

Article Type: Concepts & Questions

Concepts and Questions

## **Harnessing ecological processes to facilitate coral restoration**

Mark C Ladd<sup>1\*</sup>, Margaret W Miller<sup>2</sup>, John H Hunt<sup>3</sup>, William C Sharp<sup>3</sup>, and Deron E Burkepile<sup>1,4</sup>

*<sup>1</sup>Department of Ecology, Evolution, and Marine Biology, University of California–Santa Barbara, Santa Barbara, CA \* (mark.ladd@lifesci.ucsb.edu); <sup>2</sup>National Marine Fisheries Service, Southeast Fisheries Science Center, Miami, FL; <sup>3</sup>Florida Fish and Wildlife Conservation Commission, Fish and Wildlife Research Institute, Marathon, FL; <sup>4</sup>Marine Science Institute, University of California–Santa Barbara, Santa Barbara, CA*

### **Running heads:**

MC Ladd *et al.*

Facilitating coral restoration

**Incorporating ecological processes into restoration planning is increasingly recognized as a fundamental component of successful restoration strategies. We outline a scientific framework to advance the emerging field of coral restoration. We advocate for harnessing ecological processes that drive community dynamics on coral reefs in a way that facilitates the establishment and growth of restored corals. Drawing on decades of coral reef ecology research and lessons learned from the restoration of other ecosystems, we posit that restoration practitioners can control factors such as the density, diversity, and identity of transplanted corals; site selection; and transplant design to restore positive feedback processes – or to disrupt negative feedback processes – in order to improve restoration success. Ultimately, we argue that coral restoration should explicitly**

**This is the author manuscript accepted for publication and has undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the Version of Record. Please cite this article as doi: 10.1002/fee.1792**

This article is protected by copyright. All rights reserved

**incorporate key natural processes to exploit dynamic ecological forces and drive recovery of coral reef ecosystems.**

*Front Ecol Environ* 2018;

**In a nutshell:**

- Global declines in corals have spurred efforts to transplant species grown in underwater nurseries to recover coral populations
- An important component to restoration of degraded terrestrial, aquatic, and marine ecosystems is the reestablishment of key ecological processes
- Coral reef restoration can build on lessons learned from restoring other types of ecosystems to develop creative methods for harnessing key ecological processes, such as predation, herbivory, and nutrient cycling, that facilitate coral restoration

Although coral reefs cover less than 0.1% of Earth's surface, they support more than 30% of total marine biodiversity (Reaka-Kudla 2005), are a key source of fisheries production (Moberg and Folke 1999), and provide shoreline protection for over 100 million people living in coastal areas (Ferrario *et al.* 2014). However, corals are in rapid decline on many reefs due to global stressors associated with climate change, such as increasing sea surface temperatures that cause coral bleaching and disease, as well as local stressors like nutrient pollution, sedimentation, and overfishing (Hughes *et al.* 2017). Coral reefs in the Pacific Ocean have lost nearly half of their corals over the past four decades (Bruno and Selig 2007), and many have lost an additional 30–50% during the recent (2014–2016) global coral bleaching event (Hughes *et al.* 2017). This alarming trend is even more pronounced in the western Atlantic Ocean (henceforth, the Caribbean), where reefs have lost approximately 80% of their corals since the mid-1970s (Jackson *et al.* 2014). Although the causes of coral decline are numerous, many of the drivers of coral loss are localized, acute disturbances, making coral restoration a feasible option for reestablishing corals in many areas.

Current restoration efforts largely focus on “outplanting” (transplanting), corals raised in nurseries to augment existing populations, with the goal of restoring key foundational species on degraded reefs. These efforts have become increasingly successful at reestablishing target corals that are often threatened or endangered (Figure 1; Young *et al.* 2012). In the

Caribbean alone, there are at present more than 150 coral propagation operations in over 20 countries containing tens of thousands of nursery-raised corals for use in restoration efforts (Lirman and Schopmeyer 2016). The nascent field of coral restoration is therefore on the threshold of conducting substantial restoration programs.

Generally speaking, restoration efforts typically focus on restoring populations of foundation species that provide the physical structure upon which community members depend for shelter, resources, or reproduction (eg grasses [Werner *et al.* 2016]; trees [Elliott *et al.* 2003]; mangroves [Bosire *et al.* 2008]; seagrasses [Reynolds *et al.* 2013]). There is a long history of restoring foundation species in terrestrial systems, where planting trees has been central to restoring key ecosystem processes and services (Holl 2017). However, beyond simply reestablishing foundation species, restoration efforts often incorporate fundamental ecological processes, such as competition, succession, and herbivory, to restore communities that support important ecosystem functions (Suding *et al.* 2004). Indeed, two decades ago, Palmer *et al.* (1997) recognized the central roles that basic ecological theory and community ecology play in effective restoration. For example, manipulating community dynamics by outplanting later successional species is often used to accelerate the process of community succession in restoring terrestrial systems (Palmer *et al.* 1997; Werner *et al.* 2016). Facilitation of target restoration species using nurse plants (species used to create a more favorable environment for restored species) or specific early successional species is frequently used in the restoration of terrestrial and coastal ecosystems to reduce physical stress and improve local growing conditions (Bruno *et al.* 2003; Silliman *et al.* 2015).

The practice of harnessing positive interactions and ecological processes to expedite restoration in terrestrial systems is increasingly being applied to restore degraded aquatic and marine communities (Bruno *et al.* 2003; Halpern *et al.* 2007); for instance, promoting genetic diversity in large-scale seagrass restoration planning can restore genetically diverse populations far more rapidly than can natural regeneration via recruitment (Reynolds *et al.* 2013). Simple changes in coastal wetland restoration designs that leverage positive intra- (Silliman *et al.* 2015) and interspecific (Derksen-Hooijberg *et al.* 2017) interactions, as opposed to trying to minimize negative ones, can also greatly improve the chances of successful restoration.

Whereas facilitation and ecological processes are often incorporated into restoration approaches in many terrestrial, aquatic, and marine systems, practitioners of coral reef restoration have been slower to integrate these factors into coral restoration programs (Shaver and Silliman 2017). To assess the degree to which ecological processes are incorporated into restoration efforts on coral reefs, we surveyed 116 scientific papers on coral restoration published between 1987 and 2017 (see the WebReferences in WebPanel 1 for a full list of the papers included in the review). The majority of these studies focused on factors such as the growth and survivorship of corals either in nurseries or outplanted to reefs, whereas only 19% incorporated any aspect of ecological processes (eg recruitment, predation, herbivory; Table 1; WebPanel 1). In addition, we surveyed 21 coral restoration practitioners conducting coral restoration operations in 12 different countries and territories throughout the Caribbean region to ascertain what factors influence how practitioners choose reefs to conduct coral restoration and determine sites within those reefs to outplant corals (Table 2; WebPanel 2). Existing coral cover, available clean substrate, and water depth were the three most important factors identified by practitioners when selecting a reef to conduct restoration, whereas factors associated with ecological processes were generally ranked low in importance.

However, when selecting where to outplant corals within a reef, practitioners appeared to give ecological processes more consideration, as the three most important factors identified were choosing the best available substrate, avoiding potential benthic competitors, and outplanting near herbivores. Nevertheless, there appears to be limited data addressing how effective these different processes may be for facilitating restoration. For example, avoiding benthic competitors was the second most highly ranked criterion for selecting sites to outplant corals (Table 2), but few, if any, scientific studies have examined the impacts of competition on restored corals (Table 1). Furthermore, recruitment of fishes and corals has been the most studied process in the context of coral restoration (though composing just 5% of all restoration studies), yet these studies typically only measure recruitment following coral outplanting, with negligible consideration of how the design of restoration can facilitate or impede recruitment. Thus, there is definite interest in integrating ecological processes into coral restoration, but it is unclear how extensively ecological theory has shaped current practices.

Here, we outline a framework suggesting how restoration practitioners could potentially increase the success and rate of restoration through better integration of key ecological

processes, such as herbivory, competition, predation, and nutrient cycling, into restoration efforts. We propose that restoration practitioners can manipulate where, when, and how corals are outplanted to enhance coral survivorship and growth in order to restore positive (or to disrupt negative) feedback processes. We highlight important knowledge gaps regarding the ecological underpinnings of coral restoration that must be addressed through rigorous scientific research (WebTable 1). By explicitly incorporating methods that either take advantage of or manipulate key processes, restoration efforts may be able to utilize dynamic ecological forces to hasten the recovery of coral populations.

### **Capitalizing on important ecological processes**

#### ***Promoting herbivory in restored areas***

Herbivory by fishes and urchins is the linchpin of a series of positive feedbacks that reinforce topographically complex, coral-dominated reefs, thereby supporting ecosystem function (Mumby and Steneck 2008). Robust herbivore populations can suppress macroalgal cover, minimize coral–algal competition, increase coral growth and recruitment, and facilitate the recovery of coral populations after disturbances (Graham *et al.* 2015; Zaneveld *et al.* 2016). Restoration practitioners recognize the importance of herbivory, since “outplanting near herbivores” was ranked as the third most important criterion for selecting sites on a reef to outplant corals (Table 2). Yet only 2.5% of studies on coral restoration address herbivory at all, with only one study focusing on herbivory by fishes or urchins (WebPanel 2). Capitalizing on herbivory in concert with coral restoration, either by outplanting coral in areas where herbivory is high or promoting herbivory on reefs where it is diminished, should therefore be both a research and a restoration priority.

Whereas populations of small, coral-associated fish often decline as a result of reduced coral cover, populations of larger, roving fishes, such as herbivorous parrotfish and surgeonfish species, may persist in the immediate aftermath of coral loss (Graham *et al.* 2007). In Moorea, French Polynesia, for example, populations of herbivorous fish increased following an outbreak of coral-eating sea stars, which consumed virtually all living corals on the island’s reefs; the increased herbivory facilitated recovery by keeping the substrate free of macroalgae, thereby allowing corals to recruit back to these reefs (Holbrook *et al.* 2016). For reefs with lower coral recruitment rates, restoring corals shortly after an acute disturbance may harness

the benefits of existing herbivore populations to help jump-start recovery of coral populations, as compared to sites where rates of herbivory are lower.

In addition, restoring corals immediately following a disturbance could maintain robust herbivorous fish populations, as fish larvae, like coral larvae, are attracted to waterborne chemical cues emitted by corals (Dixon *et al.* 2014). Quickly restoring corals after a disturbance might therefore help prevent diminished recruitment of important fishes and corals in the absence of abundant coral. Initiation of such recruitment cascades could hasten the recovery not only of coral populations but also of organisms that provide key ecosystem functions like herbivory and nutrient cycling (eg Halpern *et al.* 2007). This type of scenario highlights the key ways in which larger-scale processes such as connectivity between reefs and larval supply dynamics can influence coral restoration.

Different types of herbivores likely vary in effectiveness in facilitating restoration, given that herbivores differ in the spatial extent and intensity at which they graze. Urchins represent a concentrated source of grazing over a small area of a reef ( $\sim 1 \text{ m}^2$ ), whereas herbivorous fishes may graze over more diffuse (hundreds of square meters) areas (Sandin and McNamara 2012). The steady and intense herbivory performed by urchins can ease coral–algal competition and allow transplanted or juvenile corals to establish (Sandin and McNamara 2012). Indeed, localized recovery of the long-spined urchin (*Diadema antillarum*), a historically abundant grazer on Caribbean reefs, has greatly reduced macroalgal cover and increased coral recruitment compared to adjacent areas where the urchin is absent (Carpenter and Edmunds 2006).

Establishing recovery nuclei by focusing restoration efforts on small, discrete areas to attract important community members (eg birds, rodents) that can deposit seeds, concentrate nutrients, and facilitate succession is common in forest restoration (Holl 2017). On reefs, restoring coral in areas with existing urchin populations could harness a consistent source of herbivory to facilitate coral growth and result in recovery nuclei on a degraded reef. However, it is important to consider the density-dependent nature of the benefits that urchin provide, as grazing by urchins at high densities can dislodge juvenile corals, kill coral recruits, and reduce the cover of important coral settlement substrate (McClanahan *et al.* 1996). Thus, at high densities or in the absence of adequate coral growth, the presence of urchins may work against long-term restoration goals by degrading the structural framework of reefs.

Reducing the amount of substrate available for algal colonization can force herbivores to graze more intensely on the remaining space (Williams *et al.* 2001). This might be achieved by increasing the density of corals outplanted for restoration, or by using fast-growing corals and/or coral species with morphologies that occupy relatively large amounts of surface area (Figure 2). The temporary use of non-colonizable, algal-free surfaces to reduce grazable substrate can concentrate existing herbivory (Williams *et al.* 2001). Coupling targeted high-density outplanting of corals with the restocking of grazers (eg urchins, parrotfishes) could promote positive feedbacks and hasten the development of recovery nuclei (Maciá *et al.* 2007; Obolski *et al.* 2016). Such approaches may be more feasible for discrete areas like patch reefs, where natural barriers aid in spatially restricting herbivores.

### ***Reducing coral predation and disease***

Coral predation (ie corallivory) is a chronic source of tissue loss and mortality for many species of coral (Rotjan and Lewis 2008). Common predators of coral include many types of invertebrates (eg snails, fireworms, and sea stars) and fishes (eg damselfishes, butterflyfishes, and other corallivorous species). Before the mass bleaching of 2014–2016 (Hughes *et al.* 2017), over 40% of the coral cover lost on Australia’s Great Barrier Reef over the past three decades was due to outbreaks of the corallivorous crown-of-thorns sea star (*Acanthaster planci*; De’ath *et al.* 2012). In the Caribbean, algal-farming damselfishes can be a major source of mortality for colonies of staghorn coral (*Acropora cervicornis*) outplanted for coral restoration (Figure 3; Schopmeyer and Lirman 2015). Surprisingly, our survey revealed that avoiding or managing corallivory was seen as one of the least important factors among restoration practitioners when selecting sites to outplant corals (Table 2), although corallivory has attracted more research attention in the coral restoration literature (Table 1).

Notably, there appear to be several relatively easy decisions practitioners can make to help minimize predation on restored corals. As coral cover declines, predation by roving corallivorous fishes can generate an alarming pattern in which predation intensity on corals increases as coral cover decreases (Burkpile 2012); moreover, corallivory from less mobile organisms (eg invertebrates) also intensifies as coral cover decreases and food resources become scarcer (Baums *et al.* 2003). Given this relationship, sites featuring exceptionally low coral cover may in fact be poor choices for restoration, particularly if the corals being used for

restoration are frequent targets of corallivores. Outplanting on reefs with some existing coral populations may be important for reducing damage by corallivores.

Asymmetry in prey preference can also make the outplanting of rare but preferred corals particularly problematic. Such is the case for *A cervicornis*, the primary species used for coral restoration in the Caribbean, which is the preferred prey of the corallivorous gastropod *Coralliophila abbreviata* (Johnston and Miller 2014). In regions with high spatial variability of corallivore abundance, avoiding reefs with large populations of corallivores in favor of targeting sites with low corallivore abundance could help to mitigate this negative feedback hindering coral restoration (Williams *et al.* 2014).

Current restoration efforts largely focus on restoring one or a few species of corals. However, as coral propagation techniques improve, the increasing number and diversity of corals available for restoration provide the opportunity to test and employ creative approaches to restoration. Some coral species, such as *Porites* spp in the Caribbean (Miller and Hay 1998), and *Acropora* spp and *Montipora* spp in the Pacific (White and O'Donnell 2010), are quickly consumed by corallivores when transplanted onto a reef. Limiting access by corallivores to palatable coral species by protecting them with less palatable branching corals is one creative approach to reduce corallivory and increases the diversity of corals being restored. In Florida, for instance, colonies of *A cervicornis* outplanted next to conspecifics were more quickly preyed upon than those outplanted next to different species (Johnston and Miller 2014); similarly, colonies of the leaf coral (*Pavona frondifera*) outplanted next to finger corals (*Porites cylindrica*) suffered lower predation rates than did *P frondifera* outplanted with conspecifics (Cabaitan *et al.* 2015). If the corals being used for restoration are heavily targeted by corallivores, informed use of mixed-species assemblages of corals may help reduce corallivory and its detrimental effects on coral restoration (Figure 2). Such an approach would parallel the beneficial interactions commonly used in terrestrial restoration (Bruno *et al.* 2003).

Disease is a major source of coral mortality and can have devastating effects on coral populations (Precht *et al.* 2016). Although we did not specifically ask about disease in our survey of practitioners, surprisingly, only one of the 116 studies identified in our literature search focused on disease dynamics in restored corals (Table 1), indicating that there is a clear mismatch between the importance of disease as a source of coral mortality and the level of attention it has received in coral restoration studies. Many corallivores may spread disease



agents among corals, including species used for restoration (Williams and Miller 2005); for example, the bearded fireworm (*Hermodice carunculata*), a voracious coral predator and a reservoir for coral disease (Sussman *et al.* 2003), frequently consumes *A cervicornis* (Miller *et al.* 2014). Competition between corals and the common green alga *Halimeda opuntia* can attract *H carunculata*, increasing the prevalence of coral disease and mortality (Wolf and Nugues 2013). Seeking ways to control both algal competitors, such as restoring areas with abundant fishes and/or urchins, and coral predators may also help to reduce the incidence and spread of coral diseases.

Fishes and other reef inhabitants that prey on corallivores represent potential biological controls that could be leveraged to facilitate restoration. For example, white grunts (*Haemulon plumierii*), a common Caribbean reef fish, readily consume adult *H carunculata* (Ladd and Shantz 2016), whereas the carnivorous deltoid rock snail (*Thais deltoidea*) preys on the corallivore *C abbreviata* (Sharp and Delgado 2015), which can also act as a vector for coral diseases (Williams and Miller 2005). Restoring corals in areas with abundant *H plumierii* or *T deltoidea* may therefore help to minimize the negative impacts of corallivore populations. Alternatively, deployment of structures that increase the recruitment or aggregation of fishes like *H plumierii* or actively seeding restoration areas with *T deltoidea* could help reduce the abundance of corallivores and the transmission of coral diseases in restored areas.

### ***Algal-farming fishes as context-dependent forces in coral restoration***

Processes that affect coral survivorship, and ultimately restoration efforts, may be context-dependent. For example, many damselfishes are territorial algal-gardeners that could promote or hinder restoration efforts, depending on geographic location and species-specific behavior (Figure 3). In the Caribbean, territorial damselfishes (eg *Stegastes planifrons*) destroy large amounts of live coral tissue to create algal gardens that are fiercely protected from larger herbivores (Rotjan and Lewis 2008). *S planifrons* can rapidly colonize colonies of *A cervicornis* outplanted for restoration, cause considerable partial colony mortality (Figure 3a; Schopmeyer and Lirman 2015), and may increase the prevalence of coral disease (Vermeij *et al.* 2015). Coral restoration efforts should therefore avoid areas with large damselfish populations. Furthermore, concentrating coral outplants in areas with high biomass of

piscivorous fishes may reduce the abundance of damselfishes and their negative impact on corals (Figure 3b).

Conversely, on Indo-Pacific reefs, territories of the dusky farmerfish (*Stegastes nigricans*), a common species of damselfish, can promote the survival and growth of rare corals that are otherwise rapidly consumed by corallivorous fishes (White and O'Donnell 2010). The corals within these territories are often fast-growing, branching species (eg *Acropora* spp) amenable for use in restoration (Figure 3c; White and O'Donnell 2010). Restoration efforts on reefs with abundant *S nigricans* and other, similar damselfish species may benefit if coral outplanting is focused within damselfish territories to facilitate the growth and recruitment of corals and act as nuclei of recovery. In areas with robust corallivore populations, in particular, the protection provided by farming damselfishes such as *S nigricans* may be crucial for the initial growth and establishment of outplanted corals (Figure 3d).

#### ***Fish-derived nutrients promote positive feedbacks for corals***

The structures created by living corals can aggregate fishes and concentrate fish-derived nutrients that increase coral growth (Holbrook *et al.* 2008). These fish-derived nutrient hotspots also increase grazing by herbivorous fishes and reduce algal abundance, both of which likely enhance coral growth and survivorship (Shantz *et al.* 2015). Moreover, many of the fishes that aggregate around structurally complex corals are invertivores, such as *H plumierii*, potentially increasing top-down control of coral predators (Ladd and Shantz 2016). Fish-derived nutrient hotspots appear to both facilitate the growth of existing corals and concentrate herbivory, such that the resultant benthic communities also promote coral health and recruitment.

These natural positive feedbacks on coral health may be important to capture in coral restoration designs, yet such processes and feedbacks are not typically part of coral restoration approaches (Tables 1 and 2). Fish-derived nutrient hotspots promote many of the processes central to reef recovery (eg herbivory, coral growth, habitat production, coral recruitment). Furthermore, many of the coral species commonly used for restoration (eg *Acropora* spp, *Pocillopora* spp) greatly benefit from fish-derived nutrients. Focusing coral outplanting at sites of existing fish aggregations, or capitalizing on positive density dependence of corals used for

restoration to maximize habitat production and facilitate the aggregation of fishes, could harness these beneficial feedbacks to facilitate coral reef recovery (Figure 2).

### ***Competition in the context of restoration***

Competition for limiting resources can drive population dynamics, community succession, and ecosystem function (Hillerislambers *et al.* 2012), particularly on coral reefs, where space is a highly contested resource (Chadwick and Morrow 2011). On many reefs worldwide, weedy, fast-growing species like sponges and soft corals are replacing reef-building corals (Norström *et al.* 2009) and slowing the growth and survivorship of remaining corals (Chadwick and Morrow 2011). Frequent and abundant competitive interactions can generate a series of negative feedbacks that may inhibit the regeneration of diverse, topographically complex coral reefs and impede restoration efforts.

Understanding competitive interactions among corals used for restoration and their benthic competitors could assist in restoration site selection, as practitioners are clearly interested in avoiding benthic competitors when outplanting corals (Table 2). To date, however, no studies have examined the effects of competition on coral restoration (Table 1), making this area ripe for new research (WebTable 1). Within sites, outplanting corals in such a way as to avoid superior competitors represents a relatively simple method for improving coral growth and survival. On Caribbean reefs, the encrusting gorgonian *Erythropodium caribaeorum* and the zoanthid *Palythoa caribaeorum* are two aggressive, fast-growing species that can kill or suppress the growth of *A cervicornis* (Karlson 1980; Suchanek and Green 1981). Removing these competitors when outplanting *A cervicornis* or targeting outplants to areas with a low abundance of these competitors could reduce or eliminate one factor working against restoration efforts.

### **Conclusions**

Translating ecological theory into realistic approaches for conservation practitioners is one of the most challenging aspects of ecological restoration (Figure 2). Promoting positive density-dependent processes to facilitate restoration is a fundamental component of terrestrial and aquatic restoration planning (Halpern *et al.* 2007). For example, outplanting terrestrial grasses in high densities can promote pollination, increase seed set, and hasten the recovery of

grassland ecosystems (Morgan and Scacco 2006), and outplanting saltmarsh plants in high densities can reduce abiotic stress, increase biomass production, and initiate facilitation cascades (Silliman *et al.* 2015). On coral reefs, the density of outplanted corals is a basic element of restoration planning that may drive many of the ecological processes that ultimately determine restoration success (Figure 2). For example, outplanting *A cervicornis* at moderate densities can promote positive density dependence, maximize habitat production, and minimize the spread of coral diseases and coral mortality (Ladd *et al.* 2016).

However, we lack fundamental knowledge about the mechanisms that drive density dependence, as well as the abiotic and biological contexts that mediate the strength and direction of density dependence. Although many restoration practitioners currently consider density in their restoration design (Table 2), the fact that targeted coral densities varied by more than two orders of magnitude (0.1–25 corals m<sup>-2</sup>) highlights the need for a better understanding of the mechanics of density dependence among corals to optimize restoration efforts. One such approach would be to determine whether disease transmission drives negative density dependence in high-density outplants. If this mechanism were confirmed, genotypes resistant to disease (Vollmer and Kline 2008) might facilitate successful outplanting at higher densities to hasten habitat production without increased risk of disease transmission. The potentially key role of density in restoration success underscores the need for further work to understand patterns and drivers of density dependence in species used for coral restoration.

Corals vary widely in basic traits that influence population and community structures, such as growth rates, reproductive outputs, and symbiont identities, which differ among species, populations, and individuals within a population (Madin *et al.* 2016). For example, there is substantial variability among genotypes for such traits as growth and branching rates. For coral restoration, more information about important traits of corals used for restoration would allow restoration practitioners to select species and genotypes best suited for specific restoration sites (Elliot *et al.* 2003). For example, at sites frequently impacted by thermal stress, preferentially selecting corals outplanted for restoration based on genotypes known to exhibit high thermal tolerance could better prepare the site for future thermal anomalies (Ladd *et al.* 2017). Likewise, matching coral traits with prevailing environmental conditions at a restoration site could maximize the chances of survival, thereby improving restoration effectiveness and efficiency. However, there remains a paucity of data on inter- and

intraspecific differences in many traits relevant to coral restoration, and especially their potential ecological trade-offs. Collecting information about these traits is time-consuming and expensive, but the ability to make trait-based selections of corals informed by data, while maintaining overall genotypic diversity, would provide restoration practitioners with a valuable tool for increasing restoration efficacy.

Considerable progress has been made in the field of coral restoration over the past decade, but many important questions remain, hindering our ability to restore these key foundation species (WebTable 1). As coral populations continue to decline worldwide, it is urgent that these questions be addressed, although this will not be enough to ensure the persistence of corals and coral reefs. Testing and refining innovative, non-traditional approaches to restoring corals, such as harnessing important ecological processes, is an important next step for advancing the field of coral restoration ecology. We must also make progress in reducing local sources of coral mortality, such as pollution and sedimentation, as well as in reducing carbon emissions to slow future climate change. Without the dual efforts of coral restoration and stress mitigation, corals and coral reefs face a dire future.

### **Acknowledgements**

We thank the Florida Fish and Wildlife Conservation Commission (FWC) and the US Fish and Wildlife Service (USFWS) State Wildlife Grants Program for funding a series of workshops to identify many of the research needs for coral reef ecosystem restoration reviewed in this article (State Wildlife Grant Award F13AF01085). We thank A Bourque, E McDevitt, T Moore, J Walczak, and A Whittle, who, along with the authors, served on the steering committee for the workshop and A Acosta, T Adam, A Baker, W Fitt, I Enochs, K Erickson, C Frankenfeld, D Gilliam, A Johnson, J Landsberg, E Larson, E Lipp, D Lirman, M Matz, K Maxwell, E Muller, J Parkinson, V Paul, E Peters, B Reckenbeil, R Ruzicka, S Schopmeyer, L Toth, S Vollmer, and C Woodley for their participation in the workshop. Special thanks to M Truglio of FWC's Wildlife Legacy Initiative.

### **References**

Baums IB, Miller MW, and Szmant AM. 2003. Ecology of a corallivorous gastropod, *Coralliophila abbreviata*, on two scleractinian hosts. I: Population structure of snails and

- corals. *Mar Biol* **142**: 1083–91.
- Bosire JO, Dahdouh-Guebas F, Walton M, *et al.* 2008. Functionality of restored mangroves: a review. *Aquat Bot* **89**: 251–59.
- Bruno JF, Stachowicz JJ, and Bertness MD. 2003. Inclusion of facilitation into ecological theory. *Trends Ecol Evol* **18**: 119–25.
- Bruno JF and Selig ER. 2007. Regional decline of coral cover in the Indo-Pacific: timing, extent, and subregional comparisons. *PLoS ONE* **8**: e711.
- Burkpile DE. 2012. Context-dependent corallivory by parrotfishes in a Caribbean reef ecosystem. *Coral Reefs* **31**: 111–20.
- Carpenter RC and Edmunds PJ. 2006. Local and regional scale recovery of *Diadema* promotes recruitment of scleractinian corals. *Ecol Lett* **9**: 271–80.
- Chadwick NE and Morrow KM. 2011. Competition among sessile organisms on coral reefs. In: Dubinsky Z and Stambler N (Eds). *Coral reefs: an ecosystem in transition*. Dordrecht, the Netherlands: Springer.
- Cabaitan PC, Yap HT, and Gomez ED. 2015. Performance of single versus mixed coral species for transplantation to restore degraded reefs. *Restor Ecol* **23**: 1–8.
- De'ath G, Fabricius KE, Sweatman H, and Puotinen M. 2012. The 27-year decline of coral cover on the Great Barrier Reef and its causes. *P Natl Acad Sci USA* **109**: 17995–99.
- Derksen-Hooijberg M, Angelini C, Lamers LPM, *et al.* 2017. Mutualistic interactions amplify saltmarsh restoration success. *J Appl Ecol* **55**: 1–10.
- Dixson DL, Abrego D, and Hay ME. 2014. Chemically mediated behavior of recruiting corals and fishes: a tipping point that may limit reef recovery. *Science* **345**: 892–97.
- Elliott S, Navakitbumrung P, Kuarak C, *et al.* 2003. Selecting framework tree species for restoring seasonally dry tropical forests in northern Thailand based on field performance. *Forest Ecol Manag* **184**: 177–91.
- Ferrario F, Beck MW, Storlazzi CD, *et al.* 2014. The effectiveness of coral reefs for coastal hazard risk reduction and adaptation. *Nat Commun* **5**: 3794.
- Graham NAJ, Jennings S, MacNeil MA, *et al.* 2015. Predicting climate-driven regime shifts versus rebound potential in coral reefs. *Nature* **518**: 1–17.
- Graham NAJ, Wilson SK, Jennings S, *et al.* 2007. Lag effects in the impacts of mass coral bleaching on coral reef fish, fisheries, and ecosystems. *Conserv Biol* **21**: 1291–300.

- Halpern B, Silliman B, Olden J, *et al.* 2007. Incorporating positive interactions in aquatic restoration and conservation. *Front Ecol Environ* **5**: 153–60.
- Hillerislambers J, Adler PB, Harpole WS, *et al.* 2012. Rethinking community assembly through the lens of coexistence theory. *Annu Rev Ecol Evol S* **43**: 227–48.
- Holbrook SJ, Brooks AJ, Schmitt RJ, and Stewart HL. 2008. Effects of sheltering fish on growth of their host corals. *Mar Biol* **155**: 521–30.
- Holbrook SJ, Schmitt RJ, Adam TC, and Brooks AJ. 2016. Coral reef resilience, tipping points and the strength of herbivory. *Sci Rep-UK* **6**: 35817.
- Holl KD. 2017. Restoring tropical forests from the bottom up. *Science* **355**: 455–56.
- Hughes TP, Kerry J, Álvarez-Noriega M, *et al.* 2017. Global warming and recurrent mass bleaching of corals. *Nature* **543**: 373–77.
- Jackson JBC, Donovan MK, Cramer KL, and Lam W. 2014. Status and trends of Caribbean coral reefs: 1970–2012. Gland, Switzerland: IUCN.
- Johnston L and Miller MW. 2014. Negative indirect effects of neighbors on imperiled scleractinian corals. *Coral Reefs* **33**: 1047–56.
- Karlson R. 1980. Alternative competitive strategies in a periodically disturbed habitat. *B Mar Sci* **30**: 894–900.
- Kuffner IB and Toth LT. 2016. A geological perspective on the degradation and conservation of western Atlantic coral reefs. *Conserv Biol* **30**: 706–15.
- Ladd MC and Shantz AA. 2016. Novel enemies – previously unknown predators of the bearded fireworm. *Front Ecol Environ* **14**: 342–43.
- Ladd MC, Shantz AA, Nedimyer K, and Burkepile DE. 2016. Density dependence drives habitat production and survivorship of *Acropora cervicornis* used for restoration on a Caribbean coral reef. *Front Mar Sci* **3**: 1–14.
- Ladd MC, Shantz AA, Bartels E, and Burkepile DE. 2017. Thermal stress reveals a genotype-specific tradeoff between growth and tissue loss in restored *Acropora cervicornis*. *Mar Ecol-Prog Ser* **572**: 129–39.
- Lirman D and Schopmeyer S. 2016. Ecological solutions to reef degradation: optimizing coral reef restoration in the Caribbean and western Atlantic. *PeerJ* **4**: e2597.
- Maciá S, Robinson MP, and Nalevanko A. 2007. Experimental dispersal of recovering *Diadema antillarum* increases grazing intensity and reduces macroalgal abundance on a

- coral reef. *Mar Ecol-Prog Ser* **348**: 173–82.
- Madin JS, Hoogenboom MO, Connolly SR, *et al.* 2016. A trait-based approach to advance coral reef science. *Trends Ecol Evol* **31**: 419–28.
- McClanahan TR, Kamukuru AT, Muthiga NA, *et al.* 1996. Effect of sea urchin reductions on algae, coral, and fish populations. *Conserv Biol* **10**: 136–54.
- Miller MW and Hay ME. 1998. Effects of fish predation and seaweed competition on the survival and growth of corals. *Oecologia* **113**: 231–38.
- Miller MW, Marmet C, Cameron CM, and Williams DE. 2014. Prevalence, consequences, and mitigation of fireworm predation on endangered staghorn coral. *Mar Ecol-Prog Ser* **13**: 226–27.
- Moberg F and Folke C. 1999. Ecological goods and services of coral reef ecosystems. *Ecol Econ* **29**: 215–33.
- Morgan JW and Scacco PJ. 2006. Planting designs in ecological restoration: insights from the button wrinklewort. *Ecol Manag Restor* **7**: 51–54.
- Mumby PJ and Steneck RS. 2008. Coral reef management and conservation in light of rapidly evolving ecological paradigms. *Trends Ecol Evol* **23**: 555–63.
- Norström A, Nyström M, Lokrantz J, and Folke C. 2009. Alternative states on coral reefs: beyond coral–macroalgal phase shifts. *Mar Ecol-Prog Ser* **376**: 295–306.
- Obolski U, Hadany L, and Abelson A. 2016. Potential contribution of fish restocking to the recovery of deteriorated coral reefs: an alternative restoration method? *PeerJ* **4**: e1732.
- Palmer AP, Ambrose RF, and Poff NL. 1997. Ecological theory and community restoration ecology. *Restor Ecol* **5**: 291–300.
- Precht WF, Gintert BE, Robbart ML, *et al.* 2016. Unprecedented disease-related coral mortality in southeastern Florida. *Sci Rep-UK* **6**: 31374.
- Reaka-Kudla ML. 2005. Biodiversity of Caribbean coral reefs. Lancaster, PA: DesTech Publications.
- Reynolds LK, Waycott M, and McGlathery KJ. 2013. Restoration recovers population structure and landscape genetic connectivity in a dispersal-limited ecosystem. *J Ecol* **101**: 1288–97.
- Rotjan R and Lewis S. 2008. Impact of coral predators on tropical reefs. *Mar Ecol-Prog Ser* **367**: 73–91.



- Sandin SA and McNamara DE. 2012. Spatial dynamics of benthic competition on coral reefs. *Oecologia* **168**: 1079–90.
- Schopmeyer SA and Lirman D. 2015. Occupation dynamics and impacts of damselfish territoriality on recovering populations of the threatened staghorn coral, *Acropora cervicornis*. *PLoS ONE* **10**: e1041302.
- Shantz AA, Ladd MC, Shrack E, and Burkepile DE. 2015. Fish-derived nutrient hotspots shape coral reef benthic communities. *Ecol Appl* **25**: 2142–52.
- Shaver EC and Silliman B. 2017. Time to cash in on positive interactions for coral restoration. *PeerJ* **5**: e3499.
- Sharp WC and Delgado GA. 2015. Predator–prey interactions between the corallivorous snail *Coralliophila abbreviata* and the carnivorous deltoid rock snail *Thais deltoidea*. *Biol Bull* **229**: 129–33.
- Silliman BR, Schrack E, He Q, *et al.* 2015. Facilitation shifts paradigms and can amplify coastal restoration efforts. *P Natl Acad Sci USA* **112**: 14295–300.
- Suchanek T and Green D. 1981. Interspecific competition between *Palythoa caribaeorum* and other sessile invertebrates on St Croix reefs, US Virgin Islands. *Proc 4th Int Coral Reef Symp* **2**: 679–84.
- Suding KN, Gross KL, and Houseman GR. 2004. Alternative states and positive feedbacks in restoration ecology. *Trends Ecol Evol* **19**: 46–53.
- Sussman M, Loya Y, Fine M, and Rosenberg E. 2003. The marine fireworm *Hermodice carunculata* is a winter reservoir and spring–summer vector for the coral-bleaching pathogen *Vibrio shiloi*. *Environ Microbiol* **5**: 250–55.
- Vermeij M, DeBey H, Grimsditch G, *et al.* 2015. Negative effects of gardening damselfish *Stegastes planifrons* on coral health depend on predator abundance. *Mar Ecol-Prog Ser* **528**: 289–96.
- Vollmer SV and Kline DI. 2008. Natural disease resistance in threatened staghorn corals. *PLoS ONE* **3**: e3718.
- Werner CM, Vaughn KJ, Stuble KL, *et al.* 2016. Persistent asymmetrical priority effects in a California grassland restoration experiment. *Ecol Appl* **6**: 1624–32.
- White J-SS and O’Donnell JL. 2010. Indirect effects of a key ecosystem engineer alter survival and growth of foundation coral species. *Ecology* **91**: 3538–48.

- Williams DE and Miller MW. 2005. Coral disease outbreak: pattern, prevalence and transmission in *Acropora cervicornis*. *Mar Ecol-Prog Ser* **301**: 119–28.
- Williams DE, Miller MW, Bright AJ, and Cameron CM. 2014. Removal of corallivorous snails as a proactive tool for the conservation of acroporid corals. *PeerJ* **2**: e680.
- Williams ID, Polunin NVC, and Hendrick VJ. 2001. Limits to grazing by herbivorous fishes and the impact of low coral cover on macroalgal abundance on a coral reef in Belize. *Mar Ecol-Prog Ser* **222**: 187–96.
- Wolf AT and Nugues MM. 2013. Synergistic effects of algal overgrowth and corallivory on Caribbean reef-building corals. *Ecology* **94**: 1667–74.
- Young C, Schopmeyer S, and Lirman D. 2012. A review of reef restoration and coral propagation using the threatened genus *Acropora* in the Caribbean and western Atlantic. *B Mar Sci* **88**: 1075–98.
- Zaneveld JR, Burkepile DE, Shantz AA, *et al.* 2016. Overfishing and nutrient pollution interact with temperature to disrupt coral reefs down to microbial scales. *Nat Commun* **7**: 11833.

### Supporting Information

Additional, web-only material may be found in the online version of this article at

### Figure captions

**Figure 1.** Examples of coral restoration efforts in the Caribbean and western Atlantic. (a) Corals outplanted on a degraded reef in Puerto Rico; (b) juvenile blue tang (*Acanthurus coeruleus*) sheltering within restored *Acropora cervicornis* colonies; (c) a restored *A cervicornis* colony exhibiting signs of rapid tissue loss; (d) coral nursery in the Florida Keys.

### Photo credit:

(a) S Griffin, NOAA

**Figure 2.** Recovery of corals on a degraded reef can be facilitated by positive feedbacks (center left; modified from Mumby and Steneck 2008). If restoration can promote these feedback mechanisms, the likelihood for coral recovery increases. Simultaneously, negative feedbacks also can inhibit recovery (center right). However, restoration can be designed to

*impinge on these negative mechanisms to disrupt these feedbacks and initiate recovery. Thus, promoting positive feedbacks, or reducing negative ones, can lower the threshold required to push a reef from a degraded state toward recovery (center) For example, areas of existing aggregations of fishes could be selected within a site to outplant corals and capitalize on rapid nutrient cycling to promote coral growth (top left). Similarly, outplanting corals to areas with abundant herbivorous urchins may reduce algal competition and promote coral growth (bottom left). The density of outplanted corals can be tailored to minimize competition, minimize coral mortality, and maximize habitat production (top right). Mixed-species outplanting could benefit restoration by decreasing the amount of grazable substrate available, effectively intensifying herbivory in remaining areas (bottom right).*

**Figure 3.** *Context-dependent nature of damselfishes in coral reef restoration. (a) Algal garden created by threespot damselfish (*Stegastes planifrons*) on restored *Acropora cervicornis* colonies in the Florida Keys. (b) In the Caribbean, coral reef restoration efforts would likely benefit from the selection of sites with a high biomass of piscivores to reduce the abundance of damselfish and their negative impacts on corals. (c) Extensive *Acropora* spp thicket within dusky farmerfish (*Stegastes nigricans*) territories on a patch reef in Moorea, French Polynesia. (d) On reefs in the Indo-Pacific, coral restoration efforts may benefit from targeting areas with a high abundance of territorial damselfishes to reduce predation on corals from roving corallivorous fishes.*

**Photo credits:**

(a) S Schopmeyer, U Miami RSMAS

(c) B Banka, UC Santa Barbara

**Table 1. Number of peer-reviewed articles published on coral restoration and coral reef restoration (1987–2017) broken down by the general topic addressed in each study**

<i>General topic</i>	<i>Specific topic</i>	<i>Number of publications</i>
Nursery studies <i>n</i> = 45; 39%	Propagation	34
	Growth and survivorship	30
	Genotype traits	10
	Species traits	9
	Site characteristics/effects	5
	Nursery maintenance	3
Outplant studies <i>n</i> = 70; 60%	Attachment method/substrate	23
	Outplant survivorship	58
	Outplant growth	35
	Genotype traits	10
	Species traits	8
Restoration design studies <i>n</i> = 14; 12%	Density	7
	Genotypic diversity	1
	Mixed-species assemblages	5
	Removing macroalgae	1
Studies in which an ecological process was tested or measured <i>n</i> = 22; 19%	Recruitment/reproduction	6
	Succession	6
	Predation	5
	Herbivory	3
	Fish-derived nutrients	2

	Disease	1
	Competition	0

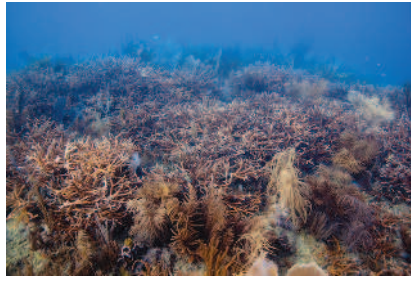
**Notes:** Publications were categorized by general topic and then reviewed for the specific topics addressed within each study. Some publications were included in multiple general topics. Percentages represent the percent of publications under a general topic out of the 116 publications reviewed. Search criteria, references for included publications, and category descriptions are presented in WebPanel 1.

Author Manuscript

**Table 2. Rankings given by restoration practitioners to criteria considered when selecting reefs at which to conduct coral outplantings (among reefs) and placement of corals at sites within a reef**

<i>Rank</i>	<i>Criteria for selecting among reef locations</i>	<i>Criteria for selecting sites within a reef</i>
1	Existing coral cover	Outplant on best available substrate
2	Available clean substrate	Avoid potential benthic competitors
3	Water depth	Outplant near herbivores
4	Presence of potential benthic competitors	Ensure corals are distributed throughout restoration site
5	Presence of herbivorous fishes	Outplant close to any existing coral
6	Abundance of coral predators	Avoid coral predators such as corallivorous snails
7	Level of human visitation	Outplant near fish aggregations
8	Presence of algal-farming damselfish	Outplant far from existing coral

**Notes:** Results are from a survey of coral restoration practitioners ( $n = 21$ ) representing 13 affiliations conducting coral restoration operations in 17 different countries and territories in the Caribbean region.

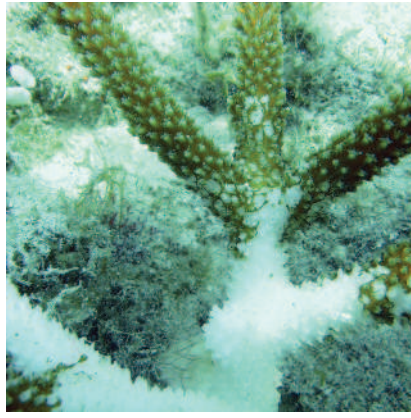


fee\_1792\_f1a.tif



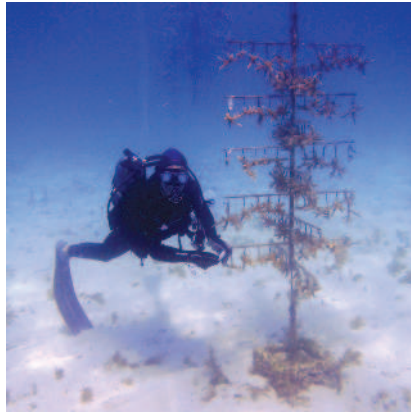
fee\_1792\_f1b.tif



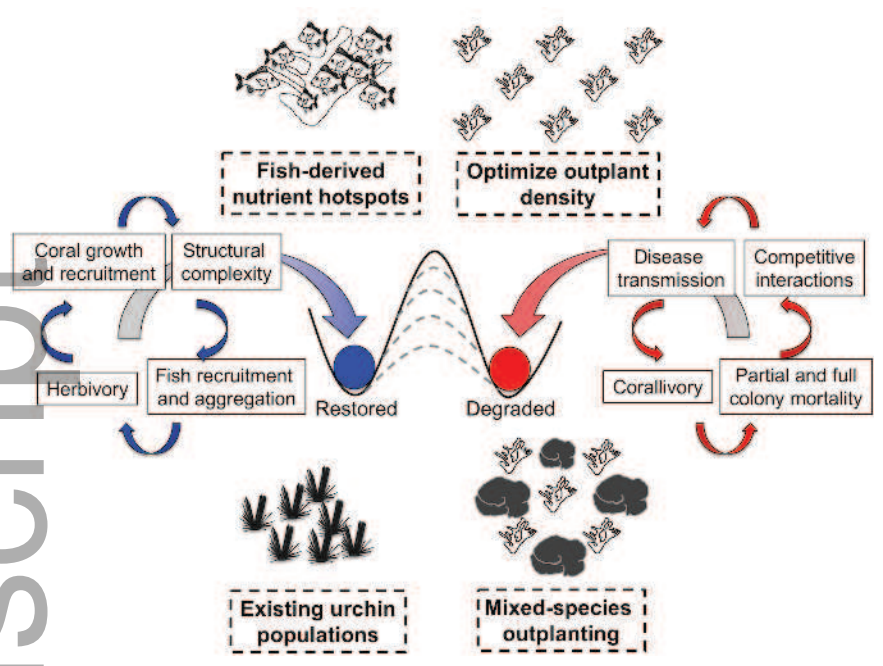


fee\_1792\_f1c.tif

# Author Manuscript



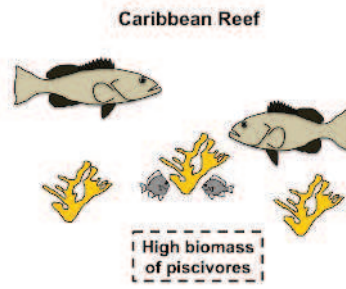
fee\_1792\_f1d.tif



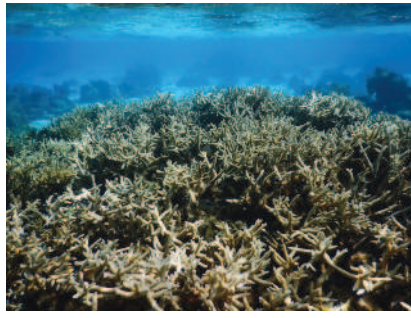
fee\_1792\_f2.tif



fee\_1792\_f3a.tif

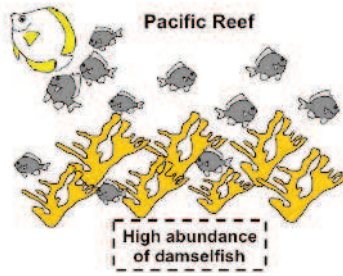


fee\_1792\_f3b.tif



fee\_1792\_f3c.tif

# Author Manuscript



fee\_1792\_f3d.tif