PLOS ONE

RESEARCH ARTICLE

Parental effects provide an opportunity for coral resilience following major bleaching events

Elizabeth A. Lenz[1], Megan J. Donahue[2], Ruth D. Gates[2†], Hollie M. Putnam[3], Eveline van der Steeg[4], Jacqueline L. Padilla-Gamiño[5]*

1 University of Hawai'i Sea Grant College Program, University of Hawai'i at Mānoa, Honolulu, HI, United States of America, **2** Hawai'i Institute of Marine Biology, University of Hawai'i at Mānoa, Kāne'ohe, HI, United States of America, **3** Department of Biological Science, University of Rhode Island, Kingston, Kingston, RI, United States of America, **4** School of Natural and Environmental Science, Newcastle University, Newcastle, United Kingdom, **5** School of Aquatic and Fishery Sciences, University of Washington, Seattle, WA, United States of America

† Deceased.
* jpgamino@uw.edu

Citation: Lenz EA, Donahue MJ, Gates RD, Putnam HM, van der Steeg E, Padilla-Gamiño JL (2025) Parental effects provide an opportunity for coral resilience following major bleaching events. PLoS ONE 20(1): e0290479. https://doi.org/10.1371/journal.pone.0290479

Editor: Atsushi Fujimura, University of Guam, GUAM

Received: August 7, 2023

Accepted: September 17, 2024

Published: January 7, 2025

Peer Review History: PLOS recognizes the benefits of transparency in the peer review process; therefore, we enable the publication of all of the content of peer review and author responses alongside final, published articles. The editorial history of this article is available here: https://doi.org/10.1371/journal.pone.0290479

Data Availability Statement: The data is currently held in a public repository on GitHub: https://github.com/ealenz/Mcap-BNB-Reproduction-SelectiveBreeding.

Abstract

Identifying processes that promote coral reef recovery and resilience is crucial as ocean warming becomes more frequent and severe. Sexual reproduction is essential for the replenishment of coral populations and maintenance of genetic diversity; however, the ability for corals to reproduce may be impaired by marine heatwaves that cause coral bleaching. In 2014 and 2015, the Hawaiian Islands experienced coral bleaching with differential bleaching susceptibility in the species *Montipora capitata*, a dominant reef-building coral in the region. We tested the hypothesis that coral bleaching resistance enhances reproductive capacity and offspring performance by examining the reproductive biology of colonies that bleached and recovered (B) and colonies that did not bleach (NB) in 2015 in the subsequent spawning seasons. The proportion of colonies that spawned was higher in 2016 than in 2017. Regardless of parental bleaching history, we found eggs with higher abnormality and bundles with fewer eggs in 2016 than 2017. While reproductive output was similar between B and NB colonies in 2016, survivorship of offspring that year were significantly influenced by the parental bleaching history (egg donor × sperm donor: B × B, B × NB, NB × B, and NB × NB). Offspring produced by NB egg donors had the highest survivorship, while offspring from previously bleached colonies had the lowest survivorship, highlighting the negative effects of bleaching on parental investment and offspring performance. While sexual reproduction continues in *M. capitata* post-bleaching, gametes are differentially impacted by recovery time following a bleaching event and by parental bleaching resistance. Our results demonstrate the importance of identifying bleaching resistant individuals during and after heating events. This study further highlights the significance of maternal effects through potential egg provisioning for offspring survivorship and provides a baseline for human-assisted intervention (i.e., selective breeding) to mitigate the effects of climate change on coral reefs.

Funding: This paper is funded in part by a grant from the National Oceanic and Atmospheric Administration, Project A/AS-1; which is sponsored by the University of Hawai'i Sea Grant College Program, SOEST, under Institutional Grant No. NA22OAR4170108 from NOAA Office of Sea Grant, Department of Commerce. The views expressed herein are those of the author(s) and do not necessarily reflect the views of NOAA or any of its subagencies. UNIHI-SEAGRANT-4941.

Competing interests: The authors have declared that no competing interests exist.

Introduction

Ocean warming caused by anthropogenic greenhouse gas emissions is one of the primary threats to the function of shallow tropical coral reefs [1,2]. Prolonged warming above the local thermal threshold for bleaching coupled with high irradiances can cause severe coral bleaching [3], the disruption of the nutritional symbiosis between the coral host and its unicellular dinoflagellates, Symbiodiniaceae (formerly, *Symbiodinium* spp.) [4]. This can subsequently result in increased rates of disease transmission [5] and mortality [6] along with reduced calcification rates and reproductive capacity in corals [7,8]. Continual declines in coral cover are predicted given the range of local and global disturbances simultaneously acting on coral reefs, with warming ranked as the most severe [9–11]. Identifying sources of resilience in coral reef ecosystems, such as locating exceptional coral genotypes that can thrive under extreme warming or temperature fluctuations, will be key in maintaining and restoring reefs for the future.

Differential bleaching susceptibility [12–14] during a thermal stress event illustrates biological variation within populations that may serve as a source of resilience and an opportunity for selection through reproductive success [15,16]. Thermal tolerance and capacity to recover after bleaching are important factors that influence sexual reproduction, recruitment, and success of future generations to adapt [7,8,17,18]. Successful sexual reproduction and recruitment are essential in maintaining coral populations [19], repopulating disturbed coral reefs [20–23], and enhancing genetic diversity within populations to overcome selective pressures [24,25]. However, parental investment in gametogenesis is energetically costly [26] and for corals reproductive cycles may exceed six to ten months [27,28]. Therefore, prolonged environmental stress can drive prioritization of energetic investment into basic metabolic function and repair, at the expense of growth and sexual reproduction [29–31]. Importantly, this tradeoff in energetic investment is likely to depend on the susceptibility and severity of coral bleaching, with greater energy available for reproduction in corals resistant to bleaching [32].

Previous studies have identified some of the way coral bleaching can impact aspects of sexual reproduction [8,33] and dampen recruitment [34,35]. For example, after the 1987 coral bleaching event in the Caribbean, *Orbicella annularis* recovered from bleaching by metabolizing tissue biomass, but did not complete gametogenesis in the following months, whereas colonies that had not bleached of the same species were able to develop and release gametes [7]. Similarly, during the 1998 bleaching event on the Great Barrier Reef, bleached corals showed high variation in reproduction compared to colonies resistant to bleaching nearby that experienced the same thermal stress. For acroporid species, reproductive polyps were more common in colonies that did not bleach, with larger eggs at higher densities per polyp than colonies that bleached and recovered [30]. More resolution is needed to better understand the impact and extent of coral bleaching events on the early life cycles of coral, from the stress event through recruitment.

Given logistical complexities and challenges, most studies have primarily investigated gametogenesis in the life cycle of coral with some understanding of cross-generational effects (i.e., parental, carry-over, or transgenerational effects) following major bleaching events. The impacts of coral bleaching may last for months to years after the initial thermal stress [36], and can manifest in life stages downstream such as fertilization [37–39], larval development, and recruitment [34,35,40]. Between the 2005 and 2010 bleaching events in Panama, Levitan et al. (2014) found that thermally tolerant *Orbicella franksi* recovered the capacity to produce and release gametes more quickly (within 3 to 5 years) than the more thermally sensitive *O. annularis*. While these studies demonstrate a range of responses in sexual reproductive biology and ecology during recovery post bleaching (i.e., gametogenesis and recruitment), few studies have followed both the intra- and intergenerational impacts of bleaching. Recent marine heatwaves

eliciting differential coral bleaching of *M*. *capitata* in Hawai'i provide an opportunity to compare the impacts of parental bleaching history on coral reproduction and offspring performance during recovery and offer potential insight on coral resilience [15,41,42].

Coral reefs in the subtropical waters of Hawai'i were largely naive to global bleaching events [43–45] with bleaching events first recorded in the Main Hawaiian Islands in 1996 and then in the Northwestern Hawaiian Islands in 2002 [43–45]. However, the Hawaiian Archipelago experienced "the blob" heatwave, followed by an El Niño that resulted in severe back-to-back coral bleaching in 2014 and 2015 (Fig 1A) [46,47]. During these consecutive bleaching events, degree heating weeks (DHW) in the Main Hawaiian Islands exceeded 8 weeks by September in both years [46,47]. In Kāne'ohe Bay (O'ahu, Hawai'i), ~70% of corals on the shallow reefs (< 2 m depth) bleached and exhibited 13–22% mortality in 2014 and 2015 [46,48–50]. During both events in Kāne'ohe Bay, colonies of the dominant reef-building coral, *Montipora capitata*, visibly bleached or remained pigmented during prolonged heat stress (Fig 1B). Despite widespread bleaching, approximately 70% of *M*. *capitata* that bleached in 2014 and 2015 were considered recovered by the following December and January based on visual coloration [12,14,15,46,51–53].

M. *capitata* demonstrates relatively high tolerance against multiple local and global stressors [54,55], with varied sensitivity among individual colonies and their traits measured under elevated temperature [15,51], such as survivorship [49], growth [45], and biomass composition [45,53,54,56–58]. Reproductive effort of *M*. *capitata*, particularly oocyte characteristics and spawning, has shown little response to warming [36,59]. This reproductive response may have contributed to its ecological success along the fringing and patch reefs of Kāne'ohe Bay in the past. However, percent of motile sperm from *M*. *capitata* declined from 80–90% in 2011 to 40.5% in 2015, corresponding with the consecutive bleaching events in Kāne'ohe Bay [36]. For *M*. *capitata*, oogenesis can begin as early as July, which means that early egg development may cooccur with severe, prolonged warming events (July-October), and later egg development continues when corals are recovering from these events (November-August). This could create a strain on energetic resources when corals are compromised during a substantial fraction of the typical gametogenic cycle [60,61]. Therefore, tracking *M*. *capitata* through subsequent spawning seasons after bleaching events can reveal the reproductive capacity of this species as ocean temperature continues to increase.

In this study, we examined cross-generation plasticity (i.e., parental effects) to determine how parental response to environmental events influence reproduction [62]. We measured the reproductive biology of *M*. *capitata* for two spawning seasons (2016 and 2017) following bleaching events (2014 and 2015). We tested the following hypotheses: (i) that parental bleaching history [bleached (B) and nonbleached (NB)] would affect reproductive performance in subsequent spawning seasons and (ii) intentional crosses of gametes from parent colonies of differential bleaching history would influence offspring success (Fig 2A). In 2016, we tested the second hypothesis and quantified the downstream effects of parental bleaching history from gamete release to settlement of the offspring in parent colonies that did and did not bleach during the 2015 warming event (Fig 2B). This study was designed to assess the impacts of consecutive bleaching events on the early stages within the coral life cycle and selective processes already occurring in nature while also testing basic breeding techniques as an intervention strategy for coral restoration to maintain genetic diversity and promote resilience.

Materials and methods

2.1 Selecting parent colonies and spawning events

Montipora capitata is a hermaphroditic broadcast spawner and its reproductive cycle, spawning dynamics, and early life stages have been extensively studied at the Hawai'i Institute of

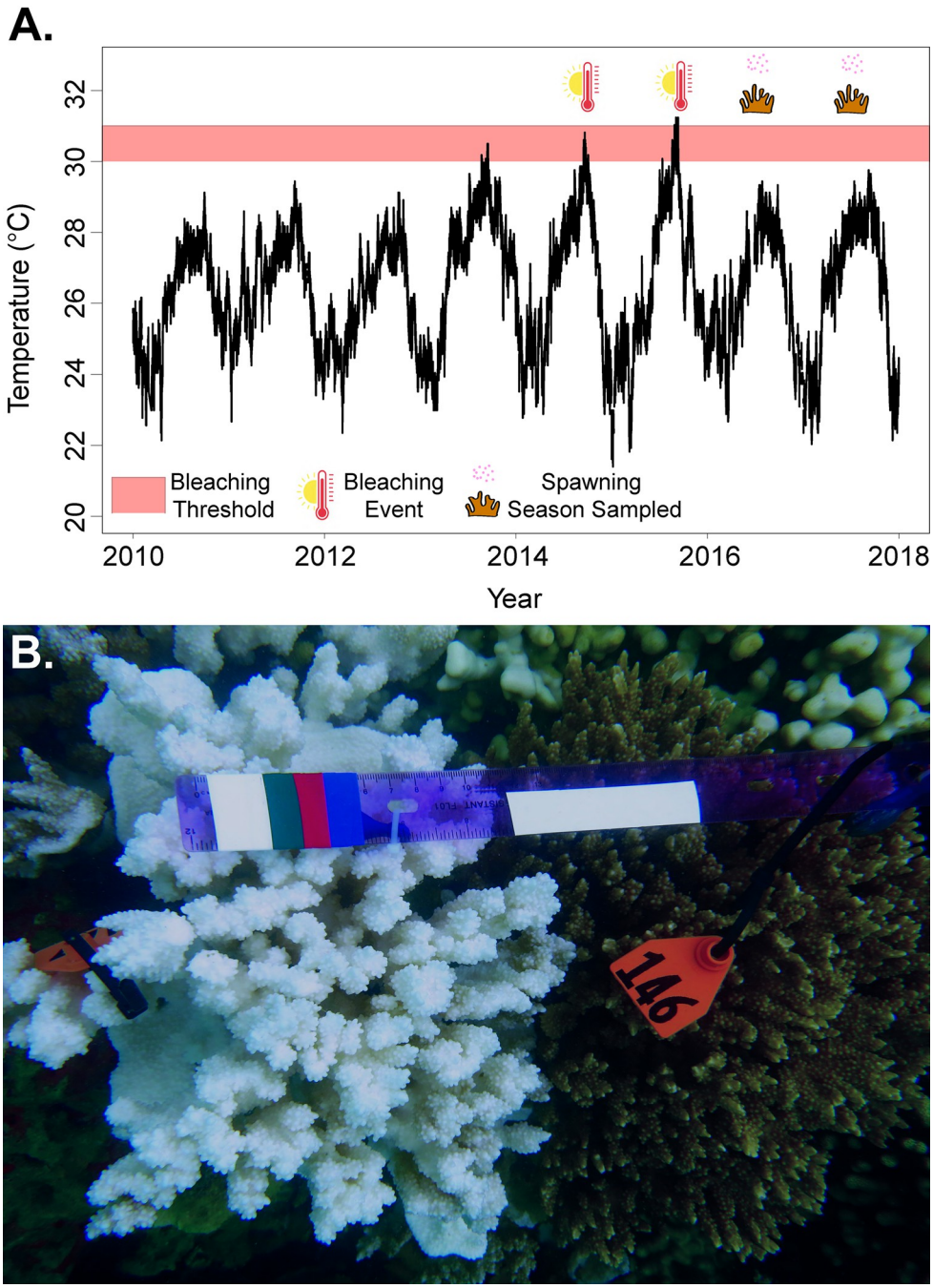

Fig 1. A) Temperature data from 2010 to 2017 (NOAA Buoy Moku o' Loe, HI Station ID: 1612480) illustrate historical patterns and identify years of bleaching events in O'ahu, Hawai'i. The bleaching threshold between 30 to 31˚C of corals in Kāne'ohe Bay (Coles et al., 2018) is shown in the shaded red, thermometers indicate the 2014 and 2015 bleaching events and the spawning corals indicate the spawning seasons. B) An image depicting the tagged bleached (left) and nonbleached (right) parental colonies in response to the 2015 heat stress in Kāne'ohe Bay.

https://doi.org/10.1371/journal.pone.0290479.g001

Marine Biology (HIMB) located in Kāne'ohe Bay, on the windward side of O'ahu, Hawai'i, USA [27,60,61,63–65]. In Hawai'i, oogenesis begins a 9–10 month period as early as July and as late as October, while spermatogenesis begins the following April to May, ca. 1 month prior to the first spawning event in May or June [28], creating the potential for differential effects of

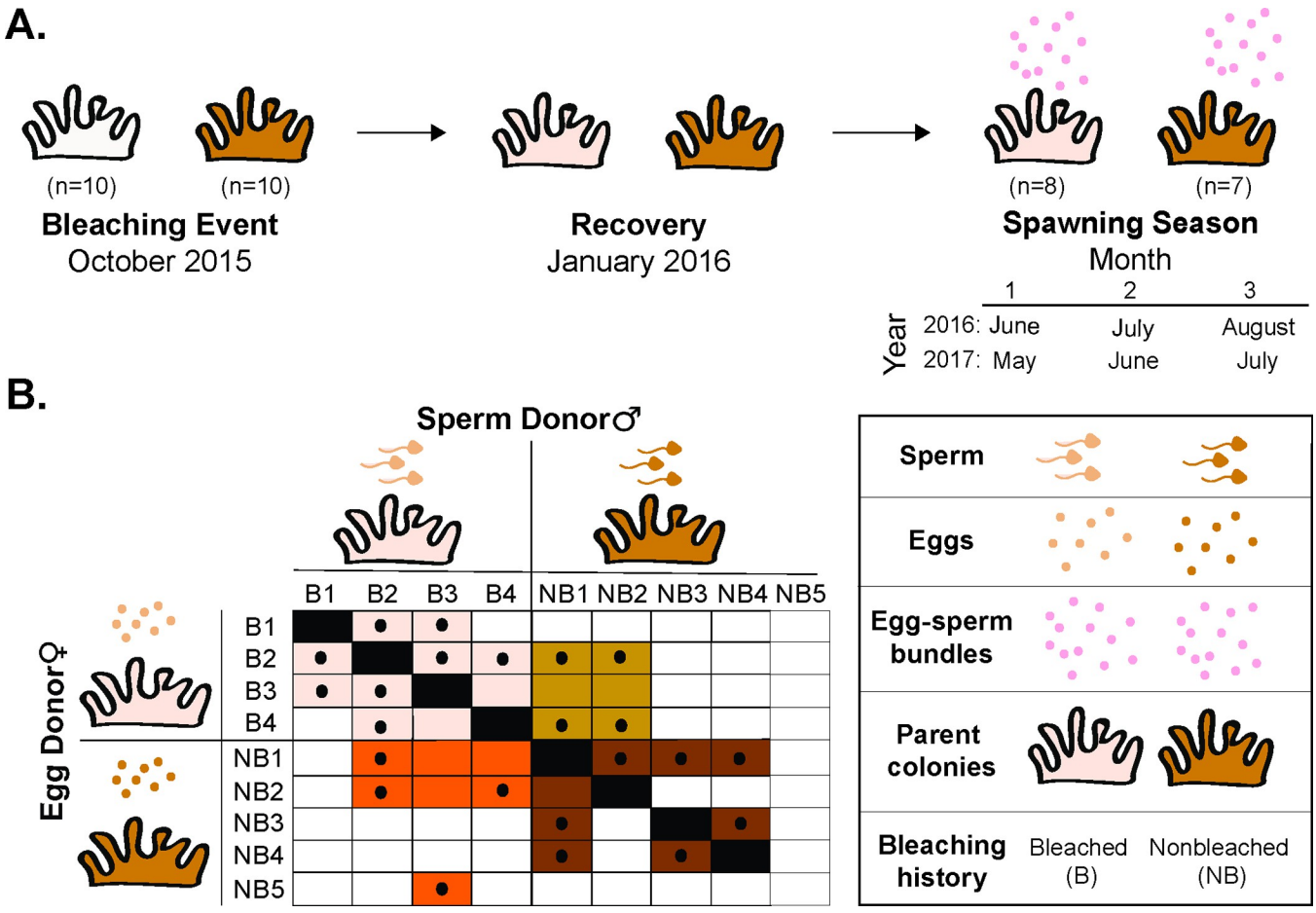

Fig 2. Experimental design of the study. A) Bleached and nonbleached colonies were tagged in October 2015 at the peak of the bleaching event. Bleached colonies in this experiment recovered by January 2016. Total reproductive output and gamete collections were measured during the 2016 and 2017 spawning seasons. Months of the spawning season differ between years because of the different timing of the new moon in 2016 and 2017. B) Selective breeding matrix illustrating the crossing of egg and sperm donors conducted in July 2016 based on parental bleaching history. Colored squares indicate the cross of individuals attempted and solid black circles indicate successful fertilization. Offspring from these crosses were used to measure survivorship of larvae and settlers and settlement.

https://doi.org/10.1371/journal.pone.0290479.g002

bleaching on oocytes and sperm. Symbiodiniaceae are vertically transferred from *M. capitata* parent colonies into eggs prior to the formation of the egg-sperm bundles, which are released during spawning [63]. Spawning in *M. capitata* extends over three, consecutive lunar months between May and September for 3 to 5 consecutive nights between 20:45 and 22:30 hrs, starting on the night of the new moon [27,60]. The second and third nights are when the largest spawning events most commonly occur [60].

During the peak of the 2015 bleaching event in Hawai'i, ten pairs of colonies (30–100 cm diameter) of *M. capitata* were identified and tagged as bleached (B) and nonbleached (NB) along the leeward side of the reef surrounding HIMB (21'26.09 N, 157'47.47' W) on 20 October 2015 (Fig 3C). These colonies remained in the field until retrieved three days prior to the new moon of the spawning months in 2016 (June, July, and August) and 2017 (May, June, and July) (Fig 3A). To examine reproductive performance of B and NB colonies of *M. capitata*, parent colonies were collected by removing the entire colony from the reef, or by breaking large fragments (30–40 cm in diameter) from tagged colonies using a hammer and chisel. These collections were first completed on 4 and 5 June 2016. Of the twenty colonies tagged, seven

colonies that had not bleached and eight colonies that had bleached and recovered were alive and used for the study. The other five colonies not recovered had either died or were missing from the reef. The fifteen colonies were transported to the wet laboratory at HIMB in 20L buckets filled with seawater from Kāneʻohe Bay at an ambient temperature of ~28 to 29˚C. Colonies were randomly allocated to two ~1,300L shaded outdoor flow-through tanks [55,66]. Both tanks had sand-filtered seawater delivered at a flow rate of ~6L minute^{-1} and a circulation pump (700 gph Magnetic Drive, Danner Manufacturing Inc. Islandia, NY, USA). Irradiance and temperature within each tank were recorded every fifteen minutes with a cosine corrected photosynthetically active radiation (PAR) sensor (Odyssey PAR loggers, Dataflow Systems Ltd, Christchurch, NZ) calibrated to a Licor 192SA sensor, and a temperature logger (Hobo™ Water Temp Pro v2 resolution ± 0.2˚C, Onset Computer Corporation, Bourne, MA, USA). Three to five days after each spawning event, colonies were returned to the original field site by attaching them to a fixed rack with cable ties and retrieved two days before the next new moon of the spawning season.

2.2 Sexual reproduction

Starting one night prior to the new moon, *M. capitata* parent colonies were monitored for seven nights. During each night of spawning, colonies were isolated at 19:30 in individual containers filled with ambient seawater from the flow-through tanks. When spawning occurred, *M. capitata* released egg-sperm bundles into the water column between 20:45 and 22:30 with peak spawning typically expected on the second night of the new moon [27,59,60]. Spawning activity of individual colonies was monitored each night and recorded as "spawn" or "no spawn". For the spawning colonies, we quantified the total volume of gametes released, number of eggs per bundle, and egg quality (i.e., area and abnormality).

Sterilized disposable pipets (2 mL) were used to gently collect all egg-sperm bundles at the water surface from each individual colony to avoid cross contamination or prematurely breaking the egg-sperm bundles. We preserved 3–5 egg-sperm bundles per colony per night to quantify the number of eggs per bundle, egg volume for size, and abnormality. Each egg-sperm bundle was placed in a 2 mL microcentrifuge tube and allowed to break up in 0.1 mL of seawater and for the eggs to hydrate for 2 hrs before preserved in zinc fixative (1:4 Z-fix, Sigma-Aldrich Inc. to 0.2 μm filtered seawater FSW). Preserved eggs from each bundle were photographed using an Olympus SZX7 dissecting microscope equipped with an Olympus America camera (SN: BH039933-H); from photographs, we counted the number of eggs per bundle and measured the egg diameter using ImageJ2 software (Schneider et al., 2012). Egg volume was calculated using the equation for a sphere with the measured egg diameter of spherical eggs. We also recorded the proportion of abnormal (irregular) eggs packaged within each bundle [36,63]. Remaining egg-sperm bundles from each colony were placed into individual 50 mL Falcon tubes to quantify the total volume of gametes of each colony per night. Annual reproductive output per colony was estimated by summing the spawn volume across the entire spawning season, normalized to planar surface area of the colony using Fiji software [67].

2.3 Fertilization success and Offspring

To compare offspring performance of bleached and nonbleached parents, we isolated the egg-sperm bundles from each parental colony that released more than 1 mL of spawn volume on the nights of 5 and 6 July 2016 (peak spawning) and placed egg-sperm bundles from each colony into a separate 50 mL falcon tube. Within one hour of the bundle breaking apart, eggs floated to the surface and sperm sank to the bottom. Sperm were pipetted from the bottom of

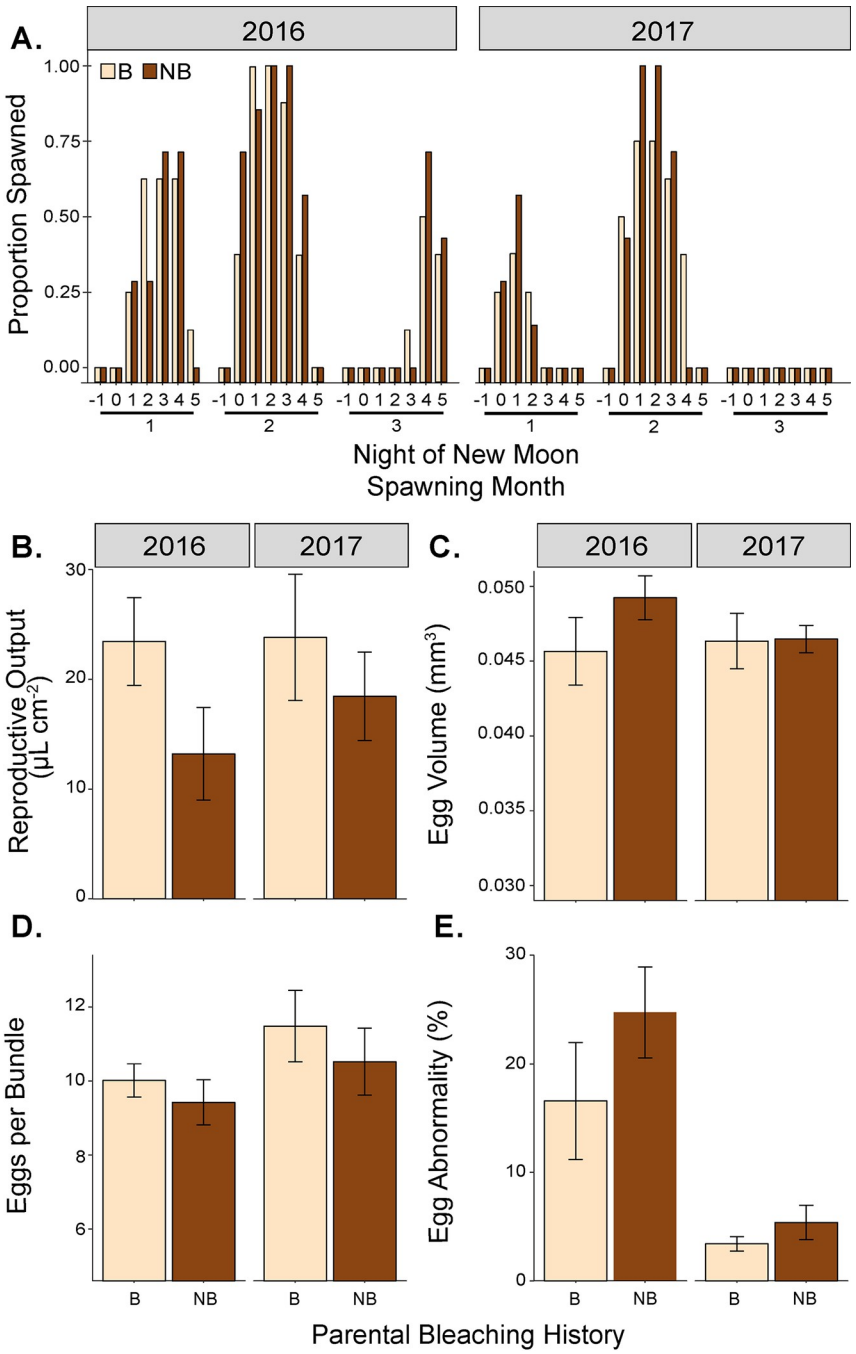

Fig 3. Reproductive traits measured from the same parent colonies in Fig 2 during 2016 and 2017 spawning seasons following the 2015 bleaching event. A) Proportion of spawning each night in 2016 and 2017 spawning seasons from parent colonies that had bleached and not bleached. "0" indicates the night of the new moon. Mean (± SE) values for B) reproductive output normalized to planar surface area, C) egg volume, D) number of eggs per bundle, and E) percent egg abnormality measured from bleached and nonbleached parents in 2016 and 2017.

https://doi.org/10.1371/journal.pone.0290479.g003

the tube, and eggs were rinsed twice with 0.2 μm filtered seawater (FSW). Sperm from each colony was placed in separate 50 mL falcon tubes and later used to fertilize eggs from specific colonies. Nine colonies had adequate spawn volume to include in crosses, and thirty individual crosses were made from gametes based on parental bleaching history to generate four cross-

types (egg donor × sperm donor): B × B (n = 8), B × NB (n = 4), NB × B (n = 4), and NB × NB (n = 7) (Fig 2B). For fertilization, the eggs (1 mL) were in a concentration of ~10^6 sperm mL^{-1} (by visual inspection) within a 50 mL falcon tube [68]. Thirty minutes after sperm and eggs were mixed, each cross type of fertilized eggs was transferred into individual 1 L conical tanks filled with UV-sterilized 1-μm FSW to avoid polyspermy. For *M*. *capitata*, self-fertilization is extremely rare [68,69]. To estimate fertilization success, three subsamples of 20–30 eggs were collected from each conical after approximately 3-hrs (i.e., when initial cleave stages are expected [70,71]), placed in a 2-μL microcentrifuge tube, and preserved in Z-fix (1:4 Z-fix to FSW). Remaining embryos in the conical tanks developed, and slow flow rate of FSW was introduced to mitigate potential effects of montiporic acid [65]. Five days post-fertilization, 10–15 larvae per conical tank were placed in a 10 mL well-plate filled with 5 mL of FSW with a chip of crustose coralline algae to track settlement through time; FSW was exchanged every other day. The proportion of planulae and settlers were examined on days 7, 28, and 53 post-fertilization while the total number of offspring alive were counted on days 6, 7, 28, 53, and 59 post-fertilization to estimate survivorship probability curves.

2.4 Statistical analysis

All analyses were conducted in R (R Core Team, 2014; v. 3.5.1). We used a generalized linear mixed effects model to determine the effects of bleaching history on spawning activity, number of eggs per bundle, and egg abnormality of the 8 B and 7 NB parental colonies observed (*glmer* in *lme4*) [72] with a binomial (spawn/no spawn and proportion of abnormal eggs) and poisson (eggs per bundle count) response. Bleaching history (B/NB) and year (2016/2017) were included as fixed effects, and spawning month (1/2/3) and colony ID were included as random effects. To analyze total reproductive output and egg size, we used linear mixed effects models (*lme* in *lme4*) [72] with bleaching history and year as fixed effects, and colony ID as a random effect. Analysis of variance (ANOVA) tables were generated using type II sum of squares (*Anova* in *car*) [73]. Post-hoc analyses were conducted to further explore significant main effects and interactions. We utilized the emmeans package [74] to calculate and compare the estimated marginal means (EMMs), which represent the predicted means of the response variable for each level of the fixed effects, adjusted for the other covariates in the model. Pairwise comparisons between the levels of the fixed effects were then performed using Tukey's Honest Significant Difference (HSD) test to adjust for multiple comparisons. This approach allowed us to identify significant differences between specific treatment groups, while accounting for the variability associated with random effects.

To test the effects of parental bleaching history on offspring performance, we first analyzed the proportion of eggs fertilized using generalized linear mixed effects models with cross-type as a fixed effect and the egg donor and sperm donor as random effects. The proportion of eggs reaching each developmental stage (2-cell, 4-cell, 8-cell, and 16-cell), the Kruskal-Wallace test was applied as the dataset did not meet the assumption of normality. For post-hoc analysis, we performed the Dunn's test for multiple pairwise comparisons to determine which specific cross-types differed. To analyze the proportion of larvae that settled at 7, 28, and 59-days post-fertilization, we used a generalized linear mixed effects model with cross-type and day (7, 28, and 59-d post-fertilization) as fixed effects and colony ID of egg donor and sperm donor as random effects. Lastly, we generated survivorship estimate curves to visualize offspring fate by cross-type with *ggsurvplot* of the census over time (i.e., days 6, 7, 23, 27, 28, 53, and 59 post-fertilization) (*survfit* in *survminer*) [75]. Cox proportional hazards (CPH) model was used to analyze the effects of cross, egg donor, and sperm donor individually on offspring survivorship (*coxph* in *survminer*) [75]. Dispersion parameters were inspected through a simulation-based approach (*DHARMa* package) [76].

Results

3.1 Sexual reproduction and egg traits

All fifteen colonies observed in this study released egg-sperm bundles one or more nights in both years (Fig 3A). When spawning was observed, colonies began releasing egg-sperm bundles between 20:20 and 21:32 hrs and ended between 20:30 and 22:15 hrs. Parental bleaching history did not affect the occurrence of spawning ($P = 0.619$) and had no interactive effect with year ($P = 0.982$). The proportion of colonies releasing gametes significantly differed by year ($P < 0.001$) which may largely be due to some spawning in 2016 compared to no spawning in 2017 during the third month (August). In 2017, the proportion of colonies participating in spawning events was 36% lower than in 2016. In both years, the second month of the spawning season had the highest proportion of colonies spawning.

In 2016, the spawning season following consecutive bleaching events, colonies that bleached and recovered had 22.5% higher mean total reproductive output than colonies that did not bleach, although this was not statistically significant (Fig 3B; Table 1; P = 0.076). There was no effect of year and no interaction between bleaching history and year on reproductive output (Fig 3B; Table 1; $P \geq 0.560$). Individual egg volume ranged from 0.032 to 0.099 mm^3 and did not differ by parental bleaching history, year, or by their interaction (Fig 3C; Table 1; $P \geq 0.462$). The number of eggs per bundle from both bleached and nonbleached parental colonies ranged from 2 to 29, and mean eggs per bundle for all colonies examined was 13.3% less in 2016 than in 2017 (Fig 3D; Table 1; P = 0.017). Eggs per bundle did not differ by parental bleaching history (Fig 3D; P = 0.249). There were 79.5% more eggs with irregularities in 2016 than in 2017 ($P < 0.001$) with no difference by bleaching history (Fig 3E; Table 1; P = 0.292).

3.2 Fertilization, survivorship, and settlement

While reproduction continued in the colonies examined, we found that cross-type did have an effect on fertilization, embryonic development, and percent larval survivorship (Fig 4;

Table 1. Statistical summary of Type II Wald χ^2 test of generalized linear mixed effects model and linear mixed effect models testing the fixed effects of spawning year and parent history of bleaching susceptibility on sexual reproduction.

Response Variables	Fixed Effects	χ^2	df	*P*-value	Post-hoc Summary
Colony-level Spawning	Bleaching History	0.248	1	0.619	
(0 = no spawn / 1 = spawn)	**Year**	22.479	1	**< 0.001**	**2016 > 2017**
	Bleaching History * Year	0.001	1	0.982	
Total Reproductive Output Log transformed	Bleaching History	3.155	1	0.076	
	Year	0.339	1	0.560	
	Bleaching History * Year	0.097	1	0.756	
Egg Volume	Bleaching History	0.108	1	0.742	
	Year	0.541	1	0.462	
	Bleaching History * Year	0.225	1	0.635	
Eggs per Bundle	Bleaching History	1.332	1	0.249	
	Year	**5.656**	1	**0.017**	**2016 < 2017**
	Bleaching History * Year	1.408	1	0.235	
Egg Abnormality	Bleaching History	1.109	1	0.292	
	Year	**191.259**	1	**<0.001**	**2016 > 2017**
	Bleaching History * Year	0.035	1	0.852	

Significance indicated in bold text.

https://doi.org/10.1371/journal.pone.0290479.t001

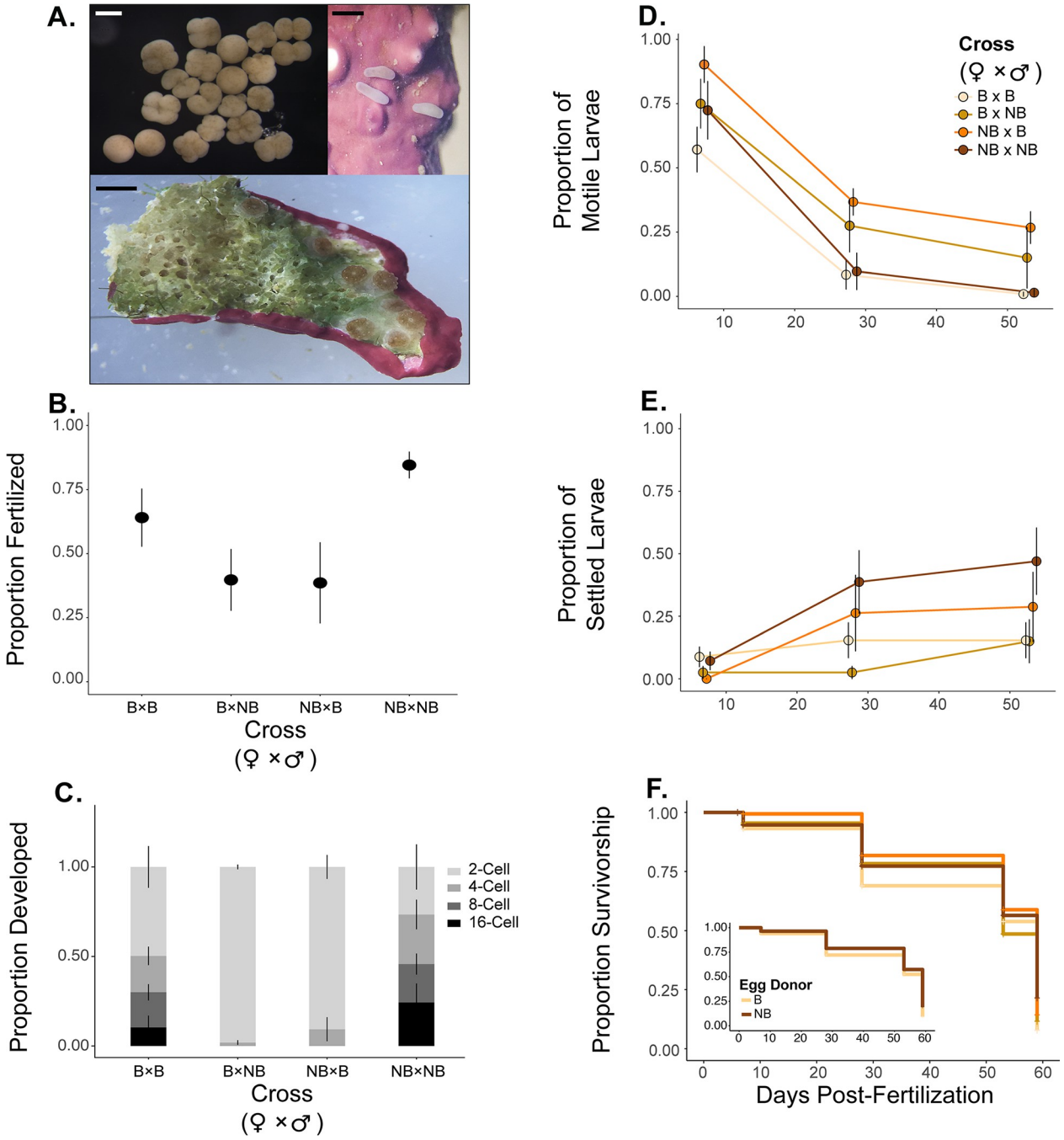

Fig 4. Offspring performance from selected crosses. A) Images of fertilized eggs and embryos (scale bar = 500 μm), planula larvae (scale bar = 500 μm), and settlement (1 mm). Mean ± SE. B) proportion of eggs fertilized by cross-type, C) proportion of cell division after 3-h fertilization D) proportion of motile larvae and E) settlers during five timepoints over a 59-d period, and F) survivorship estimate curves by cross over seven timepoints between 6 and 59-d with the figure embedded comparing the survivorship curves of offspring from bleached and nonbleached egg donors.

https://doi.org/10.1371/journal.pone.0290479.g004

Table 2). Specifically, fertilization success in the NB × NB cross-type was higher than the B × NB and NB × B cross-types (Fig 4B; Table 2; post-hoc P = 0.002 and 0.010, respectively) but not B × B (post-hoc P = 0.163). The fertilization success in cross-type B × B also did not differ between NB × B (post-hoc P = 0.250), but was higher than B × NB (post-hoc P = 0.047).

Table 2. Statistical summary of Type II Wald χ^2 test of generalized linear mixed effects model testing the fixed effects of cross-type (NB × NB, NB × B, B × NB, B × B) on the proportion of fertilized embryos and summary of the Kruskal-Wallace test for the cellular development (2-Cell, 4-Cell, 8-Cell, and 16-Cell). Statistical summary of Type II Wald χ^2 test of generalized linear mixed effects model testing the fixed effects of cross-type on larval survivorship, and settlement over three timepoints post-fertilization.

Response Variable		Effect	χ^2	df	*P*-value	Post-hoc Summary
Embryonic Development	Fertilization	**Cross**	**16.334**	**3**	**0.001**	B×B > B×NB NB×NB > B×NB, NB×B
	2-Cell		**34.071**	**3**	**<0.001**	B×B = NB×NB NB×B = B×NB
	4-Cell		**21.729**	**3**	**<0.001**	B×B = NB×NB, NB×B NB×B = B×NB
	8-Cell		**33.882**	**3**	**<0.001**	B×B = NB×NB B×NB = NB×B
	16-Cell		**20.445**	**3**	**<0.001**	B×B = NB×NB, B×NB, NB×B NB×B = B×NB
Response Variable	**Fixed Effects**					
Larval Survival *Square-root transformed*	**Cross**		**20.915**	**3**	**<0.001**	B×B ≠ NB×B
	Days Post-Fertilization		**178.595**	**2**	**<0.001**	
	Cross * Days Post-Fertilization		7.174	6	0.305	
Larval Settlement	Cross		7.623	3	0.055	
	Days Post-Fertilization		**17.214**	**2**	**<0.001**	
	Cross * Days Post-Fertilization		9.066	6	0.170	

Significance indicated in bold text.

https://doi.org/10.1371/journal.pone.0290479.t002

Cell division advanced beyond the 2-cell stage more quickly for within cross-types (B × B and NB × NB) than between cross-types (B × NB and NB × B) at 3-h post-fertilization. Embryos from both B × B and NB × NB cross-types reached the 16-cell stage at 3-h post fertilization, whereas embryos from B×NB and NB × B crosses developed at a slower rate and only reached the 4-cell stage (Fig 4C, Table 2).

Percent larval survivorship and settlement varied by cross-type, driven by egg donor bleaching history (Fig 4D and 4E; Table 3). Offspring developed from eggs from previously B egg donors had lower survivorship than those from NB egg donors. NB egg donors had a significant effect on the proportion of larvae survival (Fig 4E; $P < 0.001$). However, no difference was found in offspring survivorship from bleached or nonbleached sperm donors ($P = 0.992$). Overall, percent mortality from the initial to final time point (i.e., day 5 to 59) were 92.5% for B × B, 87.8% for B × NB, 85.6% for NB × B, and 77.3% for NB × NB (Fig 4F).

Table 3. Summary of Cox proportional hazards analysis of coral offspring survival influenced by the fixed effects: Cross-type, dam, and sire over time with model average estimates of the hazard ratio (with 95% confidence intervals; Cross (NB × NB, NB × B, B × NB, B × B): df = 3 or egg/sperm donor (NB vs. B): df = 1; *n* = 1,318; number of events = 560) for five timepoints (day 6, 7, 28, 53, and 59).

Fixed effect	Hazard ratio	z	*P*-value
Cross	0.90 (0.84–0.96)	-3.071	**0.002**
Egg Donor	0.77 (0.65–0.91)	-3.068	**0.002**
Sperm Donor	1.00 (0.80–1.24)	-0.010	0.992

Significance indicated in bold text.

https://doi.org/10.1371/journal.pone.0290479.t003

Discussion

Here, we demonstrate the influences of marine heatwaves on coral reproductive capacity and parental effects in spawning seasons following major bleaching events. It is noteworthy that the unprecedented, consecutive warming events in 2014 and 2015 in Kāneʻohe Bay, Hawaiʻi influenced the reproductive capacity of *M*. *capitata* regardless of *parental bleaching response*. When comparing the first spawning season following the 2015 bleaching event to the second, *M*. *capitata* colonies had fewer eggs packaged within the egg-sperm bundles released. While average egg volume did not differ between years, the egg abnormality was higher in 2016 than in 2017 regardless of parental bleaching history. Parental colonies that bleached and did not bleach had similar reproductive output, number of eggs per bundle and egg abnormality. However, delayed beneficial maternal effects were observed in offspring from parents resistant to bleaching. These results demonstrate that although *M*. *capitata* has the energetic capacity to continue reproduction despite bleaching response, cross-generational impacts occur (Byrne et al., 2020), with possible ecological consequences downstream.

4.1 Reproductive capacity after bleaching events

M. *capitata* appears to maintain reproductive resilience, as well as recovery with time, after consecutive marine heatwaves and coral bleaching events, as evidenced by continuing synchronous broadcast spawning and production of viable eggs and sperm. These results are consistent with prior studies examining the influence of environmental and biological factors on *M*. *capitata* gametogenesis and spawning in Kāneʻohe Bay [28,59]. For instance, Padilla-Gamiño et al. [28] found similar rates of gametogenesis along a strong sedimentation gradient. Further, Cox [59] found no differences in reproductive output, eggs per bundle, and egg size between B and NB parents in the spawning season immediately following the 2004 mild warming event. Resilience in *M*. *capitata* may be due to its capacity to maintain energetic stability under stress [53], here evident by the completion of gametogenesis even at the cost of producing fewer eggs per bundle with higher proportion of irregularity in shape in 2016 than in 2017. One hypothesis to explain similar reproductive traits in bleached and nonbleached parents, is that after the thermal stress (Septemebr-October), there is still time for the colonies to recover (~5–6 months) and develop gametes that can be released during the spawning season (May-August) [14,53,60,63]. Furthermore, Rodrigues & Padilla-Gamino [77] found that *M*. *capitata* colonies that bleached allocated 10% more carbon to gametes despite bleaching by limiting the allocation of carbon to adult tissues, with 50–80% less carbon allocated to bleached compared to non-bleached colonies. Compared to other species, *M*. *capitata* prioritizes gametogenesis at the expense of the adult colony. Maintaining egg traits such as size and biochemical composition would serve as an advantageous strategy to ensure ecological fitness of parents and their developing offspring [61,78,79]. For example, there may be an optimal egg size that needs to be achieved to ensure successful fertilization [80,81]. It is notable that the relationship between egg size and number of eggs per bundle in our study has shifted from prior studies; we found 10–12 eggs per bundle in 2016–2017 compared to 15–18 eggs per bundle in studies and egg size was 11% larger in our study than previous studies [59,60]. This apparent tradeoff in reproductive effort suggests plasticity in response to environmental changes and emphasizes the need for long-term studies to detect changes in sexual reproduction [14,35,36]. While further examination of egg traits, such as total lipid content and composition of lipid classes, was beyond the scope of this study due to limited material available, larger egg volume could be beneficial in storing lipids and carbohydrates as well as increased surface area for slower sperm to fertilize eggs in the water column.

High inter- and intraspecific variation in thermal tolerance contribute to reproductive consequences after bleaching events [8,17,33]. For example, there were no differences in percent reproductive polyps between bleached and nonbleached colonies of acroporid species at Heron Island on the Great Barrier Reef after the 1998 bleaching event [82]. Baird and Marshall [8] found that the bleaching response of *Acropora millepora* did not influence fecundity, whereas the bleaching response of *Acropora hyacinthus* strongly influenced the completion of gametogenesis. It is important to emphasize that although reproductive capacity after bleaching events can be greatly suppressed, there are species and populations that are resistant and/or more able to recover from bleaching [7,8,17,39,59,82]. Distinctive populations carrying resilient individuals are critical to identify and protect, particularly if they are successful in continuing sexual reproduction to replenish impacted neighboring reefs [83,84]. Coral reproductive modes and strategies have evolved to withstand environmental fluctuations and severe selective pressures, but the question of how much thinning can a population withstand without complete collapse remains.

4.2 Parental effects on fertilization and offspring survivorship

We demonstrate parental effects, or cross-generational plasticity, in *M. capitata*, with parent cross-type having an effect on fertilization and embryonic development with maternal effects apparent in offspring survivorship. Fertilization success differed by cross-type which may be due to gametic compatibility [85]. Such compatibility could be driven by gamete-recognition proteins that mediate fertilization through chemoattraction, binding, and fusion of egg and sperm [85–87]. Furthermore, high gamete compatibility may explain the advanced rate in cell division during embryogenesis in offspring from NB × NB and B × B cross-types. The lack of compatibility observed in crosses between B × NB and B × NB could potentially result from lineage crossing. However, in our study, we were unable to analyze the genetic composition of the parent organisms and we could not determine if they belonged to distinct parental lineages. Future studies should take into account parental lineages to better understand gamete compatibility, inheritance patterns and traits that can lead to increased genetic diversity or novel offspring phenotypes.

Egg-sperm compatibility has been observed as a mechanism for pre-zygotic isolation to select for populations that are likely to succeed under intense environmental pressures, such as temperature [88–91]. With regards to sperm selection, Henley et al. [92] demonstrated sperm motility in *M. capitata* is strained with a severe decline that may be associated with damaged mitochondria in response to heat stress. Eggs from parent colonies that were resistant to bleaching had offspring with notably higher survivorship regardless of the sperm donor bleaching history [42]. More pronounced benefits of nonbleached egg donors support previous work of maternal provisioning in coral offspring [93–95]. Previous studies have demonstrated that beneficial cross-generational plasticity can occur from maternal effects observed in offspring survivorship. Benefits of maternal effects could be associated with phenotypic traits that help overcome hurdles created by thermal stress such as energetic provisioning through lipid reserves stored in the eggs and larvae [61,96,97], mitochondria [96], or vertical transmission of Symbiodinaceae from the parent into the eggs [64,94,97].

M. capitata houses the endosymbionts *Cladocopium* spp. and *Durusdinium* spp., formerly Clade C and D, respectively. It has been shown that *M. capitata* colonies associate with *Durusdinium* spp. in more challenging environments such as high light and variable thermal regimes [61,98,99]. After a bleaching event, there was a rise in the relative proportion of the heat-tolerant symbiont *Durusdinium* spp. in *M. capitata* colonies across most areas in Kāneʻohe Bay [98]. However, despite this increase, the overall composition of Symbiodiniaceae symbionts

remained largely unchanged, and distinct regions of the bay retained their pre-bleaching compositions. In *M*. *capitata*, these symbionts are vertically transferred to the eggs creating offspring with different assemblages [64] that could confer different physiological attributes to the offspring. For example, Little et al. [100] found that *Acropora* juveniles grew faster when infected with *Cladocopium* spp. than *Durusdinium* spp. (formerly clade C and D, respectively) and Abrego et al. (2008) showed enhanced physiological tolerance and higher ^{14}C photosynthate incorporation in juveniles infected with *Cladocopium* spp. (clade C1). Padilla-Gamiño et al. [64] showed that *Cladocopium* spp. is more likely to be transferred to *M*. *capitata* eggs, but further research is needed to better understand transfer mechanisms, and how different symbionts influence survival, tolerance and/or tradeoffs in larvae and juveniles.

4.3 Interventions for thermal tolerance

Research on coral reefs has become greatly focused on identifying human interventions (i.e., assisted evolution) that support biological persistence and resilience against anthropogenic stressors [101–103]. Developing effective interventions to implement has become increasingly urgent to protect shallow-dwelling coral reef ecosystems [103]. Current strategies proposed to overcome bottlenecks in early life history include identifying genetic adaptation [104], environmental hardening through non-genetic or epigenetic mechanisms [105–110], manipulation of Symbiodiniaceae symbionts [41,111,112], cryopreservation for coral conservation [113], and selective breeding [94,95,114].

Human interventions, such as selective breeding in coral sexual propagation, has been proposed as one of the viable options to maintain genetic diversity and increase resilience in restoration efforts [15,102,103,105,115,116]; however, feasibility to potentially scale up efforts remain limited and costly without full understanding of tradeoffs [117,118]. Our study supports the potential for selective breeding and environmental hardening to have positive fitness consequences. In our study, bleaching in *M*. *capitata* did not severely disrupt reproductive output or egg traits measured (size and abnormality), but the use of eggs from NB colonies in the intentional crossing of gametes produced offspring with higher settlement and survivorship, while bleached corals had higher overall fecundity to balance reduced survivorship and settlement. These results are important to maximize restoration efforts through selective breeding by identifying candidate colonies in the natural environment or through manipulated stress tests and performing crosses using the gametes of resilient colonies. We encourage further research to test the efficacy and trade-offs of human-assisted evolution, particularly selective propagation and environmental hardening, designed to increase coral resistance that would ensure the continuation of coral reefs confronted by global climate change.

Acknowledgments

We would like to thank members of the Gates Coral Laboratory for their technical support and advice, especially Jen Davidson and Dr. James Guest. We are grateful to Mary Hagedorn, Amy Moran, and Peter Marko for their feedback on the manuscript, the many volunteers especially Dyson Chee, Megan Buras, Katie Allen, Shayne Fabian, and Kat McPherson and the security Greg Miranda and Moses at Moku o Lo'e who ensured safety and the success of this research. We dedicate this research to Dr. Ruth D. Gates and her infectious enthusiasm that pushed assisted evolution to the forefront of coral biology–you rock!

Author Contributions

Conceptualization: Elizabeth A. Lenz, Megan J. Donahue, Ruth D. Gates, Hollie M. Putnam, Jacqueline L. Padilla-Gamiño.

Data curation: Elizabeth A. Lenz, Eveline van der Steeg.

Formal analysis: Elizabeth A. Lenz, Megan J. Donahue, Jacqueline L. Padilla-Gamiño.

Funding acquisition: Elizabeth A. Lenz, Ruth D. Gates, Hollie M. Putnam.

Investigation: Elizabeth A. Lenz.

Methodology: Elizabeth A. Lenz, Ruth D. Gates, Hollie M. Putnam, Eveline van der Steeg.

Project administration: Elizabeth A. Lenz, Eveline van der Steeg.

Resources: Elizabeth A. Lenz, Ruth D. Gates.

Software: Elizabeth A. Lenz.

Supervision: Megan J. Donahue, Ruth D. Gates.

Validation: Elizabeth A. Lenz.

Visualization: Elizabeth A. Lenz.

Writing – original draft: Elizabeth A. Lenz, Jacqueline L. Padilla-Gamiño.

Writing – review & editing: Elizabeth A. Lenz, Megan J. Donahue, Hollie M. Putnam, Eveline van der Steeg, Jacqueline L. Padilla-Gamiño.

References

1. Gattuso JP, Magnan A, Billé R, Cheung WWL, Howes EL, Joos F, et al. Contrasting futures for ocean and society from different anthropogenic CO emissions scenarios. Science. 2015; 349(6243).
2. Intergovernmental Panel on Climate Change. Global warming of 1.5˚C: An IPCC special report on the impacts of global warming of 1.5˚C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of strengthening the global response to the threat of climate change, sustainable development, and efforts to eradicate poverty. 2018. Available from: https://www.ipcc.ch/sr15/.
3. Glynn PW. Coral reef bleaching: Facts, hypotheses and implications. Glob Chang Biol. 1996; 2 (6):495–509.
4. LaJeunesse TC, Parkinson JE, Gabrielson PW, Jeong HJ, Reimer JD, Voolstra CR, et al. Systematic revision of Symbiodiniaceae highlights the antiquity and diversity of coral endosymbionts. Curr Biol. 2018; 28(16):2570–2580.e6. https://doi.org/10.1016/j.cub.2018.07.008 PMID: 30100341
5. Muller EM, Bartels E, Baums IB. Bleaching causes loss of disease resistance within the threatened coral species. eLife. 2018; 7. https://doi.org/10.7554/eLife.35066.
6. Hughes TP, Anderson KD, Connolly SR, Heron SF, Kerry JT, Lough JM, et al. Spatial and temporal patterns of mass bleaching of corals in the Anthropocene. Science. 2018; 359(6371):80–83. https://doi.org/10.1126/science.aan8048 PMID: 29302011
7. Szmant AM, Gassman NJ. The effects of prolonged bleaching on the tissue biomass and reproduction of the reef coral Montastrea annularis. Coral Reefs. 1990; 8(4):217–224.
8. Baird AH, Marshall PA. Mortality, growth and reproduction in scleractinian corals following bleaching on the Great Barrier Reef. Mar Ecol Prog Ser. 2002; 237:133–141.
9. Gardner TA, Côté IM, Gill JA, Grant A, Watkinson AR. Long-term region-wide declines in Caribbean corals. Science. 2003; 301(5635):958–960. https://doi.org/10.1126/science.1086050 PMID: 12869698
10. De'ath G, Fabricius KE, Sweatman H, Puotinen M. The 27-year decline of coral cover on the Great Barrier Reef and its causes. Proc Natl Acad Sci U S A. 2012; 109(44):17995–9. https://doi.org/10.1073/pnas.1208909109 PMID: 23027961
11. Hughes TP, Kerry JT, Baird AH, Connolly SR, Chase TJ, Dietzel A, et al. Global warming transforms coral reef assemblages. Nature. 2018; 556(7702):492–6. https://doi.org/10.1038/s41586-018-0041-2 PMID: 29670282
12. Cunning R, Ritson-Williams R, Gates RD. Patterns of bleaching and recovery of Montipora capitata in Kāneʻohe Bay, Hawaiʻi, USA. Mar Ecol Prog Ser. 2016; 551:131–9.

13. Loya Y, Sakai K, Yamazato K, Nakano Y, Sambali H, van Woesik R. Coral bleaching: The winners and the losers. Ecol Lett. 2001; 4(2):122–31.

14. Wall CB, Ritson-Williams R, Popp BN, Gates RD. Spatial variation in the biochemical and isotopic composition of corals during bleaching and recovery. Limnol Oceanogr. 2019; 64(5):2011–28. https://doi.org/10.1002/lno.11166 PMID: 31598010

15. Barott KL, Huffmyer AS, Davidson JM, Lenz EA, Matsuda SB, Hancock JR, et al. Coral bleaching response is unaltered following acclimatization to reefs with distinct environmental conditions. Proc Natl Acad Sci U S A. 2021; 118(22). https://doi.org/10.1073/pnas.2025435118 PMID: 34050025

16. Johnston EC, Counsell CW, Sale TL, Burgess SC, Toonen RJ. The legacy of stress: Coral bleaching impacts reproduction years later. Funct Ecol. 2020; 34(11):2315–25.

17. Levitan DR, Boudreau W, Jara J, Knowlton N. Long-term reduced spawning in Orbicella coral species due to temperature stress. Mar Ecol Prog Ser. 2014; 515:1–10.

18. Putnam HM. Avenues of reef-building coral acclimatization in response to rapid environmental change. J Exp Biol. 2021; 224(1). https://doi.org/10.1242/jeb.239319 PMID: 33627470

19. Bramanti L, Edmunds PJ. Density-associated recruitment mediates coral population dynamics on a coral reef. Coral Reefs. 2016; 35(2):543–53.

20. Bellwood DR, Hughes TP, Folke C, Nyström M. Confronting the coral reef crisis. Nature. 2004; 429 (6994):827–33. https://doi.org/10.1038/nature02691 PMID: 15215854

21. Gilmour JP, Smith LD, Heyward AJ, Baird AH, Pratchett MS. Recovery of an isolated coral reef system following severe disturbance. Science. 2013; 340(6128):69–71. https://doi.org/10.1126/science.1232310 PMID: 23559247

22. Adjeroud M, Kayal M, Penin L. Importance of recruitment processes in the dynamics and resilience of coral reef assemblages. In: Rossi S, Bramanti L, Gori A, Orejas C, editors. Marine Animal Forests. Cham: Springer International Publishing; 2017. p. 549–69.

23. Cruz DW, Harrison PL. Enhanced larval supply and recruitment can replenish reef corals on degraded reefs. Sci Rep. 2017; 7(1):13985. https://doi.org/10.1038/s41598-017-14546-y PMID: 29070842

24. Richmond RH. Reproduction and recruitment in corals: Critical links in the persistence of reefs. In: Birkeland C, editor. Life and death of coral reefs. Boston: Springer US; 1997. p. 175–97.

25. van Oppen MJ, Gates RD. Conservation genetics and the resilience of reef-building corals. Mol Ecol. 2006; 15(13):3863–83. https://doi.org/10.1111/j.1365-294X.2006.03026.x PMID: 17054489

26. Vance RR. On reproductive strategies in marine benthic invertebrates. Am Nat. 1973; 107(955):339–52.

27. Richmond RH, Hunter CL. Reproduction and recruitment of corals: Comparisons among the Caribbean, the Tropical Pacific, and the Red Sea. Mar Ecol Prog Ser. 1990; 60:185–203.

28. Padilla-Gamiño JL, Hédouin L, Waller RG, Smith D, Truong W, Gates RD. Sedimentation and the reproductive biology of the Hawaiian reef-building coral Montipora capitata. Biol Bull. 2014; 226(1):8–18. https://doi.org/10.1086/BBLv226n1p8 PMID: 24648203

29. Richmond RH. Energetics, competency, and long-distance dispersal of planula larvae of the coral Pocillopora damicornis. Mar Biol. 1987; 93(4):527–33.

30. Ward S. Two patterns of energy allocation for growth, reproduction and lipid storage in the scleractinian coral Pocillopora damicornis. Coral Reefs. 1995; 14(2):87–90.

31. Leuzinger S, Willis BL, Anthony KR. Energy allocation in a reef coral under varying resource availability. Mar Biol. 2012; 159(1):177–86.

32. Lenz EA, Bartlett LA, Stathakopoulos A, Kuffner IB. Physiological differences in bleaching response of the coral Porites astreoides along the Florida Keys reef tract during high-temperature stress. Front Mar Sci. 2021; 8:615795.

33. Fisch J, Drury C, Towle EK, Winter RN, Miller MW. Physiological and reproductive repercussions of consecutive summer bleaching events of the threatened Caribbean coral Orbicella faveolata. Coral Reefs. 2019; 38(4):863–76.

34. Hughes TP, Kerry JT, Baird AH, Connolly SR, Chase TJ, Dietzel A, et al. Global warming impairs stock-recruitment dynamics of corals. Nature. 2019; 568(7752):387–90. https://doi.org/10.1038/s41586-019-1081-y PMID: 30944475

35. Price NN, Muko S, Legendre L, Steneck RS, van Oppen MJ, Albright R, et al. Global biogeography of coral recruitment: Tropical decline and subtropical increase. Mar Ecol Prog Ser. 2019; 621:1–17.

36. Hagedorn M, Carter VL, Lager C, Camperio Ciani JF, Dygert AN, Schleiger RD, et al. Potential bleaching effects on coral reproduction. Reprod Fertil Dev. 2016; 28(8):1061.

37. Negri AP, Marshall PA, Heyward AJ. Differing effects of thermal stress on coral fertilization and early embryogenesis in four Indo Pacific species. Coral Reefs. 2007; 26(4):759–63.

38. Howells EJ, Ketchum RN, Bauman AG, Mustafa Y, Watkins KD, Burt JA. Species-specific trends in the reproductive output of corals across environmental gradients and bleaching histories. Mar Pollut Bull. 2016; 105(2):532–9. https://doi.org/10.1016/j.marpolbul.2015.11.034 PMID: 26608503

39. Omori M, Fukami H, Kobinata H, Hatta M. Significant drop of fertilization of Acropora corals in 1999: An after-effect of heavy coral bleaching? Limnol Oceanogr. 2001; 46(3):704–11.

40. Edmunds PJ. Implications of high rates of sexual recruitment in driving rapid reef recovery in Mo'orea, French Polynesia. *Sci Rep*. 2018; 8(1):16615. https://doi.org/10.1038/s41598-018-34686-z PMID: 30413729

41. Dilworth J, Caruso C, Kahkejian VA, Baker AC, Drury C. Host genotype and stable differences in algal symbiont communities explain patterns of thermal stress response of *Montipora capitata* following thermal pre-exposure and across multiple bleaching events. *Coral Reefs*. 2021; 40(1):151–163. https://doi.org/10.1007/s00338-020-02014-4.

42. Drury C, Dilworth J, Majerová E, Caruso C, Greer L. Expression plasticity regulates intraspecific variation in the acclimatization potential of a reef-building coral. *Nat Commun*. 2022; 13:4790. https://doi.org/10.1038/s41467-022-32452-4 PMID: 35970904

43. Jokiel PL, Brown EK. Global warming, regional trends and inshore environmental conditions influence coral bleaching in Hawaii. *Glob Change Biol*. 2004; 10(10):1627–1641. https://doi.org/10.1111/j.1365-2486.2004.00836.x.

44. Jokiel PL, Coles SL. Response of Hawaiian and other Indo-Pacific reef corals to elevated temperature. Coral Reefs. 1990; 8(4):155–162.

45. Bahr KD, Jokiel PL, Rodgers KS. Relative sensitivity of five Hawaiian coral species to high temperature under high-pCO2 conditions. Coral Reefs. 2016; 35(2):729–738.

46. Bahr KD, Rodgers KS, Jokiel PL. Impact of three bleaching events on the reef resiliency of Kāne'ohe Bay, Hawai'i. Front Mar Sci. 2017; 4:398.

47. Couch CS, Burns JHR, Liu G, Steward K, Gutlay TN, Kenyon J, et al. Mass coral bleaching due to unprecedented marine heatwave in Papahānaumokuākea Marine National Monument (Northwestern Hawaiian Islands). PLoS One. 2017; 12(9).

48. Bahr KD, Jokiel PL, Rodgers KS. The 2014 coral bleaching and freshwater flood events in Kāne'ohe Bay, Hawai'i. PeerJ. 2015; 3.

49. Coles SL, Bahr KD, Rodgers KS, May SL, McGowan AE, Tsang A, et al. Evidence of acclimatization or adaptation in Hawaiian corals to higher ocean temperatures. PeerJ. 2018; 6. https://doi.org/10.7717/peerj.5347 PMID: 30123699

50. Rodgers KS, Bahr KD, Jokiel PL, Richards Donà A. Patterns of bleaching and mortality following widespread warming events in 2014 and 2015 at the Hanauma Bay Nature Preserve, Hawai'i. PeerJ. 2017; 5.

51. Matsuda SB, Huffmyer AS, Lenz EA, Davidson JM, Hancock JR, Przybylowski A, et al. Coral bleaching susceptibility is predictive of subsequent mortality within but not between coral species. Front Ecol Evol. 2020; 8:178.

52. Brown KT, Lenz EA, Glass BH, Kruse E, McClintock R, Drury C, et al. Divergent bleaching and recovery trajectories in reef-building corals following a decade of successive marine heatwaves. Proc Natl Acad Sci U S A. 2023; 120(52). https://doi.org/10.1073/pnas.2312104120 PMID: 38113265

53. Wall CB, Ritson-Williams R, Popp BN, Gates RD. Spatial variation in the biochemical and isotopic composition of corals during bleaching and recovery. Limnol Oceanogr. 2019; 64(5):2011–2028. https://doi.org/10.1002/lno.11166 PMID: 31598010

54. Gibbin EM, Putnam HM, Gates RD, Nitschke MR, Davy SK. Species-specific differences in thermal tolerance may define susceptibility to intracellular acidosis in reef corals. Mar Biol. 2015; 162(3):717–723.

55. Putnam HM, Davidson JM, Gates RD. Ocean acidification influences host DNA methylation and phenotypic plasticity in environmentally susceptible corals. Evol Appl. 2016; 9(9):1165–1178. https://doi.org/10.1111/eva.12408 PMID: 27695524

56. Grottoli AG, Rodrigues LJ, Juarez C. Lipids and stable carbon isotopes in two species of Hawaiian corals, Porites compressa and Montipora verrucosa, following a bleaching event. Mar Biol. 2004; 145 (3):621–631.

57. Grottoli AG, Rodrigues LJ, Palardy JE. Heterotrophic plasticity and resilience in bleached corals. Nature. 2006; 440(7088):1186–1189. https://doi.org/10.1038/nature04565 PMID: 16641995

58. Rodrigues LJ, Grottoli AG. Energy reserves and metabolism as indicators of coral recovery from bleaching. Limnol Oceanogr. 2007; 52(5):1874–1882.

59. Cox EF. Continuation of sexual reproduction in Montipora capitata following bleaching. Coral Reefs. 2007; 26(3):721–724.

60. Padilla-Gamiño JL, Gates RD. Spawning dynamics in the Hawaiian reef-building coral Montipora capitata. Mar Ecol Prog Ser. 2012; 449:145–160.

61. Padilla-Gamiño JL, Bidigare RR, Barshis DJ, Alamaru A, Hédouin L, Hernández-Pech X, et al. Are all eggs created equal? A case study from the Hawaiian reef-building coral Montipora capitata. Coral Reefs. 2013; 32(1):137–152.

62. Byrne M, Foo SA, Ross PM, Putnam HM. Limitations of cross-and multigenerational plasticity for marine invertebrates faced with global climate change. Glob Change Biol. 2020; 26(1):80–102. https://doi.org/10.1111/gcb.14882 PMID: 31670444

63. Padilla-Gamiño JL, Weatherby TM, Waller RG, Gates RD. Formation and structural organization of the egg–sperm bundle of the scleractinian coral Montipora capitata. Coral Reefs. 2011; 30(2):371–380.

64. Padilla-Gamiño JL, Pochon X, Bird C, Concepcion GT, Gates RD. From parent to gamete: vertical transmission of Symbiodinium (Dinophyceae) ITS2 sequence assemblages in the reef building coral Montipora capitata. PLoS One. 2012; 7(6). https://doi.org/10.1371/journal.pone.0038440 PMID: 22701642

65. Hagedorn M, Farrell A, Carter V, Zuchowicz N, Johnston E, Padilla-Gamiño J, et al. Effects of toxic compounds in Montipora capitata on exogenous and endogenous zooxanthellae performance and fertilization success. PLoS One. 2015; 10(2). https://doi.org/10.1371/journal.pone.0118364 PMID: 25714606

66. Gibbin EM, Krueger T, Putnam HM, Barott KL, Bodin J, Gates RD, et al. Short-Term Thermal Acclimation Modifies the Metabolic Condition of the Coral Holobiont. Front Mar Sci. 2018; 5.

67. Schindelin J, Arganda-Carreras I, Frise E, Kaynig V, Longair M, Pietzsch T, et al. Fiji: an open-source platform for biological-image analysis. Nat Methods. 2012; 9(7):676–682. https://doi.org/10.1038/nmeth.2019 PMID: 22743772

68. Lager CV, Hagedorn M, Rodgers KS, Jokiel PL. The impact of short-term exposure to near shore stressors on the early life stages of the reef building coral Montipora capitata. PeerJ. 2020; 8. https://doi.org/10.7717/peerj.9415 PMID: 32685286

69. Padilla-Gamiño JL, Gates RD, Medina M. Gametogenesis and reproductive output in the Hawaiian reef-building coral Montipora capitata. Coral Reefs. 2011; 30(3):451–460.

70. Willis BL, Babcock RC, Harrison PL, Wallace CC. Experimental hybridization and breeding incompatibilities within the mating systems of mass spawning reef corals. Coral Reefs. 1997; 16:53–65.

71. Babcock RC, Heyward AJ. Larval development of certain gamete-spawning scleractinian corals. Coral Reefs. 1986; 5(3), 111–116.

72. Bates D, Mächler M, Bolker B, Walker S. Fitting linear mixed-effects models using lme4. J Stat Softw. 2015; 67(1):1–48. https://doi.org/10.18637/jss.v067.i01.

73. Fox J, Weisberg S. An R companion to applied regression. 2nd ed. Thousand Oaks, CA: Sage; 2011.

74. Lenth RV. emmeans: Estimated marginal means, aka least-squares means (R package version 1.4.8). 2020. https://CRAN.R-project.org/package=emmeans.

75. Kassambara A, Kosinski M, Biecek P. survminer: Drawing survival curves using 'ggplot2' (R package version 0.4.0). 2017. https://CRAN.R-project.org/package=survminer.

76. Hartig F. DHARMa: Residual diagnostics for hierarchical (multi-level/mixed) regression models (R package version 0.2.6). 2019. https://CRAN.R-project.org/package=DHARMa.

77. Rodrigues LJ, Padilla-Gamiño JL. Trophic provisioning and parental trade-offs lead to successful reproductive performance in corals after a bleaching event. Sci Rep. 2022; 12(1):18702. https://doi.org/10.1038/s41598-022-21998-4 PMID: 36333369

78. Moran AL, McAlister JS. Egg size as a life history character of marine invertebrates: is it all it's cracked up to be? Biol Bull. 2009; 216(3):226–242. https://doi.org/10.1086/BBLv216n3p226 PMID: 19556591

79. Jacobs MW, Podolsky RD. Variety is the spice of life histories: comparison of intraspecific variability in marine invertebrates. Integr Comp Biol. 2010; 50(4):630–642. https://doi.org/10.1093/icb/icq091 PMID: 21558229

80. Levitan DR. The importance of sperm limitation to the evolution of egg size in marine invertebrates. Am Nat. 1993; 141(4):517–536. https://doi.org/10.1086/285489 PMID: 19425997

81. Levitan DR, Petersen C. Sperm limitation in the sea. Trends Ecol Evol. 1995; 10(6):228–231. https://doi.org/10.1016/S0169-5347(00)89071-0 PMID: 21237018

82. Ward S, Harrison P, Hoegh-Guldberg O. Coral bleaching reduces reproduction of scleractinian corals and increases susceptibility to future stress. Proc Ninth Int Coral Reef Symp. 2000; 2:1123–1128.

83. Underwood JN, Smith LD, Van Oppen MJH, Gilmour JP. Multiple scales of genetic connectivity in a brooding coral on isolated reefs following catastrophic bleaching. Mol Ecol. 2007; 16(4):771–784. https://doi.org/10.1111/j.1365-294X.2006.03187.x PMID: 17284210

84. Baker AC, Glynn PW, Riegl B. Climate change and coral reef bleaching: an ecological assessment of long-term impacts, recovery trends and future outlook. Estuar Coast Shelf Sci. 2008; 80(4):435–471.

85. Vacquier VD. Evolution of gamete recognition proteins. Science. 1998; 281(5385):1995–1998. https://doi.org/10.1126/science.281.5385.1995 PMID: 9748153

86. Tomaiuolo M, Levitan DR. Modeling how reproductive ecology can drive protein diversification and result in linkage disequilibrium between sperm and egg proteins. Am Nat. 2010; 176(1):14–25. https://doi.org/10.1086/652999 PMID: 20455709

87. Miller MW, Baums IB, Pausch RE, Bright AJ, Cameron CM, Williams DE, et al. Clonal structure and variable fertilization success in Florida Keys broadcast-spawning corals. Coral Reefs. 2018; 37 (1):239–249.

88. Coll JC, Bowden BF, Meehan GV, König GM, Carroll AR, Tapiolas DM, et al. Chemical aspects of mass spawning in corals. I. Sperm-attractant molecules in the eggs of the scleractinian coral Montipora digitata. Mar Biol. 1994; 118(2):177–182.

89. Baums IB, Devlin-Durante MK, Polato NR, Xu D, Giri S, Altman NS, et al. Genotypic variation influences reproductive success and thermal stress tolerance in the reef-building coral Acropora palmata. Coral Reefs. 2013; 32(3):703–717.

90. Kosman ET, Levitan DR. Sperm competition and the evolution of gametic compatibility in externally fertilizing taxa. Mol Hum Reprod. 2014; 20(12):1190–1197. https://doi.org/10.1093/molehr/gau069 PMID: 25323969

91. Vermeij GJ, Grosberg RK. Rarity and persistence. Ecol Lett. 2018; 21(1):3–8. https://doi.org/10.1111/ele.12872 PMID: 29110416

92. Henley EM, Quinn M, Bouwmeester J, Daly J, Zuchowicz N, Lager C, et al. Reproductive plasticity of Hawaiian Montipora corals following thermal stress. Sci Rep. 2021; 11(1):1–17.

93. Marshall D, Allen R, Crean A. The ecological and evolutionary importance of maternal effects in the sea. Oceanogr Mar Biol. 2008; 46:203–262.

94. Quigley KM, Willis BL, Bay LK. Maternal effects and community composition drive differential patterns in juvenile survival in the coral. R Soc Open Sci. 2016; 3(10):160471.

95. Chan WY, Peplow LM, van Oppen MJH. Interspecific gamete compatibility and hybrid larval fitness in reef-building corals: Implications for coral reef restoration. Sci Rep. 2019; 9(1):4757. https://doi.org/10.1038/s41598-019-41190-5 PMID: 30894593

96. Rivest EB, Chen C-S, Fan T-Y, Li H-H, Hofmann GE. Lipid consumption in coral larvae differs among sites: a consideration of environmental history in a global ocean change scenario. Proc Biol Sci. 2017; 284(1853):20162825. https://doi.org/10.1098/rspb.2016.2825 PMID: 28446693

97. Jones AM, Berkelmans R. Tradeoffs to thermal acclimation: Energetics and reproduction of a reef coral with heat tolerant Symbiodinium type-D. J Mar Sci. 2011; 2011(1):185890.

98. Rocha de Souza MR, Carlo C, Ruiz-Jones L, Drury C, Gates RD, Toonen RJ. Community composition of coral-associated Symbiodiniaceae differs across fine-scale environmental gradients in Kāneʻohe Bay. R Soc Open Sci. 2022; 9(2):212042.

99. Stat M, Bird CE, Pochon X, Chasqui L, Chauka LJ, Concepcion GT, et al. Variation in Symbiodinium ITS2 sequence assemblages among coral colonies. PLoS One. 2011; 6(1). https://doi.org/10.1371/journal.pone.0015854 PMID: 21246044

100. Little AF, van Oppen MJ, Willis BL. Flexibility in algal endosymbioses shapes growth in reef corals. Science. 2004; 304(5676):1492–1494. https://doi.org/10.1126/science.1095733 PMID: 15178799

101. van Oppen MJH, Oliver JK, Putnam HM, Gates RD. Building coral reef resilience through assisted evolution. Proc Natl Acad Sci U S A. 2015; 112(8):2307–2313. https://doi.org/10.1073/pnas.1422301112 PMID: 25646461

102. van Oppen MJH, Gates RD, Blackall LL, Cantin N, Chakravarti LJ, Chan WY, et al. Shifting paradigms in restoration of the world's coral reefs. Glob Change Biol. 2017; 23(9):3437–3448. https://doi.org/10.1111/gcb.13647 PMID: 28247459

103. National Academies of Sciences, Engineering, and Medicine (U.S.), Committee on Interventions to Increase the Resilience of Coral Reefs. A research review of interventions to increase the persistence and resilience of coral reefs. Washington (DC): National Academies Press; 2019. 245 p.

104. Dixon GB, Davies SW, Aglyamova GA, Meyer E, Bay LK, Matz MV. Genomic determinants of coral heat tolerance across latitudes. Science. 2015; 348(6242):1460–1462.

105. Putnam HM, Gates RD. Preconditioning in the reef-building coral Pocillopora damicornis and the potential for trans-generational acclimatization in coral larvae under future climate change conditions. J Exp Biol. 2015; 218(15):2365–2372. https://doi.org/10.1242/jeb.123018 PMID: 26246609

106. Putnam HM. Avenues of reef-building coral acclimatization in response to rapid environmental change. J Exp Biol. 2021; 224. https://doi.org/10.1242/jeb.239319 PMID: 33627470

107. Putnam HM, Ritson-Williams R, Cruz JA, Davidson JM, Gates RD. Environmentally-induced parental or developmental conditioning influences coral offspring ecological performance. Sci Rep. 2020; 10:136664. https://doi.org/10.1038/s41598-020-70605-x PMID: 32788607

108. Liew YJ, Howells EJ, Wang X, Michell CT, Burt JA, Idaghdour Y, et al. Intergenerational epigenetic inheritance in reef-building corals. Nat Clim Change. 2020; 10(3):254–259.

109. Dixon G, Liao Y, Bay LK, Matz MV. Role of gene body methylation in acclimatization and adaptation in a basal metazoan. Proc Natl Acad Sci U S A. 2018; 115(52):13342–13346. https://doi.org/10.1073/pnas.1813749115 PMID: 30530646

110. Chakravarti LJ, van Oppen MJH. Experimental evolution in coral photosymbionts as a tool to increase thermal tolerance. Front Mar Sci. 2018; 5:227.

111. Levin RA, Voolstra CR, Agrawal S, Steinberg PD, Suggett DJ, van Oppen MJ. Engineering strategies to decode and enhance the genomes of coral symbionts. Front Microbiol. 2017; 8:1220. https://doi.org/10.3389/fmicb.2017.01220 PMID: 28713348

112. Buerger P, Alvarez-Roa C, Coppin CW, Pearce SL, Chakravarti LJ, Oakeshott JG, et al. Heat-evolved microalgal symbionts increase coral bleaching tolerance. Sci Adv. 2020; 6(20). https://doi.org/10.1126/sciadv.aba2498 PMID: 32426508

113. Hagedorn M, Carter VL, Henley EM, van Oppen MJH, Hobbs R, Spindler RE. Producing coral offspring with cryopreserved sperm: A tool for coral reef restoration. Sci Rep. 2017; 7(1):14432. https://doi.org/10.1038/s41598-017-14644-x PMID: 29089578

114. Chan WY, Peplow LM, Menéndez P, Hoffmann AA, van Oppen MJH. Interspecific hybridization may provide novel opportunities for coral reef restoration. Front Mar Sci. 2018; 5:157.

115. Epstein N, Bak RPM, Rinkevich B. Applying forest restoration principles to coral reef rehabilitation. Aquat Conserv Mar Freshw Ecosyst. 2003; 13(5):387–395.

116. Hancock JR, Barrows AR, Roome TC, Huffmyer AS, Matsuda SB, Munk NJ, et al. Coral husbandry for ocean futures: leveraging abiotic factors to increase survivorship, growth, and resilience in juvenile Montipora capitata. Mar Ecol Prog Ser. 2021; 657:123–133.

117. Edwards AJ, Guest JR, Heyward AJ, Villanueva RD, Baria MV, Bollozos ISF, et al. Direct seeding of mass-cultured coral larvae is not an effective option for reef rehabilitation. Mar Ecol Prog Ser. 2015; 525:105–116.

118. Chamberland VF, Petersen D, Guest JR, Petersen U, Brittsan M, Vermeij MJ. New seeding approach reduces costs and time to outplant sexually propagated corals for reef restoration. Sci Rep. 2017; 7(1):18076. https://doi.org/10.1038/s41598-017-17555-z PMID: 29273761