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Assessing the potential for "assisted gene flow" to enhance heat tolerance of multiple coral genera over three key phenotypic traits

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ABSTRACT

Mass coral bleaching and mortality events have increased in frequency over the last 30 years, with ocean temperatures projected to reach bleaching thresholds annually by 2050. Genetic interventions like assisted gene flow may speed up adaptation in reefs with less heat-tolerant corals by increasing the frequency of heat tolerance-associated genetic variants, but the effectiveness of the intervention across species and life stages remains uncertain. To investigate, we generated reproductive crosses of corals from reefs along a thermal gradient on the Great Barrier Reef, comparing fitness traits in intra-region (same region) and inter-region (different region) offspring from three species (Acropora kenti, *A. hyacinthus*, and *Goniastrea retiformis*). Juveniles were inoculated with three heat-tolerant symbionts: Durusdinium trenchii, a heat-evolved Cladocopium goreaui strain, and "wild" symbionts from northern reef sediments, to assess symbiosis impacts on heat tolerance. Survival, growth, colour change (proxy for bleaching), and effective quantum yield of photosystem II (YII) were measured across larvae, juveniles, and adults at elevated (32 °C, 35.5 °C) and ambient (27.5 °C) temperatures. Results showed higher survival in some inter-region crosses compared to intra-region crosses from central reefs in larvae and juvenile corals, though enhancement varied by species. Furthermore, heat-tolerant parents did not always produce heat-tolerant offspring, and larval heat tolerance did not always persist to the juvenile stage. Parent genetic background influenced survival more than symbiont treatment. These findings underscore the complexity of heat tolerance acquisition in early coral life stages.

1. Introduction

Anthropogenic activities have caused the global climate to change at an alarming rate over the past several decades, leading to ocean acidification and warming (Doney et al., 2020; Donner, 2011; Zeebe and Wolf-Gladrow, 2001). Current warming rates suggest organisms must endure climatic conditions that are becoming more extreme relative to those they are currently adapted to (Buckley and Huey, 2016). Coral reefs, as highly sensitive ecosystems (Mora et al., 2016), are particularly vulnerable and must adapt quickly to shifting environmental norms, including rising seawater temperatures (Souter et al., 2021). Consequently, this accelerated rate of climate change poses severe threats to the survival and resilience of coral reef ecosystems.

On the Great Barrier Reef (GBR), increased warming, coral disease, crown-of-thorns starfish predation, and cyclones have all caused major decreases in coral cover over the past 50 years (Babcock et al., 2016; Bruno et al., 2007; De'Ath et al., 2012; Miller et al., 2009). These losses have been exacerbated by the occurrence of heat-induced mass bleaching events, now the primary driver of coral degradation worldwide, including on the GBR (Donner et al., 2017; Hughes et al., 2018a; Hughes et al., 2018b; Skirving et al., 2019; Stuart-Smith et al., 2018). Bleaching manifests when the coral-algal symbiosis breaks down, leading to the loss of the symbiotic dinoflagellates and coral mortality if heat stress persists (Douglas, 2003). These disturbances have altered coral

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species assemblages (Hughes et al., 2018b) and their symbiont communities (Quigley et al., 2022b), prompting the need to consider more active interventions to assist the conservation of coral reefs. However, ocean warming is projected to persist (Arias, 2021; Munday et al., 2009), and outplanting corals to degraded reefs may become insufficient if rates of warming exceed corals' natural capacity for acclimatisation and adaptation (Quigley et al., 2019).

Bleaching and mortality is often not spatially homogenous, as seen across the GBR (Hughes et al., 2018a), with some reefs harbouring more 'heat tolerant' adults than others (Naugle et al., 2024). Heat tolerance varies between species (Pratchett et al., 2020; Tavakoli-Kolour et al., 2023) and is determined by several heat tolerance-associated fitness traits, such as bleaching tolerance and heat stress survival. This in turn is driven by multiple factors including microbiome (Mohamed et al., 2023), phenotypic plasticity of the host (Drury et al., 2022c), and host genotype (Howells et al., 2022). One of the principal components of the coral microbiome is algae from the family Symbiodiniaceae (Bourne et al., 2016; Hoadley et al., 2019; Quigley et al., 2018), which have their own taxon dependant heat tolerance (Qin et al., 2019), and can affect the overall heat tolerance of the host coral. Furthermore, phenotypic plasticity can allow for short term acclimation to disturbance (Drury et al., 2022c), while genotypic variation within populations drives adaptation (Howells et al., 2022). Heritable genetic diversity linked to heat tolerance may occur at a higher frequency on some reefs (Dixon et al., 2015; Howells et al., 2016; Kenkel et al., 2015; Quigley and van Oppen, 2022; Weeriyanun et al., 2022) potentially due to evolutionarily prolonged exposure to elevated temperatures or frequent bleaching-related conditions (Sully et al., 2019). This adaptive variation can be leveraged to increase the presence of heat tolerance-associated genes on degraded reefs through methods like Assisted Gene Flow (AGF; Aitken and Whitlock, 2013; van Oppen et al., 2015). Here, we define AGF as the intentional translocation of warm-adapted adults or their offspring within a species range to facilitate adaptation to anticipated local conditions (Aitken and Whitlock, 2013; Baums et al., 2019). In theory, introducing enough individuals with these "pre-adapted" genotypes at the correct time should decrease mortality of those populations during subsequent heating events, thereby improving overall reef resilience (Hazraty-Kari et al., 2022b; Torda and Quigley, 2022).

Indeed, previous experiments in the laboratory and in the field with corals have demonstrated promising results in increasing survival to heat stress. For instance, inter-region larvae of *Acropora millepora* and juveniles of *A. spathulata* showed a 13- to 26-fold higher odds of survival under heat stress when compared to intra-region central corals (Dixon et al., 2015; Quigley et al., 2020b). Similarly, *Platygyra daedalea* larvae with mixed genetic backgrounds from the Persian Gulf and Indian Ocean exhibited an 84 % increase in survival after 60 h of experimental heat stress compared to individuals with both parents from the cooler Indian Ocean (Howells et al., 2021). Even more promising, breeding experiments with *A. kenti* larvae and juveniles resulted in an average increase in tolerance of ~3 °C (Quigley and van Oppen, 2022). This approach mirrors success in other biological systems, such as trees and amphibians (Aitken and Whitlock, 2013; Rudin-Bitterli et al., 2021). Collectively, these findings suggest that AGF could facilitate rapid adaptation to future warming under specific conditions (Quigley et al., 2019; Torda and Quigley, 2022).

Although significant progress has been made to develop AGF as a conservation strategy (reviewed in Drury et al., 2022b), further research is needed before it can be used to reliably and broadly contribute to restoration. First, further testing is needed on the efficacy of AGF across different coral species and genera. Secondly, it is currently unclear whether the heat tolerance of offspring from the same parents is carried across the early-life stages (i.e., in both the larval and juvenile stage), or whether heat tolerant parents produce both tolerant larvae and juveniles. To address these outstanding questions, we produced corals by reproductively crossing parents sourced from northern and central GBR reefs for three coral species (*A. kenti, A. hyacinthus,* and *Goniastrea retiformis*) and compared their heat stress survival to central intra-region controls at the larval, juvenile, and adult stages. Survival was increased in inter-region offspring in relation to central intra-region controls at multiple life stages for some species, however familial heat stress survival varied across species and life stages. Furthermore, survival did not differ among the three heat-tolerant symbiont treatments; however, these treatments significantly influenced growth and bleaching responses. These results suggest that although AGF could be an effective strategy for improving conservation efforts of some species on the GBR, it remains challenging to predict which species and target populations will provide maximum benefit.

2. Materials and methods

2.1. Coral collections

Colonies of *A. kenti* and *G. retiformis* were collected in November 2020 and *A. hyacinthus* colonies were collected in November 2021. Reefs predicted to harbor heat tolerant adult corals with high heritability were selected using predictive models based on remote sensing data and breeding experiments (Fig. 1A; Quigley and van Oppen, 2022). Davies Reef was selected as a control reef, representing a location not predicted to have a predisposition for heat-tolerant genotypes. Gravid *A. kenti* colonies were collected from five reefs across the northern and central GBR: Jewell and Parke Reef (northern outer shelf; 14.40768°S, 145.36202°E, 14.43982°S, 145.32310°E), Switzer Reef (northern inshore; 14.29289°S, 144.73738°E), Davies (central, mid-outer shelf; 18.81978°S, 147.64563°E), and Mundy Bay, off Bwgcolman in the Palm Islands (central inshore- mid shelf; 18.76431°S, 146.62412°E). *G. retiformis* colonies were collected from Jewell, Parke, and Switzer reefs. Gravid *A. hyacinthus* colonies were collected from five reefs across the northern and central GBR: Wood (northern, outer shelf; 11.811805°S, 143.981617°E), Martin (northern, mid-shelf; 14.77130°S, 145.36940°E), Arlington (northern, mid-shelf; 16.64293°S, 146.10841°E), Eumilli Island (Fantome Island) in the Palm Islands (central, inshore- mid shelf; 18.65907°S, 146.50455°E), and Davies Reef in November 2021. Site locations and environmental conditions are described in Supplementary Table 1. Gravid colonies were brought back to the National Sea Simulator (SeaSim) at the Australian Institute of Marine Science (AIMS) in Townsville, Australia.

2.2. Coral breeding design and larval rearing

The number of coral colonies used for spawning per reef for each species are shown in Supplementary Table 2. Northern intra-region crosses were generated between corals sourced from the northern reefs only. Inter-region crosses were generated between corals sourced from the northern reefs and central reefs. Intra-region crosses from central reefs were produced as controls (Fig. 1B), following established methods (Quigley et al., 2020b). To produce families with mixed genetic backgrounds, corals from different regions were required to spawn on the same night, as gametes could not be stored for longer than a few hours without producing confounding effects. Therefore, coral spawning time and day after full moon were estimated using the Indo-Pacific coral spawning database (Baird et al., 2021). The beginning of spawning for each species are as follows: *A. kenti*: 19:25, *A. hyacinthus*: 21:45, *G. retiformis*: 21:25. For *A. hyacinthus*, some reef crosses were unable to be produced due to mismatched spawning days between central and northern reefs. Gametes were gently collected from the water surface once they were released by adult colonies and 'washed' to separate eggs from sperm using a 120 μm filter and 0.2 μm filtered sea water (FSW). Sperm density from each colony was quantified using an automated sperm counter, following which sperm cells were diluted to a concentration of 1×10^6 cells per litre (Computer - Assisted Semen Analysis-CASA equipment: Finelli et al., 2021; Zuchowicz et al., 2021). Once all colonies had spawned, sperm was mixed with eggs from specific

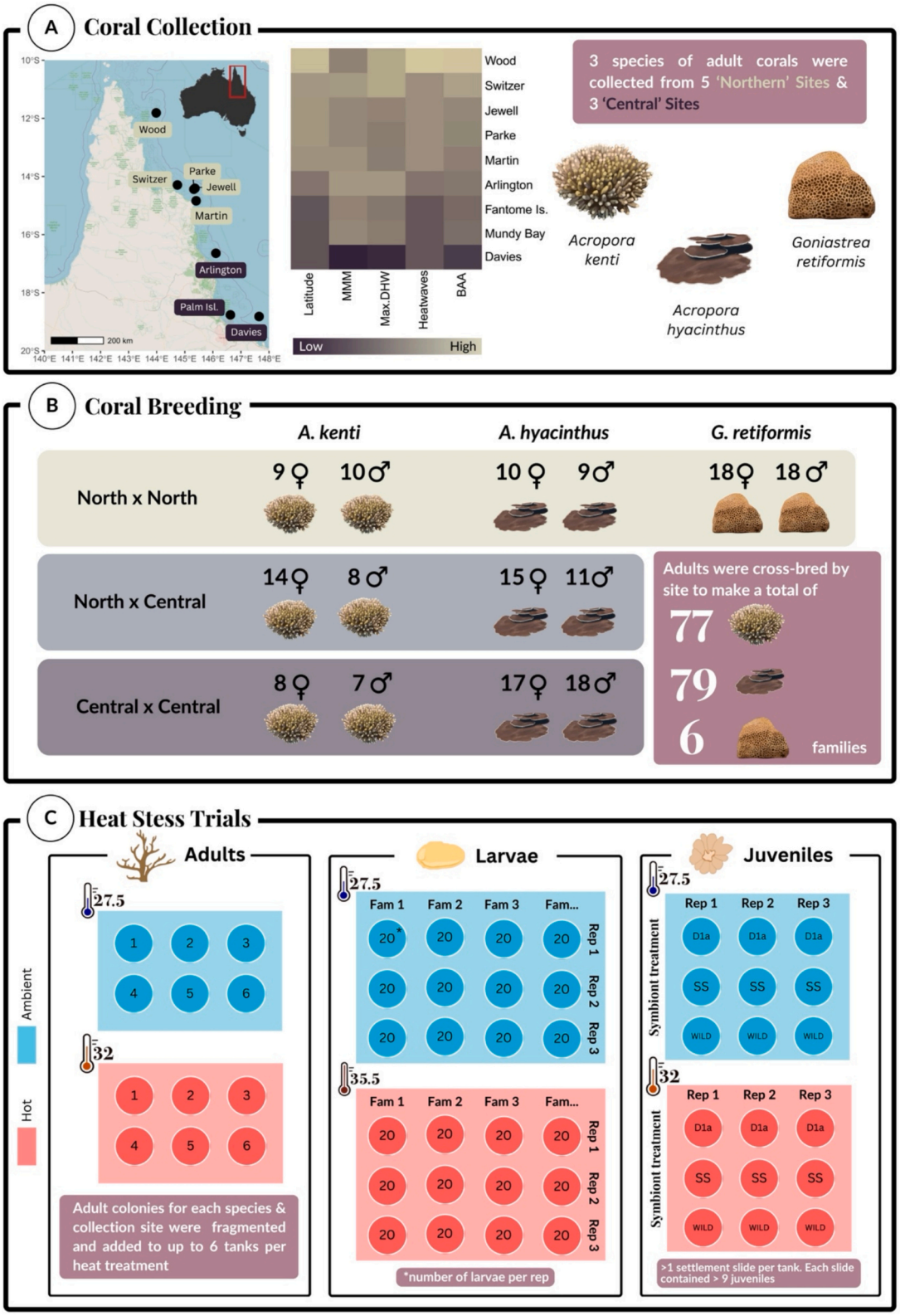

Fig. 1. Summary of coral species, collection site information, coral breeding and heat stress trials (A) Map of the Great Barrier Reef showing the sites of coral collection, a heatmap showing locations and environmental conditions for collection sites (see Supplementary Figure S1 and Supplementary Table 1 for full site information; MMM = maximum monthly mean, DHW = degree heating weeks, BAA = bleaching alert area), and images of the three study species: *A. kenti*, *A. hyacinthus* and *G. retiformis*. (B) Diagram of coral breeding of the three coral species and the resultant families. Numbers and symbols indicate the number of dams and sires used in the crosses. (C) Diagrams of the experimental setup for the three heat stress trials: adults (duration = 7 days for *A. kenti* and *A. hyacinthus*, 11 days for *G. retiformis*), larvae (duration = 61 h), and juveniles (duration = 31 days; D1a = *Durusdinium trenchii*, SS = heat-selected *Cladocopium goreaui,* wild = symbionts within Jewell reef sediments; see Methods sections 2.3, 2.4, and 2.6 for full details).

colonies to produce single crosses (one egg donor, one sperm donor) with a known sire (the male parent) and a known dam (the female parent). Fertilisation success was confirmed under microscope (Heyward and Babcock, 1986), and embryos from each family were transferred into separate 15 L conical tanks to develop.

After 24 h, each tank received constant flow-through of 0.2 μm FSW and an air bubbler to reduce water stagnation. The resultant crosses (hereby referred to as families) are detailed in Supplementary Table 3, where dam is named first and sire second. Parentage information for each cross is presented in Supplementary Table 4. 'Family' refers to offspring from the same sire and dam. 'Reef cross' refers to the reef of origin of the family's parents and were abbreviated to the first three letters of the reef (e.g. a Jewell dam and a Davies sire is JEWxDAV). 'Region-cross' refers to the combination of all reef crosses with the same region of origin (e.g., North x Central offspring is used to designate all families with a north reef dam and central reef sire). Intra-region refers to corals bred with both parents from the same region (e.g., Central x Central), while inter-region refers to corals bred with parents from different regions (e.g., North x Central).

2.3. Adult heat stress experiment

The parent colonies of *A. kenti, A. hyacinthus* and *G. retiformis* collected from northern (Jewell, Parke and Switzer for *A. kenti* and *G. retiformis*, and Martin and Wood for *A. hyacinthus*) and central reefs (Davies and Palms for *A. kenti* and *A. hyacinthus*) on the GBR were tested for thermal tolerance following spawning. Prior to and then after spawning, colonies were held at the SeaSim facility in AIMS in aquarium systems synchronized to each reef's historic temperature regime (Supplementary Table 1), to ensure that spawning timing was not disturbed (Lin and Nozawa, 2023; Paxton et al., 2016; Sakai et al., 2024). Due to post-spawning mortality, some parent genotypes could not be subjected to post-spawning heat stress conditions. However, alternate colonies collected from these reefs were tested. A band saw with a diamond encrusted blade was used to cut similar sized coral fragments (~5 cm). These were superglued onto aragonite plugs to provide at least six genetic replicates for each genotype per temperature treatment for *A. kenti*, six for *A. hyacinthus* and nine for *G. retiformis*. These fragments were left for an acclimation period of two weeks for coral fragments to heal from fragging wounds and avoid non-heat induced mortality. Once acclimated, corals were randomly distributed throughout 50 L acrylic aquaria.

Water inflow to aquaria was 0.8 L/min to allow for high turnover and circulated via an internal pump. Lighting for each aquarium was on a 24-h light/dark cycle (sunrise: 06:00 and sunset: 16:00), 2-h sunrise/sunset ramp time with photosynthetically active radiation (PAR) measuring ~150 PAR. The growth of fouling algae was cleaned every second day to support the health of coral and accuracy of readings. Feeding of corals with *Artemia* nauplii and algae was carried out at 15:00 each day.

The 5-km global product from NOAA Coral Reef Watch states that corals start to become stressed and bleach when the sea surface temperature (SST) is 1 °C warmer than the maximum monthly mean temperature (MMM) (Liu et al., 2014). A temperature of 32 °C was chosen for the adult heat stress treatment, 2 °C above the MMM of the warmest reef (Switzer reef MMM = 29.99 °C), to ensure bleaching and heat stress were induced. After an additional acclimation period of one week, the temperature in the hot treatment aquaria was increased by 0.5 °C/day from ambient (27.5 °C) to 32 °C over a period of nine days for all aquaria. The temperature of the ambient treatment aquaria remained at 27.5 °C. The resulting aquaria were $n = 6$ ambient, n = 6 hot treatments for *A. hyacinthus* and $n = 3$ ambient, n = 3 hot treatments for *A. kenti* and *G. retiformis* (see Fig. 1C for experimental setup). The first coral fitness trait measurements were taken the day after the hot aquaria reached a maximum temperature of 32 °C.

Bleaching was assessed using an Olympus TG5 camera fixed to a tripod to ensure consistent positioning and lighting conditions. Images were taken alongside a CoralWatch Health Monitoring Chart (Siebeck et al., 2006) under standardized settings (ISO: 125, f/2.0, shutter speed: 1/25, no flash). The coral fragment colour was matched to the closest category on the CoralWatch "D" coral health chart by the same observer to minimise bias. Once the temperature reached 32 °C, the experiment ran until the first coral genotype experienced 50 % mortality. This was seven days for *A. kenti* and *A. hyacinthus*, 11 days for *G. retiformis*.

2.4. Larval heat stress experiment

Two large aquaria were filled with flow through FSW. *A. kenti, A, hyacinthus* and *G. retiformis* larvae from the intra-region and inter-region crosses were placed into floating net wells (2.5 cm diameter nets fixed to plastic well; $n = 20$ larvae per well, n = 3 wells per tank), allowing water exchange (see Fig. 1C for experimental setup). Previous experiments have shown the extreme heat tolerance of coral larvae (Dixon et al., 2015; Howells et al., 2021). For continuity and comparability with a history of these experimental designs, a temperature of 35.5 °C was selected for the larval heat stress treatment due to the fact that it induced larval mortality over experimental time period in previous experiments (Quigley and van Oppen, 2022; Weeriyanun et al., 2022). One tank remained at ambient temperature (27.5 °C) while the other was gradually heated by 0.5 °C per hour until reaching 35.5 °C. Larval survival in each net well was visually counted until the first family exhibited ~50 % survival at 35.5 °C (61 h). Insufficient spawning from Wood Reef colonies prevented the creation of inter-region families with parents from this reef to be included in the experiments.

2.5. Juvenile settlement and symbiont inoculations

Non-heat stressed larvae were taken from the larval rearing tanks for settlement. All families were induced to settle onto PVC slides using a custom synthetic peptide (500 μL of GLW-amide neuropeptide Hym-248, Sigma Aldrich) at a final concentration of 1 μM (Takahashi et al., 1997). The Hym-248 peptide is derived from *Hydra* sp. and has been shown to induce settlement and metamorphosis in *Acropora* larvae (Iwao et al., 2002). Fifty distinct families of *A. kenti* and 13 families of *A. hyacinthus* larvae successfully settled onto the PVC slides (see Supplementary Table 5). No *G. retiformis* larvae successfully settled onto the slides. The slides were put into experimental tanks with two temperature treatments, 27.5 °C (ambient/control) and 32 °C (heated). *A. kenti* juveniles were then inoculated with three Symbiodiniaceae treatments (D1a = *Durusdinium trenchii* (SCF082; for details see Quigley and van Oppen, 2022), SS = artificially heat-evolved strain of *Cladocopium goreaui* (SCF055-01.01; for details see Quigley et al., 2021a), and freshly collected sediments housing Symbiodiniaceae ("wild") from Jewell Reef, using established methods for inoculation (Quigley et al., 2021a). *A. hyacinthus* juveniles were inoculated with one symbiont treatment (symbionts from sediments collected from Wood Reef). Light was set to 70 PAR (μMol/m^2/s) across all aquaria. The water temperature was maintained at 27.5 °C for 45 days to allow corals to grow and establish symbiosis with algae (assessed using Walz Microscope pulse amplitude modulation, PAM). For more information on symbiont inoculations, see Supplementary Methods 1.

2.6. Juvenile heat stress experiment

To ensure continuity with previous studies (see Quigley et al., 2020a; Quigley et al., 2020b) juveniles were exposed to the same heat stress temperature as adults. After four inoculations with the cultured symbionts, juveniles in the ambient treatment aquaria were held at 27.5 °C, while those in the heated treatment aquaria were gradually subjected to heat stress (+0.5 °C/h) until the temperature reached 32 °C, which was then maintained for the rest of the experiment. Once the temperature ramping was completed, water flow was resumed at 0.8 L/min to help maintain temperature, with the water filtered to 0.5 μm to prevent

external symbionts from entering the aquaria. For *A. kenti*, the 18 experimental aquaria were comprised of the following temperature and symbiont treatments: 27.5 °C: $n = 3$ D1a, n = 3 SS, n = 3 wild; 32 °C: n = 3 D1a, n = 3 SS, n = 3 wild (see Fig. 1C for experimental setup). The *A. kenti* tanks held 5881 individual coral juveniles, spread evenly across each treatment, resulting in ~21 (±2) juveniles per family per treatment. For *A. hyacinthus*, the six experimental aquaria were: 27.5 °C: n = 3, 32 °C: $n = 3$. The *A. hyacinthus* tanks held 248 individual coral juveniles, spread evenly across each treatment, resulting in ~6 juveniles (±1) per family per treatment. Lighting for each tank was on a 24-h light/dark cycle (sunrise: 10:00 and sunset: 18:00), 2-h sunrise/sunset ramp time with light levels measuring ~70 PAR.

Juvenile physiological traits were measured weekly throughout the experiment. These included measuring effective quantum yield of photosystem II (YII; Mueses et al., 2013) and light adapted maximum ($F_{m,}$) and minimum (F_t) fluorescence using imaging and microscopy pulse amplitude modulated (PAM) fluorometry. Images were taken weekly with a Nikon D810 camera body and Nikon AF-S 60 mm micro lens to obtain data on growth (2D area), colour (as a proxy for bleaching) using hue saturation and lightness (HSL) and survival ('alive' or 'dead'). These were later analysed using the program 'Ilastik' (Berg et al., 2019) and 'Fiji' (Schindelin et al., 2012) with a coral analysis pipeline to assess bleaching status and size for each juvenile (Macadam et al., 2021). Recording of physiological data ceased at 31 days, when the first cross reached ~50 % mortality.

2.7. Statistical analyses

Statistical analyses of adult, larval and juvenile survival were performed using hierarchical logistic models in a Bayesian framework using the brms package (Bürkner, 2017b) with 'RStan' (Guo et al., 2015). Separate models were fit for adults, larvae and juveniles.

The effect of temperature and reef identity on adult survival was analysed by fitting adult survival to a binomial distribution (number of live and dead fragments at each timepoint), where species, reef, and temperature were included as fixed effects along with terms to account for their interaction. Replicates between experimental treatments and tank were included as random effects.

The effect of temperature and reef cross identity on larval survival was analysed by fitting larval survival to a binomial distribution (number of live and dead larvae at each timepoint), where species, cross, and temperature were included as fixed effects along with terms to account for their interaction. Replicates between experimental treatments and boat (the floating device holding the larvae) were included as random effects.

Percent survival for coral juveniles was calculated for each family across each symbiont and temperature treatment. To exclude biases from fitness differences between individual and chimeric coral juveniles (i.e. juveniles that have fused during development; Rinkevich, 2019), only single coral juveniles were included in the survival statistics. Survival of coral juveniles was analysed by fitting juvenile survival to a binomial distribution (number of live and dead juveniles at each timepoint), where species, cross, symbiont treatment and temperature were included as fixed effects along with terms to account for their interaction. Replicates between experimental treatments and cassette (the device holding settlement slides) were included as random effects.

Percent change in colour, size, and YII were calculated for each individual juvenile across host reef cross and symbiont treatment. Percent change was calculated between the first and last timepoint. Growth, colour change, and YII were analysed using a GLMM in a Bayesian framework for each trait with Gaussian distribution using R package 'brms' (Bürkner, 2017a; Bürkner, 2017b) with symbiont treatment, host reef and temperature treatment as interactive fixed effects. Tank and cassette were added to the model as random variables.

All models included three No-U-Turn (Markov chain Monte Carlo; MCMC) chains of 5000 iterations, thinned to a rate of 10, with a burn-in period of 2500. MCMC mixture and convergence were assessed using trace plots, autocorrelation plots, Rhat and effective sample size diagnostics. Model assumptions were assessed using residual diagnostics using the package 'DHARMa' (Hartig, 2017). All model diagnostics passed, and values derived from histograms indicated that all Rhat parameters ≤1.008, suggest strong convergence. Models were iteratively fitted using leave-one-out (LOO) cross-validation to assess fit. Bayesian exceedance probabilities (P_e) are reported, which refers to the percent (%) confidence that the model has a greater posterior probability than any other model tested (Stephan et al., 2009). Credibility intervals are plotted for each treatment. The exceedance probability can be interpreted similarly to statistical power, and the width of confidence intervals for the exceedance probability convey the stability of a result (Segal, 2021). The P_e scale adopted for this paper is: >0.85 = week evidence, >0.9 = evidence, >0.975 = strong evidence. All results were visualised using the 'ggplot2' package (Wickham et al., 2016) in R (version 4.2.1; R CoreTeam, n.d.) and all code used to execute the statistical analyses is available online (github.com/alexmacadam241/AGF-Physiology).

The relative contributions of symbiont identity and host genetic background were quantified using statistical methods in which each factor was run separately as described in (Mizerek et al., 2018) using Marginal and Conditional R^2 values calculated with the 'rsquared' function from the 'piecewiseSEM' package (Lefcheck, 2016).

3. Results

3.1. Heat tolerance of adult corals

3.1.1. Adult survival

Adult corals underwent heat stress for a total of seven days for *A. kenti* and *A. hyacinthus* and 11 days for *G. retiformis*. Adult survival at 32 °C was 11.6 % ± 5.3, 17.1 % ± 4.0, and 10.1 % ± 2.9 lower compared to 27.5 °C for *A. kenti*, *A. hyacinthus,* and *G. retiformis* (absolute survival at 32 °C: *A. kenti* = 81 % ± 5.5, *A. hyacinthus* = 56.4 % ± 12.6, *G. retiformis* = 89.1 % ± 6.0) and varied between source reefs (Fig. 2A). The only exception to this pattern was *A. kenti* from the Palms, which exhibited higher survival at 32 °C compared to 27.5 °C (100 % ± 0 versus 82 % ± 9.0). At 27.5 °C adult coral survival was high across all three coral species (mean ± SE = 95 % ± 0–82 % ± 1.7) for all reefs, indicating that aquarium conditions for the experiment were tolerable (Fig. 2A).

G. retiformis exhibited the smallest decrease in survival at 32 °C (−10.1 % ± 1.9), although Jewell decreased by 25 % ± 14.4. This was followed by *A. kenti* (−11.6 % ± 5.3), with the lowest survival also from Jewell (−44.4 % ± 5.6). *A. hyacinthus* survival was the lowest (−17.1 % ± 4.0), especially at Davies (−36.2 % ± 5.1). Conversely, the highest survival for each species was recorded for *G. retiformis* from Parke (+2.1 % ± 1.04), *A. kenti* from the Palms (+18.3 % ± 9.1), and *A. hyacinthus* from Martin (−3.3 % ± 2.3).

3.1.2. Adult bleaching

Final baseline colour scores at 27.5 °C varied across the three species as follows (mean ± SE): *G. retiformis* = 5.5 ± 0.0, *A. kenti* = 4.5 ± 0.5, *A. hyacinthus* = 4.0 ± 0.1 (Fig. 2B). At 32 °C, bleaching responses varied between species and reefs (Fig. 2B). Relative to controls, *G. retiformis* from Jewell (−4.0 ± 0.1), *A. kenti* from Jewell (−2.4 ± 1.2) and *A. hyacinthus* from Davies (−0.8 ± 0.4) bleached the most. The lowest bleaching score relative to control per species was observed in *G. retiformis* from Switzer (−0.6 ± 0.3) *A. kenti* from the Parke (−0.0 ± 0.0) and *A. hyacinthus* from Martin (−0.2 ± 0.1).

3.2. Heat stress survival of larval and juvenile corals across reef crosses

3.2.1. Larval survival

Larval survival across all reefs at 35.5 °C was 25.7 % ± 3.2, 66.5 %

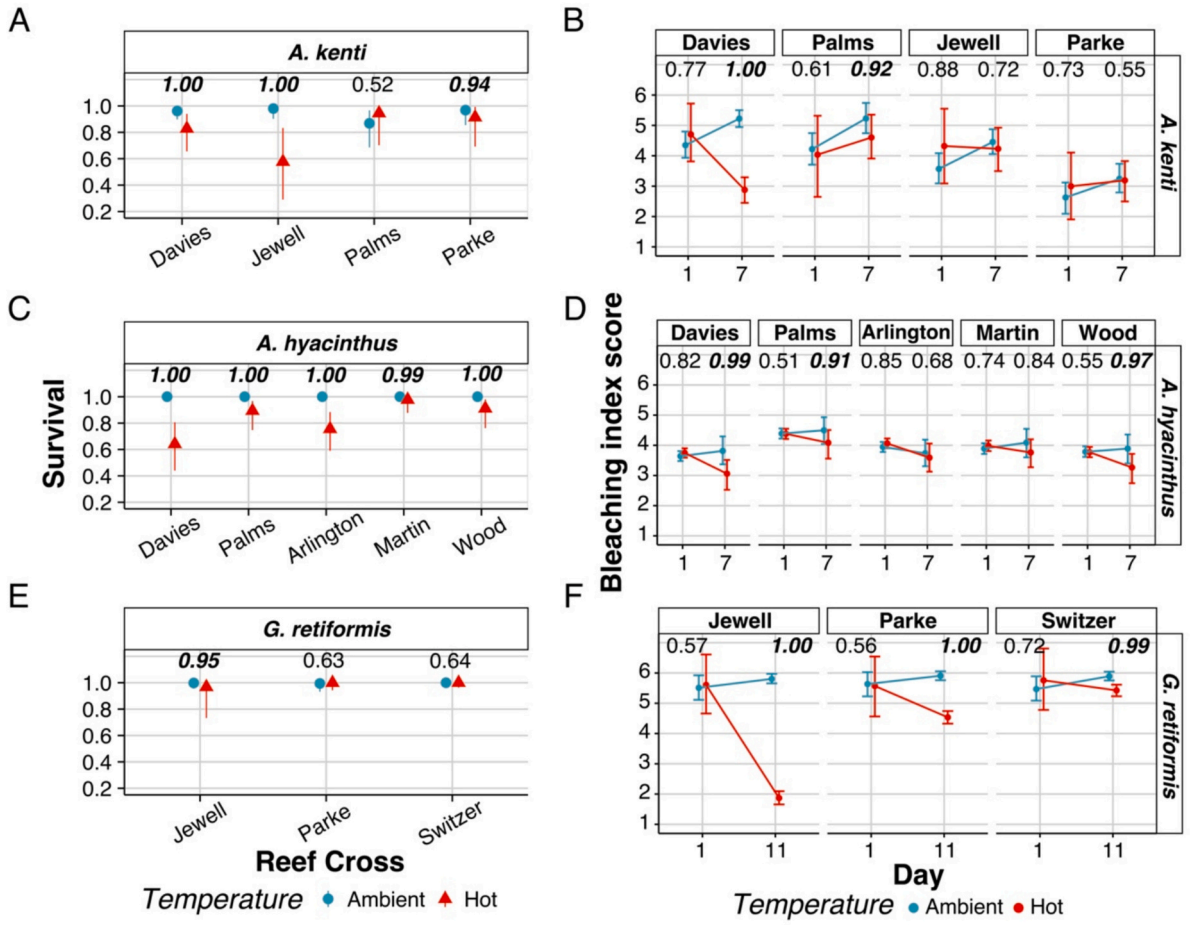

Fig. 2. Adult coral estimated marginal means (EMM) of survival and bleaching. EMM (±95 % credibility intervals) for survival of adult *Acropora kenti* (A), *A. hyacinthus* (C), and *Goniastrea retiformis* (E) coral fragments from different reefs and temperature treatments across the Great Barrier Reef. Temperature treatments were ambient/control (blue, 27.5 °C) and hot (red, 32 °C). (B) EMM (±95 % credibility intervals) for colour score (converted to CoralWatch coral health chart score using the D scale from saturation and brightness measurements) of adult *A. kenti* (B), *A. hyacinthus* (D), and *G. retiformis* (F) coral fragments from different reefs and temperature treatments between timepoint 0 and the final timepoint (day **seven** for *A. kenti* and *A. hyacinthus*, and day **11** for *G. retiformis*). Numbers correspond to exceedance probabilities (P_e) between the ambient and hot treatments. P_e above a threshold of 0.90 are in bold. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

± 2.0, and 10.3 % ± 1.6 lower compared to 27.5 °C for *G. retiformis*, *A. kenti,* and *A. hyacinthus* respectively (Fig. 3A-C; absolute survival at 35.5 °C: *A. kenti* = 30.5 % ± 0.5, *A. hyacinthus* = 65.9 % ± 0.3, *G. retiformis* = 61.1 % ± 0.9). All families had higher survival at 27.5 °C, except for WOOxMAR reef cross for *A. hyacinthus* (27.5 °C = 73.8 % ± 11.8, 35.5 °C = 75.8 % ± 9.7). Survival at 27.5 °C was high (*G. retiformis* = 85.4 % ± 2.1, *A. kenti* = 97.1 % ± 0.7, *A. hyacinthus* = 78.9 % ± 3.8) for all reef-crosses (Fig. 3A & C).

Generally, northern intra-region *A. kenti* larvae survived better at 35.5 °C compared to central intra-region larvae. Northern intra-region *A. kenti* larvae had 54 % greater odds of survival compared to central intra-region larvae (Fig. 3A, P_e = 0.943, BGLMM). Inter-region *A. kenti* larvae also had 115 % greater odds of survival compared to central intra-region larvae (Fig. 3A, P_e = 1.000, BGLMM). Specifically, survival of JEWxDAV (42.7 % ± 5.5) and JEWxPAL (38.3 % ± 5.2) larvae had 176 % (P_e = 0.999, GLMM) and 500 % (P_e = 1.000, GLMM) higher odds of survival at 35.5 °C, compared to our control reef crosses (central intra-region DAVxDAV = 34.2 % ± 4.6 and PALxPAL = 10.6 % ± 3.6). They had comparable survival rates (42.1 % ± 6.4) to the intra-region larvae from the northern reef larvae (JEWxJEW).

At 35.5 °C northern intra-region *A. hyacinthus* larvae had 296 % greater odds of survival compared to central intra-region larvae (Fig. 3B; P_e = 0.994, BGLMM). However, inter-region *A. hyacinthus* larvae did not have higher odds of survival compared to central intra-region larvae (Fig. 3B, P_e < 89.0, BGLMM). The inter-region larvae with the highest percent survival at 35.5 °C was MARxDAV (64.1 % ± 3.7), which is lower than the central intra-region controls (DAVxDAV: 68.2 % ± 3.0). *A. hyacinthus* survival at 27.5 °C was high but highly variable (range ± SE = 26.7 % ± 1.7–100 % ± 0, Fig. 3B).

At 35.5 °C, *G. retiformis* larvae with a Jewell dam (69.6 % ± 7.5) had 45 % greater odds of survival compared to those with a Switzer dam (Fig. 3C; 45.1 % ± 5.6; P_e = 0.899, BGLMM). The cross with the highest survival at 35.5 °C was JEWxSWI (78.2 % ± 10.9), while the cross with the lowest survival was SWIxPAR (36.7 % ± 6.0). Overall survival of *G. retiformis* at 27.5 °C was high (85.1 % ± 2.1).

3.2.2. *Juvenile survival*

Juvenile survival across all reef crosses at 32 °C was 16.01 % ± 2.0 and 19.9 % ± 3.1 lower compared to 27.5 °C for *A. kenti* and *A. hyacinthus,* respectively (Fig. 3D-E). All families had higher survival in 27.5 °C treatment. Survival at 27.5 °C was high (mean ± SE: *A. kenti* = 95.5 % ± 0.7, *A. hyacinthus* = 97.7 % ± 1.3) for all reef crosses (Fig. 3D-E). Survival did not significantly vary by symbiont treatment; therefore, this factor was then dropped from the model.

Generally, northern intra-region *A. kenti* juveniles survived better at 32 °C compared to central intra-region juveniles. Northern intra-region *A. kenti* juveniles had 59 % greater odds of survival compared to central

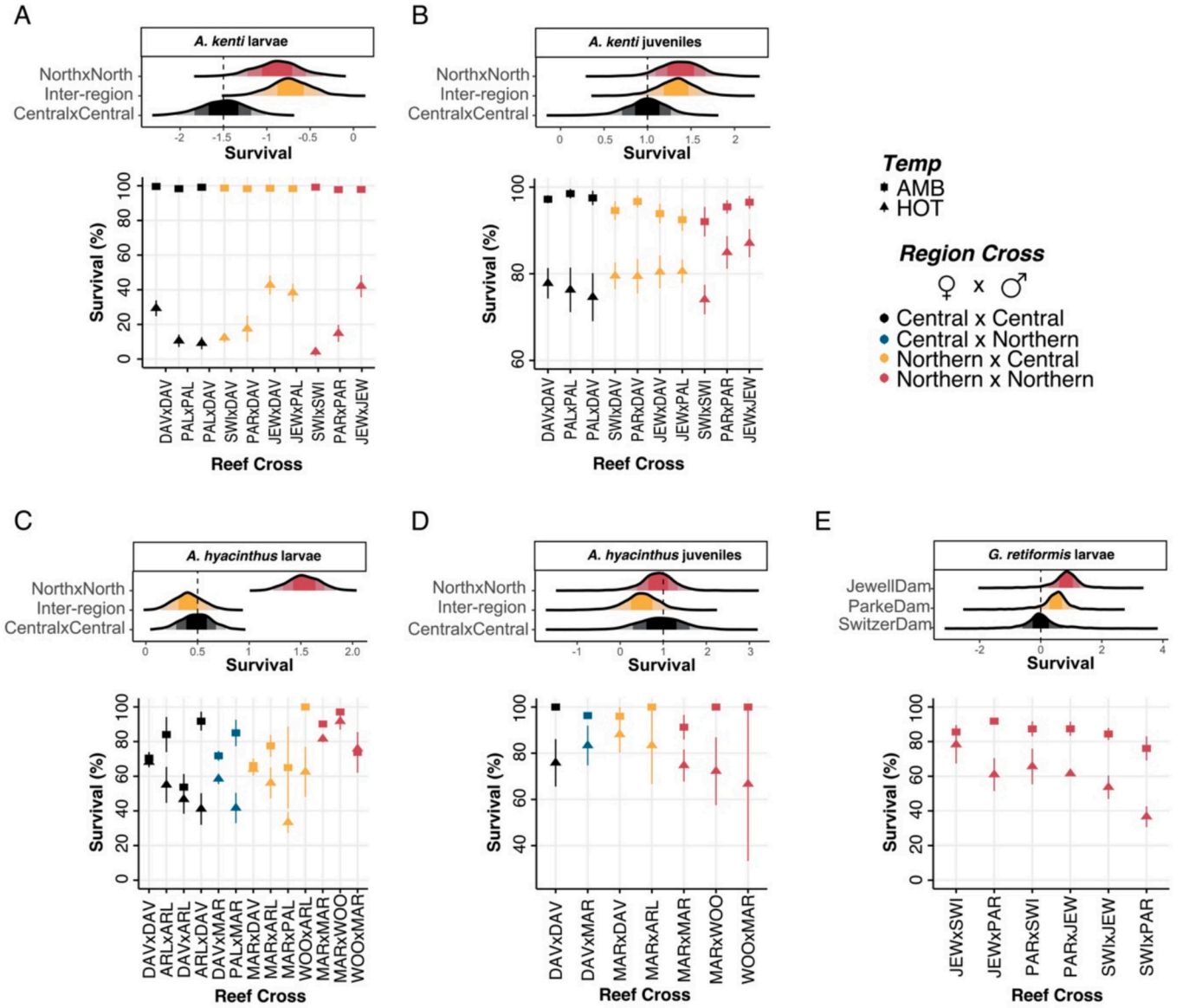

Fig. 3. Survival of early life stage corals for *Acropora kenti*, *Goniastrea retiformis*, and *A. hyacinthus* in ambient (27.5 °C) and hot (35.5 °C in larvae and 32 °C in juveniles) treatments. Survival (log-odds) of *A. kenti* larvae (A) and juveniles (for all Symbiodiniaceae treatments; B), *A. hyacinthus* larvae (C) and juveniles (D), and *G. retiformis* larvae (E). Estimated marginal means (EMM; ± 95 % credibility intervals) of survival (log-odds) in the hot (larvae = 35.5 °C, juveniles = 32 °C) treatment by region cross relative to baseline (Central × Central; top). Mean percent survival (± SE) for reef crosses subjected to ambient (27.5 °C) and hot (larvae = 35.5 °C, juveniles = 32 °C) temperature treatments (bottom). The duration of larval heat stress was 61 h. The duration of juvenile heat stress was 31 days.

intra-region juveniles (Fig. 3D, P_e = 1.000, BGLMM). Inter-region *A. kenti* juveniles also had 38 % greater odds of survival compared to central intra-region juveniles (Fig. 3D, P_e = 0.992, BGLMM). Specifically, survival of JEWxDAV (80.4 % ± 3.8) and SWIxDAV (79.5 % ± 3.1) juveniles had 66 % (P_e = 0.991, GLMM) and 27 % (P_e = 0.905, GLMM) higher odds of survival at 32 °C, compared to our control reef crosses (central intra-region DAVxDAV, 77.8 % ± 3.5).

At 32 °C northern intra-region *A. hyacinthus* juveniles did not have higher odds of survival compared to central intra-region juveniles (Fig. 3E; P_e = 0.501, BGLMM). Comparably, inter-region *A. hyacinthus* juveniles did not have higher odds of survival compared to central intra-region juveniles (Fig. 3E; P_e = 0.501, BGLMM). The inter-region cross with the highest percent survival at 32 °C was MARxDAV (88.1 % ± 7.9), which is 12.3 % ± 6.1 higher than the central intra-region controls (DAVxDAV: 75.8 % ± 10.3). *A. hyacinthus* survival at 27.5 °C was high (mean ± SE = 97.7 % ± 2.6, Fig. 3E).

Region cross did not significantly affect final size (Supplementary Figure S3A), colour score (Supplementary Figure S3B), YII (Supplementary Figure S3C), change in size (Supplementary Figure S4A), change in colour (Supplementary Figure S4B), or change in YII (Supplementary Figure S4C).

3.3. Performance of coral juveniles across symbiont treatments

While survival did not significantly vary by symbiont treatment in *A. kenti* juveniles (Fig. 4A), juvenile size, colour and YII all varied significantly (Fig. 4B-D, Supplementary Figure S2).

3.3.1. Juvenile size

Final juvenile size and change in size across all symbiont treatments at 32 °C was 0.05 mm^2 ± 0.0 and 8.34 % ± 0.5 lower compared to 27.5 °C (Fig. 4B, Supplementary Figure S2A). There was lower growth at 32 °C than 27.5 °C in all symbiont treatments (P_e > 0.935, BGLMM).

Symbiont treatment significantly affected final juvenile size at 32 °C

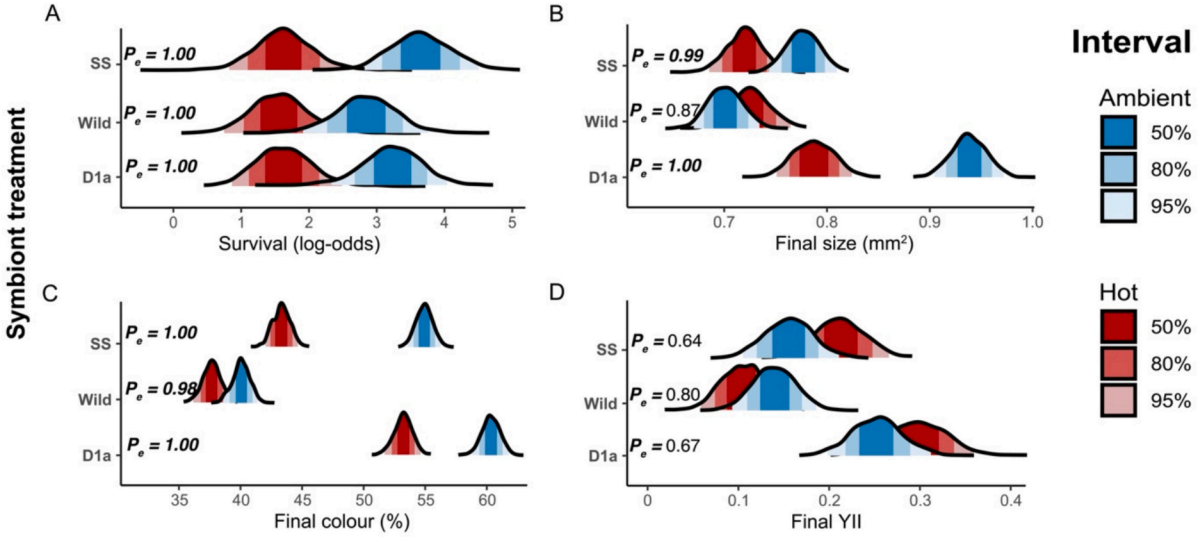

Fig. 4. Estimated marginal means of physiological parameters of *Acropora kenti* juvenile corals across Symbiodiniaceae treatments between ambient (27.5 °C) and hot (32 °C) treatments. (A) Estimated marginal means (EMM) for survival (log-odds) of *Acropora kenti* juveniles at the completion (day 30) of the experiment per symbiont and temperature treatments. (B) EMM for final size (mm^2) of *A. kenti* juveniles at the completion (day 30) of the experiment per symbiont and temperature treatments. (C) EMM of final colour (grey scale %) of *A. kenti* juveniles at the end (day 30) of the experiment per symbiont and temperature treatments. (D) EMM for final effective quantum yield (YII) of *A. kenti* juveniles at the end (day 30) of the experiment per symbiont and temperature treatments. Temperature treatments: 27.5 °C (ambient/control) and 32 °C (hot). Symbiont treatments: D1a = *Durusdinium trenchii,* SS = heat-selected *Cladocopium goreaui,* wild = symbionts within Jewell reef sediments; see Methods sections 2.3, 2.4, and 2.6 for full details). Intervals correspond to 50 %, 80 % and 95 % credibility interval. Exceedance probabilities (P_e) above the threshold of 0.90 are highlighted in bold.

(Fig. 4B). The final size of D1a juveniles was 0.07 mm (P_e = 0.994, BGLMM) and 0.06 mm (P_e = 0.983, BGLMM) larger than the SS and wild juveniles at 32 °C (Fig. 4B).

Temperature treatment affected final size more in the SS and D1a than the wild juveniles (Fig. 4B). The final size of the D1a and SS juveniles at 27.5 °C conditions was 0.15 mm (P_e = 1.000, BGLMM) and 0.06 mm (P_e = 0.991, BGLMM) larger than at 32 °C, while the final size of the wild treatment juveniles was not significantly different between temperature treatments (P_e = 0.851, BGLMM; Fig. 4B).

Symbiont treatment significantly affected change in size of juveniles at 32 °C (Supplementary Figure S2A). The SS and D1a juveniles had 10.40 % (P_e = 1.000, BGLMM) and 19.92 % (P_e = 1.000, BGLMM) larger decrease in size compared to the wild symbiont juveniles at 32 °C, while change in size was 9.53 % higher in the D1a compared to SS treatment in 32 °C (P_e = 1.000, BGLMM).

3.3.2. *Juvenile bleaching*

Final colour score was significantly lower at 32 °C than 27.5 °C for all three symbiont treatments (P_e > 0.995, BGLMM; Fig. 4C), and was overall 7.1 % ± 0.2 lower.

Symbiont treatment significantly affected final juvenile colour score at 32 °C (Fig. 4C). The final colour score of D1a juveniles was 10.0 % ± 5.0 (P_e = 1.000, BGLMM) and 15.8 % ± 7.9 (P_e = 1.000, BGLMM) higher than the SS and wild juveniles at 32 °C (Fig. 4C). Temperature treatment affected final colour score more in the SS and D1a than the wild juveniles (Fig. 4C). The final colour of the D1a and SS juveniles at 27.5 °C was 7.0 % ± 3.5 (P_e = 1.000, BGLMM) and 11.5 % ± 5.8 (P_e = 1.000, BGLMM) higher than at 32 °C, while the final colour score of the wild juveniles was 1.8 % ± 0.9 higher at 32 °C (P_e = 0.980, BGLMM; Fig. 4C).

Change in colour score was significantly lower in 32 °C than 27.5 °C for all three symbiont treatments (P_e > 1.000, BGLMM; Supplementary Figure S2B), and was 7.8 % ± 0.1 lower compared to 27.5 °C. Symbiont treatment significantly affected change in colour score of juveniles at 32 °C (Supplementary Figure S2B). Juvenile colour score decreased in SS and D1a juveniles at 32 °C, but not in wild juveniles (Supplementary Figure S2B). The wild symbiont juveniles had 4.9 % ± 2.4 (P_e = 1.000, BGLMM) and 5.5 % ± 2.7 (P_e = 1.000, BGLMM) lower change in colour score compared to D1a and SS juveniles at 32 °C.

3.3.3. *Juvenile photophysiology*

Symbiont treatment significantly affected final YII at 32 °C (Fig. 4D). The final YII of D1a juveniles was 8.7 % ± 4.3 (P_e = 0.985, BGLMM) and 19.7 % ± 9.9 (P_e = 1.000, BGLMM) higher than the SS and wild juveniles at 32 °C (Fig. 4D). Final YII did not significantly increase for any symbiont treatment at 32 °C compared to 27.5 °C (Fig. 4D; P_e < 0.800, BGLMM).

Change in YII was significantly lower at 32 °C compared to 27.5 °C for D1a and SS juveniles (P_e > 0.918, BGLMM; Supplementary Figure S2C), while there was no difference in wild juveniles (P_e = 0.831, BGLMM). Symbiont treatment significantly affected change in YII of juveniles at 32 °C (Supplementary Figure S2C). YII increased by 115.4 % ± 39.3 and 96.2 % ± 26.5 in SS and wild juveniles at 32 °C, while D1a juveniles decreased 6.7 % ± 34.9 (Supplementary Figure S2C).

3.4. *Correlations across generations and life stages*

The correlation of survival under heat stress across early life stages (larvae and juveniles) for each individual family was low (R^2 = 0.023; Fig. 5A & B). Similarly, survival of adult corals under hot conditions did not positively correlate with survival of offspring at juvenile (Fig. 5C) or larval (Fig. 5D) life stages. In fact, larval and adult survival were negatively correlated in *A. kenti* and *G. retiformis*.

Although there was no positive correlation of survival between life-history stages, relative contributions of family identity on survival of larvae were high for the two *Acropora* species (Percent explained: *A. kenti* = 97.6 %, *A. hyacinthus* = 98.6 %; Table 1). This was considerably lower in the juvenile life stage for *A. kenti* (7 %) but was substantial in the *A. hyacinthus* juveniles (61.6 %). The relative contributions of sire and dam varied between species and life stages (Table 1). Family had higher relative contributions to survival, growth, bleaching, and YII than reef cross in all species and life stages, except for in *A. kenti* juveniles, where contributions were comparable (Table 1).

At the larval stage, dam and sire contributions to survival were

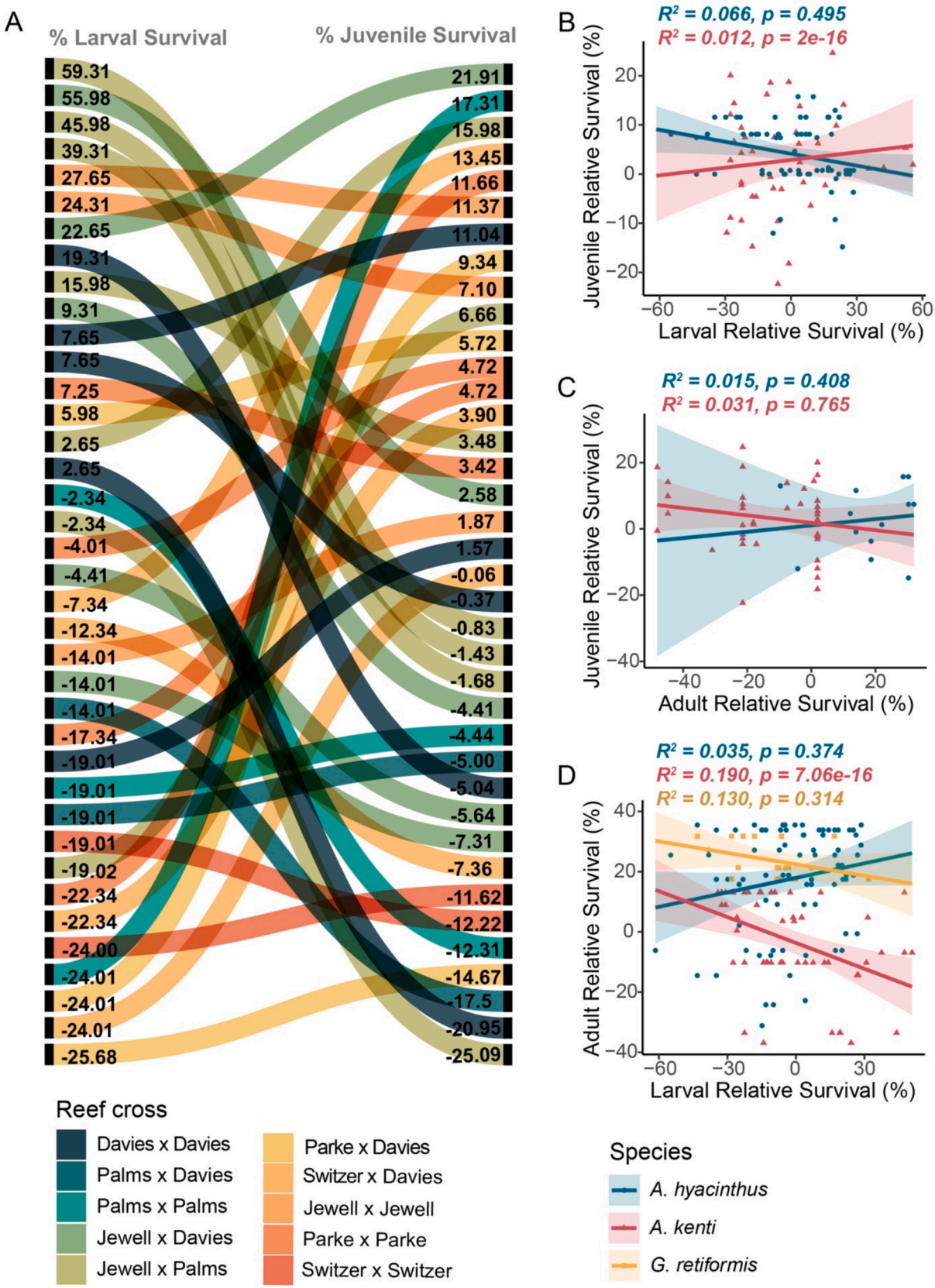

Fig. 5. Comparisons of survival across life stages. (A) Alluvial plot showing the order of survival under heat stress for larval and juvenile families. Numbers correspond to relative percent survival (%) deviance from the mean survival of all families. Colours correspond to reef cross. Correlation plots of percent survival (%) deviance between (B) larval and juvenile survival by species, (C) adult and juvenile survival by species, (D) larval and adult survival by species showing survival (%). Species: *Acropora hyacinthus* (blue), *A. kenti* (red), *Goniastrea retiformis* (yellow). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1
Relative contributions of variables across all *Acropora kenti*, *A. hyacinthus* and *Goniastrea retiformis* larvae, and *A. kenti* and *A. hyacinthus* juveniles.

	Larval survival			Juvenile survival			Juvenile growth			Juvenile bleaching			Juvenile YII		
	R2 (M)	R2(C)	% explained	R2 (M)	R2(C)	% explained	R2 (M)	R2 (C)	% explained	R2 (M)	R2 (C)	% explained	R2(M)	R2 (C)	% explained
A. kenti															
Symbiont				0	0.271	0	0.061	0.395	15.4	0.018	0.536	3.4	0.149	0.998	14.9
Reef cross	0.297	0.945	31.4	0.0018	0.258	7	0.004	0.394	1	0.007	0.531	1.3	0.033	0.998	3.3
Family	0.97	0.994	97.6	0.0018	0.292	6.2	0.02	0.404	5.4	0.037	0.544	6.8	0.022	0.149	14.8
Dam	0.648	0.94	68.9	0.04	0.262	15.3	0.006	0.396	1.5	0.009	0.532	1.7	0.073	0.998	7.3
Sire	0.261	0.95	27.5	0.066	0.275	24	0.01	0.398	2.5	0.011	0.531	2.1	0.062	0.998	6.2
All				0.165	0.403	40.9	0.108	0.412	26.1	0.258	0.548	47.2	0.199	0.999	19.9
A. hyacinthus															
Reef cross	0.255	0.905	28.2	0.018	0.082	21.9	0.02	0.256	7.9	0.106	24.5	24.5	0.067	0.999	6.7
Family	0.98	0.994	98.6	0.115	0.186	61.6	0.088	0.302	29.2	0.146	32.7	32.7	0.12	0.999	12
Dam	0.382	0.907	42.1	0.114	0.186	60.9	0.058	0.287	20.4	0.147	33.3	33.3	0.106	0.999	10.6
Sire	0.389	0.906	42.9	0.062	0.131	47.7	0.042	0.282	14.9	0.115	26.2	26.2	0.095	0.999	9.5
All				0.206	0.211	97.4	0.045	0.294	15.4	0.122	26.3	26.3	0.094	1	9.4
G. retiformis															
Reef cross	0.451	0.787	57.3												
Family															
Dam	0.336	0.787	42.7												
Sire	0.296	0.76	38.9												
All															

comparable in *A. hyacinthus* (Dam = 42.1 %, Sire = 42.9 %) and *G. retiformis* (Dam = 42.7 %, Sire = 38.9 %), while dam contributions to survival was larger than sire contributions in *A. kenti* (Dam = 68.9 %, Sire = 27.5 %). Conversely, the relative contribution to survival was larger for sires than dams in *A. kenti* juveniles (Dam = 15.3 %, Sire = 24.0 %), while the contribution of dams was stronger in *A. hyacinthus* juveniles (Dam = 60.9 %, Sire = 47.7 %).

For the *A. kenti* juveniles, symbiont treatment had the largest relative contribution to explaining variation in growth rate (15.4 %) and YII (14.9 %).

4. Discussion

Our study provides one of the most comprehensive evaluations of AGF for reef-building corals on the GBR, considering both geographical scope and species. For simplicity, we refer here to all inter-region crosses as AGF, acknowledging that these represent only the first step (inter-region crossing) in the use of AGF as an intervention in wild populations. By conducting heat stress experiments across multiple life stages, we assessed heat tolerance of 77 *Acropora kenti*, 79 *A. hyacinthus*, and five *Goniastrea retiformis* families. Our results highlight AGF's potential to enhance heat tolerance within and between species, while also revealing significant variability in its effectiveness. Notably, survival to heat stress was not consistently transferred across life stages or species, emphasizing the complexity of this trait. Parental effects had a stronger influence on survival than reef cross effects, suggesting that genetic background plays a crucial role in determining heat tolerance. Additionally, while juveniles inoculated with the two varieties of heat-tolerant symbiont treatments (heat-evolved *C. goreaui* and sediment-derived symbionts from northern reefs), these exhibited similar acquired heat tolerance to those hosting *D. trenchii* (Quigley et al., 2020b). Symbiodiniaceae treatments significantly affected other fitness traits, such as growth and bleaching tolerance. These findings underscore the need for a nuanced, species- and life-stage-specific approach when implementing AGF as a climate adaptation strategy.

4.1. Species-specific variability in heat stress survival

Our findings demonstrate that AGF can increase heat tolerance in early life stages in multiple coral species, but the degree of enhancement is variable. In *A. kenti,* inter-region larvae and juveniles exhibited significantly higher survival under heat stress compared to intra-region central crosses (controls). This is consistent with previous studies demonstrating increased tolerance in inter-region crosses from central and northern reefs (Quigley and van Oppen, 2022; Weeriyanun et al., 2022). Offspring from intra-region northern reefs (Jewell and Parke) exhibited the highest survival rates, supporting expectations that corals from warmer environments contribute beneficial alleles for enhanced thermal tolerance (Quigley et al., 2020a). However, the relationship between historic thermal regimes and heat tolerance was not always straightforward. For instance, *A. kenti* larvae and juveniles from Switzer Reef, an inshore northern reef with the highest recorded historic maximum monthly mean temperature (MMM) and Degree Heating Weeks (DHW) in the experiment, exhibited lower than expected survival under heat stress. This may reflect local adaptation to Switzer Reef's high turbidity and nutrient levels, potentially rendering them maladapted to the low-nutrient conditions of the experimental setup. In contrast, inter-region Switzer × Davies juveniles outperformed both intra-region central and northern controls, suggesting that inter-regional breeding could mitigate this potential maladaptation to inshore environmental conditions. These findings underscore the complex interplay between water-quality and heat tolerance (Morris et al., 2019) and highlight the importance of considering cumulative environmental gradients when selecting broodstock for AGF-based interventions.

Contrary to patterns seen for *A. kenti*, AGF did not significantly improve *A. hyacinthus* larval survival. While inter-region juveniles

exhibited a 12.3 % higher mean survival than intra-region central controls, this difference was not statistically significant, possibly due to high phenotypic variability or small sample sizes. Cryptic genetic variation (Sheets et al., 2018) may also have contributed to this outcome. Although we targeted a single morphotype (Ladner and Palumbi, 2012; Rose et al., 2018), low intra-region survival suggests the potential presence of putative species within reefs (supported by Naugle et al., 2024), potentially influencing compatibility during ontogeny. While offspring produced from crossing different populations may outperform both parental populations in some cases (heterosis; Hamilton and Miller, 2016), in others, incompatibility can arise when genetic mismatches between source populations result in reduced offspring fitness (outbreeding depression; Aitken and Whitlock, 2013). This can result in disruptions to co-adapted gene complexes or incompatible structural genomic differences (Kovach et al., 2016). Incorporating population genomic data with breeding experiments may be essential for successfully using *A. hyacinthus* for AGF.

For *G. retiformis,* crosses with a Jewell dam exhibited the highest survival under heat stress, similar to trends observed in *A. kenti*. Notably, adult *G. retiformis* exhibited the highest heat stress survival of all three species studied, aligning with previous findings that *Goniastrea* corals are inherently heat tolerant (Darling et al., 2012). Although our dataset for this species is preliminary, and despite the limitation that no population genetic data is available for *Goniastrea* on the GBR, these results suggest that *G. retiformis* possess a strong baseline heat tolerance that can be further increased through AGF, making it a promising candidate for future interventions that involve reproduction. This finding also demonstrates that AGF can be effective on the GBR beyond Acroporidae, as has been observed in Caribbean (Hagedorn et al., 2018) and Persian Gulf corals (Howells et al., 2021).

The varying levels of effectiveness in survival enhancement among species observed here is likely driven, in part, by a combination of population structure, standing genetic variation, and phenotypic plasticity. Genetic connectivity and population structure vary among coral species on the GBR, influencing the success of AGF. For instance, *A. kenti* exhibits isolation-by-distance (IBD) patterns and comprises at least four genetic clusters, three of which are in the northern and central regions (Matias et al., 2023). This indicates that this species is unlikely to be fully panmictic. This enables local adaptation by allowing selective pressures to vary between regions, while preventing excessive gene flow that would homogenize the population. In contrast, *A. hyacinthus* likely represents a species complex (Naugle et al., 2024), where high genetic variation between putative species may lead to incompatibility. This explains why AGF enhanced heat tolerance more effectively in *A. kenti* than in *A. hyacinthus*, as the former benefited from favourable genetic variation between regions, while the latter may have been hindered by excessive genetic divergence. These results underscore the need for species-specific assessments of genetic structure.

The presence of heritable variation in heat tolerance is a critical prerequisite for AGF (Grummer et al., 2022). Heritability estimates offer valuable insights into the genetic basis of many traits, like heat tolerance (Bairos-Novak et al., 2021); however, high heritability alone does not guarantee rapid adaptation, as this also depends on the strength of selection (Richards et al., 2023). Polygenic adaptation, driven largely by shifts in the prevalence of preexisting alleles, plays a central role in species-specific resilience to climate change (Matz et al., 2018; Rose et al., 2018). Even among closely related species, allele frequency variation across multiple loci influences protein function, gene expression, and symbiont compatibility, ultimately shaping differences in heat tolerance between species (Rose et al., 2018). Furthermore, species with higher genetic diversity within or among reef populations may exhibit greater potential for selection to act upon beneficial alleles (Ørsted et al., 2019). Despite occupying the same reef, species may experience distinct selective pressures due to microhabitat differences, which could drive patterns of local adaptation. Moreover, local adaptation can occur even in the absence of distinct genetic differentiation, driven by persistent selective pressures rather than biophysical isolation (Aitken and Whitlock, 2013). For instance, reefs exposed to recurrent extreme heat events, high daily temperature variability, and elevated MMM temperatures may harbor higher frequencies of heat tolerance-associated variants (Quigley and van Oppen, 2022). Such reefs represent potential donor populations for AGF, as they may provide adaptive alleles that enhance thermal resilience into recipient populations. These findings highlight the importance of integrating genomic tools with environmental data to identify reefs with high adaptive potential, even in the absence of strong genetic differentiation, to optimize the success of AGF in a changing climate (Quigley and van Oppen, 2022).

Beyond genetic variation, phenotypic plasticity and epigenetic mechanisms further influence interspecific differences in AGF success. A substantial proportion of heat tolerance in corals may be mediated by non-genetic factors (Liew et al., 2020). Some corals may retain the benefits of acclimation from prior heat stress exposure, potentially through transgenerational inheritance of beneficial epigenetic modifications (e.g., DNA methylation) that enhance heat tolerance without permanent genetic changes (Guerrero and Bay, 2024). However, this plasticity likely varies between species (Da-Anoy et al., 2024). Some species exhibit high plasticity in response to heat stress (Ferrara et al., 2024), enabling short-term resilience but potentially reducing the strength of selection for genetic adaptation. High plasticity may facilitate the persistence of maladapted genotypes, ultimately weakening the effects of AGF (Gilbert and Miles, 2019). Conversely, species with lower plasticity may rely more heavily on genetic adaptation, which necessitates a longer timescale for beneficial alleles to accumulate in a population (Healy et al., 2018). These findings highlight the importance of a multifaceted approach in selecting broodstock for AGF interventions. Future research should integrate quantitative and population genetic analyses, assessments of phenotypic plasticity, and multi-generational studies of AGF efficacy to refine conservation strategies (Hoffmann et al., 2021; Richards et al., 2023).

4.2. Variation in survival across life-history stages

The species-specific variability to increases to heat tolerance with AGF aligns with findings from other coral breeding studies (reviewed in Drury et al., 2022b), yet our study is among the first to experimentally demonstrate that AGF-induced enhancements differ across species and life stages. In both *Acropora* species, larval survival to heat stress at the family level did not correlate with survival in juveniles. This result aligns with expectations, since the heritability of traits can vary across life stages (Bairos-Novak et al., 2021) due to the involvement of different genes (Strader and Quigley, 2022). To date, this had not been experimentally demonstrated. Discrepancies in heat tolerance between other life stages have been reported in previous studies, including differences between larvae and adults (Weeriyanun et al., 2022) as well as between larvae and juveniles in a coral species with vertical symbiont transmission (Drury et al., 2022a). These findings underscore the complex interactions between genetic and environmental factors in determining thermal resilience across developmental stages, emphasizing the need for life-stage-specific conservation strategies over a one-size-fits-all approach.

Several factors may contribute to variation in heat tolerance across life stages, including maternal provisioning, differential selection pressures, and non-additive genetic effects. First, maternal effects, particularly lipid provisioning, are likely to play a significant role in early-stage heat tolerance (Harii et al., 2007), but this advantage diminishes as lipids are depleted (Hazraty-Kari et al., 2022a), leading to potential changes in heat tolerance as larvae transition to the juvenile stage. Some evidence suggests that maternal effects may continue to influence early juvenile growth and survival post-settlement (van Oppen et al., 2014), but the strength of this effect likely declines over time. In our study, while overall parental heat tolerance did not directly correlate with offspring heat stress survival, individual families exhibited strong

maternal influence on both larval and juvenile heat tolerance.

Secondly, life-stage specific selection pressures may drive differences in heat tolerance. Coral larvae, which are lecithotrophic and dispersive, must cope with fluctuating environmental conditions, potentially necessitating greater stress tolerance mechanisms. In contrast, juveniles are sessile and may experience relatively stable conditions compared to larvae, leading to selection for localised adaptations rather than broad stress tolerance. Gene expression patterns in responses to heat stress differ between larvae and juveniles (Strader and Quigley, 2022), suggesting that distinct genetic and physiological mechanisms underpin heat tolerance at each stage. While some genes likely contribute to heat tolerance across both life stages, the differential expression of these genes implies that selection may act on different aspects of heat tolerance depending on the developmental stage. In addition to genetic factors, non-genetic transgenerational plasticity and acclimatisation (through epigenetic modifications) may account for some life stage differences in heat tolerance (Guerrero and Bay, 2024).

Third, non-additive genetic variation, particularly epistatic interactions, may contribute to discrepancies in heat tolerance between life stages. Epistatic effects arise when the influence of an allele at one locus is modified by alleles at other loci, leading to complex trait outcomes that cannot be predicted solely from additive genetic effects (Salman et al., 2019). Such interactions are well-documented in studies of evolutionary biology and breeding, often influencing the predictability of offspring traits (Duenk et al., 2020). In corals, non-additive genetic variation may differentially impact heat tolerance at larval and juvenile stages, leading to variation in trait expression across families (Hazraty-Kari et al., 2022b; Sambucetti et al., 2013; Vijendravarma and Kawecki, 2013). Understanding these mechanisms will be critical for predicting how heat tolerance traits are inherited and expressed across generations.

Importantly, these genetic trade-offs between life stages could constrain adaptation; in which selection for heat tolerance may come at the cost of other critical traits such as growth or reproductive output (Hazraty-Kari et al., 2022b; Quigley et al., 2021b). Encouragingly, we observed no such trade-off between heat stress survival and juvenile coral growth under experimental conditions. However, given that mass bleaching events primarily impact adult corals (Álvarez-Noriega et al., 2018), with severe consequences for reef structure and reproductive capacity (Baird and Marshall, 2002; Magel et al., 2019), assessing the persistence of heat tolerance beyond the juvenile stage is essential. While enhancing juvenile thermal tolerance may reduce early life-stage mortality, it remains unclear whether these benefits extend into adulthood. If thermal resilience does not persist through reproductive maturity, the long-term effectiveness of AGF strategies may be limited. Future studies should track heat tolerance across early to later life stages, and even across multiple generations, to ensure that early-stage enhancements translate into improved adult survival and reproductive success and that outbreeding depression does not occur in later generations. This approach will be critical for developing ecologically informed predictions and refining conservation strategies aimed at increasing coral resilience in a warming ocean.

4.3. Moving beyond survival and the host: contributions of symbiont treatment to holobiont performance under heat stress

This study evaluated multiple species, life stages, and symbiotic relationships, providing the most comprehensive assessment of AGF feasibility to date. Given that algal symbionts play a crucial role in heat tolerance (Cornwell et al., 2021; Quigley and van Oppen, 2022), our approach ensures a robust evaluation of AGF success beyond survival alone, incorporating key traits like growth. Notably, we found that coral genetic background explained more variation in survival, bleaching, and photophysiology than symbiont treatment (as seen in selectively-bred *Acropora digitifera*; Humanes et al., 2024), while symbionts had the strongest influence on growth. Although previous studies have highlighted the role of symbionts in enhancing heat tolerance (Quigley et al., 2022a; Quigley et al., 2020b; Quigley and van Oppen, 2022), our results emphasize the need to consider multiple traits that influence heat tolerance and recovery potential. Both genetic background and symbiont treatment are key factors for improving reef resilience through effective restoration efforts.

In this study, juveniles inoculated with symbionts from sediments collected at hotter northern reefs exhibited survival rates comparable to those inoculated with heat-tolerant, laboratory-cultured symbionts produced through assisted evolution. Additionally, bleaching responses and photosynthetic efficiency were not significantly different between temperature treatments in juveniles hosting sediment-derived symbionts. However, the final bleaching and YII values were lower in the control group of the wild symbiont treatment compared to the two laboratory-grown symbiont treatments, suggesting that these wild symbionts may confer lower photosynthetic efficiency to juveniles (lower YII) and symbiont cell uptake may be lower (characterised by paler colour). Nevertheless, our results suggests that wild symbionts could provide comparable survival in heat stress in coral juveniles compared to lab grown or assisted evolution Symbiodiniaceae. Given the higher survivorship of coral larvae with mixed symbiont communities at 27 °C and 30 °C compared to larvae infected with only *Cladocopium* or *Durusdinium* (Matsuda et al., 2022), an effective symbiont-based intervention strategy may involve inoculating coral juveniles with a diverse symbiont community (Nitschke et al., 2024), including both lab-grown and wild symbionts with strong heat tolerance phenotypes.

Methodological considerations must also be acknowledged. The stress of relocating parent corals, particularly from historically nutrient-rich reefs to an experimental setup with lower nutrient conditions, may have influenced adult survival and gamete quality (Caballes et al., 2016; Ward and Harrison, 2000), as seen by the fact that some control treatment adult genotypes had high mortality. However, post-settlement survival of *A. kenti* and *A. hyacinthus* juveniles under ambient conditions was consistently high across all reef crosses, indicating that lower survival under heat stress was due to temperature treatment rather than experimental artifacts or handling stress. Conversely, adult corals from certain reefs (e.g., Palms) exhibited high mortality even in the control treatment. Conducting pre-spawning heat tolerance testing of parent corals could improve phenotyping accuracy while minimizing confounding effects of gamete production and collection stress.

5. Conclusions

Our study demonstrates that acquired heat tolerance varies across coral genera and life stages, including the variable transfer of tolerance from adults to larvae and juveniles. Additionally, we found that parental origin had a stronger influence on juvenile survival than symbiont treatment, and that wild sourced symbionts from warm locations provided comparable heat tolerance as lab-grown symbionts. While these findings support the potential of AGF for some species, coral reefs are highly dynamic ecosystems where microbial community acquisition and other environmental factors shape overall ecosystem resilience. To confirm the ecological relevance of this enhanced heat tolerance, outplanting and in-situ testing remain critical next steps (see Quigley et al., 2021b). Along with the necessary development of ecosystem-scale restoration practices (McLeod et al., 2022), enhancing heat tolerance across reefs through AGF may provide a valuable buffer to extend coral survival until efforts to reduce carbon emissions accelerate and climate warming is brought under control.

Acronyms

AGF	Assisted gene flow
F_m	Light adapted maximum fluorescence
FSW	Filtered sea water

F_t	Minimum fluorescence
GBR	Great Barrier Reef
HSL	Hue, saturation and lightness
LOO	Leave one out
MCMC	Markov chain Monte Carlo
MMM	Maximum monthly mean
PAM	Pulse amplitude modulation fluorometry
YII	Effective quantum yield of photosystem II

CRediT authorship contribution statement

Alex Macadam: Writing – review & editing, Writing – original draft, Visualization, Validation, Resources, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Carys Morgans:** Investigation, Data curation. **Jessica Cheok:** Investigation, Data curation. **Katarina Damjanovic:** Investigation, Data curation. **Melissa Ciampaglia:** Investigation, Data curation. **Maren Toor:** Investigation, Data curation. **Patrick Laffy:** Writing – review & editing, Validation, Supervision. **Ira R. Cooke:** Writing – review & editing, Validation, Supervision. **Jan M. Strugnell:** Writing – review & editing, Validation, Supervision. **Kate M. Quigley:** Writing – review & editing, Writing – original draft, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization.

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Declaration of competing interest

The authors declare no financial interests/personal relationships which may be considered potential competing interests.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2025.111155.

Data availability

Data will be made available on request.

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Corrigendum

Corrigendum to "Assessing the potential for "assisted gene flow" to enhance heat tolerance of multiple coral genera over three key phenotypic traits" [Biol. Conserv. 306 (2025) 111155]

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