

Review

Thermal Stress and Resilience of Corals in a Climate-Changing World

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Abstract: Coral reef ecosystems are under the direct threat of increasing atmospheric greenhouse gases, which increase seawater temperatures in the oceans and lead to bleaching events. Global bleaching events are becoming more frequent and stronger, and understanding how corals can tolerate and survive high-temperature stress should be accorded paramount priority. Here, we review evidence of the different mechanisms that corals employ to mitigate thermal stress, which include association with thermally tolerant endosymbionts, acclimatisation, and adaptation processes. These differences highlight the physiological diversity and complexity of symbiotic organisms, such as scleractinian corals, where each species (coral host and microbial endosymbionts) responds differently to thermal stress. We conclude by offering some insights into the future of coral reefs and examining the strategies scientists are leveraging to ensure the survival of this valuable ecosystem. Without a reduction in greenhouse gas emissions and a divergence from our societal dependence on fossil fuels, natural mechanisms possessed by corals might be insufficient towards ensuring the ecological functioning of coral reef ecosystems.

Keywords: thermal stress; coral resilience; bleaching events; thermally-tolerant symbionts; acclimatisation; adaptation; heterotrophy; climate change

1. Introduction

Since the last century, scleractinian coral reef ecosystems have undergone a decrease in biodiversity and ecological functioning [1–5], formerly attributed to the direct and indirect effects of overfishing [6,7], pollution from agriculture, sewage runoff, and land development [8–10]. Currently, along with the exponential increase of the human population [11] and our societal dependence on carbon fossil fuels, these local threats have been compounded by the impacts of global climate change in the oceans [12–14]. The impact of increasing greenhouse gases in the atmosphere is leading to a global increase in seawater temperatures that has caused mass bleaching events [12,14–17]. These global bleaching events are becoming more frequent (1998, 2010 and 2014–17) and severe [14,16,18–22], leaving coral reefs vulnerable and unable to recover. The 2014–2017 mass bleaching event, which lasted 36 months and spanned four calendar years, was the longest-lasting, most widespread, and probably most damaging event on record [21–29], and stands out as unique by spanning all phases of the El Niño–Southern Oscillation cycle of 2017, being the warmest non-El Niño year ever recorded [21,30].

Coral bleaching is defined as the loss of colour, due to the partial or total loss of Symbiodiniaceae dinoflagellates and/or the reduction of their photosynthetic pigments, that exposes the white calcium

carbonate of the coral skeleton (Figure 1A) [31,32]. Bleaching is a generalized stress response to environmental perturbations such as aerial exposure, sedimentation, eutrophication, exposure to heavy metals, high UV radiation, and extreme changes in salinity and temperature [17,31,33,34], however, at large scales is triggered by high seawater temperatures (exceeding normal summer maxima) in combination with high solar radiation [12,15,17,31–33,35]. Scleractinian corals possess molecular protective mechanisms, such as heat shock proteins and antioxidant enzymes to resist thermal stress [17,33,36], or mycosporine amino acids (MAA) and fluorescent pigments to resist light stress (Figure 1B) [17,33,37,38]. The cellular mechanism of bleaching starts with the photoinhibition process within the photosynthetic apparatus of the endosymbionts, which results in the build-up of free electrons that react to form reactive oxygen species (ROS) [39,40]. The proliferation of harmful ROS leads to the degradation, exocytosis, or apoptosis of symbiont cells by the coral host [39], in order to avoid cellular damage [36]. If the duration of the thermal stress extends beyond their physiological ability to recover, corals cannot survive without their main symbiotic partners [15,31,35]. Even though the molecular process of bleaching is similar across coral species, variations in the mechanism to resist and survive thermal stress exist (Figure 1B,C) [17,32,35].

Resilience is the capacity of a coral colony or an entire coral reef ecosystem to absorb, resist, and recover from perturbations [41–43]. The resilience of corals to thermal stress is contingent on the mean long-term annual maximum temperature of the region they live in [17]. Much research has been done in the past decades to understand if the resilience of corals to thermal stress might be an adaptation and/or acclimatisation process (reviewed in [17,44,45]). Here, we review current research that focuses on the capabilities of coral species to adapt and/or acclimatise to thermal events, in order to understand what the future of this irreplaceable ecosystem will be. We have included only scientific studies which have clearly identified the different general strategies to survive thermal stress, as presented in this review.

2. Mechanisms of Resilience to Thermal Stress

2.1. Thermally Tolerant Endosymbionts

By associating with stress-resistant symbionts, some coral species are able to acquire increased thermal tolerance. Within the Symbiodiniaceae, species like *Durisdinium* spp. (previously clade D) [46–48], *Cladocopium* C15 [49], and *C. thermophilum* C3 [50,51] are resistant to thermal stress. Dinoflagellates in the genus *Durisdinium* are extremophiles inhabiting environments of thermal stress, high temperature fluctuations, sedimentation and high-latitude marginal reefs [52–62]. In recent decades, *Durisdinium* spp. have generated interest because they proliferate in bleached corals [53,60,63–65], protecting against thermal stress by providing 1–1.5 °C of thermal tolerance [46]. *Durisdinium* spp. maintain high photochemical efficiency when exposed to high temperatures compared to symbionts from other genera (*Breviolum* or *Cladocopium*) [48,66,67] and are able to fix more carbon and assimilate more nitrogen [68]. Furthermore, *D. trenchii* has been found to provide tolerance to cold stress too [69,70].

When exposed to thermal stress, some species of coral are capable of shifting the relative abundance of their dominant symbionts. Background symbionts, which can represent <10% of the overall Symbiodiniaceae community [60,71], become dominant, conferring thermal tolerance to the holobiont. Even though many coral species are able to associate with a heterogeneous community of Symbiodiniaceae [72,73], others do not change their dominant symbiont even when bleaching [74], showing a long-term symbiotic adaptation between coral host and dominant symbiont [75–78].

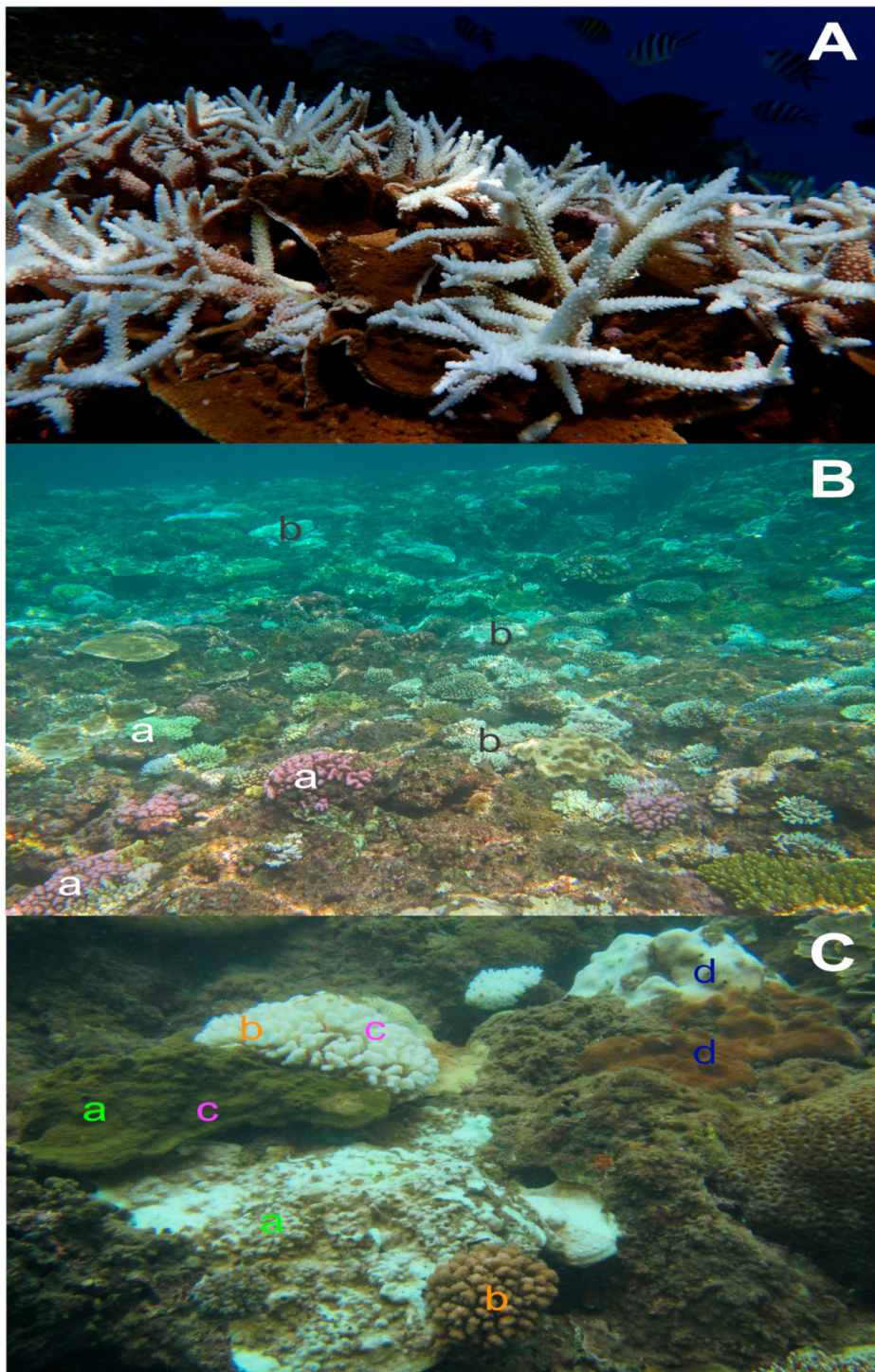


Figure 1. (A) Onset of a bleaching process in a colony of *Acropora* spp., in Kenting, Taiwan 2015 (Photo: J. Wei); (B) Bleaching event showing colonies with fluorescent pigments as a protective mechanism (a) and already bleached colonies (b), in Okinawa, Japan 2016 (Photo: S.-Y. Yang); (C) Intra-specific: between *Montipora* spp. colonies (a) and between *Isopora palifera* colonies (b), inter-specific: between *Montipora* spp. and *I. palifera* colonies (c) and intra-colony: within *Leptoria phrygia* colony (d) responses to thermal stress in Kenting, Taiwan 2016 (Photo: R. Carballo-Bolaños).

2.2. Acclimatisation (Phenotypic Plasticity)

Phenotypic plasticity refers to dissimilar phenotypes that can be generated from a single genotype in response to different environmental conditions [79]. These phenotypic changes are reversible and

dependent on the boundaries of each organism’s genotype [17]. In this context, acclimatisation refers to the phenotypic changes of corals in their natural environment, while acclimation denotes short-term phenotypic changes under manipulative experimental conditions in the laboratory. Reciprocal transplantation experiments (RTE) are a well-known method to quantify acclimatisation mechanisms by measuring differences in physiological parameters in specimens transplanted across environmentally distinct sites, locations or regions. For example, a RTE of *Porites lobata* between a fore reef (impacted by high wave action, oceanic swells and storms) and back reef (sheltered) in American Samoa, showed phenotypic plasticity in mean annual skeletal extension rates, bulk densities, and calcification rates after only six months, with all variables in transplanted corals approximating values of corals originally from the site [80]. In another study, Sawall et al. [81] found optimal calcification rates at 28–29 °C throughout all populations of *Pocillopora verrucosa* with evident differences in temperature fluctuations between the northern (21–27 °C) and southern (28–33 °C) parts of the Red Sea, supporting high phenotypic plasticity due to low genetic divergence between north and south coral host populations.

2.3. Thermal Stress Acclimatisation

Multiple studies have identified a direct link between thermal preconditioning and bleaching susceptibility (Table 1) [82–91]. After exposing corals to short-term thermal preconditioning experiments, only preconditioned corals did not bleach during a heat-stress experiment (Table 1) [82,83], despite maintaining their Symbiodiniaceae and the bacterial community [82]. Moreover, other studies have compared coral responses of the first major mass bleaching event in 1998 with subsequent stronger bleaching events [89,91]. Maynard et al. [91] surveyed the same sites in 1998 and after a more severe bleaching event in 2002, which featured exposure to twice as many degree heating weeks (DHW) and 15% higher solar irradiance, corals acclimatised, and exhibited less bleaching than in 1998. In a similar study, Guest et al. [89] demonstrated how coral bleaching was less severe after the 2010 large-scale bleaching event in Southeast Asia in locations that previously showed high bleaching in 1998 (Singapore and Malaysia), and had greater historical temperature variability and lower rates of warming. Meanwhile, corals in Indonesia were unaffected by bleaching in 1998, but showed high mortality in 2010. Consequently, corals acclimatised to previous thermal stress events, but also those living in sites with highly variable temperatures presented higher tolerance [89].

Table 1. Studies performed to test acclimatisation to thermal stress and high temperature variability at different locations around the world.

Study	Temp/DHW	Duration	Location	Species	Main Results	Ref.
Precondition + HSE	28 °C (precond.)	10 d	GBR, Australia	<i>Acropora millepora</i>	No bleaching in pre-conditioned corals	[82]
	31 °C (HSE)	8 d				
Precondition + HSE	31 °C (precond.)	2 d	GBR, Australia	<i>Acropora aspera</i>	No bleaching in pre-conditioned corals	[83]
	34 °C (HSE)	6 d				
Comparison 1998/2002 BE	DHW = 2002 > 1998	Bleaching survey	GBR, Australia	<i>Acropora</i> spp., <i>Pocillopora</i> spp., <i>Porites</i> spp.	Less mortality in 2002	[91]
Comparison 1998/2010 BE	DHW = Malaysia + Singapore > Indonesia	Bleaching survey	Indonesia, Malaysia, Singapore	<i>Acropora</i> spp., <i>Pocillopora</i> spp.,	Low bleaching in Malaysia and Singapore	[89]
Survey 2010 BE	-	Bleaching survey	Thailand	<i>Coelastrea aspera</i>	Less bleaching in high irradiance colony sides (decadal environmental ‘memory’)	[90]

Table 1. Cont.

Study	Temp/DHW	Duration	Location	Species	Main Results	Ref.
Comparison 1970/2017 HSE	31.4 °C	31 d	Hawaii, USA	<i>Montipora capitata</i> , <i>Pocillopora damicornis</i> , <i>Lobactis scutaria</i>	Higher calcification, delayed bleaching and mortality in 2017	[87]
HSE (HV and MV)	31.5 °C	5 d	American Samoa	<i>Acropora hyacinthus</i>	Mortality and photochemical efficiency decline: HV+ <i>Durusdinium</i> < MV+ <i>Durusdinium</i> < MV+ <i>Cladocopium</i>	[67]
HSE from RT (HV and MV)	34 °C	3 h	American Samoa	<i>Acropora hyacinthus</i>	Acclimatised: MV to HV increased heat resistance; HV to MV reduced chl <i>a</i> retention; Different expression of 74 genes	[92]
HSE (HV and LV)	30 °C	270 d	Taiwan	<i>Pocillopora damicornis</i> ,	Acclimatised: HV = control in all parameters	[93]
Comparison 1998/2005-06 BE (HV - LV)	-	Bleaching survey	Egypt, Madagascar, Seychelles, Australia, Guam, Kiribati, Cook Islands	Multiple species	Less bleaching in HV sites	[94]
Comparison multiple BEs (HV - LV)	-	Bleaching survey	Western Indian Ocean, Pacific Ocean, Caribbean Sea, GBR, Red Sea	Multiple species	Less bleaching in HV sites	[95]

HSE = Heat Stress Experiment, HV = Highly Variable, MV = Moderately Variable, LV = Low Variable, RT = Reciprocal Transplantation, BE = Bleaching Event, DHW = Degree Heating Weeks, d = days, h = hours, GBR = Great Barrier Reef.

Brown et al. [90] demonstrated ‘long-term environmental memory’ during the bleaching event in 2010. In 2000, coral colonies were rotated 180° in a manipulative experiment [96]. During the bleaching event of 2010, the sides of colonies exposed to high solar radiation before rotation in the 2000 experiment, retained four times as many symbionts than the sides exposed to low solar radiation, despite experiencing higher radiation for 10 years [90]. These experiments provide evidence that long-term acclimatisation to local conditions enhances thermal tolerance during bleaching events (Table 1). Coles et al. [87] showed evidence of acclimatisation to increasing seawater temperatures by replicating a bleaching experiment from 1970 at the same location in 2010. Because sea-surface temperature (SST) has steadily increased 1.13 °C over the last four decades, the authors experimentally increased 2.2 °C of ambient temperatures. Corals in 2017 showed higher calcification rates, delayed bleaching, and mortality compared to corals in 1970 (Table 1) [87]. Unfortunately, despite increased temperature tolerance in local corals, Hawaii suffered high coral mortality (34%) during the 2014–2017 global bleaching event, showing that high-temperature acclimatisation processes may not be occurring quickly enough to mitigate the projected length and intensity of future bleaching events [87].

2.4. Acclimatisation to High Temperature Variability

A series of backreef pools exhibiting tidal temperature variability on the island of Ofu, American Samoa, present a unique environment to study physiological differences between conspecific corals at small-spatial scales [97]. Using genetically identical coral fragments in a heat-stress experiment from both pools, Oliver and Palumbi [67] provided evidence of increased thermal tolerance when corals

have acclimatised to high temperature variability (Table 1). Corals from the highly variable (HV) pool showed lower mortality and higher photochemical efficiency, while those from the moderately variable (MV) pool suffered increased mortality and lower photochemical efficiency related to symbiont species. Corals associated with *Durisdinium* spp. exhibited an intermediate decline in photochemical efficiency, while those associated with *Cladocopium* spp. showed the highest decline [67]. Palumbi et al. [92] performed reciprocal transplantations of corals between HV and MV pools and subjected those corals to a heat stress experiment to test for acclimatisation responses to thermal stress (Table 1). Corals acquired heat sensitivity based on the pool they were transplanted to: MV pool corals acquired heat resistance when moved to HV pool, but not to the same extent of HV conspecifics, while HV to MV transplantees experienced reduced chlorophyll *a* retention, similar to the levels of native corals [92]. Mayfield et al. [93] performed a thermal stress experiment with corals from a site in Taiwan exhibiting high daily temperature fluctuations and found that, under HV conditions, physiological parameters behaved similarly to those in control corals, suggesting that individuals living under HV temperatures can acclimate to high temperatures that would cause bleaching and mortality in unacclimated corals from other regions (Table 1) [93].

Some studies have compiled data of past bleaching events, in an effort to link patterns of bleaching susceptibility within sites under high temperature variability, in a worldwide context [94,95]. Sites characterized by a high-frequency pattern of temperature variability experienced higher thermal stress during both bleaching events, with extensive bleaching reported during 1998. However, in 2005–2006, these sites experienced reduced bleaching compared to sites under low frequency patterns, due to the acclimatisation of corals to thermal stress after the 1998 bleaching event and selective adaptation of resilient corals that survived the bleaching event [94]. Safaie et al. [95] explored this concept further by collecting in situ data with remotely sensed datasets from different reef locations around the globe, along with spatiotemporally coincident quantitative coral bleaching observations. Corals regularly exposed to temperature fluctuations on daily or tidal timescales became acclimatised to thermal stress and resistant to bleaching events. More importantly, these patterns of high-frequency temperature variability to bleaching occur in many reefs worldwide [95].

2.5. Molecular Mechanisms for Acclimatisation

Most studies involving transcriptomic analyses and thermal stress have shown differential gene expression under high temperature stress compared to controls (Table 2) [98–103]. Corals exposed to experimental thermal stress presented an upregulation of genes involved in oxidative stress responses [98,99] and carbon metabolism [98]. A comparison of differences in gene expression in corals preconditioned to thermal stress showed seventy differentially expressed genes between non-preconditioned corals and controls, 42 between preconditioned corals and controls, and nine genes between non-preconditioned and preconditioned corals (Table 2) [102].

Table 2. Thermal stress studies looking at differences in gene expression.

Study	Method	Genes/Molecules	Response	Location	Species	Main Results	Ref.
HSE – gene expression	qPCR	HSP70, MnSOD, ferritin, Zn ²⁺ -metalloprotease	Oxidative stress response	GBR, Australia	<i>Acropora millepora</i>	Up-regulation in heat-stressed	[99]
HSE – gene expression	qPCR	HSP90, HSP70 Glyceraldehyde-3-phosphate dehydrogenase, α-ketoglutarate dehydrogenase, glycogen synthase, glycogen phosphorylase	Oxidative stress response Carbon metabolism	GBR, Australia	<i>Acropora aspera</i>	10.5-fold up-regulation in heat-stressed coral host genes	[98]
Short-term precondition—gene expression	cDNA micro-array	Lectins, heme-binding proteins, transcription factor AP-1, NF-κB inhibitor, thymosin, phosphate carrier protein, ferritin	Oxidative stress response	GBR, Australia	<i>Acropora aspera</i>	Different expression: 70 genes (non-preconditioned/control), 42 genes (preconditioned/control), 9 genes (preconditioned/non-preconditioned)	[102]
HSE—transcriptome wide gene expression (Thermally resilient vs. sensitive)	RNA-Seq	HSP70, HSP23/HSPB1, HSP16.2, CSMD1, Cu-Zn SOD TNFRs, TRAFs, NF-κB/Nfkb1, JNK/MAPK8	Oxidative stress response Apoptosis/immune response	American Samoa	<i>Acropora hyacinthus</i>	Up-regulation in thermal sensitive: 60 genes = “Frontloaded” in thermal resistant	[103]
HSE—transcriptome wide gene expression (RT HV – MV)	RNA-Seq	HSPs, Chaperonin proteins, CYPs TNFRs, TRAFs,	Oxidative stress response Apoptosis/immune response	American Samoa	<i>Acropora hyacinthus</i>	Different expression: 71 contigs based on pool of origin (HV/MV), 74 contigs based on pool transplanted	[93]

HSE = Heat Stress Experiment, HV = Highly Variable, MV = Moderately Variable, RT = Reciprocal Transplantation, qPCR = quantitative Polymerase Chain Reaction, HSP = Heat Stress Protein, SOD = Superoxide Dismutase, TNFR = Tumor Necrosis Factor Receptor, TRAF = Tumor Receptor Associated Family, GBR = Great Barrier Reef.

To understand the genomic basis of thermal resilience in corals, Barshis et al. [103] compared transcriptome-wide gene expression among thermally resilient and thermally sensitive conspecifics (Table 2). Sixty genes were up-regulated in thermally sensitive corals, while resilient corals already presented up-regulated genes under ambient conditions. These “frontloaded” genes facilitate a faster reaction to thermal stress at the protein level [103]. In a similar study, using reciprocally transplanted corals from HV and MV pools, transcriptome-wide gene expression analyses showed differential expression in 74 genes related to heat acclimation between genetically identical corals from both pools (Table 2) [93]. In a related study performed at the same sites, Ruiz-Jones and Palumbi [104] monitored the transcriptomic response of corals in the HV pool with a strong tidal cycle (high temperatures over 17 days). Their results bolstered the conclusions of Barshis et al. [103], showing that genes up-regulated during the hottest days, were enriched for “unfolded protein response”, an ancient eukaryotic cellular response to endoplasmic reticulum stress, which corals use as the first line of defence against thermal stress [104].

2.6. Adaptation

Adaptation, strictly defined, refers to changes in the genetic composition of a population that are passed onto the next generation through natural selection [17,44,105]. The major concern regarding global climate change is that the current rate of environmental changes will outpace the evolutionary capabilities of corals to adapt [12,14,16,19,106]. Recent evidence has shown that, in addition to phenotypic plasticity and acclimatisation, other adaptive responses in corals, such as trans-generational plasticity [107], epigenetics [108,109], and somatic mutations [110] might contribute to resilience under thermal stress. Moreover, the fast rate of asexual reproduction within the Symbiodiniaceae (days to weeks *in hospite*) [111] in combination with large population sizes within corals ($\sim 1\text{--}5 \times 10^6$ cells cm^{-2}) [112] provide the potential for mutations to develop that might enable corals to resist thermal stress [110].

Few studies have examined adaptation to local thermal history in Symbiodiniaceae dinoflagellates [113,114]. Howells et al. [113] demonstrated adaptive capacity in the symbiont *C. goreaui* (formerly type C1) in corals from two sites in the GBR with dissimilar thermal histories. Corals hosting *C. goreaui* from the cooler site presented photodamage and bleaching, while those from the hotter site exhibited no signs of stress and greater growth [113]. Chakravarti et al. [114] tested adaptation to thermal tolerance of *C. goreaui* through experimental evolution. Dinoflagellates were cultured *in vitro* at elevated temperature of 31 °C for ~ 80 generations (2.5 y), while wild-types were reared at 27 °C ambient temperature, then both cultures were tested at both temperatures. To measure physiological responses *in hospite*, both types (thermally selected and wild types) were inoculated into aposymbiotic recruits of three coral species and were exposed to both temperatures similar to *in vitro* experiments [114]. Symbionts reared *in vitro* performed better in photophysiology and growth at both temperatures, and showed lower levels of extracellular ROS. In contrast, wild-type symbionts were unable to photosynthesise or grow at high temperatures, and produced 17 times more extracellular ROS [114]. The differences were less obvious *in hospite* than *in vitro*. Cultures of corals inoculated with the thermally tolerant symbionts showed no difference in growth between 27 and 31 °C, while those inoculated with wild-types showed a negative growth trend at 31 °C, confirming an adaptation to thermal stress in *C. goreaui* after many generations living under high temperature [114].

Dixon et al. [115] revealed genetic data from the coral host that forms the heritable basis of temperature tolerance by performing a cross-fertilization experiment with coral colonies from two thermally divergent locations in GBR. The authors measured heat tolerance using the survivorship rate of larvae exposed to high temperatures and found that parents from the warmer location conferred significantly higher thermo-tolerance to their offspring, up to 10 fold increase in odds of survival, in comparison to parents from the cooler location. Dixon et al. [115] also identified “tolerance-associated genes” (TAGs), whose expression before stress predicted high survivorship rates in larvae under thermal stress, dissimilar from frontloaded genes [103]. When TAG expression was compared with

parental colonies after three days of heat stress, they were negatively correlated with long-term heat stress response similar to the larval response, indicating that the larval heat tolerance results from the absence of pre-existing stress and not from prior up-regulation of heat stress genes through frontloading [115].

Krueger et al. [116] presented evidence that *Stylophora pistillata* underwent selection for heat tolerance in the Red Sea, after spending 47 days at 1–2 °C above their long-term summer maximum and showed an increase in primary productivity. Fine et al. [117] demonstrated how different corals species showed no signs of stress after exposure to 33 °C for four weeks and proposed that corals that colonised the Gulf of Aqaba after the last ice age had to cross exceedingly warm waters (>32 °C in the summer) at the entrance of the Red Sea, maintaining this adaptation to heat tolerance until the present day.

2.7. Heterotrophy

Heterotrophic carbon can become a significant energy source for some coral species when phototrophic carbon is unavailable, such as during a bleaching event (Table 1) [118]. Some studies have shown how heterotrophy replenished energy reserves in corals exposed to high temperatures [119] and during the recovery phase [120]. Similarly, Borell and Bischof [121] showed higher photochemical efficiency in fed corals compared to unfed corals after a mild thermal stress experiment. Also, Borell et al. [122] demonstrated how heterotrophy sustained photosynthetic activity and energy reserves in thermally stressed corals.

In a study which developed an energy-budget model linking coral bleaching and mortality risk, authors concluded that the time between the start of severe bleaching and the beginning of mortality is influenced by the amount of lipid stores corals have before the bleaching event and their capacity to acquire energy through heterotrophy [123]. With a stable isotope ¹³C pulse-chase labelling experiment, Hughes et al. [124] demonstrated that, after exposure to high temperatures, coral hosts incorporated heterotrophic labelled carbon for storage and to stimulate endosymbiont recovery. Even after recovery from bleaching, 75% of carbon in newly acquired lipids was sourced heterotrophically [125], and corals continued assimilating heterotrophic carbon for up to 11 months after the bleaching experiment [126].

Nonetheless, the capacity for heterotrophic plasticity is compromised after two consecutive bleaching events [127]. Researchers experimentally bleached corals for 2.5 weeks, transferred corals to the field for recovery, and then repeated the bleaching experiment after one year. After the first thermal stress experiment, zooplankton and dissolved organic carbon (DOC) allowed the metabolic demand of bleached corals to be met; however, neither form of heterotrophic carbon was able to contribute to the energy budget of both species after the second bleaching experiment, suggesting that the capacity for heterotrophic plasticity is compromised under annual bleaching events [127] and corals need to depend on their energy reserves and/or symbiont association to survive repeated bleaching [128].

3. Perspectives for the Future

Because the loss of corals around the world would be a devastating consequence of human influence on earth, strategies to mitigate the damage and improve coral's thermal tolerance are currently being taken into consideration. For example, assisted colonization, migration and/or gene flow contemplate the movement of colonies or larvae of the same species living at different latitudes. 'Warm-adapted' corals can be transplanted to high latitude areas, where conspecifics living in colder environments, are vulnerable to thermal stress [129–131]. Assisted evolution has the potential to increase thermal stress tolerance in corals through various approaches: preconditioning acclimatisation (see Section: 'Thermal stress acclimatisation') and trans-generational acclimatisation, changes in microbial communities [132], selective breeding [133], mutagenesis [134], and the use of "CRISPR/Cas9" genome editing technology [135]. The use of 'strong corals' naturally adapted to high temperature extremes, such as corals originating from the Persian Gulf or Red Sea, as possible seedlings to repopulate areas where corals have disappeared [117,136–138] is also being considered. Unfortunately, none of

these measures seem to be able to keep pace with the current rate of climate change, with the time between recurrent bleaching events becoming increasingly too short to allow complete recovery of coral reef ecosystems [139]. Despite recent advances in research methods and technology, such as transcriptomics [140], financial and logistical limitations to implement these actions remain [141], especially at large scales [130], and it takes many years to safely deploy new technology after social and political scrutiny [142].

Other conservation measures under consideration include designing better marine protected areas (MPAs) [143] or networks of MPAs [144–146], taking into consideration larval dispersal, connectivity and distribution patterns in areas with thermally tolerant corals [147] and including ‘refugia’ in areas where coral reefs have proven to be resilient to climate change [21,43,148,149]. This might help avoid the “protection paradox” in MPAs, in which vulnerable species are protected from local pressures, like fishing; yet while these species recover, they might be more sensitive to global pressures, like bleaching events [144]. Nevertheless, well-protected reefs within MPAs are not shielded from thermal stress [150,151]. After the last bleaching event, this was confirmed for MPAs [152], and for remote and isolated reefs with almost no direct human pressures [23,24,27,153–155].

The integration of assisted evolution [131,134] into coral reef restoration programs [156,157] to increase the resilience of already degraded ecosystems [41] is one strategy that has proven to be successful. Morikawa and Palumbi [158] used naturally thermal-tolerant corals from American Samoa to show that resilient corals can survive multiple bleaching events, providing the first proof that ecosystem engineering for conservation might be a resilience restoration tool of great importance in our climate changed future [158].

Evidence from reciprocally transplanted coral clones between sites with different thermal histories shows how individual coral colonies can shift their thermal threshold and thermal tolerance [93,159,160]. It is clear that many coral species are acclimatising and adapting to rapid changes in climate and their mechanisms differ among species and localities [67,82,83,89,90,113,115,161]. However, under current greenhouse gas emission projections, coral reefs worldwide are likely to change into new configurations with new assemblages of species [19,149,162–165]. These changes are happening fast, the GBR being the best example. After the 2014–2017 mass bleaching event, even the most ‘pristine’ areas in the northern GBR saw high mortality regardless of reefs’ individual management status, proving that current management toolsets are insufficient to protect coral reef ecosystems from climate change [20,152]. The Paris Agreement was a first step to tackle the climate crisis, but no major industrialized country is meeting its pledges to control and reduce their greenhouse gas emissions [166]. It is imperative that societies completely change our dependence on fossil fuels, therefore addressing the root causes of climate change.

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