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Coral husbandry for ocean futures: leveraging abiotic factors to increase survivorship, growth, and resilience in juvenile *Montipora capitata*

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ABSTRACT: Reef restoration via direct outplanting of sexually propagated juvenile corals is a key strategy in preserving coral reef ecosystem function in the face of global and local stressors (e.g. ocean warming). To advance our capacity to scale and maximize the efficiency of restoration initiatives, we examined how abiotic conditions (i.e. larval rearing temperature, substrate condition, light intensity, and flow rate) interact to enhance post-settlement survival and growth of sexually propagated juvenile *Montipora capitata*. Larvae were reared at 3 temperatures (high: 28.9°C, ambient: 27.2°C, low: 24.5°C) for 72 h during larval development, and were subsequently settled on aragonite plugs conditioned in seawater (1 or 10 wk) and raised in different light and flow regimes. These juvenile corals underwent a natural bleaching event in Kāne'ohe Bay, O'ahu, Hawai'i (USA), in summer 2019, allowing us to opportunistically measure bleaching response in addition to survivorship and growth. This study demonstrates how leveraging light and flow can increase the survivorship and growth of juvenile *M. capitata*. In contrast, larval preconditioning and substrate conditioning had little overall effect on survivorship, growth, or bleaching response. Importantly, there was no optimal combination of abiotic conditions that maximized survival and growth in addition to bleaching tolerances. This study highlights the ability to tailor sexual reproduction for specific restoration goals by addressing knowledge gaps and incorporating practices that could improve resilience in propagated stocks.

KEY WORDS: *Montipora capitata* · Kāne'ohe Bay · Coral husbandry · Coral spawning · Bleaching

1. INTRODUCTION

Coral reefs around the world are subject to a combination of natural and anthropogenic stressors that have caused ecosystem-scale shifts and declines in structure and function (Hughes et al. 2018, Sully et al. 2019). Among these stressors, coral bleaching due to extreme temperature events is the most severe, leading to mass mortality at increasingly frequent intervals (Hughes et al. 2017). This problem will only become more extreme, as coral bleaching is projected to become a near yearly occurrence on most of the world's reefs by mid-century (Hughes et al. 2018, Sully et al. 2019).

Even under ideal conditions, coral reef recovery after stress can take decades (Gilmour et al. 2013, Hughes et al. 2018), so intervention in the form of active restoration has become an increasingly common strategy for mitigation (National Academies of Sciences, Engineering, and Medicine 2019). Most restoration work in the recent past has focused on asexual propagation of adult colonies maintained in

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a nursery, which produces coral fragments that are outplanted onto degraded reefs (National Academies of Sciences, Engineering, and Medicine 2019); however, sexual reproduction can also be an important tool that aids in recovery and maintains genetic diversity (Guest et al. 2014). The use of sexual propagules settled *ex situ* as material for subsequent outplanting can minimize or remove the *in situ* nursery propagation phase of the 'coral gardening' approach, but adds logistical complexity (e.g. fertilization, gamete collection). Sexual propagation for restoration has been attempted infrequently relative to asexual propagation (Omori et al. 2008, Nakamura et al. 2011, Chamberland et al. 2017), but is a growing area of research (Randall et al. 2020).

The use of sexual propagules increases the scalability and increases genetic diversity (Pollock et al. 2017), which is paramount for the success of future restoration projects (Baums et al. 2019). This method allows for the generation of orders of magnitude more propagules (compared to hundreds in asexual propagation) while simultaneously allowing the integration of targeted selection (i.e. screening with a stressor of interest), selective breeding, deliberate symbiont infection, or preconditioning (van Oppen et al. 2015, Buerger et al. 2020, Quigley et al. 2020). These are key strategies to dramatically increase coral restoration efficacy under climate change (Van Oppen et al. 2017).

Rearing of sexually produced coral offspring presents significant logistical and biological challenges, particularly survival bottlenecks during settlement, and post-settlement survivorship in the lab and *in situ* (Randall et al. 2020). Importantly, sexual recruits can take years to reach reproductive maturity, before which they contribute to the ecological structure and function of the reef but have a limited role in adaptive change. Newly settled corals are vulnerable to benthic competition (Box & Mumby 2007), predation (Wilson & Harrison 2005, Rotjan & Lewis 2008, Trapon et al. 2013), and sedimentation (Leong et al. 2018), and therefore optimization of abiotic influences (e.g. to reduce algal competition) can have strong impacts on growth and survival. Previous work has focused largely on substrate dynamics such as crustose coralline algae (CCA) communities (Harrington et al. 2004, Ritson-Williams et al. 2010) and algal overgrowth (Tebben et al. 2014). Optimization of post-settlement survival presents an opportunity to scale success. Advances in our understanding of fertilization, larval rearing, settlement strategies, and substrate influence have improved the viability of raising sexually produced corals and have created opportunities to tailor additional interventions (Guest 2010, Pollock et al. 2017, Doropoulos et al. 2019), but scaling this technique to an extent useful for restoration typically requires substantial prior knowledge that is species and location specific. For many coral species, there is a limited understanding of reproductive biology and knowledge on husbandry practices, especially post settlement.

Given the emerging importance of sexual reproduction for restoration, identifying factors that promote coral survivorship and growth for key reef-building species (or rare threatened species) can fill important knowledge gaps. Here, we examined the impact of 4 ecologically important abiotic conditions on post-settlement survivorship and growth of the broadcast spawning coral *Montipora capitata* in Kāneʻohe Bay, Oʻahu, Hawaiʻi (USA). During the summer of 2019, Kāneʻohe Bay experienced unusually warm temperatures and mild bleaching, so we opportunistically tracked bleaching response. We used over 12 000 juvenile *M. capitata* to test and optimize the effects of (1) substrate conditioning, (2) light intensity, (3) flow rate, and (4) larval rearing temperature (see Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m657p123_supp.pdf).

2. MATERIALS AND METHODS

2.1. Spawning, collection, fertilization, and larval rearing

Montipora capitata is a simultaneous hermaphrodite broadcast spawner that releases positively buoyant egg–sperm bundles in mass spawning events around the summer new moons in Hawaiʻi (Padilla-Gamiño & Gates 2012). *M. capitata* is also one of relatively few broadcast-spawning species that provision eggs with symbionts (i.e. vertical transmission; Padilla-Gamiño et al. 2012). Gamete bundles were collected near Reef 11 (21° 26′ 56″ N, 157° 47′ 45″ W) in Kāneʻohe Bay, Oʻahu, during the mass spawning event on 31 June and 1 July 2019. Egg–sperm bundles were released at approximately 21:00 h and were gathered from the ocean surface using 153 µm mesh nets until approximately 21:15 h. Bundles were gently rinsed from nets into large collection containers (19 l) of 1 µm filtered seawater. We immediately aliquoted 5 ml of intact egg–sperm bundles into 35 ml of 1 µm filtered seawater and allowed fertilization to occur for 90 min before removing concentrated sperm supernatant. Approximately 5 ml of fertilized

embryos were added per liter of filtered seawater in larval conicals (n = 58; Fig. S1). Larval rearing conicals utilized flow-through temperature-controlled seawater filtered at 1 µm that drained through a centralized banjo filter (153 µm mesh). For the first 24 h post fertilization, water input was <1 l h^{-1} to prevent physical shearing of early-stage embryos. At 24 h post fertilization, water flow was increased (~2 l h^{-1}) to minimize larvae settling on the conical walls. Additional detail can be found in Text S1.

2.2. Larval rearing temperature treatments

Embryos were reared for 3 d at ambient temperatures before temperature treatments commenced (ramping to treatment conditions over ~6 h; high: 28.9 ± 0.05°C, ambient: 27.2 ± 0.02°C, low: 24.5 ± 0.03°C, mean ± SE; Fig. S2). Larval cultures (high: n = 21, ambient: n = 29, low: n = 8) were maintained under these treatments for 72 h before returning to ambient (~6 h) immediately prior to introduction of settlement substrate. On the second day of treatments, temperatures fluctuated during a seawater supply change affecting all of the Hawai'i Institute of Marine Biology.

2.3. Plug conditioning and larval settlement

In preparation for larval settlement, aragonite plugs (2.85 cm^2 top surface) were conditioned for either 10 wk or 1 wk in flow-through sand-filtered seawater under natural sunlight. Conditioning produced a biofilm and moderate CCA coverage in the 10 wk treatment and a biofilm in the 1 wk treatment. One week after fertilization (at the conclusion of larval temperature treatments), larvae were allowed to settle on aragonite plugs in chambers (~15 cm wide × 30 cm long with plugs in 2 cm water, n = 24) with mesh bottoms (153 µm). Chambers were partially submerged in flow-through raceways to maintain larval concentrations and ensure continuous water exchange through the mesh bottom, which was elevated ~10 cm from the tank bottom. See Text S1 for additional details.

Each settlement chamber contained 83 upside-down aragonite plugs, half of which were from each substrate conditioning treatment (1 and 10 wk). Larvae were allowed to settle for 3 d in settlement chambers before plugs with newly settled juvenile recruits were removed and transferred into grow-out treatments. See Text S1 for additional details.

2.4. Post-settlement treatment conditions

Newly settled juvenile corals were raised in a fully crossed design manipulating (1) prior larval rearing temperature, (2) substrate condition, (3) light intensity, and (4) flow rate (Fig. S1). In total, 12 183 settled juveniles, including at least 201 from each fully crossed treatment combination (initial n = 201–1358 per treatment), were reared for 5 mo in outdoor flow-through seawater raceway tanks (n = 2 total raceways). Raceways were siphoned monthly to remove accumulated sediment. We did not clean individual plugs or deliberately leverage microherbivory, which can be important for coral husbandry (Craggs et al. 2019). Twice per week, 3 g of Reef Chili (commercial coral food, Bulk Reef Supply) was mixed with seawater and added to each tank for the duration of the experiment. Plugs were repositioned within treatments at each sampling timepoint (see Section 2.7). Tank temperatures closely matched those in Kāne'ohe Bay, including elevated temperatures (above mean monthly max [MMM]) from July to October and subsequent bleaching (Fig. S3).

2.5. Flow rate

An adjustable manifold (powered by 2 Danner Manufacturing magnetic drive pumps) created a high-flow environment in one raceway, and the absence of circulation pumps created a low-flow environment in the other (n = 1). Each 196 l raceway received equal seawater input (6 l seawater min^{-1}, turnover time ~0.5 h), but the high-flow tank had the equivalent of ~5300 l h^{-1} additional circulation.

2.6. Light intensity

Light levels were modified in half of each raceway (n = 2) using commercially available shade cloth to create relative high- and low-light environments (Fig. S4). Light loggers (Onset Pendants) in each treatment failed during the study, so light data were captured over a 24 h period at the end of the experiment for a representative day using replicate (n = 2) loggers in each light treatment.

2.7. Juvenile responses

To assess treatment effects on coral survivorship, growth, and bleaching susceptibility, plugs (N = 1687)

were photographed (AM 1000 MU Scope camera) immediately after settlement and at 9 subsequent timepoints (6, 13, 20, 27, 34, 63, 91, 119, 148 d). Juveniles were classified as individuals or aggregates (colony type) at the initial timepoint for downstream analysis, with aggregates defined as the clustered settlement of 2 or more juveniles in physical contact.

2.7.1. Survivorship

We tracked survivorship at each timepoint for all juveniles on n = 1687 plugs. Survivorship was determined by examining photographs of plugs and recording a juvenile as being 'alive' if a distinct coral-lite structure was present with tissue pigmentation that was distinguishable from the substrate. Juveniles were recorded as 'dead' if tissue pigmentation was not present, and corallites appeared eroded or overgrown with turf algae or CCA.

2.7.2. Growth

We calculated growth for juveniles that were alive at the conclusion of the experiment as the percent change in planar surface area (SA, mm^2) over the entire experiment (148 d). Growth measurements were calculated by tracing the outline of a juvenile coral at the beginning and conclusion, and growth was corrected for initial size $\left(\frac{SA_{final} - SA_{initial}}{SA_{initial}}\right)$. Growth measurements were collected from all corals on 15 randomly selected plugs from each treatment (n = 608 juveniles). Measurements were conducted in ImageJ (version 1.51).

2.7.3. Bleaching

During the experiment, a bleaching event occurred in Kāneʻohe Bay, resulting in temperatures above the bleaching threshold (MMM + 1°C) within the experimental tank system (Fig. S3). Bleaching susceptibility was quantified throughout the experiment using photographs described above. A juvenile was classified with a binary response either as 'bleached' if tissue bleaching was apparent and tissue integrity was preserved (i.e. not eroded calices). Unbleached juveniles were those that did not exhibit tissue paling. We calculated degree heating weeks (DHW) as the time spent above MMM + 1°C (Wyatt et al. 2020) (27.5 + 1°C; calculated for 2008–2012 from NOAA National Data Buoy Center Station MOKH1; https://www.ndbc.noaa.gov/station_page.php?station=mokh1).

2.8. Data analysis

The effects of larval rearing temperature, substrate conditioning, flow rate, light intensity, and colony type on juvenile coral response (survival, growth, bleaching) were analyzed with linear mixed effect models in the 'lme4' package (Bates et al. 2014) in R Statistical Programming (version 4.0.2) and RStudio (v1.2.5019; R Core Team 2019). Cohen's *d* effect sizes for treatment effects of variables of interest were calculated using the packages 'effsize' (Torchiano 2020) and 'rstatix' (https://CRAN.R-project.org/package=rstatix) in R.

For all response metrics, corals that fused with neighboring colonies were removed from analyses, with 'colony type' indicating those that were either individual or aggregate at the start of the experiment. Juvenile coral survivorship was analyzed as a binary response (alive or dead) for each individual. First, survivorship was analyzed with time and light intensity as fixed effects and plug number as a random intercept. As mortality was high in the low-light treatment, we then analyzed survivorship within the high-light treatment with a binomial mixed effects model with larval rearing temperature, flow rate, substrate conditioning, and colony type as fixed effects. Plug number was included as a random intercept to account for repeated measures. Significance tests were conducted using Type II ANOVA tests in the 'lmerTest' package (Kuznetsova et al. 2017). Overdispersion was examined in the 'blmeco' package (Korner-Nievergelt et al. 2015).

Juvenile coral bleaching was measured on individuals over the course of the experiment as a binary response (bleached or unbleached). Bleaching was analyzed with a binomial mixed effects model with larval rearing temperature, flow rate, substrate conditioning, and colony type as fixed effects. Plug number and time (days) were included as random intercepts. Bleaching was only analyzed for juveniles in the high-light treatment, as there was complete mortality in the low-light treatment.

Juvenile coral percent growth and final size were analyzed with larval rearing temperature, flow rate, substrate conditioning, and colony type as fixed effects. Growth was only analyzed in the high-light treatment due to high mortality in the low-light treatment. Plug number was included as a random intercept. Percent growth (square root) and final size (1/10

exponential) were transformed to meet assumptions of analysis. Normality of residuals was examined with quantile–quantile plots, and homogeneity of variance was tested with Levene's tests in the 'car' package (Fox et al. 2012). Due to violation in homogeneity of variance, a White heteroscedasticity-corrected coefficient covariance matrix adjustment was applied for both analyses of percent growth and final size. To analyze the relationship between growth and survivorship, we calculated the average growth and survivorship rate for each treatment combination and examined Spearman's correlations between survivorship and growth for (1) aggregates and (2) individuals.

For all mixed effect model analyses, significance was tested using Type II ANOVA tests in the 'lmerTest' package (Kuznetsova et al. 2017). Overdispersion in binomial models was assessed using the 'blmeco' package (Korner-Nievergelt et al. 2015).

3. RESULTS

3.1. Physical conditions

Tanks closely tracked the temperature profiles of Kāneʻohe Bay, averaging 0.43°C warmer throughout the experiment (Fig. S3). Low-light treatments had 23% of the daily light dose (integral of lux) of high-light treatments (Fig. S4A). Peak light intensity was 15% higher in the low-flow tank; however, the daily light integral was only 2.9% higher in the low-flow tank (Fig. S4B).

3.2. Juvenile survivorship

There was a large significant effect ($d = -0.91$) of light availability on juvenile survival over the course of the experiment ($p < 0.01$; Fig. 1, Table S1). Survival was higher in the low-light treatment up until 35 d post-settlement (post hoc $p < 0.01$), after which point survival was instead higher in the high-light treatment (post hoc $p < 0.01$; Fig. 1; Table S2). Mean ± SE juvenile survivorship at the end of the experiment was significantly higher in the high-light treatment (34 ± 1%) than in the low-light treatment (1 ± 0%; post hoc $p < 0.01$).

Due to high mortality in the low-light treatment (Fig. 1), we further analyzed juvenile survival, bleaching, and growth within the high-light treatment. Survival in the high-light treatment was dependent on colony type, with higher survivorship in aggregate colonies than individuals ($p < 0.01$; Fig. 2A; Table S3). Further, survival was increased with high flow ($p < 0.01$; Fig. 2B; Table S4). High-flow conditions were more favorable for individual colonies as compared to aggregate

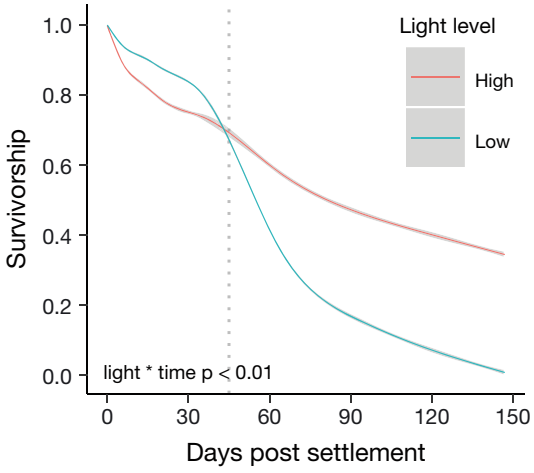

Fig. 1. Percent survivorship of *Montipora capitata* juveniles in high-light and low-light treatments over time. Survivorship was significantly higher in low-light treatments during the first 35 d post settlement. After 64 d, survivorship was significantly higher in the high-light treatment. Vertical dotted line represents time of change in relative survivorship between light treatments; shading represents 95% confidence interval

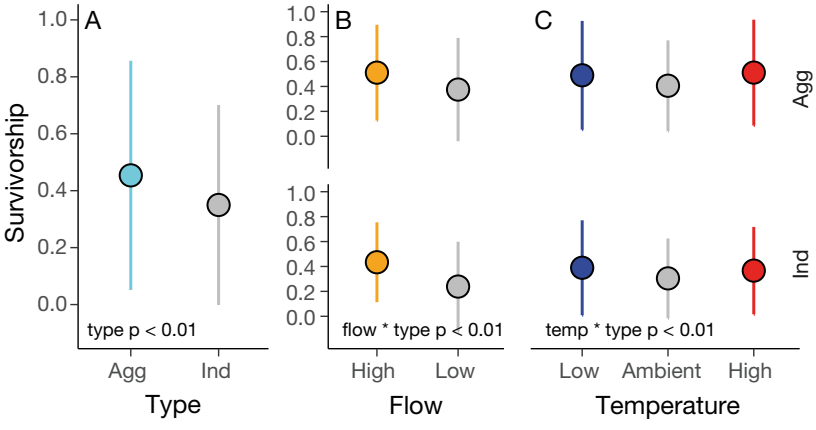

Fig. 2. End-point survivorship of settled *Montipora capitata* juveniles by light treatment, substrate conditioning, colony type (agg: aggregates; ind: individuals), and larval rearing temperature. (A) Survivorship was significantly higher in aggregate corals experiment wide. (B) There was a significant interaction of flow rate and colony type on survivorship, but high-flow treatments had higher survivorship overall. (C) There was a significant interaction between larval rearing temperature (low: 24.5°C, ambient: 27.2°C, high: 28.9°C) and colony type, although the effect sizes were small (Table S1). Error bars represent SD

colonies ($p < 0.01$; Fig. 2B). Larval rearing temperature had a small ($d = -0.02$), but significant, effect on juvenile survival ($p < 0.01$; Fig. 2C). Both aggregate and individual colonies had higher survival after larval exposure to high and low temperature treatments as compared to ambient (Fig. 2C).

Plug conditioning, colony type, and water flow created complex interactive effects on juvenile survival ($p < 0.01$; Table S4). For both aggregate and individual colonies, survival was higher on 10 wk conditioned plugs in a high-flow environment, but survival on these conditioned plugs was lower in a low-flow environment as compared to 1 wk conditioned plugs (Fig. 3; Table S3).

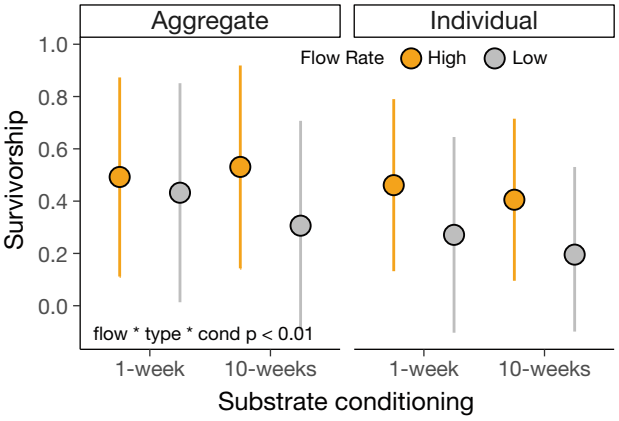

Fig. 3. Interaction of substrate conditioning, flow rate, and colony type on survivorship of settled *Montipora capitata* juveniles. There was a significant interaction between flow rate, substrate conditioning, and colony type on settled juvenile survivorship, with higher survivorship in aggregates and high-flow treatments and a diminished difference between flow rates on unconditioned aggregate plugs. Error bars represent SD

3.3. Juvenile bleaching

Corals in this experiment accumulated 5.79 DHW, and peak bleaching occurred during the first week of August (Fig. S3). Across all groups, approximately 10% of corals exhibited bleaching (Table S5). Aggregate colonies exhibited less bleaching (3%) than individual colonies (7%) ($p < 0.01$; Fig. 4A; Table S6). Juvenile corals exposed to high flow also had significantly decreased bleaching than those in low-flow conditions ($p < 0.01$; Fig. 4B).

Juveniles that were exposed to elevated temperature as larvae were more susceptible to bleaching compared to those exposed to ambient larval temperatures ($p < 0.01$; Fig. 4C). Further, the influence of larval thermal exposure was dependent on colony type, with different patterns in response to larval temperature differing between aggregate and individual colonies ($p < 0.01$; Fig. 4C).

There was also a significant effect of substrate conditioning, with elevated bleaching susceptibility for

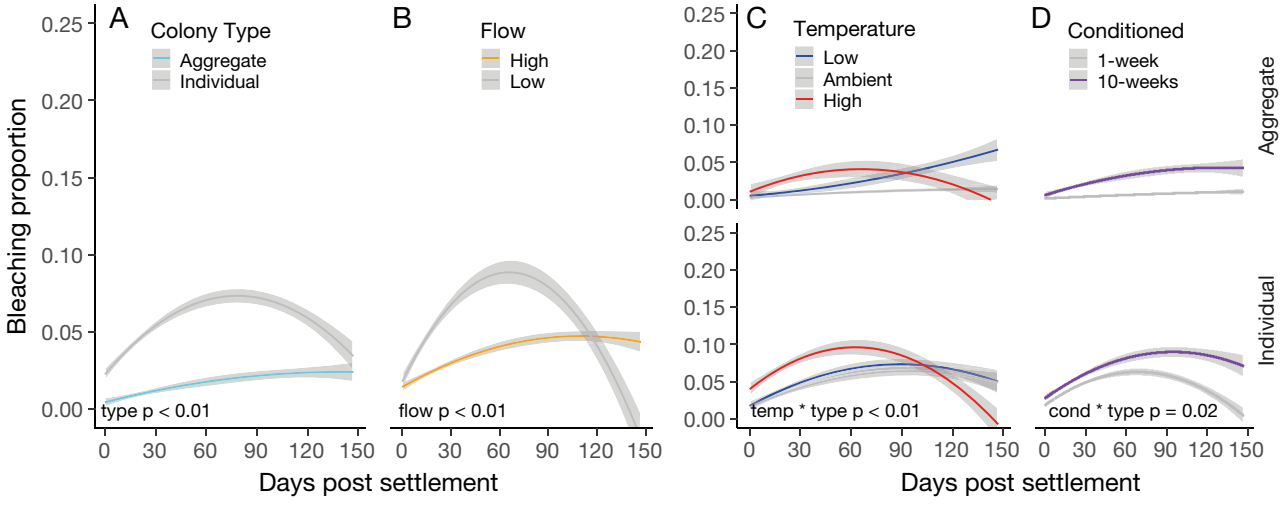

Fig. 4. Bleaching and recovery of settled juvenile *Montipora capitata* during a mild bleaching event (July–December 2019) in Kāneʻohe Bay and experimental tanks receiving ambient seawater. Bleaching rate was significantly lower (A) in aggregates than in individual settlers and (B) in high-flow treatments than in low-flow treatments. (C) The interaction of larval rearing temperature and colony type was significant, but effect sizes and overall bleaching rate were low. (D) The interaction of substrate conditioning and colony type was significant, but 1 wk substrate conditioned plugs had lower bleaching than 10 wk substrate conditioned plugs in both treatments. See Fig. S3 for long-term temperature profile and how sampling timepoints overlap temperature dynamics. Shading represents 95% confidence interval

juveniles settled on 10 wk conditioned plugs, as compared to plugs conditioned for only 1 wk ($p < 0.01$; Fig. 4D). Juvenile susceptibility to bleaching was driven by interactions between abiotic and biotic factors in this experiment, highlighting the complex nature of coral bleaching ($p < 0.05$; Table S6).

3.4. Juvenile growth

Overall, juvenile corals grew 5 ± 2% (mean ± SE) over the duration of the experiment (Table S7). Aggregates had a slower rate of growth than individual corals ($p < 0.01$; Table S8; Fig. 5A) and many had negative growth. Individual juveniles grew more quickly (size-specific growth rate), but aggregate colonies were 2.5 times larger at the end of the experiment ($p < 0.01$; Tables S9 & S10; Fig. 5B). Growth rates were higher with increased flow for both aggregates and individuals ($p < 0.01$; Table S8; Fig. 6).

3.5. Relationship between survivorship and growth

Survivorship and growth were not related in either aggregate ($\rho = -0.09$, $p = 0.78$) or individual ($\rho = 0.37$, $p = 0.23$) *Montipora capitata* corals when averaged for each treatment group (Fig. S5).

4. DISCUSSION

Identifying post-settlement rearing conditions that maximize survivorship and growth of juvenile corals is an essential step in the development of sexual reproduction as a tool for reef restoration (Craggs et al. 2019, Randall et al. 2020). Increasing our understanding of the factors that support juvenile success through early life-history bottlenecks can reduce current limitations to restoration and allow climate-focused strategies such as thermal conditioning or selective breeding to be integrated with production techniques. We reared and tracked more than 12 000 preconditioned juvenile *Montipora capitata* for 5 mo through a natural bleaching event in Kāneʻohe Bay, Oʻahu, in an *ex situ* facility. Testing multiple factors simultaneously, our study demonstrates that optimization of certain abiotic conditions can support survivorship or growth of juvenile corals.

Coral health is strongly dictated by environmental conditions (Drury et al. 2017, Putnam et al. 2017); however, most studies focus on the biology of adult corals and few have examined how many factors

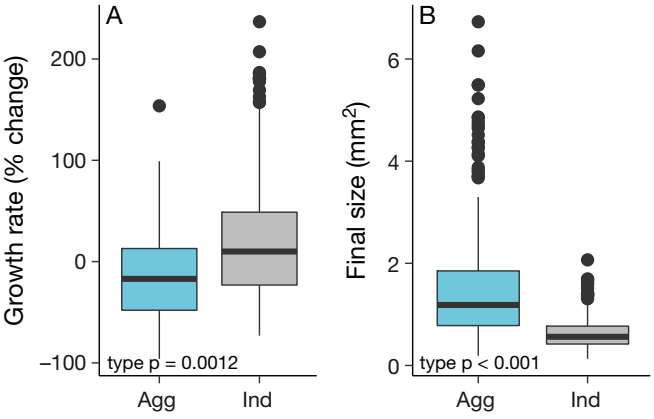

Fig. 5. Growth rate of juvenile *Montipora capitata* by colony type. (A) Individually settled corals (ind) grew significantly faster than aggregates (agg). (B) At the final timepoint, aggregates were nearly 3 times as large as individuals. Bar: median; box: interquartile range; whiskers: 1.5× the interquartile range; dots: outliers

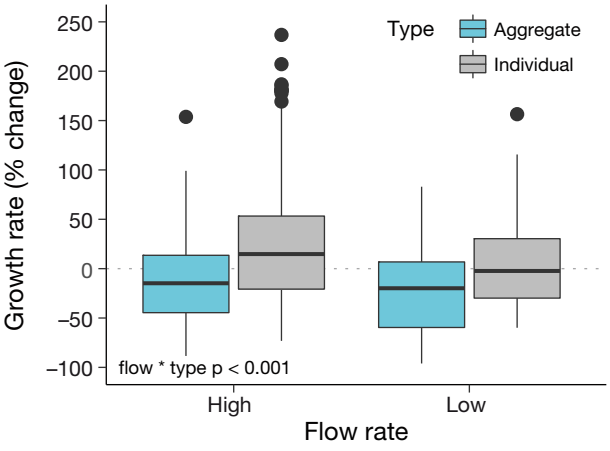

Fig. 6. Growth rate of juvenile *Montipora capitata* corals by type and flow rate. Box plot parameters as in Fig. 5

translate across life-history stages. We demonstrate the importance of manipulating flow rate and light intensity on post-settlement growth and survivorship of juvenile corals. Individual colonies had a higher growth rate than aggregates, but both grew more quickly in a high-flow environment. Forsman et al. (2012) found that adult *M. capitata* grew twice as fast in low-flow environments compared to high flow, but juvenile corals in our experiment showed opposite patterns in both aggregates and individuals. This pattern supports a size effect in flow response, because higher growth (or calcification) also has been observed in flow manipulations in other corals (Dennison & Barnes 1988). The benefits of increased flow include sediment removal, food delivery, and increased respiration and metabolic waste flushing (Jokiel 1978, Rogers 1990, Sebens et al. 1997, 2003,

Bruno & Edmunds 1998), but may impact corals of various sizes in different ways (Hoogenboom & Connolly 2009). Forsman et al. (2012) documented that flow and light requirements were species specific, but that low-light treatments yielded lower growth in adult *M. capitata* regardless of flow, corresponding to the high mortality we observed in low light. High flow can also alleviate bleaching in high-light environments (Van Woesik et al. 2005) by removing or reducing the warm boundary layer around colonies (Edmunds 2005), potentially lessening temperature stress by facilitating the removal of toxic and metabolic compounds (Fabricius 2006). Our results suggest that the benefits of exposure to adequate flow also supports survival of juveniles during bleaching stress, but the natural distribution of juveniles on the reef may prevent these benefits in some corals due to microhabitat differences where flow is lower.

Light is one of the most important factors dictating the distribution and biology of corals (Mundy & Babcock 1998, Putnam et al. 2017), and our data also suggest that optimal light exposure shifts as juvenile corals age. Most coral larvae prefer to settle within lower-light conditions in shaded microhabitats (Maida et al. 1994), and our results demonstrate that this lower-light environment is also beneficial for survivorship until approximately 1 mo post settlement. Doropoulos et al. (2016) pointed out that juvenile corals may need to settle in low-light microhabitats to avoid predation before taking advantage of high light later in life. Low light in our experiment may have benefited juvenile corals by enabling sufficient photosynthesis while limiting algal competition (Birkeland et al. 1981). We did not routinely clean juvenile coral plugs, so the impacts of light on algal competition are critically important. Other studies have sought to use microherbivory to address this time-consuming step (Craggs et al. 2019), and a combination of light and herbivory may further increase efficiency. At 1 mo post settlement, survivorship in the lower-light treatment declined significantly, potentially because the energetic needs of developing corals were not met by photosynthesis. Since *M. capitata* is a vertical transmitter (i.e. eggs are provisioned with symbionts), photosynthesis under low light may be sufficient at the earliest stages of post-settlement development due to energetic reserves or low energetic demands. Indeed, this time-dependent effect of light intensity has recently been documented in juveniles of other scleractinian species (Kuanui et al. 2020), suggesting that the manipulation of light levels over time may be used to enhance early survivorship and improve coral cultivation via sexual reproduction. As juvenile corals grow, they also develop thicker tissues which can self-shade, increasing tolerance of high-light conditions (Putnam et al. 2017).

Aggregation behavior at the time of settlement (individual or aggregate) influenced survival, growth, and bleaching throughout the experiment. Aggregate corals had higher survivorship, lower bleaching, and larger final size, although they exhibited slower growth rates. This is an important practical consideration for managers and restoration practitioners who can control aggregation via settlement density, but also highlights the dynamic interaction between abiotic and biotic influences in early juvenile development. Gregarious settlement and tissue fusion allows small, newly settled corals to overcome size-specific mortality thresholds by rapidly increasing total colony size (Raymundo & Maypa 2004, Puill-Stephan et al. 2012), and formation of chimeric aggregations may facilitate wider ranges of physiological strategies to survive stress (Amar et al. 2008, Rinkevich 2019). While our study did not intend to create aggregate colonies, numerous studies have shown that increased larval supply density positively affects total larval settlement and the potential formation of gregarious colonies (Cruz & Harrison 2017, Cameron & Harrison 2020). Therefore, future research should aim to optimize larval concentrations during settlement in order maximize the growth and survivorship of targeted species for specific restoration purposes.

Sublethal temperature exposure during the larval phase had small effects on downstream post-settlement survival, bleaching resistance, and growth. While we did observe significantly higher survivorship in juveniles that were exposed to both high and low larval rearing temperatures, the logistical constraints of creating temperature treatments may not be worth the added benefit in a restoration context, especially given the small effect sizes of larval rearing temperature during subsequent bleaching. Coral larvae undergo broad molecular changes in response to temperature stress (Polato et al. 2010, Meyer et al. 2011, Dixon et al. 2015) and suffer increased mortality in temperatures higher than the local average temperatures (Woolsey et al. 2015), so the lack of meaningful response found here may relate to treatment timing, duration, or intensity. Previous work has found positive effects of preconditioning in adult corals (Middlebrook et al. 2008, Bellantuono et al. 2012, Bay & Palumbi 2015), but this response is not ubiquitous (Schoepf et al. 2019, Dilworth et al. 2020). The lack of large effect here could also be because larval rearing temperature does not translate across life-history stages or is obscured by interactions with light or flow.

Previous work utilizing thermal preconditioning as a strategy to improve downstream traits in early life-history stages found that gamete preconditioning at 32°C could improve fertilization success rate (Puisay et al. 2018). In our study, moderate temperatures may not have elicited strong enough molecular responses to create large effects downstream. It is also possible that logistical difficulties which temporarily compromised temperature treatments contributed to this outcome. *M. capitata* eggs also contain higher levels of antioxidants than adults, which could mute the response of early life-history stages to oxidative stress (Padilla-Gamino et al. 2013). Future experiments should continue to examine the influence of timing and intensity of stress while avoiding treatments that result in high mortality and selective screening (Dixon et al. 2015). These factors should be given consideration based on the specific goals of the project.

Practitioners can manipulate abiotic conditions (including light and flow) to improve growth and survivorship of juvenile corals using simple and cost-effective techniques such as shading and increasing circulation. Our results show that the highest survivorship treatment combination for individual corals was achieved by combining high light levels, low larval rearing temperatures, unconditioned substrate, and low flow. Aggregate survivorship was maximized in high light and at low larval rearing temperatures, with high flow and 10 wk conditioned substrate. Interestingly, these treatments only supported 45% of maximum growth in individuals and led to negative growth in aggregates. There was also no significant correlation between growth and survivorship, which means that practitioners should not expect changes designed to elicit improvement in one metric to lead to improvements in another, which depends on the additive, antagonistic, or synergistic effects of treatments. Treatments may be tailored during post-settlement grow-out to maximize a specific outcome based on the goals of the specific project and tailored to fit the biology of different species.

The primary limitation of our study is the pseudo-replication of flow regime in 2 large raceway tanks: we were logistically limited by infrastructure capacity and the ability to create different flow regimes in replicate tanks. Tanks shared a water source, input flow rate was standardized daily, and the biofouling communities (mostly CCA) of each tank were similar in gross composition and biomass. Conversely, the light measurements we collected indicate that subtle but potentially important differences in maximum intensity and the shape of the daily light profile impact these tanks, although the total difference is within the measurement error of our instruments (~3%). High flow can also create substantial light scattering and may contribute to these patterns. We consistently randomized the position of plugs within tanks during measurement intervals to account for micro-scale differences in shading. Water temperature was similar between tanks (~0.1°C). Despite these similarities, unknown differences between tanks may contribute to the large effect sizes due to flow in our analysis, and future experiments should confirm this pattern with better replication. There may also be bias in our growth data, where we deliberately chose colonies that survived the experiment to maximize our efficiency. This could introduce bias for corals that grew more quickly and survived as a result, or from another unknown source of variance. Conversely, our very high replication, use of genetically diverse input, and integrative statistical analysis give us confidence in our results.

Our results provide useful practical information about the use of abiotic treatments to improve post-settlement growth, survivorship, and bleaching response in juvenile *M. capitata* corals collected from natural spawning events and reared *ex situ*. Optimization of sexual reproduction for restoration can utilize these factors to improve outcomes and create a framework in which biological interventions such as selective breeding can be applied to increase resilience in restoration stock.

Data availability. Data and scripts are publicly available at https://github.com/AHuffmyer/Mcapitata_Juvenile_Rearing. Data and scripts are available at Zenodo (doi:10.5281/zenodo.4289416).

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