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REVIEW ARTICLE

Applying coral breeding to reef restoration: best practices, knowledge gaps, and priority actions in a rapidly-evolving field

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Reversing coral reef decline requires reducing environmental threats while actively restoring reef ecological structure and function. A promising restoration approach uses coral breeding to boost natural recruitment and repopulate reefs with genetically diverse coral communities. Recent advances in predicting spawning, capturing spawn, culturing larvae, and rearing settlers have enabled the successful propagation, settlement, and outplanting of coral offspring in all of the world's major reef regions. Nevertheless, breeding efforts frequently yield low survival, reflecting the type III survivorship curve of corals and poor condition of most reefs targeted for restoration. Furthermore, coral breeding programs are still limited in spatial scale and species diversity. Here, we highlight four priority areas for research and cooperative innovation to increase the effectiveness and scale of coral breeding in restoration: (1) expanding the number of restoration sites and species, (2) improving broodstock selection to maximize the genetic diversity and adaptive capacity of restored populations, (3) enhancing culture conditions to improve offspring health before and after outplanting, and (4) scaling up infrastructure and technologies for large-scale coral breeding and restoration. Prioritizing efforts in these four areas will enable practitioners to address reef decline at relevant ecological scales, re-establish self-sustaining coral populations, and ensure the long-term success of restoration interventions. Overall, we aim to guide the coral restoration community toward actions and opportunities that can yield rapid technical advances in larval rearing and coral breeding, foster interdisciplinary collaborations, and ultimately achieve the ecological restoration of coral reefs.

Key words: broodstock selection, coral breeding, coral recruitment, coral reef restoration, coral reproduction, larval propagation, local community engagement, offspring health, scaling up, technological innovation

Implications for Practice

- Coral breeding is a rapidly-evolving and potentially-scalable approach to reef restoration, which needs further innovation to match the extent of the coral reef crisis.
- Past achievements and future successes in coral restoration all rely on committed funder support, community engagement, and fundamental knowledge of coral reproductive biology and ecology.
- Scaling and improving breeding-based coral restoration programs will require careful broodstock selection and the development of methods to increase offspring fitness (i.e. health, growth, and survivorship) before and after outplanting.
- Re-establishing self-sustaining coral communities and the ecological functions they support will also require better knowledge transfer across practitioners and the reduction of local disturbances and regional climate stresses.

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Introduction

The United Nations Decade on Ecosystem Restoration declaration stresses that active interventions are needed to prevent, halt, or reverse ecosystem degradation. Globally, coral reefs are valued at $10 trillion USD/year (Spalding et al. 2017). They maintain biodiversity, provide habitat, and protect coasts, with key roles in recreation, tourism, food security, and pharmaceutical research (Knowlton et al. 2021). However, since the 1970s, up to 50% of live coral cover has been lost (NASEM 2019) and nearly half of all coral species are now at an “elevated risk of extinction” (Carpenter et al. 2008; IUCN 2022). Further losses are predicted, threatening the livelihood and well-being of 500 million people, many from lower-income but reef-rich nations (Knowlton et al. 2021).

Recognizing that the coming decade is decisive for the future of coral reefs, transformational actions that address climate change and local stressors must be implemented now, in concert with restoration interventions (Knowlton et al. 2021; Quigley et al. 2022), to ensure the persistence of foundational taxa and their genetic diversity. One such intervention is reef restoration via coral breeding (Randall et al. 2020). By producing millions to billions of coral offspring at a time, coral larval propagation has the potential to be applied at km scales (Hardisty et al. 2019; Harrison et al. 2021) while increasing the adaptive capacity of restored populations (Baums et al. 2019).

Though still a nascent area of research and restoration, this approach has clearly demonstrated its potential and continues to advance rapidly (Figs. 1A–O & 2A–O). The basic knowledge and practices needed to consistently and successfully rear larvae now exist (Heyward et al. 2002; Harrison et al. 2021; Miller et al. 2021; Fig. 2G & 2L), and, for some species, outplanted corals have achieved reproductive size, thus completing the coral life cycle in small-scale experiments (Guest et al. 2014; Chamberland et al. 2016a; Harrison et al. 2021; Fig. 2M–O). Challenges nevertheless remain due to the sheer scale of reef degradation relative to the current methodological capacity and costs (Bayraktarov et al. 2020; Fig. 3). Scaling up sexual propagation was recently identified as one of six priorities to advance coral restoration (Vardi et al. 2021). Here, we summarize current priority actions in effectively restoring coral populations at scale using sexually-produced offspring. We propose key research directions to advance the field, highlight opportunities for interdisciplinary collaborations, and emphasize the importance of local community inclusion and training for this approach to become an effective tool in assisting coral reef recovery. We base these recommendations on eight well-established principles that underpin ecological restoration (Gann et al. 2019; Table 1).

Expanding the Number of Restoration Sites and Species

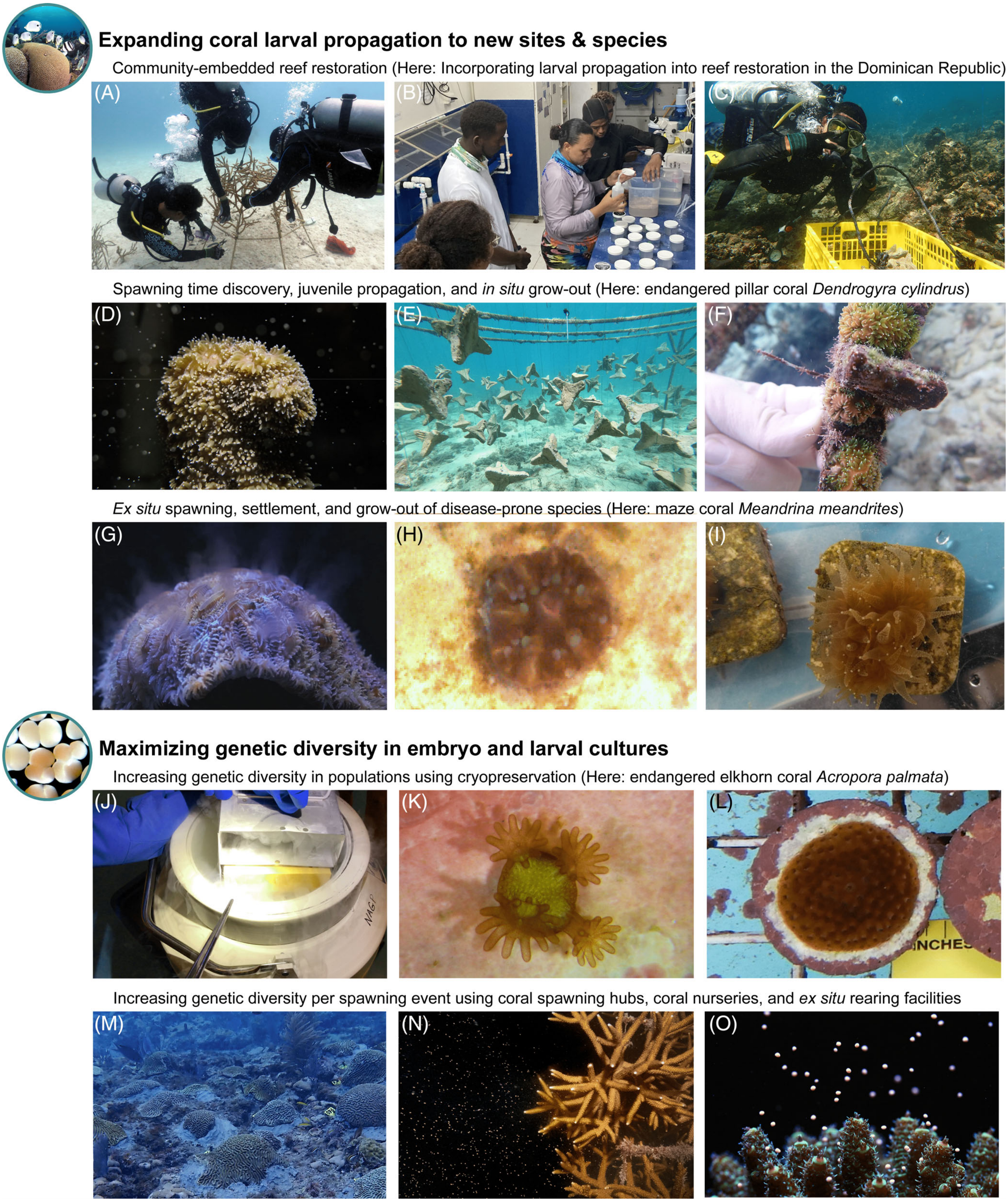
The coral life cycle has been achieved in its entirety for a few coral species. Future efforts should focus on including more species and understanding early life history traits of the many understudied species. Stronger initiatives are also needed to increase accessibility to capacity-building programs and therefore scale up by involving community members and ensuring representation from understudied regions and sites.

Investing in Reproductive Natural History to Expand the Number of Target Species

To date, most coral spawning research has been conducted on hermaphroditic species that synchronously release egg–sperm bundles on a few nights per year (Harrison et al. 1984; Harrison & Wallace 1990). For the best-studied species, decades of observation have enabled the collection of large volumes of gametes from wild populations (Heyward et al. 2002; Doropoulos et al. 2019; Harrison et al. 2021). Information on reproductive traits is available for more than 400 scleractinian species in the Indo-Pacific (Baird et al. 2009, 2021), and direct spawning observations exist for nearly all Caribbean species (Vermeij et al. 2021). Progress has also been made in propagating gonochores (taxa with separate male and female colonies) due to expanded natural history efforts and captive spawning at ex-situ facilities (Marhaver et al. 2015; O'Neil et al. 2021; Villalpando et al. 2021; Fig. 1A–I). However, inconsistent reproductive timing in wild populations from year to year is becoming more common, making spawn collections increasingly challenging for some species (e.g. *Acropora palmata*; Miller et al. 2016). This is especially true in communities impacted by bleaching, often resulting in delayed or interrupted spawning cycles (Ward et al. 2000; Levitan et al. 2014). In addition, fundamental reproductive data are missing for (1) many gonochoric species, (2) many species-rich regions in the Indo-Pacific, and (3) under-resourced regions worldwide. Without knowledge of spawning times and behaviors, it is impossible to undertake coral breeding. Thus, an essential requirement for reef restoration with sexually-produced corals is a concerted investment in reproductive studies across a broader diversity of species and sites (Fig. 4), allowing practitioners to combat declines at the community level and propagate multiple species resilient to various stressors (Principles 2, 4, and 6; Table 1). These efforts can be accelerated by workshops and conferences (Vardi et al. 2021), spawning databases (Baird et al. 2021), spawning prediction calendars (Vermeij et al. 2021), and breeding reference guides (Chamberland et al. 2023). Importantly, targeting more species multiplies opportunities for gamete collection each year, further increasing the scale and speed of restoration (Principle 7; Table 1).

Embedding Coral Restoration Programs within Communities to Secure Sustainable Outcomes

Given the technical knowledge required for successful coral breeding, community involvement is often wholly discounted or assumed to be too challenging; however, we disagree with this perspective. In fact, some of the biggest gains in implementing sexual propagation have come from community-based programs. For example, the largest breeding program for the critically endangered pillar coral *Dendrogyra cylindrus* is led by a local nonprofit organization in the Dominican Republic



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(Sellares-Blasco et al. 2021; Fig. 1A–C) with participation by local hotels, resorts, dive centers, and members of the community. Meanwhile, programs on the Great Barrier Reef (Hardisty et al. 2019), Indonesia, and Thailand (Chad Scott pers. comm.) have included Traditional Owners and collaborators in restoration projects using larval propagation. Contributing to this momentum, training workshops have made coral breeding more accessible to the restoration community (Bayraktarov et al. 2020) by establishing and disseminating standardized techniques and best practices that are effective and adaptable to local needs and resources. When participants are empowered to implement the teachings at their localities, such training programs help expand the diversity of restoration sites and species (Fig. 4; Principle 7; Table 1).

Local engagement has important long-term benefits that ultimately make restoration sustainable, equitable, and successful (Principles 1 and 2; Table 1). Involving local partners increases community understanding and support for restoration efforts. Engaging with historically-marginalized communities from the earliest planning stages ensures that cultural knowledge is integrated into restoration plans, while reducing the likelihood of harming culturally- and historically-important sites and species. Finally, community engagement represents a concerted effort to begin reversing the harm caused by colonial or "parachute science"; that is, the practice of privileged scientists from wealthy countries taking knowledge and specimens from resource-rich countries without further engagement, communication, or compensation (Stefanoudis et al. 2021).

Improving Broodstock Selection to Maximize the Genetic Diversity and Adaptive Capacity of Restored Populations

The effective integration of coral breeding within larger-scale coral reef restoration efforts will primarily depend on our ability to optimize coral offspring survival, health, and growth throughout their early life stages. An organisms' genotype will have a strong influence on its performance and eventual fitness. Thus, there is a need to identify and establish criteria for broodstock selection to maximize offspring health and genetic diversity.

Maximizing Genetic Diversity in Larval Cultures

A primary restoration objective is to re-establish self-sustaining, breeding populations with sufficient phenotypic and genetic variation to survive and adapt to climate change (Principles 2, 4, and 6; Table 1). Thus, maximizing genetic diversity is a top priority in coral breeding, both to increase the total genetic diversity created and to avoid applying unintended selective bottlenecks (Fig. 4). The current best practice is to collect gametes from as many parents as possible, ideally from a variety of habitats, to allow outcrossing and genetic recombination among many genets and thereby increase the representation of adaptive genetic variants in the population (Baums et al. 2019; Fig. 4). However, this can be challenging, in some regions, due to depleted populations, low genet diversity, asynchronous spawning times, spawning failure among remaining genets (Miller et al. 2016), and difficulties in accessing remote sites, especially at night and in rough seas.

An emerging tool for increasing genetic diversity in coral breeding is the use of cryopreserved sperm (Supplement S1; Fig. 1J–L). Due to recent innovations in sperm cryopreservation and long-term storage, frozen-thawed sperm from distant populations or habitats can be mixed with freshly-collected eggs on spawning nights and the resultant embryos can be propagated following standard methods (Grosso-Becerra et al. 2021; Hagedorn et al. 2021; Supplement S1; Fig. 4). This approach also helps prevent genetic bottlenecks due to spawning asynchrony or mate incompatibility in small populations (Chan et al. 2019). Additional emerging strategies for genetic diversification include the deliberate production of chimeric colonies or interspecies hybrids (Supplement S2).

Where populations are significantly depleted, transplanting gravid colonies to create in situ spawning hubs can enhance allelic diversity and facilitate efficient gamete collection (Gilliam et al. 2021; Fig. 1M). Similarly, harvesting spawn

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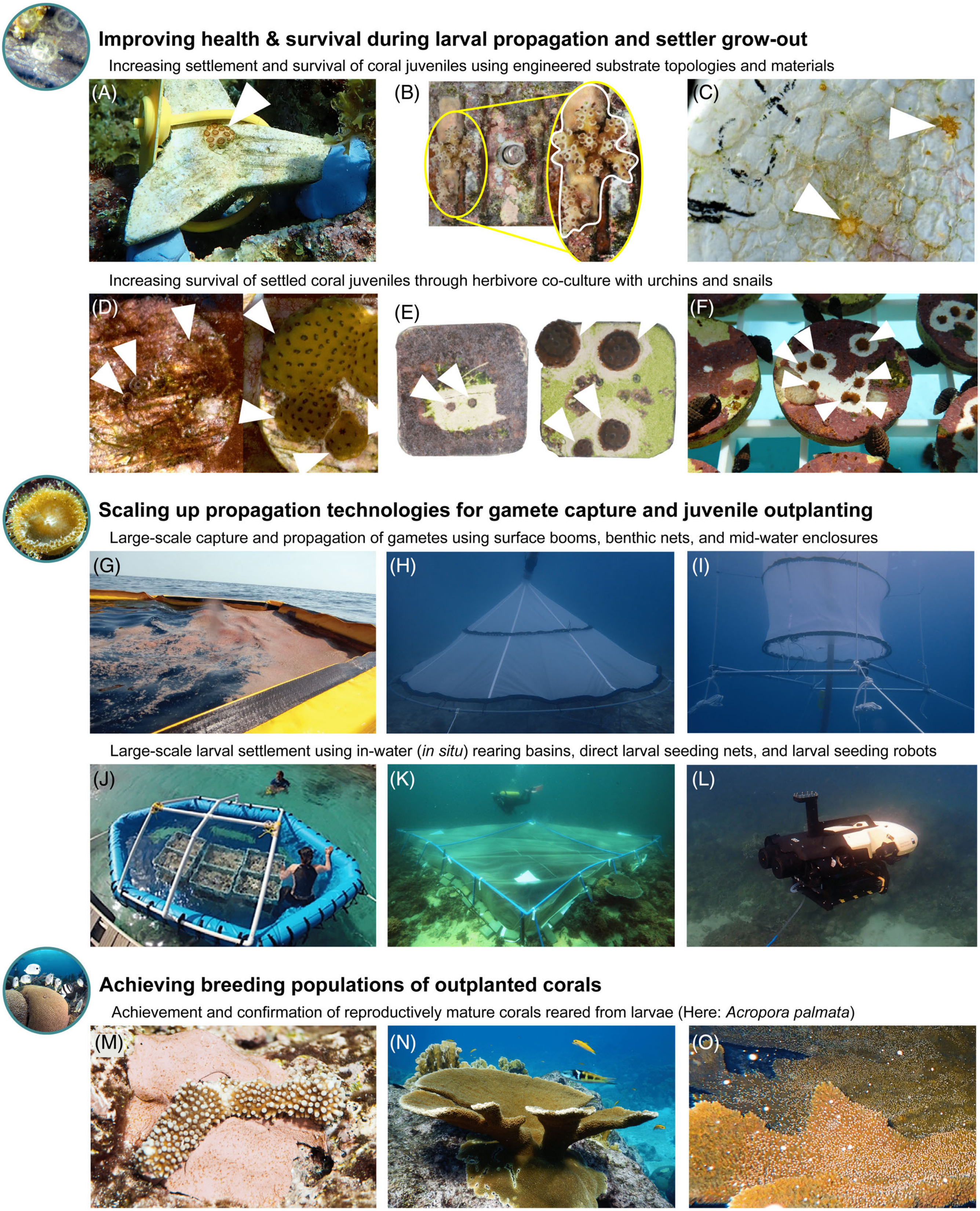
Figure 1. Success and momentum in increasing the scale of coral breeding in reef restoration: expanding training, sites, species, and genetic diversity. (A–C) Community-driven reef restoration programs incorporating larval propagation. Here: FUNDEMAR, Dominican Republic. (A) FUNDEMAR team members working on a traditional coral propagation nursery, (B) handling gametes on a spawning night in the larval propagation laboratory, and (C) outplanting coral substrates (photo credit: R. Sellares/FUNDEMAR). (D–F) Successful propagation of endangered, understudied species previously lacking data on spawning times and propagation. Here: *Dendrogyra cylindrus*. (D) Spawning *D. cylindrus* female in Curaçao (photo credit: K. Marhaver), (E) in situ underwater nursery in the Dominican Republic holding newly settled *D. cylindrus* juveniles (photo credit: M. Villalpando; also see Villalpando et al. 2021), (F) 2-year-old juvenile *D. cylindrus* propagated in the underwater nursery in the Dominican Republic (photo credit: M. Villalpando; also see Villalpando et al. 2021). (G–I) Propagation of disease-prone coral *Meandrina meandrites* in the ex situ facility at Florida Aquarium Center for Conservation. (G) Male *M. meandrites* releasing sperm (photo credit: Florida Aquarium), (H) 4-month-old, and (I) 15-month-old *M. meandrites* juveniles (photo credit: K. O'Neil). (J–L) Introduction of genetic diversity (assisted gene flow) in endangered *Acropora palmata* using cryopreserved sperm. (J) Liquid nitrogen dry shipper holding *A. palmata* sperm (photo credit: K. Marhaver), (K) settled *A. palmata* raised from cryopreserved sperm at CARMABI (photo credit: D. Flores and L. Tichy), (L) 6-month-old *A. palmata* raised from cryopreserved sperm, grown out at Mote Marine Lab (photo credit: C. Page). (M–O) Increased cohort-level genetic diversity by translocating and aggregating parent colonies. (M) Spawning hub for *Colpophyllia natans* in Broward County, Florida (photo credit: M. Miller; Gilliam et al. 2021), (N) spawning of *Acropora cervicornis* at an in-water restoration nursery in the Florida Keys (photo credit: A. Neufeld/Coral Restoration Foundation), (O) cohort-level genetic diversity can be increased by aggregating colonies in ex situ spawning systems. Here: spawning *Acropora millepora* (photo credit: J. Craggs/Horniman Museum; also see Craggs et al. 2017).



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Current challenges and stage-specific bottlenecks in applying coral larval propagation to reef restoration

Spawning adult colony	Fertilization	Developing embryos	Swimming larva (2 days)	Settled polyp (1 week)	Settled polyp (6 weeks)	Juvenile (up to 6 months)	Juvenile (up to 1 year)	Mature colony (4+ years)
Collecting high genetic diversity from multiple reef habitats	Achieving high fertilization in rare/gonochoric species	Maintaining high water quality and culture health	Providing effective settlement cues and substrates	Managing and eliminating fouling species and pests	Preventing algal overgrowth and trampling by invertebrates	Timing outplanting to avoid bleaching/ hurricanes	Preventing direct predation by fish/ invertebrates	Preserving genetic diversity in F2 crosses/ gene banking
Capturing/ fertilizing gametes from gonochores	Successfully cryopreserving and fertilizing with post-thaw sperm	Preventing genetic bottlenecks/ dominant genotypes	Preventing substrate fouling by aggressive competitors	Facilitating symbiont and microbiome establishment	Promoting rapid growth toward escape size	Selecting suitable outplanting habitats and densities	Managing fouling and overgrowth by benthic competitors	Maintaining accurate records on parentage and phenotype
Capturing gametes at aquaculture scales	Achieving high gamete concentrations in large-scale batches	Facilitating embryo development at aquaculture scales	Successfully mass-settling/ direct-seeding larvae	Maintaining stable aquarium systems and conditions for *ex situ* rearing	Determining effective feeding protocols for *ex situ* rearing	Outplanting at large scales/ reducing per-unit cost and handling time	Tracking survival/ growth/genotype on large spatial scales	Maintaining funding and capacity for long-term monitoring

Figure 3. Three main challenges and bottlenecks in applying larval propagation to reef restoration at each life stage of mass-spawning corals. Images show the life cycle of a typical mass-spawning coral (here: the grooved brain coral *Diploria labyrinthiformis*; propagation first described by Chamberland et al. 2017*b*). Ages listed in the figure correspond to the corals shown in the photos above and indicate the typical time at which each challenge or bottleneck occurs. Challenges that span multiple time points are listed under life stages at which they are commonly encountered. Although larval propagation programs continue to scale up and accelerate, practical bottlenecks still exist at each step of the rearing process. Innovation and creative solutions at each stage of collection and propagation are necessary to successfully integrate larval propagation into coral reef restoration at scale (photo credits: adult colony: Z. Ransom; all others: K. Marhaver).

from restoration nurseries and outplant sites can enable efficient gamete collection from numerous genotypes and source habitats (Fig. 1N). These approaches impose less stress on parental colonies than the collection, transport, and acclimation of corals to ex situ facilities while allowing collection from more colonies. Reef-based collection also reduces production costs as it avoids the need for the construction and maintenance of aquaculture systems (Harrison et al. 2021). However, field logistics, weather, person power, travel distances, and species biology can all affect the success of field collections and the total genetic diversity captured per spawning event. Therefore, in some cases, particularly for rare and endangered species, ex situ spawning, collection, and propagation (Supplement S3) remain the most practical way to increase parent numbers, gamete densities, and allelic diversity in a cohort (Craggs et al. 2017; O'Neil et al. 2021; López-Nandam et al. 2022; Fig. 1G–I & 1O).

Even when gametes are collected from many parents, offspring genetic diversity may be lower than expected. For example, some larval cohorts of *Acropora* spp. have yielded an over-

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Figure 2. Success and momentum in increasing the scale of coral breeding in reef restoration: improved settlement and culture methods, large scale propagation, and completing the coral life cycle. (A–C) Engineering substrates to improve coral settlement and survival. (A) 2-year-old *Orbicella annularis* on a concrete tetrapod produced by SECORE, outplanted in Mexico (photo credit: S. Mendoza), (B) tiles with wide grooves increased survival of *Acropora tenuis* by 3× relative to controls (photo credit: C. Randall; modified from fig. 2 in Randall et al. 2021); white outline denotes coral colony margin, (C) lime mortar substrates increased settlement of two species of Caribbean corals (photo credit: K. Marhaver; Levenstein et al. 2022). (D–F) Improved survival of coral settlers via herbivore co-culture. (D) Control (left) and treatment (right) coral substrates with *Acropora millepora* juveniles after 6 months in co-culture experiments with *Mespilia globulus* urchins (photo credit: J. Craggs/Horniman Museum; modified from fig. 6 in Craggs et al. 2019), (E) control (left) and treatment (right) coral substrates with *Acropora cervicornis* juveniles after 4.2 months in co-culture experiments with *Lithopoma* spp. snails (photo credit: J. Henry; modified from fig. 3 in Henry et al. 2019), (F) 2-month-old *Acropora palmata* juveniles co-cultured with *Batillaria minima* snails (photo credit: C. Page; also see Hagedorn et al. 2021). In (A) and (C–F), white arrows point to individual coral juveniles. (G–I) Large-scale gamete capture systems. (G) Floating larval culture pool system used to rear millions of larvae from coral spawn slick samples (modified from fig. 1B in Doropoulos et al. 2019; also see Harrison et al. 2021 and Harrison & dela Cruz 2022), (H–I) coral larval cradle system deployed in Japan consisting of (H) a conical net covering corals on the benthos connected to a hose and (I) a mid-water "larval cradle" chamber for receiving and holding spawn directly from the reef (photo credit: G. Suzuki; also see fig. 2 in Suzuki et al. 2020). (J–L) Large-scale rearing systems. (J) In situ larval rearing basin (CRIB) used for large-scale larval propagation and settlement (photo credit: SECORE), (k) larval seeding net deployed in Philippines (photo credit: Harrison et al. 2021), (L) LarvalBot autonomous vehicle system for larval seeding (photo credit: P. Harrison). (M–O) Reproductive populations of coral outplants. Here: A. *palmata* reared and outplanted by SECORE in Curaçao, photographed at age (M) 1 year (photo credit: P. Selvaggio), (N) 6 years (photo credit: V. Chamberland), and (O) 10 years, shown spawning (photo credit: V. Chamberland).

Table 1. Priorities that must be addressed to increase the effectiveness and scale of coral breeding and restoration. Promising areas of research and key actions are provided for each priority along with expected outcomes and associated principles that underpin ecological restoration.

Priority	*Research Directions and Key Actions*	*Expected Outcomes*	*Associated Principle(s) for Ecological Restoration (Gann et al. 2019)*
1. Expanding the number of restoration sites and species	(i) Investing in reproductive natural history to expand the number of target species	New scientific knowledge allows the propagation of more species	Principle 2: Ecological restoration draws on many types of knowledge
		Restored coral communities are more diverse and exhibit a greater resilience to different stressors	Principle 4: Ecological restoration supports ecosystem recovery processes Principle 6: Ecological restoration seeks the highest level of recovery attainable
		Breeding more species increases the number of opportunities for gamete collections and restoration each year	Principle 7: Ecological restoration gains cumulative value when applied at large scales
	(ii) Embedding restoration programs within communities to secure sustainable outcomes	Members of the community support, design, direct, and implement restoration efforts	Principle 1: Ecological restoration engages stakeholders
		Cultural knowledge is integrated into restoration plans	Principle 2: Ecological restoration draws on many types of knowledge Principle 8. Ecological restoration is part of a continuum of restorative activities
		Participation with local partners helps further expand the diversity of restoration sites and species	Principle 7: Ecological restoration gains cumulative value when applied at large scales
2. Improving broodstock selection to maximize the genetic diversity and adaptive capacity of restored populations	(i) Maximizing genetic diversity in larval cultures	Restored populations harbor sufficient phenotypic and genetic variation to survive and adapt to a changing environment	Principle 4: Ecological restoration supports ecosystem recovery processes Principle 6: Ecological restoration seeks the highest level of recovery attainable
	(ii) Considering heritability and limitations of selective breeding	Allelic diversity is preserved, and early genetic bottlenecks are prevented	Principle 7: Ecological restoration gains cumulative value when applied at large scales
	(iii) Evaluating advantages and downsides of stress exposure on broodstock	Restored populations are more resilient to different stressors	Principle 3: Ecological restoration practice is informed by native reference ecosystems, while considering environmental change
	(iv) Standardizing protocols for tracking the ancestry and stress-tolerance of broodstock, larvae, and settlers	Restored populations preserve the allelic diversity of their broodstock; cohorts are matched to environments where they thrive	
3. Enhancing culture conditions to improve offspring health before and after outplanting	(i) Providing favorable rearing conditions for embryos and larvae	Larval cohorts have low mortality and reduced stress, yielding superior offspring health and growth	Principle 2: Ecological restoration draws on many types of knowledge
	(ii) Designing and conditioning substrates for successful larval settlement and outplanting	Aquarists, materials scientists, engineers, chemists, microbiologists, and ecologists together achieve higher settlement, more efficient outplanting, and higher survival than otherwise possible	Principle 3: Ecological restoration practice is informed by native reference ecosystems, while considering environmental change
	(iii) Improving offspring health and survival using symbiotic algae and probiotic microbes	Routine mass-inoculation of larvae and settlers with beneficial algae and microbes provides additional gains in survival and stress tolerance	

Table 1. Continued

Priority	*Research Directions and Key Actions*	*Expected Outcomes*	*Associated Principle(s) for Ecological Restoration (Gann et al. 2019)*
	(iv) Feeding settlers during in situ and ex situ grow out to improve health and performance	Effective, species-specific feeding regimes increase growth during propagation and survival after outplanting	
	(v) Co-culturing settlers with beneficial grazers to reduce algal fouling	Reduced levels of competition with harmful algae improve larval settlement as well as settler health, growth, and survival	
	(vi) Standardizing protocols to allow rigorous, data-driven comparisons of restoration outcomes across sites, species, and outplanting approaches	Methodologies that significantly improve the health and survival of coral larvae, settlers, and juveniles are identified and disseminated across practitioners	Principle 3: Ecological restoration practice is informed by native reference ecosystems, while considering environmental change Principle 5: Ecosystem recovery is assessed against clear goals and objectives, using measurable indicators
4. Scaling up infrastructure and technologies for large-scale coral breeding and restoration	(i) Harvesting millions to billions of gametes from spawning events (ii) Enabling large-scale rearing of embryos, larvae, and settlers (iii) Effectively deploying larvae and settled juveniles to large areas of reef	Methodological and technological advances continually increase the size and quality of gamete collections and larval cohorts, including for gonochoric and brooding species	Principle 2: Ecological restoration draws on many types of knowledge Principle 6: Ecological restoration seeks the highest level of recovery attainable Principle 7: Ecological restoration gains cumulative value when applied at large scales
	(iv) Ensuring the availability of new technologies in low-income but reef-rich nations	Coral breeding is conducted by an increasing number of people targeting an increasing number of sites and species	
5. Achieving ecological restoration	(i) Promoting short-term performance and long-term adaptation	Selecting genotypes with high survival potential maximizes short- to medium-term benefits, while outplanting populations with high genetic and phenotypic variation promotes long-term community persistence Reducing local stressors multiplies the benefits of coral restoration on both short and long time scales	Principle 4: Ecological restoration supports ecosystem recovery processes Principle 6: Ecological restoration seeks the highest level of recovery attainable Principle 7: Ecological restoration gains cumulative value when applied at large scales
	(ii) Creating nodes of reef connectivity	The future breeding success of restored populations is maximized by choosing outplanting sites strategically Restored populations increase larval supply to nearby, down-current reef areas and help to reconnect meta-populations	
	(iii) Establishing holistic reef management	Management actions enhance restoration outcomes and ensure long-term success	Principle 1: Ecological restoration engages stakeholders Principle 2: Ecological restoration draws on many types of knowledge Principle 8: Ecological restoration is part of a continuum of restorative activities

representation of closely-related offspring (i.e. half or full siblings) and low allelic diversity (Baums et al. 2022; López-Nandam et al. 2022; Fig. 3). Although it remains unclear what causes such genetic bottlenecks during propagation, candidate mechanisms include gametic incompatibilities, differences in sperm motility or quality (Willis et al. 1997; Grosso-Becerra et al. 2021), unintended and undesirable selective pressure imposed by culture conditions, or selective pressure from environmental conditions at the destination reef (Baums et al. 2022).

Considering Heritability and Limitations of Selective Breeding

Coral health and stress tolerance are affected by genotype and thus partially inherited from parents, but the degree of heritability can vary widely across traits, individuals, species, and sites. Thermal tolerance is a trait of particular interest in coral restoration and there is preliminary evidence that it can be inherited by larvae, separate from any influence of symbionts (Baums et al. 2013; Howells et al. 2021; Drury et al. 2022). However, it remains to be determined whether this demonstrated resistance of larvae to lab-induced heat stress translates to more resilient adult colonies on reefs. Additional heritable variation in the symbiont community may also help corals adapt to changing environments (Quigley et al. 2017). Other traits important in reproduction and survival also display genetic determination, including spawning times (Levitan et al. 2011; Miller et al. 2016), settlement preferences (Kenkel et al. 2011), growth, and calcification rates (Kuffner et al. 2017).

Although there is potential for heritable trait selection in restoration programs, additional non-genetic parameters, including environmental and epigenetic factors, will also influence offspring traits. O'Donnell et al. (2018) showed that individual genets performed differently in distinct environments (nursery vs. reef sites) suggesting that caution is needed when selecting for traits in the limited environment of a single breeding program. As well, selecting broodstock to enhance a trait such as heat tolerance may lead to trade-offs in other physiological functions, such as growth, wound healing, disease resistance, toxin tolerance, fecundity, reproductive success, or even cold tolerance. Therefore, if gametes are sourced from bleaching- and disease-resistant wild colonies to help build climate resilience (van Oppen et al. 2015), we recommend undertaking such selective breeding (i.e. crosses among parents with resistant, heritable phenotypes) in combination with propagation of larval cohorts bearing high genetic diversity (i.e. crosses with as many parents of as wide a variety of phenotypes as possible; Baums et al. 2019; Principles 2, 4, and 6; Table 1).

Evaluating the Advantages and Downsides of Stress Exposure on Broodstock

Exposure to sublethal environmental stress can reduce the number and quality of gametes and larvae that parents produce (Harrison & Wallace 1990; Hartmann et al. 2017). When the goal is to produce the healthiest possible offspring for restoration, it is best to avoid breeding corals exposed to severe stressors. However, the effects of sublethal, chronic environmental stress are not universally negative. Sublethal stress may prime eggs, larvae, and settlers to tolerate these conditions (a process known as stress-hardening) and possibly select for valuable adaptive genetic variants. For example, brooded larvae from parents living near the warm and variable outflow (28.5–33°C, mean 29.2°C) of a desalination plant tolerated rearing at 31°C, while conspecific larvae from nearby parents at ambient reef temperature (mean 28.7°C) suffered 40% greater mortality when reared at 31°C (Chamberland et al. 2016*b*).

Stress-hardening may also be achieved in the laboratory by exposing parents to elevated stress (e.g. increased pCO_2), which may increase offspring survival under similar conditions (Putnam et al. 2020). Inherited forms of stress tolerance can arise via such epigenetic priming or via selection for stress-tolerant alleles (Dixon et al. 2015; Howells et al. 2021). Thus, hardier offspring could be produced for restoration by deliberately sourcing larvae from stressful and marginal environments, if indeed this stress tolerance is heritable and is maintained throughout the full life cycle (Fig. 4). A major knowledge gap exists as to whether stress-hardened, outplanted broodstock are resilient when subsequently exposed to stress events such as heat waves and disease outbreaks. A similar evaluation would be needed for resistance to diseases, pests, or pollutants.

For coral restoration to successfully preserve genetic diversity and promote adaptation, practitioners must implement effective systems for tracking the ancestry of broodstock and outplants (Supplement S4) and linking genotype and parentage with offspring performance through the life cycle. Standard protocols are also needed for stress testing broodstock, larvae, and settlers, which will provide valuable information on their performance in different environments (Principle 3; Table 1).

Enhancing Culture Conditions to Improve Offspring Health before and after Outplanting

The mass production of coral recruits via in vitro fertilization and settlement is now relatively routine, but efforts to scale up larval production are hampered by the fact that corals undergo a Type III survival bottleneck, meaning that most offspring die young (Wilson & Harrison 2005; Vermeij & Sandin 2008). Thus, for species with prolific and predictable spawning, post-settlement mortality is currently the greatest impediment to scaling up larval propagation (Fig. 3). Improving offspring health (e.g. size, lipid and protein content, pigment concentration, photosynthesis and respiration rates) and performance (growth, resistance to disease and competition), before and after outplanting, will require additional technical progress and the adoption of best practices at each stage of breeding.

Providing Favorable Rearing Conditions for Embryos and Larvae

Initial culture conditions are critical in coral breeding efforts (Fig. 3). Maintaining optimal temperature and water quality is essential during embryogenesis and larval development (Randall et al. 2020; Fig. 4). Water quality is maintained by ensuring high fertilization rates in cultures, thoroughly rinsing

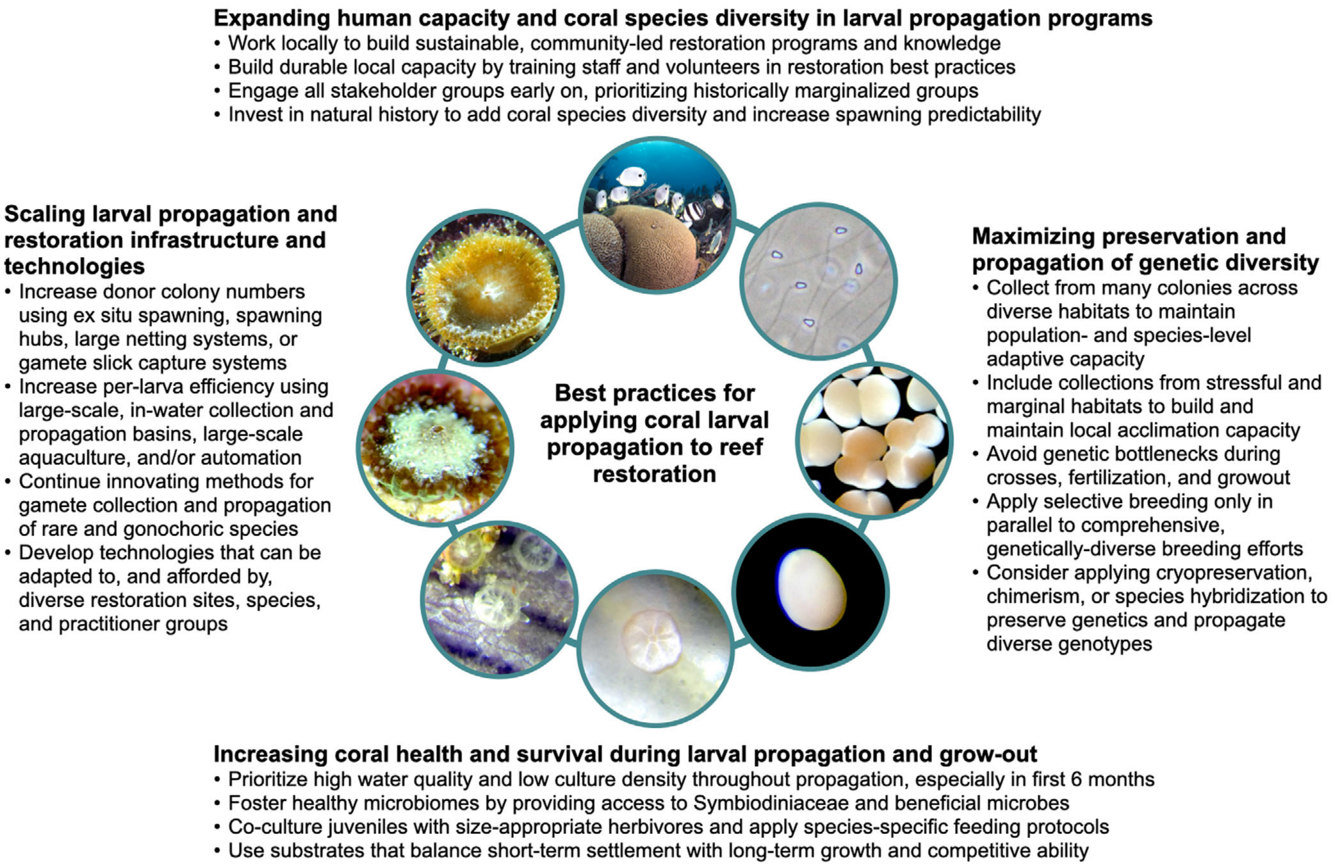

Figure 4. Best practices for applying coral larval propagation to reef restoration. As larval propagation programs continue to build momentum, methods, and equipment are changing quickly. Nevertheless, a core set of best practices have emerged; these best practices apply to small restoration start-ups as well as large scale infrastructure initiatives. Images show the life cycle of a typical mass-spawning coral (here: the grooved brain coral *Diploria labyrinthiformis*, propagation first described in Chamberland et al. 2017*b*) (photo credits: adult colony: Z. Ransom; all others: K. Marhaver).

embryos after fertilization to remove sperm and bacteria, rearing embryos at low density, and conducting frequent water changes (dela Cruz & Harrison 2017; Pollock et al. 2017). Poor culture conditions can have acute effects on larvae, including developmental delays, developmental failures, and latent effects that manifest after settlement (Pechenik 2006).

Designing and Conditioning Substrates for Larval Settlement and Outplanting

Once larvae are competent to settle, they can either be provided with artificial settlement substrates that are subsequently outplanted onto the reef (Guest et al. 2014; Chamberland et al. 2017*b*; Randall et al. 2021; Fig. 2A–C) or “seeded” directly onto the natural benthos (Edwards et al. 2015; Harrison et al. 2021; Fig. 2K). As larvae search for a suitable habitat, they can discriminate between materials, textures, colors, and shapes, but the optimal habitat for promoting initial settlement may be disadvantageous over the longer term by also attracting competitors. For example, some species prefer to settle against vertical surfaces, in deep grooves, or on rough textures, but these features may accumulate sediments, foster competition by benthic algae, or provide suboptimal light conditions for coral symbionts (Randall et al. 2021).

When designing artificial substrates, best practices include using non-toxic, sustainably-sourced materials and providing micro-scale features that attract larvae and reduce predation and competition. Promising areas of research include designing artificial substrates that further support coral growth by providing beneficial microbes, nutrients, minerals, or other additives (Levenstein et al. 2022; Fig. 2C).

To encourage settlement, practitioners typically condition artificial substrates in the ocean or in aquaria for a few weeks to months prior to spawning, until substrates are populated by biofilms and crustose coralline algae (CCA, Morse et al. 1994; Ritson-Williams et al. 2010). However, conditioning can be challenging, especially at large scales, and can yield inconsistent or unwanted results such as the growth of other benthic organisms detrimental to coral survival (Edwards 2010; Fig. 3). Co-conditioning substrates with herbivores may help reduce fouling levels before substrates are provided to larvae (K. Latijnhouwers, pers. comm.). Another possibility is to circumvent the conditioning step altogether; instead, substrates could be coated with cultured microbes or settlement cues derived from bacteria or CCA. Several microbial isolates and microbe-derived molecules have already been found to effectively trigger metamorphosis and/or settlement in laboratory settings (Negri et al. 2001; Sneed et al. 2014). Next, the isolation of cue molecules with broad activity and the development of standardized treatment protocols are needed to efficiently apply microbe-derived cues in restoration programs in different regions.

Another important consideration in settlement substrate design is the ease and speed of their deployment onto the reef. Substrates have typically consisted of flat ceramic or terracotta tiles without specific mechanisms for attachment to the reef. Manually attaching substrates using epoxy, nails, screws, or cable ties is time consuming and accounts for ~30% of restoration costs (Edwards 2010; Chamberland et al. 2015, 2017*a*), imposing a major bottleneck on scalability (Fig. 3). Newer devices are deployable within seconds and with minimal handling; these include stainless-steel clips (Suggett et al. 2020) and self-stabilizing, tetrapod-shaped substrates (Chamberland et al. 2017*a*; Fig. 2A). Designing substrates that can be efficiently deployed on reefs and that improve long-term survival and growth in the wild is an active area of research that requires interdisciplinary collaboration among propagation experts, materials scientists, engineers, chemists, ecologists, and microbiologists (Principle 2; Table 1).

Improving Offspring Health and Survival Using Symbiotic Algae and Probiotic Microbes

Most broadcast-spawning coral species do not provision eggs with symbiotic dinoflagellates (family Symbiodiniaceae), so these must be acquired from the environment. In culture systems, symbiont uptake is typically facilitated at the early post-settlement stage by exposing settlers to (1) coral fragments or colonies (Williamson et al. 2021), (2) symbionts extracted from adult corals, (3) in vitro symbiont cultures, or (4) sediment, raw seawater, or rubble collected from natural reefs, as each can be a vehicle for free-living Symbiodiniaceae (Littman et al. 2008).

Regardless of inoculation strategy, it has been generally assumed that early symbiont acquisition is most beneficial for juvenile corals. For example, Chamberland et al. (2017*b*) observed that *Diploria labyrinthiformis* settlers that acquired their symbionts within 1 month, and prior to outplanting, grew twice as fast and were four times more likely to survive to 5 months. Similarly, Hazraty-Kari et al. (2022) reported a 1.2-fold increase in the size of 4-month-old *Acropora tenuis* juveniles inoculated with lab-cultured Symbiodiniaceae during the larval stage. However, Hartmann et al. (2018) found that symbiont uptake during the larval stage could be detrimental due to increased physiological stress from symbiont metabolic activity. Chamberland et al. (2017*c*) and Kitchen et al. (2021) further reported that symbiosis at the larval stage can be particularly detrimental under heat stress. As an alternative to symbiont introduction in culture, direct larval seeding or outplanting of young (<1-month-old), aposymbiotic settlers allows the uptake of symbionts that are already adapted to the outplant habitat (Baums et al. 2019). Additional experiments are needed to determine at which ontogenetic stage symbiont introduction is most beneficial for each species (Fig. 3; Principle 2; Table 1).

For corals propagated over longer time periods in ex situ aquarium systems, optimizing lighting conditions is important for overall growth and survival once symbionts are established. These conditions will be species-specific but should generally mimic natural reef irradiation levels (Banaszak et al. 2018; Brunner et al. 2022).

In addition to dinoflagellates, corals associate with diverse microorganisms including viruses, bacteria, archaea, and protists that help maintain coral health (Knowlton & Rohwer 2003; Blackall et al. 2015). Probiotic microbes, or beneficial microorganisms for corals (BMC), can improve nutrition and growth, reduce stress caused by heat and pollutants, control pathogens, and influence early development (Peixoto et al. 2021). In larvae and settlers, BMC may supply nitrogen (diazotrophs) or act as antipathogens (e.g. *Roseobacter* spp.; Lema et al. 2014). Given their importance, the use of BMC is a proposed tool to improve health and growth of larvae and juveniles during breeding and restoration. At this time, additional research is needed prior to the large-scale inoculation of settlers with probiotic microbes (Supplement S5; Fig. 3; Principle 2; Table 1).

Feeding Settlers During Grow Out to Improve Health and Performance

Feeding settlers can provide a beneficial complement to nutrition derived from maternal lipids, symbionts, and BMCs (Petersen et al. 2008; Barton et al. 2017; Geertsma et al. 2022; Fig. 4). Supplemental nutrition can increase tissue and skeletal growth (Ferrier-Pagès et al. 2003), thereby increasing survivorship before and after outplanting (Toh et al. 2014). Live feeds such as brine shrimp (*Artemia* spp.) nauplii (Banaszak et al. 2018), rotifers (*Brachionus* spp.; Conlan et al. 2017), and microalgae (Brown & Blackburn 2013) are commonly used. However, culturing these foods can be labor intensive compared to using commercially-available foods (Hill et al. 2020). Although commercial foods are more commonly fed to adult corals (Forsman et al. 2012), they are increasingly being used during juvenile grow out (K. O'Neil, K. Marhaver, pers. comm.). Recent work has demonstrated that feeding *Acropora* larvae with homogenized *Artemia* significantly increased larval settlement and spat survival (Rodd et al. 2022).

Gaining a better understanding of the feeding capacity of coral juveniles will help to improve species-specific feeding protocols (Geertsma et al. 2022), avoid overfeeding and associated waste, pest outbreaks and poor water quality in culture systems (Conlan et al. 2017; Fig. 4). Polyp morphology, energy requirements, required dosage, feeding frequency, and water flow conditions, which may change ontogenetically, all need to be considered. Improving diets and feeding protocols can in turn reduce overall rearing costs and the time to reach target outplanting sizes (Barton et al. 2017). A close collaboration with aquaculture experts will help to determine the most effective formulae of live foods, commercial foods, and liquid supplements, as well as the optimal setting, timing, and duration of feeding to achieve good outcomes prior to outplanting (Principle 2; Table 1).

Co-Culturing Settlers with Beneficial Grazers to Reduce Algal Competition

A significant cause of settler mortality is competition with, and overgrowth by, benthic algae and cyanobacteria (Fig. 3). Co-culturing settlers with small-sized herbivores can help to mitigate these threats if incidental grazing does not cause excess damage to the coral settlers (Figs. 2D–F & 4). For example, *Acropora valida* settlers reared alongside the gastropod *Trochus niloticus* were 13% more likely to survive on the reef (Villanueva et al. 2013) and grazing by juvenile *Mespilia globulus* urchins resulted in a seven-fold increase in the survival of *Acropora millepora* settlers in laboratory tanks (Craggs et al. 2019; Fig. 2D). Small grazers can also help prevent algal blooms caused by overfeeding and resulting eutrophication in recirculating aquaculture systems (Bartlett 2013). Although co-culture efforts undoubtedly increase costs and logistical challenges, including maintenance of facilities and propagation expertise, this approach may have disproportionate benefits. For example, co-culturing the herbivorous Caribbean sea urchin *Diadema antillarum* with coral settlers has the potential to increase restoration success while restoring depleted populations of this keystone herbivore (Pilnick et al. 2021; AGRRA 2022). Herbivorous snails are also promising co-culture candidates (Henry et al. 2019; C. Page, pers. comm.; Fig. 1E & 1F).

As an increasing number of coral species are propagated to the settler stage, their species-specific interactions with diverse grazers, as well as suitable grazer sizes and densities, should be determined empirically (Villanueva et al. 2013; Craggs et al. 2019) to ensure effective algal removal while avoiding incidental grazing or predation. Little research has been done on other potentially beneficial grazers, but adaptively managing grazing pressure by micro-herbivores during coral grow out promises to increase settler size and yield, while reducing manual cleaning time and labor costs.

Regardless of the techniques employed to rear coral larvae and settlers, the use of standardized monitoring protocols is encouraged to allow accurate comparisons of restoration outcomes across sites, species, and restoration approaches (Supplement S6).

Scaling up Infrastructure and Technologies for Large-Scale Coral Breeding and Restoration

Thus far, cost, logistics, and technology gaps have limited most coral breeding and restoration activities to experimental scales that are too small to be ecologically significant (Fig. 3). However, this field is accelerating quickly, and with proof-of-concept established across a diversity of species, locations, and techniques, the field is now primed for a major expansion in scale (Figs. 2 & 3).

Harvesting Millions to Billions of Gametes from Spawning Events

Large-scale propagation requires the collection of millions to billions of gametes from spawning events (Principles 2, 6, and 7; Table 1). The feasibility of working at this scale has been demonstrated in regions where massive slicks form at the sea surface after spawning and can be concentrated using, for example, oil booms (Doropoulos et al. 2019; Fig. 2G). Similarly, the development of floating spawn collection nets and inflatable booms, which can be temporarily deployed adjacent to coral communities prior to spawning, now allows the efficient collection of tens to hundreds of millions of eggs and embryos during spawning events along with subsequent mass larval culture; these systems have already been successfully tested in the Philippines and on the Great Barrier Reef (Harrison et al. 2021; Harrison & dela Cruz 2022).

Large-scale rearing is more challenging when gametes must be collected from individual colonies rather than from surface slicks. To address this, Suzuki et al. (2020; Fig. 1H & 1I) designed the “coral larval cradle,” a gamete collector and in situ rearing system in which several million larvae can be produced per spawning event from multiple colonies simultaneously. This system is best suited for common species that are densely aggregated. For rare and dispersed species, translocating colonies to create higher-density coral “spawning hubs” could be an effective strategy (Gilliam et al. 2021; Fig. 1M).

Although the propagation scale for spawning hermaphrodites continues to rise, further innovation is needed for broadcast-spawning gonochoric corals, which release individual eggs and sperm rather than gamete bundles (Figs. 3 & 4; Principles 2 and 7; Table 1). Their gametes generally cannot be harvested with standard techniques that are dependent on buoyancy, instead being collected in smaller numbers using plastic bags or syringes. Similarly, the large-scale collection and culture of brooded larvae is not yet feasible in reef environments and requires further methodological development.

Enabling Large-Scale Rearing of Embryos, Larvae, and Settlers

Over the last decade, in-water rearing systems have been developed for large-scale embryo culture, larval rearing, settlement, and settler grow out (Suzuki et al. 2020; Miller et al. 2021; Fig. 2G–L; Principles 2, 6, and 7; Table 1). In the Philippines and the Great Barrier Reef, large, floating larval culture pools have enabled the production of >200 million coral larvae from multispecies spawning events (Harrison et al. 2021; Harrison & dela Cruz 2022; Fig. 2G). These in-water methods eliminate the costs, land-based infrastructure, and logistics of laboratory culturing, thereby reducing cost per coral while allowing propagation in remote reef environments. Meanwhile, there is a potential role for industrial-scale, intensive aquaculture methods. Doropoulos et al. (2019) trialed a large, shipborne gamete slick-collector with multiple 4,500-L larval culture tanks onboard, demonstrating that similar land-based aquaculture systems housing billions of larvae could also be feasible. In Australia, semi-automated and automated shore-based aquaculture systems are being developed to enhance recruitment on bleaching-damaged reefs, with deployment scales ranging from 1 to 20 or more reefs (RRAP 2022). Importantly, such large-scale rearing efforts can be limited during marine heat waves and hurricanes, and by under-resourcing, particularly in low- to middle-income economies.

Effectively Deploying Larvae and Settled Juveniles to Large Areas of Reef

In addition to scaling up gamete collection and larval culture, reef restoration must also scale up the delivery of larvae and settlers to restoration sites. Thus far, in situ larval culture and settlement pools have allowed the outplanting of up to 63,000 settlers per spawning event (Miller et al. 2021; Fig. 2J). Meanwhile, direct larval seeding using mesh enclosures has been applied in the Philippines (dela Cruz & Harrison 2017; Fig. 2K), Great Barrier Reef, and Curaçao, delivering millions of larvae per spawning event to replicate reef areas up to 100 m^2 (P. Harrison, pers. comm.). Because this approach still requires the manual transfer of larvae from rearing facilities or basins to the settlement enclosures, it has not yet been applied at scales greater than 1 ha.

Recently prototyped methods for directly deploying millions of larvae onto reefs include targeted release through pipe networks, the mass release of larval clouds from nets (P. Harrison pers. comm.), and robotics to disperse coral larvae at multihectare scales. On the Great Barrier Reef and in the Philippines, researchers are remotely operating an underwater drone, the "LarvalBot," to disperse hundreds of thousands of larvae at a time, covering 1,500 m^2 of reef per robot-hour (Dunbabin et al. 2020; Fig. 2L). In the future, robot and drone technology could also be used to outplant corals pre-settled on artificial substrates. Overall, enabling coral breeding at massive scales across species, nations, and reef areas will require alliances between biologists and engineers and equitable access to emerging technologies in under-resourced locations (Principles 2, 6, and 7; Table 1).

Achieving Ecological Restoration

If post-settlement survival bottlenecks are resolved, the number of reproductive adults on a reef can be enhanced by coral breeding efforts in as little as 2–4 years for fast-growing species (Guest et al. 2014; Chamberland et al. 2016a; Harrison et al. 2021). Restored populations can therefore contribute to natural spawning events and help rebuild reef structural complexity within relatively short time frames. Coral breeding and restoration have the potential to enhance key ecological processes and help repair damaged reef ecosystems when they are practiced thoughtfully, with long-term objectives in mind, following the eight principles for ecological restoration (Gann et al. 2019; Table 1).

Promoting Short-Term Performance and Long-Term Adaptation

Outplanting individual coral genotypes with demonstrated high performance under controlled conditions can help to maximize short- to medium-term restoration benefits, while restoring populations with high genetic and phenotypic variation will promote more durable, long-term community persistence by buffering against future environmental change. Because the benefits of each approach are complementary, manifesting at different times, they can and should be combined (Principles 4, 6, and 7; Table 1). Crucially, reducing local environmental stressors can multiply the benefits of larval propagation on both short- and long-term time scales, by improving offspring survival, coral health, and bleaching resilience in existing parental communities, while providing a path forward to rebuilding habitat quality for future communities (Principles 4, 6, and 7; Table 1).

Creating Nodes of Reef Connectivity

A key, but complex, consideration to ensure the long-term success of coral breeding efforts is the strategic selection of suitable outplanting sites (Supplement S7) and microhabitats (Supplement S8), so that future breeding success and population connectivity are maximized (Principles 4, 6, and 7; Table 1). Whenever possible, outplanted and seeded corals should be interspersed with wild conspecifics (but located away from parent colonies) at adequate inter-colony distances to increase the overall likelihood of outcrossing with unrelated individuals. Similarly, outplanting dense aggregations of (potential) siblings from an individual rearing effort should be avoided whenever possible to minimize the risk of inbreeding. These precautions are particularly important when larval cohorts contain limited genetic diversity due to small source populations or propagation bottlenecks (Baums et al. 2022).

When planning an outplanting effort, it is also important to consider larval dispersal and ocean currents so that restored breeding populations may increase larval supply and recruitment to nearby, down-current reefs and help to reconnect meta-populations (Harrison & Booth 2007; Harrison et al. 2021; Supplement S8; Principles 4, 6, and 7; Table 1). In some cases, outplanting may be deliberately designed to create larval "source" reefs, that is, reefs (or "spawning hubs") expected to seed downstream "sink" reefs with dispersed larvae; however, caution is warranted because most coral reef systems lack such simple and predictable "source-sink" relationships.

Establishing Holistic Reef Management

To achieve successful restoration outcomes, strategic plans should be developed in collaboration with all local partners and Traditional Owners (Quigley et al. 2022; Principles 1, 2, and 8; Table 1). Holistic management plans should include the goals of the restoration initiative, guidelines on selection of restoration sites, monitoring, data archiving, communication, timing of interventions, and risk assessments. Although site selection often focuses on no-take zones, marine protected areas, or other areas with a formal protected status, it is important to assess the actual level of management and enforcement at such sites and consider whether restoration could be just as effective or more so at unprotected, but equally valuable sites.

Conclusion

The ultimate aim of all ecosystem restoration is to achieve self-sustaining, naturally-reproducing populations that support key ecological functions. Coral restoration interventions are needed at hectare scales, that is, at much larger scales than are currently possible. We believe coral breeding should play a key role, and that these interventions should be planned strategically, collectively, and inclusively, in collaboration with local partners and Traditional Owners, using appropriate conservation and management strategies. We envision it will soon be possible to establish new coral generations that will contribute to the persistence and recovery of coral reefs and thus to the well-being of humankind through the centuries ahead.

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Supporting Information

The following information may be found in the online version of this article:

Supplement S1. Cryopreservation—a tool to maximize genetic diversity and assist gene flow.
Supplement S2. Chimerism and interspecies hybridization—prospective pathways to increase genetic diversity.
Supplement S3. Aquarium-based spawning—opportunities for assisted fertilization, managed breeding, and biological research.
Supplement S4. Tracking phenotypes and genotypes of coral broodstock and outplants.
Supplement S5. Probiotics—challenges to delivery strategies for large-scale inoculation of coral larvae and settlers.
Supplement S6. Standardized monitoring protocols—best practices to measure progress in larval propagation techniques.
Supplement S7. Outplanting—how to select and prepare sites to improve restoration outcomes.
Supplement S8. Reef connectivity—considering larval dispersal and ocean currents to help reconnect meta-populations.

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