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REPORT

Coral reef resilience differs among islands within the Gulf of Mannar, southeast India, following successive coral bleaching events

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Abstract We used a 12-yr data set of benthic cover (2005–2017), spanning two bleaching events, to assess changes in benthic cover and coral community composition along 21 islands within Gulf of Mannar (GoM), southeast India. Overall, between 2005 and 2017 reefs had a simultaneous decrease in relative coral cover (avg. = − 36%) and increase in algal cover (avg. = + 45%). Changes in benthic cover were not consistent among islands, ranging from − 34 to + 5% for coral cover and from − 0.3 to + 50% for algae. There was a spatial gradient in coral mortality, which increased among islands from west to east. However, there was a disconnect between coral loss and subsequent increases in algae. Algal cover increased more on islands in west GoM where coral loss was minimal. Environmental co-factors (coral cover, percent bleaching, degree heating weeks, fish densities, Chl-a, pollution) explained > 50% of the benthic cover responses to successive bleaching. Coral survival was favored on islands with higher fish densities and chlorophyll-a levels, and increases in algal cover were associated with higher measures of pollution from terrestrial runoff. Coral morphotypes differed in their response following successive bleaching resulting in changes in the relative abundance of different coral morphotypes. Existing climate projections (RCP8.5) indicate a 22-yr gap in the onset of annual severe bleaching (ASB) for reefs in the east versus west GoM, and ASB was ameliorated for all reefs under the RCP4.5 projections. There is limited knowledge of the resilience of GoM reefs, and this study identifies coral morphotypes and reefs that are most likely to recover or decline from successive bleaching, in the context of forecasts of the frequency of future bleaching events in GoM.

Keywords Successive bleaching events · Coral resilience · Gulf of Mannar · Southeast India · Coral morphotypes · Island-specific response · Chlorophyll-a · Reef fish

Introduction

Coral reefs are one of the most sensitive ecosystems to climate change, and repeated mass coral bleaching events caused by ocean warming (Heron et al. 2016; Hughes et al. 2018) are fundamentally altering coral reefs as we know them (Williams and Graham 2019). Based on global averages, ocean temperatures in 2015–2017 were the

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highest temperatures recorded since the 1800s (Blunden and Arndt 2019) and resulted in a 3-yr global coral bleaching event (Hughes et al. 2018; Eakin et al. 2019). Bleaching occurs when there is a breakdown between corals and their symbiotic microalgae (zooxanthellae) (Vidal-Dupiol et al. 2009) and can result in extreme nutritional stress for corals (Muscatine 1990). Thermally stressed corals have reduced growth, reproductive output, higher disease susceptibility and increased risk of mortality, depending on the duration of the heat event (Baker et al. 2008). Coral loss subsequently affects other organisms that depend on coral reefs for food and shelter (Glynn 1985; Sano 2004; Bellwood et al. 2006; Baker et al. 2008). Coral bleaching also changes the balance between reef accretion and erosion (Cantin and Lough 2014), resulting in a loss of reef topographic complexity and rugosity (Perry and Alverez-Filip 2019).

As ocean waters continue to warm under climate change, bleaching events are expected to become more frequent and severe, giving coral reefs little time to recover between disturbances (van Hooidonk et al. 2016). Coral reefs show spatial heterogeneity in the severity of coral bleaching and degree of recovery (Graham et al. 2015; Hughes et al. 2018; Safaie et al. 2018), which is influenced by factors such as bleaching severity, coral community structure, abundance of herbivores, maintenance of biodiversity, exposure to secondary stressors and gradients in oceanography and climate (Baker et al. 2008; Graham et al. 2015; Safaie et al. 2018; McClanahan et al. 2019; Head et al. 2019). For example, reefs in the Seychelles were more likely to recover to coral dominance following mass coral bleaching if they were in deeper water and had more abundant herbivore populations (Graham et al. 2015). There is still much uncertainty surrounding coral reef responses to successive bleaching events, and gathering data on the effects of recurrent bleaching on coral reefs is important to understand which coral species, reefs and regions are most likely to display resistance or resilience to climate change.

Using a 12-yr data set of benthic cover (2005–2017), spanning two bleaching events, the long-term benthic cover and coral community composition of reef sites were assessed along 21 islands within Gulf of Mannar (GoM), southeast India. GoM reefs were first impacted by bleaching in 1998, where 89% of the coral bleached and 23% subsequently died (Arthur 2000). More recently in 2010, thermal stress caused 10% bleaching and 9.7% mortality (Edward et al. 2012) and in 2016 resulted in 24% bleaching and 16% mortality (Edward et al. 2018). Our study examined the resilience of these reefs in response to successive bleaching events. Changes in benthic cover and coral community composition were examined following the two recent bleaching events, in terms of which coral morphotypes drove changes in coral community composition, and what environmental conditions were associated with changes in coral and algal cover following bleaching. Finally, global climate model predictions were used to assess future annual severe bleaching conditions for reefs in GoM associated with global climate change.

Methods

Survey methods

Four monitoring sites were established at 21 islands in the GoM, India, in 2005 (Fig. 1 and Supplemental Table 1), which have been resurveyed annually through 2017 (Edward et al. 2008a, b, 2012, 2018). At each site, three 20-m transects were laid parallel to shore with a minimum of a 20-m gap between transects (3 transects/site * 4 sites/island = 252 transect/year). Along each transect, substrate characteristics were recorded using line-intercept method with corals recorded by growth forms (morphotypes) and further categorized by corals within Acroporidae versus corals in other families following English et al. (1997) (Table 2). Other substrate categories included soft corals, algae (macroalgae and algal turf), crustose coralline algae, abiotic (sand, rock and old dead corals) and others (sponges, sea anemones, ascidia, zoanthids, crinoids, oysters, hydroids and bryozoans). Annual surveys were conducted between October and December, and additional surveys were conducted at the same sites between April and June during bleaching events in 2010 and 2016. Timing of surveys during the bleaching events was based on sea surface temperatures (SST) indicating water temperatures were passing the bleaching threshold for corals in GoM (30 °C) (Edward et al. 2018) and rapid surveys conducted at representative sites during the elevated SST time periods. In this manner, we were able to resurvey the reefs as bleaching was approximately at its peak. At each survey date, sites were relocated via GPS coordinates allowing the same area of the reef to be surveyed, but transect placement was random rather than along permanent markers.

Environmental variables

Environmental variables that could affect bleaching, mortality or recovery of benthic populations were measured in situ during annual surveys or derived from remotely sensed data (Table 2). Water clarity was measured at each site with a 20-cm Secchi disk and divided by maximum bottom depth to standardize across sites. Sedimentation was assessed annually in 2005–2008 and 2013–2017 using four replicate PVC sediment traps (10 cm height × 8 cm diameter) per island. Traps were secured adjacent to the

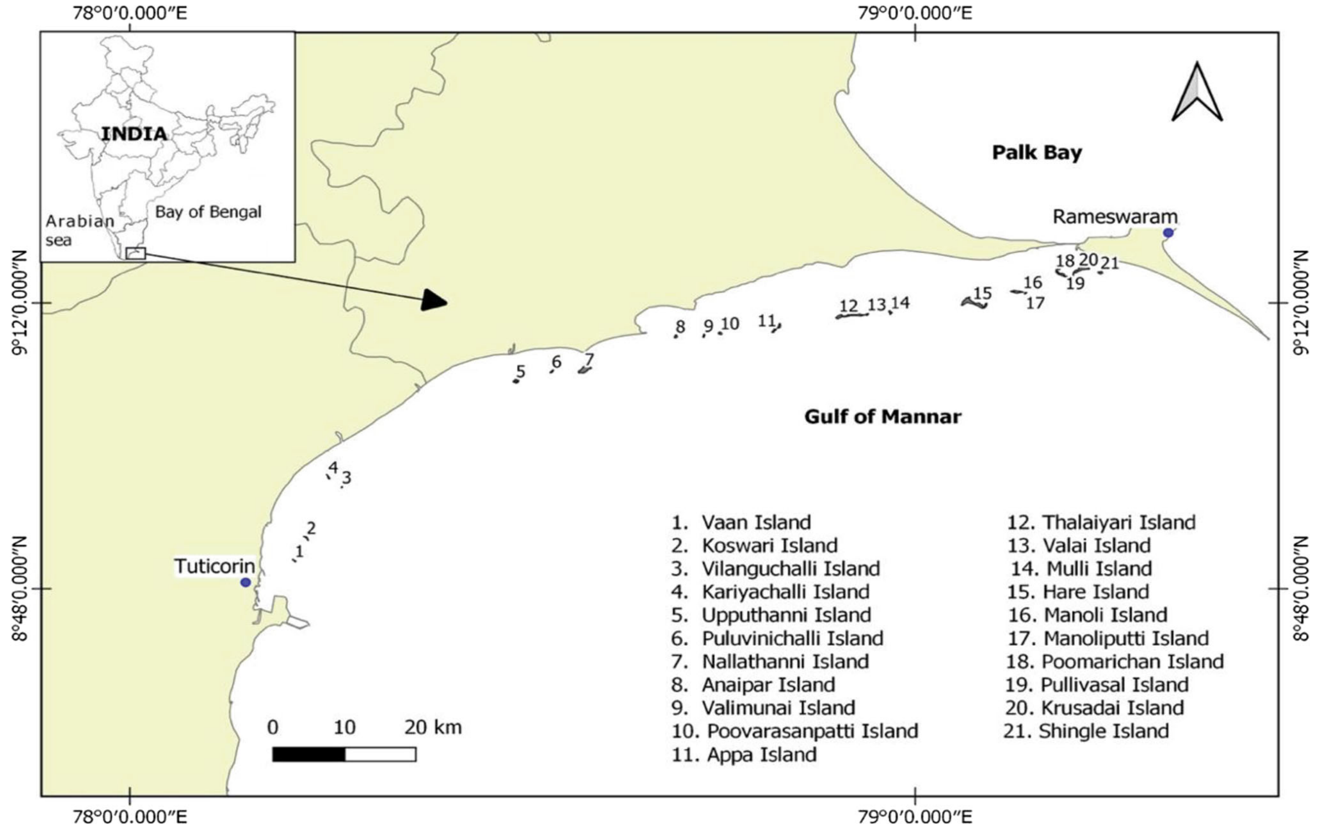

Fig. 1 Map of Gulf of Mannar, India, showing long-term monitoring sites surveyed between 2005 and 2017 and resurveyed during the bleaching events in 2010 and 2016

reef, 20 cm above the bottom, and collected after 10–15 d. Samples were dried at 70 °C and weighed to calculate milligrams of sediment deposited per cm^2 per day. At the island level, sedimentation varied little through time; therefore, mean sedimentation values per island were used in statistical analyses. Reef fish densities were recorded using visual census along six belt transects (50 × 5 m) per island between April 2014 and March 2015. Annual maximum degree heating week (DHW) values at 5-km spatial resolution were obtained for each island for the two bleaching years, 2010 and 2016, from NOAA's Coral Reef Watch (Liu et al. 2005, NOAA Coral Reef Watch 2019). Maximum monthly chlorophyll-a values (as a proxy for phytoplankton biomass) at 4-km spatial resolution for each island and bleaching year were obtained from monthly chlorophyll-a observations from NASA MODIS-Aqua (NASA 2014, 2017). Missing data at a given sampling site and date were excluded from calculation of the maximum. To account for human impacts on reefs, the 2015 human population for India (WorldPop 2017) was measured at 100-m spatial resolution. For each coast-adjacent grid cell, the total number of people living within 10 km of each survey point was found using the Zonal Statistics 2 Toolbox in ArcMap 10.1 (Environmental Systems Research, Inc.). To assess the relative impact of coastal populations on each island, the inverse distance weighted method was employed, where grid cells farther away from an island received less weight than closer cells. The population in each cell was divided by the square of the distance of that cell from the survey point to produce a weighted population measure for each survey point.

Data analysis

Analyses of benthic changes following successive bleaching events

To determine whether the mean proportional change in coral and algal cover differed across islands, we used analysis of variance (ANOVA). The response variable was the difference in coral or algal cover between 2005 and 2017 for each transect and the predictor variable (group) was island. Numerous environmental, ecological and human factors are hypothesized to affect coral bleaching resistance and resilience (West and Salm 2003; Obura 2005). We assessed the role of potential environmental drivers in explaining variability in benthic cover responses to the 2010 and 2016 bleaching events using beta regression models. The response variables in the beta regression models were calculated as the change in coral or algal cover on a transect from before and after each bleaching event (i.e., substrate change between 2009 and 2010 and 2015 and 2016), which varied from − 100 to 100% and were scaled between 0 and 1. The initial predictor variables considered in the beta regression models included a suite of environmental variables hypothesized to affect coral's ability to resist bleaching or recover following a bleaching event (Table 1); however, variables with greater than 50% correlation (based on Pearson's correlation coefficient) were removed from the analysis. Random effects of transect, nested within site, nested within island, were also included in the beta regression models. Stepwise forward selection was used to select the optimal model, sequentially adding variables to the nested random effects that reduced the AIC value by more than two. Model fit was further assessed by calculating R^2 values for model predicted outcomes with observations of substrate change. The beta regression models were conducted in *R* statistical software (hereafter referred to as *R*) using the glmmTMB function and package (Magnusson et al. 2017). The magnitude of change in coral or algal cover following the 2010 bleaching event was compared with the changes following the 2015 event using paired *t* tests, with data paired by island.

Coral community changes following successive bleaching

Permutational multivariate analysis of variance (PERMANOVA) was used to determine whether the coral community composition (based on proportion of different morphotypes) shifted following each bleaching event and across islands. For each island, a PERMANOVA was conducted where the response variable was the Bray–Curtis dissimilarity matrix from the raw percentage morphotype cover values for each transect and the predictor variable was time period with nested random effects of transect within site. There were three time periods assessed, including the period: (1) before the 2010 bleaching event (2005–2009), (2) following the 2010 bleaching event and before the 2016 bleaching event (2010–2015) and (3) following the 2016 bleaching event (2016–2017). PERMANOVAs were conducted using the vegan package (Dixon 2003) in *R*.

Table 1 Predictor variables with their description and units used to model potential environmental drivers of coral reef resilience within Gulf of Mannar, India

Variable	Description and units	Min.	Max.	Data source
Water clarity	Secchi disk divided by maximum water depth in meters	0.25	1.10	Reef survey
Sedimentation rate	mg of sediment per cm^2/d	33.94	47.39	Reef survey
Fish density	# fish per 250 m^2	213.80	1346.20	Reef survey
Surface runoff pollution	Modeled diffusive plumes in 2013 based on impervious surface runoff from watershed	0.41	78.1	Halpern et al. (2015) Ocean Health Index https://knb.ecoinformatics.org/#view/doi:10.5063/F1S180FS
Mean bleaching in 2010	% coral cover bleached during 2010 bleaching event	8	48	Reef survey
Mean bleaching in 2016	% coral cover bleached during 2016 bleaching event	27	99	Reef survey
Chlorophyll-a in 2010	Maximum chlorophyll-*a* concentration (mg/m^3) observed at survey locations March–June of year	1.91	3.45	NASA MODIS-Aqua (https://oceandata.sci.gsfc.nasa.gov/MODIS-Aqua/Mapped/Monthly/4km/chlor_a/)
Chlorophyll-a in 2016	Maximum chlorophyll-*a* concentration (mg/m^3) observed at survey locations March–June of year	1.55	2.82	NASA MODIS-Aqua (https://oceandata.sci.gsfc.nasa.gov/MODIS-Aqua/Mapped/Monthly/4km/chlor_a/)
Degree Heating Weeks (DHW) 2010	Maximum degree heating week values at 4-km spatial resolution for the 2010 bleaching year	2.40	4.78	NOAA Coral Reef Watch (ftp://ftp.star.nesdis.noaa.gov/pub/sod/mecb/crw/data/5km/v3.1/nc/v1.0/annual)
Degree Heating Weeks (DHW) 2016	Maximum degree heating week values at 4-km spatial resolution for the 2016 bleaching year	6.44	9.27	NOAA Coral Reef Watch (ftp://ftp.star.nesdis.noaa.gov/pub/sod/mecb/crw/data/5km/v3.1/nc/v1.0/annual)
Pop10k	Estimated number of people living within a 10-km radius of the survey point in 2015 divided by the distance to coast squared	0.00	0.03	WorldPop http://www.worldpop.org.uk/data/summary/?doi=10.5258/SOTON/WP00532

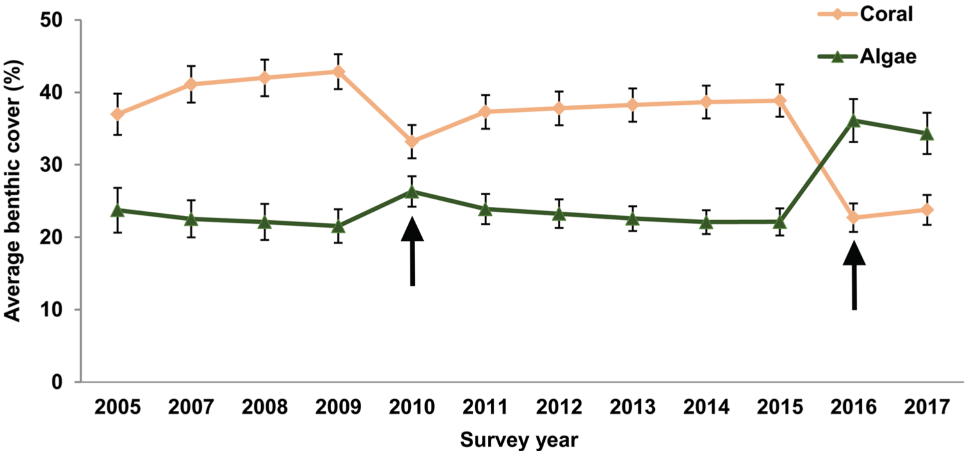

Fig. 2 Changes in average coral and algal cover on reefs subsequent to the 2010 and 2016 bleaching events (marked with arrows). Bleaching occurred in the summer of each year, and annual surveys were conducted in the following November of each year. The data show the long-term outcome from the bleaching events. Annual surveys were conducted on coral reefs at 21 islands within Gulf of Mannar. Data reflect mean and standard error of the mean (SEM) of average island values

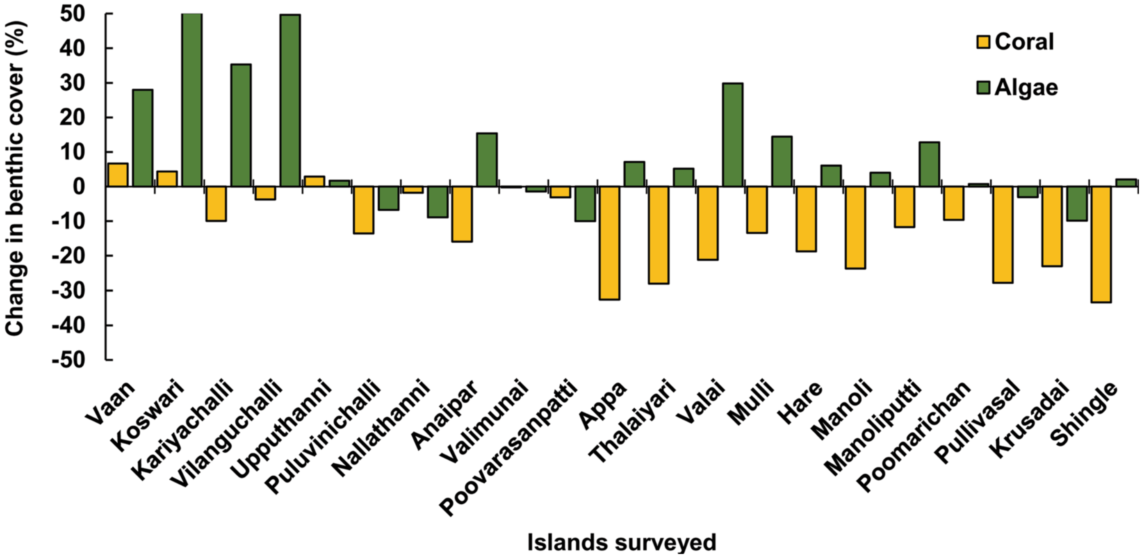

Fig. 3 Change in mean coral and algal cover between 2005 and 2017 for islands surveyed within Gulf of Mannar. These data reflect the island-specific outcome for benthic cover due to successive bleaching events. Islands are ordered from west to east

An indicator species analysis was used to identify morphotypes driving differences in the coral community composition across time periods and islands. An indicator species analysis identifies species assemblages that are characteristic of specific groups (i.e., in this study group refers to time period). This is done by combining species relative abundance and relative frequency of occurrence across all combinations of groups, where the index is maximized when a species is only found in a single group and is present in all samples associated with that group. The indicator species analysis was conducted using the multipatt function in the indicspecies package (De Caceres 2013) in *R*. Code for the ANOVAs, beta regression models, PERMANOVAs and indicator species analysis is available in the following github repository: https://github.com/jms5151/Coral_times_series_Gulf_of_Mannar.

Climate projections for Gulf of Mannar

Future bleaching frequency for the GoM was analyzed using global coral bleaching predictions from van Hooidonk et al. (2016). Downscaled (4-km resolution) climate model projections of predicted ocean surface warming over the coming decades were used to assess the 21 islands in the GoM. Ocean warming was predicted from an ensemble of Coupled Model Intercomparison Project Phase 5 models using emissions pathways RCP8.5 (high CO_2 emissions) and RCP4.5. Emissions scenario RCP4.5 represents lower

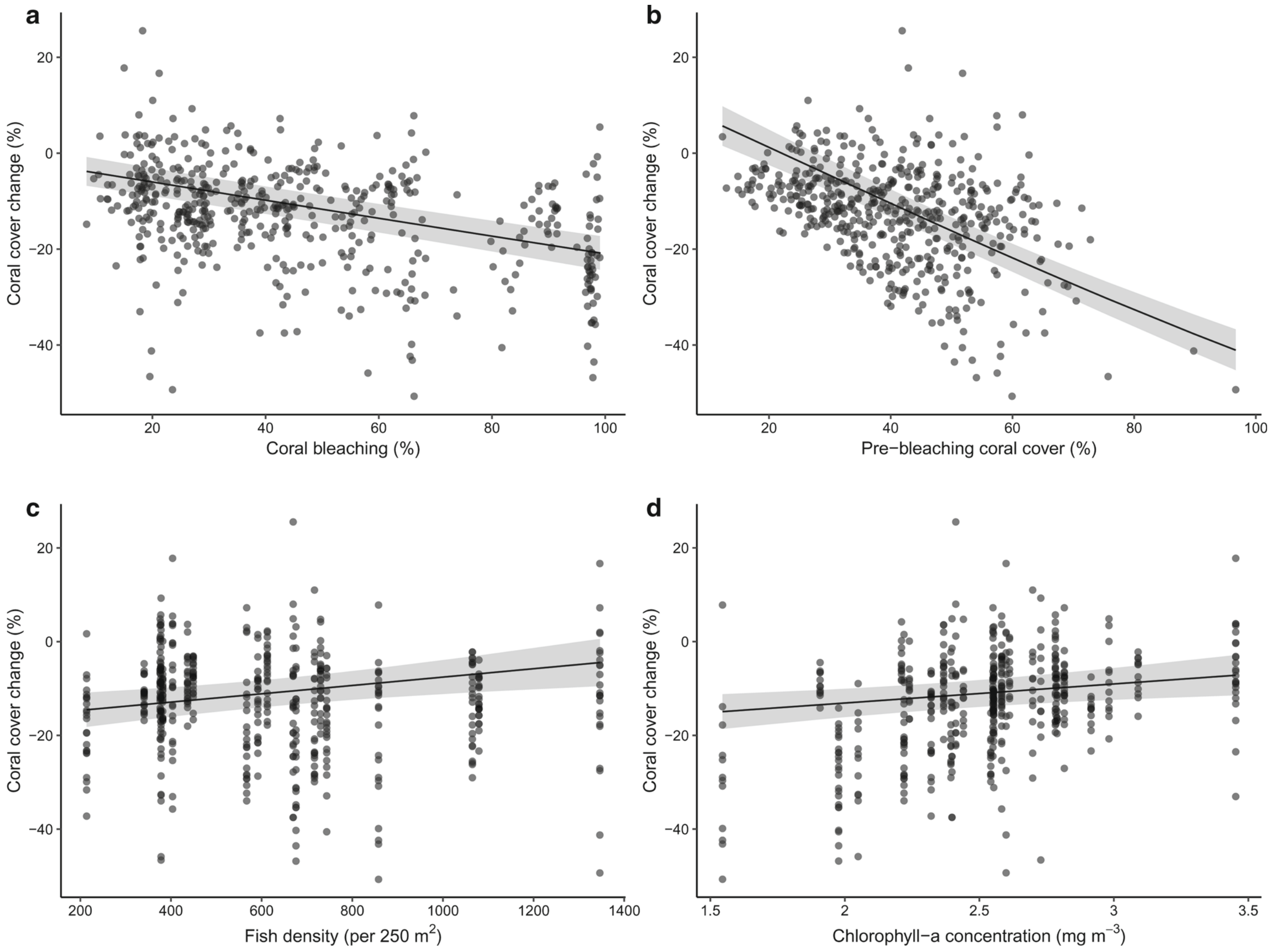

Fig. 4 Scatter plots showing modeled relationships (lines with shaded confidence intervals) between changes in coral cover subsequent to bleaching events in relation to different co-factors overlaid with survey data (points). The overlaid data points show the data used to create the model and how well they fit the model. The black line and shaded confidence interval (± 1.96 * SE) shows the marginal effect of the beta regression model for (**a**) coral bleaching, (**b**) pre-bleaching coral cover, (**c**) reef fish densities and (**d**) chlorophyll-a concentration. The marginal effects show the predicted change in coral cover associated with a change in an ecological covariate while accounting for all other factors included in the model (e.g., other ecological drivers and nested random effects)

emissions mid-century that will eventuate if pledges made following the 2015 Paris Climate Change Conference (COP21) become reality (van Hooidonk et al. 2016). From the van Hooidonk et al. (2016) data layers (available at: https://coralreefwatch.noaa.gov/climate/projections/downscaled_bleaching_4km/index.php), we calculated the decade in which reefs across the GoM are predicted to start bleaching twice per decade and 10 times per decade, referred to as Annual Severe Bleaching (ASB) (van Hooidonk et al. 2016). ASB translates to an exceedance of 8 Degree Heating Weeks (DHWs) projected to occur in each of the 10 yr per decade; 8 DHWs are higher than the mean optimum worldwide bleaching predictor of 6.1 DHWs (i.e., at 8 DHWs, thermal stress will be sufficiently great for bleaching to occur) (van Hooidonk and Huber 2009).

Results

Island-specific responses following successive bleaching

Between 2005 and 2017, average coral cover (all islands combined) declined by 36% and average algal cover increased by 45% with changes in percent cover occurring after each bleaching event and a greater magnitude of benthic response after the severe 2016 event (Fig. 2). Following the 2016 bleaching event, there was an average of 6.5% more coral cover loss ($t_{(20)} = -3.67$, $p < 0.01$) and an average increase of 9.2% more algal cover ($t_{(20)} = 3.16$, $p < 0.01$) than following the 2010 event. However, changes were not consistent among islands, ranging from − 34 to + 5% for coral cover and from − 0.3 to + 50% for algal cover (Fig. 3). There was a

Table 2 Coefficient values for model covariates

Covariate	Percent change in coral cover model	Percent change in algal cover model
Intercept	− 0.26	0.19
Initial cover (%)	− 0.15	− 0.13
Percent coral bleaching	− 0.10	
Maximum DHW		0.07
Fish density	0.05	
Human population		
Chlorophyll-a concentration	0.03	− 0.09
Pollution (impervious surface runoff)		0.13
R^2	0.53	0.51

Blank values indicate the covariate was not included in the model. Initial cover refers to the pre-bleaching percent of coral and algal cover for the coral and algal models, respectively. Human population refers to the human population size within 10 km of the nearest coastline, divided by the distance to the nearest coast squared to account for the hypothesized decreasing influence of humans with distance. Percent coral bleaching and maximum degree heating weeks were tested separately the models because they are collinear. The R^2 value was calculated based on in-sample model predictions

spatial gradient in coral mortality with islands in the eastern part of GoM (north GoM) losing more coral than islands in the western part (south GoM), but there was a disconnect between coral loss and subsequent increases in algal cover. The four western-most islands, Vaan, Koswari, Kariyachalli and Vilanguchalli, had minimal to no reductions in coral cover (+ 5%, + 2%, − 10%, − 5%), respectively, but the largest increases in algal cover (+ 31%, + 53% + 39%, + 51%), respectively (Fig. 3).

Changes in benthic cover following each bleaching event were significantly different among islands for coral ($F_{(20,\ 231)}$ = 26.21.854, $p < 0.001$) and algal cover ($F_{(20,\ 231)}$ = 31.84, $p < 0.001$). By examining the effect of each environmental covariate on benthic cover change, while accounting for all other variables in the model, we found these changes were associated with specific environmental drivers. Coral mortality was lower on islands with higher fish densities and higher chlorophyll-a levels, whereas mortality was greater on islands with more bleaching and higher than average coral cover prior to bleaching (Fig. 4). The optimal model explained 53% of the spatial variability in changes in coral cover among islands (Table 2). It must be noted that the total loss of coral cover is probably due to a combination of direct mortality caused by bleaching, as well as subsequent mortality suffered by corals, which have been stressed or suffered partial mortality, leaving them more vulnerable to algal overgrowth and diseases (West and Salm 2003). Algal cover following bleaching events increased on islands with more terrestrial runoff pollution, and higher thermal stress, with lower increases in algae found on islands with higher initial algal cover and higher chlorophyll-a levels (Fig. 5). The optimal model explained 51% of the spatial variability in algal cover change (Table 2).

Taxon-specific resilience to successive bleaching

Coral morphotypes differed in their response following successive bleaching through time. All coral morphotypes showed coral loss following the 2010 bleaching with cover stabilizing or even slightly increasing up until the 2016 bleaching. However, after the severe 2016 bleaching, most coral morphotypes had an even greater loss in coral cover, but there were two types, encrusting Acroporidae (ACE) and submassive corals (CS), which increased in absolute cover (Fig. 6). Hence, the proportional contribution of each morphotype to the overall coral community changed between 2005 and 2017 by either having a greater increase or decrease in cover relative to other morphotypes or by keeping cover constant, while other morphotypes changed in abundance (Fig. 7). The largest reduction among morphotypes was for digitate Acroporidae (ACD) which represented 17.1% of the community in 2005 and 5.1% of the community in 2017. In contrast, mounding corals (CM) had the largest increase from 31.1% of the community in 2005 to 42.8% in 2017. Ultimately, coral communities in GoM shifted following successive bleaching with some coral morphotypes becoming relative “winners” and others relative “losers” (Fig. 7).

Coral community shifts differ among islands

For all islands, the coral community shifted significantly following the severe 2016 bleaching event (Supplemental Table 2), but the degree of change differed among islands (Fig. 8). Some islands showed a more distinct shift in community structure after the 2016 bleaching event (orange polygons relative to the gray and blue polygons in Fig. 8) (e.g., Mulli), whereas others were less extreme

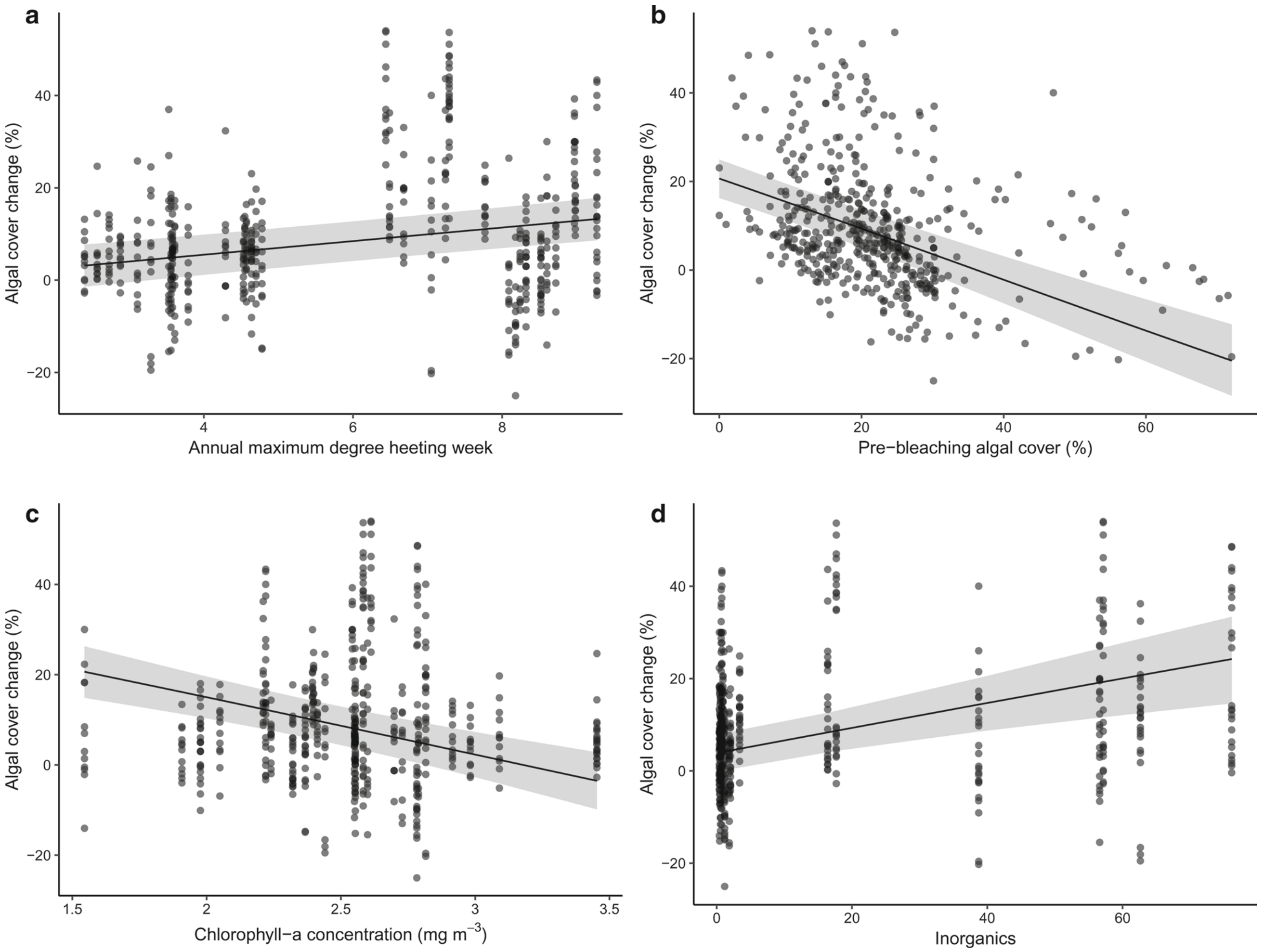

Fig. 5 Scatter plots showing significant modeled relationships (lines with shaded confidence intervals) between percent changes in algal cover subsequent to bleaching events in relation to different co-factors overlaid with survey data (points). The overlaid data points show the data used to create the model and how well they fit the model. The black line and shaded confidence interval (± 1.96 * SEM) shows the marginal effect of the beta regression model for (**a**) annual maximum degree heating weeks, (**b**) pre-bleaching algal cover, (**c**) chlorophyll-a concentration and (**d**) terrestrial runoff pollution. The marginal effects show the predicted change in algal cover associated with a change in an ecological covariate while accounting for all other factors in the model (e.g., other ecological drivers and nested random effects)

(e.g., Manoliputti). The coral types exerting the strongest influence on spatial variations in community structure also differed among islands especially following the 2016 bleaching (Fig. 9). However, some consistencies were evident such as encrusting Acroporidae (ACE) which increased in abundance at 16 of the 21 islands and foliose corals (CF) decreased in abundance at all but two islands (Fig. 9).

Climate projections for Gulf of Mannar

The downscaled climate projections showed that all islands across the GoM are predicted to experience annual severe bleaching (ASB) under a high emissions scenario (RCP8.5) prior to 2070 and bleaching twice per decade prior to 2060 (Fig. 10). However, the projections also highlighted local-scale (10 s km) spatial variability in the expected frequency of severe bleaching events (Fig. 10). For a high emissions scenario (RCP8.5), the onset of ASB showed a clear east to west gradient, with reefs toward the eastern end of the GoM (the islands of Shingle, Krusadai, Pullivasal and Poomarichan) all predicted to experience ASB before 2045. Moving west, the onset of ASB generally occurs later and by Nallathanni Island, the onset is pushed to 2061. Three islands toward the far western end (Koswari, Vilanguchalli and Kariyachalli) are not expected to experience ASB until 2067. The patterns for severe bleaching twice per decade generally show the same east to west gradient (Fig. 10). The reduced emissions scenario RCP4.5 has clear ameliorating effects and means the

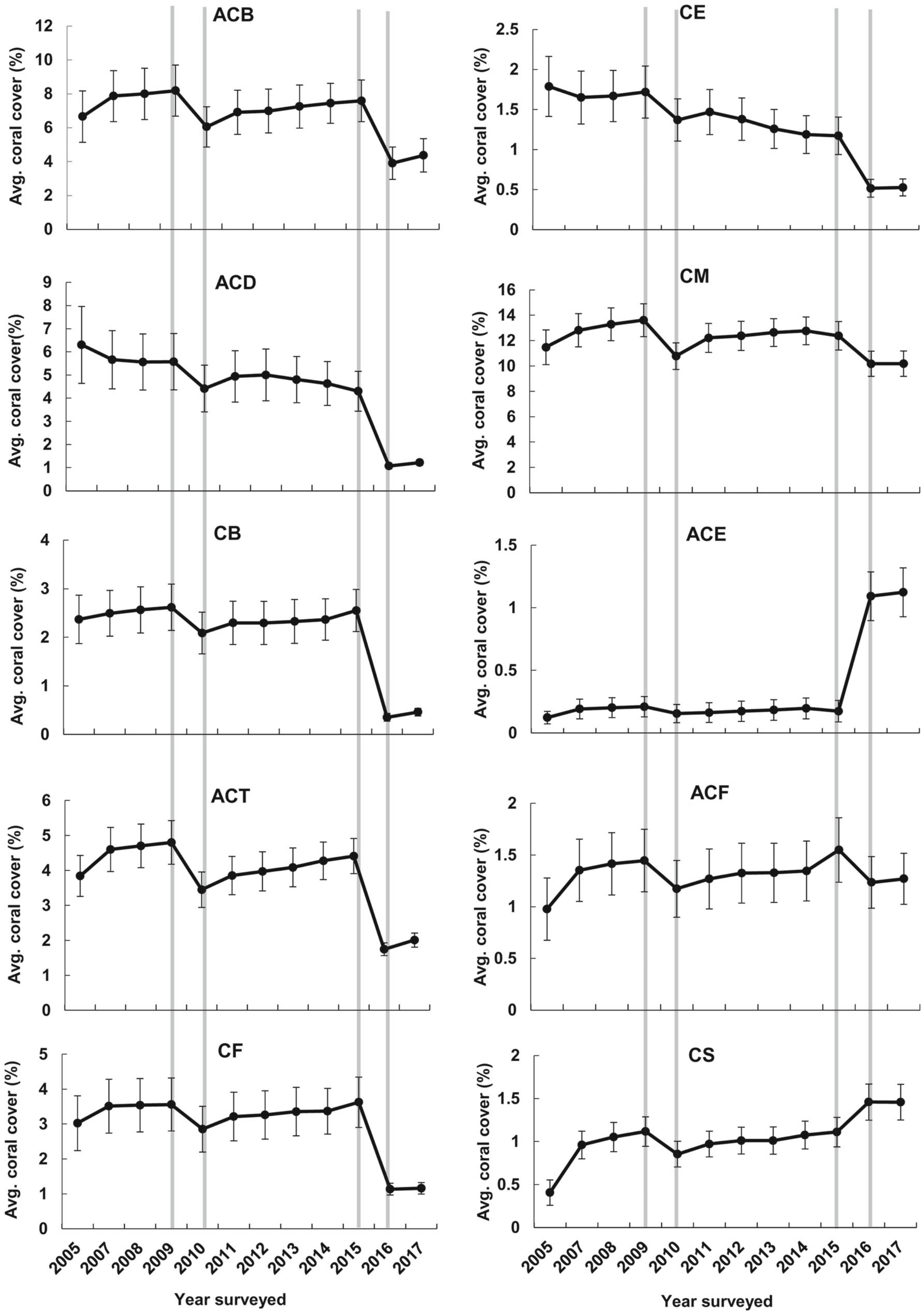

Fig. 6 Differences in cover among coral morphotypes through time. Twenty-one islands were surveyed each year. Note that the y-axis units differ among morphotypes. CS = submassive coral, ACE = encrusting Acroporidae, CB = branching coral, ACT = table Acroporidae, ACD = digitate Acroporidae, CE = encrusting coral, CF = foliose coral, ACB = branching Acroporidae, CM = massive coral. Gray vertical lines delineate the bleaching years

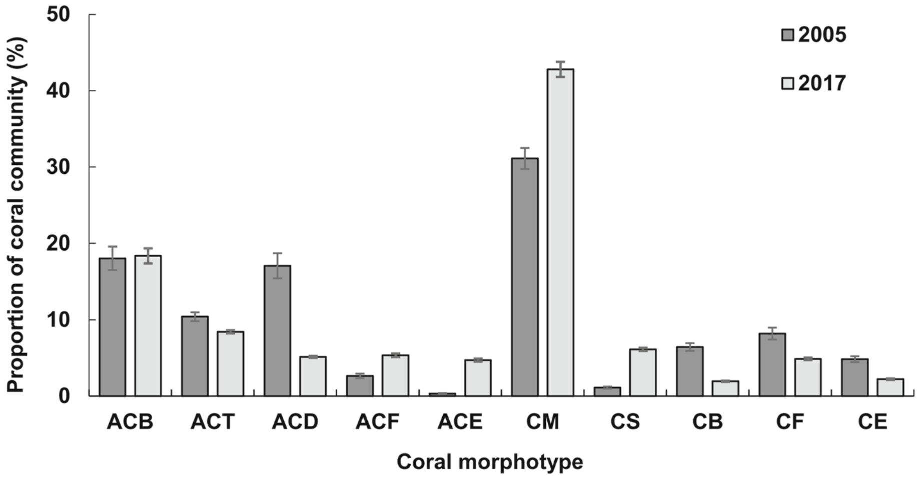

Fig. 7 Shifts in the proportional contribution of different coral morphotypes to overall coral communities in response to multiple bleaching events through time. Data show the proportion of the mean coral community represented by each morphotype in 2005 when surveys began and 2017 at the end of study. CS = submassive coral, ACE = encrusting Acroporidae, CB = branching coral, ACT = table Acroporidae, ACD = digitate Acroporidae, CE = encrusting coral, CF = foliose coral, ACB = branching Acroporidae, CM = massive coral

majority of islands would not experience ASB (or even severe bleaching twice per decade) between now and 2070. Exceptions to this pattern are the four islands toward the far eastern end of the GoM, which are still predicted to experience ASB prior to 2089 and severe bleaching twice per decade prior to 2070 under RCP4.5 (Fig. 10).

Discussion

Following successive bleaching events in the GoM in 2010 and 2016, reefs generally exhibited the classic paradigm of a simultaneous decrease in coral cover and increase in algal cover. However, there were contrasting responses among the 21 islands to the multiple bleaching events: Some islands lost significant coral cover over time, while others were able to maintain their cover. Thermal stress, expressed in degree heating weeks (DHW), experienced by GoM reefs was lower in 2010 (range 2.4–4.8) compared to 2016 (range 6.4–9.3), but varied among islands in both years, even though all islands had reefs at similar depths (< 5 m). As expected, maximum DHW and percent bleaching were significant factors explaining change in benthic cover among islands. However, other environmental variables also impacted coral bleaching, mortality or recovery. Lower coral mortality following bleaching events was found on islands with higher fish densities and chlorophyll-a levels. Reef fish play a critical role in maintaining ecosystem function and resilience of coral reef habitats (Graham et al. 2011). Grazing by herbivores generates reductions in algal cover that promotes recovery of corals (Mumby et al. 2006; Burkepile and Hay 2008) and maintaining fish diversity can mitigate threats from coral disease (Raymundo et al. 2009). Chlorophyll-a is a proxy for phytoplankton biomass and thus ocean surface primary productivity (Gove et al. 2016; Coelho et al. 2017). Historically, chlorophyll-a has been used as a proxy for water quality and eutrophication, and excess coastal nutrients can reduce coral cover and promote macroalgal cover, particularly in human-populated regions (Fabricius 2005; Wooldridge 2009). Reefs exposed to higher nutrients can also experience more severe bleaching (Woodridge 2009; Woolridge and Done 2009; Vega-Thurber et al. 2014). However, the relationship between a reef's response to thermal stress and "nutrients" is more nuanced than this (D'Angelo and Wiedenmann 2014; Williams et al. 2019). Chlorophyll-a is also strongly correlated with the abundance of zooplankton which represents a key food source for reef-building corals (Fox et al. 2018) that can promote their spatial dominance (Williams et al. 2015; Aston et al. 2019), their resilience to coral bleaching (Grottoli et al. 2006) and overall ecosystem function (Graham et al. 2018).

Higher concentrations of phytoplankton in the water might also offer some degree of protection to corals by limiting the amount of ultraviolet radiation (UVR) reaching colonies. UVR can directly damage corals (Lesser 1996; Anderson et al. 2001; Baruch et al. 2005) and is a synergistic factor increasing bleaching severity during thermal stress events (Torregiani and Lesser 2007; Ferrier-Pages et al. 2007). Factors that ameliorate the amount of UVR reaching coral colonies could reduce bleaching or other harmful effects of UVR exposure. For example, Iluz et al. (2008) found that bleaching-related colony mortality within warmer lagoon waters was lower than colonies on

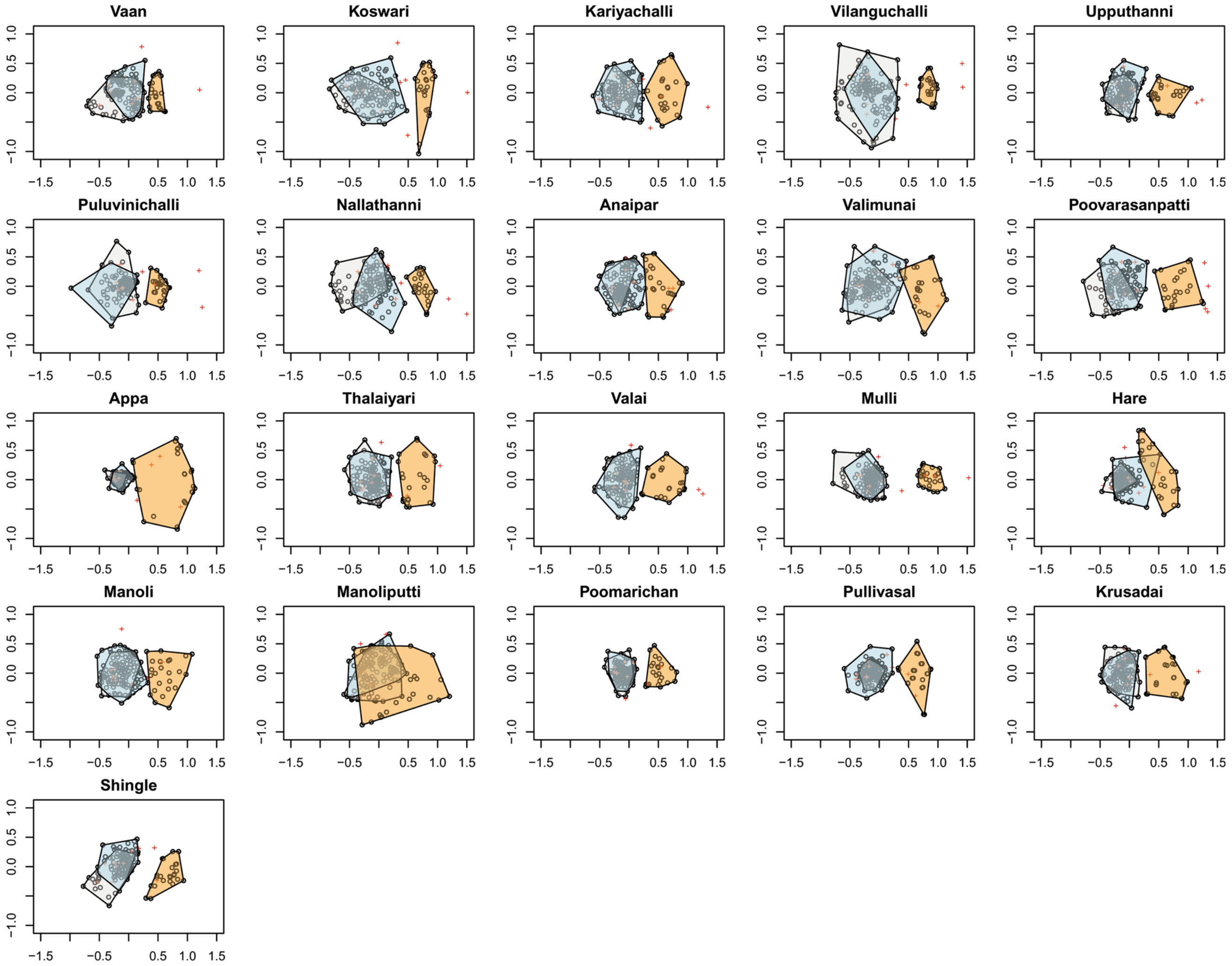

Fig. 8 NMDS plot where the points indicate mean coral community composition for every transect, site and year within an island based on a Bray–Curtis dissimilarity matrix. The convex hulls (polygons with shaded interiors) outline the multidimensional niche space of coral community composition in the three time blocks of interest: before the 2010 bleaching event (2005–2009, gray convex hulls), after the 2010 bleaching event and before the 2016 bleaching event (2010–2015, blue convex hulls) and after the 2016 bleaching event (2016–2017, orange convex hulls). Islands are ordered from west to east

surrounding slopes in cooler water. Lagoon waters had high turbidity due to seagrass leachate which attenuated UVR and protected corals from further bleaching.

Given the increasing gradient in coral mortality from west to east, it was surprising that increases in algal cover did not follow the same spatial pattern as coral mortality as has been found in other studies (e.g., coral loss is followed by subsequent increases in algal cover; Diaz-Pulido et al. 2009). Instead, the highest increases in algal cover occurred on the four islands in the west of GoM that had the lowest levels of coral loss (Vaan, Koswari, Kariyachalli and Vilanguchalli). These four islands maintained or lost little coral suggesting that increases in algae among islands were not necessarily linked to reductions in coral cover. Coral reef ecosystem recovery patterns occur against the background of local stressors. The four islands with the highest increases in algal cover were closest to the main population center of Tuticorin and a major sewer outfall for the region (Meiaraj and Jeyapriya 2019), and we found terrestrial runoff pollution as an important factor explaining spatial differences in increased algal cover among islands. Increasing levels of algae are already a problem for reefs in GoM (Jeevamani et al. 2013; Bharath et al. 2017) and may prove problematic for reef resilience, as algae can directly overgrow corals, trap sediment, prevent coral settlement and potentially harbor coral pathogens (Smith et al. 2006; Mumby et al. 2007; McClanahan et al. 2012; Vega-Thurber et al. 2012). Climate change-related coral mortality is unavoidable here, but local management actions can improve conditions allowing reefs to better recover. For example, algal growth could be minimized by reducing pollution or enhancing herbivore populations, which in turn

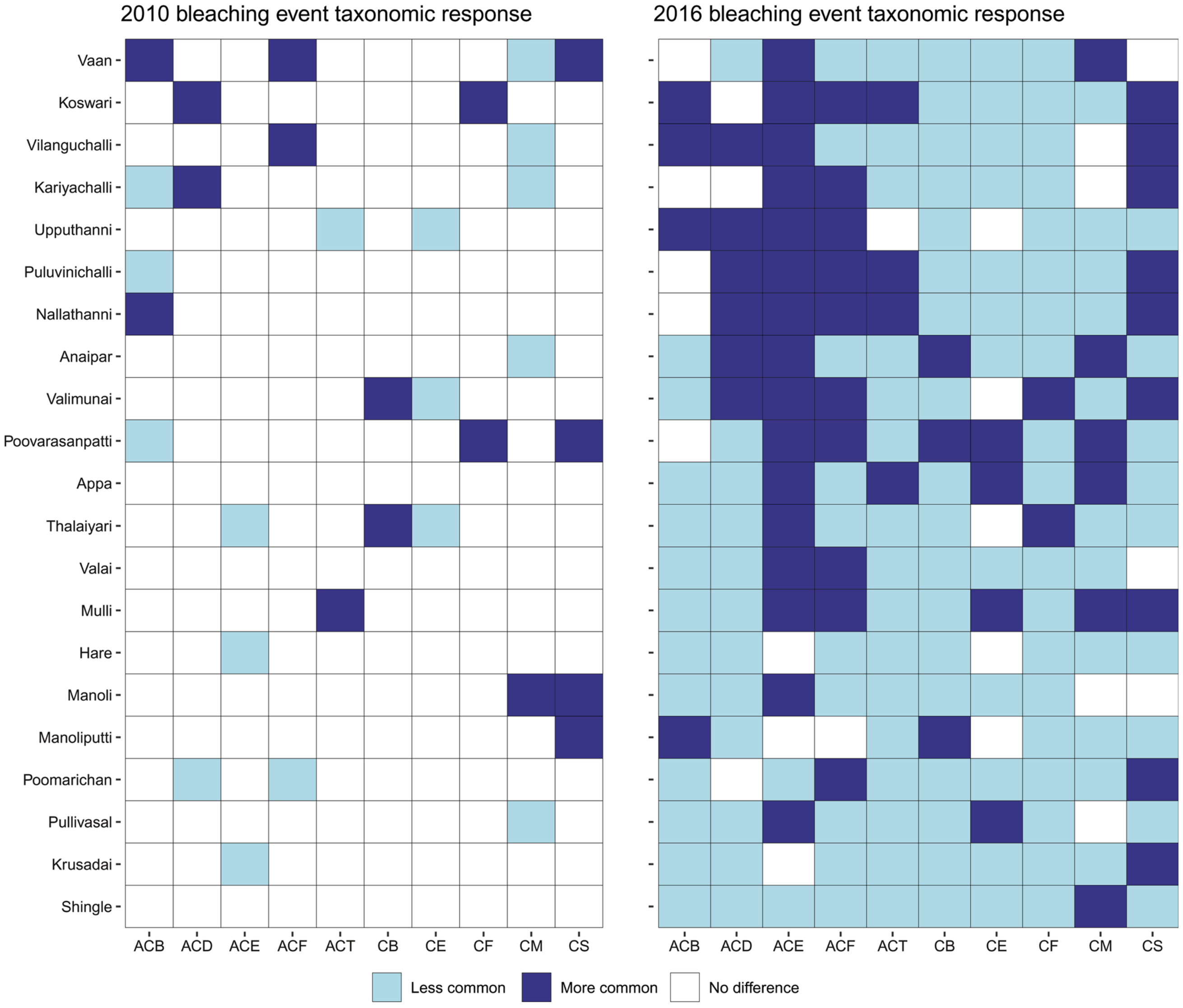

Fig. 9 Coral morphotypes influencing shifts in coral communities across islands following the 2010 and 2016 bleaching events. The left panel indicates morphotypes that significantly differed before and after the 2010 bleaching event (i.e., 2005–2009 compared with 2010–2015). The right panel indicates the morphotypes that significantly differed before and after the 2016 bleaching event (i.e., 2010–2015 compared with 2016–2017). Morphotypes were identified as less or more common based on indicator species analyses performed by island. Islands are ordered from west to east. CS = submassive coral, ACE = encrusting Acroporidae, CB = branching coral, ACT = table Acroporidae, ACD = digitate Acroporidae, CE = encrusting coral, CF = foliose coral, ACB = branching Acroporidae, CM = massive coral

will maximize the potential for coral regrowth and for the establishment of juvenile corals. This study identifies islands prone to coral mortality and/or algal overgrowth following bleaching events, providing direction for potential mitigation.

Variability in bleaching and mortality may have also arisen from local acclimation of corals to heat stress. Reefs within GoM undergo mild bleaching almost every summer that also varies among islands (Edward et al. 2012, 2018). This may have resulted in coral populations at some islands with a higher heat tolerance. Other studies have suggested that historical temperature variability affects corals' physiological tolerance under thermal stress (McClanahan et al. 2004; Oliver and Palumbi 2011) with surviving populations better adapted to withstanding further thermal stress events (Carilli et al. 2012; Palumbi et al. 2014). Conversely, Hughes et al. (2018) found no evidence for a protective effect of past bleaching (e.g., from acclimation or adaptation) along the Great Barrier Reef, Australia. They found that reefs with higher bleaching scores in 1998 or 2002 did not experience less severe bleaching in 2016.

Bleaching and subsequent mortality patterns can differ among coral genera (Edmunds 1994; Hoegh-Guldberg 1999; Marshall and Baird 2000) and growth forms (Loya

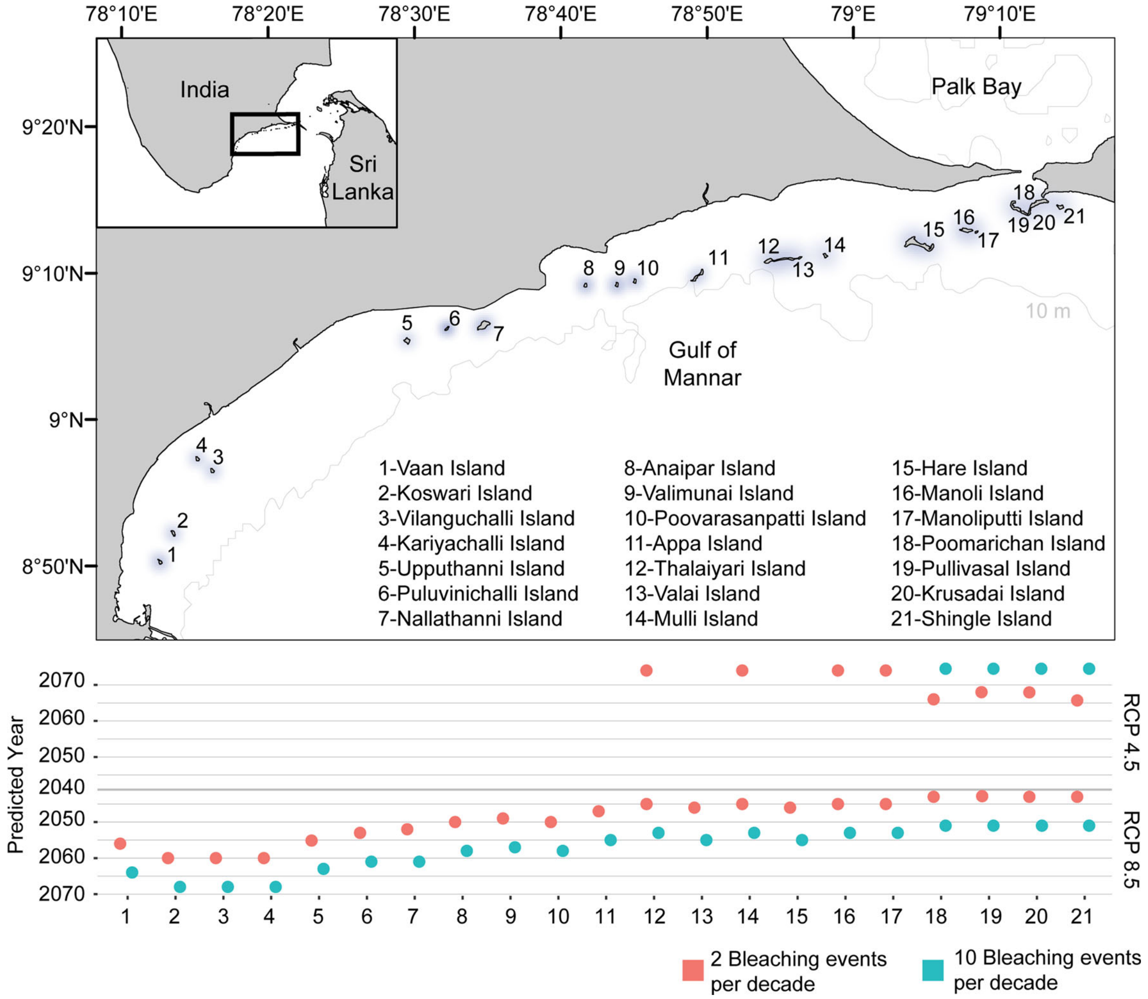

Fig. 10 The predicted frequency of future bleaching events differs across islands within Gulf of Mannar. Downscaled (4-km resolution) climate projections of predicted ocean surface warming (from van Hooidonk et al. 2016) across the Gulf of Mannar (GoM) in the coming decades and the subsequent year in which the onset of severe bleaching every 5 years (red) and annual severe bleaching (blue) conditions is predicted to occur under RCP8.5 (high emissions) and a reduced emissions scenario RCP4.5. Note the high local-scale (10 s km) variation seen in the projections across the GoM, with a clear gradient in the timing of bleaching onset from east to west for both RCP8.5 and RCP4.5. Note that for RCP4.5, several islands do not experience severe bleaching every 5 yrs (islands 1–11, 13, 15) or annual severe bleaching (islands 1–17) within the 83-yr modeled period (2006–2089)

et al. 2001; Iluz et al. 2008) and have been attributed to numerous coral host factors (Loya et al. 2001; Brown et al. 2002; Grottelli et al. 2006; Visram and Douglas 2007; Baird et al. 2009) and/or the density or types of *Symbiodinium* residing within the coral host (Bhagooli and Yakovleva 2004; Sampayo et al. 2008; Howells et al. 2012; Cunning and Baker 2013). Similarly, within GoM, coral morphotypes varied in bleaching severity and mortality following each bleaching event, resulting in a change in community structure. As some coral species died after the bleaching events, the more bleaching-tolerant species increased in relative abundance in the community. Massive corals had the largest relative increase in the community likely because this morphotype has coral taxa known to be stress tolerant such as *Porites, Dipsastraea* and *Favites* (Stafford-Smith 1993; Riegl 1999; Burt et al. 2013). Digitate Acroporidae had the largest losses as these coral morphotypes contained the more thermally sensitive coral taxa, *Acropora* and *Montipora* (Marshall and Baird 2000; Kayanne et al. 2002; McClanahan et al. 2004). It is important to note that for the current study, most coral morphotypes included multiple coral genera, which can differ in bleaching susceptibility regardless of their growth form (Baird and Marshall 2002; McClanahan et al. 2004). As the coral communities in GoM shift through time, so may the risk to reefs from different threats. As an example, *Montipora* spp. are becoming a larger component of the GoM coral community and *Montipora* spp. are known to be susceptible to outbreaks of tissue loss disease in GoM (Raj et al. 2016). In contrast, foliose corals (CF) which are important in providing habitat for fish and other marine species decreased in abundance. As coral communities continue to change through time, it would be advantageous for managers to re-evaluate local threats to GoM reefs.

A key issue for the potential resilience of all reefs is the frequency of disturbance events and whether sufficient time for recovery of mature coral assemblages can occur. When reefs bleach annually, reef recovery becomes highly unlikely (van Hooidonk et al. 2016). Islands across GoM are not predicted to experience annual severe bleaching (ASB) under a high emissions scenario (RCP8.5) until after 2040. Reefs are then expected to have a distinct east to west gradient in timing of ASB with a 22-yr gap predicted between the onset of ASB on reefs in east versus west GoM. This predicted spatial pattern of thermal stress among islands is consistent with what was found during the 2010 and 2016 bleaching events and provides some indication of how GoM reefs might respond to repetitive bleaching events in the future. The western reefs will become increasingly important, constituting spatial refugia (van Hooidonk et al. 2013) for corals which is critical for reef recovery via larval transport (Hock et al. 2017). The predictions of ASB for GoM are greatly improved under the reduced emissions scenario (RCP4.5) with only the four most vulnerable northern islands predicted to experience ASB and then not until after 2070. This is potentially good news for GoM and provides strong motivation for global policy makers to take steps to limit carbon emissions to mitigate global climate change. There is limited knowledge on the resilience of GoM reefs, and this study identifies the coral morphotypes and reefs that are most likely to recover or decline from successive bleaching events.

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Declarations

Conflict of interest On behalf of all authors, the corresponding author states that there is no conflict of interest.

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