Seabird nutrient subsidies alter patterns of algal abundance and fish biomass on coral reefs following a bleaching event

Running head: Seabird nutrients and coral bleaching

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Keywords: allochthonous input, climate change, coral bleaching, disturbance, invasive species, rats, reef fish, resilience

Paper type: Primary Research

Abstract

Cross-ecosystem nutrient subsidies play a key role in the structure and dynamics of recipient communities, but human activities are disrupting these links. Because nutrient subsidies may also enhance community stability, the effects of losing these inputs may be exacerbated in the face of increasing climate-related disturbances. Nutrients from seabirds nesting on oceanic islands enhance the productivity and functioning of adjacent coral reefs, but it is unknown whether these subsidies affect the response of coral reefs to mass bleaching events or whether the benefits of these nutrients persist following bleaching. To answer these questions, we surveyed benthic organisms and fishes around islands with seabirds and nearby islands without seabirds due to the presence of invasive rats. Surveys were conducted in the Chagos Archipelago, Indian Ocean immediately before the 2015-2016 mass bleaching event and in 2018, two years following the bleaching event. Regardless of the presence of seabirds, relative coral cover declined by 32%. However, there was a post-bleaching shift in benthic community structure around islands with seabirds, that did not occur around islands with invasive rats, characterised by increases in two types of calcareous algae (crustose coralline algae [CCA] and *Halimeda* spp.). All feeding groups of fishes had higher starting biomass around islands with seabirds, but only herbivores and piscivores sustained this higher biomass following the bleaching event. Coral-dependent fishes experienced the greatest losses, such that following bleaching there was no longer a difference in biomass of corallivores and planktivores between island types. Even though seabird nutrients did not enhance community-wide resistance to bleaching, they may still promote recovery of these reefs through their positive influence on CCA and herbivorous fishes. More broadly, the maintenance of nutrient subsidies, via strategies including eradication of invasive predators, may be important in shaping the response of ecological communities to global climate change.

Introduction

Nutrient subsidies play a key role in many ecosystems by enhancing the productivity, biomass, and diversity of recipient communities, as well as by altering population and community dynamics (Loreau & Holt, 2004; Polis, Anderson, & Holt, 1997). In both terrestrial and aquatic environments, such inputs are often provided by mobile predators that translocate consumed nutrients across different habitats (Lundberg & Moberg, 2003; Schmitz, Hawlena, & Trussell, 2010). However, human activities have greatly reduced the populations of many large animals, and as a result have diminished their capacity to move nutrients by 94% (Buckner, Hernández, & Samhouri, 2018; Doughty et al., 2016; Estes et al., 2011; Roman et al. 2014; Young, McCauley, Galetti, & Dirzo, 2016). Because allochthonous nutrients can act to stabilize recipient food webs and communities (McCann, Rasmussen, & Umbanhowar, 2005; Rooney, McCann, Gellner, & Moore, 2006), the consequences of losing these nutrient links may become exacerbated in the face of increasing human-caused environmental disturbance. Despite these theoretical predictions regarding the link between nutrient subsidies and stability, there is a lack of empirical studies testing how nutrient subsidies, and their disruption, influence the response of ecosystems to disturbances (Bernhardt & Leslie, 2013).

Seabirds are crucial providers of nitrogen and phosphorous to many ecosystems worldwide (Otero, Peña-Lastra, Pérez-Alberti, Ferreira, & Huerta-Diaz, 2018). By feeding in the open ocean and depositing guano on islands and coastal environments, seabirds stimulate primary production, with cascading influences throughout terrestrial (W. B. Anderson & Polis, 1999; Onuf, Teal, & Valiela, 1977; Polis & Hurd, 1996; Sánchez-Piñero & Polis, 2000), coastal (Bosman & Hockey, 1986; Vizzini, Signa, & Mazzola, 2016; Wootton, 1991), and marine (McCauley et al., 2012) food webs. However, the introduction of rats and other mammalian predators has decimated seabird populations, especially on islands (Jones et al., 2008; Towns, Atkinson, & Daugherty, 2006). On islands where seabirds have been lost to invasive predators, the abundance, biomass, and diversity of terrestrial primary producers and consumers are reduced (Croll, Maron, Estes, Danner, & Byrd, 2005; Fukami et al., 2006; Maron et al., 2006; Towns et al., 2009), leading to smaller and less complex food-webs (Thoresen et al., 2017). Recent research uncovered that invasive rats also disrupt the flow of nutrients from seabird colonies to adjacent coral-reef ecosystems. As a result, there is lower biomass of reef fishes at all trophic levels and reduced rates of key ecosystem functions (herbivory and bioerosion) around islands with invasive rats compared to nearby islands with large populations of seabirds (Graham et al., 2018).

The loss of nutrient subsidies may interact with global threats to coral reefs, which are some of the most vulnerable ecosystems to climate change (Barlow et al., 2018; Hoegh-Guldberg et al., 2007). Mass coral bleaching events caused by warm water anomalies are now occurring over global scales and with greater frequency, leaving little time for recovery between warming episodes (Hughes et al., 2018, 2017). Although anthropogenic nutrient inputs often increase the susceptibility of corals to bleaching (D’Angelo & Wiedenmann, 2014; Vega Thurber et al., 2014; Wiedenmann et al., 2013; Wooldridge, 2009; Wooldridge & Done, 2009), there is increasing evidence that corals respond differently to human-derived versus naturally-derived nutrient inputs (Shantz & Burkepile, 2014). Indeed, biological nutrient inputs may foster resistance to bleaching by providing nitrogen and phosphorous in optimal ratios for maintaining the mutualism between coral hosts and their algal symbionts (Allgeier, Layman, Mumby, & Rosemond, 2014; Ezzat, Maguer, Grover, & Ferrier-Pagès, 2016; Meyer & Schultz, 1985; Wiedenmann et al., 2013). However, there have been no field studies to date testing whether natural nutrient subsidies influence the response of corals to major warming events.

Beyond their effects on corals, nutrient subsidies may influence the response of entire reef communities to bleaching through a range of indirect processes. For example, nutrients from fishes promote the expansion of macroalgae when coral cover is reduced by stressors such as bleaching (Burkepile et al., 2013). Thus, allochthonous nutrients from seabirds could trigger regime shifts from coral-dominated to algae-dominated communities following bleaching events. Alternatively, the higher biomass of herbivores and rates of herbivory around islands with seabirds (Graham et al., 2018) may prevent such shifts to macroalgae from occurring (Graham, Jennings, MacNeil, Mouillot, & Wilson, 2015; Hughes et al., 2007). The complex interplay among nutrients, corals, and reef-associated processes necessitates an empirical examination of how nutrient subsidies influence the response of coral reefs to climatic disturbances.

To test whether seabirds affect the response of adjacent coral reefs to a major disturbance, we compared the benthic and fish communities before and after a mass bleaching event around islands with seabirds versus islands with invasive rats. We predicted that if nutrient inputs from seabirds promote resistance of coral reefs to bleaching, then the benthic and fish communities will remain more similar to the pre-disturbance state around islands with seabirds compared to those without. In addition, we tested whether the response to bleaching and seabird nutrients varied across different groups of benthic organisms and fishes. We hypothesized that corals would experience greater declines around islands that lack natural nutrient subsidies due to the presence of invasive rats. Consequently, fishes most dependent on corals may also experience greater declines around islands with rats compared to islands with seabirds.

Materials and methods

This study was conducted in the remote Chagos Archipelago (British Indian Ocean Territory), located in the central Indian Ocean (5° 50′ S, 72° 00′ E). The northern atolls have been uninhabited for approximately 40 years and are relatively free from local human stressors with the exception of invasive rats, which still inhabit some islands following their introduction several hundred years ago (Sheppard et al., 2012). On islands where rats were never introduced there are large populations of seabirds, including ten internationally-recognized Important Bird Areas (Carr, 2011). The region's coral reefs remain some of the most pristine in the world and are characterized by exceptionally high biomass of fishes, including ecologically-important herbivores (Graham & McClanahan, 2013; Graham et al., 2017; MacNeil et al., 2015; Sheppard et al., 2012). However, coral bleaching events have affected reefs in the Chagos Archipelago several times in the past few decades. Shallow reefs in this area recovered from the 1998 worldwide bleaching event (Sheppard, Harris, & Sheppard, 2008), but suffered widespread coral mortality again as part of the 2015-2016 mass bleaching event that affected reefs throughout the Indian and Pacific Oceans (Hughes et al., 2018; Sheppard et al., 2017). Because of these characteristics, the Chagos Archipelago is an ideal system in which to study the interactive effects of seabird nutrient subsidies and global climate change with few confounding influences.

In March-April 2015, baseline benthic and fish surveys were conducted on reefs around 12 islands across three atolls of the Chagos Archipelago (Figure 1). Half of the islands had large seabird populations (mean density = 1242 birds/ha), while the other half had invasive rats and thus few seabirds (mean density = 1.6 birds/ha) (Graham et al., 2018). These differences in seabird densities translated to 251 times greater nitrogen loads on islands with seabirds compared to those without (190 kg/ha/year versus 0.8 kg/ha/year), some of which was then assimilated by benthic organisms and fishes on adjacent coral reefs (Graham et al., 2018). Islands were otherwise similar in terms of size, location, and environment. In April 2015, sea surface temperatures in the Chagos Archipelago began exceeding the predicted bleaching threshold (degree heating weeks [DHW] > 4°C-weeks), and remained above this threshold for 247 days between April 2015 and July 2016 (Liu, Strong, Skirving, & Arzayus, 2006; NOAA Coral Reef Watch, 2018). In response to these warmer water temperatures, corals across the region began exhibiting signs of bleaching in April-May 2015, with widespread mortality beginning in 2016 and extending into 2017 (Sheppard et al., 2017). In May 2018, we replicated the surveys around ten of the same islands (five with seabirds and five with rats). Rough weather and logistical constraints precluded surveying the remaining two islands, both of which were located on the Great Chagos Bank. Although other environmental changes could have occurred between 2015 and 2018, we assume that the bleaching event was the main driver of any differences between the two surveys. This assumption is reasonable given the aforementioned temperature anomalies and evidence of coral bleaching in the Chagos Archipelago during this time (Sheppard et al. 2017), as well as the isolation of the study region from other stressors (e.g., fishing) (Graham & McClanahan, 2013; Sheppard et al., 2012).

Benthic organisms and fishes were surveyed along the reef crest on the lagoonal side of each island. The location of the site was marked by GPS in 2015 and the same sites surveyed in 2018. Four replicate 30-m transects spaced 10 m apart were surveyed, which were between 110 and 325 m from shore and at a depth of 1 to 3 m. These distances from shore are all within the range at which both benthic organisms and fishes assimilate nutrients from seabirds (Graham et al., 2018). Structural complexity of the reef along each transect was estimated by the same observer (N.A.J.G.) using a standard scale ranging from 1 (no relief) to 6 (exceptionally complex relief) (Polunin & Roberts, 1993; Wilson, Graham, & Polunin, 2007). Using line (2015) and point-intercept transects (2018), which give highly correlated estimates of benthic cover (Facon et al., 2016; Leujak & Ormond, 2007), we quantified percent cover of the following benthic groups: hard coral, soft coral, crustose coralline algae (CCA), macroalgae, sponges, pavement, rubble, sand, and other (e.g., bryozoans). Hard coral and macroalgae were further identified to genus. Because macroalgae consisted of >99% *Halimeda* spp., we refer to this category as '*Halimeda*' for the remainder of the manuscript, and include the other genera of macroalgae (*Asparagopsis*, *Caulerpa*, and *Lobophora*) in the 'other' category. We recorded the species and size (total length, visually estimated to the nearest cm) of all diurnal, non-cryptic fishes. Large and mobile fishes were counted in a 5-m wide belt during a first pass along the transect, and damselfishes (Pomacentridae) were counted in a 2-m wide belt during a second pass along the same transect. The same observer (N.A.J.G.) surveyed the fish communities in both 2015 and 2018. Fish counts were converted to biomass using published length-weight relationships (Froese & Pauly, 2018). Based on their main diet and feeding behaviour, we assigned fishes to one of the following feeding groups: herbivore, corallivore, invertivore, planktivore, piscivore, or mixed-diet (Graham et al., 2018).

To test for differences in the response of coral-reef benthic and fish communities around islands with seabirds versus islands with rats to the 2015-2016 bleaching event, we used a combination of univariate and multivariate statistics. To test whether the presence of seabirds influenced the response of various reef organisms to bleaching, we ran separate linear mixed effects models for each benthic and fish group. The response variables were percent cover for benthic groups and biomass for fish groups. Because coral bleaching can reduce structural complexity and structural complexity has a strong influence on coral-reef fishes (Graham & Nash, 2013; Graham et al., 2006), we also ran a model with structural complexity as the response variable. Because sand, soft coral, sponges, and other benthos comprised extremely low percentages of the benthos regardless of treatment or year (mean ≤ 2%), we did not conduct univariate analyses for these categories. All responses were log-transformed when necessary to meet the assumptions of normality and homogeneity. Island nested within atoll were included as random effects to account for non-independence among transects conducted at the same islands through time and the spatial distribution of islands across three atolls (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). To determine whether the presence of seabirds influenced the response of each group to bleaching, we tested for an interaction between treatment (seabird versus rat) and year (pre- versus post-bleaching) using likelihood ratio tests (Zuur et al., 2009). When the interaction was not statistically significant ($p > 0.05$), we tested for significance of the main effects of treatment and year. To compare the relative influence of the random versus fixed effects, we also conducted likelihood ratio tests of the full models against null models containing only the random effects (Supplemental Table 1). Models for fish biomass included structural complexity and hard coral cover as co-variates, to test the variables of interest while accounting for other factors that can have a large influence on coral-reef fishes.

To examine differences in overall benthic and fish community structure, we used non-metric multidimensional scaling (NMDS) on Bray-Curtis similarity matrices for proportional cover (benthos) and log-transformed abundance (fish) (Kruskal, 1964; McCune & Grace, 2002). We conducted PERMANOVAs to test for an effect of treatment (seabird versus rat), year (pre- versus post-bleaching), and the interaction between treatment*year on benthic and fish communities around each island with atoll as a blocking factor (M. J. Anderson & Walsh, 2013). To determine which organisms drove dissimilarities between communities that were significantly different from each other, we then used SIMPER analysis (Clarke, 1993). Finally, we tested for differences in multivariate dispersion, a measure of community stress response (Halford & Caley, 2009; Warwick & Clarke, 1993), among the benthic and fish communities using the PERMDISP2 procedure (M. J. Anderson, 2005; M. J. Anderson, Ellingsen, & McArdle, 2006). All statistical analyses were conducted in R version 3.3.3 with associated packages vegan, lme4, blme, jtools, and MuMIn (Barton, 2018; Bates, Maechler, Bolker, & Walker, 2015; Chung, Rabe-Hesketh, Dorie, Gelman, & Liu, 2013; Long, 2018;

Oksanen et al., 2018; R Core Team, 2017;), and we provided our data and code in an open source repository (https://github.com/cbenkwitt/seabirds-bleaching).

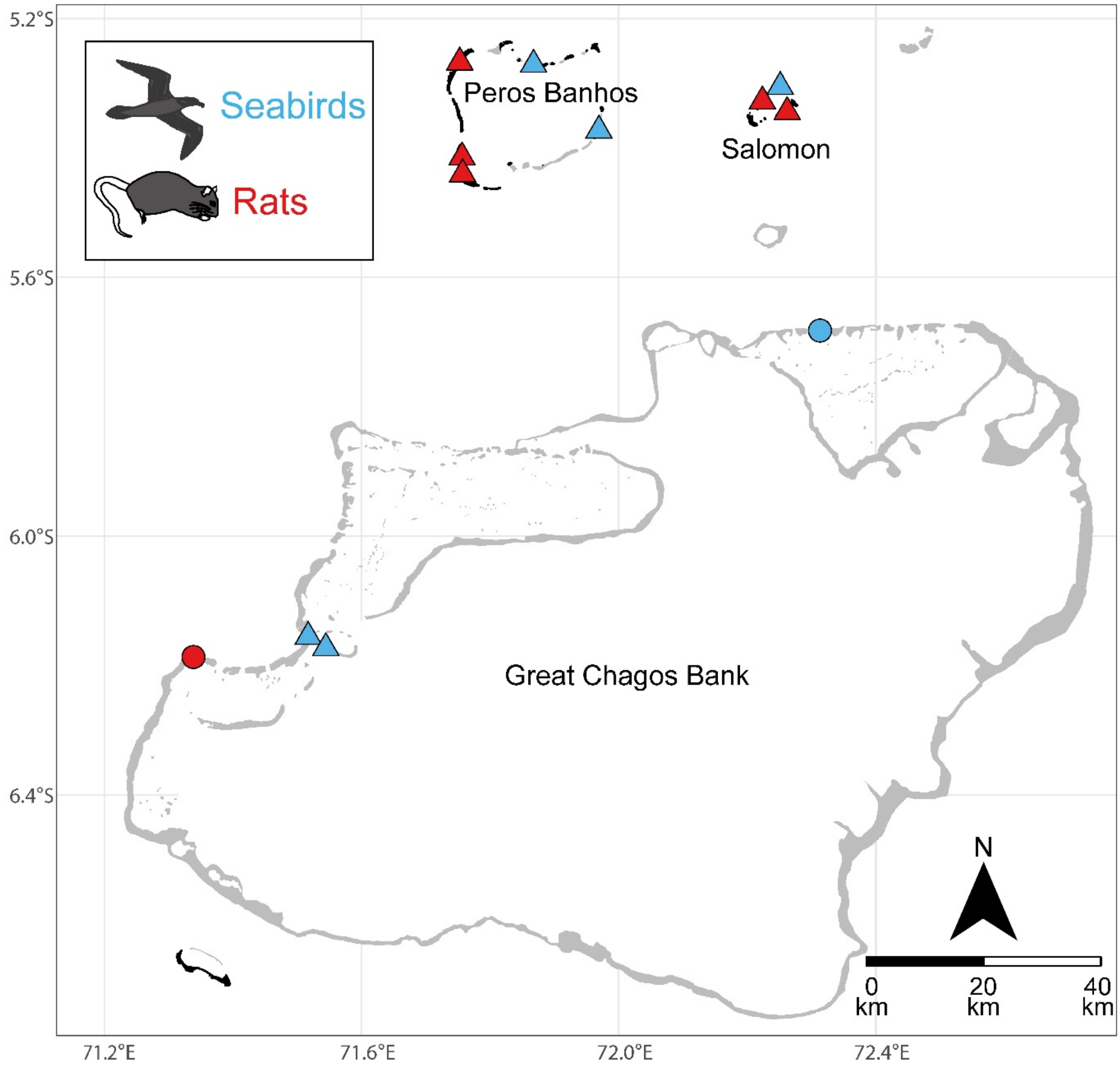

Figure 1. Map of the study region within the Chagos Archipelago, Indian Ocean. Points show the location of surveyed reefs adjacent to islands with seabirds (blue) and islands that lack seabirds due to the presence of invasive rats (red). Triangles represent sites that were surveyed in 2015 and 2018, circles represent sites that were only surveyed in 2015 due to logistical constraints.

Results

Benthos

Absolute coral cover declined by an estimated 10.6% (95% CI: 6.3 to 14.8) following the 2016 bleaching event, regardless of the presence of seabirds (Figure 2; Figure X; year χ^2= 21.20, p <0.001; treatment χ^2= 1.12, p = 0.29; treatment*year χ^2 = 0.14, p = 0.71). This reduction was primarily driven by a decline in *Acropora*, which was the most abundant genus of coral in both years (mean 47.9% and 38.7% of coral cover was *Acropora* in 2015 and 2018, respectively). Absolute percent cover of *Acropora* declined by an estimated 7.8% (95% CI: 4.6 to 11.0), the magnitude of which was unaffected by the presence of seabirds (year χ^2= 20.24, p <0.001; treatment χ^2= 1.83, p = 0.18; treatment*year χ^2 = 0.74, p = 0.39). Atoll was a more important driver than rats in the response of corals to bleaching. In the most-enclosed lagoon with the highest initial coral cover (Salomon Atoll), there was a mean reduction in pre-bleaching coral cover of only 6%, compared to 42% and 72% in the other atolls (Great Chagos Bank and Peros Banhos, respectively) (Supplemental Figure S3). These results are corroborated by the community analysis, as hard coral was the main cause of differences between Salomon Atoll and the other two atolls (SIMPER, 33% and 36% dissimilarity explained, p < 0.002).

In contrast to coral, the response of both crustose calcifying algae and *Halimeda* to the bleaching event depended on seabirds (Figure 2; Figure X; CCA treatment*year χ^2 = 6.0, p = 0.01; *Halimeda* treatment*year χ^2= 29.6, p < 0.001). Percent cover of CCA increased by an estimated 5.4 times around islands with seabirds (95% CI 3.6 to 8.1), whereas around islands with rats it increased by only 2.6 times (95% CI 1.7 to 3.9). Likewise, *Halimeda* increased by an estimated 4.2 times around islands with seabirds (95% CI: 2.9 to 6.1), but remained consistently low around islands with rats (estimated decrease by a factor of 0.87, 95% CI: 0.60 to 1.27). Three out of the five islands with seabirds underwent a shift such that

Halimeda comprised 27.9-43.7% of the benthos post-bleaching. In contrast, post-bleaching cover of *Halimeda* remained below 1.3% near the other two islands with seabirds and every island with invasive rats. Instead, pavement continued to dominate the substrate around islands with rats even after bleaching, remaining at an estimated 50.6% cover (95% CI: 41.5 to 59.6) compared to just 21.3% cover around islands with seabirds (95% CI: 12.2 to 30.3) (treatment*year χ^2= 15.4, $p < 0.001$). Percent cover of rubble did not vary by treatment or year (treatment*year χ^2= 0.003, p = 0.96; treatment χ^2= 0.36, p = 0.55; year χ^2= 2.1, p = 0.14). Structural complexity was similarly unaffected by rat-invasion status or bleaching, with estimated mean rugosity scores between 2.2 and 2.5 for all treatment-year combinations (95% CI: 2015 seabirds: 1.6 to 2.8, 2015 rats: 2.0 to 3.1, 2018 seabirds: 1.6 to 2.8, 2018 rats: 1.7 to 2.8; treatment*year χ^2= 2.18, p = 0.14; treatment χ^2= 0.95, p = 0.33; year χ^2= 1.2, p = 0.27).

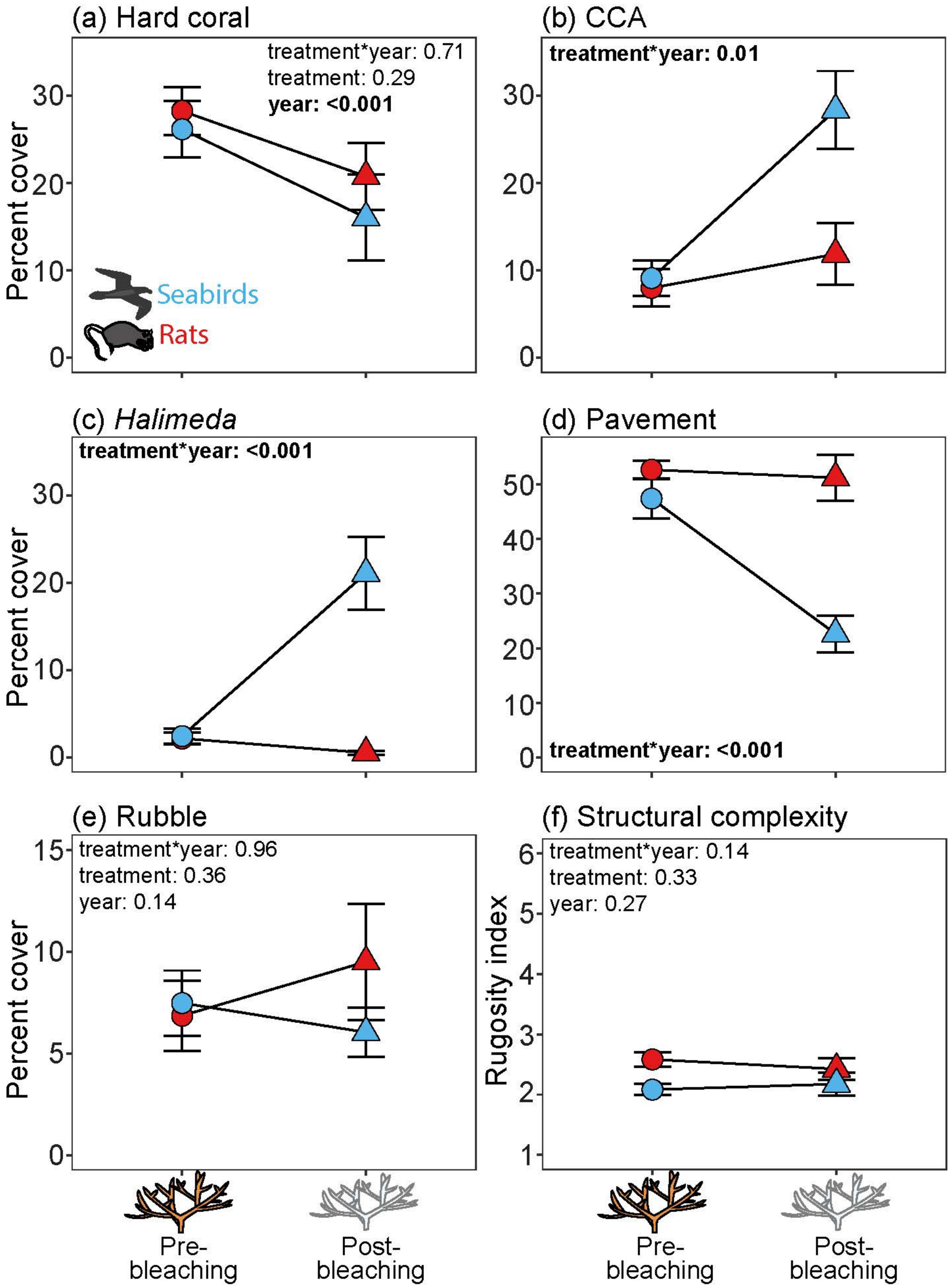

Figure 2. Percent cover (mean +/- SEM) of benthic organisms (a-e) and structural complexity (f) around islands with seabirds (red symbols) versus islands with invasive rats (blue symbols), in 2015 (pre-bleaching) and in 2018 (post-bleaching). Text shows p-values from linear mixed effects models testing for an effect of treatment (seabirds versus rats) and year (pre- versus post-bleaching), with significant p-values ($p < 0.05$) in bold. Note differences in y-axis scales.

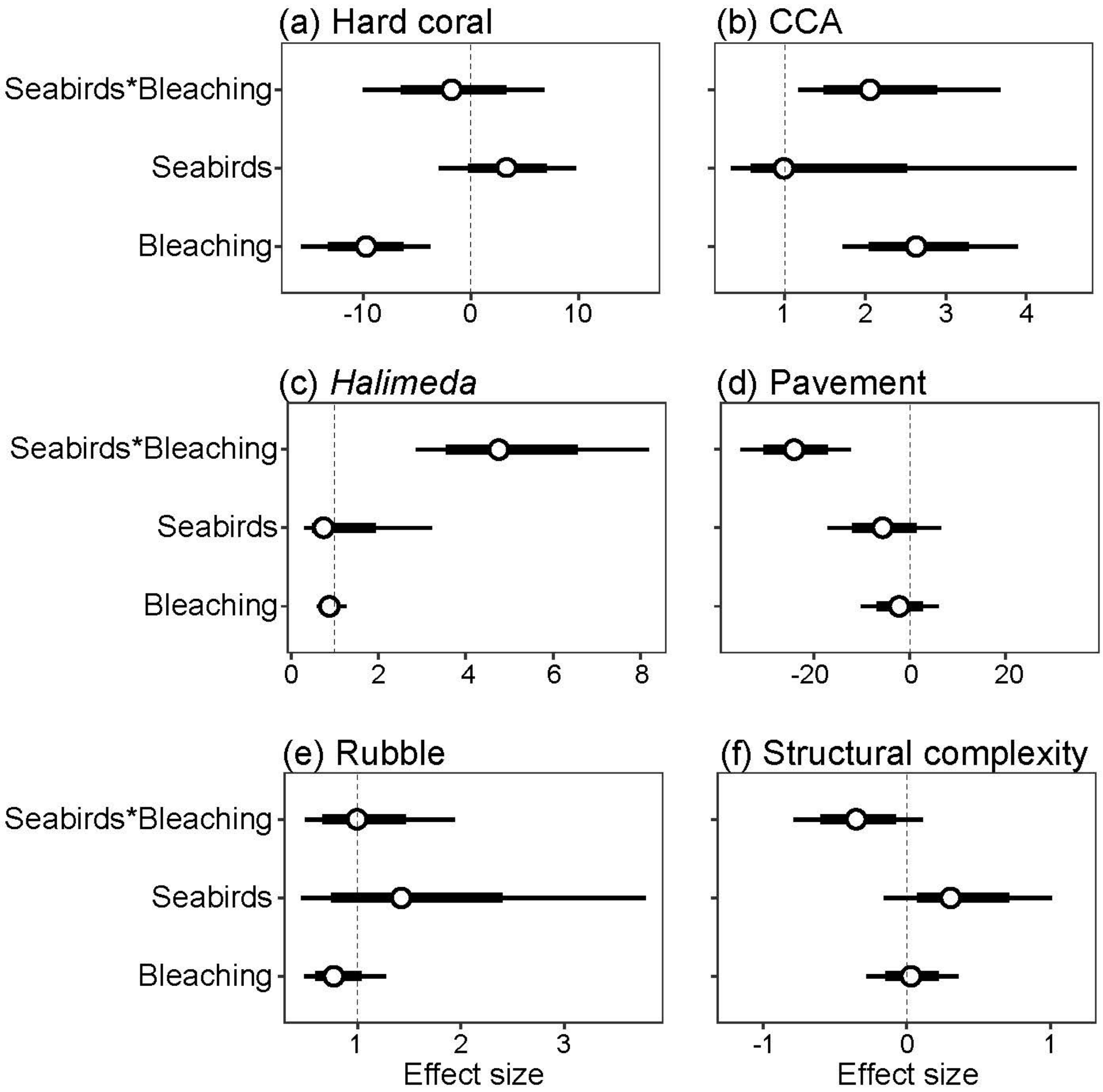

Figure X. Estimated effects from linear mixed-effects models for seabird presence, a major coral bleaching event, and their interaction on benthic organisms (a-e) and structural complexity (f). Thick bars represent 75% confidence intervals, thin bars represent 95% confidence intervals. Dashed lines indicate no estimated effect (0 for models with un-transformed responses, 1 for models with log-transformed responses).

Fish

The presence of seabirds did not modify the response of any feeding group to the bleaching event, but seabirds did have a positive effect on all groups across both years, the extent of this effect variable among feeding groups (Figure 3 and Figure Y). However, there were differences in the response of fishes to bleaching depending on feeding group (Figure 4). Biomass of herbivores and piscivores was constant through time, remaining higher around islands with seabirds than islands with rats by an estimated 222.2 (95% CI: 28.9 to 415.4) and 75.5 (95% CI: 17.8 to 133.3) kg/ha, respectively (Herbivore: treatment $\chi^2 = 5.25$, $p = 0.02$; year $\chi^2 = 0.01$, $p = 0.92$; treatment*year $\chi^2 = 0.04$, $p = 0.84$; Piscivore: treatment $\chi^2 = 7.14$, $p < 0.01$; year $\chi^2 = 0.02$, $p = 0.88$; treatment*year $\chi^2 = 0.12$, $p = 0.73$). Mixed-diet feeders were similarly unaffected by the bleaching event and exhibited a trend towards higher biomass by an estimated 1.5 times around islands with seabirds in both years, although this pattern was not statistically significant (95% CI: 0.58 to 3.9; treatment*year $\chi^2 = 0.14$, $p = 0.71$, treatment $\chi^2 = 1.92$, $p = 0.17$, year $\chi^2 = 1.6$, $p = 0.20$). In contrast, planktivores and corallivores declined by an estimated 45.0% (95% CI: 10.0 to 66.5) and 38.4 % (95% CI: 8.3 to 58.6%), respectively, following the bleaching event (Planktivore: year $\chi^2 = 6.3$, $p = 0.01$; treatment: $\chi^2 = 2.85$, $p = 0.09$; treatment*year: $\chi^2 = 0.09$, $p = 0.76$; Corallivore: year $\chi^2 = 4.1$, $p = 0.04$; treatment $\chi^2 = 1.9$, $p = 0.17$; treatment*year $\chi^2 = 0.79$, $p = 0.37$). Invertivores also appeared to decrease through time, especially around islands with seabirds, although this pattern was not statistically significant (treatment*year $\chi^2 = 0.41$, $p = 0.52$, treatment $\chi^2 = 1.74$, $p = 0.19$, year $\chi^2 < 0.01$, $p = 0.98$).

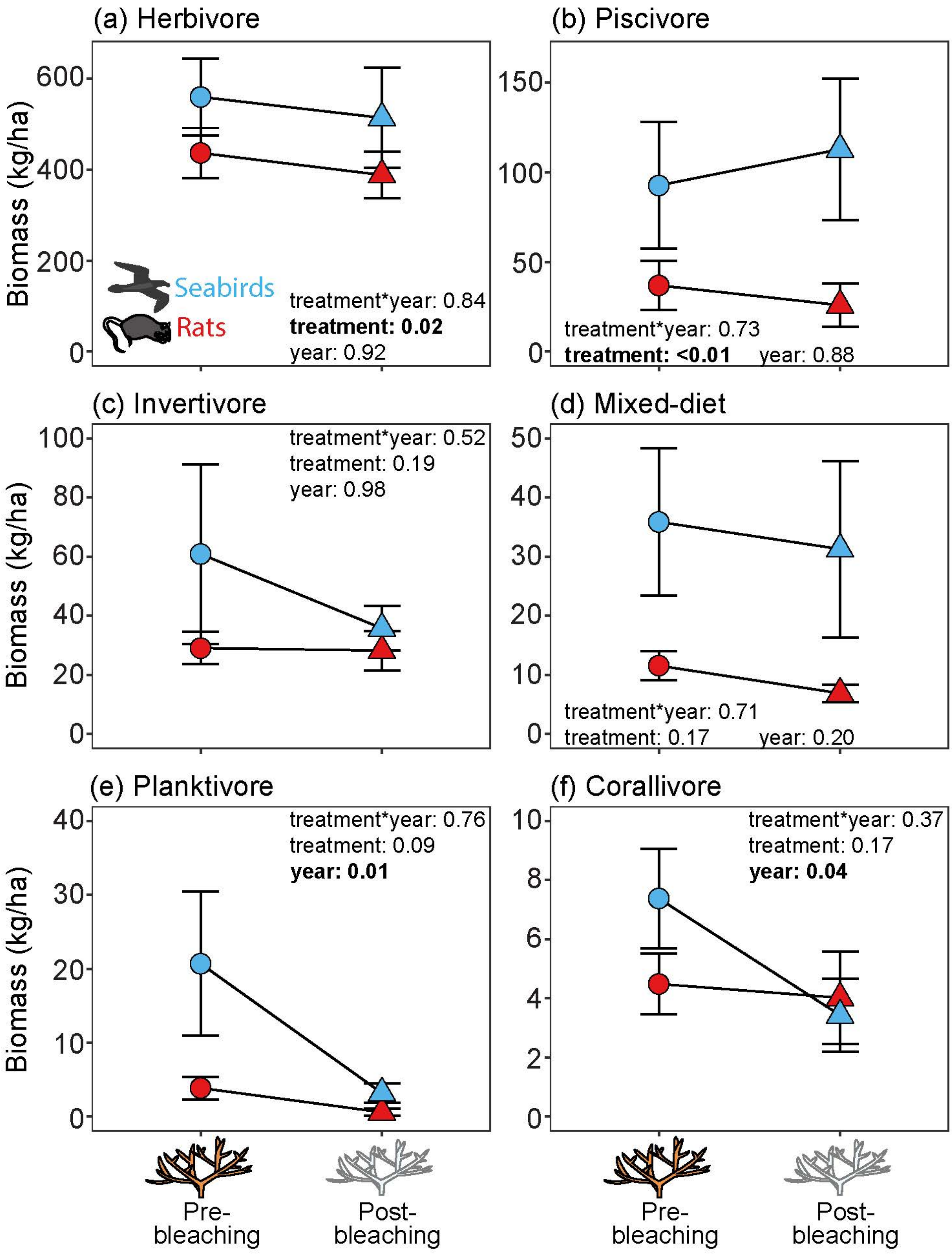

Figure 3. Biomass (mean +/- SEM) of coral-reef fishes around islands with seabirds (blue symbols) versus islands with rats (red symbols), in 2015 (pre-bleaching) and in 2018 (post-bleaching). Text shows p-values from linear mixed effects models testing for an effect of treatment (seabirds versus rats) and year (pre- versus post-bleaching), with significant p-values ($p < 0.05$) in bold. Note differences in y-axis scales.

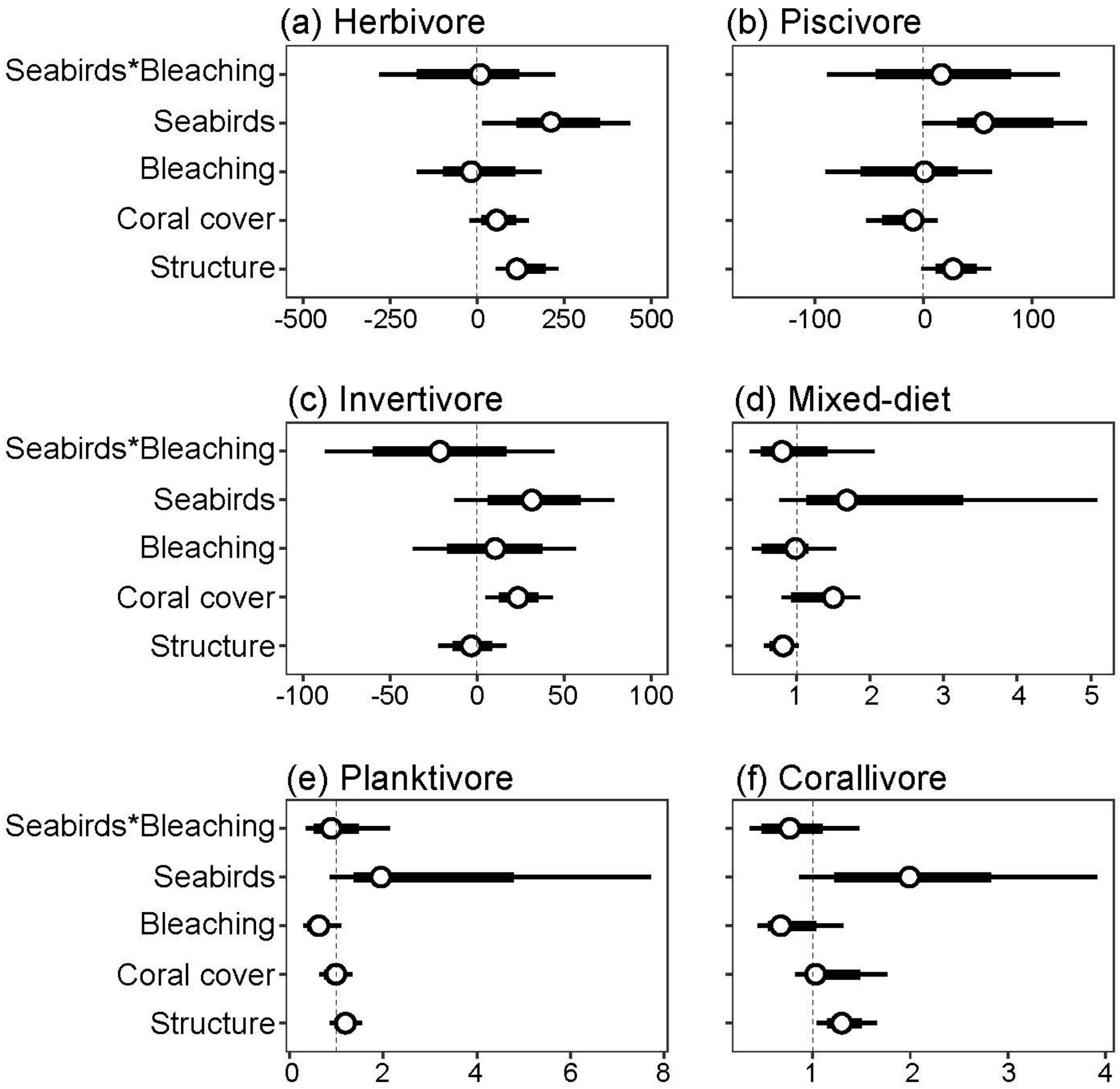

Figure Y. Estimated effects from linear mixed-effects models for seabird presence, a major coral bleaching event, and their interaction on feeding groups of fishes (a-f). Also included in the models are coral cover and structure, both of which are known to influence fish biomass. Thick bars represent 75% confidence intervals, thin bars represent 95% confidence intervals. Dashed line indicates no estimated effect (0 for models with un-transformed responses, 1 for models with log-transformed responses).

Community response

A major post-bleaching shift in benthic community structure occurred around islands with seabirds but not around islands with invasive rats (Figure 2; Supplemental Figure S1; PERMANOVA, treatment*year F = 2.15, p = 0.03). Pavement, CCA, and *Halimeda* were the primary drivers of differences between islands with rats compared to those with seabirds after the coral bleaching event, with these three groups explaining 26.8%, 19.8%, and 18.8% of the dissimilarity between island types, respectively (SIMPER, p = 0.005, 0.062, 0.007, respectively). Before the bleaching event, benthic communities around islands with seabirds and those with rats were similarly dispersed, with mean dispersion parameters of 0.21 (95% CI: 0.14 to 0.28) and 0.16 (95% CI: 0.11 to 0.21), respectively (Figure 2; Supplemental Figure S2; PERMDISP, pairwise p = 0.29). After the bleaching event, however, mean dispersion of benthic communities around islands with seabirds increased to 0.33 (95% CI: 0.25 to 0.42), which was higher than all other communities (PERMDISP, all pairwise $p \leq 0.048$). Conversely, mean community dispersion around islands with rats was 0.22 (95% CI: 0.17 to 0.28) following bleaching, which was not different than the pre-bleaching dispersion (PERMDISP, pairwise p = 0.11).

In contrast to benthic community structure, fish community structure changed following the bleaching event around islands with seabirds and islands with rats (Figure 2; PERMANOVA, year F = 3.12, p = 0.02; treatment F = 1.01, p = 0.50; treatment*year F = 1.61, p = 0.16). Planktivores and corallivores were the main drivers of community dissimilarity before versus after the bleaching (SIMPER, planktivores 32.4% of variance explained, $p < 0.01$; corallivores 26.3% of variance explained, p = 0.03). Dispersion of fish communities around islands with seabirds and islands with rats were similar within both 2015 and 2018 (Figure 2; Supplemental Figure S2; 2015 mean [95% CI]: 0.04 [0.03 to 0.06], 0.07 [0.03 to 0.11], respectively; 2018: 0.13 [0.09 to 0.17], 0.12 [0.07 to 0.18], respectively; PERMDISP, 2015 pairwise p = 0.34, 2018 pairwise p = 0.83). However, the magnitude of change differed between the island types, as there was an increase in the dispersion of fish communities around islands with seabirds (PERMDISP, pairwise $p < 0.01$), but no difference in pre- versus post-bleaching dispersion around islands with invasive rats (PERMDISP, pairwise $p = 0.15$).

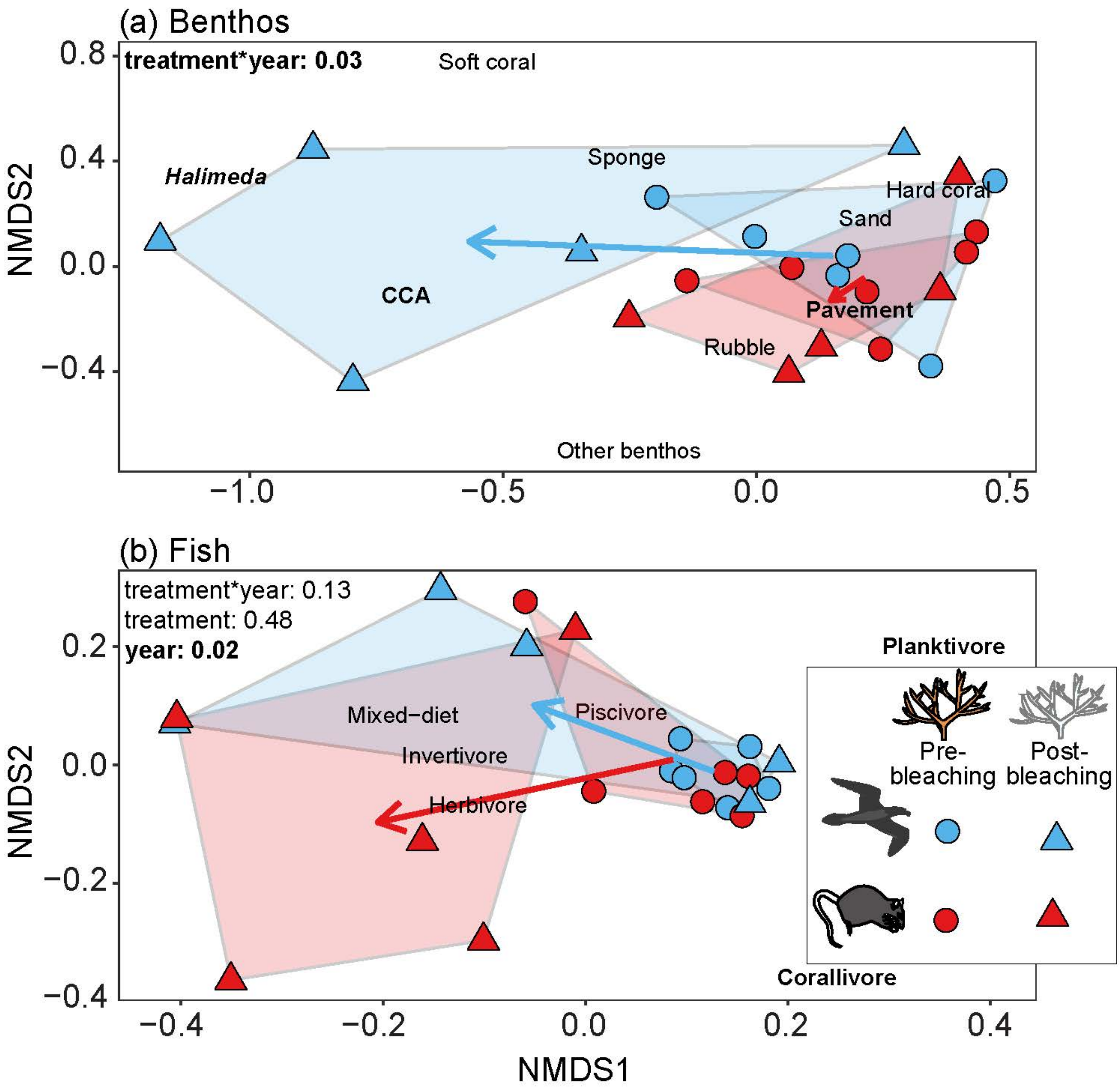

Figure 4. Non-metric multidimensional scaling (NMDS) plot of (a) benthic and (b) fish community structure as a function of whether the reef was adjacent to an island with seabirds (blue) or invasive rats (red) and whether the survey was conducted pre-bleaching (circles) or post-bleaching (triangles). Each point represents a reef in species space, with the distances among points approximating dissimilarities among communities. Shaded areas represent minimum convex hull polygons and arrows show movement of centroid before versus after bleaching. Grouping labels in bold were the primary drivers of dissimilarities among communities based on SIMPER analysis. Text shows p-values from PERMANOVAs testing for an effect of treatment (seabirds versus rats) and year (pre- versus post-bleaching) on the multivariate communities, with significant p-values ($p < 0.05$) in bold. NMDS stress = 0.11 (a) and 0.08 (b).

Discussion

Understanding local factors that alter the response of coral reefs to global climate change is necessary to effectively manage reefs in the Anthropocene (Ban, Graham, & Connolly, 2014; Knowlton & Jackson, 2008). Here, we provide the first evidence that the response of some groups of benthic organisms and fishes to a mass bleaching event depends on natural nutrient subsidies. Although nutrients from seabirds increased reef-fish production and functioning before the bleaching event (Graham et al., 2018), they did not confer community-wide resistance to bleaching in terms of reduced changes in community structure or reduced community stress response. Instead, there were greater changes in the structure and dispersion of benthic communities on coral reefs adjacent to islands with seabirds than those without seabirds due to the presence of invasive rats. Furthermore, the change in fish community structure following bleaching, as well as the dispersion of fish communities within each year, were similar between islands with seabirds and those with rats. However, the responses of coral-reef organisms to seabird nutrients following the bleaching event varied widely by functional group, which in turn may influence the pace of recovery and future community dynamics.

Contrary to our prediction, hard corals declined regardless of whether they were adjacent to islands with seabirds or islands with invasive rats. Corals assimilate nutrients from seabirds nesting on adjacent islands (Lorrain et al., 2017), and the ratio of nitrogen to phosphorous in seawater adjacent to seabird colonies is within the range considered optimal for coral growth (N:P ratio of 13-32 in seawater compared to optimal ratio of 11-29) (Allgeier et al. 2014; Savage, 2019). Therefore, we expected the large inputs of nitrogen and phosphorous from seabird guano to enhance resistance of corals to bleaching (D’Angelo & Wiedenmann, 2014; Graham et al., 2018). However, we observed no evidence to corroborate this hypothesis. One possible explanation is that nutrients confer resistance to bleaching during less extreme temperature anomalies, but the magnitude and duration of this warming event negated any differences in resistance between corals adjacent to islands with seabirds compared to those without seabirds. Indeed, sea surface temperatures during the 2015-2016 bleaching event were the warmest ever recorded (Hughes et al., 2018), and these extreme temperatures persisted for more than half of the year at some sites in the Chagos Archipelago (NOAA Coral Reef Watch, 2018; Sheppard et al., 2017).

Instead of depending on proximity to seabird colonies, the response of corals to bleaching varied by atoll. The lagoon that maintained most of its live coral is the smallest and most-enclosed, and therefore experiences the least water flow, warmest temperatures, and highest temperature fluctuations under normal conditions (Pugh & Rayner, 1981; Sheppard et al., 2017). Other field studies have similarly demonstrated reduced susceptibility to bleaching for corals in sheltered areas with low water flow (Hoogenboom et al., 2017; McClanahan, Ateweberhan, Muhando, Maina, & Mohammed, 2007; Pineda et al., 2013; Sheppard, 1999). One likely explanation for this pattern is that corals from small lagoons are adapted to warmer water and/or greater temperature variability, and thus are better able to withstand temperature stress (Donner, 2011; Guest et al., 2012; Middlebrook, Hoegh-Guldberg, & Leggat, 2008; Oliver & Palumbi, 2011; Safaie et al., 2018; Schoepf, Stat, Falter, & McCulloch, 2015).

Although seabirds did not affect coral cover, they appeared to fuel an increase in two types of calcifying algae (*Halimeda* and crustose coralline algae) that was not observed around islands with invasive rats, where pavement continued to dominate the benthos following bleaching. The high abundance of calcifying algae around islands with seabirds is noteworthy because the overall cover of calcifying organisms, rather than coral cover alone, is an important component of reef accretion budgets (Perry, Spencer, & Kench, 2008) and an indicator of ecological function (McClanahan et al., 2011). Increases in algal cover following bleaching-induced coral mortality are common, but the newly-established algal communities are typically dominated by turfs and fleshy macroalgae rather than the calcareous algal groups observed here (Birrell, McCook, Willis, & Diaz-Pulido, 2008). Still, the increase in CCA around islands with seabirds is consistent with the relative dominance model of Littler & Littler (1984), which posits that CCA will dominate benthic communities when both nutrient levels and herbivory rates are high. Most support for the relative dominance model comes from small-scale experiments using anthropogenic nutrients (Burkepile & Hay, 2009; Smith, Hunter, & Smith, 2010; Smith, Smith, & Hunter, 2001), or fish-derived nutrients which increase cover of CCA at the scale of individual coral heads (Shantz, Ladd, Schrack, & Burkepile, 2015). This study provides, to our knowledge, the first evidence that naturally-derived nutrients may also enhance CCA at the scale of entire reefs following a disturbance.

The concurrent increase in *Halimeda* around islands with seabirds, however, is inconsistent with the relative dominance model. *Halimeda* exhibits increased growth and calcification rates with nutrient enrichment (Lapointe, Littler, & Littler, 1987; Littler, Littler, & Lapointe, 1988; Smith, Smith, Vroom, Beach, & Miller, 2004; Teichberg, Fricke, & Bischof, 2013; Wolanski, Drew, Abel, & O'Brien, 1988), suggesting that, like most macroalgae, it is nutrient-limited. However, for most macroalgae the negative effects of grazing outweigh the benefits of nutrient enrichment in areas where both rates of herbivory and nutrient inputs are high (Burkepile & Hay, 2006). In contrast, in this study *Halimeda* proliferated around islands with seabirds, which have both high rates of herbivory and high nutrient inputs (Graham et al., 2018). Although *Halimeda* has morphological and chemical defences that reduce its susceptibility to grazing (Hay, Kappel, & Fenical, 1994; Lewis, 1985; Paul & Hay, 1986), it is still readily consumed by a range of herbivorous fishes (Ferrari, Gonzalez-Rivero, Ortiz, & Mumby, 2012; Hamilton, Smith, Price, & Sandin, 2014; Poray & Carpenter, 2014). Therefore, a lack of grazing on *Halimeda* is unlikely to be the sole cause for its success around islands with seabirds. *Halimeda* and other macroalgae also benefit from growing within stands of branching *Acropora*, which provide a spatial refuge from large-bodied herbivores (Bennett, Vergés, & Bellwood, 2010; Castro-Sanguino, Lovelock, & Mumby, 2016). However, *Acropora* cover and structural complexity were similar between islands with seabirds and islands with rats both before and after the bleaching event, so a difference in suitable habitat is unlikely to have driven the observed difference in the proliferation of *Halimeda*. Finally, geographic variation in abiotic conditions is unlikely to explain the differences in *Halimeda* cover post-bleaching. *Halimeda* increases calcification rates with increased temperature (Campbell, Fisch, Langdon, & Paul, 2016), but the smallest increase in *Halimeda* occurred in the atoll with the warmest temperatures. Ultimately, the simplest explanation for the increase in *Halimeda* in areas with both high nutrients and high herbivory is that *Halimeda* responds more strongly to naturally-derived nutrients than to herbivory, so the benefits of seabird nutrients outweigh the costs of increased grazing around islands with seabirds. Similar to our findings, Shantz et al. (2015) observed an increase in both *Halimeda* and CCA around individual coral heads with large aggregations of fishes, where both natural nutrients and grazing rates are high. At a broader scale, fish excretion has a larger influence on macroalgal cover than herbivore biomass in the Florida Keys (Burkepile et al., 2013). Thus, the relative importance of herbivory versus nutrients in controlling macroalgal abundance may depend on whether the nutrients are from human-derived or naturally-derived sources.

The response of fishes to bleaching depended on both feeding group and the presence of seabirds versus invasive rats. Some key groups of fishes, namely herbivores and piscivores, maintained higher biomass around islands with seabirds than islands with rats even after the bleaching event. The lack of response to bleaching by herbivores and piscivores is consistent with previous studies, which demonstrate that immediately following bleaching events, these groups are either unaffected or exhibit short-term increases in abundance due to an increase in food availability (Pratchett et al., 2008; Wilson, Graham, Pratchett, Jones, & Polunin, 2006). On the other hand, corallivores and planktivores often experience sharp declines within three years of mass bleaching events (Pratchett et al., 2008; Pratchett, Wilson, & Baird, 2006; Stuart-Smith, Brown, Ceccarelli, & Edgar, 2018; Wilson et al., 2006). Declines in these groups are directly linked to loss of live coral (Graham et al., 2008; Wilson et al., 2008, 2006), likely because corallivores rely on live coral for food while many planktivores rely on live coral for successful recruitment and effective anti-predator strategies (Booth & Beretta, 2002; Boström-Einarsson, Bonin, Munday, & Jones, 2018; Chivers, McCormick, Allan, & Ferrari, 2016; Coker, Graham, & Pratchett, 2012; Coker, Pratchett, & Munday, 2009). Similarly, we observed substantial declines in these groups despite comparable structural complexity between years. Overall, there appeared to be a convergence of biomass of planktivores and corallivores across islands with seabirds and invasive rats following the bleaching event, but the estimated effect of seabirds on biomass was still positive for all groups of fishes, including those most affected by the bleaching. .

Because this study was conducted only two years after a bleaching event, any differences in the responses of coral-reef communities between islands with birds versus rats were likely related to differences in *resistance* to change rather than *recovery* (Grimm & Wissel, 1997; Hodgson, McDonald, & Hosken, 2015; West & Salm, 2003). Coral cover in the Chagos Archipelago rebounded within 10 years following the 1998 mass bleaching event (Sheppard et al., 2012), which is within the range of recovery times observed in other regions (Baker, Glynn, & Riegl, 2008). Even though seabird nutrients did not enhance resistance to bleaching, they may still promote recovery of these reefs in the coming years, which depends on the growth of remnant colonies and recruitment of new juveniles (Baker et al., 2008; Gilmour, Smith, Heyward, Baird, & Pratchett, 2013). Natural nutrients from fishes and seabirds increase coral growth rates (Holbrook, Brooks, Schmitt, & Stewart, 2008; Liberman, Genin, & Loya, 1995; Meyer, Schultz, & Helfman, 1983; Shantz et al., 2015; Savage, 2019), so seabird nutrients may quicken recovery times following bleaching events. In addition, the high cover of CCA around islands with seabirds may enhance recruitment of juvenile corals, as some species of CCA attract coral larvae and increase post-settlement survival (Birrell et al., 2008; Harrington, Fabricius, De'ath, & Negri, 2004; Heyward & Negri, 1999; Price, 2010). Finally, herbivory is a key component of rapid recovery following bleaching events (Graham et al., 2015), thus the persistence of higher herbivore biomass around islands with seabirds may further speed recovery on these reefs. On the other hand, the dominance of *Halimeda* around some islands with seabirds may inhibit recovery due to its negative effects on both juvenile and adult corals (Birrell et al., 2008; Nugues, Smith, Hooidonk, Seabra, & Bak, 2004; Rasher & Hay, 2010). Continued monitoring will be necessary to determine how seabird nutrients influence longer-term recovery of coral reefs in the Chagos Archipelago.

Eradicating invasive rats from islands has demonstrable conservation benefits for terrestrial plants and animals (Brooke et al., 2017; Jones et al., 2016; Wolf et al., 2018). Nutrient subsidies from seabirds can be restored within 10-20 years following rat removal, with faster return times possible when combined with assisted recovery (Jones, 2010). Restoring seabird colonies and their associated nutrient inputs will likely benefit coral-reef fishes (Graham et al., 2018), but may have variable success in promoting resistance of coral reefs to bleaching. Rat invasion status had more of an effect than the bleaching event on the biomass of herbivores and piscivores, so these groups will likely continue to benefit from rat eradication. However, nutrient subsidies were insufficient to foster community-wide resistance to this severe mass bleaching event, even in a remote region that is well-protected from local human impacts (Sheppard et al., 2012). Still, given the success of de-ratting programs in achieving conservation goals in terrestrial habitats, combined with the potential for seabirds to enhance coral-reef recovery following bleaching events, integrating rat eradication with global management strategies may be an important strategy for coral-reef conservation.

Acknowledgements

We thank the United Kingdom Foreign and Commonwealth Office and the British Indian Ocean Territory Administration for granting us permission to undertake the research. This project was funded by the Royal Society and the Bertarelli Foundation and contributed to the Bertarelli Programme in Marine Science. Coral, seabird, and rat drawings were obtained from Catherine Collier and Jane Thomas, Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/imagelibrary/) and Openclipart (openclipart.org).

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