Discrete Pulses of Cooler Deep Water Can Decelerate Coral Bleaching During Thermal Stress: Implications for Artificial Upwelling During Heat Stress Events

Yvonne Sawall[1]*, Moronke Harris[1], Mario Lebrato[2], Marlene Wall[3] and Ellias Yuming Feng[3]*

[1] Marine Benthic Ecology and Ecophysiology (MABEE) Lab, Bermuda Institute of Ocean Sciences, St. George's, Bermuda, [2] Bazaruto Center for Scientific Studies, Benguerra Island, Mozambique, [3] GEOMAR Helmholtz Centre for Ocean Research Kiel, Kiel, Germany

Global warming is considered to be the most severe threat to coral reefs globally, which makes it important for scientists to develop novel strategies that mitigate the impact of warming on corals and associated habitats. Artificial upwelling of cooler deep water to the surface layer may be a possible mitigation/management tool. In this study, we investigated the effect of simulated artificial upwelling with deep water off Bermuda collected at 50 m (24°C) and 100 m (20°C) on coral symbiont biology of 3 coral species (*Montastrea cavernosa*, *Porites astreoides*, and *Pseudodiploria strigosa*) in a temperature stress experiment. The following treatments were applied over a period of 3 weeks: (i) control at 28°C (ii) heat at 31°C, (iii) heat at 31°C+ deep water from 50 m depth, and (iv) heat at 31°C+ deep water from 100 m depth. Artificial upwelling was simulated over a period of 25 min on a daily basis resulting in a reduction of temperature for 2 h per day and the following degree-heating-weeks: 5.7°C-weeks for ii, 4.6°C-weeks for iii and 4.2°C-weeks for iv. Comparative analysis of photosynthetic rate, chlorophyll-*a* concentration and zooxanthellae density revealed a reduction of heat stress responses in artificial upwelling treatments in 2 of the 3 investigated species, and a stronger positive effect of 100-m water than 50-m water. These results indicate that artificial upwelling could be an effective strategy to mitigate coral bleaching during heat stress events allowing corals to adjust to increasing temperatures more gradually. It will still be necessary to further explore the ecological benefits as well as potential ecosystem impacts associated with different artificial upwelling scenarios to carefully implement an effective *in situ* artificial upwelling strategy in coral reefs.

Keywords: coral bleaching, bleaching mitigation, artificial upwelling, pulsed upwelling, global warming, sea surface temperature rise, heat waves

INTRODUCTION

Global warming is the most severe threat to coral reefs worldwide (Hughes et al., 2017; Gattuso et al., 2018), since most reef-building corals are highly susceptible to abnormally high sea surface temperatures (SSTs). This is evident in coral bleaching, the loss of the coral's symbiotic algae (zooxanthellae) inside the coral tissue, occurring during periods of increased SST in the form of heat waves over weeks to months (Brown, 1997; Weis, 2008). Temperature-sensitive species can die quickly when exposed to heat stress (few weeks; Jones, 2008; Hughes et al., 2018b), while others die as a lack of energy through photosynthesis, if deprived of their symbiotic algae for too long (weeks to months; Grottoli et al., 2006). To date, the most devastating coral bleaching event on record occurred from 2014 to 2017 affecting numerous coral reefs worldwide (Heron et al., 2017; NOAA Coral Reef Watch,, 2018; Hughes et al., 2018a). For example, in the Great Barrier Reef in 2016, 85% of the 171 individual reefs surveyed experienced bleaching, of which 31% were exposed to 8 – 16°C-weeks (degree heating weeks – DHW), which resulted in bleaching of 70–90% of all corals (Hughes et al., 2017). Furthermore, it was found that the degree of reef protection and water quality had very little effect on bleaching susceptibility, and that previous bleaching events did not seem to have made corals less susceptible to repeated heat stress in 2016 (Hughes et al., 2017). Considering that current climate change models predict increasing frequency and severity of abnormally high SSTs (e.g., heat waves) in many regions of the world over the course of this century (Cai et al., 2014; ICPP, 2014), and considering that reefs take at least 15–25 years to recover from major destructive events (Baker et al., 2008), the future of coral reefs is on a steep trajectory of decline. This highlights the need to develop novel and unconventional reef management strategies that either equip corals with the necessary toolkit to cope with SST rise as proposed via assisted evolution approaches or that allow corals to adjust more gradually to SST rise via heat stress mitigation (Rau et al., 2012; Anthony et al., 2017; Gattuso et al., 2018; National Academics of Sciences, Engineering, and Medicine [NAS], 2019).

While rearing heat resilient coral may be a viable solution to counter reef decline (van Oppen et al., 2015; Chakravarti et al., 2017; Van Oppen et al., 2017), the research is still in its infancy. Furthermore, this approach needs to account for other unforeseen future changes and potentially is not applicable to the broad range of coral species forming coral reefs and for larger reef areas due to logistical constrains. Hence, this approach will require substantial time to be applicable and may still have its limitations. Concepts that will reduce the occurrence of thermal stress in order to allow corals to survive heat waves and to adjust more gradually to global warming may be more feasible in the near future. Different approaches of heat stress mitigation have been suggested like reef shading achieved through marine cloud brightening (cloud production from seawater aerosols; Latham et al., 2012; Kravitz et al., 2013) or large shade cloths (Rau et al., 2012). Furthermore, naturally occurring turbid waters in some near shore reefs were suggested to act as refuges from coral bleaching (Cacciapaglia and Van Woesik, 2016). Shading has two

effects: Firstly, it reduces the ocean's uptake of solar energy or heat (Latham et al., 2012), and it also reduces the stress caused by the synergetic effect of high temperature and intense light (Mumby et al., 2001; Coelho et al., 2017). While most of this research is based on modeling approaches, not much testing of their applicability has been conducted in the lab or *in situ* so far (but see, Coelho et al., 2017). An alternative way of heat stress mitigation is artificial upwelling (AU), which brings cooler deep water into warm shallow reef waters, thereby reducing SST. So far, this geoengineering technology has mainly been considered for fertilizing purposes, where nutrient-rich deep water (deeper than 100 m) is introduced into nutrient-poor surface waters to increase primary production (Williamson et al., 2009; Fan et al., 2015; Pan et al., 2016). The increase in primary production via AU aims to increase the yield of fisheries (Kirke, 2003; Viúdez et al., 2016), or to increase carbon sequestration, which reduces CO_2 in the ocean and atmosphere (Lovelock and Rapley, 2007; Pan et al., 2015; Zhang et al., 2017). A so far unstudied application of AU is surface water cooling (shown to occur by a modeling study of Oschlies et al., 2010). This may be a viable tool to mitigate thermal stress on corals, as indicated by studies in natural upwelling areas.

Localized natural upwelling has been found to reduce coral bleaching during periods of SST anomalies (Jiménez et al., 2001; Chollett et al., 2010; Bayraktarov et al., 2012; Wall et al., 2015; Schmidt et al., 2016; Riegl et al., 2018). For example, short-term cold-water intrusions due to large internal waves in the Andaman Sea, Thailand, significantly reduced coral bleaching and death on exposed reefs compared to sheltered reefs during a major bleaching event in 2010 (Wall et al., 2015; Schmidt et al., 2016). Furthermore, a modeling study proposed that certain upwelling regions in the Caribbean may be less prone to coral bleaching due to overall lower rate of SST rise (Chollett and Mumby, 2013). Although these findings are promising, studies are now required that investigate the effectiveness of different artificial upwelling regimes, including depth of upwelled water, and the rate and duration of upwelling.

If AU would be applied to cool surface waters of reefs during heat waves, it would be critical to choose a depth with a temperature that causes meaningful SST reductions, while matching as much as possible the seawater chemical composition of surface waters (e.g., inorganic nutrients, pH, dissolved inorganic carbon, oxygen). Unlike when AU is applied to fertilize surface waters, AU application for surface water cooling should minimize nutrient enrichment, which may otherwise lead to negative side effects of AU on reef communities (e.g., McCook, 1999). Furthermore, reductions of pH and changes in the seawater carbonate chemistry should be minimal to avoid negative effects on coral calcification (Schneider and Erez, 2006); and overcooling should be avoided, since this can, as well, lead to stress and bleaching in corals (Saxby et al., 2003; Kemp et al., 2011). In summer, decreased wind-induced water mixing often leads to a steep gradient in temperature with depth coinciding with the season of highest likelihood for heat stress. In the euphotic zone (>1% light of surface intensity), this is accompanied by overall low nutrient concentration and high oxygen concentration, and an increase of phytoplankton with depth (Lalli and Parsons, 1997). Below the euphotic zone,

respiration and re-mineralization decrease oxygen concentration, increase CO_2 and inorganic nutrients, and decrease seawater pH (Lalli and Parsons, 1997). Depending on region these changes are more or less pronounced, and depending on water clarity the depth of the euphotic zone varies.

In order to test the potential use of AU in mitigating coral bleaching during thermal stress, a laboratory study was carried out testing the effect of deep-water pulses from 50 m ($\sim$24°C) and 100 m ($\sim$20°C) depth on three different coral species. The 20-day study took place in Bermuda in late summer, when maximum annual SST of $\sim$28°C was reached. Thermal stress was simulated by exposing the corals to 31°C, and pulses of upwelling were applied once a day at midday reducing the temperature for a total period of 2 h. We hypothesized that both upwelling scenarios decelerate coral bleaching, while the water from 100 m is more efficient than the water from 50 m depth. Furthermore, we hypothesize that the efficiency of upwelling will vary between species. The goal of the study was to gain a first understanding about whether pulsed upwelling (sudden temperature drops) has the potential to mitigate coral bleaching in corals that are not naturally exposed to upwelling events, and – in case of a positive result - to stimulate further in-depth studies that would allow determining the most effective AU scenario(s). To facilitate the latter, the results are also discussed in a broader context, which includes further considerations for AU implementations and the potential benefits and risks that remain to be tested.

MATERIALS AND METHODS

Study Site and Study Species

The Bermuda platform is a circular pseudo-atoll ($\sim$900 km^2) comprised by a large lagoon with numerous patch reefs surrounded by a tract of shallow rim reefs that drops quickly to the mesophotic reefs and to the deep ocean (**Figure 1A**). Bermuda's reefs rank among the highest coral cover in the wider Caribbean with an estimated cover of 38.6% (Jackson et al., 2014). The oligotrophic waters surrounding the Bermuda platform are typically stratified during the summer months, with a temperature of $\sim$28°C at the surface, $\sim$24°C at 50 m depth and $\sim$20°C in 100 m depth (Steinberg et al., 2001). Inorganic nutrient concentration (nitrate + nitrite < 0.1 μmol kg^{-1}, phosphate < 0.5 μmol kg^{-1}) and concentrations of total organic carbon (60–70 μM with >95% being dissolved organic carbon) and total organic nitrogen (4–5 μM) are rather consistent within the first 100 m depth, while chlorophyll-*a* values are elevated at 100 m depth (0–50 m: <0.1 μg kg^{-1}, 100 m: $\sim$0.4 μg kg^{-1}) (Hansell and Carlson, 2001; Steinberg et al., 2001). Although no major bleaching event imposing significant mortality has been observed in Bermuda so far, coral bleaching and subsequent recovery has been observed fairly frequently in rather susceptible coral species, such as *Millepora alcicornis* (hydrozoan), *Diploria labyrinthiformis* and *Montastrea cavernosa* (Cook et al., 1990; Smith et al., 2013). Temperature threshold for coral bleaching in Bermuda is >28°C at the rim reef and >30°C at lagoonal and coastal reefs (Cook et al., 1990).
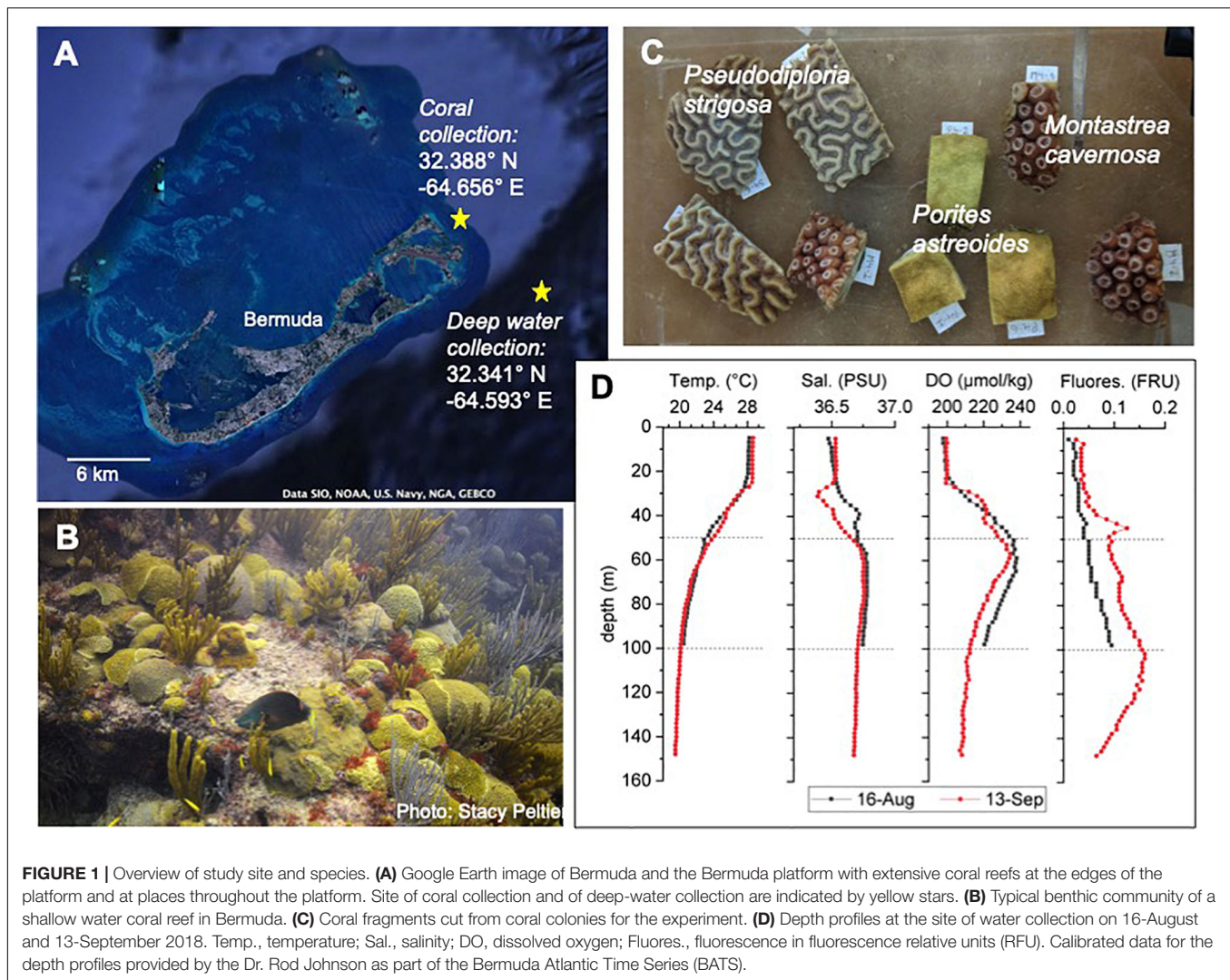
The common shallow water coral species *Montastrea cavernosa*, *Porites astreoides*, and *Pseudodiploria strigosa* (formerly *Diploria strigosa;* Budd et al., 2012) were used in the experiment, due to their importance as dominant reef builders in Bermuda reefs (**Figure 1B**). In August 2018, 6 colonies (diameter $\sim$20 cm) per species were collected (permit no. 2018071710, Department of Environment and Natural Resources, Bermuda government) with a hammer and chisel in 5 m depth from Sea Venture Shoals, a reef that is close to open ocean water (**Figure 1A**). Corals were brought to the Bermuda Institute of Ocean Sciences (BIOS) in coolers filled with seawater within 1h after collection. Each colony was divided into 9 fragments using a wet-cutting diamond saw and kept in in-door aquaria with continuous seawater flow-through for 3 weeks for recovery and acclimatization (**Figure 1C**). Seawater is constantly pumped from 2 m depth in Ferry Reach in front of BIOS. Temperature was kept at 28°C using chillers (TECO TK500) and aquarium heaters (Accu-therm, Cobalt Aquatics), and light (photosynthetic active radiation – PAR: 220 – 240 μE m^{-2} s^{-1}) was provided for 13 h each day (Indoor grow light, Sun Blaze T5 Fluorescent 44).

Experimental Setup

To test the effect of deep cold water pulses (AU) during thermal stress, the following temperature scenarios were applied, each on a subset of five replicate aquaria filled with 6 L of seawater: (i) *Control* condition – surface water at 28°C, which is the average summer temperature at shallow rim reefs; (ii) "*Heat*" treatment – surface water at 31°C, which is known to cause thermal stress and bleaching in Bermuda corals; (iii) "*Heat + 50*" m AU treatment – surface water at 31°C mixed with cooler water from 50 m depth once a day; (iv) "*Heat + 100*" m AU treatment – surface water at 31°C mixed with cooler water from 100 m depth once a day. Each subset of aquaria was kept inside a larger water basin, which was temperature-controlled by a chiller and a heater connected to a temperature controller (28°C or 31°C). Five of the 6 coral colonies per species (replicates) were used in the experiment (the 6th colony served as a back-up) and the 9 clones (fragments) of each coral colony were distributed between the 4 treatments, with 3 fragments in the control and 2 fragments in each of the heat treatments. Water flow was supplied by small aquarium pumps within each aquarium and a slow flow-through of unfiltered seawater was applied in the night after the "new" seawater has been adjusted to target temperature during the day.

AU Simulation

Prior to the experiment, a preliminary test was conducted to determine the AU regime to be applied, while considering the amount of deep water available. Deep water was collected during 2 cruises of the *RV Atlantic Explorer*, and the total amount of water available allowed a maximum addition of $\sim$5.5 L of deep water per AU aquarium per day, for a period of 20 days. For the preliminary test, we used surface water cooled down to the same temperature as in 50 m (24°C) and 100 m (20°C) depth, respectively, and we added the chilled water to 31°C warm water in different mixing ratios and flow speeds. The strongest and longest cooling effect with the available amount of water was achieved by removing 3 L of the 6 L of water in the aquarium,

FIGURE 1 | Overview of study site and species. **(A)** Google Earth image of Bermuda and the Bermuda platform with extensive coral reefs at the edges of the platform and at places throughout the platform. Site of coral collection and of deep-water collection are indicated by yellow stars. **(B)** Typical benthic community of a shallow water coral reef in Bermuda. **(C)** Coral fragments cut from coral colonies for the experiment. **(D)** Depth profiles at the site of water collection on 16-August and 13-September 2018. Temp., temperature; Sal., salinity; DO, dissolved oxygen; Fluores., fluorescence in fluorescence relative units (RFU). Calibrated data for the depth profiles provided by the Dr. Rod Johnson as part of the Bermuda Atlantic Time Series (BATS).

and then adding 5.5 L of cool water over a period of 22–24 min. This resulted in a 1:1 mixing ratio of "hot" and cool water after about 15 min, followed by continued cooling for another 7–9 min. Water warmed up again over a period of about 1.5 h until reaching the initial temperature. This AU scenario was applied to the AU treatments.

Three weeks prior to the start (16-August 2018, Batch 1) and in the middle of the experiment (13-September 2018, Batch 2), ~260 L of water per depth (50 and 100 m) were collected 3 km off the Bermuda platform (**Figure 1A**) with a rosette of 24 × 12-L Niskin bottles on board of the *RV Atlantic Explorer*. A connected CTD (regularly used and calibrated as part of the Bermuda Atlantic Time Series) allowed depth profiles of temperature, salinity, dissolved oxygen and fluorescence (**Figure 1D**). The water was filled into 25-L dark water storage containers, brought to BIOS within 3 h after collection and stored in the dark at 4°C to minimize biological activity and hence changes in water chemistry. During each day of the experiment, the amount of deep water required for one AU simulation (one per day) was poured into a larger container and was allowed to slowly come

up to room temperature. Just prior to the daily AU simulation at ~1300 h, the water from 50 m depth was adjusted to 24°C and the water from 100 m depth to 20°C with a cooler or heater. Then the deep water was added to the *Heat + 50* and *Heat + 100* treatment aquaria, respectively, following the AU scenario described above.

Measurement of Water Quality

Temperature was monitored continuously in one of the five replicate aquaria, as well as in three replicate aquaria during AU simulation, using temperature loggers (HOBO Pendant Temperature/Light loggers, ONSET). Salinity was measured twice per day (morning and evening) and small amounts of distilled water were added to the aquaria in case salinity increased as a consequence of evaporation. pH was measured in parallel to salinity, as well as just before AU simulation and after AU simulation in the AU aquaria. Conductivity (salinity) and pH sensors (Orion Star, Thermo Fisher Scientific) were calibrated weekly with standard calibration solutions. Environmental parameters of the deep water were measured, during deep-water retrieval and every 3rd day throughout the

experiment immediately before AU simulation. Those included salinity, pH, concentration of dissolved inorganic carbon (DIC) and total alkalinity (TA). For DIC and TA analysis, water samples were taken, preserved with $HgCl_2$ and later measured using two automated high-precision VINDTA systems at BIOS (model VINDTA 3C; built by L. Mintrop at Marianda Co.; Bates, 2017). TA and DIC were calibrated by measuring certified reference material (CRM; prepared by A.G. Dickson, Scripps Institution of Oceanography).

Measurements of Coral Response Parameters

Thermal stress can cause a cascade of physiological response in corals, while the loss of zooxanthellae and their photo-harvesting pigments (chlorophyll-*a*, c2 and peridinin) is the most obvious sign of a thermal stress response (coral bleaching). A number of studies suggested that the loss of zooxanthellae is the consequence of their malfunctioning photosystem caused by stress-related production of oxygen radicals in the chloroplasts (e.g., Warner et al., 1999; Lesser, 2006). More recent studies, however, indicate that the leaching of oxygen radicals from the zooxanthellae to the host – imposing a risk of cell damage to the host – triggers expulsion of zooxanthellae even if the photosystems are still intact (Gardner et al., 2017).

In this study, net photosynthetic rate was measured and standardized to surface area representing the product of zooxanthellae photosystem functioning and the amount of zooxanthellae and photo-pigments per surface area. Net photosynthetic rate was measured repetitively of one fragment per colony and per treatment (5 colonies [replicates] × 3 species × 4 treatments = 60 fragments). Always the same fragment was measured on day 3, 7, 12, 15, and 20 of the experiment, using 1 L-glass incubation chambers with a plastic lid (Glasslock USA, Inc.). The chambers were placed upside down to guarantee maximum light penetration (through glass instead of plastic) and were equipped with an oxygen sensor spot (PyroScience), a magnetic stirring bar and a grid for coral placement above the stirring bar. A tub of water was placed on a magnetic stirring plate and the chambers were submerged inside the tub to stabilize the temperature inside the chambers (28° or 31°C). Twelve fragments were incubated simultaneously over a period of 45 min starting with the fragments of the AU treatments in order to avoid interference with the AU pulse conducted in the afternoon. Five to six rounds of incubations were conducted per day until measurements of all 60 fragments were completed. Light during incubations was equal to the experimental light intensity (220–240 $\mu E\ m^{-2}\ s^{-1}$). Oxygen was measured in the beginning and at the end of the incubation by holding a fiber optic cable connected to an Optical Oxygen Meter (FireSting, PyroScience, Germany; calibrated with air-bubbled seawater as a 100% dissolved oxygen standard) from the outside of the incubation chamber against the oxygen sensor spot inside the chambers for 30 s. The change in oxygen concentration was used to calculate net photosynthesis standardized to coral surface area ($\mu mol\ O_2\ cm^{-2}\ h^{-1}$). Surface area of the coral fragment was determined by photography and subsequent picture analysis using Image J (fragments had a rather flat surface, since all

experimental coral species feature a massive growth form; **Figure 1C**).

Chlorophyll-*a* concentration and zooxanthellae density were determined as a metric for coral bleaching. For this, one fragment of each coral colony was harvested from the control treatment on day 3 (5 colonies × 3 species × 1 treatment = 15 fragments) and from all four treatments on day 12 and day 20 of the experiment (5 colonies × 3 species × 4 treatments = 60 fragments per sampling day). The tissue was removed from the skeleton with an airbrush and filtered seawater (0.47 μm pore size; ~25 ml) inside a Ziploc bag, and homogenized using an Ultraturrax homogenizer. Aliquots of the tissue slurry were frozen at −80°C (1.5 ml – chlorophyll-*a*) and −20°C (1.5 ml – zooxanthellae density) until further processing. For chlorophyll-*a* measurements, the tissue slurry was defrosted on ice, centrifuged (3100 rpm, 2 min) to collect the zooxanthellae in the pellet, the supernatant was discarded, and the pellet was re-dissolved in 0.5 ml of distilled water and mixed with 4.5 ml of 100% acetone (final concentration of acetone 90%). Chlorophyll extraction took place over 24 h at 4°C in the dark. Extract was centrifuged (3100 rpm, 4 min) and the absorbance of the supernatant containing the chlorophyll was measured in a spectrophotometer at wavelengths 663, 630 nm and 750 (absorbance at 750 is an indicator for turbidity, which was subtracted from 663 and 630), using 1 cm glass cuvettes (Parsons et al., 1984). Chlorophyll-*a* concentration was calculated following Parsons et al. (1984): Chlorophyll-*a* [μg] = (11.43 × Absorbance$_{663}$)-(0.64 × Absorbance$_{630}$). For zooxanthellae density, tissue slurry was defrosted, homogenized again, and drops of the slurry were placed on a hemocytometer and counted under the microscope (e.g., Sawall et al., 2014). The average of 6 replicate counts (6 drops) was used to calculate zooxanthellae density. Chlorophyll-*a* and zooxanthellae density were standardized to coral surface area.

Data Analysis

Degree-heating-weeks (DHW) were calculated from the temperature data following the description from NOAA (National Oceanic and Atmospheric Administration, United States). Temperature data were decomposed into weekly means and temperature anomalies per week calculated by subtracting the long-term climatological maximum monthly mean SST (28°C). The heat stress experienced by the corals in terms of DHW were derived by summing up all weekly anomalies for the experimental period only if they were ≥1°C (Strong et al., 1997; Liu et al., 2003).

One-way ANOVA and the Tukey's HSD *post hoc* test were performed with the software OriginPro2018 to examine differences between treatments at the end of the experiment (day 20). Each response parameter was tested separately for each coral species.

RESULTS

Temperature Regimes

Temperature in the *Control* treatment varied around the target temperature of 28°C with a minimum temperature of 27.1°C

and a maximum temperature of 28.8°C (**Figure 2A** and **Table 1**). Minimum temperatures occurred later in the night after several hours of fresh seawater supply, which was slightly cooler than the target temperature. Temperature in the heat treatments (*Heat*, *Heat + 50*, *Heat + 100*) varied around the target temperature of 31°C (**Table 1**), except during AU pulses (**Figure 2A**). During AU pluses, in *Heat + 50*, temperature dropped by about 3.5°C (minimum ∼27.5°C) and by about 5°C (minimum ∼26°C) in the *Heat + 100* (**Figures 2B,C**). In both AU treatments the drop in temperature occurred over a period of 25 min and the subsequent increase in temperature to 31°C required 1.5 to 2 h (**Figures 2B,C**). This resulted in daily mean temperatures of 30.9 ± 0.2°C (mean ± SD; *Heat*), 30.6 ± 0.2°C (*Heat + 50*) and 30.4 ± 0.2°C (*Heat + 100*). AU simulations were consistent between replicate aquaria (**Figure 2C**). Degree heating weeks were 5.73 ± 0.47°C-weeks for *Heat* treatment, which was reduced by 1.1°C-weeks in *Heat + 50* and by 1.56°C-weeks in *Heat + 100* (**Supplementary Figure S1**).

pH, Salinity, Total Alkalinity, Dissolved Inorganic Carbon

Parameters other than temperature were rather consistent throughout the treatments and over the duration of the experiment (**Table 1**). Mean pH_{NBS} varied between 8.11 ± 0.05 (*Heat*, mean ± SD) and 8.21 ± 0.03 (*Control*). Mean salinity ranged from 36.5 ± 0.1 (*Control*) to 36.9 ± 0.3 PSU (*Heat*), while salinities up to 37.3 PSU occurred occasionally due to evaporation in the 31°C-treatments. Short-term drops in salinities (<36 PSU) occurred in some cases during manual salinity adjustments. TA ranged from 2334 ± 15 (*Heat + 50*) to 2356 ± 31 μmol kg^{-1} (*Heat*). In the deep water, temperature of Batch 1 was 22.9°C in 50 m depth and 20.4°C in 100 m depth, while it was closer to the target temperature of 24°C (50 m: 23.8°C) and 20°C (100 m: 20.1°C) in Batch 2. The chemical properties of the deep water were similar to the aquarium water (shallow water) and varied little over time (**Table 1**). Salinity was 36.7 PSU in both depths, TA was around 2400 μmol kg^{-1} in both depths (∼50 μmol kg^{-1} higher than in the aquarium water), and DIC varied around 2100 μmol kg^{-1} (**Table 1**).

Coral Response Parameters

Most coral fragments survived the experimental period of 20 days (**Figures 3A–C** – numbers behind values of day 20). Among the few corals that died, most of them belonged to the species *P. astreoides*, where 2 of 5 fragments died in *Heat*, and 1 of 5 in both *Heat + 50* and *Heat + 100* (**Figure 3B**). *M. cavernosa* and *P. strigosa* each experienced a loss of 1 fragment in *Heat + 100* (**Figures 3A,C**). Paling (=bleaching) of corals was evident in corals in the *Heat* and *Heat + AU* treatments including corals that have died, but has not been quantified explicitly. The results of the statistical tests are presented in **Figure 3** with details provided as **Supplementary Table S1**.

Montastrea cavernosa experienced a significant loss of chlorophyll-*a* in all heat treatments, while remaining rather constant in *Control* with a final concentration of 79.9 ± 9.7 μg cm^{-2} (mean ± SE). *Heat* featured the lowest chlorophyll-*a*

concentration at the end of the experiment (13.8 ± 5.1), followed by *Heat + 50* (20.6 ± 4.0) and *Heat + 100* (29.1 ± 8.7; **Figure 3A**). A similar pattern was evident in zooxanthellae density where *Control* remained constant throughout the experiment with a final density of 14.0 ± 2.4 × 10^5 cells cm^{-2}, while the heat treatments had significantly reduced densities at the end of the experiment, albeit less pronounced in *Heat + 100* (*Heat*: 3.3 ± 0.7 × 10^5, *Heat + 50*: 3.9 ± 0.6 × 10^5, *Heat + 100*: 6.1 ± 2.4 × 10^5; **Figure 3D**). Net photosynthesis of *Control* slightly decreased over the course of the experiment (from 39.2 ± 8.7 to a final rate of 31.6 ± 3.0 μg O_2 cm^{-2} h^{-1}), rates were significantly lower in *Heat + 50* (7.7 ± 3.8) and *Heat* (5.8 ± 3.5) than *Control,* and were less reduced in *Heat + 100* with values lying between *Control* and *Heat + 50* (18.2 ± 4.6; **Figure 3G**). A decoupling between the trajectories of zooxanthellae density and net photosynthesis rate seems to be evident in the heat treatments where net photosynthesis decreased before zooxanthellae densities declined (**Figures 3D,G**).

Porites astreoides showed similar trends in the response parameters as *M. cavernosa*. A high variability between replicates and a reduced number of replicates in all heat treatments (due to coral death), however, led to non-significant results in most cases. Chlorophyll-*a* increased in *Control* over the duration of the experiment (final: 26.4 ± 6.9 μg cm^{-2}) and was higher than in all heat treatments. Second highest average chlorophyll-*a* concentration occurred in *Heat + 100* (16.1 ± 6.8) followed by *Heat + 50* (7.7 ± 3.0) and *Heat* (3.5 ± 1.3) at the end of the experiment (**Figure 3B**). Zooxanthellae density of *Control* remained high throughout the experiment with 6.9 × 10^5 cells cm^{-2} after 20 days, while densities decreased in all heat treatments with *Heat + 50* (3.3 ± 0.6 × 10^5) being amongst the lowest and the only one significantly lower than *Control* (**Figure 3E**). Net photosynthesis of *Control* was rather consistent throughout the experiment (except on day 6) with 31.7 ± 6.3 μg O_2 cm^{-2} h^{-1} at the end of the experiment. Net photosynthesis was similarly high in *Heat + 100* (29.3 ± 7.8), and lower in *Heat + 50* (20.6 ± 5.6) and *Heat* (10.3 ± 6.8), although not statistically significant (**Figure 3H**). Like in *M. cavernosa*, a decrease in net photosynthesis in the heat treatments appeared to be earlier in the experiment and remained similar or even increased (Heat + 100) toward the end of the experiment, while zooxanthellae density decreased later in the experiment (**Figures 3E,H**).

Of all study species, *P. strigosa* showed the weakest response to the treatments. Also none of the tested differences between treatments were statistically significant. Chlorophyll-*a* concentration in *Control* was rather constant throughout the duration of the experiment, but also highly variable between replicates (62.0 ± 28.6 μg cm^{-2} at the end of the experiment). In *Heat + 100,* chlorophyll-*a* was similarly high than in *Control* at the end of the experiment (75 ± 14.5), followed by *Heat* (42.2 ± 15.2) and *Heat + 50* (36.8 ± 14.7; **Figure 3C**). Zooxanthellae density decreased in *Control* over the experimental duration from 11.5 ± 2.3 × 10^5 (day 3) to 7.0 ± 1.5 × 10^5 cells cm^{-2} (day 20). At the end of the experiment, zooxanthellae density in *Heat + 100* was equally

TABLE 1 | Environmental conditions of the aquarium water (experimental units) and the deep water collected at 50 and 100 m depth.

	Aquarium water			Deep water								
				Batch 1 (collected 16-August-2018)				Batch 2 (collected 13-September-2018)				
	Mean (SD)	Min.	Max.	16-August	8-September	11-September	14-September	13-September	17-September	20-September	23-September	26-September
Heat + 50 m												
Temperature [°C]	30.5	27.3	31.8	22.9	24.0	24.0	24.0	23.8	24.0	24.0	24.0	24.0
pH	8.14 (0.04)	8.00	8.29	-	8.13	8.02	–	-	-	8.16	8.12	-
Salinity [PSU]	36.8 (0.2)	35.4	37.3	36.7	36.9	36.6	36.7	36.7	36.6	36.6	36.6	36.6
TA [μmol kg^{-1}]	2334 (15)	2307	2345	2398	2397	2408	2407	2398	2402	2403	2399	2376
DIC [μmol kg^{-1}]	–	–	–	2074	2091	2142	2111	2070	2088	2095	2084	2096
Heat + 100 m												
Temperature [°C]	30.4	25.1	31.8	20.4	20.0	20.0	20.0	20.1	20.0	20.0	20.0	20.0
pH	8.14 (0.05)	7.95	8.3	–	8.21	8.19	–	-	–	8.17	8.17	–
Salinity [PSU]	36.8 (0.1)	35.6	37.3	36.7	36.6	36.6	36.5	36.7	36.7	36.6	36.6	36.6
TA [μmol kg^{-1}]	2346 (21)	2286	2373	2405	2398	2410	2406	2405	2413	2407	2408	2381
DIC [μmol kg^{-1}]	–	–	–	2094	2093	2123	2115	2100	2125	2124	2118	2102
Control												
Temperature [°C]	27.9	27.1	28.8									
pH	8.21 (0.03)	8.13	8.39									
Salinity [PSU]	36.5 (0.1)	36.2	36.9									
TA [μmol kg^{-1}]	2350 (8)	2302	2381									
Heat												
Temperature [°C]	30.9	30.1	31.6									
pH	8.11 (0.05)	8.05	8.25									
Salinity [PSU]	36.9 (0.3)	35.4	37.3									
TA [μmol kg^{-1}]	2356 (31)	2319	2459									

TA, total alkalinity; DIC, dissolved inorganic carbon. Average values of aquarium water across the entire experimental period (7–27 September-2018) and concrete values of deep water at time of collection and every 3rd day of experiment. Missing values of pH due to sensor failure. No DIC measured in aquarium water.
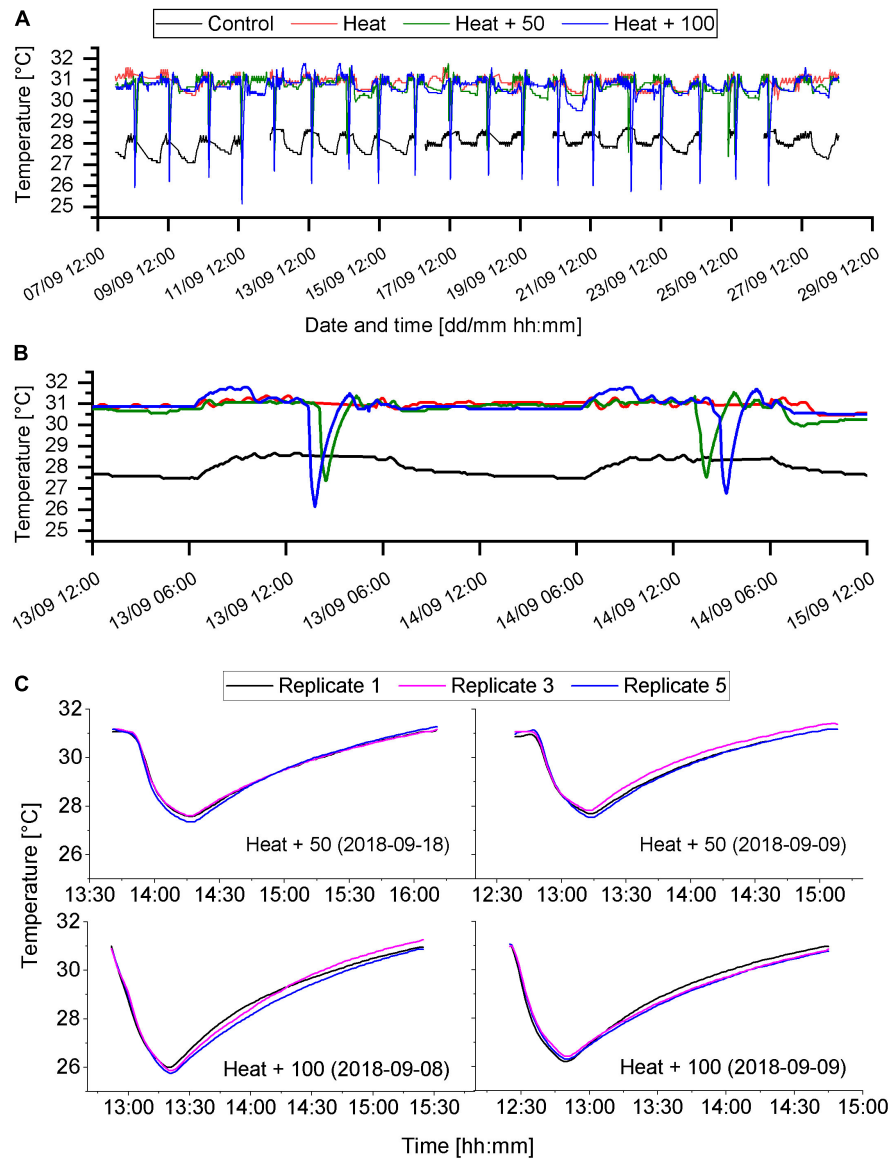
FIGURE 2 | Temperature regimes of the different treatments. **(A)** Temperature of each of the four treatments throughout the experimental phase (8th to 28th of September 2018). Sudden drops of temperature indicate AU events. Gaps in the data set indicate gaps in temperature recordings. **(B)** Close up of temperature regime of 2 experimental days (13th and 14th of September). **(C)** Examples of AU events, showing the temperature of 3 of the 5 replicate aquaria.

high as in *Control* ($7.0 \pm 2.1 \times 10^5$), but lower in *Heat + 50* ($6.1 \pm 1.7 \times 10^5$) and *Heat* ($4.7 \pm 1.6 \times 10^5$; **Figure 3F**). Net photosynthesis decreased in *Control* over the experimental duration from 35.5 ± 4.4 (day 3) to 22.5 ± 3.4 μg O$_2$ cm^{-2} h^{-1} (day 20). Net photosynthesis in *Heat + 50* (22.3 ± 12.6) and *Heat + 100* (24.8 ± 3.0) were similar as in *Control*, but lower in *Heat* (11.1 ± 4.6; **Figure 3I**) at the end of the experiment. Net photosynthesis varied slightly more between treatments on day 3 already, if compared to *M. cavernosa* and *P. astreoides* (**Figures 3G–I**).
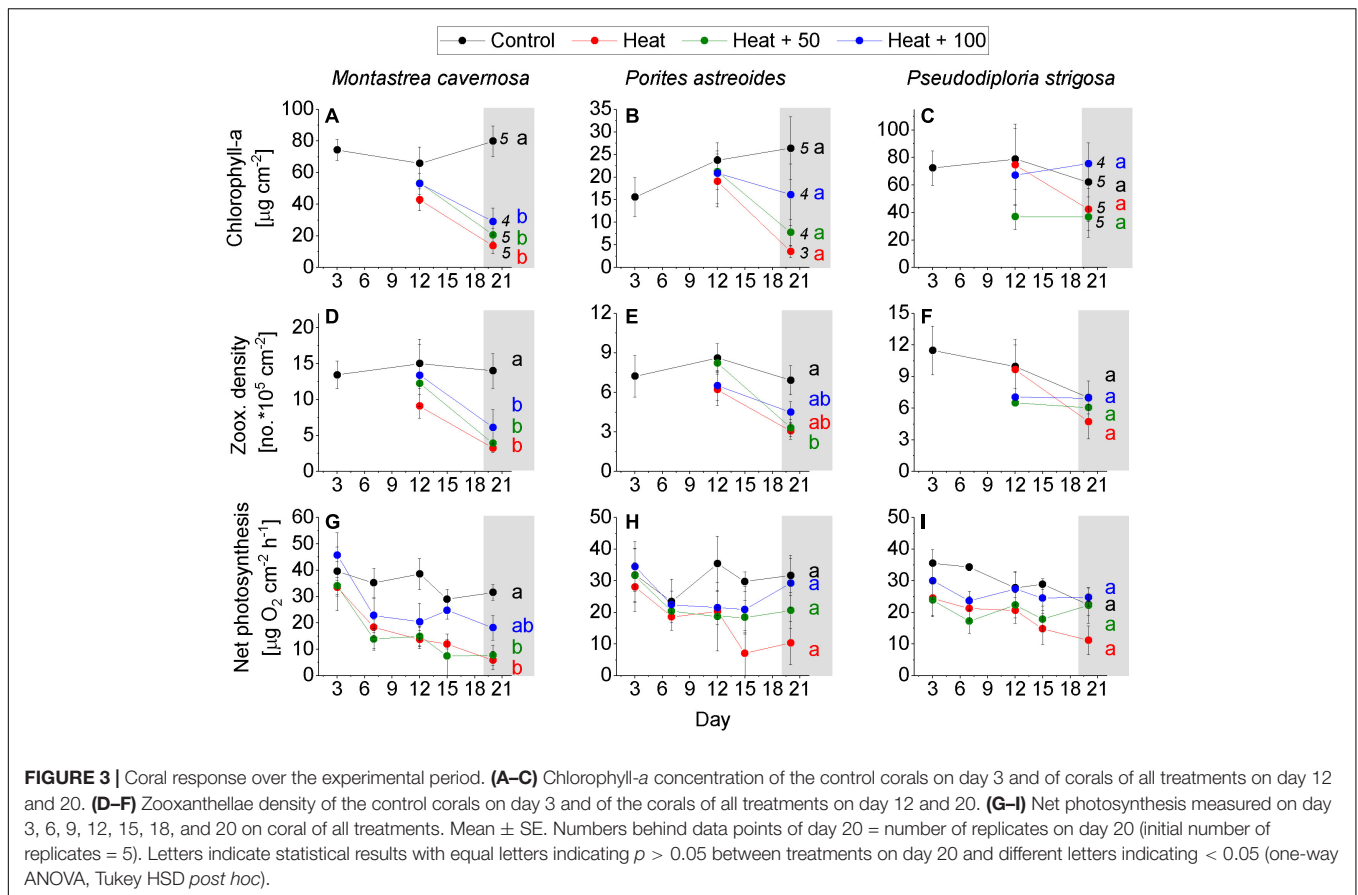
Data repository: CTD data/depth profiles collected on the research vessel are available on the BIOS website from the BATS Data Portal (cast IDs: 10350022, 10350023, 10351019, 10351020).

All other data (environmental and coral responses) are available on the PANGAEA website[1].

DISCUSSION

Artificial upwelling could be an emerging reef management tool by locally reducing SST during heat waves and hence providing a temporal refugium for corals from thermal stress. The results of our study support the hypotheses (i) that pulses of cooler deep water can reduce thermal stress responses during a heat stress

FIGURE 3 | Coral response over the experimental period. **(A–C)** Chlorophyll-*a* concentration of the control corals on day 3 and of corals of all treatments on day 12 and 20. **(D–F)** Zooxanthellae density of the control corals on day 3 and of the corals of all treatments on day 12 and 20. **(G–I)** Net photosynthesis measured on day 3, 6, 9, 12, 15, 18, and 20 on coral of all treatments. Mean ± SE. Numbers behind data points of day 20 = number of replicates on day 20 (initial number of replicates = 5). Letters indicate statistical results with equal letters indicating $p > 0.05$ between treatments on day 20 and different letters indicating < 0.05 (one-way ANOVA, Tukey HSD *post hoc*).

event, and (ii) that the water from a deeper and cooler layer in the ocean (100 m) is more efficient than from a more shallow and warmer layer (50 m). Furthermore, it is evident that species-specific differences in responses occur. Mitigation of heat stress occurred despite the rather short pulses of deep-water supply, which restricted temperature reduction ($<31°C$) to less than 2 h per day and led to an overall reduction of DHW by 1.1–1.6°C-weeks. In the following, we discuss the results in more detail, and we provide a broader picture on the implications of our results with respect to AU utilization, and what else needs to be considered and investigated from an ecological standpoint.

Efficiency of Simulated Upwelling in Coral Bleaching Mitigation

The two coral species *M. cavernosa* and *P. astreoides* showed the strongest response to the treatments with respect to both heat stress and mitigation of heat stress under simulated upwelling. Being aware of the fact that our low replication of $n = 5$ likely precludes statistically significant results between *Heat* and *Heat + AU*, the trends in zooxanthellae characteristics are reasonably clear to draw the conclusion that pulsed AU has the potential to mitigate heat stress responses in these two coral species.

Heat stress responses were first evident in a reduction of net photosynthetic rates followed by a loss of zooxanthellae

(and pigments; *M. cavernosa* and *P. astreoides*). This indicates that photo-damage may be a rapid response to heat, which is followed by the coral's expulsion of the malfunctioning zooxanthellae (Lesser, 2006; Hennige et al., 2011). Contrasting results were recently found in a heat stress experiment, where the branching corals *Acropora millepora* and *Stylophora pistillata* experienced a loss of zooxanthellae several days before a reduction in photosynthesis and photosynthetic efficiency was observed (Gardner et al., 2017), indicating species-specific heat stress responses. Interestingly, in the AU treatments net photosynthesis remained rather stable throughout the second half of the experiment (while they declined further in the *Heat* treatment, but also in *Heat + 50* of *M. cavernosa*) and even increased in *Heat + 100* in *P. astreoides*, despite the loss of zooxanthellae. The reason for this could be that a moderate loss of zooxanthellae may be counterbalanced by an increase of light available for the remaining symbionts thereby maintaining a comparatively high photosynthetic rate (non-linear relationship between cell density and photosynthesis; e.g., Hoogenboom et al., 2010; Gardner et al., 2017), in particular under AU conditions. It may also be that thermal stress led to a selection of prevalent thermally tolerant *Symbiodinium* types with potentially improved photosynthetic efficiency, or that highly abundant endolithic algae increased their photosynthetic rates due to increased availability of light (Pernice et al., 2020). In *P. astreoides*, it is worthwhile mentioning that this species

experienced the highest number of dead fragments due to heat. This could be due to lower energy reserves (less biomass), where a shortage of photosynthetic energy quickly leads to starvation (Thornhill et al., 2011). Alternatively, this could also be due to a higher susceptibility to colony fragmentation (3 weeks prior the experiment), which only becomes evident during concomitant heat stress. The consequent reduction in the number of replicates (survivors) likely explains the lack of statistical significance between treatments, despite rather clear trends.

Bleaching susceptibility of *M. cavernosa* and *P. astreoides* are generally considered to be moderate, while it is considered rather high in *P. strigosa*, as studies have shown during large-scale bleaching events in the wider Caribbean (Florida Keys – Brandt, 2009; Little Cayman – van Hooidonk et al., 2012; US Virgin Islands – Miller et al., 2009). This seems to be in contradiction with our finding, where *P. strigosa* revealed a high coral survival and the lowest differences between treatments at the end of the experiment. However, it needs to be considered that the corals in *Control* experienced a decline in zooxanthellae density and net photosynthesis over the course of the experiment as well (maybe due to fragmentation or continued acclimatization to laboratory conditions), which may distort visible changes due to heat. Therefore, the observed small differences found between treatments at the end of the heat stress experiment (lower net photosynthesis in *Heat*, compared to *Control* and *Heat + AU* conditions) may indicate beneficial effects of AU on *P. strigosa* under thermal stress, however, further studies are required to confirm this conclusion. We suggest that follow-up studies with this coral species consider larger fragment sizes (>5 cm in diameter) and longer periods for recovery from fragmentation and for acclimatization to laboratory conditions.

Implications of Results for AU Utilization and Further Considerations

In accordance with our study, pulsed natural upwelling has previously found to reduce heat stress and signs of coral bleaching during a large-scale bleaching event in Thailand (Wall et al., 2015; Schmidt et al., 2016). Large amplitude internal waves (LAIWs) deliver short-pulses of deep water into shallow reef areas of the Similan Islands (Andaman Sea, Thailand) with drops in temperature of up to 6–9°C for a period of 15–30 min (Schmidt et al., 2012). In a follow-up experiment, Buerger et al. (2015) simulated pulsed upwelling (2 pulses/day, 30 min/pulse, temperature drop of 5–6°C, pH drop 0.6 units), and found that the coral *Porites lutea* from both, exposed and sheltered reefs, experienced significantly less bleaching under upwelling conditions when exposed to thermal stress (2.3°C above average summer temperatures). These examples together with our study show that even short pulses of cold-water upwelling can substantially reduce thermal stress in corals during heat waves. One mechanism behind this could be reduced production and increased neutralization of cell damaging oxygen radicals during cool periods (Lesser, 1997). Pulsed AU, instead of sustained AU, is expected to be a preferable AU approach, since it likely reduces the risk of undesirable side effects (which, however, remains to be tested).

Undesirable side effects of AU on reefs, as well as on neighboring ecosystems, could be caused by a range of factors that are manipulated due to artificially mixing of two water bodies with different physical, chemical and biological properties. The magnitude of changes in water properties strongly depends on upwelling depth and intensity (upwelling rate and duration), as well as on the local conditions. In Bermuda, the euphotic zone extends deeper than 100 m, and the chemical properties of the water used for our experiment deviated little from the surface conditions. Therefore, the water taken at 50 and 100 m depth harbors relatively low risk of negative side effects of AU on corals and coral reefs, although we can not completely rule out the possibility that other parameters than temperatures have confounded the AU effects observed. Only chlorophyll-*a* was elevated substantially at 100 m depth as indicated by fluorescence in our study (**Figure 1D**) and as previously described (from <0.1 at surface to ∼0.4 µg kg^{-1} at 100 m depth; Steinberg et al., 2001). The influx of phytoplankton, depending on AU intensity, may lead to increased feeding and biomass of corals (Roder et al., 2010, 2011), which is considered beneficial for corals, in particular when photosynthetic energy supply decreases due to bleaching (Grottoli et al., 2006; Borell and Bischof, 2008; Buerger et al., 2015). However, sustained supply of plankton may lead to indirect negative effects on corals when it dies, since it can promote microbial activity that is potentially harmful (e.g., fostering the spread of benthic cyanobacteria mats; Brocke et al., 2015).

Upwelled water from a depth below the euphotic zone could cause substantial changes in the surface water chemistry, which might lead to negative effects overruling the benefits of cooling. More acidic water (lower pH, higher CO_2, lower aragonite saturation state) is known to hamper coral growth (calcification) and to promote bioerosion (Schneider and Erez, 2006; Jokiel et al., 2008; Schmidt and Richter, 2013). While pulses of acidic deep water in Thailand did not show a measurable effect on *P. lutea* in a laboratory study (Buerger et al., 2015), it may be responsible (together with temperature reductions) for a generally lower coral growth at LAIW-exposed reefs (Schmidt and Richter, 2013). Hence, under a more continuous upwelling scenario, more acidic deep water could certainly impact coral growth. Furthermore, CO_2-enrichment may foster (benthic) algal growth (Wu et al., 2008), and it could lead to higher CO_2-flux into the atmosphere, thereby contributing to the greenhouse effect. Decreased oxygen concentrations of deep water could lead to low oxygen stress in particular in the night when corals and other reef photosynthesizers (algae) do not produce oxygen (Murphy and Richmond, 2016). Therefore, if AU is conducted with water from below the euphotic zone, it might be desirable to limit AU applications to the daytime only. Another reason for conducting AU during the daytime is that the most stressful situation for corals occurs when high temperature coincides with high light conditions (Mumby et al., 2001; Anthony et al., 2007).

Increased nutrient supply is usually known to be either neutral or beneficial for corals by increasing zooxanthellae densities and/or zooxanthellae pigmentation, which increases photosynthetic capacity and hence energy supply (Fabricius, 2005). Negative effects of nutrients, however, have been found in

the reproductive success of corals (Loya et al., 2004) and in the thermal tolerance (e.g., Wooldridge, 2009). A decrease in thermal tolerance can be caused by an unbalanced nutrient supply (high nitrogen: phosphate ratio), where phosphate starvation produces symbionts with a low thermal tolerance (Wiedenmann et al., 2013; Ezzat et al., 2015). Furthermore, nutrient enrichment may lead to a reduced carbon translocation to the coral host, which can lead to energy shortage of the coral host in particular under thermal stress (Wooldridge, 2013). The lack of energy may consequently lead to a reduction of CO_2 supply to the symbionts thereby triggering the expulsion of symbionts (Wooldridge, 2013). At an ecosystem level, nutrient enrichment can lead to changes in the benthic community structure, where faster growing algae may spatially outcompete slower growing corals, in particular when the abundance of grazers is low (Shulman and Robertson, 1996; Murphy and Richmond, 2016). Although periodic natural upwelling has been found to be an important source of nutrients in a number of reefs (e.g., Florida – Leichter et al., 2003; Galapagos – Riegl et al., 2018; Great Barrier Reef – Andrews and Gentien, 1982), in case of AU, it will be important to assess the natural nutrient dynamics, in order to determine the upper limits of potentially harmful nutrient concentrations.

The bathymetry and hydrology of a given location determines the accessibility of cooler deep water for AU in coral reefs. In Bermuda, the most extensive coral reefs occur at the rim of the Bermuda platform. The platform drops off quickly into depths below 200 m. Here, deep water is comparatively easy to access and a suitable depth for AU could be chosen based on seawater properties. In contrast, in the central Great Barrier Reef many coral reefs are located on a wide continental shelf that is 40-80 m deep. The shelf edge, and consequently the location of deep water, is up to 50 km away from many reefs. Furthermore, large parts of the shelf experience a rather homogenous temperature throughout the water column all year around (Furnas and Mitchell, 1986), which exempt these reefs from AU applications. However, it has been found that deep-water intrusions from the adjacent deep Coral Sea can sometimes occur far onto the shelf. They occur also during summer months and can persist for several weeks, although they do not necessarily reach the surface layers of reef waters (Andrews and Gentien, 1982; Furnas and Mitchell, 1986). In case these intrusions happen concomitantly with a heat wave, this water could be targeted for AU, although no selection for the "type" of water could be done. Therefore it would be important to carefully choose an appropriate AU intensity.

CONCLUSION

Our results along with previous studies on the effect of cold water upwelling or pulses during heat stress indicate that reductions of SST via AU could be an effective tool to provide temporal refuges for corals from thermal stress. We have shown, that even short intrusions of cooler deep water (<2 h per day) are likely to mitigate thermal stress as evident in enhanced zooxanthellae performance in corals exposed to heat and AU compared to corals exposed to heat only. This effect seemed stronger in AU simulations with water from 100 m depth (temperature

reduction of 0.5°C per day; DHW 4.2°-weeks) than with water from 50 m depth (0.3°C per day; DHW 4.6°C-weeks), despite the small difference in DHW between treatments. This suggests that the absolute change in temperature during AU pulses might be a better predictor for heat stress response during pulsed AU than DHW (see also McClanahan et al., 2019). Our study also shows that the responses to AU were still comparatively small, therefore, an increase of AU duration or frequency may likely be required to mitigate heat stress and coral bleaching effectively. In order to avoid unwanted and unforeseeable side effects of AU caused by changes in other physical as well as chemical and biological parameters, pulsed AU instead of steady AU might be the desirable mode of application. While our results are promising, there are a number of studies that need to be conducted to advance our understanding on the benefits and risks of AU addressing ecological, engineering and societal aspects, before this can be applied on large scales *in situ*. Ecological aspects involve, but are not limited to (i) evaluating the effect of deep-water intrusions on reef communities rather than on individual corals, (ii) exploring the most effective and concomitantly least risky upwelling regime with respect to depth of water retrieval, volume of water upwelled, frequency and timing, (iii) assessing the effect of AU on plankton communities in the water column, (iv) evaluating the effect of AU on the hydrodynamics of reefs, and (v) assessing potential longer-term effects of AU on coral physiology (e.g., do AU induced temperature fluctuations promote higher thermal tolerance over time?).

Ocean warming and thus, the occurrence of heat waves will increase in frequency and intensity over the next decades and we will need to consider more permanent unconventional solutions to protect and sustain coral reefs. In future reef management strategies AU may be considered in combination with more conventional tools (strategies that aim to minimize local pressures such as overfishing and pollution) as well as other unconventional approaches like assisted evolution. For instance, AU and reef shading are both active ways to mitigate thermal stress and coral bleaching, while they may have different logistical constrains. Therefore, one or the other may be favorable at a given location. Traditional reef management strategies such as marine protected areas and fishing regulations are essential and will help to buffer future changes and minimize cumulative effects caused by pollution, overfishing and physical destruction. Yet we urgently need to carefully develop, test and assess unconventional approaches as novel management strategies, which are still far from being applied in the field at scale.

DATA AVAILABILITY STATEMENT

All datasets generated for this study are included in the article/**Supplementary Material**.

AUTHOR CONTRIBUTIONS

EF initiated the idea of the study. YS, EF, MW, and ML contributed to the conception and design of the study. YS and

REFERENCES

Andrews, J., and Gentien, P. (1982). Upwelling as a source of nutrients for the Great Barrier Reef ecosystem: a solution to Darwin's question? *Mar. Ecol. Prog. Ser.* 8, 257–269. doi: 10.3354/meps008257

Anthony, K., Bay, L. K., Costanza, R., Firn, J., Gunn, J., Harrison, P., et al. (2017). New interventions are needed to save coral reefs. *Nat. Ecol. Evol.* 1:1420.

Anthony, K. R., Connolly, S. R., and Hoegh-Guldberg, O. (2007). Bleaching, energetics, and coral mortality risk: effects of temperature, light, and sediment regime. *Limnol. Oceanogr.* 52, 716–726. doi: 10.4319/lo.2007.52.2.0716

Baker, A. C., Glynn, P. W., and Riegl, B. (2008). Climate change and coral reef bleaching: an ecological assessment of long-term impacts, recovery trends and future outlook. *Estuar. Coast. Shelf Sci.* 80, 435–471. doi: 10.1016/j.ecss.2008.09.003

Bates, N. R. (2017). Twenty years of marine carbon cycle observations at Devils Hole Bermuda provide insights into seasonal hypoxia, coral reef calcification, and ocean acidification. *Front. Mar. Sci.* 4:36. doi: 10.3389/fmars.2017.00036

Bayraktarov, E., Pizarro, V., Eidens, C., Wilke, T., and Wild, C. (2012). "Upwelling mitigates coral bleaching in the Colombian Caribbean," in *Proceedings of the 12th International Coral Reef Symposium*, Cairns.

Borell, E. M., and Bischof, K. (2008). Feeding sustains photosynthetic quantum yield of a scleractinian coral during thermal stress. *Oecologia* 157, 593–601. doi: 10.1007/s00442-008-1102-2

Brandt, M. (2009). The effect of species and colony size on the bleaching response of reef-building corals in the Florida Keys during the 2005 mass bleaching event. *Coral Reefs* 28, 911–924. doi: 10.1007/s00338-009-0548-y

Brocke, H. J., Polerecky, L., de Beer, D., Weber, M., Claudet, J., and Nugues, M. M. (2015). Organic matter degradation drives benthic cyanobacterial mat abundance on Caribbean coral reefs. *PLoS One* 10:e0125445. doi: 10.1371/journal.pone.0125445

Brown, B. E. (1997). Coral bleaching: causes and consequences. *Coral Reefs* 16, S129–S138.

Budd, A. F., Fukami, H., Smith, N. D., and Knowlton, N. (2012). Taxonomic classification of the reef coral family Mussidae (Cnidaria: Anthozoa: Scleractinia). *Zool. J. Linnean Soc.* 166, 465–529. doi: 10.1111/j.1096-3642.2012.00855.x

Buerger, P., Schmidt, G., Wall, M., Held, C., and Richter, C. (2015). Temperature tolerance of the coral *Porites lutea* exposed to simulated large amplitude internal waves (LAIW). *J. Exper. Mar. Biol. Ecol.* 471, 232–239. doi: 10.1016/j.jembe.2015.06.014

Cacciapaglia, C., and Van Woesik, R. (2016). Climate-change refugia: shading reef corals by turbidity. *Glob. Chang. Biol.* 22, 1145–1154. doi: 10.1111/gcb.13166

Cai, W., Borlace, S., Lengaigne, M., van Rensch, P., Collins, M., Vecchi, G., et al. (2014). Increasing frequency of extreme El Niño events due to greenhouse warming. *Nat. Clim. Chang.* 4:111.

Chakravarti, L. J., Beltran, V. H., and van Oppen, M. J. (2017). Rapid thermal adaptation in photosymbionts of reef-building corals. *Glob. Chang. Biol.* 23, 4675–4688. doi: 10.1111/gcb.13702

Chollett, I., and Mumby, P. J. (2013). Reefs of last resort: locating and assessing thermal refugia in the wider Caribbean. *Biol. Conserv.* 167, 179–186. doi: 10.1016/j.biocon.2013.08.010

Chollett, I., Mumby, P. J., and Cortes, J. (2010). Upwelling areas do not guarantee refuge for coral reefs in a warming ocean. *Mar. Ecol. Prog. Ser.* 416, 47–56. doi: 10.3354/meps08775

Coelho, V., Fenner, D., Caruso, C., Bayles, B., Huang, Y., and Birkeland, C. (2017). Shading as a mitigation tool for coral bleaching in three common Indo-Pacific species. *J. Exper. Mar. Biol. Ecol.* 497, 152–163. doi: 10.1016/j.jembe.2017.09.016

Cook, C. B., Logan, A., Ward, J., Luckhurst, B., and Berg, C. J. (1990). Elevated temperatures and bleaching on a high latitude coral reef: the 1988 Bermuda event. *Coral Reefs* 9, 45–49. doi: 10.1007/bf00686721

Ezzat, L., Maguer, J. F., Grover, R., and Ferrier-Pagès, C. (2015). New insights into carbon acquisition and exchanges within the coral-dinoflagellate symbiosis under NH4+ and NO3- supply. *Proc. R. Soc. Biol. Sci.* 282:20150610. doi: 10.1098/rspb.2015.0610

Fabricius, K. E. (2005). Effects of terrestrial runoff on the ecology of corals and coral reefs: review and synthesis. *Mar. Pollut. Bull.* 50, 125–146. doi: 10.1016/j.marpolbul.2004.11.028

Fan, W., Pan, Y., Liu, C. C., Wiltshire, J. C., Chen-Tung, A. C., and Chen, Y. (2015). Hydrodynamic design of deep ocean water discharge for the creation of a nutrient-rich plume in the South China Sea. *Ocean Eng.* 108, 356–368. doi: 10.1016/j.oceaneng.2015.08.006

Furnas, M. J., and Mitchell, A. W. (1986). Phytoplankton dynamics in the central Great Barrier Reef—I. Seasonal changes in biomass and community structure and their relation to intrusive activity. *Continent. Shelf Res.* 6, 363–384. doi: 10.1016/0278-4343(86)90078-6

Gardner, S. G., Raina, J. B., Nitschke, M. R., Nielsen, D. A., Stat, M., Motti, C. A., et al. (2017). A multi-trait systems approach reveals a response cascade to bleaching in corals. *BMC Biol.* 15:117. doi: 10.1186/s12915-017-0459-2

Gattuso, J.-P., Magnan, A. K., Bopp, L., Cheung, W. W., Duarte, C. M., Hinkel, J., et al. (2018). Ocean solutions to address climate change and its effects on marine ecosystems. *Front. Mar. Sci.* 5:337. doi: 10.3389/fmars.2017.00337

Grottoli, A. G., Rodrigues, L. J., and Palardy, J. E. (2006). Heterotrophic plasticity and resilience in bleached corals. *Nature* 440, 1186–1189. doi: 10.1038/nature04565

Hansell, D. A., and Carlson, C. A. (2001). Biogeochemistry of total organic carbon and nitrogen in the Sargasso Sea: control by convective overturn. *Deep Sea Res. Part II Top. Stud. Oceanogr.* 48, 1649–1667. doi: 10.1016/s0967-0645(00)00153-3

Hennige, S. J., McGinley, M. P., Grottoli, A. G., and Warner, M. E. (2011). Photoinhibition of *Symbiodinium* spp. within the reef corals *Montastraea faveolata* and *Porites astreoides*: implications for coral bleaching. *Mar. Biol.* 158, 2515–2526. doi: 10.1007/s00227-011-1752-1

Heron, S. F., Eakin, C. M., Douvere, F., Anderson, K. L., Day, J. C., Geiger, E., et al. (2017). *Impacts of Climate Change on World Heritage Coral Reefs: A First Global Scientific Assessment.* Paris: UNESCO World Heritage Centre.

Hoogenboom, M., Beraud, E., and Ferrier-Pagès, C. (2010). Relationship between symbiont density and photosynthetic carbon acquisition in the temperate coral *Cladocora caespitosa*. *Coral Reefs* 29, 21–29. doi: 10.1007/s00338-009-0558-9

Hughes, T. P., Kerry, J. T., Álvarez-Noriega, M., Álvarez-Romero, J. G., Anderson, K. D., Baird, A. H., et al. (2017). Global warming and recurrent mass bleaching of corals. *Nature* 543, 373–377.

Hughes, T. P., Anderson, K. D., Connolly, S. R., Heron, S. F., Kerry, J. T., Lough, J. M., et al. (2018a). Spatial and temporal patterns of mass bleaching of corals in the *Anthropocene*. *Science* 359, 80–83. doi: 10.1126/science.aan8048

Hughes, T. P., Kerry, J. T., Baird, A. H., Connolly, S. R., Dietzel, A., Eakin, C. M., et al. (2018b). Global warming transforms coral reef assemblages. *Nature* 556, 492–496. doi: 10.1038/s41586-018-0041-2

ICPP (2014). *Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Geneva: IPCC.

Jackson, J., Donovan, M., Cramer, K., and Lam, V. (2014). *Status and Trends of Caribbean Coral Reefs. Gland: Global Coral Reef Monitoring Network*. Switzerland: IUCN. Available online at: http://cmsdata.iucn.org/downloads/caribbean_coral_reefs___status_report_1970_2012.pdf

Jiménez, C., Cortés, J., León, A., and Ruíz, E. (2001). Coral bleaching and mortality associated with the 1997-98 El Niño in an upwelling environment in the eastern Pacific (Gulf of Papagayo, Costa Rica). *Bull. Mar. Sci.* 69, 151–169.

Jokiel, P., Rodgers, K., Kuffner, I., Andersson, A., Cox, E., and Mackenzie, F. (2008). Ocean acidification and calcifying reef organisms: a mesocosm investigation. *Coral Reefs* 27, 473–483. doi: 10.1007/s00338-008-0380-9

Jones, R. J. (2008). Coral bleaching, bleaching-induced mortality, and the adaptive significance of the bleaching response. *Mar. Biol.* 154, 65–80. doi: 10.1007/s00227-007-0900-0

Kemp, D. W., Oakley, C. A., Thornhill, D. J., Newcomb, L. A., Schmidt, G. W., and Fitt, W. K. (2011). Catastrophic mortality on inshore coral reefs of the Florida Keys due to severe low-temperature stress. *Glob. Chang. Biol.* 17, 3468–3477. doi: 10.1111/j.1365-2486.2011.02487.x

Kirke, B. (2003). Enhancing fish stocks with wave-powered artificial upwelling. *Ocean Coast. Manag.* 46, 901–915. doi: 10.1016/s0964-5691(03)00067-x

Kravitz, B., Forster, P. M., Jones, A., Robock, A., Alterskjær, K., Boucher, O., et al. (2013). Sea spray geoengineering experiments in the geoengineering model intercomparison project (GeoMIP): Experimental design and preliminary results. *J. Geophys. Res. Atmos.* 118, 175–111.

Lalli, C., and Parsons, T. R. (1997). *Biological Oceanography: An Introduction*. Amsterdam: Elsevier.

Latham, J., Bower, K., Choularton, T., Coe, H., Connolly, P., Cooper, G., et al. (2012). Marine cloud brightening. *Philos. Trans. R. Soc. A* 370, 4217–4262.

Leichter, J. J., Stewart, H. L., and Miller, S. L. (2003). Episodic nutrient transport to Florida coral reefs. *Limnol. Oceanogr.* 48, 1394–1407. doi: 10.4319/lo.2003.48.4.1394

Lesser, M. P. (1997). Oxidative stress causes coral bleaching during exposure to elevated temperatures. *Coral Reefs* 16, 187–192. doi: 10.1007/s003380050073

Lesser, M. P. (2006). Oxidative stress in marine environments: biochemistry and physiological ecology. *Annu. Rev. Physiol.* 68, 253–278. doi: 10.1146/annurev.physiol.68.040104.110001

Liu, G., Strong, A. E., and Skirving, W. J. (2003). Remote sensing of sea surface temperature during 2002 Barrier Reef coral bleaching. *EOS* 84, 137–144.

Lovelock, J. E., and Rapley, C. G. (2007). Ocean pipes could help the Earth to cure itself. *Nature* 449:403. doi: 10.1038/449403a

Loya, Y., Lubinevsky, H., Rosenfeld, M., and Kramarsky-Winter, E. (2004). Nutrient enrichment caused by in situ fish farms at Eilat, Red Sea is detrimental to coral reproduction. *Mar. Pollut. Bull.* 49, 344–353. doi: 10.1016/j.marpolbul.2004.06.011

McClanahan, T. R., Darling, E. S., Maina, J. M., Muthiga, N. A., D'agata, S., Jupiter, S. D., et al. (2019). Temperature patterns and mechanisms influencing coral bleaching during the 2016 El Niño. *Nat. Clim. Chang.* 9, 845–851. doi: 10.1038/s41558-019-0576-8

McCook, L. J. (1999). Macroalgae, nutrients and phase shifts on coral reefs: scientific issues and management consequences for the Great Barrier Reef. *Coral Reefs* 18, 357–367. doi: 10.1007/s003380050213

Miller, J., Muller, E., Rogers, C., Waara, R., Atkinson, A., Whelan, K., et al. (2009). Coral disease following massive bleaching in 2005 causes 60% decline in coral cover on reefs in the US Virgin Islands. *Coral Reefs* 28:925. doi: 10.1007/s00338-009-0531-7

Mumby, P. J., Chisholm, J. R., Edwards, A. J., Andrefouet, S., and Jaubert, J. (2001). Cloudy weather may have saved Society Island reef corals during the 1998 ENSO event. *Mar. Ecol. Prog. Ser.* 222, 209–216. doi: 10.3354/meps222209

Murphy, J. W. A., and Richmond, R. H. (2016). Changes to coral health and metabolic activity under oxygen deprivation. *PeerJ* 4:e1956. doi: 10.7717/peerj.1956

National Academics of Sciences, Engineering, and Medicine [NAS] (2019). *Ocean Studies Board Committee on Interventions to Increase the Resilience of Coral Reefs. A Decision Framework for Interventions to Increase the Persistence and Resilience of Coral Reefs*. Washington, DC: The National Academies Press.

NOAA Coral Reef Watch, (2018). *Status Report*. Available at: https://coralreefwatch.noaa.gov/satellite/analyses_guidance/global_coral_bleaching_2014-17_status.php (accessed August 2019).

Oschlies, A., Pahlow, M., Yool, A., and Matear, R. J. (2010). Climate engineering by artificial ocean upwelling: channelling the sorcerer's apprentice. *Geophys. Res. Lett.* 37:961.

Pan, Y., Fan, W., Huang, T.-H., Wang, S.-L., and Chen, C.-T. A. (2015). Evaluation of the sinks and sources of atmospheric CO_2 by artificial upwelling. *Sci. Total Environ.* 511, 692–702. doi: 10.1016/j.scitotenv.2014.11.060

Pan, Y., Fan, W., Zhang, D., Chen, J., Huang, H., Liu, S., et al. (2016). Research progress in artificial upwelling and its potential environmental effects. *Sci. China Earth Sci.* 59, 236–248. doi: 10.1007/s11430-015-5195-2

Parsons, T., Maita, Y., and Lalli, C. (1984). "Determination of chlorophylls and total carotenoids: spectrophotometric method," in *A Manual of Chemical and Biological Methods for Seawater Analysis*, eds T. R. Parsons, Y. Maita, and C. M. Lalli, (Oxford: Pergamon Press), 101–112.

Pernice, M., Raina, J., Rädecker, N., Cárdenas, A., Pogoreutz, C., and Voolstra, C. R. (2020). Down to the bone: the role of overlooked endolithic microbiomes in reef coral health. *ISME J.* 14, 325–334. doi: 10.1038/s41396-019-0548-z

Rau, G. H., McLeod, E. L., and Hoegh-Guldberg, O. (2012). The need for new ocean conservation strategies in a high-carbon dioxide world. *Nat. Clim. Chang.* 2, 720–724. doi: 10.1038/nclimate1555

Riegl, B., Glynn, P. W., Banks, S., Keith, I., Rivera, F., Vera-Zambrano, M., et al. (2018). Heat attenuation and nutrient delivery by localized upwelling avoided coral bleaching mortality in northern Galapagos during 2015/2016 ENSO. *Coral Reefs* 38, 1–13.

Roder, C., Fillinger, L., Jantzen, C., Schmidt, G., Khokiattiwong, S., and Richter, C. (2010). Trophic response of corals to large amplitudal internal waves. *Mar. Ecol. Prog. Ser.* 412, 113–128. doi: 10.3354/meps08707

Roder, C., Jantzen, C., Schmidt, G., Kattner, G., Phongsuwan, N., and Richter, C. (2011). Metabolic plasticity of the corals *Porites lutea* and *Diploastrea heliopora* exposed to large amplitude internal waves. *Coral Reefs* 30, 57–69. doi: 10.1007/s00338-011-0722-x

Sawall, Y., Al-Sofyani, A., Banguera-Hinestroza, E., and Voolstra, C. (2014). Spatio-temporal analyses of zooxanthellae physiology of the coral *Pocillopora verrucosa* along large-scale nutrient and temperature gradients in the Red Sea. *PLoS One* 9:e103179. doi: 10.1371/journal.pone.103179

Saxby, T., Dennison, W. C., and Hoegh-Guldberg, O. (2003). Photosynthetic responses of the coral *Montipora digitata* to cold temperature stress. *Mar. Ecol. Prog. Ser.* 248, 85–97. doi: 10.3354/meps248085

Schmidt, G. M., Phongsuwan, N., Jantzen, C., Roder, C., Khokiattiwong, S., and Richter, C. (2012). Coral community composition and reef development at the Similan Islands, Andaman Sea, in response to strong environmental variations. *Mar. Ecol. Prog. Ser.* 456, 113–126. doi: 10.3354/meps09682

Schmidt, G. M., and Richter, C. (2013). Coral growth and bioerosion of *Porites lutea* in response to large amplitude internal waves. *PLoS One* 8:e73236. doi: 10.1371/journal.pone.073236

Schmidt, G. M., Wall, M., Taylor, M., Jantzen, C., and Richter, C. (2016). Large-amplitude internal waves sustain coral health during thermal stress. *Coral Reefs* 35, 869–881. doi: 10.1007/s00338-016-1450-z

Schneider, K., and Erez, J. (2006). The effect of carbonate chemistry on calcification and photosynthesis in the hermatypic coral *Acropora eurystoma*. *Limnol. Oceanogr.* 51, 1284–1293. doi: 10.4319/lo.2006.51.3.1284

Shulman, M. J., and Robertson, D. R. (1996). Changes in the coral reefs of San Blas, Caribbean Panama: 1983 to 1990. *Coral Reefs* 15, 231–236. doi: 10.1007/s003380050048

Smith, S. R., Sarkis, S., Murdoch, T. J., Weil, E., Croquer, A., Bates, N. R., et al. (2013). "Threats to coral reefs of Bermuda," in *Coral Reefs of the United Kingdom Overseas Territories*, ed. C. R. C. Sheppard, (Cham: Springer), 173–188. doi: 10.1007/978-94-007-5965-7_13

Steinberg, D. K., Carlson, C. A., Bates, N. R., Johnson, R. J., Michaels, A. F., and Knap, A. H. (2001). Overview of the US JGOFS Bermuda Atlantic Time-series Study (BATS): a decade-scale look at ocean biology and biogeochemistry. *Deep Sea Res. Part II Top. Stud. Oceanogr.* 48, 1405–1447. doi: 10.1016/s0967-0645(00)00148-x

Strong, A. E., Barrientos, C. B., Duda, C., and Sapper, J. (1997). "Improved satellite techniques for monitoring coral reef bleaching," in *Procedings of the 8th International Coral Reef Symposium*, Panama City, FL.

Thornhill, D. J., Rotjan, R. D., Todd, B. D., Chilcoat, G. C., Iglesias-Prieto, R., Kemp, D. W., et al. (2011). A connection between colony biomass and death in Caribbean reef-building corals. *PLoS One* 6:e29535. doi: 10.1371/journal.pone.029535

van Hooidonk, R. J., Manzello, D. P., Moye, J., Brandt, M. E., Hendee, J. C., McCoy, C., et al. (2012). Coral bleaching at little cayman, Cayman Islands 2009. *Estuar. Coas. Shelf Sci.* 106, 80–84. doi: 10.1016/j.ecss.2012.04.021

Van Oppen, M. J., Gates, R. D., Blackall, L. L., Cantin, N., Chakravarti, L. J., Chan, W. Y., et al. (2017). Shifting paradigms in restoration of the world's coral reefs. *Glob Chang. Biol.* 23, 3437–3448.

van Oppen, M. J., Oliver, J. K., Putnam, H. M., and Gates, R. D. (2015). Building coral reef resilience through assisted evolution. *Proc. Natl. Acad. Sci. U.S.A.* 112, 2307–2313. doi: 10.1073/pnas.1422301112

Viúdez, Á, Balsells, M. F.-P., and Rodríguez-Marroyo, R. (2016). Artificial upwelling using offshore wind energy for mariculture applications. *Sci. Mar.* 80, 235–248. doi: 10.3989/scimar.04297.06b

Wall, M., Putchim, L., Schmidt, G., Jantzen, C., Khokiattiwong, S., and Richter, C. (2015). Large-amplitude internal waves benefit corals during thermal stress. *Proc. R. Soc. Lond. B Biol. Sci.* 282:20140650. doi: 10.1098/rspb.2014.0650

Warner, M. E., Fitt, W. K., and Schmidt, G. W. (1999). Damage to photosystem II in symbiotic dinoflagellates: a determinant of coral bleaching. *Proc. Natl. Acad. Sci. U.S.A.* 96, 8007–8012. doi: 10.1073/pnas.96.14.8007

Weis, V. M. (2008). Cellular mechanisms of Cnidarian bleaching: stress causes the collapse of symbiosis. *J. Exper. Biol.* 211, 3059–3066. doi: 10.1242/jeb.009597

Wiedenmann, J., D'Angelo, C., Smith, E. G., Hunt, A. N., Legiret, F.-E., Postle, A. D., et al. (2013). Nutrient enrichment can increase the susceptibility of reef corals to bleaching. *Nat. Clim. Chang.* 3, 160–164. doi: 10.1038/nclimate1661

Williamson, N., Komiya, A., Maruyama, S., Behnia, M., and Armfield, S. W. (2009). Nutrient transport from an artificial upwelling of deep sea water. *J. Oceanogr.* 65, 349–359. doi: 10.1007/s10872-009-0032-x

Wooldridge, S. A. (2009). Water quality and coral bleaching thresholds: formalising the linkage for the inshore reefs of the Great Barrier Reef, Australia. *Mar. Pollut. Bull.* 58, 745–751. doi: 10.1016/j.marpolbul.2008.12.013

Wooldridge, S. A. (2013). Breakdown of the coral-algae symbiosis: towards formalising a linkage between warm-water bleaching thresholds and the growth rate of the intracellular zooxanthellae. *Biogeosciences* 10, 1647–1658. doi: 10.5194/bg-10-1647-2013

Wu, H., Zou, D., and Gao, K. (2008). Impacts of increased atmospheric CO_2 concentration on photosynthesis and growth of micro- and macro-algae. *Sci. China Ser. C Life Sci.* 51, 1144–1150. doi: 10.1007/s11427-008-0142-5

Zhang, Y., Zhao, M., Cui, Q., Fan, W., Qi, J., Chen, Y., et al. (2017). Processes of coastal ecosystem carbon sequestration and approaches for increasing carbon sink. *Sci. China Earth Sci.* 60, 809–820. doi: 10.1007/s11430-016-9010-9