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Bleaching in sponges on temperate mesophotic reefs observed following marine heatwave events

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ABSTRACT

Climate change driven extreme events such as marine heatwaves (MHWs) can have dramatic impacts on ecosystems, with thermal stress often resulting in localised die-offs and visible signs of impacts such as bleaching of organisms. Such impacts are reported widely in shallower ecosystems but are less studied on deeper mesophotic ecosystems (MEs) where collecting data is more expensive. However, these deeper ecosystems are often biodiverse and play important ecological roles, and so understanding climate change impacts at these depths is important. Here we use benthic imagery collected as part of a large-scale monitoring program to explore bleaching in a cup sponge 'morphospecies' (i.e. morphologically distinct organisms readily identified in imagery) in MEs across eastern Tasmania, a region experiencing rapid ocean warming. We find an increased incidence of bleaching in surveys following MHWs, but currently no evidence for mass mortality following bleaching. Our results suggest that this cup sponge morphospecies may be useful for tracking climate change impacts on MEs in the region. Future efforts should be directed towards a better understanding of the physiological limits of this morphospecies across its range and timing surveys to more closely follow MHW events. Sponges form an important and dominant component of temperate MEs and monitoring the impacts of climate change on sponges across these ecosystems should therefore be an ongoing priority.

Introduction

Coastal marine ecosystems are undergoing dramatic changes due to increased frequency and severity of extreme oceanographic events associated with climate change [1–3]. This is particularly the case in regions where changing oceanographic conditions have resulted in dramatically altered thermal regimes [4]. When warming conditions are present for an extended period it can lead to a phenomenon known as "marine heatwaves" [MHWs; 5]. In recent decades, such events have increased in frequency and severity, with a global average of 50% more MHW days recorded annually [6].This increased frequency of MHWs is altering shallow-water temperate habitat-forming communities that could have consequences for the structure and function of the entire ecosystem [7], as well as on the human populations that depend on them [8].

Long-term, large-scale monitoring programs are particularly valuable to understand the response of complex marine ecosystems to extreme oceanographic events [9], such as MHWs. The high cost of collecting such ecological monitoring data, particularly in mesophotic ecosystems [MEs, ~30–150 m depth; 10], is focussing efforts on sentinel species acting as early indicators of change [11,12]. Sponges are one such organism as they provide important structural habitat as well as critical cycling of nutrients and organic material [13,14]. Sponges in tropical regions may benefit under future climate change scenarios as many species have been noted to have higher tolerances to warming and acidification compared to other dominant benthic species such as corals [15–17]. However, many sponges contain symbiotic algae, and similarly to corals that contain symbiotic zooxanthellae, may be susceptible to increases in bleaching, necrosis, disease, and mortality due to thermal stress [15,18–20]. Most studies examining the impacts of temperature stress on sponges have focused on shallower tropical locations as part of wider studies examining coral bleaching events [e.g. 17,19]. Studies in temperate regions are rarer [but see 21], and studies spanning larger latitudinal extents across temperate regions where temperature gradients exist through time are currently lacking.

It is particularly valuable to monitor sentinel species, species that may give early warnings of impacts, in regions where ocean surface temperatures have changed rapidly and are projected to continue to do so [22]. The waters of the east coast of Tasmania are one such area, being considered a global hotspot for marine climate change [23,24]. The increasing penetration of the poleward flowing East Australian Current (EAC) has resulted in an increase in extreme events, and a predicted change of 2–4 °C from 1990 to 2060 [25]. In this region impacts on shallower kelp dominated ecosystems have been dramatic, par-

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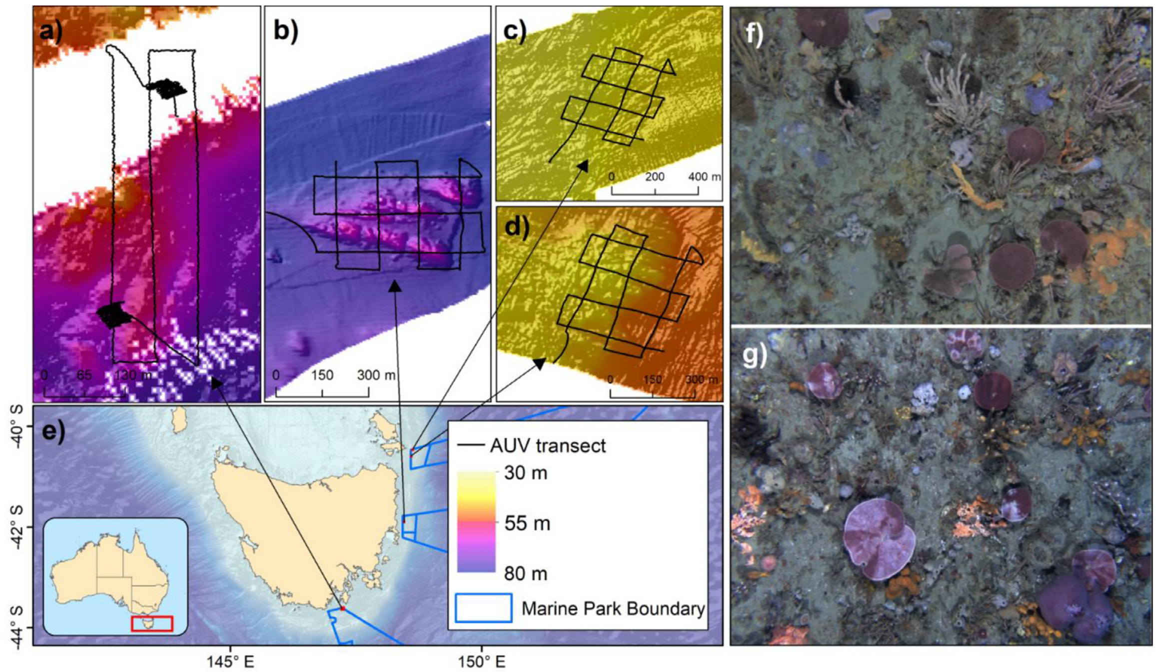

Fig. 1. The study region on the east coast of Tasmania (e), with study sites in Huon (a), Freycinet (b) and Flinders (*c* = NW, *d* = W*)* marine parks; and example images from the Flinders West site, showing unbleached cup sponge morphospecies in 2013 (f) and bleached in 2017 (g).

Table 1
Location of sites included in the study, depth range of sites, years surveyed, and the number of images annotated each year.

Site	Location	Depth range (m)	Years surveyed	Images annotated
Flinders northwest (NW)	40° 27′ 54″S, 148° 37′ 40″E	41–45	2013, 2017	1638, 2258
Flinders west (W)	40° 36′ 3″S, 148° 35′ 39″E	43–52	2011, 2013, 2017	1588, 1507, 2233
Freycinet	41° 53′ 59″S, 148° 27′ 1″E	59–83	2011, 2014, 2016	1783, 1488, 2285
Huon	43° 36′ 59″S, 147° 13′ 25″	45–71	2009, 2010, 2014	2015, 2160, 1713

ticularly through the overgrazing of a range-extending urchin species [e.g. 26,27]. However, impacts on organisms in adjacent MEs are less well documented due to the cost of collecting monitoring data at these depths. Environmental conditions in MEs are typically more stable, with the potential to act as refuge from MHWs [e.g. 28] or provide long-term refugia [see 29]. Conversely, the lack of previous acclimation to such events may make communities in MEs more susceptible [30]. Understanding the impacts of MHWs on MEs is important as these ecosystems often contain undescribed biodiversity [31] and provide important ecosystem services including the support of valuable fisheries [32]. As many species in MEs are currently undescribed or difficult to taxonomically identify from imagery, scientists often focus is often on 'morphospecies' [e.g. 33]. These morphologically distinct organisms are reliably identified in imagery and are known to correlate well with true taxonomic diversity [34].

Here, we use benthic imagery from an autonomous underwater vehicle (AUV) that spans a latitudinal gradient of approximately 350 km (from 40.46 to 43.62° South) to examine the incidence of bleaching in a conspicuous and widespread cup sponge morphospecies between 2007 and 2016. We also examine the occurrence and timing of MHW events over this period as a possible driver for bleaching events.

Methods

Data collection and image annotation

AUV derived imagery was collected on deep shelf rocky reefs within Flinders, Freycinet and Huon marine parks between 2009 and 2017 (Fig. 1 and Table 1). The AUV deployments followed protocols outlined in Monk et al. [33]. All imagery was subsequently annotated using the online platform Squidle+ (https://squidle.org/). Imagery was subset to every fifth image along the transects so that overlapping images were not included, resulting in > 1500 images per year (Table 1). In each image all individuals of the target cup sponge morphospecies were counted, and where 50% or more of an individual exhibited bleaching those individuals were tagged as 'bleached'.

Modelling

We assessed the proportion of bleaching through time using a Bayesian spatial modelling approach, where images form the basis of the analysis and spatial correlation between images is accounted for [for more details see 26]. We treated the response as binomial, where the number of bleached individuals in an image is the number of 'successes' and the total number of individuals is the number of trials. The survey year was treated as a categorical variable and depth was treated as a continuous covariate. For each site, the intercept estimate represents the initial survey. Additionally, a second model with a Poisson response was specified for the total counts of the target cup sponge morphospecies (i.e. bleached and unbleached combined) to estimate changes in abundance.

All modelling was conducted using the Integrated Nested Laplace Approximation [INLA; 35] approach in the R statistical package. The same Bayesian priors described in Perkins et al. [26] were used. As model fixed effect estimates are Bayesian, posterior distributions for each effect are given, with evidence for an effect being those distributions that

Table 2
Model estimates of year and depth effects on proportion of bleaching at each site. Coefficients are on the logit scale.

Site (depth range)	Fixed effect	mean	sd	0.025 quantile	0.975 quantile
Flinders	Intercept (2013)	−2.001	0.164	−2.329	−1.684
NW	year 2017	0.572	0.184	0.215	0.936
	depth	0.021	0.104	−0.181	0.226
Flinders	Intercept (2011)	−2.034	0.104	−2.239	−1.831
W	year 2013	−0.294	0.112	−0.514	−0.076
	year 2017	0.696	0.099	0.502	0.892
	depth	0.304	0.067	0.172	0.436
Freycinet	Intercept (2011)	−0.295	0.205	−0.699	0.106
	year 2014	−0.813	0.250	−1.305	−0.323
	year 2016	−0.286	0.247	−0.771	0.200
	depth	0.287	0.108	0.076	0.498
Huon	Intercept (2009)	−1.935	0.085	−2.104	−1.769
	year 2010	0.403	0.102	0.204	0.604
	year 2014	0.310	0.106	0.103	0.519
	depth	0.400	0.044	0.314	0.486

do not include zero in the 95% credible interval, and larger effects being distributed further from zero. Post hoc comparisons for the survey year were conducted by examining the posterior distributions for linear combinations of each pairwise comparison. This comparison was not conducted for Flinders Northwest, which only had two sampling events. Model coefficient estimates are on the logit scale, and probabilities of bleaching were made by calculating the inverse logit, $\frac{\exp(\beta)}{\exp(\beta)+1}$. For the count-based model, coefficient estimates are on the log scale and multiplicative changes in mean counts per image were calculated by exponentiating the estimates, $\exp(\beta)$.

The relationship between the probability of bleaching and the occurrence of MHW events was made through visual examination of the occurrence of MHWs and whether bleaching was found to increase following such events.

Quantifying heatwaves

Daily ocean temperature records at depth were extracted from the Eastern Tasmania ocean circulation model (ETAS) which provides 3D records for the period of 1993 to 2016 [36]. The ETAS model does not cover the Flinders AMP sites and the closest grid cell (approx. 20–30 km away) had to be used as a proxy for the temperature record at these sites. However, an exploratory analysis showed similar trends across the shelf waters and sites included in this region.

The heatwaveR R package [37] was used to explore the historical daily site-level temperature data and to quantify MHW events between 2007 and 2016. The MHW definitions used in the package follow those outlined by Hobday et al. [5], where MHW events are classed as those that exceed a 90% climatological seasonal threshold for a period of 5 days or more. As we were interested in summertime heatwaves (i.e. January - March), which may push temperatures past a biological threshold for our target cup sponge morphospecies, we used the 'exceedance' function in the heatwaveR package to quantify periods where the summertime threshold was exceeded.

Results

Model results

The proportion of the bleached target cup sponge morphospecies revealed strong evidence for change across the survey periods at each site (Table 2 and Appendix A). Estimates of the year effect at Flinders NW showed a strong increase in bleaching between 2013 and 2017, with the probability of bleaching increasing from 11.9 to 19.3% (Table 2 and Fig. 2). At Flinders W there was a decrease in bleaching between 2011 and 2013 from 11.6 to 8.9%, and then a large increase in the probability of bleaching to 20.8% in 2017 (Table 2 and Fig. 2). At Freycinet there was a large decrease in the probability of bleaching from 42.7% 2011 to 22.9% in 2014, and an increase to 32.1% in 2016. At Huon there was an increase in bleaching from 12.6% in 2009 to 17.8% in 2010, and a small non-significant (Appendix A) decrease to 16.4% in 2014. Bleaching had a positive correlation with depth for all sites except Flinders NW, where depth was found to be non-significant (Fig. 3).

Estimates from the count-based model for abundance (both bleached and unbleached) of the target cup sponge morphospecies displayed evidence for shifts in abundance across the years at each site (Appendix B), with no apparent relationship with bleaching. Both sites at Flinders had increases in abundance between 2013 and 2017, with mean counts per image increasing by 0.33 at the NW site and 0.46 per image at the W site. At Freycinet, a large increase in counts per image of 0.99 was observed between 2011 and 2014, followed by a decrease of 0.58 per image between 2014 and 2016. Counts were stable between 2009 and 2010 at Huon, followed by a decrease of 0.42 per image between 2010 and 2014.

Marine heatwaves

Between 2007 and 2016 two summertime MHWs occurred at the Flinders and Huon sites and one summertime event occurred at Freycinet (Table 3). The most severe MHW in terms of temperature intensity occurred across both the Flinders sites during the summer of 2014 when temperatures exceeded the 90% threshold by a maximum of 1.25 °C at Flinders NW and a maximum of 1.16 °C at Flinders W, in events that lasted for a period of 16 days. Shorter and less intense summertime MHWs occurred at the Flinders sites in 2010. Less intense, but much longer lasting summertime events occurred at Huon during the summers of 2010 and 2013. A single short-lived summertime MHW event occurred at Freycinet during the summer of 2007, 3 years prior to the initial survey.

Threshold temperatures for MHW classification decreased from north to south (Table 2), with the southernmost Huon site having a threshold of approximately 2.5 °C less than that at the northernmost site (Flinders NW).

Relationship between bleaching and marine heatwaves

The increase in bleaching observed at both Flinders sites between the surveys in 2013 and 2017 followed a strong MHW event in 2014 where temperatures peaked at more than 1 ^{0}C above the 90% seasonal threshold and lasted for 16 days (Table 3, Fig. 2). The probability of bleaching approximately doubled at both Flinders sites between the surveys in 2013 and 2017. At Freycinet, the only summertime MHWs occurred prior to the initial survey; however, the overall probability of bleaching was highest at this site. Significantly lower bleaching was observed between the initial 2011 survey and the survey in 2014 with the probability of bleaching in 2016 being similar to 2011. At Huon, the probability

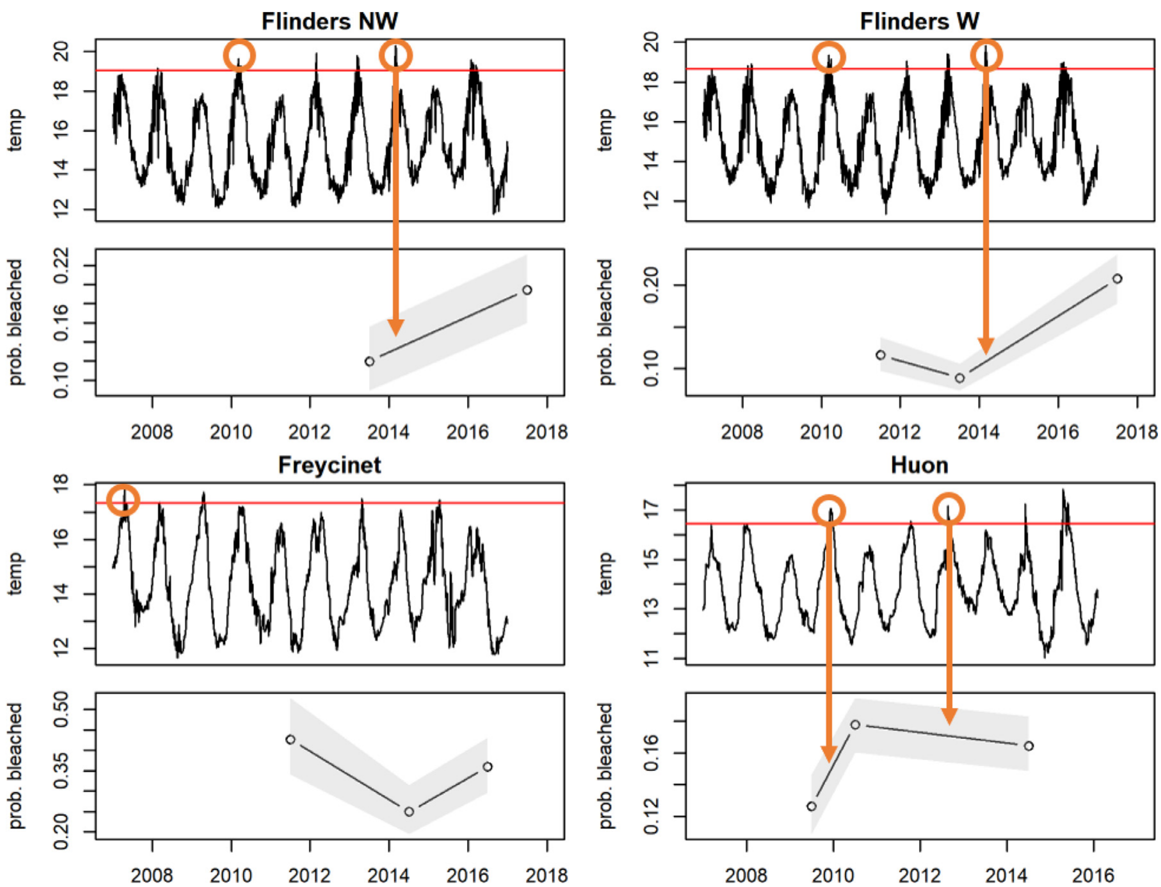

Fig. 2. The relationship between MHWs and the modelled probability of bleaching of the target cup sponge morphospecies between 2007 and 2016. Grey shading indicates 95% credible intervals. Upper panels for each site show the daily temperature records with the horizontal line indicating the 90% seasonal threshold. Orange circles highlight periods where the threshold was exceeded by five days or more with orange arrows showing where these events occurred in relation to surveys.

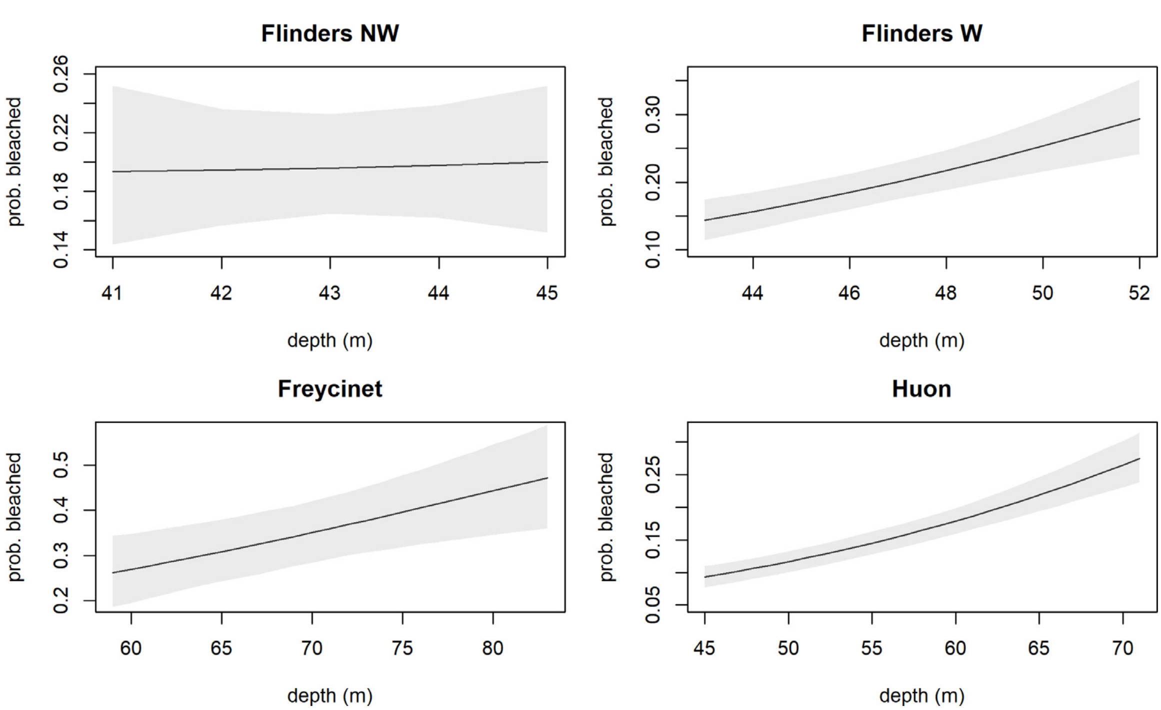

Fig. 3. Depth effect on bleaching at each site calculated based on the last year surveyed. Solid lines show the mean probability of bleaching and shading is the 95% credible interval.

Table 3
Marine heatwave events at each survey site between 2007 and 2016 that exceeded the 90% threshold temperature for a duration of at least five days.

Site	90% threshold temperature	Duration (days)	Start date	Peak date	Maximum intensity (above threshold)
Flinders	19.03	5	2010–03–05	2010–03–07	0.617 °C
NW	°C	16	2014–02–24	2014–03–03	1.25 °C
Flinders	18.66	5	2010–03–05	2010–03–08	0.704 °C
W	°C	16	2014–02–24	2014–03–01	1.16 °C
Freycinet	17.34 °C	6	2007–04–16	2007–04–18	0.491 °C
Huon	16.46	29	2010–03–16	2010–03–29	0.593 °C
	°C	19	2013–03–15	2013–03–16	0.724 °C

of bleaching approximately doubled between 2009 and the survey in 2010. A long lasting (29 days, Table 1) MHW occurred between these two surveys in the summer of 2010. A higher probability of bleaching was maintained in 2014 compared to 2010 at Huon, with a shorter (19 days, Table 1) MHW occurring in the summer of 2013.

Discussion

Here we report for the first time the incidence of bleaching in a cup sponge morphospecies across MEs on the east coast of Tasmania. Increased bleaching was noted in surveys following MHW events, suggesting that this could be a driver of observed bleaching. Bleaching has been shown to persist in corals for longer than 12 months [e.g. 38,39]; however, persistence of bleaching after warming events is not as well reported for sponges and the persistence of bleaching in our cup sponge morphospecies is unclear, indicating the need for surveys more closely coupled with MHW events. This region is known to be a marine global warming 'hotspot', with warming events predicted to increase in severity and frequency in coming decades [25]. Impacts of warming and changing oceanographic conditions on shallow reef systems in the region are historically reported [e.g. 23,26], and here we report what appears to be an early warning sign of the impacts of MHWs on deeper MEs. Our findings are important from a conservation perspective, as these deeper reefs are known to be biodiverse and are likely to contain species that are not yet described by science. Present evidence points to our target cup sponge morphospecies being a potential indicator for ongoing monitoring of the impacts of warming events across MEs in the south-east marine park network as it is reliably identified, widespread and relatively abundant [12]. Clearly, further work is required to establish threshold temperatures and exposure durations for bleaching to occur, how long bleaching persists for, how these factors differ across the range of this cup sponge morphospecies, and to better couple the timing of surveys with MHW events.

Mass mortality of sponges following periods of abnormally elevated water temperatures has been reported elsewhere [e.g. 18,19,20,21,40]. Evidence to date indicates that mass mortality in our target cup sponge morphospecies has not occurred due to the bleaching, with abundance estimates increasing concurrently with an increase in bleaching at both Flinders sites, and no clear relationships between bleaching events and abundance at the other sites. However, the fate of the cup sponge morphospecies individuals, how long bleaching persists for and effects on health and reproductive output are currently unclear and will require ongoing monitoring and manipulative experiments. Surprisingly, we found a trend for increased bleaching with depth at three of our four sites. It is currently unclear what is driving this pattern and these results require further investigation. This cup sponge morphospecies appears to be only found within mesophotic ecosystems (> 30 m) in our region, with no records from nearby diver-based surveys (N. Barrett personal communication). Therefore, if MHW events are capable of impacting these ecosystems, as our results suggest, then depth is unlikely to act as a refuge for this morphospecies.

When exploring the effects of MHWs, care should be taken in distinguishing between anomalous oceanographic conditions and what is biologically significant. We used the default definition for MHWs developed by Hobday et al. [5], which uses a 90% threshold with a minimum duration of 5 days. The 90% threshold differed across our sites, with lower thresholds in southerly sites. In fact, mean temperatures in the northern (i.e. Flinders) sites would be classified as MHW events at the southern (i.e. Huon) site. Our results indicate that acclimation to local temperatures appears to be important for our sponge morphospecies as bleaching occurs across the entire latitudinal gradient under different mean temperature regimes.

Many monitoring programs in MEs are currently in their infancy and knowledge on the distribution and baseline levels of change is typically being built as data is collected. As knowledge grows, developing indicators and approaches for monitoring important drivers of ecosystem change is an important component of such programs. For the present study, a targeted scoring approach was taken whereby all non-overlapping AUV images were annotated. This is in contrast to the common approach used in baseline surveys that aim to quantify overall community composition [see 12,33]. Previous work on MEs across the region has shown that most morphospecies have low percent cover (< 2%) and thus tracking changes in individual morphospecies requires considerable sampling effort [12,41]. Once indicators are chosen, a targeted annotation approach makes the most of the large amount of imagery collected by the AUV, providing much larger sample sizes for tracking changes in abundance and metrics such as the proportion of bleaching. Future efforts could also be directed at examining bleaching across size classes for the target cup sponge morphospecies and bleaching in other sponge morphospecies. We conclude that ongoing monitoring should take into consideration the timing of MHWs, with a higher frequency of visits to sites, and particularly immediately following warming events allowing for a stronger assessment of the correlation between warming and bleaching to be made.

Declaration of Competing Interest

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

Appendix A.

Tables A1 and A2

Table A1
Pairwise comparison of bleaching between years at each site.

Site	Comparison	mean	sd	0.025 quantile	0.975 quantile
Flinders	2013–2011	−0.294	0.112	−0.514	−0.076
W	2017–2011	0.696	0.099	0.502	0.892
	2017–2013	0.991	0.109	0.777	1.206
Freycinet	2014–2011	−0.813	0.250	−1.305	−0.323
	2016–2011	−0.286	0.247	−0.771	0.200
	2016–2014	0.527	0.217	0.104	0.954
Huon	2010–2009	0.403	0.102	0.204	0.603
	2014–2009	0.310	0.106	0.102	0.519
	2014–2010	−0.093	0.072	−0.093	0.048

Table A2
Raw counts of bleached and unbleached sponges across years at each site.

Site	Year	Bleached	Unbleached	Total
Flinders	2013	75	528	603
NW	2017	184	682	866
Flinders	2011	298	1840	2138
W	2013	249	1981	2230
	2017	774	2917	3691
Freycinet	2011	65	85	150
	2014	83	209	292
	2016	128	231	359
Huon	2009	416	2184	2600
	2010	984	3940	4924
	2016	576	2675	3251

Appendix B.

Tables B1 and B2

Table B1
Output of model-based analysis of counts of red cup sponges at each site over time.

Site	Fixed effect	mean	sd	0.025 quantile	0.975 quantile
Flinders	intercept	0.031	0.364	−0.685	0.745
NW	year 2017	0.278	0.086	0.109	0.448
	depth	−0.760	0.109	−0.974	−0.547
Flinders	intercept	1.368	0.041	1.287	1.448
W	year 2013	−0.108	0.043	−0.193	−0.024
	year 2017	0.111	0.040	0.033	0.189
	depth	−0.282	0.029	−0.338	−0.225
Freycinet	intercept	0.181	0.055	0.072	0.289
	year 2014	0.604	0.058	0.49	0.718
	year 2016	0.298	0.059	0.181	0.414
	depth	−0.136	0.030	−0.194	−0.078
Huon	intercept	0.951	0.046	0.861	1.041
	year 2010	0.094	0.055	−0.013	0.201
	year 2014	−0.064	0.056	−0.173	0.046
	depth	−0.047	0.026	−0.098	−0.047

Table B2
Pairwise comparison of counts of red cup sponges between years at each site.

Site	Comparison	mean	sd	0.025 quantile	0.975 quantile
Flinders	2013–2011	−0.294	0.112	−0.514	−0.076
W	2017–2011	0.696	0.099	0.502	0.892
	2017–2013	0.991	0.109	0.777	1.206
Freycinet	2014–2011	0.604	0.058	0.490	0.718
	2016–2011	0.298	0.059	0.181	0.414
	2016–2014	−0.306	0.054	−0.413	−0.200
Huon	2010–2009	0.094	0.055	−0.013	0.201
	2014–2009	−0.064	0.056	−0.173	0.046
	2014–2010	−0.157	0.030	−0.216	−0.099

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