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Exploring Traits of Engineered Coral Entities to be Employed in Reef Restoration

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Abstract: Aggregated settlement of coral larvae results in a complex array of compatible (chimerism) and incompatible (rejection) allogenic responses. Each chimeric assemblage is considered as a distinct biological entity, subjected to selection, however, the literature lacks the evolutionary and ecological functions assigned to these units of selection. Here, we examined the effects of creating chimera/rejecting partners in terms of growth and survival under prolonged field conditions. Bi/multichimeras, bi/multi-rejecting entities, and genetically homogenous colonies (GHC) of the coral *Stylophora pistillata* were monitored under prolonged field conditions in a mid-water floating nursery in the northern Red Sea. Results revealed an increased aerial size and aeroxial ecological volume for rejected and chimeric entities compared to GHCs. At age 18 months, there were no significant differences in these parameters among the entities and traits, and rejecting partners did not differ from GHC. However, survival probabilities were significantly higher for chimeras that further revealed disparate initiation of up-growing branches and high diversity of chimeric phenotypes. These results suggest enhanced fitness for chimerism, augmenting earlier alluded chimeric benefits that trail the increased size at crucial early life-stages. Adding chimerism to the tool-box of reef restoration may enhance coral fitness in mitigating anthropogenic/climate change impacts.

Keywords: coral chimerism; growth rates; survival; genetic homogenous; ecological engineering; active restoration; climate change; costs and benefits; nursery; coral transplantation

1. Introduction

Chimeras are organisms possessing simultaneously cells, tissues, or organs originating from two or more conspecific individuals [1] and natural chimerism has been documented in at least 10 phyla including protists, animals (vertebrates and invertebrates, marine and terrestrial), plants, and fungi [2–9]. One of the taxa studied for chimerism are reef building corals that document a widely distributed chimerism in nature, recorded already from millions of year old fossils [10,11] and from a variety of contemporary coral species [2,12–17]. In colonial invertebrates such as sponges, cnidarians, and tunicates, chimerism is the outcome of allogenic fusions between two or more closely-settled colonies, young or adults [18–31], or following fusions between larvae or among embryos [32–35]. The literature reveals that when two or more conspecifics of many marine invertebrates come into direct contact, they either fuse to form a chimeric entity or reject each other, creating tissue necroses [14,20,21,26–31,36]. There are cases where no fusions nor tissue destructions are developing, the outcomes of indifference [37–39]. In many marine invertebrates including reef corals, allogeneic fusions and chimeras development often occur at early astogenic stages, before the maturation of the

allorecognition machinery (usually within a define window in astogeny), and the capacity to fuse has also been hypothesized to be associated with genetic relatedness [8,20,26,27,29,30,36].

In reef corals, although fusion among aggregated juveniles was first described in 1902 [40], and various aspects of chimerism were followed by numerous studies (literature above), the literature is deficient on the costs and benefits of chimerism, primarily when considering prolonged field conditions. In colonial ascidians, the cost for chimerism is associated with colonial resorption and the threat of germline parasitism [29,41–44]. In hard and soft coral chimeras, absorption or post-fusion rejection was sometimes documented [28,29,45] as overgrowth and delayed cytotoxicity [46,47], and in reef building hydrozoans such as *Millepora* growth without calcification has also been documented [48]. However, despite the cost involved in chimerism and aggregated settlement, chimerism carries some major benefits. In corals, the benefits of chimerism include the increase in genotypic diversity [2,12,15], fast wound healing [25], and increase in size, with consequences in traits like earlier sexual maturity and increased survival [14,26,49]. Under laboratory settings, chimeras of the branching coral species *Stylophora pistillata* grew to larger colonies than genetic homogenous colonies (GHC; regular colonies) in the first seven months following settlement, where chimeras of multi-partners (multi-chimeras) were bigger than two partner chimeras (bi-chimeras) and had higher survival rates [26]. Similarly, eight month old chimeric colonies of *Pocillopora damicornis* exhibited larger sizes and higher survival rates for multi-chimeras and bi-chimeras [49]. Puill-Stefan et al. [14] also reported an increased surface area of four month old chimeric *Acropora millepora* colonies studied in two different regions.

The overall proposed array of benefits for coral chimerism have led to the proposition that chimerism can be regarded as an evolutionary rescue tool for accelerating adaptive responses to environmental impacts(including global climate change) and as an integral part of the active reef restoration tenet [50–52]. Although studies on coral chimerism were conducted primarily in the laboratory or in short-term field experiments [14,26,49], harnessing chimerism and its advantages to the active reef restoration 'toolbox' may clearly alleviate or mitigate climate change impacts [50–52]. However, comprehensive studies are required to elucidate the advantages, disadvantages, and properties of chimerism under prolonged field settings. Here, for the first time, we followed, under field conditions, chimeric and rejecting *S. pistillata* entities interacting with sibling partners for several biological traits (growth, size, survival) compared to genetic homogenous colonies (GHC).

This study revealed that chimeras are augmented in size compared to GHC following the crucial first few months under field conditions, levelled at 1.5-year-old colonies. However, significantly enhanced survival rates in chimeras were observed after a year-long field condition. Traits for rejecting partners did not differ from GHC. For the first time, we reveal an effect of chimerism on the coral early branching astogeny. Results are discussed following the deliberations of employing chimerism as an integral part of the ecological engineering toolbox developed for active reef restoration.

2. Materials and Methods

2.1. Planulae Collection, Rearing, and Creating Chimeras

Coral planulae were collected with planulae traps during two reproductive seasons (2018–2019) from the shallow reef (3–5 m) in front of the Inter University Institute (IUI) for Marine Science in Eilat (Gulf of Eilat/Aqaba, Red Sea). Planulae traps were placed at sunset over healthy, large (15–25 cm diameter) *Stylophora pistillata* colonies and collected the following morning as described in Shefy et al. [53]. The content of each trap was placed in separate Petri dishes (PD) covered by a polyester film with a double-sided matte ("Maylor paper"; manufactured by Jolybar, Israel), preconditioned for one month for a microbial film that encourages larval settlement [26,54]. Planulae in each PD (10–150) were siblings, sharing the same maternal colony and an unknown sperm donor. PDs were then transferred to a running seawater table, where each PD was filled with seawater and sealed with a lid to minimize evaporation, secured by a weight (small stone). The PDs were placed in the water table in a way that ~75% of each PD was submerged in the water to keep ambient water

temperature. Water in each PD was exchanged daily. Then, two settlement patterns (aggregation and solitary) were followed. Two or more planulae that had been settled when touching each other or were at distances shorter than 1 mm were labeled as settlements in aggregation, while settled planulae >1 mm away, were labeled as solitary settlements. Aggregations with two primary polyps that fused were termed as 'bi-chimeras' and aggregation with more than two fuse genotypes were term as 'multi-chimeras'. Attaching primary polyps that did not fuse were labeled as 'bi-rejected' or 'multi-rejected' entities (as in aggregations, respectively). All selected rejected entities (colonies that showed incompatible reaction) exhibited a relatively stable connection between the genotypes (i.e., did not fall apart when moved to a different substrate). All rejected sample did not have tissue necrosis (when transferred to the nursery) in the contact area, although few entities had a suture formation in the contact area, creating de facto few separated colonies (as described in [46]). Solitary primary polyps were designated as 'genetically homogenous colonies' (GHC). At the average age of seven months, GHC/chimeras/rejecting entities were removed from the "Maylor paper", each as a single unified unit, glued on plastic pins, and translocated to a mid-water floating nursery at the north beach of Eilat (29°32'24.02" N, 34°58'28.77" E; sea bottom at 23 meters, the nursery floats at 10–11 meters depth; [22]).

2.2. Monitoring

Each sample was repeatedly photographed (using a Canon X7 camera equipped with an underwater housing) every 1–4 months from above (aerial view photos) and from the side (side view photos) until the colony reached the age of 18 months (Figure 1). Aerial size (a, mm^2), which represents the aerial 3D projection of the colony onto a plane area (revealing the surface area intimately impacted by the colony), was measured from the aerial view photos (using the software ImageJ). The side view photos revealed the colonial heights (h, mm) or the upward axial colony plane and were measured in ImageJ. A third metric was the aeroaxial ecological volume (a × h; mm^3), representing the captured space of the colony including the skeletal and surrounding volumes, ecologically engineered by the colony.

When in the coral nursery, we applied the "common gardening" method [55], and the locations of the colonies were continuously swapped every 4–8 weeks. Along the monitoring period, the status (dead or alive) of each colony was documented. Before taking a picture, the plastic pin substrates next to the colony edges were cleaned (using soft tooth brush) to accurately mark the colonial boundaries for the ImageJ software. At the end of the monitoring period, final documentations were taken from GHC/chimeras/rejecting entities older than one year old including the number of upgrowing branches (UB), reflecting initial branching events.

2.3. Statistical Analysis

Statistical analyses were conducted using R software [56]. For the colonial type (bi-chimeras, multi-chimeras, bi-rejected, multi-rejected, and GHC) effect on the aerial size, height, and aeroaxial ecological volume, we used the lme4 and lsmean packages [57,58]. A series of 13 linear mix models were fitted with and without the fixed effect of the colony type, with or without the interaction effect of age (months) and with different combinations of random slopes and intercept (Tables S1–S3). In all models, age (month) was defined as a covariate, colony type as a fixed variable, and the colonies as random variables. Since all dependent variables did not meet the mixed linear models' assumptions, $\log_e$ transportation was applied. The best-fitted models were selected by the lowest Akaike Information Criterion (AIC), which measures the model's relative quality for the dataset. Multi comparisons between colony types were performed with the ls mean package with Bonferroni correction. The models' marginal mean age of the samples during their stay in the nursery (mean age, adjusted for the other variables in the model, i.e., the mean age of all the samples at the time of sampling while in the nursery) was 10.8 months. Results are presented as estimated marginal mean (EMM) ± standard error (SE) values as predicted from the models. For the survival analyses, we used the Kapan–Meier survival analysis (using the package survival [59]). Survival analyses were executed

on all samples until they reached a full year in the nursery. For final sizes at the genotype level, we used data gathered at the age of 18 months from colonies that had been sampled at that age. This was performed by summing up the aerial sizes and the aeroxial volumes (not transformed values), divided by the number of samples. This analysis was not performed on multi partner entities due to differences in the number of genotypes within each entity.

Differences in the number of first branches (UB; initial upgrowing branches) were examined using the Fisher exact test for independence. Pairwise comparisons with Bonferroni correction were applied when we compared the differences in UB between the types of coral entities. In order to eliminate the effect of bi-associations when compared with the single GHCs, we generated a simulated new colonial type, 'bi-GHC pairs', by permuting the original GHC list in all pairwise combinations, creating a new list of bi-GHC. Then, we summed the number of branching events in all bi-GHC pairs exhibiting 0, 1, or 2 branches.

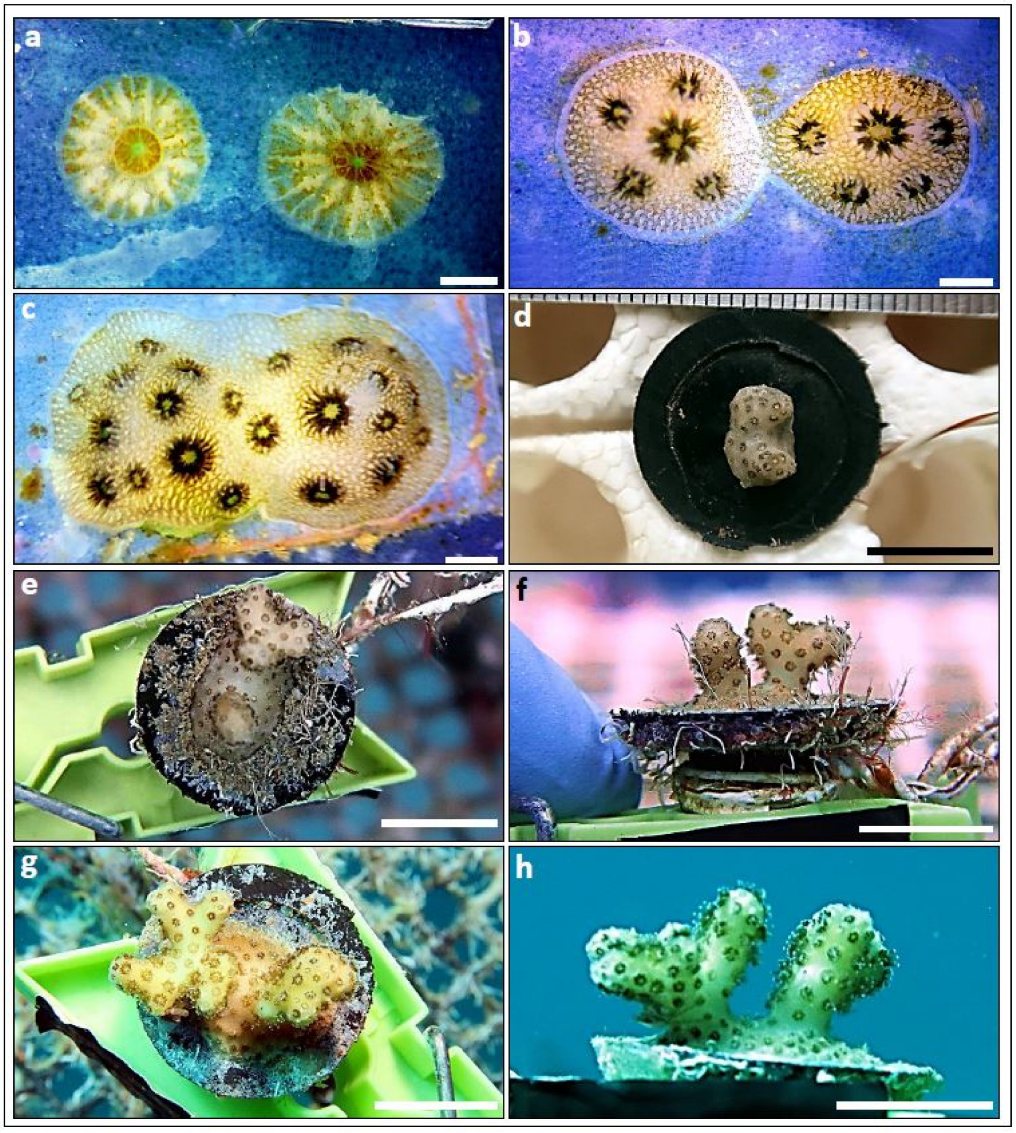

Figure 1. The formation of a bi-chimera colony under laboratory conditions (**a**–**c**) and the chimera development in the nursery under field conditions (**d**–**h**). (**a**) 16 days old, two spat; (**b**) 37 days old; at fusion event; (**c**) established chimera, 127 days old; (**d**) 191 days old developing chimeric entity; (**e**) 343 day old; aerial view; (**f**) 343 days old; side view; (**g**) 541 days old; aerial view; (**h**) 541 days old; side view.

3. Results

Several hundreds of the five types of colonial entities were established during two reproductive seasons and were held for 7 ± 2 months (mean ± sd) at IUI in the outdoor water table. A total of 222 healthy colonial entities were then glued onto plastic pins and translocated to a mid-water floating nursery as follows: 74 GHC (genetically homogenous colonies), 62 bi-chimeras, 22 multi-chimeras, 32 bi-rejected, and 32 multi-rejected. The colonies experienced the ambient conditions of the four seasons (summer, fall, winter, and spring) with yearly surface water temperatures ranging from 21.5 °C to 28.5 °C [60,61] and summer/winter variations of sun irradiation. Several rain events occurred during the stay of the colonies in the nursery, with a few particularly intense rain storms that brought considerable runoff and suspended sediment to the sea. The monitoring came to an end after a super-storm that hit the gulf on March 2020.

3.1. Aerial Size

The best fitted model included random slopes, random intercepts, and the effect of the colony type and interaction effect between age (months) and colony type (Table S1, Figure 2a). Marginal R^2 and conditional R^2 of this model were 0.926 and 0.398, respectively. Results revealed a significant effect of the colony type on the intercepts and slopes ($X^2_{df=8} = 52.839$, $p < 0.0001$). The highest estimated marginal mean (EMM) intercepts (age 0; i.e., initial size) were observed for multi-chimeras and multi-rejected (3.10 ± 0.23 (SE) and 3.23 ± 0.18 log aerial size; $p > 0.05$; Tables S4 and S5), followed by bi-chimera that had significantly higher values than GHC (2.97 ± 0.13 and 2.23 ± 0.13 log aerial size; $p = 0.01$; Tables S4 and S5, Figure 2a). Bi-rejected had an EMM intercept of 2.72 ± 0.19 that was not significantly different with the EMM intercepts of the other colonial types. GHC exhibited the lowest EMM intercept value (2.23 ± 0.13) that was significantly different from bi-chimeras, multi-chimeras, and multi rejected ($p = 0.001$, $p = 0.01$, $p = 0.0001$; respectively; Tables S4 and S5, Figure 2a).

A multi comparison of EMM at the age of 10.8 months (the marginal mean age of the samples during their stay in the nursery; i.e., the average age of all the samples at the time of sampling while in the nursery) showed significantly lower EMM values for GHC when compared to bi-chimeras, multi-chimeras, and multi-rejected (3.75 ± 0.06, 4.25 ± 0.07, 4.41 ± 0.12, 4.09 ± 0.1; $p < 0.0001$, $p < 0.0001$, $p = 0.046$; respectively; Tables S4 and S5), when compared between bi-chimeras and bi-rejected (4.25 ± 0.07, 3.88 ± 0.1; $p = 0.41$), between bi-rejected to multi-chimera (3.88 ± 0.1, 4.41 ± 0.12, $p = 0.01$) and between multi chimera to multi-rejected 4.41 ± 0.12, 4.09 ± 0.1; $p = 0.041$; Tables S4 and S5). However, a multi comparison among EMM at the end time point of the model (age = 18 months) did not show any significant difference in the EMM log aerial size. A multi comparison between slopes showed a significant difference only between GHC to multi rejected ($p = 0.03$; Tables S4 and S5, Figure 2a). Comparisons between aerial sizes (age of 18 months) at the genotype level within each type of entity and GHC genotypes elucidated that each genotype in bi-chimeras and bi-rejected was 17% and 30% (respectively) smaller, on average (Table S6), a possible cost for the allogeneic interactions.

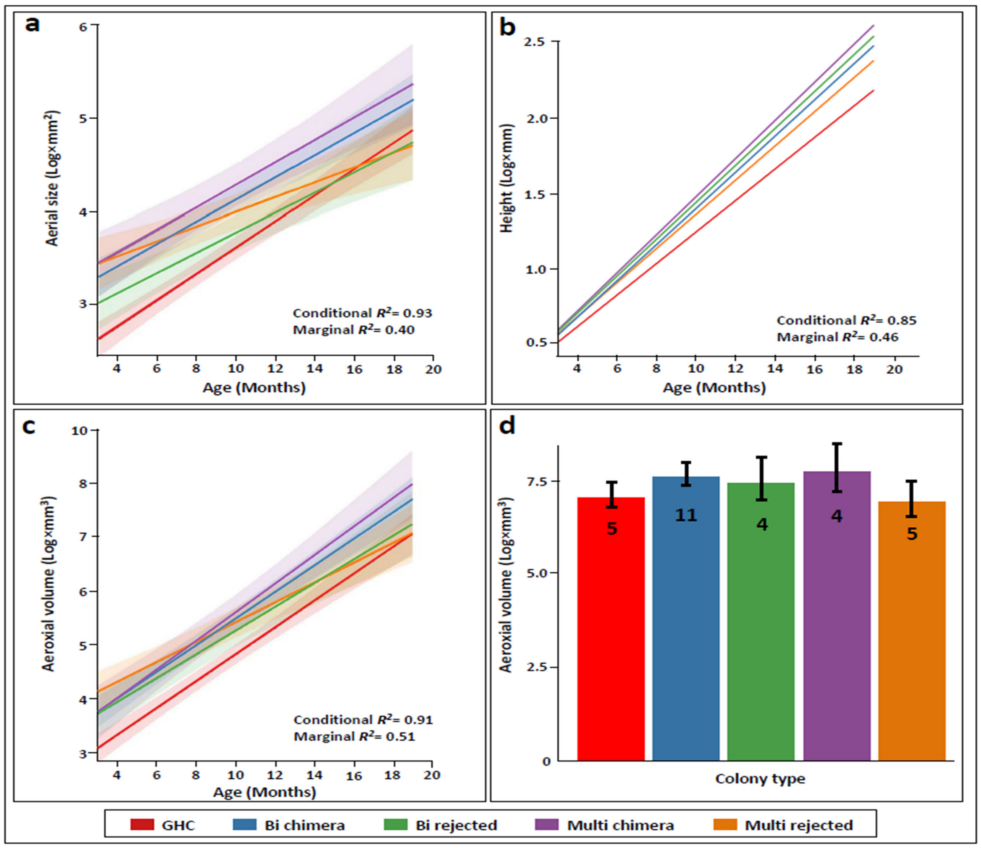

Figure 2. The best fitted mix linear models for (**a**) areal size (mm^2), (**b**) height, and (**c**) aeroxial volume. Covariate (*X*-axis) is age in months, random factors are the samples. Each line represents a linear model for each colony type as described in the caption. Conditional R^2 (the proportion of variance explained by the whole model) and marginal R^2 (proportion of variance explained by the fixed factor alone) are attached to each sub-figure. (**d**) Mean log aeroxial volumes with SE in colonies sampled at the age of 18 months (real values, not from the model). Number above bars depicts the number of samples.

3.2. Height

The best fitted model recognized random slopes, random intercepts, and the interaction between age (months) and colony type (slope only model; Tables S7 and S8). Marginal R^2 and conditional R^2 of this model were 0.854 and 0.464, respectively (Figure 2b). In this model, the combined interaction of colony type and the age (months) had a significant effect on the height of the colonies ($X^2_{df=4} = 13.753$, $p = 0.008$; Figure 2b). However, a multi comparison analysis of the slopes revealed that only the slopes of multi-chimeras and GHC were significantly disparate from each other, whereas multi-chimeras had steeper slopes (trends: 0.130 ± 0.0079, 0.106 ± 0.006; $p = 0.04$; respectively Tables S7 and S8).

3.3. Aeroaxial Ecological Volume

The best fitted model characteristics included random slopes, random intercepts, the effect of colony type, and the effect of the interaction between age (months) and colony type (Table S3; Figure 2c). Marginal R^2 and conditional R^2 of this model were 0.909 and 0.51, respectively (Figure 2c). Results revealed a significant effect of the colony type on the intercept and slopes ($X^2_{df=4} = 927$, $p < 0.0001$). Similar to the aerial size, GHC had the lowest EMM intercept values (2.51 ± 0.13 log volume (mm^3), significantly lower than bi-chimeras, multi-chimeras, and multi-rejected (3.17 ± 0.13, 3.29 ± 0.2, 3.17 ± 0.16; multi-comparison: $p < 0.0001$, $p = 0.001$, $p = 0.0012$; respectively; Tables S9 and S10). A multi-comparison of EMM at the age of 10.8 months (half resident time in the nursey) showed significantly lower MME values for GHC followed by multi-rejected, bi-chimera, and multi-chimera (5.08 ± 0.1, 5.75 ± 0.11, 5.88 ± 0.18; multi-comparison: $p = 0.001$, $p = 0.001$, $p = 0.02$, respectively;

Tables S9 and S10), but not a significant difference from bi-rejected (multi comparison 5.5 ± 0.15, $p = 0.21$; Tables S9 and S10). No significant differences were revealed among all colony types at the 18 month time-point (multi-comparisons, all $p > 0.05$: Tables S9 and S10). A multi-comparison analysis on the actual calculated aeroxial volumes among colonies (not on the model) also did not reveal a significant difference (pair-wise ANOVA: $p > 0.05$ for all comparisons; Figure 2d). There were no significant differences among slopes (multi-comparisons, all comparisons were $p > 0.25$; Tables S9 and S10). Comparing the aeroxial volumes (age of 18 months) at the genotype level between bi-chimeras, bi-rejected entities, and GHC genotypes elucidated that each genotype in bi-chimeras gained 20% surplus volume (on the average) compared to the GHC genotypes, while genotypes in bi-rejected entities did not lose or gain volume compared to GHC genotypes (Table S6), an emerged possible benefit for chimeric interactions.

3.4. Survival

A total number of 219 entities participated in the survival analyses following the removal of corals that died from unrelated anthropogenic impacts (e.g., divers). This list included 65 GHC, 59 bi-chimeras, 33 bi-rejected, 22 multi-chimeras, and 40 multi-rejected. The colony type had a significant effect on the cumulative survival probability of the corals after one year in the nursery (Kaplan–Meier: $X^2_{(df = 4)} = 14.4$, $p = 0.006$). Chimerism (multi-chimeras and bi-chimeras) had a positive significant effect on the cumulative survival probabilities compared to GHC and the two types of rejected colonies (Kaplan–Meier multi-comparison with Bonferroni correction, $p < 0.05$; Table S11; Figure 3).

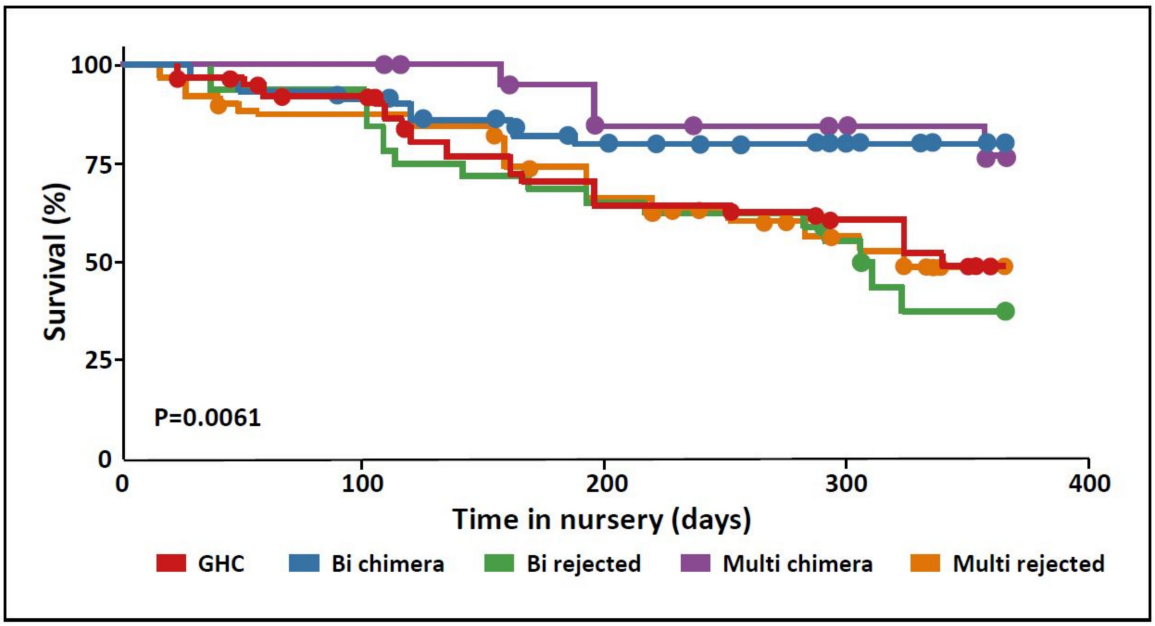

Figure 3. Kaplan–Meier survival curves (with the p value) for all colony types along a period of one-year in the midwater coral nursery under ambient field conditions. The Y-axis depicts the cumulative survival probabilities and the X-axis is the time in the nursery in days. Circles on lines indicate census dates.

3.5. Astogenic Statuses for Early Branching Events

Astogeny in young *Stylophora pistillata* colonies starts with the deposition of calcareous skeletons on the substrates (basal plates), concurrent with the extra-tentacular mode of polyp budding, where at the yet undisclosed astogenic stage, up-growing branches initiate by apical growth, usually as a single apical structure ramified from each basal plate [62]. Here, we examined the presence and the numbers of early branching events (up-growing branches, UB) in colonies older than one year. Results revealed that the colony type has a significant effect on UB numbers (Fisher test: $p < 0.0001$).

UB distributions were significantly different between GHC to other colonial types (Fisher pairwise comparison: $p < 0.0001$), but did not differ among the other types of colonies (bi-chimera, multi-chimera, bi-rejection, and multi-rejection; Fisher pairwise comparison: $p > 0.05$). While GHC colonies developed only a single branch or none (0 UB: 22%, 1 UB: 78%; Figure 4), some of the bi- and the multi-chimeras developed up to three initial branches (bi-chimeras: 0 UB: 21%%, 1 UB: 46%, 2 UB: 31%, 3 UB: 2%; multi-chimeras: 0 UB: 15%%, 1 UB: 30%, 2 UB: 45%, 3 UB: 10%; Figure 4). UB numbers in bi-rejected colonies were not significantly different from bi-chimeras, multi-chimeras, and multi-rejected colonies (bi-rejected: 0 UB: 6%, 1 UB: 36%, 2 UB: 58%, 3 UB: 0%; Fisher pairwise comparison: $p > 0.5$). Although one multi-rejected colony (3%) developed four upgrowing branches, the UB appearance in this type of entity was not significantly different from other colony types (multi-rejected: 0 UB: 9%, 1 UB: 47%, 2 UB: 28%, 3 UB: 12%, 4 UB: 3%; Fisher pairwise comparison: $p > 0.5$).

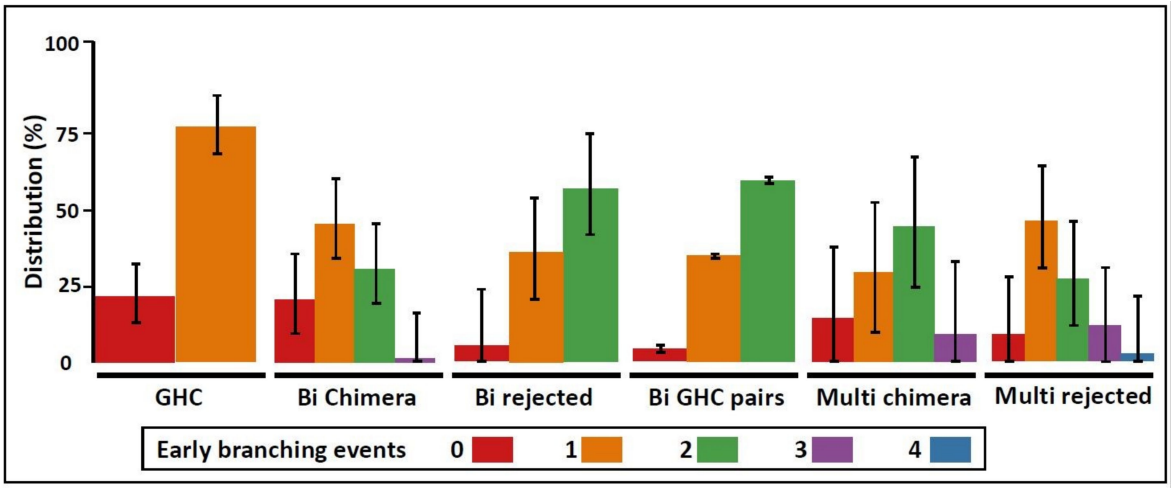

Figure 4. Distributions (%) of the colony early branching events in all *S. pistillata* colonial types. 'Bi-GHC pairs' are the permuted GHC pairs. The different branching events (0–4) are depicted by colors in the caption. Error bars are 95% confidence intervals.

Analyses performed on the permutated 'bi-GHC pairs' yielded dramatically different UB distributions. While nonsignificant to the bi-rejected (Fisher pairwise comparison: $p = 0.75$), results were significantly different from the UB distributions in other colony types (permutated bi-GHC pairs: 0 UB: 5%, 1 UB: 35%, 2 UB: 60%; Fisher pairwise comparison: $p < 0.001$).

4. Discussion

While aggregated settlement of coral larvae has been repeatedly documented for more than a century [19,33,40,63], the repercussion of this behavior on either the aggregated entity to be formed or at the population level has gained limited attention. A gregarious settlement of coral spat originating from the same species (allogenic contacts) will lead to histocompatible reactions (tissue fusions between interacting spat) or histoincompatible reactions (necrotic areas at points of contacts rejections). Regardless of the interactions developing in the chimeric or rejecting entities, the initial sizes are directly correlated with the number of genotypes in the entity, a trait that may govern survival benefits [49,64]. Xenogenic (with other species) contacts will result in just a wide array of rejection types [46,65–68].

Coral chimerism, an entity possessing cells from two or more conspecifics, had been postulated to affect the colony fitness under natural conditions [26,49–52], even though this claim was not tested in the field. For the first time, this study demonstrates, under prolonged field conditions, some costs and benefits and life history effects for coral chimerism, as compared to regular colonies and rejected entities. Parameters examined were size properties (aerial dimension, height, and aeroxical ecological volume), survival, and early-branching astogeny. Results revealed that multi-chimeras, multi-rejections, and bi-chimeras that indeed experienced larger earlier sizes and aeroxial ecological volumes than GHC

(genetically homogenous colonies; as documented in laboratory studies [14,26,49]) did not continue with faster growth rates and at the age of 18 months, there was no significant difference in aerial size nor aeroxial volume among any of the colonial types. These results further suggest that growth rates (slope) were not affected by the entity type. In contrast, the best fitted model for the height did not show any difference in heights nor height growth rates (slope) except between multi-chimera and GHC. At the genotype level, there is a loss of aerial size in chimeras, however, aeroxial volume is augmented compared to GHC. Chimeric benefits are also assigned to the survival rates of chimeric colonies (field results, age of 18 months) that were significantly higher than the GHC and the rejected colonies' survivorships. Furthermore, this study revealed a chimeric bearing on primary up-growing branches, affecting early astogenic stages.

It is of interest to note that under laboratory conditions, *S. pistillata* chimeras from the Red Sea exhibited enhanced sizes compared to GHC entities for the first seven months of their life but had equal survivor rates [26]. Similar observations for enhanced chimeric sizes (three months old chimeras) were obtained by Puill-Stephan et al. [14] on *Acropora millepora* from the Great Barrier Reef, Australia and in young chimeric colonies of *Pocillopora damicornis* from the Philippines that further revealed higher survival rates [49]. The present study further showed that the immediate increase in size due the fusion between genotypes was not followed by enhanced growth rates, however, the fitness of larger colonial sizes, primarily at the very early life stages [49,64], should not be ignored. While not studied here, enhanced fitness could also be attained by an earlier onset of sexual maturation [69,70] and improved regeneration power [71]. Immediate increase in size due to fusion of coral spat (very small and young colonies) and juveniles may lessen the mortality rates caused by grazers [72,73] or by bottom associated processes (e.g., scouring sand, allogenic and xenogenic interactions).

In contrast, and despite the size equality between chimeras and rejected entities at the age of 18 months, the last colonial type had lower survival rate, indicating additional deleterious process developing in the reject entities. Histoincompatible reactions between conspecific ramets of *S. pistillata* and between xenogenic interaction have negative effects on the partners in contact in terms of reproduction and growth [68,74]. Therefore, it is feasible that stress-related processes negatively compensate for the size benefits.

In contrast to the benefits above-mentioned, chimerism in other sedentary marine invertebrates is considered to be associated with a wide range of costs including somatic and germ cell parasitism [29,41–44,75,76], morphological resorption of genotypes in soft corals [28] and tunicates [77,78], outcomes not documented in scleractinian corals. In stony corals, the cost for chimerism, as depicted in the literature and in this study, is mainly reflected in the relative aerial size of each genotype participating in the chimera as compared to GHCs, estimated in the literature, as 12–64% loss of potential sizes [26]. Chimerism in other organisms such as colonial marine invertebrates and mammals may lead to the development of phenotypes not recorded in non-chimeric organisms [74,79,80], an outcome that emerged in the present research that impacts on early branching events. While GHCs developed zero to a single upgrowing (UG) branch at the age of one-year, chimeric colonies developed two to three UG branches. Further analyses revealed similarity in UG branch distributions between 'bi-GHC pairs' and the bi-rejected entities, suggesting the cumulative effect of the two genotypes in the entity. On the other hand, bi-chimeras exhibited significantly different UG branch distributions, indicating early astogenic processes impacted by the fusion event.

The recorded highlighted survivorship in coral chimeric entities may impose benefits on the within-species biodiversity, despite the documented costs (e.g., impacts on early life stages sizes). Not only did more colonial entities survive, but intra-species biodiversity was augmented by at least two-fold for each survived chimeric entity, directly reliant on the number of genotypes per survived chimera. Furthermore, as evolution works on the entire chimeric entity and not on each genotype individually, less adapted genotypes [81] to temporary environmental conditions (e.g., a heat wave sensitive forming a chimera together with a heat wave tolerant partner) may gain chimeric shelter, escaping mortality. They may then pass on these protected genetic repertoires to

future generations, boosting the population's genetic diversity and fitness by increasing phenotypic diversity [82]. In principle, chimerism may serve as a bypass through an environmental bottleneck, allowing a range of genotypes to survive through harsh conditions. At the colony level, higher genetic repertoires in chimeras may diversify gene expressions, improving this entity fitness against capricious environmental changes [43].

Climate change and anthropogenic disturbances are rapidly leading coral reefs to accrue degradation and biodiversity loss [81,83,84], necessitating the corals' fast adaptation to changing environments. The failed passive management acts (such as the creation of marine protected areas) to reverse this trend [85–87], reflecting the need for alternative scientific and applied tactics such as active restoration and ecological engineering approaches [50–52,88,89]. This rationale further takes into consideration that ecological engineering is "the design of sustainable ecosystems that integrate human society with its natural environment for the benefit of both" [90]. The most promising active reef restoration approach, based on the gardening tenet, is made on two basic operational steps: farming of large stocks of corals in nurseries (whether from fragments or propagules) and then transplanting them into degraded reefs [22,23,48,91–99]. Coral chimerism may serve as one of the tools in the gardening approach, and provide an evolutionary rescue mechanism that enhances population genetic diversity [50–52]. High genetic and genotypic diversity and large populations are presumed to be necessary for creating resilience and resistance in the 'reef of tomorrow' and to mitigate climate change impacts [100–102]. In the nursery phase, which is basically an aquaculture venture, large stocks of coral colonies are endeavored as fast as possible and of improved genetic background [22,91,98]. Improved survival and increased colonial size at early life stages characteristics of chimeric colonies may positively affect this gardening step and increase overall genotypic diversity in nursed coral populations. Large chimeric entities (primarily of multi-chimeras), when fragmented, may further serve as a source for new colonies exhibiting different percentages of participating genotypes, increasing genotypic repertoire of farmed corals with a minimum negative influence on the natural population. Following their transplantation, chimeric colonies may increase genotypic diversity at restored reefs, following plant restoration practices, for faster recovery [103–106]. It was noted that sites with aggregated adult colonies of the coral *Acropora cervicornis* with higher genotypic diversity had higher coral cover compared to sites with lower diversity [107]. Chimeric colonies can therefore increase phenotypic diversity in the population, an essential evolution mechanism to adapt to the changing environment [108]. However, although few studies have raised or partly tested the use of chimeras in restoration acts [22,23,109], there is an urgent need for the development of advancement methods and of a better understanding of the responses of chimeric coral colonies to environmental stress.

Supplementary Materials: The following are available online at http://www.mdpi.com/2077-1312/8/12/1038/s1, Table S1: Aerial size model selection, Table S2: Height model selection, Table S3: Aeroxial ecological volume model selection, Table S4: Descriptive statistics for the best fitted aerial size model, Table S5: Multi-comparison for colony types in the best fitted aerial size model, Table S6: Sizes and volume relative differences at the genotype level, Table S7: Descriptive statistics for the best fitted height data model, Table S8: Multi-comparison for colony types in the best fitted height model, Table S9: Descriptive statistics for the best fitted aeroxial ecological volume model, Table S10: Multi-comparison for colony types in the best fitted aeroxial ecological volume model, Table S11: A Kaplan–Meier survival multi comparison analysis among colony types.

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References

1. Rinkevich, B. Quo vadis chimerism? *Chimerism* **2011**, *2*, 1–5. [CrossRef]
2. Schweinsberg, M.; Weiss, L.C.; Striewski, S.; Tollrian, R.; Lampert, K.P. More than one genotype: How common is intracolonial genetic variability in scleractinian corals? *Mol. Ecol.* **2015**, *24*, 2673–2685. [CrossRef]
3. Magor, B.G.; De Tomaso, A.; Rinkevich, B.; Weissman, I.L. Allorecognition in colonial tunicates: Protection against predatory cell lineages? *Immunol. Rev.* **1999**, *167*, 69–79. [CrossRef]
4. Rinkevich, B.; Weissman, I.L. Variation in the outcomes following chimera formation in the colonial tunicate *Botryllus schlosseri*. *Bull. Mar. Sci.* **1989**, *45*, 213–227.
5. Adams, K.M.; Nelson, J.L. Microchimerism: An investigative frontier in autoimmunity and transplantation. *J. Am. Med. Assoc.* **2004**, *291*, 1127–1131. [CrossRef]
6. Buss, L.W. Somatic cell parasitism and the evolution of somatic tissue compatibility. *Proc. Natl. Acad. Sci. USA* **1982**, *79*, 5337–5341. [CrossRef]
7. Ross, C.N.; French, J.A.; Orti, G. Germ-line chimerism and paternal care in marmosets (*Callithrix kuhlii*). *Proc. Natl. Acad. Sci. USA* **2007**, *104*, 6278–6282. [CrossRef]
8. Ilan, M.; Loya, Y. Ontogenetic variation in sponge histocompatibility responses. *Biol. Bull.* **1990**, *179*, 279–286. [CrossRef]
9. Albarella, S.; De Lorenzi, L.; Catone, G.; Magi, G.E.; Petrucci, L.; Vullo, C.; D'Anza, E.; Parma, P.; Raudsepp, T.; Ciotola, F.; et al. Diagnosis of XX/XY blood cell chimerism at low percentage in horse. *J. Equine Vet. Sci.* **2018**. [CrossRef]
10. Noble, J.P.A.; Lee, D. First report of allogeneic fusion and allorecognition in tabulate corals. *J. Paleontol. Soc.* **1991**, *65*, 69–74. [CrossRef]
11. Helm, C.; Schülke, I. Contact reactions and fusion of Late Jurassic ramose coral *Thamnasteria dendroidea* in a patch reef environment. *Coral Reefs* **2000**, *19*, 89–92. [CrossRef]
12. Puill-Stephan, E.; Willis, B.L.; van Herwerden, L.; van Oppen, M.J.H. Chimerism in wild adult populations of the broadcast spawning coral *Acropora millepora* on the Great Barrier Reef. *PLoS ONE* **2009**, *4*, e7751. [CrossRef]
13. Hennige, S.J.; Morrison, C.L.; Form, A.U.; Büscher, J.; Kamenos, N.A.; Roberts, J.M. Self-recognition in corals facilitates deep-sea habitat engineering. *Sci. Rep.* **2014**, *4*, 6782. [CrossRef]
14. Puill-Stephan, E.; van Oppen, M.J.H.; Pichavant-Rafini, K.; Willis, B.L. High potential for formation and persistence of chimeras following aggregated larval settlement in the broadcast spawning coral, *Acropora millepora*. *Proc. R. Soc. Lond. Ser. B Biol. Sci.* **2012**, *279*, 699–708. [CrossRef]
15. Rinkevich, B.; Shaish, L.; Douek, J.; Ben-Shlomo, R. Venturing in coral larval chimerism: A compact functional domain with fostered genotypic diversity. *Sci. Rep.* **2016**, *6*, 19493. [CrossRef]
16. Maier, E.; Buckenmaier, A.; Tollrian, R.; Nürnberger, B. Intracolonial genetic variation in the scleractinian coral *Seriatopora hystrix*. *Coral Reefs* **2012**, *31*, 505–517. [CrossRef]
17. Oury, N.; Gelin, P.; Magalon, H. Together stronger: Intracolonial genetic variability occurrence in *Pocillopora corals* suggests potential benefits. *Ecol. Evol.* **2020**, *10*, 5208–5218. [CrossRef]
18. Fidler, A.E.; Bacq-Labreuil, A.; Rachmilovitz, E.; Rinkevich, B. Efficient dispersal and substrate acquisition traits in a marine invasive species via transient chimerism and colony mobility. *PeerJ* **2018**, *6*. [CrossRef]
19. Cameron, K.A.; Harrison, P.L. Density of coral larvae can influence settlement, post-settlement colony abundance and coral cover in larval restoration. *Sci. Rep.* **2020**, *10*, 5488. [CrossRef]
20. Nozawa, Y.; Loya, Y. Genetic relationship and maturity state of the allorecognition system affect contact reactions in juvenile *Seriatopora corals*. *Mar. Ecol. Prog. Ser.* **2005**, *286*, 115–123. [CrossRef]
21. Wijayanti, D.P.; Hidaka, M. Is genetic involve in the outcomes of contact reactions between parent and offspring and between siblings of the coral *Pocillopora damicornis*? *ILMU Kelaut. Indones. J. Mar. Sci.* **2018**, *23*, 69. [CrossRef]
22. Linden, B.; Rinkevich, B. Elaborating an eco-engineering approach for stock enhanced sexually derived coral colonies. *J. Exp. Mar. Bio. Ecol.* **2017**, *486*, 314–321. [CrossRef]
23. Linden, B.; Rinkevich, B. Creating stocks of young colonies from brooding coral larvae, amenable to active reef restoration. *J. Exp. Mar. Bio. Ecol.* **2011**, *398*, 40–46. [CrossRef]
24. Chang, E.S.; Orive, M.E.; Cartwright, P. Nonclonal coloniality: Genetically chimeric colonies through fusion of sexually produced polyps in the hydrozoan *Ectopleura larynx*. *Evol. Lett.* **2018**, *2*, 442–455. [CrossRef]

25. Toh, T.; Chou, L. Aggregated settlement of *Pocillopora damicornis* planulae on injury sites may facilitate coral wound healing. *Bull. Mar. Sci.* **2013**, *89*, 503–504. [CrossRef]
26. Amar, K.O.; Chadwick, N.E.; Rinkevich, B. Coral kin aggregations exhibit mixed allogeneic reactions and enhanced fitness during early ontogeny. *BMC Evol. Biol.* **2008**, *8*, 126. [CrossRef]
27. Amar, K.O.; Rinkevich, B. Mounting of erratic histoincompatible responses in hermatypic corals: A multi-year interval comparison. *J. Exp. Biol.* **2010**, *213*, 535–540. [CrossRef]
28. Barki, Y.; Gateño, D.; Graur, D.; Rinkevich, B. Soft-coral natural chimerism: A window in ontogeny allows the creation of entities comprised of incongruous parts. *Mar. Ecol. Prog. Ser.* **2002**, *231*, 91–99. [CrossRef]
29. Frank, U.; Oren, U.; Loya, Y.; Rinkevich, B. Alloimmune maturation in the coral *Stylophora pistillata* is achieved through three distinctive stages, 4 months post-metamorphosis. *Proc. R. Soc. Lond. Ser. B Biol. Sci.* **1997**, *264*, 99–104. [CrossRef]
30. Hidaka, M. Tissue compatibility between colonies and between newly settled larvae of *Pocillopora damicornis*. *Coral Reefs* **1985**, *4*, 111–116. [CrossRef]
31. Nozawa, Y.; Hirose, M. When does the window close? The onset of allogeneic fusion 2–3 years post-settlement in the scleractinian coral, *Echinophyllia aspera*. *Zool. Stud.* **2011**, *50*, 396.
32. Jiang, L.; Lei, X.; Liu, S.; Huang, H. Fused embryos and pre-metamorphic conjoined larvae in a broadcast spawning reef coral. *F1000Research* **2015**, *4*. [CrossRef]
33. Rivera, H.E.; Goodbody-Gringley, G. Aggregation and cnidae development as early defensive strategies in *Favia fragum* and *Porites astreoides*. *Coral Reefs* **2014**, *33*, 1079–1084. [CrossRef]
34. Mizrahi, D.; Navarrete, S.A.; Flores, A.A.V. Groups travel further: Pelagic metamorphosis and polyp clustering allow higher dispersal potential in sun coral propagules. *Coral Reefs* **2014**, *33*, 443–448. [CrossRef]
35. Mercier, A.; Sun, Z.; Hamel, J.-F. Internal brooding favours pre-metamorphic chimerism in a non-colonial cnidarian, the sea anemone *Urticina felina*. *Proc. R. Soc. B Biol. Sci.* **2011**, *278*, 3517–3522. [CrossRef]
36. Hidaka, M.; Yurugi, K.; Sunagawa, S.; Kinzie, R.A. Contact reactions between young colonies of the coral *Pocillopora damicornis*. *Coral Reefs* **1997**, *16*, 13–20. [CrossRef]
37. Rinkevich, B. Allorecognition and xenorecognition in reef corals: A decade of interactions. *Hydrobiologia* **2004**, *530–531*, 443–450. [CrossRef]
38. Rinkevich, B. Conserved histocompatible machinery in marine invertebrates? *Invertebr. Surviv. J.* **2015**, *12*, 170–172.
39. Rinkevich, B.; Weissman, I.L. Incidents of rejection and indifference in Fu/HC incompatible protochordate colonies. *J. Exp. Zool.* **1992**, *263*, 105–111. [CrossRef]
40. Duerden, J.E. Aggregated Colonies in Madreporarian Corals. *Am. Nat.* **1902**, *36*, 461–471. [CrossRef]
41. Pancer, Z.; Gershon, H.; Rinkevich, B. Coexistence and possible parasitism of somatic and germ cell lines in chimeras of the colonial urochordate *Botryllus schlosseri*. *Biol. Bull.* **1995**, *189*, 106–112. [CrossRef]
42. Stoner, D.S.; Rinkevich, B.; Weissman, I.L. Heritable germ and somatic cell lineage competitions in chimeric colonial protochordates. *Proc. Natl. Acad. Sci. USA* **1999**, *96*, 9148–9153. [CrossRef]
43. Rinkevich, B.; Yankelevich, I. Environmental split between germ cell parasitism and somatic cell synergism in chimeras of a colonial urochordate. *J. Exp. Biol.* **2004**, *207*, 3531–3536. [CrossRef]
44. Rinkevich, B.; Weissman, I.L. Chimeras vs. genetically homogeneous individuals: Potential fitness costs and benefits. *Nord. Soc. Oikos* **1992**, *63*, 119–124. [CrossRef]
45. Boschma, H. *On the Post Larval Development of the Coral Maeandra areolata*; Carnegie Institution for Science: Washington, DC, USA, 1929.
46. Chadwick-Furman, N.; Rinkevich, B. A complex allorecognition system in a reef-building coral: Delayed responses, reversals and nontransitive hierarchies. *Coral Reefs* **1994**, *13*, 57–63. [CrossRef]
47. Rinkevich, B.; Frank, U.; Bak, R.P.M.; Müller, W.E.G. Alloimmune responses between *Acropora hemprichi* conspecifics: Nontransitive patterns of overgrowth and delayed cytotoxicity. *Mar. Biol.* **1994**, *118*, 731–737. [CrossRef]
48. Frank, U.; Brickner, I.; Rinkevich, B.; Loya, Y.; Bak, R.P.M.; Achituv, Y.; Ilan, M. Allogeneic and xenogeneic interactions in reef-building corals may induce tissue growth without calcification. *Mar. Ecol. Prog. Ser.* **1995**, *124*, 181–188. [CrossRef]
49. Raymundo, L.J.; Maypa, A.P. Getting bigger faster: Mediation of size-specific mortality via fusion in juvenile coral transplants. *Ecol. Appl.* **2004**, *14*, 281–295. [CrossRef]

50. Rinkevich, B. The active reef restoration toolbox is a vehicle for coral resilience and adaptation in a changing world. *J. Mar. Sci. Eng.* **2019**, *7*, 201. [CrossRef]
51. Rinkevich, B. Ecological engineering approaches in coral reef restoration. *ICES J. Mar. Sci.* **2020**. [CrossRef]
52. Rinkevich, B. Coral chimerism as an evolutionary rescue mechanism to mitigate global climate change impacts. *Glob. Chang. Biol.* **2019**, *25*, 1198–1206. [CrossRef]
53. Shefy, D.; Shashar, N.; Rinkevich, B. The reproduction of the Red Sea coral *Stylophora pistillata* from Eilat: 4-decade perspective. *Mar. Biol.* **2018**, *165*, 27. [CrossRef]
54. Baird, A.H. The Ecology of Coral larvae: Settlement Patterns, Habitat Selection and the Length of the Larval Phase. Ph.D. Thesis, James Cook University of North Queensland, Townsville, Australia, 2001.
55. Rinkevich, B. Conservation of coral reefs through active restoration measures: Recent approaches and last decade progress. *Environ. Sci. Technol.* **2005**, *39*, 4333–4342. [CrossRef]
56. R Core Team. *R: A Language and Environment for Statistical Computing*; R Core Team: Vienna, Austria, 2014.
57. Bates, D.; Mächler, M.; Bolker, B.; Walker, S. Fitting Linear Mixed-Effects Models Using lme4. *J. Stat. Softw.* **2015**, *67*, 1–48. [CrossRef]
58. Lenth, R.V. Least-Squares Means: The {R} Package {lsmeans}. *J. Stat. Softw.* **2016**, *69*, 1–33. [CrossRef]
59. Therneau, T.M. A Package for Survival Analysis in R 2020 Version 3.2-7. Available online: https://cran.r-project.org/package=survival (accessed on 2 September 2020).
60. Shaked, Y.; Genin, A. The Israel National Monitoring Program in the Northern Gulf of Aqaba 2018. Available online: https://iui-eilat.huji.ac.il/Research/NMPReports.aspx (accessed on 16 April 2019).
61. Sheked, Y.; Genin, A. The Israel National Monitoring Program in the Northern Gulf of Aqaba 2019. Available online: https://iui-eilat.huji.ac.il/Research/NMPReports.aspx (accessed on 2 September 2020).
62. Rinkevich, B. The Branching Coral *Stylophora pistillata*: Contribution of Genetics in Shaping Colony Landscape. *Isr. J. Zool.* **2002**, *48*, 71–82. [CrossRef]
63. Goreau, N.; Goreau, T.; Hayes, R. Settling, survivorship and spatial aggregation in planulae and juveniles of the coral *Porites porites* (Pallas). *Bull. Mar. Sci.* **1981**, *31*, 424–435.
64. Connell, J.H. Population ecology of reef-building corals. *Biol. Geol. Coral Reefs* **1973**, *2*, 205–245.
65. Buss, L.W.; Jackson, J.B.C. Competitive networks: Nontransitive competitive relationships in cryptic coral reef environments. *Am. Nat.* **1979**, *113*, 223–234. [CrossRef]
66. Rinkevich, B.; Loya, Y. Intraspecific competitive networks in the Red Sea coral *Stylophora pistillata*. *Coral Reefs* **1983**, *1*, 161–172. [CrossRef]
67. Müller, W.E.G.; Müller, I.; Zhan, R.; Maidhof, A. Intraspecific recognition system in scleractinian corals: Morphological and cytochemical description of the autolysis mechanism. *J. Histochem. Cytochem.* **1984**, *32*, 285–288. [CrossRef]
68. Rinkevich, B.; Loya, Y. Intraspecific competition in a reef coral: Effects on growth and reproduction. *Oecologia* **1985**, *66*, 100–105. [CrossRef]
69. Wallace, C.C.; Harrison, P.L. Reproduction, dispersal and recruitment of scleractinian corals. In *Ecosystems of the World*; Coral Reefs; Dubinsky, Z., Ed.; Elsevier Science Publishing Company, Inc.: Amsterdam, The Netherlands, 1990; Volume 25, pp. 133–207.
70. Rinkevich, B.; Loya, Y. The reproduction of the Red Sea coral *Stylophora pistillata*. I. Gonads and planulae. *Mar. Ecol. Prog. Ser.* **1979**, *1*, 145–152. [CrossRef]
71. Oren, U.; Benayahu, Y.; Lubinevsky, H.; Loya, Y. Colony integration during regeneration in the stony Coral *Favia favus*. *Ecology* **2001**, *82*, 802–813. [CrossRef]
72. Christiansen, N.A.; Ward, S.; Harii, S.; Tibbetts, I.R. Grazing by a small fish affects the early stages of a post-settlement stony coral. *Coral Reefs* **2009**, *28*, 47–51. [CrossRef]
73. Penin, L.; Michonneau, F.; Baird, A.H.; Connolly, S.R.; Pratchett, M.S.; Kayal, M.; Adjeroud, M. Early post-settlement mortality and the structure of coral assemblages. *Mar. Ecol. Prog. Ser.* **2010**, *408*, 55–64. [CrossRef]
74. Rinkevich, B. Do reproduction and regeneration in damaged corals compete for energy allocation? *Mar. Ecol. Prog. Ser.* **1994**, *143*, 197–302. [CrossRef]
75. Mueller, W.A.; Rinkevich, B. Cell Communication-mediated nonself-recognition and -intolerance in representative species of the animal kingdom. *J. Mol. Evol.* **2020**, *88*, 482–500. [CrossRef]
76. Simon-Blecher, N.; Achituv, Y.; Rinkevich, B. Protochordate concordant xenotransplantation settings reveal outbreaks of donor cells and divergent life span traits. *Dev. Comp. Immunol.* **2004**, *28*, 983–991. [CrossRef]

77. Rinkevich, B.; Weissman, I.L. Allogeneic resorption in colonial protochordates: Consequences of nonself recognition. *Dev. Comp. Immunol.* **1992**, *16*, 275–286. [CrossRef]
78. Rinkevich, B.; Weissman, I.L. Chimeras in colonial invertebrates: A synergistic symbiosis or somatic-cell and germ-cell parasitism? *Symbiosis* **1987**, *4*, 117–134.
79. Jaraud, A.; Bosse, P.; de Citres, C.D.; Tiret, L.; Cache, V.; Abitbol, M. Feline chimerism revealed by DNA profiling. *Anim. Genet.* **2020**, *4*, 631–633. [CrossRef]
80. Lipsker, D.; Flory, E.; Wiesel, M.; Hanau, D. Between light and dark, the chimera comes out. *Arch. Dermatol.* **2008**, *144*, 327–330. [CrossRef]
81. Bindoff, N.L.; Cheung, W.W.L.; Kairo, J.G.; Arístegui, J.; Guinder, V.A.; Hallberg, R.; Hilmi, N.; Jiao, N.; Karim, M.S.; Levin, L.; et al. Changing Ocean, Marine Ecosystems, and Dependent Communities. In *IPCC Special Report on the Ocean and Cryosphere in a Changing Climate*; IPCC: Geneva, Switzerland, 2019.
82. Bolnick, D.I.; Amarasekare, P.; Araújo, M.S.; Bürger, R.; Levine, J.M.; Novak, M.; Rudolf, V.H.W.; Schreiber, S.J.; Urban, M.C.; Vasseur, D.A. Why intraspecific trait variation matters in community ecology. *Trends Ecol. Evol.* **2011**, *26*, 183–192. [CrossRef]
83. Sully, S.; Burkepile, D.E.; Donovan, M.K.; Hodgson, G.; van Woesik, R. A global analysis of coral bleaching over the past two decades. *Nat. Commun.* **2019**, *10*, 1264. [CrossRef]
84. Bruno, J.F.; Selig, E.R. Regional decline of coral cover in the Indo-Pacific: Timing, extent, and subregional comparisons. *PLoS ONE* **2007**, *2*, e711. [CrossRef]
85. Bruno, J.F.; Côté, I.M.; Toth, L.T. Climate change, coral loss, and the curious case of the parrotfish paradigm: Why don't marine protected areas improve reef resilience? *Ann. Rev. Mar. Sci.* **2019**, *11*, 307–334. [CrossRef]
86. Gill, D.A.; Mascia, M.B.; Ahmadia, G.N.; Glew, L.; Lester, S.E.; Barnes, M.; Craigie, I.; Darling, E.S.; Free, C.M.; Geldmann, J.; et al. Capacity shortfalls hinder the performance of marine protected areas globally. *Nature* **2017**, *543*, 665–669. [CrossRef]
87. Bates, A.E.; Cooke, R.S.C.; Duncan, M.I.; Edgar, G.J.; Bruno, J.F.; Benedetti-Cecchi, L.; Côté, I.M.; Lefcheck, J.S.; Costello, M.J.; Barrett, N.; et al. Climate resilience in marine protected areas and the 'Protection Paradox'. *Biol. Conserv.* **2019**, *236*, 305–314. [CrossRef]
88. Rinkevich, B. Rebuilding coral reefs: Does active reef restoration lead to sustainable reefs? *Curr. Opin. Environ. Sustain.* **2014**, *7*, 28–36. [CrossRef]
89. Rinkevich, B. Management of coral reefs: We have gone wrong when neglecting active reef restoration. *Mar. Pollut. Bull.* **2008**, *56*, 1821–1824. [CrossRef]
90. Mitsch, W.J. What is ecological engineering? *Ecol. Eng.* **2012**, *45*, 5–12. [CrossRef]
91. Epstein, N.; Rinkevich, B. Applying forest restoration principles to coral reef rehabilitation. *Aquat. Conserv. Mar. Freshw. Ecosyst.* **2003**, *13*, 387–395. [CrossRef]
92. Shafir, S.; Van Rijn, J.; Rinkevich, B. A mid-water coral nursery. In Proceedings of the 10th International Coral Reef Symposium, Okinawa, Japan, 28 June–2 July 2006; pp. 1674–1679.
93. Amar, K.O.; Rinkevich, B. A floating mid-water coral nursery as larval dispersion hub: Testing an idea. *Mar. Biol.* **2007**, *151*, 713–718. [CrossRef]
94. Shafir, S.; Rinkevich, B. The underwater silviculture approach for reef restoration: An emergent aquaculture theme. In *Aquaculture Research Trends*; Schwartz, S.H., Ed.; Nova Science Publishers, Inc.: Hauppauge, NY, USA, 2008; pp. 279–295. ISBN 9781604562170.
95. Golomb, D.; Shashar, N.; Rinkevich, B. Coral carpets—A novel ecological engineering tool aimed at constructing coral communities on soft sand bottoms. *Ecol. Eng.* **2020**, *145*, 105743. [CrossRef]
96. Horoszowski-Fridman, Y.; Izhaki, I.; Rinkevich, B. Long-term heightened larval production in nursery-bred coral transplants. *Basic Appl. Ecol.* **2020**, *47*, 12–21. [CrossRef]
97. Rinkevich, B. Restoration strategies for coral reefs damaged by recreational activities: The use of sexual and asexual recruits. *Soc. Ecol. Restor.* **1995**, *3*, 241–251. [CrossRef]
98. Rinkevich, B. Steps towards the evaluation of coral reef restoration by using small branch fragments. *Mar. Biol.* **2000**, *136*, 807–812. [CrossRef]
99. Shafir, S.; Van Rijn, J.; Rinkevich, B. Nubbing of coral colonies: A novel approach for the development of inland broodstocks. *Aquar. Sci. Conserv.* **2001**, *3*, 183–190. [CrossRef]
100. Ayre, D.J.; Hughes, T.P. Climate change, genotypic diversity and gene flow in reef-building corals. *Ecol. Lett.* **2004**, *7*, 273–278. [CrossRef]

101. Van Oppen, M.J.H.; Souter, P.; Howells, E.J.; Heyward, A.; Berkelmans, R. Novel genetic diversity through somatic mutations: Fuel for adaption of reef corals? *Diversity* **2011**, *3*, 405–423. [CrossRef]
102. Baums, I.B. A restoration genetics guide for coral reef conservation. *Mol. Ecol.* **2008**, *17*, 2796–2811. [CrossRef]
103. Reusch, T.B.H.; Ehlers, A.; Hammerli, A.; Worm, B. Ecosystem recovery after climatic extremes enhanced by genotypic diversity. *Proc. Natl. Acad. Sci. USA* **2005**, *102*, 2826–2831. [CrossRef]
104. Hughes, A.R.; Stachowicz, J.J. Genetic diversity enhances the resistance of a seagrass ecosystem to disturbance. *Proc. Natl. Acad. Sci. USA* **2004**, *101*, 8998–9002. [CrossRef]
105. Crutsinger, G.M.; Collins, M.D.; Fordyce, J.A.; Gompert, Z.; Nice, C.C.; Sanders, N.J. Plant genotypic diversity predicts community structure and governs an ecosystem process. *Science* **2006**, *313*, 966–968. [CrossRef]
106. Letters, E. Additive and interactive effects of plant genotypic diversity on arthropod communities and plant fitness. *Ecol. Lett.* **2006**, *9*, 24–34. [CrossRef]
107. Drury, C.; Greer, J.B.; Baums, I.; Gintert, B.; Lirman, D. Clonal diversity impacts coral cover in *Acropora cervicornis* thickets: Potential relationships between density, growth, and polymorphisms. *Ecol. Evol.* **2019**, *9*, 4518–4531. [CrossRef]
108. Carne, L.; Kaufman, L.; Scavo, K. Measuring success for *Caribbean acroporid* restoration: Key results from ten years of work in southern Belize. In Proceedings of the 13th International Coral Reef Symposium, Honolulu, HI, USA, 19–24 June 2016; pp. 352–368.
109. Linden, B.; Vermeij, M.J.A.; Rinkevich, B. The coral settlement box: A simple device to produce coral stock from brooded coral larvae entirely in situ. *Ecol. Eng.* **2019**, *132*, 115–119. [CrossRef]