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Flow rates alter the outcome of coral bleaching and growth experiments

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Abstract
It is important to consider flow rate explicitly in coral growth and bleaching studies across multiple species with differing life histories to guide coral conservation, management and captive culture. We quantified growth rates and coral bleaching responses to thermal stress (approx. 18 DHW) in flow-through aquaria with various current velocities to test whether flow conditions alter experimental outcomes. Across natural flow rates (< 1 to over 50 cm/sec), *Montipora capitata*, *Pocillopora acuta*, and *Pocillopora meandrina* showed increased growth and bleaching recovery at intermediate flow rates. Growth rates for all species increased from no flow to intermediate (50–100 turnovers-per-hour, ~ 10–30 cm/s), but then decreased at highest flow (> 190 tph, > 50 cm/s) although this trend was not significant for *P. meandrina*. The flow treatment with highest recovery from temperature stress differed across species, ranging from 4 tph in the flow-loving *P. meandrina* to 210 tph in the lagoonal *M. capitata*, indicating that natural flow regime alone is not predictive. Fragments from the same individual (e.g., *P. acuta* colony 8) held under identical thermal conditions continue bleaching and die under one flow regime (4 tph), whereas they recover from bleaching (30 tph) or grow fastest (105 tph) under different flow treatments. Flow is rarely reported in the literature, but uncontrolled flow effects may help to explain some of the variation in coral bleaching results reported across the literature. Significant differences among individual colonies, and colony-by-flow interactions, preclude generalizations beyond that flow rates can alter the outcome of both coral growth and bleaching experiments.

Keywords Coral nursery · Survivorship · Bleaching recovery · *Montipora* · *Pocillopora* · *Porites*

1 Introduction

Coral reefs are one of the most diverse ecosystems on the planet and provide a wealth of ecosystem services that are negatively impacted by anthropogenic threats [1–3]. Rising sea surface temperatures (SST) are a substantial stressor to the coral-algal symbiosis that induces a breakdown in the mutualistic relationship between corals and their endosymbiotic dinoflagellates (Symbiodiniaceae) that can provide ~ 90% of the energy required by corals [4]. Loss of endosymbionts in the coral tissue reveals the skeleton underneath and results in paling of corals, a phenomenon termed coral bleaching

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[5–7]. Coral bleaching reduces the translocation of nutrients to the coral animal, and can lead to mortality when bleaching is severe or prolonged [8–10].

Coral bleaching due to thermal stress, leading to coral mortality and decline of reef habitat, has emerged as one of the greatest threats to coral reefs worldwide [3, 11, 12]. Coral bleaching events on global scales are a recent phenomenon attributed to anthropogenic climate change [13–15]. The frequency and severity of thermal stress has increased significantly in recent decades with the 2014–2017 El Niño representing an unprecedented marine heat wave that resulted in the longest, most widespread and destructive global mass coral bleaching event ever recorded [14, 16]. Followed soon after by the 2023–2024 global heatwave which was particularly devastating in the Atlantic, with 99.7% of reefs experiencing bleaching and unprecedented widespread bleaching mortality of corals throughout the entire Atlantic Ocean basin [16]. The combined effect of anthropogenic impacts have led many to predict complete collapse of these iconic ecosystems by the end of this century [17–19]. As the situation becomes more dire, people have become increasingly motivated to move beyond reporting the decline of coral reefs and pursue human interventions to conserve and actively restore coral reefs [20–24].

The continued decline of coral reefs despite global conservation efforts has juxtaposed the desire to conserve coral reefs in their natural form with the desire to maintain ecosystem services provided by reef habitats in the face of increasing anthropogenic threats [21]. As a result, coral reef conservation efforts have transitioned from being focused on passive habitat protection to a surge of research and activities focused on active coral restoration and rehabilitation of degraded coral reefs [25–27]. Efforts to propagate corals for reef restoration and rehabilitation have evolved quickly from the early beginnings of live coral propagation to coral farming at scales required to outplant tens of thousands of coral fragments [28–32]. Likewise, while the cost of reef restoration remains high, considerable advances have been made in more cost-effective options for restoration activities [33]. Improvements to techniques to rear and transplant corals have made it feasible to minimize impacts on wild stocks while maximizing production [34], or incorporating thermally tolerant colonies that have a better chance of surviving increasingly frequent marine heatwaves [20, 35–37].

The importance of water flow to corals has long been recognized [38–40] and it is well-known that flow regime contributes to coral nutrient uptake, growth, and post-bleaching recovery [41–44]. Yet experimental flow conditions are not reported in > 95% of published coral bleaching studies to date [12, 45], and rarely considered explicitly in the design of coral husbandry or restoration projects [27, 46]. Increased flow improves diffusion of heat [47, 48] along with metabolites, oxidative radicals, and essential nutrients [43, 49–52] across the coral boundary layer. Increased diffusion reduces oxidative stress for respiration and improves photosynthesis and nitrogen fixation [43, 49–53]. Increased flow also enhances calcification rates for growth [48, 49, 52, 53] and in some cases encourages zooxanthellae re-recruitment following bleaching [50, 51]. Flow can also modify colony morphology, surface area, polyp density, and probability of detachment or breakage in the field, all of which can have impacts on coral growth or survivorship among environments, and ultimately the success of coral restoration efforts [41, 54–56].

To address this gap in understanding the ideal water flow under which to maintain nursery corals for restoration activities, we undertook experiments to assess the effects of flow on coral growth, survival, and post-bleaching recovery rates. By following coral fragments maintained in a controlled flow-through aquarium setting, we address three primary hypotheses: (1) flow rates will significantly alter coral growth rates in aquaria, (2) coral species and individuals within species will react differently to the same flow conditions, and (3) unreported differences in flow can influence the outcome of laboratory coral growth and bleaching experiments. The results of our study will help inform environmental conditions for future coral bleaching studies and are especially relevant to coral farming and reef restoration activities in Hawai'i as temperatures continue to increase and marine heat waves become more common.

2 Materials and methods

2.1 Definitions of flow

Here we include a variety of measurements of water movement that are easily confused if not clearly defined. For the purposes of this paper, we used the terms water *exchange*, *turnover,* and *flow rate* as defined here. Water *exchange* measures the time taken for incoming raw seawater to completely refill the aquariums in which corals are maintained. This is the rate at which the holding tank volume is replaced with raw ambient seawater, measured in liters per hour. Because a large pump will create more bulk water movement in a small tank than a large one, we standardized each pump-to-tank-size ratio by dividing the manufacturer rating of pump output by the volume of water as *turnovers per hour* (tph).

We note that this value depends on manufacturer pump ratings, which we found to be inaccurate when measuring flow rates reported in Table 1. Water *flow rate* is the current velocity at which water travels within the tank, measured in centimeters per second. We measured flow rate using a Nortek Vectrino 3D fixed stem Acoustic Doppler Velocimeter (ADV) (Nortek, Boston MA), sampling at 2 Hz (1.8 mm transmit length with a 2.5 mm sample bin). We performed multiple measures throughout the tank area and found that the turbulent flow conditions through time at a single point location in the tank were greater than the mean differences among locations within the tank or among pump sizes (Table 1). Therefore, we report XY flow speeds measured in two locations: (1) mid-tank at the front of the 18 × 18 cm mesh plate where coral fragments were placed during the experiment, and (2) at the far side of the mesh plate near the back of the tank away from the pump (Supplementary). Based on our flow measurements (Table 1), the experimental flow rates here encompass the range of flow speeds observed on natural reefs from which these coral species were originally collected. For example, near the protected HIMB coral nursery in Kāne'ohe Bay, natural flow rates are on the order of 5–10 cm/s [57]. Flow conditions on forereefs are typically higher, reaching 30 cm/s [58] but can exceed 50 cm/s in some locations [59, 60].

2.2 Species selection

We selected three of the eight most abundant coral species in Hawai'i that together comprise more than 95% of coral cover [61], could be collected within ~ 1 km radius of the HIMB Coral Nursery, and showed differing flow regime preferences and thermal tolerances for this experiment. *Montipora capitata* (Dana, 1846), and *Pocillopora acuta* Lamarck, 1816 are common species on reefs throughout Kāne'ohe Bay, but are typically restricted to the lower end of the flow regime (< 20 cm/s) mentioned above [62–64]. In contrast, *Pocillopora meandrina* Dana, 1846 is typically restricted to the upper end of that flow regime (> 20 cm/s) and is only really found along the edges of the Sampan Channel within Kāne 'ohe Bay [63] where flow rates are 10–20 cm/s [57], but likely enhanced by both natural wave energy and frequent boat wakes within the channel. These species were selected because they are commonly used in coral restoration activities in Hawai'i [65, 66], and rank among the eight most common corals that collectively account for over 95% of cover on Hawaiian reefs [61, 67]. Furthermore, they represent a range of life history, colony morphology, preferred flow regime habitats and thermal tolerance. Bleaching susceptibility of these species differs markedly, with *Montipora* being generally more resistant to bleaching than *Pocillopora* [8], and *P. meandrina* being the most sensitive of Hawaiian coral species to thermal stress [68, 69].

Table 1 Summary of aquarium pump ratings and measured flow rates for each treatment aquarium

Pump	Lph	Tph	Max X (cm/s)	Min X (cm/s)	Mean X (cm/s)	SD(X)	Max Y (cm/s)	Min Y (cm/s)	Mean Y (cm/s)	SD(Y)
Front of coral rack (nearest pump)										
Nothing	0	0	0.710	0.010	− 0.017	0.220	0.710	0.000	0.022	0.202
Airstone	38	4	1.930	0.010	0.167	0.550	3.210	0.310	− 1.646	0.589
70GPH	265	30	11.760	0.010	0.248	3.834	23.500	0.040	− 0.404	4.652
250GPH	946	105	47.410	0.500	− 9.027	14.390	41.910	0.310	− 3.333	13.573
500GPH	1893	210	36.340	0.030	3.667	12.438	51.530	0.100	2.856	9.030
950GPH	3610	401	65.820	0.880	0.275	24.828	59.290	0.120	1.581	25.720
Back of coral rack (away from pump)										
Nothing	0	0	1.040	0.000	0.040	0.310	1.160	0.000	− 0.050	0.251
Airstone	38	4	1.850	0.000	0.727	0.449	1.400	0.000	0.009	0.465
70GPH	265	30	17.230	0.000	− 5.318	4.158	5.980	− 19.160	− 2.741	3.510
250GPH	946	105	33.070	0.010	− 4.445	7.454	28.240	0.100	− 1.102	8.204
500GPH	1893	210	41.480	0.140	− 7.223	11.603	48.510	0.020	− 0.501	10.449
950GPH	3610	401	72.590	0.180	3.582	22.852	67.840	0.320	2.385	25.389

Flow was measured using a Nortek Vectrino 3D fixed stem Acoustic Doppler Velocimeter (ADV) sampling at 2 Hz (1.8 mm transmit length with 2.5 mm sample bin) averaging over 120 measurements. Based on these results and our pilot study, we selected the 0–500GPH pump array for our experimental treatments. A graphical representation of measurement locations and a 120 measurement time series of flow per location and flow treatment are provided in the Supplementary Materials

2.3 Experimental setup

Four coral colonies per species were collected from nearby sites in Kāneʻohe Bay under Hawaiʻi Department of Land and Natural Resources Special Activity Permits SAP-2018–03 and SAP-2019–16 issued to HIMB. Previous work shows extremely low rates of clonality in these species [70–72], but to maximize the chance that each colony was a distinct genet, field collections targeted colonies at least 3 m apart. Each replicate aquarium had a single 2–3 cm long coral nubbin (ramet) from each of the 4 coral colonies (genets) and all three coral species (3 species × 4 colonies × 5 flow treatments × 3 replicate tanks = 180 fragments), as illustrated in Fig. 1. Coral ramets were attached using IC-Gel Insta-Cure Coral Frag Glue (Bob Smith Industries, Atascadero CA) to a 1.5 mL plastic centrifuge tube, containing a single 2.5 g round split shot fishing weight and unique label, sealed using PC-Marine epoxy putty (Protective Coating Company, Allentown PA). Each sample's initial wet weight (g) was then measured and fragments were allowed to recover in the field under natural conditions (~ 1.5 m depth) in the HIMB midwater floating coral nursery for ~ 2 weeks before being used in any of the experiments, which employed 30% shade cloth to approximate field conditions (Supplementary). We chose to use total wet mass over buoyant weight as our measure of coral growth because corals can shift growth between calcification and tissue mass (particularly during times of stress), and buoyant weight excludes neutrally buoyant tissue mass [73].

After reef recovery from the 2018 bleaching, we began our experiment to determine the effects of flow on the outcome of coral growth experiments. Based on results from a pilot experiment (Supplementary), we selected pumps to create a range of flows from 0 up to roughly 200 tph. Corals were now maintained in commercial 10 L Zebrafish Rearing Tanks (Pentair Aquatic Eco-Systems, Apopka FL) set in a large-volume flow-through seawater table (Fig. 1) that maintained corals under the field conditions via constant flow-through with surrounding ocean water for temperature control and irradiance equivalent to 1.5 m depth at which corals were collected via Agfabric 30% shade cloth (Agfabric, Corona CA; see Supplementary for temperature and light data). Water exchange with ambient seawater was kept equal and consistent among experimental tanks using Hydroport Adjustable 8-outlet Manifolds (RainDrip NDS, Woodland Hills CA), which were cleaned daily to prevent clogging from organic matter passing through the unfiltered HIMB flow-through seawater system. We measured exchange rates periodically throughout the experiment to confirm water in our treatment tanks was flushed at a rate of 4.82–6.91 complete exchanges per day with raw, unfiltered seawater. Unfiltered seawater on this line has been shown sufficient to recruit and support a diverse and healthy natural coral reef community in flow through mesocosms [74]. For this experiment, we performed three spot checks in which we filtered water for 5 min each from the raw seawater line and collected an average of 1.8 zooplankton/min, providing a continuous food supply of ~ 10 zooplankton/fragment/hr during the course of the experiment.

Samples were secured in raised mesh plates and exposed to five water flow treatments (Fig. 1). The first treatment relied entirely on the water turnover from the Hydroport manifolds with no additional flow (0 tph), while the second treatment included an air stone for circulation (4 tph) because we could not find any aquarium pump small enough for this gap. The remaining flow treatments were generated by commercial aquarium pumps as follows: Koralia Nano Pumps (Hydor Ferplast, Italy) rated at 265 Lph (30 tph), Aquaneat Submersible Aquarium Pumps (Aquaneat, China) rated at 946 Lph (105 tph), and Aqueon Circulation Pumps (Aqueon, Franklin, WI) rated at 1893 Lph (210 tph). We established 15 tanks creating 3 replicates of each of the 5 flow conditions with a single coral fragment from each parent colony of each species housed in each tank (Fig. 1). Experimental treatments covered the full range these corals might experience on natural reefs in Kāne'ohe Bay, ranging from roughly 0–50 cm/s [57, 58] as reported in Table 1.

With twelve nubbins of each species per treatment (4 genets × 3 ramets with one in each of three replicate tanks), we had 60 nubbins per species and 180 total coral fragments in the experiment (Fig. 1). Fragments were measured weekly via wet mass and tanks were scrubbed clean every other week to remove algal growth and prevent fouling. Tank position was randomized weekly and HOBO temperature loggers were deployed along the outer middle sections of the water table to test for potential effects of tank positioning on temperature. These temperature profiles were compared with a 2-sample t-test in RStudio (1.4.1103, R > 4.1.2). Differences in growth by flow treatment were tested by ANOVA and non-parametric Kruskal–Wallis because of unequal variances among treatments in JMP (18.0.2) based on the a priori experimental design. Based on referee feedback, we also analyzed the data using a random effect mixed model in JMP (18.0.2), but the results were consistent with our a priori statistical design, so we present only the latter here. Post-hoc Tukey HSD tests in JMP evaluated differences among all pairs of treatment. Finally, differences in growth by colony (genets) among flow treatments for each coral species were also assessed with ANOVA and Tukey HSD tests in JMP (18.0.2).

After 8 weeks of normal growth in these aquaria, a natural bleaching event began as water temperatures in Kāne'ohe Bay began to rise, and first exceeded the local bleaching threshold of 28.0 °C [18] in mid-August of 2019 (Supplementary).

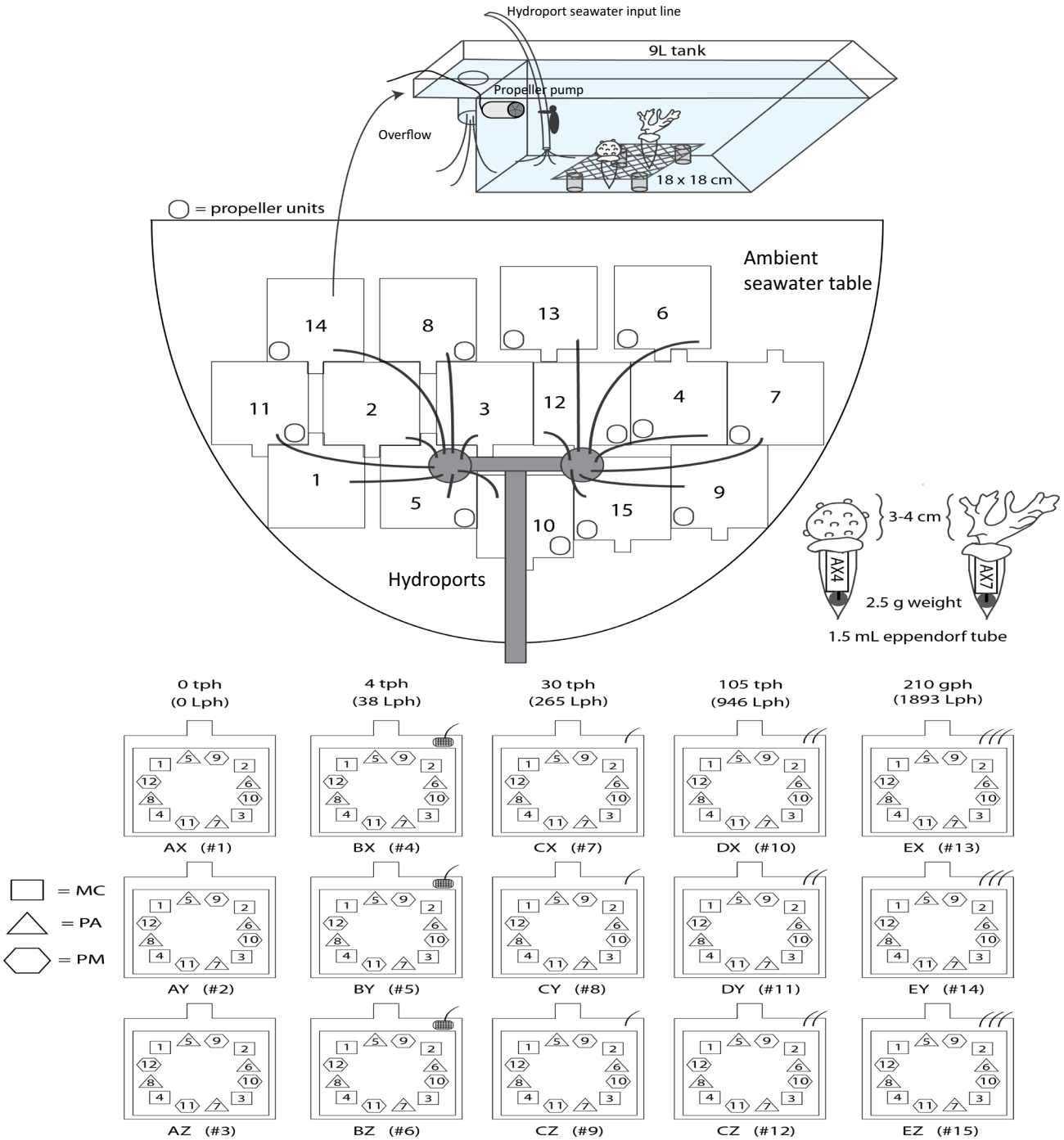

Fig. 1 Experimental design for investigation of various flow rates on the outcome of growth and coral bleaching experiments using *Montipora capitata*, *Pocillopora acuta* and *Pocillopora meandrina*. Upper portion of the figure depicts the tank setup and the lower portion is the labeling system for coral fragments. Tanks were arranged in an outdoor water table with constant flow through seawater, and each tank had equal input of fresh unfiltered seawater from hydroport tubes. The tank order was randomly assigned and the position of tanks was reshuffled each week. Flow treatment is denoted by symbols in the upper right of each tank: **A** = no flow, **B** = airstone, **C** = 70gph pump, **D** = 250 pgh pump, **E** = 500 gph pump. Each nubbin was assigned a unique label based on the flow treatment (A-E), flow replicate number (X–Z), and the species replicate number (*MC M. capitata*: 1–4, *PA P. acuta*: 5–8, *PM P. meandrina*: 9–12) with colony number representing the genet from which each replicate ramet was fragged

At this point, we transitioned the experiment from growth to study the effect of flow regime on coral bleaching in response to thermal stress, mortality, or subsequent recovery from bleaching. To minimize stress, we stopped growth measurements after 8 weeks and instead began to visually quantify coral bleaching scores using the Hawaiian Koʻa Card [75], through the full extent of the natural bleaching event. Temperatures regularly exceeded 28.0 °C and thermal stress continued to accumulate through 15 November (Supplementary), so a final wet weight for growth measurement taken one month later, at the end of the 23-week experiment. We selected the Koʻa Cards as a minimally invasive method of evaluating coral bleaching state to avoid any potential bias in mortality rate by adding human handling stress to the thermal stress corals were already experiencing. Further, these standardized coral color cards were developed through a series of controlled laboratory studies followed by field validations of over 1400 colonies to directly link color changes to specific physiological state and health (e.g., symbiont density, chlorophyll levels, photosynthetic efficiency) for each of the most common coral species in Hawaiʻi [75]. Thus, the Koʻa Color Scale (KCS) provides a non-invasive method of linking visual color to experimentally validated physiological conditions for Hawaiian corals [75].

Coral bleaching and recovery was evaluated for 15 weeks following the onset of the 2019 mass bleaching event in mid-August [76]. Each species was scored with the specific quadrant of the Hawaiian Koʻa Card based on its species-specific natural range of coloration (*M. capitata*: 19–27, *P. acuta*: 1–9, *P. meandrina*: 10–18) from weeks 9 through 23. Hereafter we refer to the color value as the Koʻa Card Score (KCS) and changes in color value as the Koʻa Card Score difference (ΔKCS). These species-specific changes in reference color, with lower values indicating paling associated with reduced symbiont density, chlorophyll levels, and photosynthetic performance [75], were analyzed with ANOVA and Tukey HSD tests in JMP (18.0.2). Dead corals were removed from the analysis because they cannot be assigned a KCS color score.

3 Results

3.1 Flow effects on coral growth and bleaching recovery

Based on a pilot study (Supplementary), commercial aquarium pumps ranging from 0 to roughly 200 tank volume turnovers per hour (tph) for our coral growth and bleaching experiment. We established 15 tanks with 3 replicates of each of 5 flow conditions (Fig. 1). The aquarium pump treatments created different flow regimes that covered the natural range that corals might see on local reefs (0–70 cm/s), but these differences are not reflected in the mean flow conditions (Table 1). Instead, the variability in measured flow (SD) and maximum flow speeds (cm/sec) both scale in a more consistent manner with pump manufacturer ratings (Table 1). Temperature and light exposure were measured for one week with HOBO loggers in tanks at the outer edge and the middle section of the water table to quantify consistency across tank positions. Throughout the experiment, between noon and 2 pm daily, irradiance averaged 1408 ± 369 μmol/m^2/s reaching the tanks. Spot checks with a Li-Cor LI-193 Spherical Quantum Sensor (Li-Cor, Lincoln NE) indicated consistent transmission at ~ 70% of those values (985 ± 258 μmol/m^2/s) through the shade cloth throughout the array (Supplementary). Temperature differed slightly but significantly ($t = 7.83$, $df = 672$, $p < 0.01$) between the center (28.90 °C) and outer edge of the water Table (28.67 °C). However, experimental tanks were rotated among positions and would alternate between the central and outer positions weekly, so all fragments experienced these small temperature differences (0.23 °C) equally for 4 of the 8 weeks throughout the experiment. There was 100% survivorship and up to 20% growth among coral fragments during this initial 8-week growth period.

Observed increases in growth rate of replicate clonal fragments held under differing flow rate (Fig. 2) are consistent with the pilot experiment (Supplementary), during which exact flow rates were not measured. Mean growth across all fragments increased from 0.395 ± 0.05 g wet weight at 0 tph, to 0.463 ± 0.05 g at 4 tph, 0.588 ± 0.05 g at 30 tph, 0.526 ± 0.05 g at 105 tph and 0.403 ± 0.05 g at 210 tph ($F_{6,177} = 6.84$, $p < 0.01$). Despite considerable variation among individual genets, coral growth again tended to increase with flow within all three species, although it was only significant for *Montipora capitata* ($F_{4,55} = 3.64$, $p = 0.01$; $\chi^2 = 11.1$, $df = 4$, $p = 0.03$) and for *Pocillopora acuta* with parametric ($F_{4,55} = 2.70$, $p = 0.04$), but not non-parametric statistics ($\chi^2 = 8.4$, $df = 4$, $p = 0.07$). Growth of *M. capitata* increased from 0.244 ± 0.06 g wet weight at 0 tph, to 0.379 ± 0.06 g at 4 tph, 0.434 ± 0.06 g at 30 tph, 0.510 ± 0.06 g at 105 tph and then declined significantly to 0.248 ± 0.06 g at 210 tph (Tukey HSD, $p = 0.028$). Growth of *P. acuta* increased from 0.622 ± 0.09 g wet weight at 0 tph, to 0.633 ± 0.09 g at 4 tph, 0.826 ± 0.09 g at 30 tph, 0.734 ± 0.09 g at 105 tph and then declined significantly to 0.406 ± 0.09 g at 210 tph (Tukey HSD, $p = 0.025$). Although, *Pocillopora meandrina* shows a similar trend of increasing growth with flow for the first 3 treatments, and reduced growth at higher flows, but increased variability with 2 outlier points (Fig. 2) among the highest flow treatment renders this trend nonsignificant ($F_{4,55} = 1.32$, $p = 0.27$; $\chi^2 = 5.32$, $df = 4$,

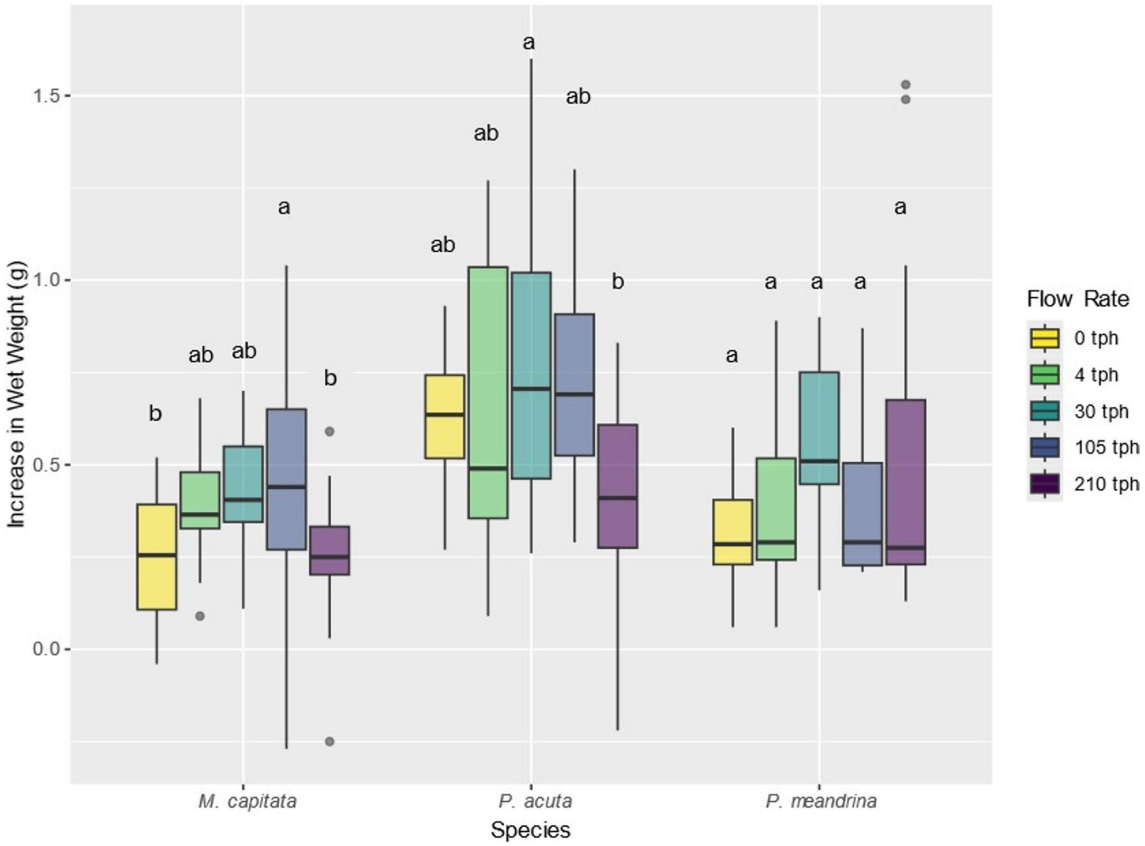

Fig. 2 Box plot of growth (increase in wet weight) for *Montipora capitata*, *Pocillopora acuta*, and *Pocillopora meandrina* maintained under differing flow treatments. Each box shows median and upper and lower quartiles for mass increase among the twelve nubbins during eight weeks of experimental treatments. Vertical lines represent min and max values while outliers are plotted as individual points. Statistically insignificant differences between treatments, as defined by Tukey's multiple comparison test ($p < 0.05$), are indicated by shared letter labels above the bars; each species was assessed independently.

$p = 0.26$). Growth of *P. meandrina* fragments throughout this experiment increased from 0.318 ± 0.09 g wet weight at 0 tph, to 0.378 ± 0.09 g at 4 tph, 0.553 ± 0.09 g at 30 tph, 0.403 ± 0.09 g at 105 tph and 0.518 ± 0.09 g at 210 tph.

3.2 Intraspecific variation in response to flow rates

Although we included only 4 individual colonies (genets) for each species in these experiments, significant variation in growth was recorded among colonies for both *P. acuta* ($F_{3,16} = 6.02$, $p < 0.01$) and *P. meandrina* ($F_{3,16} = 3.95$, $p = 0.03$), but not for the more variable *M. capitata* ($F_{3,16} = 0.55$, $p = 0.65$). Overall, *M. capitata* colonies averaged 3.89 ± 0.73 g with no significant differences among individuals 1–4. In contrast, *P. acuta* (colonies 5–8) shows a two-fold difference among individuals with colony 6 averaging 10.95 ± 1.01 g of growth whereas colony 7 averaged only 5.00 ± 1.01 g (Fig. 3A). *P. meandrina* falls intermediate to these two with significant differences among colony 10 averaging 3.19 ± 0.34 g of growth whereas colony 9 averaged only 1.60 ± 0.34 g over the same period.

Among flow treatments *M. capitata* likewise shows high individual variation, with colony 4 growing fastest in the 30 tph treatment, colony 1 growing fastest in the 105 tph treatment, and the other two colonies showing no difference in growth across flow treatments. Yet, despite this individual variation, there remains a significant overall influence of flow treatment on growth rate of genets of *M. capitata* ($F_{4,55} = 2.81$, $p = 0.038$). In contrast, *P. acuta* showed clear differences among genets in both differences in overall growth rate among genets ($F_{3,55} = 8.83$, $p < 0.001$) and the mean growth rate of clonal fragments held under differing flow treatments within the genets ($F_{4,55} = 3.84$, $p = 0.01$). Differences in growth rate among genets were more consistent in *P. acuta* than *M. capitata*, with colony 6 showing significantly higher growth than all other colonies across all treatments in these experiments (vs. Colony 5 $p = 0.05$; vs. Colony 7 $p < 0.001$; vs. Colony 8 $p = 0.01$, Tukey HSD). Likewise, *P. meandrina* shows a significant effect of genet ($F_{3,59} = 4.29$, $p = 0.01$) and flow ($F_{4,59} = 2.63$, $p = 0.049$) on overall growth rates

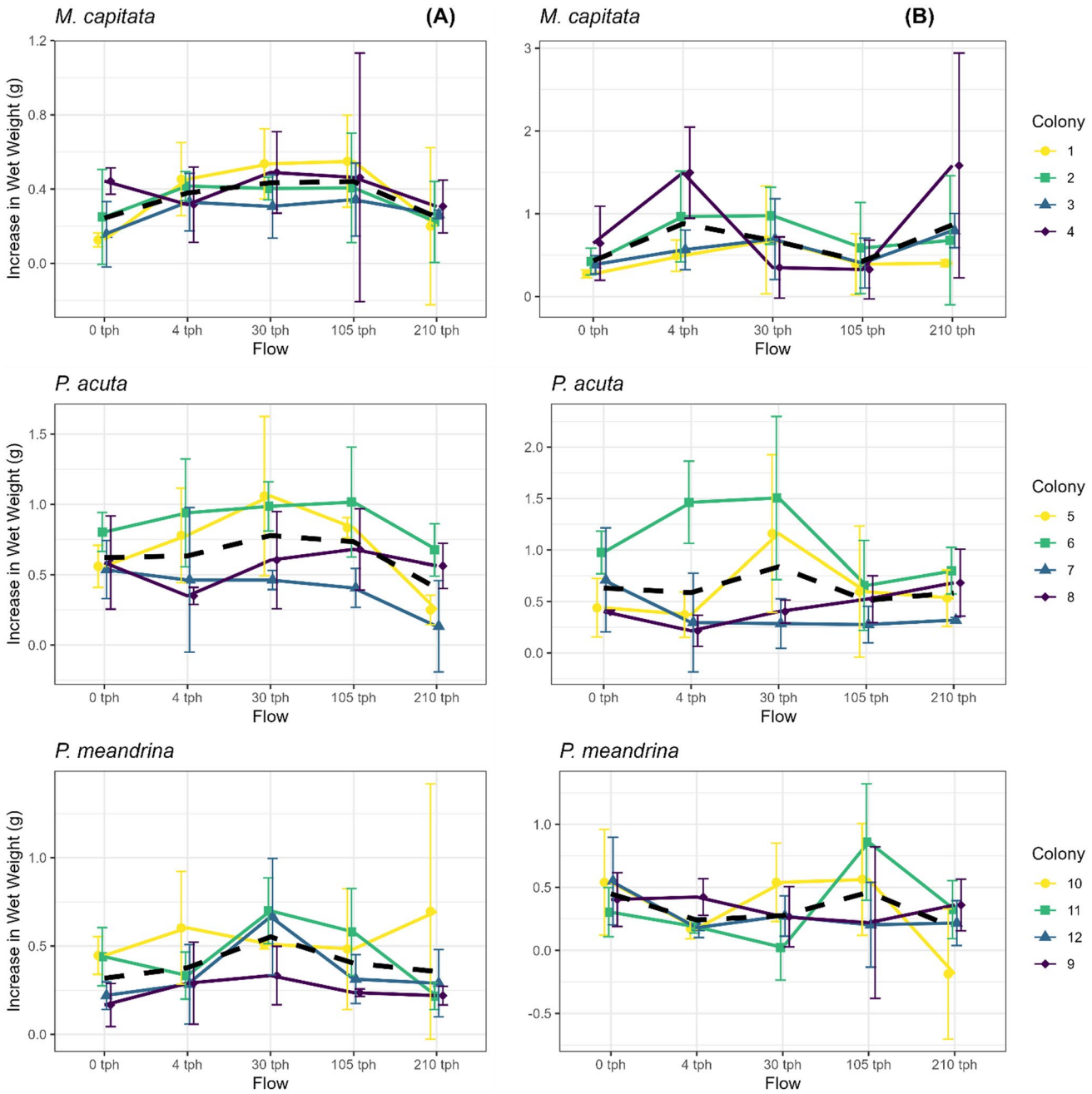

Fig. 3 Mean change in wet weight of 3 replicate fragments maintained in each of the flow treatments by coral colony (each of 4 genets in different colors) and species, with variable axis scales to better visualize differences among flow treatments. The overall mean result from all 12 fragments of each species is plotted as a dashed line in black. **A** Individual variability in coral growth during 8 weeks of normal temperatures. Each point represents the average of triplicate nubbins grown under differing flow regimes (0–210 tph) with 1 clonal ramet/genet in each of the 3 replicate tanks per flow treatment as outlined in Fig. 1. The same four genets for each species—*M. capitata* (colonies #1–4), *P. acuta* (colonies #5-8), and *P. meandrina* (colonies #9–12)—were used throughout the entire 23 week experimental period, but when temperatures rose to the bleaching threshold after 8 weeks, the experiment became a bleaching response experiment beginning with week 9 and running for 15 weeks. **B** Individual variability in coral growth throughout the 15 weeks following the growth experiment, showing increased individual variability and differential responses to bleaching by experimental flow condition.

among differing flow regimes, with colony 10 performing consistently better than average across all treatments. There is also a significant interaction of colony and flow for both *P. acuta* ($p = 0.001$) and *P. meandrina* ($p = 0.002$), with some individuals performing comparatively well or poorly in different flow treatments (Fig. 3A). For example, despite Colony 6 of *P. acuta* always showing the highest growth rate, there was no difference in mean growth rate of fragments held in the 0 tph and 4

tph flow treatments, whereas Colony 8 shows a significant decrease in mean growth rate, while Colony 5 shows a significant increase in mean growth rate between these same treatments. However, no such effect is detected for *M. capitata* ($p = 0.59$).

3.3 Coral bleaching and recovery among flow treatments

Temperatures above the Maximum of the Monthly Mean (MMM), 26.98 °C for the Main Hawaiian Islands (NOAA Reef Watch), tend to exceed the upper tolerance threshold for corals and result in coral bleaching when prolonged. The product of duration and intensity by which MMM is exceeded over a 3-month period (12 week sliding window) is referred to as Degree Heating Weeks (DHW). When DHW reaches 4 °C-weeks (which could result from 1 week at + 4 °C or 4 weeks at + 1 °C), significant coral bleaching is likely to occur, and values beyond 8 DHW typically result in severe and widespread bleaching and mortality [77]. Between August and November 2019, temperatures exceeded the bleaching threshold by an average of 5.3 °C-week, with peak values of 7 °C-week in October, resulting in ~ 80% of corals showing signs of bleaching in Kāne'ohe Bay [76]. This marine heatwave, during which sea water temperatures in Kāne'ohe Bay averaged 28.4˚C with roughly 13 DHW accumulated for most locations, resulted in some of the highest bleaching mortality reported to date for Hawai'i [69, 77]. While we used natural seawater for our experiment, seawater lines and tanks on land warm in the sun, so aquarium temperatures are always slightly higher (Supplementary), such that corals accumulated almost 18 DHW with a max of 11.45 °C-week above the bleaching threshold. Each treatment started with 12 healthy fragments (100% survivorship from the previous 8-week growth experiment), per species distributed with a single ramet from each genet per replicate flow treatment (Fig. 1).

Again, we were able to detect significant variation among how genets responded to thermal stress among the flow treatments (Fig. 3B). Observed variation followed the same relative rank, with *M. capitata* showing the greatest variation, followed by *P. acuta* and then *P. meandrina*. However, the flow conditions under which a colony shows the highest growth rate is not consistent with the flow rate under which there is greatest recovery from bleaching (Fig. 3B). Growth data during the bleaching experiment are complicated by the fact that there was substantial mortality during the heatwave and too few survivors in some treatments for analyses (Fig. 4). Average KCS for fragments between the end of that growth period (week 8 for growth = week 0 for bleaching) and the end of the bleaching and recovery period at week 23 (15 additional weeks) shows an interaction between bleaching response by species and flow (Fig. 4a). The mean score for each treatment of each species is plotted for weeks 8, 15, and 23 except for *P. meandrina*, which had too few fragments survive bleaching for analyses in week 23 (Fig. 4b).

As expected, the bleaching-sensitive *P. meandrina* was hit particularly hard by ~ 18DHW of thermal stress, with nearly complete mortality and only 4 fragments surviving through the end of the experiment (Fig. 4). Bleaching effects were species-specific ($F_{2,172} = 47.12$, $p < 0.001$) and significantly influenced by flow ($F_{4,172} = 2.48$, $p = 0.046$) with a significant interaction between species and flow ($F_{8,172} = 2.00$, $p = 0.049$). The significant interaction arises from differences in the performance of *M. capitata* and *P. acuta* under different flow treatments, with some ramets showing recovery from bleaching under one flow condition whereas the same colony continued bleaching and decline under a different flow treatment (Fig. 4). Differences among species were largely driven by *P. acuta*, with an average of 1.7 points less bleaching than *M. capitata* ($p = 0.007$) and 5.1 points less bleaching than *P. meandrina* ($p < 0.001$). Differences in bleaching severity match the mortality rates with 50% of *M. capitata* fragments dying, and 94% mortality of *P. meandrina* by the end of the experiment. In contrast, *P. acuta* experienced significantly less bleaching ($F_{1,59} = 9.44$, $p = 0.003$) and only 15% mortality throughout the experiment (Fig. 4c). *P. acuta* shows the greatest survivorship and recovery from bleaching ($\Delta KCS = 1.1$) under intermediate flow (30 tph, 23.5 cm/s max). *M. capitata* likewise showed lowest mortality under intermediate flow (30 tph, 23.5 cm/s max), but the greatest recovery from bleaching ($\Delta KCS = 0.3$) was observed under the highest flow treatment (210 tph, 51.5 cm/s max). Despite being the species found under the highest flow conditions in the field, *P. meandrina* exhibited the greatest survivorship and recovery from bleaching ($\Delta KCS = 0.1$) under low (4 tph, 3.2 cm/s max) flow conditions (Fig. 4).

4 Discussion

Previous studies have documented the importance of water flow on coral growth, morphology, bleaching, and post-bleaching recovery [41–43, 48, 52, 54, 78]. Yet very few published bleaching experiments (< 5%) report any aspect of the flow conditions under which bleaching experiments have been carried out [12, 45]. Further, flow regime is not even mentioned as a factor in a systematic review of methods, successes, failures, and future directions for coral restoration projects [27]. Flow clearly matters to restoration activities, however, because coral nurseries are almost always low flow

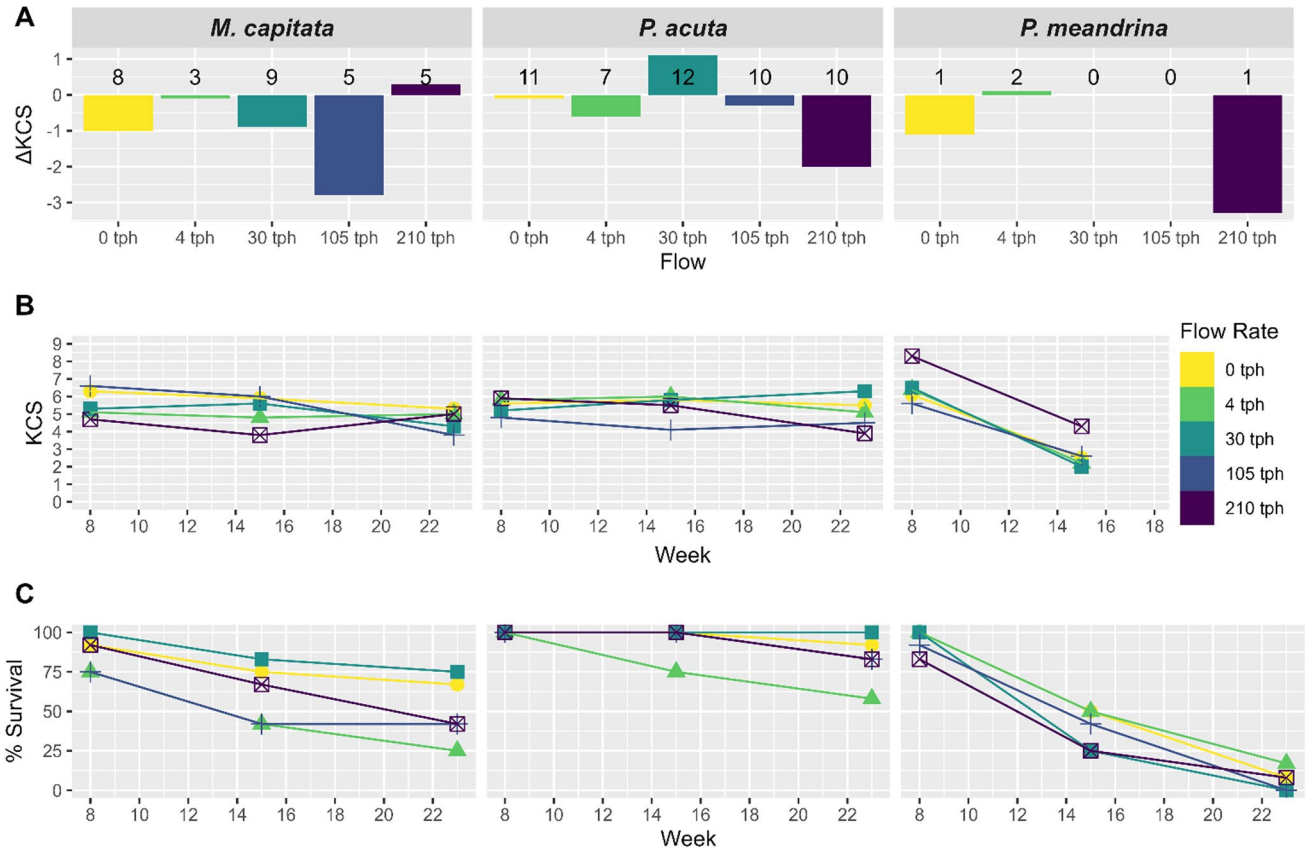

Fig. 4 Bleaching and survival of 12 coral fragments maintained under various flow treatments with 1 clonal ramet per each of 4 genets in each of 3 replicate tanks per flow treatment. **A** Cumulative difference in average KCS among surviving fragments, where a negative difference signifies continued paling or bleaching through the end of the experiment, and a positive difference signifies retention or recovery of color among surviving fragments at week 23. Final sample sizes (from 12 initial replicates) after 15 weeks of treatment are listed as the number of surviving fragments above each bar. **B** Average KCS by treatment and week for each species. Only 4 *P. meandrina* survived to the end of the experiment, so KCS was not reported for this species at week 23 due to near complete mortality. **C** Survivorship curves for percentage of fragments alive each week in each flow treatment by species.

environments relative to coral reefs. For example, colonies grown under lower flow conditions tend to develop rougher growth morphologies to increase frictional drag and thin the boundary layer, allowing them to benefit from the same mass-transfer effects of corals with smoother morphologies living in higher flow environments [59, 79, 80]. Flow can also modify overall colony morphology, surface area, polyp density, feeding efficiency, and the probability of detachment or breakage in the field [41, 54–56, 78]. Such plasticity indicates likely consequences for corals whose morphology is poorly matched to their environment, which may in turn impact the growth and survival of outplanted corals [81, 82]. Thus, there are a wide range of factors affected by flow that can clearly impact both the outcome of laboratory experiments involving corals and ultimately the success of coral restoration efforts.

The fact that the vast majority of studies to date fail to report the flow regime under which coral research or restoration activities have been performed [12, 45] suggests a lack of appreciation for its importance by coral reef researchers. Here we present results to document how experimental evaluations of coral growth, survival, and post-bleaching recovery rates can all be altered by flow regime. Furthermore, there is an interaction between individual colony and flow regime (Fig. 3). This interaction may derive from different fragments having different surface roughness at the start of the experiment or from individuals having differing responses to flow such that not all individuals of a species show highest growth or recovery from bleaching under the same flow regime. We did not quantify the morphology or surface roughness of each fragment, so we cannot distinguish among these alternative mechanisms, although it seems an important area for future research. Regardless of the underlying mechanism, it is important to note that the interaction of parent colony (genet) with flow regime means that conflicting experimental results could be obtained within a single species depending on which colony was selected and may explain some of the variability among experimental bleaching outcomes seen across the literature.

Here we sought to answer three primary questions: (1) what are optimal flow rates for growth of these Hawaiian corals, (2) does optimal flow rate differ among coral species or individuals within species, and (3) does higher flow reduce rates of coral bleaching, post-bleaching mortality, or speed recovery from bleaching among fragments that survive? To address the first question, all three species in our pilot study showed the highest mean growth around 100 tph, followed by a decline in the highest (> 200 tph) flow treatments (Supplementary). Based on that result, we focused on the flow range of about 0 to 200 tph as best we could with available aquarium products, which covered the natural range of flows from which these corals were originally collected (Table 1). We found similar results in the flow experiment (Fig. 2) for both *M. capitata* and *P. acuta*, with highest mean growth in the 105 tph treatment, and lowest mean growth rate at 210 tph. The replacement of *Por. compressa* from our preliminary experiment with *P. meandrina* in the refined experiment prevents us from comparing between experiments for these species, but *P. meandrina* was the only species that did not show the same pattern. Instead, none of the differences in growth among the treatments were statistically significant for *P. meandrina* which appeared to have slightly higher growth at lower flow rates (30 tph) than the rest (Fig. 2). It is interesting to note that *P. meandrina* is not typically found throughout Kāne'ohe Bay, because it is most common in areas of higher flow and wave energy [61], and the only site in the bay at which it is abundant is along a shipping channel where oceanic swells and frequent boat wakes increase wave energy locally. Thus, while we see a consistent trend towards maximum growth under flow rates on the order of 100 tph for both experiments using the lagoonal coral species we tested here, we caution against applying that flow rate universally. Likewise, Nakamura and colleagues [42] found that bleached colonies of *Stylophora pistillata* maintained under low flow (≤ 3 cm/s) conditions remained pale throughout their 7-week experimental period, whereas colonies maintained under moderate flow conditions (20 cm/s) recovered rapidly over the same time period. Here, we find that growth of coral fragments is maximized under moderate flow rates (30–105 tph, 14–37 cm/s), but that both survival and recovery from bleaching is highest at the lower rather than the upper end of this range (30 tph, ~ 15 cm/s).

Bleaching responses were variable among species and flow rates, with survival generally being reduced by increasingly severe bleaching in the lowest and highest flow treatments (Fig. 4). It is not surprising that corals performed relatively poorly in the no flow (0 tph) treatment. Flows on the order of 1 cm/s as seen in our 0 tph treatment, have been shown to be stressful to corals by limiting gas exchange, nutrient flux and photosynthesis [41, 83, 84]. Conversely, high flows increase coral metabolic rate because of increased oxygen supply to tissues, especially at night or during bleaching when photosynthesis is not happening [41, 83]. Without the energetic contribution of symbionts, increased metabolism can be a large energetic cost to the corals and may explain why growth tended to decrease and bleaching was generally more severe in the highest flow treatments. However, such generalizations are not universal because *M. capitata* shows recovery from bleaching in only the highest flow treatment (Fig. 4). The flow speeds measured in these experimental treatments are highly variable and a fragment could experience temporally variable flows that exceed the full range of treatment values through time in our higher flow treatments (Supplementary). Regardless, the 30–105 tph treatments generally correspond to flows on the order of 10–30 cm/s, which fall within the natural flow range for many reefs. However, mean, maximum and variability of flow all differ among treatments (Table 1), so it is hard to say exactly which aspect of flow the corals are responding to.

In fact, given the variability among both species and individuals reported here, we would argue that there is unlikely to be any single optimal flow rate for coral growth. Instead, we show significant variation among both species, and among individuals within species, for the flow rates under which maximal growth rates were obtained. For species such as *M. capitata*, some individuals (colony 1 & 4) differ significantly from the mean pattern and show maximal growth at different flow rates than others (Fig. 3). In contrast, *P. acuta* shows more similar trends among individuals, although the absolute magnitude of growth varies significantly among the colonies with colony 6 consistently outperforming all others (Fig. 3). This variability precludes a single optimal flow rate for all individuals even within a single species, and likely has implications for how such colonies would perform if outplanted to the field also. Knapp et al. [66] found similar variability among individual colonies and showed that growth varied by up to 1000% and survival by up to 40% among fragments of the same genet outplanted across an environmental gradient in Kāne'ohe Bay. Together these results indicate that at least some individuals show preferential growth and survival under differing flow environments and that no single condition appears optimal for all individuals.

Finally, we confirmed that variable flow rates could impact results and conclusions drawn from a laboratory bleaching experiment, because bleaching responses are significantly altered by flow, and with a significant interaction between flow and species. The outcomes of the experimental tests resulted in a considerable difference in survivorship for *M. capitata* (75 to 25%) and *P. acuta* (100 to 58%) of the same individuals held under different flow regimes in the bleaching experiments (Fig. 4). Furthermore, each species showed opposite responses to thermal stress among some flow conditions as

evidenced by the crossing lines in Fig. 3B among flow treatments. Individual variability in genet performance did not overshadow general species trends among flow treatments, however. For example, *P. acuta* showed increasingly severe paling in the 210 tph treatment, whereas the exact same individuals showed simultaneous recovery under a flow rate of 30 tph (Fig. 4). *M. capitata* likewise showed increased severity of bleaching in the 105 tph treatment, compared to mean recovery of corals in the 210 tph treatment. Mortality was too high in the most bleaching sensitive species, *P. meandrina*, to analyze the data, but this species also showed opposite trends among the few surviving fragments: there was recovery among the 2 survivors in 4 tph compared to increasingly severe paling of the single individual surviving in both the lowest and highest flow (0 and 210 tph) treatments (Fig. 4). However, we also note that the 4 tph treatment is the only one created by an airstone rather than an aquarium pump, which may have potentially confounding effects such as altering the levels of dissolved gases or evaporative cooling, beyond simply flow rate. Regardless, the fact that at least one coral genet within all three species exhibits opposite trends, with a clonal fragment from the same parent colony showing increased bleaching severity under one flow regime whereas another shows recovery when maintained in a different flow treatment (Fig. 3B), highlights the importance of reporting flow when trying to compare among bleaching experiments [12]. A recent survey of the coral bleaching literature revealed that more than 95% of coral bleaching studies to date have failed to report any detail of the flow conditions under which the study was performed [45]. Such interaction of the flow regime and experimental bleaching outcomes combined with oversight in reporting of flow conditions may explain some of the variability seen in the literature among studies performed with the same species. Here we show it is possible to draw opposite conclusions from bleaching experiments using the same individual at the same time under differing flow regimes, and until flow is reported and standardized, it is impossible to directly compare coral bleaching responses and recovery among studies.

5 Conclusions

Water flow is a major factor in coral health and growth but is rarely incorporated into laboratory experimental design or the rapidly expanding coral nursery and restoration literature. Here, we found that four species of coral (*Montipora capitata*, *Pocillopora acuta*, *Pocillopora meandrina* and *Porites compressa*) generally exhibit increased growth across our flow treatments from 0 to about 100 tph, but slow or possibly decrease growth at greater flow rates. Although we observed the highest growth rates in our moderate flow treatments (30–105 tph), bleaching recovery rates for the same individuals were generally higher at the lower end of this range (4–30 tph). Surprisingly, we showed that it was possible to draw the opposite conclusions from a coral bleaching study conducted with the same individuals under differing flow conditions. But results were both species- and individual-specific. For example, *P. acuta* generally showed continued paling and decline at flow rates more typical of field conditions (210 tph) as opposed to recovery of the same individuals maintained under low flow more typical of laboratory experiments (30 tph). *M. capitata* showed the opposite trend with increased severity of bleaching at lower flow (105 tph) compared to recovery at 210 tph, but there is considerable individual variation within each species. Interestingly, the 105 tph treatment was also the one in which we observed greatest growth of *M. capitata*, indicating that conditions for optimizing growth and bleaching recovery are likely to differ. The complex interaction of coral genet and flow reported here also highlights the value of variability in coral farming and restoration activities to increase chances of matching the conditions for success. Overall, these results highlight the importance of considering flow rate explicitly in coral research and reporting them explicitly in publications, and may explain differences among outcomes in the coral bleaching literature.

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Author contributions R.J.T., Z.H.F., and M.E.L. designed the study. M.E.L., R.J.T. and Z.H.F. collected and fragmented the corals, and set up and maintained the experiments with help from many in the acknowledgements. M.E.L., R.J.T., and E.B.F. analyzed the data and M.E.L. and E.B.F. created the figures. D.W.H.S. and R.J.T. performed flow measurements using the ADV and created the Supplementary file with flow data. M.E.L. and R.J.T. led writing of the initial draft of the paper in communication with all authors. All authors read and approved the final manuscript.

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Data availability The datasets generated during this study and R markdown scripts for analysis and visualization are available as supplementary materials to this submission, and in the Lentz-et-al.Flow-Rates-Affect-Coral repository, https://github.com/melentz/Lentz-et-al._Flow-Rates-Affect-Coral.git.

Declarations

Competing interests The authors declare no competing interests.

References

1. Hoegh-Guldberg O, Mumby PJ, Hooten AJ, Steneck RS, Greenfield P, Gomez E, Harvell CD, Sale PF, Edwards AJ, Caldeira K, Knowlton N, Eakin CM, Iglesias-Prieto R, Muthiga N, Bradbury RH, Dubi A, Hatziolos ME. Coral reefs under rapid climate change and ocean acidification. Science. 2007;318:1737–42. https://doi.org/10.1126/science.1152509.
2. Pandolfi JM, Connolly SR, Marshall DJ, Cohen AL. Projecting coral reef futures under global warming and ocean acidification. Science. 2011;333:418–22. https://doi.org/10.1126/science.1204794.
3. Hughes TP, Barnes ML, Bellwood DR, Cinner JE, Cumming GS, Jackson JBC, Kleypas J, van de Leemput IA, Lough JM, Morrison TH, Palumbi SR, van Nes EH, Scheffer M. Coral reefs in the anthropocene. Nature. 2017;546:82–90. https://doi.org/10.1038/nature22901.
4. Muscatine L, Porter JW. Reef corals: mutualistic symbioses adapted to nutrient-poor environments. Bioscience. 1977;27:454–60. https://doi.org/10.2307/1297526.
5. Brown BE. Coral bleaching: causes and consequences. Coral Reefs. 1997;16:S129–38. https://doi.org/10.1007/s003380050249.
6. Douglas AE. Coral bleaching–-how and why? Mar Pollut Bull. 2003;46:385–92. https://doi.org/10.1016/S0025-326X(03)00037-7.
7. van Oppen MJH, Lough JM. Coral bleaching–patterns, processes, causes and consequences. vol. 2. Springer; n.d.
8. Pratchett MS, McCowan D, Maynard JA, Heron SF. Changes in bleaching susceptibility among corals subject to ocean warming and recurrent bleaching in Moorea, French Polynesia. PLoS ONE. 2013;8:e70443. https://doi.org/10.1371/journal.pone.0070443.
9. Heron SF, Maynard JA, van Hooidonk R, Eakin CM. Warming trends and bleaching stress of the world's coral reefs 1985–2012. Sci Rep. 2016;6:38402. https://doi.org/10.1038/srep38402.
10. McClanahan T. Changes in coral sensitivity to thermal anomalies. Mar Ecol Prog Ser. 2017;570:71–85. https://doi.org/10.3354/meps12150.
11. Veron JEN, Hoegh-Guldberg O, Lenton TM, Lough JM, Obura DO, Pearce-Kelly P, Sheppard CRC, Spalding M, Stafford-Smith MG, Rogers AD. The coral reef crisis: the critical importance of<350 ppm CO2. Mar Pollut Bull. 2009;58:1428–36. https://doi.org/10.1016/j.marpolbul.2009.09.009.
12. Grottoli AG, Toonen RJ, van Woesik R, Vega Thurber R, Warner ME, McLachlan RH, Price JT, Bahr KD, Baums IB, Castillo KD, Coffroth MA, Cunning R, Dobson KL, Donahue MJ, Hench JL, Iglesias-Prieto R, Kemp DW, Kenkel CD, Kline DI, Kuffner IB, Matthews JL, Mayfield AB, Padilla-Gamiño JL, Palumbi S, Voolstra CR, Weis VM, Wu HC. Increasing comparability among coral bleaching experiments. Ecol Appl. 2021;31:e02262. https://doi.org/10.1002/eap.2262.
13. Hughes TP, Anderson KD, Connolly SR, Heron SF, Kerry JT, Lough JM, Baird AH, Baum JK, Berumen ML, Bridge TC, Claar DC, Eakin CM, Gilmour JP, Graham NAJ, Harrison H, Hobbs J-PA, Hoey AS, Hoogenboom M, Lowe RJ, McCulloch MT, Pandolfi JM, Pratchett M, Schoepf V, Torda G, Wilson SK. Spatial and temporal patterns of mass bleaching of corals in the anthropocene. Science. 2018;359:80–3. https://doi.org/10.1126/science.aan8048.
14. Lough JM, Anderson KD, Hughes TP. Increasing thermal stress for tropical coral reefs: 1871–2017. Sci Rep. 2018;8:6079. https://doi.org/10.1038/s41598-018-24530-9.
15. Sully S, Burkepile DE, Donovan MK, Hodgson G, van Woesik R. A global analysis of coral bleaching over the past two decades. Nat Commun. 2019;10:1264. https://doi.org/10.1038/s41467-019-09238-2.
16. Thiem H. How does 2023–24 global coral bleaching compare to past events? ClimateGov 2024. https://www.climate.gov/news-features/featured-images/how-does-2023-24-global-coral-bleaching-compare-past-events. Accessed on October 14 2024.
17. Cinner JE, Maire E, Huchery C, MacNeil MA, Graham NAJ, Mora C, McClanahan TR, Barnes ML, Kittinger JN, Hicks CC, D'Agata S, Hoey AS, Gurney GG, Feary DA, Williams ID, Kulbicki M, Vigliola L, Wantiez L, Edgar GJ, Stuart-Smith RD, Sandin SA, Green A, Hardt MJ, Beger M, Friedlander AM, Wilson SK, Brokovich E, Brooks AJ, Cruz-Motta JJ, Booth DJ, Chabanet P, Gough C, Tupper M, Ferse SCA, Sumaila UR, Pardede S, Mouillot D. Gravity of human impacts mediates coral reef conservation gains. Proc Natl Acad Sci USA. 2018. https://doi.org/10.1073/pnas.1708001115.

18. Jury CP, Toonen RJ. Adaptive responses and local stressor mitigation drive coral resilience in warmer, more acidic oceans. Proc R Soc B. 2019;286:20190614. https://doi.org/10.1098/rspb.2019.0614.
19. Van Oppen MJH, Gates RD, Blackall LL, Cantin N, Chakravarti LJ, Chan WY, Cormick C, Crean A, Damjanovic K, Epstein H, Harrison PL, Jones TA, Miller M, Pears RJ, Peplow LM, Raftos DA, Schaffelke B, Stewart K, Torda G, Wachenfeld D, Weeks AR, Putnam HM. Shifting paradigms in restoration of the world's coral reefs. Glob Change Biol. 2017;23:3437–48. https://doi.org/10.1111/gcb.13647.
20. van Oppen MJH, Oliver JK, Putnam HM, Gates RD. Building coral reef resilience through assisted evolution. Proc Natl Acad Sci USA. 2015;112:2307–13. https://doi.org/10.1073/pnas.1422301112.
21. Anthony K, Bay LK, Costanza R, Firn J, Gunn J, Harrison P, Heyward A, Lundgren P, Mead D, Moore T, Mumby PJ, van Oppen MJH, Robertson J, Runge MC, Suggett DJ, Schaffelke B, Wachenfeld D, Walshe T. New interventions are needed to save coral reefs. Nat Ecol Evol. 2017;1:1420–2. https://doi.org/10.1038/s41559-017-0313-5.
22. Knowlton N, Corcoran E, Felis T, Ferse S, de Goeij J, Grottoli A, Harding S, Kleypas J, Mayfield A, Miller M, Obura D, Osuka K, Peixoto R, Randall C, Voolstra C, Wells S, Wild C. Rebuilding coral reefs: a decadal grand challenge. Int Coral Reef Soc Future Earth Coasts. 2021. https://doi.org/10.5364/NRKY9386.
23. National Academies of Sciences, Engineering, and Medicine. A research review of interventions to increase the persistence and resilience of coral reefs. Washington, D.C.: National Academies Press; 2019.
24. National Academies of Sciences, Engineering, and Medicine. A decision framework for interventions to increase the persistence and resilience of coral reefs. Washington, D.C.: National Academies Press; 2019.
25. Kleypas J, Allemand D, Anthony K, Baker AC, Beck MW, Hale LZ, Hilmi N, Hoegh-Guldberg O, Hughes T, Kaufman L, Kayanne H, Magnan AK, Mcleod E, Mumby P, Palumbi S, Richmond RH, Rinkevich B, Steneck RS, Voolstra CR, Wachenfeld D, Gattuso J-P. Designing a blueprint for coral reef survival. Biol Cons. 2021;257:109107. https://doi.org/10.1016/j.biocon.2021.109107.
26. Anthony KRN, Helmstedt KJ, Bay LK, Fidelman P, Hussey KE, Lundgren P, Mead D, McLeod IM, Mumby PJ, Newlands M, Schaffelke B, Wilson KA, Hardisty PE. Interventions to help coral reefs under global change—a complex decision challenge. PLoS ONE. 2020;15:e0236399. https://doi.org/10.1371/journal.pone.0236399.
27. Boström-Einarsson L, Babcock RC, Bayraktarov E, Ceccarelli D, Cook N, Ferse SCA, Hancock B, Harrison P, Hein M, Shaver E, Smith A, Suggett D, Stewart-Sinclair PJ, Vardi T, McLeod IM. Coral restoration—a systematic review of current methods, successes, failures and future directions. PLoS ONE. 2020;15:e0226631. https://doi.org/10.1371/journal.pone.0226631.
28. Delbeek JC. Coral farming: past, present and future trends. Aquarium Sci Conserv. 2001;3:171–81. https://doi.org/10.1023/A:1011306125934.
29. Young C, Schopmeyer S, Lirman D. A review of reef restoration and coral propagation using the threatened genus *Acropora* in the Caribbean and Western Atlantic. Bms. 2012;88:1075–98. https://doi.org/10.5343/bms.2011.1143.
30. Leal MC, Ferrier-Pagès C, Petersen D, Osinga R. Coral aquaculture: applying scientific knowledge to *ex situ* production. Rev Aquac. 2016;8:136–53. https://doi.org/10.1111/raq.12087.
31. Barton JA, Willis BL, Hutson KS. Coral propagation: a review of techniques for ornamental trade and reef restoration. Rev Aquac. 2017;9:238–56. https://doi.org/10.1111/raq.12135.
32. Forsman ZH, Kimokeo BK, Bird CE, Hunter CL, Toonen RJ. Coral farming: effects of light, water motion and artificial foods. J Mar Biol Ass. 2012;92:721–9. https://doi.org/10.1017/S0025315411001500.
33. Bayraktarov E, Stewart-Sinclair PJ, Brisbane S, Boström-Einarsson L, Saunders MI, Lovelock CE, Possingham HP, Mumby PJ, Wilson KA. Motivations, success, and cost of coral reef restoration. Restor Ecol. 2019;27:981–91. https://doi.org/10.1111/rec.12977.
34. Lirman D, Thyberg T, Herlan J, Hill C, Young-Lahiff C, Schopmeyer S, Huntington B, Santos R, Drury C. Propagation of the threatened staghorn coral *Acropora cervicornis*: methods to minimize the impacts of fragment collection and maximize production. Coral Reefs. 2010;29:729–35. https://doi.org/10.1007/s00338-010-0621-6.
35. 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;40:151–63. https://doi.org/10.1007/s00338-020-02024-3.
36. Caruso C, Hughes K, Drury C. Selecting heat-tolerant corals for proactive reef restoration. Front Mar Sci. 2021;8:632027. https://doi.org/10.3389/fmars.2021.632027.
37. Drury C, Caruso C, Quigley K. Selective breeding to enhance the adaptive potential of corals. In: van Oppen MJH, Aranda Lastra M, editors. Coral reef conservation and restoration in the omics age. Cham: Springer International Publishing; 2022. p. 71–84.
38. Darwin C. Geological observations on coral reefs, volcanic islands, and on South America: Being the geology of the voyage of the Beagle, under the command of Captain Fitzroy, RN, during the years 1832 to 1836. Smith, Elder, & Company; 1851.
39. Jokiel PL. Effects of water motion on reef corals. J Exp Mar Biol Ecol. 1978;35:87–97. https://doi.org/10.1016/0022-0981(78)90092-8.
40. Edmondson CH. Growth of Hawaiian Corals. Honolulu HI: Bernice P. Bishop Museum; 1929.
41. Sebens KP, Helmuth B, Carrington E, Agius B. Effects of water flow on growth and energetics of the scleractinian coral *Agaricia tenuifolia* in Belize. Coral Reefs. 2003;22:35–47. https://doi.org/10.1007/s00338-003-0277-6.
42. Nakamura T, Yamasaki H, van Woesik R. Water flow facilitates recovery from bleaching in the coral *Stylophora pistillata*. Mar Ecol Prog Ser. 2003;256:287–91. https://doi.org/10.3354/meps256287.
43. Nakamura T, van Woesik R, Yamasaki H. Photoinhibition of photosynthesis is reduced by water flow in the reef-building coral *Acropora digitifera*. Mar Ecol Prog Ser. 2005;301:109–18. https://doi.org/10.3354/meps301109.
44. Falter JL, Atkinson MJ, Lowe RJ, Monismith SG, Koseff JR. Effects of nonlocal turbulence on the mass transfer of dissolved species to reef corals. Limnol Oceanogr. 2007;52:274–85. https://doi.org/10.4319/lo.2007.52.1.0274.
45. McLachlan RH, Price JT, Solomon SL, Grottoli AG. Thirty years of coral heat-stress experiments: a review of methods. Coral Reefs. 2020;39:885–902. https://doi.org/10.1007/s00338-020-01931-9.
46. Hancock J, Barrows A, Roome T, Huffmyer A, Matsuda S, Munk N, Rahnke S, Drury C. Coral husbandry for ocean futures: leveraging abiotic factors to increase survivorship, growth, and resilience in juvenile *Montipora capitata*. Mar Ecol Prog Ser. 2021;657:123–33. https://doi.org/10.3354/meps13534.

47. Jokiel PL, Coles SL. Effects of temperature on the mortality and growth of Hawaiian reef corals. Mar Biol. 1977;43:201–8. https://doi.org/10.1007/BF00402312.
48. Jokiel PL, Morrissey JI. Water motion on coral reefs: evaluation of the "clod card" technique. Mar Ecol Prog Ser. 1993;93:175–81.
49. Stambler N, Popper N, Dubinsky Z, Stimson J. Effects of nutrient enrichment and water motion on the coral *Pocillopora damicornis*. Pac Sci. 1991;45:299–307.
50. Sebens KP, Grace SP, Helmuth B, Maney EJ Jr, Miles JS. Water flow and prey capture by three scleractinian corals, Madracis mirabilis, *Montastrea cavernosa* and Porites porites, in a field enclosure. Mar Biol. 1998;131:347–60. https://doi.org/10.1007/s002270050328.
51. Nakamura T, Yamasaki H. Requirement of water-flow for sustainable growth of *Pocilloporid* corals during high temperature periods. Mar Pollut Bull. 2005;50:1115–20. https://doi.org/10.1016/j.marpolbul.2005.06.025.
52. Comeau S, Edmunds P, Lantz C, Carpenter R. Water flow modulates the response of coral reef communities to ocean acidification. Sci Rep. 2014;4:6681.
53. Dennison WC, Barnes DJ. Effect of water motion on coral photosynthesis and calcification. J Exp Mar Biol Ecol. 1988;115:67–77. https://doi.org/10.1016/0022-0981(88)90190-6.
54. Schutter M, Crocker J, Paijmans A, Janse M, Osinga R, Verreth AJ, Wijffels RH. The effect of different flow regimes on the growth and metabolic rates of the scleractinian coral *Galaxea fascicularis*. Coral Reefs. 2010;29:737–48. https://doi.org/10.1007/s00338-010-0617-2.
55. Marti-Puig P, Forsman ZH, Haverkort-Yeh RD, Knapp IS, Maragos JE, Toonen RJ. Extreme phenotypic polymorphism in the coral genus <I>Pocillopora;</I> micro-morphology corresponds to mitochondrial groups, while colony morphology does not. BMS. 2014;90:211–31. https://doi.org/10.5343/bms.2012.1080.
56. Paz-García DA, Hellberg ME, García-de-León FJ, Balart EF. Switch between Morphospecies of *Pocillopora* Corals. Am Nat. 2015;186:434–40. https://doi.org/10.1086/682363.
57. Lowe RJ, Falter JL, Monismith SG, Atkinson MJ. A numerical study of circulation in a coastal reef-lagoon system. J Geophys Res. 2009. https://doi.org/10.1029/2008JC005081.
58. Lowe RJ, Falter JL, Bandet MD, Pawlak G, Atkinson MJ, Monismith SG, Koseff JR. Spectral wave dissipation over a barrier reef. J Geophys Res. 2005. https://doi.org/10.1029/2004JC002711.
59. Monismith SG. Hydrodynamics of coral reefs. Annu Rev Fluid Mech. 2007;39:37–55. https://doi.org/10.1146/annurev.fluid.38.050304.092125.
60. Rogers JS, Monismith SG, Koweek DA, Dunbar RB. Wave dynamics of a Pacific Atoll with high frictional effects. JGR Oceans. 2016;121:350–67. https://doi.org/10.1002/2015JC011170.
61. Franklin E, Jokiel P, Donahue M. Predictive modeling of coral distribution and abundance in the Hawaiian Islands. Mar Ecol Prog Ser. 2013;481:121–32. https://doi.org/10.3354/meps10252.
62. Hunter CL, Evans CW. Coral reefs in Kaneohe Bay, Hawaii: two centuries of western influence and two decades of data. Bull Mar Sci. 1995;57:501–15.
63. Bahr KD, Jokiel PL, Toonen RJ. The unnatural history of Kāneʻohe Bay: coral reef resilience in the face of centuries of anthropogenic impacts. PeerJ. 2015;3:e950. https://doi.org/10.7717/peerj.950.
64. Stimson J. Recovery of coral cover in records spanning 44 yr for reefs in Kāneʻohe Bay, Oaʻhu, Hawaiʻi. Coral Reefs. 2018;37:55–69. https://doi.org/10.1007/s00338-017-1633-2.
65. Forsman Z, Maurin P, Parry M, Chung A, Sartor C, Hixon M, Hughes K, Rodgers K, Knapp I, Gulko D, Franklin E, Del Rio TL, Chan N, Wolke C, Gates R, Toonen R. The first Hawaiʻi workshop for coral restoration & nurseries. Mar Policy. 2018;96:133–5. https://doi.org/10.1016/j.marpol.2018.08.009.
66. Knapp ISS, Forsman ZH, Greene A, Johnston EC, Bardin CE, Chan N, Wolke C, Gulko D, Toonen RJ. Coral micro-fragmentation assays for optimizing active reef restoration efforts. PeerJ. 2022;10:e13653. https://doi.org/10.7717/peerj.13653.
67. Rodgers KS, Jokiel PL, Brown EK, Hau S, Sparks R. Over a decade of change in spatial and temporal dynamics of Hawaiian coral reef communities. Pac Sci. 2015;69:1–13. https://doi.org/10.2984/69.1.1.
68. Jokiel PL, Coles SL. Response of Hawaiian and other Indo-Pacific reef corals to elevated temperature. Coral Reefs. 1990;8:155–62. https://doi.org/10.1007/BF00265006.
69. Bahr KD, Rodgers KS, Jokiel PL. Impact of three bleaching events on the reef resiliency of Kāneʻohe Bay, Hawaiʻi. Front Mar Sci. 2017;4:398. https://doi.org/10.3389/fmars.2017.00398.
70. Gorospe KD, Karl SA. Genetic relatedness does not retain spatial pattern across multiple spatial scales: dispersal and colonization in the coral, *Pocillopora damicornis*. Mol Ecol. 2013;22:3721–36.
71. Johnston EC, Forsman ZH, Toonen RJ. A simple molecular technique for distinguishing species reveals frequent misidentification of Hawaiian corals in the genus *Pocillopora*. PeerJ. 2018;6:e4355. https://doi.org/10.7717/peerj.4355.
72. Caruso C, De Rocha Souza M, Ruiz-Jones L, Conetta D, Hancock J, Hobbs C, Hobbs C, Kahkejian V, Kitchen R, Marin C, Monismith S, Madin J, Gates R, Drury C. Genetic patterns in *Montipora capitata* across an environmental mosaic in Kāneʻohe Bay, Oʻahu, Hawaiʻi. Mol Ecol. 2022;31:5201–13. https://doi.org/10.1111/mec.16655.
73. Johnston NK, Burns AS, Hay ME. Response of a temperate coral to temperature stress: a comparison of populations across sites. J Exp Mar Biol Ecol. 2023;560:151863. https://doi.org/10.1016/j.jembe.2022.151863.
74. Timmers MA, Jury CP, Vicente J, Bahr KD, Webb MK, Toonen RJ. Biodiversity of coral reef cryptobiota shuffles but does not decline under the combined stressors of ocean warming and acidification. Proc Natl Acad Sci USA. 2021;118:e2103275118. https://doi.org/10.1073/pnas.2103275118.
75. Bahr KD, Severino SJL, Tsang AO, Han JJ, Richards Dona A, Stender YO, Weible RM, Graham A, McGowan AE, Rodgers KS. The Hawaiian Koʻa card: coral health and bleaching assessment color reference card for Hawaiian corals. SN Appl Sci. 2020;2:1706. https://doi.org/10.1007/s42452-020-03487-3.
76. Yadav S, Roach TNF, McWilliam MJ, Caruso C, de Souza MR, Foley C, Allen C, Dilworth J, Huckeba J, Santoro EP, Wold R, Simpson J, Miller S, Hancock JR, Drury C, Madin JS. Fine-scale variability in coral bleaching and mortality during a marine heatwave. Front Mar Sci. 2023;10:1108365. https://doi.org/10.3389/fmars.2023.1108365.

77. Winston M, Oliver T, Couch C, Donovan MK, Asner GP, Conklin E, Fuller K, Grady BW, Huntington B, Kageyama K, Kindinger TL, Kozar K, Kramer L, Martinez T, McCutcheon A, McKenna S, Rodgers K, Shayler CK, Vargas-Angel B, Zgliczynski B. Coral taxonomy and local stressors drive bleaching prevalence across the Hawaiian Archipelago in 2019. PLoS ONE. 2022;17:e0269068. https://doi.org/10.1371/journal.pone.0269068.
78. Sebens KP. Adaptive responses to water flow: morphology, energetics, and distribution of reef corals. Proceedings of the 8th International Coral Reef Symposium 1997;2:1053–8.
79. Baird AH, Hughes TP. Competitive dominance by tabular corals: an experimental analysis of recruitment and survival of understorey assemblages. J Exp Mar Biol Ecol. 2000;251:117–32. https://doi.org/10.1016/S0022-0981(00)00209-4.
80. Nakamura T, van Woesik R. Water-flow rates and passive diffusion partially explain differential survival of corals during the 1998 bleaching event. Mar Ecol Prog Ser. 2001;212:301–4. https://doi.org/10.3354/meps212301.
81. Henley EM, Bouwmeester J, Jury CP, Toonen RJ, Quinn M, Lager CVA, Hagedorn M. Growth and survival among Hawaiian corals outplanted from tanks to an ocean nursery are driven by individual genotype and species differences rather than preconditioning to thermal stress. PeerJ. 2022;10:e13112. https://doi.org/10.7717/peerj.13112.
82. Todd PA. Morphological plasticity in scleractinian corals. Biol Rev. 2008;83:315–37. https://doi.org/10.1111/j.1469-185X.2008.00045.x.
83. Patterson MR, Sebens KP, Olson RR. In situ measurements of flow effects on primary production and dark respiration in reef corals. Limnol Oceanogr. 1991;36:936–48. https://doi.org/10.4319/lo.1991.36.5.0936.
84. Badgley BD, Lipschultz F, Sebens KP. Nitrate uptake by the reef coral *Diploria strigosa*: effects of concentration, water flow, and irradiance. Mar Biol. 2006;149:327–38. https://doi.org/10.1007/s00227-005-0180-5.