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Chimerism as a strategy to improve the resilience of boulder corals

Sandra Mendoza-Quiroz[1,2,3]✉, Margaret W. Miller[1,3]✉, Raúl Tecalco-Rentería[1,2], Gandhi Germán Ramírez-Tapia[1,2] & Anastazia T. Banaszak[2,3]

Chimeras form by the fusion of at least two distinct genets. Such genetic heterogeneity has been hypothesized to increase resilience of clonal invertebrates, and, given the changing environment of coral reefs, may provide important benefits in coral restoration. Intra- and interspecific pairs of six- and 18-month-old *Orbicella faveolata* and *O. annularis* recruits were actively staged in aquaria. Successful fusion was observed in intraspecific pairs, especially in the younger recruits of *O. faveolata* (70%). Fusion success between other intraspecific pairings ranged from 20 to 40%. Survival and growth of the fused chimeras were evaluated over two years following outplanting alongside large (>1 cm diameter) and small (<1 cm diameter) singleton recruits selected from the same cohorts. Chimeras showed 43–57% mortality over the first year, but no subsequent mortality and positive growth rates were maintained, even during the 6 months of the 2023 severe heatwave. Singletons of both size classes suffered continuous whole-colony mortality over the study period and negative growth rates during the heatwave. No chimeras formed between interspecific pairings over six months. This study provides important evidence of fusion success rates in Caribbean boulder corals and of the hypothesized greater resilience of chimeras in a restoration setting independent of colony size.

Keywords Mexican Caribbean, *Orbicella annularis*, *Orbicella faveolata*, Bleaching event, Coral recruits

Chimerism, a phenomenon in which an organism is formed by the fusion of two or more distinct genets, is widely documented in nature in unicellular eukaryotes, invertebrates, plants, algae as well as vertebrates such as fish, mammals, and humans[1,2]. It occurs naturally in modular invertebrates via colony fusion[3] and, in reef corals, colony fusion often results from gregarious larval settlement[4]. Corals with such genetic heterogeneity have been readily observed in wild populations[5–7], though the required genetic sampling (i.e., analyzing multiple tissue samples from locations spread across a colony to compare genotypes) likely underestimates prevalence[8]. Colony fusion has been repeatedly shown to benefit corals via the simple mechanism of size; larger chimeric juvenile sizes resulting from the fusion of young corals can show enhanced survivorship in this vulnerable life phase[9–11] and may thus be leveraged in a restoration context to help overcome persistent post-settlement mortality bottlenecks that impair the efficiency of coral seeding and population enhancement efforts[12].

The likelihood of colony fusion is expected to be affected by age and genetic relatedness. The fusion of allogenic colonies is believed to be facilitated in young colonies due to the immaturity of histocompatibility and immune responses, and higher genetic relatedness provides less contrast to trigger histocompatibility systems. Several studies in corals have suggested that four months of age is a threshold for successful fusion[13,14], though opportunistic fusion has been observed in juvenile and adult corals at older ages[15].

In the Anthropocene era, rapidly changing climate as well as local environmental impacts present existential threats to coral populations and coral reef ecosystems. There is considerable debate as to whether reef-building corals have adequate adaptive capacity that can be expressed rapidly enough to persist under such threats[16]. It has been more recently hypothesized that chimerism may provide an added source of both genetic and phenotypic variability as well as enhanced resilience in specific environmental conditions, through an enhanced 'genetic repertoire'. This advantage may arise from both drawing on genetic variants of multiple individual and from the potential adjustment of somatic composition among the constituent genets[17]. Partial, short-term tests of this hypothesis have involved comparing the performance of chimeric and singleton recruits of brooding coral species under ~ one month laboratory thermal stress exposures[18] and 48 h field stress exposures by moving recruits to shallow depths (10 m to 2 m)[19]. The latter study compared gene expression between chimeras and singletons, concluding that chimeras show greater constitutive expression of stress response genes, suggesting that 'frontloading' of transcriptional stress response may be a genetic mechanism contributing to greater chimeric resilience[19]. Non-silent intracolony Single Nucleotide Polymorphisms (SNPs) have also been reported

[1]SECORE International, Miami 33145, FL, USA. [2]Unidad Académica de Sistemas Arrecifales, Universidad Nacional Autónoma de México, Puerto Morelos, 77580 Quintana Roo, Mexico. [3]Sandra Mendoza-Quiroz, Margaret W. Miller and Anastazia T. Banaszak contributed equally to this work. ✉email: s.mendoza@secore.org; m.miller@secore.org

in *Pocillopora acuta*[7], validating the concept of an enhanced 'genetic repertoire' in chimeric corals. Notably, no prior studies have addressed this hypothesis of increase stress resilience of chimeras in the context of Caribbean corals, broadcast spawning species, nor long-term performance under field conditions.

Our two-phased study addressed the formation and resilience of chimeras in the endangered Caribbean reef-building corals, *Orbicella annularis* and *O. faveolata*. In phase one, pairs of corals were placed in close contact and evaluated in the lab over six months to document their likelihood of fusing into chimeric colonies and the influence of polyp age (Fig. 1A). In phase two, the resulting fused chimeras of each species were outplanted to a natural reef, alongside singleton colonies of two separate size classes from the same-aged cohorts (Fig. 1B). Their survivorship and growth were followed over an additional two years, during which the record-breaking 2023 heat wave[20] provided a unique opportunity to evaluate long-term resilience of chimeras vs. singletons during a severe bleaching event.

Methods

In September 2019 and 2020, spawning of *Orbicella annularis* and *O. faveolata* colonies was monitored in Jardines and La Bocana reefs in Puerto Morelos, Quintana Roo, Mexico, between the fourth and ninth night after full moon, according to local spawning predictions for these species (http://crc.reefresilience.org/wp-content/uploads/2020/06/Coral-Spawning-Predictions-Puerto-Morelos-2020.pdf). When spawning occurred, gametes were collected using conical collectors placed over the colonies[21].

Gametes were returned to the Reef Systems Academic Unit in Puerto Morelos for fertilization and larval culture. For each cohort, gamete bundles containing both eggs and sperm from four or five parent colonies (details in Suppl. Table 1) were mixed for one hour, after which fertilization was verified via observation of the

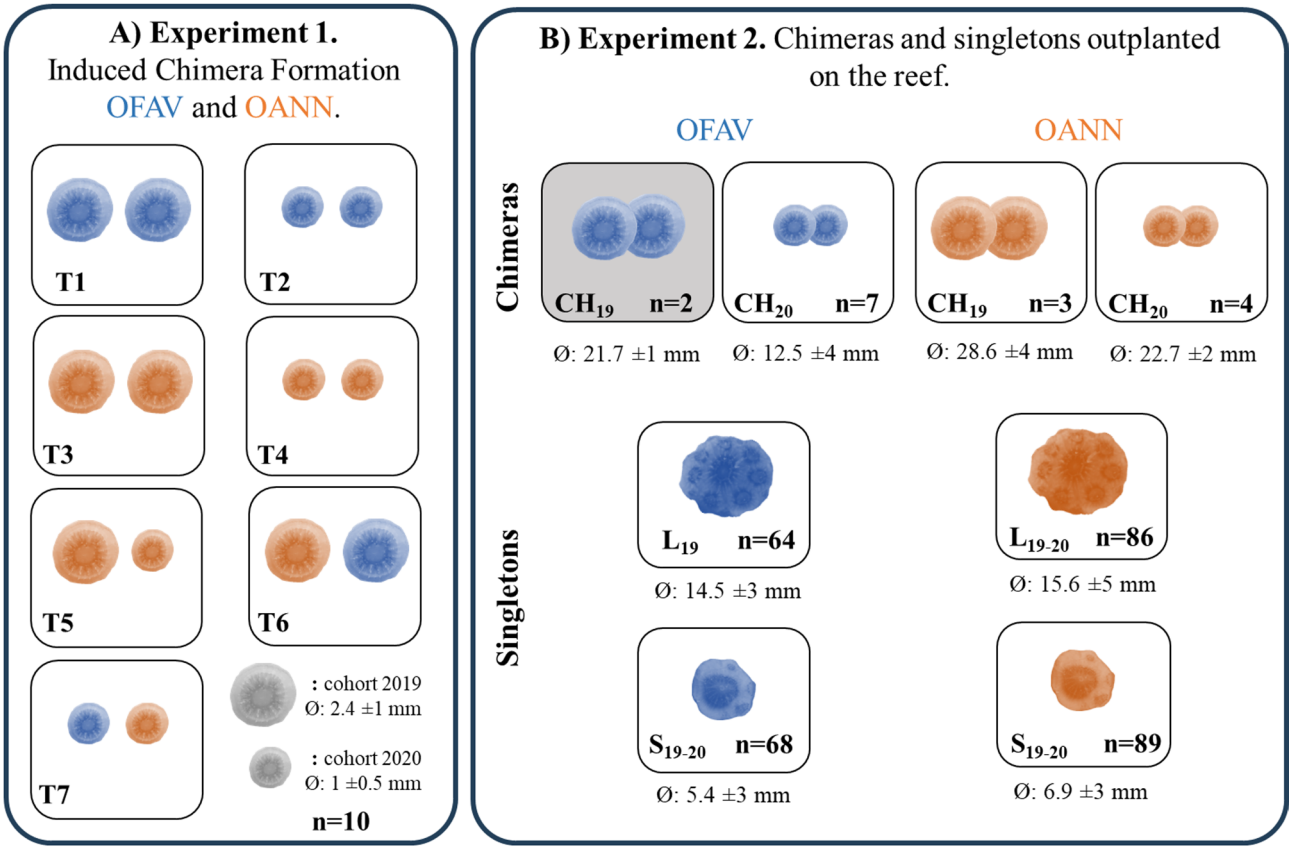

Fig. 1. Experimental treatments with *Orbicella* species recruits from two cohorts born in 2019 and 2020 (indicated by subscripts and size of the polyp icons). **(A)** Experiment 1: Staged pairs of *Orbicella faveolata* (blue) and *Orbicella annularis* (orange) recruits from two cohorts examined for induced chimera formation. The 2019 cohort was 6 mos of age and the 2020 cohort was 18 mos of age at the start of this experiment. The first four treatments (T_1-T_4) matched the same species and cohorts (intraspecific pairs). The remaining three treatments (T_5-T_7) combined pairs of recruits from different species or cohorts. **(B)** Experiment 2: All successfully fused chimeras of each *Orbicella* species from Expt 1 were outplanted on the reef alongside singleton colonies divided into two size class treatments: Large (L; > 10 mm) and Small (S; < 10 mm). Members of singleton treatments were pooled from colonies of both age cohorts (indicated by subscripts). The shaded box indicates chimeras which were excluded from statistical analysis in order to standardize colony size between chimeras and large singletons. n: number of replicates per treatment; Ø indicates mean diameter (± 1 standard deviation) per treatment.

first division of embryos and quantified (# dividing embryos/ [# dividing embryos + # nondividing eggs])[21]. The embryos and larvae were reared in an indoor static seawater system under controlled conditions. The seawater was pretreated with ultraviolet C radiation and filtered for sediment and particle retention to 1 micron, with 30% water changes every third day. When the larvae were ready to settle (~ 60 h post fertilization), they were offered cement (type II tetrapod[22]) and 3-D printed ceramic substrates, previously conditioned in the sea for two months. After settlement, the corals were fed for two weeks with CoralAmino and Koralle-VM liquid supplements (Brightwell Aquatics, USA) following the manufacturer's recommendations. The substrates with settled corals were then transferred to a closed, recirculating, outdoor aquarium system. Feeding continued three times a week with recently hatched *Artemia* nauplii. Natural light (350–480 µmol quanta m^{-2} s^{-1}), temperature (27–28 °C), and salinity (35–37 ppt) were continuously monitored and regulated as needed. The seawater in the outdoor system was filtered through 20-micron cartridge filters, and 30% was renewed every third day.

Experiment 1 was initiated in March 2021 to analyze the potential for inducing chimera formation in *O. annularis* and *O. faveolata* colonies of different ages (18 months old from the 2019 cohort, mean colony diameter 2.4 ± 1 mm and 6 months of age from the 2020 cohort, mean colony diameter 1 ± 0.5 mm). Ten replicates of each of seven treatment combinations (Fig. 1A) were constructed by carefully detaching each colony from its substrate using a Dremel 3000 rotary tool (Bosch Power Tools BV, The Netherlands) along with ~ 3 mm of the substrate and adhering each to a new substrate with Apoxie sculp (Aves Studio, LLC, USA). Each replicate consisted of two colonies placed at a 3 to 5 mm distance between them on a square tile (3 cm x 3 cm) composed of limestone encrusted with fragments of shells and corals. To identify the species throughout the study, a mark was placed in the lower right corner of every tile with Colony 1 glued to the left side and Colony 2 glued to the right side. A replicate number was marked under the substrate. The colony pairs were reared in the lab in an outdoor aquarium system under the previously mentioned conditions for 6 months. Fusion and survival were evaluated monthly using images of the substrates to identify fusion or rejection between colonies. Specifically, five types of interaction were distinguished (Fig. 2). No Rejection or Fusion (NRF) was observed when each colony grew away from the other without their tissues coming into contact. Fusion (F) of tissue between colonies was determined when the tissue of each colony was uniformly united and the boundary between the colonies could not be visually distinguished; Rejection (R) was determined when colonies remained in contact but the boundary between the colonies could be distinguished; Rejection Mortality (RM) was distinguished by observing tissue mortality of one or both colonies in the contact area between the colonies, as opposed to Natural Mortality (NM) which was designated when mortality of one of the colonies occurred prior to them growing into contact, primarily at the beginning of the experiment (and likely attributable to the initial handling when attaching the colonies to the tiles). The proportion of interaction types between age treatments for each species (i.e. T1 versus T2, and T3 vs. T4, Fig. 1A) was compared using the X^2 test in JASP v 0.19 software[23] to determine if the likelihood of Fusion and Rejection responses depended on age. For this analysis, Natural Mortality and No Rejection or Fusion interaction types were excluded (as no interaction between these colony pairs in fact occurred) and Rejection Mortality and Rejection categories were pooled.

In Experiment 2, fused chimeras formed from both species were outplanted on Jardines reef in September 2021 to evaluate their relative performance alongside singletons of different sizes. The overall density of outplants was five colonies per m^2. Small (S; <1 cm diameter) and large (L; >1 cm diameter) singleton colonies were selected from a pooled population of the same cohorts (~ 1 year and ~ 2 years of age) that had been cultured under the same conditions (that is, single colonies in each size class were of mixed ages). Sample sizes for each treatment (n) are given in Fig. 1B. Surveys were conducted at 1, 3, 6, 13, and 17 months after outplanting to assess colony survival (by visual inspection) and size (diameter, by in situ measurement using a millimeter-graduated ruler).

Due to the unprecedented and unexpected heatwave that affected the region during May-December of 2023[20] (months 20–27 of Expt 2), additional surveys were conducted in months 24 (survival and size; at 17.6 DHW), 26 (survival; at 9.9 DHW) and 28 (survival; after return to 0 DHW). Kaplan-Meyer survival analyses followed by Log-rank (Mantel-Haenszel) tests were performed separately for each species to compare survival curves across the three treatments (Large singletons, Small singletons and Chimeras). The Kaplan-Meyer survival analysis with Log-rank test was repeated for *O. faveolata*, excluding the two larger chimeras from the 2019 cohort (resulting in a total of $n = 7$ chimeras) to control for size between the chimera and large singleton treatments (see sizes in Fig. 1B). Due to the small sample size of chimeras and the consequent unbalanced nature of their comparison to singletons, we also performed nonparametric bootstrapping using $n = 1000$ resamplings of the data, refitting the Kaplan-Meier curves for each iteration and visualized these with 95% confidence intervals.

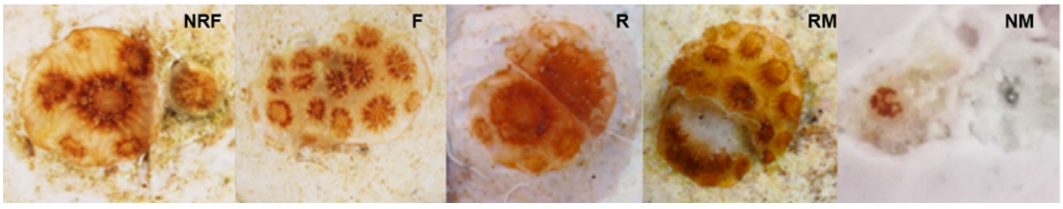

Fig. 2. Interaction responses during chimera formation that were recorded in *Orbicella faveolata* and *O. annularis*. NRF: No rejection or fusion, F: Fusion, R: Rejection, RM: Rejection mortality and NM: Natural mortality. Monthly interactions are shown in Supplementary Fig. S1.

For each colony that survived 24 months, growth was calculated as the change in diameter (cm) per month during the pre-heatwave interval (i.e. months 0–17) and during the heatwave (interval from months 17–24). A nonparametric Wilcoxon paired signed-ranks test was performed within each colony-type treatment to compare growth before vs. during the heatwave. All statistical analyses were performed in JASP v 0.19[23] or Rstudio 2025.09.2 (RStudio 2025.09.2 + 418 "Cucumberleaf Sunflower" Release (12f6d5e22720bd78dbd926bb344efe12d0dce83d, 2025-10-20) for Windows).

Results

Experiment 1: interactions among intra- and interspecific pairs

The full time course of interactions among colony pairs in the seven treatments is given in Suppl Fig. 1. The fusion success of *Orbicella faveolata* after six months was dependent on age ($X^2 = 5.051$; $p = 0.025$ for T_1 versus T_2; Fig. 1A), with 20% of older colony pairs and 70% of younger pairs forming integrated chimeras (and all remaining replicates showing rejection; Fig. 3A). *Orbicella annularis* pairs showed no influence of age ($X^2 = 0.00$; $p = 1.00$ for T_3 versus $T_{4;}$ Fig. 1A), with the proportion of Fusion: Rejection of 40%:60% in both age treatments (Fig. 3B). Meanwhile, no fused chimeras were formed in any 'mismatched' pair treatments (i.e., neither interspecies T_{6-7} nor different aged pairs, T_5, Fig. 1A) with active rejection observed in at least 80% of these treatment pairs (Fig. 3C).

Experiment 2: chimeras vs. singleton performance on the reef

Survival

Chimeras of both *Orbicella faveolata* and *O. annularis* outplanted on the reef had a higher survival probability than singletons. For *O. faveolata* survival curves (Fig. 4A), the Log-rank (Mantel-Haenszel) test indicated significant differences among all treatments (Log-rank test $X^2 = 16.17$; $p < 0.001$). Chimera survival at the end of the experiment (57%) was 12 times higher than the large singleton colonies (4.5%). Although these large *O.*

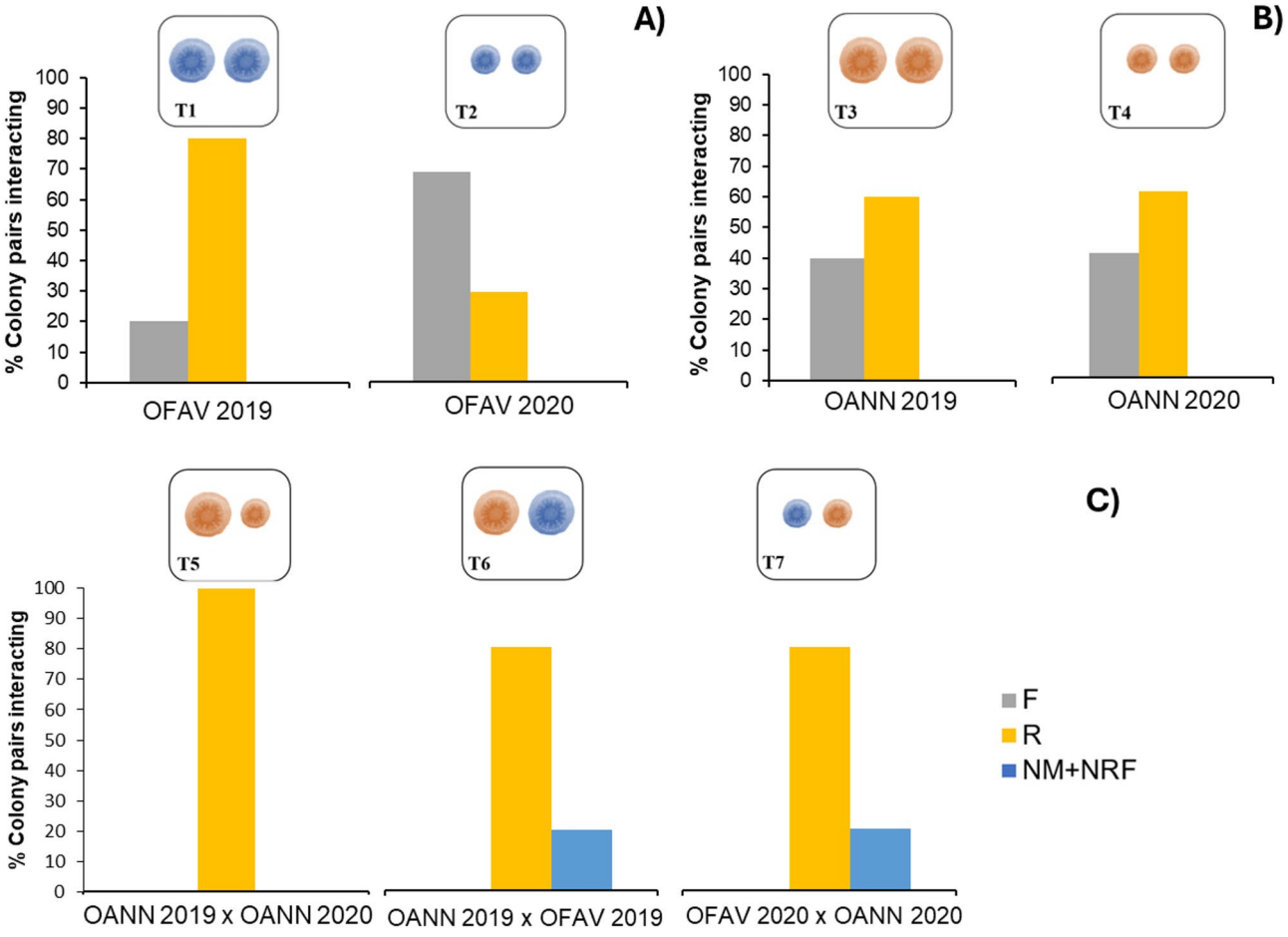

Fig. 3. Frequency of interaction responses (see Fig. 2 for definitions) in colony pairs for each treatment (described in Fig. 1A) after 6 months of rearing under laboratory conditions. (A) *Orbicella faveolata* (OFAV) and (B) *Orbicella annularis* (OANN) treatments with matched pairs from 2019 and 2020 cohorts. (C) 'Mismatched' treatments with pairs combining different species or age-cohorts. NM + NRF: Natural Mortality plus No Rejection or Fusion, F: Fusion, R: Rejection (including Rejection Mortality, RM). $n = 10$ replicate pairs for each treatment.

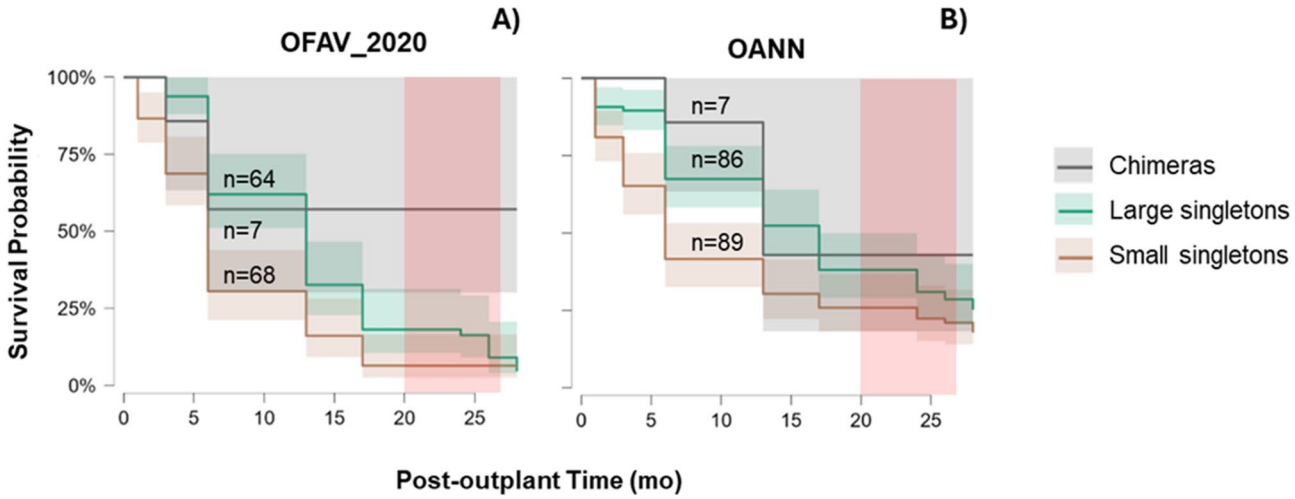

Fig. 4. Kaplan-Meier survival plots (with shaded 95% confidence intervals) of chimeras and singletons of *Orbicella faveolata* (A; OFAV) and *O. annularis* (B; OANN) outplanted on the reef. (A) Survival probability plot of OFAV chimeras from 2020 cohort only (larger, 2019 chimeras were excluded to better match the size between chimeras (for this subset, Ø: 12.5 ± 4 mm (mean ± SD) and the large singletons (Ø: 14.5 ± 3 mm)). The red band indicates the duration of the severe heatwave during 2023 (20–27 months after outplanting).

faveolata singletons had higher survivorship than the small singletons throughout most of the study, they ended slightly lower than smalls (at 6.4%). These results (Fig. 4A) are for the comparison in which the larger chimeras (from the 2019 cohort; see Fig. 1B) are excluded to control for size differences between chimeras (cohort 2020; Ø: 12.5 ± 4 mm) and large singletons treatments (Ø: 14.5 ± 3 mm). A similar pattern and statistical result occurs when all the *O. faveolata* chimeras are included ($n = 9$; Suppl. Figure 2). For *O. annularis*, the Log-rank test also indicated significant variation in survival patterns among treatments (Log-rank test $X^2 = 7.7$; $p = 0.018$) (Fig. 4B). Chimeras again showed the highest survival (43%) followed by large (25%) and small (18%) singletons, though these three curves have overlapping confidence intervals. For both species, the survival probability of the chimeras remained constant after an initial post-outplant decline (six months in *O. faveolata* and one year in *O. annularis*), even including the heatwave period, whereas singletons of both species showed continued mortality throughout the 28 months of post-outplant observations. Bootstrapping the Kaplan-Meier curves for each species showed an overall similar pattern with clear differentiation of confidence intervals between chimeras and singletons for *O. faveolata*, and somewhat greater overlap for *O. annularis* (Suppl. Figure 3).

Growth

For both *Orbicella* species (combined due to low numbers of surviving colonies), the monthly change in colony diameter was highly variable among individual colonies of all treatments. It was positive on average for the period prior to the heatwave event (up to 17 months after outplanting) for all treatments (Fig. 5). During the heatwave, growth was negative on average for both large and small singletons (Fig. 5B-C), whereas chimeras maintained positive growth (Fig. 5A). Results of the nonparametric Wilcoxon Signed-Ranks test indicated that chimeras showed no change in diameter ($W = 11.0$; $p = 0.500$), whereas singletons showed significant declines in growth rate (to negative means) after the heatwave event for both small ($W = 100.0$; $p < 0.001$) and large ($W = 174$; $p = 0.004$) treatments (Fig. 5).

Discussion

The results of our current study provide evidence to support the hypothesis proposed by Rinkevich (2019) that chimerism improves coral resilience. Prior literature on fusion in reef-building corals has focused on branching Indo-Pacific species, dominated by *Stylophora pistillata*, *Pocillopora* spp., and *Acropora* spp[4,9–11,13,18,19,24,25]. Here, we extend characterization of formation and field performance of chimeras to the Caribbean reef-building boulder coral *Orbicella* spp. including during an intense heatwave event.

Bi-chimerism (i.e., chimeras comprised of precisely two genets, as addressed in this current study) confers a substantial benefit to *Orbicella* spp. during the crucial juvenile life history phase (Fig. 4), which has been identified as the most important bottleneck to efficiently extending coral population enhancement to ecologically and evolutionarily meaningful scales[12,26]. For *O. faveolata*, we found a 12x improvement in post-outplant survivorship (Fig. 4A), whereas for *O. annularis*, though survivorship was improved over singletons, the margin was lower than the 2x (based on the higher survival of singletons; Fig. 4B) that would be required to compensate for the number of initial settling larvae.

Our results also support the hypothesis that chimeras can display increased stress resilience[17] and, at least for *O. faveolata*, this effect is not accounted for simply by increased colony size. The occurrence of the worst marine heatwave to date during the latter portion of our second, field-based experiment (months 20–24)[20] provided an important real-world test of climate stress resilience and confirmed that chimeras performed better under long-

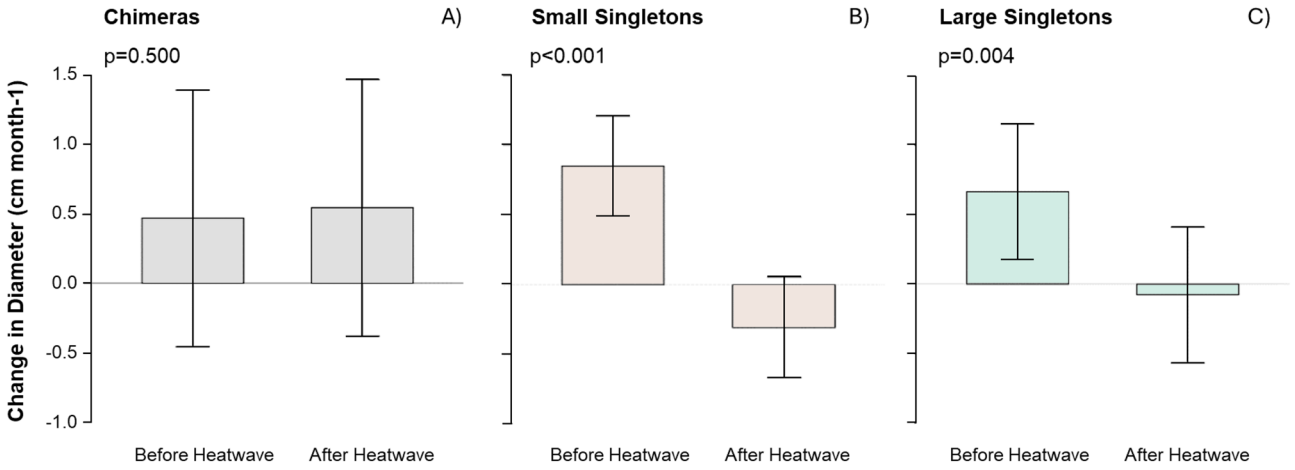

Fig. 5. Change in diameter of *Orbicella* of three colony types, chimeras (A) and two size classes of singletons (B: Small and C: Large) that survived the entire study duration outplanted on the reef. The two species are combined due to the low number of surviving colonies (total $n = 6$ for Chimeras, $n = 14$ for Small Singletons; $n = 34$ for Large Singletons). Growth intervals are depicted before (~ 17 mos) and during (months 17–24 mos) a regional severe heatwave. Bar plots show mean values; error bars represent 95% CI.

term (> six months) temperature stress. Chimeras of both species showed no mortality during this heatwave and no effect on their albeit highly variable growth rates, in comparison to continued whole colony mortality (Fig. 4) and reduction to mean negative growth rates of singletons (Fig. 5). The mechanisms by which genetic heterogeneity confer this increased heat resistance warrants further investigation.

The hypothesis that chimerism may confer particular resilience to climate stressors[17] has previously had limited empirical support. Jiang et al.[25] exposed *Acropora austera* chimeras resulting from aggregated settlement (hence with up to seven fused polyps per colony) and singletons to short term (two-week) laboratory exposure to elevated temperature and pCO_2. The rate of symbiont uptake and overall survivorship were higher for chimeras irrespective of temperature and pCO2 exposure treatments, likely simply attributable to larger size (see below). However, the polyp-specific growth rate was lower for chimeras than singletons, and even more so in the elevated temperature treatment. Vidal-Dupiol et al.[19] induced a multifaceted experimental stress (elevated temperature and light) on chimeras and singletons of *Stylophora pistillata* that had been growing at 10 m depth in a field nursey for one year by raising them to 2 m depth for 48 h to compare their transcriptomes. While the chimeras had displayed higher survivorship over the previous year of growout in the field nursery, no mortality was observed in the short stress exposure. However, the transcriptomic comparison of the stressed and unstressed chimeras versus singletons suggested that the chimeras had fundamental differences in their transcriptomic stress response, with greater constitutive expression of stress genes. This suggests a mechanism that could account for greater stress resistance of chimeras.

Many previous studies have demonstrated enhanced performance of coral chimeras in various settings and response types, such as field survivorship[9,10,19], symbiosis establishment or bleaching[25,27], or disease resilience[28]. However, all of these previous examples are confounded by, and often explicitly attributed to, colony size. That is, fused corals are larger, and larger corals have higher survivability in general due to their modular architecture. For example, Williamson et al.[28] showed higher survival probability of chimeric brain coral recruits with more component genets during experimental disease exposure. However, the chimeras with more contributing genets were larger, and thus less likely to succumb to gradual disease mortality. We specifically incorporated conspecific singleton colonies from multiple age cohorts to attempt to control for chimera size, with partial success. Although the *O. annularis* chimeras were still substantially larger than any of the singletons, in *O. faveolata*, our chimeras from the 2020 cohort had a mean (± SE) diameter of 12.7 ± 4 mm compared to the Large Singleton treatment with a diameter of 14.7 ± 3 mm. These *O. faveolata* chimeras out-performed these singletons of similar size (Fig. 4A), especially during heatwave conditions (Fig. 5), despite quite low sample sizes.

We show that the key Caribbean reef-building corals, *Orbicella faveolata* and *Orbicella annularis*, both broadcast spawning hermaphroditic boulder corals, are capable of colony fusion up to 18 months of age. Indeed, *O. annularis* showed no effect of age (i.e., identical fusion rates between 6- and 18-month-old recruits, Fig. 3B) while *O. faveolata* demonstrated the expected age effect with younger colonies showing 2.5x higher fusion rates than older (Fig. 3A); but all were at least 50% older than the four-month age threshold previously described in Pacific branching corals[13,14]. Previous work has also suggested different age cutoffs when rejection responses mature to a level that fusion is not successful; e.g., Nozawa & Hirose[15] showed successful fusion of coral recruits up to three years of age.

In addition to immaturity of immune and histocompatibility systems, genetic relatedness is also expected to influence allorecognition and hence the likelihood of successful colony fusion in modular invertebrates[5,11]. The results of our study show that chimeras do not form between *O. faveolata* and *O. annularis* thus suggesting that there is some level of non-self-recognition even in early-stage corals[29]. One prior study suggests that inter-species chimeric tissue is implicated in a pathological condition in *Montipora* spp. corals[30], though earlier work

suggested that xenografts could be successful between closely related species of *Hydra* (reviewed by Campbell and Bibb[31]. Meanwhile, intraspecific genetic relatedness was not strictly controlled in our fusion experiment as individual colonies were haphazardly selected from fertilization batches of either four or five parent colonies. Hence, it is possible that each pair represented either sibs, half-sibs, or un-related pairs, with the likelihood of related pairs (conferring higher fusion probability) being theoretically higher in the cohorts with fewer contributing parents (i.e., the younger cohort of *O. faveolata* and the older cohort of *O. annularis*; see Suppl. Table 1). Thus, we conclude that the observed age effect for *O. faveolata* fusion success may have been enhanced by potentially greater genetic relatedness in the younger treatment given that there were four contributing parents (compared to five for the older ones).

Our results confirm previous calls that the greater performance of chimeric coral recruits might be leveraged to improve the outcomes of coral restoration[10,17] especially because many restoration efforts now consider how corals will respond to the changing conditions of today's oceans. Chimerism may serve to increase genetic variation of coral populations in the face of global climate change[17]. Our experiment involved 'constructing' two-entity chimera by gluing two young singleton recruits in close proximity on a new substrate and this was a labor-intensive process not suitable for restoration scale application. Nonetheless, corals often settle gregariously and fuse naturally, so chimeras certainly enter restoration pipelines at some frequency. However, we currently lack techniques to control this process, making it challenging to leverage bi-chimerism actively in large scale restoration. It is possible that limiting co-settling larval batches to highly related, full-sib crosses would increase the frequency of polyp fusion[4,5], but this confounds (or at best complicates) the intent to maximize genetic diversity in resultant outplanted cohorts[32]. Studies have also shown that increasing the larval supply (relative to available settlement space) can also increase aggregated settlement[33], but gregarious settlement can be overdone, resulting in density-dependent mortality of settlers[34–36] and likely increased frequency of multi-entity versus bi-chimeras. While not studied here, multi-chimeras (i.e., chimeras formed from a larger contributing number of initial polyps/genets) might have a higher threshold of survival to represent a net, per-larva benefit. For example, Ligson et al.[24] showed survivorship to peak at a group size of 6–9 (across different group sizes of aggregated/fused settlers up to 28) but with a maximum survival increment of only about 3x, and Shefy et al.[10] showed similar survival probabilities, less than 2x, for so-called bi-chimeras and multi-entity chimeras. Thus, in larval-limited restoration practices, two-entity chimeras may be expected to provide greater net benefit over larger entities. Considerable work remains to develop effective means to control the spatial distribution of gregarious settlement to encourage chimera formation while ensuring net benefit in the per-larva production of surviving corals on the reef.

Data availability

All data generated or analyzed during this study are included in Supplementary Information files accompanying this publication.

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Author contributions

SQM, MWM, and ATB conceived the study, SQM, RTR, and GGRT performed the experiments, SQM and MWM analyzed the results, and SQM, MWM, and ATB drafted the manuscript. All authors reviewed the manuscript.

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Competing interests

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Additional information

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Correspondence and requests for materials should be addressed to S.M.-Q. or M.W.M.