

Two spatial scales in a bleaching event: Corals from the mildest and the most extreme thermal environments escape mortality

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Abstract

In summer 2010, a bleaching event decimated the abundant reef flat coral *Stylophora pistillata* in some areas of the central Red Sea, where a series of coral reefs 100–300 m wide by several kilometers long extends from the coastline to about 20 km offshore. Mortality of corals along the exposed and protected sides of inner (inshore) and mid and outer (offshore) reefs and in situ and satellite sea surface temperatures (SSTs) revealed that the variability in the mortality event corresponded to two spatial scales of temperature variability: 300 m across the reef flat and 20 km across a series of reefs. However, the relationship between coral mortality and habitat thermal severity was opposite at the two scales. SSTs in summer 2010 were similar or increased modestly (0.5°C) in the outer and mid reefs relative to 2009. In the inner reef, 2010 temperatures were 1.4°C above the 2009 seasonal maximum for several weeks. We detected little or no coral mortality in mid and outer reefs. In the inner reef, mortality depended on exposure. Within the inner reef, mortality was modest on the protected (shoreward) side, the most severe thermal environment, with highest overall mean and maximum temperatures. In contrast, acute mortality was observed in the exposed (seaward) side, where temperature fluctuations and upper water temperature values were relatively less extreme. Refuges to thermally induced coral bleaching may include sites where extreme, high-frequency thermal variability may select for coral holobionts preadapted to, and physiologically condition corals to withstand, regional increases in water temperature.

Coral reef ecosystems have been declining for centuries (Pandolfi et al. 2003), and in the last few decades, the frequency of regional coral mortality events has increased (Hughes et al. 2003). In particular, coral bleaching is a formidable threat to contemporary coral reefs (Hoegh-Guldberg et al. 2007; Pandolfi et al. 2011). Elevated temperature and solar radiation can produce coral bleaching, the whitening of corals due to the expulsion or degradation of symbiotic zooxanthellae. Much of the research on coral bleaching has justifiably focused on biological and ecological processes, from the molecular physiology of the coral holobiont, to individual and species-specific patterns in bleaching, to community dynamics after bleaching events. Physical processes have received relatively less attention, yet physical processes may determine the scale and the frequency of bleaching disturbances, which in turn interact with life history, ecological, and suborganismal processes to determine patterns of acclimatization, adaptation, and ultimately evolution and extinction.

The spatial scales of bleaching vary strikingly. Healthy and bleached coral patches can be separated by a few tens of meters or tens of kilometers (regional scale) (Berkelmans and Oliver 1999). Knowledge of this spatial variability is fundamental for identifying refuges to regional and large-scale

bleaching events, and this understanding may be critically important to coral reef conservation in face of anthropogenic climate change (West and Salm 2003). However, an understanding of the causes of spatial variability in bleaching, and how processes operating at different spatial scales can interact in producing refuges to coral bleaching, is missing. Temperature variability in coral reefs is determined by multiple processes, including (1) large-scale interannual variability, such as El Niño Southern Oscillation (ENSO; Glynn 1985); (2) mesoscale eddies (Jokiel and Coles 1990); (3) cross-shore (perpendicular to the coastline) spatial gradients (Blythe et al. 2011); (4) internal waves, which can bring cool water to reefs (Wang et al. 2007); and (5) shallow topography interacting with wave flow (Davis et al. 2011). Furthermore, there are indications that the surface ocean is warming in response to anthropogenic climate change (Bindoff et al. 2007), and mass coral reef bleaching associated with warmer temperatures might already be occurring (reviewed by Glynn 1993; Hoegh-Guldberg et al. 2007).

Hydrodynamic processes leading to local water temperature increase can play a key role in the ecology of coral bleaching. For example, ENSO and processes leading to reduced mixing of surface waters can cause coral bleaching (Glynn 1985; Skirving and Guinotte 2001). How the coral holobiont responds to temperature variability and whether this leads to bleaching are dependent on various biological and abiotic processes. From the physical side, factors include the seasonal timing of the temperature anomaly,

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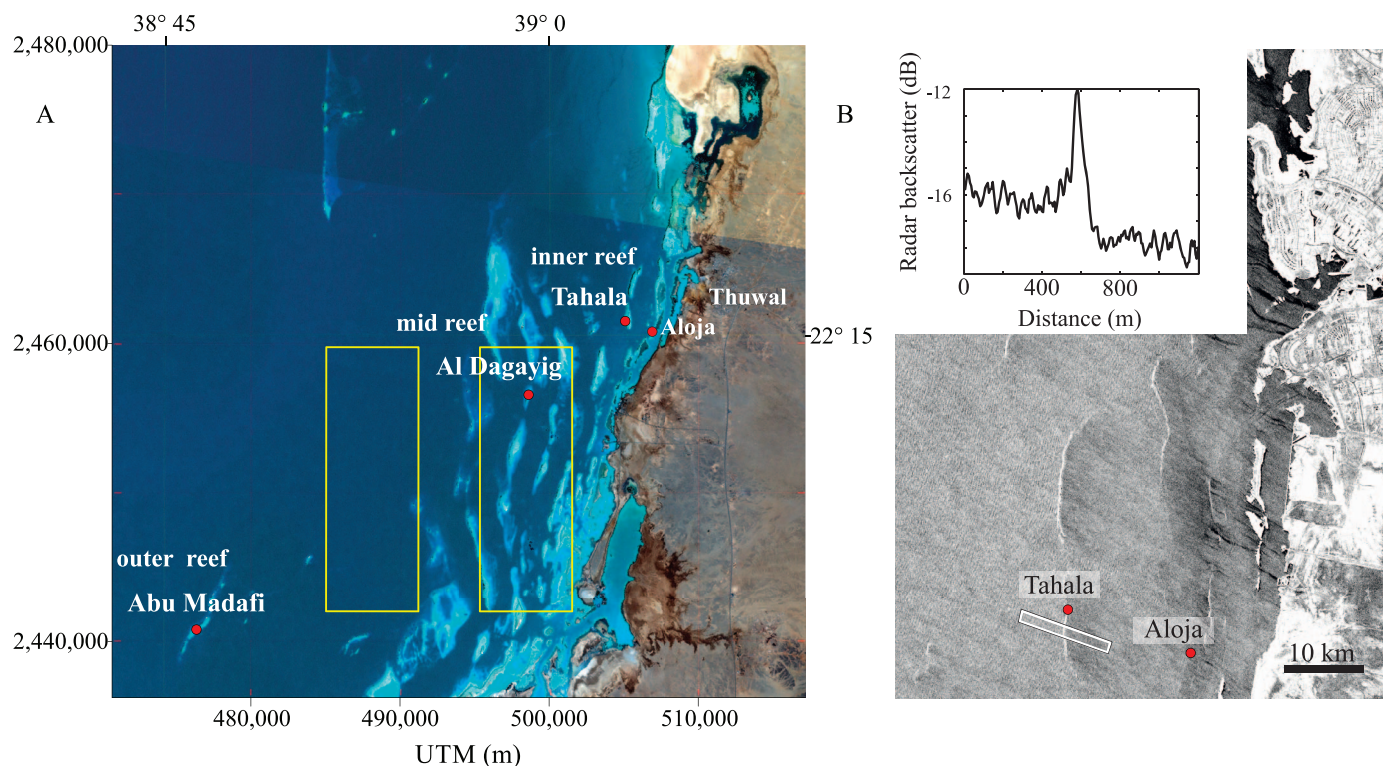


Fig. 1. (A) Landsat image of the study area with yellow boxes including inshore and offshore areas where SST averages and their gradient were derived. (B) TerraSAR-X synthetic aperture radar image (spotlight mode, vertical transmit, and vertical receive VV polarization) of Tahala and other inshore reefs, 25 June 2008. Note the attenuation of the wave field near the protected side of the reefs. The radar backscatter level on the exposed side is followed by an intense variation (+ 4 dBs) resulting from wave breaking and then, on the protected side of the reef, an area where radar power falls by more than 1 dB relative to the exposed side (see radar backscatter plot inset). The development on land is King Abdullah University of Science and Technology (KAUST). Landsat image acquired before the SAR image. Map units in degrees and minutes and in Universal Transverse Mercator (UTM) coordinates.

the magnitude and duration of the anomaly, and the seasonal amplitude of temperature variability. For instance, researchers suggest that temperatures 1–2°C above maximum seasonal temperatures for weeks would result in bleaching (Jokiel and Coles 1990; Glynn and D'Croz 1991). Furthermore, corals in sites with large seasonal temperature variability might be more resistant to bleaching than those in sites with smaller seasonal variability (McClanahan et al. 2007). On the other hand, hydrodynamic phenomena that cause a localized temperature decrease during regional-scale warming events might create spatial refuges to coral reef bleaching. For example, topographic and wind-driven upwelling and internal waves might bring cool water to stressed coral reefs (reviewed in West and Salm 2003; see Wang et al. [2007] for an example involving internal waves). A less obvious refuge to thermally induced bleaching might exist in thermally extreme, shallow-water habitats. Diurnal thermal variability is common in shallow inshore coral reef environments (reviewed in Brown 1997). Large diurnal temperature fluctuations and high temperatures in these habitats might select for holobiont genotypes that are adapted to high temperatures or for corals that can acclimate. Observational and experimental studies indicate that corals from habitats exposed to diurnal variability and high temperatures are more stress resistant than corals exposed to less variable and milder conditions just 100 m to

a few kilometers away (Barshis et al. [2010] for experimental evidence; Hoeksema [1991] and Castillo et al. [2012] for observational studies). Can highly fluctuating extreme thermal environments act as refuges during regional bleaching events?

Here, we use in situ and remote physical observations to document two spatial scales of a bleaching event at the end of the summer of 2010 in the central Red Sea, off Thuwal, Saudi Arabia. In this region, a series of reefs 100–300 m wide and several kilometers long are aligned parallel to the shore and extend up to 20 km offshore (Fig. 1A). The reef flats in this region are shallow, from occasionally exposed on some sites, to about 1.5 m deep. Deeper waters surround the offshore and onshore sides of these reefs, and the reef slopes tend to be very steep on the offshore side and quasi-vertical in the onshore side. As surface waves approach the shallow reef topography on the exposed (offshore) side of the reefs, they break and drive a flow across the reef flat (Fig. 1B; S. Lentz unpubl.) The waters warm as they flow toward the protected (onshore) side in the daytime, but at night, patterns reverse, and waters sometimes cool as they cross the reef flat (Davis et al. 2011). Similarly, but at a cross-shore scale of ~ 20 km across the series of reefs, in situ point measurements and recent satellite imagery off Thuwal indicate that inshore waters tend to be warmer than waters ~20 km offshore during the summer. During

the winter, however, patterns reverse, and inshore waters are cooler than offshore waters (Blythe et al. 2011).

We hypothesized that these two scales of temperature variability have physiological and ecological effects on corals living on the shallow reef flats. One of the most abundant scleractinian corals on the region's reef flat (pers. obs.) is *Stylophora pistillata*, a brooding "opportunistic" species (Loya 1976) that extends its vertical distribution to subtidal habitats. A. Tarrant et al. (unpubl.) found that within these shallow reef flat environments, *S. pistillata* corals always contained *Symbiodinium* subclade A1 symbionts, with subclade C3 also present in about 20% of the corals. Subclades were identified by using denaturing gel electrophoresis of the internal transcribed spacer 2 (ITS2) region followed by sequencing, and by sequencing clone libraries. Furthermore, inshore corals had higher lipid content than offshore corals.

Information about bleaching events in the Red Sea is scant, but isolated instances of bleaching in the Red Sea were reported recently for Eilat, Israel, and Hurghada, Egypt (Loya 2004; Mohammed and Mohamed 2005). Unpublished reports indicate bleaching also occurred in 1998 in a site 50 km north of Thuwal (Y. Fadlallah pers. comm.). In 2010, widespread bleaching was reported in south Asia (Guest et al. 2012). We first observed extensive bleaching near Thuwal, in the central Saudi Arabian Red Sea, in early August 2010. Surveys of bleached reefs in September 2010 found the highest incidence of bleaching on inner reefs and a higher incidence of bleaching in shallow (5 and 10 m) parts of reefs compared with deeper parts (15 m; Furby et al. 2013). A wide variety of coral taxa (12 families) were affected by this bleaching event, with oculinid taxa suffering the highest mortality. Furby et al. (2013: p. 505) measured bleaching of the coral taxa "during the peak of this thermal stress," in September 2010, then revisited the sites 7 months later, in April 2011, and inferred that the 2010 bleaching event caused the mortality observed in April 2011. In this study, we did not measure bleaching; however, we infer that the bleaching event that Furby et al. (2013) documented caused the mortality we measured 8 months after the event.

In this study, we use an array of remote and in situ temperature observations resolving two distinct scales to address the following questions. What are the spatial scales of variability in the 2010 summer bleaching and mortality event? Do mortality spatial patterns of the coral *S. pistillata* correspond to the across-the-reef and cross-shore scales of temperature variability documented in the region? Is the most severe mortality seen in the most thermally extreme habitats at the across-the-reef scale, as well as at the cross-shore scale?

Methods

Water temperature and mortality of corals *S. pistillata* were measured at sites on the protected and exposed sides of three reefs near Thuwal in the central Saudi Arabian Red Sea. Tahala, Al Dagayig, and Abu Madafi represented inner, mid, and outer reefs (Fig. 1A). (Here, we use "inner," "mid," and "outer" to designate a reef's relative

distance from the shore, with inner, mid, and outer reefs closest, in between, and most distant from the shore, respectively.) The distances between the exposed and protected sites were 290 m for the inner reef Tahala, 110 m for the mid reef Al Dagayig, and 230 m for the outer reef Abu Madafi. These observations thus encompass two scales: across the reef, ~ 300 m, and cross-shore, ~ 20 km.

Reef flat in situ temperature—Reef flat temperature at each of the six sites was measured with two Hobo WaterTemp Pro (Onset) temperature loggers separated along the reef by 10–15 m at each site. The sampling interval was 6.5 min in 2009 and 15 min in 2010. Instruments were fixed 10–30 cm above the bottom, at a water depth that varied over the year between approximately 40 cm in the summer to 1 m in the winter. Reef flat temperature data were used raw or were filtered with the use of a 33 h lowpass filter.

Satellite derived sea surface temperature: Cross-shore gradients and time series—Moderate-resolution imaging spectroradiometer (MODIS) sea surface temperature (SST) retrievals were based on the 11 μ m National Aeronautics and Space Administration (NASA) SST algorithm (Walton et al. 1998). Orbital data were processed into a 1.0 km grid. SST retrievals are each assigned a quality level of 0–4, with 0 being the highest quality. Data must pass 13 different tests to gain a quality level of 0 (http://oceancolor.gsfc.nasa.gov/DOCS/modis_sst/). For this analysis, retrievals with a quality level of 0 or 1 are used.

Cross-shore gradients and large-scale SST features—SST data for the region were derived from MODIS sensors aboard the Aqua and Terra satellites. Data were downloaded from the NASA OceanColor website (<http://oceancolor.gsfc.nasa.gov>). The average temperature in an inshore rectangular area and an offshore area, each about 16 km by 6 km (alongshore by cross-shore) was computed. Inshore and offshore areas were centered at about 5 km and 16 km from the shore (Fig. 1A). Only nighttime data were used because nighttime temperatures are less influenced by transient solar heating of the ocean's surface layer (Gentemann et al. 2008), which is prominent in this area (Davis et al. 2011). The cross-shore temperature gradient was calculated by subtracting the average offshore SST from the average inshore SST (Blythe et al. 2011).

SST images from 2010 were inspected to assess large-scale features that might have influenced local temperatures. The 2010 images that were obtained and processed were from 26 May (comprising satellite passes from 24–28 May, 30 June, 25 July, and 04 August).

Time series—SST measurements from 1985 through 2010 were obtained using the Coral Reef Temperature Anomaly Database (CoRTAD), Version 4, the high-resolution global SST product of the U.S. National Oceanic and Atmospheric Administration (NOAA) released in June 2012. These time series include a global record of SSTs and indices indicative of heat stress on coral reefs from 1985 through 2010. CoRTAD retains the ca.

4 km resolution of the Pathfinder SST product on which it is based, and day and night satellite passes are part of the weekly average reported (Selig et al. 2010). We downloaded the data for the southern Red Sea, which corresponds to the global tile from row 3, column 9 (<http://www.nodc.noaa.gov/sog/cortad/>), and selected the pixels from the inshore reef area at Thuwal for further analysis. We were primarily interested in the SST climatological indexes of sea surface temperature anomaly (SSTA, calculated as SST minus climatological SST), and temperature stress anomaly degree heating week (TSA_DHW, where the anomaly is calculated as SST minus the maximum weekly climatological SST; see <http://www.nodc.noaa.gov/sog/cortad/>). We calculated the average of the eight pixels in the inshore study area available for each week.

Meteorological observations—Wind speed and direction were measured with improved meteorological sensors (Hosom et al. 1995) deployed on a buoy about 30 km offshore from Abu Madafi (Farrar et al. 2009). Depth at the site was about 700 m. Winds were measured every minute and were smoothed for analysis with a 7 day lowpass filter.

Coral mortality and coral surveys—In 2008 and 2009, as part of a study on *S. pistillata* holobiont physiology (A. Tarrant et al. unpubl.) and ecology, eight to nine coral colonies were tagged with plastic tags at the exposed and protected sites of Tahala and Abu Madafi. Each colony was surveyed in February 2010, before the bleaching event, and again after the event, in May 2011 and September–October 2011.

In October of 2011 and June 2012, we conducted belt transects to estimate the number of dead corals at six sites: the protected and exposed sides of Tahala, Al Dagayig, and Abu Madafi. A transect line was laid on the bottom along the reef at 0.8–1.5 m water depth. We assessed the first 30 *S. pistillata* colonies found along the tape within a belt 2–4 m wide (depending on the density of colonies within each site). Three transects were conducted at each of the six sites, and each transect ran parallel to the long axis of the reef. The separation between transects was 10–15 m. Small (< 8 cm) coral colonies were measured across the largest horizontal dimension. Colonies < 4 cm across were considered to have settled after the bleaching event (Loya 1976). Corals on each transect were classified as dead or alive on the basis of a visual evaluation of the colony. Statistical analyses to compare coral mortality across and between reef sites were done with Systat 13 (Systat Software).

Results

Seasonal and diurnal temperature patterns—In situ reef flat water temperatures were highest from July to September and lowest from January to February (data for Tahala, Fig. 2). Diurnal temperature variability, with highest temperatures in the afternoon and lowest at night, occurred throughout the year at the exposed and protected sides of all reefs and was more conspicuous in spring and summer. Fluctuations in temperatures were larger on the

protected than on the exposed side of the reef, with diurnal fluctuations of up to 6.5°C on the protected side on the inner reef, Tahala.

Reef flat temperature in 2009 and 2010 and spatial temperature gradients—Thirty-three hour low-passed reef flat summer temperatures in 2009 were consistently warmer on the inner reef, Tahala, than on the mid and outer reefs (Fig. 3). Al Dagayig and Abu Madafi, consistent with the results of Blythe et al. (2011) for a multiyear time series (2000–2009) in the same region. These cross-shore gradients were exacerbated in the summer of 2010 relative to 2009 (Fig. 3). Box plots and the distribution of raw temperature data from May to November 2010 also indicate a cross-shore gradient, with higher mean, median, 75%, 95%, and 99% percentiles at the inner reef and lowest values at the outer reef (Fig. 4). Maximum temperatures do not follow these patterns, however, with some of the highest temperatures observed on the protected side of the outer reef, Abu Madafi. High water temperatures on the protected site of the outer reef are likely the result of in situ warming on the ~ 300 m wide Abu Madafi reef crest. The protected inner reef, however, features the highest values for all the statistics, a likely outcome from in situ warming superimposed on the cross-shore gradient.

Seasonal range in 2010 low-passed temperature was about 9.5°C, 8°C, and 7°C for the inner, mid, and outer reefs. Temperatures at the inner and mid reefs, Tahala and Al Dagayig, were about 1.4°C and 1°C higher in the summer of 2010 than in 2009. However, 2009 and 2010 maximum reef flat temperatures on Abu Madafi appear of the same order. The pronounced cross-shore temperature gradient in 2010 was the result of increased temperatures in inshore waters. Superimposed on the 2010 seasonal variability in the inner reef, diurnal temperature variability ranged from negligible to up to 6.5°C (Fig. 2).

Cross-shore gradients in satellite-derived SSTs show anomalously high values in 2010, with the largest values in the time series (Fig. 5), and the steep gradients are consistent with the in situ reef flat trends for 2010 (Fig. 3). These results support the observed exacerbated cross-shore temperature gradients in 2010. In the summer of 2010, inshore waters were warmer than in 2009, whereas offshore waters remained cool.

A large-scale offshore feature may have influenced water temperature on the outer reef. A cool core eddy was detected offshore of Abu Madafi on 26 May 2010 (Fig. 6). The eddy persisted until 30 June, but by 04 August, it was not seen in the SST satellite images (results not shown for 30 June and 04 August).

CoRTAD time series—The satellite-derived SSTs show positive anomalies from January to May and then from August to September (Fig. 7A). The August–September anomalies occurred when seasonal temperature is at its peak. The TSA_DHW shows a steep increase in late summer, from August to November (Fig. 7B).

Meteorological observations—In late spring and summer of 2009, winds were upwelling favorable with north wind

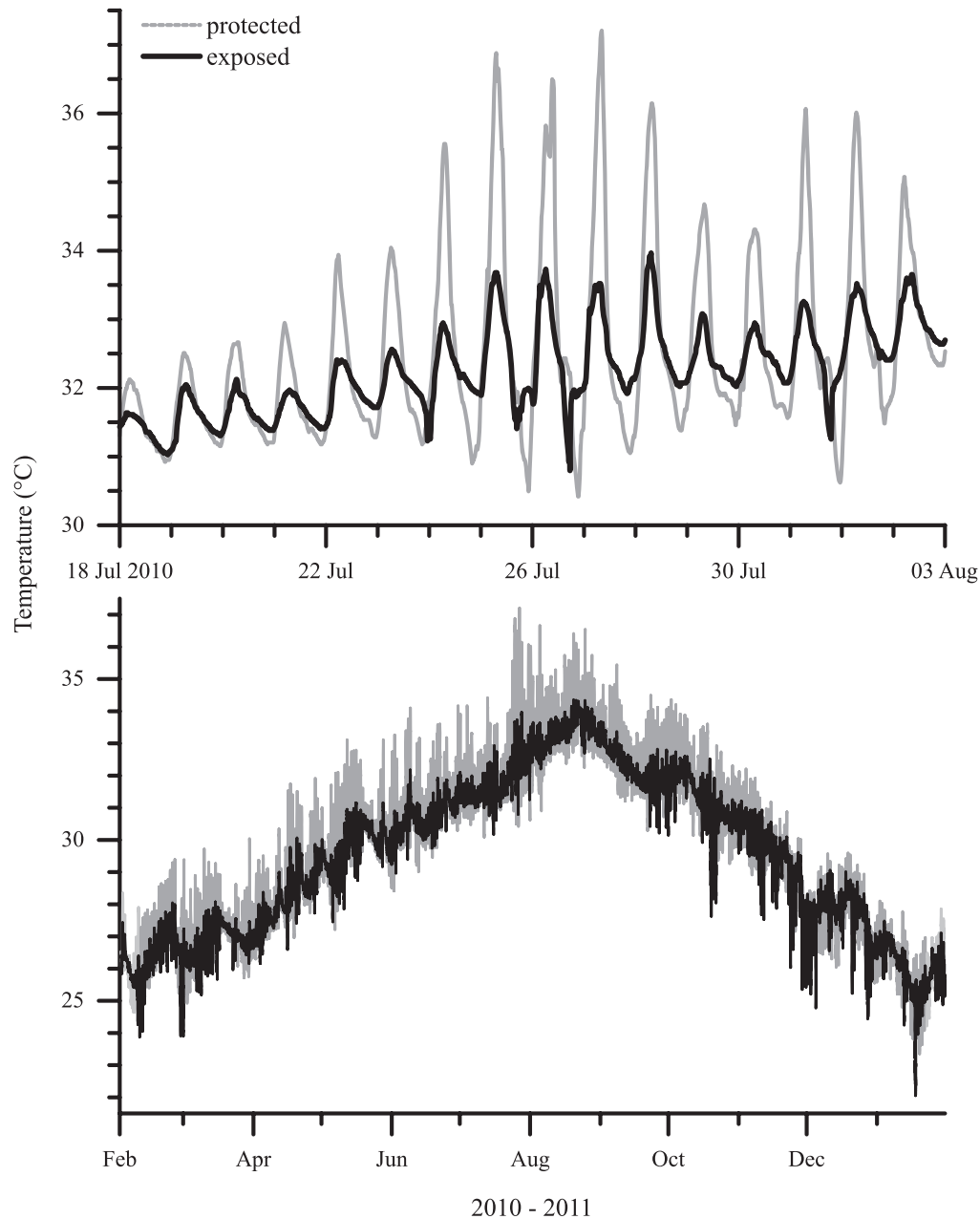


Fig. 2. Yearly seasonal temperature time series at the exposed and protected sides of Tahala reef and details of the diurnal variability.

events $> 5 \text{ m s}^{-1}$ in May, August, and September (Fig. 8). In 2010, after downwelling favorable winds in early May, winds turned from north to south. North and east winds were energetic from mid-May to early July 2010. After an event with downwelling favorable winds in mid-July, north and east winds were very weak until early September, when east and north winds intensified. This period of weak winds coincided with the onset of the bleaching event in summer 2010.

Coral mortality—*S. pistillata* mortality varied sharply within and among reefs. After the bleaching event, none of the tagged colonies were found alive at the exposed side of the inner reef (Tahala). On the protected side of this reef,

however, the percentage of tagged colonies found alive was comparable to both the exposed and protected sides of the outer reef (Abu Madafi; Fig. 9). The proportions of live, dead, and missing tagged corals in the exposed and protected sides of Tahala and Abu Madafi were significantly different (Pearson chi-square 17.44, $df = 7$, $p = 0.015$). The largest Freeman–Tukey deviates were for Tahala exposed side (-3.6), which had fewer live corals than expected, and for Abu Madafi's exposed side, which had fewer dead corals than expected (-2.2).

Coral survey—The number of dead *S. pistillata* colonies on the belt transects also varied strikingly within and

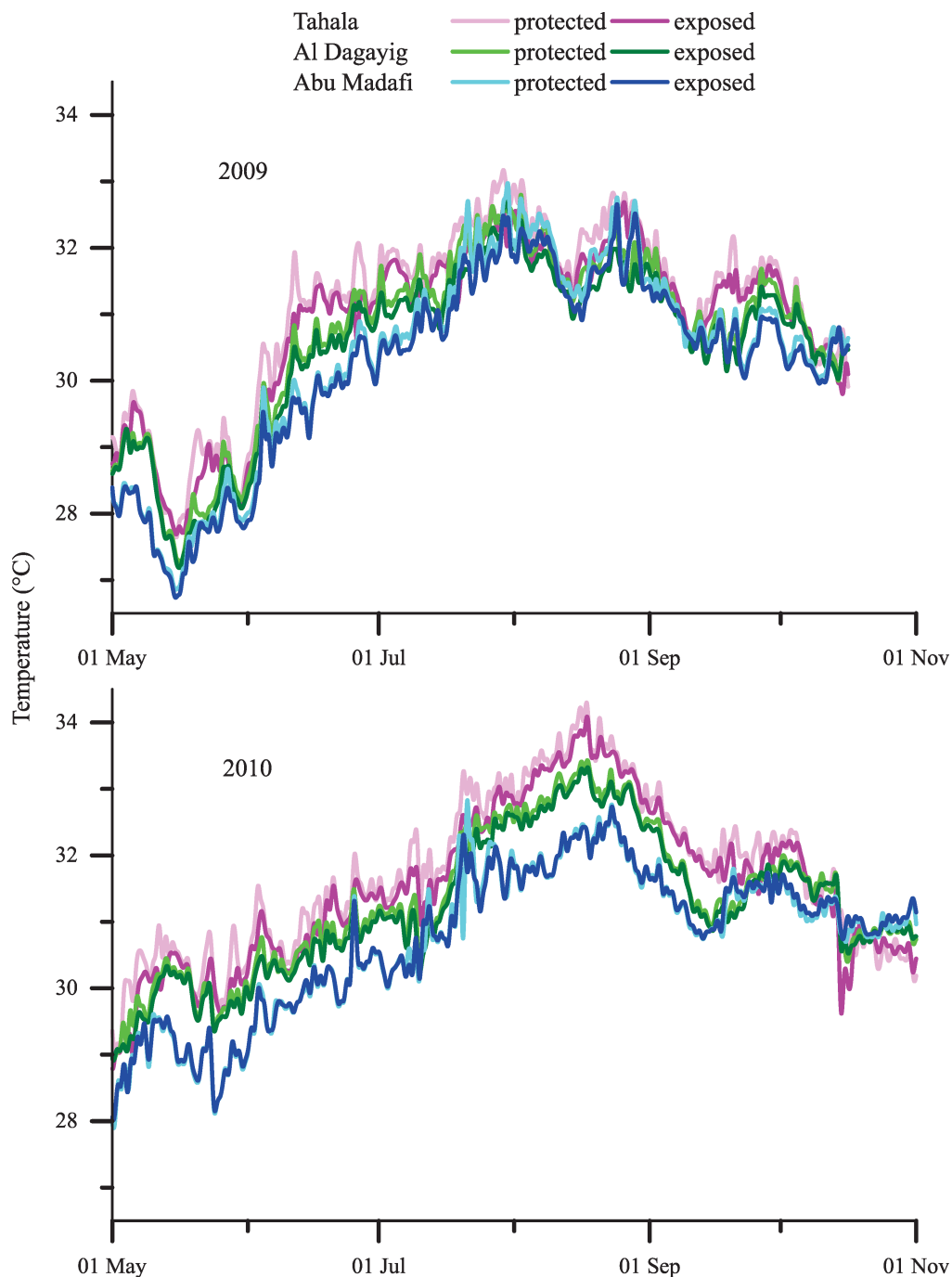


Fig. 3. Reef flat low-passed temperature time series on the exposed and protected sides of Tahala, Al Dagayig, and Abu Madafi in 2009 and 2010.

among the reefs, with more dead colonies at the exposed side of the inner reef, Tahala, than at any other reef site in 2011 and 2012 (Fig. 10). One out of 90 colonies was found alive at the Tahala exposed site in 2011, with a small increase in number of live colonies in 2012.

Transect data were first analyzed to determine whether the three transects within each of the sites were homogeneous, to check whether pooling data for subsequent testing would confound results. In 2011, the three transects did not differ within any site except at the Abu Madafi

exposed site (chi-square = 12.61, $df = 2$, $p = 0.002$). At this site, 15 out of 30 colonies were dead in one transect, whereas the two other transects had 4 or 5 dead colonies out of 30 surveyed. In 2012, the proportion of dead colonies in one of the three transects in the Tahala protected site was significantly different from the other two transects (17 dead out of 30 vs. 8 and 9 dead out of 30) (chi-square = 6.90, $df = 2$, $p = 0.032$). In 2012, transects for Al Dagayig and Abu Madafi, exposed and protected sides, did not differ in the proportion of dead colonies.

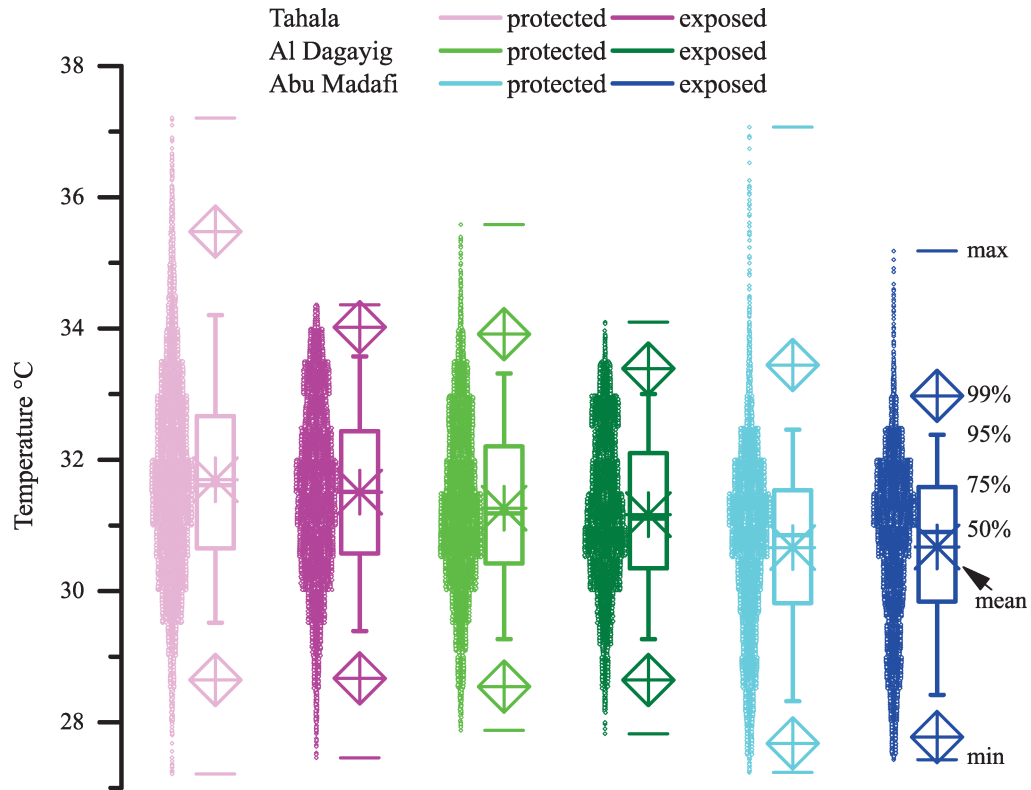


Fig. 4. Box plot of temperature and its distribution from the study sites, 02 February 2010 to 13 March 2011. All data points sampled at 15 min intervals are plotted. Box plots feature maximum; 99%, 95%, 75%, 50% (median), 25%, 5%, and 1% percentiles; minimum; and the mean.

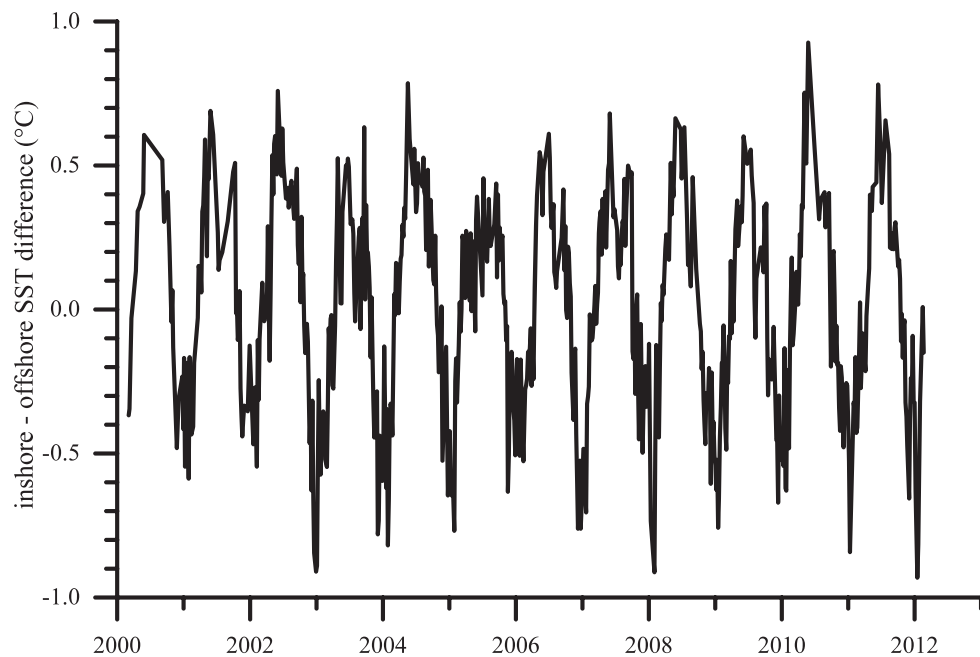


Fig. 5. Time series of the inshore-offshore gradient in SST. Inshore and offshore areas are about 16 by 6 km, as depicted in Fig. 1A.

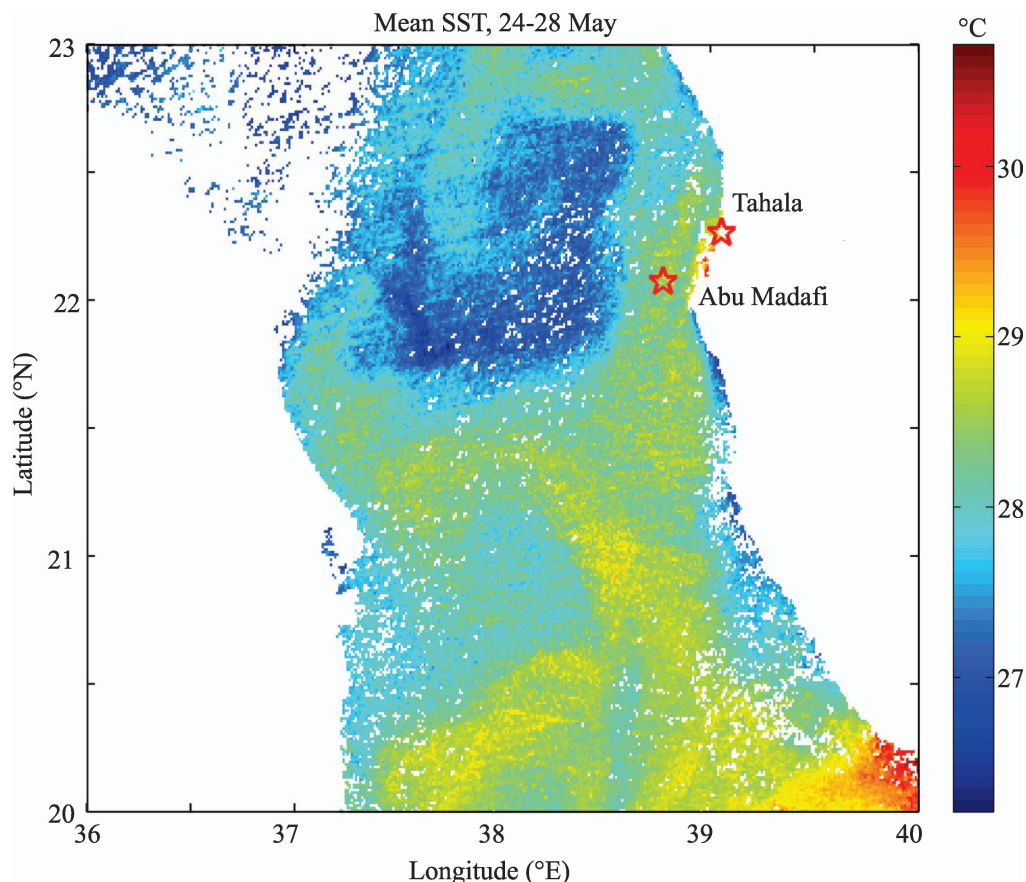


Fig. 6. SST image of a cool eddy derived from two satellite passes: one from MODIS flying on the Aqua satellite and the other from MODIS flying on the Terra satellite.

The transect data were pooled in subsequent statistical comparisons.

The difference in the proportion of dead colonies within a reef was reef dependent. In October 2011, 89 of 90 colonies on the exposed side of the inner reef were dead, and this was significantly higher than the proportion of dead corals on the protected side (31 out of 90; chi-square = 84.10, $p < 0.0001$; Fig. 10). The single live colony on the exposed side of the inner reef in 2011 was a recruit (< 4 cm). Excluding the recruits (colonies < 4 cm) from the analysis did not change the results; the proportion of dead corals in the exposed site was larger than in the protected side (chi-square = 83.01, $p < 0.001$). The proportion of dead colonies at the mid reef protected side was higher than at the exposed side (12 out of 90 dead vs. 4 out of 90 dead; chi-square = 4.39, $df = 1$, $p < 0.036$), although these mortalities were not as high as at Tahala or Abu Madafi. The proportions of dead colonies in the exposed and protected side of the offshore reef Abu Madafi were not significantly different (chi-square = 0.77, $df = 1$, $p = 0.383$), with 24 out of 90 dead colonies in the exposed side compared with 19 out of 90 dead colonies in the protected side.

Eight months later, in June 2012, the proportion of dead colonies in the exposed side of the inner reef, Tahala, continued to be significantly higher than in the protected side (83 out of 90 dead, vs. 34 out of 90 dead; chi-square =

58.63, $df = 1$, $p < 0.0001$). Similar to 2011, excluding the recruits (< 4 cm) from the analysis did not change the results; the proportion of dead corals in the exposed site was larger than in the protected side (chi-square = 46.79, $p < 0.001$). One of the live colonies on the exposed side of Tahala was a recruit (< 4 cm), and the six other live colonies on the same site were < 7 cm in diameter, and probably recruited after the bleaching event. The proportion of dead colonies on the exposed and protected sides of the mid reef, Al Dagayig, did not differ (13 out of 90 dead vs. 19 out of 90 dead; chi-square = 1.37, $df = 1$, $p = 0.242$). Similarly, the proportion of dead colonies on the exposed and protected sides of Abu Madafi did not differ (15 out of 90 dead vs. 22 out of 90 dead, Chi-square = 1.67, $df = 1$, $p = 0.197$).

Recruits and large colonies, within reef comparisons—We compared the proportion of recruits (colonies < 4 cm) to large colonies in the exposed vs. the protected sides of each reef in October 2011 and June 2012. The only reef that had significant differences in the proportion of recruits to large colonies at the two exposure locations was Tahala in 2012. (Chi-Square = 12.29, $df = 1$, $p = 0.0005$. Only < 4 cm recruits included in this test.) In 2012, only one of the 90 colonies was a recruit (< 4 cm) on the exposed side, whereas 14 of 90 colonies were recruits (< 4 cm) on the protected side. (In the previous year, 2011, one out of 90

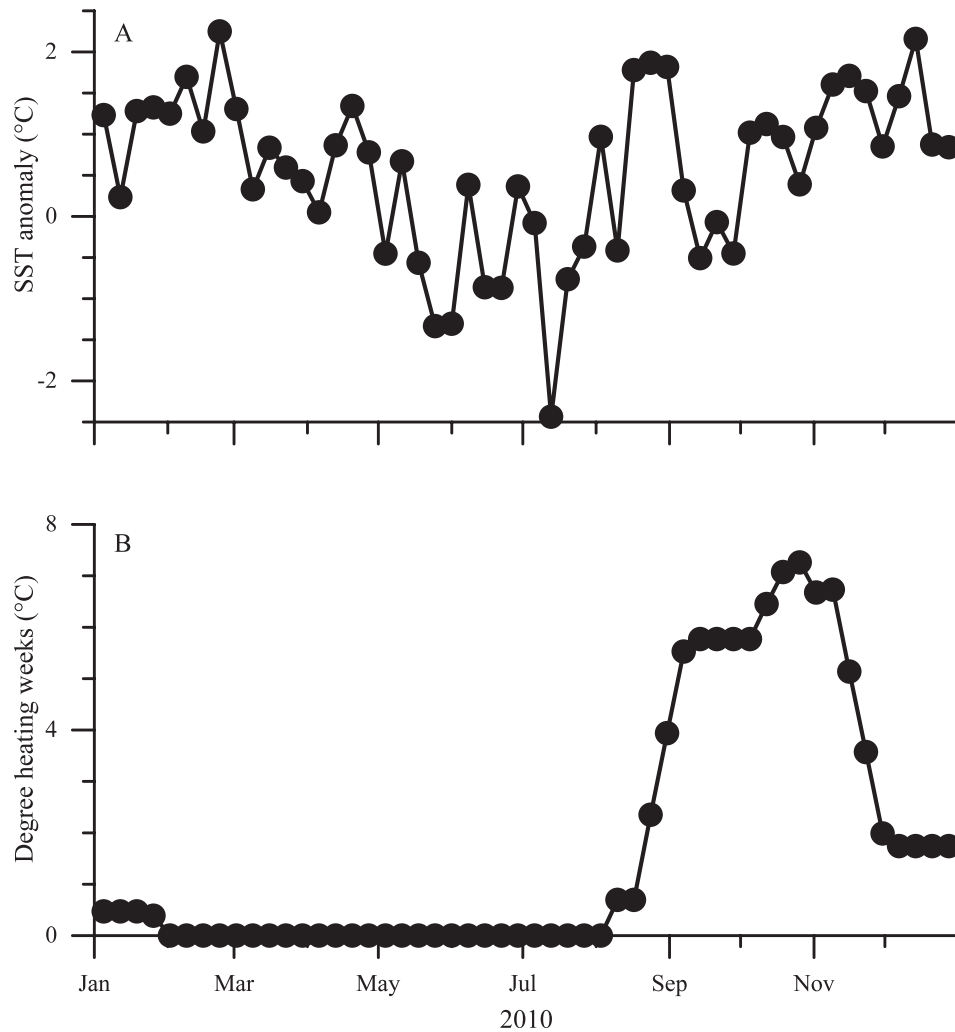


Fig. 7. (A) Satellite-derived CoRTAD SST anomaly for the region inshore in Thuwal (SSTA). Anomalies are weekly SST minus the weekly yearly average (climatology). (B) NOAA CoRTAD degree heating week, the sum of the previous 12 weeks when the thermal surface anomaly was $\geq 1^{\circ}\text{C}$ (TSA_DHW). The anomaly is calculated relative to the highest seasonal temperature of the yearly weekly average.

colonies was a recruit on the exposed side whereas 4 out of 90 colonies were recruits on the protected side.)

At Al Dagayig, the exposed side had 17 recruits in 2011 and 16 in 2012; the protected side had 11 and 14 recruits in each year. At Abu Madafi reef, the exposed side had 18 recruits in 2011 and 27 recruits in 2012; the protected side had 25 and 30 recruits in each year.

Recruits and large colonies, among-reef comparisons—To compare the proportion of recruits among reefs in 2011, the data were pooled over exposure locations within a reef. We found significant differences in proportions among reefs (chi-square = 33.69, $df = 2$, $p < 0.001$). The inner reef, Tahala, had far fewer recruits than expected in 2011 (5 out of 180; Freeman–Tukey deviate = -4.0). On the other hand, Abu Madafi had more recruits than expected (43 out of 180, Freeman–Tukey deviate = 3.5).

The results from June 2012 follow similar trends, with proportion of recruits significantly different among the

three reefs (chi-square = 31.50, $df = 2$, $p < 0.001$). Tahala had a lower than expected proportion of recruits (15 of 180; Freeman–Tukey deviate = -3.38), and Abu Madafi had a higher than expected proportion of recruits (57 of 180; Freeman–Tukey deviate = 3.79).

Discussion

The bleaching and mortality event in summer 2010 affected populations of *S. pistillata* on central Red Sea reef flats, with variability in mortality at two scales. At the cross-shore (20 km) scale, corals on the inner reef were affected, but little mortality occurred at the mid and outer reefs. At the across-the-reef (~ 300 m) scale, *S. pistillata* mortality was extreme at the exposed side of the inner reef but modest at the protected side of the same reef. The spatial patterns in *S. pistillata* mortality correspond to two prominent spatial and temporal scales of temperature variability in coastal Red Sea coral reefs: cross-shore, with

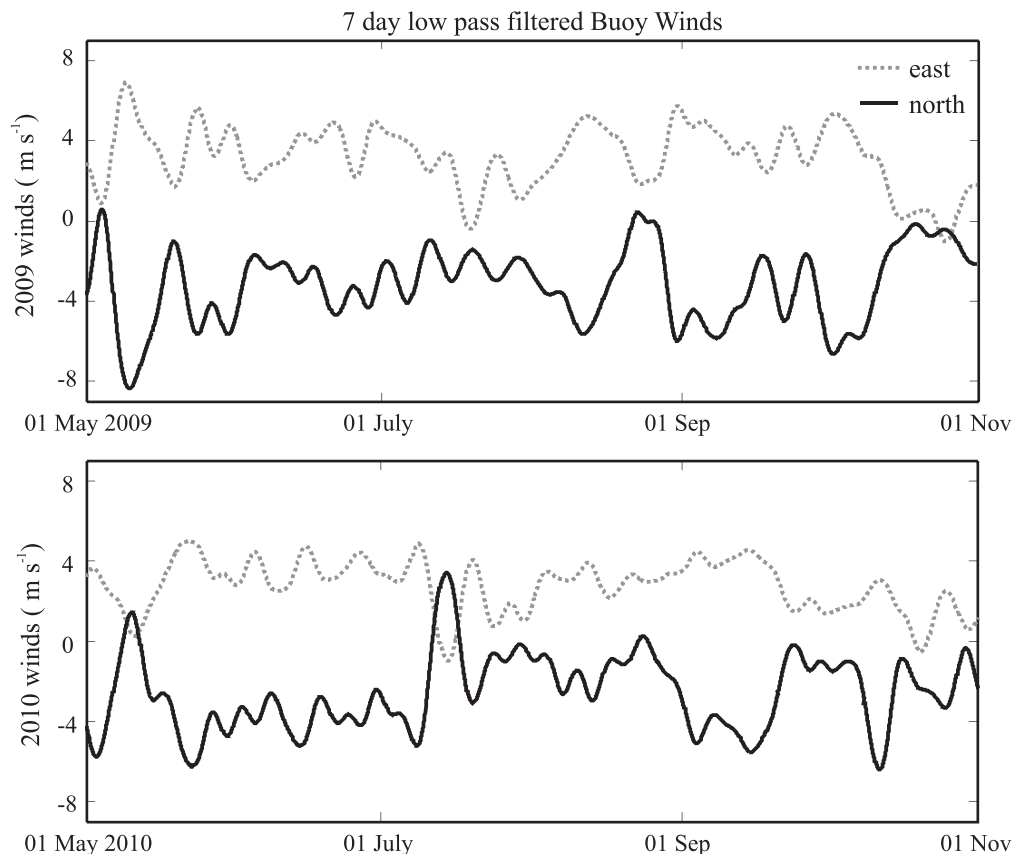


Fig. 8. Wind speed and direction measured with meteorological sensors deployed on a buoy about 30 km offshore from Abu Madafi. Positive north and east winds are northward and eastward.

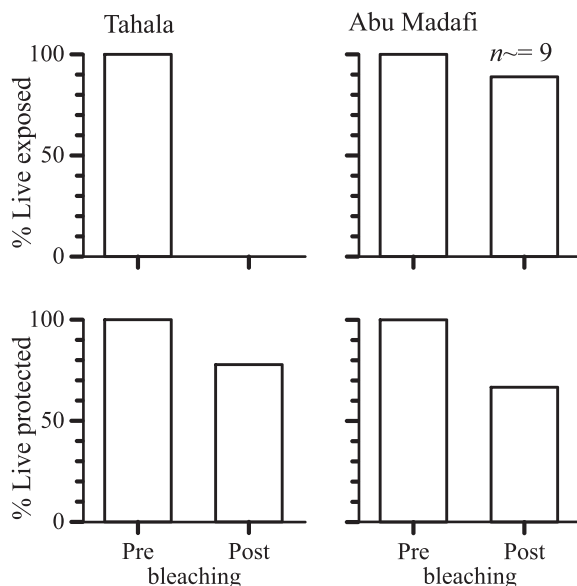


Fig. 9. Percentage of live tagged coral colonies before and after the bleaching event at Tahala and Abu Madafi exposed and protected sites ($n = 9$ or 8). After the bleaching event, five tagged colonies were found dead, and three tagged corals were missing at the Tahala exposed site. On the protected side of Tahala, seven tagged colonies were alive, and two were dead. In Abu Madafi, eight corals were alive, and one was missing on the exposed side, and on the protected side, six colonies were alive, two were dead, and one was missing.

seasonal temporal scales, and across the reef, with diurnal scales (Figs. 2, 5; Blythe et al. 2011; Davis et al. 2011). With observations at two spatial scales in temperature variability and mortality, this study represents an important step toward identifying the scales and potential processes associated with refuges to bleaching events.

Mortality in the inner reef was associated with an increase in 2010 summer reef flat temperatures relative to 2009 (Fig. 3) and with an anomalously large gradient in inshore to offshore SST temperatures (Fig. 5). CoRTAD temperature anomalies relative to the seasonal weekly average (climatology) indicate that 2010 SSTs tended to be anomalous from January to May and again in August and September (Fig. 7A). Seasonal peak temperatures on Thuwal reef flats occur in July–September (Figs. 2, 3). Therefore, anomalously high temperatures in August and September exposed reef flat corals to temperatures higher than typical peak seasonal temperatures, which might cause stress, bleaching, or mortality because corals can die in thermal environments $1\text{--}2^{\circ}\text{C}$ above the average seasonal maxima (Jokiel 2004). These anomalous conditions on top of the seasonal high are reflected in the Degree Heating Week plot derived from CoRTAD satellite data, showing “accumulated” anomalies higher than the yearly maximum from August to September (Fig. 7B). For reefs in which the in situ water temperature increase in 2010 relative to 2009

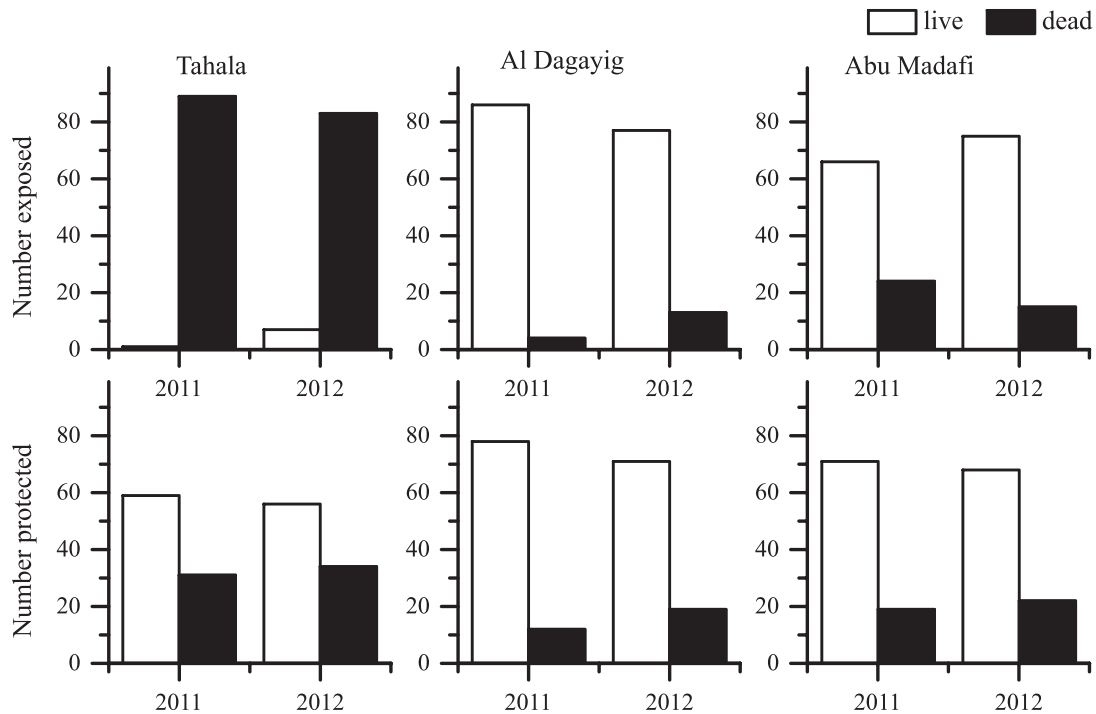


Fig. 10. Dead and live colonies on belt transects in 2011 and 2012 after the bleaching event.

was modest (mid reef, Al Dagayig) or not apparent (outer reef, Abu Madafi; Fig. 3), little bleaching and mortality were observed. Several authors reported coral bleaching events in Southeast Asia in the summer of 2010, including Guest et al. (2012). Furby et al. (2013) surveyed the exposed side of eight reefs, including Tahala and Abu Madafi, and found that bleaching affected a wide range of corals at 5, 10, and 15 m depth, with overall highest mortality for agaricids and oculinids and lowest for mussels. Bleaching and mortality was most prevalent in the inner reef (Tahala) and more rare in mid and outer reefs. In the Thuwal region, exposed sides of other inner reefs such as Aloja (Fig. 1A) and Fsar were also decimated (Furby et al. 2013; J. Pineda and V. Starczak pers. obs.) Despite the variability in mortality among coral taxa found by Furby et al. (2013), the cross-shore patterns in spatial mortality the authors documented correspond to the patterns we observed for *S. pistillata*. The bleaching event in 2010 clearly affected numerous nearshore reefs; in the central Red Sea region, inner reefs similar to Tahala are among the most dominant of reef types (Sheppard et al. 1992).

The local mechanisms responsible for the high SSTs in the summer of 2010 and its cross-shore heterogeneity are not known, but two phenomena might be involved. First, north and east winds from mid-July to the end of August 2010 were very weak compared with winds before and after this period and relative to the same period in 2009 (Fig. 8). Reduced wind speeds would cause a decrease in upper layer mixing and lead to heat accumulation and reduction of evaporative cooling in surface waters; weak winds and little mixing have been implicated in bleaching events (see review in Glynn 1993; Skirving and Guinotte 2001). However, the cross-shore structure of the temperature gradient in 2010

might be the result of other processes. Specifically, we speculate that the cool water eddy observed in late May might have influenced surface temperatures in the offshore reef, Abu Madafi (Fig. 6), but it is unlikely to have influenced the SSTs near the mid and inner reefs. The eddy persisted at least through late June but dissipated or moved away from the site by early August (results not presented).

The positive relationship between increased temperature and bleaching and mortality at the cross-shore scale (Furby et al. 2013; this study), however, does not hold at the across-the-reef scale (Fig. 11). Within Tahala, mortality of *S. pistillata* was modest on the protected side, which features the largest temperature fluctuations and maxima, yet mortality was extreme at the exposed side, with milder thermal conditions (Figs. 2, 4; Davis et al. 2011). Coral bleaching and mass mortality of many coral taxa on the exposed side extended to depth (5–15 m, Furby et al. 2013; J. Pineda pers. obs. for depths up to 5 m).

Interactions between physical factors and the coral holobiont operating characteristically at two scales might explain the observed patterns in mortality. First, an offshore-to-inshore increase in SST, with temperatures exceeding the thermal tolerance of the *S. pistillata* holobiont, might have determined the cross-shore patterns in bleaching and mortality; it is well known that anomalously elevated temperatures result in coral bleaching (reviews in Glynn 1993; Hoegh-Guldberg 1999; Jokiel 2004). Second, a previous biological adaptation or acclimatization to high-frequency, small-scale physical variability might have accounted for the patterns at the across-the-reef scale, where *S. pistillata* at the most extreme thermal habitat, the protected site, suffered less mortality than at the relatively thermally milder exposed environment

Processes that create refugia to thermally induced bleaching events at the 300 m and at the 20 km scales

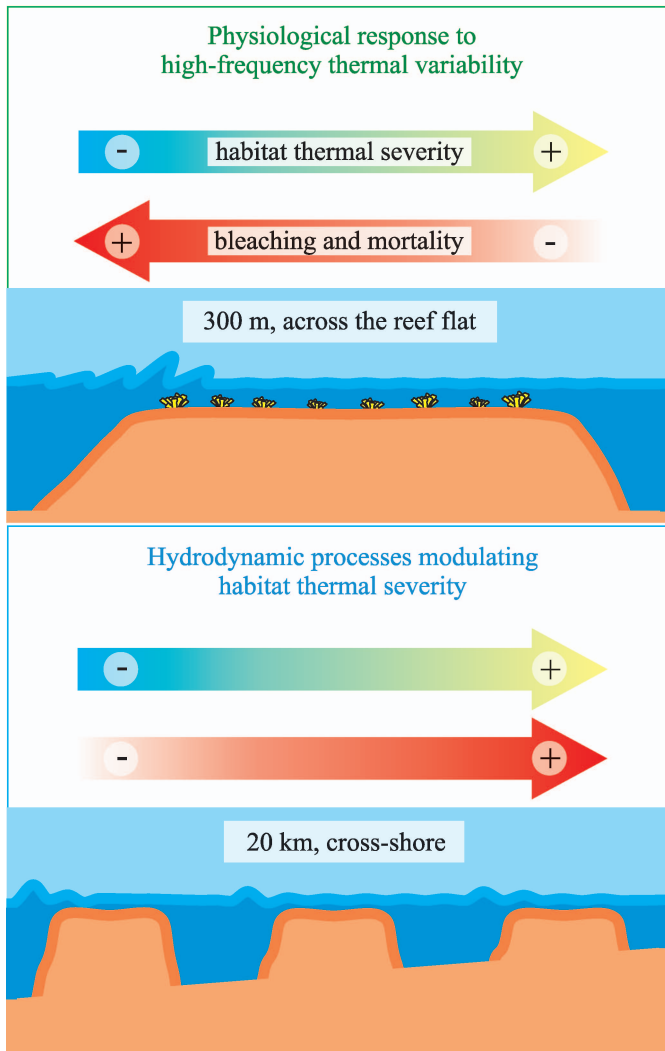


Fig. 11. Hypotheses of types of processes that create refugia to thermally induced bleaching events at the diurnal, ~ 300 m scale, and the seasonal, ~ 20 km scale, and schematic representation of the relationships between habitat thermal severity and coral bleaching and mortality at the two scales.

(Figs. 9–11). Recent experimental studies suggest that corals in habitats with high-frequency thermal variability have distinct physiology and elevated thermal tolerance relative to nearby sites with smaller fluctuations (Barshis et al. 2010; Oliver and Palumbi 2011). Furthermore, a minor bleaching event at Palmyra Atoll had fewer effects on corals in habitats with larger temperature variability and a higher mean than in relatively less extreme habitats, although habitat depth differed (Williams et al. 2010). Finally, an apparent regional increase in SST off southern Belize over the last 30 yr correlated with a decrease in skeletal growth rates in *Siderastrea siderea* in offshore exposed reefs, but growth rates did not change in more variable nearshore thermal environments (Castillo et al. 2012).

The response of corals to thermal stress can be mediated by *Symbiodinium* symbiont type (Rowan 2004), by host

genotype, and by acclimatization (Barshis et al. 2010; Oliver and Palumbi 2011). Both symbionts and hosts can adapt locally to stressful thermal conditions, and adaptation has been found at small spatial scales. For example, *Symbiodinium* C1 can adapt to different thermal environments, and this adaptation has been shown to contribute to the performance of the coral host (Howells et al. 2012). *Porites lobata* colonies in thermally variable back reef environments were physiologically more tolerant than corals in less variable fore reef environments (Barshis et al. 2010). Furthermore, Barshis et al. (2010) found a strong genotypic component in explaining the tolerance to stressful back reef conditions, with a weaker phenotypic response. In a recent study on coral physiology at our study sites, A. Tarrant et al. (unpubl.) found no clear patterns in the spatial distribution of Red Sea *S. pistillata* symbionts cross-shore, from outer to inner reefs, or across the reef. All corals had subclade A1, with some also containing subclade C3. Moreover, ribosomal deoxyribonucleic acid sequences of *S. pistillata* ITS1 region from our study sites did not show evidence of genetic structure, although the study by A. Tarrant et al. (unpubl.) was not intended for elucidating fine genetic structure within the host populations. Future studies investigating the genotypic and phenotypic expressions of corals in response to the environmental gradients addressed in the present study might reveal the underlying mechanisms of resistance to bleaching events and their thresholds.

Thus, we speculate that differences in mortality across the reef in the Thuwal area might be related to differences in host or symbiont physiology adapted to a high-frequency fluctuating thermal environment, which could be due to acclimation or fine-scale genetic variation. Symbionts and hosts in the protected, thermally stressful environments might have been preadapted and escaped mortality in the bleaching event, which is consistent with the experimental results of Oliver and Palumbi (2011) that suggest that corals in fluctuating thermal environments are more tolerant of thermal stress than corals in relatively more stable thermal environments.

Coral recruitment can be dependent on adult density and fecundity (Hughes et al. 2000), and we speculate that recruitment at the exposed side of the inner reef was affected by the extreme mortality of the local population. *S. pistillata* is a brooder, releasing planula larvae that settle only 1–2 days after reproduction (Shlesinger and Loya 1985, for the northern Red Sea). Our coarse estimates of recruitment in October 2011, about 1 yr after the bleaching event, indicate lowest recruitment at the site with the most severe mortality, the exposed side of the inner reef, where recruitment was also low in mid 2012. Larvae dispersing from offshore reefs to the inner reefs might be rare. The protected inner reef, where mortality was less severe, had relatively higher recruitment in 2011 and 2012, whereas the mid and outer reefs had the largest recruitment in 2011 and 2012. Although we did not measure recruitment before the bleaching event, and little recruitment could be the result of poor survivorship of the coral settlers at the Tahala exposed site, the decimation of the local population at the exposed inner reef site might have resulted in a reduction of larval supply, settlement, and recruitment.

Reefs feature dramatic community structure differences among reef zones. Differences in environmental conditions, such as temperature fluctuations demonstrated here between exposed and protected sites, likely contribute to the resultant community compositions. Species such as *S. pistillata* that experience these within-reef environmental gradients are ideal models to explore how organisms handle sublethal stresses created by these gradients. Sublethal stresses might affect reproductive output in corals (Baird and Marshall 2002), although it is not well known how these stresses subsequently affect associated reef fauna. Persistent, low levels of stresses or disturbances could have long-term implications on overall reef community structure (Berumen and Pratchett 2006). Understanding how environmental forcing, with characteristic disturbance and stress regimes, shapes reef communities requires continued study of phenomena such as the mortality event captured here.

In conclusion, we found that *S. pistillata* corals in the mildest and in the most extreme thermal environments escaped mortality in a widespread bleaching event (Fig. 11; Furby et al. 2013). Coral reefs in the Thuwal area experience predictable seasonal and diurnal temperature variability. The seasonal range in 2010 low-passed temperature was about 9.5°C in the inner reef, which was 2.5°C greater than in the outer reef. Summer temperatures in 2010 were 1°C higher than in 2009 at the inner and mid reefs. Superimposed on seasonal variability, diurnal temperature variability ranged from negligible to up to 6.5°C, with the largest diurnal variability in the summer. *S. pistillata* corals subjected to the most extreme seasonal and diurnal temperature variability and upper temperature maxima survived, but most of those exposed to subextreme variability and slightly smaller temperature ranges perished. Our results further suggest the hypothesis that predictable high-frequency temperature variability predominate in generating genotypes and phenotypes that can resist anomalous high-temperature events leading to bleaching and mortality. Understanding how high-frequency thermal variability enables the coral holobiont to escape bleaching characteristically associated with anomalously high temperatures and the spatial scales of coral bleaching and their relationship to the hydrodynamic processes that create predictable patterns in temperature at a variety of scales might offer clues for identifying refuges to thermal bleaching, a severe threat for contemporary coral reefs.

Finally, our results indicate that both cross-shore seasonal and across-reef diurnal physical processes play a role in the thermal ecology of coral holobionts and bleaching. A correspondence exists between the spatial and temporal scales of physical oceanic processes (Stommel 1963). For example, physical processes with small spatial scales generally have short temporal scales. Many have speculated that some biological variables follow similar trends and have argued that larger scale physical processes are the most important in determining biological patterns because larger scale processes explain most of the variability in biological variables (Haury et al. 1978). In our study system, we found that both across-the reef 300 m and cross-shore 20 km scales were important in producing

spatial patterns of coral mortality, with the potential for long-term effects on the community structure of the entire reef. A caveat in our study is that conclusions at the cross-shore scale are based on only one sample of inner, mid, and outer reefs. On the other hand, Furby et al. (2013) documented similar patterns of bleaching and mortality at the cross-shore scale on the exposed sides of other reefs, suggesting that the cross-shore patterns in bleaching and mortality we report might not be singular. High-frequency diurnal fluctuations were superimposed on the peak of the seasonal cycle, and these fluctuations might have been superimposed on the elevated surface water temperature trend that caused widespread bleaching in the central Saudi Arabian Red Sea and south Asia. Biological acclimation and adaptation to small-scale, high-frequency thermal variability might influence coral reef flat community response to climate change. The effects of temperature extremes on coral reefs might not necessarily scale up in a way that would allow us to predict large-scale patterns of coral bleaching from climate change (i.e., more moderate temperature at the 20 km scale had the opposite trend with mortality than on the 300 m scale). Therefore, predicting coral bleaching might require a more sophisticated understanding of how temperature varies at a variety of temporal and spatial scales, as well as an appreciation of the “interactive effects” from biology (e.g., coral holobiont acclimation and adaptation). In the face of anthropogenic climate change, some have suggested that protecting mild habitats may offer cool refuges to corals during warming events (West and Salm 2003), and a recent review identified stress-resistant coral species and symbionts and large annual temperature variability as the three most important factors in promoting coral resilience against anthropogenic climate change (McClanahan et al. 2012). Experimental studies and the results presented here suggest that protecting corals living in extreme thermal habitats with large diurnal fluctuations might preserve resilient shallow-water coral holobionts. Protecting these corals could be challenging because their shallow water habitats are some of the most vulnerable to human activities and development.

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