

Cooling and shading corals: in-situ mitigation of bleaching through engineered refuges

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Abstract

Marine heatwaves are driving recurrent coral bleaching and mass mortality, threatening reef persistence as ocean warming outpaces coral adaptive capacity. Locally reducing temperature or irradiance could mitigate bleaching and its physiological consequences, yet the conservation potential of these interventions remains poorly resolved, particularly for artificial cooling, which has yet to be demonstrated under natural reef hydrodynamics. Here, we show that sustained deep-seawater cooling of up to 2°C largely prevented severe heat stress accumulation during a marine heatwave and bleaching across three coral species, including a highly susceptible foundational species, effectively preserving coral-algal symbiosis, symbiont associations and host energetic integrity. By contrast, 83% shading reduced bleaching and mortality only in moderately susceptible species but imposed species-specific energetic and growth constraints. Temporarily manipulating temperature and light can thus help protect corals during climate extremes, providing opportunities to engineer climate-resilient conservatories to preserve coral diversity supporting adaptation to ocean warming.

Introduction

Marine heatwaves (MHWs) have become a major driver of coral reef decline, triggering recurrent mass bleaching and mortality events worldwide¹. Their frequency, intensity and duration have increased markedly over recent decades, with successive global bleaching events affecting even historically resilient reef systems². Thermal anomalies of only ~ 1–2°C above local summer maxima are sufficient to disrupt cellular homeostasis in both the coral host and its *Symbiodiniaceae* symbionts, generating oxidative stress that can break down the symbiosis, thus triggering bleaching³. Under high irradiance, bleaching severity is further exacerbated as heat-impaired photosystem repair promotes the accumulation of photodamage in symbionts^{3,4}.

Because *Symbiodiniaceae* supply up to 90% of the coral host's energetic requirements⁵, their loss rapidly compromises carbon acquisition and metabolic performance, ultimately threatening survival if stress persists^{6,7}. Even when colonies survive, they frequently experience sublethal effects persisting for months to years following bleaching, including depleted energy reserves, reduced calcification, impaired reproduction and diminished capacity to withstand subsequent disturbances^{8–12}. As global warming continues to intensify, many reefs are projected to experience annual or near-annual bleaching within decades¹³, leaving insufficient time for recovery and ultimately threatening coral population and ecosystem persistence worldwide^{14,15}.

Although rapid reductions in greenhouse gas emissions remain essential to curb climate change, mitigation efforts are lagging behind while coral reefs continue to decline¹⁶. Consequently, growing attention has been directed towards complementary local interventions capable of reducing bleaching and subsequent mortality to preserve vulnerable coral populations until broader climate mitigation efforts take effect¹⁷. This may be particularly important where recurrent mass mortality substantially

reduces population sizes and standing genetic variation, progressively filtering out susceptible species and genotypes and constraining the diversity upon which acclimation and, crucially, adaptation can act¹⁸. Locally protecting ecologically valuable coral populations through acute climate extremes could therefore help retain ecological function while maintaining the adaptive potential needed for persistence under ocean warming,

Protecting vulnerable components of coral diversity through acute climate extremes could therefore prevent their local extinction^{19,20}, while preserving living biological resources for future reproduction, population replenishment and restoration²¹. Such targeted protection may help retain both ecological function and the adaptive potential needed for persistence under continued ocean warming.

Natural environmental refuges provide compelling evidence that moderating the main environmental drivers of bleaching can substantially increase coral resistance during MHWs. Corals inhabiting shaded reef habitats, mesophotic depths or areas influenced by cold-water upwelling often experience reduced thermal and/or light stress, resulting in lower bleaching prevalence, greater survival and, in some cases, enhanced recovery^{7,22–25}. Engineering similar protective conditions through the injection of deeper, colder seawater to alleviate thermal stress, or through artificial shading to reduce the light-dependent component of bleaching, could therefore help create temporary refuges during extreme heat events²⁶. However, despite nearly a decade of research, their conservation potential remains largely unresolved as current evidence mostly derives from short-term thermal stress experiments conducted *ex situ*, and has primarily focused on immediate bleaching responses^{27–33}. Artificial cooling, in particular, has so far been explored only through modelling and aquarium experiments^{33–35}, leaving its technical feasibility and effectiveness in mitigating bleaching under natural reef hydrodynamics unresolved. More broadly, whether shading and cooling interventions can not only prevent coral bleaching and mortality but also preserve the physiological functioning and energetic integrity that underpin long-term coral performance and resilience during a real MHW remains unknown.

Here, we tested whether temporarily manipulating temperature or irradiance *in situ* could reproduce the protective features of natural refuges during the major 2024 MHW at Tetiaroa atoll, French Polynesia. Cold deep seawater (11°C; from 960m) discharged from an existing seawater air-conditioning (SWAC) system³⁶ was continuously diffused over coral nurseries to reduce thermal stress, while high-attenuation shading was evaluated comparatively as a simpler and more readily deployable mitigation strategy specifically targeting light stress. Across three coral species (*Acropora globiceps*, *Pocillopora cf. tuahiniensis* and *Pavona duerdeni*) spanning contrasting bleaching susceptibilities and life-history strategies, we assessed responses across multiple biological scales, from symbiont photopigments, densities and community composition to host energetics, growth and survival, from pre-bleaching conditions through post-heatwave recovery. We hypothesized that both interventions would mitigate bleaching by alleviating environmental stress and preserving the coral-algal symbiosis, but that cooling would provide broader physiological protection by directly reducing temperature – the main driver of bleaching³ – without restricting light available for photosynthesis, whereas shading could impose

energetic and growth trade-offs³⁷. Deep-water diffusion generated sustained localized cooling reaching $\sim 2^{\circ}\text{C}$ under natural reef hydrodynamics and prevented most heat stress from accumulating, providing a proof-of-concept for coral cooling. Cooling consequently prevented bleaching across all three species, maintained initial symbiont associations and preserved host energetic integrity, whereas shading reduced bleaching and mortality only in moderately susceptible species and imposed species-specific physiological trade-offs. Together, our results provide evidence that environmental refuges can be engineered, opening opportunities to locally safeguard vulnerable coral diversity under accelerating climate change.

Results

Mitigation of bleaching-inducing stressors

The 2024 MHW developed from February to July, reaching 4.4 Degree Heating Weeks (DHW), matching the intensity of the previous and most intense MHW recorded locally (Fig. 2a; Supplementary Fig. 1). Cooling and shading were deployed on 1 March, when thermal anomalies above the maximum monthly mean (MMM) had already begun accumulating ($\text{AHS}_{0^{\circ}\text{C}}$), and maintained for 4.5 months until thermal stress had dissipated in mid-July (Figs. 1, 2a in grey shading).

Under natural reef hydrodynamics, diffusion of 11°C deep seawater³⁶ generated sustained localized cooling throughout the intervention. Cooling intensity was strongly modulated by current speed, following a sigmoidal relationship ($R^2 = 68\%$; Fig. 2b-c). Temperature reductions exceeding 0.5°C occurred under low current, at speeds $< 0.16 \text{ m s}^{-1}$, conditions that prevailed 63% of the monitored period (Fig. 2c-d). Cooling of $1.0\text{--}1.5^{\circ}\text{C}$ occurred approximately one-quarter of the time, with episodic maxima reaching 1.9°C relative to ambient seawater (Fig. 2d; Supplementary Fig. 2). Overall, daily mean temperature was reduced on every day of the intervention, by $0.15\text{--}1.25^{\circ}\text{C}$, with an average cooling of $0.71 \pm 0.01^{\circ}\text{C}$ ($\pm \text{se}$; $p < 0.001$; Fig. 2e-f, Supplementary Table 1). Cooling also increased the daily thermal range experienced by corals by 42% ($1.18 \pm 0.03^{\circ}\text{C}$, up to 2.3°C) relative to control ($0.83 \pm 0.03^{\circ}\text{C}$, up to 1.7°C ; $p < 0.001$; Fig. 2g; Supplementary Table 1).

This sustained temperature reduction substantially limited the accumulation of *in-situ* heat stress (AHS). Low-magnitude heat stress ($\text{AHS}_{0^{\circ}\text{C}}$) had already reached $2.6^{\circ}\text{C-weeks}$ before interventions were deployed, and subsequently peaked at $8.1^{\circ}\text{C-weeks}$ in control and shaded nurseries, but was nearly halved under cooling ($4.4^{\circ}\text{C-weeks}$; Fig. 2a). More severe heat stress, accumulating above $\text{MMM} + 1^{\circ}\text{C}$ ($\text{AHS}_{1^{\circ}\text{C}}$), was largely avoided under cooling ($0.4^{\circ}\text{C-weeks}$ vs $3.4^{\circ}\text{C-weeks}$ uncooled) and dissipated one month earlier (Fig. 2a).

In parallel, shade cloths installed above nursery frames strongly reduced irradiance, without affecting thermal exposure (Fig. 1d). Midday photosynthetically active radiation (PAR; 10:00–14:00) declined from $418 \pm 9 \mu\text{mol m}^{-2} \text{ s}^{-1}$ (max $1370 \mu\text{mol m}^{-2} \text{ s}^{-1}$) under ambient conditions to $67 \pm 3 \mu\text{mol m}^{-2} \text{ s}^{-1}$ (max

363 $\mu\text{mol m}^{-2} \text{s}^{-1}$) under shading. Daily light integral was consequently reduced by 83%, from 10.3 ± 0.5 to $1.7 \pm 0.2 \text{ mol photons m}^{-2} \text{d}^{-1}$ (Friedman $\chi^2(1) = 30$, $p < 0.001$; Fig. 3).

Cooling-induced nitrogen enrichment

Beyond thermal mitigation, injection of water pumped at 960m depths³⁶ altered the chemical environment surrounding cooled corals. Dissolved oxygen and pH were only marginally reduced under cooling, by 0.05 mg L^{-1} and 0.018 units, respectively (both $p < 0.001$), while phosphate ($\sim 0.253 \mu\text{M}$, $p = 0.719$) and ammonium concentrations ($\sim 0.100 \mu\text{M}$; $p = 0.053$) remained comparable to ambient seawater (Supplementary Fig. 3; Supplementary Table 2). Conversely, nitrate concentrations increased 13-fold, from $0.095 \pm 0.016 \mu\text{M}$ under ambient conditions to $1.236 \pm 0.210 \mu\text{M}$ under cooling ($p < 0.001$), while nitrite concentrations declined by 40% ($p = 0.019$), but contributed little to overall nutrient availability ($0.013 \pm 0.002 \mu\text{M}$ in control vs $0.008 \pm 0.001 \mu\text{M}$ under cooling). Overall, deep-seawater diffusion increased dissolved inorganic nitrogen (DIN) approximately 6-fold, from $0.21 \pm 0.03 \mu\text{M}$ to $1.37 \pm 0.22 \mu\text{M}$ ($p < 0.001$; Supplementary Table 2).

Bleaching and photophysiological responses

After nearly two months of intervention, at peak heat stress in late April, bleaching responses differed markedly among species under ambient conditions. All *Acropora globiceps* genotypes bleached, 80% severely, whereas bleaching affected 0.40 ± 0.13 of *Pocillopora cf. tuahiniensis* genotypes, mostly partially, and 0.27 ± 0.07 of *Pavona duerdeni* genotypes, mostly severely (Figs. 4, 5, Supplementary Figs. 4, 5).

Cooling prevented bleaching across all three species, preserving the coral-algal symbiosis throughout thermal stress (Figs. 4, 5, Supplementary Figs. 4, 5). Symbiont densities were 14-fold higher than controls in *A. globiceps* ($p < 0.001$), 72% higher in *P. cf. tuahiniensis* ($p = 0.007$), and twice as high in *P. duerdeni* ($p < 0.001$) during active cooling (Supplementary Fig. 10). Cellular chlorophyll a content was also 33–37% higher in *A. globiceps* ($p = 0.024$) and *P. duerdeni* ($p = 0.009$; Supplementary Fig. 6). Four months after cooling ceased, in November, most photophysiological differences had dissipated as symbiont densities and photopigments decreased in previously cooled fragments, converging towards recovering control levels (Supplementary Figs. 6, 7). *P. duerdeni* was the exception, retaining elevated symbiont densities from April to November ($p = 0.313$), remaining still visibly darker than controls in November ($p < 0.001$; Fig. 5, Supplementary Figs. 6, 7, 8).

By contrast, shading provided species-dependent bleaching protection. It provided no detectable protection in the highly susceptible *A. globiceps*, with all genotypes bleaching as under ambient conditions (all $p > 0.16$; Fig. 5, Supplementary Figs. 6, 8). However, it reduced bleaching incidence more than 4-fold across *P. cf. tuahiniensis* and *P. duerdeni* (treatment effect: $\chi^2(1) = 7.21$, $p = 0.007$), with only one genotype of each bleaching (treatment x species effect: $\chi^2(1) = 0.13$, $p = 0.716$; Supplementary

Fig. 9). Symbiont densities remained comparable to controls during active shading ($p > 0.1$), while cellular chlorophyll a and c_2 contents were 49–79% higher relative to controls in both species ($p < 0.03$; Supplementary Figs. 6, 7). These photoacclimatory responses were reversible, with no photophysiological differences remaining four months after shade removal (all $p > 0.09$; Supplementary Figs. 6, 8).

Survival and recovery trajectories

Bleaching translated into markedly different recovery trajectories among species. Despite severe bleaching, *A. globiceps* was highly resilient, with all but one bleached control genotype recovering following the heatwave. By contrast, only half of bleached *P. duerdeni* were resilient, while none of the *P. cf. tuahiniensis* recovered (Fig. 4, Supplementary Fig. 5).

By preventing bleaching, cooling therefore prevented any bleaching-related mortality (Fig. 4). However, this did not translate into higher overall survival (all $p > 0.4$), because mortality unrelated to bleaching partly offset these benefits. This was particularly evident in cooled *P. cf. tuahiniensis*, for which mortality from other causes was 5-fold higher relative to controls ($p = 0.001$; Supplementary Fig. 10a-b). These mortalities were frequently associated with algal mats progressively overgrowing live tissue (Supplementary Fig. 10c).

Where shading reduced bleaching, it also reduced subsequent mortality. Bleaching-related mortality was sixfold lower in shaded *P. cf. tuahiniensis* than in controls ($p = 0.028$), although this did not significantly increase overall survival ($p = 0.182$). In *P. duerdeni*, shading prevented mortality entirely, compared with 40% mortality under ambient conditions ($p = 0.005$; Supplementary Fig. 10a-b).

Energetic performance

Cooling prevented the energetic depletion and growth impairment associated with bleaching during peak heat stress (April; Fig. 6). In both *A. globiceps* and *P. duerdeni*, protein, lipid and carbohydrate reserves remained elevated relative to controls, resulting in 43–75% greater total energy reserves (all $p < 0.007$; Supplementary Fig. 11) and 52–64% higher growth rates (both $p < 0.010$; Supplementary Fig. 12). In *P. cf. tuahiniensis*, energy reserves did not differ from controls (all macromolecules $p > 0.5$), while growth was 82% higher under active cooling ($p < 0.001$).

Benefits of cooling largely persisted after thermal stress had subsided, even four months post-intervention, as energy reserves and growth remained elevated in all three species. Energy reserves and growth remained stable between April and November in cooled *P. duerdeni* and *P. cf. tuahiniensis* (all $p > 0.5$; Fig. 6, Supplementary Fig. 11). As control *P. cf. tuahiniensis* accelerated growth during recovery (+80% in April–November vs February–April, $p = 0.004$), however, growth no longer differed between cooled and control fragments by November ($p = 0.787$; Supplementary Figs. 7, 12). As growth did not change in control *P. duerdeni* post-MHW ($p = 0.577$), cooled fragments still exhibited 38% higher growth rates than

control fragments ($p = 0.048$; Fig. 6, Supplementary Fig. 12). In *A. globiceps*, the legacy of severe bleaching remained evident seven months after peak heat stress: energy reserves of control fragments remained 19% lower than those of previously cooled fragments ($p = 0.031$; Supplementary Fig. 11). Although growth increased during recovery in both control (+ 42%, $p = 0.026$) and previously cooled fragments (+ 52%, $p = 0.007$), growth remained 61% higher in the latter ($p = 0.003$; Supplementary Fig. 12).

In contrast, shading constrained growth despite relatively limited effects on energy storage. Shaded *A. globiceps*, in which bleaching was not mitigated, followed the same trajectory as controls, with comparable depletion of energy reserves and reduced growth (all $p > 0.07$; Fig. 6, Supplementary Figs. 7, 11, 12). In *P. duerdeni*, energy reserves remained unaffected ($p > 0.1$), yet growth was 32% slower than in controls during shading ($p = 0.014$), and subsequently recovered after shade removal (control vs shade $p = 0.429$). Physiological constraints were strongest in *P. cf. tuahiniensis*, where total stored energy was 22% lower ($p = 0.009$), and growth was 5.4-fold lower than in controls during active shading (both $p < 0.01$; Supplementary Figs. 11, 12). Despite partial replenishment of energy reserves after shade removal, growth remained less than half that of controls during recovery ($p < 0.001$). Energy reserve composition remained stable across treatments and timepoints (Supplementary Fig. 13).

Symbiodiniaceae community dynamics

Prior to intervention (February, t_0), *Symbiodiniaceae* communities, characterized from ITS2 type profiles, differed strongly among host species ($p < 0.001$, $R^2 = 48\%$; Supplementary Table 3). Most corals hosted a single dominant ITS2 type profile within the genus *Cladocopium* (Fig. 6a). *A. globiceps* exclusively hosted C3-type profiles (85% C3f/C3ae-C3h-C3j-C3bj-C3g-C3ph-C3ba-C3cv; 3 profiles identified), *P. cf. tuahiniensis* was dominated by C1-type profiles (mostly C1d/C42.2/C1-C1b-C3cg-C42bg-C115k-C3-C1au; 4 profiles), whereas *P. duerdeni* harboured more diverse assemblages, largely co-dominated by C42.2/C1 and C21 profiles (12 profiles; Fig. 7a, Supplementary Fig. 14).

Symbiont communities remained stable throughout the experiment in *P. duerdeni* and *P. cf. tuahiniensis*, regardless of treatment (PERMANOVA treatment x timepoint: $p = 0.270$ and $p = 0.357$ respectively; Table 1), indicating that bleaching mitigation occurred without consistent restructuring of associations.

Table 1

Permutational analysis of variance (PERMANOVA) results on Symbiodiniaceae assemblages within coral hosts. PERMANOVA were performed separately for each species on the most abundant ITS2 profiles (> 0.01%).

Species	Variable	Df	SumOfSqs	R ²	F	p	
Acropora globiceps	Timepoint	2	1,416	0,058	4,369	0,0013	***
	Treatment	2	1,807	0,074	5,575	0,0001	***
	Timepoint:Treatment	4	1,693	0,069	2,612	0,0101	*
	Residual	121	19,612	0,800			
	Total	129	24,529	1,000			
Pocillopora cf. tuahiniensis	Timepoint	2	0,057	0,011	0,570	0,6939	
	Treatment	2	0,100	0,019	1,002	0,2836	
	Timepoint:Treatment	4	0,193	0,036	0,968	0,3573	
	Residual	100	4,993	0,934			
	Total	108	5,344	1,000			
Pavona duerdeni	Timepoint	2	0,370	0,008	0,481	0,707	
	Treatment	2	0,665	0,014	0,865	0,1532	
	Timepoint:Treatment	4	1,117	0,024	0,726	0,2704	
	Residual	114	43,823	0,953			
	Total	122	45,975	1,000			

By contrast, symbiont communities in *A. globiceps* shifted significantly during bleaching under ambient conditions (February vs April, $p = 0.018$), primarily through changes among *Cladocopium* lineages towards C1-type profiles (Fig. 7, Supplementary Fig. 15, Supplementary Table 4). These communities did not shift further during recovery (April vs November: $p = 0.077$) and remained significantly different from their initial composition (February vs November: $p = 0.037$, $R^2 = 22\%$). Shading did not prevent this bleaching-associated restructuring (February vs April, $p = 0.005$; control vs shade $p = 0.100$), although communities partly shifted back towards their initial composition after shade removal (April vs November: $p = 0.036$; February vs November: $p = 0.010$, $R^2 = 9\%$). In contrast, symbiont communities of cooled *A. globiceps* remained stable throughout the experiment (all temporal comparisons $p > 0.2$, $R^2 = 3\text{--}7\%$), thereby preventing the bleaching-associated symbiont restructuring (control vs cooled $p < 0.02$; Supplementary Table 4).

Discussion

Sustained localized sub-2°C cooling under natural reef hydrodynamics provided substantial protection to coral species spanning contrasting bleaching susceptibilities and life-history strategies during a severe MHW, effectively preserving coral-algal symbiosis, host energetic condition and growth. By translating artificial cooling from previous aquarium experiments^{27,33} and modelling approaches^{34,35} into natural reef conditions, our study demonstrates that moderate thermal refuges can be engineered to escape the major effects of MHWs even on an exposed reef experiencing continuous hydrodynamic forcing. Under ambient conditions, combined thermal and light stress led to the partial or even complete breakdown of the symbiosis, triggering canonical bleaching cascades. Severe symbiont loss in all *Acropora globiceps*, as well as a subset of *Pavona duerdeni*, and partial loss in *Pocillopora cf. tuahiniensis* disrupted photoautotrophic carbon acquisition, likely compounded by reduced carbon translocation from remaining symbionts³⁸. Although increased heterotrophy can partly compensate for this loss³⁹, it rarely fully offsets autotrophic deficits and may itself be impaired under heat stress^{40,41}. Consequently, corals catabolized stored energy reserves, particularly evident in severely bleached *A. globiceps*, likely to sustain respiratory and metabolic demands exacerbated under stress⁴². Growth was concomitantly reduced, consistent with the reallocation of limited energetic resources away from calcification towards maintenance and survival, as often documented during and after bleaching^{10,11,38}. Despite largely surviving severe bleaching, unprotected *A. globiceps* still exhibited depleted energy reserves and reduced growth rates seven months after peak thermal stress, illustrating the prolonged physiological legacy that typically follow bleaching^{9,12,14}, as recovery of nutrient transfer and host energy stores to pre-bleaching levels can require up to a year in resilient corals^{12,43}.

Cooling prevented this physiological cascade from unfolding by preventing severe heat stress from accumulating, thereby keeping corals below dysbiosis thresholds. By maintaining high symbiont densities and chlorophyll content, cooled corals retained their photoautotrophic capacity³⁹, preserving host energetic reserves and investment in growth throughout thermal stress and subsequent recovery. Cooling also helped maintain initial symbiotic associations, preventing, for instance, the restructuring among *Cladocopium* lineages observed following bleaching in *A. globiceps*. Although the functional consequences of shifts within *Cladocopium* spp. remain poorly resolved⁴⁴, maintaining stable symbiotic partnerships may contribute to sustaining holobiont carbon budgets and energetic performance^{45,46}. More broadly, bleaching commonly promotes shifts toward more thermotolerant symbionts such as *Durussdinium* spp.^{45,47}, which may enhance short-term tolerance and resilience^{48,49}, but can also reduce photosynthetically derived carbon translocation to the host⁵⁰, constraining growth, reproduction and thus long-term demographic performance^{46,51}. Consequently, here, thermal stress was sufficiently alleviated to prevent destabilization of the coral-algal symbiosis, providing benefits that extend well beyond immediate bleaching prevention. Cooling can therefore preserve holobiont function while preventing prolonged physiological trade-offs typically accompanying bleaching and subsequent recovery.

Engineering thermal refuges through deep-water injection inevitably modifies environmental conditions beyond mean temperature, requiring consideration of potential co-benefits and trade-offs. Together with

thermal stress mitigation, the increased thermal variability generated by cooling may also have contributed to stress acclimation and enhanced thermotolerance^{52,53}. Importantly, however, temperature range remained within biologically safe bounds, limiting risk of secondary stress. Natural internal wave and upwelling events commonly reduce temperatures by 1–4°C for hours or days, alleviating bleaching^{24,54}, whereas large-amplitude and abrupt cooling of 5–9°C, usually short-lived (< 1h), have been shown to induce cold stress, particularly when corals are not acclimatized^{27,55,56}. Additionally, large-amplitude intermittent cooling may have limited capacity to reduce cumulative heat exposure when pulses are too infrequent – for instance, a daily ~ 30-min pulse of ~ 5°C cooling experimentally reduced severe thermal stress by only 26% in laboratory settings³³. By contrast, the sustained sub-2°C cooling achieved here was both safer, avoiding extreme fluctuations, and more effective at mitigating thermal stress, suggesting that relatively small but persistent temperature reductions may provide greater protection.

Deep-water injection also altered local nutrient availability, increasing dissolved inorganic nitrogen (DIN) 6-fold to ~ 1.37 µM – primarily by enriching nitrates. Excess nitrogen availability can destabilize the symbiosis and increase bleaching susceptibility, when phosphate is limiting, as coral hosts normally regulate nitrogen supply to their symbionts (N:P ratio > 15; Wiedenmann et al. 2013; Rosset et al. 2017; Jung et al. 2025). However, background phosphate concentrations were relatively high at Tetiaroa (~ 0.25 µM; N:P ratio = 5.5:1), thereby limiting the risk of nutrient imbalance associated with nitrate enrichment under cooling^{58,60}. Instead, moderate nitrogen enrichment stimulated symbiont proliferation and increases in photopigments, suggesting enhanced photosynthetic capacity rather than nutrient-driven dysbiosis here⁶⁰. Responses nevertheless differed among hosts: whereas *P. duerdeni* maintained elevated symbiont densities without detectable energetic and physiological costs after cooling ceased, *A. globiceps* subsequently reduced symbiont abundance while growth increased, suggesting contrasting host-symbiont regulatory strategies to nitrate enrichment. This trade-off in *A. globiceps*⁵⁰ remained nonetheless minor relative to the energetic depletion observed in unprotected bleached corals. Nutrient enrichment may, however, have contributed to turf proliferation on some cooled (younger) *P. cf. tuahiniensis* fragments, consequently offsetting bleaching-related survival benefits. Because such cooling would be intended for temporary deployment during episodic heat events rather than continuous operation, risks associated with nutrient enrichment and broader community shifts appear limited – except in areas where algal competitors are already favoured⁶¹.

Artificial shading mitigated bleaching through a fundamentally different physiological pathway from cooling. Rather than reducing thermal stress, shading decreased irradiance by 83%, thereby alleviating the light-dependent amplification of thermal stress that promotes photoinhibition and accelerates bleaching^{3,28–30}. This effectively reduced bleaching incidence more than 4-fold in moderately bleaching-susceptible *P. cf. tuahiniensis* and *P. duerdeni*. Unbleached fragments exhibited typical photoacclimatory responses to reduced light availability, increasing cellular chlorophyll a and c₂ content rather than symbiont densities to enhance light harvesting without substantially increasing symbiont maintenance costs^{62,63}. However, photoacclimation, and potentially increased heterotrophic feeding³⁹, only partly

compensated for reduced irradiance. Unlike cooling, the bleaching protection provided by shading came with physiological trade-offs, consistent with reduced autotrophic carbon acquisition under prolonged light limitation^{37,39}. While energy reserves remained unaffected in shaded *P. duerdeni*, growth was moderately and temporarily reduced. By contrast, both energy reserves and growth were substantially and persistently reduced in *P. cf. tuahiniensis*, revealing energetic constraints comparable to those observed in severely bleached corals^{11,43}. Such contrasting responses likely reflect species-specific capacities to downregulate metabolism⁶⁴ or compensate heterotrophically under resource limitation³⁹. Shading can therefore prevent the energetic costs associated with bleaching while simultaneously imposing a different form of resource limitation when too intense. Lower shading intensities may reduce these energetic trade-offs, but effective protection will still likely require sufficient light attenuation to reduce irradiance below levels at which excess excitation pressure exacerbates thermal stress²⁹. This balance may be particularly important on very shallow reefs, where incident irradiance can be substantially higher and strong attenuation may therefore be required to achieve physiologically protective light levels and, crucially, maximize protection.

The effectiveness of shading also depended strongly on species-specific susceptibility to thermal stress, making deployment timing particularly important. Because shading can only alleviate light stress and its interaction with temperature^{28,30,65}, its protective capacity may decline once heat-driven damage has already accumulated⁶⁶. Elevated temperatures can damage host proteins, increase metabolic reactive oxygen species (ROS) production, and inhibit photosystem repair³. Crucially, substantial low-magnitude heat stress had already accumulated before deployment. If repair capacity was already compromised at this stage, reducing irradiance alone may have been insufficient to mitigate photoinhibition and bleaching^{3,66}, as suggested by the lack of protection observed in *A. globiceps* here. Earlier deployment of shading, before any thermal anomalies begin to accumulate, could therefore substantially improve protection for highly bleaching-susceptible taxa⁶⁶, for which even minimal thermal anomalies may be sufficient to initiate physiological damage. Importantly, despite its physiological trade-offs, shading retained substantial conservation value where bleaching was successfully mitigated, as survival improved in both protected species. Optimizing shade intensity and deployment timing will therefore be critical to maximize bleaching protection while minimizing prolonged resource limitation.

Beyond nursery settings, both interventions have potential for broader deployment. Several deep ocean water systems, such as SWAC and Ocean Thermal Energy Conversion (OTEC) technology, are already operational, planned or under construction, in many tropical reef regions worldwide to provide low-carbon cooling, electricity and freshwater^{67,68}. Cold-water discharge from such infrastructures could therefore be repurposed for reef conservation through relatively simple agriculture-like diffusion networks. Cooling intensity and spatial distribution can be tuned by adjusting cold-water flow rate, pipe-network density, and outlet diameter and spacing, allowing future systems to be adapted to local hydrodynamic conditions and MHW severity, and potentially extended over reef areas on the order of tens of square meters³⁴ – although whether comparable thermal mitigation can be achieved at these spatial scales remains to be demonstrated. Temperature reductions on the order of 1–2°C may be

sufficient to offset much of the thermal anomaly associated with contemporary MHWs⁶⁹. Here, sustained sub-2°C cooling largely prevented severe heat stress from accumulating when ambient temperatures exceeded the local maximum monthly mean by up to 1.6°C. Unlike natural upwelling or internal-waves events, whose occurrence may not coincide with peak thermal anomalies to mitigate bleaching^{7,70,71}, engineered cooling can be aligned with heatwave progression to create temporary thermal refuges during periods of greatest bleaching risk. Nevertheless, the suitability of deep-water cooling will remain strongly site dependent. Hydrodynamic conditions determine cold-water retention and dispersal, while deep-water chemistry, benthic responses, infrastructure requirements, energetic costs and governance constraints will determine whether implementation provides a net conservation benefit⁶⁷. Where access to deep seawater can be achieved and suitable infrastructures exist⁷², cooling appears particularly suited to protecting nurseries with endangered or rare species, or high-value reef habitats. Shading is comparatively cheaper and more broadly deployable, but its effectiveness will ultimately depend on local coral assemblage composition^{28,30} and comes with greater physiological trade-offs. Floating shading systems could provide a readily deployable means of protecting larger reef areas, with modelling suggesting that large-scale shading could substantially increase coral cover relative to unshaded reefs under future warming scenarios⁷³.

With MHWs and bleaching events projected to become near-annual within decades¹³, preserving the long-term energetic integrity of corals may be as critical as preventing immediate mortality. Incomplete energetic and physiological recovery between successive events can ultimately turn “winners” into “losers”¹⁴, progressively eroding coral fitness, reproductive capacity and demographic resilience^{8,9,74}. By maintaining symbiosis, growth and lipid reserves that support future reproductive investment⁷⁴, cooling may therefore help sustain local demographic and reproductive processes that underpin reef persistence⁷⁵. Shading, despite its energetic trade-offs, still offers substantial conservation value through its capacity to prevent bleaching and subsequent mortality. Importantly, such interventions need not protect entire reef ecosystems to provide conservation value. By buffering highly diverse coral nurseries from acute climate extremes, climate-resilient coral biodiversity conservatories could be established as living repositories of vulnerable species, populations and genotypes that might otherwise be progressively lost from natural reefs under recurrent marine heatwaves^{20,76}. Such protected repositories could preserve living biological diversity for future reproduction, restoration and population replenishment, while maintaining standing genetic variation upon which adaptation can act. While not substitutes for global emissions reductions, these localized interventions could therefore complement broader conservation portfolios and help prevent coral biodiversity loss from outpacing the capacity of populations to persist and adapt to warming oceans.

Methods

Study site and cooling system

The study was conducted on the south-western outer reef slope of Tetiaroa atoll, in French Polynesia (17°0'48.21"S, 149°35'53.76"W), between 12 and 14m depth (Supplementary Fig. 16). This location was selected for its direct proximity to a deep seawater air conditioning (SWAC) outlet, providing a rare opportunity to experimentally manipulate seawater temperature *in-situ* on coral reefs under realistic field conditions. Powered by renewable solar energy, the SWAC system draws cold (5–7°C) seawater from ~960m depth to cool onshore infrastructures before discharging the water, unaltered, onto the outer reef slope at 30m, averaging 11°C³⁶.

To exploit this previously unused cold-water resource for coral cooling, a derivation system was installed in June 2023. Approximately 80% of the SWAC outlet was intercepted and diverted through PVC pipes (50 mm diameter; Supplementary Fig. 17a-b), conveying cold water upward to diffusion networks at a depth of 12-14m (Fig. 1e, Supplementary Fig. 17c-d). The high discharge rate at the SWAC outlet (150–200 m³ h⁻¹; ³⁶) provided sufficient pressure to maintain continuous and homogeneous flow throughout the derivation system. Cold water was distributed over experimental galvanized-iron tables, anchored to the reef pavement using steel cables fixed at each leg (Supplementary Fig. 17c-d). On each table (0.5m high, 1.5 x 1.5m), the diffusion system consisted of a rigid horizontal PVC frame of identical dimensions supporting 10 parallel PVC pipes (40 mm diameter), secured with heavy-duty cable ties. To maximize contact between cooled water and coral fragments, each pipe was perforated with twelve 4-mm outlets, spaced every 10 cm and oriented toward the substrate to promote downward diffusion and generate a cold-water plume encompassing the entire table (Fig. 1f-g). Two cooled tables were installed, one at 12m and a second at 14m (Supplementary Fig. 17d).

Coral collection and experimental nurseries

To test the bleaching mitigation potential of cooling and shading, three coral species were selected based on their high local abundance around the study site and their contrasting thermal sensitivities observed during previous bleaching events: branching *Acropora globiceps* and *Pocillopora cf. tuahiniensis*, and massive *Pavona duerdeni*. During the 2019 bleaching event, *Acropora* spp. exhibited high bleaching prevalence (98%) and coral cover loss (77%), *Pocillopora* spp. showed intermediate responses (57% bleaching, 33% cover loss), whereas *Pavona* spp. was comparatively tolerant (8% bleaching, 1% cover loss; unpublished data).

Coral nurseries were established in March 2023 to allow fragments to heal following fragmentation. Fifteen medium-sized, visually healthy donor colonies were sampled for each species between 7 and 20m depth on the western outer reef slope of Tetiaroa, in the vicinity of the study site. To minimize the probability of sampling clonal individuals, colonies were haphazardly selected at least 15m apart for each species⁷⁷. Although donor colonies were not genotyped, they are hereafter referred to as distinct “genotypes” for clarity, while acknowledging that this approach may not fully exclude clonality. Nine fragments (~ 5 cm) were collected from each donor colony, yielding a total of 405 fragments.

Fragments were tagged (unique ID), attached to 10cm stainless-steel rods (4-mm diameter) using cable ties (Fig. 1a-c), and then acclimated in a control nursery located approximately 30m north-east of the

cooled tables (17°0'45.70"S, 149°35'52.05"W), at 13m depth (Supplementary Fig. 16). This separation ensured that acclimation occurred under ambient, non-influenced thermal conditions. The nursery also consisted of galvanized-iron tables (0.5m high, 1.5 x 1.5m) supporting a PVC frame composed of ten parallel pipes (1.35 x 1.5m), attached 30 cm above the substrate (i.e. 20cm below the top of the table; Fig. 1a). Rods with fragments were inserted through pre-drilled holes in the PVC frame and protruded 2–3 cm below the frame, allowing secure yet removable attachment for repeated monitoring. Fragments were spaced 10 cm apart, accommodating up to 96 fragments per table (no fragments on the first and last PVC pipes). Following unexpected mortality of several *Pocillopora* fragments during acclimation, a completely new set of 15 donor colonies was sampled in early January 2024 to replenish stocks prior to the experiment. Acclimation was thus shorter for *P. cf. tuahiniensis* fragments (2 months), compared with *A. globiceps* and *P. duerdeni* (12 months).

Cooling and shading interventions

Ahead of the forecasted marine heatwave, coral fragments were randomly allocated to 3 experimental nurseries, with 3 fragments per genotype assigned to each nursery: (i) a cooled nursery supplied with deep cold seawater through the diffusion system described above, (ii) an artificially shaded nursery, and (iii) an unmanipulated control nursery. Artificial shading was achieved using high-density polyethylene shade cloths providing 60% theoretical light attenuation, selected based on shading levels previously shown to alleviate bleaching under thermal stress in aquaria^{28–30}. Actual light reduction was subsequently verified through *in-situ* PAR measurements (see Environmental data section). Shade cloths were tensioned 40 cm above fragments on larger galvanized tables (0.7m high, 2 x 2.2m) using heavy-duty cable ties with a tightening tool to withstand local hydrodynamic conditions. Shade cloths extended 25 cm beyond all table edges to ensure full-day shading coverage for all fragments (Fig. 1d). Fragments were arranged in mirrored configurations across nurseries to minimize positional effects and facilitate monitoring.

Baseline surveys (t_0) were conducted 23–27 February 2024, when NOAA bleaching outlooks reached “Warning” levels, allowing interventions to be proactively deployed ahead of peak thermal stress. Cooling and shading interventions were subsequently deployed on 1 March and maintained throughout the 2024 MHW (Fig. 2a, in grey shading). Shaded and control nurseries remained at the acclimation site, while fragments assigned to the cooling treatment were transferred to cooled tables and positioned 15 cm below the diffusion system (i.e. supporting PVC frames were 20 cm below), with one cold-water outlet located directly above each fragment to maximize exposure (details in Supplementary Fig. 18). This configuration ensured consistent exposure to cooled water among fragments while maintaining comparable spatial arrangement to other treatments (Supplementary Fig. 19). Peak-stress survey (t_1) was conducted 25–28 April, and shade cloths were concurrently cleaned with wire brushes. After 4.5 months of treatment, once the MHW had receded, interventions were terminated 13 July (Fig. 2a). Shade cloths were removed and cooling stopped, returning to control configurations and fragments were surveyed again (t_2 ; 13–14 July). Post-intervention recovery was monitored 4 months later, 6–9 November (t_3), allowing assessment of delayed effects and longer-term coral performance.

Environmental monitoring

Seawater temperature was recorded every 15 minutes at the control site throughout the experiment and on cooled tables using calibrated HOBO Pro v2 loggers (Onset; resolution 0.02°C, accuracy < 0.05°C at 25–30°C; ⁷⁸). Loggers were deployed at the center of each cooled table over the entire cooling period, with sensors positioned vertically 15 cm below the cold-water diffusion system around the average height of fragments. This positioning ensured that recorded temperatures closely reflected the thermal conditions experienced by coral fragments. Current speed and direction were monitored every 10 minutes using a Marotte HS current meter deployed on top of a cooled table from t_0 to t_1 to assess the influence of hydrodynamic conditions on cooling efficiency.

To evaluate the spatial uniformity of the cold-water plume within a table, horizontal diffusion was assessed between 1 and 23 June 2024 using 9 temperature loggers deployed 15 cm below the diffusion system in a grid pattern. Loggers were positioned at the table center, at the midpoint of each edge and at each corner (Supplementary Fig. 19).

Treatment-specific heat exposure trajectories were quantified through Accumulated Heat Stress (AHS), calculated from daily *in-situ* means relative to an *in-situ*-corrected maximum monthly mean (MMM = 28.67°C), following the NOAA Coral Reef Watch framework for Degree Heating Week computation (Supplementary Methods: AHS computation). Two metrics were thus computed: $AHS_{0^\circ C}$, integrating temperatures exceeding MMM to capture low-magnitude heat stress and $AHS_{1^\circ C}$, integrating temperatures exceeding $MMM + 1^\circ C$ to capture moderate-to-severe stress⁷⁹.

To assess physicochemical changes associated with deep-water injection, pH, dissolved oxygen and nutrient concentrations were measured. During four consecutive days in mid-April 2024, at peak marine heatwave intensity (t_1), pH loggers (HOBO MX pH, Onset) and dissolved oxygen loggers (HOBO U26-001, Onset) were deployed at fragment height, 15 cm below the cold-water outlet at the center of a cooled table, and in the control area. All sensors were calibrated according to manufacturer guidelines prior to deployment. Water samples were collected in triplicate on six different days and at different times of day to account for natural variability associated with currents. Seawater samples were collected 10–15 cm below the diffusion system and in the control area, preserved at -20°C until processing using a Seal Analytical AA3 HR autoanalyzer for nitrate (NO_3^-), nitrite (NO_2^-), ammonium (NH_4^+), phosphate (PO_4^{3-}) and silicic acid ($Si(OH)_4$)⁸⁰.

Underwater photosynthetically active radiation (PAR, 400-700nm) was recorded every 15 minutes using DEFI2-L light loggers (JFE Advantech). One logger was positioned at the center beneath a shade cloth at fragment height, and one logger was deployed comparatively on a control table. Loggers were deployed at t_0 and maintained throughout the intervention period, being retrieved at t_1 and redeployed until t_2 . Because visits to the experimental site were limited to the survey periods described above, biofouling progressively reduced sensor light transmission between visits. To avoid associated measurement bias,

only the first two weeks after each deployment were retained for analysis. Therefore, we acknowledge that measured light conditions characterize discrete periods of the intervention rather than the entire treatment duration.

Coral health monitoring

For each genotype and treatment, one of the three fragments was randomly selected for non-destructive monitoring of bleaching susceptibility, survival, growth and pigmentation throughout the experiment ($n = 135$). To assess photophysiological and host energetic responses (see physiology and energy reserves section), the remaining pair of fragments from the same genotype and treatment was destructively sampled at peak bleaching in April (t_1) and during recovery in November (t_3). When only a single fragment had survived in November, it was first processed for non-destructive measurements and subsequently snap-frozen (total $n = 235$, details in Supplementary Table 5). Each time, entire fragments were snap-frozen in liquid nitrogen and stored at -20°C until further processing. Fragments were carefully transported in seawater-filled coolers to the Tetiaroa Society aquaria supplied with seawater from the adjacent lagoon. Measurements were completed immediately on arrival, and corals were frozen within one hour to preserve biochemical integrity.

At each survey, the health status of all live fragments was visually assessed and categorized as healthy, partially bleached (10–70% of the surface depigmented), severely bleached ($> 70\%$), or dead ($< 10\%$ remaining living tissue). Physiological monitoring complemented visual assessments. Growth rates ($\% \text{ day}^{-1}$) were quantified as the daily relative change in buoyant weight between surveys, encompassing both the stress period (February–April, t_0 – t_1) and the recovery period (April–November, t_1 – t_3). Pigmentation was quantified from standardized photographs using a continuous color score derived from a principal component analysis of standardized RGB channels (Supplementary Methods: Color score quantification). Increasing color scores indicate paling associated with symbiont loss, whereas decreasing scores indicate darkening linked to increasing concentrations of photosynthetic pigments and/or symbiont densities⁸¹. All photographs were taken under standardized lighting and camera settings to ensure comparability across timepoints.

Symbiont community composition

To monitor changes in endosymbiotic algal communities, $\sim 0.5 \text{ cm}^2$ clippings were collected from each fragment at t_0 , t_1 and t_3 , and preserved in 96% ethanol at -20°C until processing ($n = 370$). DNA was extracted using the E.Z.N.A. Mollusc DNA Kit (Omega Bio-Tek) following the manufacturer's instructions. For each sample, the *Symbiodiniaceae* ITS2 region of the rDNA was amplified using the primers SYM_VAR_5.8S2 and SYM_VAR_REV⁸² with Illumina MiSeq adapters. PCR reactions were performed by adding 1 μL of extracted DNA to 1 μL of each primer, 7 μL of Master Mix (QIAGEN Multiplex PCR Kit) and 15 μL of DNase-free ultrapure water. Thermal cycling consisted of an initial denaturation at 95°C for 15 min, followed by 35 cycles of 95°C for 30s, 56°C for 90s and 72°C for 30s, with a final extension of 10min at 72°C and a hold at 4°C . Negative controls were included during extraction and PCR amplification to detect potential contamination. Amplification success was verified by electrophoresis of 2 μL of PCR

product on a 2% agarose gel, with all samples showing pronounced bands except negative controls. Indexed ITS2 libraries were prepared and sequenced using paired-end sequencing (v2, 2 x 250bp) on an Illumina MiSeq platform at Bio-Environnement (University of Perpignan Via Domitia, France). Symbiont identity was determined using SymPortal⁸³, which detects and defines intragenomic variants (DIVs) and ITS2 type profiles based on their co-occurrence. Rare ITS2 sequence variants and type profiles (relative abundance < 0.01%) were excluded from downstream analyses, resulting in the retention of 197 DIVs out of 499 and 35 profiles out of 42. Nine samples failed to yield successful sequencing and were excluded from further analysis. Symbiont communities of samples were classified as *Durussinium*-dominated or *Cladocopium*-dominated when a single genus represented more than 80% of the profiles, or as mixed otherwise.

Photophysiology and energy reserves

Coral tissue was removed from skeletons by airbrushing fragments in 0.22 µm filtered seawater. The resulting slurry was homogenized, aliquoted (1mL) and stored at -20°C until processing. When processed, aliquots were thawed on ice and centrifuged at 13,000 rpm for 3min at 4°C to separate host tissue from endosymbiont cells.

Microalgal endosymbiont densities were quantified by performing six replicate counts of 10µL of resuspended algal pellet (in filtered seawater) using a Neubauer hemocytometer under a compound microscope. Chlorophyll pigments (chlorophyll a and c₂) were extracted by resuspending the algal pellet in 1mL of 90% acetone and incubating samples 24h at 4°C in the dark. After centrifugation at 13,000rpm for 3min at 4°C, absorbance of the supernatant was read at 663, 630 and 750nm using a spectrophotometer (Epoch 2, Agilent Biotek). To ensure all pigments were thoroughly quantified, extraction was performed a second time on the algal pellet remaining from the 24h-extraction, and chlorophyll concentrations were calculated⁸⁴.

Total host protein, carbohydrate and lipid contents were quantified from the host tissue slurry using colorimetric assays performed in triplicate on 96-well plates. Protein content was quantified by a BCA assay with bovine serum albumin (BSA) as a standard (Pierce BCA Protein Assay Kit, Thermo Fisher Scientific). Carbohydrate content was quantified using a modified phenol-sulfuric acid method with L-glucose as a standard⁸⁵. Lipid content was quantified using the sulfo-phospho-vanillin method, with corn oil as a standard⁸⁶.

Using the enthalpies of combustion for protein (23.9 J mg⁻¹), carbohydrate (17.5 J mg⁻¹), and lipid (39.5 J mg⁻¹; ⁸⁷), we estimated the total energy available from each macromolecular reserve. These values provide an estimate of relative energetic reserves rather than absolute caloric content, allowing comparison across treatments. All physiological metrics, including symbiont densities and energy reserves, were standardized to total tissue volume and skeletal surface area using the paraffin wax-dipping technique⁸⁸.

Statistical analysis

All statistical analyses were performed using R v.4.4.2⁸⁹. Daily mean seawater temperature and daily thermal range during the intervention period were compared among treatments using linear mixed-effects models (LMMs) with treatment as a fixed effect and date as a random intercept. Cooling efficiency was further assessed by modelling the temperature difference between cooled and control tables as a function of current speed using a generalized additive mixed model (GAMM), with date included as a random effect. Nutrient concentrations were analysed using generalized linear mixed models (GLMMs) including treatment, nutrient type and their interaction as fixed effects, and total dissolved inorganic nitrogen (DIN; $\text{NH}_4^+ + \text{NO}_3^- + \text{NO}_2^-$) was further analysed with treatment as a fixed effect and sampling date as a random intercept. Seawater pH and dissolved oxygen were analysed using LMMs with treatment as a fixed effect and date and time of day included as random intercepts. Daily light integrals (DLI; cumulative photosynthetic photon flux density throughout the day) were compared among treatments using non-parametric Friedman tests followed by pairwise Wilcoxon post-hoc comparisons, while midday irradiance (10:00–14:00) was analysed using mixed-effects models with treatment as a fixed effect and date and time as random intercepts. Bleaching susceptibility (if ever bleached, whether partially or severely) and survival outcomes (survival, bleaching-related mortality or other causes of death) were analysed using binomial and multinomial GLMMs (package *mclogit*⁹⁰) including treatment, species and their interaction as fixed effects, with genotype as a random intercept. Physiological responses, including pigmentation (color score), symbiont density, chlorophyll a and c_2 content per symbiont, host energy reserves (proteins, lipids, carbohydrates and total energy content) and growth rates were analysed using GLMMs with treatment, species, timepoint and their interactions as fixed effects, and genotype and, when relevant, fragment identity nested within genotype as random intercepts to account for repeated measurements.

Model structure was selected using likelihood ratio tests, and assumptions were assessed by inspecting residual distributions, quantile-quantile plot for normality and residuals vs fitted values for homoscedasticity. When relevant, data were log-transformed to reduce the data skew and increase normality. Response-specific distributions, link functions and final model structures are reported in Supplementary Table 6. Gaussian, binomial and negative binomial mixed-effects models were fitted using *lme4*⁹¹, while gamma models with log links were fitted using *glmmTMB*⁹². Effects of fixed variables were assessed using Type II Wald tests with Kenward-Roger degrees of freedom, and post-hoc comparisons were conducted on estimated marginal means and adjusted using the Benjamini-Hochberg procedure (package *emmeans*⁹³). When applicable, estimates were bias-corrected for link-function nonlinearity (Jensen's inequality⁹³). Results are reported as estimated marginal means $\pm$ SE unless stated otherwise.

A three-way PERMANOVA was first conducted on the full ITS2 type profile dataset, including species, treatment, and timepoint as fixed effects and their interactions. Because *Symbiodiniaceae* communities were primarily structured by host species, subsequent analyses were performed separately for each species. *Symbiodiniaceae* community composition was analysed separately for each species using non-metric multidimensional scaling (nMDS) and permutational analysis of variance (PERMANOVA) on Bray-

Curtis dissimilarities of square-rooted relative abundance of ITS2 type profiles. PERMANOVA included treatment, timepoint and their interaction as fixed effects (package *vegan*⁹⁴). Permutation schemes were constrained within genotype strata to account for non-independence of repeated measures. When significant effects were detected, temporal changes among treatments were explored using pairwise PERMANOVA with Benjamini-Hochberg correction (package *pairwiseAdonis*⁹⁵). To resolve finer-scale patterns, additional nMDS ordinations were performed on square-root-transformed relative abundances of ITS2 sequence variants (DIVs). Variants were fitted onto ordination space using the function *envfit* (*vegan*) to identify those significantly associated with temporal and treatment-driven community shifts.

Declarations

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Data availability

All scripts and data necessary to replicate the analysis can be publicly accessed here:

<https://github.com/clr-btl/Cooling-shading-corals>.

Code availability

Code used for this analysis and figure generation can be accessed at <https://github.com/clr-btl/Cooling-shading-corals>

Contributions

CBT, SP and LH contributed to the study conception and design. CBT, CG, HB and CBP planned and carried out the fieldwork. CBT, OM and JN conducted the lab work. EB supervised and helped in DNA extractions and downstream processing and analysis. CBT conducted the data analysis. SP and LH secured funding for and supervised this research. The manuscript was written by CBT with input from SP and LH. All authors read, reviewed and approved the final manuscript.

Competing interests

The authors declare that they have no conflict of interest.

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Figures



Figure 1

Experimental mitigation strategies applied to coral fragments during the 2024 bleaching event. (a-c) Representative fragments of *Acropora globiceps* at the peak of bleaching in late April 2024 (t_1): bleached fragments under control conditions (a), bleached fragments under shading (b), and unbleached

fragments under cooling (c). (d) Shading structure, consisting of woven polyethylene shade cloths stretched 30cm above coral fragments using heavy-duty zip ties; the cloths extended 25cm beyond the edges of the nursery tables, ensuring continuous shading throughout the day. (e) Derivation of cold deep water at the SWAC outlet and upward transport to the upper reef to coral tables (12-14m depth), where (f-g) water was diffused over coral fragments using perforated PVC frames. Note the cold-water stratification at the SWAC outlet, extending over at least 1m in (e), illustrating the high discharge flow rate, which allows cold water to be maintained under pressure and transported over several tens of meters. The cold-water plume generated by the diffusion system was visualized at the end of the experiment in November 2024 using fluorescein dye (non-toxic, commonly used for leak detection), highlighting (f) the downward propagation of cold water in the water column over coral fragments and (g) its spatial coverage at the scale of an entire nursery table.

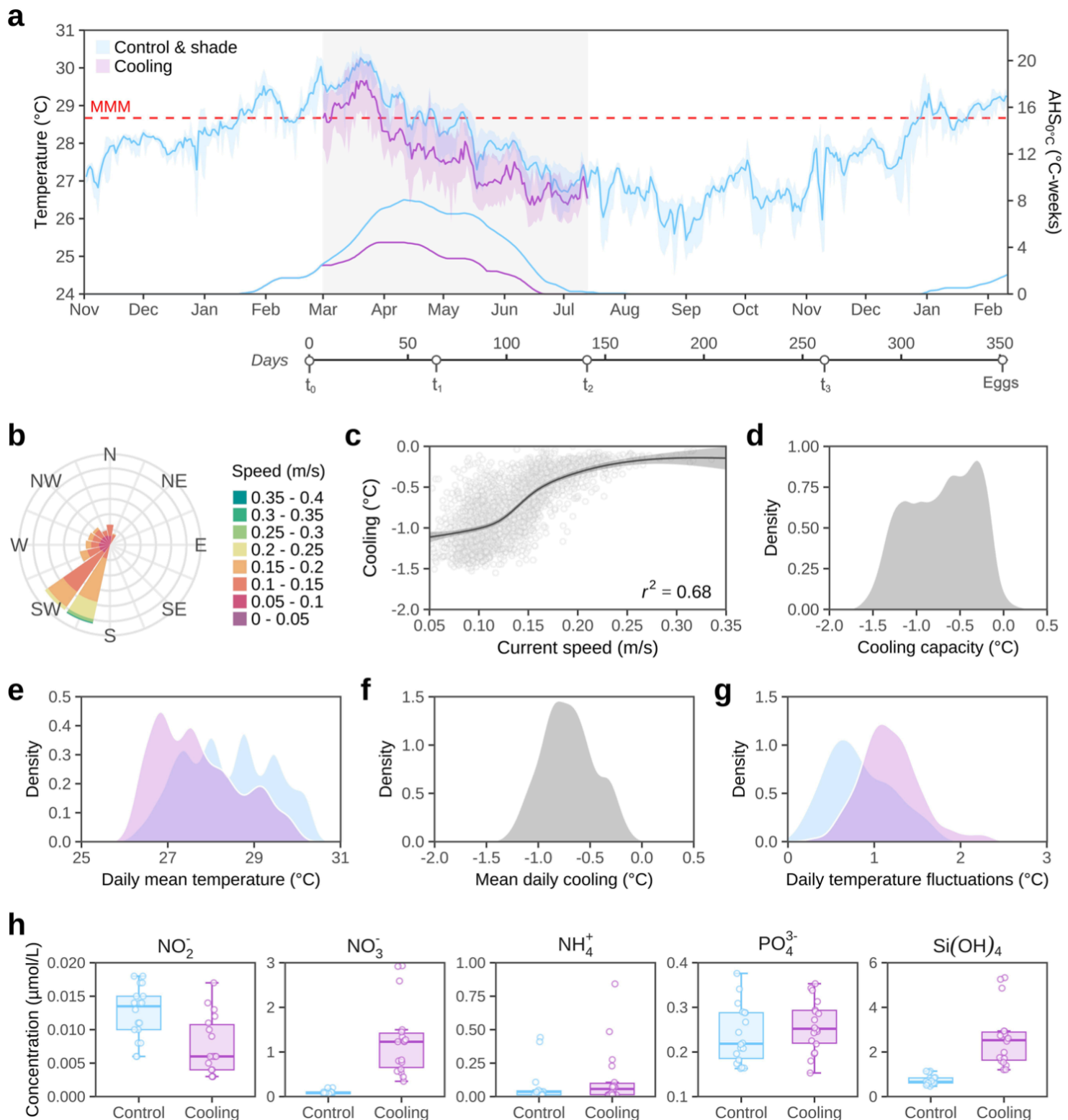


Figure 2

Thermal performance and environmental context of the deep cold-water cooling system applied to coral nurseries. (a) *In-situ* daily mean temperatures (solid lines) and daily thermal range (ribbons) recorded under cooled nursery tables (purple; mean of the two cooled tables) and under control and shaded tables (blue). The cooling intervention period is indicated in grey (1 March-13 July 2024). Accumulated heat stress (AHS $_{0^{\circ}\text{C}}$; right axis), indicating low-magnitude *in-situ* thermal stress

accumulating when daily mean temperatures exceeded the *in-situ* corrected maximum monthly mean (MMM; red dashed line), is shown for each treatment. The experimental timeline indicates nursery sampling times (t_0 - t_3 ; eggs indicate when fragments of *A. globiceps* were visually inspected for the presence of mature oocytes). (b) Current direction and speed measured during the first half of the cooling period (early March to late April, t_0 - t_1), illustrating the prevailing hydrodynamic conditions at the nurseries. (c) Relationship between current speed and cooling efficiency (temperature difference between cooled and control tables), described using a generalized additive model (GAM; predictions $\pm$ 95% confidence interval), revealing a sigmoidal decline in cooling capacity with increasing current speed and optimal cooling under low-flow conditions ($< 0.16 \text{ m s}^{-1}$; inflexion point). (d) Density plot of temperature difference between cooled and control tables, measured every 15 minutes. (e) Density plot of daily mean temperatures, and (f) resulting daily mean cooling efficiency, and (g) daily temperature range for control and shaded nurseries (blue) and cooled nurseries (purple) during the intervention period. (h) Nutrient concentrations measured in control and cooled nurseries (from left to right: nitrite, nitrate, ammonium, phosphate, and silicate), indicating an enrichment of nitrate and silicate in the vicinity of cooled fragments. Boxplots include the median (centre lines), upper and lower quartiles (box limits), 1.5x interquartile range (whiskers). Points correspond to raw data.

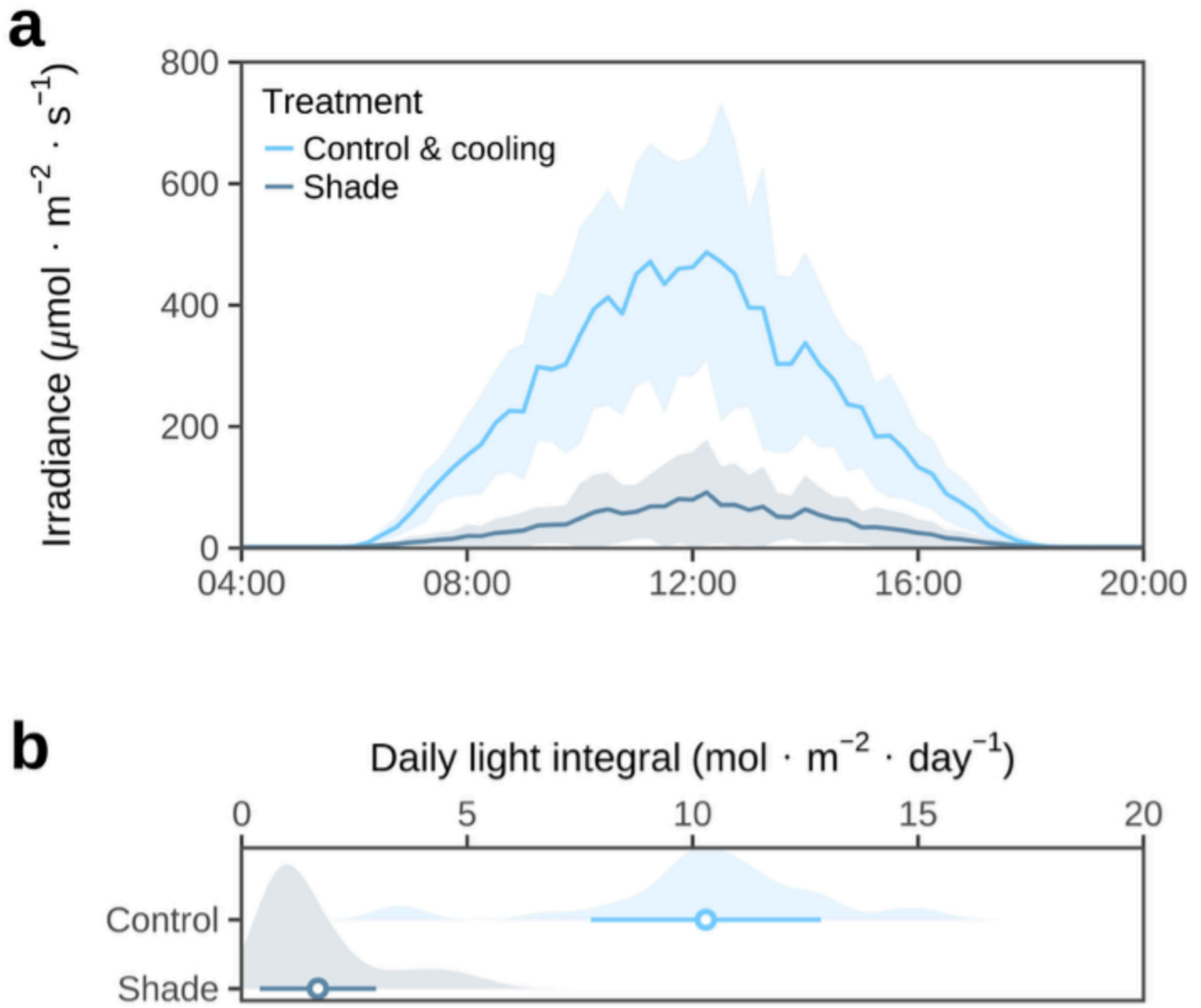


Figure 3

Light regimes in unshaded (control and cooling) and shaded nurseries.

(a) Mean diel profiles of photosynthetically active radiations (PAR; 400-700nm) averaged at 15-min intervals ($\pm$ standard deviations). (b) Mean ($\pm$ sd) and distribution of daily light integral (DLI) experienced across nurseries.

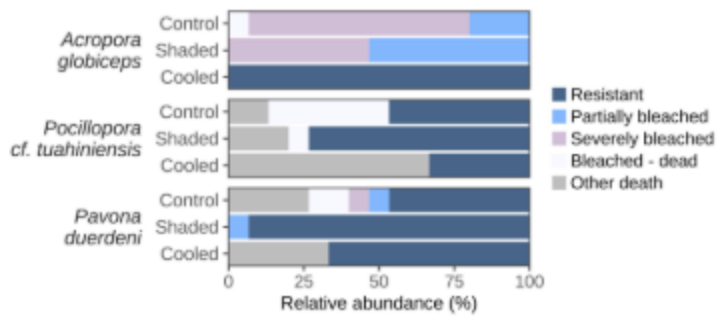


Figure 4

Health trajectories as relative abundances of bleaching responses and survival outcomes. Fragments were categorized as follows: resistant (alive in November with no visible bleaching response over time), partially bleached (10-70% surface depigmented followed by recovery), severely bleached (>70% depigmentation followed by recovery), bleached-dead (partial or severe bleaching without recovery), and other mortality (death without prior visible bleaching).

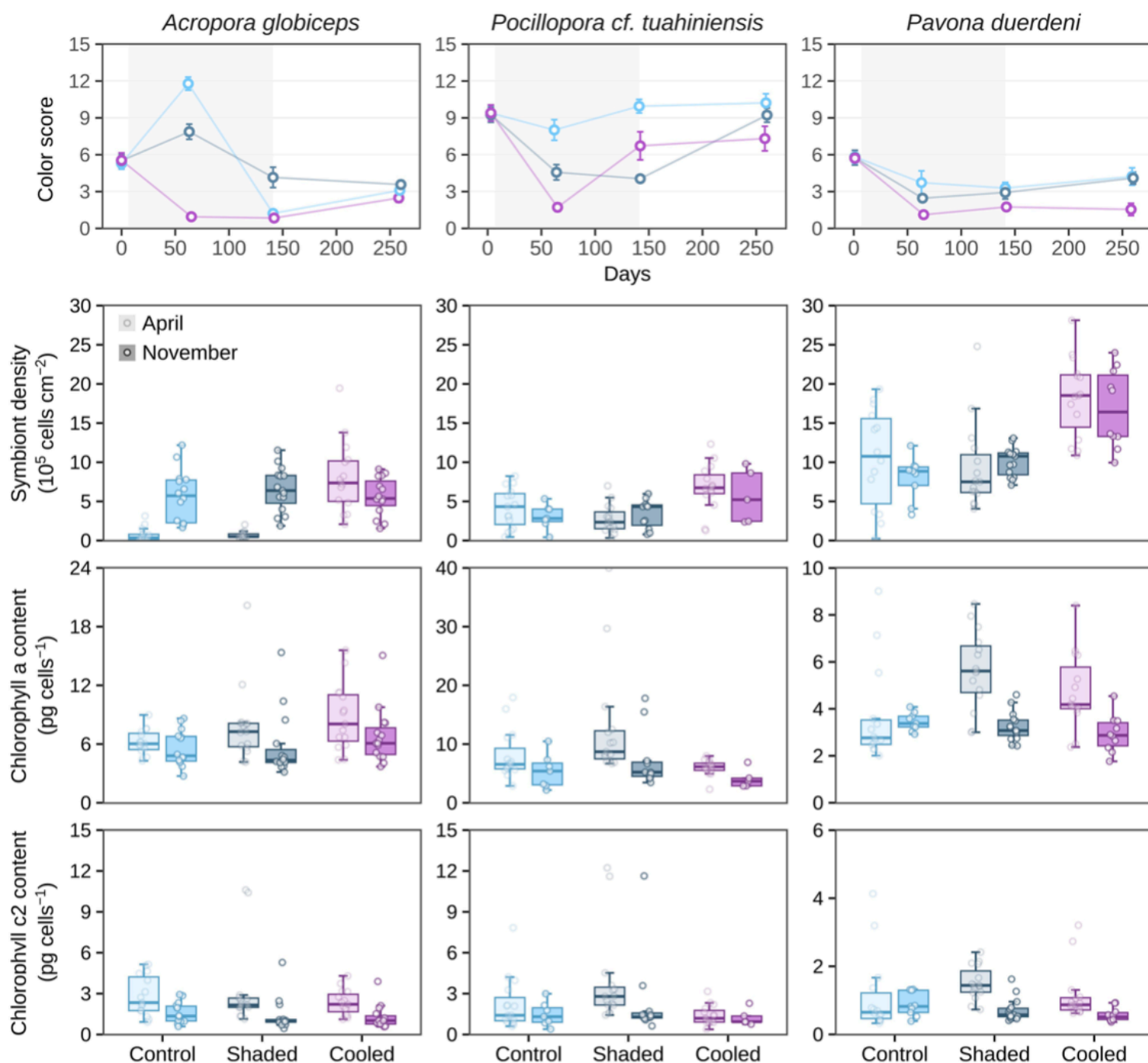


Figure 5

Temporal trajectories of bleaching severity and symbiont photophysiology under shading and cooling across species. An increasing color score indicates paling, whereas a decreasing color score indicates darkening (points are means and errorbars are standard errors; intervention period is indicated by grey shading). Boxplots of symbiont densities, chlorophyll a and c2 content per symbiont cell display the median (center lines), upper and lower quartiles (box limits), 1.5x interquartile range (whiskers). Points correspond to raw data. For each treatment pair, lighter colors (left) correspond to peak heat stress (April), and darker colors (right) correspond to recovery four months post-intervention (November).

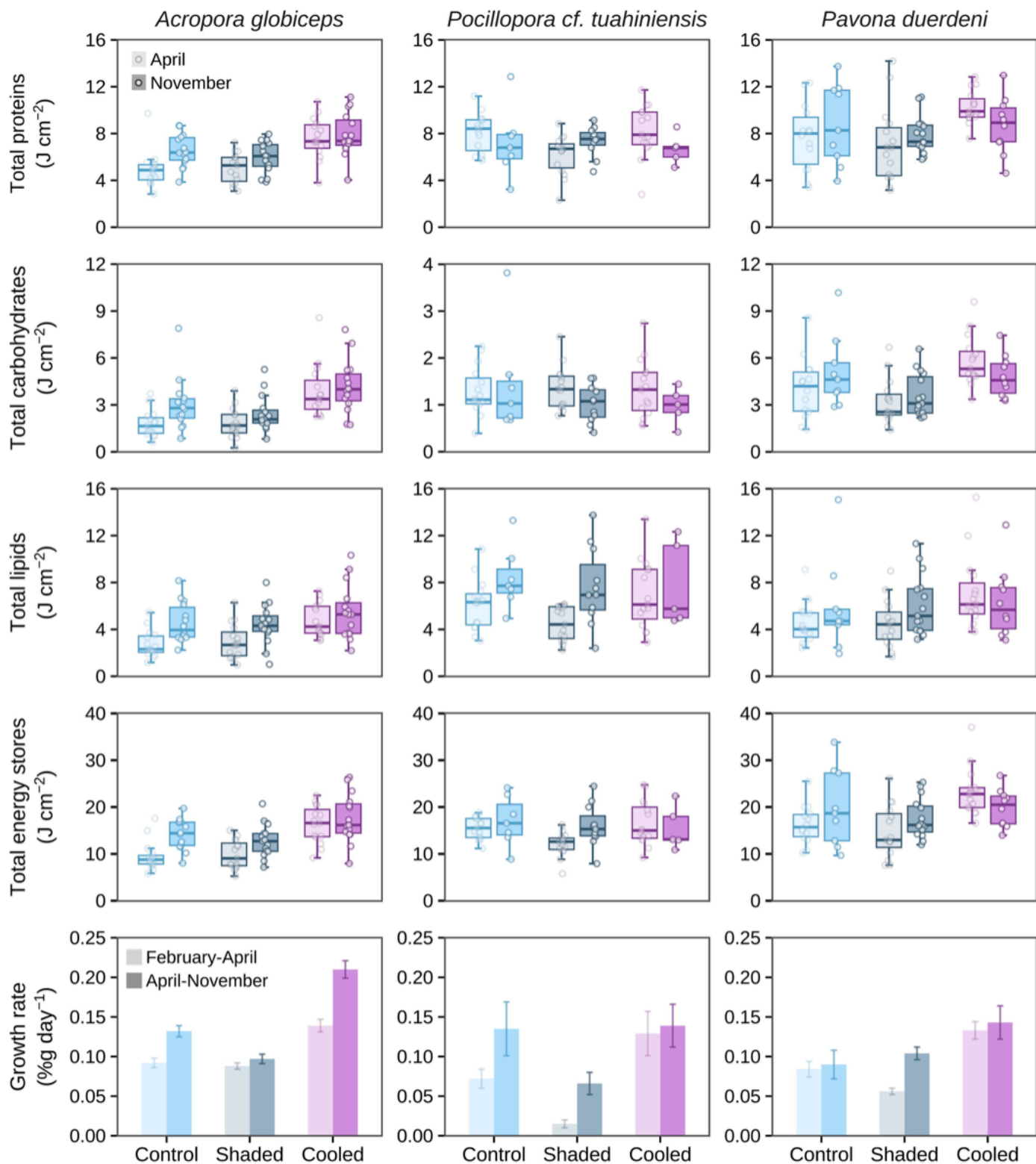


Figure 6

Energetic state and investment into growth trajectories under shading and cooling across species.

Boxplots of protein, lipid, carbohydrate and total reserves display the median (center lines), upper and lower quartiles (box limits), 1.5x interquartile range (whiskers). Points correspond to raw data. Growth rates (daily relative weight gain) were measured between February and April (from intervention deployment to peak heat stress), and April and November (from peak heat stress to 4 months post-

interventions). For each treatment pair, lighter colors (left) correspond to peak heat stress (April), and darker colors (right) correspond to recovery four months post-intervention (November). Bar indicate mean while errorbars indicate standard error.

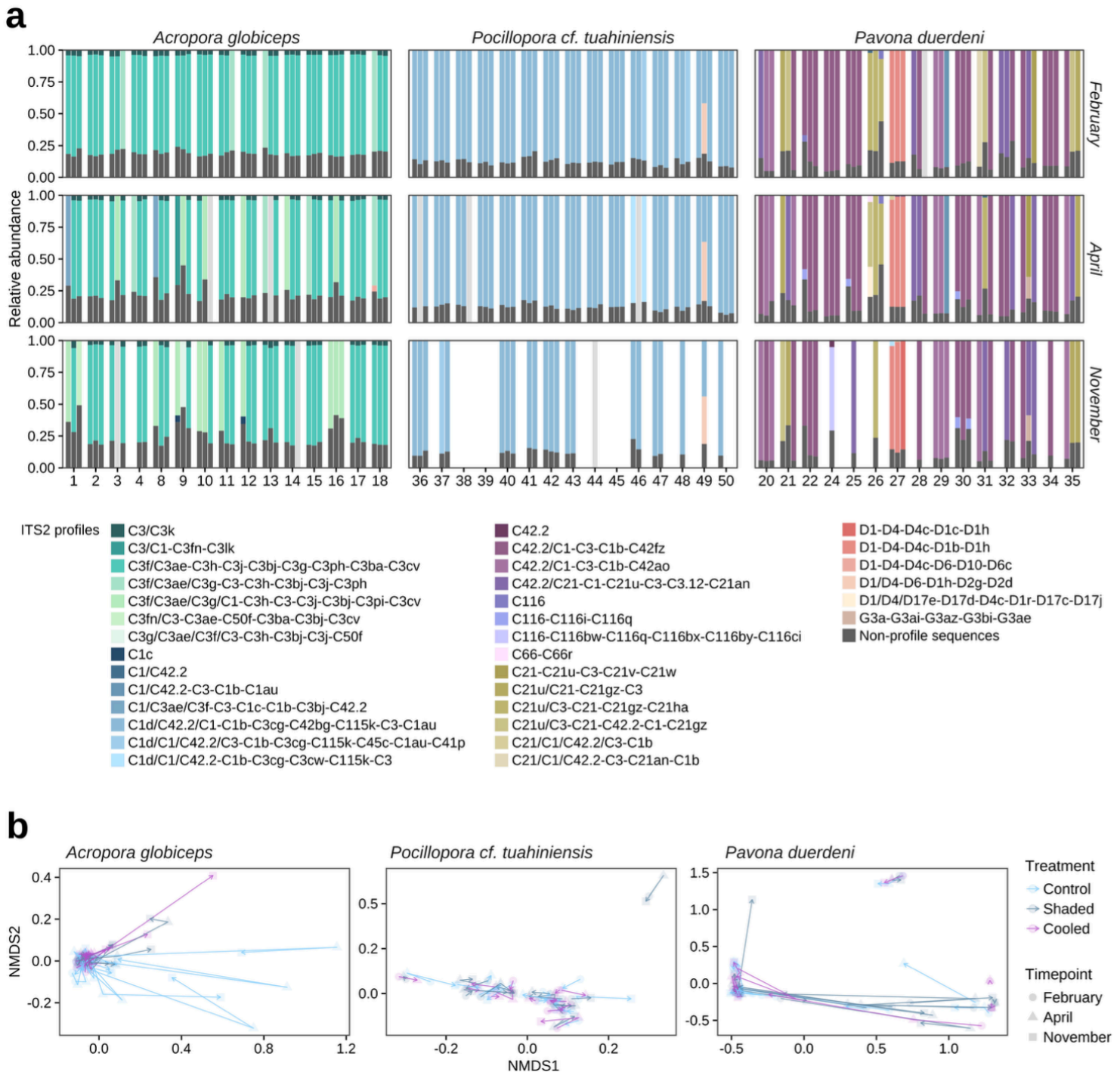


Figure 7

Temporal evolution of *Symbiodiniaceae* communities within individual coral fragments across treatments. (a) Relative abundance of the most abundant (> 0.01%) ITS2-type profiles, with each vertical bar representing a single fragment at a given timepoint: February (pre-intervention), April (peak marine heatwave), and November (4 months post-intervention, recovery phase). For each genotype within each

species, three adjacent bars correspond to control, shaded, and cooled treatments (left to right). Light grey bars correspond to samples with unsuccessful sequencing. Sequences not assigned to any ITS2 profile are shown in dark grey. (b) Non-metric multidimensional scaling (nMDS) ordination based on the most abundant defining intragenomic variants (DIVs) illustrates fine-scale temporal shifts in community composition.

Supplementary Files

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