Abstract

Successful restoration of coral reefs depends on the survival of outplanted species. Research shows that outplanting survival is mixed, with outplants often experiencing rapid mortality in response to various stressors. We used published results on outplant monitoring to investigate the role of sea surface temperature in the survival rates of corals. We find that the maximum temperature experienced at an outplanting site is very important in determining outplant survival, with ~50% mortality occurring if temperatures reach 30.5 °C. Some genera, however, are more tolerant than others. Outplant survival increases when sites experience greater variability in temperature, where outplants are exposed to temperatures both warmer and cooler than the long-term mean. Similar results were found when considering temperature conditions of the site in the year prior to outplanting. Thus, sea surface temperature data can be used as a tool to assess whether a restoration site is appropriate, with sites chosen to increase outplant survival.

1. Introduction

Coral reef restoration is rapidly growing as a crucially important effort to restore and sustain reefs, especially as environmental and human stressors continue to threaten these ecosystems [1]. A key method for restoring reefs is through the outplanting of coral fragments [2–4], and numerous organizations are involved in reef restoration with tens of thousands of corals outplanted every year [5]. The outplanting of fragments onto reefs aims to restore foundational species, increase coral biomass, generate coastal protection, increase reef complexity, and provide habitat for associated fauna [5].

Coral propagation methodologies are well-developed, and protocols for enhancing growth rates are established and underway among numerous nurseries [3]. Conversely, outplanting success is mixed as outplants can experience rapid mortality due to various abiotic and biotic stressors [5–7]. Outplanting is one of the most expensive and time-consuming steps in the restoration process [4, 6], so choosing the best place to outplant is crucial to restoration success.

The median reported cost to restore one hectare of coral reef is approximately $400 000 USD [8]. Despite this high cost, relatively little is known about conditions that lead to outplant mortality because long-term monitoring is rare and/or of highly variable quality [9]. With the continued decline of coral reef habitats, best-practice strategies are needed to optimize the success of restoration. Currently, one of the main barriers to increased restoration rests in finding a scalable reef restoration strategy that is both ecologically and economically achievable [10], and considering temperature conditions prior to outplanting is a key step that can be incorporated into coral outplanting methodologies [5]. When choosing where to place coral outplants, the majority of practitioners consider available substrate, avoidance of benthic competitors, and presence of herbivores [5]. A plethora of parameters can be considered by restoration practitioners, and we have suggested that the use of remote sensing could be used to optimize the process of site selection [11].

Temperature is fundamental to determining coral health and survival, especially as thermal anomalies of just 1 °C lasting for more than a few weeks can cause bleaching [1]. Sea surface temperature (SST) monitoring is long established, can be remotely sensed in a variety of ways, and continues to increase in both accuracy and spatial resolution. SST data are already used to predict coral bleaching and disease events [12, 13], and thus SST has an important application for reef restoration. The impacts of various temperature
conditions on outplant survival are not well known, although in several projects, warming events have been pinpointed as the cause of restoration failure (e.g. [14–16]).

Here we pair global, satellite-based SST and thermal anomaly data with peer-reviewed, published reef restoration projects to determine the role of temperature in coral outplant success, contrasting the effects across coral genera to ascertain differences in thermal limits of outplants. We also examine historical, pre-outplanting temperature data for each restoration project (i.e. thermal conditions of the restoration site prior to outplanting) to assess whether survival success of outplants can be predicted by considering the thermal history of the site. Doing so would determine whether historical site data can be used to assess whether that site is appropriate for restoration, or to choose between multiple sites to maximize outplant survival.

2. Material and methods

2.1. Literature search and data collection for coral outplant survival rates

We conducted a systematic literature search using Web of Science (Core collection; Thomson Reuters, New York, U.S.A.) with the topic search terms ‘coral rest’∗ OR ‘coral reef rest’∗ OR ‘coral transplant’∗ OR ‘coral outplant’∗. We also mined the references of relevant papers, including two recent reviews on coral restoration projects [5, 8]. Studies were included if coral outplant survival rate, location and date of outplant were provided with summaries of the results shown in figure 1 and figure S1 (stacks.iop.org/ERL/15/074045/mmedia). Information on coral genera and length of monitoring period were also recorded. In total, we identified 82 studies that met our criteria. A single study could contain more than one observation [1]: if studies included multiple monitoring times (e.g. monitored every month for one year), each record was included as a data point, especially as survival success is extremely variable month to month and [2] if success of multiple species were individually monitored, each was treated as a separate data point. In total, we had 539 observations.

2.2. Sea surface temperature data

The US National Oceanic and Atmosphere Administration (NOAA) Coral Reef Watch program (CRW) generates daily, satellite-derived global 5 km resolution sea surface temperature (SST), dating back to 1985 [17]. From the SST observations, CRW also generates sea surface temperature anomaly (SSTA) by subtracting the long-term (seven years) SST mean from the SST at that given location at that same time of year, with a positive anomaly indicating the SST is warmer than average.

CRW temperature data were available for 519 of the original 539 observations in the outplanting survival dataset (accessed at https://coralreefwatch.noaa.gov/satellite/hdf/index.php). For each restoration site, SST and SSTA were downloaded for two separate time periods [1]: ‘during’ the full outplanting period as specified for each study and [2] for the full one-year period ‘prior’ to the outplanting. For each outplanting location, the 5 km × 5 km cell nearest to the outplanting location was used for data extraction. A one-year prior period was chosen as temperature conditions over longer time periods might not be as analogous to conditions experienced by the outplants, as annual SST trends can be very variable over longer periods [18]. For both the ‘during’ and ‘prior’ time periods, the maximum, minimum, range, and standard deviation of both SST and SSTA were computed.

2.3. Statistical analyses

The ‘during’ and ‘prior’ temperature variables and effects on outplant survival were considered in separate models. Variables were checked for multicollinearity using Pearson’s correlations, where variables that exhibited a correlation coefficient of more than 0.7 were checked [19]. In these instances, the variable that exhibited the highest number of collinear relationships was removed. Variables were also visually inspected to assess non-linear relationships. Lastly, multicollinearity was checked using the variance inflation factor (VIF) where the final variables included in the ‘during’ and ‘prior’ model were less than 1. Maximum, minimum, standard deviation and range of SST and SSTA variables showed numerous correlations and thus only two variables were included in the final models: SSTA range and SST maximum. These variables displayed either no relationships, or the lowest collinearity with other variables as well as the lowest VIF. These variables and their importance to coral survival were also biologically apparent.

Data were assessed following best practice guidelines as per [20, 21]. The first model aimed to determine the effect of the SST and SSTA variables on coral outplant survival success. Temperatures that outplants experienced during the full outplanting period were considered in the model. The effects of SSTA range and SST maximum experienced during the outplanting period on coral survival were analyzed with generalized linear mixed models (GLMMs) using the glmer function from the lme4 package in R (v1. 1–21; [22]), coral genus and length of outplanting were included as random terms within the model, and the model was run with a binomial error distribution and a logit link function.

We performed model selection on the GLMM by testing all combinations of variables in the model using the dredge function from the MuMIn package.
Models that were within $\Delta AIC$ Akaike information criterion (AIC) were averaged. We calculated 95% confidence intervals (CIs) and standardized beta coefficients to determine the strength of each model-averaged variable, where predictor variables with intervals that did not overlap zero were considered to contribute significantly to the model. For these significant, model-averaged variables, response plots were generated. To visualize the effects of the temperature predictors on coral outplant survival, we generated prediction plots for the top-ranked model. Modelling was also performed using the same temperature variables, (i.e. SSTA range and SST maximum), prior to outplanting utilizing the same analysis methodology. Since the original dataset included 42 different genera (figure S1), and many of these genera were only represented once, the original dataset was reduced to include only the prevalent genera (*Acropora, Echinopora, Merulina, Pocillopora* and *Porites*) which we represented by 30 or more different outplanting studies resulting in 358 observations. In this manner, genus could be considered as a fixed factor, and the interaction between genus and each SST and SSTA variable experienced during outplanting could be considered following the above analyses.

3. Results

3.1. Global variation in coral restoration success

Considering the full dataset ($n = 539$, see methods for details), mean survival of coral outplants was $62.5 \pm 31.0\%$ with an average project monitoring length of $13.1 \pm 15.8$ months (mean $\pm$ standard deviation). Figure 1 maps the location of restoration sites considered in this study, denoting percent survival in tercile categories. Locations where the majority of survival success was less than $33\%$ include Curaçao and Guam. In contrast, locations where survival success was mostly greater than $66\%$ include Pacific Mexico, Zanzibar and Male. Hotspots of coral restoration projects were found in Puerto Rico, northern regions of the Red Sea and the Philippines (figure 1).

Coral outplant success decreased with outplant age; however, there are comparatively few data entries for 24 months and beyond ($n = 44$) (figure S1). When considering outplanting genera, a total of 43 different genera have been used, displaying variable survival rates (figure S1). The majority of genera showed 50% or higher survival rates, with *Acropora* by far the most commonly outplanted genus ($n = 194$), followed by *Echinopora* ($n = 42$) and *Merulina* ($n = 40$) (figure S1).

3.2. Temperature conditions experienced by outplants

The following statistics represent an average value of specific thermal conditions experienced by coral outplants across all sites at which we obtained temperature data ($n = 519$). The mean temperature experienced by outplants was $27.4 \pm 2.0$ °C, with a maximum temperature of $29.7 \pm 1.3$ °C.

The mean temperature anomaly experienced by outplants was $0.4 \pm 0.4$ °C. The maximum SSTA experienced was on average $1.5 \pm 0.5$ °C, with a minimum SSTA on average of $-0.9 \pm 0.7$ °C. The average range of temperature anomalies experienced by outplants, i.e. the difference between the maximum and minimum, was $2.4 \pm 0.9$ °C. Since the range of SSTAs were greater than $1.5$ °C, this means that many outplanting sites experienced SST temperatures higher and lower than their long-term average.

3.3. Temperature effects on coral outplanting success

SSTA range and SST maximum were retained in the best models as indicated by the AIC selection procedure. SST maximum correlated negatively and most strongly with coral outplant survival ($\beta = -0.87; 95\%$ CI lower $= -1.17$, upper $= -0.56$; table 1). Specifically, survival decreased with increases in maximum temperature, dropping below $50\%$ at about $30.5$ °C (figure 2(a)). A larger range of SST anomalies increased outplant survival success ($\beta = 0.41; 95\%$ CI lower $= 0.06$, upper $= 0.76$; table 1, figure 2(b)).

3.4. Predictability of coral outplant survival

SSTA range and SST maximum were retained in the best model. A collinearity matrix of the same variables
Table 1. Model-averaged coefficients and 95% confidence intervals (CIs). Coefficients where CIs do not overlap zero are shown in bold font.

|                      | β coefficient | Lower 95% CI  | Upper 95% CI |
|----------------------|---------------|---------------|--------------|
| **Temperature conditions experienced by outplants** |               |               |              |
| SST range            | 0.41          | 0.06          | 0.76         |
| SST max              | −0.87         | −1.17         | −0.56        |
| **Temperature conditions of site prior to outplanting** |               |               |              |
| SST range            | 0.31          | 0.06          | 0.57         |
| SST max              | −0.28         | −0.48         | −0.09        |
| **Interaction between genera and temperature variables** |               |               |              |
| SST range            | 0.03          | −0.26         | 0.33         |
| SST max              | −0.19         | −0.43         | 0.02         |
| Echinopora           | 46.4          | 13.3          | 87.20        |
| Merulina             | 51.1          | 15.7          | 92.10        |
| Pocillopora          | 2.32          | −12.4         | 20.00        |
| Porites              | 15.6          | −17.0         | 56.20        |
| Echinopora* SST max  | −1.55         | −2.91         | −0.45        |
| Merulina* SST max    | −1.68         | −3.02         | −0.51        |
| Pocillopora* SST max | −0.07         | −0.65         | 0.43         |
| Porites* SST max     | −0.50         | −1.84         | 0.58         |

Figure 2. Smoothed predictor variables with 95% CIs (shaded regions) for coral outplant survival. SST maximum and SST anomaly (SSTA) ranges experienced during the outplanting period are shown in the left panels, with SST maximums and SSTA ranges for the year prior to outplanting shown in the right panels.

measured the year prior to outplanting with those measured during the outplanting period shows that they are highly correlated, i.e. SSTA range and SST maximum data prior to outplanting and during outplanting are very similar with Pearson correlations of 0.83 and 0.75 respectively (table S1).

SST maximum values in the year prior to outplanting correlated negatively with coral outplant survival \((\beta = -0.28; 95\% \text{ CI lower} = -0.48, \text{upper} = 0.09; \text{table 1})\). Similar to what was observed with SST maximum values experienced by outplants, survival was more likely to decrease at sites
Figure 3. Effects of maximum temperatures experienced during outplanting on coral survival shown across different genera. The shaded regions represent 95% confidence intervals.

with higher maximum temperatures (figure 2(c)). Survival showed a positive correlation with the range of SSTAs at the site prior to outplanting ($\beta = 0.31$; 95% CI lower = 0.06, upper = 0.57; table 1; figure 2(d)).

3.5. Effects across coral genera

SSTA and its interaction with coral genus was not retained in the best model as indicated by the AIC selection procedure. When considering the five most common coral genera used in outplant studies, Echinopora and Merulina performance differed significantly from that of Acropora, Pocillopora and Porites (table 1). This was due to significant negative interactions of Echinopora and Merulina with maximum temperature experienced during outplanting, where survival of outplants in these genera decreased steeply at approximately 29 °C (figure 3). For Echinopora and Merulina, this suggests a lower maximum thermal limit than the other three genera and a smaller range of temperatures at which they can survive.

4. Discussion

Our findings indicate that the survival of outplanted corals is likely to drop below 50% when maximum temperatures experienced at outplanting sites exceed 30.5 °C. Increased mortality at this temperature is closely linked with normal functioning of corals, reflecting the critical role of thermal limits. With ocean temperatures expected to continue warming in excess of 1.5 °C and outplants already showing 50% mortality at ~30.5 °C, generating thermally-tolerant genotypes across coral outplant species will be essential in ensuring reef restoration is successful in the face of climate change. Using naturally-occurring thermally-resilient corals to create coral nurseries is possible [29] and should be rapidly expanded to maximize restoration success.

The survival rate of outplants also increased with increases in the range of SSTA experienced at outplanting locations. On average, the maximum SSTA experienced at sites was 1.5 °C, but the range of SSTAs experienced by outplanting sites was 2.4 °C, indicating that outplanting sites experienced SST temperatures higher and lower than their long-term average. In this case, low temperatures experienced by outplants might have offered reprieve, thereby explaining why outplant survival rate increased with greater SSTA ranges. For the symbiotic Cnidarian Cassiopea, exposure to lower temperatures increased the bleaching threshold of this species [30] and could help explain our results. A global synthesis of field observations of coral bleaching from 1998–2017 found that bleaching was significantly lower in areas with high SSTA variance [31]. Similarly, SST variability reduced coral mortality and promoted coral tolerance in the west Indian Ocean [32] and was shown to be a factor that provides the greatest resistance to climate change [33]. On a smaller spatial scale, in the reefs of American Samoa, Acropora exposed to more thermally variable pools showed greater coral-algal thermal tolerance [34]. Results from our global study of coral outplants agree with these in-situ findings: Variability in temperature is key for increasing coral outplant survival.

The maximum temperature experienced during outplanting was a strong predictor of coral survival, reflecting the critical role of thermal limits. With ocean temperatures expected to continue warming in excess of 1.5 °C and outplants already showing 50% mortality at ~30.5 °C, generating thermally-tolerant genotypes across coral outplant species will be essential in ensuring reef restoration is successful in the face of climate change. Using naturally-occurring thermally-resilient corals to create coral nurseries is possible [29] and should be rapidly expanded to maximize restoration success.

The survival rate of outplants also increased with increases in the range of SSTA experienced at outplanting locations. On average, the maximum SSTA experienced at sites was 1.5 °C, but the range of SSTAs experienced by outplanting sites was 2.4 °C, indicating that outplanting sites experienced SST temperatures higher and lower than their long-term average. In this case, low temperatures experienced by outplants might have offered reprieve, thereby explaining why outplant survival rate increased with greater SSTA ranges. For the symbiotic Cnidarian Cassiopea, exposure to lower temperatures increased the bleaching threshold of this species [30] and could help explain our results. A global synthesis of field observations of coral bleaching from 1998–2017 found that bleaching was significantly lower in areas with high SSTA variance [31]. Similarly, SST variability reduced coral mortality and promoted coral tolerance in the west Indian Ocean [32] and was shown to be a factor that provides the greatest resistance to climate change [33]. On a smaller spatial scale, in the reefs of American Samoa, Acropora exposed to more thermally variable pools showed greater coral-algal thermal tolerance [34]. Results from our global study of coral outplants agree with these in-situ findings: Variability in temperature is key for increasing coral outplant survival.

The dominant genera used in outplanting studies (Acropora, Echinopora, Merulina, Pocillopora and
Porites) showed significantly different tolerances to the maximum temperature experienced at outplanting sites. Merulina and Echinopora underwent steep declines in survival when maximum temperatures exceeded 29 °C, in contrast to Acropora, Pocillopora and Porites that showed much more gradual decreases in survival with increasing temperature. There are several studies that show species-specific responses to high SST; however, the susceptibility of each coral genus depended on reef location. Acropora and Pocillopora were found to be the least susceptible taxa in response to bleaching events on Singaporean reefs [35], whereas Echinopora underwent the greatest decreases in relative coral cover in response to thermal stress [36]. On Maldivian reefs; however, Acropora and Pocillopora, but not Porites, were the genera most severely affected by bleaching [37]. In the case of coral outplants, and not established corals, we find that Merulina and Echinopora corals were the most susceptible to increases in temperature.

Merulina and Echinopora belong to the family Merulinidae [38]. Furthermore, the majority of the Merulina genus outplanted was comprised of the species Merulina scabricula, and for Echinopora, it was Echinopora lamellosa. These corals have laminar growth forms in contrast to the branching and finger-like growth forms of Acropora, Pocillopora and Porites. Thus, the lower thermal tolerance of Merulina and Echinopora may indicate that outplants with a laminar growth form are more susceptible to mortality, especially as growth form is a strong predictor of bleaching susceptibility [39]. As Merulina and Echinopora show lower thermal limits and thus a more limited temperature range, sites in which they can be successfully outplanted are limited and highlights the importance of considering outplant genera when restoring a reef.

When considering SST maximum and SSTA range of the site for the year prior to outplanting, our results are similar to the findings for temperatures actually experienced by outplants at those sites. This suggests that considering SST and SSTA of a site prior to outplanting are a good predictor of coral survival, allowing comparison among potential restoration sites. Bearing in mind that the mean spatial extent of restoration projects is 108 ± 4542 m², with a median cost of the outplanting phase at around $400,000 USD [8], any measure taken to increase outplant survival rates is extremely valuable. Use of freely available SST and SSTA prior to outplanting can readily be incorporated into restoration efforts.

It is important to note that SST measurements apply to the ocean surface, and temperature below the surface can differ from that estimated from satellites. Sub-surface temperatures are usually cooler than SST measurements taken by satellite from Earth orbit, and thus our upper thermal tolerance estimates may be biased slightly high in shallow waters (i.e. <5 m depth) and more so in deeper coral restoration sites (5–20 m depth) [40]. Additionally, it is important to note that our analyses did not consider the length of time spent at the maximum temperature recorded for each restoration project, the size of the outplants, or conditions experienced during the nursery phase.

Despite these study limitations, the role of temperature in determining coral outplant success has emerged in our analysis: A maximum SST of 30.5 °C at outplanting sites can be used as a guide to prevent survival dropping below 50%, although this value can vary among coral basins. Counterbalancing this effect, variability in site temperatures can help to increase coral outplant survival. As the ocean continues to warm, generating thermally-tolerant genotypes of coral outplants will be central to the success of restoration efforts. Site selection is key to successful restoration. Because remotely sensed temperature data are available worldwide, they provide a key avenue to assess whether a potential restoration site is appropriate, thereby accelerating efforts to scale up coral reef saving efforts.

Acknowledgments

We thank David Knapp for preparing temperature data for the analysis, and to Nick Vaughn, Luke Evans and Rachel Carlson for helpful comments on the manuscript. This study was supported by the John D. and Catherine T. MacArthur Foundation. SF and GA conceived the manuscript, were involved in discussing the results and writing the final manuscript. SF analysed the data. The authors declare no competing interests.

Data availability statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

ORCID iDs

Shawna A Foo  https://orcid.org/0000-0002-7083-2377
Gregory P Asner  https://orcid.org/0000-0001-7893-6421

References

[1] Hughes T P et al 2017 Global warming and recurrent mass bleaching of corals Nature 543 373–7
[2] Rinkevich B 2005 Conservation of coral reefs through active restoration measures: recent approaches and last decade progress Environ. Sci. Technol. 39 4333–42
[3] Lirman D and Schopmeyer S 2016 Ecological solutions to reef degradation: optimizing coral reef restoration in the Caribbean and western Atlantic PeerJ. 4 e2597
[4] Hein M Y, Willis B L, Beeden R and Bittles A 2018 The need for broader ecological and socioeconomic tools to evaluate the effectiveness of coral restoration programs Restor. Ecol. 25 873–83
[5] Ladd M C, Miller M W, Hunt J H, Sharp W C and Burkepile D E 2018 Harnessing ecological processes to facilitate coral restoration Front. Ecol. Environ. 16 239–47
[6] Fabian R, Beck M and Potts D 2013 Reef restoration for coastal defense: a review (Tech. Rep. Santa Cruz, CA: University of California, Santa Cruz)
[7] Muehllehner N, Langdon C, Venti A and Kadlo D 2016 Dynamics of carbonate chemistry, production, and calcification of the florida reef tract (2009–2010): evidence for seasonal dissolution Global Biogeochem. Cycles 30 661–88
[8] Bayraktarov E, Stewart-Sinclair P J, Brisbane S, Bostrom-Einarsson L, Saunders M I, Lovelock C E, Possingham H P, Mumbry P J and Wilson K A 2019 Motivations, success, and cost of coral reef restoration Restor. Ecol. 27 961–91
[9] Fox H E, Harris J L, Darling E S, Ahmadia G N and Estradivari T B 2019 Razak, Rebuilding coral reefs: success (and failure) 16 years after low-cost, low-tech restoration Restor. Ecol. 27 862–9
[10] Gillies C L et al 2015 Scaling-up marine restoration efforts in Australia Ecol. Manage. Rest. 16 84–85
[11] Foo S A and Anser G P P 2019 Scaling up coral reef restoration using remote sensing technology Front. Mar. Sci. 6 79
[12] Liu G, Strong A E, Skirving W J and Arzayus L F 2006 Overview of NOAA coral reef watch program’s near-real-time satellite global coral bleaching monitoring activities Proc. of the 10th Intl. Coral Reef Symp. (Okinawa)pp 1783–93
[13] Liu G, Eakin C M, Chen M, Kumar A, De La Cour J L, Heron S F, Geiger E F, Skirving W J, Tirak K V and Strong A E 2018 Predicting heat stress to inform reef management: NOAA Coral Reef Watch’s 4-month coral bleaching outlook Front. Mar. Sci. 5 57
[14] Yap H T 2004 Differential survival of coral transplants on various substrates under elevated water temperatures Mar. Pollut. Bull. 49 306–12
[15] Shaish L, Levy G, Katez G and Rinkivich B 2010 Coral reef restoration (Bolíniao, Philippines) in the face of frequent natural catastrophes Restor. Ecol. 18 285–99
[16] Dela Cruz D W, Rinkivich B, Gomez E D and Yap H T 2015 Assessing an abridged nursery phase for slow growing corals used in coral restoration Ecol. Engineer. 84 408–15
[17] NOAA Coral Reef Watch 2017 Updated daily. NOAA Coral Reef Watch Version 3.0 Daily Global 5-km Satellite Virtual Station Time Series Data for Southeast Florida, 12 March 2013–11 March 2014. College park, maryland, USA: NOAA Coral reef watch. Data set 2019-12-8(available at https://coralreefwatch.noaa.gov/vv/data.php)
[18] Deser C, Alexander M A, Xie S P and Phillips A S 2010 Sea surface temperature variability: patterns and mechanisms Ann. Rev. Mar. Sci. 2 115–43
[19] Dormann C F et al 2013 Collinearity: a review of methods to deal with it and a simulation study evaluating their performance Ecography 36 27–46
[20] Zuur A F, Ieno E N and Elphick C S 2010 A protocol for data exploration to avoid common statistical problems Methods Ecol. Evol. 1 3–14
[21] Harrison X A, Donaldson L, Correa-Canó M E, Evans I, Fisher D N, Goodwin C E D, Robinson B S, Hodgson D J and Inger R 2018 A brief introduction to mixed effects modelling and multi-model inference in ecology PeerJ. 6 e4794
[22] Bates D, Maechler M, Bolker B and Walker S 2015 Fitting linear mixed-effects models using lme4 J. Stat. Softw. 67 1–4
[23] Barton K 2009 Mu-Mln: multi-model inference. R Package Version 0.12.2 r18
[24] Lough J M 2012 Small change, big difference: sea surface temperature distributions for tropical coral reef ecosystems, 1950–2011 J. Geophys. Res. 117 C09018
[25] Bayraktarov E, Pizarro V, Eidsen C, Wilke T and Wild C 2013 Bleaching susceptibility and recovery of Colombian Caribbean corals in response to water current exposure and seasonal upwelling PLoS One 8 e60536
[26] Tošić M and Navas-Camacho R 2012 Long-term monitoring of temperature in coral reef waters of the Colombian Caribbean. Joint ICTP-TWAS Workshop on Climate Change in Mediterranean and Caribbean Seas, Guayaquil, Ecuador
[27] Manzello D P, Berkelmans R and Hendee J C 2007 Coral bleaching indices and thresholds for the Florida Reef tract, bahamas, and St. Croix, US virgin Islands Mar. Pollut. Bull. 54 1925–31
[28] Lough J M, Anderson K D and Hughes T P 2018 Increasing thermal stress for tropical coral reefs: 1871–2017 Sci. Rep. 8 6079
[29] Morikawa M K and Palumbi S R 2019 Using naturally occurring climate resilient corals to construct bleaching-resistant nurseries PNAS 116 10586–91
[30] Klein S G, Pitt K A, Lucas C H, Hung S H, Schmidt-Roach S, Aranda M and Duarte C M 2019 Night-time temperature reprieves enhance the thermal tolerance of a symbiotic cnidarian Front. Mar. Sci. 6 453
[31] Sully S, Burkkepile D E, Donovan M K, Hodgson G and van Wees C R 2019 A global analysis of coral bleaching over the past two decades Nat. Commun. 10 1264
[32] Atewebaner M and McClanahan T R 2010 Relationship between historical sea surface temperature variability and climate change-induced coral mortality in the Western Indian Ocean Mar. Pollut. Bull. 60 964–70
[33] McClanahan T R et al 2012 Prioritizing Key Resilience indicators to support coral reef management in a changing climate PLoS One 7 e42884
[34] Oliver T A and Palumib S R 2011 Do Fluctuating temperature environments elevate coral thermal tolerance? Coral Reefs 30 49–40
[35] Guest J R, Baird A H, Maynard J A, Muttaqin E, Edwards A J, Campbell S J, Yewdall K, Afdi Y A and Chou L M 2012 Contrasting patterns of coral bleaching susceptibility in 2010 suggest an adaptive response to thermal stress PLoS One 7 e33353
[36] Guest J R et al 2016 Coral community response to bleaching on a highly disturbed reef Sci. Rep. 6 20717
[37] Pitaia C, Burn D and Pratchett M 2019 Changes in the population and community structure of corals during recent disturbances (February 2016–October 2017) on Maldivian coral reefs. Sci. Rep. 9 8402
[38] Huang D, Benzioni F, Fukami H, Knowlton N, Smith N D and Budd A F 2014 Taxonomic classification of the reef coral families Merulinidae, Montastraeidae, and Diplastraeidae (Cnidaria: anthozoa: scleractinia) Zool. J. Linn. Soc. 171 277–355
[39] McCowan D M, Pratchett M S and Baird A 2012 Bleaching susceptibility and mortality among corals with differing growth forms Proc. of the 12th Int. Coral Reef Symp.
[40] Kennedy J J 2014 A review of uncertainty in in situ measurements and data sets of sea surface temperature Rev. Geophys. 52 1–32