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Marine heatwaves reveal coral reef zones susceptible to bleaching in the Red Sea

Running head: Marine heatwaves reveal bleaching-prone zones

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Abstract

As the Earth's temperature continues to rise, coral bleaching events become more frequent. Some of the most affected reef ecosystems are located in poorly-monitored waters, and thus, the extent of the damage is unknown. We propose the use of Marine Heatwaves (MHWs) as a new approach for detecting coral reef zones susceptible to bleaching, using the Red Sea as a model system. Red Sea corals are exceptionally heat-resistant, yet bleaching events have increased in frequency. By applying a strict definition of MHWs on >30-year satellite-derived sea surface temperature observations (1985–2015), we provide an atlas of MHW hotspots over the Red Sea coral reef zones, which includes all MHWs that caused major coral bleaching. We found that: 1) if tuned to a specific set of conditions, MHWs identify all areas where coral bleaching has previously been reported; 2) those conditions extended farther and occurred more often than bleaching was reported; and 3) an emergent pattern of extreme warming events is evident in the northern Red Sea (since 1998), a region until now thought to be a thermal refuge for corals. We argue that bleaching in the Red Sea may be vastly underrepresented. Additionally, although northern Red Sea corals exhibit remarkably high thermal resistance, the rapidly rising incidence of MHWs of high intensity indicates this region may not remain a thermal refuge much longer. As our regionally-tuned MHW

algorithm was capable of isolating all extreme warming events that have led to documented coral bleaching in the Red Sea, we propose that this approach could be used to reveal bleaching-prone regions in other data-limited tropical regions. It may thus prove a highly valuable tool for policy-makers to optimise the sustainable management of coastal economic zones.

Introduction

Corals rely on an endosymbiotic relationship with algae of the family Symbiodiniaceae (LaJeunesse et al., 2018), which serve as their main energy source (Falkowski et al., 1984). One of the major threats to corals is the loss of those zooxanthellae, a phenomenon referred to as coral bleaching, which is a response to the coral's exposure to stress. The primary cause of mass coral bleaching is prolonged exposure to anomalously high sea surface temperatures (SSTs) (Glynn, 1993). Mortality is not certain, as corals may be repopulated by the endosymbiont if environmental conditions return to their habitual level soon after. However, bleached corals cannot fulfil the ecological role of live corals, and even if mortality does not occur, bleaching can nevertheless leave corals with noticeable long-term effects (Baker et al., 2008). For instance, depleted energy stores during heat stress may impact coral reproductive success (Omori et al., 2001; Szmant and Gassman, 1990; Ward et al., 2002), which in turn bring risks linked to a reduced gene pool (Bassim et al., 2002; Knowlton, 2001). If mortality does ensue, corallivores (e.g. crown-of-thorns sea stars, gastropods) would aggregate around the remaining live corals, accelerating coral deterioration and culminating in corallivore depletion (Kayal et al., 2012). This process can result in a change of coral assemblage, or a complete shift away from coral-dominant landscapes (Aronson et al., 2004; Hughes, 1994; Hughes et al., 2018b). Reef fish responses will vary depending on their diet and their reliance on coral for settlement or habitat (Baker et al., 2008; Pratchett et al., 2008), as some fish species have specificity for certain coral species (Sano, 2004), and dead coral structures tend to be cleared by bioerosion (Eakin, 2001). However, it is observed that the rarest coral species often suffer the most from bleaching (Monroe et al., 2018). A general decrease in reef community diversity is therefore likely, as species-specific organisms will drop with declining coral diversity.

Coral bleaching thresholds vary according to coral species, endosymbiotic assemblage, and location (Anthony et al., 2009; Furby et al., 2013; Rosenberg et al., 2007). However, markedly warmer conditions may soon be reached, as climate change is increasing global marine temperatures as well as the frequency and intensity of El Niño events (Cai et al., 2014). Water temperatures are now closer to coral thermal stress thresholds, exposing them to heightened threats to their life history (Cantin et al., 2010) and bleaching recovery (Ainsworth et al., 2016). The higher frequency of El Niño events may also shorten the periods of time when oceanic temperatures are cooler, therefore diminishing the time for corals to recover (Baker et al., 2008). Moreover, temperatures during La Niña, El Niño's cold counterpart, are now recorded to be as hot as temperatures during El Niño three decades ago (Hughes et al., 2018a). It is estimated that the world's coral reefs have seen a resulting 8-fold increase in bleaching events since the 1997/1998 El Niño (Donner et al., 2017).

We have gained knowledge of bleaching mechanisms from the many studies performed on the Caribbean and Great Barrier Reefs, yet many reefs remain unexplored or are poorly monitored. A prime example is the Red Sea, which is one of the warmest seas in the world yet has been the subject of relatively few studies (Berumen et al., 2013). Red Sea corals were thought to be at low risk from climate change due to acclimatisation, but the Red Sea experienced a sudden 0.7°C rise in SST in the mid-90s (Raitsos et al., 2011), which was followed by a severe and widespread mass bleaching event during the next El Niño in 1998

(Devantier et al., 2000; Pilcher and Alsuhaibany, 2000). Bleaching events have occurred at increasing frequency and number of sites since then, having been recorded at various locations in the Red Sea in 2007, 2010, 2012 and 2015 (Osman et al., 2018).

Corals in the Red Sea can withstand exceptionally high temperatures; typical summer temperatures would cause coral bleaching in most other tropical seas (Osman et al., 2018; PERSGA, 2010). The Red Sea SSTs increase southwards, ranging from a summer (mid-May to mid-September) average of 25°C at the Gulf of Suez (North) to 31.5°C at the Farasan Islands (South) (Racault et al., 2015; Raitsos et al., 2013). Although corals in the southern Red Sea are subjected to higher SSTs, reefs in the northern parts experience more severe heating events relative to their habitual temperatures, as measured in degree heating weeks (DHWs) (Osman et al., 2018). Despite this, they saw no bleaching events before 2007, and the few instances recorded since were mild in nature (Osman et al., 2018). Meanwhile, mass coral bleaching events have occurred in the central and southern regions of the Red Sea on several occasions, most recently in 2015 when the warm El Niño temperatures caused up to 67% of coral cover to bleach on inshore reefs off Thuwal (Saudi Arabia) (Monroe et al., 2018). Due to the ability of corals in the northern Red Sea to withstand temperatures far exceeding their maximum summer means, this region has been termed a "thermal refuge" for coral species (Fine et al., 2013; Osman et al., 2018). However, climate change and the increase in frequency of extreme El Niño events raise concerns over the possible emergence of a new pattern of bleaching in the Red Sea. The occurrence of bleaching events in the northern central Red Sea in southern Egypt (i.e. Wadi El Gemal and further south) in 2007 and 2012, as well as the increase in northern Red Sea SSTs of 0.4-0.45°C $decade^{-1}$ (Chaidez et al., 2017), suggest northern reefs may no longer be protected by their high thermal tolerance.

This increase in the frequency of bleaching events in the Red Sea highlights the pressing need to establish a management framework to limit the impacts they may have on the ecosystem and the livelihoods that rely upon it. It is therefore necessary to identify the regions in the Red Sea that are at risk of coral bleaching, as well as to understand the temporal evolution of environmental conditions that have caused the present patterns. However, DHWs have been known to over-report bleaching in the northern Red Sea (Osman et al., 2018), as well as to miss bleaching in Thuwal (western Saudi Arabian coast) (Monroe et al., 2018). This is perhaps due to the fact that they are calculated by setting a fixed thermal threshold at a given temperature (usually 1ºC) above the long-term climatological mean maximum (Liu et al., 2006, 2003), and are therefore not able to detect unusual warming in cooler periods. Indeed, some bleaching events have been known to occur after months exhibiting the peak mean climatology (Osman et al., 2018). Marine heatwaves (MHWs), a recently established hierarchical approach for detecting heating events, can detect such occurrences as they use a percentile-based threshold calculated by pooling daily SSTs around each day of the year, thus following the climatology variability (Hobday et al., 2016). As it is possible to tune their definition to any environment and to isolate events in space and time, we adapted the MHW definition to the environmental conditions documented to have caused coral bleaching in the Red Sea in the past, to reveal reef zones susceptible to bleaching in the future. We produce a concise and high-resolution atlas of extreme warming events in the Red Sea over the last 30 years, revealing the MHW hotspots over the coral reef zones, as well as past heating trends. This method has, to the best of our knowledge, never been used to detect coral bleaching thresholds, neither has it been used to identify regions of warming in the Red Sea. Specifically tailored to MHWs that can cause Red Sea corals to bleach, we envisage that our atlas will be a valuable tool for optimising the management of the Red Sea coastal economic zone. Furthermore, our approach may serve as a precedent for detecting bleaching-prone coral reef zones in other tropical region lacking rigorous monitoring.

Materials and methods

This study used the definition and statistical methodology developed by Hobday *et al.* (2016) to identify MHWs over the Red Sea from satellite-derived daily-averaged SST time series. This methodological approach was tailored to account for the unique conditions of the Red Sea and tuned to yield only the most extreme heating events, while still detecting all MHWs that have caused the documented coral bleaching events in the Red Sea.

Datasets

Satellite-derived daily SST data spanning 31 years (1985–2015) were acquired from the Operational SST and Sea Ice Analysis (OSTIA) system (Donlon et al., 2012; Stark et al., 2007). This global SST analysis provides daily-averaged SST fields on a 1/20° horizontal resolution (~5–6 km in the Red Sea). This merged SST product has the highest spatial resolution currently available over the Red Sea and provides a detailed description of the coastline regions. OSTIA uses a blend of satellite data from microwave and infrared satellite instruments provided by international agencies via the Group for High Resolution SST (GHRSST), together with in-situ observations from the International Comprehensive Ocean-Atmosphere Data Set (ICOADS) database. The OSTIA products have been validated by inter-comparisons with other historical datasets and are continuously monitored and validated with in-situ measurements.

Bathymetry data were acquired through the General Bathymetric Chart of the Oceans (GEBCO_2014 Grid, version 20150318, http://www.gebco.net), to identify the areas shallow enough to accommodate coral reefs. The positions of coral reefs shown in Figure 1 were taken from the Global Distribution of Coral Reefs dataset (version 2018) produced by UNEP-WCMC (www.unep- wcmc.org). Data analysis was performed in R, using the package RmarineHeatWaves, Version 0.16.1 (Hobday et al., 2016; Smit et al., 2018) [note: this package has now been updated by HeatwaveR (Schlegel and Smit, 2019)]. Red Sea coral bleaching events were based on reports found in the available literature (Hughes et al., 2018a; Osman et al., 2018).

Marine heatwaves: overview

MHWs are described as "discrete prolonged anomalously warm water events that can be described by their duration, intensity, rate of evolution, and spatial extent" (Hobday *et al.* 2016). This methodology uses a percentile-based threshold to allow for the identification of events at all times of the year for areas exhibiting different SST variabilities, and yields numerous indices to characterise such events. To highlight regions in the Red Sea that are potentially susceptible to intense warming, we opted to focus on the following five descriptors: i) the number of MHWs; ii) the mean intensity of events (described as the average SST (°C) above the climatological mean during an event); iii) the mean duration of events; iv) the cumulative intensity of events (the mean intensity multiplied by the duration of an event), and v) the number of MHW days, calculated during the entire three-decade dataset.

Red Sea marine heatwaves and coral bleaching

The 31-year (1985–2015) satellite-derived daily SST dataset was used to establish the seasonally varying climatological SST mean and percentile threshold relative to each day of the year. These were calculated by pooling the daily SST values within an 11-day window centred on the specific date of interest, to account for the inherent variability of daily SST data (Hobday et al., 2016). They were then further smoothed using a 31-day moving window, which is deemed optimal for obtaining a useful climatology from daily data (Hobday et al., 2016). A MHW was considered when the daily SST consistently exceeded the established percentile threshold for a given minimum number of days. Our objective was to find a combination of these two criteria that would yield the most extreme MHWs in the Red Sea and encompass all known events that caused coral bleaching (1998, 2007, 2010, 2012 and 2015). To do so, we examined a number of different SST percentile thresholds (90th, 95th, 98th and 99th) and different event durations (5, 7, and 10 days). We also investigated different thermal thresholds (30, 30.5, 31, 31.5 and 32°C average SST during events) to set as an additional restriction to MHWs, as corals in the northern Red Sea exhibited a high tolerance relative to their maximal summer SST means (Fine et al., 2013; Osman et al., 2018). We found that values exceeding the 95th percentile threshold for a minimum duration of 7 days and a minimum average SST of 30°C over the duration of the event was the best combination to meet our objective. Identified MHW events were considered continuous if intermittent periods lasted less than two days. The modified definition of Hobday et al. (2016) MHWs was applied pixel-by-pixel for the whole time series (1985–2015), to reveal spatial patterns in MHW frequency, and their intensity and duration over the Red Sea.

MHWs were identified throughout the year, but only MHWs that originated during the months of July to October were extracted, as warming-related events during summer months are the most relevant to coral bleaching (Maynard et al., 2008). Finally, as coral reefs occur along shallower coastal waters, only pixels that represented depths of less than 150 metres were considered for the analysis to restrict the depth yet not exclude deep regions which contain small areas of shallow reefs.

We therefore define Red Sea MHWs capable of causing coral bleaching as extreme heating events that: 1) exhibit SSTs above the 95th percentile for at least 7 consecutive days, 2) have a mean SST of 30°C or higher during the event, and 3) occur during summer months (July-October) over shallow depths (<150 m).

Potential bias

Although we acquired one of the longest high-resolution daily SST datasets available, the usage of satellite-derived SST data very near the coast, islands or inside lagoons has acknowledged weaknesses (Donlon et al., 2012; Stark et al., 2007; Van Wynsberge et al., 2017). Thus, the MHWs calculated over coastal zones may potentially present lower accuracy. However, the regions that we identify for the atlas (Fig. S1-S15) are relatively broad, and as we average SSTs over their entire surface to obtain one single value, the bias is minimal. Additionally, we may not detect MHWs that occur within areas smaller than the dataset's resolution (~5 km). However, the focus here is on extreme events evident in large regions, and where coral bleaching has been reported. Thus, even more events might be identified if a higher resolution dataset were used and/or a less strict definition of MHWs were adopted for alternative research aims.

Results

Spatial and temporal patterns of Red Sea marine heatwaves

A substantial part of the Red Sea coastal zone is occupied by corals (Fig. 1a). The temporal evolution of the number of MHWs along latitudes reveals an increase of events in the northern Red Sea since 1998 previously devoid of MHWs (Fig. 1b), which also translates into an increase in total MHW days (Fig. 1c). We also observed a gradual decrease in events in the southern section of the Red Sea (12–16°N). MHWs also exhibited unique spatial patterns in terms of total number of events, as well as duration and intensity (Fig. 2a,b,c). The eastern coast of the northern region and the southernmost tip of the Red Sea experienced the highest number of MHWs while the most intense events were observed at the western coast of the southern region, and events at the eastern coast of the southern region were the most persistent. In the following section, in order to provide a more detailed description, we divided the Red Sea into four regions following Raitsos *et al*. (2013): the Northern Red Sea (NRS; 25.5–30°N), the North-Central Red Sea (NCRS; 22-25.5°N), the South-Central Red Sea (SCRS; 17.5–22°N), and the Southern Red Sea (SRS; 12.5-17.5°N).

Northern Red Sea (NRS). This region experienced the highest rate of increase in summer SSTs, estimated from our dataset at 0.37°C per decade during 1985–2015. MHWs were not observed over the whole NRS until 1998, yet they were common and longer afterwards, affecting the entire coastal region (Fig. 1b,c). Exceptions were the Gulfs of Aqaba and Suez where no MHWs were detected, as the mean SST was below 30°C during all warming events. Throughout this 31-year study, fewer events were observed over the western region, with most of the events occurring on the eastern coast (Fig. 2a). The identified events were characterised by a high intensity throughout the region, at approximately 1.5°C above the percentile threshold, and were highest at the northernmost tip, at around 1.7°C (Fig. 2b).

MHWs were generally of short duration (about 8 days) over most of the coastline, with the eastern coast also exhibiting more persistent events of ~12 days (Fig. 2c). MHWs over the NRS are intense, although their duration tends to be short in comparison with other regions. Despite their recent emergence, they have occurred regularly throughout the past decade, while continuously increasing their spatial extent.

North-Central Red Sea (NCRS). Summer SSTs have increased at an estimated rate of 0.26°C per decade over the NCRS region. Until 1998, our methodological approach detected only two MHWs, located in small and isolated areas. However, after that period the NCRS exhibits the most systematic pattern of MHWs, experiencing events that tended to spread across the whole region and to persist more than 20 days (Fig. 1b,c). Many of the events occurred over the east coast (~10 events), reaching 12 events in the Yanbu region (Fig. S5), while noticeably fewer are observed over the western coast (4) (Fig. 2a). On the eastern coast, mean MHW intensity was ~1.4°C in the south, increasing towards the north to ~1.6°C (Fig. 2b). The opposite pattern is observed on the western coast, with higher mean intensity during the events in the south (~1.5°C) than in the north (~1.2°C). Mean duration was relatively short throughout the region, ranging from 7 to 10 days (Fig. 2c). The east coast appears to be the area most at risk. Specifically, the region of Yanbu exhibits one of the highest numbers of events of the NCRS (12), which are relatively short in duration yet amongst the most intense of the whole Red Sea (1.7°C).

South-Central Red Sea (SCRS). Summer SSTs over the SCRS region increased at an estimated rate of 0.17°C per decade. No regular temporal pattern of MHWs is noticeable: they spread over a large part of the region on three occasions, while all other events occurred in patches, generally covering small areas, where the total number of MHW days for each summer remained below 20, except during 2015 where they exceeded 40 days (Fig. 1b,c). The western coast has been subjected to few events (5 on average, Fig 2a), which were generally mild (intensity less than 1.2°C, Fig. 2b) and of short duration (~5 days, Fig. 2c). Most of the east coast experienced few events, apart from the northern region, where a maximum of 10 fairly widespread events were recorded. MHWs in the east coast were also more intense (reaching 1.5°C near Al Lith), and tended to persist longer, with a recorded maximum duration of 21 days in the south. In general, the SCRS has experienced a moderately low number of events, which were amongst the mildest on the west coast. A noticeable exception was the area near Al Lith (east coast), which exhibited few but intense and persistent MHWs.

Southern Red Sea (SRS). The SRS exhibits the lowest increase in summer SSTs, estimated at 0.14°C per decade, although the SSTs remain overall the highest in the Red Sea. MHWs appear to occur regularly between 13°N and 15°N, but the areas affected remain localised, and their spatial extent appears to diminish over time, as well as the count of MHW days (Fig. 1b,c). On average, a rather small number of events occurred over the SRS coastline (up to 6), except over the Dahlak Archipelago (13-15°N on the west coast, Eritrea) and the southernmost tip, which experienced the highest number of MHWs in the Red Sea (Fig. 2a). The mean intensity on the east coast was mostly low (1.2°C or less) except in an isolated area near the Farasan region (1.5°C; Fig. S9), whereas the mean intensity of events reached values as high as 2.1°C on the west coast (Fig. 2b). MHWs were generally short (less than 10 days), apart from those that occurred over a large area near Farasan and the southern tip (>16 days, Fig. 2c). In conclusion, although large areas of the region experience few MHWs, and MHWs over half of the area are of low intensity, the observed SSTs remain amongst the highest of the Red Sea and some areas exhibit extreme conditions. Notably, more MHWs occurred over the southernmost tip of the Red Sea (Eritrea) than anywhere else in the Red Sea (14), which were intense (~1.9C) and of long duration (up to 31 days) (Fig. 2a,b,c). Many extreme MHWs also occurred over the area around the Dahlak Archipelago (up to 14 events, with ~2.1°C mean intensity), while MHWs over the Farasan region were few but intense and long.

Marine heatwaves over established and probable coral bleaching events

The SSTs were spatially averaged over the regions where coral bleaching was comprehensively reported in the literature (i.e. Fig. 3, black boxes shown on the heat maps), to generate a single daily SST time series covering 1985–2015. This also smoothed the high-frequency variability between pixels. The tailored MHW algorithm was then applied over each region, from which a set of summary figures were derived to complement the atlas (Fig. 3, 4, and Fig. S1-S15). Through this methodological approach, we isolated the MHWs that caused all recorded coral bleaching events in the Red Sea (Fig. 3). Evidently, the high temperatures recorded at the reported bleached zones extended far beyond those localised areas, and regions presenting even higher SSTs were observed (Fig. 3). It seems that in all cases of coral bleaching, a much wider region was above this threshold, suggesting the bleaching may have spread farther than reported.

Other areas were identified which are likely to have had unreported bleaching events, as they presented MHWs with similar characteristics to those causing known bleaching events. We discuss here the example of Al Wajh in the northern Red Sea (Fig. 4), a good representative of the NRS as it exhibits the characteristic pattern of MHWs emerging after 1998. We also provide similar plots for other regions (Figs. S1-S15) covering the majority of the coral reef complexes along the Red Sea coast.

Al Wajh experienced severe MHWs during 2010 and 2015, the same years that bleaching was recorded in Yanbu and Thuwal in the eastern NCRS (Figs. 3, S5, S7). This could indicate that the bleaching events reported in these positive El Niño years (Raitsos et al., 2015) extended at least as far north as Al Wajh. Furthermore, we have detected 4 more MHWs that occurred in non-El Niño years (2001, 2003, 2008 and 2014) (Fig. 4c). The 2014 event was exceptionally intense (1.5°C) and lasted more than 20 days. Although a typical example of the NRS, Al Wajh still appears to be at frequent risk of bleaching, exhibiting severe MHWs both during and outside El Niño years.

Discussion

This study linked extreme warming events to coral bleaching using a recent methodological approach (Hobday et al., 2016) for analysing MHWs, which has the advantage of being tailorable to any marine environment in the world. We applied a set of strict conditions that were specifically tailored to our region of interest, the Red Sea, on a satellite-derived daily SST dataset (1985–2015), to isolate the MHWs over the Red Sea coral reef zones, which are likely to cause coral bleaching. We produced an atlas which: 1) revealed that MHWs in the Red Sea are more widespread and numerous than those reported during bleaching events, and 2) uncovered an emergent (1998) pattern of increasing MHWs over the northern Red Sea. We discuss below the implications of these results, both for the Red Sea and for the application of this methodology as a management tool for tropical marine ecosystems where monitoring is limited.

Undetected bleaching events in the Red Sea

Although our definition of MHWs is restrictive, we were able to isolate MHWs during all coral bleaching events in the Red Sea. However, these extreme conditions spanned much larger areas and occurred more frequently than the reported coral bleaching events, and additional MHWs have also been detected during other years and/or in other areas. For instance, severe bleaching (>30% cover at a scale of 10-100km) in Thuwal (Saudi Arabia) has been reported in 1998, 2010 and 2015 (see supp. mat. Hughes et al., 2018a), but we have found MHWs of similar or more extreme characteristics in 1995, 2001, 2003 and 2005 (Fig. S7), during which bleaching has not been reported. This could suggest that the extent of coral bleaching may be greatly underestimated. Indeed, the Red Sea is a highly unexplored area, having been subjected to relatively few in-situ studies despite its rich biodiversity (Berumen et al., 2013; Raitsos et al., 2013). Apart from the bleaching reports issued from several research and monitoring efforts (e.g. coral reef status by PESGA, research institutes in Israel, Saudi Arabia, Egypt and Jordan), which we have used to tune the MHW model, divers (commercial and touristic) also report bleaching events in the Red Sea. However, as the methods are not standardised, the extent of bleaching events reported in this way is hard to quantify (Donner et al., 2017). While these types of reports have not been used by most studies, we consider them (in addition to the published events) as indications that SSTs have reached a bleaching threshold. Firstly, our example of Al Wajh as a region susceptible to bleaching can be confirmed to some extent by sightings of bleaching in 2010 reported by Riegl *et al.* (2013). We have also identified the Dahlak region (western SRS) as a hotspot for intense MHWs. Its strongest MHW occurred during the 1998 El Niño, yet bleaching was only reported in the nearby region of Massawa (Wilkinson, 2000). Our results indicated that the extreme temperatures during the event extended beyond the reported area (Fig. 3), and observations of bleaching over the Dahlak archipelago following the El Niño have indeed been put forward (see Benayahu *et al.*, 2002). Our atlas also shows the Farasan islands to experience very long MHWs. Most recently, a strong event occurred during the 2015 El Niño (Fig. S9), which could be the same as the one that caused bleaching in the nearby Al Lith region (Fig. 3). Although details have yet to be published, bleaching has been reported near Farasan (Monroe et al., 2018). We have also observed MHWs of high intensity over the northern NRS, and some bleaching was confirmed at Ras Qisbah (eastern northernmost coast) in 2006 (Bruckner and Dempsey, 2015).

Although the limited monitoring prevents the confirmation of bleaching during all severe MHWs seen in the atlas, the lack of such occurrences may in some cases be due to the higher thermal tolerance of some corals. For instance, it has been suggested that the bacterial community associated with corals can be linked to thermal tolerance, as some taxa are consistently present in heat tolerant corals and not in sensitive corals (Ziegler et al., 2017). Reefs exposed to regular temperature variability (e.g. strong diurnal fluctuations, lack of cool water flow) also exhibit a higher resilience than those exposed to waves as the corals and their endosymbionts are preadapted to extreme thermal conditions (Davis et al., 2011; Oliver and Palumbi, 2011; Pineda et al., 2013). These different habitats may be found at scales of 100 m apart (Oliver and Palumbi, 2011; Pineda et al., 2013), and thus cannot be observed with the ~5 km resolution SST data used. Factors that reduce the aggregation of harmful reactive oxygen species, that are created by the endosymbionts as a result of the heat stress (Lesser et al., 1990), have also been shown to increase coral thermal tolerance (Nakamura and Van Woesik, 2001). These can be inherent to some strains of endosymbionts in the presence of high salinity through their production of an antioxidant in response to osmotic stress (D'Angelo et al., 2015; Gegner et al., 2017; Ochsenkühn et al., 2017), or be due to the oceanographic circulation (e.g. currents, eddies) that displaces the particles with the flow (Nakamura, 2010; Osman et al., 2018). The effects of circulation may however be detected through the distribution of MHWs in the NRS, as they appear to occur predominantly on the eastern coast, a pattern that is also observed in the NCRS and partly in the SCRS (Fig. 2a). This may be linked in the NRS and NCRS to the strong flows induced by the prevalent cyclonic circulation (Zhan et al., 2014) that would affect the African coastal region most due to its deeper bathymetry, which increases its exposure (Fig. 1a). The western SCRS hosts the

Tokar Wind Jet (Sudanese coast, ~19ºN) caused by summer monsoonal winds channelled through a gap in the mountain range over the Red Sea (Viswanadhapalli et al., 2017), that may reduce thermal stress through evaporative fluxes as well as by intensifying the local circulation by creating a semi-permanent dipolar eddy (Zhai and Bower, 2013). Meanwhile in the SRS, less MHWs are observed over the Saudi Arabian coast than the African coast (Fig. 2a). This is potentially due to the strong southward winds occurring during summer, which may induce upwelling at the eastern coast and a corresponding downwelling in the west (Sofianos and Johns, 2003). The intrusion of cool water into the intermediate layer from the Bab El Mandeb strait may also act to further cool the corals in the Saudi Arabian coast during upwelling (Dreano et al., 2017).

There are therefore multiple factors that may have prevented coral bleaching during MHWs, some of which may not be detected with SST data and/or be occurring at spatial scales below that of our analysis. However, while coral bleaching has not been reported at all areas and times we have detected a MHW, oceanic temperatures are rising rapidly throughout the Red Sea (Chaidez et al., 2017), as well as the intensity and duration of MHWs throughout the world (Frölicher et al., 2018). Therefore, all areas we highlight through our atlas should nevertheless be considered at risk of future affliction. As the available coral bleaching data is sparse and highly localised, additional data collection from around the Red Sea would aid in further refining the MHW criteria for each region.

A probable emerging susceptible region for bleaching

Studies have suggested the northern Red Sea to be a thermal refuge for corals, as they can withstand temperatures far above their mean summer maximum SST (Fine et al., 2013; Osman et al., 2018). Indeed, the few bleaching events observed were mostly categorised as mild (1-10% of coral cover bleached) (Bruckner and Dempsey, 2015; Kotb et al., 2008;

Osman et al., 2018), while corals in the central and southern RS have experienced widespread bleaching events (Monroe et al., 2018; Osman et al., 2018). However, our results provide evidence for the recent emergence (since 1998) and rapid increase in MHWs in the NRS, to a point that they are more frequent than those in the SRS. This is the first time that this trend of emergent and increasing extreme warming events has been reported, but it coincides with an abrupt increase in the overall temperature of the Red Sea observed in 1994 (Raitsos et al., 2011). Additionally, our study supports the findings of Chaidez *et al.* (2017) that SSTs in the NRS are currently rising faster than in the rest of the Red Sea. Though the NRS has experienced less severe bleaching events than the CRS and SRS, it exhibited a higher occurrence of MHWs. This is likely because the SSTs in those regions (particularly the SRS) are much closer to the corals' bleaching threshold than in the NRS (Fine et al., 2013; Osman et al., 2018) as temperatures remain considerably cooler throughout the year in the NRS (Raitsos et al., 2013). However, it has been recently revealed that annual MHWs days have increased by more than 50% over the last century (Oliver et al., 2018), and MHWs are projected to become more frequent and intense over the next century as global warming continues to take effect (Frölicher et al., 2018). As the changes seen here have occurred rapidly, we may soon observe an altered coral bleaching regime in this region. Mass bleaching afflicting thermally resistant corals is not unprecedented, having occurred in northwestern Australia as recently as 2016 (Le Nohaïc et al., 2017). The sightings of bleaching in Ras Qisbah in 2006 (Bruckner and Dempsey, 2015), Hurghada in 2004, 2005 and 2007 (Hughes et al., 2018a), Gulf of Aqaba in 2007 (Kotb et al., 2008) and Al Wajh in 2010 (Riegl et al., 2013) were mostly characterised as mild. However, they are already a cause for concern due to their recent emergence and high frequency. As such changes are occurring so rapidly in the NRS, it may not remain a thermal refuge much longer.

The Red Sea already hosts touristic regions, such as Sharm El Sheikh (Egypt, northern NRS). The Kingdom of Saudi Arabia has initiated the construction of a large-scale tourism project stretching from Al Wajh to Umluj (NRS) termed the Red Sea Project, as well as NEOM, a "giga-project" for an enormous city in eastern NRS near Ras Qisbah (Public Investment Fund, 2017). These regions (will) rely on the renowned diversity of the Red Sea coral reefs to attract divers and other eco-tourists, as well as for food provision. Mass bleaching in this area would be added to existing pressures, such as reduced food availability in the NRS driven by increasing SSTs (Gittings et al., 2018). These have lowered the abundance of phytoplankton blooms, as well as delayed their onset and advanced their termination. Therefore, careful integrated conservation management will be necessary if MHWs continue to increase in frequency and intensity. Failing this, the renowned reef scenery could undergo drastic changes, which would certainly impact upon the tourism sector, as well as their related ecosystem services (food provision, coastal protection) (Chen et al., 2015; Doshi et al., 2012).

The MHW atlas as a conservation management tool

As we have shown, our atlas can identify coral reef regions that experience frequent and severe MHWs, thus revealing regions most at risk of bleaching. Furthermore, as this methodological approach can be tuned to any environment, it may be reproduced for any region that is either unexplored or does not have rigorous coral bleaching monitoring schemes. It is a cost-efficient way of revealing areas at high risk of bleaching and any emergent patterns, as it requires only remotely-sensed data and some records of coral bleaching to tailor the MHW definition.

The Red Sea MHW atlas has allowed us to highlight two threatened regions of particular interest. Firstly, we have detected a rising risk of bleaching for the NRS. As it is also a region reliant on tourism, we suggest the NRS (in particular the northern and eastern NRS) will soon require management, which should be implemented as soon as possible. We also suggest the NCRS to be a prime candidate, as it also exhibits a similar increase in MHWs and numerous bleaching events. In addition, it is a highly biologically-important region. Raitsos et al. (2017) have identified it as the most highly physically connected region of the Red Sea, which is echoed in the observed genetic dispersal. It is in this region that the "mother reefs" (Coghlan, 2017; Raitsos et al., 2017) are located, which are at the source of a significant proportion of gene flow throughout the Red Sea that spreads with the dynamic circulation flow (Raitsos et al., 2017). The NCRS may consequently sustain numerous communities of organisms throughout the Red Sea. It is also one of the regions (alongside the SCRS) that has seen a drastic decline of shark populations, one of the most profitable fisheries in the Red Sea, due to overexploitation (Spaet et al., 2016). As this region is vital for the continued survival and dispersal of certain species, yet shows an accumulation of different threats, there is a pressing need for this region to receive adequate management. The world's reefs are projected to decline by an estimated 70-90% by mid-century (Beyer et al., 2018; Donner et al., 2005; Frieler et al., 2013), yet the remaining corals could serve to repopulate the devoid reefs (Hoegh-Guldberg, 2014). A recent study therefore proposed 50 coral reefs that could serve that role, based on an analysis of multiple factors that relate to their risk of bleaching-related mortality and their connectivity with neighbouring areas, which include some reefs in the Red Sea (Beyer et al., 2018). The metrics used for their analysis of warming trends were all based on DHWs, yet we have shown that coral bleaching may be induced by warming during cooler periods, which is below that detected using that methodology. An integration of MHWs to this initiative could therefore provide further insights in determining which reef zones are most susceptible to coral bleaching when studying data-poor regions where the DHW method may not be applicable. Due to the lack of extensive in-situ bleaching data in the Red Sea, it is hard to relate a MHW index to bleaching severity. For instance, Yanbu (Fig.

S5) and Al Khawkhah (Fig. S10) experienced medium bleaching (10-30%) in 1998 (Osman et al., 2018) yet their MHWs showed duration: 13 vs 11 days, maximum intensity: 2.3 vs 1.7 ºC, cumulative intensity: 26 vs 14 ºC-days, respectively. However, a bleaching severity indicator may be unearthed with further in-situ research and analysis into the additional metrics offered by this methodology (Hobday et al., 2016).

The next step is to use this information, by developing management action plans that address the threats to the ecosystem brought by coral bleaching. These may be local, for example by reducing fishing pressure, culling corallivores (i.e. crown-of-thorns sea star) and enhancing herbivory and larval recruitment. This can delay biological responses to change, thereby allowing more time for the ecosystem to recover (Hughes et al., 2017). These methods have the purpose of increasing the resilience of the reef to avoid a phase shift towards a microalgae ecosystem (Bellwood et al., 2006; Graham et al., 2013; Hughes et al., 2010, 2005; Lam et al., 2017). However, it is important to note that by addressing issues at a local scale only, management plans may overlook the larger-scale processes and underlying distal causes (Hughes et al., 2017). For instance, if the source reefs mentioned above were ignored and reefs were managed only locally, recruitment could still diminish significantly if the source reefs are not protected and degrade (i.e. through bleaching), or if connectivity between reefs is not facilitated. Setting bans on fishing or regulating certain fisheries may also be ineffective if there is limited compliance. Indeed, an optimal management plan for the 50-reef initiative has been proposed, that involves a combination of actions on multiple scales, including global compliance with the Paris agreement to halt greenhouse gas emissions, cooperation between nations, organisations and stakeholders to develop management plans that consider both long and short timescales, and regional policies that directly involve the community to improve local ecosystems (Hoegh-Guldberg et al., 2018). It is therefore important to address the social norms, poverty or market demands which may drive overfishing and other local threats (Cinner et al., 2016; Hughes et al., 2017). In fact, it has been proposed that rapid changes in these social drivers can constitute early indicators of impending phase shifts (Hicks et al., 2016). If coral reef management plans incorporated both social and distal drivers of change, environmental protection would be much more robust, as more effective action could be taken even before effects are revealed by ecological indicators. Consequently, while the MHW atlas is needed to detect spatial and/or temporal patterns of bleaching risk, research on other possible threats to the ecosystems remains necessary to optimise ecosystem management.

We have demonstrated that the MHW atlas may serve as a reliable tool for detecting areas at risk of coral bleaching, and consequently propose its adaptation to other tropical regions which lack monitoring of coral reefs. The Red Sea was used as a model system as it is one of the warmest marine ecosystems on Earth, and may provide insights into the future functioning of global tropical oceans, since it exhibits conditions that are predicted to occur in other marine ecosystems several decades from now. By implementing this approach on this model system, we showed that bleaching is potentially more widespread than has been reported in the literature. It is therefore possible that the renowned resistance of Red Sea corals to bleaching is overestimated, and the sparsity of reports is the result of a lack of monitoring. Furthermore, we have shown that MHWs in the northernmost and north-central Red Sea are increasing in numbers, after having been absent before 1998. This study is the first to report this trend of emergent and increasing extreme warming events, and although the northern Red Sea has not been found to experience severe bleaching events yet, it is alarming that MHWs are so frequent given their very recent emergence. This highlights the need for cautious management of the northern and central Red Sea, particularly as these regions serve other ecologically-important roles and will face future pressures due to the imminent construction of large cities on the Saudi Arabian coast. We therefore recommend that management plans take these findings into consideration, and carry out more spatially- and temporally-extensive monitoring. We also propose that this cost-effective approach for the detection of coral bleaching risk be implemented in other unexplored tropical regions, alongside the analysis of local social pressures (increased market demand, poverty) that may serve as early indicators.

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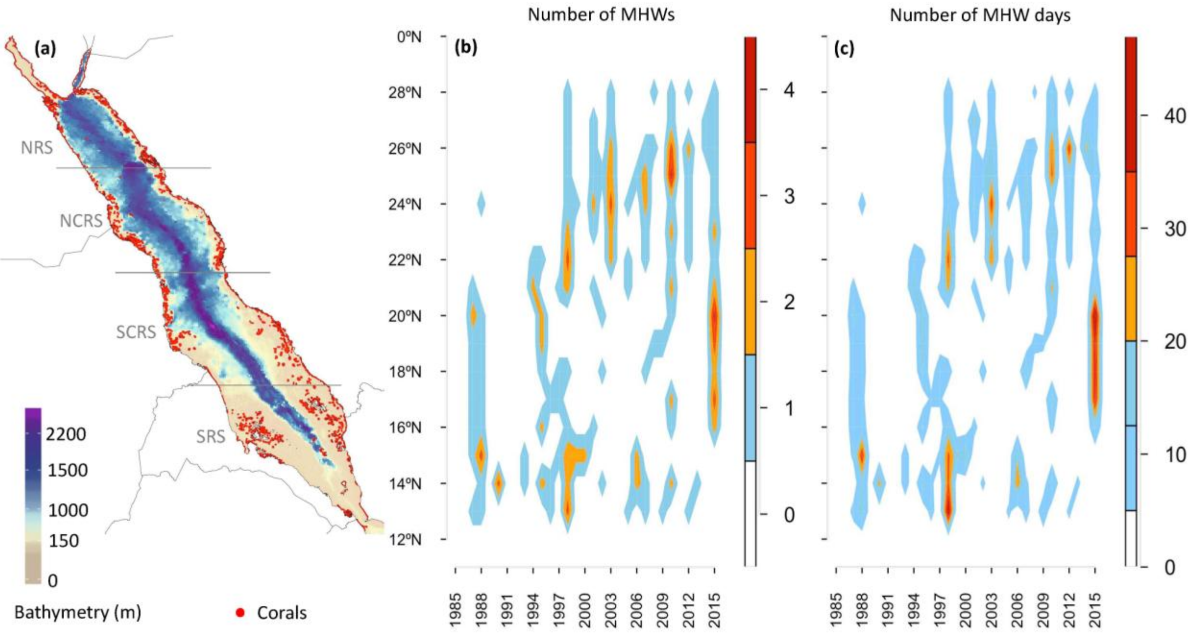
Figure captions

Figure 1: The map of the Red Sea shows the bathymetry and coral reefs (a), Hovmöller diagrams represent the number of marine heatwave events (b), and the total number of MHW days (c). The MHW algorithm was applied during summer over the Red Sea coastal waters (depth <150 m) along the latitudinal axis during 1985–2015. The Red Sea is divided into four regions, following Raitsos et al. *(2013): Northern Red Sea (NRS), North-Central Red Sea (NCRS), South-Central Red Sea (SCRS) and Southern Red Sea (SRS).*

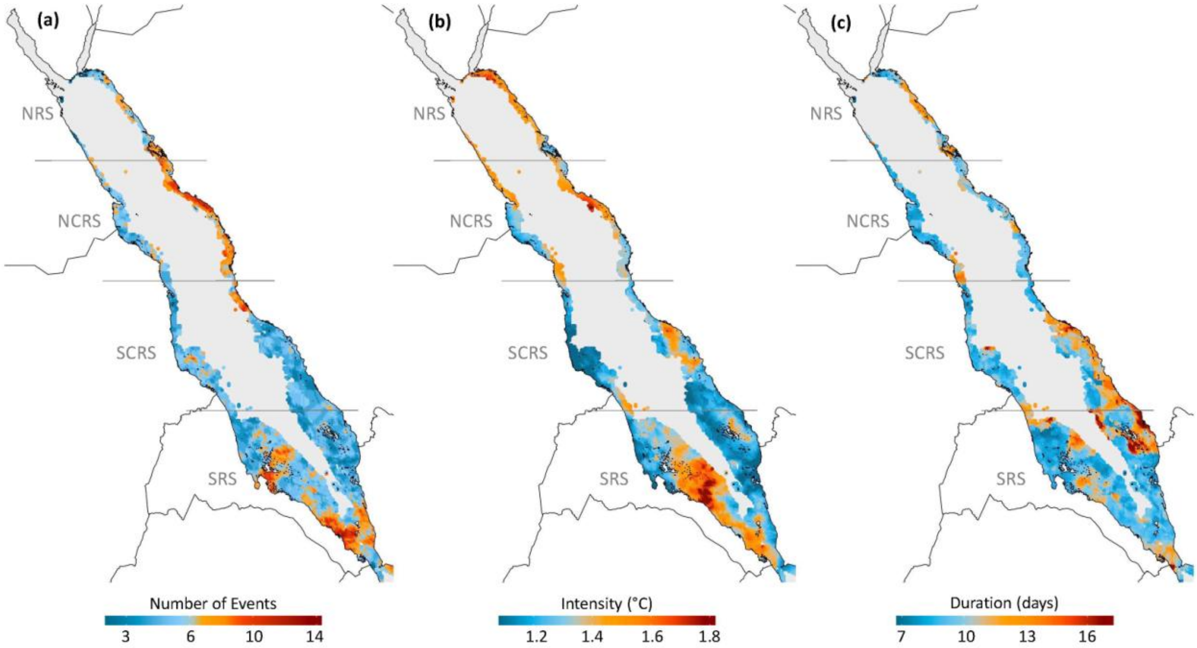
Figure 2: Atlas of marine heatwave hotspots over the Red Sea coral reef zones during 1985–2015. The maps represent: a) the total number of events, b) the average mean intensity of events, and c) the average duration of events.

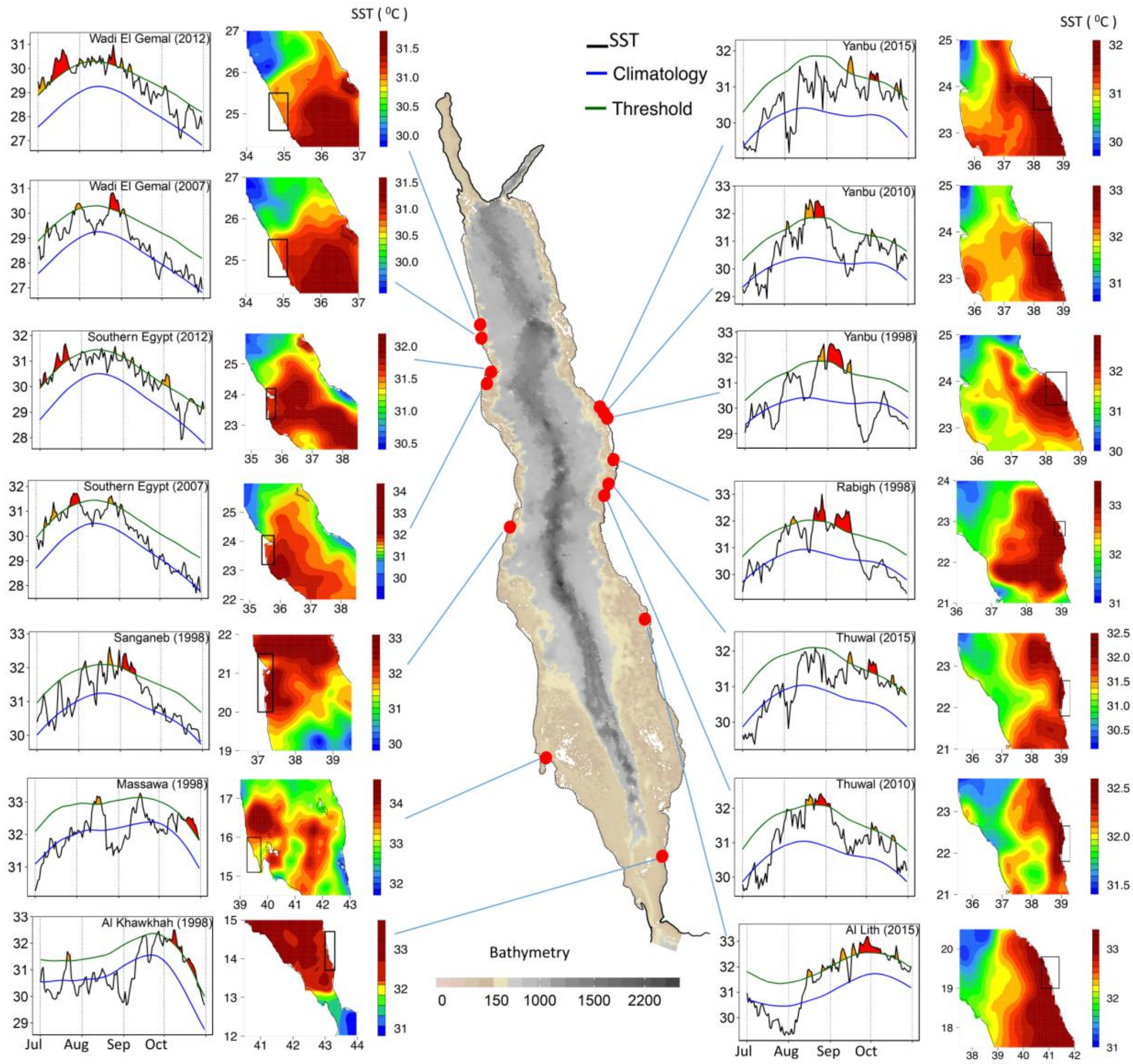
Figure 3: Marine heatwaves (MHWs) during recorded coral bleaching events in the Red Sea during 1985–2015. The colour maps show the sea surface temperature (SST) during the hottest day of the MHW at the bleached area, where the areas shown in black rectangles were spatially-averaged to construct the time-series plots. These show SST (in black), SST climatology (in blue) and 95th percentile threshold (in green). In the series-plots, the red filled area reveals the SSTs and duration of the MHWs, while the orange shaded areas highlight the SSTs above the threshold that did not meet the other conditions of a MHW. Note: the heat maps have different colour scales to make the MHWs clearly visible in space and time in each example.

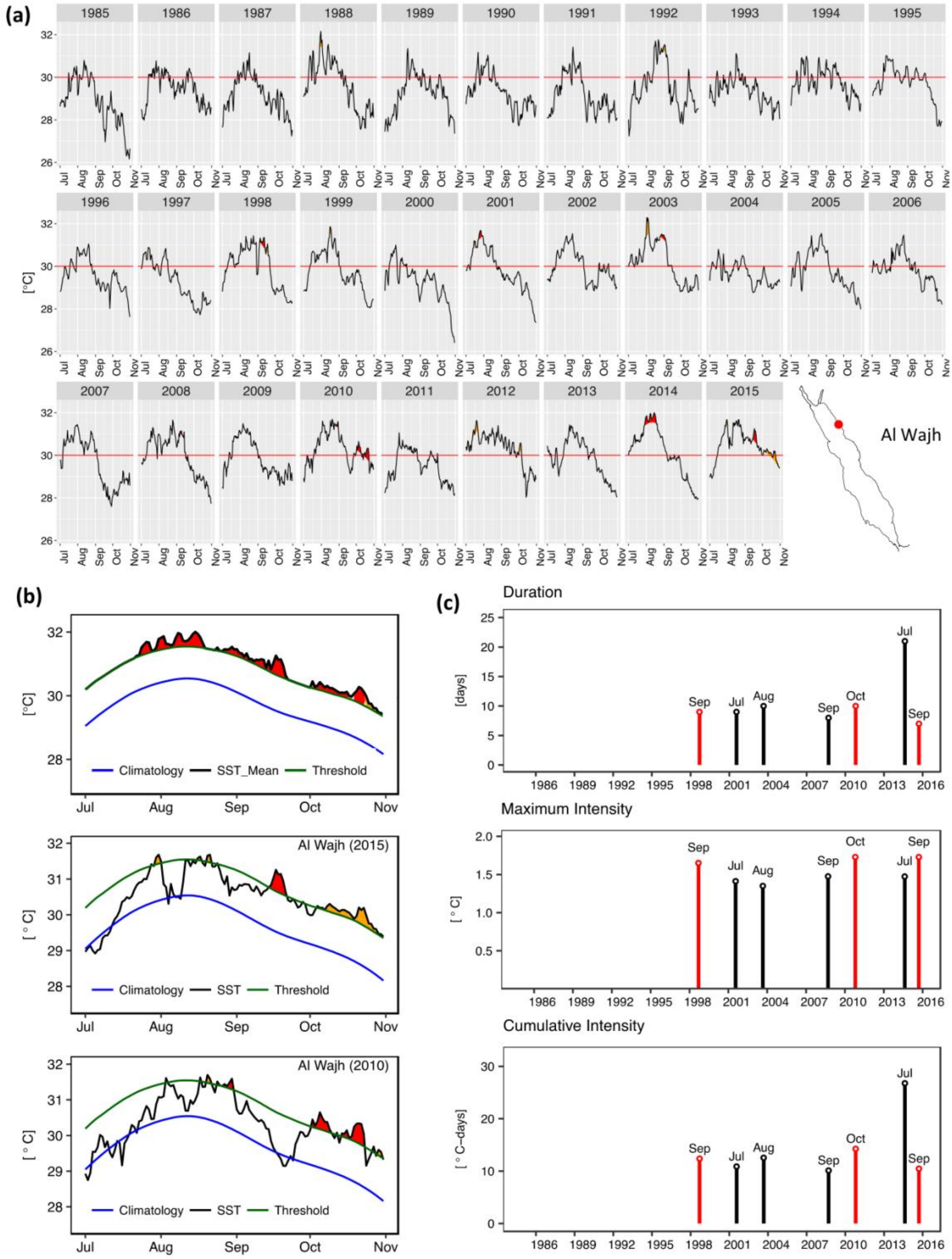
Figure 4: Summary plots of marine heatwaves (MHWs) detected from spatially-averaged sea surface temperature (SST) time-series in the Al Wajh region. (a) Event line showing the daily SST during summer months (July-October). The red filled areas reveal the SSTs above the percentile threshold associated with MHWs, the yellow areas highlight SSTs exceeding the percentile threshold but not representing a MHW, and the red line shows the base temperature of coral bleaching of 30°C. (b) Daily mean SST during summer MHWs (top), time-series of SST during the most recent bleaching year of 2015 (middle), and during the widespread bleaching year of 2010 (bottom) along with climatology and percentile threshold. (c) Lollipop charts showing the duration (top), maximum intensity (middle) and cumulative intensity (bottom) of all MHWs at Al Wajh; El Niño years are in red. Additional summary plots for other important regions around the Red Sea coastline can be found in the Supplementary Materials (Figs. S1-S15).



(a)
NRS
NCRS
SCRS
SRS
2200
1500
1000
150
0
Bathymetry (m)
Corals
Number of MHWs
(b)
0ºN
28ºN
26ºN
24ºN
22ºN
20ºN
18ºN
16ºN
14ºN
12ºN
1985
1988
1991
1994
1997
2000
2003
2006
2009
2012
2015
4
3
2
1
0
Number of MHW days
(c)
40
30
20
10
0


(a)
(b)
(c)
NRS
NCRS
SCRS
SRS
Number of Events
3
6
10
14
Intensity (°C)
1.2
1.4
1.6
1.8
Duration (days)
7
10
13
16


SST (⁰C)
SST
Climatology
Threshold
Wadi El Gemal (2012)
Wadi El Gemal (2007)
Southern Egypt (2012)
Southern Egypt (2007)
Sanganeb (1998)
Massawa (1998)
Al Khawkhah (1998)
Yanbu (2015)
Yanbu (2010)
Yanbu (1998)
Rabigh (1998)
Thuwal (2015)
Thuwal (2010)
Al Lith (2015)
Jul
Aug
Sep
Oct
Bathymetry
0
150
1000
1500
2200


(a)
1985
1986
1987
1988
1989
1990
1991
1992
1993
1994
1995
1996
1997
1998
1999
2000
2001
2002
2003
2004
2005
2006
2007
2008
2009
2010
2011
2012
2013
2014
2015
[°C]
Al Wajh
(b)
Climatology
SST_Mean
Threshold
Al Wajh (2015)
SST
Al Wajh (2010)
Jul
Aug
Sep
Oct
Nov
(c)
Duration
[days]
Maximum Intensity
[° C]
Cumulative Intensity
[° C–days]
1986
1989
1992
1995
1998
2001
2004
2007
2010
2013
2016