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The Third Global Coral Bleaching Event on the Marginal Coral Reefs of the Southwestern Indian Ocean and Factors That Contribute to Their Resistance and Resilience

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Abstract: Coral reefs reach their southernmost limits in the southwestern Indian Ocean in Maputaland, South Africa. Here, we investigate the recent global coral bleaching event of 2016, the thermal dynamics of these marginal high-latitude reefs and the potential environmental factors regulating the responses of coral communities. Pre-, peak- and post-bleaching surveys of over 9850 coral colonies from 29 genera were undertaken over 3 years across 14 sites spanning 120 km of coastline using point-intercept and visual bleaching index survey methodologies. Bleaching data were related to several environmental variables including temperature, degree heating weeks (DHW), depth, latitude, and upwelling intensity. These reefs have experienced a history of relatively low thermal stress based on DHW. Long-term in situ temperature records nevertheless showed no obvious trend of increase. In situ temperatures also displayed poor relationships, with temperatures predicted by the Representative Concentration Pathway models. Mild coral bleaching with no significant mortality was recorded across sites with taxon-specific bleaching responses evident. Latitude and cumulative daily DHW were significantly related to the bleaching index whereas depth and interactions of depth with latitude and DHW were not. While upwelling of cooler water may offer some refuge to coral communities, especially in the Central and Southern Reef Complexes where it is more pronounced, this may only be transient as the upwelled water may also experience some degree of warming in future, thereby limiting such protection from global warming.

Keywords: climate change; coral communities; degree heating weeks; depth; high-latitude reefs; latitude; Maputaland; shelf edge; submarine canyons; upwelling

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1. Introduction

Coral reefs are highly valued natural assets [1,2]. Despite their value, coral reefs are becoming increasingly threatened by both global and local stressors [3]. Warming by anthropogenic climate change is a significant global threat and has resulted in high losses of live coral [4]. Anomalously warm temperatures can cause coral bleaching which is a consequence of the loss of zooxanthellar algae from the host tissue and often results in mortality [5]. There have been several global bleaching events with one of the most severe occurring in 2014–2017 [6], which also affected parts of the south-west Indian Ocean [7].

The southern-most coral reefs in the south-west Indian Ocean are located in South Africa [8–10]. The ecological functioning and biological characteristics of these reefs have been reviewed by Schleyer et al. (2018) [11] and described in detail by Schleyer and Porter (2018) [12]. Despite these reef's marginal nature, they exhibit relatively high levels of biodiversity and are protected in the iSimangaliso Wetland Park World Heritage Site [11,13]. They are not typical accretive coral reefs but consist of submerged fossil dunes encrusted by corals. Soft coral cover of 30% is dominant over hard coral cover of 23% [14]. The reefs are considered to be almost pristine as they have not been significantly impacted by local-scale pressures [11] or climate-related coral bleaching [15].

During the largest mass coral bleaching and mortality event that impacted much of the Western Indian Ocean (WIO) in 1998 [16,17], only negligible coral bleaching was recorded on the high-latitude reefs of South Africa [18]. While some reefs in the WIO experienced more than 90% mortality due to bleaching [19], less than 1% of the hard corals bleached in South Africa [18,20]. This was mostly due to bleaching in widely spaced colonies of *Montipora* [18]. No bleaching was recorded in the following year of 1999 [21]. Subsequently, Floros et al., (2004) [22] recorded an increase in bleaching across the coral community of between 5 and 10% in 2000–2001. *Montipora* was again detected as being the most bleached genus. The bleaching was associated with increased sea temperatures characterized by high seasonal peaks, as well as high radiation levels during the summer months of 2000 [21].

During this period (2000), Celliers and Schleyer (2002) [21] measured similar levels of bleaching of the total living cover of up to 12% at Sodwana Bay. This was largely restricted to Two-mile Reef with the other reefs in the Central Complex either showing no bleaching or levels of ~1%. They found that most hard corals that bleached belonged to the genera *Montipora* and *Alveopora*, and that an encrusting sponge *Suberites kelleri* was also found to bleach. Of the coral colonies that manifested bleaching, 47% were completely white whilst 44% were partially bleached. No whole colony mortality was ever recorded but partial mortality was detected in 9% of bleached corals. Bleaching was also inconsistent among colonies of the same species of *Montipora*, as colonies displayed variable levels of bleaching across the two reefs where bleaching was detected [21].

Bleaching was not documented again in South Africa until 2005, when the bleaching response index across all hard coral taxa was as high as 40 during a warm-water anomaly in the southern Indian Ocean [23]. *Montipora* spp. were again found to show some of the highest incidences of bleaching, with bleaching response indexes of up to 65. Sebastian et al. (2009) [24] recorded bleaching responses across the coral community during this time, ranging from 11 at Nine-mile Reef in the Central Complex to 30 at Tridacna on Saxon Reef in the Northern Complex. Generally, deeper sites suffered less from bleaching [24]. Since then, only negligible levels of bleaching have been recorded up until 2016.

Over the last twenty-five years, bleaching-induced mortality on South African reefs has been minimal and, as such, the cover of hard coral has remained relatively consistent for the past decade [15]. Glynn (1996) [25] hypothesised that reef environments " ... at moderate depth, in upwelling centres, on oceanic banks or island shores exposed to vigorous circulation, and at some high latitude sites ... " could be potential refuge sites. The high latitude of these reefs in South Africa and the narrow shelf has provided them some protection from bleaching in the past [21]. The reefs are also located in relatively deep water (~$\geq$12 m) that is naturally turbulent and they experience periodic upwelling events in summer which help to cool the surface waters [21,26]. However, the characteristically clear water of this region may exacerbate bleaching [10,21]. Furthermore, reefs in the Northern Complex are furthest from the shelf edge and submarine canyons relative to reefs further south, and are likely to experience reduced canyon-induced upwelling and cooling effects, making them potentially more vulnerable to bleaching [14]. Understanding the responses of high-latitude coral communities to thermal stress driven by climate change will provide an indication of their ecological resilience and be important in predicting their future and potential for range expansion [27].

Ecological resilience is a measure of the amount of change needed before an ecosystem is transformed from one set of processes and structures to an alternative set of processes and structures [28]. Some coral communities are displaying evidence of resilience to global warming [29], such as those in the Phoenix Islands, central Pacific [30]. In certain circumstances, resilience may be due to ecological resistance, a component of ecological resilience [31]. In this respect, resistance is a characteristic of communities or populations that remain unchanged when subjected to disturbance [32]. Ideally, coral communities may be able to either resist a disturbance such as bleaching in the first place or quickly recover from it through the contribution of critical resilience factors [33].

During the third global bleaching event of 2014–2017 [34], surveys of the percentage cover of bleached coral and bleaching indexes were undertaken across all three reef complexes. The aim of this study was to investigate the spatial and temporal dynamics of bleaching and potential environmental factors regulating the associated responses of these marginal coral communities. Historical and recent temperature indices, including degree heating weeks (DHW), as well as the role of upwelling in the region, depth and latitude were investigated. We predicted that coral communities exposed to higher DHW and those located at lower latitudes and shallower depths would be most affected by bleaching.

2. Materials and Methods

2.1. Temperature Data

Three types of temperature data were utilized—in situ records from four sites over various periods, degree heating week records and projected sea-surface temperature data.

In situ temperatures at hourly mean intervals have been recorded at Nine-mile Reef, South Africa since 1994, initially using Hugrun underwater temperature recorders (UTRs) and after 2000 with Starmon mini UTRs, providing a long-term record [15] (Figure 1). In addition, Hobo temperature loggers were deployed at Tridacna and Chain Reef and Leadsman Shoal at 9 m, 16 m and 18 m depths, respectively, where bleaching index surveys were conducted from December 2014 to April 2016; these quantified temperatures were taken at 30-min mean intervals. These in situ temperature records were supplemented with daily 5 km resolution degree heating week (DHW) records acquired from the NOAA Satellite and Information Service [35] for the same 3 sites. Furthermore, historical daily DHW data were acquired from 1985 and extracted for several sites where bleaching surveys were conducted, spanning all three reef complexes, using python language scripts with Jupyter Notebook 6.20. and Anaconda Navigator 1.10.0 to provide an overview of historical thermal stress in the region.

Projected sea-surface temperature data from the Coupled Model Intercomparison Project Phase 5 (CMIP5) for Representative Concentration Pathways (RCPs) 2.6, 4.5, 6.0 and 8.5 were acquired for the area encompassing Nine-mile Reef from the Earth System Grid Gateway—National Centre for Atmospheric Research (ESG-NCAR) Climate Data Gateway [36–38]. The data included all of the ensemble runs for each of the four RCPs and were compared to in situ temperature records to provide an overview of how well the projected data corresponded with the empirical data.

2.2. Coral Bleaching Data

Two independently collected datasets on coral bleaching were analysed—point-intercept data on bleaching severity and bleaching index data following the method of McClanahan (2004) [39].

Point-intercept data on bleaching severity and benthic cover were collected from 5 sites ranging in depth from 9–18 m on Two-mile Reef, Central Reef Complex (Figure 1). At each site, 4–7 replicate 10-m long weighted transects, with intervals marked every 50 cm, were haphazardly placed on areas of reef using SCUBA. Depending on the number of transects, sites were ~1600–2800 m^2 in extent. A GoPro video camera was used to survey each transect at a distance of ~1 m above the reef. These surveys were conducted in December 2015 and again in May and September 2016, at the same five sites, corresponding to pre-, peak- and post-bleaching periods, respectively. The benthic cover and the bleaching severity beneath each 50-cm interval along the video transects were extracted in the laboratory. Bleaching severity was scored according to a four-level ordinal scale where: 0 = no bleaching; 1 = pale but not white; 2 = white; and 3 = recently dead.

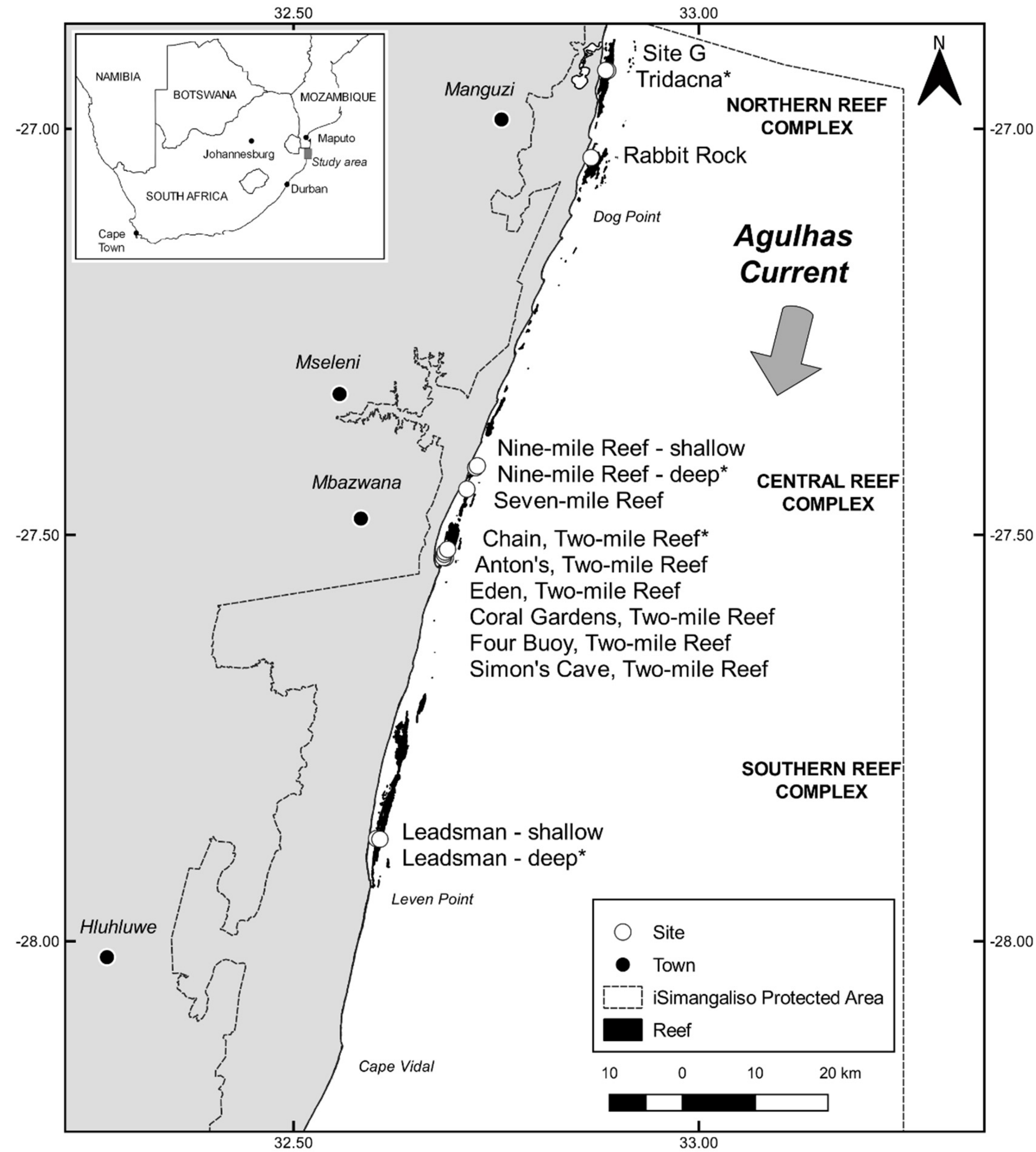

Figure 1. Coral reefs in the southwestern Indian Ocean of the Maputaland region of South Africa indicating study sites where bleaching surveys were conducted. * indicates sites where underwater temperature recorders were present.

Bleaching was also assessed using the method and bleaching index described by McClanahan (2004) [39]. This provides an index of the proportion of bleached corals relative to the total number of corals surveyed. This method allowed for taxon- and site-specific bleaching indices to be calculated, as well as the determination of the proportion of hard coral colonies bleached relative to the total number of hard coral colonies assessed. These surveys were conducted during May 2015, 2016, and 2017 at 13 sites situated across all three reef complexes in Maputaland, South Africa at depths of 6–19 m (Figure 1).

2.3. Data Analysis

In situ quantified temperatures since 1994 from Nine-mile Reef were summarised into monthly and yearly average, -minimum and -maximum metrics and linear regression models fitted to determine temporal trends only. In situ temperatures from the Nine-mile Reef and those predicted by the CMIP5 RCPs 2.6, 4.5, 6.0 and 8.5 were compared from 2006 to 2019. We consider the relationship between empirically derived in situ temperatures and those predicted by CMIP5 RCPs to be relevant, but not causal. Monthly, yearly average and yearly maximum monthly temperature metrics were compared. Trends for each temperature metric over time were calculated with linear regression to derive the slope of the relationship only. Before correlations between in situ temperatures and those from the RCPs were derived, the data were explored graphically with scatterplots and assessed for normality and homogeneity of variance using Shapiro-Wilks and Fisher's *F* tests, respectively. Furthermore, each timeseries was tested for a seasonal and a linear trend using the *nsdiff* and *ndiff* commands in the R version 4.0.2 forecast package, respectively [40,41], as timeseries data are usually serially correlated. Seasonal trends were detected in all five monthly timeseries and, therefore, the monthly timeseries were differenced by a factor of 1 and a lag of 12 using the *diff* command in the R base package to seasonally detrend them. Linear trends were not detected in the yearly-average and yearly maximum timeseries, nor the seasonally detrended monthly timeseries, therefore, no further detrending by differencing was required. The removal of seasonal and linear temporal trends in the timeseries by differencing was conducted in order to avoid spurious correlations that may occur, as one trended timeseries regressed against another will often reveal a strong but false relationship [42]. Although exploratory analyses indicated that the data were normally distributed, variances were heterogeneous, and scatterplots indicated monotonic relationships between in situ temperatures and those derived from the RCPs. Therefore Spearman-rank correlations were calculated to assess relationships between empirically derived in situ temperatures and those of the RCPs using the *corr.test* command in the R base package.

One-way univariate permutational analyses of variance (permANOVA) were run using 9999 permutations of residuals under a reduced model with type I sums of squares based on the Euclidian distance metric, to investigate whether temperatures differed in magnitude between in situ records and those derived from the four RCPs, as the data were non-parametric and non-independent [43]. The ANOVA was supplemented with univariate permutational analyses of dispersion (permDISP), also using 9999 permutations [44]. All permutation-based analyses were conducted with PERMANOVA+ for PRIMER [45].

Upwelling intensities were investigated at three sites located over a coastline distance of 110 km, using the Hobo temperature logger data and classified according to Berkelmans et al. (2010) [46], where daily amplitudes of 0–0.5 °C were defined as no upwelling, 0.5 < 1.0 °C as low-intensity upwelling, 1.0 < 2.0 °C as medium-intensity and >2.0 °C as high-intensity upwelling. Seasonal patterns in upwelling intensity at the same three sites were also investigated using the daily temperature coefficient of variation. The coefficient of variation was employed to adjust for any influence due to seasonal warming as there is naturally greater variation in daily temperatures during summer, when temperatures are warmer [47].

The bleaching severity data derived from the point intercept transects were analysed using a three-factor permANOVA supplemented with a permDISP. *Period* (pre-, peak- & post-bleaching) was treated as a fixed factor while *site* and *transect* were included as random factors with *transect* nested in *site* and *period*. The analysis was run using type III sums of squares based on the Euclidian distance measure with 9999 permutations of residuals under a reduced model. *Post hoc* permANOVA analyses were further conducted on the fixed effects term *period*. The permDISP was run with the same model with pairwise comparisons focused initially on groups of replicate transects to investigate higher-order dispersions among groups at this level.

For the bleaching index data, the multivariate relationship between scleractinian community composition and the bleaching index at each site was assessed using distance-based linear models (DistLM) based on root-transformed abundance (count) data and the Bray-Curtis similarity to determine if there was a significant relationship between community composition and bleaching index for each of the three years it was quantified. This was conducted to ensure that the coral community itself was not a confounding factor prior to subsequent analyses of bleaching index. The bleaching index data were then analysed using a permutational analysis of covariance (permANCOVA) to explore their association with several environmental factors that could be influencing the degree of bleaching intensity. *Year* was considered a random factor while *latitude*, *depth* and *cumulative DHW* (from 6 months prior to bleaching surveys) were fitted as covariates. Type I sequential sums of squares were used so that the covariates could be investigated first, and the analysis was set to run 9999 Monte-Carlo permutations of the residuals under a reduced model [45]. The inclusion of *latitude* in the model also allowed for 91% of the spatial variation in sampling location to be accounted for by modelling the spatial dependence between the sites prior to fitting *depth* and *cumulative DHW*.

3. Results

3.1. Temperature

Cumulative degree heating weeks (DHW) since 1985 were highest at Tridacna, the northernmost site in the Northern Reef Complex, at 2276.8 °C and lowest at Leadsman, the southernmost site in the Southern Complex at 1253.3 °C (Figure 2). Since the start of DHW records in 1985, all five sites in each of the three reef complexes indicated accumulated thermal stress, with stepped inclines during ~1988–1999, ~2005–2010 and most markedly during 2016–2017 (Figure 2). Results for Tridacna and Rabbit Rock in the Northern Complex indicated similar DHW trajectories over time, which diverged from the other sites in the Central and Southern Complex which had relatively similar DHW trajectories.

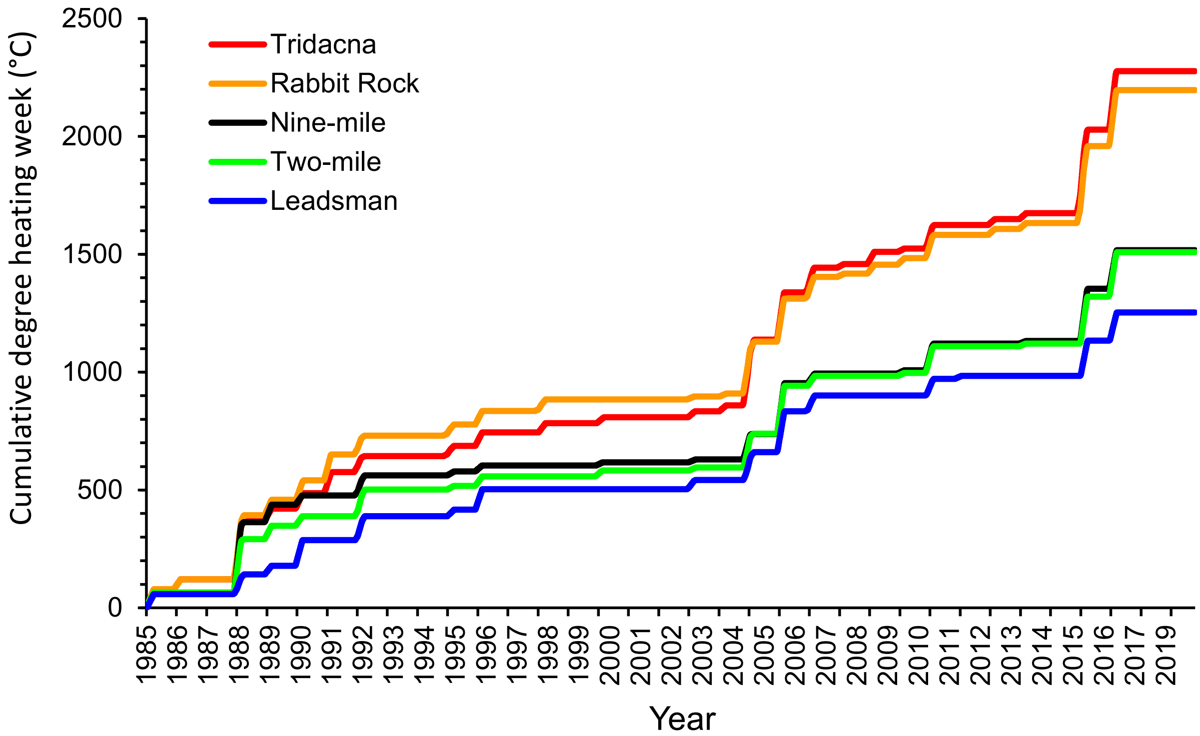

Figure 2. Cumulative daily degree heating weeks (°C) for several sites spanning the Northern, Central and Southern Reef Complexes in Maputaland, South Africa.

In situ measured temperatures at Nine-mile Reef since 1994, based on hourly measurements, have shown a declining trend at a rate of −0.0876 °C per decade. Monthly average, -minimum and -maximum metrics also showed declining trends (−0.0010 to −0.0013 °C Month^{-1}) (Electronic Supplementary Material 1, Figure S1a), as did the yearly average and -maximum metrics (−0.0115 and −0.0077 °C Year^{-1}, respectively) (ESM 1, Figure S1b). Only the yearly minimum metric indicated an increasing trend of 0.0046 °C Year^{-1}. In situ temperatures at Nine-mile Reef based on monthly, yearly average and yearly maximum metrics, all displayed decreasing trends with time since 2006 when Representative Concentration Pathway (RCP) temperatures are available (Table 1, Figure 3, ESM 2 Figure S1a,b). Similarly, monthly temperature trends predicted by each of the four RCPs displayed decreasing trends with time (Table 1, Figure 3). Contrastingly, temperature trends for the yearly average and yearly maximum metrics for all four of the RCPs displayed increasing trends (Table 1, ESM 2, Figure S1a,b). Strong seasonal patterns were evident for all monthly timeseries (Figure 3).

Table 1. Temperature trends from 2006 to 2019 at Nine-mile Reef according to each temperature model and associated temporal metric, and spearman correlation coefficients and associated probability values, as well as *post hoc* permutational ANOVA probability values, between in situ temperatures and the four Representative Concentration Pathway (RCP) modelled temperature timeseries. Significant differences are highlighted in bold (α = 0.05).

Model	Trend			Spearman Correlation Coefficient			$P_{(Spearman)}$			$P_{(perANOVA)}$		
	Monthly	$Yearly_{Ave}$	$Yearly_{Max}$	Monthly	$Yearly_{Ave}$	$Yearly_{Max}$	Monthly	$Yearly_{Ave}$	$Yearly_{Max}$	Monthly	$Yearly_{Ave}$	$Yearly_{Max}$
In situ	−0.002	−0.0053	−0.0374	–	–	–	–	–	–	–	–	–
RCP2.6	−0.0006	0.0132	0.0177	0.063	−0.283	0.070	0.4386	0.3273	0.8129	**0.0001**	**0.0001**	**0.0001**
RCP4.5	−0.0015	0.0022	0.0041	0.034	0.631	−0.234	0.6720	0.1410	0.4210	**0.0001**	**0.0001**	**0.0001**
RCP6.0	−0.0014	0.004	0.0081	0.286	0.669	−0.172	**0.0003**	**0.0088**	0.5565	**0.0001**	**0.0001**	**0.0001**
RCP8.5	−0.0006	0.0129	0.0150	0.113	0.0171	−0.272	0.1611	0.9537	0.3477	**0.0001**	**0.0001**	**0.0001**

Spearman correlation coefficients between the monthly temperatures predicted by all four RCPs and the in situ monthly temperatures were all positive and generally low (Table 1). However, the correlation between in situ and RCP6.0 monthly temperatures was relatively high and significant (rho = 0.286; $p = 0.0003$). Correlations between yearly average RCP temperatures and in situ temperatures were generally positive and non-significant. However, a statistically significant relationship was detected between yearly average in situ and RCP6.0 temperatures (rho = 0.669; $p = 0.0088$). Contrastingly, correlations based on yearly maximum temperatures were generally negative and yielded no significant relationships between in situ and RCP temperatures.

For all three temperature metrics (monthly, yearly average & yearly maximum), in situ temperatures were at least a degree lower than those derived from the RCP models (Figure 3 and ESM2, Figure S1a,b). Permutational ANOVA analyses indicated significant differences among in situ temperatures and those predicted by the four RCPs for all three temporal metrics ($p < 0.0001$), with *post hoc* analyses detecting differences between in situ and projected temperatures for all RCPs and temporal metrics ($p < 0.0001$) (Table 1). Significant differences in dispersion were detected between in situ temperatures and those projected by all four RCP scenarios for both yearly average ($p < 0.05$) and yearly maximum ($p < 0.005$) metrics, but not for the monthly temperature metric ($p = 0.8149$).

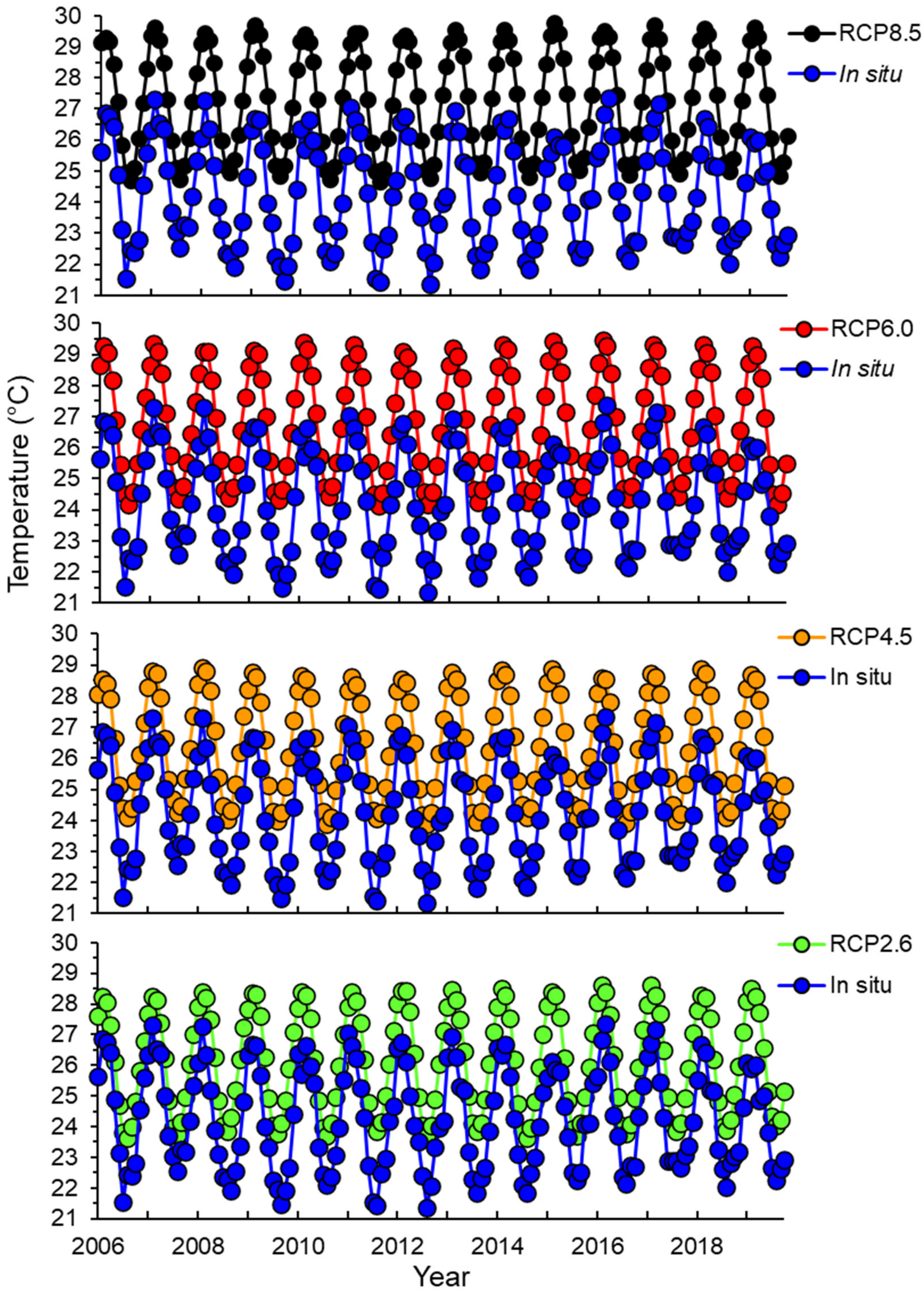

Figure 3. Temperature timeseries from 2006 based on monthly data derived from in situ measurements and Representative Concentration Pathway (RCP) models for Nine-mile Reef, Sodwana Bay, South Africa. Monthly in situ data are at least a degree centigrade cooler compared to the different monthly temperatures derived from the various RCP models.

In situ temperatures at Tridacna, Chain and Leadsman where some of the bleaching surveys were conducted (2015–2017) were highest during March 2016 (Figure 4). A maximum temperature of 28.96 °C was recorded at Chain, although temperatures at each of the sites were on average highest at Tridacna followed by Chain and Leadsman, respectively. Rapid decreases in temperatures of >2 °C within 6 h at all sites were detected. Daily DHW temperatures followed a similar pattern to temperatures at all sites where they were highest at Tridacna (max = 4.21) followed by Chain (2.40) and Leadsman (1.79) from February–May 2016 (Figure 4). The daily temperature coefficients of variation at Tridacna, Chain and Leadsman ranged from 0.001–0.076 and had an average ± standard deviation (SD) of 0.010 ± 0.011 (Figure 5). All three sites indicated the full range of upwelling intensities (no upwelling to high upwelling) with Tridacna showing the least and Leadsman showing the most (ESM 3, Figure S1). Medium- to high-upwelling intensities were particularly prevalent during the austral summer and autumn periods at all three sites whereas no and low-upwelling intensities characterised sites during the winter and spring periods (Figure 5).

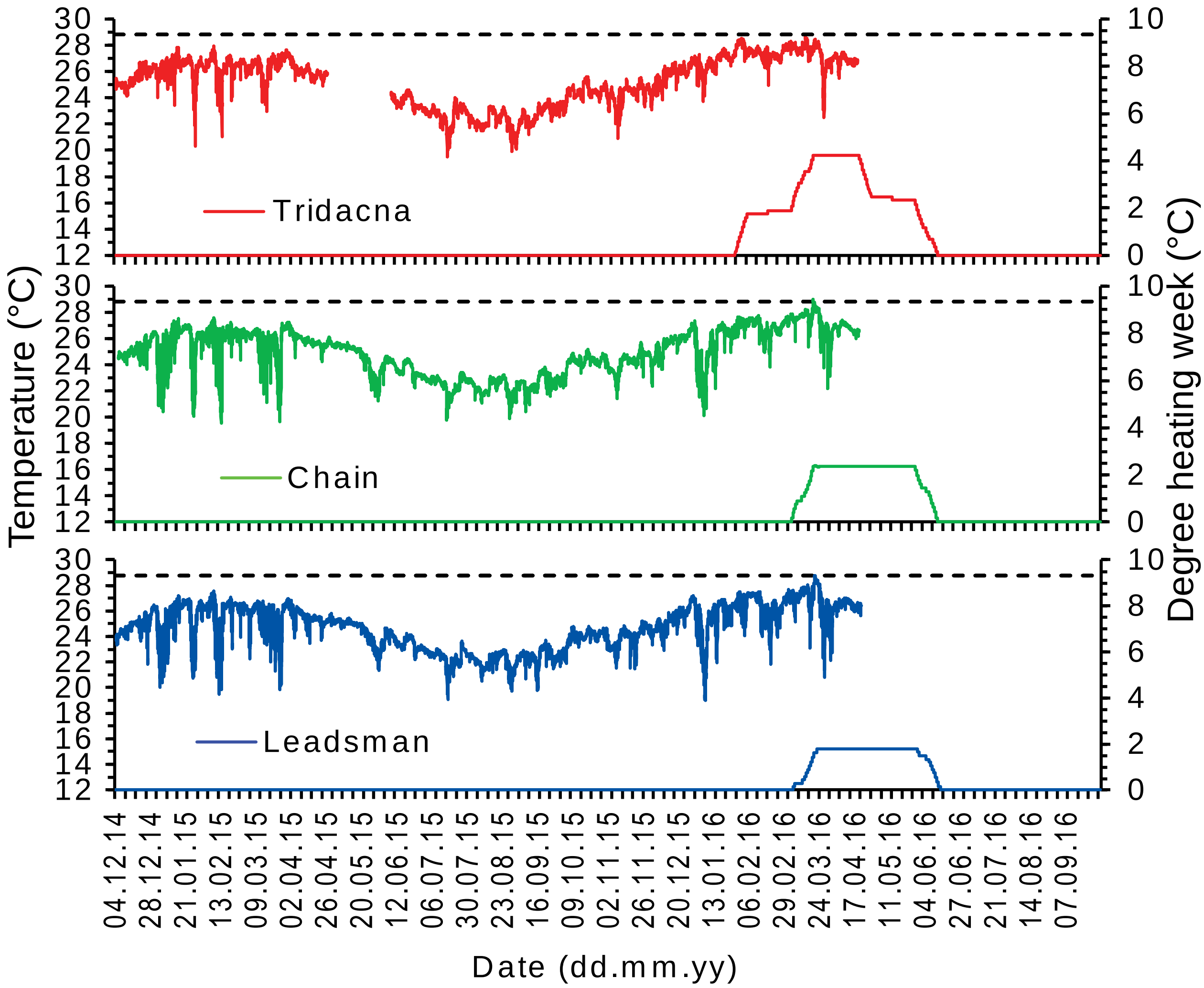

Figure 4. Temperature timeseries and degree heating weeks at Tridacna, Chain and Leadsman Shoal in Maputaland, South Africa during bleaching surveys conducted in December 2015, April–May 2016 and September 2016. The dashed line indicates the local bleaching threshold temperature [21].

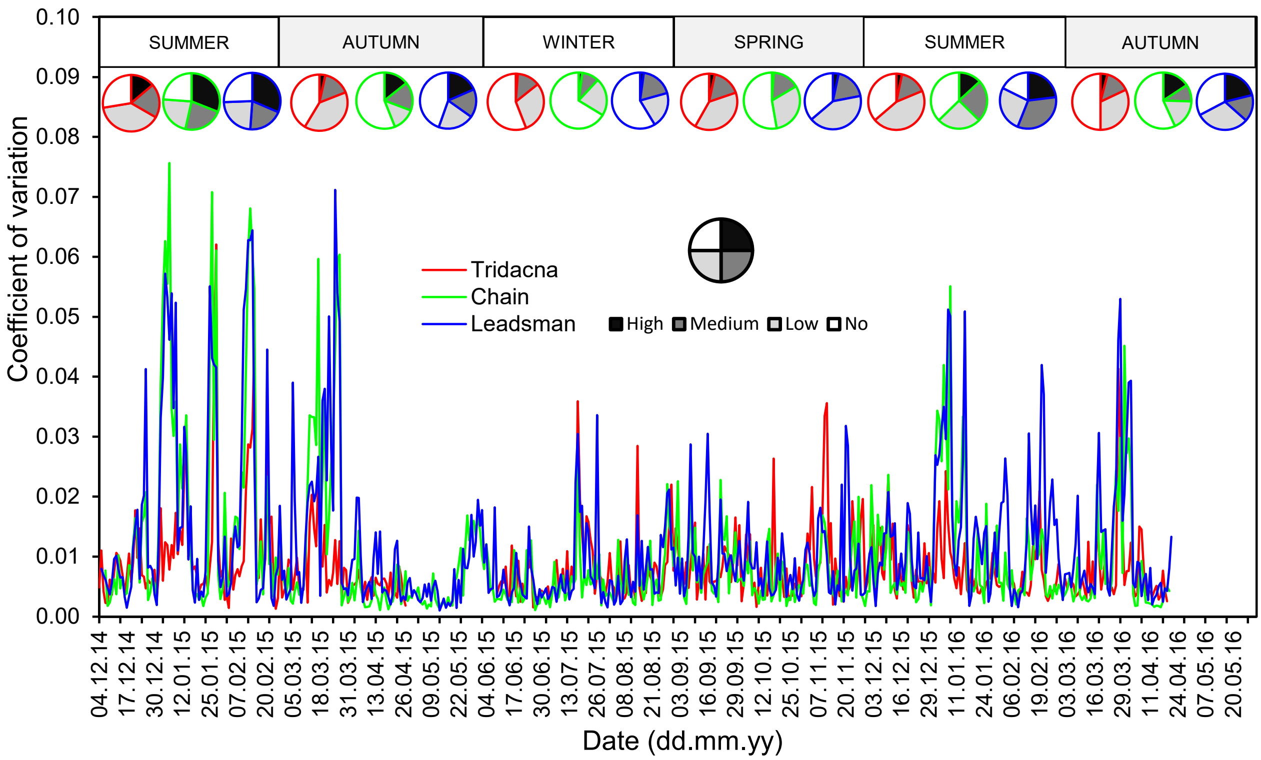

Figure 5. Temperature timeseries of daily temperature coefficients of variation (coloured lines) measured at Tridacna, Chain and Leadsman, Maputaland, South Africa as well as the relative frequencies of upwelling intensity's (coloured pie graphs) according to each site and season leading up to peak coral bleaching surveys in April-May 2016. Colours indicate the site, whilst shading in the pie graphs indicates upwelling intensity ranging from no upwelling (white) through to high intensity upwelling (black) for each season.

3.2. Coral Bleaching

A total of 978 point-intercepts were recorded during the pre- (289), peak- (409) and post-bleaching (280) severity surveys on Two-mile Reef. The average ± standard error bleaching severity across the five sites on Two-mile Reef was highest during the peak-bleaching period at 0.13 ± 0.02, followed by pre- (0.07 ± 0.02) and post-bleaching (0.01 ± 0.01) periods. During peak bleaching, this translated into 90.6 ± 2.7% of the coral cover being assessed as normal, 4.8 ± 2.1% as pale and the remaining cover of 4.6 ± 1.4% as bleached (Figure 6). Peak-period bleaching on Two-mile Reef reached a maximum at Eden of 9.0% of the coral cover. Contrastingly, the pre-bleaching period did not record any bleached coral although 3.6 ± 1.2% and 0.6 ± 0.4% of the coral cover was recorded as pale or recently dead, respectively. Post-bleaching surveys indicated that 98.9 ± 0.7% of the coral cover was normal with the remaining 1.1 ± 0.7% being pale. The permutational ANOVA (permANOVA) on bleaching severity detected a significant difference among the *periods* when bleaching assessments were conducted ($P_{(perm)} = 0.0223$). *Post hoc* pairwise permANOVA analyses found that bleaching severity was significantly higher during the peak-bleaching period compared to the post-bleaching period ($P_{(perm)} = 0.0099$) but did not differ between pre- and peak- ($P_{(perm)} = 0.1771$) nor pre- and post-bleaching periods ($P_{(perm)} = 0.1459$). Permutational analyses of dispersion found significant differences between most transects for peak- and post-bleaching pairwise comparisons within their respective sites ($p < 0.05$).

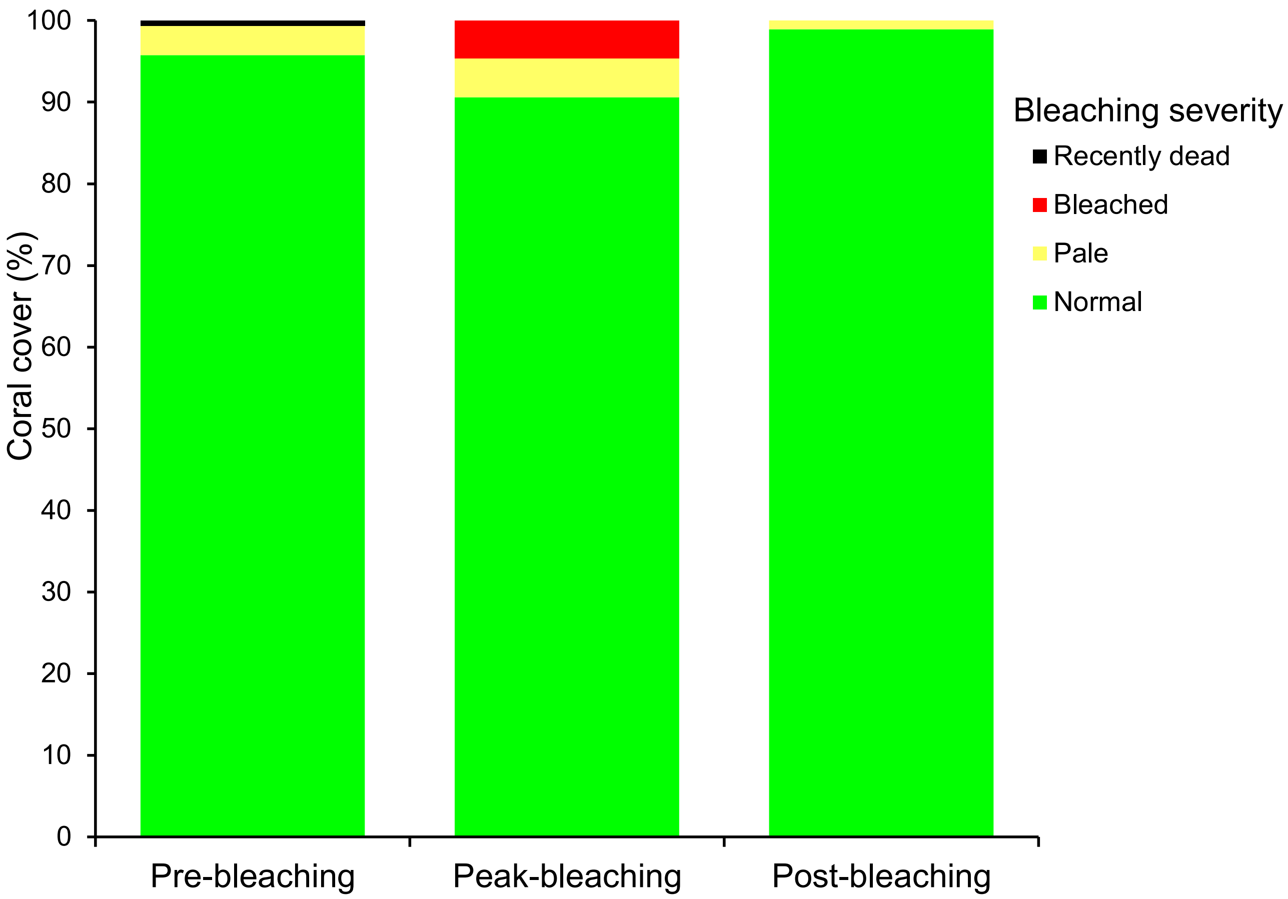

Figure 6. Average bleaching severity as a proportion of total coral cover, assessed at five sites on Two-mile Reef, Central Reef Complex, using point-intercept transects during pre-, peak- and post-bleaching periods (2015–2016).

The bleaching indices of 9855 scleractinian colonies were assessed over the three-year period. The average ± standard deviation bleaching index at a site was 9.8 ± 3.1 across the three years and ranged from 3.8 at Leadsman Deep in 2016 to 16.7 at Rabbit Reef in 2016 (Figure 7d). The average ± SD annual bleaching index was 7.9 ± 2.3 in 2015, 10.8 ± 3.6 in 2016 and 10.7 ± 2.3 in 2017. Over the three-year period, 6226 colonies were assessed as normal and 2468 colonies as pale while the remaining 1161 colonies showed some degree of bleaching or recent mortality. Distance-based analyses of a linear model (DistLM), assessing the relationship between scleractinian community composition and bleaching index at each site, detected non-significant relationships during all three years ($P_{(perm)} > 0.05$). The amount of variation in the bleaching index explained by scleractinian community composition ranged between 13.2 and 14.8% depending on the year. Nevertheless, different scleractinian genera had different bleaching indexes (Figure 8). Of the genera where twenty-five or more colonies were assessed, bleaching indexes were highest for *Montipora* (28.8) followed by *Paramontastraea* (20.2) and *Goniastrea* (12.1), and lowest for *Fungia* (0.0), *Pavona* (0.3) and *Gyrosmilia* (1.3). The bleaching index showed increasing trends with a decrease in latitude and an increase in cumulative daily DHW, while the bleaching index decreased with increasing depth (Figure 7a–c). The permutational analysis of covariance (permANCOVA) found that latitude and cumulative daily DHW were significantly related to the bleaching index at each site ($P_{(Monte\text{-}Carlo)} = 0.0015$ and $P_{(Monte\text{-}Carlo)} = 0.0062$, respectively) (Table 2). The other independent variables and all interaction terms were not significant ($p > 0.05$).

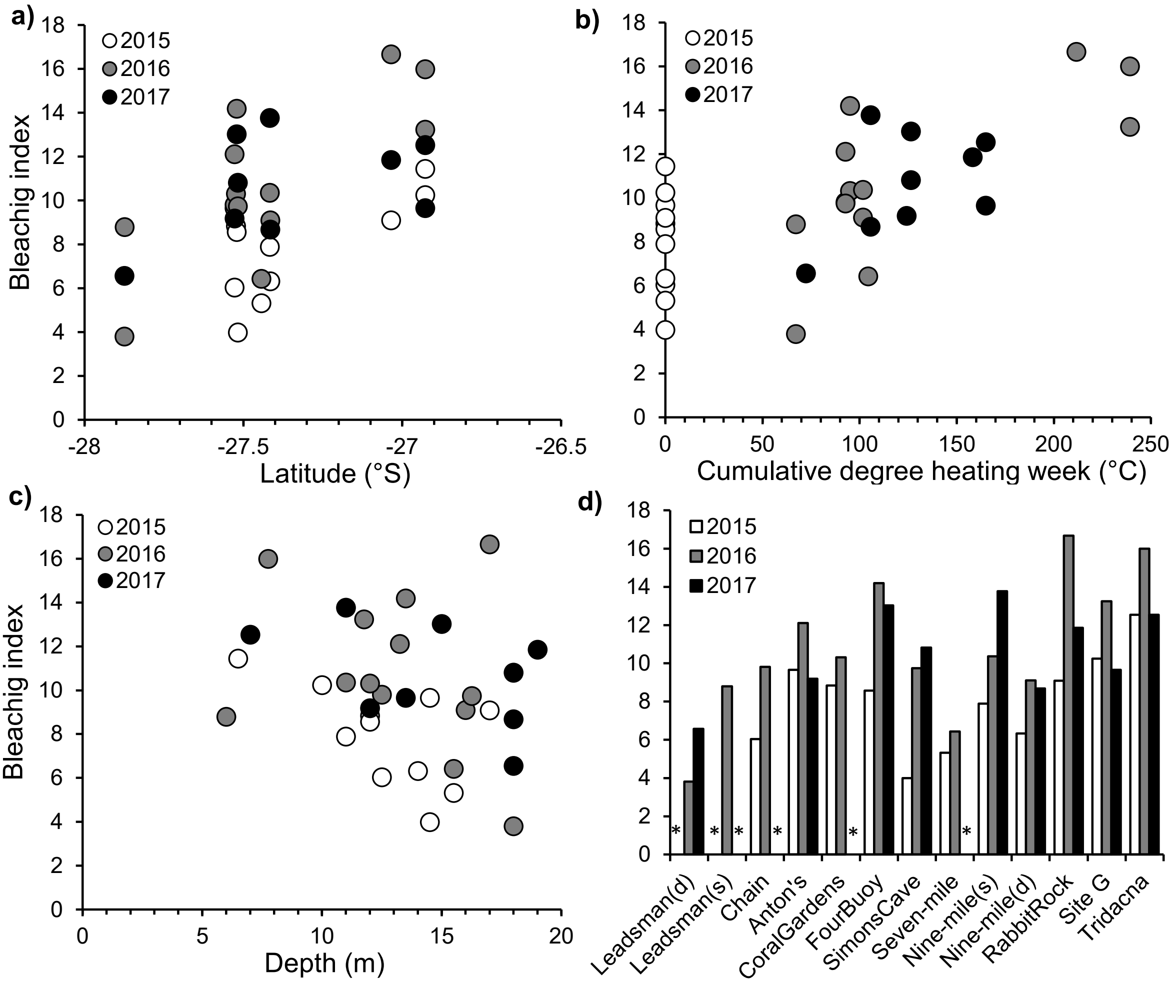

Figure 7. Bleaching index of coral communities from 13 sites in Maputaland surveyed in 2015, 2016, and 2017 in relation to (**a**) latitude (°S), (**b**) cumulative degree heating weeks (°C), (**c**) depth (m) and (**d**) site. * = no data.

Table 2. Permutational analysis of covariance investigating variation in bleaching index according to latitude, depth, cumulative daily degree heating week (DHW) and year on reefs in the south-west Indian Ocean from 2015–2017. Significant effects are indicated in bold (α = 0.05).

Source of Variation	df	MS	Pseudo-F	$P_{(\text{Monte-Carlo})}$
Latitude	1	87.864	16.122	**0.0015**
Depth	1	6.2642	1.2233	0.2842
Degree heating week (DHW)	1	86.742	175.19	**0.0062**
Year	2	0.32103	0.056779	0.9443
Latitude × Depth	1	4.2134	0.7452	0.3974
Latitude × DHW	1	23.499	4.1561	0.0652
Latitude × Year	2	3.0228	0.53462	0.5929
Depth × DHW	1	2.2216	0.39293	0.5413
Depth × Year	2	0.3426	0.060594	0.9434
DHW × Year	1	3.1902	0.56424	0.468
Latitude × Depth × DHW	1	2.4955	0.44136	0.5076
Latitude × Depth × Year	2	3.0243	0.53489	0.5955
Latitude × DHW × Year	1	7.3053	1.292	0.2754
Depth × DHW × Year	1	1.2777	0.22597	0.6399
Latitude × Depth × DHW × Year	1	0.068484	0.012112	0.9164
Residual	13	5.654		
Total	32			

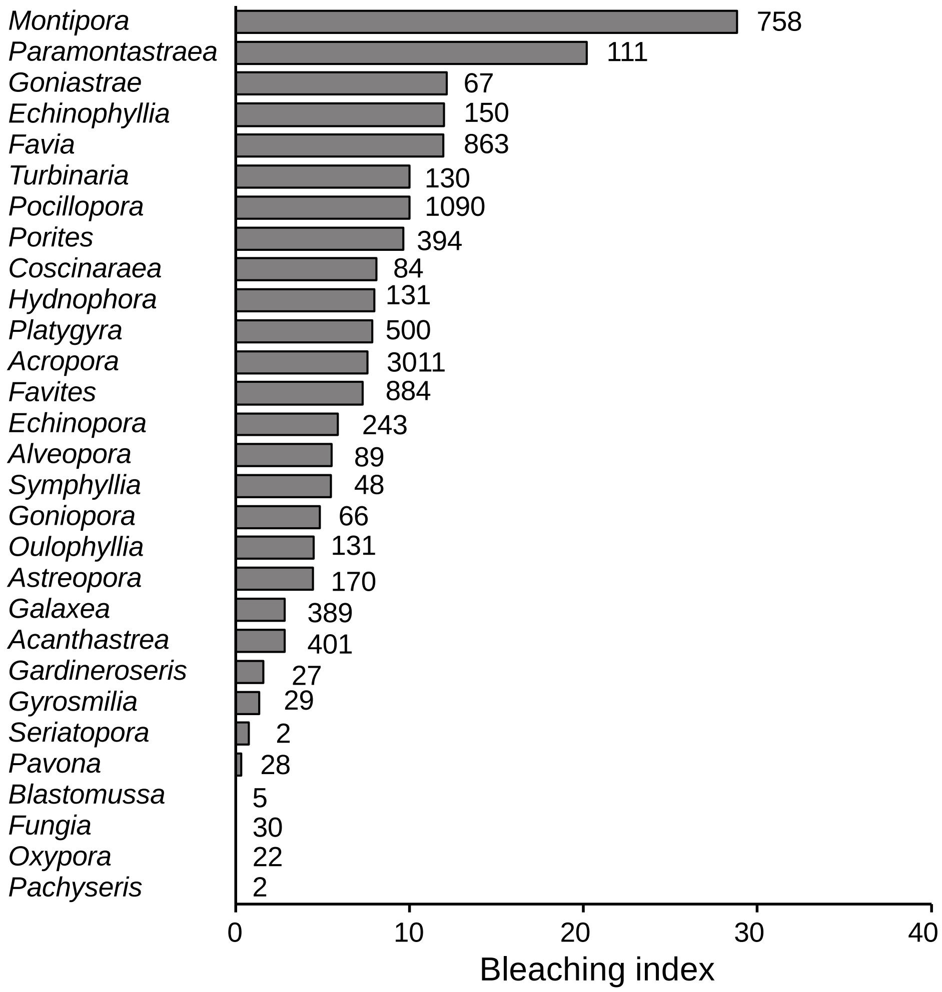

Figure 8. Taxonomic bleaching index for scleractinian genera surveyed across 13 sites on Maputaland high-latitude reefs from 2015 to 2017. Numbers adjacent to bars indicate the total number of colonies assessed.

4. Discussion

This study investigated the spatial and temporal dynamics of bleaching and potential environmental factors regulating the responses of coral communities comprised of 29 genera on the marginal reef of the southwestern Indian Ocean during the third global coral bleaching event. Peak bleaching occurred in 2016 and as predicted, coral communities exposed to higher degree heating weeks (DHW) and lower latitudes were most affected by bleaching. Although bleaching decreased with depth, this relationship was not significant during the period investigated. Patterns in historical and recent temperature indices are discussed first, followed by patterns and trends in bleaching.

4.1. Temperature

Cumulative degree heating weeks since 1985 showed several stepped periods of marked increases across reefs in all reef complexes (Figure 2). The first period of increase in the late 1980s corresponds to the 1987 El Niño event and at a time when large-scale bleaching on many reefs around the world was first reported [4,48,49]. The second marked increase during the mid-2000s corresponded with a period of anomalously warm water in the south-west Indian Ocean [50]. Most notably, there was no increase in DHW during 1998 when reefs bleached further north in the WIO and globally [19]. The most recent period of marked increase in 2016 resulted from a positive Indian Ocean dipole associated with an extreme El Niño that caused the third global coral bleaching event [51]. Despite this, long-term temperatures at Nine-mile Reef have been relatively stable, with a negligible overall decline in temperature with time at a rate of 0.0876 °C per decade (ESM 1, Figure S1a).

The different trajectories of cumulative daily DHW between sites in the Northern Reef Complex and those in the Central and Southern Reef Complexes may relate to meso-scale (~50 km) oceanographic factors in the region such as upwelling [26]. Reefs in the Northern Complex are further from the shelf edge and further from submarine canyons relative to reefs in the Central and Southern Complexes and are therefore likely to experience less effects of cooler oceanic and upwelled water [14]. However, reefs in the Central and Southern Complexes which are characteristically closer to the shelf edge and canyons will probably experience temperatures that are mitigated by these oceanographic factors, causing relatively cooler shelf water to prevail where coral communities occur [14]. In this respect, reefs in the Central and Southern Complexes, although having experienced thermal stress historically, may offer some refuge to coral communities in the future relative to their northern neighbours.

The 2015–2016 timeseries of daily temperature coefficients of variation confirmed upwelling events were present during the lead up to minor coral bleaching in the region, mainly in the summer and autumn months, and indicated that upwelling was most pronounced at Chain and Leadsman, sites investigated in the Central and Southern Reef Complexes, respectively, compared to Tridacna, a site investigated in the Northern Complex (Figure 5; ESM 3, Figure S1). These periodic upwelling events in the Central and Southern Complexes may have reduced temperatures more profoundly than would typically occur at cooler higher latitudes in the region, thus contributing to resistance of coral communities to bleaching. Despite this, anomalously warm temperatures were detected in late summer of 2016 when four DHWs were measured and were briefly on par with or exceeded the local bleaching threshold temperature of 28.8 °C at all three sites in each of their respective reef complexes [21] (Figure 4).

In situ temperatures at Nine-mile Reef manifested poor congruence with temperatures projected by the Representative Concentration Pathway (RCP) models (Figure 3; ESM 2, Figure S1a,b). This was largely because in situ temperatures showed declining trends in temperature with time whereas the RCP models manifested declining monthly trends but increasing annual trends (Table 1). An overall declining trend in temperature with time at Nine-mile Reef has been detected since 1994 [15], and continues to show a declining trend despite the anomalously warm temperatures of the recent 2016 El Niño (ESM 1, Figure S1a–c). Furthermore, temperatures measured in situ and those that were modelled differed significantly in all cases. Interestingly, monthly and yearly average temperatures predicted by RCP 6.0 were significantly correlated with those measured on Nine-mile Reef, however modelled temperatures were consistently warmer than those measured in situ.

At a global scale, CMIP5 predictive models have shown discrepancies with measured temperatures and generally predict too little warming in the past and too much warming in recent years [52]. These models are also often deficient when applied to regional seas [53], as they are typically coarse in resolution (1–3°) [54], which results in their inability to incorporate key processes that may play a dominant role in local responses to global warming [55]. For example, the characteristic local upwelling and oceanographic processes associated with the shelf-edge in the region are unlikely to be accounted for by the global RCP models which are likely to require downscaling to smaller spatial scales to study the effects of climate change on local reefs and their potential future impacts [56]. In the Red Sea, only some of the CMIP5 models produced results comparable to medium and high resolution hindcasts, and the models generally performed more accurately inside the Red Sea than outside, in the Gulf of Aden [57]. As such, the suitability of CMIP5 models for a particular region and parameter must thus be evaluated on a case-by-case basis [58].

4.2. Coral Bleaching

The pre-bleaching condition of sites at Two-mile Reef in terms of coral cover provided a reasonable baseline on which to assess peak- and post-bleaching levels and indicated negligible recent mortality and paling but no bleaching (Figure 6). Although these reefs lie within a marine protected area and World Heritage Site and are generally not exposed to many of the pressures affecting reefs north of South Africa, natural mortality, pollutants from the terrestrial environment and even upwelling of cooler water may account for some of the paling and mortality [11,59]. Three pronounced upwelling events of cooler water by >2 °C within 24 h were detected at Two-mile Reef during a two-week period leading up to pre-bleaching surveys in mid-December 2015. Bleaching severity during the peak-bleaching assessment in May 2016 indicated obvious but limited paling and bleaching of coral cover, and corroborated previous studies indicating local bleaching when temperatures reach 28.8 °C and/or ~4 DHW [13,60]. During 2016, widespread bleaching was recorded in the Western Indian Ocean when some sites experienced 15 DHW and 37% of these sites were affected by high or extreme bleaching [7,61]. Post-bleaching surveys in September 2016 detected no mortality and only negligible paling on the South African reefs, approximating pre-bleaching levels as expected, after degree heating weeks returned to zero in June, corresponding with the cooler austral winter months (Figures 4 and 6).

As expected, the bleaching index of coral communities across all three reef complexes peaked in 2016, corresponding to the 3rd global coral bleaching event and widespread bleaching in the Western Indian Ocean [7,62] (Figure 7a). The average bleaching index of 10.8 recorded in this study in 2016 in terms of equivalent percentage coral cover equates, for example, to 75% normal, 15% pale and 10% full colony bleaching. Previous bleaching index assessments in 2005 at sites spanning the same reefs we assessed, recorded indexes ranging from 11–30, with an average of 17 [24]. This was during an anomalously warm period in the region when temperatures peaked at 28 °C at Two-mile Reef, and followed an unusually large temperature change on 26th December when temperatures rose from 18.3 to 25.1 °C over 33 h. The peak bleaching index we measured also corresponds with subsequent surveys by McClanahan and Muthiga (2021) [27] in Mauritius in 2019, which averaged 17 and ranged between 0 and 56 depending on the site.

Although limited bleaching was detected in 2015 and 2017 on these marginal reefs, DHWs were zero in 2015. This suggests potential biases in the surveys, methodology, or that local heating of the reefs undetectable in the 5 km spatial resolution of the data underpinning DHW could account for this [60] (Figure 7b). During 2017, DHWs and minor bleaching were detected at magnitudes less than that experienced in 2016. The significant and positive relationship detected between the bleaching index and the cumulative DHWs confirmed our prediction that local coral communities exposed to higher DHW would experience higher incidences of bleaching (Table 2). Degree-heating weeks have been shown to be a significant predictor of coral bleaching in the region [50] and in the north-western Pacific [60].

The bleaching index was also significantly related to latitude and displayed an increasing relationship with decreasing latitude as one moved closer to the equator (Figure 7a). A similar pattern was measured in the bleaching responses of coral communities in the region during anomalously warm temperatures in 2005 [24] and the bleaching susceptibility across coral reefs in the Western Indian Ocean was also found to be significantly related to latitude that year [50]. Although the bleaching index declined with increasing latitude, minor bleaching was nevertheless detectable on the southern-most reefs in the southwestern Indian Ocean. Our findings and those of Moore et al. (2012) [63] for south-western Australian reefs and Kim et al. (2019) [64] for high-latitude reefs in eastern Australia, therefore casts doubt over hypotheses proposing that future thermal impacts on coral reefs under predicted warming may be mitigated by high-latitude refugia. Furthermore, the relatively small spatial extent over which our study focused (120 km) further highlights the importance of latitude on these reefs as far as their susceptibility to bleaching is concerned, particularly because we found evidence that reefs in the north of our study area experience less cooling from canyon-induced upwelling and shelf edge effects compared to reefs in the south of our study area, as hypothesised by Porter and Schleyer (2019) [14].

Although we found that the bleaching index decreased with increasing depth as expected, the two were not significantly related (Figure 7c; Table 2). This was despite a previous study in the region detecting a significant relationship between bleaching index and depth in 2005 [24]. The results we obtained, however, align with a previous study by McClanahan et al. (2007) [50] who did not find a significant relationship between bleaching index and depth in their analyses of coral bleaching on reefs in the Western Indian Ocean during 2005. Furthermore, we found that the interaction of depth with latitude was not significant either, and there was therefore limited evidence that coral communities in the region at relatively greater depth and higher latitude were less susceptible to bleaching during this period. However, depending on the magnitude of future thermal anomalies, depth may still be an important factor in mitigating coral bleaching on these marginal and relatively deep reefs as it reduces solar irradiance, ultraviolet radiation and localised heating, thus contributing to the bleaching resistance of local coral communities [15,21]. Furthermore, the low levels of nutrients characterising these waters due to the narrow shelf, dearth of riverine input, absence of cities and adjacent low-density rural populations [10], is likely to further contribute to the resistance and potential resilience of coral communities here as improved water quality can mitigate the effects of climate change on corals [65]. This is dissimilar to many other locations where terrestrial sources of nutrients are likely to increase the probability of bleaching, such as on the Great Barrier Reef [66], although there is evidence that there are high frequencies of bleaching-resistant alleles in corals from localities with poor water quality and large variations in temperature [67]. The role of these factors in mitigating bleaching in the region needs further research.

Taxon-specific differential responses in bleaching indices were obvious among many scleractinian genera (Figure 8). Encrusting *Montipora* colonies, the only growth form of this genus found on local reefs, were by far the most bleached genus of coral in the region based on its bleaching index. This is consistent with previous findings in the region where *Montipora* displayed the highest incidences of bleaching [18,21]. Further north in Mozambique, *Montipora* was again found to show some of the highest bleaching indices, as high as 80 in 1998 and 2005, and, on average, it ranked third in terms of its bleaching index after *Alveopora* and *Stylophora*, respectively, in the Western Indian Ocean [23]. *Alveopora* was also previously noted to undergo relatively high levels of bleaching in the region by Celliers and Schleyer (2002) [21] but we did not find this during the most recent surveys. Similar inconsistencies in bleaching index among coral taxa over different time periods have been found in Mauritius between 2004 and 2019 [27]. Such inconsistencies in bleaching index among genera exposed to different levels of thermal stress over varying timescales may be due to different taxon-specific non-linear responses and threshold effects. For example, McClanahan et al. (2020) [68] found that taxon-specific patterns in bleaching responses to thermal stress during 2016 indicated novel responses relative to historical reports [39], and that different thermal metrics were associated with different taxon-specific bleaching responses. Furthermore, taxon-specific bleaching responses in the Indian Ocean prior to and during 2016 were characterised by weak relationships and that a weak slope in the relationships suggested that historically sensitive corals bleached relatively less than previously tolerant taxa did in 2016 [68].

Genetic resilience to bleaching may well become a factor on the South African coral reefs. On the one hand, genetic connectivity between the regional reefs is poor [69]; this could, in fact, reduce reef resilience. However, two of the South African reefs amongst those studied manifest both allelic richness and a high number of private alleles in their populations of *Acropora austera* and *Platygyra daedalea*. The reefs in question are Rabbit Rock in the Northern Reef Complex and Nine-mile Reef in the Central Complex, both being considered as 'landing sites' for the recruitment for migrants from further afield. Their allelic richness and private alleles are indicative of natural variation. The aforementioned variability in bleaching in *Montipora* colonies [21], and the reduced levels of bleaching more recently recorded in *Alveopora* [21], this study also provide evidence of resilience.

Furthermore, the South African coral communities are speciose, comprising 93 species of Scleractinia and 39 species of Alcyonacea [11]. Such attributes afford populations resilience.

5. Conclusions

Over the period of available degree heating week (DHW) data (since 1985), the high-latitude coral reefs of the southwestern Indian Ocean have experienced a history of relatively low thermal stress. These reefs are also likely to be differentially affected by cooler upwelled water in the region; evidence suggests that reefs in the Central and Southern Complexes are influenced more than reefs in the Northern Complex due to their closer proximity to canyons and the shelf edge. Upwelling is likely to be a key resistance factor in mitigating the effects of global warming on coral communities in parts of the region. Long-term in situ temperature records at Nine-mile Reef over the last 27 years nevertheless showed no obvious trend of increase. In situ temperatures at Nine-mile Reef also displayed poor relationships with temperatures derived from the Representative Concentration Pathway (RCP) models, with absolute differences greater than 1 °C lower than the RCP projected temperatures.

Slight coral bleaching with no significant mortality has been recorded in the region in the past and the most recent 2016 bleaching event was similar in severity. Latitude and cumulative DHW were significantly related to the bleaching index whereas depth and interactions of depth with latitude and DHW were not. The results indicated that, although these reefs are relatively deep and at high latitude, they may be vulnerable to future bleaching. While upwelling of cooler water may offer some refuge to these reefs, especially in the Central and Southern Reef Complexes, this may only be transient as the upwelled water may experience some degree of warming too, in future, thereby offering limited protection from global warming. Nevertheless, genetic resilience to bleaching may be latent, or may be emerging, within the local coral biodiversity and its natural variability.

Further research needs to be undertaken to investigate the role of depth and canyon- and shelf-induced upwelling of cooler waters in the region in contributing to resistance and mitigating bleaching, and the potential for coral communities to adapt to global warming. With temperatures predicted to warm and signs of mild bleaching in the region already, it is important that the long-term monitoring in the region is urgently expanded to provide a comprehensive overview of the responses of these marginal reefs to future warming and local stressors to provide the necessary foundation for resilience-based management.

Supplementary Materials: The following are available online at https://www.mdpi.com/article/10.3390/d13100464/s1. ESM 1: emperature timeseries for Nine-mile Reef in Maputland for (a) hourly, (b) monthly and (c) yearly metrics. Values in brackets indicate the slopes of the temperature trends derived from linear regression models. ESM 2: Temperature timeseries from 2006 to 2019 at Nine-mile Reef derived from in situ measurements and Representative Concentration Pathway (RCP) models for Nine-mile Reef based on (a) yearly average and (b) yearly maximum metrics. ESM 3: Temperature variation showing overall daily temperature amplitudes (upwelling intensities) measured at Tridacna, Chain and Leadsman, Maputaland, South Africa from December 2014 to April 2016 leading up to peak coral bleaching surveys that were conducted in April–May 2016.

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