

Observations of the 2021/2022 La Niña mass coral bleaching event on the soft coral genus *Sarcophyton* at Magnetic Island (Australia)

Stefano Borghi

`stefano.borghi@my.jcu.edu.au`

James Cook University Faculty of Science and Engineering: James Cook University College of Science and Engineering <https://orcid.org/0000-0002-5458-9514>

Riccardo Mandolini

James Cook University Faculty of Science and Engineering: James Cook University College of Science and Engineering

Nicholas D. Briggs

James Cook University Faculty of Science Engineering and Information Technology: James Cook University College of Science and Engineering

Saara J. Wilson

James Cook University Faculty of Science Engineering and Information Technology: James Cook University College of Science and Engineering

Hillary A. Smith

James Cook University Faculty of Science Engineering and Information Technology: James Cook University College of Science and Engineering

Claudia Trave

James Cook University Faculty of Science and Engineering: James Cook University College of Science and Engineering

Research Article

Keywords: Octocorallia, soft coral diversity, bleaching, *Sarcophyton*, Great Barrier Reef

Posted Date: January 13th, 2025

DOI: <https://doi.org/10.21203/rs.3.rs-5765630/v1>

License:   This work is licensed under a Creative Commons Attribution 4.0 International License.

[Read Full License](#)

Abstract

Coral reef ecosystems are declining globally due to climate change. As most ecological studies have focused on stony corals, the distribution of other benthic communities and their susceptibility to bleaching remain largely overlooked. Soft corals can form diverse and ecologically important assemblages; hence it is important to understand their distribution and quantify the impacts of heatwaves on soft coral demographics. We surveyed soft corals on two inshore fringing reefs: Geoffrey Bay (19°09'13.7"S, 146°52'09.5"E) and Alma Bay (19°08'52.9"S, 146°52'13.7"E) at Magnetic Island. We aimed to survey soft corals to genus level. Then, we quantified the size frequency distribution of *Sarcophyton* colonies as the most abundant genus between substrate types, and examined the susceptibility of *Sarcophyton* to bleaching during the La Niña mass coral bleaching event in January-March 2022. We found the reefs at Magnetic Island to support diverse soft coral communities. *Sarcophyton* was one of the dominant soft coral genera on rock, rubble and sand beds, and colonies of all sizes experienced bleaching. Bleaching occurrence was lower in Alma Bay than Geoffrey Bay (26.66% and 52.27% of *Sarcophyton* colonies bleached, respectively). Bleaching was found to be depth- and size-dependent, as deeper and larger colonies had a greater likelihood to bleach. Since larger *Sarcophyton* colonies were more susceptible to bleaching, the impacts on reproduction, mortality and ecosystem functioning are likely to be significant. This is the first assessment of the soft corals at Magnetic Island and of the susceptibility of a common soft coral genus on the GBR to bleaching.

Introduction

Coral reefs have suffered widespread and frequent heatwaves since the 1980s, which have often resulted in bleaching of coral tissue (Baker et al. 2008; Hughes et al. 2018; Smale et al. 2019). Successive years of severe and large-scale bleaching events during the last decade have now impacted virtually every coral reef, causing reef degradation (Harrison et al. 2019; Pratchett et al. 2021). When prolonged, bleaching can cause extensive mortality in corals (Chakravarti and van Oppen 2018; Claar and Baum 2019), and other cumulative changes in demographic rates (e.g., compromised growth and reproduction) can take place over time (Bak and Meesters 1998; Baker et al. 2008; Kramer et al. 2020). These short- and long-term impacts have been extensively studied in hard corals (Hughes 1984; Babcock 1991; Kramer et al. 2020), while responses to bleaching remain poorly understood in other benthic marine groups, such as soft corals.

Soft corals are abundant and ecologically important on many reefs (Dinesen 1983), contributing to reef structure (Ferrari 2017) and ecosystem functioning by providing habitat, shelter, and foraging opportunities for a variety of marine taxa (Lau et al. 2019; Long et al. 2020). Similar to hard corals, soft corals are also impacted by bleaching. Severe and prolonged bleaching events have been documented to lead to extensive mortality in soft corals, sometimes exceeding that of reef-building hard corals (Maucieri and Baum 2021). Long-term implications on their reproduction and survival have also been reported. In some soft coral genera, sexual reproduction in bleached colonies can fail over multiple annual spawning seasons, significantly reducing the reproductive output of soft coral populations and

therefore their survival post-bleaching (Michalek-Wagner and Willis 2001). However, despite their ubiquity, ecological importance, and known susceptibility to bleaching, the influence of colony size and other factors on soft coral demographic processes during bleaching events, including growth, reproduction, and mortality, remains poorly understood. For instance, in hard corals there is a complex link between species-level and size-dependent susceptibility to bleaching, where the impact of bleaching events on corals varies in severity among colonies of different sizes, with larger colonies expected to be more susceptible (Brandt 2009; Burn et al. 2022).

Numerous reef-wide coral bleaching events have been reported on fringing reefs around Magnetic Island, in the central GBR since 1979 (Jones et al. 1997, Marshall and Baird 2000; Hughes et al. 2018; Smith, Prenzlau, et al. 2022). Increasing seawater temperatures, as well as high macroalgal cover on reef flats around this continental island, have negatively impacted hard coral assemblages (Ceccarelli et al. 2020; Smith, Brown, et al. 2022). However, there are limited records on the impacts of these bleaching events on the local soft coral community (Marshall and Baird 2000), and studies on the soft corals of Magnetic Island only focus on few soft coral genera (e.g., *Sarcophyton* and *Lobophytum*) (Coll et al. 1995; Morrissey 1980), possibly underestimating their diversity and ecological importance. Documenting the diversity in soft coral assemblages and their demography during bleaching is necessary to understand how these corals are impacted by increasing temperature over prolonged periods of thermal anomalies, and to provide baseline knowledge to underpin future investigations of broader ecological implications.

This study aims to evaluate the soft coral diversity of Magnetic Island, with a focus on their susceptibility of bleaching during an extreme La Niña. To address this, we firstly assessed the genus-level diversity of soft corals on two reefs at Magnetic Island to characterise the local biodiversity. Then, among the genera identified, *Sarcophyton* was selected for further investigation due to its dominant abundance both at the study site and along the GBR (Fabricius and Alderslade 2001). For a more comprehensive evaluation of the *Sarcophyton* assemblages within the study sites, we characterised the size-frequency distribution of *Sarcophyton* colonies among three different substrate types, including rock, mud/sand and rubble beds. Finally, we examined the bleaching susceptibility of *Sarcophyton* in relation to colony size, depth, and location during the 2022 La Niña mass coral bleaching event.

Methods

Study area

We surveyed two adjacent reefs: Geoffrey Bay (19°09'13.7"S, 146°52'09.5"E) and Alma Bay (19°08'52.9"S, 146°52'13.7"E) at Magnetic Island in the central inshore region of the GBR (Fig. 1). Within the study area, reefs are characterised by rocky reef flats of hard coral and macroalgae (Smith et al. 2022; Smith, Prenzlau, et al. 2022), with a shift to rubble on the outer reef flat, and a sandy/mud slope toward the middle of the bays (Fig. 1).

Soft coral distribution and abundance surveys

We conducted photographic surveys of the soft corals encountered at Geoffrey Bay and Alma Bay. Each day, we conducted two surveys using a standard amount of searching time of 1 hour. Soft coral assemblages were surveyed on 4 February and 20 March 2022 in Alma Bay, and 12 and 27 February 2022 in Geoffrey Bay. During surveys, we identified all encountered soft corals to genus level and visually estimated the abundance of the genera into 4 categories: dominant, abundant, sporadic and rare (see Benayahu et al. 2004). This was done on the inner-mid reef flat, outer reef flat and sandy slope, to provide information on local coral diversity between substrate types. For this study, we consider as soft corals all the octocorals that are not from the former sub-order Calcaxonia and Holaxonia, and the systematics follow the revision of McFadden et al. (2022). Colonies were not collected for further taxonomic examination, hence their classification to species-level was not possible.

Soft coral bleaching susceptibility surveys

Of the 14 soft coral genera observed, *Sarcophyton* occurred in both bays and across all substrate types and therefore was selected for further analyses. Bleaching of *Sarcophyton* colonies was first observed in Geoffrey Bay on 10 January 2022. By the end of January, reports of hard coral bleaching in both Geoffrey and Alma Bay, as well as sea surface temperature (SST) data from the National Oceanic and Atmospheric Administration (NOAA), indicated a possible mass bleaching event impacting the central GBR. Thus, we investigated the potential for soft coral bleaching on 4 February and 20 March in Alma Bay, and 12 and 27 February in Geoffrey Bay. We used photographic surveys to further ensure the same colonies were not recorded multiple times. We conducted SCUBA surveys recording all *Sarcophyton* colonies encountered while swimming from the middle reef flat to sandy slopes and back at depths of ~ 4 to 10m. Colony size was measured as the stalk basal circumference, which was estimated from photos using underwater scale bars. In *Sarcophyton* colonies, the stalk basal circumference is considered to represent the most accurate area measurement, since polyp and stalk height shrink and expand frequently over a 24h period (Hellström and Benzie 2011). For each colony, we recorded the bleaching status, depth, and substrate type (sand, rubble or rock). Bleaching was recorded as a binary variable (presence-absence) rather than a gradient (bleaching score) to reduce potential errors and biases linked to photography-based colour assessment, particularly across colonies with different baseline colouration.

Sea surface temperature (SST) data were obtained from satellite-derived sources. These include SST data for the central GBR from the 5km daily-resolution Regional Virtual Stations product from the Coral Reef Watch (CRW) program (<https://coralreefwatch.noaa.gov/>) for regional time series data. Data were extracted for both Geoffrey Bay and Alma Bay from the PolarWatch program (<https://polarwatch.noaa.gov/>) for a localised time series. SST data were sourced from 1 November 2021 to 17 May 2022 for the region (CRW data), and to 1 May 2022 for Geoffrey and Alma Bay (PolarWatch data). For the regional data, we investigated the relationship between temperature and the

occurrence of bleaching using the accumulation and magnitude of heat stress measured in Degree Heating Weeks (DHW). This cumulative variable has been extensively applied as a coral bleaching index globally, with bleaching expected at values ranging from 4°C-weeks to 8°C-weeks, and severe bleaching and coral mortality predicted at values > 8°C-weeks (Gleeson and Strong 1995; Kayanne 2017; Sakai et al. 2019). Finally, local SST data was used to compare the mean temperature at Magnetic Island specifically with the mean SST of the region.

Statistical analyses

The size-frequency distribution (SFD) of *Sarcophyton* assemblages was assessed using the basal circumference data for colonies on each substrate type. The basal circumference data were log-transformed to meet normality, which was assessed using Shapiro-Wilk tests. Then, we analysed SFDs by looking at the coefficient of variation (CV), skewness and kurtosis. The CV indicates dispersion in size measurements, while skewness and kurtosis identify the presence of either small or large colonies within observed assemblages and possible extreme values in the distribution tails, respectively. When analysing skewness and kurtosis, we further ensured normality by running Jarque-Bera tests, which is a goodness-of-fit test that measures the similarity between skewness and kurtosis to a normal distribution. Finally, we performed two-sample Kolmogorov-Smirnov tests (KS tests) to compare the SFDs of *Sarcophyton* between substrate types.

To assess the size-, depth-, and location-specific bleaching susceptibility of *Sarcophyton* colonies, we modelled the probability of bleaching using a generalised linear mixed effects model with binomial distribution and logit link, in the R package glmmTMB (REF). A range of models were created and model selection was performed using Akaike Information Criterion adjusted for small sample size (AICc). The most parsimonious model structure incorporated the additive effect of all three factors (size, depth, and location). Model validation utilised a simulated residuals plot and tests for overdispersion and zero inflation, all of which were satisfactory.

Results

Soft coral diversity and distribution

Photographic surveys revealed differences in the composition of soft coral genera between Alma Bay and Geoffrey Bay (Fig. 2). Overall, we identified 15 genera of soft corals, most of which were present in Geoffrey Bay (n = 14 genera), compared to 7 genera in Alma Bay. In Geoffrey Bay, the boulders along the shorelines continue in the inner-mid reef flat zone of the bay, providing habitat for localised assemblages of *Iciligorgia* and *Scleronephthya* corals. In the outer reef flat, abundant assemblages of *Sarcophyton* and *Lobophytum* colonies, and more sporadic *Briareum*, *Cladiella* and *Sclerophytum* colonies, occurred on the rocky reef and rubble bed. The majority of the soft coral genera (n = 11), however, occurred on the deeper sand/mud slope. The sandy habitat was dominated by aggregations of *Umbellulifera* and

Briareum soft corals. Genera that are known to prefer mud-sandy habitats were also sporadically observed, including colonies of *Studeriotites* and *Dendronephthya*.

By contrast, the shallow inner-mid reef flat in Alma Bay was inhabited only by sporadic colonies of *Sarcophyton* and occasional colonies of *Lobophytum*. Sporadic assemblages of *Lobophytum*, *Sclerophytum*, *Xenia* and *Briareum* were found in the outer reef flat, where *Sarcophyton* colonies were more abundant. Similar to Geoffrey Bay, the greatest diversity of soft coral genera in Alma Bay was observed on the sandy slope ($n = 6$ genera). This deeper area was dominated by the genus *Sarcophyton*, intermingled with *Briareum* colonies. Other genera observed in the sandy slope of Geoffrey Bay, however, were only rarely observed in Alma Bay, such as *Studeriotites* and *Dendronephthya*.

Although no specimens were collected for further identification to species level, we observed colonies of a species of *Briareum* on sandy slopes and rubble beds in both bays that consists of brown polyps with a white oral disks and white lines that run along the entire length of each tentacle (Fig. 2I). Hence, we identified these colonies as *Briareum cf. hamrum* (see Samimi-Namin and van Ofwegen 2016). Since the species is only known from the Western Indian Ocean and East African reefs, this could represent the first observation of the species in Australian waters, but a further taxonomic examination is necessary to establish the presence of the species at Magnetic Island.

Bleaching was observed to impact most of the dominant zooxanthellate genera in both bays (Fig. 3). The genus *Sarcophyton* was found to be the only soft coral genus present in both bays and from the shallow reefs down to sandy slopes. *Sarcophyton* colonies were also the first observed to show signs of bleaching (first observed ~ 10 January 2022), and one of the last to regain pigmentation (no complete recovery observed in the last exploratory dive in 16 April, 2022).

Regional and local sea surface temperature and cumulative heat stress

Regional SST data revealed that mean daily temperatures were consistently higher during the survey period compared to the long-term averages (Fig. 4). We found SST anomalies ranging from $+0.39^{\circ}\text{C}$ on 21 February 2022, with a peak on 11 March 2022 ($+2.77^{\circ}\text{C}$). In the region, the accumulated daily heat stress (DHW) peaked at $10.91^{\circ}\text{C-weeks}$ on 16 March 2022, indicating possible widespread bleaching occurring from mid-January 2022, and severe bleaching and high mortality likely occurring between mid-March to mid-April 2022.

Daily SST data from Geoffrey Bay (PolarWatch data) revealed the inshore reef was consistently warmer than the average regional measurements, with most values being closer to the daily maximum regional values (Fig. S1). The highest value was recorded on 8 March 2022 (31.27°C).

Sarcophyton population structure

We observed and measured a total of 89 *Sarcophyton* colonies across the two study sites. Of these, 45 colonies were measured in Alma Bay and 44 in Geoffrey Bay, with a mean basal circumference of 18.62 cm (± 1.86 cm SE) and 16.50 cm (± 1.09 cm SE) respectively. After pooling observations from the two locations, we found that the majority of the colonies were on rubble (52.81%; $n = 47$ colonies) rather than sand (24.72%; $n = 22$) or rock (22.47%; $n = 20$) (Fig. 5). *Sarcophyton* assemblages exhibited little variation in their size-frequency distribution over different substrata. The KS tests showed that SFDs in *Sarcophyton* assemblages varied significantly between rocky and sandy areas only ($p = 0.01$). Assemblages growing on all substrate types were normally distributed (Shapiro-Wilk test > 0.05), with the lowest dispersion on sand (CV = 39.45) and the greatest on rock (CV = 66.47). Following log-transformation, all assemblages showed platykurtic distributions over substrate types.

Influence of colony size and environmental variables on bleaching susceptibility.

Overall, bleaching was recorded to be less prevalent in Alma Bay (26.7% of colonies affected) than in Geoffrey Bay (52.27% of colonies affected), and there was a statistically significant increased risk of bleaching in Geoffrey Bay (GLMM, $z = 2.68$, $p = 0.007$; Fig. 6A). Furthermore, we found the likelihood of bleaching to be significantly depth-dependent, with increasing probability of bleaching with greater depth ($z = 2.31$, $p = 0.02$; Fig. 6B). Colony size had a positive relationship with bleaching probability, though this relationship was not statistically significant ($z = 1.86$, $p = 0.06$; Fig. 6C).

Discussion

Soft corals form abundant and diverse assemblages on many reefs globally. However, these diverse communities are often overlooked, and their demography poorly understood (Dinesen 1983; Yesson et al. 2012). This study aimed to bridge this gap by providing insight on the soft coral diversity and susceptibility to bleaching in a representative inshore location of Australia's GBR. We assessed soft coral diversity to genus level from inner reef flats to deeper sandy habitats at Geoffrey and Alma Bay (Magnetic Island). The results indicate a considerable soft coral diversity in both bays, but some genera form localised assemblages on sand beds. Higher soft coral diversity is typical of inner shelf reefs in the first ~ 10 m (Benayahu et al. 2002; Benayahu et al. 2004), where there are genus-specific preferences to settle on hard substrata and/or on sandy/muddy substrates (Fabricius and Alderslade 2001; Poulos et al. 2013; Jenkins and Stevens 2022). For instance, we observed *Umbellulifera* and *Studeriotis* soft corals to grow predominantly in sandy habitats, while *Sarcophyton* colonies were widespread in both hard and soft bottom habitats (Fabricius and Alderslade 2001).

In the context of coral reef degradation due to climate change, the analysis of soft coral population dynamics can provide valuable insights into the ecological integrity of local reef ecosystems. In particular, the size-frequency distributions can provide information on the number of sexually-mature colonies and/or the likelihood of coral assemblages to recover after disturbance (Bak and Meesters 1998). In this study, the size frequency distribution of the common and zooxanthellate soft coral genus *Sarcophyton* showed that assemblages on rocky habitats had the greatest dispersion in colony sizes.

Indeed, rock is the substrate habitat that promotes greatest growth, while unconsolidated rubble and sand beds form dynamic habitats that can be hostile for the establishment and development of soft corals (Duckworth and Wolff 2011). For instance, while some species may exhibit higher resilience, larger colonies can be subjected to higher scouring frequency and mortality on rubble beds (Kenyon et al. 2020), which could explain the infrequent occurrence of large colonies on sand and rubble beds in this study. Similarly, soft corals may struggle to cope with sediment deposition on sandy substratum, and have been reported to be more susceptible to sedimentation than their hard coral counterparts (Riegl 1995). This can explain the lowest dispersion in colony size we observed on sand, where colonies may spend most of their energy to remove sediments that deposit on the polyps rather than promote colony growth (Riegl 1995).

The presence of *Sarcophyton* colonies on unstable substrata, as well as the impacts of more frequent heatwaves in recent years, can have implications on the population dynamics of the genus. For instance, we found 68.54% of all colonies to have a basal stalk circumference equal or smaller than 20 cm (48.31% of them being ≤ 16 cm). This size threshold is important when considering sexual maturity in the genus *Sarcophyton* (see Hellström et al. 2010). Previous studies found *Sarcophyton* colonies to reach sexual maturity when measuring ~ 16 cm (Hellström et al. 2010). Given these observations, our 20 cm threshold likely represents a substantial portion of colonies that may still not be sexually mature. A high number of small colonies can also indicate new recruits in healthy hard coral populations (Kramer et al. 2020), but in coral communities a skewed distribution toward small colony size can also represent a long-term impact of past bleaching events (Álvarez-Noriega et al. 2018). During disturbances, soft corals have been reported to shift to smaller sizes as a defensive mechanism (McFadden 1986). This decrease in size can occur in both hard and soft corals, with colonies expected to shift to a pre-reproductive state (Done 1999; Baker et al. 2008; McClanahan et al. 2008). This can have implications on the future of these populations in Geoffrey and Alma Bays, if colonies settle on unstable substrata and are maintained by asexual reproduction only.

While some soft coral genera observed in our study are azooxanthellate and therefore can withstand bleaching events (e.g., the genera *Studeriotis* and *Nephtyigorgia*) (Fabricius and Alderslade 2001), other soft coral genera are zooxanthellate, such as *Sarcophyton* and *Sclerophyllum*, and have shown high susceptibility to bleaching during past heatwaves at Magnetic Island (Marshall and Baird 2000). Thermal stress during the study period was extreme, as the bleaching event reached a peak of 10.91°C-weeks DHW. We observed, however, that bleaching susceptibility in *Sarcophyton* colonies differed between bays. We found bleaching occurrence was greater in Geoffrey Bay, suggesting that small-scale variations in physical parameters (e.g., currents) can occur and influence the impacts of heatwaves (Green et al. 2019; Page et al. 2019; Decarlo et al. 2020), and therefore estimations of such environmental parameters should be included in further studies. We also found that the susceptibility to bleaching was size-dependent in both bays, where the probability to bleach in smaller colonies was lower than in larger colonies. Our findings corroborate previous observations of other *Sarcophyton* assemblages across the West Pacific during the same bleaching event, which found larger colonies to be more susceptible to bleaching (Shenkar et al. 2005; Baran et al. 2023). Although *Sarcophyton* assemblages are widespread

and abundant in tropical regions (Fabricius and Alderslade 2001), our observations of bleaching susceptibility highlight the complex relationship between this genus and thermal stress. The presence of *Sarcophyton* in the face of prolonged back-to-back bleaching events suggests potential resilience mechanisms that necessitate further investigation. Future studies should focus on understanding the long-term impacts of bleaching on *Sarcophyton* populations, including potential trade-offs between susceptibility and recovery, to better predict responses of these soft coral communities to climate change.

In this study, bleaching susceptibility differed between bays also in relation to depth. The *Sarcophyton* assemblages showed an overall greater likelihood to bleach in the deep. This is surprising, considering that the study sites were all less than ~ 10m deep where coral reefs are known not to experience substantial temperature differences (Riegl and Piller 2003; Hoogenboom et al. 2017). Indeed, we observed no variation in temperature during our surveys (pers. obs.). Hence, temperature alone is unlikely to explain higher occurrence of bleaching in deeper *Sarcophyton* colonies in our study sites, and further works should include other physical parameters.

Conclusion

Our study provides the first comprehensive assessment of soft coral diversity at Magnetic Island, revealing previously undocumented assemblages, particularly in sandy habitats. We found that many zooxanthellate soft coral genera experienced bleaching during the 2021/2022 La Niña thermal stress event, with the widespread genus *Sarcophyton* showing complex patterns of bleaching susceptibility. The unexpected depth-dependent bleaching pattern in the absence of clear temperature stratification in *Sarcophyton* colonies suggests that bleaching in soft corals is driven by complex interactions between multiple environmental and biological factors. While our study examined depth, location, and colony size, other potentially important variables such as water flow, light penetration, sedimentation rates, and colony genetics were not quantified. The relative importance of these factors in determining soft coral bleaching susceptibility remains poorly understood. Our findings highlight that soft coral assemblages are vulnerable to thermal stress. Future research should focus on identifying the mechanisms underlying bleaching susceptibility in soft corals, particularly the interaction between population dynamics and environmental and physical parameters. Such work will be crucial for informing future ecological works and understanding soft coral changes driven by bleaching on a local scale.

Declarations

Conflict of interest

The authors have no relevant financial or non-financial interests to disclose.

Compliance with Ethical Standards

This work did not require ethical approval from an animal welfare committee. All applicable international, national and/or institutional guidelines for the care of organisms for the study have been followed and all necessary approvals have been obtained.

Funding

The authors declare that no funds, grants, or other support were received during the preparation of this manuscript.

Acknowledgments

We thank the crew of the Pleasure Divers dive center at Magnetic Island for providing the dive gear.

Data availability

The authors confirm that the data supporting the findings of this study are available from the corresponding author upon request.

Contributions

SB: Conceptualisation, Methodology, Formal analysis, Investigation, Validation, Data Collection, Data curation, Project administration, Writing- Original Draft, Writing- Review & Editing, Visualisation; RM: Data Collection, Methodology, Data Curation, Formal analysis, Writing- Reviewing and Editing, Visualisation; CT: Methodology, Writing- Reviewing and Editing; SJW: Data Collection, Writing- Reviewing and Editing; NDB: Data Collection, Writing- Reviewing and Editing; HAS: Methodology, Formal analysis, Investigation, Writing- Review & Editing, Visualisation.

References

1. Álvarez-Noriega M, Baird AH, Bridge TCL, Dornelas M, Fontoura L, Pizarro O, Precoda K, Torres-Pulliza D, Woods RM, Zawada K, Madin JS (2018) Contrasting patterns of changes in abundance following a bleaching event between juvenile and adult scleractinian corals. *Coral Reefs* 37(2):527–532. <https://doi.org/10.1007/s00338-018-1677-y>
2. Babcock RC (1991) Comparative Demography of Three Species of Scleractinian Corals Using Age- and Size-Dependent Classifications. *Ecol Monogr* 61(3):225–244. <https://doi.org/10.2307/2937107>
3. Bak RPM, Meesters EH (1998) Coral population structure: The hidden information of colony size-frequency distributions. *Mar Ecol Prog Ser* 162:301–306. <https://doi.org/10.3354/meps162301>
4. Baker AC, Glynn PW, Riegl B (2008) Climate change and coral reef bleaching: An ecological assessment of long-term impacts, recovery trends and future outlook. *Estuarine, Coastal and Shelf Science*, 80(4), 435–471. <https://doi.org/10.1016/j.ecss.2008.09.003>
5. Baran CC, Luciano RMA, Segumalian CS, Valino DAM, Baria-Rodriguez MV (2023) Genus and size-specific susceptibility of soft corals to 2020 bleaching event in the Philippines. *Mar Biol Res* 0(0):1–

12. <https://doi.org/10.1080/17451000.2023.2198242>
6. Benayahu Y, Jeng MS, Perkol-Finkel S, Dai CF (2004) Soft Corals (Octocorallia: Alcyonacea) from Southern Taiwan. II. Species Diversity and Distributional Patterns. *Zoological Stud* 43(3):548–560
7. Benayahu Y, Yosief T, Schleyer MH, Schleyerc MH, Yosief T, Schleyerc MH (2002) Soft Corals (octocorallia, Alcyonacea) of the Southern Red Sea. *Isr J Zool* 48(4):273–283. <https://doi.org/10.1560/HYC7-TUTH-EV77-BEUQ>
8. Brandt ME (2009) The effect of species and colony size on the bleaching response of reef-building corals in the Florida Keys during the 2005 mass bleaching event. *Coral Reefs* 28(4):911–924. <https://doi.org/10.1007/s00338-009-0548-y>
9. Burn D, Matthews S, Pisapia C, Hoey AS, Pratchett MS (2022) Changes in the incidence of coral injuries during mass bleaching across Australia's Coral Sea Marine Park. *Mar Ecol Prog Ser* 682:97–109. <https://doi.org/10.3354/meps13935>
10. Ceccarelli DM, Evans RD, Logan M, Mantel P, Puotinen M, Petus C, Russ GR, Williamson DH (2020) Long-term dynamics and drivers of coral and macroalgal cover on inshore reefs of the Great Barrier Reef Marine Park. *Ecol Appl* 30(1):e02008. <https://doi.org/10.1002/eap.2008>
11. Chakravarti LJ, van Oppen MJH (2018) Experimental Evolution in Coral Photosymbionts as a Tool to Increase Thermal Tolerance. *Front Mar Sci* 5:227. <https://doi.org/10.3389/fmars.2018.00227>
12. Claar DC, Baum JK (2019) Timing matters: survey timing during extended heat stress can influence perceptions of coral susceptibility to bleaching. *Coral Reefs* 38(4):559–565. <https://doi.org/10.1007/s00338-018-01756-7>
13. Coll JC, Leone PA, Bowden BF et al (1995) Chemical aspects of mass spawning in corals. II. (-)-Epithunbergol, the sperm attractant in the eggs of the soft coral *Lobophytum crassum* (Cnidaria: Octocorallia). *Mar Biol* 123(1):137–143. <https://doi.org/10.1007/BF00350332>
14. DeCarlo TM, Gajdzik L, Ellis J, Coker DJ, Roberts MB, Hammerman NM, Pandolfi JM, Monroe AA, Berumen ML (2020) Nutrient-supplying ocean currents modulate coral bleaching susceptibility. *Sci Adv* 6(34):eabc5493. <https://doi.org/10.1126/sciadv.abc5493>
15. Dinesen ZD (1983) Patterns in the distribution of soft corals across the central Great Barrier Reef. *Coral Reefs* 1(4):229–236. <https://doi.org/10.1007/BF00304420>
16. Done TJ (1999) Coral Community Adaptability to Environmental Change at the Scales of Regions, Reefs and Reef Zones1. *Am Zool* 39(1):66–79. <https://doi.org/10.1093/icb/39.1.66>
17. Duckworth AR, Wolff CW (2011) Population dynamics and growth of two coral reef sponges on rock and rubble substrates. *J Exp Mar Biol Ecol* 402(1):49–55. <https://doi.org/10.1016/j.jembe.2011.03.017>
18. Fabricius K, Alderslade P (2001) Soft Corals and Sea Fans: A comprehensive guide to the tropical shallow water genera of the central-west Pacific, the Indian Ocean and the Red Sea. Australian Institute of Marine Science
19. Ferrari R (2017) The hidden structure in coral reefs. *Coral Reefs* 36(2):445–445. <https://doi.org/10.1007/s00338-017-1540-6>

20. Gleeson MW, Strong AE (1995) Applying MCSST to coral reef bleaching. *Adv Space Res* 16(10):151–154. [https://doi.org/10.1016/0273-1177\(95\)00396-V](https://doi.org/10.1016/0273-1177(95)00396-V)
21. Green RH, Lowe RJ, Buckley ML, Foster T, Gilmour JP (2019) Physical mechanisms influencing localized patterns of temperature variability and coral bleaching within a system of reef atolls. *Coral Reefs* 38(4):759–771. <https://doi.org/10.1007/s00338-019-01771-2>
22. Harrison HB, Álvarez-Noriega M, Baird AH, Heron SF, MacDonald C, Hughes TP (2019) Back-to-back coral bleaching events on isolated atolls in the Coral Sea. *Coral Reefs* 38(4):713–719. <https://doi.org/10.1007/s00338-018-01749-6>
23. Hellström M, Benzie JAH (2011) Robustness of size measurement in soft corals. *Coral Reefs* 30(3):787–790. <https://doi.org/10.1007/s00338-011-0760-4>
24. Hellström M, Kavanagh KD, Benzie JAH (2010) Multiple spawning events and sexual reproduction in the octocoral *Sarcophyton elegans* (Cnidaria: Alcyonacea) on Lizard Island, Great Barrier Reef. *Mar Biol* 157(2):383–392. <https://doi.org/10.1007/s00227-009-1325-8>
25. Hoogenboom MO, Frank GE, Chase TJ, Jurriaans S, Álvarez-Noriega M, Peterson K, Critchell K, Berry KLE, Nicolet KJ, Ramsby B, Paley AS (2017) Environmental Drivers of Variation in Bleaching Severity of *Acropora* Species during an Extreme Thermal Anomaly. *Front Mar Sci* 4. <https://www.frontiersin.org/article/10.3389/fmars.2017.00376>
26. Hughes TP (1984) Population Dynamics Based on Individual Size Rather than Age: A General Model with a Reef Coral Example. *Am Nat* 123(6):778–795. <https://doi.org/10.1086/284239>
27. Hughes TP, Kerry JT, Simpson T (2018) Reef Ecol 99(2):501–501. <https://doi.org/10.1002/ecy.2092>. Large-scale bleaching of corals on the Great Barrier
28. Jenkins TL, Stevens JR (2022) Predicting habitat suitability and range shifts under projected climate change for two octocorals in the north-east Atlantic. *PeerJ* 10:e13509. <https://doi.org/10.7717/peerj.13509>
29. Jones RJ, Berkelmans R, Oliver JK (1997) Recurrent bleaching of corals at Magnetic Island (Australia) relative to air and seawater temperature. *Mar Ecol Prog Ser* 158:289–292. <https://doi.org/10.3354/meps158289>
30. Kayanne H (2017) Validation of degree heating weeks as a coral bleaching index in the northwestern Pacific. *Coral Reefs* 36(1):63–70. <https://doi.org/10.1007/s00338-016-1524-y>
31. Kenyon TM, Doropoulos C, Dove S, Webb GE, Newman SP, Sim CWH, Arzan M, Mumby PJ (2020) The effects of rubble mobilisation on coral fragment survival, partial mortality and growth. *J Exp Mar Biol Ecol* 533:151467. <https://doi.org/10.1016/j.jembe.2020.151467>
32. Kramer N, Tamir R, Eyal G, Loya Y (2020) Coral Morphology Portrays the Spatial Distribution and Population Size-Structure Along a 5–100 m Depth Gradient. *Front Mar Sci*. [7https://www.frontiersin.org/articles/10.3389/fmars.2020.00615](https://www.frontiersin.org/articles/10.3389/fmars.2020.00615)
33. Lau YW, Poliseno A, Kushida Y, Quéré G, Reimer J (2019) The Classification, Diversity and Ecology of Shallow Water Octocorals. *Encyclopedia of the World's Biomes*. <https://doi.org/10.1016/B978-0-12-409548-9.12109-8>

34. Long S, Sparrow-Scinocca B, Blicher ME, Hammeken Arboe N, Fuhrmann M, Kemp KM, Nygaard R, Zinglensen K, Yesson C (2020) Identification of a Soft Coral Garden Candidate Vulnerable Marine Ecosystem (VME) Using Video Imagery, Davis Strait, West Greenland. *Front Mar Sci* 7. <https://www.frontiersin.org/articles/10.3389/fmars.2020.00460>
35. Marshall PA, Baird AH (2000) Bleaching of corals on the Great Barrier Reef: Differential susceptibilities among taxa. *Coral Reefs* 19(2):155–163. <https://doi.org/10.1007/s003380000086>
36. Maucieri DG, Baum JK (2021) Impacts of heat stress on soft corals, an overlooked and highly vulnerable component of coral reef ecosystems, at a central equatorial Pacific atoll. *Biol Conserv* 262:109328. <https://doi.org/10.1016/j.biocon.2021.109328>
37. McClanahan TR, Baird AH, Marshall PA, Toscano MA (2004) Comparing bleaching and mortality responses of hard corals between southern Kenya and the Great Barrier Reef, Australia. *Mar Pollut Bull* 48(3):327–335. <https://doi.org/10.1016/j.marpolbul.2003.08.024>
38. McFadden CS (1986) Colony fission increases particle capture rates of a soft coral: Advantages of being a small colony. *J Exp Mar Biol Ecol* 103(1):1–20. [https://doi.org/10.1016/0022-0981\(86\)90129-2](https://doi.org/10.1016/0022-0981(86)90129-2)
39. McFadden CS, van Ofwegen LP, Quattrini AM (2022) Revisionary systematics of Octocorallia (Cnidaria: Anthozoa) guided by phylogenomics. *Bull Soc Syst Biologists* 1(3). Article 3. <https://doi.org/10.18061/bssb.v1i3.8735>
40. Michalek-Wagner K, Willis BL (2001) Impacts of bleaching on the soft coral *Lobophytum compactum*. I. Fecundity, fertilization and offspring viability. *Coral Reefs* 19(3):231–239. <https://doi.org/10.1007/s003380170003>
41. Morrissey J (1980) Community structure and zonation of microalgae and hermatypic corals on a fringing reef flat of magnetic island (Queensland, Australia). *Aquat Bot* 8:91–139. [https://doi.org/10.1016/0304-3770\(80\)90045-5](https://doi.org/10.1016/0304-3770(80)90045-5)
42. Page CE, Leggat W, Heron SF, Choukroun SM, Lloyd J, Ainsworth TD (2019) Seeking Resistance in Coral Reef Ecosystems: The Interplay of Biophysical Factors and Bleaching Resistance under a Changing Climate. *BioEssays* 41(7):1800226. <https://doi.org/10.1002/bies.201800226>
43. Poulos DE, Harasti D, Gallen C, Booth DJ (2013) Biodiversity value of a geographically restricted soft coral species within a temperate estuary. *Aquat Conservation: Mar Freshw Ecosyst* 23(6):838–849. <https://doi.org/10.1002/aqc.2362>
44. Pratchett MS, Heron SF, Mellin C, Cumming GS (2021) Recurrent Mass-Bleaching and the Potential for Ecosystem Collapse on Australia's Great Barrier Reef. In J. G. Canadell & R. B. Jackson (Eds.), *Ecosystem Collapse and Climate Change* (pp. 265–289). Springer International Publishing. https://doi.org/10.1007/978-3-030-71330-0_10
45. Riegl B (1995) Effects of sand deposition on scleractinian and alcyonacean corals. *Mar Biol* 121(3):517–526. <https://doi.org/10.1007/BF00349461>
46. Riegl B, Piller WE (2003) Possible refugia for reefs in times of environmental stress. *Int J Earth Sci* 92(4):520–531. <https://doi.org/10.1007/s00531-003-0328-9>

47. Sakai K, Singh T, Iguchi A (2019) Bleaching and post-bleaching mortality of *Acropora* corals on a heat-susceptible reef in 2016. *PeerJ* 7:e8138. <https://doi.org/10.7717/peerj.8138>
48. Samimi-Namin K, van Ofwegen LP (2016) Overview of the genus *Briareum* (Cnidaria, Octocorallia, Briareidae) in the Indo-Pacific, with the description of a new species. *ZooKeys* 557(557):1–44. <https://doi.org/10.3897/zookeys.557.6298>
49. Shenkar N, Fine M, Loya Y (2005) Size matters: Bleaching dynamics of the coral *Oculina patagonica*. *Mar Ecol Prog Ser* 294:181–188. <https://doi.org/10.3354/meps294181>
50. Smale DA, Wernberg T, Oliver ECJ et al (2019) Marine heatwaves threaten global biodiversity and the provision of ecosystem services. *Nat Clim Change* 9(4) Article 4. <https://doi.org/10.1038/s41558-019-0412-1>
51. Smith HA, Prenzlau T, Whitman T, Fulton SE, Borghi S, Logan M, Heron SF, Bourne DG (2022) Macroalgal canopies provide corals limited protection from bleaching and impede post-bleaching recovery. *J Exp Mar Biol Ecol* 553:151762. <https://doi.org/10.1016/j.jembe.2022.151762>
52. Yesson C, Taylor ML, Tittensor DP, Davies AJ, Guinotte J, Baco A, Black J, Hall-Spencer JM, Rogers AD (2012) Global habitat suitability of cold-water octocorals: Global distribution of deep-sea octocorals. *J Biogeogr* 39(7):1278–1292. <https://doi.org/10.1111/j.1365-2699.2011.02681.x>

Figures

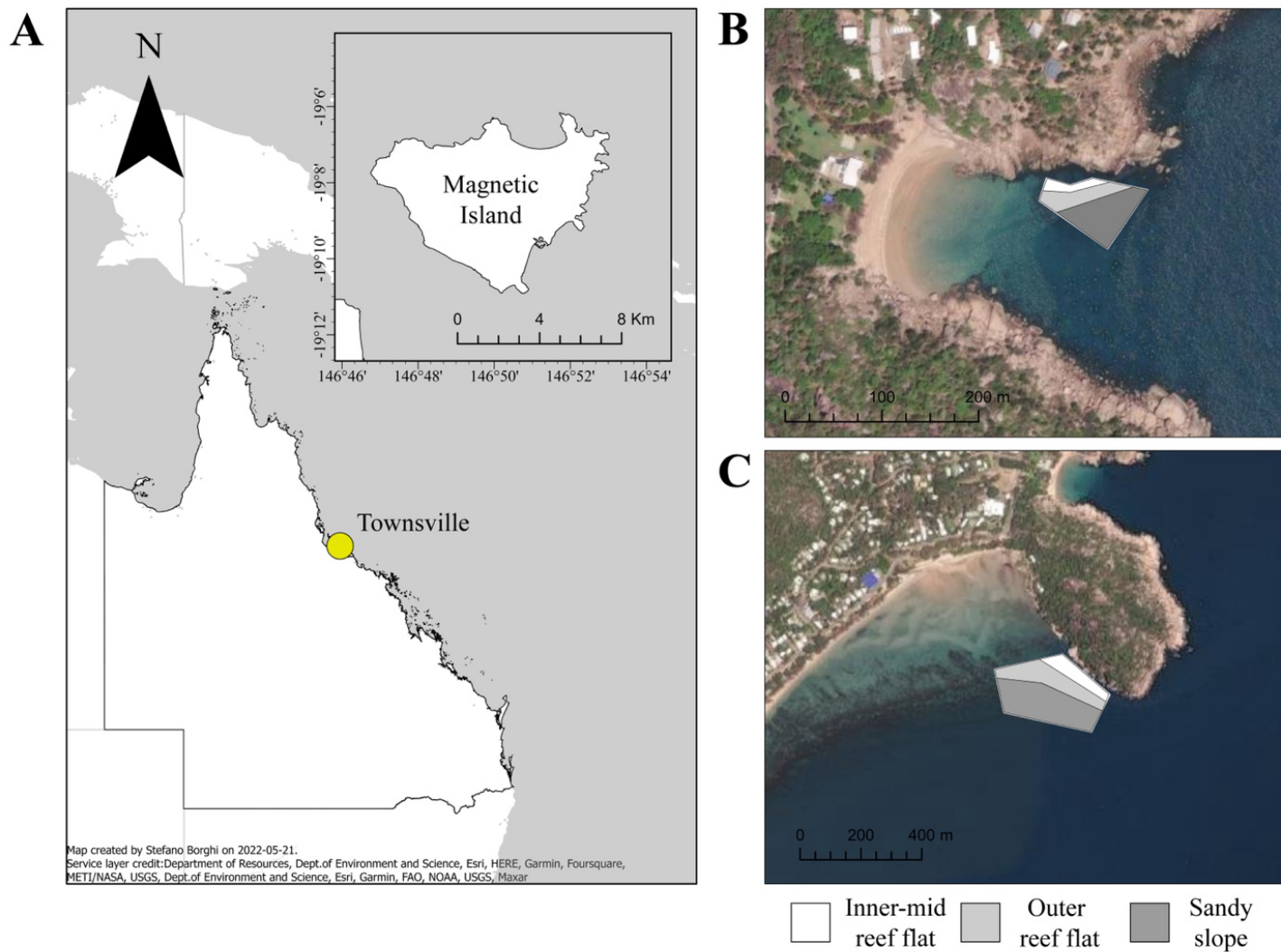


Figure 1

(A) Map of the study sites on Magnetic Island, ~8 km offshore from Townsville QLD, Australia. Estimated survey areas in (B) Alma Bay and (C) Geoffrey Bay with reef zonation highlighted.

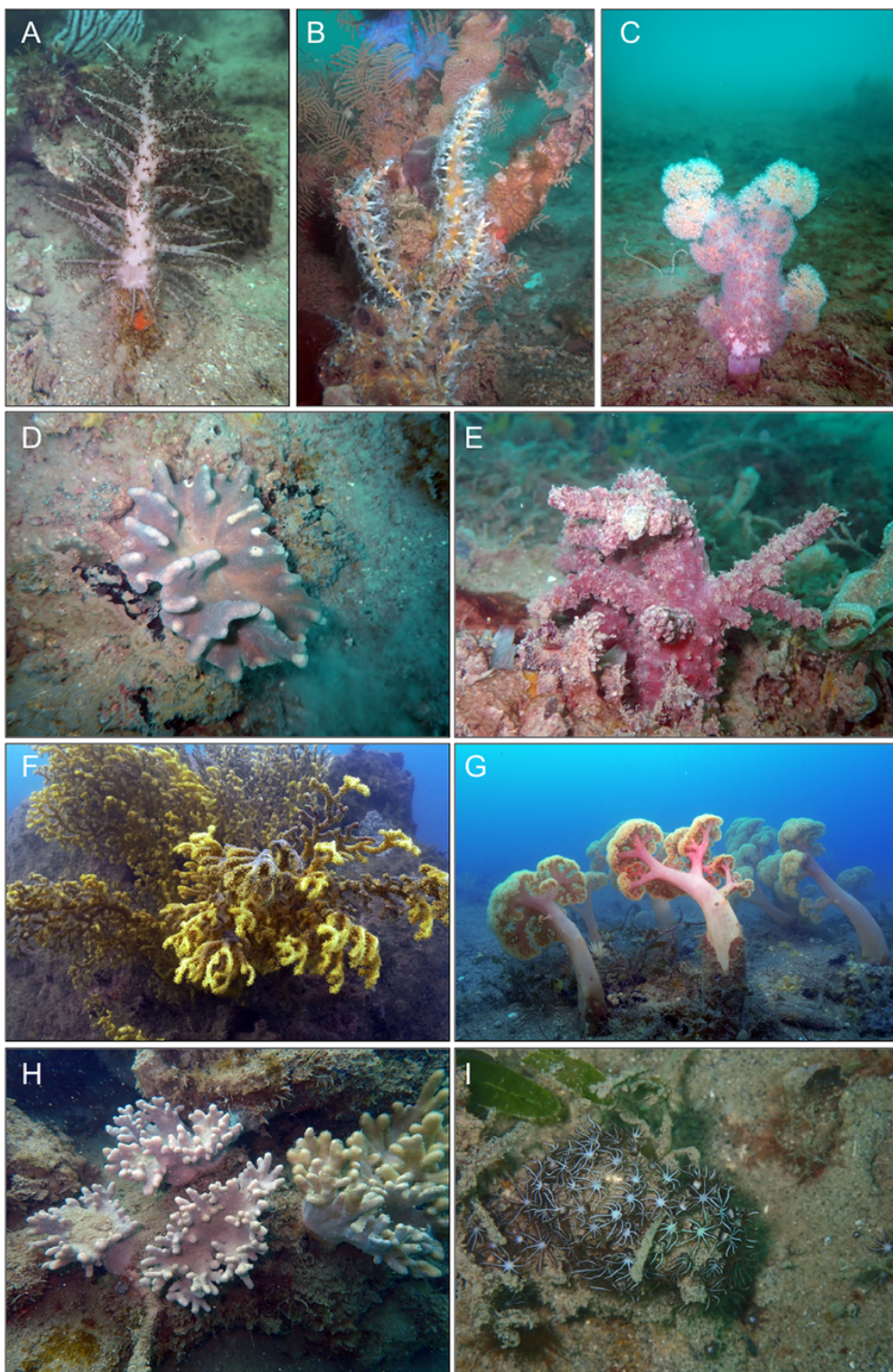


Figure 2

Photos of some of the soft corals observed in Geoffrey Bay, including the genera (A) *Studeriotetes*, (B) *Carijoa*, (C) *Dendronephthya*, (D) *Lobophytum* and (E) *Nephthyigorgia*, (F) *Iciligorgia*, (G) *Umbellulifera*, (H) *Sclerophytum* and (I) the species *Briareum cf. hamrum* (Gohar, 1948).

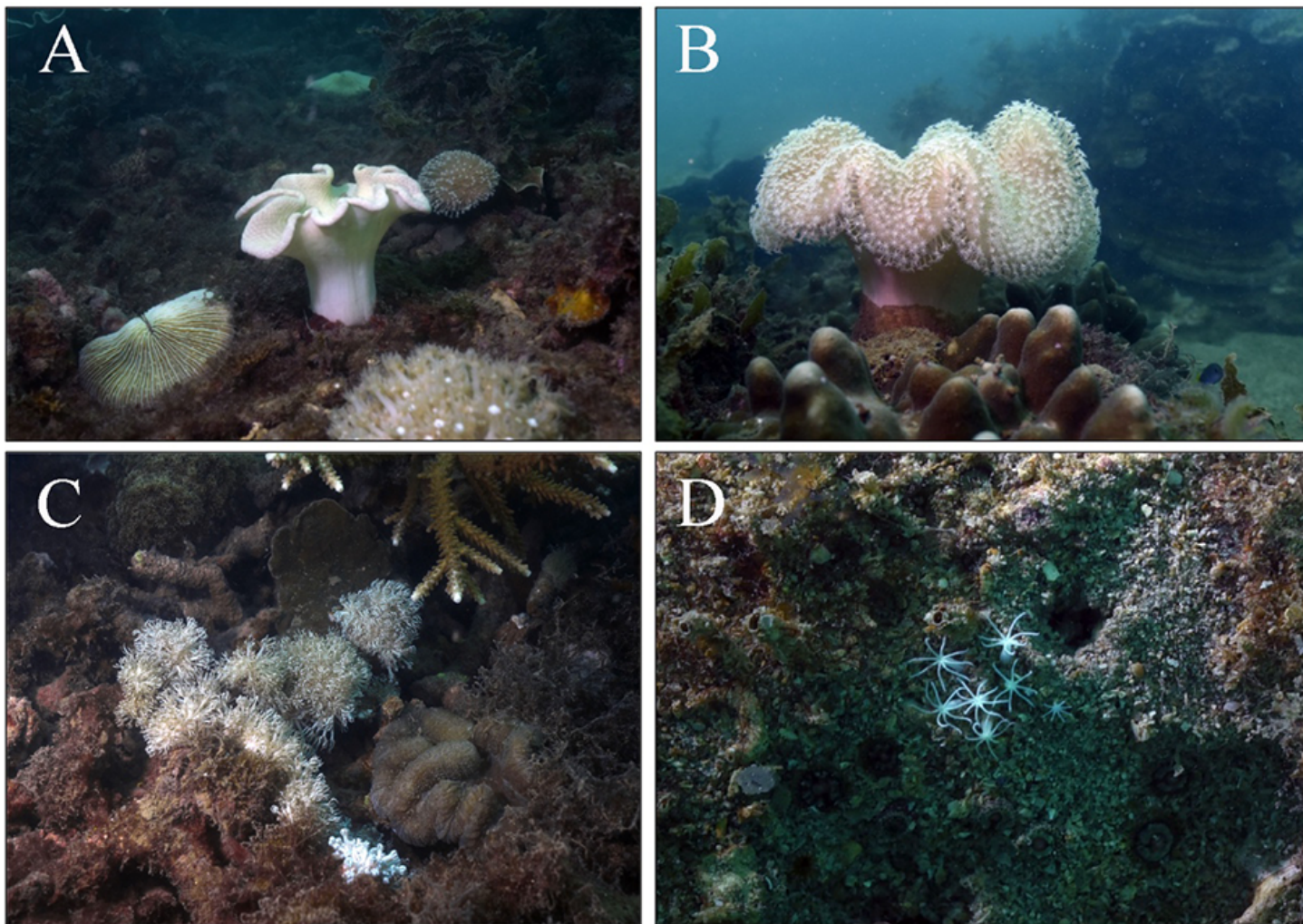


Figure 3

Observations of bleaching of a range of soft coral genera.

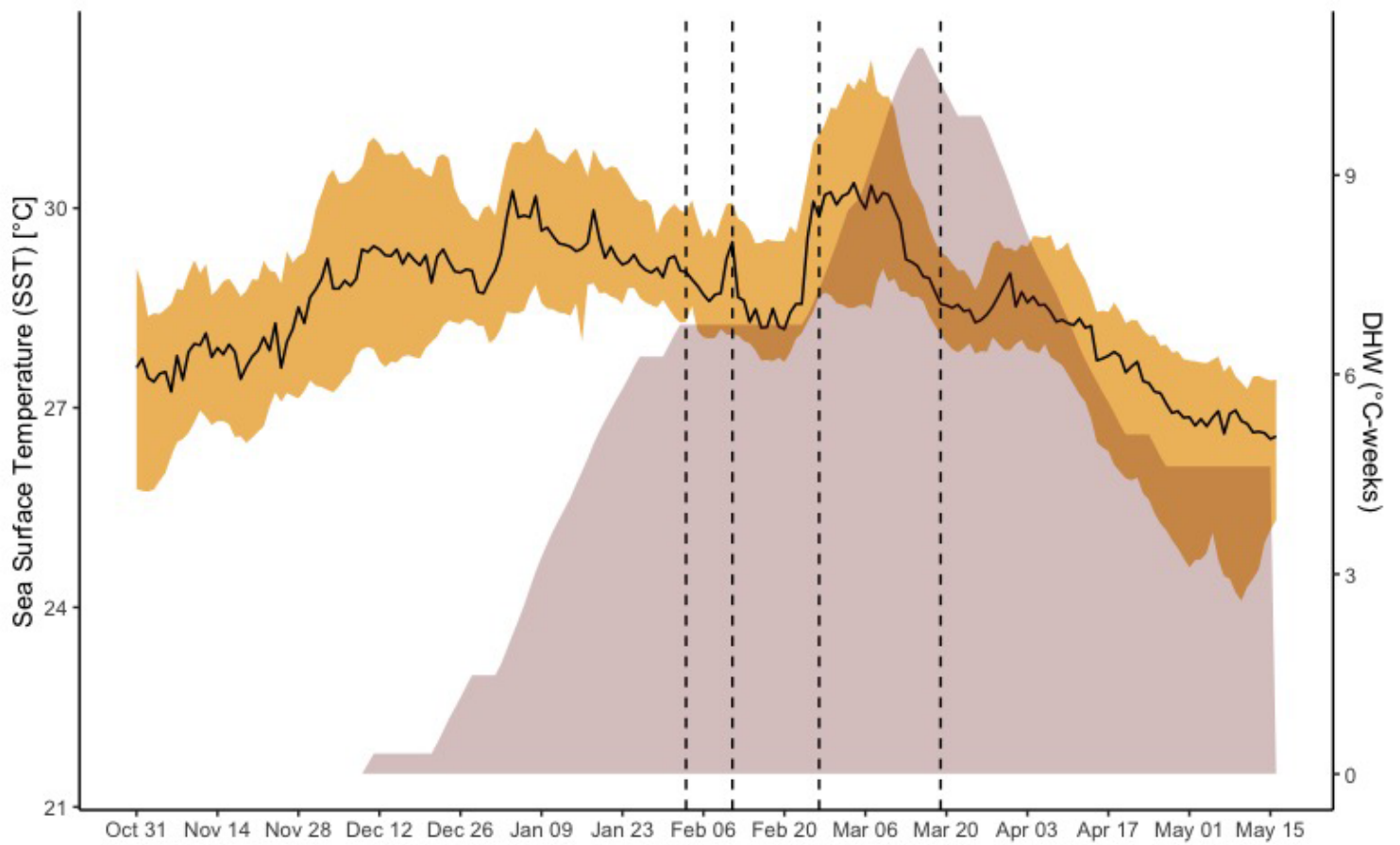


Figure 4

Satellite-derived SST (black line) and daily temperature range (yellow shading) in the central GBR region (~5km resolution). Accumulated daily heat stress (DHW; red shading) revealed consistently warmer conditions across the region. Vertical black dashed lines indicate survey dates.

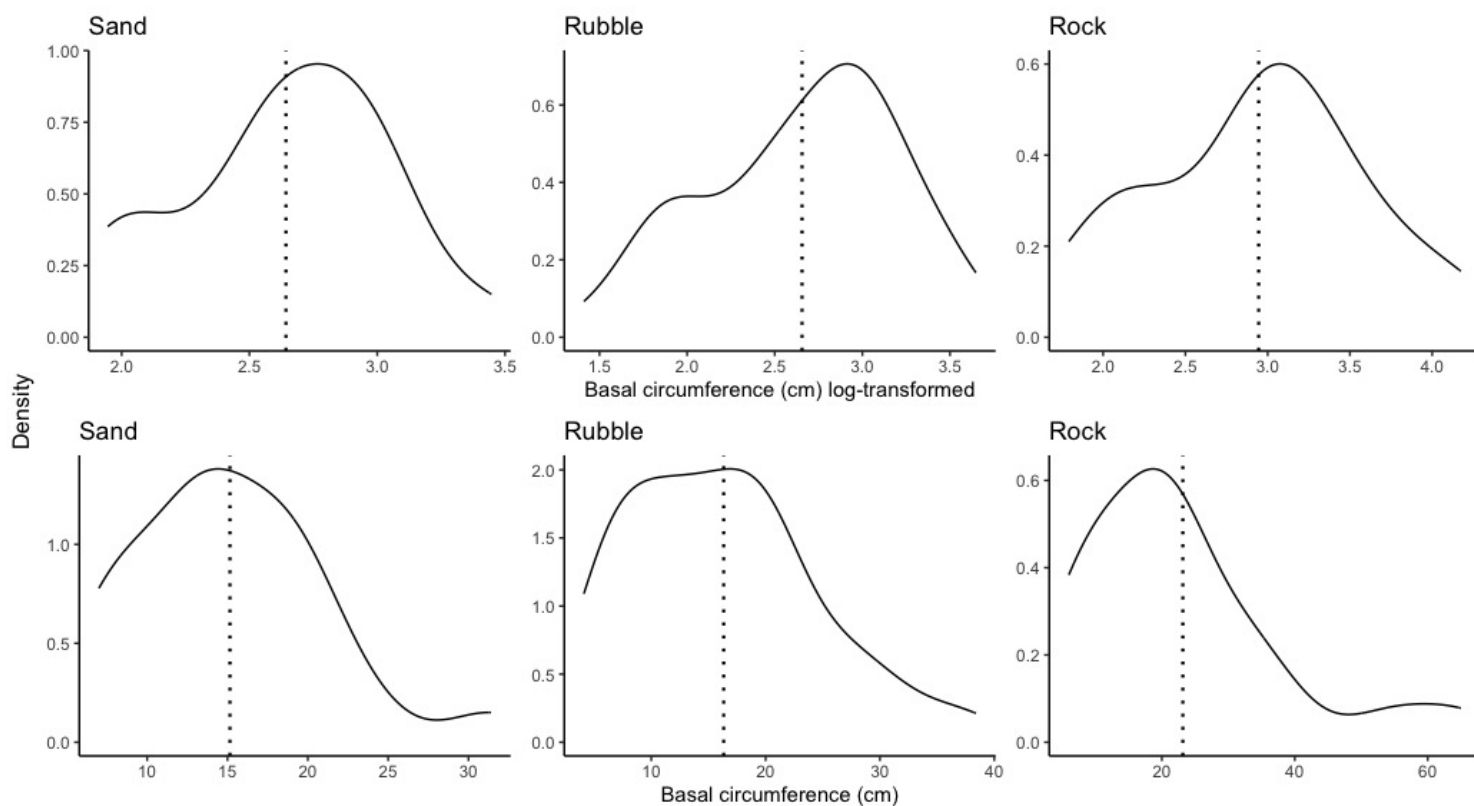


Figure 5

Differences in size-frequency distribution (SFD) over sand, rubble, rock. The SFDs of *Sarcophyton* assemblages over substrate types are based on basal circumference measurements and their log-transformation.

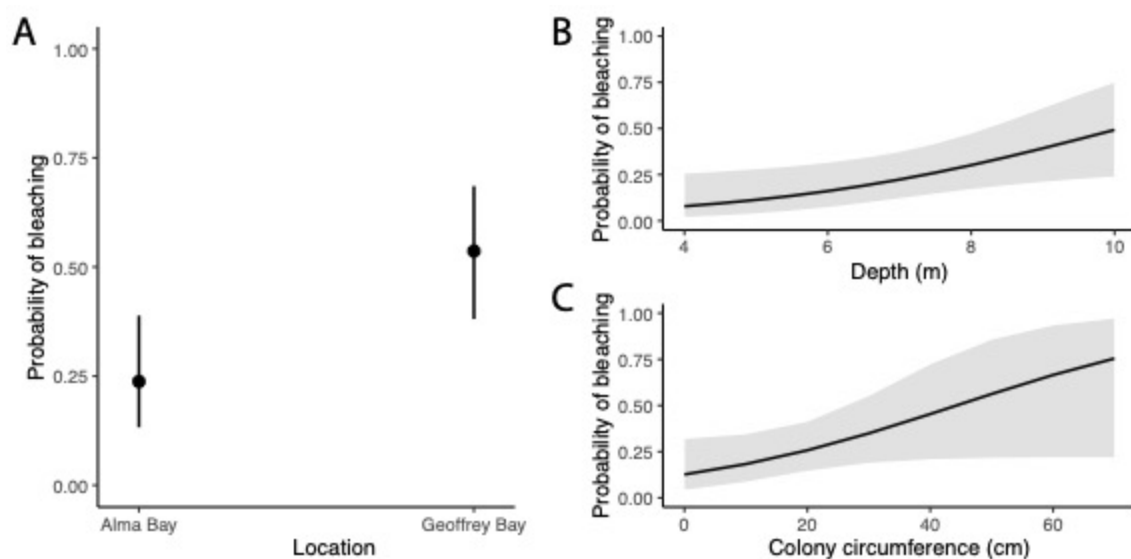


Figure 6

Partial effects plots showing the probability of bleaching to occur in colonies (A) between locations; (B) among depths; and (C) among colony sizes.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [SupplementaryMaterial.docx](#)