Tracking widespread climate-driven change on temperate and tropical reefs

Highlights

- Reef fish communities responded to sea temperature and habitat change over 10 years

- Southeastern Australian communities clearly re-organized with warmer seas

- Generalist fishes became more dominant at many coral reefs as coral cover declined

- Specificity of ecological indicators to pressures can vary spatially, hiding trends

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In brief

With data from diver-based monitoring around Australia over the last decade, Stuart-Smith et al. reveal large-scale responses of reef fish communities to shifting ocean temperatures and habitat cover (corals and kelps). Warming impacts are observed in temperate zones and habitat loss impacts in tropical zones but with high spatial variability.

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Article

Tracking widespread climate-driven change on temperate and tropical reefs

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SUMMARY

Warming seas, marine heatwaves, and habitat degradation are increasingly widespread phenomena affecting marine biodiversity, yet our understanding of their broader impacts is largely derived from collective insights from independent localized studies. Insufficient systematic broadscale monitoring limits our understanding of the true extent of these impacts and our capacity to track these at scales relevant to national policies and international agreements. Using an extensive time series of co-located reef fish community structure and habitat data spanning 12 years and the entire Australian continent, we found that reef fish community responses to changing temperatures and habitats are dynamic and widespread but regionally patchy. Shifts in composition and abundance of the fish community often occurred within 2 years of environmental or habitat change, although the relative importance of these two mechanisms of climate impact tended to differ between tropical and temperate zones. The clearest of these changes on temperate and subtropical reefs were temperature related, with responses measured by the reef fish thermal index indicating reshuffling according to the thermal affinities of species present. On low latitude coral reefs, the community generalization index indicated shifting dominance of habitat generalist fishes through time, concurrent with changing coral cover. Our results emphasize the importance of maintaining local ecological detail when scaling up datasets to inform national policies and global biodiversity targets. Scaled-up ecological monitoring is needed to discriminate among increasingly diverse drivers of large-scale biodiversity change and better connect presently disjointed systems of biodiversity observation, indicator research, and governance.

INTRODUCTION

Shallow rocky and coral reefs are valuable natural laboratories for understanding relationships between environmental change and biodiversity, connected by widely dispersing larvae, ocean currents, and broad environmental gradients. Reefs support a diversity and density of life that makes it feasible to study hundreds of species, their interactions, and extraordinary productivity at scales and depths where direct observations by scuba diving are often possible. This high diversity and density of life make

reefs extremely valuable to people but also a key pathway through which the changing climate is impacting ecosystems and human populations. Reef fishes represent a core component of this pathway of climate impact, forming the basis for nutrition, recreation, tourism, and numerous critical ecological functions.[1–4]

Reef fishes are rapidly responding to environmental change,[5–7] but general patterns in ecological change have been difficult to extract from a diverse range of studies and regions. Published studies have presumably been heavily biased toward those from locations where significant ecological change has occurred,[8] while the amount of unpublished monitoring data showing little or no change remains unknown. A further hurdle for understanding broader patterns of change arises through the independent study of tropical and temperate reefs. Reefs in these latitudinal realms can sometimes share fish species, functional groups, and ecological processes but are usually considered in isolation by studies using different methods and with different research foci and paradigms. For example, the effects of elevated sea temperatures on reef fishes in the tropics have often been considered in the context of impacts from coral bleaching events[9–12] (i.e., as indirect effects through habitat loss). In temperate regions, a major focus has been on species' range shifts[13,14] (i.e., direct effects on populations). More observations of range shifts are emerging from the tropics,[15] however, and impacts of large-scale macroalgal loss have been evident in temperate regions.[16–18] These two (direct and indirect) mechanisms of climate impact are clearly not constrained by latitude, but the question remains whether they differ in relative importance between temperate and tropical zones.

We evaluated trends in reef fish communities that may be broadly associated with these two key mechanisms of climate impact over a 12-year period of reef monitoring by three diver-based programs, encompassing diverse tropical and temperate reef systems around the entire Australian continent (see STAR Methods). Our data span locations that have experienced major heatwaves and temperature fluctuations as well as a small number of locations that experienced only minor sea temperature change. To set expectations for the influences of broad environmental change, we used habitat data (living hard coral and macroalgal canopies, the latter hereafter referred to as "kelp") obtained along the same underwater transects surveyed for fishes and trends in remotely sensed sea surface temperatures (SSTs). To evaluate biodiversity responses most likely related to each of these, we used the data on fish community structure to calculate two ecological indicators: the reef fish thermal index (RFTI,[19] also known as the community temperature index), and the community generalization index (CGI[20]). These are calculated from the same fish community structure data but respectively use species-level characterizations of realized thermal or habitat niches as traits to better isolate and distinguish directional changes relating to changing temperatures or habitats. While links between heatwaves or habitat degradation and the responses in fish communities measured with these indicators have been observed through observational studies in temperate and tropical realms,[6,13,20] trends in these two indicators through time have not simultaneously been investigated for any region, let alone a continent. Thus, in addition to better understanding temperate–tropical differences in the relative importance of sea

temperature and habitat driven changes in reef fishes, a second aim of our study was to consider the strengths and weaknesses of these indicators in the context of tracking progress towards global biodiversity targets related to climate change.

RESULTS

Repeated underwater observations from 1,251 sites spanning Australian continental and offshore reef systems highlight shifting community structure of reef fishes over a decadal scale, often in directions consistent with temperature or habitat change. These ecological changes were visible over broad regions in synoptic maps of change (Figure 1), as well as through interannual trends over a 12-year period at 18 long-term monitoring locations distributed around the continent (Figures 2 and 3). Reef ecosystems appear to be extremely dynamic, with fish community restructuring occurring within 2 years of environmental or habitat change in most cases in which change was observed (Figures 2 and 3; Tables S1 and S2).

Spatial patterns in mean change in the RFTI[19] from the 2010–2015 to 2016–2020 periods were largely consistent and positively associated with SST change across temperate and subtropical zones (Figure 1) (p < 0.01; linear mixed effects models; Table S1; Figure S2). These patterns represent regional scale reshuffling of local reef communities in a way that reflects changes in the oceanographic thermal environment. A net regional "warming" of the fish community occurred in southeastern Australia, where all monitored temperate and subtropical locations that showed strong evidence for changes in RFTI through time (eight out of twelve) also experienced concurrent increases in SST (p < 0.05; Figure 2; Table S2). A net "cooling" of the fish community was observed in southwestern Australia (Figure 1B), following a previous increase in RFTI values associated with the 2011 marine heatwave (Figures 2G and 2J).

Time-series trends in RFTI suggested varying lag periods associated with different thermal anomaly events but with consistency between locations. For example, peaks in RFTI in 2011 and 2016 across southeastern Australia relate to peaks in oceanographic SST in 2010 (with 1 year lag) and 2016 (with no lag), respectively (Figures 2E, 2F, 2K, 2L, 2Q, and 2R), caused by the El Niño–Southern Oscillation impacts on the East Australian Current.[21] In southwestern Australia, the impacts of the 2011 marine heatwave on fishes that have been previously reported[6,18,22] peaked after 2 to 3 year lag (Figures 2G and 2J). A temporal lag of 2 years was best supported at the national scale, although evidence for a relationship between interannual RFTI and SST changes remained with no lag applied in the models (p < 0.001; Table S1; Figure S3).

Despite coherent and predictable changes in RFTI across temperate and subtropical regions, spatial patterns in RFTI deviated from expectations across large parts of tropical Australia. Minor declines in RFTI were observed across a large portion of the central Great Barrier Reef (GBR) and Coral Sea, even where a 2016 heatwave resulted in the widely reported mass coral bleaching (and subsequent heatwave in 2017).[23] Although some individual reefs in this region showed increased RFTI by up to 1.2°C, many of the surrounding reefs showed a "cooling" of the fish community, particularly post-heatwave in 2018 and 2019 (Figures 1 and 2).
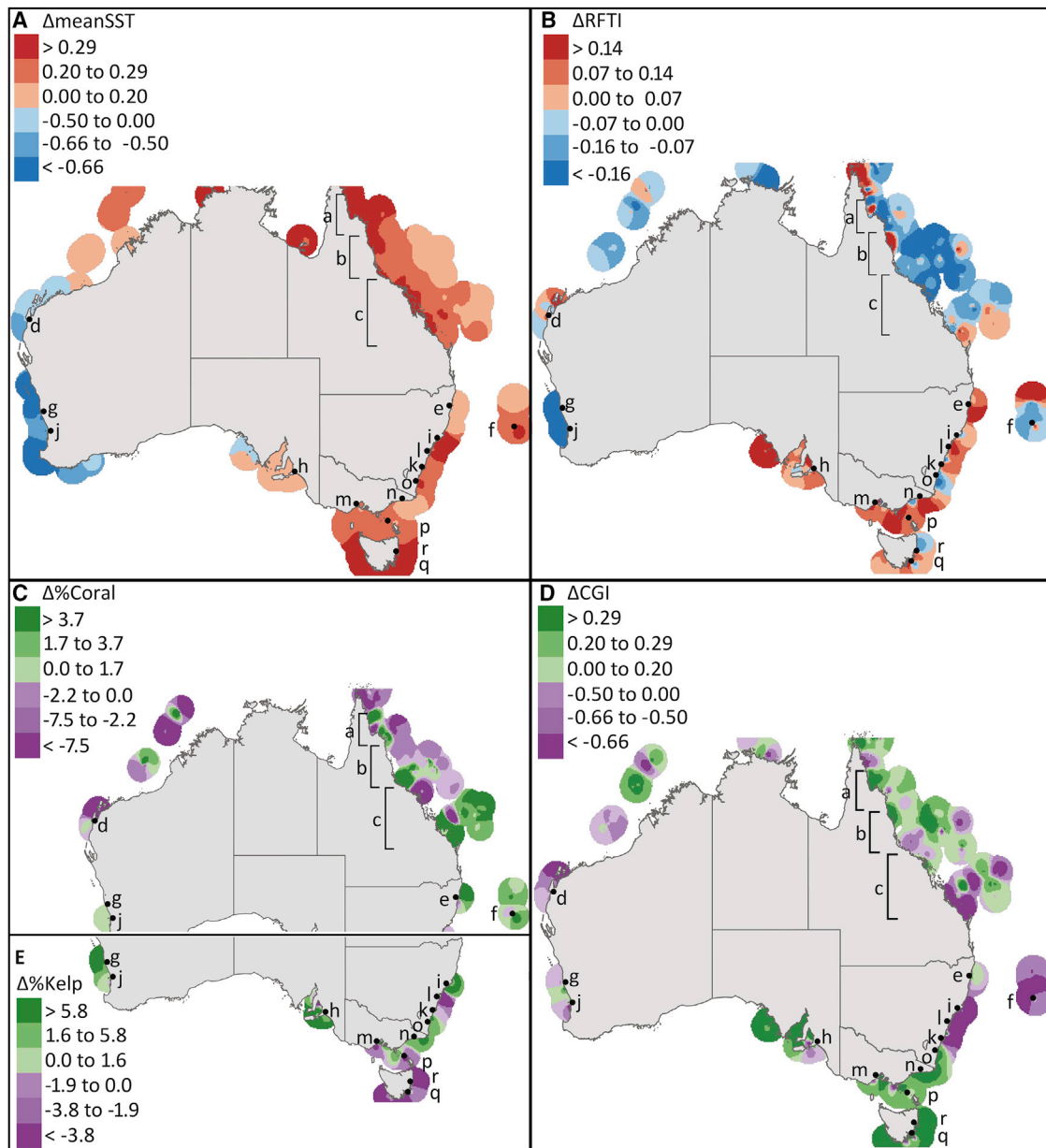
Figure 1. Change in reef fish communities around the Australian continent over the last decade in relation to sea temperature trends and reef habitat integrity

Heat maps on the left show patterns of environmental change, while maps on the right show the biodiversity change based on indicators designed to capture directional change in reef fish communities associated with these. Data are from 764 shallow rocky and coral reef sites that have been surveyed by Reef Life Survey divers on multiple occasions, and in each of the periods 2010–2015 and 2016–2020, with the difference in means between these two periods (expressed as change per year) represented by the color scale. A buffer of 150 km extends around each reef survey site, with values interpolated between survey sites within the buffer zone.

(A and B) Reds reflect positive change in SST (A) and the reef fish thermal index (RFTI; B), while blues represent negative changes. Thus, matching regions of red across maps indicate warmer seas (A) and associated shifts to fish communities typical of warmer climates (B).

(C and D) Greens reflect positive change in coral cover (in tropical locations) or kelp cover (in temperate locations) and the community generalisation Index (CGI; D), while purples represent negative changes. Thus, regions that are purple on the habitat map (C) and green on the CGI map (D) indicate where habitat degradation has led to shifts towards communities increasingly dominated by habitat generalist reef fishes.

Letters relate to long-term monitoring locations shown in Figures 2 and 3.
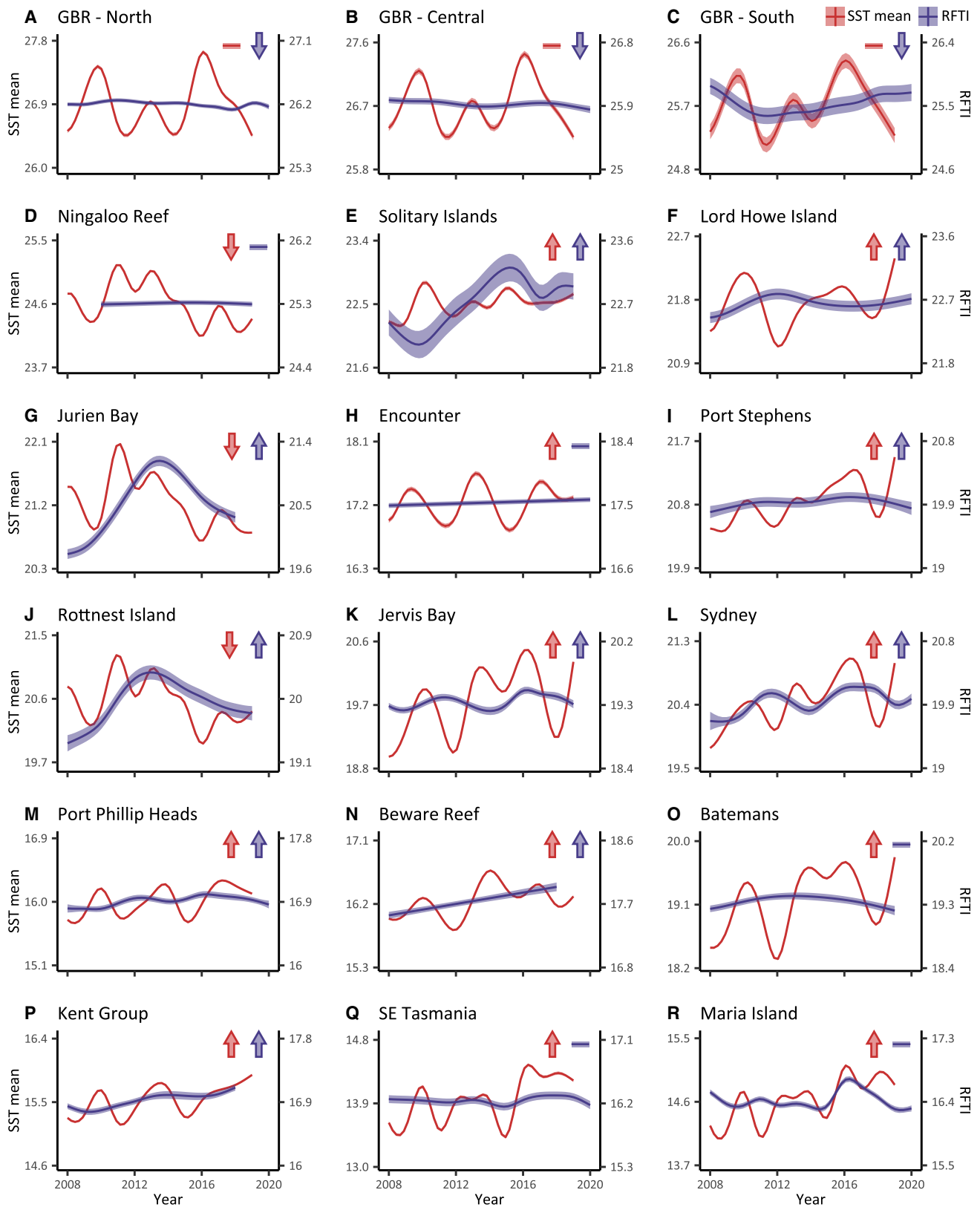
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Trends in the CGI observed around Australia, in this first broad-scale temporal analysis of this indicator, suggested changing coral and kelp cover (and other macroalgal canopy) are likely having widespread impacts on reef fishes, especially on coral reefs. Our synoptic maps suggest many broadly matching regions of increasing CGI (generalization) with reductions in coral and kelp cover (Figure 1), although matching spatial patterns in habitat and CGI change were not statistically supported at this larger scale (Table S1). Time-series trends at monitoring locations (Figure 3) also indicated increased dominance of habitat generalist fishes during years of declining habitat cover; opposing trajectories in CGI and coral cover were observed over interannual time scales across tropical locations ($p < 0.001$; Table S1; Figure S3), but no evidence for a relationship between CGI and kelp cover was found for temperate locations ($p = 0.058$; Table S1; Figure S3). All locations at which both habitat and CGI changed from 2008 to 2020 (seven of eighteen locations) showed opposite trajectories of habitat and CGI values (indicating generalization with habitat degradation; see Table S2 for coefficient estimates). Relatively little kelp loss was observed in many southeastern Australian monitoring locations, however, and large fluctuations in CGI in this region were instead correlated with RFTI change (see below and Figure S1).

DISCUSSION

Climate-driven ecological change on reefs

Temperate Australian fish communities responded to both cyclical and extreme temperature events. SST and RFTI showed corresponding variation, but different lag periods are suggested for independent events. Consistency in the direction and lag of the fish community response, or RFTI, to each of these warm years, across locations spaced hundreds of kilometers apart, implies potentially important differences in the mechanisms underlying community change. Further research is required to understand this variation, but the seasonal timing and magnitude of thermal anomalies provide possible explanations, through different influences on the relative contributions of immigration, emigration, and abundance shifts to overall community change. For instance, the arrival of climate immigrants may lead to immediate responses if warmer seas coincide with peak recruitment seasons for reef fishes.[24] On the other hand, demographic responses of local species may lead to lagged responses if elevated temperatures coincide with peak breeding season and result in reduced recruitment or abundance in subsequent years.

Detailed observations from reefs in southwestern Australia following the 2011 heatwave[22] illustrate these mechanisms; the large but "smoothed" and lagged response of the fish community post-heatwave (Figures 2G and 2J) occurred as many of the tropical immigrants that arrived during the heatwave became less frequently observed on survey transects, varying in how many years they were able to maintain populations at higher latitudes. The warm years that followed the heatwave likely boosted the number of immigrating species and promoted persistence of new populations. Meanwhile, temperate species extirpated during the heatwave[22] appear to have been slower to return or have not yet returned.

Effects of habitat change on reef fishes were most evident on tropical coral reefs. The first study to test the CGI on reef fishes[20] found localized responses of the fish community to coral loss as a result of a cyclone at Ningaloo Reef and the 2016 mass coral bleaching event on the GBR, and this study confirms longer-term fluctuations in CGI that are generally in line with coral cover changes at larger scales (and with an independent dataset for the GBR; see STAR Methods). Our results are also suggestive of CGI responding to kelp (macroalgal canopy) cover changes in some temperate locations (areas of contrasting purple and green across bottom panels of Figures 1, 3G, 3N, and 3P), although statistical support for this trend was relatively low (Table S1), and the overall test for temperate locations was clearly influenced by other locations in which responses were highly varied.

Our observations of reef fishes, using indicators that theoretically relate population trends and community composition to changes in ocean temperatures and reef habitats, showed impacts of these two (often linked) components of environmental change to be widespread and substantial over relatively short time periods. While confirming broader generality in the magnitude of change observed in more localized studies,[12,13,25] our results suggest the longevity and spatial consistency of community-wide responses may be lower than expected on the basis of knowledge accumulated from previous studies. With respect to spatial consistency, communities were highly dynamic, and responses were observed over very large scales, but an assumption that the same responses occurred at every location that experienced change in temperature or habitats would not be justified. Without the high spatial and temporal resolution of biodiversity change provided by this study, conclusions on the relative importance of these impacts at the national scale would thus have included more uncertainty.

Indicators for tracking biodiversity in relation to climate change

Our study not only highlights nuances in how the impacts of climate-related pressures on biodiversity aggregate up over larger scales but also provides important lessons for tracking impacts to inform the public and policy makers of the most important threats to biodiversity. These include the following:

1. Local-scale data are needed to capture important ecological detail, but detection of systematic change requires

Figure 2. Trends in sea surface temperature and the reef fish thermal index (RFTI) through time at 694 sites across 18 long-term monitoring locations distributed around the Australian continent

Change in mean annual SST (in °C) is shown in red, and changes in the RFTI (also in °C) are in purple. Trend lines represent generalized additive mixed model (GAMM) predictions accounting for different numbers of surveys at different sites within each location (A–R), with shaded ribbons representing the standard error around the mean. Arrows in the top right of each plot represent direction of overall change through time, where $p < 0.05$ (linear mixed effects model; see Table S2 for coefficients). Increases in RFTI reflect increased dominance of warm affinity fishes amongst community members.
Letter codes on plots identify the positions of these locations on the maps in Figure 1.
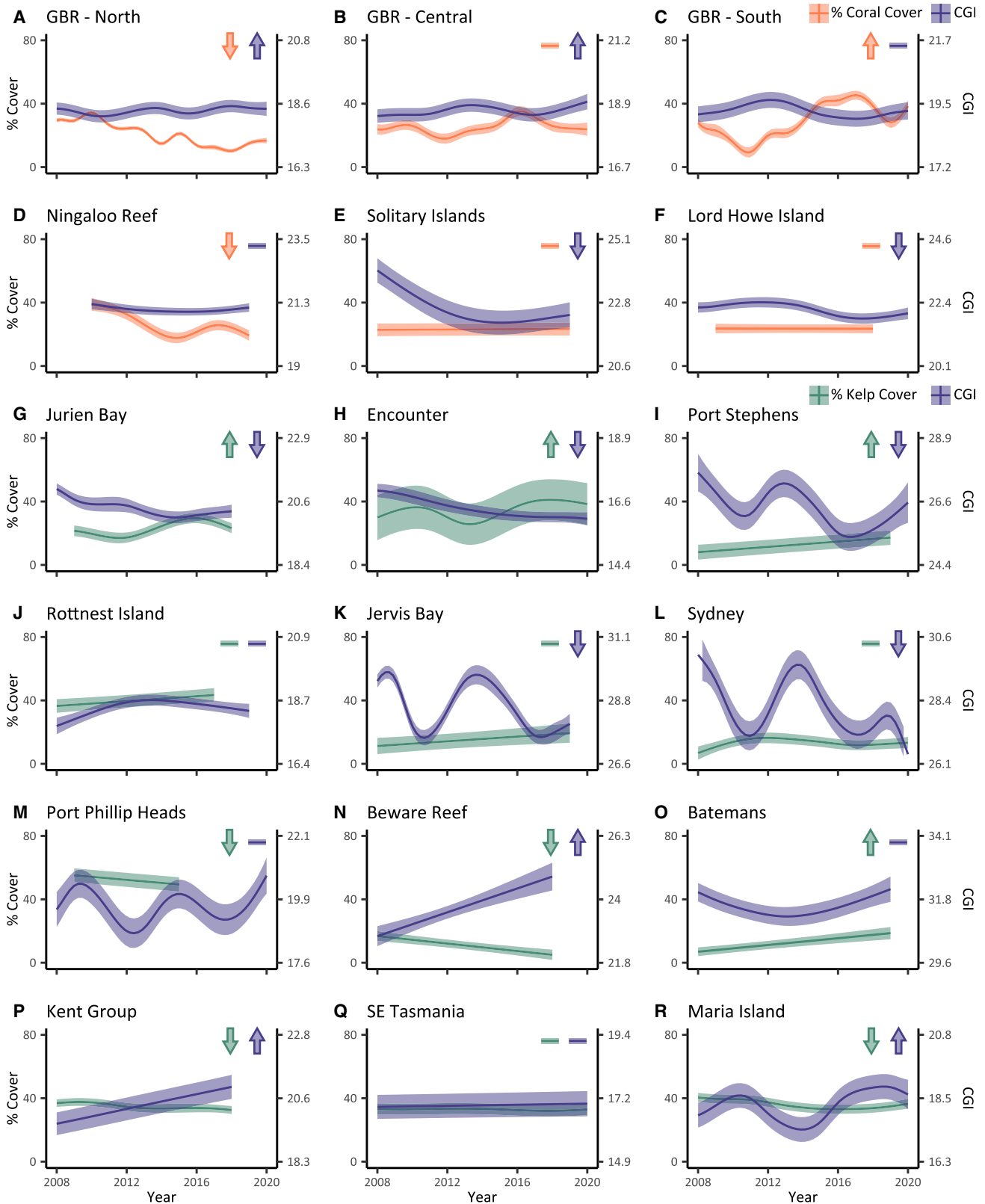
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compilation at larger scales than those currently covered by most existing types of monitoring programs.

2. Substantial variability exists in biodiversity responses, as evidenced by spatial patchiness; consequently, broader conclusions of biodiversity change need to account for what is effectively a mosaic of change rather than relying on a limited set of local case studies.
3. Generally informative indicators that may be sensitive to individual pressures can still show correlated or spurious trends in some regions (i.e., the "specificity" of an indicator to a particular pressure can vary spatially).
4. Ecological communities in temperate and tropical regions differ in ways that may affect indicator responsiveness, complicating interpretation of biodiversity responses to major pressures.

These are discussed in greater detail below.

Local detail for global insight

We used directly compatible data from some of the most spatially (Reef Life Survey) and temporally (Australian Temperate Reef Collaboration and Australian Institute of Marine Science; see STAR Methods) extensive reef monitoring programs worldwide to achieve a detailed national and decadal coverage for Australia. While Australia is approximately 1.5 times the size of Europe and spans a very broad range of reef habitats and faunas, scaling this level of effort up globally remains an enormous challenge. Essential ocean variables[26] and essential biodiversity variables[27] are the focus of globally coordinated and aggregated data streams for calculating indicators to track global biodiversity targets, but it is important that these data streams can be used to generate the most useful indicators. A lack of compatibility in data at the finest levels of taxonomic, spatial, and quantitative resolution will inevitably limit the range of indicators that can be calculated with such data streams. The indicators applied here, using what are among the best available standardized data (for the scales investigated), revealed important caveats (as discussed below), so the utility of aggregated global data streams represents a concern that should be addressed early for these processes to have maximum impact.

Spatial variability

Patchiness in biodiversity responses was clearly evident, highlighting caveats associated with scaling up results from more detailed localized studies or using different methods for monitoring in different regions (potentially introducing further patchiness through methodological bias). The impacts of habitat transformation illustrate this point particularly well, where conclusions on the consequences of cyclones or mass bleaching events for regional biodiversity can vary considerably depending

on the spatial and temporal scope of the study.[23,28,29] To better understand the impacts of habitat degradation over broad scales, a key unanswered question is: "At what point do the patches of degradation become large or numerous enough to be considered at a scale of importance to the broader public, national policies, ecosystem service provision, and global biodiversity conservation?" Fine-scale, locally matching habitat and biodiversity data that can be investigated together at the global scale are critical for answering this question. Further research using such data could then also quantitatively evaluate changes in conclusions that arise by trialing varying levels of spatial aggregation in the data and could possibly best guide the most informative scales for understanding and tracking each indicator.

Correlated or misleading trends

One reason for unusual trends observed at some locations is that indicators may be correlated with each other and/or responding to another pressure. Indeed, the specificity of indicators to the pressure of interest is one of the most important criteria for choosing indicators, albeit not often tested and less often met.[30] Our results identify an additional potential issue in that specificity may vary spatially. Few, if any, global indicators have likely been tested for such variation.

The indicators used here distill detailed monitoring data into metrics designed to characterize directional change in fish communities in relation to temperature and habitat change, but they may also be influenced by other factors not investigated (e.g., extractive use of reef species or variation in oceanographic productivity). In addition, both are ultimately based on the same underlying fish community structure data. Correlation between them can occur where local bias exists: for example, where habitat generalists are also the subset of the community with the warmest affinity. This appears to be the case at opposite ends of the Australian continent—the warmest affinity species tended to be habitat generalists in the southeast (positive correlation between traits) and habitat specialists in the tropics (negative correlation between traits; Figure S1).

The implications of correlations between traits associated with temperature affinity or habitat generalization therefore differ between temperate and tropical regions. The RFTI increased across southeastern Australia, indicating a relatively coherent regional "warming" of the fish community, which strongly matched expectations from SST change. CGI showed unusual responses in a subset of these locations, in some cases widely fluctuating despite very limited change observed in the dominant habitat cover (kelp in this region). At the other end of the continent (northern), the CGI largely followed trends expected to result from the losses in coral cover in large parts of the GBR and Coral Sea, while some of these locations showed a

Figure 3. Trends in the percent cover of live hard corals and canopy kelps and the community generalization Index (CGI) through time at 293 sites across 18 long-term monitoring locations distributed around the Australian continent
Change in the cover of hard corals is shown in orange, kelps in green, and CGI in purple. Trend lines represent generalized additive mixed model (GAMM) predictions accounting for different numbers of surveys at different sites within each location (A–R), with shaded ribbons representing the standard error around the mean. Arrows in the top right of each plot represent direction of overall change through time, where p < 0.05 (linear mixed effects model; see Table S2 for coefficients). Increases in CGI reflect increased dominance of habitat generalist fishes amongst community members.
Letter codes on plots identify the positions of these locations on the maps in Figure 1.

"cooling" of the fish community (decreasing RFTI values). This cooling effect probably reflected the negative correlation between traits for the species found in this region (habitat generalists tended to be those with relatively cooler affinity).

The underlying causes and generality of these trait correlations remain unknown, but they strongly emphasize the need for local context, tracking the pressures themselves as well as the biodiversity responses (in this case, SST and habitat trends) and investigating species-level patterns to collectively inform which of the pressures may be the dominant local driver of change. Tracking "pressures" with associated biodiversity change (i.e., "state") usually forms part of most biodiversity reporting frameworks (e.g., DPSIR—drivers, pressures, states, impacts, and responses—and derivatives[31]). Our results show this is important for interpreting indicator trends. Both the indicators we applied here have previously been tested for sensitivity and shown to respond to the pressure of interest (particularly the RFTI, which has been widely applied in various forms).[6,20,32,33] We thus expected change in a particular direction when the change in pressure was known. Our analyses confirmed relationships between SST and RFTI change overall (spatially and temporally; Table S1) and CGI and habitat change in the tropics (Table S1). The lack of a relationship with habitat change we observed in southeastern Australia, however, indicated that CGI trends were not likely representing impacts of habitat degradation in the reef fish community there. Likewise, the warming seas in the northeast suggested the RFTI decline in some parts of this region was not likely driven primarily by changing sea temperatures (which was supported by investigation of the trends in individual species).

At continental to global scales, incorrect conclusions on the drivers of change may not be problematic if idiosyncratic responses are swamped by signals from more numerous locations where the indicators describe directional change well. This appears to have been the case at the continental scale, where the general conclusions from our analysis only need slight modification after considering the trends in the pressures themselves. That is, with the context of changes in sea temperatures and habitats, the direct effects of temperature-driven change in the fish communities may be slightly underestimated in some parts of the tropics by our results and habitat-driven change overestimated in some temperate regions.

Notably, for this study, we applied the CGI to provide an indication of the impacts of habitat degradation on fishes in a comparative sense with more direct impacts of temperature change on fishes. For tracking general biodiversity change, monitoring habitats directly is important in its own right and appears to be a necessary prerequisite for understanding impacts on the fishes using CGI. For future application of the CGI for reef fishes, we recommend (1) only interpreting trends in CGI in regions where habitat change has been confirmed and (2) that more research is undertaken to better understand the underlying causes for spatial patterns in the correlation between species' thermal affinities and habitat generalization traits.

Temperate-tropical differences

Temperature-related changes in reef fish communities (RFTI) appeared to be stronger than habitat-related changes in temperate

regions over the last 12 years of monitoring, a conclusion that holds regardless of a correlation between traits used for the two indicators. Our results also suggest that habitat-related changes (CGI) were likely stronger in tropical than temperate regions. A key remaining question is whether temperature or habitat change has been a stronger driver of the observed responses in fish communities across Australia's extensive tropical coral reef regions. The answer is obscured by the likelihood that temperature effects have been underestimated in the tropics (as discussed above).

Patterns of CGI change amongst coral reefs in the northern GBR and offshore Western Australia (Figure 1) indicate increased proportions of generalist reef fishes in areas where coral cover declined and increased specialists where coral cover increased. This signal was reasonably coherent and stronger than any signal associated with RFTI in the tropics. On first impressions, this could indicate that coral reef fish community changes are driven more strongly by changes in coral cover than directly by temperature. Historical focus of studies of bleaching impacts on fishes has been directed toward the effects of the lost coral habitat[9–11,34,35] rather than the thermal anomalies responsible,[15] perhaps reflecting some form of unofficial consensus by the coral reef research community that habitat is more important than temperature in driving change in reef fish community structure. Coral reefs tend to have greater structural complexity than kelp forests at scales relevant for fishes, and tropical fishes are, on average, more towards the habitat specialization end of the spectrum for the habitat niche breadth trait used to calculate CGI.[20]

Despite the clear importance of live coral cover habitat for tropical reef fishes, substantial evidence for temperature-associated reshuffling of community structure continues to grow for tropical reef fishes. Species-level and trophic-group-level changes in reef fishes were observed following the 2016 mass bleaching event on the GBR that were consistent with elevated temperatures, but not spatially related to coral loss,[15] and some patches of elevated RFTI were evident in the northern and southern GBR in this study (Figure 2). Yet the question remains as to why changes in RFTI observed across large parts of the central GBR and Coral Sea regions in this study were not consistent with elevated temperatures. With thermal affinity positively correlated with habitat generalization among species in the broader region, one explanation is that the spatial mosaic in trends in CGI and RFTI reflects the outcomes of whichever was the stronger of the two drivers at any given location. In other words, temperature effects may have been strong enough to dominate the community change signal in the north and south of the GBR and Coral Sea region, but habitat change impacts prevailed in the central part of the region. Given heat stress can often cause coral loss, the impacts of these two pressures are probably regularly confounded in the literature and will always be difficult to tease apart, even using species-level approaches (as opposed to the community-level approach used here).

With respect to other differences between temperate and tropical fish community responses, change in tropical fish communities is probably also more difficult to evaluate than that in temperate communities when using the community weighted

means approach used here for the RFTI and CGI. Not all species in a given ecological community respond to each pressure, and the number of non-responders for a given pressure may be greater in the tropics due to the extraordinarily high species richness of coral reef fish communities and far more complex food webs and ecological dynamics.[36] This could generate more "ecological inertia" in community-level responses and reduce the signal-to-noise ratio. Thus, a lack of indicator trends may not mean a lack of any ecological change.

The future of marine global biodiversity monitoring

The four key points discussed above can be collectively addressed through broader application of organized, high-level citizen science to complement existing large-scale scientific monitoring and cover the massive scales required (points 1 and 2). Reporting trends in a broad suite of indicators is also needed, ideally in combination with measures of change in pressures and an understanding of local context (points 3 and 4). The scientific community should lead these steps, along with the testing of the sensitivity and specificity of indicators and modeling, to achieve the best possible integration of diverse data streams. But effective translation of global monitoring to improved biodiversity outcomes also requires a shift in the way scientists and policy makers connect. More than 500 global environmental conventions or multilateral environmental agreements (MEAs) are in place to address transboundary global environmental issues,[37] and the present situation for tracking their success appears ineffective, as a mix of top-down (policy) and bottom-up (scientific) processes that do not meet in the middle. From the top, biodiversity goals and targets are not informative or specific enough to adequately guide monitoring and indicator development, while from the bottom, the limited quantity, distribution, and interoperability of biodiversity data available are not sufficient for the questions and scales that drive decision-making by policy makers[38] (leading to an over-reliance on small-scale case studies).

Our results also highlight the importance of ensuring that climate change is explicitly recognized in new and existing targets and indicators, thus providing an opportunity to add further impetus for governments to improve national climate policies. Climate change clearly has a huge impact on marine biodiversity, with changes we observed around the Australian continent over short time scales indicating that much larger changes are likely over the next half century as ocean warming progresses,[39] currents change in intensity,[21] and heatwaves increase in frequency.[39,40] Consideration of climate impacts on marine ecosystems currently focusses on coral reefs because of the highly visible impacts of increased frequency of coral bleaching and storm damage. Our results support not only the need to include climate-specific impacts on biodiversity in new targets and indicators for the post-2020 global biodiversity framework but also to broaden the scope of relevant marine indicators beyond coral reefs and coral cover and to encompass biodiversity change in addition to biodiversity loss.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

AUTHOR CONTRIBUTIONS

R.D.S.-S. led the study design and writing of the manuscript with C.M. and G.J.E.; C.M. undertook data analysis and prepared figures with E.C.; G.J.E., R.D.S.-S., M.J.E., and N.S.B. led field data collection, with input from most authors; E.S.O. and M.J.E. led digitization of benthic imagery; all authors contributed to the writing of the manuscript.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Raw data	This paper analysed existing data available through the National Reef Monitoring Network (NRMN).	Data are available through https://portal.aodn.org.au
Software and algorithms		
R Studio		http://www.rstudio.com

RESOURCE AVAILABILITY

Lead contact
Further information and requests for resources should be directed to the lead contact, Rick Stuart-Smith (rstuarts@utas.edu.au).

Materials availability
This study did not generate new unique reagents.

Data and code availability

- This paper analysed existing data available through the National Reef Monitoring Network (NRMN), Australia's Integrated Marine Observing System (IMOS) – IMOS is enabled by the National Collaborative Research Infrastructure Strategy (NCRIS). Data are available through https://portal.aodn.org.au/. The Australian Institute of Marine Science Long-term Monitoring data used for the Great Barrier Reef will be shared by Author M. Emslie upon request.
- This paper does not report original code
- Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request.

EXPERIMENTAL MODEL AND SUBJECT DETAILS

All three reef monitoring programs providing data for these analyses collect quantitative data on reef biodiversity on standardised visual censuses along 50 m transect lines set on hard reef substrate (rocky or coral).

METHOD DETAILS

Field data collection
For the Reef Life Survey (RLS) and Australian Temperate Reef Collaboration (ATRC) data, fishes are surveyed in duplicate 5 m wide belts on either side of the transect line, with abundance and binned size recorded for all species observed during a single swim along each side of the line. All species sighted within the blocks are recorded, including unidentified individuals, which are usually photographed for later identification with the assistance of taxonomic experts. For RLS surveys, multiple transects are usually surveyed at each site, often laid parallel at different depths (typically in 4 – 15 m depth), while ATRC data collection involves four end-on-end transects along either the 5 or 10 m depth contour. The only other difference between these two programs is how the habitat data are collected. For RLS, this involves the divers taking photoquadrats (20 images per 50 m transect, spaced at 2.5 m intervals) and later scoring the percentage cover of major benthic functional groups using annotation software such as Squidle+ (https://squidle.org/). For the ATRC, the percentage of macroalgal species is scored underwater using *in situ* quadrats (5 quadrats per 50 m transect, each 0.5 m x 0.5 m). Full details of RLS survey methods are provided in[41,42] and an online methods manual (at http://reeflifesurvey.com) and for the ATRC, in.[43]

    The Australian Institute of Marine Sciences Great Barrier Reef Long-Term Monitoring program (AIMS LTM) data collection involves underwater visual surveys for fishes and digital imagery for coral cover along permanently marked transects on 103 reefs spread across the length and breadth of the Great Barrier Reef.[44,45] Five transects are set between 6 and 9 m in a standard reef slope habitat in each of three sites at each reef. A subset of 210 species of reef fishes from 9 families are counted, and lengths have been estimated since 2017 (but were not required for this study). Forty benthic images from each transect are analysed by identifying the benthic taxa to the lowest taxonomic level possible under each of five points per image. Sites monitored by AIMS were divided into three regions along the Great Barrier Reef to allow independent examination of regional trends in time-series analyses.

Monitoring involved dive teams returning to the same sites (identified by GPS coordinates and depth) and resurveying multiple transects in any given location, where a location is loosely described as a collection of sites visited during a monitoring campaign, usually within ∼30 km of each other (but broader across the more remote parts of the continent and the Great Barrier Reef, where sites within a 'location' may span up to 500 km, for example). The frequency of monitoring varied among sites, typically annual for many locations, with surveys targeting the same time of year each year. Some locations, such as Lord Howe Island (RLS) and parts of the Great Barrier Reef (AIMS) are surveyed biennially. Some gap years exist for many sites, however, where either weather or funding continuity interfered with the ability of field teams to cover those sites. The imbalance in monitoring coverage among sites within locations ad years was explicitly considered for analysis of trends in indicators (see below).

Indicator calculation

The Reef Fish Thermal Index (RFTI) is the same as the Community Temperature Index,[19,46] calculated for the reef fish community. It is a Community Weighted Mean (CWM) value of the thermal affinity values of fish species recorded on each 50 m transect, weighted by the log of their abundances. Thermal affinities, or Species Temperature Index (STI) values, were calculated as the midpoint of the thermal niche breadth of fish species, as calculated by[47] using the full range of seasonal sea temperatures experienced at all species record locations. RFTI values are always calculated at the level of standardised area for individual fish surveys before analysis.

The Community Generalisation Index (CGI) is calculated in the same way as the RFTI but represents a CWM of Species Generalisation Index values (SGIs), which effectively estimate the habitat niche breadth of each species. CGI is also weighted by the log of the species' abundance on the transect. SGI values were calculated using co-located fish and habitat data from across the global distributions of the fishes, using three-dimensional kernel density estimation with the kde function in the R package ks. It estimates the probabilistic 'habitat volume' occupied by a species, expressed as a proportion of the total volume of surveys across all ecoregions it has been recorded in. Full rationale and details are provided in,[20] but it effectively identifies habitat generalists with higher values.

The RFTI has been applied in a number of studies for reef fishes in recent years, and is recognised by the Global Biodiversity Indicators Partnership for tracking biodiversity in relation to international targets (https://www.bipindicators.net/indicators/reef-fish-thermal-index). The CGI was only recently developed.[20]

QUANTIFICATION AND STATISTICAL ANALYSIS

Synoptic maps of biodiversity change

Although annual monitoring is undertaken in numerous locations around the Australian continent through the combination of the three programs, as shown in the individual panels of Figures 2 and 3 (and described above), the RLS program has also undertaken surveys at 764 sites around the continent for which data are available for at least one point in time in each of the two major time windows covered by this study (2010-2015 and 2016-2020). Although less frequent and consistent as the monitoring undertaken in the locations shown in individual plots, this spatially rich dataset enabled change in indicator values to be investigated for a much broader range of the coastline, including some large remote areas not frequently surveyed by any scientific institution, industry or government agency. For these sites, we calculated the difference in the mean indicator values from all surveys undertaken in each of these two time windows. We then expressed these differences in change per year to account for the varying number of years between surveys among sites, and mapped values using inverse-distance weighting to visualise mean values through a 150 km buffer around each survey site (Figure 1). This buffer size was chosen to allow visualisation of patterns at the scale presented, and while not all of the coloured area in the maps represents shallow reef habitat, the maps should be interpreted as the value of indicator change per year that occurred, on average, for reef sites surveyed within the coloured area. Breaks in the colour gradients were determined using the quantile method, which sets breaks to have an equal number of pixels in each level. Maps of biodiversity change were computed in R using the 'raster', 'gstat' and 'tmap' packages.

Evidence for relationships between indicator and pressure maps in Figure 1 was tested using linear mixed effect models (LMEs) with site-level mean annual change in RFTI (ΔRTFI) as a function of mean annual change in SST (SST) in the first model (Equation 1) and mean annual change in CGI (CGI) as a function of mean annual change in habitat cover (either coral or kelp; ΔHabitat) as the second model (Equation 2). In both models, we included an interaction with the realm considered (tropical or temperate) to test whether the magnitude and/or direction of these relationships differed between realms. We also included a 'location' random effect to account for the non-independence of multiple survey sites within each location. We assumed a gaussian error distribution and verified the normality of model residuals using Q-Q plots. The absence of spatial autocorrelation in model residuals was verified through spatial correlograms of Moran's I and two-sided probability values p > 0.05 after applying a Bonferroni correction. Model coefficient estimates and associated probability values (approximated using the normal distribution) are presented in Table S1; and plots of effect sizes and partial effects are presented in Figure S3.

$$\Delta RTFI \sim \Delta SST * Realm + (1|Location) \quad \text{(Equation 1)}$$

$$\Delta CGI \sim \Delta Habitat * Realm + (1|Location) \quad \text{(Equation 2)}$$

TEMPORAL TRENDS IN INDICATORS

Temporal trends shown for each indicator and at each location shown in Figures 2 and 3 were modelled using Generalised Additive Mixed Models (GAMMs), where the indicator values were modelled as a function of year, with thin plate smoothing splines and a 'site' random effect to account for the hierarchical structure of the dataset (i.e., individual surveys at the transect level nested within sites at each location). Only sites with at least 4 years' of data available post-2008 were retained for this analysis. GAMMs were calibrated in R using the 'mgcv' package. Mean annual sea surface temperature data were calculated using extracted daily values for each site surveyed using down-scaled Coral Reef Watch temperature data[48] (available through https://coralreefwatch.noaa.gov/product/5km/).

Evidence for relationships between trends in indicators and pressures were assessed using LMEs, with lag periods ranging from zero to 2 years tested in a multi-model comparison based on the Akaike Information Criterion corrected for small sample sizes (AICc). The RFTI model included SST as a fixed effect, as well as an interaction with the realm (temperate or tropical), and a 'site-within-location' random effect to account for the temporally replicated and spatially structured nature of the dataset (Equation 3). The lag-zero model predicted RFTI in year t as a function of SST observed in the same year; the lag-one model as a function of SST observed in year t-1, and the lag-two model as a function of SST observed in year t-2. The model with the smallest AICc was selected.[49] The CGI model was structured the same way; however, as habitat was measured in a different response variable in temperate and tropical locations (i.e., kelp cover values would naturally differ from coral cover values), separate models were run for tropical versus temperate locations (as indicated by the habitat cover used for Figure 3) (Equations 4 and 5). We assumed a gaussian error distribution and verified the normality of model residuals using Q-Q plots. Results from the LMEs are presented in Table S1; and plots of effect sizes and partial effects are presented in Figure S3.

$$RTFI \sim SST * Realm + (1|Location / Site) \quad \text{(Equation 3)}$$

$$CGI_{trop} \sim \%Coral + (1|Location / Site) \quad \text{(Equation 4)}$$

$$CGI_{temp} \sim \%Kelp + (1|Location / Site) \quad \text{(Equation 5)}$$

In addition to analysing year-to-year links between indicators, further LMEs were run for each indicator x location combination to assess significance of overall change in the time series. For each location, evidence for a temporal trend in each indicator over the time series considered was assessed through LMEs with a 'year' fixed effect and a 'site' random effect (therefore analogous to the GAMMs plotted in Figures 2 and 3 but without the smoothing splines). Coefficients and p-values for each model are provided in Table S2, and all significant trends are shown with coloured arrows in individual plots of Figures 2 and 3.

INDICATOR CORRELATIONS

In order to investigate causes for some unexpected trends in indicator values, we evaluated the relationship between the traits that underlie the RFTI and the CGI; i.e. the species' thermal affinities (STI values) and their habitat niche breadth (SGI values), on a location-by-location basis. For this we took the entire list of reef fish species recorded over the study period at each location surveyed by the RLS program. This provided the most comprehensive species list and allowed spatial aggregation at the scale of ~30 km locations for much of the country. Pearson correlation was calculated for STI vs SGI values for species in each location and plotted on a map to visualise spatial patterns. This identified a gradient from a positive correlation in the south (where warmer affinity species tend to be more generalist) to a negative correlation in the north (where warmer affinity species tend to be more specialist) (Figure S1). The correlation was weak or non-existent for many locations in mid-latitudes.

FISHING PRESSURE

It is also likely that spatial differences and temporal changes in fishing pressure may have influenced some of the trends observed. Unfortunately, robust metrics for fishing pressure on shallow reefs around the Australian coastline (which is heavily dominated by recreational fishing) are not available and we could not adequately test whether this may affect trends in RFTI or CGI. We make an assumption that changes in these indicators related to fishing (or lack of) will be present in either a dampening or exaggeration of trends, rather than through reversal of trends. I.e. the magnitude of change may vary depending on fishing in particular locations, but the direction should not.