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Optimizing sexual reproduction of *Montipora capitata* for restoration: effects of abiotic conditions and light acclimation on juvenile survival and growth

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ABSTRACT: The worldwide decline of coral reefs necessitates development of tools and methods for active conservation of reef structures and their ecological function. Aquaculture of sexually produced corals is a potential strategy for reef restoration efforts, but existing methods require greater scalability and optimization. To address these needs, we reared *Montipora capitata* larvae from Kāne'ohe Bay and raised them in an *ex situ* facility to examine patterns of growth and survivorship under different abiotic conditions, building from previous best practices and manipulating light levels during early life-history stages. Larvae were reared using different stocking densities and settled at varied densities (25, 125, and 225 larvae per plug) on conditioned plugs (1 or 4 wk). Juveniles were raised and tracked under different flow, shade, and light acclimation regimes for 135 d. Results show that recruitment increased with settlement density. Juvenile survivorship was maximized in high flow and intermediate shade levels, while growth was maximized by low shade environments in both aggregate and individual settlers. Light acclimation treatments yielded intermediate survivorship and tradeoffs between growth and survival compared to corals reared in static shade conditions. Importantly, no abiotic treatment combinations optimized growth and survivorship simultaneously. This study demonstrates interactions of abiotic factors and provides insight into how they can be manipulated to scale the sexual reproduction of corals for conservation.

KEY WORDS: Coral husbandry · Light acclimation · *Montipora capitata* · Coral spawning · Restoration

1. INTRODUCTION

Coral reefs are vitally important ecosystems that foster biodiversity and provide essential resources for coastal communities (Fisher et al. 2015, Woodhead et al. 2019). For example, in Hawai'i, where this study was conducted, coral reefs are vital features of Indigenous and contemporary cultural landscape, so in the course of this research we hope to honor the legacy of the waters known as Ke Kai o Malulani in the He'eia region of Kāne'ohe Bay (Friedlander et al. 2013, Gregg et al. 2015). Despite the biological, economic, and social value of reefs worldwide, they currently remain in a state of serious decline due to a combination of local stressors (e.g. pollution, overfishing) and global climate change (Pandolfi et al. 2003, Donner & Potere 2007, Hughes et al. 2018, Woodhead et al. 2019). As a result, active restoration tools are increasingly considered essential interventions to preserve coral reefs and their associated ecosystem functions (Rinkevich 2005, Boström-Einarsson et al. 2020). In order for such interventions to be effective, these tools must be able to produce the large number of corals that will be required to rehabilitate reefs at an ecological scale (Pollock et al. 2017, Craggs et al. 2019). Restoration utilizing sexu-

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ally produced coral propagules is an emerging technique which potentially offers scalability of this magnitude (Randall et al. 2020).

In recent decades, coral restoration and out-planting efforts have mostly relied on asexual reproduction methods such as coral gardening, where coral stock is produced by fragmentation (Bowden-Kerby 2001, Nama & Akter 2021). However, these techniques present several significant constraints, in particular the limited genetic diversity and potentially reduced resilience associated with asexually produced corals (Baums 2008, Guest et al. 2014, Omori et al. 2016, Baums et al. 2019). Additionally, these practices often require fragmenting and/or removing healthy coral from source areas, which may negatively affect source reefs and donor colony health (Edwards & Clark 1999, Forsman et al. 2006, Lirman et al. 2010). Due to concerns about such negative impacts, obtaining appropriate permits is also a considerable logistical challenge to this methodology, and represents another barrier to upscaling these practices (Lirman et al. 2010, Boström-Einarsson et al. 2020). Alternatively, generating corals through a sexual reproduction pipeline, in which coral gametes are collected and reared through early life stages into juveniles, is an emerging approach which addresses many of these limitations (Randall et al. 2020, Hancock et al. 2021). Importantly, methods using sexual reproduction promote genetic diversity and allow for potential incorporation of additional techniques such as selective breeding or assisted gene flow (Baums 2008, van Oppen et al. 2017, Humanes et al. 2021). Additionally, sexual reproduction pipelines minimize damage to existing reefs because they do not require the extraction or fragmentation of adult corals, instead utilizing a small portion of gametes, collected *in situ* during spawning events, as source material (Edwards 2010, Randall et al. 2020). Sexual propagation also offers the opportunity to significantly upscale the current production of restoration by taking advantage of the high fecundity of corals, which may produce billions of larvae during mass spawning events (Álvarez-Noriega et al. 2016, Pollock et al. 2017, Craggs et al. 2019).

Despite the potential benefits of sexually produced corals (e.g. scalability, genetic diversity), biological bottlenecks associated with the early life history stages of coral development present significant challenges to implementing these methodologies (Vermeij & Sandin 2008, Penin et al. 2010, Guest et al. 2014). Embryogenesis, larval development, larval settlement, and post-settlement survivorship are all early life history phases that present unique obstacles to the feasibility of large-scale restoration efforts (Guest et al. 2014, Randall et al. 2020). In particular, high mortality rates associated with larval stages and sensitivity of newly settled recruits to environmental conditions make larval settlement and post-settlement survivorship prime areas for improvement (Craggs et al. 2019, Hancock et al. 2021). Species-specific techniques which improve these processes are being developed worldwide in order to facilitate large-scale restoration efforts (Pollock et al. 2017, Craggs et al. 2019). Yet, for most coral species, essential rearing and husbandry protocols have yet to be defined or specifically tailored for maximum output. In particular, larval cultures and recruitment are known to have density-dependent thresholds that have yet to be quantified for many species (Pollock et al. 2017, Randall et al. 2020). For example, even in *Montipora capitata,* where sexual reproduction has been studied extensively, optimal densities for larval rearing and settlement remain unknown (Padilla-Gamiño & Gates 2012, Hancock et al. 2021). While it has been observed that success of larval recruitment increases with larval abundance supplied, densely stocked larvae may lead to high rates of mortality in *ex situ* cultures (Suzuki et al. 2012, Doropoulos et al. 2017, Cameron & Harrison 2020). Additionally, previous studies have also demonstrated the importance of substrate biofilms in the settlement of coral larvae (Webster et al. 2004, Ritson-Williams et al. 2010, Hancock et al. 2021). Larvae of many coral species have been shown to actively select a position for permanent settlement based on external chemical cues that induce metamorphosis (Heyward & Negri 1999, Tran & Hadfield 2011). Balancing these factors and defining effective larval rearing techniques and optimal substrate conditions are imperative steps in establishing protocols which maximize output at all stages of the sexual reproduction pipeline (Pollock et al. 2017, Randall et al. 2020).

Newly settled recruits are particularly sensitive to abiotic factors, such as light intensity and water flow, which are known to be influential drivers of post-settlement survival in the *ex situ* grow-out phase of juvenile *M. capitata* (Forsman et al. 2012, Hancock et al. 2021). Interestingly, as juvenile corals age, optimal rearing conditions may shift, particularly in response to light, representing a potentially important opportunity to enhance post-settlement husbandry techniques (McMahon 2018, Kuanui et al. 2020). Previous experiments have indicated that the light needs of juvenile *M. capitata* may change after 1 mo post-settlement, where juveniles may prefer darker conditions immediately after settlement but may sub-

sequently benefit from increased light availability (Hancock et al. 2021). Light intensity impacts coral growth as well as the photosynthetic capabilities of symbiotic zooxanthellae, which has strong influence on colony health and survival (Kühl et al. 1995, Kuanui et al. 2020). Excessive light availability can lead to increased oxidative stress and reduced photosynthetic efficiency which can result in coral bleaching, as well as algal overgrowth (Kühl et al. 1995, Richier et al. 2008). Therefore, determination of optimal light conditions is of high priority for rearing sexually propagated corals. Here, we examine how light acclimation, the process of incrementally increasing the light intensity available to juvenile corals, affects the survivorship and growth of juvenile *M. capitata*. By initially heavily shading early recruits and subsequently increasing light availability, we aim to enable juvenile survival and growth through enhanced photosynthetic capabilities (Kuffner et al. 2006, Ritson-Williams et al. 2009, Kuanui et al. 2020).

In this study, we fine-tune current post-settlement and larval rearing practices and incorporate an understudied coral husbandry tool, light acclimation, in an attempt to enhance the sexual reproduction pipeline for *M. capitata*. We present the most recent improved practices for rearing *M. capitata* in Hawai'i and determine (1) optimal substrate conditioning, (2) enhanced embryo and larval stocking densities, (3) effects of multiple light and flow regimes, and (4) impacts of light acclimation on post-settlement survival and growth.

2. MATERIALS AND METHODS

2.1. Gamete collection, embryo stocking densities

Montipora capitata is a hermaphroditic broadcast spawner that releases egg-sperm bundles in mass spawning events during the summer months in Hawai'i (Padilla-Gamiño & Gates 2012). During mass spawning events in June and July 2020, gamete bundles were collected near Reef 11 in Kāne'ohe Bay, O'ahu. Egg-sperm bundles were released at approximately 21:00 h and were collected from the ocean surface using mesh nets (153 µm mesh) for approximately 15 min. Gametes were gently rinsed from collection nets into a large collection bucket (19 l) containing seawater. After the completion of gamete collection, 5 ml of egg-sperm bundles were immediately aliquoted into approximately 35 ml of seawater within a 50 ml falcon tube. Egg-sperm bundles were then transported to an *ex situ* facility on Moku o Lo'e (Hawai'i Institute of Marine Biology) and were allowed to fertilize until bundles visibly separated, after approximately 60 min. Following the successful collection of gametes and fertilization period, concentrated sperm supernatant was removed from the gamete-seawater solution. Fertilized embryos were then transferred into 15 l larval rearing conicals at 9 volumes (5, 7.5, 10, 12.5, 15, 17.5, 20, 22.5, 25 ml l^{-1}) in June for the embryo stocking density experiment and at 15 ml in July for the post-settlement experiment. Here, embryo stocking density refers to the number of fertilized embryos that were added to each rearing conical. Embryos were gently stirred into the conicals in order to dilute any additional sperm water, which was then drained approximately 90% before refilling. The larval rearing conicals were supplied with 1 µm filtered seawater at ambient temperature and overflow was passed through a submerged banjo filter (153 µm mesh) to prevent the loss of embryos and larvae. For 24 h immediately following fertilization, flow through the conicals was minimal (<1 l h^{-1}) in order to minimize physical damage to the embryos. Water flow through the conicals was increased at 24 and 48 h post-fertilization to prevent larvae from settling on conical surfaces (~2 l h^{-1}).

2.2. Larval rearing and quantification

Fertilized embryos were reared for 5 d at ambient temperatures. The temperature of all rearing conicals was recorded 4 times within the 2 d immediately after fertilized embryos were added and averaged 27.1°C. Cultures were cleaned every hour during the first 5 d of rearing. Cleaning included removing visibly dead embryos, stirring embryos in order to prevent settling on the side of the conicals or banjo filter, and removing any biofilm present on the surface of the conicals. At 5 d post fertilization, production of competent larvae was volumetrically quantified from each stocking density culture. Twelve 1 ml samples were aliquoted from a homogenized conical mixture and counted to calculate average larvae produced from each stocking density. In July, we used the same volumetric technique to quantify larvae for settlement.

2.3. Plug conditioning, larval settlement, larval stocking density

In preparation for settlement in June, aragonite plugs (~1.9 cm diameter) were conditioned for either 4 or 1 wk in a flow-through seawater tank under 2

layers of shade cloth. In July, plugs were conditioned in the same tank environment for 4 wk. After 4 wk, conditioning produced a biofilm as well as notable growth of filamentous algae. Efforts were taken to remove any macroalgae on the plugs before settlement. At 5 d post-fertilization, larvae were placed into settlement bins with mesh bottoms (~15 cm wide × 30 cm long; 153 µm mesh), each containing 80 aragonite plugs submerged in approximately 2 cm of water. In June, larvae were introduced to settlement chambers at low, medium, and high densities (25, 125, and 225 larvae per plug, n = 8 bins per density) and were allowed to settle for either 24 or 72 h (n = 4 bins per time point). In July, larvae were added to 38 settlement bins at a density of 125 larvae per aragonite plug, all plugs were checked for settled larvae at both 24 and 72 h time points. At each time interval, plugs with newly settled corals were removed from the settlement chambers and placed into a holding tank until all plugs with settled corals were transferred into their respective treatments.

2.4. Coral husbandry

The newly settled recruits in post-settlement treatments were reared for 5 mo (July 2020 to December 2020) in experimental tank treatments designed to test effects of light intensity, flow, and light acclimation. Each treatment was replicated in 2 raceway tanks. The raceway tanks were periodically siphoned to remove accumulation of sand and sediment from the bottom of tanks. In addition, these tanks experienced a large bloom of macroalgae which began in September 2020 and continued until the beginning of November 2020. In order to prevent complete overgrowth of the juvenile corals, algae was manually removed from plugs and plug racks, and tanks were cleaned on a weekly basis. Importantly, this maintenance was solely to prevent corals from being smothered by mat-forming macroalgae and was not an attempt to represent any form of herbivory, a factor which can be influential when raising corals in an *ex situ* environment (Craggs et al. 2019, Henry et al. 2019). Despite these efforts, this algal bloom interfered with data collection and no data was recorded in September due to extensive algae cover.

Once a month for the duration of this experiment, 15 ml of commercially available coral food (Reef Chili) was mixed with 1000 ml of water and added to each tank (Reef Chili not added in September due to level of algae overgrowth). Additionally, temperature loggers (HOBO Pendant, Onset Computer) were placed into all raceway tanks and recorded temperature measurements every 15 min from 30 July 2020, 17:00 h until 8 February 2020, 17:00 h. All tanks closely tracked each other as well as the temperature of Kāneʻohe Bay.

2.5. Post-settlement shade, flow, and light acclimation treatments

2.5.1. Shade treatments. Three different static shade treatments were tested (1x, 2x, and 3x) within each flow tank (n = 4). Utilizing commercially available shade cloth, shade coverings were constructed for each light treatment with 1 layer (1x), 2 layers (2x), or 3 layers (3x) of shade cloth. Therefore, the 1x treatment received the most sunlight and the 3x treatment received the least. Every raceway tank was modified to accommodate all 3 light treatments. This arrangement allowed for the racks to be periodically rearranged within the tanks to account for variability in light or flow. We measured photosynthetically active radiation (PAR, in units of photosynthetic photon flux density or PPFD) values under each shade cloth treatment using a Li-COR light meter. PAR measurements were taken at noon on a sunny day in August in order to represent maximum light intensity expected to reach the corals over the duration of the experiment. In the light acclimation treatment, a subset of plugs (n = 30) within each raceway tank were transferred 36 d post-settlement from high shade (3x) to low shade (1x) treatments. Plugs were re-randomized within racks after transfer.

2.5.2. Flow treatments. Relatively high and low flow treatments were tested in this experiment. A manifold powered by 2 Danner Manufacturing pumps created the high flow environment in 2 tanks, while a manifold powered by 1 pump created a low flow environment in remaining tanks (n = 2). The seawater input to each raceway tank was equivalent (6 l min^{-1}, turnover time ~0.5 h). The high flow tank had the equivalent of approximately 5300 l h^{-1} circulation while the low flow tank had the equivalent of approximately 2650 l h^{-1} circulation.

2.6. Juvenile survivorship and recruitment density

The effects of the light, flow, and light acclimation treatments on the survivorship and growth of juvenile corals were assessed by photographing all plugs (n = 2699) immediately after settlement and at 4 additional time points (36, 64, 106, 134 d post-settle-

ment). Photographs were taken of every plug using a Canon EOS 6D camera and Canon EF 24-70mm f/4.0L IS USM standard zoom lens. Living juveniles were classified as individuals or aggregates based on initial settlement for downstream analysis, whereby aggregates represent 2 or more corals that have settled in physical contact with each other. Survivorship of all juvenile *M. capitata* was tracked on 200 plugs (30 per shade/flow treatment) for all time points. Survival was determined by examining photos and recording a juvenile as alive if a distinct corallite structure was present and there was pigmentation distinguishable from the substrate directly underneath the coral. The number of living individual and aggregate juvenile corals on each plug was recorded. Aggregate survivorship was determined by the state of the whole aggregate colony rather than the survival of individual polyps within an aggregate structure. If a coral appeared to be overgrown by macroalgae or crustose coralline algae, or lacked distinct tissue pigmentation, the coral was not counted as living. The same methodology was used to determine recruitment density from June plugs, which were settled at different larval densities.

2.7. Juvenile growth

Growth rate was calculated for corals that were alive at the conclusion of the experiment as a percent change in planar surface area (mm^2) over the entire experiment (135 d; approximately 5 mo). Growth measurements were collected from a random subset of 10 plugs from each treatment (n = 295 juveniles). The outline of every individual and aggregate coral alive at the December time point was traced using ImageJ software to determine the final surface area (SA_{final}). The aggregate or individual was then identified in the plug from the July time point and the initial surface area ($SA_{initial}$) of the same juvenile was determined using ImageJ software. Growth was then calculated for every juvenile using the formula:

$$\text{Growth} = \frac{SA_{final} - SA_{initial}}{SA_{initial}} \quad (1)$$

2.8. Data analysis

For all data analysis corals were grouped into 'juvenile type', either aggregate or individual, based on initial settlement patterns. Survival was examined as a binary response (dead or alive). Growth was determined using Eq. (1). First, 2-way analysis of variance (ANOVA) was used to test the effect of larval stocking density and time on the total number of settlers. An independent-samples *t*-test was used to compare total recruitment in the 1 and 4 wk conditioning treatments. A Wilcoxon signed-rank test analyzed survival in high and low flow conditions. As mortality in the low flow treatment was high, the effect of light and juvenile type on survivorship was analyzed within the high flow treatment with a quasibinomial general linearized model.

Juvenile growth was also analyzed within the high flow treatment. A 2-way ANOVA was used to examine effects of shade treatment and juvenile type on growth. To analyze the relationship between growth and survival, the average growth and survivorship for all treatment combinations was calculated and examined as a linear regression between survival and growth for aggregates and individuals. All analyses and visualizations were performed in R Statistical Programming (version 4.1.2) and RStudio (version 1.1.463) using the tidyverse, janitor, plotrix, lubridate, car, emmeans, and cowplot packages (Fox et al. 2007, Lenth et al. 2018, Wickham et al. 2019, Wilke et al. 2019, Lemon et al. 2021). For appropriate analyses, homogeneity of variance was tested with a Levene's test in the car package (Fox et al. 2007). Post-hoc analysis to determine pairwise significance was conducted in the emmeans package (Lenth et al. 2018).

3. RESULTS

3.1. Larval stocking density, plug conditioning, larval output

In July, a total of 2699 plugs had new recruits present, with an average of ~5.0 individuals and ~3.6 aggregate recruits per plug. The total number of recruits was significantly enhanced by higher larval stocking densities, the density of larvae supplied to settlement bins, at both 24 and 72 h time points (F = 28.6, $p < 0.001$; Fig. 1B). There was no significant effect of conditioning on the number of new recruits (F = 1.79, p = 0.32; Fig. 1A); however, recruitment was 25% higher on plugs with 4 wk of conditioning. Average recruitment at 24 h was 35% higher than at 72 h, although recruitment across time treatments was not significantly different (F = 3.65, p = 0.06; Fig. 1B). There was a positive relationship between the volume of embryos added to a rearing conical and the number of larvae produced (R^2 = 0.33, p = 0.053). The average number of fertilized embryos in 1 ml was found to be 13 931 across 110 samples,

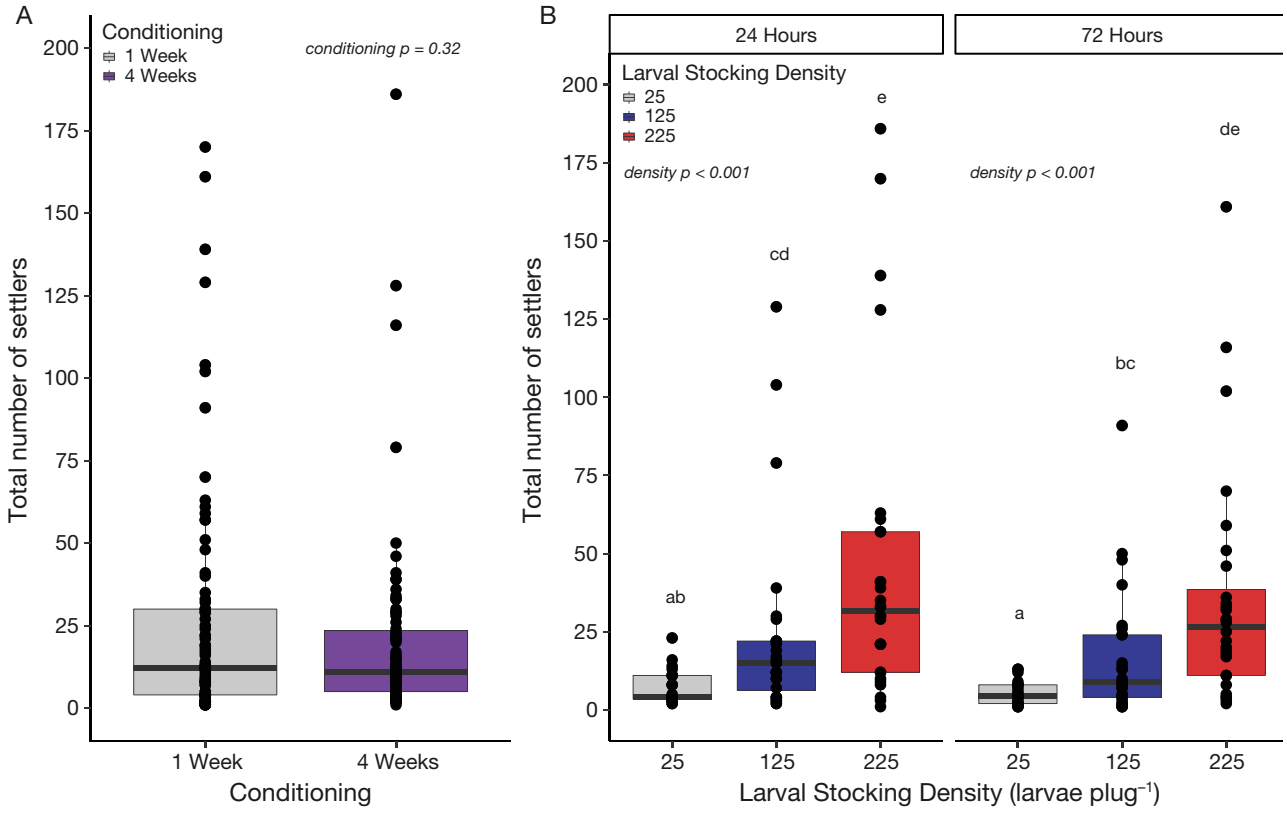

Fig. 1. (A) Conditioning (1 vs. 4 wk) exhibited no significant effect on the total number of settled recruits. (B) Recruitment was enhanced by the highest larval stocking density (differences between treatments indicated by letter groupings); time exhibited no significant effect on recruitment. Bar: median; box: interquartile range (IQR); whiskers: max./min. values within 1.5 × IQR above/below box; dots: individual plugs

meaning embryo stocking density ranged from ~69 655 (5 ml) to ~348 275 (25 ml) embryos per 15 l conical. After 5 d, moderate embryo volumes, 17.0 and 17.5 ml, produced the greatest yields of larvae for maximum outputs of 131 333 ± 1016 and 112 833 ± 895 larvae, respectively. These densities are equivalent to a starting point of ~15 embryos ml^{-1} and an end point of ~8 larvae ml^{-1}.

3.2. Juvenile survivorship

High flow conditions exhibited ~2.9 times better survival than low flow conditions across juvenile type and shade treatment (W = 4547, p < 0.001; Fig. 2B). These results strongly indicate that high flow environments are preferable for juvenile coral survivorship; therefore, all further analyses were conducted exclusively within the high flow treatments. Across all treatments, there was no significant effect of juvenile type (individual or aggregate) on overall survivorship (F = 0.042, p = 0.84; Fig. 2A). Across all shade and flow treatments, average individual survivorship was 18.3%, while average aggregate survivorship was 16.7%.

Light dramatically impacted survivorship in juvenile corals, with generally lowest survival in low shade and highest survival at intermediate light levels (p < 0.001; Fig. 3). Over time, individuals in the 3x light treatment survived ~3.4 times better than individuals in the 1x shade treatment (Table 1). Interestingly, individuals in the 2x shade treatment survived

Table 1. Juvenile survivorship across shade treatments (see Fig. 4B for PAR values) in a high flow environment. Survival was determined as a percentage of initial settlers

Type	Shade treatment	Survival (%)
Individual	1x	10.5
	2x	34.2
	3x	37.2
	3x to 1x	21.2
Aggregate	1x	12.9
	2x	38.6
	3x	27.3
	3x to 1x	27.7

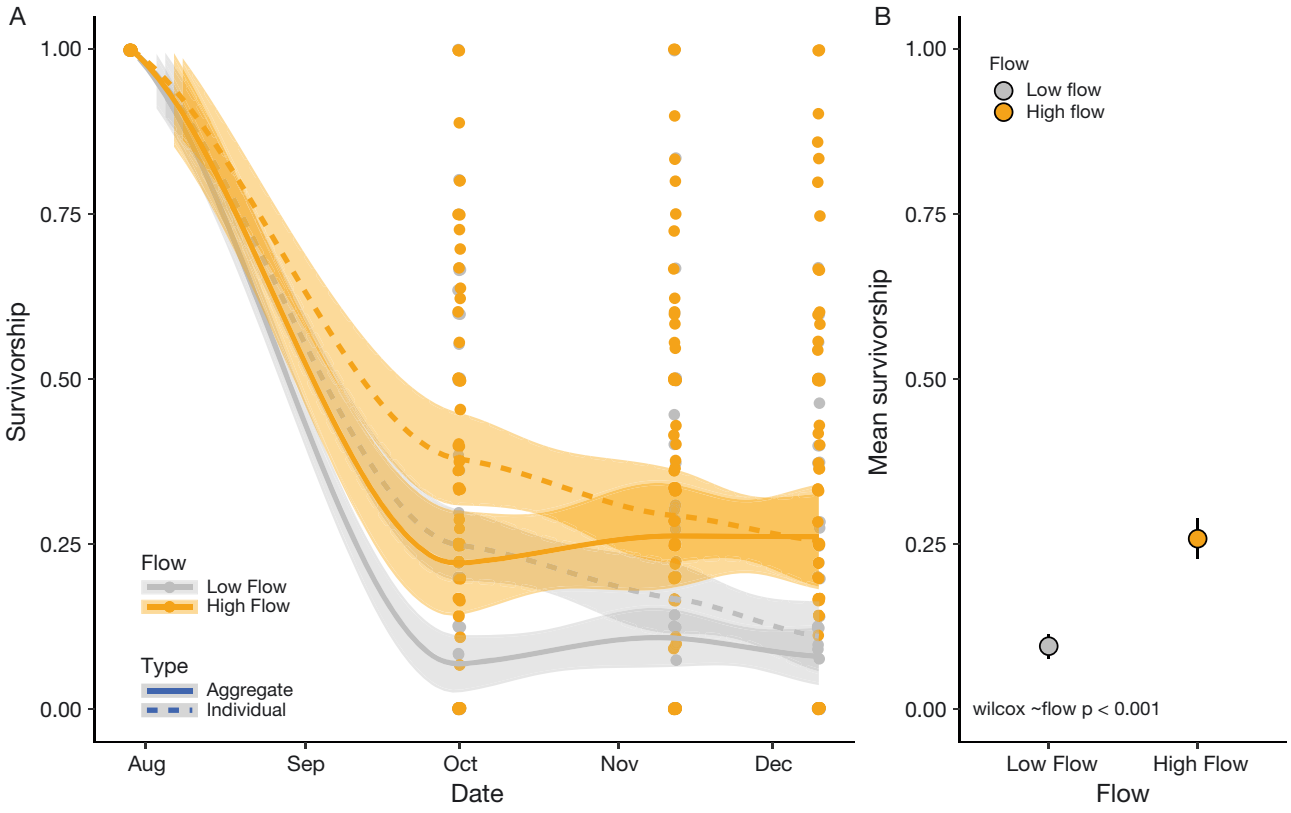

Fig. 2. (A) Proportion survivorship of individual and aggregate juvenile *Montipora capitata* in high and low flow treatments over time. There was no significant difference in overall survivorship between aggregate and individual juveniles. Points represent tracked aggregates and individuals in high and low flow treatments. (B) Across aggregates and individuals, survivorship was significantly higher in the high flow treatment. Error bars represent SD

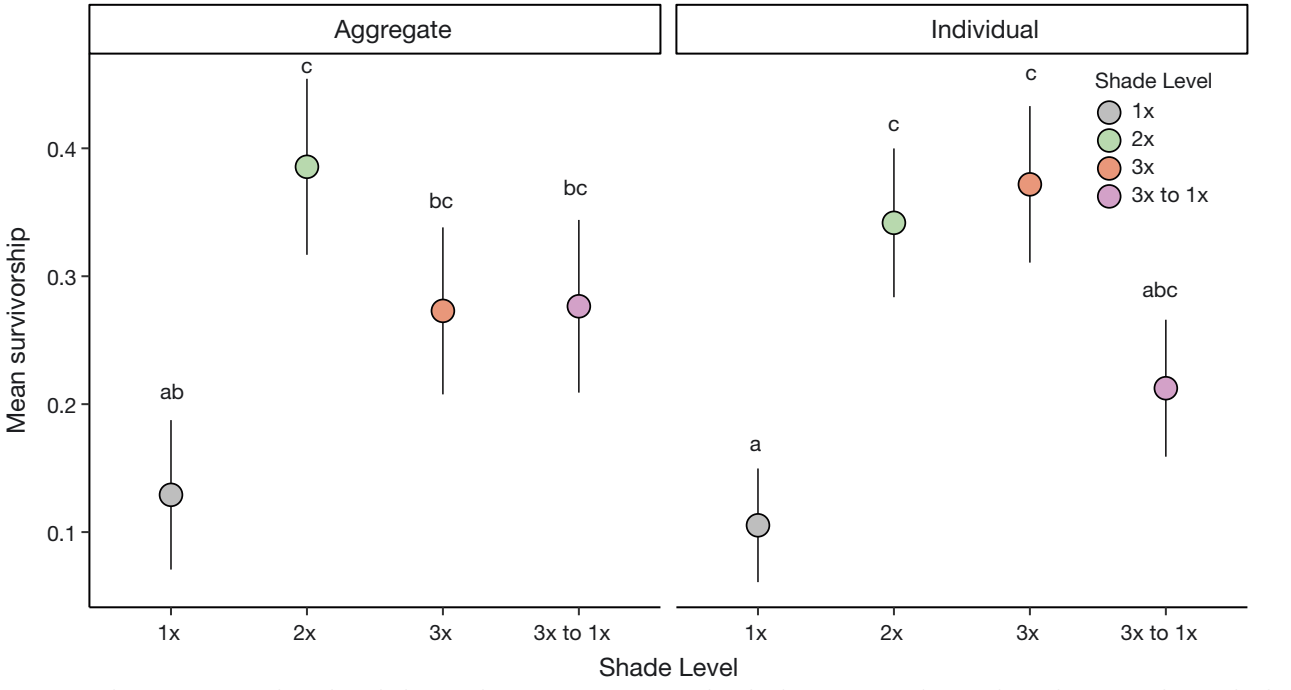

Fig. 3. End point survivorship of settled juvenile *Montipora capitata* by shade treatment. Survival was lowest in the 1x shade treatment in both aggregates and individuals (differences between treatments indicated by letter groupings). Error bars represent SD

~4.1 times better in the high flow environment when compared to the low flow conditions. Aggregate colonies in the 2x shade treatment exhibited the highest survival of all treatments, with 38.6% survivorship (Table 1). Aggregates in the high flow, 2x shade treatment exhibited ~4 times better survival than aggregates in the low flow, 2x shade treatment. In both aggregate colonies ($p > 0.08$) and individuals ($p > 0.07$), survivorship in the light acclimation treatment was not significantly different from that in static shade treatments.

3.3. Juvenile growth

Overall, individual corals grew significantly more than aggregate corals over the course of the experiment ($W = 7870$, $p < 0.001$; Fig. 4A). On average, individual corals grew 4.15 $\mu m^2\ d^{-1}$ and aggregate corals grew −2.67 $\mu m^2\ d^{-1}$, although aggregate colonies were ~2.3 times larger than individual corals at the end of the experiment. There was no significant effect of flow on either individual ($W = 1866$, $p = 0.29$) or aggregate growth ($W = 2300$, $p = 0.31$). However, indi-

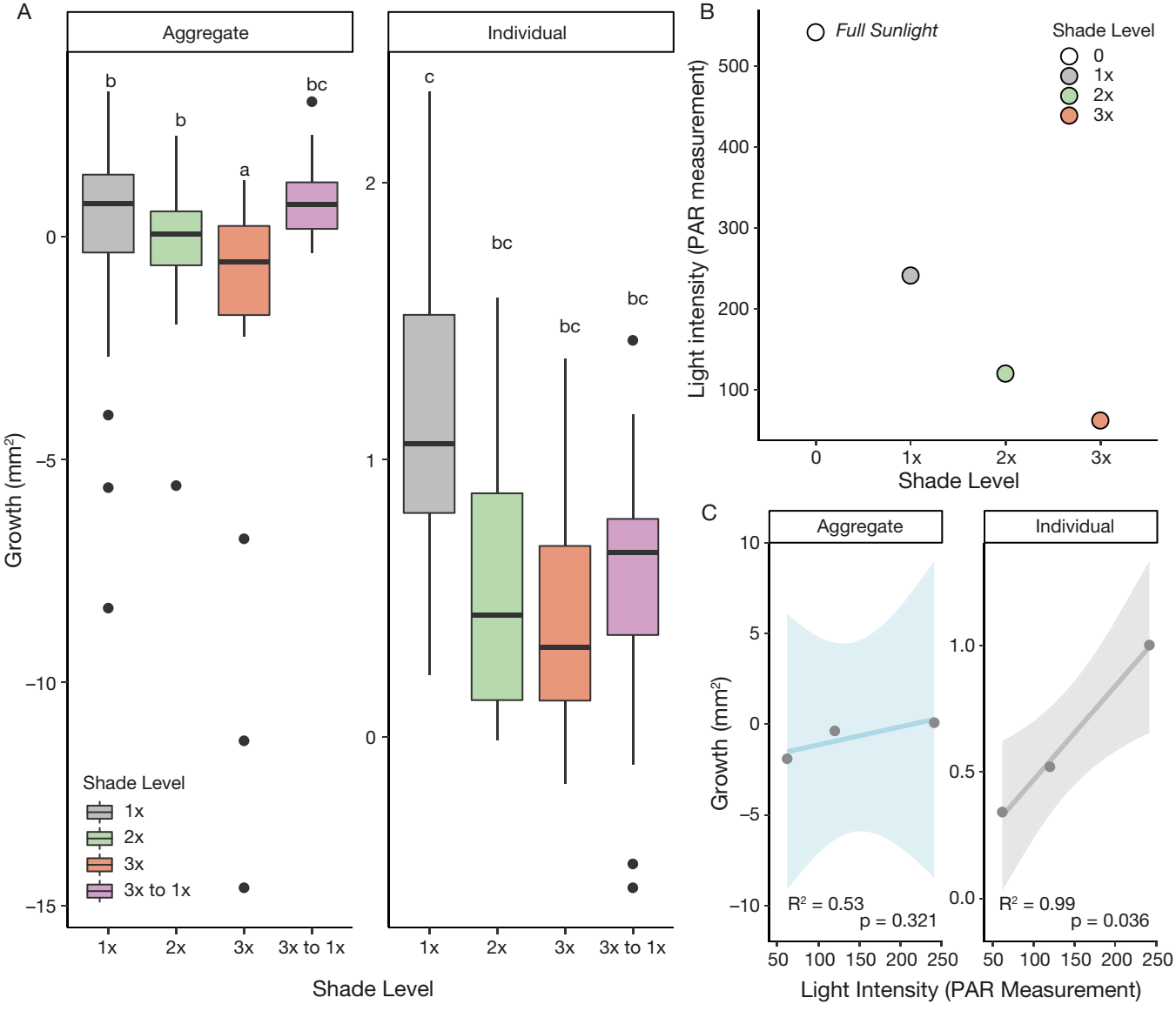

Fig. 4. (A) Shade level significantly impacted growth of individual and aggregate *Montipora capitata*. Individuals grew significantly more than aggregates over the course of the experiment (dots: outliers; other boxplot details as in Fig. 1; differences between treatments indicated by letter groupings). Note different *y*-axis scales. (B) Average light intensity across shade treatments. (C) Relationship between light intensity and growth in both aggregate and individual juveniles. Particularly in individuals, light intensity was strongly related to juvenile growth

viduals and aggregates grew 42% and 34% more in a high flow environment, respectively. Shade level significantly affected juvenile growth ($F = 12.21$, $p < 0.001$; Fig. 4A). On average, aggregates in the 3x to 1x shade treatment grew fastest, at 1.41 $\mu m^2\ d^{-1}$, across all shade treatments, while individuals in the 1x shade treatment grew ~1.6 times faster than those in any other shade treatment.

In full sun, and 1x, 2x, and 3x shade, PAR measurements were 542.18, 241.36, 120.14, and 62.08 PPFD, respectively (Fig. 4B). Overall light levels were highly predictive of growth in individuals, almost completely explaining the variance ($R^2 = 0.99$, $p = 0.04$; Fig. 4C). In aggregates, PAR measurements did not significantly predict growth, but did explain 53% of observed variance ($R^2 = 0.53$, $p = 0.32$; Fig. 4C).

3.4. Relationship between growth and survivorship

Across treatments, there was no relationship between survivorship and growth in aggregate ($R^2 = -0.17$, $p = 0.99$; Fig. 5) or individual corals ($R^2 = -0.02$, $p = 0.38$; Fig. 5).

4. DISCUSSION AND CONCLUSIONS

Upscaling is one of the primary challenges to current active restoration efforts which seek to recover reef ecosystem functions lost due to anthropogenic stressors (van Oppen et al. 2017, Craggs et al. 2019). A focus on increasing productivity and maximizing efficiency during the sexual propagation of corals is fundamental to improving overall yield and enabling the success of such interventions (Randall et al. 2020). However, despite the various benefits of using sexually produced coral propagules, few publications have detailed methods to optimally rear corals through such techniques (Guest et al. 2014, Pollock et al. 2017, Hancock et al. 2021). In this study, we were able to raise thousands of juvenile *Montipora capitata* from Kāneʻohe Bay, Oʻahu, produced by sexual reproduction in an *ex situ* facility. By examining the effects of different stocking densities, and shade, flow, and light acclimation treatments, this study highlights the benefits of defining optimal rearing techniques and grow-out conditions for sexually propagated corals. Importantly, our findings suggest that light acclimation is a husbandry tool which potentially mitigates traditional tradeoffs between growth and survivorship conditions. Continued development and improvement of light acclimation protocols may be key in improving the overall capacity of sexual reproduction pipelines.

Defining appropriate embryo and larval stocking densities is a significant component of overcoming the biological bottlenecks associated with invertebrate larval stages and increasing overall yield during sexual propagation (Capo et al. 2002, Liu et al. 2006, Abidin et al. 2019). The dynamic relationship between embryo stocking density and larval health/development has been defined for many invertebrate

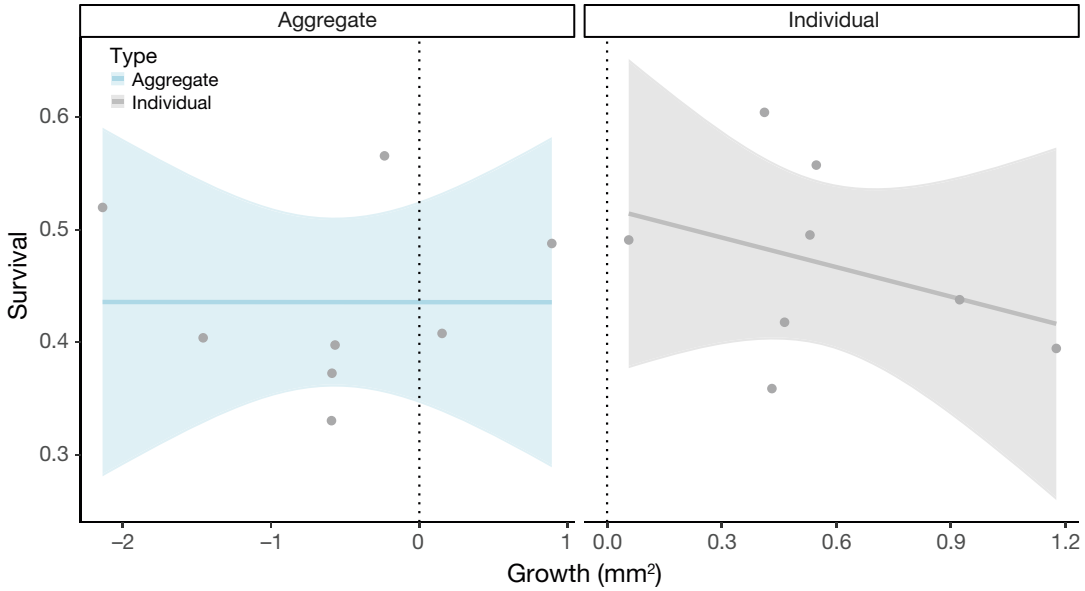

Fig. 5. Linear regression of average growth and survivorship across all treatments for both individuals and aggregates. Survival and growth were not significantly correlated in either juvenile type. Vertical dotted lines denote where juvenile growth is zero

organisms in an aquaculture setting (Asmani et al. 2017, Ren et al. 2018). Yet, optimal densities have not been quantified for most coral species, including *M. capitata*, despite the acute sensitivity of this phase of the coral life cycle (Edwards 2010, Pollock et al. 2017, Randall et al. 2020). An optimized embryo stocking density is one which limits overcrowding, disease spread, and density-related mortality, and thereby maximizes both larval output and survival (Edwards 2010).

Here, we found an optimal embryo stocking density of approximately 17 ml of fertilized embryos per 15 l conical, which exhibited a high larval output (~130 000 larvae) and substantial survivorship (~55%). In culture, many of the embryo densities investigated here experienced substantial declines in quality within 24 h of fertilization, resulting in strongly reduced larval yield. It is possible that damage to embryos and larvae triggered the release of toxic compounds, including montiporic acid, which are known to reduce fertilization success and damage healthy cells (Hagedorn et al. 2015). While the ecological function of such compounds remains unknown, the presence of these toxins in cultures can make rearing *M. capitata* embryos difficult, especially at high densities (Hagedorn et al. 2015). Anecdotally, we found that surviving *M. capitata* larvae were competent to settle as early as 96 h post-fertilization, although time to competency is species-specific and is known to be influenced by external factors such as temperature (Nozawa & Harrison 2002, Guest 2010). External conditions are also particularly influential in settlement processes (Babcock & Mundy 1996, Petersen et al. 2005, Strader et al. 2015). Specifically, the presence of a biofilm community and the conditioned substrate provide essential cues for larval settlement and metamorphosis (Heyward & Negri 1999, Tran & Hadfield 2011). We did not find a significant difference between recruitment on substrate that was conditioned for 1 wk when compared to substrate that was conditioned for 4 wk. This suggests that a biofilm which encourages settlement is established quickly, even in an *ex situ* tank environment, a valuable practical consideration for restoration practitioners. Consistent with previous studies, our findings indicated that settlement rate increased with larval supply (Doropoulos et al. 2017, Cameron & Harrison 2020). However, it has been shown that intraspecific competition may negatively affect long-term survival of densely settled recruits (Cameron & Harrison 2020). Further research is required to assess the long-term effects of larval stocking density on the survivorship of *M. capitata* post-settlement.

The effects of various coral husbandry regimes on post-settlement survival and growth of juvenile corals have been demonstrated by several previous analyses (Guest et al. 2014, Craggs et al. 2019, Hancock et al. 2021). These studies highlight the importance of tailoring *ex situ* environmental conditions and husbandry protocols to the targeted coral species and location (Forsman et al. 2012, Cooper et al. 2014, Hancock et al. 2021). High flow positively impacts the survivorship and growth of juvenile *M. capitata*, but only relative high flow (2 circulation pumps) and no flow (circulation pumps absent) regimes have been previously investigated, highlighting the need for further exploration (Hancock et al. 2021). Here, we tested a similar relatively high flow environment, consisting of 2 circulation pumps per raceway tank, and a low flow environment, consisting of 1 circulation pump per raceway tank. We found that the high flow environment significantly enhanced the survival of both aggregate and individual *M. capitata*. This finding importantly indicates that high flow is preferable to both a low flow environment (1 circulation pump) and the previously investigated 'no flow' environment (Hancock et al. 2021). High flow is known to benefit coral health through sediment removal, enabling particle capture and increasing the exchange rate between coral tissue and the environment (Jokiel 1978, Helmuth & Sebens 1993, Forsman et al. 2012, Jones et al. 2019). By removing the warm boundary layer that directly surrounds coral tissue, flow may also improve coral survivorship by mitigating light and temperature stress (Fabricius 2006). Here, our findings suggest that understanding such interactions between light and flow is essential to the optimization of post-settlement survival. Nonlinear interactions between light and flow makes understanding the additive or synergistic effects of these 2 environmental conditions essential to successful husbandry in an *ex situ* environment (Hoogenboom & Connolly 2009). Our survivorship trends, particularly those in the intermediate light treatment (2x), emphasize the positive interactive effects of flow and light, with increased flow enabling corals to survive in higher light intensities. Future work should continue to investigate and define the mechanistic relationship between these influential factors and fundamental metabolic processes in corals at different life history stages.

In addition to flow, this study clearly demonstrates the significant effects of different shade regimes on juvenile coral survival and growth. The fundamental relationship between light intensity and coral health has been well documented; however, there still

remain many key gaps in our understanding of how this abiotic factor can be manipulated *ex situ* to improve restoration efforts (Huston 1985, Putnam et al. 2017, Randall et al. 2020). Our results demonstrate that an intermediate shade environment (77.8% reduction from full sunlight) is beneficial for the survival of both individual and aggregate corals for the first 5 mo post-settlement. An environment with minimal shading (55.5% reduction from full sunlight) was not found to be favorable for survival, and resulted in the lowest survivorship across juvenile type. Interestingly, we also found that 88.5% reduction in light (3x shade cloth) can decrease survivorship when compared to intermediate treatments (2x). This may be due to competitive interactions within an aggregate colony, where newly settled recruits grow on top of each other potentially shading parts of the colony and thereby increasing the light requirement relative to individual settlers. The intermediate (2x) and high (3x) shade treatments may have been especially beneficial to the survival of juvenile corals in this time frame, limiting algal presence and competition (Harriott 1983). Other studies have addressed these competitive benthic algae interactions through the addition of herbivores such as sea urchins (Craggs et al. 2019). It is likely that optimal conditions will combine and balance the interactions between herbivory and shade treatment, representing another potentially beneficial coral husbandry tool which future research should explore. While intermediate to high shade conditions promoted survival of juvenile corals, our data indicates opposite trends for juvenile growth, with minimal shade maximizing growth. Individuals were found to have a higher growth rate than aggregates; however, aggregates were larger at the conclusion of the experiment. Both juvenile types grew most in the least shaded environment (1x). Light intensity is known to have a significant impact on the growth and health of corals which contain symbiotic zooxanthellae (Muscatine & Cernichiari 1969, Kuanui et al. 2020). Zooxanthellae utilize light in the process of photosynthesis to produce oxygen and organic sugars. When excess amounts of these products are generated they are shifted to the coral host for growth and other functions (Muscatine & Cernichiari 1969). Our results clearly reflect these biological processes, by providing corals with high light availability in the lowest shade treatment (1x) we are enabling photosynthetic capabilities and production of organic compounds and thereby enhancing overall growth. However, in the context of restoration, it is imperative to consider the tradeoffs between shade conditions which maximize growth and those which maximize survival, and to apply tools which can promote both metrics.

While the impact of light on coral biology has been studied more extensively than many other environmental factors, we still lack a comprehensive understanding of how light impacts corals at different ages and life stages (Kuanui et al. 2020). Previous work has demonstrated that, within 1 mo post-settlement, juvenile *M. capitata* survive better in low light availability, while after the first month, juvenile corals survive better in higher light availability (Hancock et al. 2021). Studies have also shown that maximizing the growth of corals of different ages requires different light intensities, suggesting that light may be manipulated in an *ex situ* environment over time to optimize growth and survival (Kuanui et al. 2020). We attempted to accommodate these changing optimal conditions by moving juvenile corals into a higher light environment at 36 d post-settlement, based on our previous results. Light acclimation exhibited promising trends for aggregate juveniles and improved upon survival in the low (1x) shade treatment. This indicates that, by manipulating available light throughout the aquaculture period, we can better align abiotic conditions with the changing biological needs of juvenile corals to improve survivorship. While aggregate survival was better than in both high and low shade treatments, light acclimation was not as effective as the static intermediate (2x) shade environment. This trend in survivorship likely reflects the stress experienced by corals during the light acclimation process. The abrupt transition from a low light environment to a high light environment may have caused stress or even photobleaching in some of the light-acclimated corals. Presumably, stress from the transition itself or excessive light intensity in the minimal shade treatment caused mortality in some corals and reduced survivorship relative to the most effective static shade treatment. It may be possible that, by gradually increasing light availability, such stress can be mitigated and survivorship be further optimized through this technique. While the light acclimation treatment did not maximize survivorship, it did maximize aggregate growth, further demonstrating the potential benefits of this husbandry tool. The dynamic changing physiological requirements during coral early life history stages likely drives fluctuations in coral–symbiont associations (Little et al. 2004). In corals with horizontal acquisition of symbionts during early life history stages, light acclimation is likely even more influential, especially if it impacts preference for symbiont type (Little et al. 2004). Aligning dynamic shifts in

symbiont associations with complementary light intensities holds important potential for maximizing post-settlement growth in sexual propagation. In individuals, survival in the light acclimation treatment was only improved over the low shade (1x) environment, while growth was improved over both the intermediate (2x) and high shade (3x) treatments. These trends, while less promising than those exhibited by aggregates, still indicate light acclimation achieved some improvements over static light treatments. Potentially, chimeric aggregates are more biologically suited to survive the environmental stress associated with light acclimation, explaining these differences in performance (Rinkevich 2019). Further refinement in the application of light acclimation protocols is needed to maximize the potential benefits of this promising coral husbandry tool.

Our results show that high flow and static intermediate shade (2x) treatments achieved the highest survivorship for aggregate corals, while individual survival was maximized in heavy shading (3x). In contrast, the highest individual growth rates were achieved by the static low shade (1x) treatment, and highest aggregate growth rates achieved by the light acclimation treatment. Simple techniques such as shading or increasing circulation represent powerful tools for coral practitioners and restoration managers who aim to rear sexually propagated juveniles for restoration purposes. Fine-tuning these practices through the addition of more complex coral husbandry tools, such as light acclimation, demonstrates the immense potential for optimizing and scaling up current restoration efforts. Importantly, our study does not reveal an ideal set of abiotic conditions that simultaneously maximizes the growth and survivorship of juveniles. This is a critical piece of knowledge for restoration management and highlights the importance of designing restoration efforts for the goals of a specific project. Overall, this study provides important practical and logistical information about the abiotic conditions and husbandry practices that best produce juvenile *M. capitata* for restoration purposes. The continued development and improvement of these protocols will enable current practices to be expanded to ecologically meaningful scales and allow for the incorporation of other climate-related techniques like selective breeding and symbiont manipulation (van Oppen et al. 2017, Buerger et al. 2020). In the face of global climate change, the combination of such efforts is an essential step in increasing the efficiency of active restoration practices in order to significantly contribute to coral conservation.

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