Direct and indirect effects of climate change-amplified pulse heat stress events on coral reef fish communities

JENNIFER M. T. MAGEL,[1] SEAN A. DIMOFF,[1] AND JULIA K. BAUM[1,2,3]

[1]*Department of Biology, University of Victoria, PO Box 1700 STN CSC, Victoria, British Columbia V8W 2Y2 Canada*
[2]*Hawai'i Institute of Marine Biology, University of Hawai'i, 46-007 Lilipuna Road, Kāne'ohe, Hawaii 96744 USA*

Abstract. Climate change-amplified temperature anomalies pose an imminent threat to coral reef ecosystems. While much focus has been placed on the effects of heat stress on scleractinian corals—including bleaching, mortality, and loss of reef structural complexity—and many studies have documented changes to reef fish communities arising indirectly from shifts in benthic composition, the direct impacts of heat stress on reef fish are much less well understood. Here, we quantify the direct and indirect effects of heat stress on reef fishes, using underwater visual censuses of coral reef fish communities conducted before, during, and after the 2015–2016 El Niño-induced global coral bleaching event. Surveys took place at the epicenter of this event, at 16 sites on Kiritimati (Republic of Kiribati; central equatorial Pacific) spanning across a gradient of local human disturbance. We expected that heat stress would have both direct and indirect negative effects on the reef fish community, with direct effects resulting from physiological stress during the event and indirect effects manifesting afterward as a consequence of coral mortality, and that the ability of fish communities to recover following the heat stress would depend on levels of local human disturbance. We found that total reef fish biomass and abundance declined by >50% during heat stress, likely as a result of vertical migration of fish to cooler waters. One year after the cessation of heat stress, however, total biomass, abundance, and species richness had recovered to, or even exceeded, pre-heat stress levels. However, the biomass of corallivores declined by over 70% following severe coral loss, and reefs exposed to higher levels of local human disturbance showed impaired recovery following the heat stress. These findings enhance understanding of the projected impacts of climate change-associated marine heatwaves on reef fishes, and highlight the interacting effects of local and global stressors on this vital component of coral reef ecosystems.

Key words: climate change; El Niño; functional group; local disturbance; marine heatwaves; multiple stressors; pulse disturbance; reef fish; thermal stress; trophic group.

INTRODUCTION

Pulse heat stress events (i.e., marine heatwaves) and associated coral bleaching have moved to the forefront of scientific research on coral reefs over the past two decades, and are now recognized as the most prominent threats facing tropical coral reefs this century (Hoegh-Guldberg 2011, Hughes et al. 2018). In particular, El Niño-associated heat stress has precipitated several mass coral bleaching events since the early 1980s (Heron et al. 2016), leading to widespread bleaching and mass coral mortality throughout the Pacific, Indian, and Atlantic Oceans (Wilkinson 1998, Eakin et al. 2010, Hughes et al. 2017). The losses of live coral cover and reef structural complexity resulting from such events have been shown to trigger subsequent short-term declines in local

reef fish abundance and diversity (i.e., changes visible within 1–3 yr; Wilson et al. 2006, Pratchett et al. 2011), and may also lead to shifts in the structure of reef fish communities that are still evident over a decade after the initial coral mortality (Bellwood et al. 2012, Graham et al. 2015, Robinson et al. 2019). These indirect effects of ocean warming on reef fish, mediated by changes in benthic community composition, have been well documented. However, there has been very little research to date examining the direct effects of ocean warming, and pulse heat stress events in particular, on tropical reef fish communities (but see López-Pérez et al. 2016).

The most recent global coral bleaching event, which occurred during the 2015–2016 El Niño, was the most extreme warming event to date (Claar et al. 2018), and resulted in unprecedented levels of bleaching and mortality in several regions. Effects were particularly severe in the central Pacific Ocean; on Jarvis Island, the loss of over 95% live coral cover resulted in substantial declines in total reef fish biomass, while changes in primary

productivity as a result of warming negatively affected planktivores (Brainard et al. 2018). On parts of the Great Barrier Reef that suffered substantial coral mortality, declines in the abundance of corallivores and decreased fish species richness were evident 8–12 months after bleaching (Stuart-Smith et al. 2018). Signs of biotic homogenization were also visible on the Great Barrier Reef only six months after the mass mortality event, as reef fish communities became more taxonomically and functionally similar compared to those present only 1 yr prior (Richardson et al. 2018). While these studies provide valuable insight into the short-term indirect impacts of a severe warming event on tropical reef fishes, the potential direct effects of heat stress on reef fish communities remain largely unknown.

The projected direct impacts of climate change on fish distributions and abundances (Cheung et al. 2009, 2010) are primarily expected to manifest through effects on fish physiology, specifically, through the oxygen limitation of thermal tolerance (Farrell 2016, Pörtner and Knust 2007; but see Clark et al. 2013, Norin et al. 2014 for the limitations of this approach). A fish's capacity to perform aerobic activity is highly temperature dependent, as increases in temperature lead to an increase in oxygen demand within bodily tissues (Fry 1947). A fish's ability to tolerate thermal extremes therefore hinges on its capacity to supply oxygen to the tissues to meet this demand—a capacity that is maximized within its optimal thermal window. Tropical ectotherms such as reef fish generally have narrower thermal tolerances than temperate organisms (Tewksbury et al. 2008, Deutsch et al. 2008), making them particularly vulnerable to the effects of ocean warming (Comte and Olden 2017). Several species of reef fish already appear to be living close to, or even above, their thermal optima (Rummer et al. 2014), suggesting that even small increases in sea surface temperatures (SSTs) may result in decreased performance. For example, experimental increases in water temperature of 2°–3°C above present-day values have been shown to have direct negative impacts on the growth and reproduction of the coral reef damselfish *Acanthochromis polyacanthus* (Munday et al. 2008, Donelson et al. 2010). To avoid supra-optimal temperatures, lab studies have shown that fish may seek out cooler waters during periods of warming (Nay et al. 2015), which could result in changes in their distribution and abundance in the wild. This has previously been documented in pelagic fish communities of the eastern tropical Pacific (Barber and Chavez 1983, Ñiquen and Bouchon 2004), and it is suspected that mobile reef fish species also seek out more favorable habitat to escape the effects of severe disturbances (Wilson et al. 2006).

Understanding the effects of pulse heat stress events on reef fish communities has both social and ecological implications. Fish comprise a large proportion of the consumer biomass on coral reefs, and play a number of important ecological roles. Herbivores help to maintain the reef in a coral-dominated state (Burkepile and Hay 2008) and can facilitate coral recruitment (Mumby et al. 2007), while mobile fish species play key roles in energy transfer and nutrient provisioning (Meyer et al. 1983, Allgeier et al. 2014, 2017). Worldwide, coral reef fisheries are valued at over US$6.8 billion annually and are an invaluable source of food and income for many small island nations (Burke et al. 2011). Studying the impacts of present-day pulse heat stress events on the abundance and diversity of reef fish could serve as a window into the future, foreshadowing the potential long-term consequences of climate change-induced ocean warming for both coral reef ecosystems and tropical coastal communities. Knowledge of the short-term impacts of these events will also be highly relevant over the next few decades, in light of projected increases in the frequency and intensity of marine heatwaves (Frölicher et al. 2018, Oliver et al. 2018). To inform reef fish conservation and management under these changing conditions, it is increasingly important that we understand the direct effects of pulse heat stress events on reef fish populations.

In this study, we exploit an extreme temperature anomaly, which occurred on Kiritimati (Republic of Kiribati) in the central Pacific Ocean during the 2015–2016 El Niño, to examine the direct and indirect effects of heat stress on tropical reef fishes. During this event, Kiritimati's reefs were subjected to unprecedented levels of heat stress, with SST anomalies exceeding 1°C above Kiritimati's historical maximum monthly temperature for nine months (Claar and Baum 2019, Claar et al. 2019). We conducted underwater reef fish surveys across the atoll's gradient of local human disturbance to quantify the effects of a severe heat stress event on the biomass, abundance, species richness, and structure of reef fish communities. To the best of our knowledge, this study is one of the first to examine the direct effects of pulse heat stress events on tropical coral reef fishes. Our specific objectives were to (1) assess changes in reef fish communities both during the heat stress itself (i.e., the direct effects of heat stress, prior to major changes in coral cover) and after the mass coral mortality event (which caused a loss of almost 90% of the atoll's coral cover; J. K. Baum, *unpublished data*) and (2) investigate the effect of local human disturbance on the response of reef fish communities to the heat stress. We hypothesized that anomalously high water temperatures would negatively impact fish species across the atoll, resulting in declines in total fish biomass, abundance, and species richness, potentially due to the movement of fish to less stressful thermal environments (e.g., deeper, cooler waters). However, we also expected that larger fishes might respond more strongly than smaller ones due to greater mobility, and that some species and functional groups would have stronger responses to the elevated water temperatures, leading to shifts in reef fish community structure. Moreover, we predicted that severe declines in coral cover would be followed by decreases in corallivore abundance and concomitant increases in herbivore abundance, due to changes in their preferred food

sources. Finally, we hypothesized that reef fish communities at all levels of human disturbance would be negatively impacted by the heat stress event, but those subjected to minimal disturbance would show the greatest recovery following the heat stress.

METHODS

Study site and design

We surveyed reef fish communities before, during, and after the 2015–2016 El Niño at 16 forereef sites around Kiritimati (Christmas Island, Republic of Kiribati; Fig. 1). Located in the central equatorial Pacific Ocean (01°52′ N 157°24′ W), Kiritimati is the world's largest coral atoll by land mass. The atoll supports a population of approximately 6,500 people (Kiribati National Statistics Office 2016), the vast majority of which are highly dependent on reef resources for subsistence and income due to the atoll's geographic isolation and lack of alternate livelihoods (Burke et al. 2011, Watson et al. 2016). Reef fish in particular are a vital resource, with over 95% of households on Kiritimati actively engaged in fishing activities (Watson et al. 2016).

Concentration of the local population in villages on the northwest side of the atoll has resulted in a spatial gradient of human disturbance across the surrounding reefs, including distinct differences in benthic community composition around the atoll (Appendix S1: Fig. S1, Tables S1 and S2). We quantified local disturbance at each site by combining spatial data on fishing intensity and human population density (Appendix S1: Table S1). Using fishing intensity data from Watson et al. (2016), we first generated a kernel density function with ten steps to calculate the intensity of subsistence fishing pressure at each site. We then extracted data from the 2015 Population and Housing Census (Kiribati National Statistics Office 2016) and calculated the number of people within a 2 km radius of each site, as a proxy for immediate point-source disturbances (e.g., pollution and sewage runoff) from villages into the marine environment. Combining these two metrics, we calculated a quantitative measure of local disturbance for each site (Appendix S1: Table S1), which we used as a covariate in our models. For visualization purposes, we also grouped sites into four distinct human disturbance levels (very low, low, medium, very high) based on clear breakpoints in the continuous measure (Fig. 1). These terms should be regarded as being relative to other levels of disturbance around the atoll, rather than absolute levels of human disturbance. Beyond these differences, upwelling along the western (leeward) side of the atoll normally causes variation in primary productivity across sites (Walsh 2011).

Surveys were conducted prior to the El Niño (in July–August of 2011 and 2013), 2 months into the warming event (July 2015), and 1 yr after the end of the event (July 2017). At the time of our July 2015 sampling, Kiritimati's waters had experienced 15°C-week degree heating weeks (Appendix S1: Fig. S2; Claar et al. 2019), placing them well above Bleaching Alert Level 2, an amount of heat stress at which coral mortality is expected (Liu et al. 2013). Heat stress continued on the island until April 2016 (Claar et al. 2019). We conducted 82 fish surveys in total, with some sites surveyed twice in a single year at different times of day: 2011 ($n = 15$ surveys), 2013 ($n = 23$), 2015 ($n = 22$), and 2017 ($n = 22$).

Reef fish communities

Underwater visual censuses (UVCs) of the reef fish communities were conducted using standard belt transect methods, following Sandin et al. (2008). At each site, reef fish species identification, abundance, and sizes (to the nearest cm) were recorded by a pair of trained scientific divers swimming in tandem along a belt transect. Three 25 m transects laid along the 10–12 m isobath were surveyed during each dive, with adjacent transects separated by 10 m. For each transect, divers first counted fishes ≥20 cm total length in an 8 m wide strip while the transect was being laid, then counted fishes <20 cm total length in a 4 m wide strip while swimming in the reverse direction. Following this, divers also conducted presence/absence surveys by swimming in a zig-zag pattern in a 30 m wide strip along the transect and noting any additional species that were not observed during the UVCs. All surveys took place during daylight hours. Surveys were conducted by a total of five divers, with the same two individuals conducting all surveys within a given year, and the two most experienced divers conducting surveys in 2 and 3 yr, respectively. Scientific divers were highly experienced, and also spent one to two days on Kiritimati prior to commencing the surveys re-familiarizing themselves with the atoll's fish species and underwater size estimation. Size estimation accuracy was checked using PVC objects of known length (Bell et al. 1985), until divers could consistently estimate fish lengths to the nearest 2 cm.

Prior to analysis, we standardized the sampling area for each UVC by doubling the number of small fishes recorded on each transect, as in Robinson and Baum (2016). Length estimates for each fish were converted to body mass (grams) using published species-specific length-weight relationships (Kulbicki et al. 2005). In cases where individuals could not be identified to species level, or higher-level length–mass relationships were not available, we calculated mean length–mass parameters based on species from the same genus or family. To minimize inflation of biomass estimates we excluded all sharks and jacks from our analyses (MacNeil et al. 2015, Williams et al. 2015, Robinson et al. 2017), as the abundance of these highly mobile species may be over-estimated in non-instantaneous UVCs (Ward-Paige et al. 2010).

To assess changes in reef fish community structure, we assigned each fish species to one of eight trophic groups
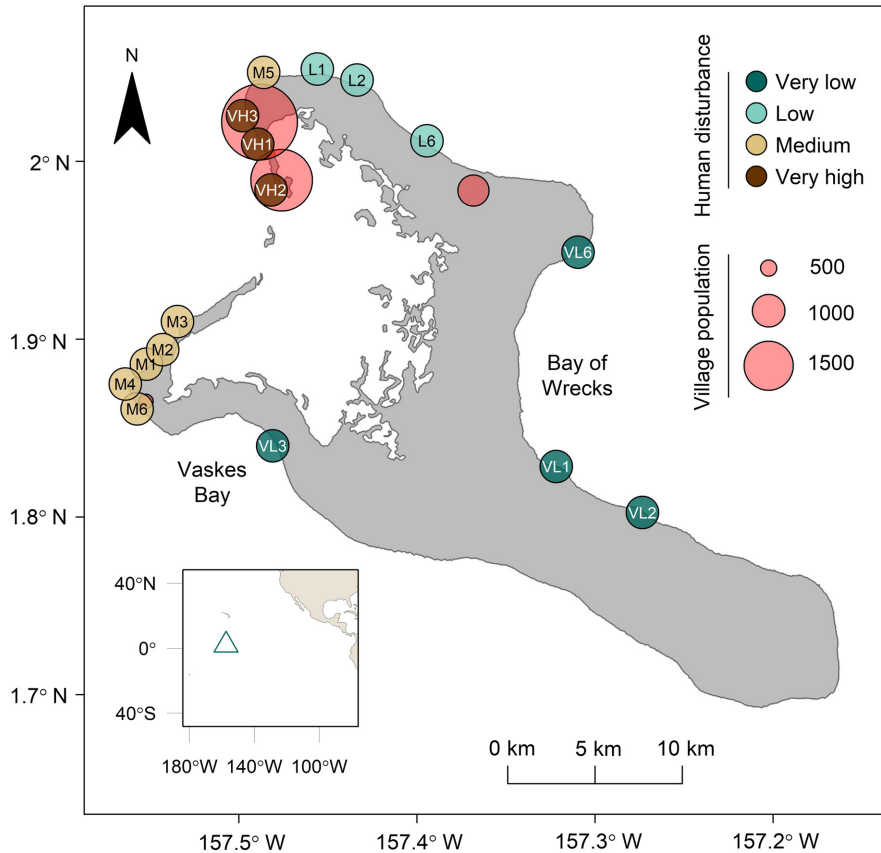
FIG. 1. Map of forereef study sites and villages on Kiritimati. Sites are categorized by the level of local human disturbance that they experience (detailed in Appendix S1: Table S1), and villages (red circles) are scaled to human population size. Inset shows Kiritimati's location in the central equatorial Pacific Ocean.

(corallivore [C], detritivore [D], generalist carnivore [GC], herbivore [H], invertivore [In], omnivore [Om], piscivore [Pi], and planktivore [Pl]) based on its dietary preferences, following Yeager et al. (2017a). For species that were not categorized in Yeager et al. (2017a), trophic groups were assigned based on dietary information from Randall (2005) or the primary literature, or were inferred from family- or genus-level trophic assignments (Appendix S1: Table S3). Additionally, to assess if body size modulated responses to heat stress, we divided the fish community into large (≥20 cm total length) and small (<20 cm total length) fishes. For each site, we then calculated total fish biomass, total fish abundance, and species richness, as well as the biomass and abundance of each trophic group, and of large and small fishes. Species richness was defined as the total number of unique species observed at each site.

Statistical analyses

All statistical analyses were conducted using R version 3.5.1 (R Core Team 2018). To examine the combined effects of local and global disturbances on reef fish biomass, abundance, and species richness, we fit generalized linear mixed-effects models (GLMMs) for each fish metric. In all models, we included our two main covariates of interest, heat stress and local human disturbance, as fixed effects; the former was categorical (before, during, after), the latter continuous. We also modeled their interaction, to allow for the effects of heat stress to differ by the level of human disturbance. We included three additional environmental and temporal variables (as fixed effects) in our models, to control for their potential influence on reef fish communities. (1) Maximum net primary productivity (NPP; mg $C \cdot m^{-2} \cdot d^{-1}$), which can positively influence reef fish biomass (Robinson et al. 2017), especially that of planktivores and piscivores (Williams et al. 2015), was modeled as a continuous variable using data obtained from the Marine Socio-Environmental Covariates (MSEC) open source data product (Yeager et al. 2017b).[4] MSEC productivity values are calculated over a 2.5-arcmin grid based on data from NOAA CoastWatch, which models net primary productivity using satellite-derived measures of photosynthetically available radiation, SST, and chlorophyll a concentrations. (2) Time of day (range 07:35–17:33) was

[4] https://shiny.sesync.org/apps/msec/

modeled as a quadratic (second-order) polynomial, to allow for the fact that any relationship with the fish community would likely peak at some point during the day, rather than increasing (or decreasing) linearly. (3) Lunar phase, which can cause short-term shifts in fish assemblages (e.g., transient spawning aggregations; Bijoux et al. 2013), was modeled as the sine of lunar day to account for its periodicity. Prior to analysis, continuous input variables were standardized to a mean of zero and a standard deviation of 0.5 using the *rescale* function in the arm package (Gelman and Su 2018). Finally, we included site and observer as random effects (i.e., varying intercepts) in all models to account for the nonindependence of observations made by the same diver and at the same site (i.e., multiple surveys in the same year, and across years).

We modeled each response variable using the above GLMM framework, tailored to the response depending on its probability distribution. Total fish biomass, the biomass of each trophic group, and the biomass of large and small fishes were modeled using a Gamma distribution (R package lme4; Bates et al. 2015), which is appropriate for positive continuous data; total fish abundance, trophic group abundance, and the abundance of large and small fishes were modeled with a negative binomial distribution (R package glmmadmb; Fournier et al. 2012, Skaug et al. 2016), which is appropriate for overdispersed data (Zuur et al. 2009); and species richness was modeled using a Poisson distribution (R package lme4), which is appropriate for count data that are not overdispersed (McCullagh and Nelder 1989, Zuur et al. 2009). All models were fit with a "log" link function. To enable use of the Gamma distribution (which only accommodates positive, non-zero values) for the four trophic groups containing zeros, one-half of the smallest non-zero observation was added to the zero values of each group prior to fitting the biomass models; this resulted in very minor additions to the data (<0.001– 0.400 g/m^2) and avoided having to fit more complex hurdle models. For the abundance models, we fit additional zero-inflated negative binomial models for each trophic group that contained over 5% zeros, and compared these to the non-zero-inflated models using AIC (Warton 2005). The zero-inflated model was found to provide a better fit for detritivore abundance, and so was used as the final model for this group. Model assumptions were evaluated visually through the use of residual plots, and in each case appeared to indicate a reasonable fit.

To examine changes in reef fish community structure, we used multivariate statistical and ordination techniques implemented through the R package vegan (Oksanen et al. 2018). Site × species matrices were created for the entire fish community and for each individual trophic group using measures of species biomass. First, we performed a multivariate ordination (principal coordinates analysis; PCoA) using the *betadisper* function to visualize differences in reef fish community structure across heat stress periods. Next, to test for

significant differences in fish community structure, we conducted permutational multivariate analysis of variance (PERMANOVA) tests with 999 permutations and Bray-Curtis distances using the *adonis* function. Heat stress, human disturbance, primary productivity, time of day, and lunar day were included as fixed effects in each model, while site was incorporated as a blocking factor using the strata term in *adonis*. Finally, to determine the species responsible for driving any observed differences in community structure, we used the *simper* (similarity percentages) function to identify influential species among heat stress time points.

Results

In total, we enumerated 171 445 individual reef fishes of 245 species on Kiritimati.

Biomass and abundance

Heat stress was the primary determinant of total reef fish biomass and abundance throughout the study period (Table 1). Total fish biomass declined by over half while under heat stress, from a mean of 116.8 ± 9.5 g/m^2 per site (mean $\pm$ SE) prior to heat stress to just 53.6 ± 6.4 g/m^2 during it ($t = -4.50$, $P < 0.001$); biomass then rebounded following heat stress ($t = 2.25$, $P = 0.025$), to a mean of 141.1 ± 18.3 g/m^2 (Fig. 2a). Similarly, total fish abundance declined significantly during the heat stress ($z = -9.64$, $P < 0.001$), from a mean of $2,499 \pm 198$ fish per site prior to stress, to just $1,035 \pm 95$ during it, but then increased back to levels similar to that prior to the heat stress ($2,358 \pm 236$) by 2017 (Fig. 2b). We also found significant declines in the biomass and abundance of both small and large fishes during heat stress, and rebounds following heat stress (Table 1, Appendix S1: Fig. S3).

Six out of eight trophic groups (H, In, Pl, Pi, GC, C) also exhibited significant declines in biomass during the heat stress (Fig. 2a). This pattern was most notable for the invertivores ($t = -6.29$, $P < 0.001$) and planktivores ($t = -4.22$, $P < 0.001$), for which heat stress caused estimated losses of 72.7% and 54.3%, respectively (Table 1). Five of these same six trophic groups (excluding the generalist carnivores), also exhibited significant declines in abundance during the heat stress event (Table 1, Fig. 2b). One year after the end of the heat stress and mass coral bleaching event, the biomass and abundance of corallivores (biomass $t = -3.33$, $P < 0.001$; abundance $z = -6.89$, $P < 0.001$) and the biomass of generalist carnivores ($t = -2.41$, $P = 0.016$) had declined significantly, whereas the biomass and abundance of herbivores (biomass $t = 3.08$, $P = 0.002$; abundance $z = 4.14$, $P = <0.001$) and the biomass of omnivores ($t = 2.19$, $P = 0.029$) had increased significantly (Table 1).

Total reef fish biomass was significantly impacted by local human disturbance ($t = 2.10$, $P = 0.036$), time of day ($t = 2.38$, $P = 0.018$), and lunar day ($t = 2.07$,

TABLE 1. Results (parameter estimates) for fixed effects from generalized linear mixed-effects models examining changes in reef fish biomass, abundance, and species richness.

Model	Heat stress		Human disturbance	Productivity NPP	Time of day		Lunar day	Heat × disturbance	
	During	After			Time	Time^2		During	After
Biomass									
All fish	**−0.548*****	**0.394***	**0.701***	−0.523	0.021	**1.280***	**0.165***	0.014	**−0.380***
Small fish	**−0.447*****	0.312	0.531	−0.168	0.984	0.666	**0.300*****	0.078	**−0.391***
Large fish	**−0.589*****	**0.627***	**0.714***	**−0.720***	−0.499	1.353	0.065	0.016	−0.297
Herbivores	**−0.679*****	**0.642****	0.712	−0.191	−0.013	**1.334***	**0.308****	**0.417***	**−0.464***
Invertivores	**−1.262*****	0.078	0.952	−0.182	**−2.404***	0.028	−0.105	−0.552	**−0.948****
Planktivores	**−0.783*****	0.481	0.958	−0.379	0.774	0.498	**0.255***	**−0.863****	**−0.584****
Piscivores	**−0.690****	−0.011	−0.523	−0.176	0.324	1.939	0.306	0.398	0.231
Omnivores	0.283	**1.092***	0.393	**−1.241***	1.918	1.595	−0.139	−0.108	−0.143
Generalist carnivores	**−0.448****	**−0.559***	−0.497	0.217	**−1.711***	1.172	0.192	0.157	−0.318
Corallivores	**−0.686***	**−1.072*****	0.325	0.247	−1.026	0.127	0.154	−0.352	0.589
Detritivores	0.207	0.172	0.094	−0.022	0.092	−0.297	0.359	−0.223	**−2.379*****
Abundance									
All fish	**−0.915*****	0.257	0.266	0.242	−0.393	0.246	**0.228*****	**−0.347***	**−0.776*****
Small fish	**−0.926*****	0.250	0.250	0.265	−0.399	0.240	**0.235*****	**−0.343***	**−0.788*****
Large fish	**−0.380***	**0.664****	**0.918****	**−0.857*****	0.068	0.637	0.007	−0.168	−0.222
Herbivores	**−0.389*****	**0.704*****	0.024	0.010	0.522	0.699	0.078	0.175	−0.166
Invertivores	**−0.812*****	0.299	**0.876***	0.416	−0.534	−0.271	0.077	**−0.652*****	**−1.245*****
Planktivores	**−1.097*****	0.278	0.217	0.299	−0.598	0.216	**0.259*****	**−0.535****	**−0.817*****
Piscivores	**−1.051*****	0.029	0.283	−0.106	1.152	0.551	**0.216***	−0.355	−0.030
Omnivores	0.199	−0.235	**−0.896***	−0.068	−1.060	−0.232	0.033	0.074	**1.374*****
Generalist carnivores	−0.092	−0.138	0.124	0.332	−0.442	1.015	0.046	0.176	−0.150
Corallivores	**−0.576*****	**−1.679*****	**−0.615***	**0.717****	−1.477	1.124	0.057	**−0.690***	**0.714***
Detritivores	−0.135	−0.252	**1.257****	−0.200	0.242	0.924	−0.011	**1.041*****	**−2.560*****
Species richness									
All fish	**−0.180*****	**0.249*****	0.073	**0.178***	−0.259	0.209	0.048	−0.091	**−0.216*****

Notes: During refers to 2015, during the heat stress event; after refers to 2017, after the heat stress event; NPP, net primary productivity; time, first-degree polynomial; time^2, second-degree polynomial. Values in boldface type are statistically significant at $\alpha = 0.05$, and asterisks indicate levels of significance (*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$). Trophic groups are ordered from most to least biomass.
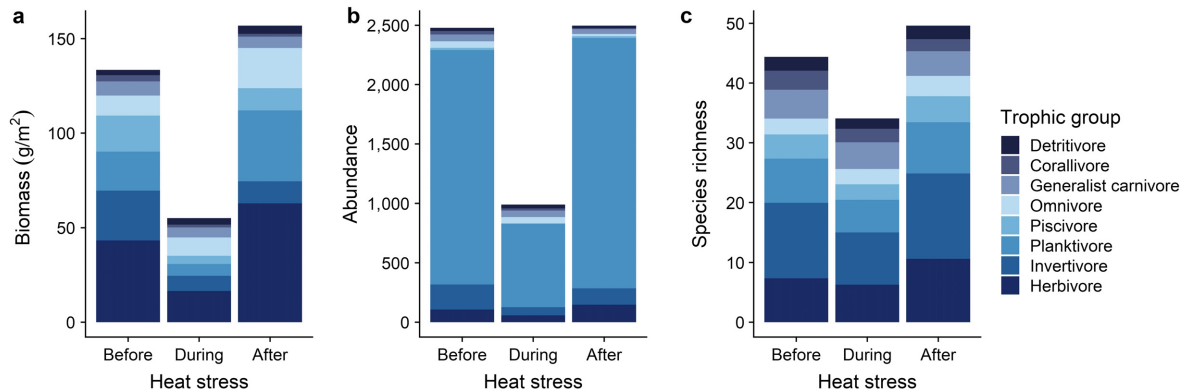
Fig. 2. Relative contribution of individual trophic groups to total reef fish (a) biomass, (b) abundance, and (c) species richness at each heat stress time point. The y-axes represent mean site-level values for each metric combined across all sites and disturbance levels, with trophic groups ordered from most to least biomass, as in the legend (detritivores at the top of each bar and herbivores at the bottom).

$P = 0.038$; Table 1). While total fish abundance did not vary significantly across the human disturbance gradient, the abundance of individual trophic groups exhibited variable responses to human disturbance (Table 1, Appendix S1: Fig. S4). The abundance of invertivores ($z = 2.36$, $P = 0.018$) and detritivores ($z = 2.84$, $P = 0.004$) was significantly higher at higher levels of human disturbance, while omnivore ($z = -2.27$, $P = 0.023$) and corallivore ($z = -2.07$, $P = 0.039$) abundance was significantly lower at these sites. Total fish abundance was also significantly affected by lunar day, while neither abundance nor biomass responded significantly to net primary productivity. Individual trophic groups were also largely unaffected by net primary productivity, time of day, or lunar day (Table 1).

Finally, local disturbance modulated the response of the reef fish community to heat stress (Table 1, Fig. 3, Appendix S1: Fig. S4). Sites subjected to higher levels of local disturbance had significantly lower total fish biomass ($t = -2.14$, $P = 0.033$) and abundance ($z = -5.41$, $P < 0.001$) after the heat stress, compared to sites at lower disturbance levels (Table 1, Appendix S1: Fig. S4). Declines in the biomass and abundance of detritivores, invertivores, and planktivores were similarly exacerbated by local disturbance following the heat stress (Table 1). Herbivore biomass also suffered greater declines at higher-disturbance sites following the heat stress, while the abundance of corallivores and omnivores was significantly higher at such sites after the warming event (Table 1).

Species richness

Reef fish species richness declined significantly during the heat stress period (Table 1), from a mean of 44 ± 1 species observed per site prior to the event to 34 ± 1 species per site during the heat stress ($z = -4.21$, $P = <0.001$; Fig. 2c). Notably, four species (three invertivores and one planktivore) were not observed at any of the study sites while subjected to heat stress (Appendix S1: Table S4). Although reef fish species richness increased significantly (relative to predisturbance levels) to a mean of 48 ± 1 species per site following the heat stress ($z = 3.80$, $P < 0.001$), five species—one corallivore, one piscivore, one herbivore, and two invertivores —disappeared during this time (Appendix S1: Table S4). Species richness was not strongly influenced by local human disturbance, but was significantly higher in more productive waters ($z = 2.40$, $P = 0.016$; Table 1). Species richness was also influenced by the interaction between heat stress and local human disturbance: richness was significantly lower at higher disturbance sites following the heat stress event ($z = -3.64$, $P = <0.001$), compared to sites with lower levels of disturbance (Table 1).

Community structure

Overall reef fish community structure varied significantly across heat stress periods (pseudo $F = 3.05$, $R^2 = 0.06$, $P = 0.001$; Fig. 4a, Appendix S1: Table S5). Over 70% of the dissimilarity in community structure under heat stress (compared to pre-heat stress composition) was attributable to changes in the biomass of 31 species, including representatives from all eight trophic groups (Appendix S1: Table S6). The structure of each individual trophic group was also significantly influenced by the heat stress event (Fig. 4b–i, Appendix S1: Table S5). With the exception of the detritivores and omnivores, these shifts in community structure during heat stress largely appear to be the result of species declines (Appendix S1: Table S6). For example, the biomass of important herbivore (*Scarus frenatus*, *Scarus rubroviolaceus*, *Scarus ghobban*), piscivore (*Lutjanus bohar*), and planktivore (*Pterocaesio tile*) species plummeted during heat stress (Appendix S1: Table S6). Conversely, influential species in several trophic groups experienced increases in biomass following heat stress (Appendix S1: Table S7).
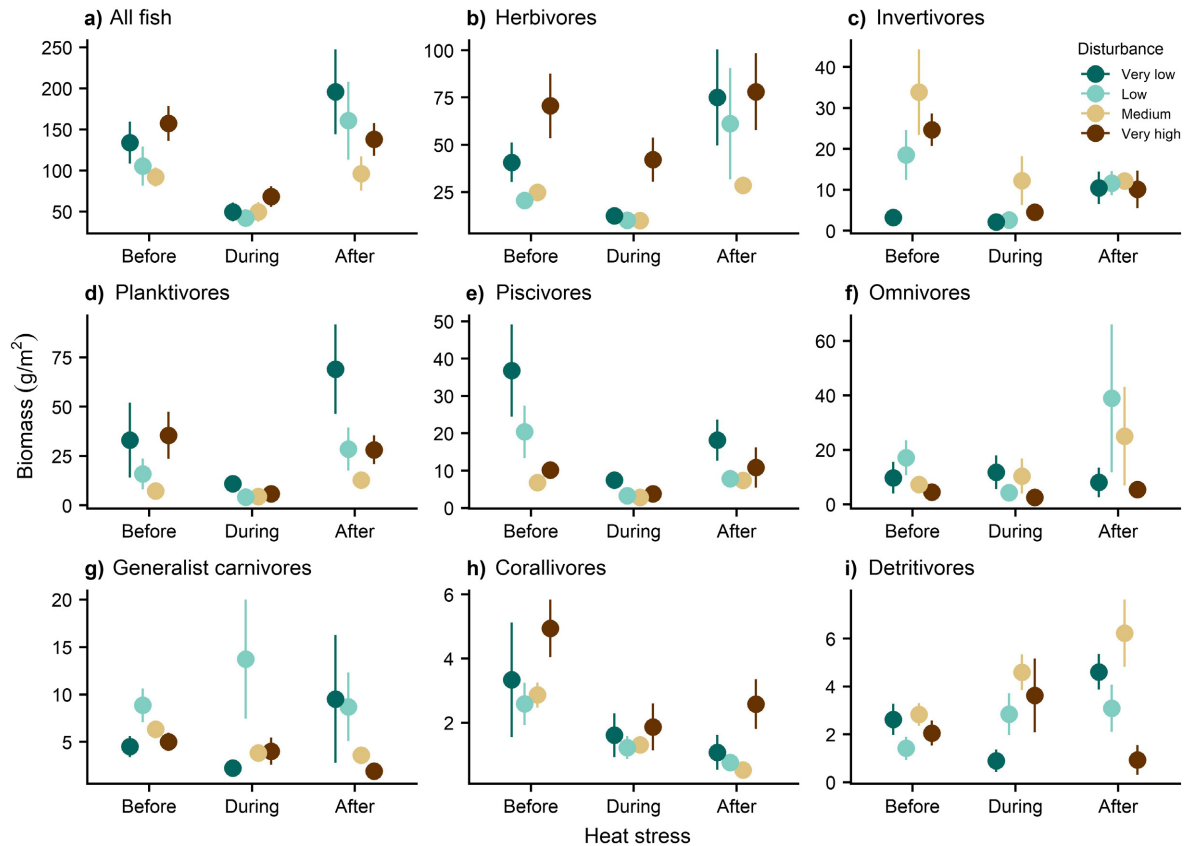
Fig. 3. Mean site-level biomass of (a) all fish and (b–i) individual trophic groups at each of the four human disturbance levels on Kiritimati before, during, and after the heat stress event. Dots represent mean ± SE, and are colored by the level of local human disturbance. Trophic groups are ordered from most to least biomass.

Overall reef fish community structure also varied significantly across the local human disturbance gradient (pseudo $F = 10.67$, $R^2 = 0.11$, $P = 0.001$; Appendix S1: Table S5). When trophic groups were considered individually, all groups except for the piscivores exhibited significant differences in structure across the local disturbance gradient (Appendix S1: Table S5). Net primary productivity also had a significant effect on overall community structure (pseudo $F = 3.07$, $R^2 = 0.03$, $P = 0.004$), and influenced the structure of four of the eight trophic groups (the herbivores, invertivores, planktivores, and generalist carnivores; Appendix S1: Table S5). There was also a significant interaction between heat stress and local human disturbance for the reef fish community as a whole (pseudo $F = 1.41$, $R^2 = 0.03$, $P = 0.001$), which suggests that the effect of heat stress on community structure is influenced by the intensity of local human disturbance. This effect was also present for the herbivores, invertivores, planktivores, and generalist carnivores (Appendix S1: Table S5).

DISCUSSION

Understanding how coral reef fishes respond to ocean warming, and the direct vs. indirect effects of pulse heat stress events on reef fish communities, are two of the major unanswered questions facing coral reef ecologists today (Wilson et al. 2010). Although El Niño-associated heat stress events tend to be relatively short lived (<1 yr in duration), they can have devastating effects on tropical coral reef ecosystems. Studying the effects of such events on reef fish communities may foreshadow the more serious long-term consequences of future ocean warming for both coral reef ecosystems and the coastal communities that depend on them. Here, we document significant changes in reef fish biomass, abundance, species richness, and community structure in direct response to a severe pulse heat stress event, patterns that have been largely overlooked by the majority of previous studies, which have focused on the lagged, indirect responses of reef fish to heat stress arising through shifts in benthic composition following coral bleaching and mortality.

Biomass and abundance

Consistent with our predictions, total fish biomass and abundance declined significantly when subjected to heat stress. These declines occurred quickly: both metrics had dropped by over 50% at the time of our 2015
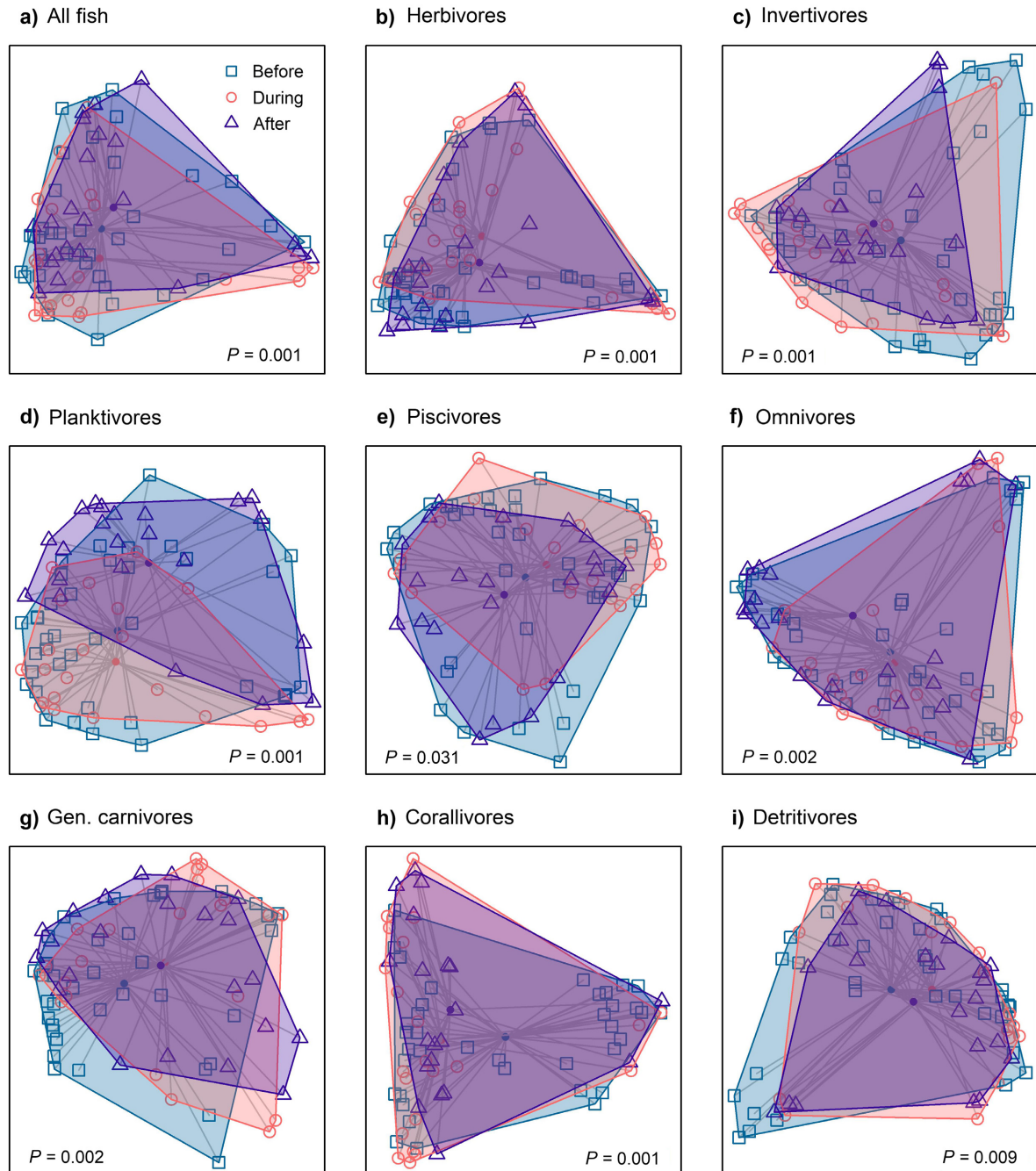
FIG. 4. Multivariate ordination (PCoA) of reef fish communities, showing differences in community structure through time for (a) the entire reef fish community and (b–i) individual trophic groups. Points represent individual sites, colored by sampling time, and shaded polygons indicate the boundaries of observed community space for each time point.

surveys, two months into the warming event. Coral bleaching was still minimal and structural complexity unchanged around the atoll at this time (J. K. Baum, *unpublished data*), which suggests that rather than responding to bleaching-induced shifts in benthic composition, the observed fish declines resulted directly from increased water temperatures (which exceeded

Kiritimati's historical maximum monthly mean temperature by more than 1°C) or other El Niño-associated changes. When water temperatures exceed a species' thermal optimum, performance capacity may become constrained and the organism may approach its upper thermal tolerance limits (Pörtner and Knust 2007, Deutsch et al. 2008, Clark et al. 2013, Farrell 2016).

Under such conditions, if thermal refugia exist, fish may move to areas with more preferred temperatures (Nay et al. 2015); if not, population declines may ensue due to decreased fitness (e.g., impacts on growth or reproduction [Munday et al. 2008, Donelson et al. 2010] or survival [Rummer et al. 2014]). The relatively short time frame in which the populations declined and subsequently recovered suggests that the observed changes in biomass and abundance resulted from shifts in reef fish distribution, rather than negative impacts on reef fish fitness. As Kiritimati is a highly isolated atoll (Watson et al. 2016), movement to deeper waters, rather than lateral movement to nearby reefs, is the most likely explanation. However, as the present study only surveyed fish communities on shallow forereefs, further studies will be needed to determine the utility of deeper reefs as thermal refugia for tropical reef fish during heat stress events.

Contrary to expectations, we did not find evidence of greater declines in larger (and theoretically more mobile) species; rather, both large and small fishes declined significantly during the heat stress. Although many of the small fishes in our surveys are likely not capable of moving large distances, short-distance migrations to deeper waters should be possible for the majority of the fish community (Chapman and Kramer 2000), as we did not document many site-attached species (e.g., small blennies and gobies).

Despite undergoing drastic declines during heat stress, total reef fish biomass exceeded pre-disturbance levels just 1 yr after the heat stress dissipated, and total fish abundance had rebounded to its former level. Although this contradicts the findings of several previous studies (Sano 2004, Wilson et al. 2006, Heenan et al. 2018), our results are in accordance with those of Lindahl et al. (2001), who reported increases in overall fish abundance on Tanzanian reefs 1 yr after the 1998 mass bleaching event, mainly resulting from an increase in herbivores. Both the decline and subsequent increase in total fish biomass on Kiritimati appear to have largely been driven by changes in herbivores and invertivores (Fig. 2a), while patterns in total fish abundance were primarily influenced by changes in small planktivores (Fig. 2b, Appendix S1: Fig. S3). Although relatively little is known about the thermal tolerances of herbivorous reef fish, previous research on planktivores (e.g., *Chromis* sp.; Rummer et al. 2014, Habary et al. 2017) suggests that these fish are highly sensitive to changes in water temperature. However, this trophic group also appears to respond strongly to levels of net primary productivity (Williams et al. 2015), which may be altered during El Niño (Barber et al. 1996, Lo-Yat et al. 2011). As we were unable to monitor changes in productivity throughout the heat stress event, the ultimate driver behind our observed declines in planktivore abundance remains unclear. Future studies examining the impacts of heat stress on reef fish communities should also take into account potential shifts in net primary productivity that may occur during El Niño.

As predicted, both the biomass and abundance of corallivorous fishes declined significantly following the mass coral bleaching event. These findings are consistent with a large body of literature documenting the negative effects of coral mortality on this trophic group (Shibuno et al. 1999, Sano 2004, Wilson et al. 2006, Pratchett et al. 2008). For example, corallivores on Japanese coral reefs had declined significantly at Ishigaki Island (Shibuno et al. 1999) and disappeared completely from Iriomote Island (Sano 2004) just one month after the 1998 mass bleaching event. Notably, the corallivores *Arothron meleagris* and *Plectroglyphidodon johnstonianus* declined substantially in our surveys, while *Chaetodon trifascialis* has not been observed at all since the heat stress (Appendix S1: Table S4). The latter species' disappearance, which has also been observed on reefs in Australia (Pratchett et al. 2006) and the Seychelles (Graham et al. 2009) following severe coral bleaching, suggests that it is particularly vulnerable to coral loss. While past studies have reported the disappearance of this species and others within 4–7 yr of severe coral bleaching, our results suggest that local disappearances and declines in fish biomass following a severe heat stress event may occur more quickly than previously thought (i.e., within 1 yr of the end of the heat stress).

Consistent with our expectations, both the biomass and abundance of herbivorous fishes increased following heat stress-induced mass coral mortality, in conjunction with increased turf and macroalgal abundance at several sites (J. K. Baum, *personal observation*). These results are consistent with previous studies that have reported increases in herbivore abundances within 1–3 yr of coral bleaching (Pratchett et al. 2008). For example, Lindahl et al. (2001) observed significant increases in herbivore abundance on reefs of transplanted corals six months after severe coral mortality, and Shibuno et al. (1999) reported increases in herbivores just one month after severe coral bleaching. These changes were primarily driven by increases in parrotfish (Scaridae) and surgeonfish (Acanthuridae), the same families that dominate the herbivore community on Kiritimati. While relatively little is known about the effects of coral loss on groups other than corallivores (Wilson et al. 2010), our results lend support to the idea that declines in coral cover may significantly alter herbivorous fish populations in the short term (i.e., <2 yr after a severe heat stress event).

Our results also suggest that, for the sites surveyed, total reef fish biomass was related to local human disturbance, although there was no significant difference in total fish abundance across the disturbance gradient. While local disturbance may impact the abundance of commercially important fish species or trophic groups (Friedlander and DeMartini 2002, Advani et al. 2015, Kadison et al. 2017), these individuals comprise a relatively low percentage of total reef fish abundance on Kiritimati, where the majority of the fish community is composed of highly abundant, ubiquitous planktivores (Fig. 2b, Appendix S1: Fig. S4). However, the positive

relationship between human disturbance and biomass is unexpected, as negative effects of local fishing pressure and human population density on tropical reef fish biomass have been documented extensively (Mora 2008, Cinner et al. 2013, Williams et al. 2015). These negative effects tend to apply to large, piscivorous fishes, and indeed on Kiritimati piscivorous fish biomass declined as disturbance increased (Fig. 3). Closer examination of our survey data also suggests a high biomass of two large herbivorous fish species (*Acanthurus olivaceus* and *Scarus ghobban*) at the highly disturbed sites on Kiritimati that are rarely found at lower levels of human disturbance, as well as higher biomass of several other large- to mid-sized herbivores, invertivores, and planktivores at the highly disturbed sites. Interviews conducted at households across Kiritimati (J. K. Baum, *unpublished data*) suggest that *A. olivaceus* and *S. ghobban* are not targeted by fishers, potentially due to the association of these two species with ciguatera fish poisoning (White 2010, Wu et al. 2011; T. Kirata, *personal communication*); such species may therefore be contributing to the maintenance of high fish biomass in otherwise disturbed areas. Alternatively, despite the known gradient of fishing pressure on Kiritimati (Watson et al. 2016) and extensive impacts of local disturbance on coral reef health (Appendix S1: Fig. S1, Table S1), the atoll's relatively small human population could mean that fishing pressure is not high enough even on the highly disturbed reefs to have an appreciable effect on total reef fish biomass.

Species richness

Similar to the observed patterns in total fish biomass and abundance, reef fish species richness also declined during the heat stress event, but was significantly higher than pre-disturbance levels during recovery in 2017. There is limited precedent for these results in the scientific literature, and previous studies reporting changes in reef fish species richness in relation to heat stress events show varying results. Whereas Sano (2004) found no change in species richness on Japanese coral reefs two months into the 1998 coral bleaching event, Stuart-Smith et al. (2018) reported declines in species richness on the Great Barrier Reef <1 yr after the 2015–2016 El Niño at sites that were heavily impacted by the mass bleaching. The mechanism driving our observed increase in species richness therefore remains unclear. While some of the new species appearing on reefs after the El Niño were previously observed at additional sites around Kiritimati in 2013, it is possible that others may have come from areas of the island that have not been surveyed previously. Given the unique functional roles that individual species may play in coral reef ecosystems (Bellwood et al. 2006, Cvitanovic and Bellwood 2009, Hoey and Bellwood 2009), both local extinctions and the appearance of new species during El Niño, together with their roles in the marine food web, should be taken into consideration when predicting the impact of heat stress events on coral reef ecosystems and adjacent coastal communities.

Interacting effects of heat stress and local disturbance

Although total reef fish biomass, abundance, and species richness returned to, or even exceeded, pre-disturbance levels relatively quickly following the 2015–2016 El Niño, levels of recovery varied across the local human disturbance gradient. We found a significant negative interaction between heat stress and local disturbance for all three of our fish metrics, with significantly lower biomass, abundance, and species richness at higher levels of disturbance (relative to sites with lower levels of disturbance) after the heat stress event. This suggests that local disturbance may impair the ability of reef fish communities to recover following severe heat stress. One potential explanation for this pattern is differences in underlying levels of reef structural complexity across the human disturbance gradient. The ability of coral and reef fish communities to recover following a severe bleaching event is strongly influenced by initial (i.e., pre-bleaching) levels of reef structural complexity (Graham et al. 2015), which on Kiritimati are inversely related to local human disturbance (Magel et al. 2019). Moreover, although some of the physical structure of the reef remained intact 1 yr following the heat stress event, Magel et al. (2019) detected significant declines in reef structural complexity, and complexity was still higher at less disturbed sites. Thus, lower levels of structural complexity at the high disturbance sites may have limited the number of fish returning to these reefs after the El Niño. This suggests that the most important fishing sites on Kiritimati (given their proximity to the island's major villages) may be the ones to suffer the sharpest ecological impacts in the face of increasing climate change.

Community structure

The structure of the reef fish community as a whole also changed as a result of the heat stress. A significant shift in reef fish community structure during heat stress has previously been observed on southern Mexican reefs in conjunction with a strong El Niño (López-Pérez et al. 2016). However, while the shift in assemblage structure on Kiritimati was driven by declines in the majority of trophic groups, the shift observed by López-Pérez et al. (2016) was driven by both increases and decreases, likely as a result of much milder coral bleaching. Short-term shifts in reef fish community structure were also observed six months after the 1998 mass coral bleaching event on reefs in Tanzania (Lindahl et al. 2001). These shifts were primarily driven by increases in herbivorous parrotfishes and surgeonfishes and occurred in conjunction with substantial (88%) loss of coral cover, similar to the results of our study. While few studies to date have formally examined short-term shifts in reef fish

community structure either during or after coral bleaching, these comparisons suggest that the trophic groups responsible for shifts in community structure may largely be tied to the severity of coral loss on associated reefs. When interpreting these results, however, it should be noted that the R^2 values for our PERMANOVA tests were quite low, suggesting that heat stress explained little variation in reef fish community structure. As such, additional studies are needed to further examine the effects of heat stress on the structure of reef fish communities, and to determine whether such changes have implications for ecosystem function.

Implications and future studies

The short-term shifts in reef fish communities documented here suggest that future studies on El Niño should focus not only on the impacts of bleaching-associated coral loss, but also the immediate impacts of elevated water temperatures on coral reef fish communities. In particular, our observed declines in reef fish biomass and abundance have several implications for the maintenance of healthy coral reef ecosystems in the face of increasing climate change and human coastal development. Marine heatwaves have already increased in frequency and duration over the past few decades (Oliver et al. 2018), and are projected to become even more severe with continued climate change (Frölicher et al. 2018). Our results suggest that the biomass of important fisheries-targeted species (e.g., herbivores and piscivores) declines during heat stress, which could severely impact coastal communities, especially those on remote island nations, whose livelihoods are centered around these important reef resources. However, it should be noted that these observed declines occurred at the epicenter of the 2015–2016 El Niño and mass coral bleaching event. More research will be needed to better understand how both the magnitude and duration of warming impact the response of reef fish communities to severe heat stress events, and to what extent these changes impact local reef-dependent communities.

Ocean warming is also predicted to lead to changes in local levels of net primary productivity (Sarmiento et al. 2004, Behrenfeld et al. 2006), which may be problematic for species that are strongly influenced by this factor. Small planktivorous fishes such as damselfish and anthias are a critical component of the marine food web, serving as prey for higher trophic-level piscivores (e.g., groupers) that may be important to local fisheries (Jennings and Polunin, 1995, Pet-Soede et al. 2001). Declines in planktivores at increased water temperatures may therefore have cascading effects that ripple up to higher levels of the coral reef food web and eventually to human coastal communities. Climate change is likely to have profound consequences for tropical fisheries, with maximum catch potential in the tropical Pacific projected to decline by up to 42% by 2055 (Cheung et al. 2010). These changes are predicted to occur in connection with warming-related shifts in both species distributions and local primary productivity. Knowing the responses of individual species to El Niño-associated heat stress and their place in the coral reef food web, combined with knowledge of which species are most important to local fisheries, could help to predict and mitigate the impacts of ocean warming on small island nations that depend heavily on local reef fisheries.

Conclusion

Climate change impacts on coral reef ecosystems are predicted to increase substantially in the coming decades (Hoegh-Guldberg et al. 2019), while human populations continue to expand. In this study we document the negative effects of a severe pulse heat stress event on the tropical reef fish community of an isolated coral atoll, foreshadowing the consequences of more frequent marine heatwaves and continued ocean warming for coral reef ecosystems around the world. Many small island nations, including Kiribati, are predicted to be incredibly vulnerable to the impacts of climate change on coral reefs, in large part due to their dependence on reef fish as a source of food and income (Burke et al. 2011). Our results enhance understanding of the projected effects of climate change on coral reef fishes, and may help managers and reef-reliant communities to better prepare for these impacts. Our finding that the recovery of reef fish communities is impaired by higher levels of local human disturbance also emphasizes the importance of mitigating local stressors currently impacting coral reefs. Successful conservation of our remaining coral reef ecosystems will require action at both local and global scales, to minimize the impacts of ocean warming on coral reef fishes and the millions of people who depend on them.

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