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A standardised national assessment of the state of coral and rocky reef biodiversity

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EXECUTIVE SUMMARY

Increasing human pressures on marine ecosystems raise the need to monitor the response of marine organisms over broad spatial and temporal scales in order to evaluate regional changes in habitat condition and population trends. This report presents findings about the status and trends of coral and rocky reef biodiversity around Australia, inferred from the integration of three long-term monitoring programs that repeatedly surveyed benthic, fish and invertebrate communities at a total of >3000 sites distributed around the continent. Based on these integrated long-term surveys, we modelled trends in individual reef species, as well as those in biodiversity indicators that can be linked to pressures such as exploitation or global warming. Our findings show that:

- Populations of many temperate species declined over the past decade, as did populations of many tropical fish species. Temperate invertebrate species showed particularly strong population declines, with significant declines for ~30% of invertebrates observed on Tasmanian transects. A significant decline in the Living Planet Index for tropical fishes was also detected from 2016 onwards.
- Habitat-forming organisms such as corals and kelps experienced variable changes over time, including widespread, yet patchy, coral mortality in response to marine heatwaves on the Great Barrier Reef, Northwest Shelf and throughout the Coral Sea. Kelp cover remains low at many monitoring locations in the temperate east, but showed a moderate rebound at Jurien Bay (WA) after the 2011 heatwave, and small increases at Encounter Marine Park (SA) and elsewhere.
- The footprint of warming sea surface temperatures was remarkably clear nationally, with rapid tropicalisation observed in the community structure of reef fishes mostly in SE Australia during the last decade.
- Previously identified declines in large fish biomass in response to fishing pressure appear to have slowed down, although this could be partly influenced by the survey design where most fished locations included in long-term monitoring programs are in the vicinity of no-take zones.
- Across northern Australia, the structure of coral communities reflected the strong influence of environmental conditions including net primary productivity, sea surface temperature and distance to land.
- The 2016 marine heatwave was most severe in northwest Australia and had a highly variable footprint among different benthic communities, with most communities showing substantial declines in coral cover (yet with large variation among sites), and others showing increases in encrusting leathery algae and green calcified algae.

- Coral cover decline was primarily associated with the magnitude of heat stress, however the extent of species reshuffling within benthic communities was mostly influenced by the pre-heatwave community composition, likely reflecting the disturbance history prior to surveys.

Our results represent a considerable advance in our understanding of the response of coral and rocky reef ecosystems to changing climate and fishing pressures over the last decades. Future research should develop further these investigations through (i) coupling long-term monitoring data with environmental conditions and past disturbance history, (ii) developing new ecological indicators reflecting the vulnerability of different biological communities to human impacts, and (iii) establishing reference points for key biodiversity indicators to provide informed targets for management interventions. Extended data collection in areas not associated with protected areas is also needed to better understand changes in the status of reef fishes related to fishing pressure.

1. INTRODUCTION

Accelerated rates of climate change are impacting the world's marine biodiversity, simultaneously threatening the provision of associated ecosystem services. Few data exist to assess decadal trends in marine biodiversity and how they respond to warmer oceans. To date, the most documented impacts are on exploited populations, yet long-term fisheries catch statistics are generally confounded by changing effort and deliberate fish-down of populations (Edgar et al. 2018). Moreover, even less documented impacts (for example on rare and/or cryptic species) can have flow-on effects on the entire ecosystem through biotic interactions and trophic pathways (Mouillot et al. 2014). Not all populations are declining, and the magnitude of impacts can vary greatly between regions and ecological communities - emphasizing the need for comprehensive assessments of ecosystem responses to environmental change, and the potential for human intervention to mitigate such impacts.

In Australia, extensive coral losses have been observed in north Western Australia, the Coral Sea, and along the Great Barrier Reef following the 2016 and 2017 marine heatwaves and mass bleaching events (Hughes et al. 2017, Stuart-Smith et al. 2018, Edgar et al. 2020a). In temperate regions, habitats dominated by kelps and other canopy-forming macroalgae are threatened through human-mediated ecological processes (e.g. sea urchins and fishing interactions (Ling et al. 2009)) and changing ocean climate (Wernberg et al. 2016). Yet many gaps remain in our understanding of how marine populations and species communities respond to environmental change.

Improved oceanographic and physical data products are now increasingly available to support an understanding of the magnitude and pace of environmental change, and thus the possible drivers of ecosystem degradation (e.g. Integrated Marine Observing System; <https://imos.org.au>). Ecological data, in contrast, have traditionally remained geographically or temporally limited, and/or constrained by the motivation or ecological question justifying the collection of a particular dataset. Quantitative long-term reef monitoring programs arguably represent the best mechanism for understanding the magnitude of broad-scale changes in marine ecosystems (Edgar et al. 2017c). However, long-term reef monitoring programs are generally limited to shallow reefs in non-turbid seas and typically differ from a methodological perspective (e.g., biomass records), complicating the development of systematic ecosystem assessments at a continental scale.

The overall aim of this project was to undertake a comprehensive assessment of the status and trend of coral and rocky reef biodiversity, and their ecological responses to decadal environmental change. To address this, we integrate ecological data streams from three of the largest long-term reef monitoring programs worldwide: Reef Life Survey (RLS; Edgar and Stuart-Smith 2014), Australian Temperate Reef Collaboration (ATRC; Edgar and Barrett 2012), and the Australian Institute for Marine Science (AIMS) Long Term Monitoring program (LTMP; Sweatman et al. 2008). Our analysis combined inferred population trends for individual species, as well as ecological indicators reflecting the potential impacts of exploitation and ocean warming. We also analysed the impact of acute disturbance events

such as marine heatwaves on habitat-forming coral communities, and assessed potential direct human impacts (e.g., fishing) on reef biodiversity.

In Chapter 2, we undertake the most comprehensive assessment of marine species population trajectories to date at a continental scale. These time-series collectively extend from 1992 to 2020, cover >1800 marine fishes, 800 mobile invertebrates and 400 macrophytes distributed around Australia, and utilise consistent diver counts of species' densities in 50 m-long transect blocks (Stuart-Smith et al. 2017a). This component seeks to address the lack of adequate assessment of threat for marine species not covered by the Environment Protection and Biodiversity Conservation listing process (i.e., the majority of fishes and invertebrates). It represents the largest national-scale assessment of the net population trends for reef species, and complements taxon-specific initiatives (e.g., National Shark Action Plan).

In Chapter 3, we develop a quantitative and directly comparable assessment of trends in the status of marine biodiversity in the national State of the Environment (SoE) report. The 2016 SoE report included the first nationally standardised quantitative assessment of change in reef biodiversity, and this chapter follows up with an extension of trends in the same indicators from 2008 to 2020, using the same data sources, albeit with some new indicators available for inclusion. It links to, and builds on, the previous hub project C2 (*Continental-scale tracking of threats to shallow Australian reef ecosystems*). This component uses and aligns the AIMS, ATRC and RLS long-term monitoring datasets, and includes new data collected subsequent to the previous analysis for the SoE.

National trends in key indicators (e.g., biomass of large fishes, community temperature Index) were modelled and compared to trends in the relative abundance of key habitat-forming organisms (kelp, corals) to help tease apart indirect impacts of habitat degradation from direct effects of exploitation and warming. For the first time, we also compiled the "Living Planet Index" for tropical and temperate fish and invertebrates, as a synoptic index of aggregated population trends over time, providing an overview of whether populations are generally declining or increasing across entire species' distributions.

In Chapter 4, we analysed a unique dataset documenting the relative abundance of reef-building corals identified to the species level across Australia's tropical reefs, before and after the 2016 marine heatwave that induced a region-wide decline in coral cover on the Great Barrier Reef. Impacts in other coral reef regions have, however, mostly remained undocumented (but see Edgar et al. 2020a). We took advantage of the development of a unique dataset of corals identified to the species level to analyse community responses to disturbance, in addition to the more commonly considered trends in total live coral cover.

Collectively, the three components of this project provide the first national assessment of the response of coral and rocky reef biodiversity to environmental change over >10 years, evaluated from ecological indicators at the species (Chap 2 & 4) and community (Chap 3 & 4) levels. This assessment provides a benchmark for the evaluation of ecological responses

to future changes, and the potential for management and intervention to mitigate further impacts of climate change on marine biodiversity.

2. ASSESSMENT OF NATIONAL THREAT STATUS FOR REEF SPECIES BASED ON POPULATION TRAJECTORIES

2.1 Methods

2.1.1 Reef monitoring data

To assess population trends amongst reef species distributed around Australia, density data from three long-term reef monitoring initiatives were analysed: Reef Life Survey (RLS; 2007-20) (Edgar and Stuart-Smith 2014), Australian Temperate Reef Collaboration surveys (ATRC; 1992-2020) (Stuart-Smith et al. 2010, Edgar and Barrett 2012), and the Australian Institute for Marine Science Long Term Monitoring program (AIMS; 1992-2019) (Sweetman et al. 2008, Emslie et al. 2020). All apply comparable underwater visual searches along 50 m transect lines (Stuart-Smith et al. 2017a, Emslie and Cheal 2018): 5 m block width for fishes (all programs); 1 m block width for small fishes (all programs) and mobile invertebrates (RLS and ATRC); photo-quadrats (RLS and AIMS) and quadrats scored by divers (ATRC) for macroalgae. The geographic scope of the three programs differed. RLS extended Australia wide; AIMS was restricted to the Great Barrier Reef (north-eastern Australia); ATRC encompassed temperate locations from south-western Western Australia to south-eastern Australia including Tasmania. AIMS surveys were confined to 210 fish species from 10 families. ATRC and RLS considered all major taxa, although RLS macroalgal data were restricted to few locations where photoquadrats were assessed to the species level (e.g. Lord Howe Island (Edgar et al. 2010)). Consequently, no macroalgal data were available for northern Australia. Coral taxa were identified to species from RLS photoquadrats by E. Turak, a coral taxonomist.

Time series analyses were based on the subset of 1613 sites surveyed at the same GPS position in at least two separate years (915 RLS sites; 419 ATRC sites; 279 AIMS sites), where each AIMS site included three survey locations a few hundred metres apart on a single reef. The 3166 taxa recorded across all programs were reduced for analysis to the 718 most frequently encountered species with at least 50 separate observations. The majority were fishes (506 species), while 94 mobile invertebrates, 13 corals and 105 algae were also considered. Abundance data for RLS surveys are available at www.reeflifesurvey.com.

2.1.2 Population trend analysis

Site data were aggregated by calculating the mean abundance of each species recorded in different transects at each site in each year. Zeros (i.e. absence records) were inserted when a species was recorded at a site but not in the particular year. Data were interpolated for years lacking survey data within each site as the linear proportion between data for each species for nearest year surveyed before and after. As site data were highly clumped, a mean value for each year and species was calculated for 1° latitude x 1° longitude grid cells, thereby providing equal weighting for cells regardless of number of sites surveyed within.

Because population trends through time were rarely linear, the significance of long-term trends for each species was assessed without interpolation by using Spearman rank correlation. This was calculated as the average standardised abundance across all 1° latitude by 1° longitude grid cells in any year versus year of survey for the period 2008-2020. Trend direction was noted for species showing significant trends with year ($p < 0.05$; two-tailed test).

Latitudinal trends depicting continental scale patterns were mapped around Australia by calculating species lists for each 1° latitude x 1° longitude grid cell that possessed survey data. The total number of species in each major taxonomic group in each of three trend categories (significant population increase, significant decrease, or a non-significant trend) were tabulated for each grid cell and then percent increase and percent decrease mapped. These data thus depict the proportion of species in each grid cell showing overall national change rather than change within the grid cell itself. Grid cell data were also graphed after averaging by latitude.

2.2 Results

Analysis of population trends for the 718 species with most extensive observations (recorded with more than 50 separate records) indicates a wide range in trajectories through the 26-year monitoring period. Populations of many temperate species declined, as did many tropical fishes, whereas almost all tropical macroinvertebrate populations remained stable or increased rather than decreased (Figure 1). Only 1 of 13 coral species assessed showed a significant continental-scale population decline from 2008-18 (7% of total), while none showed significant population increases. The number of mobile macro-invertebrates with declining populations (18; 19% of total) was much higher than the number increasing (1; 1% of total). Similarly, more fishes were decreasing (64; 13% of total) than increasing (23; 5% of total), as also the case for macroalgae (14, 13% of total; 8, 8% of total; respectively).

Tasmania exhibited an anomalously high proportion of invertebrate species with declining population numbers across their full range (Figure 1), and also more fish and macroalgal species with declining than increasing populations. The number of species with declining populations decreased northwards for invertebrates and algae, but with a substantial increase in the number of fish species with declining populations at latitudes less than 25°.

Inspection of spatial patterns around the continental margin revealed pronounced invertebrate declines in species distributed across southern Australian temperate rocky reefs (Fig. 2), and also for fish species on the Great Barrier Reef.

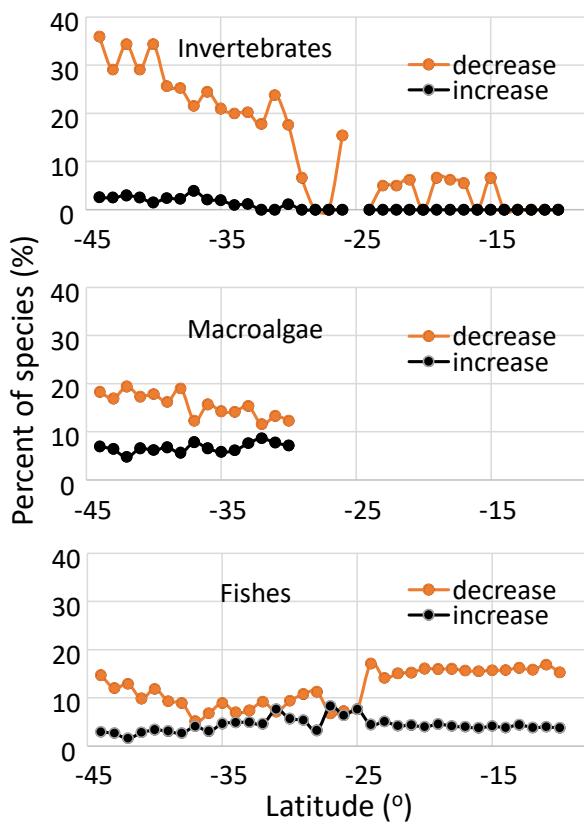


Figure 1. Percentage of reef species for three major taxa (fish, mobile invertebrate and macroalgal species) with populations that are significantly decreasing or increasing across Australia versus latitude.

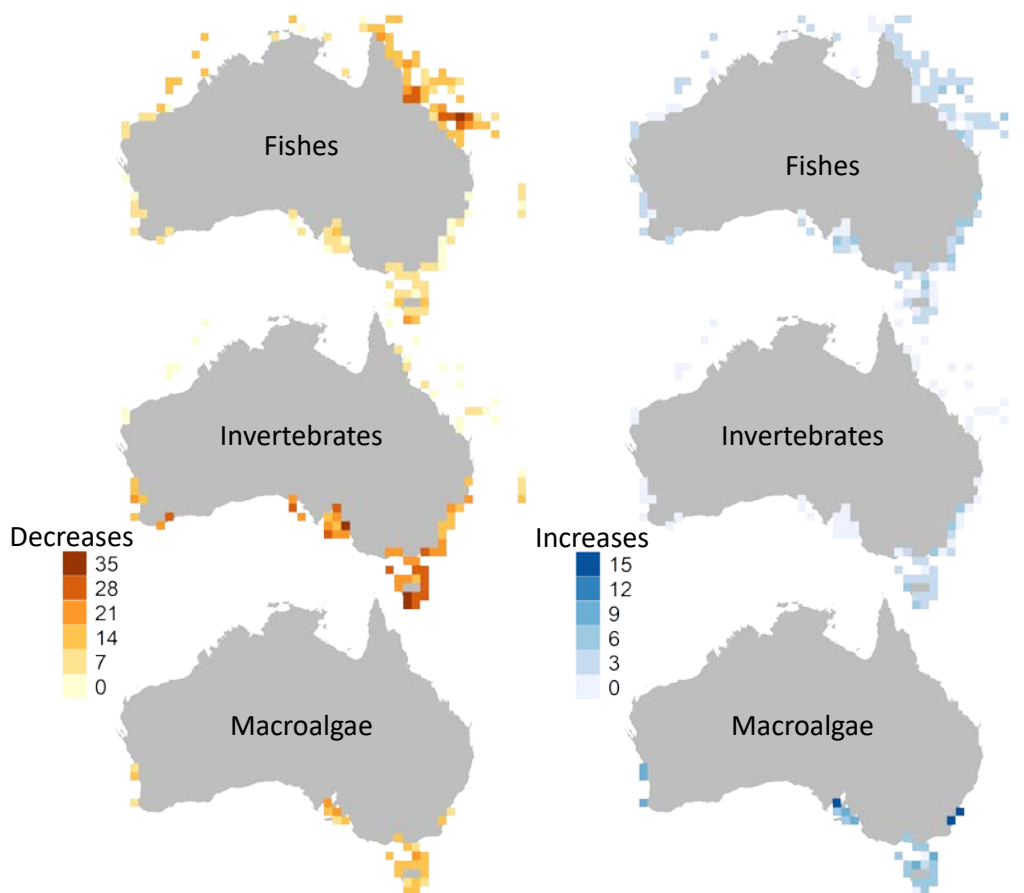


Figure 2. Recent change in population density amongst reef species in Australia waters. Plots show proportion of fish, invertebrate and macroalgal species in each 1° x 1° grid cell with population sizes that are significantly declining (left, red shading) or rising (right blue shading) across Australia over two decades of monitoring.

A total of 62 species with significantly declining populations qualified as threatened using the IUCN Red List criteria (IUCN Standards and Petitions Working Group 2008) for the 12 year period from 2008-20; 2 species qualified as Critically Endangered (>80% decline), 15 species as Endangered (>50% decline), and 45 species as Vulnerable (>30% decline). The set of threatened taxa comprised 8 algal species, 1 coral species, 12 invertebrate species, and 41 fish species. Most threatened invertebrate species possessed temperate distributions, whereas almost all threatened fish species were closely associated with tropical coral reefs.

Table 1. Species with significant continent-wide population declines for period 2008-18, with magnitude of decline exceeding IUCN Red List criteria trigger points for recognising threatened species. *temperate species.

Critically Endangered (>80% decline)	Endangered (>50% decline)	Vulnerable (>30% decline)
	Fishes	
	<i>Amblyglyphidodon leucogaster</i>	<i>Acanthurus pyroferus</i>
	<i>Chaetodon rafflesii</i>	<i>Acanthurus triostegus</i>
	<i>Chrysiptera talboti</i>	<i>Amblyglyphidodon curacao</i>
	<i>Lethrinus obsoletus</i>	<i>Aracana aurita*</i>
	<i>Neoglyphidodon melas</i>	<i>Bolbometopon muricatum</i>
	<i>Parequula melbournensis*</i>	<i>Chaetodon melannotus</i>
	<i>Pomacentrus imitator</i>	<i>Chaetodon ornatissimus</i>
	<i>Siganus argenteus</i>	<i>Chaetodon ulietensis</i>
	<i>Trachurus declivis*</i>	<i>Cheilinus fasciatus</i>
		<i>Cheilinus undulatus</i>
		<i>Cheilodactylus ephippium</i>
		<i>Chelmon rostratus</i>
		<i>Choerodon fasciatus</i>
		<i>Chromis klunzingeri*</i>
		<i>Chromis xanthura</i>
		<i>Dischistodus melanotus</i>
		<i>Girella tricuspidata*</i>
		<i>Hemigymnus fasciatus</i>
		<i>Hemigymnus melapterus</i>
		<i>Hypoplectrodes maccullochi*</i>
		<i>Lutjanus carponotatus</i>
		<i>Lutjanus lutjanus</i>
		<i>Monacanthus chinensis</i>
		<i>Notolabrus inscriptus</i>
		<i>Pomacentrus grammorhynchus</i>
		<i>Pseudophycis bachus*</i>
		<i>Scarus oviceps</i>
		<i>Scarus psittacus</i>
		<i>Scarus spinus</i>
		<i>Siganus corallinus</i>
		<i>Siganus vulpinus</i>
		<i>Zanclus cornutus</i>
	Coral	
		<i>Isopora palifera</i>
	Mobile Invertebrates	
	<i>Meridiastra gunnii*</i>	<i>Cenolia trichoptera*</i>
	<i>Strigopagurus strigimanus*</i>	<i>Conus anemone*</i>
	<i>Tosia magnifica*</i>	<i>Meridiastra calcar*</i>
		<i>Nectria ocellata*</i>
		<i>Petricia vernicina*</i>
		<i>Phyllacanthus irregularis*</i>
		<i>Scutus antipodes*</i>
	Macroalgae	
	<i>Caulerpa geminata*</i>	<i>Durvillaea potatorum*</i>
	<i>Curdiea irvineae*</i>	<i>Euptilota articulata*</i>
	<i>Gelidium asperum*</i>	<i>Lessonia corrugata*</i>
		<i>Sargassum sonderi*</i>
		<i>Xiphophora gladiata*</i>
<i>Comanthus tasmaniae*</i>		
<i>Tripneustes gratilla</i>		

2.3 Discussion

Given the impact of recent regional heatwaves and the overriding influence of temperature on continental-scale patterns, the predominant threat to Australian reef biodiversity appears to be increasing global water temperature. Population gains as well as losses were, however, evident, but with only about one-third the extent of population losses.

Population declines were most evident amongst coral reef fishes and temperate invertebrates. The former was expected given the number of prior studies that have emphasised recent biodiversity losses on coral reefs (Hughes et al. 2017). Detailed analysis of the Great Barrier Reef and Coral Sea regions affirms a decline in butterflyfishes and other species closely associated with corals following the 2016 bleaching event (Stuart-Smith et al. 2018), at least over the short-term, but also detected notable increases in some fish populations. These increases do not appear to have persisted long-term, perhaps because dead coral structure had not disintegrated at the time of the earlier study. Ecological change associated with the 2016 and 2017 bleaching events could possibly progress beyond the period investigated here if dead coral structure, on which many reef fishes depend, further disintegrates.

Continental patterns described here using site observations may progress to loss of species richness around the continent in the near future. Total species numbers must decline if rapid temperature-related ecosystem change continues, due to loss of some species and no gains other than through immigration from warmer climes (which possess an equatorial limit (Stuart-Smith et al. 2017b)). Thus, a temporal mismatch currently exists between loss of species over decades, as evident in our study, and evolution of new species over hundreds of thousands to millions of years.

Our analysis revealed a number of species with rapidly declining populations over the past decade that putatively qualify as threatened (Table 1). These should be investigated further as candidates for formal listing on threatened species schedules, depending on other available data, including information from non-reefal habitats. Given the number of species with declining populations that are closely associated with tropical coral reefs and temperate macroalgal habitats, management actions to safeguard these species may occur more effectively and efficiently through habitat rather than individual species recovery plans, or through 'threatened community' rather than 'threatened species' legislation. Such broad-based management should at least be considered, particularly given current Commonwealth listing of the *Macrocystis pyrifera* community as threatened, and other large kelp species (*Durvillaea potatorum* and *Lessonia corrugata*) were found in our study to be significantly declining.

While media interest focuses on coral reefs, temperate Australian invertebrate species appear to be in equal or greater jeopardy of extinction than tropical species, for multiple reasons. Firstly, as 67% of Australia's population lives within 50 km of the temperate coast (Bennett et al. 2016) there is considerable population pressure that translates to stress and ecological impacts. Measurable ecological change is evident in all inshore habitats due to the

cumulative influences of numerous stressors associated with high population density (urban effluent, nutrient runoff, fishing, aquaculture, introduced species, foreshore development, litter, modified freshwater flows, catchment land clearance) (Edgar and Barrett 2000, Edgar et al. 2005, Gaylard et al. 2020, NSW DPI 2017). Also, due to the large geographic extent and varying management drivers across coastal temperate waters, less attention has historically been directed towards assessing and monitoring pressures and condition of temperate rocky reefs. Recent developments in threat assessment (e.g. Doubleday et al. 2017, BMT WBM, 2017) and integrated monitoring (Aither 2019) will provide an improved understanding of the status of temperate reef biodiversity, and allow focussed management responses that are likely to involve managing threats and evaluating restoration options. Further investment in coordinating, managing and delivering the monitoring data is also required to improve management outcomes.

Secondly, cool temperate species appear highly sensitive to recent warming, with a high current incidence of population decline. For invertebrates and macroalgae, population reduction through predation and loss of macroalgal habitat following increased densities of fish predators and herbivores in a warming climate (Bates et al. 2017, Edgar et al. 2017b) are probably at least as important as the direct effects of temperature. Further, climate predictions indicate south-eastern Australia is a global hotspot for future warming, so impacts of climate change are ongoing and will continue to be particularly intense in this region (Johnson et al. 2011, Last et al. 2011, Popova et al. 2016, Oliver et al. 2018b).

Thirdly, southern Australian species inhabit a climate trap, having no shallow reef habitat in a poleward direction to retreat into as conditions warm (Edgar et al. 1991). Analogous climate traps exist for inshore species along east-west continental margins of southern Africa, South America, Antarctica and the Arctic.

Fourthly, in contrast with the large ranges of most tropical species, temperate species typically have small ranges and a high degree of endemism, and thus lack distant refuges from which to re-establish. Most temperate species investigated here are endemic to Australia (77%), compared to only 7% of tropical species. Temperate species also possess much deeper phylogenetic roots – the temperate fish species assessed here are classified within 41 families, whereas twice as many tropical fishes investigated belong to fewer (37) families. Substantial loss of temperate marine species would represent a major decline in the deep phylogenetic diversity of all life on earth.

While our investigation was focused on Australian reef-dwelling species, outcomes likely extend to other realms and continents. Changes affecting reef ecosystems presumably extend more broadly given movement of individuals of many species between different habitat types (Speed et al. 2010, Lennox et al. 2018), including life-history shifts between locations by species utilising separate nursery habitats (Aburto-Oropeza et al. 2008, Lefcheck et al. 2019). Elsewhere, a multi-decadal investigation of Californian inshore and pelagic fish communities found marked population declines since the 1970s for most studied species, with disproportionately large decreases amongst the colder water taxa (Koslow et al. 2015).

Regardless of disproportionate threats to temperate species, an acute contrast exists between tropical and temperate biomes in marine conservation focus and resourcing. This disparity is clear in Australia, where, for example, the main spatial tool used for conservation – no-fishing marine protected areas – are predominantly located in the tropics: 0.8% of cool-temperate coastal waters around Tasmania are protected in ‘no-fishing’ marine reserves, compared to 4.6% of warmer temperate waters across the states of Western Australia, South Australia, Victoria and NSW, and 7.1% of tropical waters in Queensland, Northern Territory and Western Australia (Grech et al. 2014). Internationally, no-fishing reserves are virtually absent (<1%) from the continental coasts of Europe, Asia and North America north of California and Florida, while very large (>100,000 km²) tropical no-fishing reserves are located in European overseas and US Pacific territories (World Database on Protected Areas; <https://www.protectedplanet.net/marine>).

Given the scale of population declines evident in our analysis, additional investment, management focus, and research are all needed to safeguard universal biodiversity values associated with temperate as well as tropical habitats. Marine monitoring programs urgently need expansion to allow assessment of extinction risk for macroalgae and invertebrates (Johnson et al. 2011, Krumhansl et al. 2016, Edgar et al. 2017b), and for understanding the roles of direct, indirect and cumulative stressors causing loss of temperate marine invertebrates and macroalgae. An important initial step is recognition that human activity and threats are concentrated on the continental shelf and upper slope in mid latitudes, and this is also where most of the world’s deep phylogenetic diversity resides.

3. UPDATED QUANTITATIVE ASSESSMENT OF THE “STATE OF AUSTRALIAN REEFS” CASE STUDY FOR THE STATE OF THE ENVIRONMENT 2022 REPORT

3.1 Methods

3.1.1 Reef monitoring data

All available standardised underwater visual census data collected by large-scale monitoring programs since 2008 were used for indicator calculation and trend assessment. These data came from the RLS (2165 sites), ATRC (695 sites) and AIMS LTMP (144 sites) programs, with the former two collated and accessed through the National Reef Monitoring Network sub-facility of IMOS. The data used included those used in the previous chapter, plus data from the Parks Victoria Long-term MPA monitoring program (hereafter referred to inclusively with the ATRC). The base unit of reef fish data used was 500 m² transects (50 m x 10 m), 50 m² for invertebrates and % cover for corals and algae, as scored from photoquadrats or in situ quadrats along each 50 m reef transect. Full details of data collection procedures are available in the methods manuals for the respective programs available online, and in numerous publications (Edgar and Stuart-Smith 2014, Edgar et al. 2020b).

Data available between 2008 and 2020 included annually repeated sites at long term monitoring locations distributed around the country, which formed the basis for time series analysis (see below and trends in Fig 3). Synoptic patterns in change were also investigated using all data from sites that had been surveyed at least once between each of the 2011-2015 and 2016 – 2020 periods, allowing the change in mean values from these periods to be mapped. While only representing snapshot change to be investigated, the latter covered more of the Australian shallow reef areas, and thus provides complementary information to the more detailed time-series analyses.

3.1.2 Ecological indicators

Indicators used for this national assessment included: habitat quality (expressed as the % of cover of live hard corals OR canopy forming macroalgae, depending on whether the site was tropical or temperate); the Reef Fish Thermal Index (also known as the Community Temperature Index) (Stuart-Smith et al. 2015, Stuart-Smith et al. 2017a) and the Large Reef Fish Indicator (also known as B20, or the biomass of large reef fish). The latter two were used in the previous national assessment, using these same data sources, for the 2016 State of the Environment report (Stuart-Smith et al. 2017a), and are accepted indicators (and data sources) for global biodiversity reporting by the UN-mandated Biodiversity Indicators Partnership (e.g. see <https://www.bipindicators.net/indicators/large-reef-fish>). Calculation details are provided in these other references and on the RLS website, where interpretation details are also explained (<https://reeflifesurvey.com/indicators/>).

For habitat quality, three different methods were used for evaluating percentage cover of substrate categories. For the ATRC, five quadrats of 0.5 x 0.5 m are placed on the bottom for each 50 m transect line (i.e., every 10 m), and the taxon under each of 50 points within the

quadrat is scored. For RLS, photoquadrats encompassing ~0.25 m² are taken every 2.5 m along the line, and were later scored in Squidle+, with the functional groups of habitat scored under each of 5 points per image, 100 points per transect. Categories scored are from an RLS standard vocabulary that aligns with the CATAMI classification system (Althaus et al. 2015). For the AIMS data, percent coral cover was estimated from digital images from each transect using point sampling of a randomly selected sequence of images (Jonker et al. 2008, Jonker et al. 2020). The benthic organisms were identified to the lowest taxonomic resolution possible under five points arranged in a quincunx pattern in each image (n = 200 points per transect) and the data were converted to percent cover. In this study, we focused on hard coral benthic categories, summing up their percent cover to determine total hard coral cover. All large canopy-forming brown macroalgal species or categories scored by RLS and ATRC were summed and considered ‘kelps’ for these analyses, and all living hard coral species and categories scored by RLS and AIMS were summed and considered ‘corals’.

Data for individual monitoring locations was only analysed from a single data source, to avoid issues of combining data from different methods. The synoptic maps (see below) were based only on RLS photoquadrat data.

3.1.3 Statistical analyses

We modelled temporal trends for each ecological indicator and at each location using generalized additive mixed models (GAMM) (Wood 2004) with a ‘year’ fixed effect and a ‘site’ random effect to account for the hierarchical structure of the dataset (i.e., transects nested within sites at each location). A ‘marine protected area’ fixed effect was included for locations with multiple fishing closure levels. Only sites with at least 3 years of survey post-2008, and locations with at least three of such sites, were retained for the analysis. GAMMs were calibrated in R using the ‘mgcv’ package.

We computed maps of temporal change in each indicator before and after 2016 by calculating, for each site, the mean estimate from surveys conducted between 2011-2015 and those conducted between 2016-2020, respectively. The mean annual change in each indicator was calculated as the difference between these two estimates, divided by the average resampling interval. Values of mean annual change were then interpolated using inverse-distance weighting (Cressie 1993) with a weighting power of 5 and within a 150 km buffer around survey sites. Given the maps show trends in raw indicator values and depend on which sites were surveyed in which periods (i.e., imbalance in which sites were surveyed in which years could not be accounted for as in the GAMMs), trends shown on the map may not exactly match trends shown by the GAMMs in some cases.

To summarise temporal trends in the abundance of fish and invertebrates on temperate and tropical reefs, we calculated the Living Planet Index (LPI) (Loh et al. 2005, McRae et al. 2017) for each major taxon and realm, and plotted corresponding trends between 2008 and 2020. Trends in LPI represent the geometric mean of population trends within each taxonomic group (with population size being defined as the log-transformed mean abundance of each species at each survey site) for all monitored species, with correction for the total number of species within biogeographical realms (following the method of McRae et al. 2017).

3.2 Results

Reef communities around Australia changed considerably between 2008 and 2020 in terms of habitat quality, overall reef fish community composition and structure, and in the population trajectories of the fish and invertebrate species. In terms of habitat quality, coral cover trends varied very clearly along the length of the GBR, with well-documented mortality (Hughes et al. 2017) and widespread yet patchy (Stuart-Smith et al. 2018) reductions in live coral cover in the northern region monitored (Figure 3). Central and southern GBR did not show equivalent declines, however, with a continued longer-term recovery of coral cover in the southern region. These overall patterns were largely mirrored in the Coral Sea, where before and after heatwave data showed losses in northern reef and gains in southern reefs (see map in Figure 3). Coral cover declined at some monitored sites at Ningaloo Reef, largely a result of Cyclone Olwyn destroying substantial tracts of shallow table coral gardens near Coral Bay in 2015. Coral cover substantially declined at Scott Reef in the North-West (Edgar et al. 2020a), has been stable at Lord Howe Island and the Solitary Islands, and patchy increases and declines have occurred elsewhere. More details on the coral changes are covered in the next chapter, with Figure 3 providing an overview of total coral cover trends.

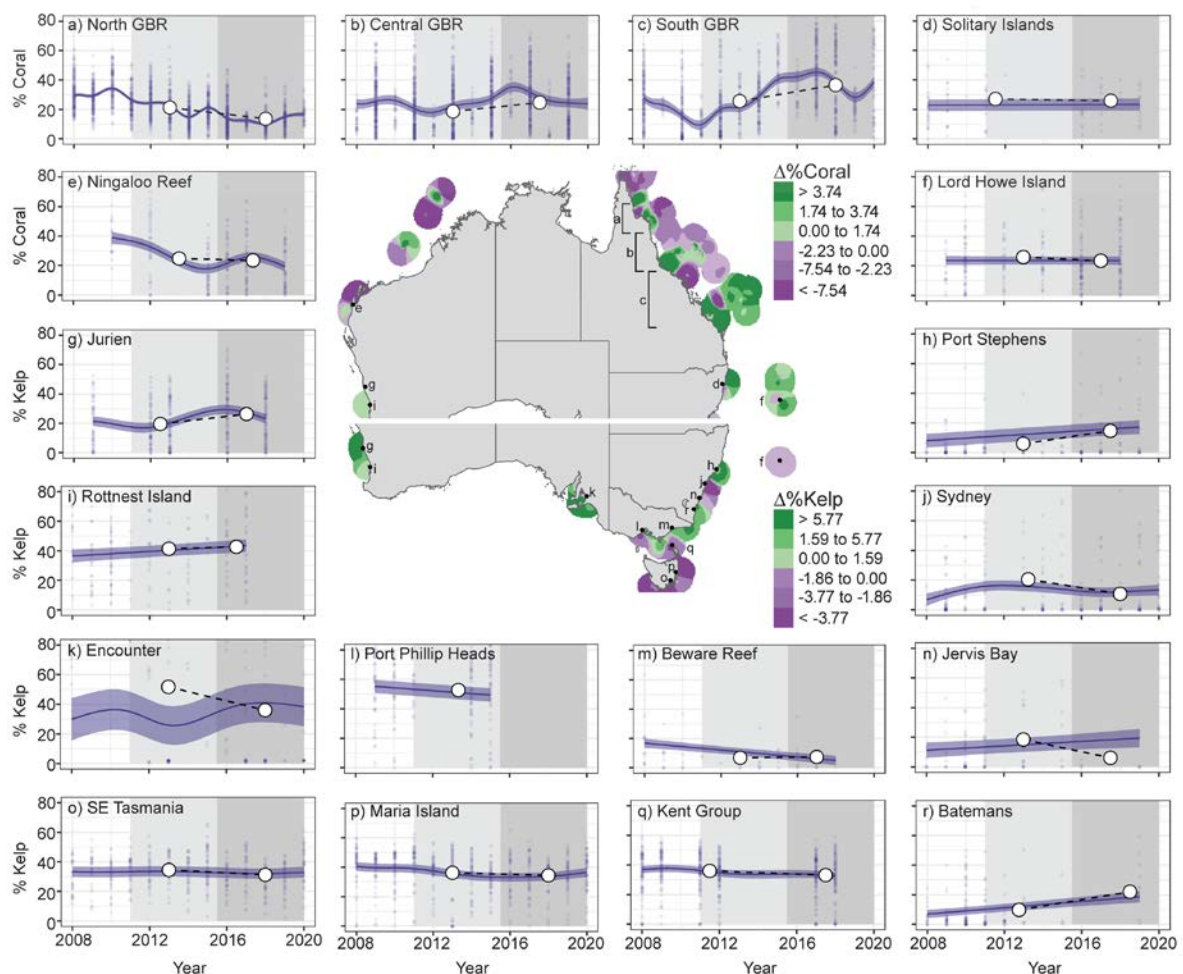


Figure 3. Changes in the cover of live coral and large canopy forming seaweeds (labelled collectively in the figure as 'Kelp') at national monitoring locations surveyed as part of the RLS, AIMS and ATRC programs.

[>Coral cover is the sum of the % cover of all live hard corals, and kelp cover is the sum of all canopy-forming seaweeds (including laminarian kelps and furoid seaweeds). % cover was estimated using quadrats (scored by divers underwater or from images of the reef surface). Trends through time shown in individual graphs for monitored locations are from statistical models (GAMMs) that account for different numbers of surveys for different sites within each location. The coloured map shows synoptic patterns in the differences in average raw values for regions across the last two 5-year periods (i.e., the difference between the 2011-2015 average and the 2016 - 2020 average, represented by the white dots and corresponding to the two grey shaded periods in the individual trend plots). Green regions on the map show *increases* in coral or kelp cover, while purple regions show declines over the same period.]

Temperate regions have experienced variable, but largely minor changes in canopy forming seaweed cover. The most notable change in kelp cover among the monitored locations was at Jurien Bay, where a small rebound in kelp cover has occurred following the decline observed from the 2011 marine heatwave. Other locations showed quite variable trends and sometimes mismatches between the regional signal shown in the map (and represented by the white points in the trend plots) and the trends in long-term monitoring sites (as shown by the trend lines in the individual plots). At Beware Reef, *Centrostephanus* sea urchins have caused substantial local impacts, while kelp cover remains patchy along the NSW coast, with trends difficult to detect as a result of high local variability and low kelp cover in general. Minor increases in NSW may represent increased cover of the dominant *Ecklonia radiata* kelp, or altered composition towards more cover of furoid algae (e.g. *Sargassum* spp.), and require more detailed investigation.

While reef habitats were clearly influenced by the marine heatwaves at some locations (as described above), the reef fish community structure reshuffled with changing sea temperatures (SST) in most monitoring locations (Figure 4). SST changes (see Appendix A. Appendix A) included medium-term cycles of 5-7 years in SE Australia, presumably associated with El Niño cycles, and reef fish communities followed these general patterns, with minimal lag (in most cases the following year of the Reef Fish Thermal Index reflected the change in SST over the last year). The Solitary Islands have shown rapid tropicalisation during the last decade, but fish communities have generally become ‘warmer’, on average, across much of SE Australia in the last five years. The ‘cooling’ of SW Australian fish communities reflects a slow return towards pre-heatwave community structures at Rottnest Island and Jurien Bay. Despite declines in the Reef Fish Thermal Index, a number of temperate species that were locally extirpated have still not returned or bounced back to pre-heatwave numbers.

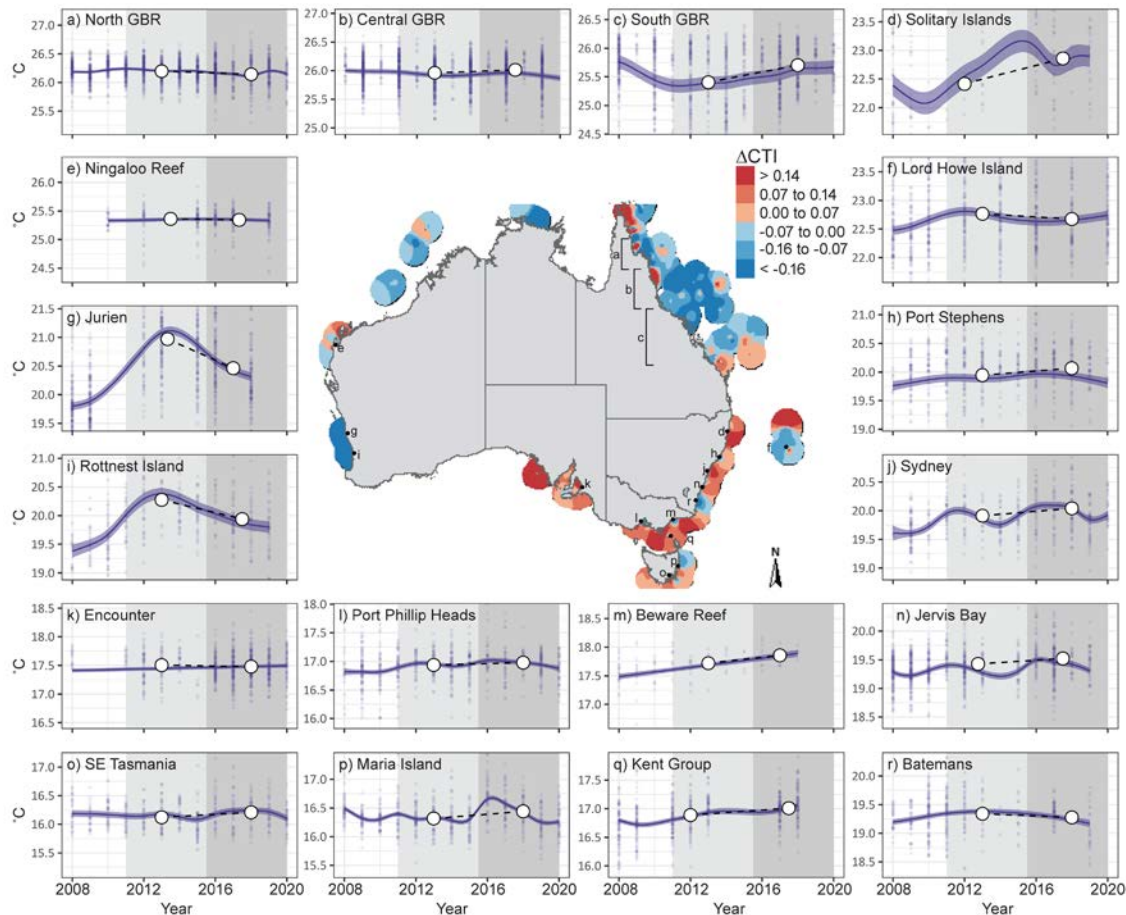


Figure 4. Trends in the Reef Fish Thermal Index, an indicator of biodiversity responses to ocean warming. Increases in this index show when the composition and local abundance of reef fish species changes in a way that favours species with preferences for warmer temperatures, while decreases show change towards communities made of up species that prefer cooler temperatures.

[> The values can be interpreted as the typical temperature preference for an individual fish recorded on underwater surveys (measured in °C). Trends through time shown in individual graphs for monitored locations are from statistical models (GAMMs) that account for different numbers of surveys for different sites within each location. The coloured map shows synoptic patterns in the differences in average raw values for regions across the last two 5-year periods (i.e., the difference between the 2011-2015 average and the 2016 - 2020 average, represented by the white dots and corresponding to the two grey shaded periods in the individual trend plots). Red shows shifts to fish communities typical of warmer regions, while blue shows shifts towards those typical of cooler waters.]

In terms of fishing pressure, previously identified declines (Edgar et al. 2018) appear to have stabilised or slowed (Figure 5). Signs of local depletion of reef fishes are still very clear around Sydney and the southern GBR, where the Large Reef Fish Indicator is significantly lower in areas that allow fishing of any type, when compared to no-take protected areas. Increases in large reef fish biomass occurred at the Solitary Islands, and in the last 4-5 years of data for a number of locations in the SE, although this was patchy. Importantly, all of the monitored locations here are associated with Marine Protected Areas, so the ‘fished’ sites sometimes have particular fishing restrictions (which differ depending on the local MPA regulations), and most ‘fished’ sites are still within the same general area as the ‘No Take’

sites in the MPA. The Solitaries did not have enough fished sites monitored to evaluate trends, so the upward trajectory in large reef fish biomass could be associated with recovery through protection from fishing, warmer seas allowing booms in growth rates of tropical fish populations or individuals, or a combination of the two (i.e. an interaction between protection from fishing and warming). This requires more research. Declines at Batemans Bay are significant, but reduced data availability in recent years reduces certainty in this result.

The equivalent analysis for the last SoE report that included the 2013 RLS data from the North-west region (Stuart-Smith et al. 2017a) indicated that Ashmore Reef had some of the clearest evidence of fishing impacts on reefs in Australian waters. Despite protected status and the Memorandum of Understanding with the Indonesian Government that had rules prohibiting the take of reef fishes, Ashmore sites clearly had reduced large fish biomass compared with other reefs in the region and more broadly. Illegal fishing has historically plagued this reserve, so that recovery of target populations appeared negligible in previous surveys (Field et al. 2009, Ceccarelli et al. 2013, Edgar et al. 2017a). More strict protection in recent years by Customs vessels appears to have assisted recovery of large reef fishes. This finding is consistent with a recent independent study in the region (Speed et al. 2019).

The recent mass bleaching events appear to have had varied impacts on the large reef fishes, with more increases (shown in green on the map) than declines on the GBR, but declines on reefs in NW Australia (other than Ashmore, as above).

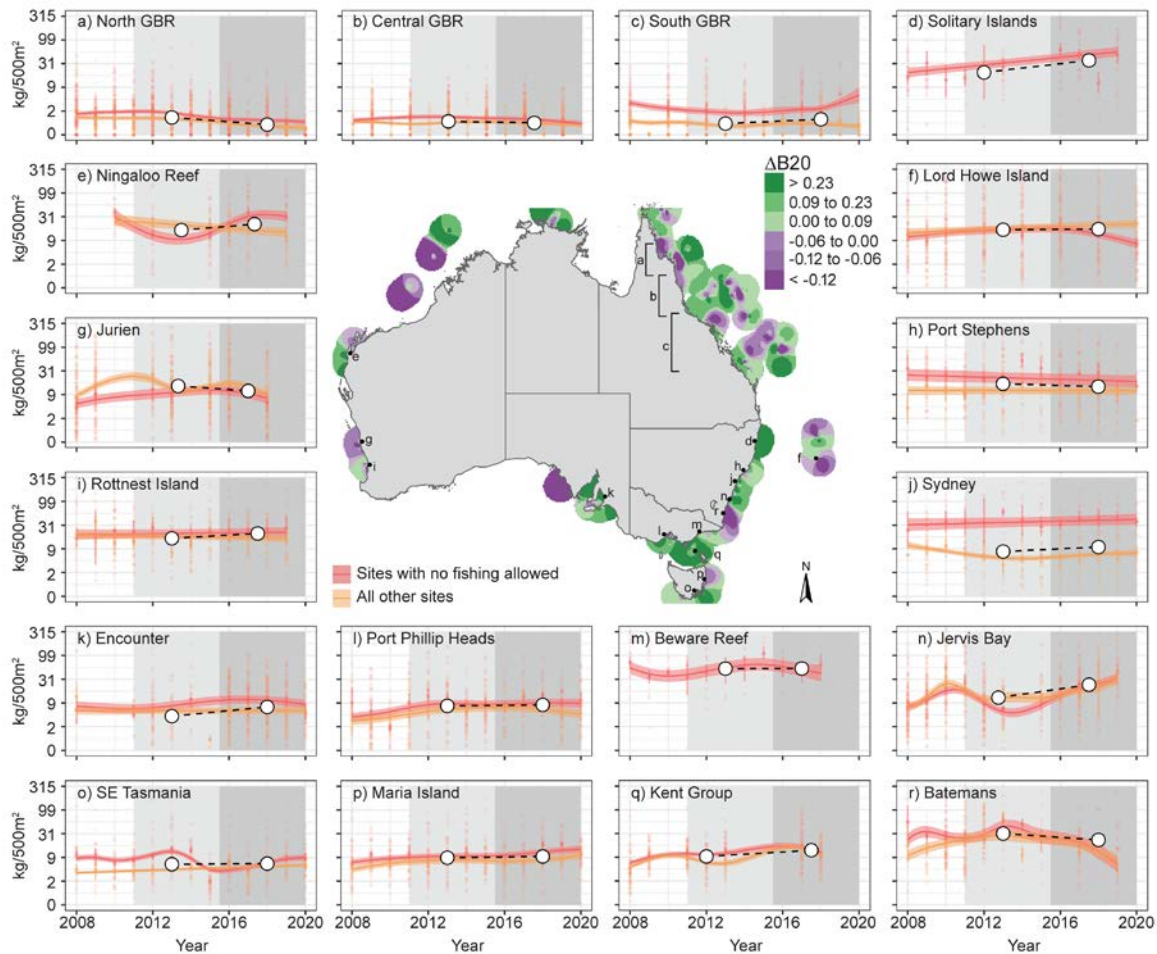


Figure 5. Trends in the biomass of large fishes (20+ cm) at long-term reef biodiversity monitoring locations around Australia (values are log-transformed kg per 50 x 10 m patch of reef).

[> Trends through time shown in individual graphs for monitored locations are from statistical models (GAMMs) that account for different numbers of surveys for different sites within each location. Separate trends are shown for sites monitored inside Marine Protected Areas with no-take regulations (red lines), versus areas with some or all fishing allowed (orange lines). The coloured map shows synoptic patterns in the differences in average raw values for regions across the last two 5-year periods (i.e., the difference between the 2011-2015 average and the 2016 - 2020 average, represented by the white dots and corresponding to the two grey shaded periods in the individual trend plots). Green regions on the map experienced *increases* in large fish biomass, while purple regions experienced decreases.]

When the population trajectories of the reef fish and invertebrate species are considered collectively in the Living Planet Index, different trends emerge for temperate and tropical species, and fishes and invertebrates (Figure 6). These trends summarise the more nuanced findings presented in the second chapter, with temperate invertebrates experiencing the most significant overall declines, and tropical invertebrates the least. While many tropical fishes have experienced increases in population numbers, the overall trend for this group appears to have turned down after the 2016 marine heatwave.

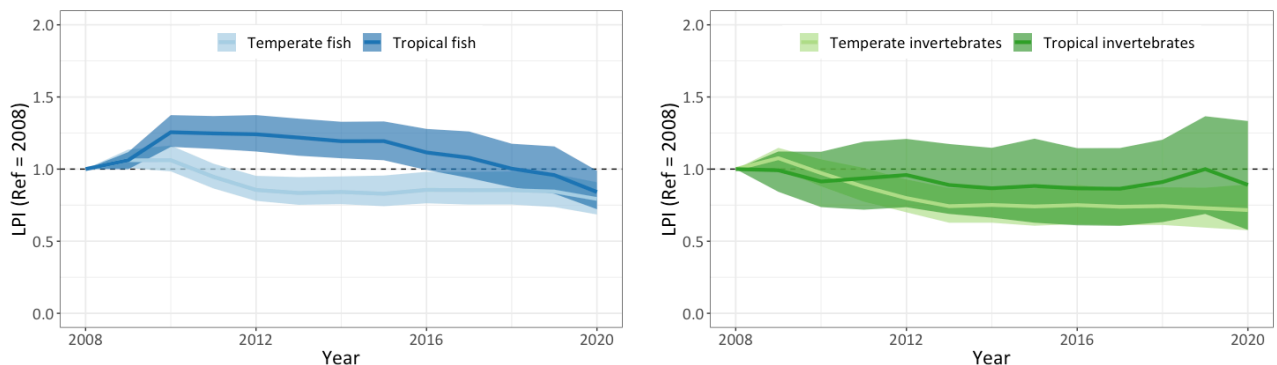


Figure 6. The Living Planet Index for reef fishes and invertebrates in temperate and tropical Australia.

[> Trends represent the geometric mean of population trends within each taxonomic group (with population size being defined as the log-transformed abundance of each species in a given location) for all monitored species and corrected for the total number of species within biogeographical realms (following the method of McRae et al 2017). Solid coloured lines show the average trend and shaded regions show the 95% confidence interval of that trend.]

3.3 Discussion

Changing ocean climate appears to have been a strong agent of change for reef communities nationally over the last decade, more so than fishing pressure. While fishing pressure was likely to have driven some substantial changes in large fish biomass in the previous SoE reporting period (Stuart-Smith et al. 2017a), such fishing impacts appear to have slowed during this period, or possibly overwhelmed by temperature effects on species and habitats. Temperature effects were especially acute on coral communities of the northern Great Barrier Reef and Ningaloo Reef, and on fish communities of south-eastern Australia that are progressively becoming more tropicalised. Notable exceptions were for Jurien Bay and Rottnest Island in Western Australia, where fish communities have progressively returned towards their pre-2011 heatwave composition, although many temperate species that were locally extirpated still have not recovered.

The regional trends presented here and broad scale of analysis notably include the combination of local scale detail from monitoring locations, as shown in the trend plots, and broader synoptic picture shown by the heatmaps. Our results typically match the biodiversity change reported in numerous local and regional studies from around the coast (e.g. Smith et al. , Vergés et al. 2016, Smale et al. 2017, Gilmour et al. 2019, Speed et al. 2019), but it is important to note that some local studies highlight important local nuances not recognised here. For example, while aggregate habitat indices such as total coral or kelp covers are useful to monitor national trends over time, they do not capture underlying shifts in species composition. Yet for the same level of habitat loss, the extent of community reshuffling can be highly variable at local to regional scales (Mellin et al. 2019). For example, we only detected a minor decline of kelp cover in SE Tasmania, but more substantial changes in the mix of fucoid algae like *Sargassum* and *Cystophora* versus laminarian kelps such as

Macrocystis and *Ecklonia*. This result is also consistent with significant declines in many canopy species highlighted in Chapter 2.

Likewise, coral cover changes can obfuscate a reshuffling of species within coral communities, whereby stress-sensitive taxa are likely to be extirpated first, thus affecting the relative proportion of different coral growth forms and life histories (but see next chapter). Such community reshuffling is likely to have further consequences for ecosystem functioning and biodiversity (Stuart-Smith et al. 2018), but requires more detailed investigation. The increasing availability of coral data identified to the species level as part of this project offers a unique opportunity for understanding the relative sensitivity of different coral taxa exposed to similar magnitude of heat stress, and how this translates to temporal shifts in coral community composition.

Our findings indicate that fishing impacts are unlikely to have increased since the last SoE report. In most cases, the trends in B20 (Large Reef Fish Index) in no-take areas were mirrored by those in fished areas. The largest apparent fishing impacts remain for Sydney, where large fish biomass in no-take zones was almost 1.5 times that in fished areas. Sydney has the least protected sites and smallest protected areas, but also the largest human population, which could exacerbate these differences through recreational fishing and indirect human impacts. Caution is nevertheless required in interpreting Figure 5 given that all of the long-term monitoring locations shown in the trend plots are associated with marine protected areas, with the possibility that some fished sites may benefit from being in the vicinity of no-take zones. More long-term monitoring locations along coastlines away from marine protected areas are needed to provide a clearer picture of national trends.

Our LPI estimates showed similar trends for both temperate fishes and invertebrates, with a sharp decline of combined abundances between 2010 and 2012 and no signs of subsequent recovery. For tropical invertebrates, the LPI showed slight fluctuations over this time period, but no significant departure from the 2008 baseline. Conversely, a recent decline was evident in the tropical fish LPI (mostly since 2016), which could be due to ocean warming and the impact of the 2016 marine heatwave – either directly or indirectly through habitat loss. In a separate study, we showed that tropical generalist species are better able to cope with habitat loss and penetrate into temperate areas (Stuart-Smith et al. in press), suggesting a high level of variation in abundance trends within tropical fish species that is not captured by the LPI. The calculation of the LPI also means that it is influenced differently by trends in the most abundant species than the rarest, and is possibly more likely to exacerbate the appearance of general declines. More investigations are required for abundance trends of individual species at particular locations to shed light on interspecific responses to ocean warming and subsequent habitat loss.

4. NATIONAL ASSESSMENT OF CORAL COMMUNITY RESPONSES TO THE 2016 MARINE HEATWAVE

4.1 Methods

4.1.1 Reef monitoring data

Benthic communities were surveyed before and after the 2016 tropical marine heatwave at a total of 289 sites across Northern Australia, encompassing four main regions that include Ningaloo Reef (N = 23), the Northwest Shelf (N = 99), the Great Barrier Reef and Coral Sea (N = 167). Pre-heatwave data were obtained between 2013 and 2015, and post-heatwave data between 2016 (8-12 months after coral bleaching) and 2018.

Two 50-m transects were usually surveyed at each site, on predominantly coral reef habitat, and generally parallel at different depths. Depth contours were restricted by depth variations in individual reefs, but where possible were selected to encompass a wide depth range (e.g., 5 – 16 m). Constraints associated with diving bottom time and air consumption generally limited depths to above 20 m.

All surveys were conducted using the standardised underwater visual census methods applied globally by Reef Life Survey, as described elsewhere (Edgar et al. 2020b). Photoquadrats (PQs) of the substrate were taken along each transect to quantify benthic cover. These were taken vertically downward every 2.5 m along each transect, and later scored in Squidle+ using a grid overlay of 5 points per image, 100 points per transect. For this project, NESP MBH Synthesis Project SS3 provided funding to score corals in the PQs to species level (or the highest taxonomic resolution possible) by E. Turak for ca. 75% of all transects. The remainder were scored to the genus level (or combination of genus and growth form) by other experienced observers. As a result, a total of 400 benthic categories were scored across all sites and surveys, including 259 corals identified to the species level, 109 corals scored to the genus level (or combination of genus and growth form), and 32 categories of algae, invertebrates, substrate type, and recently dead or bleached coral. Categories of 'substrate', 'hard substrate/encrusting' and 'turf' were removed prior to statistical analysis as these require careful consideration of observer bias (C. Mellin & L. Oh, pers. obs) and were not the focus of the present study. Total algal cover (%) and total live hard coral cover (%) were calculated for each transect as the sum of all live algae and hard coral categories, respectively.

4.1.2 Environmental covariates

The severity of the 2016 marine heatwave at each site was estimated through two metrics of thermal stress: the annual maximum degree heating weeks (DHW) and annual maximum sea surface temperature anomaly (SSTA). DHW represents the accumulation of positive temperature anomalies over a 12-week rolling window and is the most common predictor of coral bleaching risk; values of DHW > 4 typically correspond to a Level 1 bleaching alert, and DHW > 8 to a Level 2 alert (Eakin et al. 2010). By definition however, DHW does not distinguish mild but prolonged heat stress from short but acute stress - which can induce

very different responses of corals in terms of bleaching and subsequent mortality (e.g., McClanahan et al. 2019). Therefore, we also included SSTA to capture this distinction. This metric is defined as the maximum difference between satellite-derived daily SST observed during 2016 and the climatological maximum monthly mean (Eakin et al. 2010). We extracted maximum annual DHW and SSTA at each survey site for the 2016 marine heatwave from the National Oceanographic and Atmospheric Administration (NOAA) Coral Reef Watch v3.1 daily global 5 km satellite composite product (Liu et al. 2014) (Appendix B). DHW and SSTA were uncorrelated across all survey sites (Pearson's $r = 0.06$, $P = 0.267$). In addition to DHW and SSTA that reflected thermal stress experienced in 2016, we extracted the long-term mean annual sea surface temperature and its intra-annual (seasonal) standard deviation from the NOAA Coral Reef Watch climatology (1985-2012).

Additional environmental covariates were obtained from the Marine Socio-Environmental Covariates (MSEC) dataset for the global oceans, which consists of environmental and anthropogenic variables summarized in ecologically relevant ways (Yeager et al. 2017). This dataset included four sets of environmental variables related to biophysical conditions (long-term mean and seasonal variation of net primary productivity corrected for shallow-water reflectance, wave energy including sheltered-coastline corrections) and landscape context (coral reef and land cover within a 20-km radius). We included two sets of anthropogenic variables, human population density in 2015 (within a 20-km radius) and fishing closure status (open / closed / restricted), which can serve as indicators of local human impacts. All environmental covariates and corresponding sources are described in Appendix C.

4.1.3 Statistical analysis

We first characterized pre-heatwave benthic communities using multivariate regression trees (MRT) (De'ath 2002), which model the relationship between species community composition and environmental covariates. MRT forms clusters of sites by repeated splitting of the data, with each split determined by environmental characteristics and corresponding to a distinct species assemblage. We calibrated MRT using the pre-heatwave matrix of site-by-benthic covers (square-root transformed) as the response variable, and covariates describing long-term environmental conditions as predictors (Appendix C). We determined the best tree size (i.e., number of leaves or clusters formed by the tree) as the one minimizing the cross-validated relative error (CVRE), which varies from zero for a perfect predictor to nearly one for a poor predictor. We subsequently characterized each pre-heatwave benthic community (i.e., cluster) by its indicator taxa based on the Dufrêne-Legendre index, which integrates the relative abundance and frequency of each benthic category within a given cluster (Dufrêne and Legendre 1997). The index varies between 0, no occurrences of a species within a cluster, to 100, if a species occurs at all sites within the cluster and in no other cluster. The index is associated with the probability of a random pattern, based on 250 reallocations of sites among clusters. MRT were fit in the R 4.0.2 (R Development Core Team 2020) package 'mvpart', and the Dufrêne-Legendre index was calculated using the 'labdsv' R package.

Second, we quantified the change in benthic community composition following the 2016 heatwave using distance-based redundancy analysis (db-RDA) (Legendre and Anderson 1999). We used the Bray-Curtis dissimilarity matrix calculated from square root-transformed

benthic cover to reduce the influence of high values. For visualization purposes, the db-RDA ordination plots included total live (or dead) coral cover, total algal cover, and DHW as illustrative covariates (i.e., these variables did not contribute to the ordination but their position on the plot indicate how they correlate with changes in benthic communities over time). To aid visual interpretation of the ordination plots, we included a 'Pre/Post' heatwave factor associated with repeated surveys at each site (to maximize separation between pre- and post-heatwave communities), as well as a constraint to control for the variable resampling interval between survey sites (from 2 to 5 years). However, for inclusion in the boosted regression trees (BRT; see below), we reran the db-RDA without the 'Pre/Post' factor to avoid any redundancy with temporally varying predictors; this new analysis is thus equivalent to a principal coordinate analysis (PCO). The db-RDA was performed in the R package 'vegan'.

Using the same pre- vs. post-heatwave species-by-site matrices, we also calculated the temporal beta-diversity index (TBI) (Legendre 2019) for each survey site as a univariate proxy measuring the magnitude of change in species composition between pre- and post-heatwave surveys. We verified the assumption that, for each survey site, the temporal beta-diversity index was correlated with the distance between 'pre' and 'post' heatwave site coordinates on the 2D ordination plots. We identified benthic categories that significantly changed in % cover over time using a paired *t*-test for each benthic category corrected for multiple testing (Legendre 2019).

Last, we identified the main drivers of benthic community response to disturbance among biotic (i.e., pre-disturbance community composition) and abiotic (i.e., thermal stress) variables, and anthropogenic variables (human density, fishing closure) using boosted regression trees (BRT). Boosted regression trees are a machine learning algorithm that uses many simple decision trees to iteratively boost the predictive performance of the final models (Elith et al. 2008). Model settings include the learning rate (*lr*) that controls the contribution of each tree to the final model and tree complexity (*tc*) that determines the extent to which interactions were fitted. The number of trees (*nt*) that achieved minimal predictive deviance (i.e. the loss in predictive performance because of a suboptimal model) was determined using cross-validation (function *gbm.step* with *tc* = 2, *lr* = 0.001 and bag fraction = 0.5) (Elith et al. 2008). BRT were further simplified by dropping unimportant predictors (i.e., without affecting the model predictive performance) using a 10-fold cross-validation. We ran two BRT models on the absolute change in total hard coral cover (%) and the temporal beta-diversity index respectively, to test whether these response variables were explained by different predictors. BRT were fit in R using package 'gbm' and functions provided by Elith et al. (2008).

4.2 Results

4.2.1 Structure of pre-heatwave communities

Pre-heatwave benthic communities were strongly structured along latitudinal and longitudinal gradients at a regional scale, reflecting the major influence of environmental drivers including primary productivity, sea surface temperature and distance to land (Figure 7).

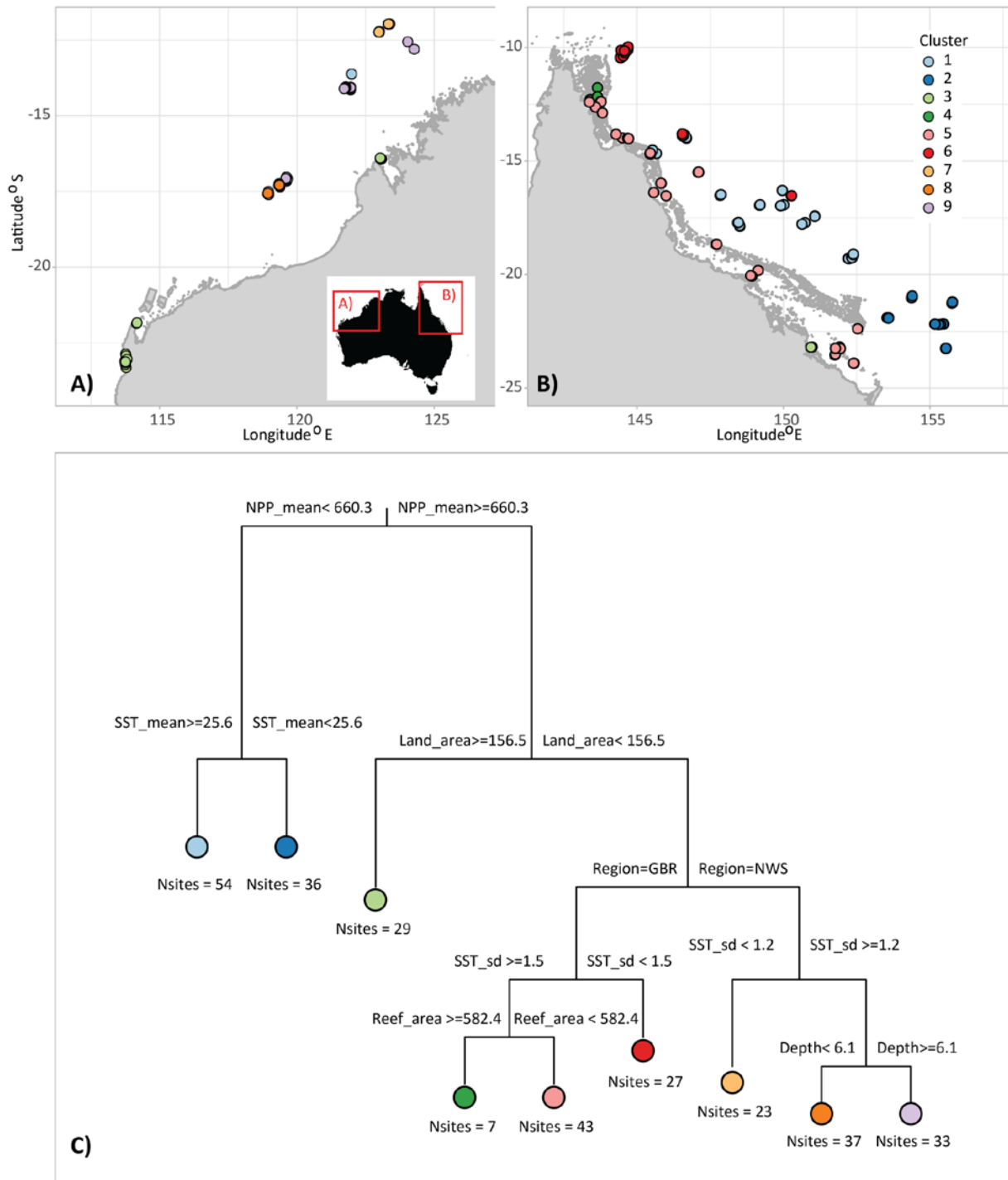


Figure 7. Spatial structure and environmental predictors of pre-heatwave benthic communities identified by multivariate regression trees.

[>Clusters (1-9) are indicated for survey sites of the western (A) and eastern (B) Australian coasts. Major environmental predictors and values associated with each split of the trees are indicated on (C). See Appendix C for variable codes.]

MRT identified a total of 9 benthic communities ('clusters') across all survey sites, primarily split between low (clusters 1-2; offshore reefs) and high (clusters 3-9) levels of net primary

productivity (Figure 7). Indicator taxa of communities exposed to both low primary productivity and warmer mean annual temperatures (cluster 1; mostly central offshore Coral Sea) included green calcified algae and *Halimeda* spp., whereas soft corals, *Porites lichen* and encrusting *Isopora* spp. corals characterized sites with cooler mean annual temperature (cluster 2; mostly southern offshore Coral Sea) (Appendix D). Among more productive environments, inshore sites including Ningaloo Reef (cluster 3) were associated with greater representation of medium foliose brown algae, encrusting leathery algae and corals, *Pocillopora* and tabular *Acropora* corals (Appendix D).

The 'region' explained the fourth split, followed by the seasonal variation in SST within both the GBR (clusters 4-6) and Northwest Shelf (cluster 7-9) regions. Within the former, mid-shelf sites with low seasonal variation in SST (cluster 4-5) were characterized by turf, branching, foliose and plate corals, while outer-shelf sites exposed to more seasonally variable SST (cluster 6) had a particularly high representation of massive *Porites*, and coral species including *Stylophora pistillata* and *Physogyra lichtensteini*. Within communities of the Northwest Shelf, the northernmost sites (e.g., Ashmore and Cartier; cluster 7) were characterized by low seasonal variation in net primary productivity, with indicator taxa that included *Favia fava*, *Seriatopora hystrix*, *S. caliendrum*, *Merulina scabricula*, in addition to erect sponges and medium foliose red algae. Among sites of high seasonal variation in primary productivity, shallow communities of Scott and Seringapatam reefs (depth < 6 m; cluster 8) had many indicator coral species (e.g., *Isopora brueggemanni*, *Acropora abrolhosensis*; Appendix D), while deeper communities composing cluster 9 were characterized by hemispherical *Porites*, encrusting *Montipora* and other coral species (e.g., *Pavona varians*, *Pocillopora verrucosa*, *Montipora grisea*; Appendix D). MRT explained a total of 22.9% variation in benthic communities (CVRE).

4.2.2 Pre- vs. post-heatwave changes in benthic communities

The 2016 marine heatwave had a highly variable footprint among different benthic communities (Figure 8A). Most benthic communities responded to heat stress through significant increase of dead coral cover (clusters 1-6; $P < 0.05$), with the largest changes in community composition (i.e., longest arrows on Figure 8A) observed for northernmost sites of the eastern region (cluster 6, at Ashmore and Boot Reefs in the Coral Sea) as well as Ningaloo and other inshore reefs (cluster 3). However, three benthic communities specific to the northwest shelf (cluster 7-9) showed a different pattern, with no increases in dead coral cover ($P > 0.05$), but significant increases in encrusting sponges and corals, encrusting leathery algae and green calcified algae (*Halimeda*), as well as *Isopora palifera* and *Porites lichen* (cluster 7) and *Acropora digitifera* (cluster 8) ($P < 0.001$) (Appendix E). Such different responses for clusters 7-9 induced a divergence of their community composition further away from other communities following the heatwave. These communities were also exposed to the greatest heat stress in 2016, with the highest DHW observed for Ashmore & Cartier (cluster 7) and highest SSTA for Scott and Seringapatam reefs (clusters 8 and 9) (Appendix B).

Changes in hard coral cover were highly variable within a given community, with significant coral cover declines for Ningaloo Reef and other inshore sites (cluster 3; $-10.4 \pm 20.7\%$; mean \pm sd), northernmost sites of the GBR and Coral Sea (cluster 6; $-7.3 \pm 10.2\%$) and shallow communities of Scott and Seringapatam reefs (cluster 8; $-5.7 \pm 12.9\%$) (Figure 8B). The cluster identity only explained 5.5% of variation in coral cover change across all survey

sites ($P = 0.003$), but up to 16.3% of variation in TBI ($P < 0.001$), which was the greatest for Ningaloo Reef and other inshore sites (cluster 3; Appendix F). TBI was strongly correlated to the distance between pre- and post-heatwave site coordinates on the db-RDA ordination plan (Pearson's $r = 0.38$, $P < 0.001$; Appendix G-A); this relationship was maintained using distances calculated from the PCO unconstrained ordination ($r = 0.37$; $P < 0.001$; Appendix G-B). TBI was, however, less correlated with the absolute change in live hard coral cover ($r = -0.22$; $P = 0.002$; Appendix G-B), indicating that changes in benthic community composition were partly decoupled from the magnitude of coral cover decline observed at the survey sites.

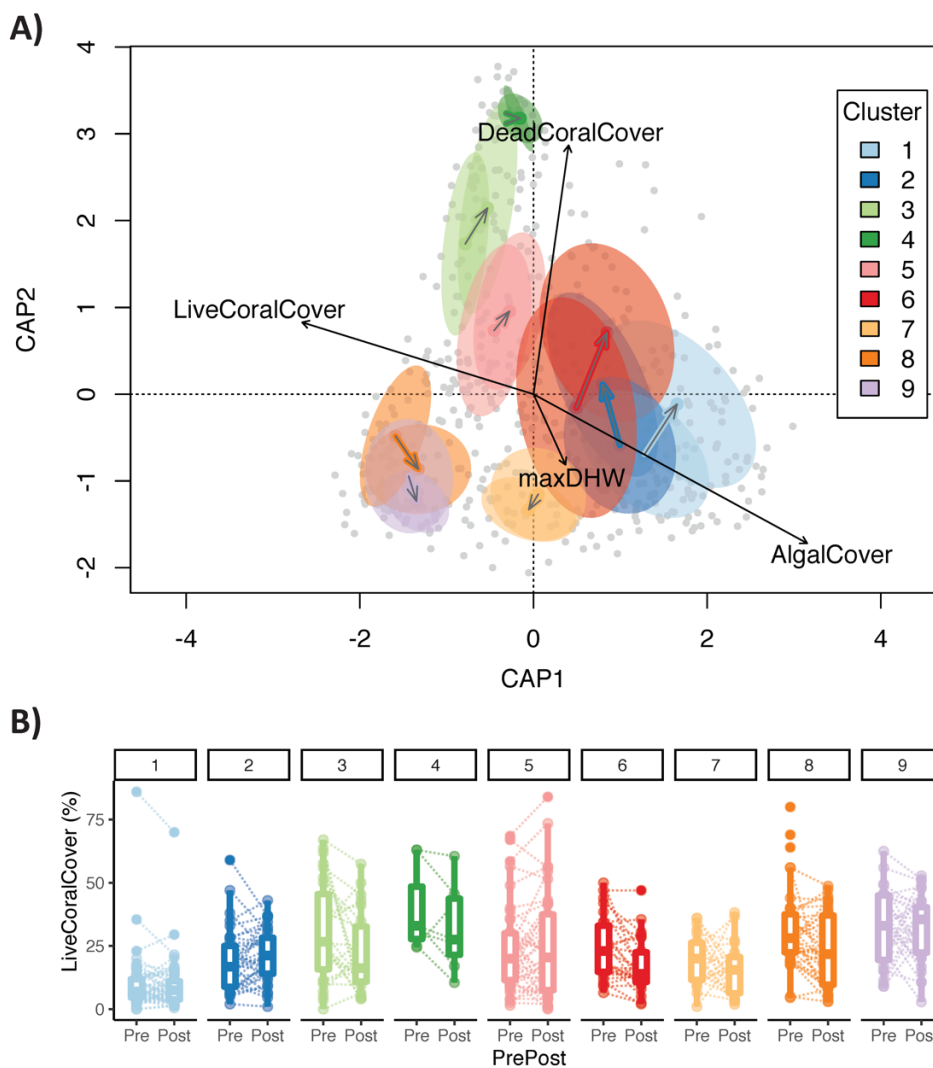


Figure 8. Change in benthic communities before and after the 2016 marine heatwave.

[> (A) Distance-based redundancy analysis showing site ordination for both pre- and post-heatwave surveys (i.e., each site corresponds to two grey dots) and temporal change in benthic community composition for each benthic cluster (ellipses and arrows; see Fig. 1 for cluster description). Ellipses encompass 1SD of all survey sites and arrows link ellipses centroids for pre- and post- benthic surveys. (B) Changes in %coral cover for sites within each

cluster. Each site corresponds to one 'pre' and one 'post' dots linked by a dotted line. Boxplots show the median (horizontal line), interquartile range (hinges), 90% confidence interval (whiskers) and outliers (dots). Numbers and colours for each cluster correspond to those mapped in Fig. 7]

4.2.3 Drivers of benthic community responses to the heatwave

BRT identified very different drivers of the change in live hard coral cover, on the one hand, and the temporal beta-diversity index, on the other (Figure 9). A total of 48.3% deviance in coral cover change was explained by BRT, primarily as a function of thermal stress (combined DHW and SSTA relative importance = 44.5%), with steep declines in coral cover at DHW > 8 and 16°C weeks, and SSTA > 2.8°C (Figure 9A).

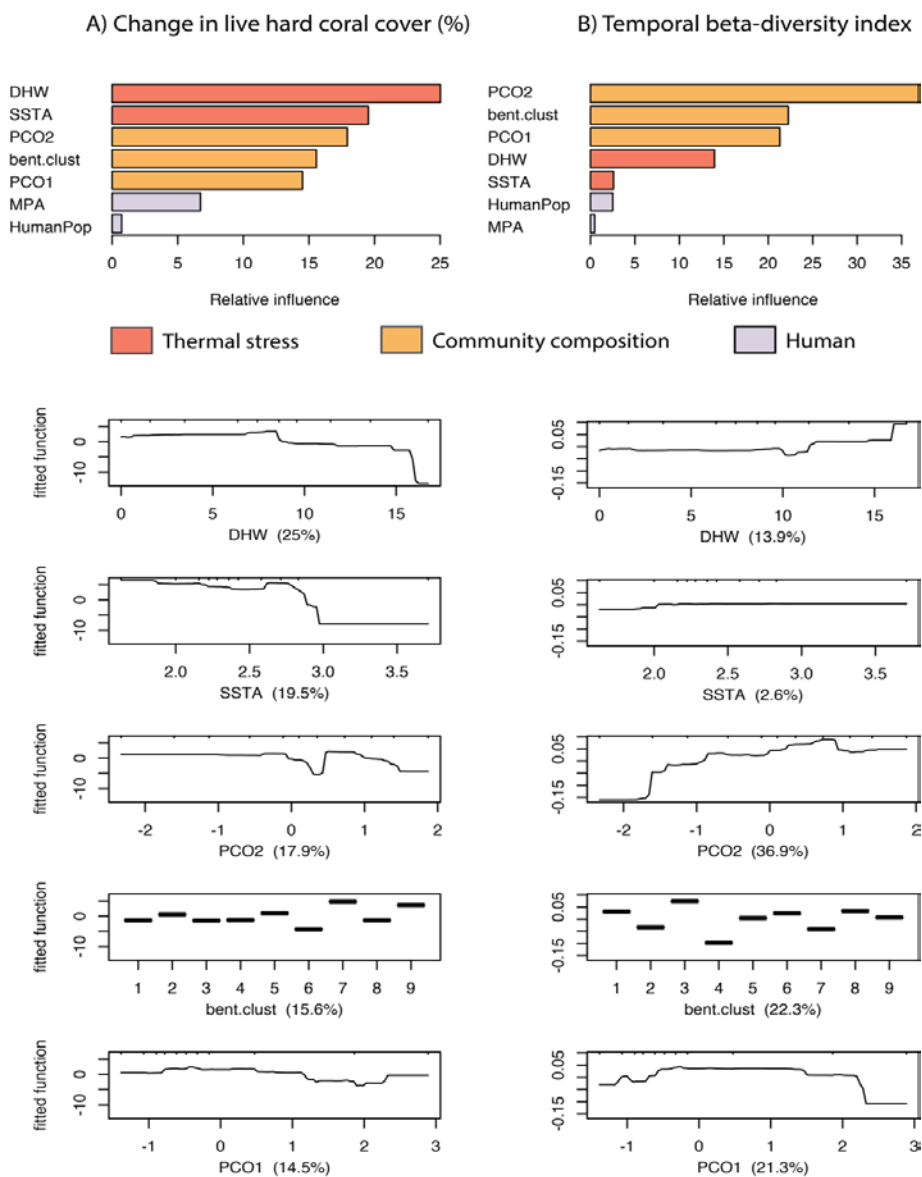


Figure 9. Influence of thermal stress, pre-heatwave community composition and human stressors on benthic responses to the 2016 marine heatwave based on (A) the change in live hard coral cover and (B) the temporal beta-diversity index.

[> The bar plot (top panel) shows the relative importance of different predictors (%), and bottom panels show marginal responses to each predictor, as determined by boosted regression trees. Thermal stress metrics include maximum degree heating weeks (DHW) and sea surface temperature anomaly (SSTA). Proxies for pre-heatwave community composition included the benthic cluster (bent.clust; Fig. 7) as well as the 'pre-heatwave' site coordinates on the PCO ordination (PCO1 and PCO2; Appendix H). Human stressors, including human population within a 20-km radius (HumanPop) and marine protected area status (MPA), did not significantly contribute to the deviance explained and are thus excluded from the marginal plots.]

In contrast, proxies for the pre-heatwave community composition were the best predictors of temporal beta-diversity (combined relative importance = 80.5%; Figure 9B), with a total of 45.9% deviance in TBI explained by all predictors collectively. In particular, communities dominated by *Porites* hemispherical, *Montipora* encrusting or *Acropora muricata* before the heatwave (i.e., positive values on PCO2; Figure 9B; Appendix H) showed the largest marginal changes in community composition subsequent to the heatwave (i.e., highest TBI assuming all other predictors constant). Conversely, a high proportion of green calcified algae (*Halimeda*), such as in cluster 1, was associated with lesser post-heatwave change in the composition of benthic communities (i.e., negative values on PCO2; Figure 9B; Appendix H). Thus, communities dominated by *Halimeda* were affected by the 2016 heatwave and other recent stressors much less than communities dominated by *Porites*, *Montipora* and *Acropora muricata*.

The benthic cluster was the second most important predictor of TBI, with a strongly positive marginal effect for Ningaloo Reef and other inshore sites characterized by medium foliose brown algae, encrusting leathery algae and corals, *Pocillopora* and tabular *Acropora* corals (cluster 3) and negative for the northernmost inshore reefs of the GBR characterized by *Acropora*, branching, foliose and plate corals (cluster 4; Figure 9B). Human stressors had low relative importance in both cases and were dropped from the set of predictors without affecting the deviance explained by either BRT.

4.3 Discussion

Coral reef communities worldwide are impacted by increasingly frequent and severe marine heatwaves, yet coral responses to heat stress vary geographically according to factors that remain poorly understood (but see Stuart-Smith et al. 2018, Darling et al. 2019, McClanahan et al. 2019). Our analysis showed that, on Australian tropical reefs, exposure to thermal stress was the main driver of coral cover decline following the 2016 heatwave, while the pre-heatwave community composition primarily determined the extent of community reshuffling (as measured by the temporal beta-diversity index). These findings have important implications for understanding ecological successions within benthic communities as marine heatwaves increase in frequency and severity (Oliver et al. 2018a), and for identifying benthic communities that are more or less vulnerable to warming oceans (Hughes et al. 2018a, Darling et al. 2019).

Our finding that the pre-heatwave composition of coral communities mostly determined their response to the heatwave likely indicates the footprint of past disturbance history (or 'ecological memory', *sensu* (Hughes et al. 2018b)) whereby the most sensitive taxa are extirpated first, and the less sensitive ones remain until the next disturbance. For example,

communities characterized by green calcified algae (*Halimeda* spp.) and relatively low coral cover were associated with the least change in community composition, possibly because they had already undergone species reshuffling in response to previous disturbances. Specifically, green calcified algae (*Halimeda* spp.) were characteristic of benthic communities within the central Great Barrier Reef and Coral Sea (cluster 1), an area that has previously been identified as a hotspot of past cyclone activity (Mellin et al. 2020). Low coral cover at those reefs before 2016 has thus likely resulted from repeated impacts due to frequent disturbances that maintain reef communities in a disturbed state prior to the 2016 heatwave.

The major influence of disturbance history is also likely to be particularly important in Ningaloo Reef, where some of our pre-heatwave data were collected before Tropical Cyclone Olwyn that caused a major decline in coral cover in 2015 (Figure 3 in Chapter 3 and (Stuart-Smith et al. in press)). Comparatively, further coral cover decline following the 2016 marine heatwave was moderate in Ningaloo Reef, yet highly variable among sites (see cluster 3 in Figure 8B). This stresses the need to account for local variation in disturbance impacts, which can differ among reefs and survey sites based on local habitat characteristics such as depth and wave exposure. Spatially explicit information on cyclone severity was lacking for Ningaloo Reef, preventing us from quantifying cyclone impacts on benthic communities in the same way as we did for thermal stress. Resolving the relative impact of multiple disturbances over time ultimately requires reconstructing disturbance history at high spatiotemporal resolutions. This was achieved across the Great Barrier Reef at a 1-km resolution from 1985 to 2016 (Matthews et al. 2019) but is yet to be modelled at a national scale and beyond, opening up important opportunities for future research.

The extent of coral cover decline following the heatwave was mostly driven by the magnitude of heat stress, as measured by DHW (corroborating e.g., Hughes et al. 2017), but also SSTA. While DHW and SSTA showed different spatial footprints in 2016, they were both the highest on the Western coast, which has comparatively been less studied than the GBR (but see Gilmour et al. 2013, Edgar et al. 2020a). The recently available coral dataset at the species level used in this study opens up unique opportunities for better understanding interspecific variability in coral susceptibility to heat stress. A potential caveat in our analysis nevertheless lies in possible observer bias, as some photoquadrats were scored by different observers (see Methods). This might have introduced bias based on the varying level of taxonomic definition (species vs. genus), but also in the way that different observers classified bleached or dead corals. An update of this dataset is underway with all photoquadrats being scored by the same expert (E. Turak), which will allow an improved understanding of coral community composition. Such improved understanding will ultimately enable the development of ecological indicators predicting the vulnerability of coral communities based on the relative importance of stress-sensitive vs. stress-tolerant taxa. Future research should also focus on quantifying functional ecosystem changes at those reefs, which might be particularly acute if reef organisms such as fish and invertebrates are already close to their thermal distribution limits (Stuart-Smith et al. 2018).

CONCLUSIONS

The overall aim of this project was to infer the status and trends of coral and rocky reef biodiversity around Australia, building on a unique integrated dataset merging three long-term monitoring programs. We used a multifaceted approach looking at (i) temporal trends in population size for individual species in Chapter 2, (ii) spatiotemporal patterns in ecological indicators reflecting the impacts of warming and fishing pressure in Chapter 3, and (iii) impacts of a major marine heatwave on coral species communities in Chapter 4.

All three chapters indicated a predominant effect of increasing sea surface temperature on reef biodiversity, both from gradual ocean warming and acute marine heatwaves. Notably, pronounced declines were evident in population sizes for species distributed across southern Australian temperate rocky reefs, in particular where sustained water temperatures were $>1^{\circ}\text{C}$ above long-term means. Major marine heatwaves over the study period (2011 in temperate Australia, 2016 on northern tropical reefs) impacted habitat-forming organisms such as kelps and corals, with consequences on fish communities and the relative importance of species with cool vs. warm affinities.

RECOMMENDATIONS

While all results relating to ocean warming and extreme events point to the need for longer-term national efforts to reduce climate change through reduced carbon emissions, shorter term recommendations largely relate to further research needs. A logical and much needed continuation of this work would include the development of improved models to quantify the relative impact of gradual warming and marine heatwaves on different components of coral and rocky reef ecosystems, detect possible lag effects between environmental change and ecological responses, and estimate ecological recovery potential following acute disturbances such as marine heatwaves.

Compared to the impact of ocean warming, that of fishing pressure seems to have slowed since the last SoE, which is encouraging. However, a better appreciation of fishing impacts would rely on additional surveys away from marine protected areas, and models integrating proxies of both commercial and recreational fishing pressure such as distance to nearest market or density of human population. Moreover, a critical avenue for future research would be the inference of reference points, for example the large fish biomass that can be expected at a particular location given its local and broadscale social-environmental context, and the potential increase anticipated under different management options. Such reference points would therefore help assess the performance of a given ecological indicator at different locations and jurisdictions based on its expected value and inform on the effectiveness of current management interventions in place.

Our analysis also highlighted a high level of variability in how species and communities respond to the same amount of pressure or heat stress. This was partly linked to species thermal affinity, with many temperate communities being progressively tropicalized, and species close to their thermal distribution limits likely to be extirpated first. While thermal affinity is progressively being resolved for fish species, the equivalent for many invertebrate and coral species remains a major knowledge gap. Until this project, coral identification was

mostly possible to the genus level (or a combination of genus and growth form). The availability of data at the species level thus opens up new opportunities for understanding, among coral species and benthic communities in general, the 'winners' and the 'losers' of climate change. This will also greatly improve our understanding of the spectrum of functional ecosystem changes anticipated for coral communities that are more or less vulnerable to future environmental change.

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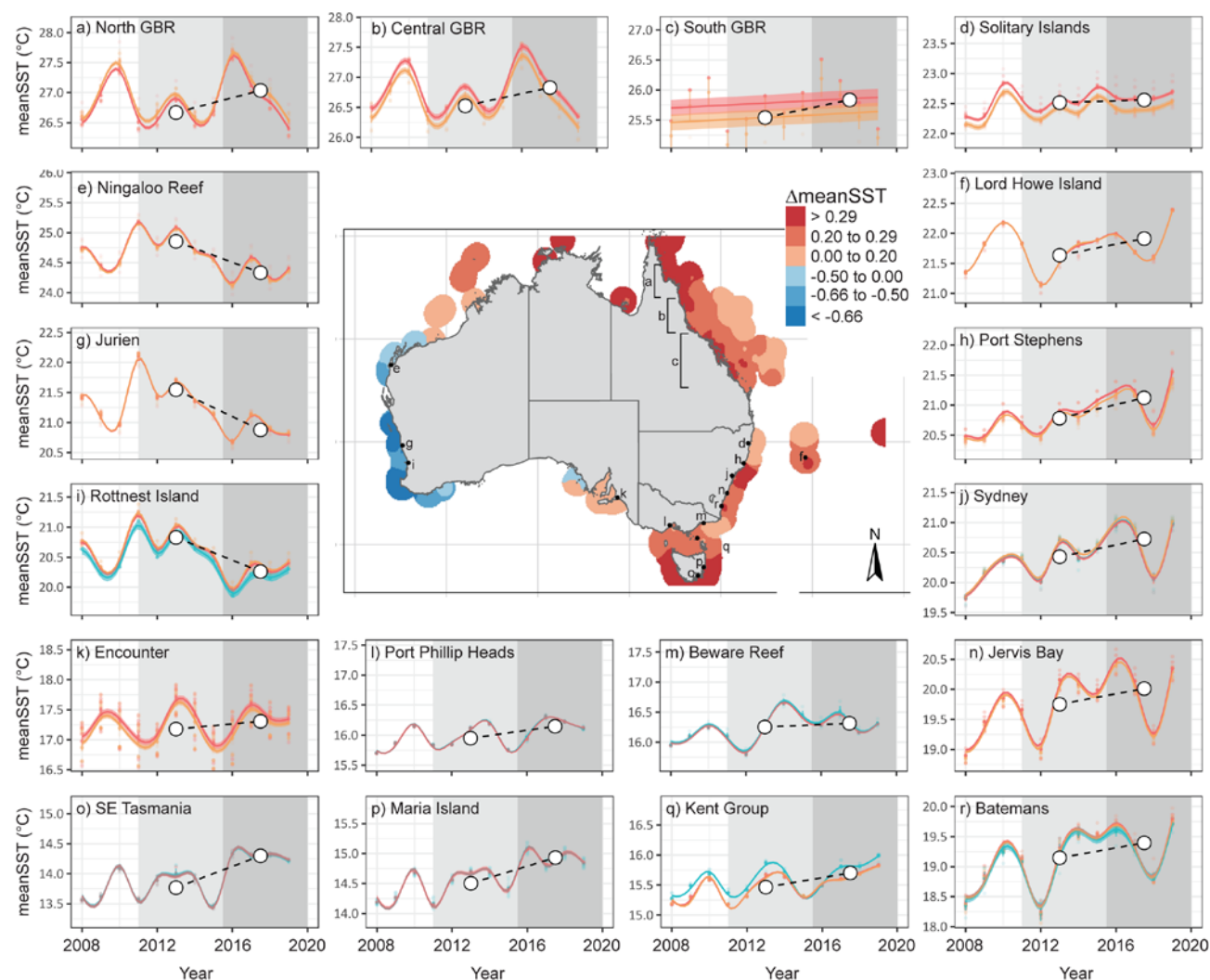
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APPENDIX A

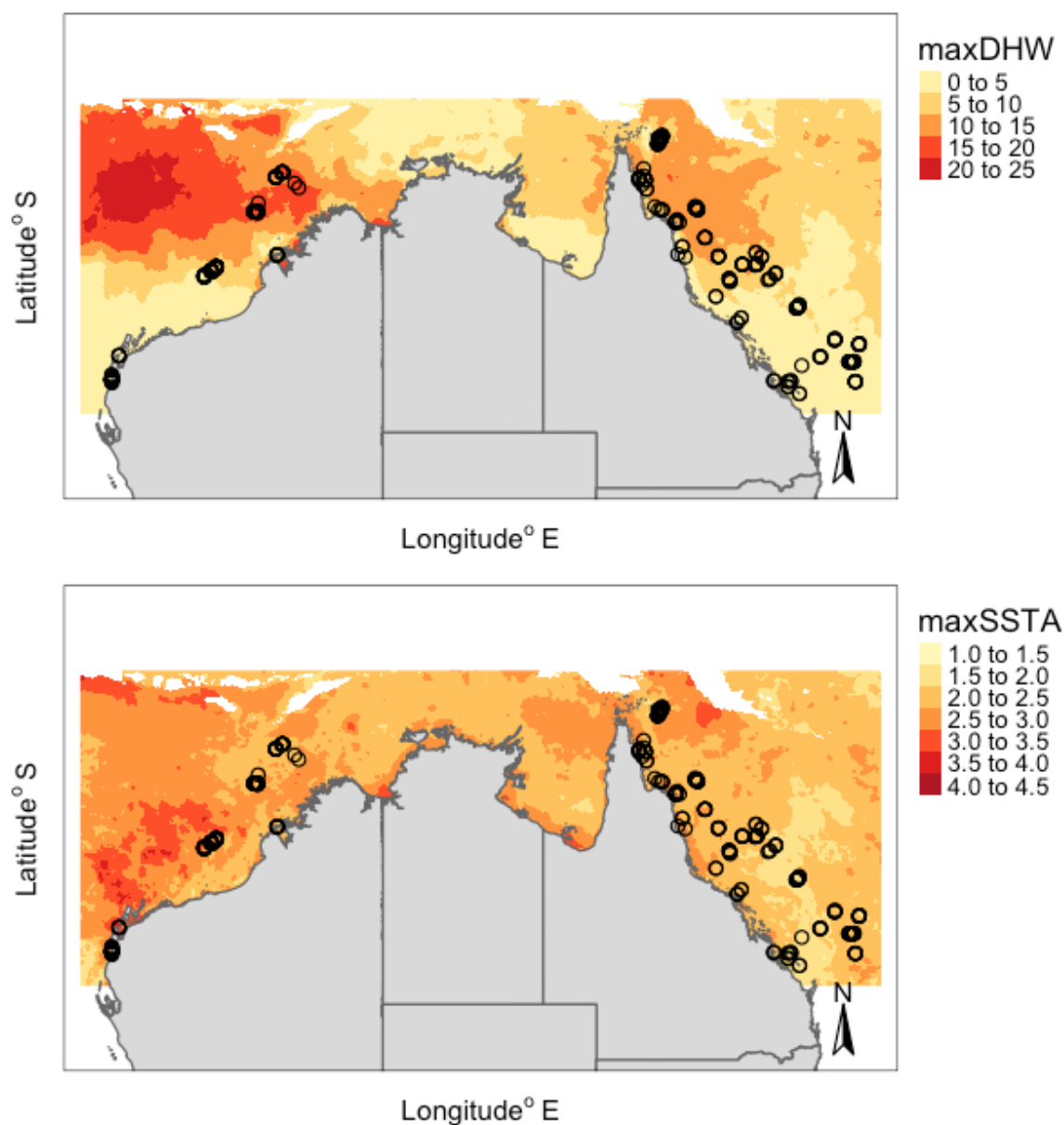


Appendix A. Overall change in mean annual sea surface temperature (°C) between 2008 and 2020 at ecological monitoring locations surveyed as part of the RLS, AIMS and ATRC programs.

[>Trends through time shown in individual graphs for monitored locations are from statistical models (GAMMs) that account for different numbers sites within each location. The coloured map shows synoptic patterns in the differences in average raw values for regions across the last two 5-year periods (i.e., the difference between the 2011-2015 average and the 2016 - 2020 average, represented by the white dots and corresponding to the two grey shaded periods in the individual trend plots). Red regions show increases in mean annual sea surface temperature, while blue regions show declines over the same period.

Mean annual sea surface temperature data were extracted for each site from the National Oceanographic and Atmospheric Administration Coral Reef Watch dataset [ref]

APPENDIX B



Appendix B. Spatial patterns in thermal stress metrics for the 2016 marine heatwave, including maximum annual degree heating week ($^{\circ}\text{C week}$) and maximum annual sea surface temperature anomaly ($^{\circ}\text{C}$). Black open symbols indicate the location of survey sites before and after the 2016 heatwave.

APPENDIX C

Appendix C. Environmental covariates used in multivariate regression trees (MRT) and boosted regression trees (BRT).

Variable	Description	Unit	Source	Covariate in:
SST_mean	Sea surface temperature, climatological overall mean (1985-2012)	°C	NOAA Coral Reef Watch climatology	MRT
SST_sd	Sea surface temperature, climatological intra-annual standard deviation (1985-2012)	°C	NOAA Coral Reef Watch climatology	
NPP_mean	Net primary productivity of carbon, overall mean (2003-2013)	mg C m ⁻² day ⁻¹	Yeager et al.	
NPP_sd	Net primary productivity of carbon, intra-annual standard deviation (2003-2013)	mg C m ⁻² day ⁻¹	Yeager et al.	
Wave_mean	Wave energy flux, overall mean	kW m ⁻¹	Yeager et al.	
Wave_sd	Wave energy flux, intra-annual standard deviation	kW m ⁻¹	Yeager et al.	
Land_area	Coral reef area within a 20 km radius	km ²	Yeager et al.	
Reef_area	Land area within a 20km radius	km ²	Yeager et al.	
Depth	Average transect depth at each site	m	This study	
Region	Categorical: GBR and Coral Sea / Ningaloo Reef / Northwest Shelf.	-	This study	
DHW	Degree Heating Weeks: maximum annual (2016)	°C wk ⁻¹	NOAA Coral Reef Watch	BRT
SSTA	Sea surface temperature anomaly: maximum annual (2016)	°C	NOAA Coral Reef Watch	
MPA	Marine Protected Area, categorical: open to fishing / closed / restricted	-	This study	
HumanPop	Human population (2015) within a 20km radius	-	Yeager et al.	

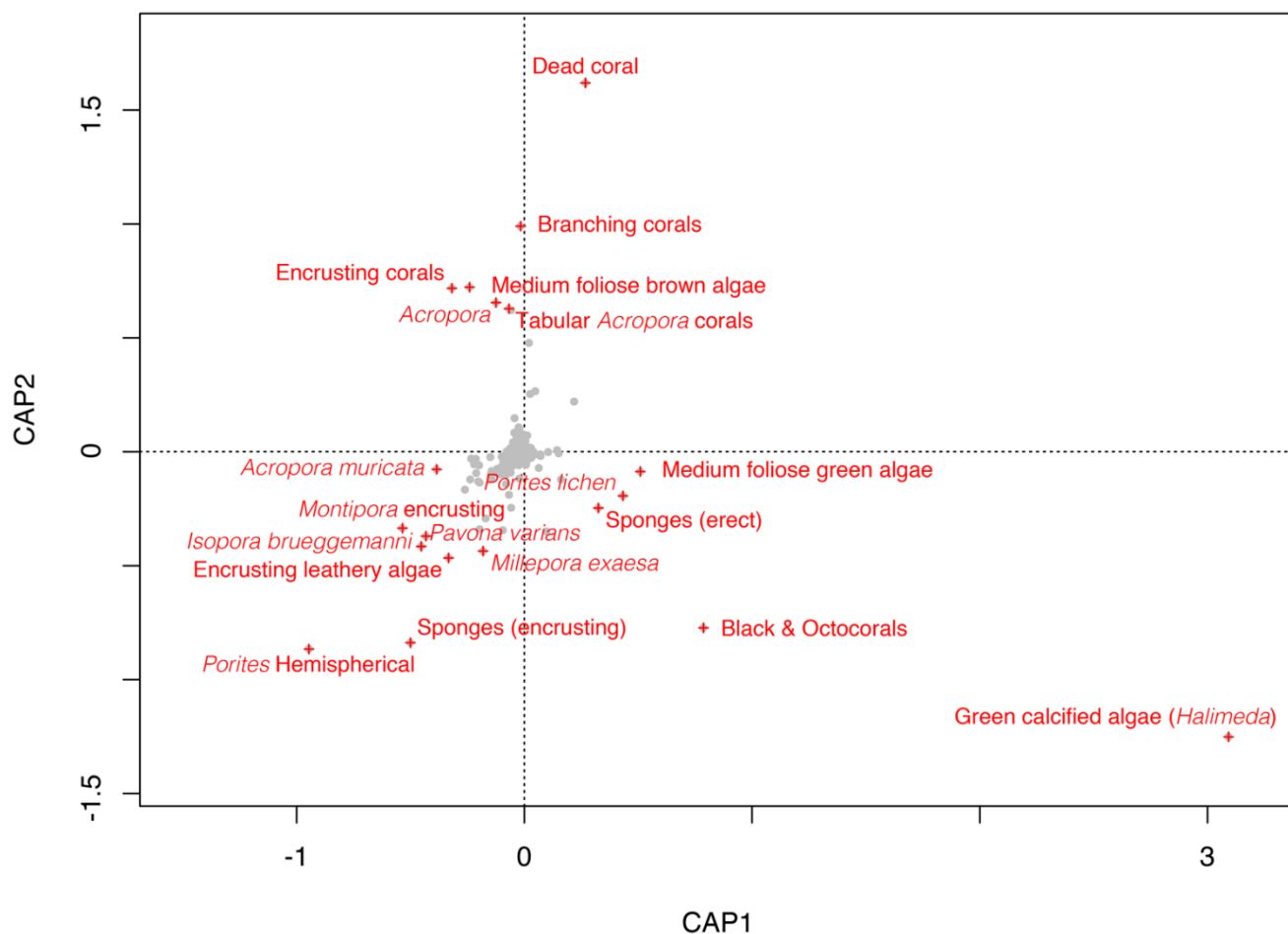
APPENDIX D

Appendix D. Pre-heatwave indicator benthic categories and taxa associated with each benthic community and identified based on the Dufrene-Legendre index ($P < 0.05$). Categories highlighted in bold indicate those that significantly decreased in relative cover following the 2016 heatwave ($P < 0.01$), and asterisk indicate categories that were no longer an indicator after the heatwave.

Cluster #	Indicator benthic categories and taxa
1	<i>Astreopora myriophthalma</i> * Green calcified algae (<i>Halimeda</i>) Medium foliose green algae
2	<i>Acropora abrotanoides</i> <i>Acropora austera</i> * Soft corals <i>Isopora</i> (encrusting) <i>Isopora palifera</i> <i>Porites lichen</i>
3	Encrusting corals* Encrusting leathery algae Filamentous algae (epiphyte)* Macroalgae* Large polyp stony corals (free living) Medium foliose brown algae Molluscs* <i>Montipora aequituberculata</i> <i>Platygyra daedalea</i> * Pocillopora* Tabular <i>Acropora</i> corals
4	<i>Acropora</i> Branching corals Dead coral Foliose Plate corals Massive corals
5	<i>Porites rus</i> *
6	<i>Physogyra lichtensteini</i>* <i>Porites massive</i> * <i>Stylophora pistillata</i>*
7	<i>Ctenactis</i> <i>Favia fava</i> * <i>Goniopora</i> Hemispherical Medium foliose red algae*

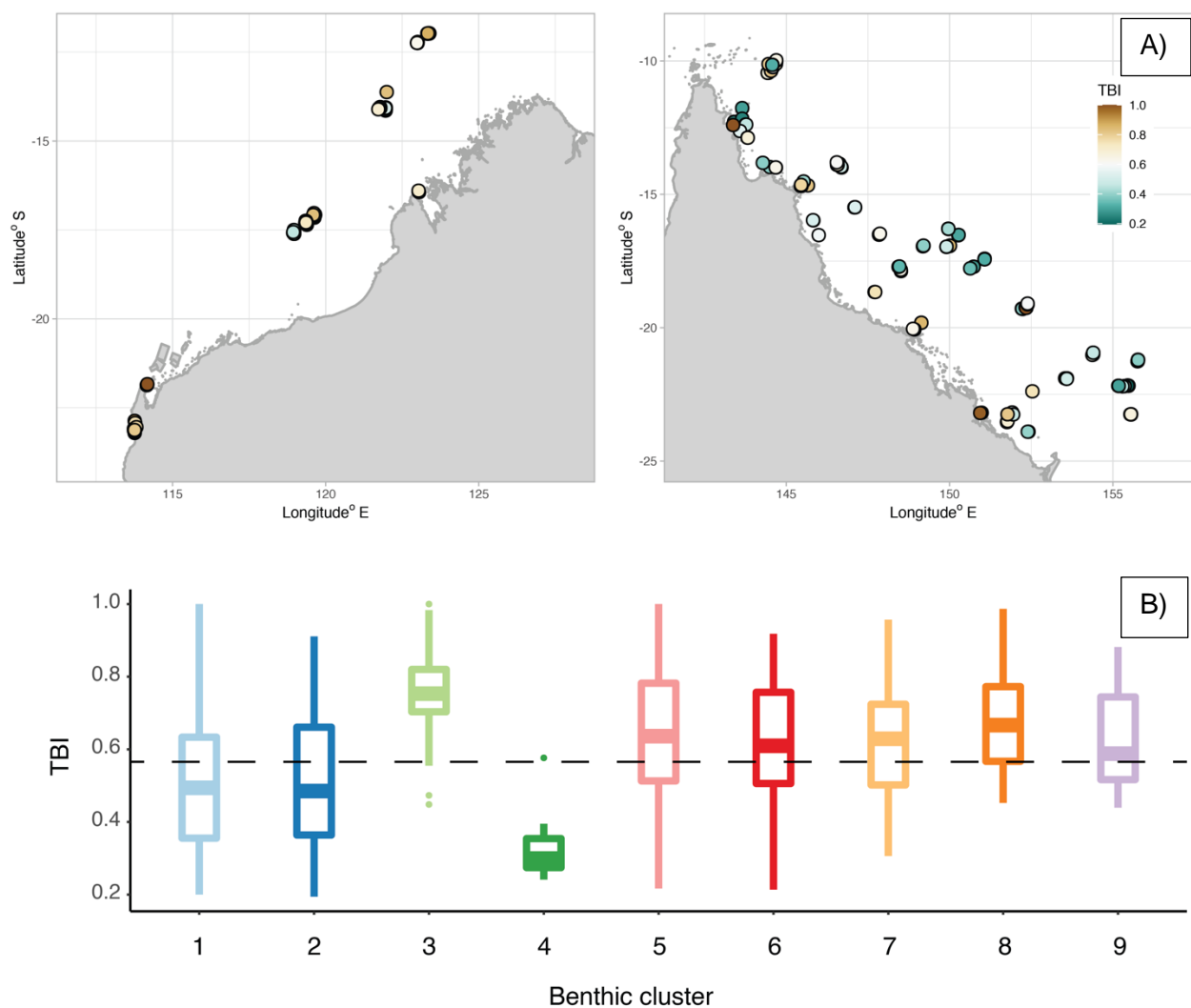
Cluster #	Indicator benthic categories and taxa
	<i>Merulina scabricula</i> * <i>Porites cylindrica</i> <i>Porites nigrescens</i> * <i>Seriatopora caliendrum</i> <i>Seriatopora hystrix</i> Sponges (erect)
8	<i>Acropora abrolhosensis</i> <i>Acropora cerealis</i> * <i>Acropora loisetteae</i> * <i>Acropora muricata</i> <i>Acropora pulchra</i> <i>Acropora turaki</i> <i>Galaxea astreata</i> * <i>Goniastrea edwardsi</i> <i>Hydnophora rigida</i> * <i>Isopora brueggemanni</i> <i>Montipora danae</i> * <i>Montipora hoffmeisteri</i> * <i>Montipora tuberculosa</i> <i>Phymastrea magnistellata</i> *
9	<i>Acropora cytherea</i> * <i>Acropora gemmifera</i> <i>Acropora humilis</i> * <i>Acropora hyacinthus</i> <i>Acropora latistella</i> * <i>Cyphastrea</i> (encrusting)* <i>Diploastrea heliopora</i> <i>Favia</i> <i>Favia stelligera</i> <i>Goniastrea pectinata</i> <i>Millepora exaesa</i> <i>Montipora</i> (encrusting) <i>Montipora grisea</i> <i>Pavona varians</i> <i>Pocillopora meandrina</i> <i>Pocillopora verrucosa</i> <i>Porites</i> (hemispherical)

APPENDIX E



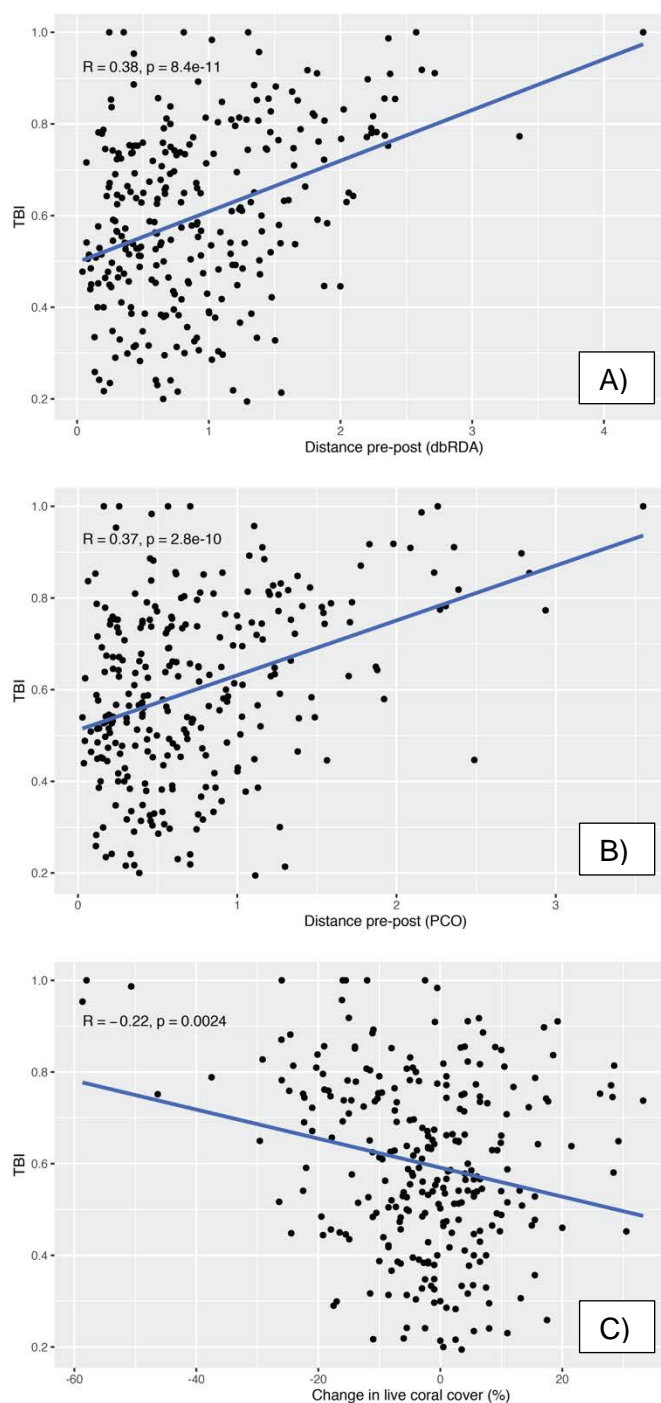
Appendix E. Distance-based redundancy analysis species plot. For clarity, only taxa contributing >30% of the fit are labelled.

APPENDIX F



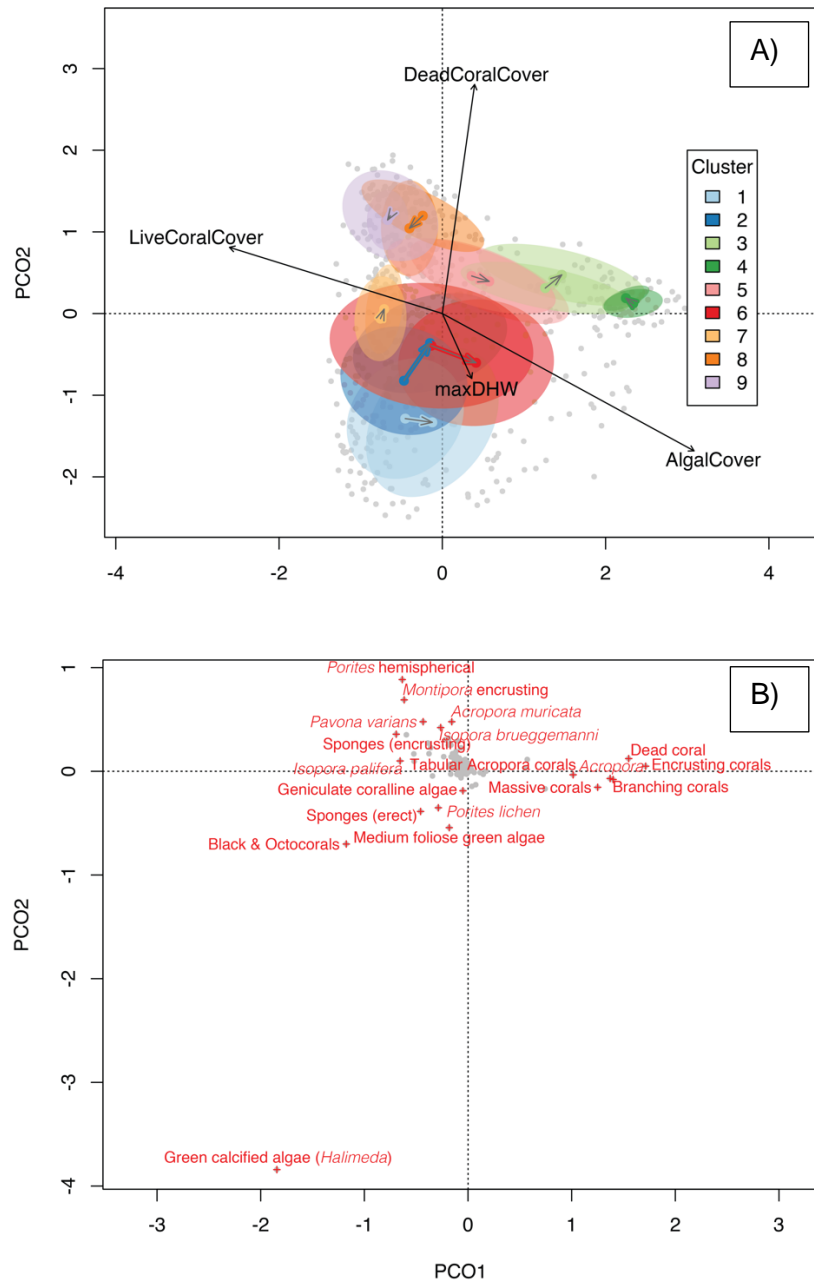
Appendix F. Spatial variation in the temporal beta-diversity index, (A) mapped across the study area and (B) plotted for each benthic cluster. Boxplots show the median (horizontal line), interquartile range (hinges), 90% confidence interval (whiskers) and outliers (dots). The dotted horizontal line shows the overall median across all survey sites.

APPENDIX G



Appendix G. Relationships between the temporal beta-diversity index (TBI) and the distance between pre- and post-heatwave community composition based on the first two axes of the distance-based redundancy analysis (db-RDA) (A), or the first two axes of the principal coordinate analysis (PCO) (B), and the absolute change in hard coral cover (C).

APPENDIX H



Appendix H. Principal coordinate analysis showing (A) site ordination for both pre- and post-heatwave surveys (i.e., each site corresponds to two grey dots) and temporal change in benthic community composition for each benthic cluster (ellipses and arrows; see Fig. 1 for cluster description). Ellipses encompass 1SD of all survey sites and arrows link ellipses centroids from pre- to post-2016 samples. (B) Species ordination plan showing taxa that mostly contributed to the dissimilarity between surveys.



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