Impacts of heat stress on soft corals, an overlooked and highly vulnerable component of coral reef ecosystems, at a central equatorial Pacific atoll

Dominique G. Maucieri, Julia K. Baum [*]

Department of Biological Sciences, University of Victoria, Victoria, British Columbia V8P 5C2, Canada

ABSTRACT

Climate change threatens coral reefs, with recent heatwaves causing widespread coral bleaching and mortality. Soft corals (order Alcyonacea) provide reef structure and habitat, but most reef research has instead focused on reef-building hard corals (order Scleractinia). Reviewing the primary literature documenting the effects of recent (2014–2020) marine heatwaves on corals, a period including the third global coral bleaching event, we found that only 20% (19/94) of studies presented any results of heat stress effects on soft corals, and even fewer (5%) presented taxonomic-specific results, highlighting the need for further study. Using images ($n = 6265$) collected on 16 expeditions to the world's largest atoll (Kiritimati; central equatorial Pacific) between 2007 and 2019, we quantified soft coral cover around the atoll's shallow (10-12 m depth) forereefs before and after a prolonged heatwave (the 2015/2016 El Niño). Prior to the heatwave, soft coral accounted for 3.0% of the benthic community, with greater cover at more sheltered sites with lower net primary productivity; *Lobophytum* and *Sinularia* were the most common genera. We documented a complete loss of soft coral after the heatwave within our sites. New soft corals were detected in 2019, three years after the heatwave. Photos of individual colonies tracked over time revealed that soft coral structures can persist for several years post-mortality, and hard corals can recruit onto these structures. Our study exposes the vulnerability of soft corals to heat stress, which has received scant previous documentation. Future studies examining the effects of heatwaves on coral bleaching and mortality should include soft corals.

1. Introduction

Coral reefs, which are the most biologically diverse marine ecosystems and provide essential ecosystem services to hundreds of millions of people (Hoegh-Guldberg, 2011), are seriously threatened by climate change (Hoegh-Guldberg et al., 2019; Hughes et al., 2017). Increases in the frequency and duration of marine heatwaves threaten the survival of corals due to coral bleaching (Cai et al., 2014; Claar et al., 2018; Hughes et al., 2018; Oliver et al., 2018). When corals become stressed by factors such as temperature anomalies their symbiotic relationship with the photosynthetic algae (family Symbiodiniaceae) living within their cells break down, leading to the ejection of the symbionts and coral bleaching. In the absence of temperature reductions, this generally leads to coral mortality (Brown, 1997; Glynn, 1983; Putnam et al., 2017). Between 2015 and 2016 an extreme El Niño (L'Heureux et al., 2017) led to widespread coral bleaching and mortality on many reefs around the world, with higher accumulated heat stress on corals than any previously documented El Niño event (Claar et al., 2018; Eakin et al., 2016;

Hughes et al., 2018). A major focus of the coral literature since has been to understand how this El Niño, and the broader 2014–2017 global coral bleaching event (Eakin et al., 2016; Heron et al., 2017), affected reef-building corals and the conditions that lead to coral bleaching and mortality (Eakin et al., 2016). This is important, not only because of the diversity of corals that are threatened, but also because widespread coral losses could have major negative consequences for marine biodiversity more broadly (Burke et al., 2011), as well as for people, through the loss of food, livelihoods and coastal protection (Moberg and Folke, 1999).

Reef building scleractinian corals (order Scleractinia) are important ecosystem engineers and the foundation of tropical coral reef ecosystems (Moberg and Folke, 1999; Putnam et al., 2017). These organisms not only provide important nutrients to their community (Wild et al., 2004) in their oligotrophic environments, but also create critical habitat structure, and provide many other ecosystem services (Moberg and Folke, 1999; Putnam et al., 2017). Soft corals (order Alcyonacea) have skeletons formed of small calcium carbonate sclerites, which allow a degree of rigidity, but they do not form the large calcium carbonate

---

structures of scleractinian corals, which form reefs (Rahman and Oomori, 2008). However, soft corals can still be considered ecosystem engineers, as they provide structure and habitat complexity to their communities, and are also able to regulate sedimentation and affect water currents (Paoli et al., 2017; Poulos et al., 2013; Sánchez, 2017; Valisano et al., 2016). Some predatory fish species are closely associated with soft coral species (Sánchez, 2017). Although soft corals are important components of coral reef communities, most studies focus on reef-building corals, while information and investment into monitoring soft corals is generally lacking (Dinesen, 1983; Richardson et al., 2017a). Consequently, less is known about how soft coral communities will react to increasing heat stress events in the future, let alone under the multiple disturbances associated with global climate change (Côté et al., 2016).

Our objectives here were twofold: *1)* to evaluate the extent to which the impacts of recent heat stress events on soft corals have been studied and *2)* to assess the vulnerability of soft corals to prolonged heat stress. To meet these objectives, we first conducted a systematic literature review to quantify the extent to which soft corals are represented in studies examining the effects of marine heatwaves on corals, focusing specifically on the past seven years, which includes the most recent global coral bleaching event (2014–2017). We then conducted our own empirical analysis, examining the effects of the 2015/2016 El Niño event on soft coral relative abundance on the world's largest atoll, Kiritimati, which experienced ten months of anomalously high temperatures during this period (Claar et al., 2019, 2020). Four genera of soft

coral have been identified on Kiritimati: *Lobophytum, Sinularia, Sarcophyton,* and *Cladiella* (see Fig. S1 for live and bleaching photos). Using community composition data from small benthic photoquadrats, we quantified changes in soft coral cover over a thirteen-year period (2007 to 2019) that included this heatwave. We hypothesized that the relative abundance of soft coral (overall and individual genera) would vary spatially around the atoll's forereefs due to differences in chronic local disturbance and environmental conditions across sites, and that the atoll's El Niño-induced prolonged heatwave would cause significant declines in soft coral cover at all sites.

2. Methods

2.1. Literature review

We first conducted a systematic literature review to quantify the extent to which field studies assessing the impacts of recent marine heatwaves (i.e., 2014 to 2020) on corals included soft corals. This date range was selected to examine heatwaves that included the same time span as the El Niño event that we examined on Kiritimati Island, and to encompass the third global coral bleaching event. On August 25, 2020, we conducted two searches for papers published between 2015 and 2020 using all databases on the Web of Science: one using the search terms: ((coral*) AND (mortal* OR bleach* OR cover* OR health*) AND ("El Niño" OR "El Nino" OR ENSO OR "heat stress" OR "heatwave" OR
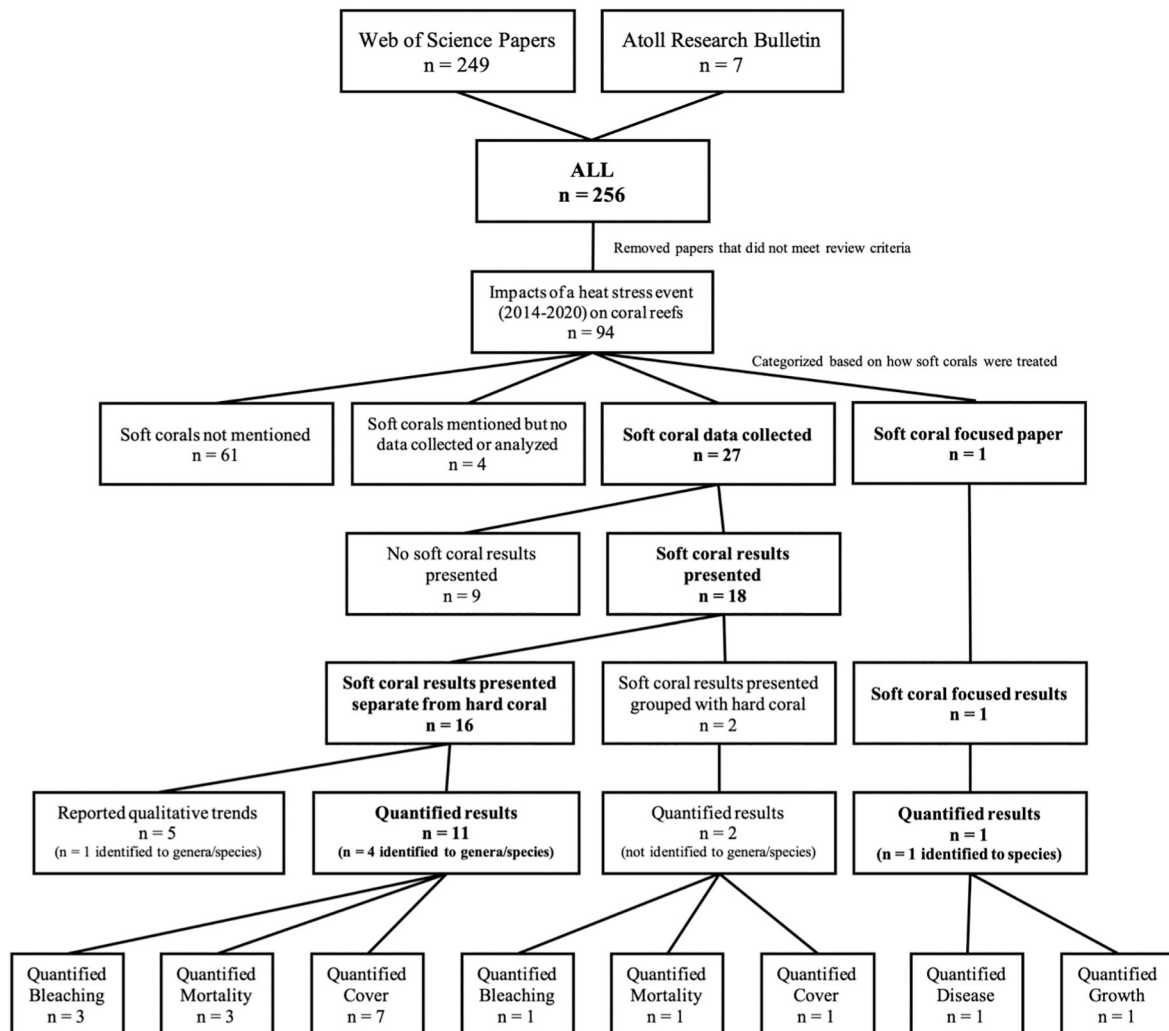

Fig. 1. PRISMA diagram showing results of literature review of the documentation of recent heat stress events (2014–2020) on soft corals.

"thermal stress" OR "temperature anomaly")); a second using the search terms: (("soft coral" OR octoc* OR alycon*) AND (mortal* OR bleach* OR cover* OR health*) AND ("El Niño" OR "El Nino" OR ENSO OR "heat stress" OR "heatwave" OR "thermal stress" OR "temperature anomaly")). On September 2, 2020, we also conducted a search using the previously mentioned search terms on Google Scholar, specifically searching for papers from the Atoll Research Bulletin because this journal is not included in Web of Science.

We evaluated each paper that was returned from these searches, reviewing the titles, abstracts and method sections, to determine if they examined corals during a heatwave between 2014 and present day (Fig. 1). We excluded papers describing lab-based studies or heatwaves prior to 2014 (Fig. 1). The remaining papers that met our criteria, were classified based upon: i) if the study mentioned soft corals (using the terms 'soft coral' or 'octocoral'), ii) if data was collected about soft corals, iii) if results were presented about soft corals, iv) if soft corals were included in figures, v) if soft corals were identified as being from specific genera, or species, vi) if quantitative results were presented, and vii) if there were quantitative results reported, were they regarding bleaching, mortality, growth, cover or disease (Fig. 1).
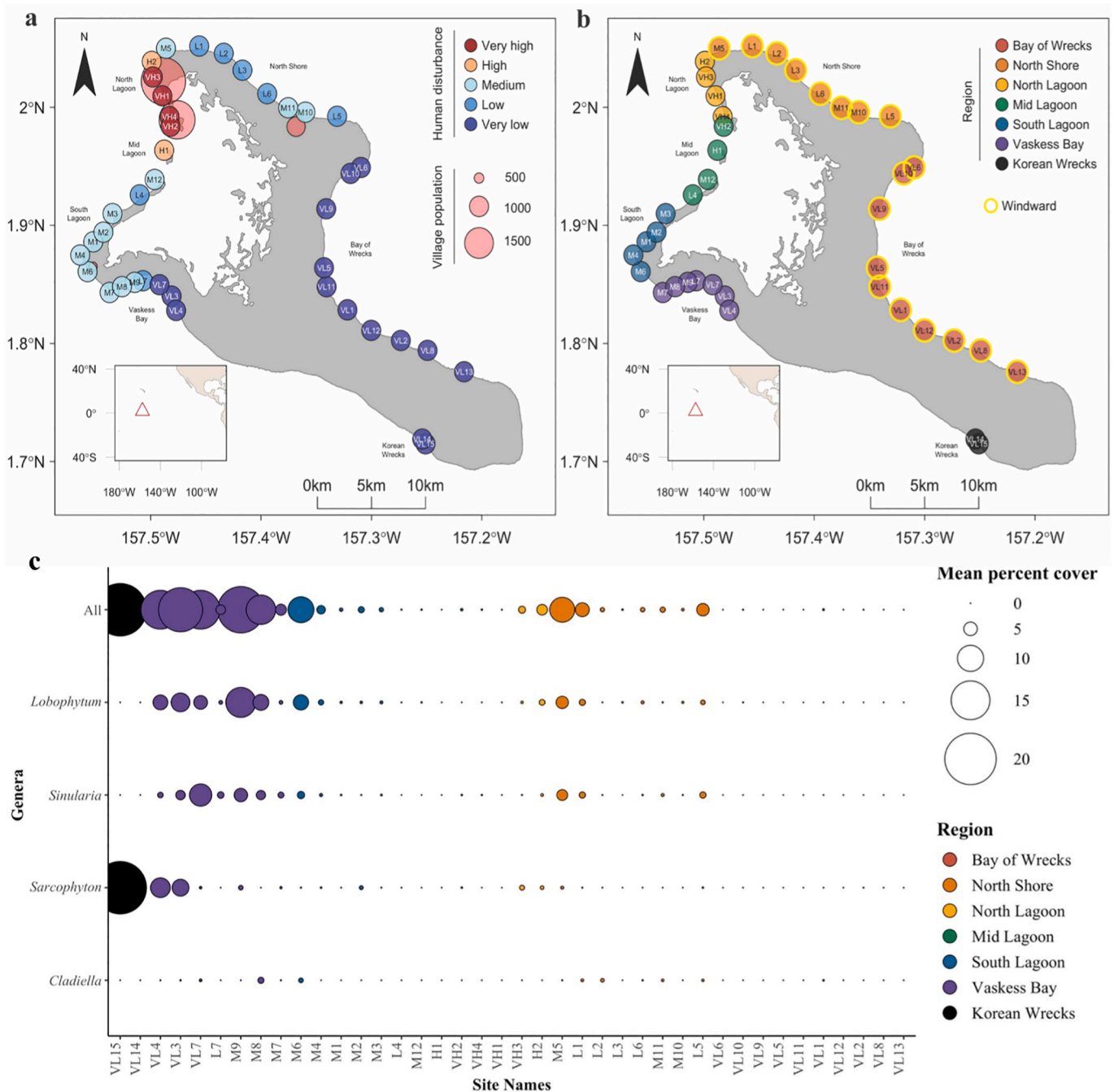

Fig. 2. Monitoring sites on Kiritimati (Christmas Island) classified by: (a) level of chronic local human disturbance, with village locations also shown; (b) regions and wind exposure (i.e., classified as 'windward' if on the side of the atoll exposed to the predominant wind direction; Bosserell et al., 2015). Inset shows the location of Kiritimati in the central equatorial Pacific Ocean; (c) mean soft coral (All and individual genera) for each site, starting with the Korean Wrecks region and going clockwise around the atoll. Size of the circles shows relative coral cover.

2.2. Study site and design

Kiritimati (01°52′N, 157°24′W), Republic of Kiribati, located in the central equatorial Pacific Ocean, is the world's largest atoll by land mass (388 km^2 with 150 km perimeter), and has a population of approximately 6500 people (Kiribati National Statistics Office, 2016). The atoll's villages are concentrated on the northwest coast, with few people living in the southeast, creating a spatial gradient of the local population and associated disturbances across the atoll (Watson et al., 2016; Magel et al., 2020; Fig. 2). Chronic local human disturbance for each of 40 shallow forereef monitoring sites has previously been quantified by combining data on the size of the human population within a two-kilometer radius of each site and the location of fishing activities, calculated from a kernel density of fishing activity (Claar et al., 2019; Watson et al., 2016). For visualization purposes, sites were also grouped into five categorical local human disturbance categories (Very Low, Low, Medium, High and Very High), based on clear breakpoints in the continuous local disturbance measure, as in Magel et al. (2020) and Claar et al. (2020). Reef sites also varied due to oceanographic factors, including primary productivity and wind exposure. We defined site-level exposure (i.e., windward versus sheltered) based on the dominant wind direction (southeasterly; Bosserell et al., 2015), with sheltered sites grouping leeward sites with other sites that are protected from the dominant wind direction. Additionally, we extracted site-level maximum net primary productivity (mg C m^{-2} day^{-1}) data and wave energy (kW m^{-1}; only available for a subset of sites, see Fig. S2) from the Marine Socio-Environmental Covariates (MSEC), an open source data product that uses satellite-derived measures of photosynthetically available radiation, SST, chlorophyll-*a* concentrations and climatology model hindcast reanalyses (Yeager et al., 2017). The MSEC net primary productivity data product is based on NOAA CoastWatch and the wave energy is based on NOAA WAVEWATCH III hindcasts, with both calculated over a 2.5 acrmin grid (Yeager et al., 2017).

Around the atoll, the forereef monitoring sites were surveyed in 16 expeditions between 2007 and 2019, although all sites were not surveyed in every expedition (mean = 16.7 sites/expedition) due to weather and timing constraints (Table S1). Of these, 37 sites are the same as Walsh (2011), which were established in 2007, along with three additional sites (L2, VL12 and H1) established in 2009. At each site, transects were laid along the 10-12 m isobath, and photos of the benthic substrate were taken at each of 20 to 35 randomly selected points along the transect. Quadrats of 0.54 m^2 (0.9 m by 0.6 m) were used from 2007 to 2011, and 1m^2 quadrats were used from 2013 to 2019.

Coral reefs on Kiritimati sustained heat stress for 10 months during the 2015/2016 El Niño event, reaching ~25 °C-weeks (degree heating weeks; DHW) according to NOAA Coral Reef Watch remotely-sensed data (Claar et al., 2019, 2020) and 31.6 °C heating weeks according to in situ temperature loggers (Claar et al., 2019, 2020). Jarvis, a nearby island to Kiritimati, is the only other location to experience heat stress of this intensity (Vargas-Ángel et al., 2019). These two islands were at the epicenter of this El Niño event, one of the most extreme El Niño events on record (Claar et al., 2018, 2019; Eakin et al., 2016). Benthic surveys were conducted on Kiritimati before, during and after the heat stress event.

To examine how quickly soft corals degrade following mortality, we also examined images of permanent 4 m × 4 m photoquadrats, in which the same individual corals were photographed at multiple time points between 2015 and 2019. These photoquadrats were established at nine of the Kiritimati monitoring sites (three per site), along the 10-12 m isobath in early 2015 as part of a separate study (Bruce, 2021; Magel et al., 2019). These have been photographed before (May 2015), during (March 2016) and after the El Niño event (November 2017, July 2017 and July 2019). We visually examined the soft corals in the photoquadrats from two sites (VL3 and M1) as they had large soft coral colonies that could be relocated in subsequent years to allow for the documentation of the bleaching and death of soft corals during the heat stress event and the persistence of structure after the heat stress event.

2.3. Data processing

We identified benthic substrate (*n* = 6381 quadrats) using randomly placed points overlaid on each image using CoralNet, an opensource program created for analysing coral benthic communities (Beijbom et al., 2015). We placed 54 and 100 random points on the 0.54m^2 and 1m^2 sized quadrats, respectively, in order to maintain an average density of one point per cm^2 of quadrat. Additionally, for coral cover analysis, we cropped the 1m^2 quadrats after all benthic substrate annotations were completed, so that the quadrat area would be 0.54m^2 and match the smaller sized quadrats. These cropped quadrats contained an average of 54 randomly annotated points, with variation due to the randomly placed annotation points, and any quadrats that had fewer than 35 or more than 65 were removed from analysis (31 quadrats, 0.49%). The identity of the substrate under each randomly placed point was determined, and soft corals were identified to genus based on visual characteristics. We were unable to identify soft corals to species as this would have required examination of sclerites or genetic analysis, neither of which was able to be performed as the necessary data were not collected. We determined percent cover for each coral genus by dividing the number of points for members of that genus by the total number of useable points in each quadrat. Unusable points included shadows, transect and quadrat hardware or unclear points where accurate identification was not possible. Quadrats where more than 10% of the annotated points were unidentifiable were removed from analysis (85 quadrats; 1.3%). In total, 6265 quadrats (98.1%) were used in analysis.

2.4. Statistical analysis

All statistical analyses were conducted in RStudio (R version 4.0.1). To examine variability in soft coral cover prior to the heat stress event, we fitted a series of generalized linear mixed models, each with a zero inflated beta probability distribution and a logit link function because soft coral cover (i.e., the response variable) was calculated as a proportion of benthic cover. Models were fit using the 'glmmTMB' package (Brooks et al., 2017). As these data spanned eight expeditions before the heat stress event (July 2007–May 2015), we averaged soft coral cover across years for each site after testing for and confirming that there was no trend over time in soft coral cover within this timespan.

We designed 7 models based on a set of a priori hypotheses about the relationship between soft coral cover, site exposure (windward vs sheltered), local human disturbance, and net primary productivity (mg C m^{-2} day^{-1}; all fixed effects). Local human disturbance and net primary productivity were continuous variables and were centered and scaled for analysis. Akaike Information Criterion (AIC) was used for model selection and all models within 6 AIC units from the best model were considered to be part of our final model set. We also ran separate models for each individual soft coral genera to examine if relationships between the overall soft coral community and abiotic factors held at this finer taxonomic scale. As wave energy data was only available for a subset of sites (Fig. S2), a separate model between soft coral cover and wave energy was also performed on the subset of data with this variable.

Finally, to examine the effect of the heat stress event on soft coral cover, we qualitatively examined the amount of soft coral cover present on the reefs during the three years after the heat stress event as exploratory analyses showed there were no soft corals in the three years after the heat stress event. Percent soft coral cover loss was determined for each region around the atoll, except for Korean Wrecks as it was not sampled after the El Niño event (Table S1).

All data, as well as the code for figures and data analyses is publicly available through GitHub (https://github.com/baumlab/Maucieri_Baum_2021_BioCon) and archived through Zenodo.

3. Results

3.1. Literature review

Our literature search returned 256 papers, of which 94 met the scope of our study, being papers that examined the impacts of a recent marine heatwave (2014–2020) on coral reefs (Fig. 1). Of these 94 papers, only one (1.1%) was soft coral focused (Quintanilla et al., 2019), but a further 27 (28.7%) collected data on soft corals along with hard corals. Over two thirds of papers (69.1%), however, either did not mention soft corals at all (64.9%) or mentioned them in passing but did not collect or analyze soft coral data (4.3%; Fig. 1). The single paper focused on soft corals considered one species, *Pacifigorgia cairnsi* (Breedy & Guzman, 2003), and examined how El Niño events affected environmental conditions, which in turn affected the soft coral's growth (Quintanilla et al., 2019). Only 18 of the 27 other papers that collected data on soft corals presented any results on soft corals, and of these, five (5.3%) only presented qualitative trends (Fig. 1). Of the thirteen general coral papers that did present quantitative results on the impacts of heat stress on soft corals, the majority ($n = 9$) did not classify soft corals into specific species or even genera, and two papers grouped soft coral results with that of hard corals. When quantitative soft coral results were presented, some papers only included soft coral on plots, and others included a sentence or two summarizing the changes observed in soft corals. For papers other than the one focused on soft corals, results related to soft corals were not investigated further and the focus was on understanding the patterns in hard coral cover. Most papers that were not focused on soft corals found small changes in soft coral cover and low amounts of soft coral mortality, though one paper, which focused on documenting soft coral species diversity more thoroughly than other papers found that there was a 93% decline in soft coral cover resulting in soft coral cover being less than 1% of the reef (Cerutti et al., 2020).

3.2. Pre-heat stress soft coral cover

Within our focal study location, Kiritimati, soft coral accounted for 3.0% (± 0.18 SEM) of the benthic community cover, on average across sites around the atoll, prior to the 2015/2016 El Niño (Fig. 3b). Overall, *Lobophytum* was the most common soft coral genus (1.3% ± 0.12 SEM), *Sinularia* (0.87% ± 0.087 SEM) the second most common, *Sarcophyton* (0.67% ± 0.093 SEM) the second least common, and *Cladiella* (0.19 ± 0.042 SEM) the rarest genus (Fig. 2c). The abundances of the different genera did show some spatial variability across the atoll, with *Lobophytum* the most common soft coral in most regions other than the south sheltered area (Korean Wrecks), where *Sarcophyton*, despite not being abundant elsewhere on the island, was most common (Fig. 2c).

Mean soft coral cover varied significantly amongst sites, with wind exposure, human disturbance and net primary productivity all being significant predictors in at least one model in the final model set (Table 1, S1). The top model included wind exposure, net primary productivity, and human disturbance, though the latter was not statistically significant (Table 1, Fig. 3). Mean soft coral cover was significantly higher at more sheltered sites, and also significantly negatively related to net primary productivity (Table 1, Fig. S3). All top models included local human disturbance, with a negative relationship between the two, but the relationship was only statistically significant when net primary productivity was not a variable in the model (Table 1, Fig. S3). These patterns – significant relationships between soft coral cover and wind exposure and net primary productivity, but not for human disturbance – held for the two most abundant soft coral genera (*Lobophytum* and *Sinularia*; Table 2, Fig. S3); there were no significant relationships for the two least abundant soft coral genera (*Sarcophyton* and *Cladiella*; Table 2). When wave energy was examined on a subset of sites, there was a tendency for soft coral cover to decline with increasing wave energy, but the effect was not statistically significant (Fig. S2; glm, $z = -1.79$, $p = 0.0728$).
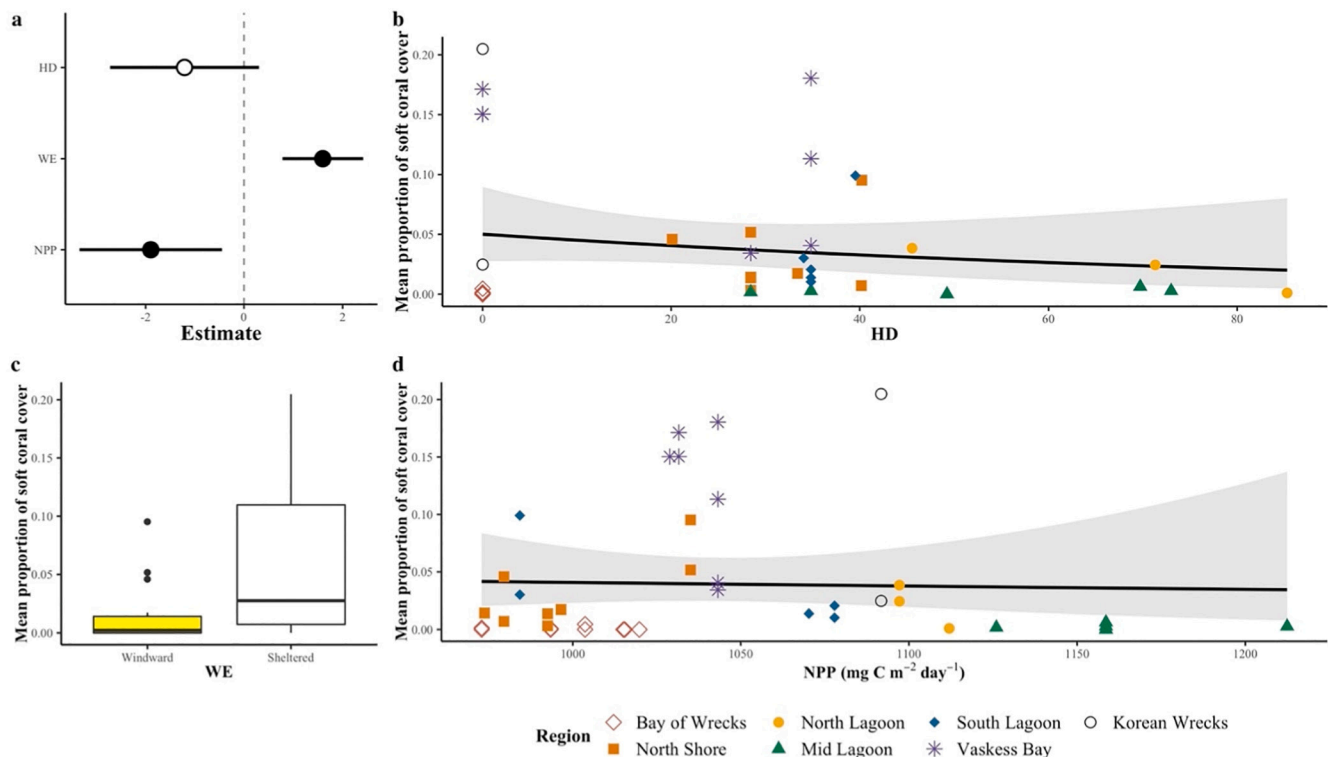

Fig. 3. Soft coral cover prior to the El Niño event for different abiotic factors. (a) Model parameter estimates and 95% confidence intervals for the best model (local human disturbance (HD), wind exposure (WE), maximum net primary productivity (NPP)). (b) Mean soft coral proportion cover for different wind exposures (WE). (c) Mean soft coral proportion cover versus local human disturbance, with colors and shapes showing each region. (d) Mean soft coral proportion cover versus maximum net primary productivity, with colors and shapes showing each region. Colors in (b-d) match region and wind exposure colors in Fig. 2.

Table 1
Parameter estimates for fixed effects from generalized linear mixed effects models describing the factors influencing mean soft coral cover prior to the heat stress event. Years analyzed were July 2007 to May 2015.

Rank	HD	WE	NPP	HD * WE	df	AICc	ΔAICc	w_i
1	−1.21	**1.60**[*]	−1.90[*]		6	−93.8	0	0.665
2	4.58	**1.49**[*]		−6.60	6	−90.9	2.88	0.157
3	**−1.64**[*]	**0.868**[*]			5	−90.2	3.56	0.112

Note: HD = local human disturbance; WE = wind exposure; NPP = max net primary productivity; df = degrees of freedom; AIC$_c$ = AIC corrected for small sample sizes; ΔAIC$_c$ = difference from the lowest AIC$_c$ value, models with ΔAIC$_c$ < 6 are shown, all models available in Table S2; w_i = model weight for each model. Boldface and asterisk indicate statistical significance (α = 0.05).

[*] $p < 0.05$.

Table 2
Parameter estimates for fixed effects from generalized linear mixed effects models describing the abiotic factors influencing each soft coral genera's mean cover prior to the heat stress event. Years analyzed were July 2007 to May 2015.

Model	HD	WE	NPP
Lobophytum	−1.08	**1.61**[*]	**−2.20**[*]
Sinularia	−0.861	**1.13**[*]	**−2.05**[*]
Sarcophyton	−1.48	0.702	0.351
Cladiella	−0.237	0.246	−3.54

Note: HD = local human disturbance; WE = wind exposure; NPP = max net primary productivity. Boldface and asterisk indicate statistical significance (α = 0.05).

[*] $p < 0.05$.

3.3. Heat stress event

In the two years following the prolonged heatwave (sampled during three expeditions: November 2016, July 2017, June 2018), we did not observe any live soft corals in any photoquadrats ($n = 1439$ quadrats), suggesting 100% loss of soft coral cover due to the heat stress event, at least on shallow forereefs around the atoll. Examination of individual soft coral colonies in permanent photoquadrats showed that although *Lobophytum* and *Sinularia* colonies bleached and died during the prolonged heat stress event, the colony structures persisted for at least three years providing a structure which hard corals recruited to (Fig. 4). In contrast, *Sarcophyton* colonies in the permanent photoquadrats all died and completely degraded between the 2015 and first 2016 sampling seasons (Fig. 4). Three years after the end of the 2015/2016 El Niño event, during our July 2019 expedition, we observed five sites with one colony each of healthy, young soft corals (Fig. 5).

4. Discussion

Our literature review reveals how little is known about how heat stress events impact soft coral communities and demonstrates the literature's focus on hard corals. We also found that on a large coral atoll (Kiritimati), soft coral cover varied spatially across the atoll's shallow forereefs. Our subsequent models suggested that this spatial variation might be attributed to differences in wind exposure and net primary productivity amongst sites; local human disturbance was not found to significantly affect soft coral cover in our top model, which was unexpected. However, as expected, a prolonged El Niño event had devastating consequences on the soft coral community, with a documented 100% loss of soft coral in our study area. Finally, we found evidence of soft corals leaving behind structures on the reef after they die, adding to reef structural complexity, as well as initial signs of soft coral recovery three years after the heatwave.

Our literature review indicates that few studies have examined how heat stress events affect soft coral communities, even when overall benthic community cover data have been collected. Soft coral assemblages provide habitat, structure and can alter environmental conditions for organisms living on or around the corals (Paoli et al., 2017; Poulos et al., 2013; Sánchez, 2017; Valisano et al., 2016), however the minimal

understanding of how soft corals are affected by heat stress means that we do not know how these environments have been altered, or how they will recover. While not all coral reefs have soft coral assemblages present, this literature review shows that the majority of reef studies do not acknowledge soft corals, which suggests that they may be overlooked on many reefs, not just absent from them. Some research groups collected data on soft coral benthic cover, but did not analyze these data in detail or at all. This is problematic because it means the scientific literature is not reflective of the amount and types of data being collected. There needs to be a greater effort put into not only collecting soft coral data, but collecting these data at higher taxonomic resolutions (i.e., species or genera), in order to understand dynamics between different soft coral assemblages and the fish and invertebrate assemblages associated with them (Sánchez, 2017). Data being collected by current researchers regarding soft coral in different areas and being exposed to different environmental stressors also needs to be reported in the literature to help inform conservation and restoration initiatives, and to help us understand how reefs will continue to change into the future. As recommended by Claar et al.'s (2018) meta-analysis, when heat stress events are being reported in the literature, along with information on hard coral, researchers should also record and report soft coral taxonomic composition, species- or genera-specific responses to heat stress, and the overall community response of all soft corals.

In our empirical analysis of Kiritimati's forereefs, we found that prior to heat stress, wind exposure, net primary productivity, and local human disturbance were all negatively related to mean soft coral cover, but only the effects of the first two were statistically significant. Indeed, areas on the southern side of the island (Vaskess Bay and Korean Wrecks), which are sheltered from the predominant wind direction, have lower net primary productivity, and minimal exposure to disturbance, with no infrastructure or pollution and virtually no fishing in them, had the highest soft coral cover (Fig. 2c). Soft corals tend to grow in more sheltered sites with lower wave energy as wave energy is known to be damaging to soft corals and to inhibit their growth so this needs to be studied further (Dinesen, 1983; Fabricius, 1997). These more sheltered sites, along with those on the leeward side of the island are sheltered from trade winds and likely experience lower wave exposure, though this needs to be confirmed with the use of in situ current meters. Although we found no significant effect of wave energy on soft corals, this was likely due to low sample sizes and a lack of data from sites experiencing heavier wave action in the Bay of Wrecks. The effects of local anthropogenic disturbance have been understudied in soft corals, but we hypothesized that higher nutrient concentrations, pollution, and physical damage from dredging near human populations would lead to a decrease in soft coral cover (Cornish and DiDonato, 2004; Januar et al., 2015). We speculate that our inability to detect such an effect is due to some confounding of our three main variables, rather than a true lack of effect. Our study instead suggests that other abiotic factors, which may be related to local human disturbance such as net primary productivity have a negative relationship with mean soft coral cover. However, net primary productivity variation is not only due to human activity (Walsh, 2011), but also upwelling (Claar et al., 2019), which therefore may play a crucial role in soft coral growth and may also be difficult to disentangle
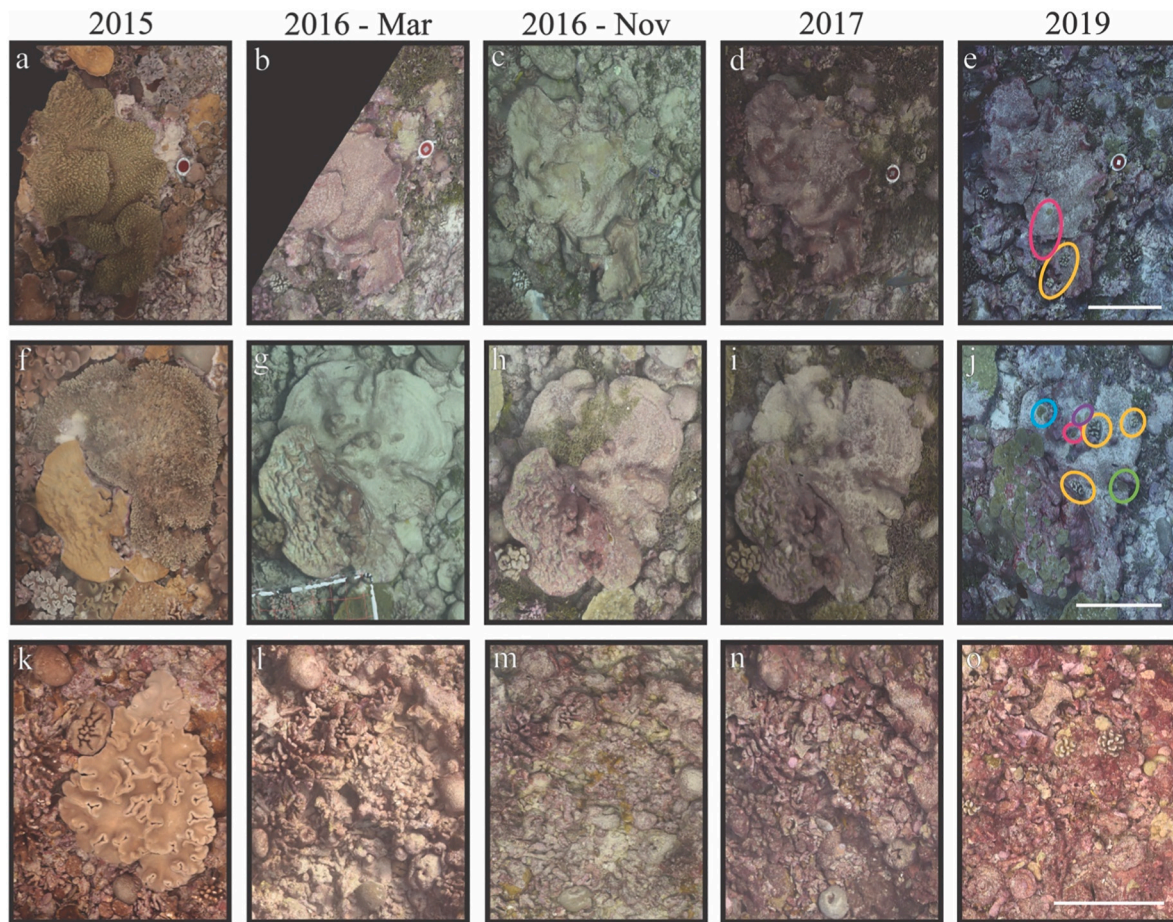
Fig. 4. Photos of three individual soft coral colonies (top - *Lobophytum* sp., middle - *Sinularia* sp., bottom - *Sarcophyton* sp.) taken in permanent photoquadrats at two forereef sites VL3 (top, middle rows) and M1 (bottom row) on Kiritimati over a four-year period, showing the progression from live coral, to mortality and decay. 2015 sampling period was before the El Niño event, March of 2016 was during the El Niño event, and November 2016, 2017 and 2019 sampling periods were after the El Niño event. Circles in panels (e) and (j) show location of hard coral recruits on dead soft coral structures with colors representing different genera; orange for *Pocillopora*, blue for *Porites* and purple, pink and green for separate morphotypes. Note: some hard coral recruit identities are only to morphotype as genera cannot be accurately determined at this size. White bar in panels (e), (j) and (o) show scale bars representing 50 cm for each row. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

from local human disturbance.

We also found spatial variation in the dominant soft coral genera amongst sites, suggesting variability in environmental preferences amongst different soft coral taxa. Our analyses of the relationships between individual soft coral genera and environmental variables did not, however, shed light on the factors underlying these differences because the two most common soft coral genera (*Lobophytum* and *Sinularia*) showed similar relationships, with both negatively influenced by wind exposure and primary productivity. This similarity may have arisen because of these species' phylogenetic relatedness, as both genera are from the Alcyoniidae family (McFadden et al., 2006), or similar life history characteristics. As these were the most abundant soft coral genera, these genera likely influenced the total soft coral cover. The other two genera (*Sarcophyton* and *Cladiella*) were rare, which likely led to a lack of power to detect relationships, as there were no significant main effects in these models. In general, little is understood about how soft coral species differ in their responses to environmental conditions and stressors, but there have been documented differences in survival amongst species due to stressors (Loya et al., 2001; Slattery et al., 2019). Further studies with soft coral from these and other families will help researchers to better understand if there are clear genera specific differences within the response of soft coral communities to abiotic factors and heat stress events which would allow for similar conservation actions being able to assist many genera, instead of general or species-

specific actions needed to maintain soft coral communities.

Our study also revealed that prolonged heat stress can be devastating for soft corals, with a complete loss of soft coral cover at our study sites over the course of the 2015/2016 El Niño event. The mortality of soft corals (100%) exceeded that of hard corals on Kiritimati Island (Baum unpublished data), suggesting soft corals are especially sensitive to extreme sea temperatures. Soft coral skeletons are made of calcified sclerites, which are not as solid as hard coral skeletons, but permanent photoquadrats on Kiritimati island documented the persistence of soft coral skeletons after coral death. *Sinularia* and *Lobophytum* soft corals in our study left behind a structure that contributed to the overall complexity of the reef and provided structure for new hard coral recruits to settle on for three years post-mortality (Fig. 4). Some soft corals from the genus *Sinularia* are known to lithify individual calcitic sclerites at the base of the colony, with a cement known as spiculite, which consists of aragonite crystals (Jeng et al., 2011; Konishi, 1982; Shoham et al., 2019). We propose this may be occurring in some corals from the genus *Lobophytum* as well. These corals, after they die, left structures behind which became areas colonized by turf algae and crustose coralline algae growth, eventually allowing for the settlement and recruitment of at least five hard coral species (including *Pocillopora* and *Porites*), which to our knowledge is the first documentation of hard coral recruitment on soft coral skeletons (shown in Fig. 4). The mechanism of this settlement warrants further investigation to determine if soft coral skeletons have
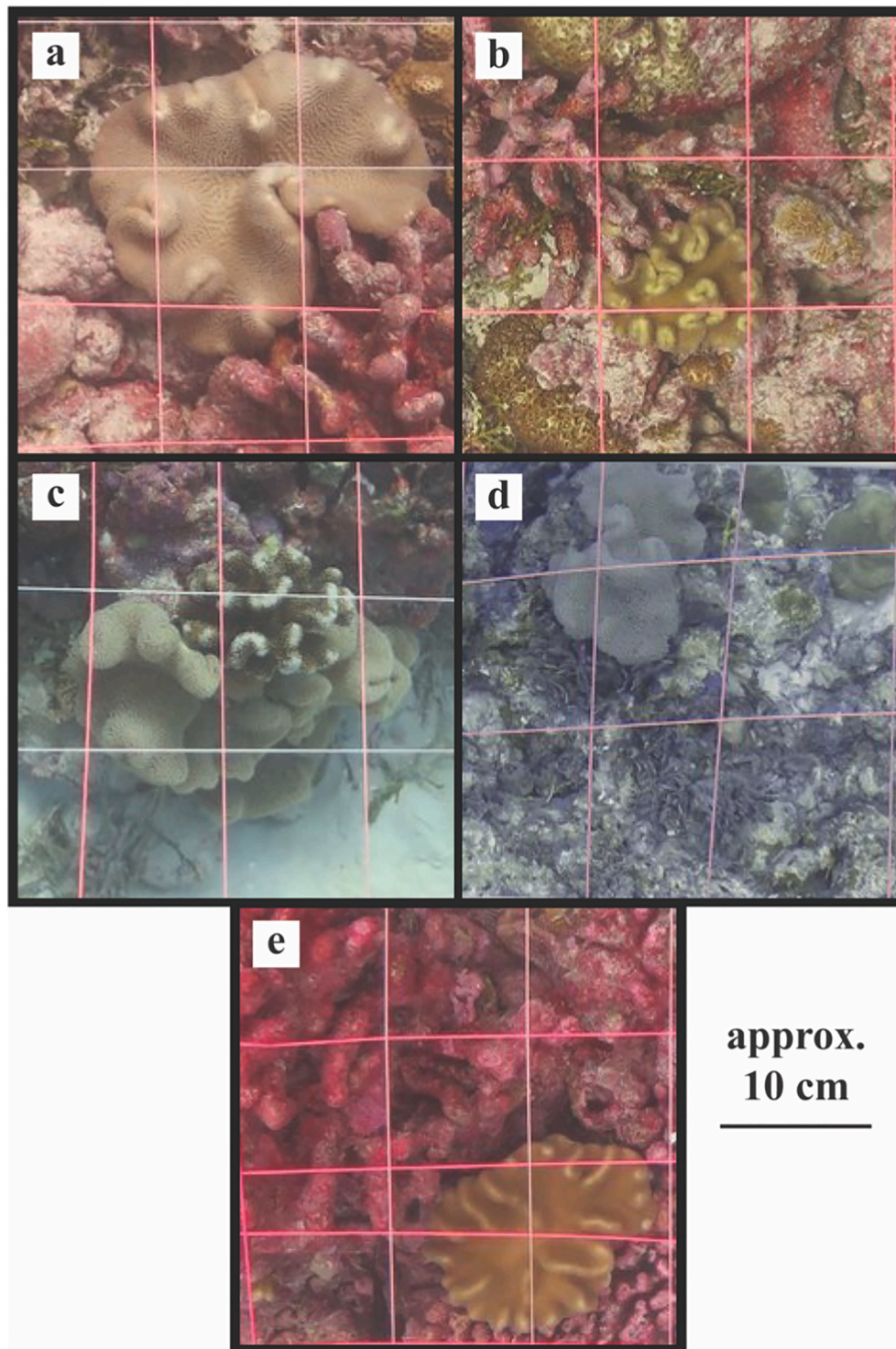
Fig. 5. Photos of the recorded soft corals from small photoquadrats present on Kiritimati after the 2015/2016 El Niño event. All are from 2019 and provide the first evidence of recovery following the El Niño event. (a–d) *Sarcophyton* from sites VL4, M6, M1 and M2 respectively (e) *Lobophytum* from site M12.

higher rates of hard coral recruitment than the surrounding benthos.

The structure that soft corals provide while they are alive is not well understood, with only a few papers examining soft coral community habitat complexity (Richardson et al., 2017a, 2017b; Wilson et al., 2007). Recent studies suggest that soft corals contributed important habitat to reef and fish communities (Epstein and Kingsford, 2019) and that under current ocean acidification projections, we may see a shift from hard coral communities to those dominated by soft corals (Gómez et al., 2015; Inoue et al., 2013). Even less is known about the structure

provided by dead soft corals, but if soft corals are contributing the formation of reefs, they could still influence reef composition. Hard coral skeletons are formed of aragonite crystals while soft coral sclerites consist of calcite crystals, some of which have been recorded as being high magnesium calcite and others low magnesium calcite (Januar et al., 2017; Konishi, 1982; Rahman et al., 2011; Shoham et al., 2019). The composition of soft coral sclerites would influence the solubility of reefs as high magnesium calcite is more soluble than aragonite, making reefs that are formed from high magnesium calcite soft corals more

susceptible to ocean acidification (Andersson et al., 2005; Eyre et al., 2014; Rahman et al., 2011). Soft coral reef formation needs to be studied further in order to understand how reef structures will react to changing oceanic conditions. The role of soft corals in community structure, reef recovery, and coral recruitment also needs to be better understood in order to know how to conserve coral reefs and their biodiversity.

Despite apparent local extinction of soft corals during the El Niño event, we found initial signs of recovery three years after the event, with the detection of a small number of young colonies. Although it is possible that some soft corals persisted in shallow areas outside of our monitoring sites, we suspect that the source of these new corals was colonies in deeper waters than those we surveyed (10 to 12 m) that had survived the event. Soft corals may not be as restricted by depth as hard corals, which may have provided conditions that allowed for soft coral survival in deeper waters (Pupier et al., 2019). Soft corals are known to quickly colonize the benthos after a mass mortality of hard corals (Richardson et al., 2017b). However, with such an extreme loss of soft coral cover, there may not be enough adult soft coral colonies to be able to recolonize and dominate the benthos of Kiritimati. Further sampling to determine how the soft coral populations recover from the bleaching event will allow for better-informed conclusions about how surviving soft corals will affect patterns of soft coral recovery.

In conclusion, there is a lack of understanding in the current scientific literature of how global heat stress events impact soft coral cover. We provide some new insights in this regard, by examining changes in a soft coral community during a prolonged marine heatwave on the world's largest atoll. First, by examining shallow forereefs on the atoll prior to the heatwave, we found evidence that spatial variability in soft coral cover may have arisen due to differences in wind exposure and net primary productivity, both of which negatively influenced soft coral cover. We then documented a 100% loss of soft coral in our study area during the 2015–2016 El Niño-induced heatwave, indicating that soft coral species are very susceptible to prolonged thermal stress. We also showed that soft coral skeletons can persist for several years after the colony dies, and that the remaining structures can provide substrate for hard corals to settle on, leading to increases in reef complexity even after the death of the soft corals. Finally, we recorded initial signs of soft coral community recovery, however, it is too soon to tell how the soft coral community will recolonize, so further studies are needed to understand rates of soft coral recover after extreme mortality events.

CRediT authorship contribution statement

D.G.M. and J.K.B. conceived of the study. J.K.B. and the Kiritimati field teams collected the data. D.G.M. collated and cleaned the data. D.G.M. conducted the data analysis and wrote the manuscript with input from J.K.B.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2021.109328.

References

Andersson, A., Mackenzie, F., Lerman, A., 2005. Coastal ocean and carbonate systems in the high CO2 world of the Anthropocene. Am. J. Sci. 305, 875–918. https://doi.org/10.2475/ajs.305.9.875.

Beijbom, O., Edmunds, P.J., Roelfsema, C., Smith, J., Kline, D.I., Neal, B.P., Dunlap, M.J., Moriarty, V., Fan, T.-Y., Tan, C.-J., Chan, S., Treibitz, T., Gamst, A., Mitchell, B.G., Kriegman, D., 2015. Towards automated annotation of benthic survey images: variability of human experts and operational modes of automation. PLoS ONE 10, 1–22. https://doi.org/10.1371/journal.pone.0130312.

Bosserell, C., Reddy, S., Lai, D., 2015. WACOP Wave Climate Reports. WACOP Kiritimati, Kiritimati.

Brooks, Mollie E., Kristensen, Kasper, van Benthem, Koen J., Magnusson, Arni, Berg, Casper W., Nielsen, Anders, Skaug, Hans J., Maechler, Martin, Bolker, Benjamin M., 2017. glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. The R Journal 9, 378–400. https://doi.org/10.3929/ethz-b-000240890.

Brown, B.E., 1997. Coral bleaching: causes and consequences. Coral Reefs 16, S129–S138. https://doi.org/10.1007/s003380050249.

Bruce, K., 2021. Application of Structure-from-motion Photogrammetry to Quantify Coral Reef Structural Complexity Change Following a Mass Mortality Event. University of Victoria, Victoria, Canada.

Burke, L., Reytar, K., Spalding, M., Perry, A., 2011. Reefs at risk revisited. World Resour. Inst. 1–130.

Cai, W., Borlace, S., Lengaigne, M., van Rensch, P., Collins, M., Vecchi, G., Timmermann, A., Santoso, A., McPhaden, M.J., Wu, L., England, M.H., Wang, G., Guilyardi, E., Jin, F.-F., 2014. Increasing frequency of extreme El Niño events due to greenhouse warming. Nat. Clim. Chang. 4, 111–116. https://doi.org/10.1038/nclimate2100.

Cerutti, J.M.B., Burt, A.J., Haupt, P., Bunbury, N., Mumby, P.J., Schaepman-Strub, G., 2020. Impacts of the 2014–2017 global bleaching event on a protected remote atoll in the Western Indian Ocean. Coral Reefs 39, 15–26. https://doi.org/10.1007/s00338-019-01853-1.

Claar, D.C., Szostek, L., McDevitt-Irwin, J.M., Schanze, J.J., Baum, J.K., 2018. Global patterns and impacts of El Niño events on coral reefs: a meta-analysis. PLoS ONE 13, 1–22. https://doi.org/10.1371/journal.pone.0190957.

Claar, D.C., Cobb, K.M., Baum, J.K., 2019. In situ and remotely sensed temperature comparisons on a Central Pacific atoll. Coral Reefs 38, 1343–1349. https://doi.org/10.1007/s00338-019-01850-4.

Claar, D.C., Starko, S., Tietjen, K.L., Epstein, H.E., Cunning, R., Cobb, K.M., Baker, A.C., Gates, R.D., Baum, J.K., 2020. Dynamic symbioses reveal pathways to coral survival through prolonged heatwaves. Nat. Commun. 11, 1–10. https://doi.org/10.1038/s41467-020-19169-y.

Cornish, A.S., DiDonato, E.M., 2004. Resurvey of a reef flat in American Samoa after 85 years reveals devastation to a soft coral (Alcyonacea) community. Mar. Pollut. Bull. 48, 768–777. https://doi.org/10.1016/j.marpolbul.2003.11.004.

Côté, I.M., Darling, E.S., Brown, C.J., 2016. Interactions among ecosystem stressors and their importance in conservation. Proc. R. Soc. B Biol. Sci. 283, 1–9. https://doi.org/10.1098/rspb.2015.2592.

Dinesen, Z.D., 1983. Patterns in the distribution of soft corals across the central Great Barrier Reef. Coral Reefs 1, 229–236.

Eakin, C.M., Lui, G., Gomex, A.M., De La Cour, J.L., Heron, S.F., Skirving, W.J., Geiger, E. F., Tirak, K.V., Stong, A.E., 2016. Global coral bleaching 2014–2017: status and an appeal for observations. Reef Encount. 31, 20–26.

Epstein, H.E., Kingsford, M.J., 2019. Are soft coral habitats unfavourable? A closer look at the association between reef fishes and their habitat. Environ. Biol. Fish 102, 479–497. https://doi.org/10.1007/s10641-019-0845-4.

Eyre, B.D., Andersson, A.J., Cyronak, T., 2014. Benthic coral reef calcium carbonate dissolution in an acidifying ocean. Nat. Clim. Chang. 4, 969–976. https://doi.org/10.1038/nclimate2380.

Fabricius, K.E., 1997. Soft coral abundance on the central Great Barrier Reef: effects of *Acanthaster planci*, space availability, and aspects of the physical environment. Coral Reefs 16, 159–167.

Glynn, P.W., 1983. Extensive "bleaching" and death of reef corals on the Pacific coast of Panamá. Environ. Conserv. 10, 149–154.

Gómez, C.E., Paul, V.J., Ritson-Williams, R., Muehllehner, N., Langdon, C., Sánchez, J.A., 2015. Responses of the tropical gorgonian coral *Eunicea fusca* to ocean acidification conditions. Coral Reefs 34, 451–460. https://doi.org/10.1007/s00338-014-1241-3.

Heron, S.F., Eakin, M.C., Douvere, F., Anderson, K., Day, J.C., Geiger, E., Hoegh-Guldberg, O., van Hooidonk, R., Hughes, T., Marshall, P., Obura, D., 2017. Impacts of Climate Change on World Heritage Coral Reefs: A First Global Scientific Assessment. UNESCO World Heritage Centre, Paris.

Hoegh-Guldberg, O., 2011. Coral reef ecosystems and anthropogenic climate change. Reg. Environ. Chang. 11, 215–227. https://doi.org/10.1007/s10113-010-0189-2.

Hoegh-Guldberg, O., Jacob, D., Taylor, M., Bolaños, T.G., Bindi, M., Brown, S., Camilloni, I.A., Diedhiou, A., Djalante, R., Ebi, K., Engelbrecht, F., Guiot, J., Hijioka, Y., Mehrotra, S., Hope, C.W., Payne, A.J., Pörtner, H.-O., Seneviratne, S.I., Thomas, A., Warren, R., Zhou, G., 2019. The human imperative of stabilizing global climate change at 1.5°C. Science 365, 1–11. https://doi.org/10.1126/science.aaw6974.

Hughes, T.P., Barnes, M.L., Bellwood, D.R., Cinner, J.E., Cumming, G.S., Jackson, J.B.C., Kleypas, J., van de Leemput, I.A., Lough, J.M., Morrison, T.H., Palumbi, S.R., van Nes, E.H., Scheffer, M., 2017. Coral reefs in the Anthropocene. Nature 546, 82–90. https://doi.org/10.1038/nature22901.

Hughes, T.P., Anderson, K.D., Connolly, S.R., Heron, S.F., Kerry, J.T., Lough, J.M., Baird, A.H., Baum, J.K., Berumen, M.L., Bridge, T.C., Claar, D.C., Eakin, C.M., Gilmour, J.P., Graham, N.A.J., Harrison, H., Hobbs, J.-P.A., Hoey, A.S., Hoogenboom, M., Lowe, R.J., McCulloch, M.T., Pandolfi, J.M., Pratchett, M., Schoepf, V., Torda, G., Wilson, S.K., 2018. Spatial and temporal patterns of mass bleaching of corals in the anthropocene. Science 359, 80–83. https://doi.org/10.1126/science.aan8048.

Inoue, S., Kayanne, H., Yamamoto, S., Kurihara, H., 2013. Spatial community shift from hard to soft corals in acidified water. Nat. Clim. Chang. 3, 683–687. https://doi.org/10.1038/nclimate1855.

Januar, H.I., Chasanah, E., Tapiolas, D.M., Motti, C.A., Liptrot, C.H., Wright, A.D., 2015. Influence of anthropogenic pressures on the bioactivity potential of sponges and soft corals in the coral reef environment. Squalen Bull. Mar. Fish. Postharvest Biotechnol. 10, 51–59. https://doi.org/10.15578/squalen.v10i2.108.

Januar, H.I., Zamani, N.P., Soedharma, D., Chasanah, E., 2017. Bioactive cembranoid composition in the soft coral of *Sarcophyton glaccum* on the response to changing pH. Indones. J. Mar. Sci. 22, 25–30. https://doi.org/10.14710/ik.ijms.22.1.25-30.

Jeng, M.-S., Huang, H.-D., Dai, C.-F., Hsiao, Y.-C., Benayahu, Y., 2011. Sclerite calcification and reef-building in the fleshy octocoral genus *Sinularia* (Octocorallia: Alcyonacea). Coral Reefs 30, 925–933. https://doi.org/10.1007/s00338-011-0765-z.

Kiribati National Statistics Office, 2016. 2015 Population and Housing Census, vol. 1. Kiribati National Statistics Office, Bairiki, Tarawa, Kiribati.

Konishi, K., 1982. Alcyonarian spiculite: limestone of soft corals. Proc. 4th Int. Coral Reef Symp. 1, 643–649.

L'Heureux, M.L., Takahashi, K., Watkins, A.B., Barnston, A.G., Becker, E.J., Liberto, T.E.D., Gamble, F., Gottschalck, J., Halpert, M.S., Huang, B., Mosquera-Vásquez, K., Wittenberg, A.T., 2017. Observing and predicting the 2015/16 El Niño. Bull. Am. Meteorol. Soc. 98, 1363–1382. https://doi.org/10.1175/BAMS-D-16-0009.1.

Loya, Y., Sakai, K., Yamazato, K., Nakano, Y., Sambali, H., Woesik, R. van, 2001. Coral bleaching: the winners and the losers. Ecol. Lett. 4, 122–131. https://doi.org/10.1046/j.1461-0248.2001.00203.x.

Magel, J.M.T., Burns, J.H.R., Gates, R.D., Baum, J.K., 2019. Effects of bleaching-associated mass coral mortality on reef structural complexity across a gradient of local disturbance. Sci. Rep. 9, 1–12. https://doi.org/10.1038/s41598-018-37713-1.

Magel, J.M.T., Dimoff, S.A., Baum, J.K., 2020. Direct and indirect effects of climate change-amplified pulse heat stress events on coral reef fish communities. Ecol. Appl. 30, 1–15. https://doi.org/10.1002/eap.2124.

McFadden, C.S., France, S.C., Sánchez, J.A., Alderslade, P., 2006. A molecular phylogenetic analysis of the Octocorallia (Cnidaria: Anthozoa) based on mitochondrial protein-coding sequences. Mol. Phylogenet. Evol. 41, 513–527. https://doi.org/10.1016/j.ympev.2006.06.010.

Moberg, F., Folke, C., 1999. Ecological goods and services of coral reef ecosystems. Ecol. Econ. 29, 215–233. https://doi.org/10.1016/S0921-8009(99)00009-9.

Oliver, E.C.J., Donat, M.G., Burrows, M.T., Moore, P.J., Smale, D.A., Alexander, L.V., Benthuysen, J.A., Feng, M., Sen Gupta, A., Hobday, A.J., Holbrook, N.J., Perkins-Kirkpatrick, S.E., Scannell, H.A., Straub, S.C., Wernberg, T., 2018. Longer and more frequent marine heatwaves over the past century. Nat. Commun. 9, 1–12. https://doi.org/10.1038/s41467-018-03732-9.

Paoli, C., Montefalcone, M., Morri, C., Vassallo, P., Bianchi, C.N., 2017. Ecosystem functions and services of the marine animal forests. In: Rossi, S., Bramanti, L.,

Gori, A., Orejas, C. (Eds.), Marine Animal Forests: The Ecology of Benthic Biodiversity Hotspots. Springer International Publishing, Cham, pp. 1271–1312. https://doi.org/10.1007/978-3-319-21012-4_38.

Poulos, D.E., Harasti, D., Gallen, C., Booth, D.J., 2013. Biodiversity value of a geographically restricted soft coral species within a temperate estuary. Aquat. Conserv. Mar. Freshwat. Ecosyst. 23, 838–849. https://doi.org/10.1002/aqc.2362.

Pupier, C.A., Fine, M., Bednarz, V.N., Rottier, C., Grover, R., Ferrier-Pagès, C., 2019. Productivity and carbon fluxes depend on species and symbiont density in soft coral symbioses. Sci. Rep. 9, 1–10. https://doi.org/10.1038/s41598-019-54209-8.

Putnam, H.M., Barott, K.L., Ainsworth, T.D., Gates, R.D., 2017. The vulnerability and resilience of reef-building corals. Curr. Biol. 27, 528–540. https://doi.org/10.1016/j.cub.2017.04.047.

Quintanilla, E., Madurell, T., Wilke, T., Sánchez, J.A., 2019. Dynamic interplay of ENSO events and local hydrodynamic parameters drives demography and health status of gorgonian sea fan populations on a remote tropical Eastern Pacific island. Front. Mar. Sci. 6, 1–9. https://doi.org/10.3389/fmars.2019.00694.

Rahman, M.A., Oomori, T., 2008. Structure, crystallization and mineral composition of sclerites in the alcyonarian coral. J. Cryst. Growth 310, 3528–3534. https://doi.org/10.1016/j.jcrysgro.2008.04.056.

Rahman, M.A., Oomori, T., Wörheide, G., 2011. Calcite formation in soft coral sclerites is determined by a single reactive extracellular protein. J. Biol. Chem. 286, 31638–31649. https://doi.org/10.1074/jbc.M109.070185.

Richardson, L.E., Graham, N.A.J., Hoey, A.S., 2017a. Cross-scale habitat structure driven by coral species composition on tropical reefs. Sci. Rep. 7, 1–11. https://doi.org/10.1038/s41598-017-08109-4.

Richardson, L.E., Graham, N.A.J., Pratchett, M.S., Hoey, A.S., 2017b. Structural complexity mediates functional structure of reef fish assemblages among coral habitats. Environ. Biol. Fish 100, 193–207. https://doi.org/10.1007/s10641-016-0571-0.

Sánchez, J.A., 2017. Diversity and evolution of octocoral animal forests at both sides of tropical America. In: Rossi, S., Bramanti, L., Gori, A., Orejas, C. (Eds.), Marine Animal Forests: The Ecology of Benthic Biodiversity Hotspots. Springer International Publishing, Cham, pp. 111–143. https://doi.org/10.1007/978-3-319-21012-4_39.

Shoham, E., Prohaska, T., Barkay, Z., Zitek, A., Benayahu, Y., 2019. Soft corals form aragonite-precipitated columnar spiculite in mesophotic reefs. Sci. Rep. 9, 1–9. https://doi.org/10.1038/s41598-018-37696-z.

Slattery, M., Pankey, M.S., Lesser, M.P., 2019. Annual thermal stress increases a soft coral's susceptibility to bleaching. Sci. Rep. 9, 1–10. https://doi.org/10.1038/s41598-019-44566-9.

Valisano, L., Notari, F., Mori, M., Cerrano, C., 2016. Temporal variability of sedimentation rates and mobile fauna inside and outside a gorgonian garden. Mar. Ecol. 37, 1303–1314. https://doi.org/10.1111/maec.12328.

Vargas-Ángel, B., Huntington, B., Brainard, R.E., Venegas, R., Oliver, T., Barkley, H., Cohen, A., 2019. El Niño-associated catastrophic coral mortality at Jarvis Island, central Equatorial Pacific. Coral Reefs 38, 731–741. https://doi.org/10.1007/s00338-019-01838-0.

Walsh, S.M., 2011. Ecosystem-scale effects of nutrients and fishing on coral reefs. J. Mar. Biol. 2011, 1–13. https://doi.org/10.1155/2011/187248.

Watson, M.S., Claar, D.C., Baum, J.K., 2016. Subsistence in isolation: fishing dependence and perceptions of change on Kiritimati, the world's largest atoll. Ocean Coast. Manag. 123, 1–8. https://doi.org/10.1016/j.ocecoaman.2016.01.012.

Wild, C., Huettel, M., Klueter, A., Kremb, S.G., Rasheed, M.Y.M., Jørgensen, B.B., 2004. Coral mucus functions as an energy carrier and particle trap in the reef ecosystem. Nature 428, 66–70. https://doi.org/10.1038/nature02344.

Wilson, S.K., Graham, N.A.J., Polunin, N.V.C., 2007. Appraisal of visual assessments of habitat complexity and benthic composition on coral reefs. Mar. Biol. 151, 1069–1076. https://doi.org/10.1007/s00227-006-0538-3.

Yeager, L.A., Marchand, P., Gill, D.A., Baum, J.K., McPherson, J.M., 2017. Marine socio-environmental covariates: queryable global layers of environmental and anthropogenic variables for marine ecosystem studies. Ecology 98, 1976. https://doi.org/10.1002/ecy.1884.