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Assisted Evolution as a Coral Reef Restoration Strategy


Picture: John Burns

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Abstract

Anthropogenic influences threaten coral reefs worldwide. A major threat is climate change, which results in ocean warming and ocean acidification. These effects cause coral bleaching: the breakdown of the symbiosis between corals and their zooxanthellae. Prolonged bleaching caused widespread coral mortality and bleaching events are predicted to increase in intensity and frequency. The conservation and restoration of coral reefs are important because the anthropogenic value of coral reefs is significant. Coral reefs provide ecosystem services including fisheries, coastal protection, and tourism. Growing evidence indicates that the rate of climate change exceeds the adaptive potential of corals. Conventional restoration strategies use the native, natural coral stock, and are therefore becoming unsustainable. A new approach is assisted evolution: the acceleration of natural evolutionary processes to enhance desirable traits. In coral reef restoration, desirable traits are traits increasing tolerance against ocean warming and acidification. Targets to enhance stress tolerance are genetic, epigenetic, and microbiome evolutionary changes. This thesis explores whether assisted evolution is a viable strategy for coral reef restoration. Research on assisted evolution for coral reef restoration is still in an early phase, but initial findings show potential for transgenerational adaptation, selective/interspecific breeding, and endosymbiont evolution. However, certain risks and ethical considerations are associated that should be examined and reflected upon before implementation. Risks include breeding invasive species, transferring pathogens, and changing the genetic community composition. Therefore, methods with lower intervention should be considered first. But, because climate change effects are increasing fast, assisted evolution is a promising strategy for coral reef restoration and its practices should be explored further to become readily available.

Keywords: assisted evolution, coral reefs, climate change, restoration, adaptation, microbiome evolution

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Introduction

Worldwide, anthropogenic influences threaten natural ecosystems. Human activities have led to, e.g., climate change, habitat fragmentation, and pollution (Crowley, 2000; Baur & Erhardt, 1995; Appannagari, 2017). These environmental changes lead to a decrease in ecosystem stability via biodiversity loss (Hautier et al., 2015). One system under threat is the coral reef ecosystem (Hoegh-Guldberg, 1999). Over the past four decades, over 40% of the world's coral reefs have been lost (Burke et al., 2011). A major threat is ocean warming, which is caused by climate change. Warming ocean temperatures can break down the symbiosis between coral animals and their zooxanthellae (Hoegh-Guldberg, 1999). This process is referred to as 'coral bleaching' as corals turn white during a bleaching event. A prolonged bleaching event leads to coral mortality and consequently, reef degradation. Another major threat is ocean acidification, caused by increasing atmospheric carbon dioxide concentrations. Ocean acidification also leads to coral bleaching, besides lower calcification rates (Anthony et al., 2008). Other anthropogenic threats are, for example, overfishing, sunscreen use, and harmful land use (Danovaro et al., 2008; Carlsson et al., 2019). Projected rises in temperature and atmospheric carbon dioxide concentrations lead to the prediction that coral reefs will erode faster than they can rebuild by 2050 (Silverman et al., 2009).

Coral reefs are high biodiversity ecosystems, containing a third of marine species in only 0.2% of the ocean (Pandolfi et al., 2011). Most coral reefs are located in south-eastern Asia (53%), the Pacific (19%), the Atlantic Ocean (15%), and the Red Sea (9%; Sorokin, 1993). They consist of a rigid calcareous framework containing the interlocked, encrusting skeletons of reef-building corals and calcareous red algae (Wells, 1957). Symbiotic systems comprising micro-algae (zooxanthellae) living within the tissues of sponges and cnidarians (corals, zoanthids, anemones) form the basis for primary production where energy is generated through photosynthesis (Jaap, 2000). Coral reefs are populated by many species of, e.g., fish, algae, invertebrates, and bacteria. But, corals are considered the ecosystem-engineers which gives them a central role (Hoegh-Guldberg, 1999). Corals and their zooxanthellae form a mutualistic symbiosis, where corals receive sugars and amino acids as photosynthetic products, and supply the zooxanthellae with crucial plant nutrients (Hoegh-Guldberg, 1999).

Coral reefs are threatened, yet these ecosystems must be restored and conserved. They are of great value and importance to humans, as they provide costly ecosystem services, including fisheries, tourism, and coastal protection (Moberg & Folke, 1999). Cesar et al. (2003) estimated that coral reefs provide goods and services worth 30 billion US$ Netto yearly. Additionally, coral reefs act as carbon sinks (Carlson & Asner, 2019) and are thereby important in decreasing climate change effects.

Research has shown that corals can become more adaptive to bleaching (Maynard et al., 2008). But, there is great concern among scientists that coral adaptations cannot keep up with the effects of climate change and that conventional restoration methods are not sustainable (van Oppen et al., 2015; Anthony et al., 2017). A new restoration method that might increase coral tolerance against major stressors such as ocean warming and acidification is (human-)assisted evolution. Assisted evolution is ‘the acceleration of natural evolutionary processes to enhance certain traits’ (van Oppen et al., 2015). Coral adaptation can be accelerated by artificially inducing genetic adaptation, transgenerational adaptation by epigenetics, and community composition modification of associated microbes (van Oppen et al., 2015). This involves practices like stress exposure, selective breeding, and genetic modification. Assisted evolution is a new, innovative approach in coral reef restoration, but it has certain risks that have to be assessed, along with ethical considerations.

For commercial purposes, the practices of assisted evolution have been used widely in the past and present. Examples are increased nutritional quality in crops (Uncu et al., 2013), enhanced meat yield in aquaculture and farm animals (Forabosco et al., 2013), and increased biomass production and wood quality in trees (Harfouche et al., 2011). Non-commercial assisted evolution used for natural ecosystem restoration is rare. Research into how assisted evolution might help restore marine ecosystems is still in an early stage and largely unexplored.

This thesis investigates if assisted evolution could work for coral reef restoration by addressing the research question: ‘Is assisted evolution a viable method for coral reef restoration?’. Topics that will be addressed are assisted evolution in general, assisted evolution in corals, the suitability of corals for assisted evolution, associated risks, and ethical considerations.

Assisted evolution

Anthropogenic influences could become so severe that the original, native species (natural stock) cannot adapt. Then, the natural stock is unsuitable to be used for restoration. As an alternative, assisted evolution might be a solution. With assisted evolution, natural evolutionary processes are artificially accelerated to create organisms with higher stress tolerance or desirable traits. Accelerated adaptation can be induced by genetic, epigenetic, and/or microbiome evolutionary changes (van Oppen et al., 2017). The non-commercial use of assisted evolution, namely, for ecological restoration, is assessed here. The definition of 'ecological restoration' by the Society for Ecological Restoration (SER), "the process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed" (Gann et al., 2019), will be used.

To clarify the different processes within assisted evolution, the difference between 'adaptation' and 'acclimatization' has to be considered. Adaptation, sometimes referred to as 'hard inheritance', involves a genetic change between generations through natural selection, inducing a change in phenotype. Acclimatization is a non-genetic phenotypic response to environmental changes, possibly enhancing fitness. Recent findings suggest that acclimatization is sometimes heritable (Mirouze & Paszkowski, 2011). Heritable acclimatization is referred to as transgenerational acclimatization, and occurs through epigenetic mechanisms: the heritable external modifications of gene functions without altering the DNA sequence (Dupont, 2009). The external modification causes a change in gene expression levels, and thereby a change in phenotype. Well-studied epigenetic mechanisms are DNA methylation, chromatin remodeling, histone tail modification, and biogenesis of small non-coding RNAs (Danchin et al., 2011).

In some organisms, the next generation inherits associated microbes (the microbiome; van Oppen et al., 2015). Changes in the microbiome can cause a change in the host phenotype (van Oppen et al., 2015). Therefore, the modification of the microbiome is an extra target for assisted evolution, next to adaptation and transgenerational acclimatization.

The genetic and epigenetic mechanisms which are targeted in assisted evolution are applied at different levels of intervention. A low-level intervention example is selective breeding. Jones & Wark (2010) developed a new green needle grass variety (Fowler Germplasm) through artificial selection of five natural plant populations. The new variety is expected to be used for habitat enhancement and restoration projects. A practice with a high level of intervention is the use of genetically modified organisms (GMOs). An example of this is the chestnut tree (*Castanea dentata*) population in North America (Thompson, 2012). The Asian fungus, introduced by humans, severely reduced the population of four billion trees to only a few trees remaining in the early 1900s. Through genetic engineering, trees resistant to the fungus were created. The first resistant individuals were planted in 2006, and today a population exists of over 1000 individuals in New York State (Thiele, 2020).

Assisted evolution in corals

Opposed to conventional coral reef restoration strategies, assisted evolution focuses on creating enhanced coral stock, rather than using the natural stock. Van Oppen et al. (2015) proposed four processes through which corals may be enhanced, varying in intensity of intervention (Fig. 1). The first one is inducing acclimatization (within and between generations) through epigenetic mechanisms by exposing the natural stock to stressors. Second is the modification of the community composition of associated microbes. Third is the selective breeding to create genotypes with higher stress tolerance. The fourth method includes the evolution of the algal endosymbionts (*Symbiodinium* spp.) in the lab through selection and/or mutagenesis. The four proposed methods are explained more elaborately in the following paragraphs.

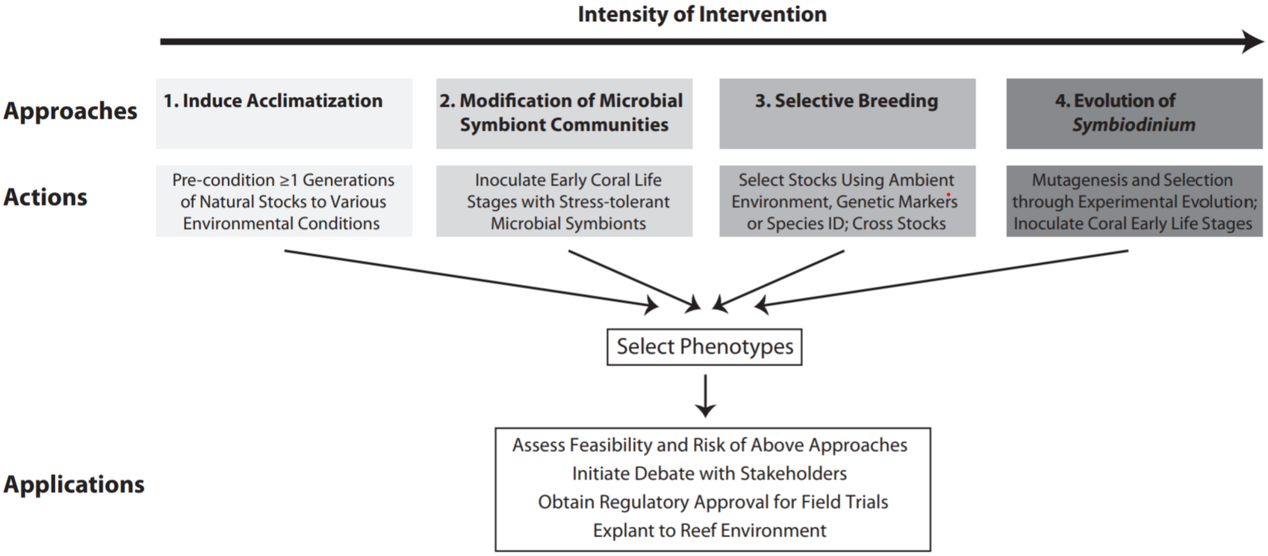

Figure 1: *Diagram with the four assisted evolution approaches proposed by van Oppen et al. (2015) along an intensity of intervention scale. (van Oppen et al., 2015)*

Inducing acclimatization may be achieved by exposing the natural stock to stressors, such as high temperatures and more acid waters. Natural and experimental observations have shown that induced acclimatization can lead to increased tolerance to bleaching (Palumbi et al., 2014). Research indicates that this acclimatization can be induced by several processes involving the algal endosymbiont community (Brown & Cossins, 2011). These processes include physiological or biochemical changes of the zooxanthellae; shifts in the dominant clades or types of zooxanthellae populations in the coral; or the replacement of bleaching-susceptible zooxanthellae by more bleaching-resistant types (Brown & Cossins, 2011). Although largely understudied, early work on transgenerational adaptation involving epigenetic mechanisms suggests it is an important process for stress tolerance in brooding corals (Putnam, 2012), which internally fertilize and brood their larvae. In adult corals exposed to higher temperatures and increased ocean acidification, performance was negatively affected. However, larvae brooded by these adults were exposed to these stressors and showed positive metabolic acclimatization (Putnam, 2012).

The second approach explores how microbial symbiont modification might lead to enhanced stress tolerance in corals. Reef-building corals form obligate symbiotic relationships with *Symbiodinium* dinoflagellates, from which several types exist. No evidence exists that adult corals can form a stable symbiosis with new *Symbiodinium* types (Coffroth et al., 2010). However, most coral eggs and larvae lack *Symbiodinium*, which creates the potential for a new, more beneficial symbiosis with a more stress-tolerant *Symbiodinium* type. Corals are also hosts to varied communities of prokaryotes, which are fundamental for coral fitness and physiology (Bourne & Webster, 2013). The manipulation of these coral prokaryotic communities could be another target to enhance coral stress tolerance. But, whether this is possible is still unknown and provides an opportunity for research.

Selective breeding is the third proposed method. Mixing genotypes leads to offspring with different genotypes producing novel, potentially better adapted, phenotypes. Van Oppen et al. (2015) suggest a method with low environmental risks, where a naturally produced interspecific hybrid is exposed to near-future conditions in the lab. This way, selection can identify the genotypes leading to the highest survival and growth rates in elevated ocean temperature and acidification conditions. Subsequently, these genotypes can be used for further breeding. For this method to be successful, the selected trait has to exhibit significant heritability in order to create better-adapted corals within a few generations. The variation in the trait, therefore, needs a genetic basis.

The fourth proposed method is the facilitation of genetic adaptation in *Symbiodinium* strains. By subjecting *Symbiodinium* to environmental stress in the lab, adaptation can take place by selection on random mutations. This has been demonstrated in the unicellular, asexually reproducing micro-algae *Emiliania huxleyi* (Lohbeck et al., 2012). In a selection experiment, *E. huxleyi* populations were exposed to increased CO_2 levels for 500 generations. The adapted strains exhibited higher growth rates than the control group under ocean acidification conditions (Lohbeck et al., 2012). The mutation rate can be accelerated by the use of a mutagen (e.g. a chemical, UV radiation, or X-rays; Cordero et al., 2011). As proposed in the second method, the selected *Symbiodinium* strains can be used to form a symbiosis with early coral life stages.

Van Oppen et al. (2017) integrated the proposed assisted evolution methods of van Oppen et al. (2015) into a coral reef restoration strategy (Fig. 2). The strategy first considers the lowest level of intervention and then proceeds to more aggressive intervention when necessary. First, the necessity of restoration is considered. When restoration is required, the coral community has to be recoverable for restoration to be effective. A coral reef may not be recoverable when it is, for example, exposed to a high disturbance frequency or chronically polluted. In these cases, restoration efforts will be immediately undone. Factors disturbing recoverability first have to be eradicated by, for example, designating the region as a marine protected area. When a coral reef is recoverable, the underlying problem has to be assessed. Based on this, the desired restoration strategy can be selected. Underlying problems might be, for instance, low suitability of reef structures for larval recruitment or low larval supply (van Oppen et al., 2017). Or, the natural coral stock is not resilient enough. In case of low coral resilience, one option is to enhance early life stage survival through protected nurseries. The more interventional option is to increase coral resilience to environmental stress by assisted evolution.

In two of the approaches of van Oppen et al. (2015), the genetic correspondence of the enhanced stock to the natural stock can be scaled: microbial community modification and selective breeding. Van Oppen et al. (2017) stress that, with developing enhanced stock, the most ‘local’ option must always be considered first to minimize the level of intervention.

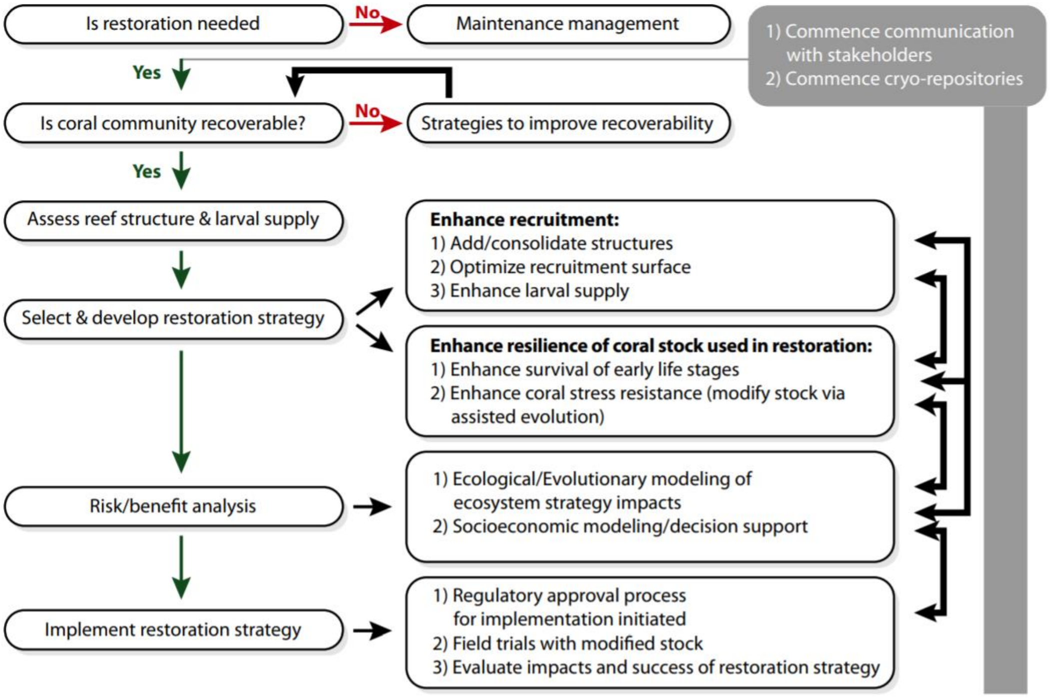

Figure 2: *Decision tree proposed by van Oppen et al. (2017) regarding coral reef restoration, including assisted evolution. The choice of restoration strategy depends on the underlying causes and the restoration targets. (van Oppen et al., 2017)*

Assisted evolution is still in an early phase of research, but studies are finding evidence that it may work for corals. Research indicates that when corals acclimate to higher temperatures during their lifetime, this thermal tolerance is highly heritable (Drury, 2020). Putnam & Gates (2015) showed transgenerational acclimatization in the brooding coral *Pocillopora damicornis*. Adults were exposed to high (28.9 ºC, 805 µatm $p\mathrm{CO}_2$) or ambient (26.5 ºC, 417 µatm $p\mathrm{CO}_2$) temperature and ocean acidification conditions. Larvae exhibited metabolic acclimation when their parents were exposed to high stressor treatment during the brooding period. Additionally, parental conditioning to acidification resulted in greater offspring settlement and survivorship (Putnam et al., 2020). These findings show that by stress exposure, corals can acclimate and that this acclimation is heritable.

Another practice of assisted evolution, showing potential to enhance coral stress tolerance, is the modification of microbial symbiont communities, including the evolution of *Symbiodinium*. The temperature range and the upper temperature tolerance of *Symbiodinium* type C1 increased after laboratory thermal selection of ±80 asexual generations (Chakravarti et al., 2017). Selected cells showed superior growth rate and photo-physiological performance, and lower reactive oxygen species levels, relative to wild-type cells at a bleaching-relevant temperature of at 31 ºC. Also in other types of *Symbiodinium* (A3c, G3, and F1), adaptive changes were observed after 41-69 generations (Chakravarti & van Oppen, 2018). Adaptive changes included faster growth rates and sometimes higher photosynthetic efficiency. Next steps for research are to investigate if corals can be infected with these strains and if, consequently, their stress tolerance would increase. Buerger et al. (2020) assessed this for another coral micro-algal endosymbiont. They evolved 10 strains of a *Cladocopium goreaui* for ± 120 asexual generations in 4 years, which enhanced thermal tolerance in all strains. After introduction into coral larvae, 3 of the 10 endosymbionts increased coral bleaching tolerance. Symbioses with higher tolerance exhibited lower levels of reactive oxygen species in the algae, higher expression of algal carbon fixation genes, and higher expression of heat tolerance genes in corals. These findings demonstrate the potential for enhanced climate resilience in corals via assisted endosymbiont evolution.

More knowledge is acquired about which genes and functional pathways are important for thermal tolerance in algal symbionts. Chakravarti et al. (2020) compared transcriptional responses at 27 ºC and at 31 ºC in a wild-type and a selected-strain of *Symbiodiniacae*, which was experimentally evolved to increased temperature over 80 generations in 2.5 years. At 31 ºC, selected strains showed a stable transcriptomic response and downregulation of stress response genes that were upregulated by the wild-type strains. These stress response genes were involved in processes such as protein repair, molecular chaperoning, protein degradation, and DNA repair. The most upregulated genes in the selected strain at 31 ºC included algal transcription factors and a gene likely from bacterial origin, encoding a type II secretion system protein.

Information about involved genes and pathways could be used for genetic engineering experiments to develop thermally tolerant strains. Coral microbiome engineering is still in a conceptual phase. Research concepts already exist (Epstein et al., 2019), based on successes in other fields, e.g., medicine and agriculture. Three research priorities were proposed by Epstein et al. (2019): (1) the identification of beneficial microbial functions, (2) the identification and maintaining of stable associations with microbial symbionts, and (3) the manipulation of coral microbiomes in trial experiments. These research priorities explore critical knowledge gaps and offer insight into the biological challenges regarding coral microbiome engineering.

Research on interspecific hybridization in corals also shows promising findings. The opportunity for interspecific hybridization incorporates the creation of new gene combinations, increasing genetic diversity and thereby enhancing adaptive potential. Chan et al. (2019a) found that hybrid corals showed equal or better survival and faster growth in elevated temperature and acidification. These results show the possibility of achieving high hybrid fitness, indicating that interspecific hybridization may enhance coral climate resilience. Next steps are to assess hybrid reproductive potential and fitness of following hybrid generations in field trials. Chen et al. (2019b) provided a decision tree regarding the suitability of hybridization as a conservation tool.

Putting things into perspective, early research on assisted evolution in corals show the potential of assisted evolution to be a viable strategy for coral reef restoration. The findings on intergenerational acclimatization, selective breeding, and microbiome adaptations lay a groundwork for further research. By exploring these mechanisms further, a deeper understanding can be acquired of how assisted evolution can be implemented in coral reef restoration. This is crucial in order to create a toolkit including several options for coral reef restoration using assisted evolution approaches. From these options, the appropriate method for the specific case of restoration necessity can then be selected.

Suitability of corals for assisted evolution

The suitability of assisted evolution for coral reef restoration depends on whether corals can rapidly adapt. Corals possess certain life-history traits that promote evolvability (van Oppen et al., 2015). Evolvability is “an organism’s capacity to generate heritable phenotypic variation” (Kirschner & Gerhart, 1998). High evolvability may implicate that corals are able to adapt fast.

A trait promoting coral evolvability is, for example, the existence of sexual reproduction as well as asexual reproduction via fragmentation or colony fission (Harrison & Wallace, 1990). This gives the potential to create a more tolerant coral via sexual reproduction, and subsequently increase the number of tolerant coral individuals asexually. Additionally, the germ cell is not segregated from the somatic cell line in all coral species (van Oppen et al., 2011). Instead, germ cells arise from somatic cells. Therefore, many cell divisions take place before gamete formation. Somatic mutation rates are higher than germ line mutation rates (Lynch, 2010). This results in a higher probability of somatic mutations becoming integrated in coral gametes. Thus, selection can act on somatic mutations enhancing fitness which theoretically increases coral adaptive potential. Another trait is the symbiosis with a wide range of potentially fast-evolving microbes. Microbes contribute to coral function through nutrient cycling, waste removal, stress tolerance, and defense (Gates & Ainsworth, 2011). These traits influence coral fitness and environmental stress tolerance, making the symbiotic element an extra target for assisted evolution. Coral populations already possess high genetic diversity and in some taxa, interspecific hybridization occurs (van Oppen et al., 2011). This provides an extensive set of possibilities for selective breeding programs. Last, Wright et al. (2019) studied genetic associations in corals subjected to three stressors: increased temperature (30 ºC), acidification (pH = 7.8, 700 ppm CO_2), and infectious disease prevalence (10^6 CFU/ml *Vibrio owensii*), compared to a control group (27°C, pH = 8.0, 400 ppm CO_2, no added *V. owensii*). Survival, coral color (as a proxy for *Symbiodiniaeceae* density), growth rate, and nine physiological indicators for coral and algal health were assessed from 40 coral colonies. No trade-offs between tolerances to different stressors were observed, but rather a reinforcement effect where an individual tolerant to one stressor was also more tolerant to the other stressors. This shows the potential to enhance coral tolerance to several stressors simultaneously, which is useful as corals are threatened by different stressors.

These findings support the potential for rapid adaptation in corals, in combination with the potential to enhance corals to several stressors simultaneously. Therefore, it can be concluded that corals are suitable for the practices of assisted evolution. From this perspective, assisted evolution is considered a viable strategy for coral reef restoration.

Risks

Assisted evolution includes the genetic manipulation of organisms and the alteration of natural community compositions within the ecosystem, which comes with certain risks.

Captively bred or genetically modified organisms may become invasive as their novel traits might give them a selective advantage over the native population. For example, in South Africa, 44 freshwater fish species were introduced, of which 37% are considered invasive species (Ellender & Weyl, 2014). Or, introduced species might hybridize with native species (or other introduced species) and produce invasive hybrids. In plants, interspecific hybridization commonly leads to invasiveness (Moran & Alexander, 2014). Some invasive coral species have been identified. In the Southwestern Atlantic, *Tubastraea tagusensis* is spreading over the Abrolhos Bank (Costa et al., 2014) and in the northern Gulf of Mexico, the population of the invasive coral species *Tubastraea nicranthus* is expanding (Sammarco et al., 2014). These invasive exotic species were introduced by human activities unintentionally. But, these examples show that coral reefs are vulnerable to invasive exotics. Therefore, corals should only be introduced when they are compatible with natural species, corals should be distributed within the range of their wild conspecifics, and only naturally sympatric coral species should be selected for hybridization (van Oppen et al., 2015).

Another concern is that introduced species may carry parasites or pathogens affecting the health of the native population. This happened with the re-introduction of a rare toad species by a captive breeding program (Walker et al., 2008). The species, the Mallorcan Midwife Toad (*Alytes muletensis*), was infected by a pathogen (*Batrachochytrium dendrobatidis*) upon re-introduction. *B. dendrobatidis* is now recognized as the driver of mass extinction in amphibians (Fisher & Garner, 2007). This example shows the necessity of extensive monitoring to check on infectious agents prior to the introduction of captively bred coral species.

Other concerns of introducing captively-bred species are the loss of genetic variation, loss of adaptations, and a change of genetic composition, discussed by Laikre et al. (2010). A strong inflow of genes by introducing a captively-bred species can swamp the existing genetic variation of the natural community. This can lead to the loss of adaptations when alleles conferring local adaptation are replaced by non-adaptive alleles. It can also cause the breakup of co-adapted gene complexes: alleles at various loci that work cooperatively to enhance fitness. Also, increasing evidence shows that a genetic change in one species can affect entire communities and ecosystems (Whitham et al., 2006). Lakre et al. (2010) stress that before introduction, genetic monitoring should take place where knowledge is gathered about: (1) the genetic characteristics of the natural population(s); (2) the possible alterations of these characteristics by the introduced species; and (3) the biological consequences. Monitoring is essential for maintaining biodiversity.

Assisted evolution practices have been explored for terrestrial systems, but not yet thoroughly for marine conservation, and almost exclusively for coastal systems (Halpern et al., 2015). Thus, experience and knowledge to understand the consequences for marine systems are still lacking. This is especially a problem because of how marine systems differ from terrestrial systems. In the ocean, modified systems are hard to isolate from natural ones because of the roughly constant flow of nutrients, organisms, and resources (Filbee-Dexter & Smajdor, 2019). Therefore, a negative impact in one area may negatively influence surrounding areas more easily.

Some authors argue that the benefits of assisted evolution outweigh the associated risks. For example, a newly engineered coral genotype dominating a reef may turn out a benefit when native coral genotypes will decline under climate change (Anthony et al., 2017). Also, it could become necessary to develop ‘engineered’ reef habitats to protect species that depend on the reef, including fish and invertebrates (Anthony et al., 2017). The risk of unintended ecosystem disruption and transformation of reefs into new or hybrid systems could be outweighed because currently, reefs are already transitioning as a response to environmental change (Graham et al., 2014). Last, there is the argument of time. Species are rapidly lost to climate change. Therefore, the apparently no-risk decision to delay the implementation of practices like assisted evolution could become an even larger risk by limiting future options (Anthony et al., 2017).

The risks associated with assisted evolution should be taken seriously. Before introduction of a coral species, extensive genetic monitoring must take place, and infectious agents should be detected. Arguments in favor of using assisted evolution practices despite the risks are convincing. Especially because time is a crucial factor in coral reef restoration and because of the high degree of other organisms depending on the reef. To minimize the risks, the level of intervention should be minimized.

Ethics

In assisted evolution, the approach is radically different from conventional nature restoration and conservation techniques. The intention is not to return to a previous ecosystem state but to modify it. This inevitably leads to the rise of ethical questions, because humans turn from ‘protectors’ to ‘designers’ of nature.

Filbee-Dexter & Smajdor (2019) discuss the ethical considerations regarding assisted evolution in marine conservation. They emphasize on the target, motivation, and ethical rightness of assisted evolution. The target is a better survival of the ecosystem through genetic interventions by humans. This raises the question of whether this newly designed ecosystem is still natural or not. There are two types of motivations for using assisted evolution: (1) ensuring the supply of goods and services, and benefits that the ecosystem provides us; and (2) solely conserving the existence of the ecosystem. Filbee-Dexter & Smajdor (2019) conclude that the tools of assisted evolution should be understood and available in case of no other, less drastic option for conservation. A justification could be that the practices of assisted evolution are consistent with the history of the modification of the natural environment by humans to achieve anthropogenically valuable results.

Thiele (2020) states that we cannot neglect our responsibility to explore practices like assisted evolution because we are responsible for the grim prospects for nature. This is a different view because here, the motivation is the moral obligation to conserve the ecosystem.

The different motivations require different ethical considerations in order to decide on the ethical rightness. One could find one motivation rightful and the other not. Whether the motivation is the value of coral reefs to humans, reflected by ecosystem services, or our moral obligation to preserve natural habitats, the target is the same. The target is the preservation of the coral reef ecosystem. Assisted evolution could be a useful tool to reach the target. Therefore, the combination of both motivations provides a sound foundation to use assisted evolution as a restoration strategy.

Conclusions

Environmental changes caused by climate change are outpacing the rates of adaptation in corals. Early research shows that the practices of assisted evolution are promising for coral restoration. Studies have found potential for using microbiome evolution and engineering, selective breeding, and transgenerational acclimatization to enhance coral stress tolerance. Most studies focus on enhancing tolerance against increasing ocean temperatures and ocean acidification, as these are the primary threats for coral reefs. However, assisted evolution practices might enhance tolerance against other or future stressors. Risks associated with assisted evolution include the breeding of invasive species, the transfer of pathogens, and deleterious changes in the genetic composition of the natural population. Therefore, conservative and restorative methods with a lower level of intervention should be considered first. However, because time is limited and anthropogenic influences have such large, fast-changing effects, high levels of intervention on a large scale might be needed to restore coral reefs. Therefore, assisted evolution is considered a viable strategy for coral reef restoration, and the tools it provides us should be understood thoroughly to be readily available for implementation.

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