Enhancing Coral Reef Resilience through Ecological Restoration: Concepts and Challenges

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Abstract

The combination of environmental and anthropogenic stressors has driven the global decline of coral reefs. Changing demographics of the human population and growing dependence on coral reef resources have necessitated mitigation measures to improve the sustainable use of the reef ecosystem. While management measures are useful in slowing the unprecedented loss of coral reefs, active restoration can be pivotal to facilitating the recovery of impacted reefs. With the rapid development of reef restoration techniques in the past decade, there is a need for a review and synthesis of restoration initiatives to identify factors that contribute to its efficacy. We reviewed the variety of reef restoration projects attempted to date and identified the key biological and ecological processes governing the different techniques. An analysis was made to elucidate the effects of biological, management and socio-economic challenges faced by restoration practitioners and used to examine how these factors might synergistically impact the success of future reef restoration efforts. Finally, we recommend the proper management of environmental and anthropogenic stressors before any attempts at active restoration are made, as well as the use of appropriate techniques to address the underlying causes of reef degradation. This study provides a comprehensive understanding of the drivers that contribute to the success of reef restoration as a tool for sustainable coastal development and resource management.

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INTRODUCTION

Coral reefs are one of the world's most important environmental and economic assets. The provision of refugia and food by coral reefs makes them an ideal habitat for resident and transient populations of marine organisms. Over one million species, including over 4000 fish species, reside in coral reefs within the Coral Triangle alone (Burke *et al.*, 2011). In addition to the maintenance of key fishery stocks, the ecological processes associated with coral reefs, such as nutrient cycling and coastal protection, provide critical benefits to coastal communities. The total ecosystem goods and services provided by coral reefs globally is estimated to be US\$375 billion annually (Costanza *et al.*, 1997) and they support more than 275 million people residing within 30 km of the reefs (Burke *et al.*, 2011).

However, more than 60% of the world's coral reefs are now under immediate and direct threats from coastal development, pollution, unsustainable and destructive fishing practices (Burke *et al.*, 2011). These anthropogenic pressures have been further intensified by rapid population growth and the increased dependence on coastal resources. At the global scale, changes in climate and ocean chemistry have also severely threatened coral reefs. The combination of effects from both local and global threats has resulted in an unprecedented worldwide decline of coral reefs and an overall depression of coral reef resilience, even in well managed sites such as the Great Barrier Reef (Hughes *et al.*, 2010; De'ath *et al.*, 2012), hence raising concerns of the ecosystem's potential collapse.

Resilience is the ability of an ecosystem to maintain key functions and processes in the presence of recurrent disturbances by either resisting or recovering from the impacts, without switching to alternative stable states (Holling, 1973; Hughes *et al.*, 2005). There is general consensus that the increase in the slow drivers of change such as pollution and climate change have led to a decrease in the capacity of coral reefs to absorb impacts caused by the acute disturbances (Fig. 1). Recent observations suggested the possibility of large-scale phase shifts from the original coral-dominated state to an alternative stable state dominated by macroalgae and other assemblages (Done, 1992; Bellwood *et al.*, 2004). This drastic shift in community dynamics can severely decrease coral cover and productivity, with flow-on effects on other species dependent on coral reefs (Hughes *et al.*, 2010).

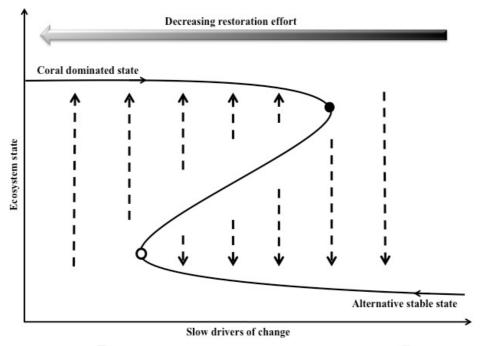


Fig. 1. Non-linear transition of coral reefs to alternative stable states dominated by other assemblages in response to increased slow drivers of change (or stressors) such as overfishing, pollution and climate change. Increasing the intensity of stressors past the threshold level (•) results in the deviation of coral reefs from a coral-dominated state (→) to an alternative stable state. Decreasing stressor intensity can reverse this trajectory (←) with the tipping point at a substantially lower threshold level (o). The occurrence of acute disturbances (such as cyclones and bleaching events) can displace the ecosystem from its equilibrium state, but the ecosystem has the capacity to return to the original state provided that the displacement does not exceed the critical threshold. Resilience, or the capacity of each state to resist change due to acute disturbances (represented by dotted arrows), decreases with elevated stressor intensity for ecosystems in the coral-dominated state, but increases for ecosystems in the alternative stable state. The extent of restoration efforts required (represented by the block arrow) thus decreases with the reduction in slow drivers of change. (Modified from Hughes *et al.*, 2010).

In an attempt to reverse this phenomenon, several strategies have been proposed to restore and rehabilitate coral reefs. The most cost-effective approach is the passive management of coastal zones through legislation and enforcement (Edwards, 2010; Haisfield et al., 2010) to regulate the activities carried out within designated Marine Protected Areas (MPA) or marine reserves. However, for impacted reefs where little or no recovery has taken place even with proper management, active interventions have instead been pivotal in assisting their recovery (Rinkevich, 1995; Edwards, 2010). Over the past few decades, numerous reef restoration approaches have been developed to increase coral cover and enhance the resilience of coral reefs, with techniques designed to address biological and ecological bottlenecks that hinder natural recovery (Edwards, 2010). Active restoration can be broadly classified into physical and biological approaches (Fig. 2) - the former involves substrate modification or stabilization to provide suitable substrata for coral growth and settlement, while the latter requires the direct or indirect transplantation of coral materials onto the reef using source materials derived from asexually or sexually propagated corals. More recently, the incorporation of an intermediate nursery phase has been strongly advocated to augment coral growth rates and survivorship prior to transplantation (Shafir et al., 2006).

As a result of the heightened awareness of the global decline of coral reefs, substantial research has been devoted to improving these techniques, and coral reef restoration has since been increasingly adopted as a key management tool for coastal managers (Rinkevich, 1995). Given the dynamic and complex nature of coral reefs, the identification of the underlying causes of reef degradation is vital to achieving success in reef restoration initiatives. In this review, we examine the key biological and ecological attributes that are of practical relevance to different reef restoration techniques, as well as the challenges that will impact the success of future restoration efforts.

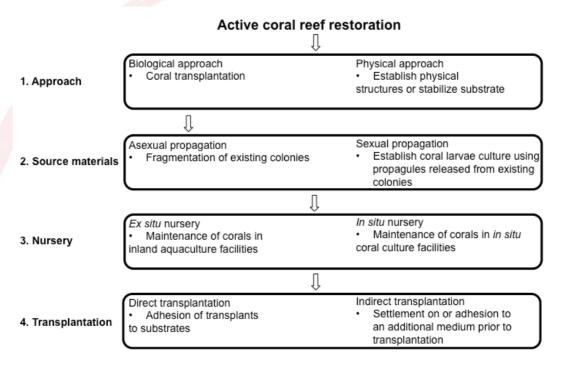


Fig. 2. Overview of active coral reef restoration approaches. A mix of biological and physical approaches can be employed, but the sequence: (1) selection of overall restoration approach, (2) sourcing for coral material, (3) establishment of nursery and (4) transplantation, is generally followed.

SCLERACTINIAN CORAL BIOLOGY

Coral reproduction and developmental biology

The reproductive biology of scleractinian corals is among the most extensively studied of marine clonal organisms. They reproduce asexually to generate genetically identical clones, predominantly through polyp budding to facilitate growth and wound healing after fragmentation (Sammarco, 1986; Richmond, 1997). However, other unique asexual reproductive modes have also been reported. Brooding corals such as *Pocillopora damicornis* have been shown to release both sexual and asexual coral larvae, and it was hypothesized that asexual larvae developed as a result of parthenogenesis of unfertilized eggs (Stoddart, 1983). Polyp bailout and polyp expulsion, where new coral polyps extend away from the parent colony, and are subsequently released to recolonize other substrata, have also been observed (Sammarco, 1982; Kramarsky-Winter *et al.*, 1997). The ease of generating large amounts of source material rapidly via coral fragmentation makes this one of the most popular coral restoration techniques (Rinkevich 1995; Edwards, 2010). However, species such as *Pectinia lactuca* exhibit much higher mortality rates upon

fragmentation than others such as *Acropora hyacinthus* for which natural fragmentation is a reproduction strategy (Yap *et al.*, 1992; Toh *et al.*, 2012). Coral fragmentation as a restoration tool should thus be exercised with caution to reduce any collateral damage to the parent colonies.

Sexual reproduction in scleractinian corals consists of two sexual systems (Fig. 3). Corals can either be hermaphroditic (both eggs and sperms developing within and attached to the gut of the coral polyps) or gonochoric (single-sex colonies) (Harrison & Wallace, 1990). A mixed sexual system (having both male and female polyps within the same colony) has also been observed in corals, but such occurrences are rare (Baird *et al.*, 2009). The development of coral larvae (planulae) can also be classified into two reproductive modes (Fig. 3). Brooding corals take up sperm released from other colonies to fertilize the eggs internally. Subsequently, the embryos develop within the polyp, which releases coral planulae. Conversely, broadcast spawning corals release their gametes into the water column and fertilization occurs externally. Coral gametogenic cycles can take months to complete (Guest et al 2012), but embryogenesis is usually completed within 18 to 24 hours after fertilization (Toh et al 2012).

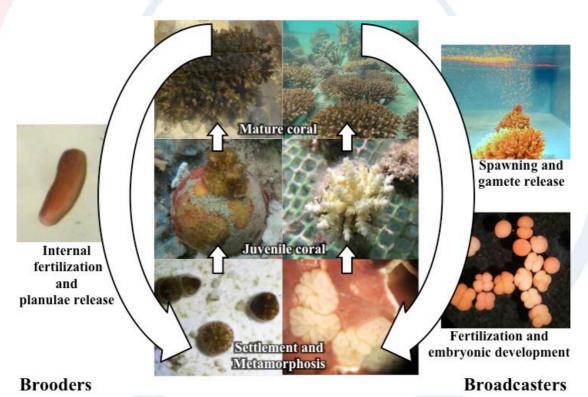


Fig. 3. Sexual systems and reproductive modes in scleractinian corals. Mature broadcast-spawning corals release gametes into the water column, and fertilization and embryogenesis occur externally. Brooding corals undergo internal fertilization instead and release the coral planulae through their polyps. The motile larvae then settle onto a suitable substrate and undergo metamorphosis to form a primary polyp.

The high fecundity of scleractinian corals and the capacity to produce large numbers of propagules have prompted studies to experiment with the use of sexually propagated corals for reef restoration as a means to enhance genetic diversity (Omori et al., 2008; Guest et al., 2010; Toh et al., 2012). The process of accurately determining the timing for propagule release is achieved by conducting extensive histological and field studies. Coral spawning usually occurs during specific periods

within a year and the timing can vary across geographical locations and among species (Baird *et al.*, 2009). The subsequent larval rearing stage has to be conducted *ex situ* under controlled conditions to minimize physical damage to the developing embryo and reduce bacterial fouling (Toh *et al.*, 2012).

Coral larvae settle and metamorphose in response to biochemical cues derived from a range of sources, including bacterial biofilm, algae and conspecifics (Gleason & Holfmann, 2011; Toh & Chou, 2013). Many of these chemicals have been used, both in the purified and unpurified form, to enhance coral settlement prior to transplantation. The most cost-effective method is to biologically condition the settlement substrates in seawater for biofilm development but isolated compounds can also be coated on the substrates to direct the settlement pattern (Guest *et al.*, 2010). However, in addition to the long culture time and expertise required, the financial costs of culturing sexually propagated corals can increase significantly as coral juveniles are often subjected to a range of post-settlement stressors, such as fouling which can lead to high mortality rates.

The establishment of stable structures such as artificial reefs has also been developed based on the knowledge on coral developmental biology. In areas where the structural integrity of the reef has been compromised due to activities such as blast fishing, coral larval settlement is compromised and post-settlement mortality is increased due to the damaging effects of moving rubble pieces on coral tissue (Fox, 2004). Substrate stabilization techniques would thus be particularly useful in assisting the recovery of degraded sites that are not limited by larval supplies (Fox *et al.*, 2005; Raymundo *et al.*, 2007).

Coral life history traits

Scleractinian coral growth rates are highly variable among species and are non-linear, with rapid growth early in life but declining as the colony ages. Fast-growing corals such as corals from the family Acroporidae can grow up to 4 cm per year (Toh *et al.*, unpublished data), but are prone to mechanical damage and are less resilient to disturbances such as tropical storms and acute *El Niño* warming events. Hence, their populations tend to be more dynamic, with large spatial and temporal variation in sizes (Hughes & Jackson, 1985). Conversely, slow-growing corals are more resistant to stress and populations are more robust (Hughes & Jackson, 1985), but their growth rates can be as low as 0.2 cm per year (Toh *et al.*, unpublished data). In addition, coral growth rates can be augmented by facilitation. Under favorable conditions, such as that provided in a nursery, coral size can be increased by more than 13 times over a span of 4 months (Shafir *et al.*, 2006).

The differences in coral life histories thus affect the choice of species and restoration strategy. Transplantation of fast-growing corals facilitates rapid re-colonization of the denuded site and as their calcium carbonate skeletons are more fragile than those of the slow-growing species, they are easier to fragment for asexual propagation. However, due to their low resilience to stressors, fast-growing corals often exhibit high mortality rates if they are transplanted to areas prone to disturbances or with currents that are too strong. Restoration of these sites can be achieved via the transplantation of the more robust slow-growing corals, although their growth rates are significantly slower. Hence, it is crucial to transplant a variety of both fast- and

slow-growing corals to increase both, heterogeneity and resilience of the restoration site to disturbances.

Coral nutrition

Scleractinian corals are capable of carrying out both autotrophy and heterotrophy (Goreau et al., 1971), enabling them to adapt to different environmental conditions and supplementing their diet with a diverse range of nutrients (Houlbrèque & Ferrier-Pagès, 2009). Autotrophy is the predominant means through which corals fulfill their nutritional needs, and is achieved by the translocation of photosynthates formed by symbiotic zooxanthellae present in coral tissues (Muscatine & Porter, 1977). The availability of solar irradiation is thus an important consideration for reef restoration, especially during the mariculture and transplantation phase. Excess irradiance can lead to the production of toxic by-products (such as hydrogen peroxide) in the zooxanthellae, leading to stress and the expulsion of the zooxanthellae from the coral tissue (Glynn, 1996), making the corals appear white, or 'bleached'. This bleaching response prevents the over-accumulation of toxins. Although corals have the ability to recover upon the re-establishment of the zooxanthellae, they tend to be more susceptible to diseases and exhibit elevated mortality rates (Glynn, 1993; Hughes et al., 2010). Conversely, irradiance-attenuating factors such as sedimentation will reduce photosynthetic rates (Barnes & Chalker, 1990). This results in a nutrient deficit, with the corals undergoing metabolic starvation and eventually death (Houlbrèque & Ferrier-Pagès, 2009). Therefore, the design of coral nurseries should not only include adaptive measures such as shading to prevent excessive irradiation, but also ensure that nurseries in locations experiencing elevated light attenuation rates are sited at shallow depths to ensure sufficient irradiation. The implementation of these adaptive measures, in conjunction with frequent monitoring efforts will facilitate timely responses to changes in environmental conditions and reduce unnecessary coral mortality.

Heterotrophy accounts for 15-35% of the total daily metabolic requirements in scleractinian corals and provides alternative sources of carbon and inorganic nutrients (Houlbrèque & Ferrier-Pagès, 2009). The food sources are diverse, and can include zooplankton, dissolved organic matter and suspended particulate matter (Houlbrèque & Ferrier-Pagès, 2009). Corals are capable of capturing and ingesting zooplankton as early as two days after settlement (Toh et al., 2013) and nutrient enhancement in corals enhances tissue growth, skeleton calcification rate and photosynthesis (Dubinsky et al., 1990; Ferrier-Pages et al., 2003; Petersen et al., 2008). In addition, heterotrophy compensates for the reduced photosynthetic activity experienced during low light conditions caused by events such as high levels of sedimentation, as well as bleaching episodes (Anthony & Fabricius, 2000; Ferrier-Pagès et al., 2011). Since corals are sessile and rely primarily on their tentacles and mucus for prey capture (Lewis & Price, 1975), physical processes such as hydrodynamic forces constitute the key determinants of prey capture and assimilation rates. Flow rate in particular, increases the prey encounter rate but high flow rates can result in coral polyp deformities and reduce the contact time required for prey ingestion (Sebens et al., 1997; Piniak, 2002). Prey density affects coral ingestion rates, and prolonged increase in prey numbers can facilitate coral growth (Petersen et al., 2008). The literature on the feeding biology of corals to date indicates that nutrient enhancement should be practiced in ex situ nurseries to augment coral growth, and that in situ coral nurseries should be constructed in relatively sheltered sites with low to moderate flow rates.

Furthermore, since flow rates are one of the key drivers structuring the distribution of corals on the reef (Sebens & Johnson, 1991), transplantation should be conducted in sites where the coral species are known to exist, to ensure that the hydrodynamic conditions are optimal for the species.

ECOLOGY OF CORAL REEFS

Connectivity

The life cycle of scleractinian corals includes a mobile planktonic phase. Physical and biological processes direct the dispersal of coral larvae and influence the genetic linkages between coral reef populations (Roberts *et al.*, 2001; Tay *et al.*, 2011; Toh *et al.*, 2012). Hydrodynamic forces transport larvae among populations and are key determinants of the source and sink sites of genetic material (Lugo-Fernández et al., 2001; Cowen & Sponaugle 2006) Therefore, variations in hydrodynamic patterns due to seasonal changes or coastal developments can influence the larval supplies received by any reef (Fiechter *et al.*, 2008). Biological factors such as coral planulae settlement competency, longevity and vertical migration affect both the dispersal range and the duration that coral larvae remain in the water column (Szmant & Meadows, 2006; Tay *et al.*, 2011).

Establishing the extent of connectivity between populations provides useful estimates for the recovery potential of degraded reefs. A site receiving limited larval supply, for instance, would have a reduced juvenile population, thus the renewal and natural recovery of the reef from disturbances would be extremely slow (Hughes *et al.*, 2010). Additionally, understanding the connectivity between coral populations maximizes the efficacy of restoration projects and facilitates spatial prioritization for restoration and conservation. The establishment of a network of protected sites (Jones *et al.*, 2007) coupled with the strategic restoration of identified source sites (such as via coral transplantation) to create a series of inter-connected 'restoration networks' can generate large amounts of larvae to seed distant or inaccessible sites. The larval supply will be increased several folds if multiple inter-connected source sites have been restored. Moreover, the spillover effects of the restored sites can also benefit adjacent sites not included in the scope of the intended restoration project, and serve to increase larval supply and recruitment rates (Halpern, 2003).

Community interactions

Competition for resources is an essential part of survival. For scleractinian corals, the amount of light and food received by a colony is determined in part by the suitability of the site that the larva has recruited on (Harrison & Wallace, 1990), and competition for these resources inevitably ensues upon settlement. Competition among scleractinian corals can result in a myriad of responses. Some, such as intraspecific fusion produce no apparent negative impacts, but most other interactions produce deleterious effects such as tissue damage, growth retardation and increased mortality rates on one or both of the corals involved. This may arise due to one of the following mechanisms: mesenterial filament extrusion, extension of sweeper tentacles and polyps, overgrowth and histo-incompatibility, with spatial ranges of up to 10 cm (Lang & Chornesky, 1990). Hence, the proximity among which coral colonies are placed in nurseries or transplanted should be considered carefully. The nursery-rearing of fast-growing and aggressive corals would benefit from spacing the colonies

further apart from each other to reduce the risks of overgrowth and tissue damage to other corals.

Fouling organisms such as sponges, algae and barnacles are detrimental to coral health. The scientific literature is replete with studies of fouling organisms impacting coral growth, survival and reproduction through overgrowth, abrasion, shading and allelopathy (Tanner, 1995; McCook et al., 2001). Macroalgae overgrowth in particular, can rapidly reduce coral cover (Tanner, 1995; Hughes et al., 2010). Biological controls can limit the proliferation of fouling communities and are thus vital to the maintenance of coral populations. However, anthropogenic disturbances having altered the dynamics of many biological communities are driving major phase shifts across the globe. For example, nutrient inputs from land developments often lead to algal blooms in coastal areas, while overfishing has drastically reduced the numbers of biological controls to levels below what is required to keep fouling organisms in check (Fig. 4; Hughes et al., 2010). Several strategies have been tested to reduce the effects that fouling communities can have on reef restoration projects. Regular maintenance of coral nurseries and transplant sites including the manual removal of surrounding fouling organisms and the use of anti-fouling paints are common means of reducing the establishment and proliferation of fouling communities (Edwards, 2010). These approaches tended to be more labour- and costintensive and may not be sustainable in the long-term. Alternatively, the introduction of biological controls has been demonstrated to be effective in controlling fouling algal communities in ex situ nurseries (Ng et al., 2013, Toh et al., in review) although the advantages for *in situ* applications (Villanueva et al., 2010) are limited.

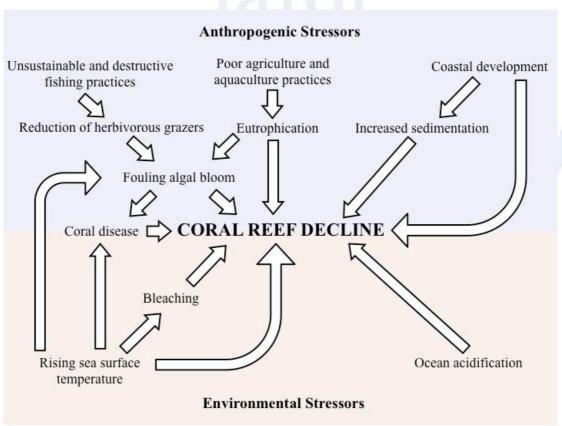


Figure 4. The impacts of environmental and anthropogenic stressors on coral reefs.

REEF RESTORATION: FUTURE CHALLENGES

Changing environmental and social dynamics

The rapidly changing environmental and social dynamics of the world today pose complex challenges to reef restoration. Environmental perturbations have ramifications on coral reefs around the world (Fig. 4), even for those in well-managed sites (De'ath et al., 2012). Climate change has resulted in increased global sea surface temperatures and acute disturbances such as typhoons are projected to be more intense and frequent in the next decade (Easterling et al., 2000). The combined effects of chronic and acute natural disturbances further depress the resilience of coral reefs, and reduce the recovery time between disturbances (Hughes et al., 2010). Rising sea surface temperatures and ocean acidification have been particularly detrimental to the survival of scleractinian corals. Ocean acidification impairs coral skeletal development and severely attenuates growth rates, while the increase in sea surface temperatures have resulted in more frequent episodes of coral bleaching, with associated increases in mortality and disease due to depressed immunity (Glynn, 1996; Brown, 1997). At elevated temperatures, coral larvae are also shown to exhibit decreased longevity, and tend to settle and metamorphose much earlier (Edmunds et al., 2001; Nozawa & Harrison, 2002), thus posing limits on their dispersal range and reducing genetic diversity.

The increasing reliance on resources derived from coral reefs continues to exert pressure on existing reefs (Fig. 4). In contrast to environmental perturbations, anthropogenic stressors are more localized (Burke et al., 2011). However, the effects tend to be more periodic and long-lived. Coastal development presents one of the major challenges in rapidly developing and highly urbanized countries. Countries such as Singapore have lost 60% of its coral reefs since the 1960s due to extensive land reclamation, dredging and coastal development (Chou, 2008; Burke et al., 2011). In addition, surface runoff and eutrophication resulting from agriculture and aquaculture activities have also increased the incidences of harmful algal blooms, intoxicating and asphyxiating coral reef organisms (Anderson et al., 2002). Unsustainable fishing practices represent another major source of anthropogenic pressures, especially in many developing coastal nations (Burke et al., 2011). Even though destructive fishing practices have been banned in several countries, the demand for seafood continues to increase (Burke et al., 2012). To meet these demands, commercial fishing and trawling activities are especially widespread in these developing coastal nations, quickly decimating the vital fish populations required to sustain healthy reefs (Turner et al., 1999).

As coastal development, land reclamation and unsustainable fishing practices persist unabated, and the global climate and ocean chemistry continue to change, the existence and recovery of coral reefs is unequivocally threatened (Fig. 5). The synergistic effects of environmental and anthropogenic pressures will thus hinder the long-term success of restoration activities (Fig. 4). Localized anthropogenic factors generates downstream effects which impacts coral reefs directly by increasing coral mortality rates and habitat loss, or indirectly by changing the community dynamics. The impacts are magnified due to the increased occurrence of acute natural perturbations, which further depresses the resilience of coral reef and hinders the natural recovery of impacted reefs. Hence, it is important to incorporate risk assessments during the planning phase of any reef restoration project, and make provisions for timely and adaptive management during the implementation phase.

Furthermore, as time and resources are limited, effective resource allocation is critical in reef restoration projects. A concerted effort among stakeholders, policy makers and scientific experts should be encouraged to maximize the benefits of restoration projects.

Effective management of stressors and the cost of reef restoration

Active restoration is never an alternative to proper coral reef management. The cost of reef restoration projects is substantially higher than that required to conserve and manage natural habitats (Edwards, 2010). Haisfield *et al.* (2010) demonstrated that utilizing enforcement to protect Indonesian coral reefs was 70 times more cost-effective than active rehabilitation. Furthermore, management of the reefs has the added benefit of preventing further destruction to coral reefs by restricting the type and extent of fishing activities in the area (Haisfield *et al.*, 2010). Embarking on reef restoration without proper management of coral reefs is counter-productive and may cause further damage to the reefs (Edwards, 2010).

Clearly, the management of stressors is crucial when engaging in coral reef restoration, but this may be complicated in most instances. The balance between socio-economic interests and habitat conservation and restoration presents a challenge to many coastal managers. Cultural practices have been a major driving force in many coastal cities where fishing is the primary means of livelihood (Lieber, 1994; Price, 1996). Although the reliance on coastal resources may be reduced by switching to alternative livelihoods such as tourism and industrial activities, these efforts require immense governmental support and commitment (Allison & Ellis, 2001), which are often met with resistance from the coastal communities to abandon their local traditions (Ikiara & Odink, 1999). Additionally, legislation to regulate activities within the marine reserves may exist, but the effectiveness may be hampered by the lack of enforcement and compliance (Qiu *et al.*, 2009). The persistent use of destructive fishing practices near restoration sites for example, will inevitably hinder the success of restoration initiatives (Fig. 5).

Some studies have also attempted to provide a monetary valuation for natural habitats to demonstrate that habitats are worth more preserved than destroyed (e.g. Costanza *et al.*, 1997), but these efforts tend to be ignored largely due to the disparity between short and long-term benefits (Botsford *et al.*, 1997). The scarcity of land has driven both urban and developing coastal nations to reclaim parts of their coastal waters to accommodate their immediate economic aims. Even with measures such as silt screens to reduce excessive sedimentation, the benefits are limited and temporary. Furthermore, proponents of coastal development often argue that lost habitats can be adequately substituted by artificial modifications, but they fail to recognize that coastal modification irreversibly alters natural systems such as hydrodynamic forces and increases terrestrial surface runoff. The ecosystems services subsequently provided by the artificial habitats will not be at the same levels as those provided by the original habitats (Perkol-Finkel & Airoldi, 2010).

The cost of coastal management and restoration can be high, with slow returns on investment (Spurgeon & Lindahl, 2000; Perkol-Finkel & Airoldi, 2010). Most of the associated benefits are intangible and are often perceived as having a lower value compared to immediate monetary benefits. The cost of restoration can range from US\$13,000 to \$100 million per hectare (Spurgeon & Lindahl, 2000) and is hardly

viable on a large scale, especially for developing nations (Edwards & Clark, 1998). However, the use of cost-benefit analysis has been useful in justifying the economic feasibility of restoration projects. The adoption of the total economic value approach to account for the direct and indirect value of coral reefs has shown that the benefits far outweigh the initial costs incurred for reef restoration in the long run (Spurgeon, 2001). To improve the cost-effectiveness of reef restoration, the cost can be substantially lowered through public involvement (such as using volunteers and members of the local community) to reduce labor and operating costs, and improving the effectiveness of existing restoration techniques. Strategic partnerships between projects can further reduce the startup costs and maximize the use of the resources, while the inclusion of community training and education initiatives provide long-term indirect benefits for restoration projects.

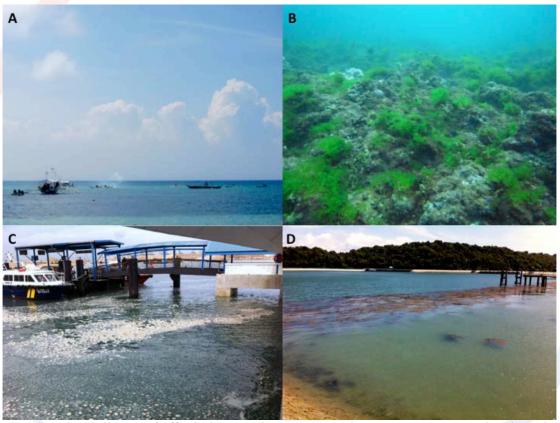


Figure 5. The challenges of effectively managing anthropogenic stressors. (a) Destructive dynamite fishing continues in one of the designated Marine Reserves in Cebu, Philippines due to noncompliance by the local community, (b) the phase shift from a previously coral-dominated to an algae-dominated reef in Bolinao, Philippines raises doubts if the reef will recover even though this site is within a Marine Reserve, (c) Sea foam resulting from a nearby land reclamation project in Singapore in spite of precautionary measures, and (d) excessive surface runoff due to coastal modifications in Singapore.

CONCLUSION

Active coral reef restoration is an important coastal management tool to supplement existing approaches. However, compared to terrestrial restoration, the science underlying coral reef restoration is still in its infancy. Most of these techniques have been based on theories developed for terrestrial restoration and empowering reef restoration practitioners and coastal managers with more knowledge of marine ecology and biology is critical to the success of restoration projects. In this paper, we have highlighted the key biological and ecological concepts essential to reef

restoration and identified the major future challenges which can hinder its effectiveness. More importantly, we recommend that the proper management of environmental and anthropogenic stressors be in place before restoration is attempted. The choice of restoration techniques should address the underlying causes of the degradation. Additionally, the inclusion of risk assessments and adaptive management should be integrated into the planning of any restoration project, to facilitate timely responses to possible changes in the social, political and environmental climate.

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REFERENCES

Allison, E.H. & Ellis, F. 2001. The livelihoods approach and management of small-scale fisheries. Marine policy 25(5):377-388.

Anderson, D.M., Glibert, P.M., & Burkholder, J.M. 2002. Harmful algal blooms and eutrophication: nutrient sources, composition, and consequences. Estuaries 25(4):704-726.

Anthony, K.R.N. & Fabricius, K.E. 2000. Shifting roles of heterotrophy and autotrophy in coral energetic under varying turbidity. Journal of Experimental Marine Biology and Ecology 252:221-253.

Baird, A.H., Guest, J.R. & Willis, B.L. 2009. Systematic and biogeographic patterns in the reproductive biology of scleractinian corals. Annual Review of Ecology, Evolution, and Systematics 40:551–571.

Barnes, D.J. & Chalker, B.E. 1990. Calcification and photosynthesis in reef-building corals and algae. In: Dubinsky, Z. (ed.), Coral Reefs Ecosystems of the World 25. Elsevier, Amsterdam. Pp. 109-131.

Bellwood, D.R., Hughes, T.P., Folke, C. & Nyström, M. 2004. Confronting the coral reef crisis. Nature 429:827-833.

Botsford, L.W., Castilla, J.C., & Peterson, C.H. 1997. The management of fisheries and marine ecosystems. Science 277(5325):509-515.

Brown, B.E. 1997. Coral bleaching: causes and consequences. Coral reefs 16(1):129-138.

Burke, L., Reytae, K., Spalding, M. & Perry, A. 2011. Reef at risk revisited. World Resources Institute, Washington DC, USA. 113 pp.

Chou, L.M. 2008. Nature and the sustainability of the marine environment. In: Wong.

T.C. et al. (eds.), Spatial planning for a sustainable Singapore. Springer Science, Singapore. Pp. 169-182.

Costanza, R., d'Arge, R., de Groot, R., Farber, S., Grasso, M., Hannon, B., Limburg, K., Naeem, S., O'Neill, R.V., Paruelo, J., Raskin, R.G. & Sutton, P. 1997. The value of the world's ecosystem services and natural capital. Nature 387:253–260.

Cowen, R.K. & Sponaugle, S. 2009. Larval dispersal and marine population connectivity. Annual Reviews of Marine Science 1:443-466.

De'ath, G., Fabricius, K.E., Sweatman H. & Puotinen, M. 2012. The 27-year decline of coral cover on the Great Barrier Reef and its causes. Proceedings of the National Academy of Sciences 109(44):17995-17999.

Done, T.J. 1992. Phase shifts in coral reef communities and their ecological significance. Hydrobiologia 247:121-132.

Dubinsky, Z., Stambler, N., Ben-Zoin, M., McCloskey, L.R., Muscatine, L. & Falkowski, P.G. 1990. The effect of external nutrient resources on the optical properties and photosynthetic efficiency of *Stylophora pistillata*. Proceedings of the Royal Society of London Series B 239:231–246.

Easterling, D.R., Meehl, G.A., Parmesan, C., Changnon, S.A., Karl, T.R., & Mearns, L.O. 2000. Climate extremes: observations, modeling, and impacts. Science, 289(5487):2068-2074.

Edmunds, P., Gates, R., & Gleason, D. 2001. The biology of larvae from the reef coral Porites astreoides, and their response to temperature disturbances. Marine Biology 139(5): 981-989.

Edwards, A.J. & Clark, S. 1998. Coral transplantation: a useful management tool or misguided meddling? Marine Pollution Bulletin 37:474-487.

Edwards, A.J. 2010. Reef Rehabilitation Manual. Coral Reef Targeted Research & Capacity Building for Management Program, St Lucia, Australia ii. 166 pp.

Ferrier-Pagès, C., Hoogenboom, M. & Houlbrèque, F. 2011. The role of plankton in coral trophodynamics. In: Dubinsky, Z. & Stambler, N. (eds.), Coral Reefs, an Ecosystem in Transition. Springer, Netherlands. Pp. 215–229.

Ferrier-Pagès, C., Witting, J., Tambutte, E. & Sebens, K.P. 2003. Effect of natural zooplankton feeding on the tissue and skeletal growth of the scleractinian coral *Stylophora pistillata*. Coral Reefs 22:229-240.

Fiechter, J., Haus, B.K., Melo, N. & Mooers, C.N.K. 2008. Physical processes impacting passive particle dispersal in the Upper Florida Keys. Continental Shelf Research 28:1261-1272.

Fox, H.E. 2004. Coral recruitment in blasted and unblasted sites in Indonesia: assessing rehabilitation potential. Marine Ecology Progress Series 269:131-139.

Fox, H.E., Mous, P.J., Pet, J.S., Muljadi, A.H. & Caldwell, R.L. 2005. Experimental assessment of coral reef rehabilitation following blast fishing. Conservation Biology, 19(1):98-107.

Gleason, D.F. & Hofmann, D.K. 2011. From gametes to recruits. Journal of Experimental Marine Biology and Ecology 408:42–57.

Glynn, P.W. 1993. Coral reef bleaching: ecological perspectives. Coral Reefs 12:1-17.

Glynn, P.W. 1996. Coral reef bleaching: facts, hypotheses and implications. Global Change Biology 2:495-509.

Goreau, T.F., Goreau, N.I., & Yonge, C.M. 1971. Reef corals: autotrophs or heterotrophs? The Biological Bulletin 141:247-260.

Guest, J.R., Heyward, A.J., Omori, M., Iwao, K., Morse, A., Boch, C. & Edwards, A.J. 2010. Rearing coral larvae for reef rehabilitation. In: Edwards, A.J. (ed.), Reef Rehabilitation Manual. Coral Reef Targeted Research & Capacity Building for Management Program, St. Lucia. Australia. Pp. 73-92.

Haisfield, K.M., Fox, H.E., Yen, S., Mangubhai, S., & Mous, P.J. 2010. An ounce of prevention: cost-effectiveness of coral reef rehabilitation relative to enforcement. Conservation Letters 3(4):243-250.

Halpern, B.S. 2003. The impact of marine reserves: do reserves work and does reserve size matter? Ecological applications 13(1):117-137.

Harrison, P.L. & Wallace, C.C. 1990. Reproduction, dispersal and recruitment of scleractinian corals. In: Dubinsky, Z. (ed.), Coral Reefs Ecosystems of the World 25. Elsevier, Amsterdam. Pp. 133-207.

Holling, C.S. 1973. Resilience and stability of ecological systems. Annual Reviews of Ecology and Systematics 4:1-23.

Houlbrèque, F. & Ferrier-Pagès, C. 2009. Heterotrophy in tropical scleractinian corals. Biological Reviews 84:1-17.

Hughes, T.P. & Jackson, J.B.C. 1985. Population Dynamics and Life Histories of Foliaceous Corals. Ecological Monographs 55(2):141-166.

Hughes, T.P., Bellwood, D.R., Folke, C., Steneck R.S. & Wilson, J. 2005. New paradigms for supporting the resilience of marine ecosystems. Trends in Ecology and Evolution 20:380–386.

Hughes, T.P., Graham, N.A.J., Jackson, J.B.C, Mumby, P.J. & Steneck, R.S. 2010. Rising to the challenge of sustaining coral reef resilience. Trends in Ecology and Evolution 25(11):633-642.

Ikiara, M.M. & Odink, J.G. 1999. Fishermen resistance to exit fisheries. Marine Resource Economics 14(3):199-214.

Jones, G.P., Srinivasan, M. & Almany, G.R. 2007. Population connectivity and conservation of marine biodiversity. Oceanography 20(3):12.

Kramarsky-Winter, E., Fine, M. & Loya, Y. 1997. Coral polyp expulsion. Nature 387:137.

Lang, J.C. & Chornesky, E.A. 1990. Competition between scleractinian reef recorals. In: Dubinsky, Z. (ed.), Coral Reefs Ecosystems of the World 25. Elsevier, Amsterdam. Pp. 209-252.

Lewis, J.B. & Price, W.S. 1975. Feeding mechanisms and feeding strategies of Atlantic reef corals. Journal of Zoology: Proceedings of the Zoological Society of London 176:527-544.

Lieber, M.D. 1994. More than a living: fishing and the social order on a Polynesian atoll. Westview Press Inc, USA. 235 pp.

Lugo-Fernández, A., Deslarzes, K.J.P., Price, J.M., Boland, G.S. & Morin, M.V. 2001. Inferring probable dispersal of Flower Garden Banks Coral Larvae (Gulf of Mexico) using observed and simulated drifter trajectories. Contental Shelf Research 21(1):47-67.

McCook L.J., Jompa J. & Diaz-Pulido G. 2001. Competition between corals and algae on coral reefs: a review of evidence and mechanisms. Coral Reefs 19:400-417.

Muscatine, L. & Porter, J.W. 1977. Reef corals: mutualistic symbioses adapted to nutrient-poor environments. Bioscience 27:454–460.

Ng C.S.L., Toh, T.C., Toh, K.B., Guest, J. & Chou, L.M. 2013. Dietary habits of grazers influence their suitability as biological controls of fouling macroalgae in *ex situ* mariculture. Aquaculture Research DOI: 10.1111/are12128.

Nozawa, Y. & Harrison, P.L. 2002. Larval settlement patterns, dispersal potential, and the effect of temperature on settlement of larvae of the reef coral, Platygyra daedalea, from the Great Barrier Reef. Proceedings of the 9th International Coral Reef Symposium 1: 409-415.

Omori, M., Iwao, K., & Tamura, M. 2008. Growth of transplanted *Acropora tenuis* 2 years after egg culture. Coral Reefs 27:165.

Pandolfi, J.M., Possingham, H.P., Sala, E., Jackson, J.B.C., Baron, N., Bradbury, R.H., Guzman, H.M., Hughes, T.P., Kappel, C.V., Micheli, F. & Ogden, J.C. 2005. Are U.S. Coral reefs on the slippery slope to slime? Science 307:1725-1726.

Perkol-Finkel, S., & Airoldi, L. 2010. Loss and recovery potential of marine habitats: an experimental study of factors maintaining resilience in subtidal algal forests at the Adriatic Sea. PLoS one 5(5):e10791.

Petersen, D., Wietheger A. & Laterveer, M. 2008. Influence of different food sources on the initial development of sexual recruits of reef building corals in aquaculture. Aquaculture 277: 174-178.

Piniak, G.A. 2002. Effects of symbiotic status, flow speed, and prey type on prey capture by the facultatively symbiotic temperate coral *Oculina arbuscula*. Marine Biology 141:449-455.

Price, R. 1966. Caribbean fishing and fishermen: A historical sketch. American Anthropologist 68(6):1363-1383.

Qiu, W., Wang, B., Jones, P. J. & Axmacher, J. C. 2009. Challenges in developing China's marine protected area system. Marine Policy 33(4):599-605.

Raymundo, L.J., Maypa, A.P., Gomez, E.D. & Cadiz, P. 2007. Can dynamite-blasted reefs recover? A novel, low-tech approach to stimulating natural recovery in fish and coral populations. Marine Pollution Bulletin 54:1009-1019.

Richmond, R.H. 1997. Reproduction and recruitment in corals: critical links in the persistence of reefs. In Birkeland, C. (ed.), Life and death of coral reefs. Chapman & Hall, New York, USA. Pp. 175-197.

Rinkevich, B., 1995. Restoration strategies for coral reefs damaged by recreational activities - the use of sexual and asexual recruits. Restoration Ecology 3(4):241-251.

Roberts, C., Halpern, B., Palumbi, S., Warner, R. 2001. Designing marine reserve networks: Why small, isolated protected areas are not enough. Conservation 2(3): 10-17.

Sammarco, P.W. 1982. Polyp bail-out: an escape response to environmental stress and a new means of reproduction in corals. Marine Ecology Progress Series 10:57-65.

Sammarco, P.W. 1986. Coral reproduction, dispersal, and survival. Oceanus 29(2):28-19.

Sebens, K.P. & Johnson, A.S. 1991. Effects of water movement on prey capture and distribution of reef corals. Hydrobiologia 226:91-101.

Sebens, K.P., Witting, J. & Helmuth, B. 1997. Effects of water flow and branch spacing on particle capture by the reef coral *Madracis mirabilis* (Duchassaing and Michelotti). Journal of Experimental Marine Biology and Ecology 211:1-28.

Shafir, S., Van Rijn, J. & Rinkevich, B. 2006. Steps in the construction of underwater coral nursery, an essential component in reef restoration acts. Marine Biology 149:679-687.

Spurgeon, J.P.G. & Lindahl, U. 2000. Economics of coral reefrestoration. In: Cesar, H.S.J (ed.), Collected essays on the economics of coral reefs. CORDIO, Sweden. Pp.125–136.

- Spurgeon, J.P.G. 2001. Improving the economic effectiveness of coral reef restoration. Bulletin of Marine Science 69(2):1031-1045.
- Stoddart, J.A. 1986. Coral genetics: new directions. Oceanus 29(2): 41.
- Szmant, A.M. & Meadows, M.G. 2006. Developmental changes in coral larval buoyancy and vertical swimming behavior: implications for dispersal and connectivity. Proceedings of the 10th International Coral Reef Symposium 1: 431-437.
- Tanner, J.E. 1995. Competition between scleractinian corals and macroalgae: An experimental investigation of coral growth, survival and reproduction. Journal of Experimental Marine Biology and Ecology 190:151-168.
- Tay, Y.C., Guest, J.R., Chou, L.M.. & Todd, P.A. 2011. Vertical distribution and settlement competencies in broadcast spawning coral larvae: Implications for dispersal models. Journal of Experimental Marine Biology and Ecology 409:324-330.
- Toh, T.C., Ng, C.S.L., Guest, J.R. & Chou, L.M. (In review). Grazers improve health of coral juveniles in *ex situ* mariculture.
- Toh, T.C., Guest, J.R. & Chou, L.M. 2012. Coral larval rearing in Singapore: Observations on spawning timing, larval development and settlement of two common scleractinian coral species. In: Tan, K.S. (ed.), Contributions to Marine Science. National University of Singapore, Republic of Singapore. Pp. 81-87.
- Toh, T.C. & Chou, L.M. 2013. Aggregated settlement of *Pocillopora damicornis* planulae facilitates coral wound healing. Bulletin of Marine Science 89(2):583-584.
- Toh, T.C., Peh, J.W.K & Chou, L.M. 2013. Early onset of zooplanktivory in equatorial reef coral recruits. Marine Biodiversity DOI:10.1007/s12526-013-0156-5.
- Turner, S.J., Thrush, S.F., Hewitt, J.E., Cummings, V.J., & Funnell, G. 1999. Fishing impacts and the degradation or loss of habitat structure. Fisheries Management and Ecology 6(5):401-420.
- Villanueva, R.D., Edwards, A.J. & Bell, J.D. 2010. Enhancement of grazing gastropod populations as a coral reef restoration tool: predation effects and related applied implications. Restoration Ecology 18(6), 803-809.
- Yap, H.T., Alino, P.M. & Gomez, E.D. 1992. Trends in growth and mortality of three coral species (Anthozoa: Scleractinia), including effects of transplantation. Marine Ecology Progress Series 83: 91–101.

