Ecosystem restructuring along the Great Barrier Reef following mass coral bleaching

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ABSTRACT

Global warming is dramatically changing diverse coral reef ecosystems through an increasing frequency and magnitude of mass bleaching events[1-3]. How local impacts scale up over affected regions depends on numerous factors, including patchiness in coral mortality, metabolic effects of extreme temperatures on populations of reef-dwelling species[4], and interactions between taxa. Here we use 'before and after' data to evaluate ecological change in corals, algae, fishes and mobile invertebrates at 186 sites along the full latitudinal span of the Great Barrier Reef and western Coral Sea following the 2016 mass bleaching event. One year post-bleaching, reductions in live coral cover of up to 51% were observed on surveyed reefs that experienced extreme temperatures, but regional patterns of coral mortality were patchy. Consistent declines of coral-feeding fishes were evident at the most heavily impacted reefs, whereas few other short-term responses of reef fishes and invertebrates could be attributed directly to changes in coral cover. Nevertheless, substantial region-wide ecological changes occurred that were largely independent of coral loss, and instead appeared directly linked to sea temperatures. Community-wide trophic restructuring was evident, with weakening of strong pre-existing latitudinal gradients in the diversity of fishes, invertebrates and their functional groups. In particular, fishes that scrape algae from reef surfaces, considered important for recovery following bleaching[2], declined on northern reefs, whereas other herbivorous groups increased on southern reefs. The full impact of the 2016 bleaching event may not be realised until dead corals erode through the next decade[5,6], but our short-term observations suggest that recovery processes, and the ultimate scale of impact, are affected by functional changes in communities, which in turn depend on the thermal affinities of local reef-associated fauna. Such change will vary geographically, and may be particularly acute at locations where many fishes and invertebrates are close to their thermal distribution limits[7].

MAIN TEXT

The 2016 mass bleaching event affected coral reefs world-wide, with catastrophic impacts reported in the Red Sea, central Indian Ocean, across the Pacific, and in the Caribbean[3,8,9]. The Australian Great Barrier Reef (GBR), the largest coral reef system in the world, experienced the warmest temperatures on record for the region. An estimated 91.1% of reefs along the GBR experienced some bleaching[3], resulting in an estimated loss of ~30% of live coral cover over the following six months[10]. The event was thus comparable to the 1998 mass bleaching event in the Indian Ocean in terms of reported impacts on corals[2,11]. We surveyed 186 reef sites along the GBR and at less-studied isolated reefs in the Coral Sea before and after the 2016 bleaching event to investigate reef- and regional-scale impacts of the extreme thermal anomaly and realised coral mortality on the rich reef-associated fish and mobile invertebrate fauna. At each site, globally standardised Reef Life Survey census methods[12] were used to quantify changes to coral cover, reef fishes and mobile macroinvertebrates at multiple depths (overall mean 6.7 m, range 0.8 – 17.0 m). 'Before' data were from 2010 to 2015, and 'after' data were from 8-12 months post-bleaching.

As reported elsewhere[10], live hard coral cover declines were widespread (Fig. 1), although we found the regional pattern to be more spatially heterogeneous than was found in the previous report, in which field surveys were standardised at 2 m depth[10]. Forty-four of 186 sites surveyed experienced absolute declines in live coral cover exceeding 10% (up to 51% loss for one site at Osprey Reef), with the northern Coral Sea reefs suffering the most consistent losses (Fig. 1a, b). The magnitude of coral cover change was related to the local sea temperature anomalies (Fig. 1d; ED Fig. 1), but coral loss varied considerably, and not all reefs in regions that experienced the greatest temperature anomalies experienced losses in live coral cover. In some cases, such as the central Coral Sea reefs, a history of cyclone damage meant there was relatively little coral to lose. Thus, geographic patterns in pre-bleaching cover played a critical role in the realised impacts of bleaching on corals (Fig. 1d). Coral cover losses of greatest magnitude occurred in disparate locations, including in the northern Coral Sea (Boot and Osprey Reefs; mean ~15% absolute cover loss, or ~40% of the pre-bleaching live coral cover), and the southern GBR (most southerly Swain Reefs; 28% loss, or 100% of pre-bleaching cover). The northern reefs in the GBR experienced the most extensive bleaching of those surveyed during the 2016 event[3], but not all reefs in that area suffered the extreme rates of live coral cover loss more generally observed[10] (Fig. 1a, b). The fate of bleached corals can vary considerably[13,14], and a reasonable proportion of corals on some of these reefs must have regained their zooxanthellae and survived the bleaching event. Algal cover substantially increased across the majority of reefs that experienced coral declines (Fig. 1c; ED Fig. 2).

Not all coral declines observed during the study could be assumed to be solely due to the bleaching event (other disturbances, such as cyclones, may have also had impacts on corals at particular locations; see methods). To investigate impacts on reef fauna that could be most clearly attributable to the bleaching event, we quantified changes on a subset of reefs that experienced extreme heating and substantial live coral cover loss (see methods for criteria). On these reefs, the abundance of coral-eating fishes (corallivores) consistently declined, and declines in local fish species richness were also common (ED Fig. 3). Such changes have previously been observed as rapid responses to coral bleaching events[5,15,16], and are clearly concerning as a distinctive form of reef-scale biodiversity loss resulting from bleaching. These changes were not observed on a subset of comparison reefs that also experienced extreme heating, but that did not experience noticeable loss of live coral cover (ED Fig. 3). Other previously reported short-term impacts of bleaching, such as increased herbivore abundance[15] in response to a boom in algal resources[5,16], occurred on some study reefs, but were not consistent features of those reefs with the clearest impacts on coral cover attributable to bleaching (ED Fig. 3).

Coherent patterns of ecological change were evident when assessing regional-scale trends between survey periods across the full range of sites surveyed. The latitudinal gradient in local species richness of mobile fauna[17] declined in slope through a combination of decreased local fish richness on northern reefs and markedly increased richness of macro-invertebrates and small cryptic fishes on southern reefs (Fig. 2; ED Fig. 4). Fish community structure on southern reefs became more similar to those in the north (ED Fig. 5), a broad-scale homogenisation that resulted in a slight decline in the overall number of fish species recorded across all surveys (from 532 to 494). Invertebrate communities also changed considerably between survey periods (Fig. 2; ED Fig. 4), characterised most clearly by sea urchins occurring less frequently on northern reefs and increasing in abundance on southern reefs after the bleaching event.

A key outcome of these changes was the regional alteration to the functional structure of reef communities, with potentially important consequences for the recovery of impacted reefs. Functional richness (represented by the number of unique functional trait combinations comprised by fishes and invertebrates on each survey) increased on southern reefs, where the potential for local herbivory also increased through herbivorous fish biomass gains (Fig. 2; ED Fig. 4; ED Fig. 6) and patchy sea urchin abundance gains. In contrast, the frequency of occurrence and biomass of fishes that scrape algae and microscopic autotrophs off coral-rock surfaces (scraping herbivores) and the frequency of sea urchins declined on northern reefs, while plankton-feeding fish biomass increased (Fig. 2; Fig. 3; ED Fig. 4).

Most of these rapid, regional-scale ecological changes could not be linked to coral loss (ED Fig. 4), and so cannot be assumed to be indirect effects of the bleaching event (or any other causes of coral degradation during the study). Some of these changes could nevertheless result from changes in the local composition and community structure of corals and algae, independently of the total amount of coral loss, but the spatial footprint of changes in the fishes and the invertebrates suggests at least some independence of changes in the benthic cover. The consistency of ecological change along the latitudinal gradient differs from the heterogeneous patterns in coral and algal cover change, particularly along the GBR, while the southern Coral Sea reefs showed very clear ecological change, despite largely escaping bleaching. The loss of large predatory fishes in remote locations, such as in the northern GBR and on some reefs in the southern Coral Sea (ED Fig. 6), could potentially be associated with expansion of the fishing footprint, but this needs further investigation. Changes in fishing pressure are unlikely to have resulted in most of the other coherent regional scale patterns of community change, because few herbivorous fishes, cryptic fishes and reef-dwelling invertebrates are targeted by fishers in this region.

Another potential explanation for rapid community restructuring relates to more direct effects of region-wide anomalously warm temperatures and altered currents on species' local occupancy and abundance[18]. Marine heatwaves and short-term temperature variation have been shown to dramatically affect temperate rocky reef communities[19], but have not been well investigated on coral reefs. The sea temperatures experienced during the bleaching event (up to 32 °C) in the northern GBR[18] exceeded those at the warm limits of the distributions for the majority of reef fishes recorded in the region[7], and many species on northern reefs probably experienced thermal stress.

We used Species Temperature Index (STI) values for those species recorded on surveys of the northern reefs to investigate the possibility that reduced fish species richness and altered trophic structure on the warmer northern reefs was due to disproportionate impacts on species with an affinity for relatively cooler seas. STI values are derived from the realised thermal distributions of species across their entire range[7,20], and provide a nuanced and continuous measure of the ocean climate each species' distribution is centred on. On average, patterns of change in the frequency of occurrence of species in each trophic group were positively related to their STI values (Fig. 3). Specifically, those species that declined between surveys across northern reefs tended to be corallivores and scraping herbivores with distributions through relatively cooler waters; a pattern that was consistent between GBR and Coral Sea fish communities, which have different biogeographic affinities[21] (ED Fig. 5). Fishes that feed by excavating the coral-rock surface tended to have the warmest affinities (i.e. higher STI values), and became more common on surveys in both the north and south (Fig. 3), although increased frequency in the north did not also translate to increased local biomass (Fig. 2, ED Fig. 4).

A bias in thermal affinities of reef fishes related to their trophic group has not previously been investigated in detail, and the generality of this phenomenon is unknown. In this case, the pattern was characterised by high variability (Fig. 3), and becomes increasingly influenced by excavators at the scale of the full GBR. The opposite situation may occur on temperate reefs, where herbivorous fishes have warmer STIs than other trophic groups[22]. Further investigation is needed to determine whether biases in STIs of trophic groups is idiosyncratic and location-dependent, or whether coherent geographic patterns emerge for particular trophic groups. The decreased frequency of occurrence of corallivores at northern reefs observed here could also be related to coral mortality, with this effect potentially confounded with inferred impacts of thermal stress (or other causes not investigated).

Ecological change on southern reefs included an increasing similarity of fish community structure to that on northern reefs (ED Fig. 5), which is consistent with a potential influence of warmer temperatures, but could also result from altered currents and possible enhanced fish recruitment of northern species in the south. No clear signal of a substantial recruitment event was evident, however, with local densities of juveniles no greater after the bleaching event than before (ED Fig. 7). Instead, the majority of positive changes in the south related to taxa of relatively small body size – both invertebrates and cryptic fishes. These could be more sensitive to temperature changes and/or capable of increases in local population size more rapidly, and/or could experience rapid numerical or behavioural release if predation pressure was reduced. Although less probable, release from predation may have resulted from minor decreases in the frequency of predatory fishes in the Coral Sea (ED Fig. 6) and benthic invertebrate consumers in the GBR (Fig. 3).

Our broad-scale field surveys did not allow a definitive test of causation for the rapid regional ecological change observed. Regardless of the causes, however, a critical feature is that the short-term impacts of the bleaching may have been masked in some cases. For example, we observed an increase in fish species richness on a reef in the Swains area, despite concurrent coral devastation (albeit highly localised in a region otherwise little impacted by bleaching[3]). Likewise, at the regional scale, local fish species richness increased on 40% of reefs surveyed, despite mass bleaching, net coral loss, and an overall decline in regional species richness. Such trends appear remarkable, given that a reduction in fish species richness has been amongst the most consistently and rapidly observed local ecological responses to coral loss observed in previous studies[6,16].

The regional-scale reshuffling and trophic reorganisation observed here appears to be extremely rapid, observable less than one year following the bleaching event. Rapid changes have previously been noted, such as increasing densities of herbivores[15], and have been hypothesised to be due to redistribution on reefs[23] rather than to a demographic response[5]. Our pre-bleaching surveys were mostly undertaken in 2013 (ranging from 2010 to 2015), and many of the observed changes could have resulted from a number of consecutive warm years, rather than the single 2016 bleaching event. In addition to the 2016 event, the study period included two of the next nine warmest years on record for the GBR region (http://www.bom.gov.au/climate/change/; accessed Sept 2017). The observed patterns may thus in part represent accumulated responses over multiple exceptionally warm years, and could provide valuable signs of the potential trajectory of ecosystem change through a warmer future with increasingly prevalent extreme events[24].

Our observations of ecological change over an extreme heating event, with ecosystem consequences at least in part independent of coral mortality, may help explain a lack of consistency among responses to bleaching observed in prior studies. For example, variability has previously been noted in herbivore responses[25], despite relatively consistent increases in algal resources following coral death[23]. This response is of critical importance, as the biomass of herbivorous fishes can be highly influential in determining the recovery trajectories of bleached reefs[2]. Scraping herbivores are considered particularly important in supporting reef recovery[26], and declined on northern reefs in our study. Whether losses of scraping herbivorous fishes in the northern GBR and Coral Sea will affect recovery of some of the most impacted reefs in the region remains an important question.

Ecosystem impacts of coral loss are likely to increase through the next decade in the GBR and Coral Sea if widespread erosion of dead corals occurs[1,5,6,15]. The extent to which the 2016 mass bleaching event proves ecologically catastrophic remains uncertain, as does the sum of accumulated impacts from multiple bleaching events (as highlighted in[3,24,27]). However, rapid local recovery may occur on some reefs[28]. Either way, the trajectories of bleached reefs will be greatly influenced by the new community structures we observed during a critical stage of reef recovery, and are thus inextricably linked with warming-related reshuffling of reef communities.

Overall, our results highlight the need for managers and researchers to consider broad spatial and temporal responses to the marine heating events amongst fishes and other biota, beyond the more readily observable impacts on coral habitat[29]. For example, potential ecological consequences of the changes observed in the northern GBR and Coral Sea could be exacerbated if herbivorous fishes were targeted by fisheries in these regions, while equivalent herbivore exploitation may not be an urgent management concern in locations where gains in herbivores occur (such as the southern GBR in our study). Likewise, functional changes in fish and invertebrate communities driven by extreme events may either complement or work against efforts to save reefs through restoration and assisted evolution of corals. Geographic location has been recognised as an important input into conservation planning and management from the perspective of considering patterns in ocean thermal regimes[30]. Our study highlights how location can additionally be important from the perspective of thermal affinities of community members. Considering the realised thermal niches of species in key functional groups may allow managers to more explicitly consider the trade-off between managing areas in which more species and functional groups are vulnerable to warming events, versus those in which fewer negative effects are expected. The former could potentially prolong local persistence of species and ecological stability by removing extractive pressures, while the latter may provide important reference areas for determining the importance of novel ecological interactions in shaping future reef ecosystems.

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AUTHOR CONTRIBUTIONS

GJE and RSS collected the data with the assistance of other Reef Life Survey divers, CJB undertook the data analysis and preparation of figures with assistance from RSS, DMC analysed the photoquadrats for benthic cover data, RSS drafted the paper with input from all other authors.

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FIGURES

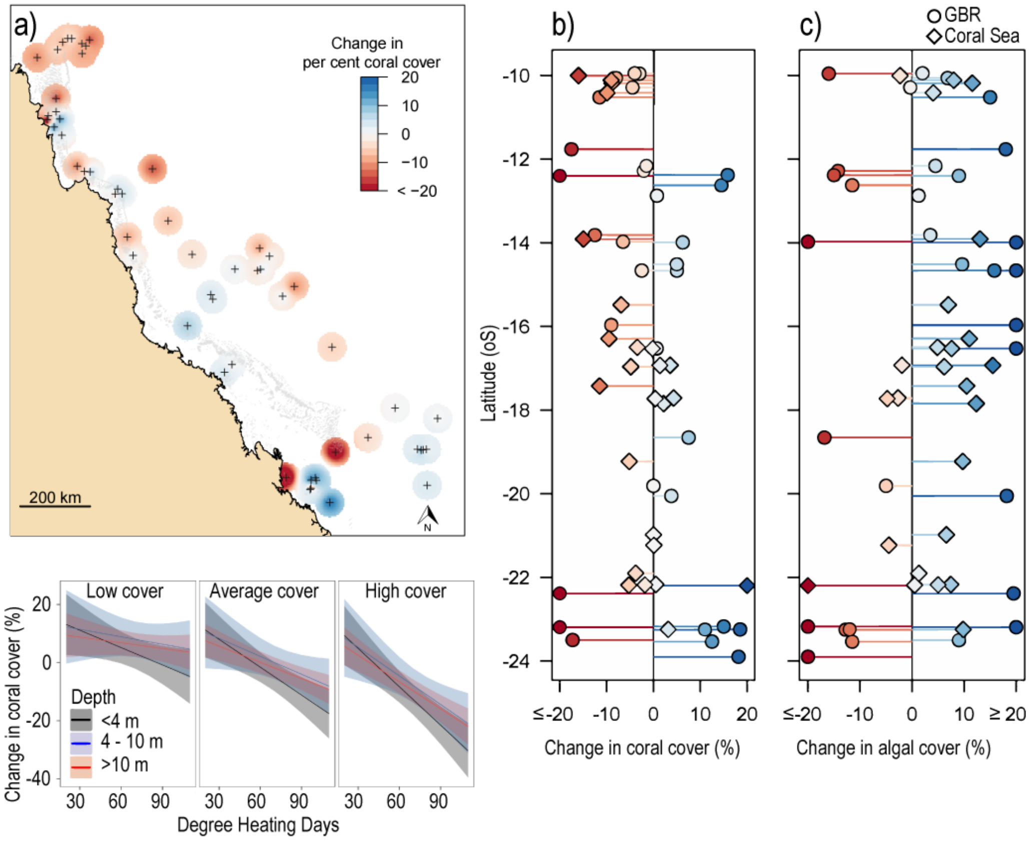

Figure 1. Observed changes in live hard coral cover from the 2016 mass bleaching event across the Coral Sea (CS) and Great Barrier Reef (GBR). Reefs in the CS showed relatively consistent losses of live corals (a, b) and gains in algal cover (c) in the north, while changes along the GBR were highly patchy. Absolute changes in live coral cover are mapped for individual sites (*n* = 186), with aggregation of sites at the reef scale shown as crosses (*n* = 53). Coral cover loss was related to the local heat anomaly from Jan-Mar 2016 regardless of depth (d), an effect which increased in strength according to pre-bleaching cover of live corals. Average pre-bleaching cover for the region was 26% (middle plot; d), while low and high

(left and right panels; d) are shown for ±1SD (19%) from average pre-bleaching live coral cover. Effects in (d) are from Bayesian mixed effects models, with shading representing 95% credibility intervals.

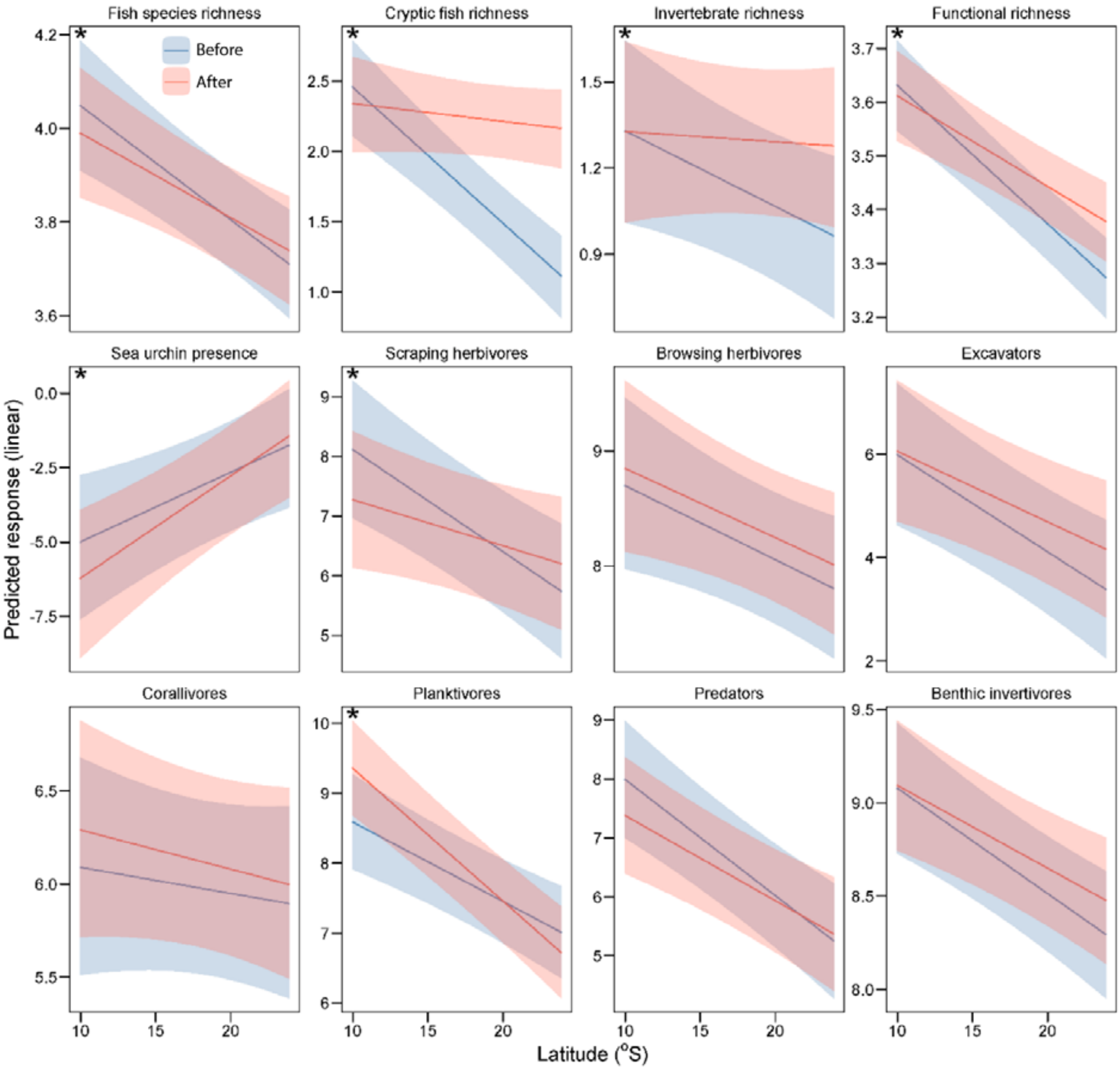

Figure 2. Changes in latitudinal trends in reef fish and invertebrate communities associated with the 2016 mass coral bleaching event. Plots in the top row relate to local richness (log scale), and all others except sea urchin presence (log-odds) relate to biomass (logged). Latitudinal trends are median effect estimates from Bayesian generalized linear mixed effects models (*n* = 233 site by depth-category combinations). Shaded regions show the marginal 95% credibility intervals, and asterisks indicate those metrics for which the term for the change in latitudinal slopes (the interaction between latitudinal and time period effects) has 95% credibility intervals that do not overlap zero (model effect sizes with credibility intervals all predictors are shown in ED Fig 4). Y-axes are on the link scale (log for poisson and normal and logit for urchins).

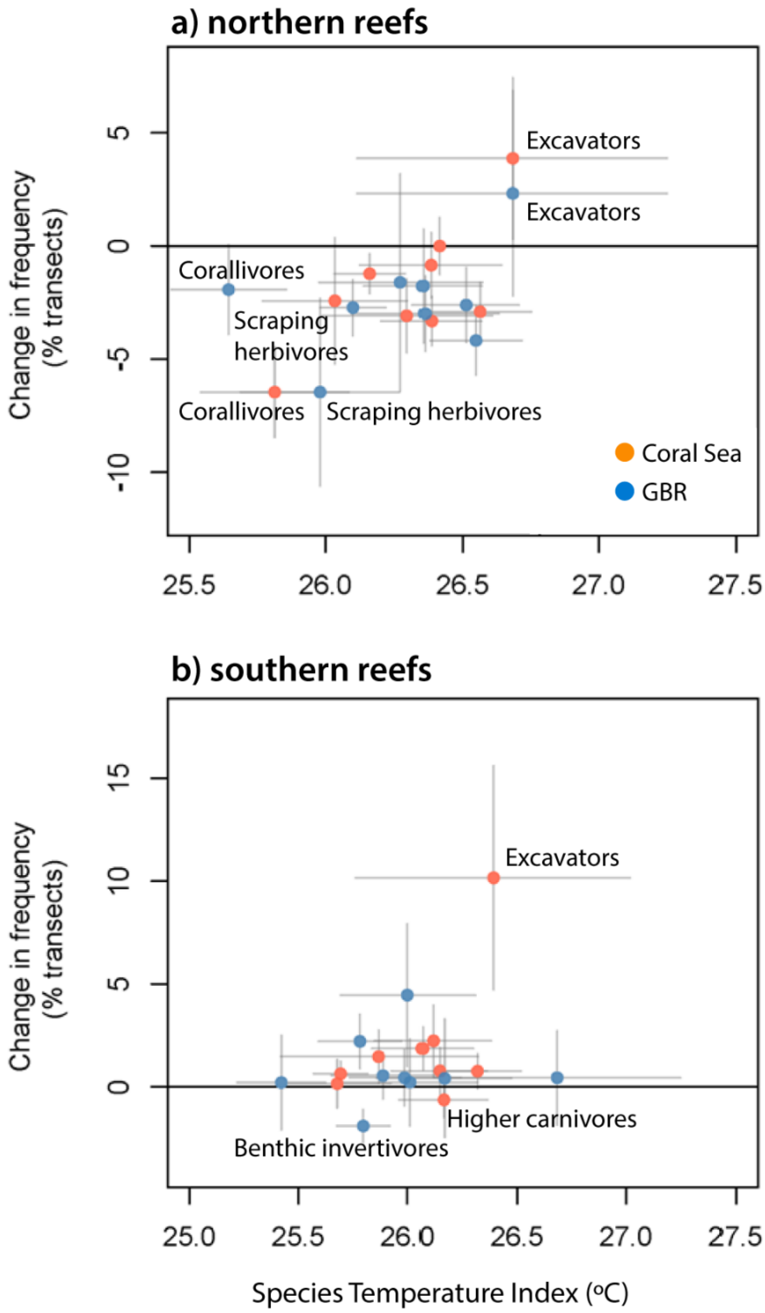

Figure 3. **Changes in the frequency of fish functional groups with differing temperature affinities**
354 **on reef surveys following the bleaching event**. Corallivores and scraping herbivores, the coolest-affinity trophic groups (lower Species Temperature Index values, on average), declined in frequency on transects at northern reefs (a; reefs north of 12°S latitude, *n*= 321 species in GBR, 301 species in
357 Coral Sea). Excavators, the trophic group consisting of species with the warmest Species Temperature Index values, became more common on transects on northern reefs of the GBR and Coral Sea, and southern reefs in the Coral Sea (b; south of 19°S latitude, *n*= 320 species in GBR, 305
360 species in Coral Sea). Points are means of species in each trophic group, shown separately for species recorded in the Great Barrier Reef (blue) and Coral Sea (orange). Error bars show standard error.

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METHODS

Survey methods

Standardised data were obtained on fishes, mobile invertebrates, coral and macroalgae along 768 50-m underwater transects by trained scientific and recreational divers participating in the citizen science Reef Life Survey (RLS) program. Full details of census methods are provided elsewhere[31-33], and an online methods manual (www.reeflifesurvey.com) describes all data collection methods. Data quality and training of divers are detailed in[31,34]. All observed fish species were counted in duplicate 5 m-wide transect blocks and aggregated as densities per 500 m^2 transect, and cryptic fishes and mobile invertebrates >2.5 cm total length in duplicate 1-m wide transect blocks (aggregated to 100 m^2 transect area) on the same transect lines. Fish length and abundance estimates were converted to biomass using species-specific length-weight coefficients obtained from FishBase (www.fishbase.org), as used in previous studies with the RLS data (including[35,36]). Invertebrate classes used for this study were Asteroidea, Cephalopoda, Crinoidea, Echinoidea, Gastropoda, Holothuroidea, and Malacostraca. All individuals from these classes exceeding 2.5cm total length were included in richness estimates for invertebrates, and in functional richness analyses.

Photoquadrats were taken vertically downward of the substrate every 2.5 m along each of the same transect lines, and later scored using a grid overlay of 5 points per image, 100 points per transect. Categories of benthic cover scored were from a set of 50 morphological and functional groups of algae and corals (ED Table 1), as detailed in[33] and aligning with the standard Australian hierarchical benthic classification scheme[37]. Analyses undertaken for this study were based on the sum of all live hard coral categories (i.e. % live hard coral per transect), and the sum of all algal categories (% algal cover per transect), with categories listed in ED Table 1.

Survey design

Matching before-after bleaching surveys were undertaken at 186 GPS-referenced sites at 53 reefs (See Fig. 1 for distribution of reefs; mean = 3.5 sites per reef) along the full length of the GBR and western Coral Sea region within the Australian EEZ. At each site, multiple surveys (mean = 2.1 transects per site) were undertaken at different depths, with transects laid along a depth contour. Depths were binned (see covariates section below), such that site by depth bin was the level of replication, making 233 matching site by depth replicates surveyed both before and after the bleaching event.

Different divers often surveyed the fishes and the invertebrates along the same transect line. Pre-bleaching surveys were largely undertaken from a survey cruise along the entire GBR and Coral Sea in 2015 (42% of pre-bleaching surveys) and a previous survey cruise through the Great Barrier Reef and Coral Sea in 2013 (39% of pre-bleaching surveys). Additional ‘before data’ (19%) were collected at Lizard Island, Great Keppel Island and the Whitsundays in 2010, and some sites in the central Coral Sea and GBR in 2012. All post-bleaching data were collected during a survey cruise through the entire region from November 2016 to March 2017. No strong biases were apparent in the interval between pre and post-bleaching surveys along the latitudinal gradient or locations experiencing different heating anomalies (ED Fig. 8).

Seven of the 10 divers who undertook pre-bleaching surveys also undertook post bleaching surveys, and authors GJE and RSS together undertook 45% of all fish surveys (and led 85% of survey voyages before and 92% after the bleaching event). There was thus a substantial element of consistency in divers during the study. To explore the effect of different divers undertaking surveys at different times, however, we re-ran the models for Fig. 2 and ED Fig. 4 with “diver” included as a random effect. This resulted in no changes in the effect sizes or conclusions. Hence, results are presented for models without the diver effect, so that marginal uncertainty intervals include site-to-site variation but not observer variation.

Species traits

All fishes and invertebrates were allocated into one of the following trophic groups: Corallivores, Scraping herbivores, Benthic invertivores, Algal farmers, Browsing herbivores, Omnivores, Planktivores, Higher carnivores, Excavators, Detritivores, Suspension feeders and Cleaners. Additional traits used for calculation of functional richness were maximum body size (included as 10 cm bins up to 50 cm, and all species which grow to >50 cm binned together), and water column position (benthic, demersal, pelagic site-attached, and pelagic non site-attached). All traits were taken from the dataset used for[38]. Functional richness was calculated as the richness of functional entities per 50 m transect, where all species with the same combination of trait levels for those three traits were considered functionally equivalent.

Species Temperature Index values were taken for each species from the dataset used by[20], and represent the midpoint between the 5th and 95th percentile of local sea surface temperature values from all occurrence locations of the species. It thus represents the centre of each species’ range when expressed as a range of sea temperatures experienced across their distribution, and provides a nuanced means of ordering species by their preferences for warmer or cooler environments. Full details, including discussion of strengths and weaknesses, are provided in [20] and [7].

Covariates

The mean depth contour of each reef transect was recorded by divers during surveys, with surveys then allocated into three depth bins (<4m, 4-10m, >10m). For any before-after comparison, we first obtained the mean values of univariate responses taken from among all transects within each depth bin at a given site (i.e. site by depth bin combinations). This gave 233 site by depth combinations, with a mean of 76 sites and 35.3 reefs per depth class. For each site, we also applied a four level categorical measure for wave exposure: (1) sheltered, with only wind waves from non-prevailing direction, (2) wind generated waves from the prevailing direction, (3) exposed to ocean swells, either indirectly with exposure to prevailing winds, or directly but sheltered from prevailing winds, or (4) exposed to open ocean swell from prevailing direction. There was a mean of 62 sites and 24 reefs per exposure category. Reef habitat categories are often used for ecological studies of coral reefs (e.g. Slope, Crest, Flat, Lagoon), but delineation between similar or adjacent habitats can sometimes be difficult. Instead of making these delineations for our survey sites, we considered that these two environmental axes of wave exposure and depth together appropriately capture the important variation between such reef habitat classifications with respect to their importance in describing potential for bleaching[2].

Sea surface temperature (SST) anomalies used in analyses relating coral cover change to Degree Heating Days (DHDs) was obtained from the ReefTemp Next Generation product from the Bureau of Meteorology (http://www.bom.gov.au/environment/activities/reeftemp/reeftemp.shtml; accessed

August 2017:)[39]. Fine scale anomalies for the January-March 2016 period were matched to survey sites.

Analysis or coral and algal cover change

We modelled the response of change in coral and algal cover as a function of Degree Heating Days (DHD) using a Bayesian mixed effects model (n = 211 site-depth combinations where benthic cover data were available). Additional fixed covariates included the depth of survey, the four wave exposure categories, a factor for whether the survey was in the GBR or the Coral Sea, the initial cover of corals or algae, an interaction between DHD and depth and an interaction between DHD and initial cover. We included a random effect for reef. We did not include a random effect for sites nested within reefs because only 36 had measurements at more than one depth across both time-periods (before and after bleaching). Change in coral and algal cover was modelled with Gaussian errors and standard model checks confirmed that this assumption was appropriate. We scaled the model's variance by the number of years between before and after surveys (maximum = 7 years, mean = 3.3 years), because we expect greater variance in the measured change in coral cover when those measurements were taken a longer time apart. We compared models with and without the variance scaling using the Widely Applicable Information Criteria (WAIC)[40,41]. The WAIC indicated that for the coral cover model with the variance scaling provided an enhanced fit to the data (1658 versus 1721), whereas for the algae cover model the unscaled model had an enhanced fit (1801 versus 1806) so we present results from these best model. However the estimated effects of the covariates were nearly identical regardless of model used in both cases.

We present the median estimated effects of DHD on coral and algal cover in ED Fig. 1, and credibility intervals are 95% quantiles. We also predict median change and the 95% marginal credibility intervals for change in coral and algal cover across the range of DHD for each depth category values for low wave exposure reefs in the GBR (Fig. 1d). Credibility intervals for predictions were integrated across all random effects, so they should be interpreted as effect sizes relative to variation across reefs. For the coral model there was a strong interaction effect of initial coral cover with DHD, so we separately plotted predicted effects for the mean initial coral cover and ± 1SD in initial coral cover.

We fitted the Bayesian mixed effects models using the INLA framework[42] implemented in the R programming language[43] using the INLA R package (version 17.06.20; www.r-inla.org, accessed 4th Oct 2017). The prior for the precision on the random effect used the log-gamma prior with shape = 1 and rate = 1x10-5, though use of other standard priors did not change the results. Priors for fixed effects had mean = 0 and precision = 0.001.

Mapped coral change values in Fig. 1a represent absolute change in live hard coral cover at each site, with the change values interpolated using an inverse-distance weighting and a buffer of 50 km applied from around each reef surveyed (implemented with the gstat package in the R program[44]). Symbols on the map thus represent the reef locations, although coral change values come from the aggregation of smaller scale data at individual sites within reefs.

Comparison of bleaching-impacted vs unaffected reefs

To isolate ecological impacts most likely arising from bleaching-associated coral loss, we used the following criteria to define 'bleaching-impacted' reefs: (1) Pre-bleaching live hard coral cover >20% on average (across all transects at the reef). This meant that the starting community was more likely one to be comprised of coral-associated fish and invertebrate species; (2) Loss of live coral cover >40% of pre-bleaching values, on average; and (3) Experienced more than 40 DHDs. These criteria were collectively used as a means to show the maximum likely impact of the loss of coral from bleaching, by ensuring there was adequate coral cover to start with (criterion 1), and that coral losses were at least typical of the mortalities observed in other studies[11] (criterion 2), while providing some confidence that observed coral loss was most likely attributable to bleaching (criterion 3). We cannot be certain about the latter (see comments below about other potential impacts on coral during the study period), but 40 DHDs well exceeds the threshold for bleaching identified by[3] for this same bleaching event. Reefs defined as 'bleaching-impacted' were widely dispersed along the Great Barrier Reef and Coral Sea (ED Fig. 3).

To provide an objective contrast with these reefs, we also selected reefs which were clearly unaffected by the bleaching. We used the same criteria as above, but instead of losing at least 40% of live coral cover, we selected only those which experienced >1% mean gain in live hard corals on average (using the mean % coral cover change, rather than mean pre-bleaching minus mean post-bleaching cover). For all these bleached and unaffected reefs, we examined responses in key metrics of the coral, fish and invertebrate communities, as shown in ED Fig. 3.

Regional community structure change

Non-metric multidimensional scaling was undertaken separately on reef fish and invertebrate community data to show broad regional change in community structure and visualise consistencies in the direction of community change among regions between before and after surveys (ED Fig. 5). Mean biomass per fish species (kg per 500 m^2) and mean abundance per mobile invertebrate species (individuals per 100 m^2) were calculated across all surveys within each 2° latitudinal band, separately for the GBR and Coral Sea. Biomass and abundance data were log-transformed and Bray-Curtis dissimilarity matrices used for ordination of each. The analysis was undertaken in PRIMER[45], with symbols subsequently colour coded for data collected before vs after the bleaching event, and labels indicate GBR vs Coral Sea regions.

Analysis of regional-scale ecological changes

We analysed the response of nine fish and invertebrate metrics to bleaching using Bayesian generalized linear mixed effects models. Each metric value on each survey was modelled with covariates for latitude, depth, coral cover, protection status (no-take 'green' zone vs all other zone types), GBR or coral sea, wave exposure, time (before or after the bleaching event) and an interaction between time and latitude. The interaction was included to allow for the possibility that latitudinal gradients in each metric changed from before to after the bleaching event. We included random effects for reefs and sites within reefs.

We chose error distributions appropriate for each metric. These were the Poisson with the log-link for the richness metrics, log-normal with the identity link for the biomass metrics, and binomial with the logit link for urchin presence. We added 0.5 to the logged biomass data so that zero values were not excluded. Checks of residuals confirmed that the log-normal was appropriate for the biomass data. Rootograms[46] and Dunn-Smyth residuals[47] were used to confirm the count models fitted appropriately.

We used the INLA framework to fit the Bayesian GLMMs, using the same settings as for the coral change model. We give effect sizes as median effects of each covariate in Fig. 2 and ED Fig. 4 with 95% credibility intervals. We term CIs that did not overlap zero in ED Fig. 4 as 'significant'. We also predict metrics across the latitudinal gradient before and after the bleaching event with marginal 95% credibility intervals. Predictions across latitude were made for a reef of <4 metres depth, with the mean level of hard coral cover, inside a protected area with low wave exposure and for the GBR. Thus positive and negative effects in ED Fig. 4 can be interpreted in relation to these levels of the relevant covariates. Choosing other covariate values for the baseline would affect the magnitude of the patterns but not the overall trend.

Possible recruitment events

We tested whether patterns metrics before and after bleaching could be related to a coincident fish recruitment event. We analysed the mean density of juvenile fishes per reef (29 reefs in total from extreme north and south) as a function of three binary covariates: before versus after bleaching, coral sea versus GBR and north versus south, using a linear model, implemented in the INLA framework[42] from the R programming language[43]. Juveniles were defined as any individuals 10 cm or less, for species that exceed 12.5 cm in maximum size. No significant change in the density of juveniles was evident before and after bleaching (mean difference = 1.70 with lower and upper 95% CIs of -0.6 to 4.0), with the distribution of data shown in ED Fig. 7.

Other potential effects on results

Few trends in fishes and invertebrates were related to changes in coral cover when considered at the scale of the whole study region, and primary study conclusions do not rest on the assumption that all observed coral mortality was driven by the 2016 bleaching event. Cyclones, crown of thorns seastars and pollution and sediment from riverine outputs are other potential impacts on corals across the region. We checked the database of past tropical cyclone tracks on the Bureau of Meteorology website (http://www.bom.gov.au/cyclone/history/index.shtml, accessed 7/4/2018) for intersection of cyclone tracks with our survey sites. Surveys were completed before Cyclone Debbie (2017), and the only surveys done before cyclone Yasi (2011) (Lizard Is, Port Douglas, Whitsundays, Keppel) were in areas outside of the destructive path of this cyclone. However, Cyclone Ita was reported to have impacts on corals in the Lizard Island area during the study period[48], and there is a possibility that other smaller cyclones caused highly localised impacts. Thus, caution is required in ruling out cyclone damage as contributing to coral cover changes observed in some locations.

We cannot be certain crown of thorns seastars did not affect coral cover at our sites in between surveys, but these are also recorded on the surveys of mobile invertebrates and were found in extremely low densities (mean 1.4 individuals per 50 m^2 when found, only at 15 sites). It is not impossible that a wave of crown of thorns sea stars came through and reduced live coral cover at a small number sites, but such effects at very small number of sites would unlikely have a detectable impact on results or conclusions of the study. Likewise, pollution and sediment from riverine sources could not have been responsible for any changes in the Coral Sea (>250 km offshore), and would be unlikely to have impacted any sites other than a small number of inshore locations. No substantial pollution events (e.g. oil spills) were noted near survey locations in the period. Regardless, care is required in inferring causality for observed coral cover change in this study, and no assumption should be made that all coral loss was attributable to bleaching.

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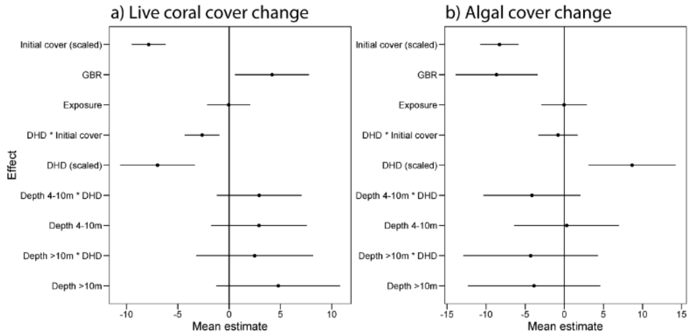
DATA AVAILABILITY

Raw reef fish and invertebrate abundance data and photoquadrats of coral cover are available online through the Reef Life Survey website: www.reeflifesurvey.com

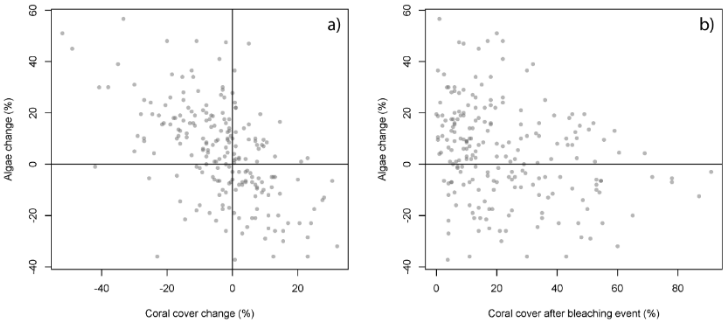
EXTENDED DATA FIGURE AND TABLE LEGENDS

ED Table 1. Categories of coral and algal cover scored from photoquadrats. Mean % cover values from before and after the bleaching event are shown for sites the Coral Sea and Great Barrier Reef. Categories are for live cover, with dead or bleached individuals or colonies scored as such (bleached corals were scored if white at the time of surveys, and only summed bleached corals included here). Soft corals were excluded from summed cover for analysis of live hard coral.

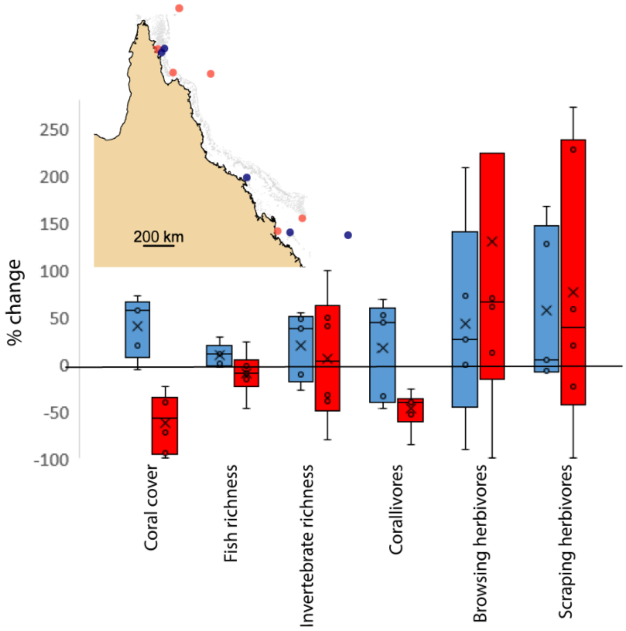
		Coral Sea		**Great Barrier Reef**	
Category	**Functional group**	**Before**	**After**	**Before**	**After**
Algae	*Caulerpa* spp.	3.6	4.6	4.7	11.4
	Crustose coralline algae	21.1	26.1	9.7	15.3
	Diatom/cyanobacterial slime	5.6	4.6	18.8	5.1
	Encrusting leathery algae	4.5	3.5	3.5	2.3
	Filamentous algae	2.2	1.6	3.7	1.4
	Foliose red algae	1.0	2.0	3.5	1.3
	Geniculate coralline algae	4.0	3.9	2.3	1.2
	Green calcified algae	16.7	20.0	2.5	3.9
	Other foliose green algae	4.9	8.5	1.0	17.0
	Small to medium foliose brown algae	1.5	15.4	4.6	4.0
	Turfing algae (<2 cm)	15.3	17.8	33.6	32.7
Coral	Ahermatypic corals	1.8	1.5	0	0
	Bleached coral	3.8	3.1	1.0	8.3
	Bottlebrush corals	5.7	16.2	4.5	3.2
	Branching *Acropora*	9.9	6.4	12.0	7.5
	Columnar corals	2.0	7.3	3.0	3.7
	Corymbose corals	2.9	2.8	4.3	5.1
	Digitate corals	3.8	1.4	1.9	2.2
	Encrusting corals	9.7	7.9	5.1	5.5
	Foliose corals	4.9	6.9	6.0	5.6
	Hydrocoral	2.3	5.4	3.9	1.3
	Large-polyp stony corals	1.5	1.2	1.8	1.3
	Massive corals	5.0	4.5	6.0	8.1
	Organ-pipe coral (*Tubipora*)	1.0	1.3	0	0
	Other branching/erect corals	5.1	8.7	7.3	10.9
	Pocillopora	3.3	3.2	2.6	3.1
	Soft corals and gorgonians	8.3	8.1	7.8	7.1
	Submassive corals	3.5	2.8	2.9	4.8
	Tabular Coral	4.7	3.4	9.6	12.8



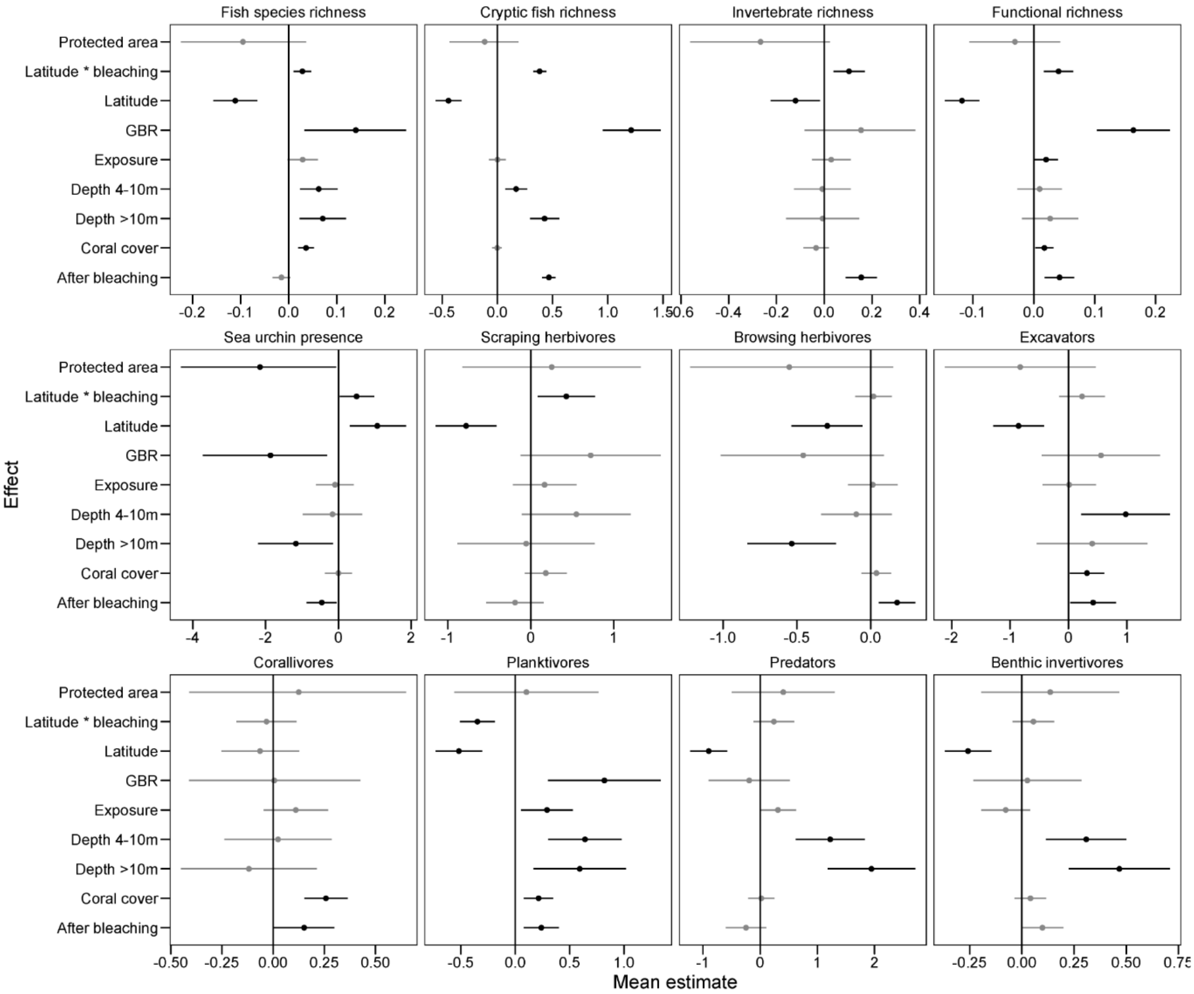
ED Figure 1. Results of GLMMs for coral (a) and algal (b) cover changes during the 2016 bleaching event. Change in cover is modelled as a function of the influences of starting cover (of corals and algae, respectively), wave exposure, thermal anomaly (Degree Heating Days, DHD), the interaction between DHD and starting cover, depth category (depths between 4 and 10 m and >10 m modelled in comparison to <4 m depth), and the interaction between depth category and DHD. Effects from Bayesian mixed effects model (*n* = 211 site-depth combinations) are considered significant if credibility intervals do not overlap zero. All continuous predictors were normalised to mean zero and SD = 1 for comparative purposes.



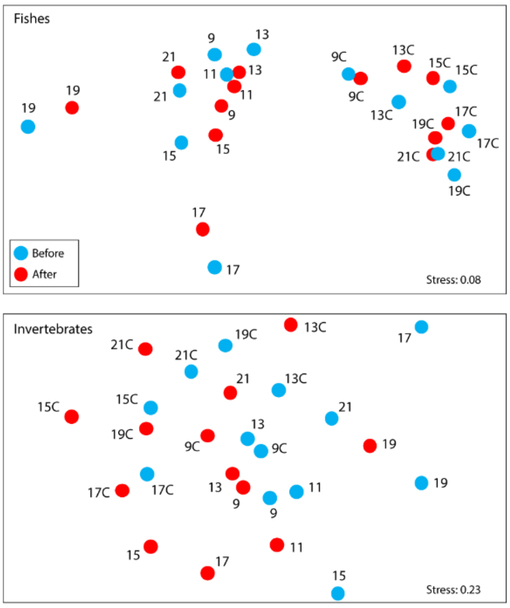
ED Figure 2. Changes in algal and coral cover spanning the 2016 bleaching event. Coral and algal cover change (a) were negatively correlated (ρ = -0.56), and greatest algal cover increases (b) occurred at sites with lowest coral cover after the bleaching event (ρ = -0.28). *n* = 211 site-depth combinations.



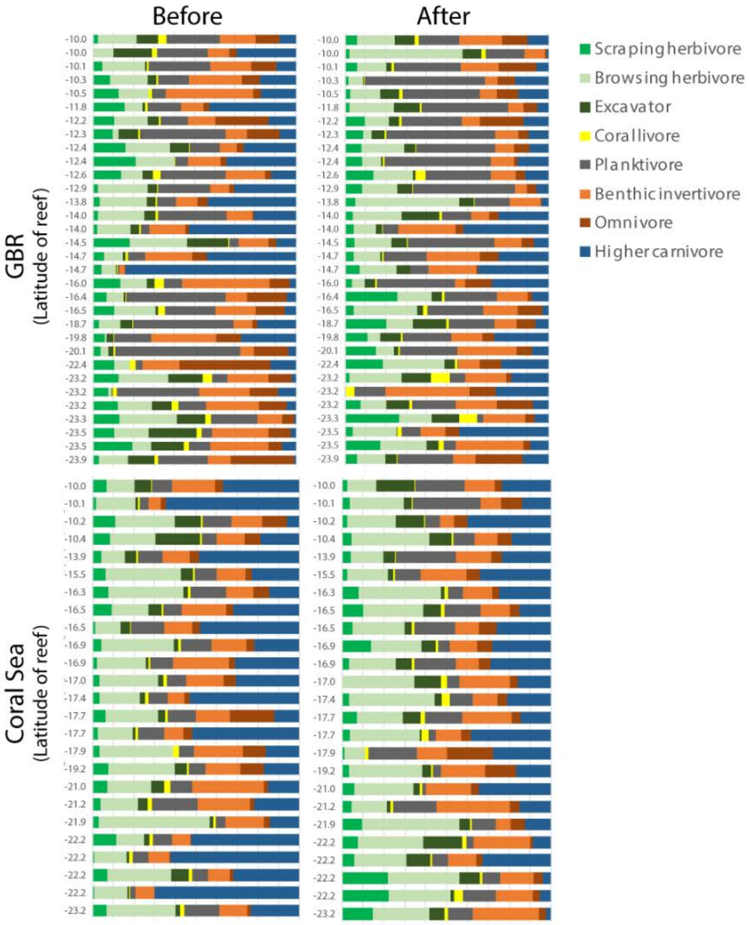
ED Figure 3. Ecological changes on surveyed reefs most clearly affected by coral bleaching (red) versus un-impacted reefs (blue). Reefs categorised as bleached were those with >20% pre-bleaching live coral cover, experienced >40 Degree Heating Days and lost >40% of pre-bleaching coral cover (see methods for rationale). The un-impacted reefs were those that had >20% pre-bleaching live coral cover and experienced >40 Degree Heating Days, but did not show a reduction in coral cover. The vertical axis is the percentage change of each metric across the reefs in each category (*n*=6 bleached, *n*=5 unbleached reefs), and horizontal lines on box plots show quartiles, *X* symbols are means and circle symbols are individual reefs within quartiles. Corallivores, browsing herbivores and scraping herbivore values describe change in densities of species in these groups. Densities and species richness are means per 500 m^2 (fishes) or 100 m^2 (invertebrates). Bleached and unbleached reefs each include reefs from both northern and southern regions. Only coral cover differed significantly between these two groups of reefs (mean difference = -72%, with 95% CIs from 25-107%), though there was a small decline in corallivore densities post-bleaching (mean difference = 42% with 95% CIs from - 0.24 to 78.0).



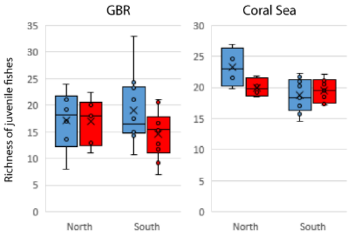
ED Figure 4. Effect sizes from GLMMs of regional change for each ecological metric. Effect sizes from Bayesian generalized linear mixed effects models (n = 233 site by depth-category combinations) give the median additive effect of each covariate on the linear expectation for each metric (95% CIs given by bars). Effect sizes are on a log-scale for all metrics, except for sea urchin presence, which gives the effect on the log-odds of presence versus absence. The influences of latitude, and its change from before to after the bleaching event (the interaction between “Latitude*bleaching”) are modelled in relation to differences between the Great Barrier Reef and Coral Sea reefs (“GBR”), wave exposure (“Exposure ”), depth of the survey (depths between 4 and 10 m and >10 m modelled in comparison to <4 m depth), the percentage cover of live hard corals on the survey (“Coral cover”) and before vs after the bleaching event (“After bleaching”). Significant effects are taken as those where credibility intervals do not overlap zero and are indicated with black, rather than grey, points and error bars.



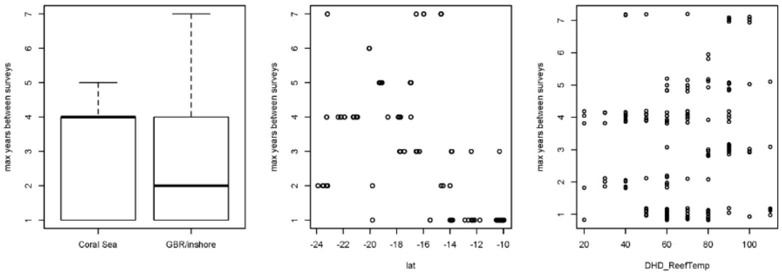
ED Figure 5. **Non-metric multidimensional scaling plots for reef fish (top) and mobile invertebrate (bottom) communities along the Great Barrier Reef (GBR) and Coral Sea**. Fish biomass data and invertebrate abundance data were averaged across surveys within 2° latitudinal bands, with number labels representing the northern latitude (i.e. 21 represents the 2° band from 21° to 23° south). Coral Sea reefs distinguished from those in the GBR by “C” in the label. Symbols have been colour coded for data collected before vs after the bleaching event (*n*=13 latitudinal bands each before and after).



ED Figure 6. **Changes in the trophic structure of reef fishes following the 2016 mass bleaching event on the Great Barrier Reef and Coral Sea**. Bars represent the proportion of total biomass made up by each trophic group, averaged across surveys on each reef, and reefs ordered by latitude. Cleaners and algal farmers were removed due to small contributions to biomass.



ED Figure 7. **Local species richness of juvenile fishes (500 m^{-2}) before (blue) and after (red) the 2016 mass bleaching event on the Great Barrier Reef (left) and Coral Sea (right).** 'North' reefs were north of 12^{o}S (n=10 reefs), and 'South' reefs were south of 19^{o}S (n=19 reefs). Juveniles were classified as any individuals 10 cm or less, for species that exceed 12.5 cm in maximum size. A Bayesian linear model indicated juvenile richness differed between the GBR and Coral Sea, but not between north and south or before vs after the bleaching event (mean difference = 1.70 with lower and upper 95% CIs of -0.6 to 4.0). Horizontal lines on box plots show quartiles, *X* symbols are means.



ED Figure 8. The distribution of sampling effort through space and time. The temporal gap between pre- and post-bleaching surveys (*n*=768 surveys total) between Great Barrier Reef and Coral Sea, along the latitudinal gradient, and locations experiencing different heating anomalies. For the box plot, the box shows the interquartile range and whiskers 1.5*interquartile range.