

A coral reef refuge in the Red Sea

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Abstract

The stability and persistence of coral reefs in the decades to come is uncertain due to global warming and repeated bleaching events that will lead to reduced resilience of these ecological and socio-economically important ecosystems. Identifying key refugia is potentially important for future conservation actions. We suggest that the Gulf of Aqaba (GoA) (Red Sea) may serve as a reef refugium due to a unique suite of environmental conditions. Our hypothesis is based on experimental detection of an exceptionally high bleaching threshold of northern Red Sea corals and on the potential dispersal of coral planulae larvae through a selective thermal barrier estimated using an ocean model. We propose that millennia of natural selection in the form of a thermal barrier at the southernmost end of the Red Sea have selected coral genotypes that are less susceptible to thermal stress in the northern Red Sea, delaying bleaching events in the GoA by at least a century.

Keywords: climate change, coral bleaching, coral reefs, Gulf of Aqaba, Red Sea

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Introduction

Coral reefs, Earth's richest and most diverse ecosystem, are deteriorating rapidly (De'ath *et al.*, 2012) with the possibility that stony corals will no longer dominate reefs (Hoegh-Guldberg *et al.*, 2007) by 2100. This may have severe ecological and socio-economical consequences as the recovery from such a state might be slow and prolonged. Among the causes, ocean acidification and global warming are often considered the most critical issues. The latter, already affecting coral reefs world-wide, is manifested as mass coral bleaching events.

Observational and experimental evidence (Hoegh-Guldberg, 1999) indicates that corals bleach when ambient water temperatures exceed the local summer maximum by 0.5–1.5 °C (hereafter 'bleaching rule'). During bleaching the symbiosis between the coral host and its *Symbiodinium* dinoflagellates (zooxanthellae) weaken, resulting in the loss of the coral's main energy source and in deceleration of calcification. As this symbiosis with *Symbiodinium* allowed for the prosperity of coral reefs in tropical, oligotrophic waters over a long geological history, an increase in the prevalence of bleaching events is alarming.

Susceptibility of coral reefs to and recovery from bleaching events is hitherto unclear (Brown & Cossins,

2011). Repetitive exposures to thermal stress were suggested as one of the mechanisms leading to increased tolerance (Brown *et al.*, 2002; Van Woesik *et al.*, 2012; Barshis *et al.*, 2013). Corals occupying areas with variable conditions are also reported to have a higher thermal resistance (McClanahan *et al.*, 2007; Guest *et al.*, 2012) and lower sensitivity to bleaching (Oliver & Palumbi, 2011). Overall, the sensitivity/resilience of corals to bleaching is species specific (Marshall & Baird, 2000) and depends on the coral host, its symbionts (Rowan, 2004; Berkelmans & Van Oppen, 2006) and their acclimatization history (Oliver & Palumbi, 2011). Recent advances in genomic techniques explain the inherent thermal resilience of corals in their ability to express or shut down an array of heat stress-related genes (Desalvo *et al.*, 2010; Barshis *et al.*, 2013; Granados-Cifuentes *et al.*, 2013) these in turn, up or down-regulate expression of cellular mechanism such as heat shock proteins (Leggat *et al.*, 2011), programmed cell death (Kvitt *et al.*, 2011), and antioxidant enzymes (Granados-Cifuentes *et al.*, 2013) which determine the physiological capacity to withstand heat stress. Yet, the general perception is that given the current trends of global warming, an increase in intensity and frequency of mass bleaching events are inevitable and will threaten some of the world's richest reefs.

Rinkevich (2005) highlighted the need to conserve the gene pool of reef building corals for possible future reseeded of lost reef areas. Conserving coral gene pool is motivating both *in vitro* (Hagedorn *et al.*, 2012) and

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in situ (Horoszowski-Fridman *et al.*, 2011) actions, including 'Assisted Colonization', that is, transplantation of corals to identified 'refugia' (Hoegh-Guldberg *et al.*, 2008) but see (Howells *et al.*, 2013). Here, we propose that the Gulf of Aqaba (GoA), northern Red Sea, is a natural refugium due to its latitudinal location, topography, oceanography, and especially its recent geological history.

More than three decades after the first reported mass bleaching event, coral reefs in the GoA have remained bleaching-free, even when sea surface temperatures exceeded the local average summer maximum by 2.0 °C as in 2010 and 2012. This cannot be explained by the high latitude of the GoA (28–29.5°N) alone, since severe bleaching events have also been reported from high latitude (Debose *et al.*, 2013) and the world's southernmost reefs (32.0°S) (Dalton & Carroll, 2011; Harrison *et al.*, 2011). Similarly, it cannot be explained by repetitive exposures to increased or variable temperature. During the 1997–1998 and 2010 world-wide bleaching events, many areas in the Gulf of Aden, outside the Red Sea, were affected by bleaching (Kotb *et al.*, 2004), while within the Red Sea the bleaching was limited to some shallow-water reefs near Eritrea and Yemen where seawater temperature exceeded 38 °C (Kotb *et al.*, 2004).

In this study, we present a plausible explanation to why corals inhabiting the reefs of the GoA do not follow the 'bleaching rule'. We hypothesize that a selection process, occurring over the last few millennia at the straits of Bab el Mandeb (southern Red Sea) and the southern Red Sea, favors thermally resistant coral genomes. When these corals disperse northward and settle in cooler water of the GoA, they live much below their bleaching threshold.

Material and methods

Laboratory experiments

This study was performed at the Interuniversity Institute for Marine Science (IUI, Eilat, Red Sea, Israel; 29°30'N, 34°56'E). The sensitivity of GoA corals to high temperatures was tested with the following five common species, all known to bleach in Indo-Pacific reefs (Pandolfi *et al.* 2011): the branching *Stylophora pistillata*, *Pocillopora damicornis*, and *Acropora eurystoma* and the massive *Favia fava* and *Porites* sp. The corals were collected at 3–5 m depth in front of the IUI, fragmented, and allowed to recover and acclimate at ambient temperature for 3 weeks before the onset of the experiment. Incubation took place in 25 5-l aquaria (5 per species, 5 fragments per aquarium) with running seawater (water replacement rate of 2 h⁻¹). Heaters and chillers were used to control temperature and data loggers were used to record temperature fluctuations in the aquaria.

Incubation experiments were conducted in winter (February) and summer (August) 2010 when the average seawater temperatures were 22.5 and 27.2 °C, respectively. Light intensity was adjusted using a shade cloth to match light levels at the collection depth (mid-day levels of 500–750 and 750–1200 $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$ in February and August, respectively).

Corals were incubated for 4 weeks in water temperatures of up to 33 °C, ca. 6 °C warmer than the average summer maximum. We define summer maximum as the multi-annual (1988–2012) average sea surface temperature (SST) for the summer period (July–September, = 26.1 °C).

Temperature was raised 1 °C per 72 h and corals were sampled ($n = 4$) at five sampling points along the temperature gradient (23, 26, 28, 30, and 33 °C in February; 26, 29, 32, 33, and 34 °C in August). The remaining five fragments per species were incubated for additional 3–4 weeks at the highest temperature and observed for signs of bleaching.

Biological examination included quantification of zooxanthellae and chlorophyll concentration per cell. Zooxanthellae cell counts were normalized to coral tissue biomass (total protein content) and chlorophyll concentration was calculated per zooxanthella cell (Krief *et al.*, 2010).

The photosynthetic capacity of symbiotic dinoflagellates in the examined species were examined using an imaging pulse amplitude modulated fluorometer (I-PAM, Walz GmbH, Effeltrich, Germany) at every sampling point on the fragments that were later sacrificed for zooxanthellae counts and chlorophyll concentration measurement. A rapid light curve (RLC) was performed to measure changes in F_v/F_m following the incubation in elevated temperature. Measurements of maximal quantum yield were performed following a 20 min dark acclimation.

Warming trends and bleaching prediction

Warming trends were calculated for the warmest month in each region: August in the GoA, September in the southern Red Sea, and June in the Gulf of Aden. SST data for the northern GoA were obtained from measurements made since 1988 once a day between 08:00 hours and 09:00 hours (local time) at the Eilat Coral Reef Nature Reserve at a fixed point, ca. 10 m seaward of the reef flat, using a standard 'bucket thermometer' (± 0.05 °C precision) lowered to the water from the pier of the Underwater Coral Observatory Park. SST for non-working days (weekends and holidays) was calculated based on interpolation between the two proximal measurements. Daily SST anomalies were calculated for the summer period (July–September) of each year as the deviation of the daily SST from the long-term (1988–2012) average of those 3 months (26.1 °C).

Sea surface temperature data for the Red Sea and the Gulf of Aden were obtained from the world-wide coastal warming assessment webpage (Lima & Wetthey, 2012). Four sites in each location were selected and the average warming trend of the warmest month in each region was calculated (°C per decade). We then extracted the predicted maximum SST in 2030, 2050 and 2100.

Larval dispersal modeling

Using an ocean model [MITgcm (Marshall *et al.*, 1997a, b)] adapted to the Red Sea (Biton *et al.*, 2008, 2010), we evaluated the spatial extent of the dispersal of larvae entering the Red Sea from the south. The model domain included the entire Red Sea area and the northern Gulf of Aden, extending to 45°E. The bathymetry in our model is based on 2 min Worldwide Bathymetry/Topography dataset (ETOPO2) (ETOPO2 data are available at <http://www.ngdc.noaa.gov/mgg/bathymetry/relief.html>.) A full surface mixed layer scheme, referred to in the literature as the K-Profile Parameterization scheme, is employed (Large *et al.*, 1994). The spatial resolution was 2' across the Red Sea and 5' along its main axis. The water column is resolved by 13 levels in the vertical, with seven of these layers concentrated in the upper 200 m to capture the complex dynamics of the upper ocean.

To simulate the present-day conditions, at the surface we impose monthly average climatological atmospheric data, including surface zonal and meridional wind vector components, surface air temperature, specific humidity, precipitation, incoming short-wave and long-wave radiation, all based on Da Silva *et al.* (1994). Evaporation and surface turbulent flux components such as latent heat, sensible heat, and wind stress were calculated by the model based on the applied atmospheric data and used the methodology described in Large & Pond (1981, 1982). Overall, the model results for the present-day Red Sea reproduce rather well the main features of circulation and hydrography of the Red Sea, including the surface circulation and the exchange flux at the Strait of Bab el Mandab (Biton *et al.*, 2008, Supplementary Information).

To simulate the circulation during the Holocene, we conduct a series of experiments designed to investigate the sensitivity of the Red Sea to sea level and atmospheric changes (that are plausible for the Holocene), as detailed in Biton *et al.* (2010). Model results for the early Holocene (a relatively humid period) and late Holocene (a relatively dry period) were compared with available proxy records from the Red Sea, and show good correspondence (Biton *et al.*, 2010). For our simulation described below, we used the model results for the early Holocene. More details on the model configuration can be found in Biton *et al.* (2008, 2010).

One thousand coral planula larva-like virtual particles were seeded on the sea surface at the entrance to the Red Sea and then tracked as they were passively advected by the model climatological currents. Since reef building corals in the Red Sea are asynchronous (Shlesinger & Loya, 1985) with some reproducing over winter and spring while others reproduce in summer, simulations were run for both February and August and we examined their position after 1–4 weeks. In the Red Sea, the majority of corals are hermaphroditic, gamete-releasing species. Among the studied GoA species, *S. pistillata* is a winter to summer planulating species, *A. eurystoma*, *P. damicornis* and *F. favus* and *Porites* sp. are summer spawners and it is likely that in the Gulf of Aden these species release their propagules in the same season (Bauman *et al.*, 2011).

Statistical analysis

The effect of temperature on chlorophyll concentration was analyzed separately for each species, using a one-way analysis of variance (ANOVA).

For analyses of chlorophyll fluorescence, one-way ANOVA and Tukey's post hoc multiple comparison tests were performed to detect significant differences over data points and between treatments (temperature, SPSS).

Kolmogorov–Smirnov normality test and Levene's homogeneity of variance test were used to identify whether the assumptions of the parametric ANOVAs were satisfied. Arcsine transformations were used where these assumptions were not met. Unless otherwise specified, mean values are presented \pm SD.

Results

Temperature record and warming trend in the GoA

Temperature summer maxima in the GoA have been rising over the last 24 years at a rate of 0.034 °C yr⁻¹ (Fig 1a) with average temperatures in August rising at an annual rate of 0.04 °C (pier measurements) to 0.05 °C (www.coastalwarming.com). February, the coldest month, has warmed by 0.028 °C yr⁻¹. At the present rate, seawater temperature in the GoA by the end of this century may exceed 31.5 °C, which is 2–2.5 °C above the expected bleaching threshold for this region (based on the local mean summer maxima). Temperature records indicate an increasing frequency of excursions from summer (July to September) maxima average (Fig 1b). In both 2007 and 2012 for example, over 12 days were 2–2.7 °C warmer than average summer maxima.

Thermal stress of GoA corals

None of the incubated corals showed any visual signs of bleaching in spite of the fact that mass bleaching conditions are generally formed at +1.5–2 °C over average summer maxima. Only at 34 °C (7 °C above summer maximum) did *S. pistillata*, *P. damicornis* and *A. eurystoma* have an average reduction of 25 \pm 3.5, 35 \pm 5.2, and 45 \pm 2.1% in zooxanthellae density, respectively. Massive corals *Porites* sp. and *F. favus* were less affected with zooxanthellae average loss of 13 \pm 3.6 and 18 \pm 3.1%, respectively.

No significant difference was detected in chlorophyll concentration per host cell between all temperature treatments ($P > 0.05$, $n = 20$). This pattern was recorded in all five species.

Chlorophyll fluorescence of the five examined coral species revealed a species-specific response to elevated temperature, as evident from both changes in

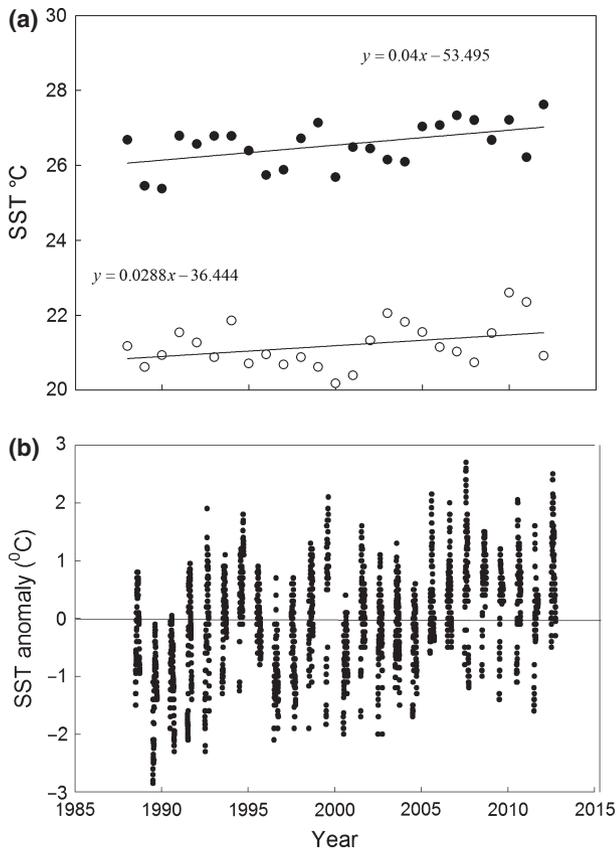


Fig. 1 (a) A 25-year (1988–2013) temperature record and regression line for August (black) and February (blank) in the northern Gulf of Aqaba, demonstrating a sharper temperature rise in the warmest month. (b) Anomalies from average summer (July, August, and September) temperatures over the last 25 years. Each data point designates one day.

dark-adapted F_v/F_m (maximal yield) and a RLC (Fig. 2). At the beginning of the incubation period, F_v/F_m was similar between species. No significant difference in dark-adapted F_v/F_m was recorded between species at temperatures between 26 and 32 °C ($P > 0.05$, $n = 5$). A 12–15% drop in dark-adapted F_v/F_m was recorded at 34 °C, except for *S. pistillata* which did not show a significant decrease ($P > 0.05$, $n = 5$). More pronounced changes in photosynthetic performance were evident along the RLC with distinct species-specific response (Fig. 2). While the variable fluorescence at 34 °C was consistently lower than that under the lower temperature treatments ($P < 0.01$), in all coral species (Tukey's post hoc comparisons), *S. pistillata*, *Acropora euristoma*, and *Favia fava* showed a significantly greater response (lower Yield, $P < 0.01$) than *Pocillopora damicornis* and *Porites* sp. No significant difference in variable fluorescence was detected between temperature treatments 26 °C, 29 °C, and 32 °C ($P > 0.05$) for all species.

Larval dispersal simulations

Simulations were run for both February and August and we examined the larvae position after 2 and 4 weeks. In both cases, the larvae remain within the warm (>32 °C) region of the southern Red Sea (Fig. 3a, b), indicating that the ancestors of corals that eventually colonized the northern Red Sea and GoA had to survive to reproduction age (≥ 1 year) in water that was >5 °C warmer than the maximum found at present in the GoA.

Discussion

Clearly, common GoA corals do not follow the global 'bleaching rule' (Table 1). Thermal tolerance of a coral is often considered dependent on the *Symbiodinium* type it hosts (Lajeunesse *et al.*, 2010). This cannot explain the thermal resistance of the corals in this study as most corals in the GoA host clade A and the widely distributed clade C (Karako-Lampert *et al.*, 2004; Byler *et al.*, 2013), both known to be relatively sensitive to thermal-driven stress. The heat-tolerant *Symbiodinium* clade D was never recorded in the GoA examined species.

We propose that the exceptional thermal resistance of GoA corals is the outcome of the unique geography and topography of the Red Sea. This elongated sea (ca. 2000 km, 12.5–29.5°N) is connected to the open ocean via a narrow, shallow (137 m) strait at its southernmost end (Bab el Mandeb). Consequently, during the last glacial maximum, when global sea level dropped ca. 120 m below present sea level (Peltier, 1994, 2004), the Red Sea became nearly disconnected from the open ocean leading to a dramatic increase in salinity (Hemleben *et al.*, 1996; Rohling *et al.*, 1998; Fenton *et al.*, 2000; Siddall *et al.*, 2003) and local decimation of corals (Braithwaite, 1987) and plankton (Fenton *et al.*, 2000). Reestablishment of coral reefs started after sea level returned to within 20 m of the present level, around 8 kyr before present (Braithwaite, 1987). As the only possible source of coral larvae for recolonization was the Gulf of Aden, each coral larva entering the Red Sea had to pass through the exceedingly warm waters (>32 °C in summer) in the entrance to the Red Sea. The palaeoceanographic conditions in the northern and central Red Sea were similar to present day or warmer at the time corals started to recolonize the Red Sea 6–7 kyr before present (Trommer *et al.*, 2010). Since the duration of the corals' planktonic larval stage is in the order of days to weeks (Cetina-Heredia & Connolly, 2011), and since it takes >1 year for recently settled corals to start reproducing, the colonization of the northern Red Sea and GoA must have occurred via stepping

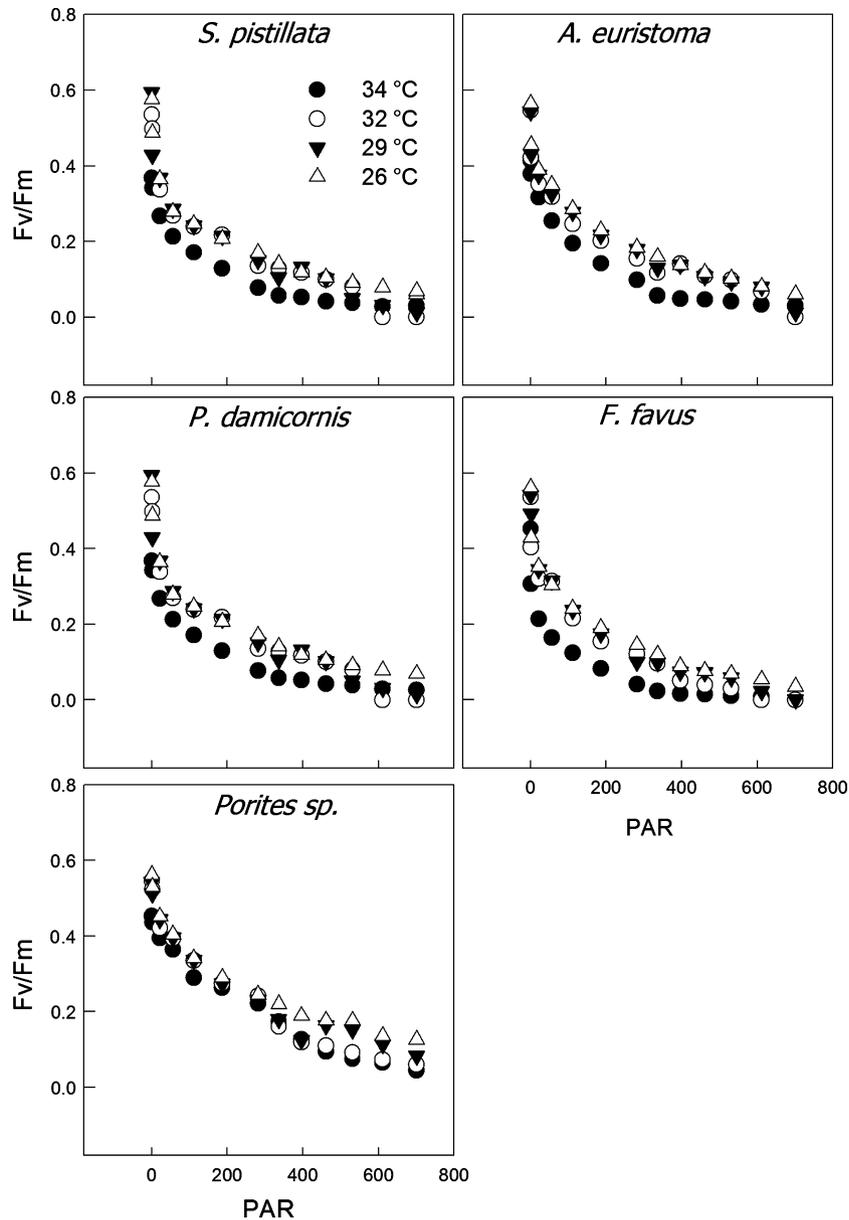


Fig. 2 Rapid light curve of the five examined species in four temperature treatments. The F_v/F_m per light intensity at a given temperature is indicative of the sensitivity of the PSII to increased irradiance as temperature increases.

stones, whereby larvae reached some distance into the Red Sea, settled, grew, released larvae, and so on.

At present, the exchange flow between the Red Sea and the Gulf of Aden changes from a two-layer exchange in winter (with inflow into the Red Sea at the surface) to a three-layer exchange in summer (with surface outflow from the Red Sea into the Gulf of Aden (Murray & Johns, 1997; Siddall *et al.*, 2002; Smeed, 2004; Sofianos *et al.*, 2002). Simulation for various stages during the Holocene (Biton *et al.*, 2010) suggest that the two-layer exchange pattern prevailed throughout the year with stronger inflow into the Red Sea in winter.

Therefore, the simulation for February (Fig. 3) represents an upper bound to the northward reach of larvae.

We propose that the southern Red Sea served as a selective barrier for heat-tolerant coral host genotypes. Based on the aforementioned 'bleaching rule', corals in the GoA should start bleaching when water temperature reaches 32.5 °C (summer maximum in the southern Red Sea +0.5–1.5 °C). Hence, under the present local warming rate (ca. 0.04 °C yr⁻¹), no mass bleaching should be expected in GoA reefs in the next 100 years. Summer temperatures in the central Red Sea often exceeds 32 °C, primarily in shallow water.

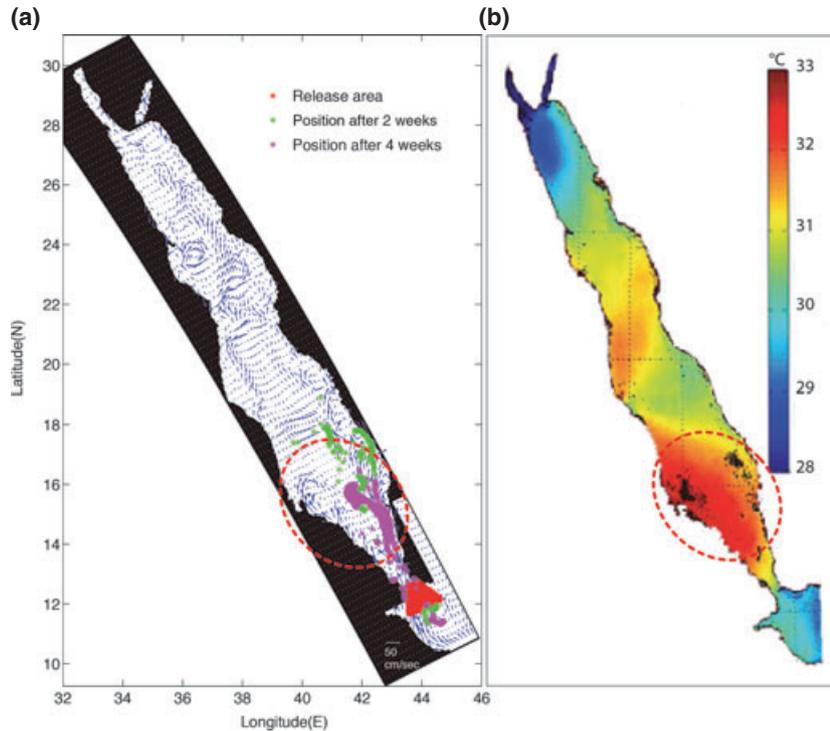


Fig. 3 (a) Model of northward dispersal of coral planula larvae ($N = 1000$), after release in the Bab el Mandab Straits in February (when the maximal northward penetration is expected). (b) Red Sea summer temperatures demonstrating the sharp latitudinal temperature gradient between the warm southern section of the Red Sea and cooler water in the Gulf of Aqaba. Dashed red circle indicates the 'warm barrier' in the southern Red Sea.

Table 1 Thermal tolerance experiments in the Gulf of Aqaba. Results of the incubation experiments, presenting the absence of bleaching at up to 7 °C above summer maximum and changes in the density of symbiotic dinoflagellates at the maximum temperature examined

Species, (<i>Symbiodinium</i> clade)	Incubation temperature/period	°C above summer maxima	Bleaching signs	% change <i>Symbiodinium</i> density	Source
<i>Stylophora pistillata</i> , (A)	31/3 weeks	4	None	ND	(Winters <i>et al.</i> , 2006)
	34/4 weeks	7	None	-25 ± 3.5	Present study
<i>Pocillopora damicornis</i> , (C)	31/3 weeks	4	None	N.D.	(Winters <i>et al.</i> , 2006)
	34/4 weeks	7	None	-35 ± 5.2	Present study
<i>Favia fava</i> , (C)	31/3 weeks	4	None	ND	Present study
	34/4 weeks	7	None	-18 ± 3.1	Present study
<i>Acropora eurystoma</i> , (C)	34/3 weeks	7	None	-45 ± 2.1	Present study
<i>Porites</i> sp. (C)	34/4 weeks	7	None	-13 ± 3.6	Present study

Although corals in that region are well acclimatized to warm seawater temperature, they live close to their bleaching threshold and occasionally bleach (records from 2007 and 2010) when this threshold is crossed (Furby *et al.*, 2013). We argue GoA corals are of the same origin but live way below their bleaching threshold.

While this hypothesis is yet to be validated by genetic markers, there are other supporting arguments. The

measured slow growth rate (linear extension) of corals in the GoA, half that of corals in the northern Red Sea and a fifth to an order of magnitude slower than in the southern Red Sea, suggests that corals originating in warmer waters of the Red Sea grow much slower in suboptimal cooler environments of the GoA. While coral growth in the central and southern sections of the Red Sea may decrease with warming (Cantin *et al.*, 2010), an increase in the linear extension of *Porites*

corals was recorded in the GoA beginning in the 1980s (Heiss, 1996). If so, warming of the northern Red Sea may promote reef building coral growth rate, and thus offset reduced coral calcification due to ocean acidification (Silverman *et al.*, 2009). At the same time, it is important to note that coral sensitivity to thermal stress may be increased by ocean acidification (Anthony *et al.*, 2008).

The predicted bleaching threshold at the latitudinal range of the northern GoA, as recorded for high-latitude reefs (Dalton & Carroll, 2011; Fig. 4), is 27 °C. However, the actual bleaching threshold is at least 5 °C higher. Considering the rate of warming in the region, by the time the Gulf of Aden and southern Red Sea reefs (as well as many other indo-pacific reefs) will cross their threshold and experience temperatures above 35 °C in 2100, corals in the GoA will still be experiencing maximum summer temperatures below 31 °C, which is under their bleaching threshold.

These findings call for special efforts to protect this exceptional refuge from anthropogenic damage, such as pollution, eutrophication, and breakage. Hoegh-Guldberg *et al.* (2008) suggested *in situ* 'Assisted Colonization', that is, transplantation of thermally resistant low-latitude corals to 'refugia' in higher latitudes where they will grow in waters far colder than their bleaching threshold. Recently, Howells *et al.* (2013) doubted the feasibility of the Assisted Colonization idea on the basis of experimental evidence, demonstrating that corals and their symbiotic *Symbiodinium* are also limited by a lower thermal limit (Howells *et al.*, 2013). The deep,

narrow GoA and relatively warm deep water temperature prevents from surface water of the gulf to drop below 20 °C. To date, no cold weather bleaching was observed in the GoA, suggesting that the corals and their symbionts have well acclimatized to these winter temperatures. We suggest that colonization of coral propagules, originating in warm areas and settling in high-latitude cooler waters of the GoA for millennia, provides a 'natural proof' of the concept that the coral symbioses is pre-adapted (and conservative) to their historical thermal limits. Coral thermal tolerance may be the result of a resilient coral host, symbiotic dinoflagellates (Berkelmans & Van Oppen, 2006) or associated microorganisms (Bayer *et al.*, 2013). It may also be the resilience of a particular combination (holobiont). Environmental change leading to changes in holobiont composition may compromise thermal tolerance (Zilber-Rosenberg & Rosenberg, 2008). Future research should focus on identifying the source of thermal resistance in the GoA at the genetic level; the *Symbiodinium*, associated microorganisms, the coral host population or a combination of all.

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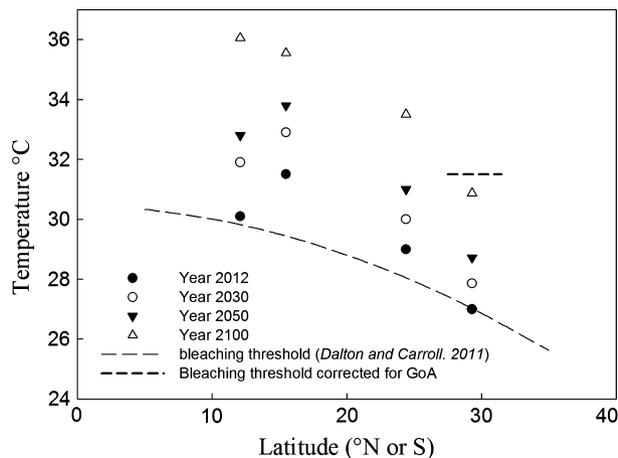


Fig. 4 Estimates of thermal bleaching threshold by latitude (Dalton & Carroll, 2011; polynomial curve) on which present and future Red Sea SST were plotted. SST predictions are for the warmest month in each region, demonstrating that although present-day temperatures in the Gulf of Aqaba are already crossing the predicted local bleaching threshold, the actual bleaching threshold (thick dashed line), experimentally identified, will not be crossed even by 2100.

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