Closing the Coral Life Cycle: A service blueprint to overcome the coral recruitment crisis through research, restoration, and innovation

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Keywords

Coral, coral reefs, restoration, marine biodiversity, endangered species, reproduction, life cycle, service blueprint, coral sexual recruitment

Abstract

Coral reefs underpin marine biodiversity and the functioning of oceanic ecosystems, yet since the 1970s they have experienced unprecedented degradation, with the Caribbean region exhibiting some of the most acute declines. Global climate change—through warming, acidification, and intensified storm activity—combined with local stressors such as sedimentation, eutrophication, and over-exploitation, now impedes every stage of the coral life cycle and has precipitated a chronic failure of sexual recruitment in the region's dominant reef-building taxa. In this synthesis we (i) delineate the complete life cycle of Caribbean reef-building corals, (ii) identify the known principal barriers that prevent successful transition from gamete to recruit, and (iii) evaluate the suite of mitigation and restoration strategies currently available. We highlight interventions that (a) curb greenhouse-gas emissions, (b) protect habitats from sediment and pollutant influx, (c) enhance adult colony health through targeted feeding and probiotic applications, (d) preserve genetic diversity via assisted gene flow, and (e) increase adult density and improve settlement substrate quality. Our review also exposes critical knowledge gaps that hinder the development of effective strategies to overcome barriers to coral recruitment: (1) the historical trajectory of recruitment failure, (2) species-specific, quantitative in-situ recruitment data, (3) reliable, low-cost methods for determining colony age, (4) robust tracking of larval dispersal and supply, (5) the dynamics of symbiont availability and uptake, (6) identity and fine-scale measurements of pollutants, and (7) disentangling the interactive effects of multiple stressors on early-life stages. To bridge these gaps we propose a research agenda that integrates (i) inexpensive age-dating techniques, (ii) rapid diagnostic and standardized stress-assay platforms, (iii) next-generation sensors for contaminant detection, (iv) molecular tools for symbiont identification, and (v) coupled biophysical-eRNA methods to quantify larval transport and settlement. Finally, we present a service-blueprint that aligns reef managers, scientists, restoration practitioners, and funders around coordinated decision-making pathways for research prioritisation, restoration design, and investment allocation. Implementing this blueprint will accelerate our mechanistic understanding of coral recruitment, enable evidence-based mitigation of global change impacts, and ultimately safeguard the persistence of Caribbean coral reefs.

Keywords: Coral life cycle, sexual recruitment, conservation, climate change, local factors, human activities, knowledge gaps, research directions.

Introduction

Coral reefs are crucial for the livelihoods of people in tropical and subtropical regions and for maintaining marine biodiversity and global ocean health (Hoegh-Guldberg et al. 2007; Sing Wong et al. 2022; Rogers et al. 2023). Unfortunately, these vital ecosystems have been severely degraded since the 1970s, with particularly alarming declines in the Caribbean (Gardner et al. 2003; Jackson et al. 2014). The combination of global climate change caused by greenhouse gas emissions and local factors such as pollution, nutrient enrichment, infectious diseases, coastal construction, and overfishing compromises corals at all life stages. Historically, coral cover in the Caribbean was approximately 50% of available reef substrate, but current estimates indicate that most areas now have less than 20% (Jackson et al. 2014; Lester et al. 2020; Reverter et al. 2024a). This decline is particularly concerning, given that only five species of reef-building corals are responsible for the vast majority of reef accretion in the region (*Acropora palmata*, *A. cervicornis*, *Orbicella annularis*, *O. faveolata*, *O. franksi*), and all five have experienced dramatic population declines (Cramer et al. 2021). For example, the population sizes of *A. palmata* and *A. cervicornis* on Florida's coral reef had been estimated at 468,000 and 10 million colonies in the early 2000's, respectively (Miller et al. 2013). However, in 2025, remnant acroporid colonies are scarce, reduced by upwards of 99.99% for *A. palmata* with only 37 founder genets remaining after the 2023 bleaching event (Williams et al. 2024). These scant colonies are spread across Florida's reefs, which precludes natural sexual reproduction as a means of population recovery or habitat restoration.

Similar patterns of decline have been observed in all major reef-building coral species throughout the Caribbean. Indeed, half of Atlantic reef-building coral species are currently at a high risk of extinction (Gutierrez et al. 2024). Historically, Caribbean coral populations have been able to recover from local, episodic population declines, such as those following storms or bleaching events. Critical to recovery was the success of sexual recruitment, i.e., sexual reproduction and subsequent growth of settled larvae into mature colonies. However, in the major reef-building Caribbean corals, the life cycle no longer completes, preventing successful sexual recruitment, stymying recovery, and accelerating the collapse of this important ecosystem (Figure 1, 2).

While some Caribbean coral species still recruit sexually (e.g., species in the Siderastreidae, Agariciidae, Poritidae, and Faviidae (Green and Edmunds 2011; Harper et al. 2023)), the major reef-building acroporid and orbicellid populations show little sign of replenishment via sexual recruitment (Hughes and Tanner 2000; Quinn and Kojis 2005; Williams et al. 2008; Harper et al. 2023; Jones and Gilliam 2024). The lack of sexual recruits is difficult to document, partly due to the general invisibility of coral recruits,

and the reliance of these species on asexual fragmentation of existing adults, which can mask the paucity of sexually-produced recruits (Baums et al. 2006; Miller et al. 2018; Manzello et al. 2019). This problem has also been compounded by the lack of species-level surveys of coral recruits that predate the 1980s. Even now, it remains challenging to identify small recruits to the species level without applying expensive genetic analyses (O'Cain et al. 2019). Without sexual recruitment, the outcome is inevitable; coral populations cannot recover or adapt, and coral reef accretion will slow or stop. Reef dissolution will outpace accretion and therefore reef structures will gradually disappear (Eyre et al. 2018).

To address this critical conservation challenge, the "Closing the Coral Circle" alliance brought together experts in coral biology, ecology, advanced forensics, biological engineering, robotics, and other areas to discuss causes and solutions for the lack of unassisted recruitment of reef-building corals in the Caribbean. The group focused primarily on acroporids and orbicellids, the key Caribbean reef-building genera for which sexual recruitment failure appears to be the most severe. Below we first describe the life cycle of these taxa (Figure 1) and outline the series of highly sensitive, sequential processes that must be successfully completed to close the coral life cycle, both in nature and captive breeding. We then (1) consider the larger environmental context of the coral reef crisis and its role in perpetuating coral recruitment failure, (2) summarize the well-understood barriers that hinder sexual coral recruitment and outline possible solutions, and (3) identify knowledge gaps in our understanding of sexual recruitment that confound and delay the search for solutions. We have also synthesized these insights into a service blueprint for improving and recovering successful coral recruitment (Figure 2, 3, Appendix 1), i.e., a visual map of the coral life cycle overlaid with known challenges, knowledge gaps, and potential solutions and interventions. This resource is intended to further the goals of funders, managers, researchers, and practitioners who aim to improve coral recruitment both in wild and captive-bred populations.

The coral life cycle

The coral life cycle is the ordered sequence of stages required for sexual reproduction to produce a genet in the next generation. For convenience, we present this circle of life in five stages; gametogenesis and spawning, larval development, settlement, symbiosis, and growth and development. We denote "sexual recruitment" as the process by which a new demographic cohort of corals is generated from sexual reproduction (forming "genets"), completing the coral life cycle. In this paper, we do not further consider the generation of new colonies (ramets) via asexual reproduction through fragmentation or the impact

of somatic mutations on genetic diversity. Currently, there are no data on how important somatic mutations may be relative to germline mutations in driving coral's evolutionary responses (adaptation), and this topic requires separate treatment (Van Oppen et al. 2011; Reusch et al. 2021; Vasquez Kuntz et al. 2022).

Gametogenesis and spawning

The major reef-building coral species in the Caribbean are hermaphroditic, seasonal broadcast spawners (Figure 1). After reaching a critical size and undergoing puberty, coral colonies require sufficient nutrition and favorable environmental conditions to produce healthy gametes. Following the onset of gametogenesis, reproductive cells begin to develop into eggs, then two to three months later, sperm development commences (Harrison and Wallace 1990; Vargas-Ángel et al. 2006). Globally, broadcast-spawning corals rely on environmental spawning cues, including annual temperature, diel, and moonlight cycles, which together with hormone signaling, enable the synchronization of gamete release (Tarrant et al. 2004; Van Woesik et al. 2006; Levitan et al. 2011; Harrison 2024). In the northern hemisphere summer, acroporids and orbicellids release gametes following the full moon, typically in August and September, but ranging from July to October, and often split across two sequential months. During spawning, these species release bundles of eggs and sperm into the water column, where they break apart, allowing fertilization to take place. Successful fertilization usually requires contact between gametes from different genets (i.e., genetically-distinct colonies), as the percentage of colonies that can self-fertilize is low (Baums et al. 2013; Vasquez Kuntz et al. 2022). However, gametes from different genets are not always compatible with one another; pairwise fertilization rates range from 0% to >90% under controlled laboratory conditions (Fogarty et al. 2012; Baums et al. 2013). Little is known about unassisted coral fertilization rates on reefs but colony-specific fertilization rates of the Pacific plating acroporid *A. hyacinthus* averaged between 12%- 34% in situ (Levitan et al. 2014; Mumby et al. 2024). Importantly, the distance between a colony and its nearest neighbour has a strong bearing on fertilization success, with greater proximity conferring much higher success (Mumby et al 2024). Evidence for such 'Allee effects' has also been found for orbicellids in the Caribbean (Levitan et al 2004).

In many locations throughout the Caribbean, wild and restored colonies of *A. palmata* and *A. cervicornis* have been observed to spawn reliably in years without significant disturbances (i.e., bleaching events or hurricanes). Similarly, wild orbicellid species spawn predictably and reliably, and a single restored colony has been observed spawning in Florida (H. Koch, pers comm). The regular success of "assisted reproduction" efforts by researchers who collect wild gametes from these taxa indicates that most

acroporid and orbicellid colonies produce viable eggs and sperm (Quiroz et al. 2023; Renegar et al. 2024) capable of fertilization and normal development, at least in years without major disturbances. Subsequently, the same researchers have often found that during assisted reproduction where eggs and sperm are combined manually, fertilization rates are very high (>90%). Hundreds to thousands of resulting larvae have been reared to the juvenile stage and some acroporids have been raised to adulthood in *ex-situ* farms and *in-situ* nurseries (Figure 1)(Chamberland et al. 2015; Koch et al. 2022a, 2022b). Thus, we know that members of these species *do* spawn and can produce viable offspring, at least when cultivated *ex-situ* through assisted reproduction.

Larval development

Coral embryos undergo cell division and differentiation, supported by egg nutrients, and eventually become planula larvae within the first 24-72 hours after fertilization (Harrison and Wallace 1990). During these early stages, embryos and larvae are vulnerable to bacterial infections, predation, mechanical damage, and environmental stressors, such as temperature and pollution, which can cause mortality, disrupt development, and deplete energy reserves (Randall and Szmant 2009; Baums et al. 2013; Banaszak et al. 2023). For a period lasting from days to months (depending on species), larvae drift in the water column on ocean currents, using their natural lipid reserves for buoyancy and energy. Dispersing larvae use their limited swimming abilities and high sensitivity to a diverse suite of environmental cues to locate and navigate toward the reef habitat (Jones et al. 2009; Tay et al. 2011; Hata et al. 2017). Little is known, however, about what happens to coral embryos and larvae in the “black box” of the water column. There are indications that altered larval dispersal pathways due to changes in ocean circulation patterns (McManus et al. 2021), and accelerated larval development from ocean warming (Randall and Szmant 2009; Baums et al. 2013), may lead to premature settlement (Figueiredo et al. 2014) and energy exhaustion (Figueiredo et al. 2022). The near-complete lack of data on the fate of coral embryos and larvae during their time in the planktonic stage could well conceal important changes in the completion rate of the coral life cycle compared to previous periods (Harrison 2024).

Settlement and recruitment

After early development and navigation in the water column, coral larvae must settle onto the reef substrate to continue their development and metamorphosis. Settlement involves an initial period of testing and attaching to substrata as a precursor to successful metamorphosis. While preliminary larval attachment and exploration of the substrate are reversible, allowing the larvae to swim back into the

water column, metamorphosis is generally irreversible, resulting in the formation of the initial or "primary" settled coral polyp and the commencement of skeletogenesis.

During settlement, the larvae examine available substrate for positive and negative cues (reviewed in Randall et al. 2020; Banaszak et al. 2023; Pysanczyn et al. 2023). Positive cues include chemical/olfactory signals that reflect a healthy reef environment (e.g., presence of crustose coralline algae, related adult corals, beneficial bacteria, calcification ions, and symbionts), stable substrate, protective crevices, sufficient but relatively low light, and sounds of the reef (Ritson-Williams et al. 2010, 2016; Vermeij et al. 2010; Levenstein et al. 2022b, 2022a; Quinlan et al. 2023; Giorgi et al. 2024). Further studies identified biofilms, bacterial strains of the genus *Pseudoalteromonas,* and several chemical cues isolated from these bacteria to induce coral larval settlement and metamorphosis (Sneed et al. 2014, 2024; Tebben et al. 2015; Petersen et al. 2021; Fiegel et al. 2025). Light and water flow also influence settlement and appear to be actively sensed by the larvae (Hata et al. 2017). Negative cues include turf and macroalgae, unstable substrate, low oxygen content, and sediment (Kuffner et al. 2006; Ritson-Williams et al. 2010; Mallon et al. 2023). The relative strengths and total diversity of available natural cues for settlement such as bacterial cues are difficult to quantify, as there are many unknowns (Sneed et al. 2014; Aoki et al. 2018; Giorgi et al. 2024). If a larva does not find a suitable place to settle within its competency period, it will exhaust its energy reserve and die (Figueiredo et al. 2014).

Once metamorphosed, coral recruits compete and interact with other benthic organisms, ranging from algae to other corals, for space on the substrate (Cruz and Harrison 2017; Doropoulos et al. 2017). Predation by reef organisms, such as corallivorous fish and invertebrates, reduces the abundance of settled coral (Ritson-Williams et al. 2010) (Figure 1).

Symbiosis

A critical component for scleractinian coral development, growth, and survival is the establishment of their mutualism with certain species of Symbiodiniaceae. *Ex-situ*, this occurs within the first 20-60 days of settlement for broadcasting species (Williamson et al. 2021; Koch et al. 2022b), which are the focus here. These dinoflagellate photosynthetic endosymbionts provide essential nutrition to the coral host, enhancing growth and calcification (Pearse and Muscatine 1971; Muscatine and Porter 1977). Caribbean reef-builders obtain their symbionts horizontally through heterotrophy (i.e., through filter feeding after the formation of a mouth and digestive tract) followed by phagosomal arrest (Mohamed et al. 2016). Diverse Symbiodiniaceae species, necessary for recruit infection, are found free-living in the water column and sediments (Adams et al. 2009; Quigley et al. 2017). Adult coral colonies also continually

release excess symbionts into the water column (Titlyanov et al. 1996) where they can be acquired by other corals (Hoegh-Guldberg and Smith 1989; Williamson et al. 2021). Such shedding from adults may be an important source of symbionts for recruits. In many coral species, including *A. palmata*, coral settlers may associate with multiple symbiont species, but these mixtures are winnowed over time such that most adult colonies retain the symbiont species they are most compatible with in a given habitat or environment (Coffroth et al. 2001; del C. Gómez-Cabrera et al. 2008). For example, sexually-propagated recruits of *A. palmata* in cultivation can harbor symbiont species atypical for wild coral colonies, including *Durisdinium trenchii* and *Cladocopium goreaui*. After outplanting to the reef, these coral colonies may retain *D. trenchii* and *C. goreaui* for years (Elder et al. 2023) before a symbiosis with the primary symbiont, *S. 'fitti'* is established [E Muller pers comm, (Baums et al. 2014)]. In wild coral colonies, the relationship between a colony and a symbiont is typically maintained for life, even after bleaching and symbiont repopulation (Stat et al. 2008; Baums et al. 2014; Hartmann et al. 2019; Quigley et al. 2022).

In addition to the algal symbionts, a coral needs a plethora of other prokaryotes, eukaryotes, and viruses to build a stable and functioning holobiont (Marhaver et al. 2008; Bonacolta et al. 2023). These microorganisms influence a coral colony's health and resilience (Thompson et al. 2015). The breakdown of symbiotic interactions often results in disease (Sweet and Bulling 2017). Disease in recruits is difficult to quantify because of the rapid rate at which a disease would kill off the settled polyp or entire 'colony' at this small size. It is thus unknown to what extent disease plays a role in the early life stages of corals (Demko et al. 2025).

Growth and development

Coral growth proceeds by polyp budding or division, an asexual (mitotic) process, resulting in a coral colony, composed of multiple interconnected polyps. Colony growth rates, which depend on genetics, the energy reserve of the colony, and the microenvironment where it grows, are generally in the order of 2-12 cm of linear extension per year (Bravo and Schoepf 2024). There are contrasting results on whether sexual maturity depends on colony size or on age (Randall et al. 2020; Rapuano et al. 2023), and this threshold is species dependent (Kai and Sakai 2008). Typically, it takes 3-7 years for a Caribbean *Acropora* coral to grow from a primary polyp to a sexually mature, reproductive adult colony (Chamberland et al. 2016). However, this time window varies based on colony health, and environmental conditions. Fragmentation of adult colonies, as a result of predation or physical disturbance (e.g., storms), is an important mode of asexual reproduction for Caribbean acroporids and orbicellids. Fragmentation can

generate extensive thickets of multiple colonies, all of which are clonemates (individually referred to as ramets) of the founding colony. Together, all ramets that originate from the founding colony comprise a genet (Baums et al. 2006; Foster et al. 2013; Drury et al. 2019; Manzello et al. 2019). This process decouples size from age so that small colonies can stem from a very old genet that recruited long ago. The oldest genets of Caribbean reef-builders can be several hundred to thousands of years old (Devlin-Durante et al. 2016; Irwin et al. 2017).

Coral - ecosystem connections and environmental challenges

Changes in the ecosystem dynamics of tropical coral reefs, and compounding environmental challenges at multiple scales, have arisen concomitant with the decline in sexual recruitment of reef-building corals in the Caribbean. The causal relationships between these factors are unclear, but are almost certainly cumulative, which makes it difficult to disentangle a single cause. Therefore, a single solution is unlikely to restore sexual recruitment, and holistic and multifaceted approaches are needed to address the broken life cycle in Caribbean major reef-building corals.

Considering biotic ecosystem factors, stony corals (although being the foundation of the reefs) are far from the only species impacted by environmental change. For well over a century, anthropogenic activities have influenced populations of sea turtles, fish, sea urchins, and sea cucumbers, for example, throughout the Caribbean (Jackson 1997; O'Dea et al. 2025). The loss of the sea urchin *Diadema antillarum,* the low biodiversity of herbivorous fishes, and the depletion of herbivores have contributed to "phase shifts," whereby reefs that were once dominated by stony corals are now dominated by macroalgae, soft corals, sponges, and increasing amounts of sediment (Hughes et al. 2007; Mumby and Steneck 2018; Steneck et al. 2018; Hylkema et al. 2023). Importantly, the Caribbean is predisposed to macroalgal blooms, which happen faster and with greater intensity than in the Indo-Pacific (Roff and Mumby 2012). The reasons for this remain uncertain though it seems unlikely to be a simple eutrophication issue and the potentially high bioavailability of iron has been implicated. Sea cucumbers, important for filtering sediments, removing toxic organics from particles, and changing the sediment microbiome, have been overharvested (Maritan et al. 2025). With fewer herbivores grazing algae and fewer sea cucumbers to filter sediments, the substrate has become less conducive to coral settlement, juvenile survival, and coral growth (described in detail below).

Considering abiotic ecosystem factors, heat and light regimes have changed greatly in recent decades and are well known to impact coral reproduction profoundly. When corals experience prolonged heat stress, colonies expel their algal symbionts in a process called bleaching, and colonies may starve and die

if symbionts are not reacquired. Prior to the 1990s (when thermal-induced bleaching became a regular occurrence), corals were mostly impacted by coastal development, associated water quality issues and removal of grazers. Light pollution (artificial light at night), primarily associated with coastal development, has long been known to disrupt breeding behavior in sea turtles. More recently, studies have shown that artificial light at night can also alter the physiology and reproductive synchrony of reef-building corals (Ayalon et al. 2019, 2021; Rosenberg et al. 2022). Artificial light at night is likely occurring across reef systems where there is significant associated urban development and/or coastal fishing, threatening reproduction (Davies et al. 2023).

Water quality remains a huge hurdle, e.g., affecting Mexican Caribbean coral reefs (Banaszak 2021). Water quality is influenced by sedimentation, nutrient content, plastics, chemicals, and other factors (Nalley et al. 2021). Negative impacts on corals can be exacerbated by increased temperatures, overfishing and harmful algal bloom events, such as Sargassum and red tide (Zaneveld et al. 2016). Blooms of the toxin producing dinoflagellate *Karenia brevis* occur almost annually on the West Florida Shelf and may affect Florida Keys' reefs where water flows from the shelf to the Straits of Florida and impact corals (Liu et al. 2016; Weisberg et al. 2019); (Reynolds et al. 2020).

As atmospheric CO_2 levels continue to rise (a direct result of industrialization and population growth), corals are not only threatened by global warming but also ocean acidification. In 2025, a planetary boundary for ocean acidification was breached and an acidified ocean can impact coral larval development, survival and metamorphosis (Nakamura et al. 2011; Findlay et al. 2025).

Principal barriers that prevent successful transition from gamete to recruits and ways to reduce these barriers

Our systematic mapping of the entire life cycle of reef-building corals in the Caribbean provides a new way to clarify where the science is clear enough and where it is still lacking to understand the barriers corals face to sexually reproduce (Fig 2). Here we describe the known major barriers corals face in completing their life cycle for which we can suggest potential solutions. Sexual recruitment failure and disruption of the coral circle of life are caused by multiple factors, additively or synergistically, which may produce the same outcome, making the coral recruitment problem particularly difficult. While multiple stressors are almost certainly present, any individual stressor may impact various stages of the coral life cycle. For example, high temperature stress events have increased in frequency, magnitude, and duration and impact the entire life cycle of reef-building corals (McWhorter et al. 2022). A critical step to 'solving' the coral recruitment crisis is therefore reducing greenhouse gas emissions because this will

reduce heat stress affecting all stages of the coral life cycle, and strategies to moderate global warming scenarios have been developed elsewhere. However, high temperature stress interacts with other factors to disrupt the life cycle. Since cooling the ocean is not a likely short-term outcome, it is of utmost importance to reduce all other stressors (Donovan et al. 2021), especially in the context of those that diminish the chances of successful sexual reproduction in coral. Further, in light of the catastrophic lack of sexual recruitment for the major reef-building species across the Caribbean region, even a partial improvement of sexual recruitment rates could yield measurable benefits for species survival. Below, we first outline the key issues impacting sexual recruitment and life-cycle disruption issues. We then highlight some possible solutions.

Poor adult health: Environmental stressors have reduced adult health and compromised gamete production

Corals require sufficient nutrition and favorable environmental conditions to produce healthy gametes. Corals allocate energy to reproduction only after meeting metabolic maintenance and growth demands, and under stress, investment in gametogenesis is reduced, leading to lower fecundity, smaller larval output, and decreased settlement success (Adjeroud et al. 2017). Poor water quality, pollution, and sedimentation can weaken corals and hinder gametogenesis (Fabricius 2005). Infectious disease outbreaks may also disrupt the production and maturation of gametes as energy reserves are depleted (Mazurek et al. 2025). In the Caribbean, many colonies of at least 25 species of corals, including *Orbicella* species, are currently plagued by stony coral tissue loss disease (SCTLD), first reported in 2014 (reviewed in Papke et al. 2024). Elevated temperatures and recent bleaching can similarly deplete coral energy reserves, deteriorate gamete quality, or prevent gametogenesis altogether. For example, thermal stress events can significantly reduce coral reproductive output (Ward et al. 2000; Johnston et al. 2020), with some species showing declines in larval production of over 50% and over multiple years following a heat stress event (Levitan et al. 2014). Declining sexual reproductive output is often accompanied by a reduction in growth rate (Hoey et al. 2016).

Potential solutions to poor adult health:

Enforcing regulations to protect coral habitats from sedimentation, especially during the spawning season, is recommended because it protects the feeding apparatus of adult corals by preventing clogging, whereas clear water enables photosynthesis of the algal symbionts.

Increasing food available to corals, at key time intervals (e.g., one month prior to spawning) may give them an additional energy for reproduction and survival, especially during episodes of bleaching

(Grottoli et al. 2025). While Caribbean acroporid and orbicellid larvae are not expected to be able to ingest particulate organic matter during their planktonic phase given the lack of a fully formed mouth, supplemental feeding with dissolved organic matter, amino acids and other nutrients may improve settlement rates and early post settlement survival (Sorokin 1973; Baird and Morse 2004; Rodd et al. 2022). How to scale these potential solutions for field applications is an unsolved problem.

Poor adult health due to infectious diseases can sometimes improve after treatment with probiotics and antibiotics. For example, the successful treatment of stony coral tissue loss disease with natural probiotics has recently been demonstrated (Ushijima et al. 2023) and other studies show considerable promise (Pitts et al. 2025). Antibiotic treatments are also effective but their widespread application *ix-situ* is discussed controversially because of the risk of increasing antibiotic resistance of marine bacteria (Neely et al. 2020; Ushijima et al. 2023).

The development of low-cost test kits could also allow for rapid, non-destructive evaluation of gamete production during the ramp-up to coral spawning months, e.g. via swabbing the colony surface and conducting a dipstick test (Meng et al. 2022). Development costs for such a method could be justified in endangered coral species where breaking off a branch tip for visual inspection of gamete development is not possible (because of their massive growth form) or advisable. Improving coral researchers' abilities to identify reproductively viable corals and make decisions around controlled breeding practices would help with resource allocation in reproduction research. This may include decisions on which colonies to target for gamete collection and which colonies to cross according to a genetic management plan (Baums et al. 2022) .

Land-based rescue may offer a last-ditch attempt to save genetic diversity by bio-banking corals (Hagedorn et al. in press). With appropriate and diligent husbandry practices, such facilities allow for controlled spawning, maintaining the broodstock in peak condition during the complete circle of life, especially through gametogenesis. Such farms or aquaria have the benefit of enabling research to continue and explore some of the unanswered questions posed above, whilst simultaneously producing recruits for outplanting activities, safeguarding cryopreserved gametes and aquacultured colonies.

Low adult density: Widespread coral mortality from multiple stressors has left fewer adults on the reef

The low density of adult coral is a significant issue resulting from widespread mortality from the multiple aforementioned stressors. The low density of adults has led to an Allee effect with several negative

impacts on population growth rate (Shantz et al. 2011). For instance, the signaling between colonies that triggers spawning may be compromised, causing spawning asynchrony or stopping it entirely. Further, low adult density also compromises fertilization success (Mumby et al. 2024). Successful fertilization in corals depends on the compatibility of gametes from different genets as well as optimal sperm concentration and mobility. Furthermore, the reduced larval pool may be more vulnerable to predation, and fewer larvae are available to settle.

Over time, continued loss of adult corals results in a loss of genetic diversity. This loss of genetic diversity can increase a population's vulnerability to inbreeding and the accumulation of harmful mutations, leading to a decline in fitness, or inbreeding depression. Genome-wide heterozygosity (a measure of genetic diversity), is already significantly lower in Caribbean acroporids than the heterozygosity of corals elsewhere (Locatelli et al. 2024). While data on inbreeding depression in corals are only now beginning to emerge (Hernández-Agreda et al. 2024), low fertility, poor neonate survivorship, and other inbreeding effects are so widespread throughout plants and animals that conservation management generally presumes inbreeding depression will be a problem in any given species unless proven otherwise (Frankham et al. 2017). Inbreeding can, in extreme cases, lead to population collapse.

Another factor that might contribute to low fertilization success in major framework building corals is widespread asexual reproduction. The branching morphology of acroporids can create genets via branch fragmentation that are distributed over more than 30 m along a reef (Baums et al. 2006). Widespread clonality is also found in *O. annularis*, in regions with acute hurricane disturbance (Foster et al. 2013). Given that most Caribbean spawners have limited selfing ability, clonality effectively creates another Allee effect, forcing genetically-distinct colonies to become farther apart. Restoration efforts can increase the genet diversity of colonies within spawning distance.

As they mature, most coral species require specific symbiont species that may primarily be shed from adult colonies (Abrego et al. 2009), so the lack of donor adults nearby can hinder symbiosis establishment and ultimately result in lower survival rates.

Potential solutions to low adult density:

To address low adult density, restoration activities could focus on building toward adequate densities of adult colonies to overcome Allee effects. "Spawning hubs" that aggregate a diverse assemblage of adult corals could also be located in strategic areas predicted to be good "source" areas based on larval

dispersal models (King et al. 2023). We recommend that this approach be integrated with existing restoration planning. However, it is essential to consider potential caveats, such as the possibility that increasing adult density may increase disease prevalence (Yakob and Mumby 2011). Moreover, despite higher adult densities in the past 10-20 years due to ongoing restoration efforts in some locations (Carne et al. 2016), sexual recruitment has still been limited, suggesting that overcoming Allee effects will be important but insufficient to solve the problem. Gamete densities could be increased to enhance chances of fertilization and cross-fertilization, and this can be scaled up by developing large-scale spawn catcher gamete collection and concentration devices (Harrison et al. 2021; Harrison 2024).

Assisted evolution (e.g. assisted gene flow or genetic rescue) is a reproduction technique that can help mitigate the loss of genetic diversity by introducing alleles from elsewhere to increase fertilization success (Hagedorn et al. 2021). For example, adult corals can be translocated, or cryopreserved gametes can be used to fertilize local corals. We note that cryopreserved gametes have reduced fertilization rates and therefore scalability is limited (so far). These activities should be guided by a genetic management plan to prevent the unintended loss of genetic diversity in breeding programs (Baums et al. 2022). Regulatory reforms are needed to aid in the process of bio-banking and transferring genetic diversity (Baker et al. 2025).

Sensory pollution: Corals fail to spawn synchronously

Corals rely on environmental cues, including increasing water temperature, moonlight during the lunar cycle, and time after sunset, in addition to signals from other corals, to synchronize spawning as described above (see also (Harrison 2024)). Artificial light at night and ocean warming can disrupt or mask the environmental cues used to synchronize spawning, preventing successful fertilization (Shlesinger and Loya 2019). Increased eutrophication and sedimentation, and consequently turbidity, may also prevent detection of moonlight cues that are key to synchronize spawning.

Potential solutions to sensory pollution:

To address this issue, raising awareness and supporting campaigns to reduce artificial light at night along coasts with reefs should be scaled up. Such programs can be implemented through education and outreach efforts that encourage individuals, communities, and governments to reduce their use of artificial lighting, particularly in areas with high conservation value (McDermott 2023). However, there are likely to be challenges with funding and political will to make such changes at any meaningful scale. Turtle conservation efforts may provide a blueprint for how to effectively implement such a strategy

(Gomez Isaza et al. 2025), and there has been a call to bring this front and centre into the sustainable development goals, where it is currently absent (Lyytimäki 2025).

Unsuitable substrate for larval settlement: Excessive turf, sediment, and macroalgae on the reef surface

Excessive sediment-laden turf and macroalgae on the reef surface are unsuitable for coral settlement. This unsuitable substrate has several negative impacts on coral reefs. For instance, coral larvae tend to avoid areas with abundant algae (Duran et al. 2024) and actively avoid toxic species of *Dictyota* and *Lobophora* (Paul et al. 2011). They also require a hard bottom to attach successfully, so reefs with substantial sediment cover are similarly unsuitable (Ricardo et al. 2017). Additionally, the lack of available and appropriate crustose coralline algae (CCA) that attract larvae to the reef further exacerbates the problem (Arnold et al. 2010; Ritson-Williams et al. 2016). Once settled, small recruits are easily overgrown by algae and smothered by sediment (Moeller et al. 2017), which can serve as a vector for disease, further reducing their chances of survival. Furthermore, competition with algae reduces space and uses up vital resources that may have helped juvenile corals grow (Hartmann et al. 2013). Survival and sexual maturity are size-dependent (Soong 1993) such that slower colony growth increases mortality risk (Lirman 2000) and prolongs the time until sexual maturity is reached.

Potential solutions to improve substrate suitability:

To address this issue, several potential solutions can be explored. In the Caribbean, where herbivores have become scarce, one approach is to expand the aquaculture of herbivores, such as sea urchins, and crabs, to restock reefs, boost herbivore biomass, and increase grazing pressure on turf and macroalgae (Butler et al. 2024; Wilson et al. 2025). Compared to previous years, progress has been made in the aquaculture of these herbivores and the loss of herbivores after release has been reduced. Cultured herbivores can be released alongside corals, or in suspected "sink" areas where coral larvae might settle (Chilma-Arias et al. 2025). However, potential caveats include a lack of standardized aquaculture protocols for target species, difficulty retaining herbivores at specific sites and predation on transplanted animals (Wijers et al. 2024; Lachnit et al. 2025). Using more nuanced urchin ‘seeding’ devices or collectors may also be considered (Hylkema et al. 2022; Williams 2022). The young urchins can then either be collected for use in aquaria or bio-banks and/or placed directly on reefs next to newly settled natural coral recruits. Likewise, aquaculture of holothurians could provide additional sediment processing and reduce harmful sediment effects.

Another opportunity is to improve diagnostics of the entire community that makes up the environment where recruits need to establish. Environmental DNA (eDNA) sequencing can identify the organisms present from bacteria to algae and other small organisms that are difficult to track with other methods. Analyses of eDNA to reveal community networks can point to key contributors to "healthy" environments for recruits to establish. eDNA can complement herbivore introductions, and track pathogens that may lurk in systems (Giroux et al. 2022), while also identifying microorganisms that are associated with reducing pathogens and algal growth along with tracking other stressors to young corals. A key challenge for application of this approach to Caribbean reefs is that “healthy” reference sites with high levels of successful sexual recruitment would have to be identified *a priori*, and it is not clear that such sites exist.

We may also turn towards the use of designed substrates (Reichert et al. 2025). Recent findings have demonstrated that clay-based substrates for example, when preconditioned at a healthy reef, harbor a rich community of invertebrates and beneficial microbes, which in turn enhance coral photophysiology, endosymbiont density, and oxidative stress resilience after transplantation to a degraded site (Levy et al. 2024). Advances in material science have recently led to the development of non-toxic antifouling coatings that reduce competitive algae while promoting coral growth (Karimi et al. 2025). These coatings can also be optimized to enhance the survivorship of coral recruits (Karimi et al. 2025). In parallel, biomimetic materials, designed to release settlement-inducing cues, have shown promise (Kundu et al. 2025). For example, application of the cnidarian neuropetide Hym-248 resulted in high settlement rates of Caribbean acroporid corals (e.g. 90 - 100% settlement and metamorphosis in *A. palmata*) (Erwin and Szmant 2010). Settlement cues such as tetrabromopyrrole (TBP) are also effective and highly specific for multiple Caribbean coral species (Sneed et al. 2014). Integrating such material-based ‘solutions’ with other intervention strategies could lead to powerful approaches enhancing recruitment success on artificial and degraded reefs.

Finally, an effective intervention to encourage settlement may be removing algae and sediment through natural or technological means (Smith et al. 2022). As already mentioned, populations of natural algae and sediment removers, such as sea urchins and sea cucumbers, could be translocated to reefs. Physical removal of fleshy algae by teams of divers including citizen scientists has been shown to be effective at increasing recruitment on algal dominated reef areas on the Great Barrier Reef (Smith et al. 2022) but were less successful in the Caribbean (McClanahan et al. 2011). Alternatively, unmanned underwater vehicles could be deployed to remove algae and sediment more effectively ahead of spawning events.

Major knowledge gaps in our understanding of the coral life cycle

Above we discussed the aspects of the coral life cycle where enough evidence exists to outline possible interventions. Below, we describe the aspects of the coral life cycle where substantial knowledge deficiencies hinder our capacity to rigorously assess the effects of diverse factors on key developmental stages, thereby limiting the development of effective conservation and management strategies. Once these knowledge gaps have been filled, it will be possible to develop solutions to newly identified factors impacting the coral life cycle.

History of the sexual recruitment problem

The lack of historical survey data prior to the 1950s, the difficulties with identifying small recruits to species level, the complex life cycle of corals, the multi-cue triggers for gametogenesis, spawning and settlement and metamorphosis, and the high cost of molecular-clock tools to age coral colonies, make it challenging to assess when the sexual recruitment problem began in the Caribbean. Pinpointing when sexual recruitment (as opposed to adult population decline) started to fail might enable examination of the changes occurring in the region at that time, which in turn could help identify the root causes of the problem.

Quantitative *in-situ* data collection on coral recruit abundance using direct observations and recruitment tiles was made possible following the invention of SCUBA in the 1940s, and even now, diver-deployed recruitment tiles remain a standard to assess levels of coral larval recruitment (Edmunds 2023). More recently, repeated large-area imaging has been used to track the fate of coral recruits (Sarribouette et al. 2022). However, the small size of the recruits and their similar morphology make it difficult to identify them to the species level in the field or digitally via imagery. Mitochondrial DNA is not as variable in corals as in other taxa (Hellberg 2006), hence alternative genetic markers have to be developed that can be used to identify taxa using non-destructive sampling, such as mucus swabs from colony surfaces. There are technologies available to capture thousands of DNA or RNA markers across the genome from the small amount of target DNA in swabs, but costs and time to process samples in the lab are still prohibitive until more economic solutions become more available (Kitchen et al. 2020).

Standard methods that investigate the size structure of a population to infer age distribution are also not applicable to corals. This is because adult coral colonies of the major Caribbean reef-builders often fragment, and so size is uncoupled from age (Baums et al. 2006). Previously, a coalescent model of

neutral somatic mutation accumulation to age genets was first applied to corals based on microsatellite markers (Devlin-Durante et al., 2016). The maximum age detected for *A. palmata*, was 838 to 6500 years, depending on mutation rate. Subsequently, a novel universal clock for modular organisms was developed based on genome-wide somatic mutations that accumulate and segregate among a genet's ramets through a somatic genetic drift process (Yu et al. 2020). In modular organisms, like corals, a key finding is that fixation among modules can happen in the absence of selection (Yu et al., 2020). This allows for the use of these fixed mutations to determine the age of genets and it has already been applied to corals with great accuracy (Conn et al. 2025). This approach relies on next-generation sequencing of several samples per genet and is therefore expensive.

To overcome the above cost challenges, we suggest developing cheaper methods for aging colonies, such as more affordable molecular clock tools based on DNA and/or epigenetic mutations (Yao et al. 2023) and methods for identifying very small coral recruits to the species level without harming the recruits, such as via water sampling or swabbing the surface. Through research investment in these areas, we will better understand when the sexual recruitment problem began, what factors contributed to its development and what the current status is.

Larval dispersal and supply

Coral gametes, embryos, and larvae are tiny [<500 um; most species <300 um; (Szmant 1986)] and therefore difficult to track in the field, which hampers our ability to resolve the processes of fertilisation, larval dispersal, development, and settlement on reefs.

To address this knowledge gap, we need to accurately characterize all coral life cycle processes and stages *in-situ*. Firstly, is fertilisation occurring primarily in the water column or at the sea surface and does it proceed at rates sufficient to generate viable embryos? This information will define the pool of larvae available for subsequent settlement and recruitment. Secondly, of the embryos produced, what proportion are of high enough quality to develop into larvae that make it through development to the planula stage? What are the local transport pathways of larvae? Are larvae arriving at the locations predicted by physical-biological models? Do they settle in the habitats where we expect them to? Answering these fundamental questions will clarify the potential for sexual recruitment across different reefs in the region.

A suite of complementary approaches can be employed to obtain the required data. High-resolution, coupled physical-biological models can be used to simulate micro- and meso-scale dispersal (from a few

metres to a few kilometres), which is most relevant for individual coral colonies. To date, most biophysical modeling has been applied to regional coral dispersal (Wood et al. 2016; Saint-Amand et al. 2023; Ishmael-Lalla et al. 2025) and extending these models to finer spatial scales will improve predictions of larval trajectories. Direct observation of the small, soft-bodied larvae is challenging; therefore, environmental RNA (eRNA) sampling offers a non-invasive alternative for detecting and discriminating between larval and adult stages in water samples (Parsley and Goldberg 2024). Future work should refine spatial and temporal sampling designs and develop such stage-specific eRNA markers for corals (Parsley & Goldberg 2024). These are challenging problems but if overcome combined, biophysical modelling and eRNA surveys could pinpoint larval hotspots, infer dispersal routes, and identify likely settlement zones.

Close-up, high-resolution imaging techniques can also be used to capture newly settled recruits in reef surveys (Gouezo et al. 2023). Molecular methods can then be combined with these imaging techniques to identify recruits to the genus or species level. These methods should be minimally invasive to avoid harming recruits, such as by analyzing coral mucus rather than tissue. This approach can help us identify the species composition of recruits and understand the settlement patterns of different coral species.

Finally, attempting free release and tracking of larvae in the Caribbean, as developed by research teams in the Philippines and on the GBR (Cruz and Harrison 2017; Harrison et al. 2021; Harrison 2024) may provide valuable insights into the fate of larvae and increase their availability for settlement.

Symbiosis establishment

Despite several laboratory studies, our knowledge of symbiont availability and uptake by coral colonies in the field remains largely unknown. Are preferred symbiont species/strains readily available on reefs where coral larvae may settle? If not, we may need to intervene to provide appropriate symbiont sources by culturing and providing symbiont donors. In addition, are the natural processes of symbiont acquisition functioning in new settlers on the reef? For example, do corals recognize and take up symbionts in a normal and healthy manner? Stressors may hinder uptake, which could have significant implications for coral health and resilience.

To answer these questions, we can inventory symbiont types and abundances across reef habitat types (Cunning et al. 2015; Fujise et al. 2021) and identify areas where symbionts may be scarce. The development of a species-resolving set of symbiont-specific primers and a sequence reference library would be an important step forward, something akin to a higher-resolution SymPortal database for

Caribbean broadcasters (Hume et al. 2019). Another approach is to monitor aposymbiotic recruits (i.e., recruits that have not yet attained symbionts) after outplanting to reef environments to track symbiont acquisition in the field (Poland and Coffroth 2017). This can help us understand natural processes of symbiont acquisition and identify potential bottlenecks or challenges. Developing new tools to detect symbiont type within coral recruits non-invasively (for example, via fluorescence-based phenotyping), would allow us to study symbiont acquisition in the field (Hoadley et al. 2023). This would enable the repeat sampling of the same juveniles over time, track the types of symbionts present in different locations or coral species, and identify any potential differences in symbiont acquisition. Additional laboratory studies may also provide valuable insights into symbiont availability and uptake. For example, development of reliable, large-scale cell cultures of as yet unculturable symbiont species may allow for inoculating juveniles with specific symbiont strains prior to outplanting, which could help improve their chances of survival (Krueger and Gates 2012; Nitschke et al. 2022).

Environmental pollution

While the effects of sediment load on reproduction are well documented and can be controlled and managed (Jones et al. 2015; Ricardo et al. 2015, 2016; Humanes et al. 2017), there is a lack of data and inadequate understanding of the presence and effects of many pollutants on coral survival, growth and reproduction (Richmond et al. 2018). Potential sources of pollutants include chemicals from agricultural runoff, heavy metals from industrial activities, microplastics and other plastic debris, nutrients from sewage and agricultural runoff, UV-blockers and pharmaceuticals, and oil spills or other petroleum-based pollutants (Dubinsky and Stambler 1996).

We know very little about the presence and effect of pollutants that impede coral growth or survival during early life stages, with a few exceptions like the oil spills (Hartmann et al. 2015). As such, it is challenging to develop conservation strategies to protect coral reefs from their impacts.

We thus suggest developing rapid, standardized assays to test how pollutants impact corals during various life stages. This can be done through laboratory experiments that expose corals to different pollutants and measure their effects on coral reproductive success, survival, and growth. While there is increasing effort in developing and standardizing ecotoxicological tests for corals (Conway et al. 2021; Miller et al. 2022; Brefeld et al. 2024), there is not yet an international ecotoxicological standardized test available. Having such a test (which could be implemented by numerous laboratories), would allow comparison of the effects of various pollutants among coral species and habitats to identify those with the most impact, including the long-term and latent effects of exposure. An approved International

Organization for Standardization (ISO) and/or Organization for Economic Cooperation and Development (OECD) standardized test would also enable governmental agencies to take regulatory action. Once the most important pollutants are identified, we suggest developing sensors to measure these pollutants across larger scales. By using sensors to monitor pollutant levels on reefs that may be sources or sinks of larvae, we can better understand the types and amounts of pollutants present and identify areas of particular concern. Developing and deploying assays and sensors will require significant investment and collaboration among researchers, policymakers, and industry stakeholders. However, the benefits of this research will be substantial, as it will help us to develop more effective and localized conservation strategies, to allow for human activities while limiting impact on the coral reproductive cycle (e.g., limiting runoff during spawning).

Reef community function

In the context of a changing environment, we have a limited understanding of how the various members of the coral reef community interact with each other on the very small scale (<1 cm) in cryptic habitats and over short time scales (days - weeks) (Doropoulos et al. 2016; Reverter et al. 2024b). To fill this knowledge gap we need to identify the key species that not only play a crucial role in increasing coral larval settlement and early post-settlement survival on this small scale, but also can be effectively introduced or transplanted to support coral recovery. Many mariculture and stocking efforts are underway targeting herbivorous species, as the enhancement of herbivory on coral reefs represents a solution to address the proliferation of macroalgae that are deleterious to corals (Butler et al. 2024). Recent progress includes successful experimental spawning and rearing of *Diadema antillarum* through settlement in captivity (Pilnick et al. 2021; Wijers et al. 2023), and demonstrated effectiveness of Caribbean King crab (*Maguimithrax spinosissimus*) stocking in reducing macroalgal cover by 50-85% on coral patch reefs (Spadaro and Butler 2021). However, questions about the viability of such efforts remain, including significant challenges with recurring urchin mortality events, urchin retention on reefs, high predation pressure on outplanted individuals, and the need for repeated stocking events due to emigration and mortality (Butler et al., 2024). As such, further refinement and rigorous, long-term monitoring is needed to determine the impacts of such efforts and scale up production to meaningfully affect the coral life cycle.

A call for demonstration sites

To test the interventions proposed in this review, we suggest the establishment of demonstration sites that serve as comprehensive testing platforms. Ideally, these sites should be strategically selected to

provide easy access to diverse reef environments, existing laboratory and aquarium infrastructure, and streamlined permitting procedures. For instance, given that we have identified sediment and algal cover as major barriers to coral recruitment, these demonstration sites could serve as test beds for large-scale removal of both (either through natural or technological means). The demonstration sites could also be critical for testing various interventions, in isolation and in combination, in an in-ocean context rather than the laboratory. For example, simply introducing or transplanting beneficial animals to a reef ecosystem is not enough. We also need to know whether they will enhance post-settlement survival and coral sexual recruitment under real-world conditions. Successful establishment of these demonstration sites will require substantial collaborative effort between researchers, policymakers, and conservation organizations to design and implement a comprehensive research program capable of providing the necessary insights to inform effective conservation strategies. The research program should encompass two primary components: conducting *in situ* experiments to address critical knowledge gaps (such as larval tracking) and testing intervention strategies designed to address already-identified problems. This systematic approach will bridge the gap between laboratory research and real-world application, providing the evidence base necessary for scaling successful interventions across broader reef systems while building the collaborative framework essential for effective coral reef conservation.

What happens if we do not act

Caribbean coral populations have already declined dramatically. In particular (because of a lack of adult corals and a paucity of sexual recruits), populations of the reef-building *Acropora spp.* are unlikely to recover in the foreseeable future without significant human intervention. The example of Florida is especially alarming, where only 37 founder genets of *A. palmata* remain in the wild following the 2023 bleaching event. If we do not act, dominant reef-building corals will face local extirpation and the possibility of regional extinction. Consequently, Caribbean coral reef communities will likely continue their shift towards non-reef-building coral species and algae. This shift has already resulted in negative reef accretion and impacted the essential biodiversity values and other ecosystem services that reefs offer humankind. Ultimately, if we do not protect our reefs, we will need to find substantial amounts of funding to fill the gaps left in their place, from replacing food resources for millions of people, industries worth billions of USD, and structures that save lives and protect vital infrastructure by preventing coastal flooding.

Conclusion

Coral populations cannot recover without sexual recruitment of larvae. ‘Closing’ the coral life cycle for acroporids and other reef-building corals in the Caribbean is an extraordinary challenge. ‘Solving’ this pressing conservation issue will require targeted investment, strategic research, and effective management actions from the local to the global scale. Here, we present a service blueprint for improving our understanding of sexual coral recruitment, with the goal of visualizing this complex problem in a way that can be interpreted and used by different stakeholders. We hope the service blueprint provides a clear yet concise guide to the coral life cycle (circle of life), identifying key knowledge gaps, and positioning interventions within a cohesive framework, inviting researchers, managers, and funders alike to prioritize and tackle this challenge.

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Figures

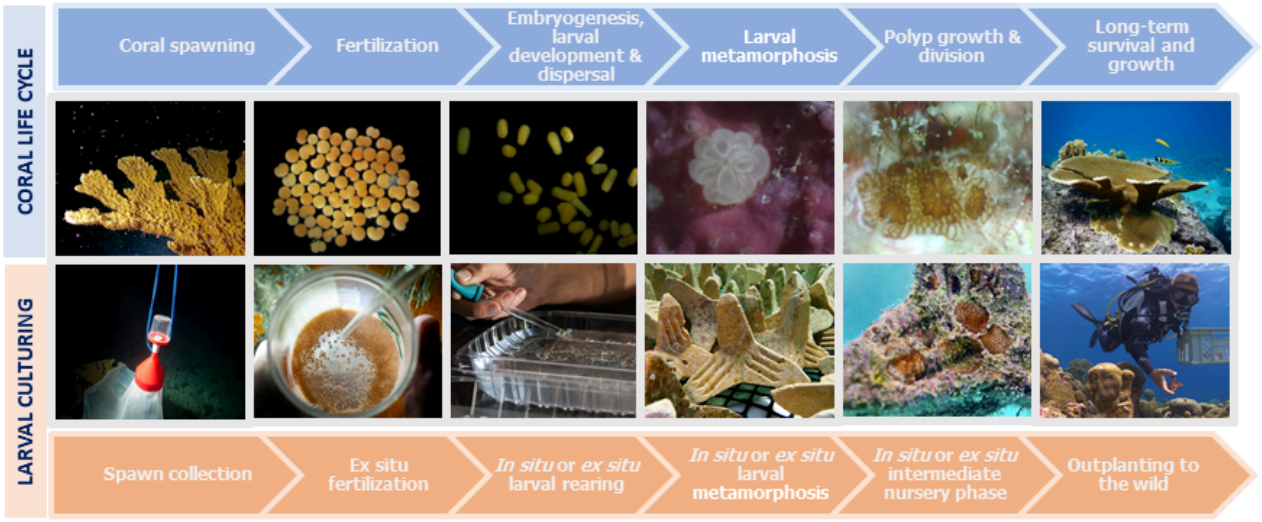

Figure 1 Major coral life cycle stages in the wild and under human care (modified from **(Baums et al. 2022)** .

ruptions, and opportunities for future research and intervention

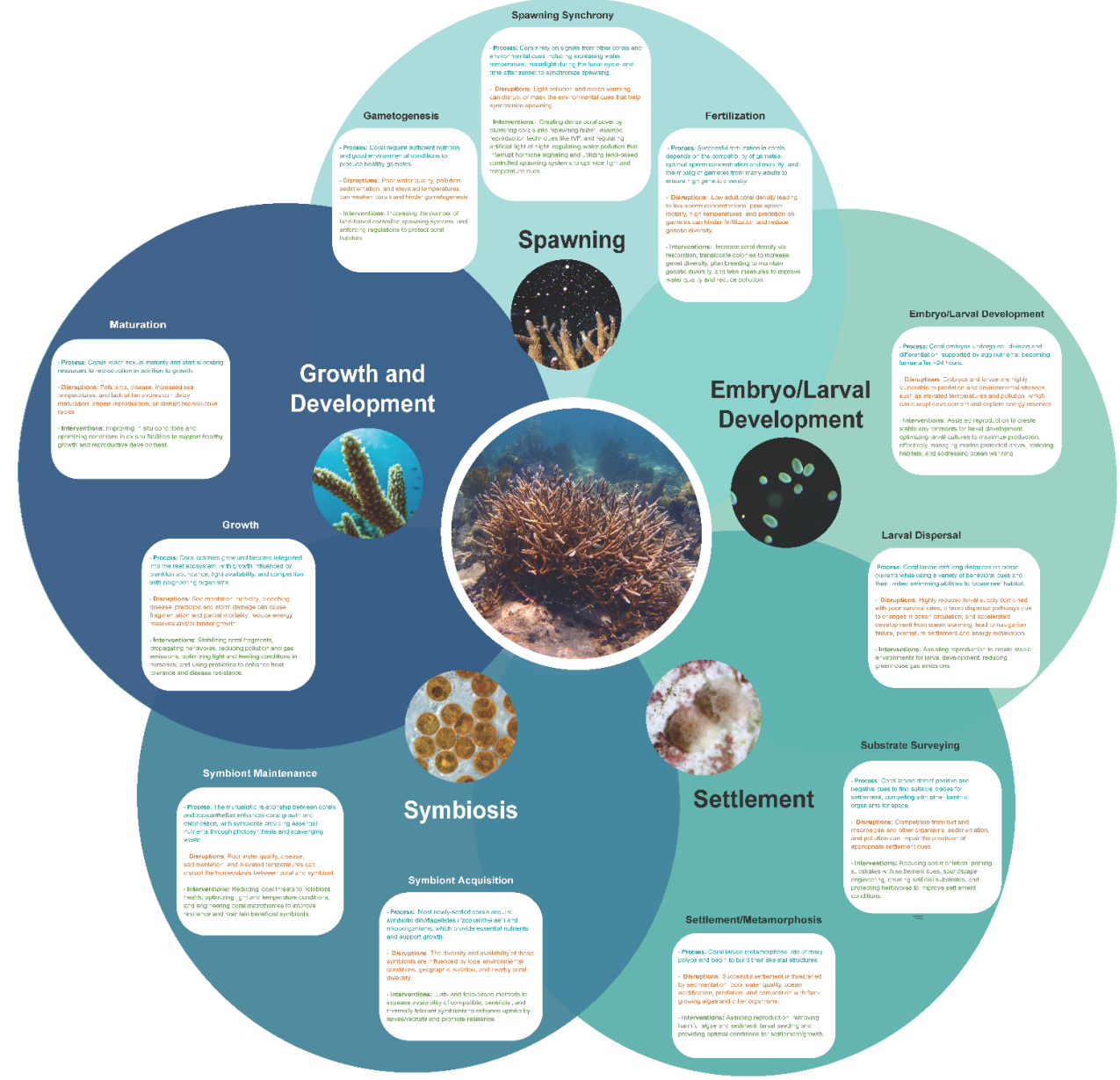

Figure 2 Simplified overview emphasizing the cyclical nature of coral sexual reproduction. Successful completion of all stages in a coral's life cycle is needed to ensure healthy coral populations. Full version available at https://doi.org/10.5281/zenodo.14893236

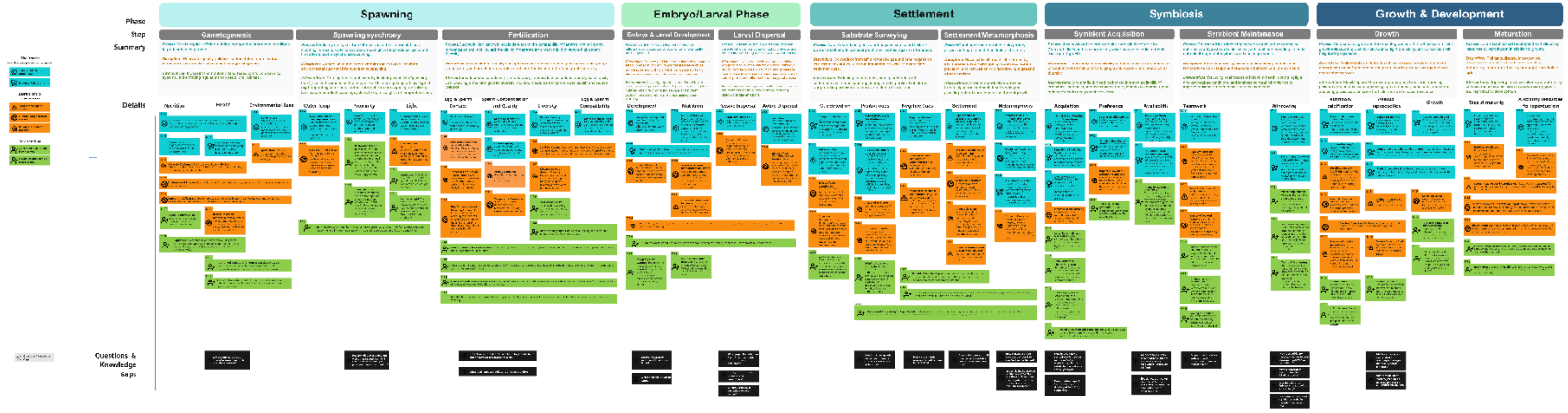

Figure 3 Detailed representation of all life stages, processes, and layers. The linear blueprint is organized hierarchically, beginning with major life phases, each contributing to the coral life cycle. Each phase is subdivided into steps, then further broken down with details on specific processes and their associated factors. Full version available at https://doi.org/10.5281/zenodo.14893236

Supplements

Blueprint user guide and extended abstract available at https://doi.org/10.5281/zenodo.14893236

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