RESTORING CORAL REEFS:

AN EXAMINATION OF METHODOLOGIES IN USE

WORLDWIDE

by

ERIN PARKER

A THESIS

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Abstract – Corals reefs are one of the most biodiverse ecosystems on the planet and they provide vitally important habitat for a host of marine species. They also provide humans with many goods and services. These ecosystems are in rapid decline worldwide due to the combined effects of many anthropogenic stressors ranging from global climate change to more local factors like pollution and overfishing. In response, methods of active reef restoration by direct human intervention began to appear, and over the past three decades the field of reef restoration has grown rapidly to include a wide variety of methods and dozens of species of corals. While restoration is now generally accepted as a viable means of restoring the biodiversity and ecosystem function of coral reefs, it is a relatively new field that is still developing. Many restoration efforts are not set up in ways that are conducive to being written up as formal studies. Consequently, they typically lack rigor and critical evaluation of their effectiveness which hinders attempts to critically compare the efficacy of various methods. Several reviews and meta-analyses of reef restoration methodologies have already been conducted, yet most of these studies do not directly compare quantitative and qualitative data of methods and the results those methods produce. This thesis

assesses the breadth of restoration methods in use and compares them in terms of how they affect survival of corals. My thesis also includes qualitative information on other factors that influence the success of restoration efforts. I used both graphical and statistical methods to analyze survivorship data. Data on growth were not amenable to quantitative analysis due to the disparity of growth metrics. My investigation provides substantial evidence for the need to tailor restoration methods to the species. I also identify several shortcomings in how restoration studies report their data and I use these findings to propose necessary components of a standardized framework for reporting. Standardization will allow future meta-analyses of reef restoration to assess what methods are likely to produce the highest success rate for a given restoration site and species. Standardization of reporting is critical to the future of the field so that techniques may be improved, thereby maximizing the impact that restoration efforts make toward rehabilitating the biodiversity and ecosystem function of a degraded reef ecosystem.

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Introduction

Coral reefs cover less than one-tenth of 1% of the ocean floor yet support 25% of all marine life (Spalding et al. 2001). They are critical habitat for one-third of all marine fish including commercially valuable species during at least some part of their life cycle. Along with rainforests, these vibrant habitats are one of the most biodiverse habitats on Earth (Reaka-Kudla 1996). Due to anthropogenic disturbances including ocean warming and acidification, reefs worldwide are bleaching and dying at unprecedented rates. Between the early 1980s and early 2000s, live coral cover on reefs has decreased by an average of more than 20% in the Indo-Pacific and 80% in the Caribbean with little regional variation (Gardner et al. 2003; Bruno and Selig 2007). Declines have continued since, with some coral species now listed as endangered (Quinn and Kojis 2006). The field of coral reef restoration has grown rapidly in the past three decades. Currently, attempts to prevent further destruction of coral reef habitat include forming marine protected areas (MPAs) around reefs and active restoration of reefs by a variety of methods, many of which involve transplanting pieces of coral to degraded reef sites. My research compares these varied methods based on the quantitative and qualitative findings of the available literature. In doing so, I identify strengths and weaknesses present in the field as a whole.

The traditional method of conservation through MPAs has been referred to as a 'passive' means of counteracting reef degradation because they operate on the assumption that an area will be able to recover by natural processes with little to no human intervention if damaging factors like overfishing are removed from the system (Rinkevich 2008). This is contrasted with 'active' restoration where humans directly

intercede to aid in the recovery of a degraded reef. The Society for Ecological Restoration International Science and Policy Working Group defines ecological restoration as the process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed (SER 2004). There is an emerging consensus that traditional methods of preserving reef habitats through management and MPAs alone are not capable of restoring degraded ecosystems. While they may promote recovery by eliminating fishing and other destructive practices (Edgar et al. 2007), their effectiveness is often compromised by factors such as poor regulation and the tendency of organisms and pollutants to move without regard to human-delineated boundaries. Establishing MPAs does not address the issues of ocean warming and acidification, both of which have devastating effects on corals (Rinkevich 1995; Yap 2000; Parnell 2005, Sale 2008). MPAs have been criticized for only slowing the rate of reef degradation (Rinkevich 1995; Rinkevich 2008). The limitations of MPAs have contributed to the increasing popularity and implementation of active restoration methods for improving the health of reef environments, and past efforts have shown that it is feasible (Yap 2000).

Some of the earliest coral transplantation experiments were performed in the mid-1960s (Shinn 1966), as part of a study examining coral biology, and not for developing restoration methodologies. Transplantation aimed at restoring reefs degraded by anthropogenic activity appears to have begun in the late 1970s and early 1980s (Birkeland et al. 1979; Kojis and Quinn 1981; Alacala 1982) and the health of coral reefs did not become a concern of international political agendas until the late 1980s (Veron 2000). Early efforts were aimed at counteracting localized damage (from

fishing, factory effluent pollution, ship groundings, etc.) rather than the global threats of ocean warming and acidification. Restoration initially required designing and building large, complex engineering projects meant to reproduce the three-dimensional structure of the reef, which would otherwise take centuries to regrow naturally, yet the scope of such projects meant they still took several years to complete (Lirman and Schopmeyer 2016). In the last two decades, restoration efforts have expanded to include a wide variety of methods involving dozens of species of corals all over the world and both the cost and feasibility of these efforts have greatly improved as methods have evolved. One method in particular, referred to as "gardening the reef" (Rinkevich 1995) involves a two-step process where fragments of coral colonies (or frags) harvested from healthy reefs are reared in an *in situ* nursery before being outplanted to degraded reef sites. These nurseries also provide new sources for frags and act as sources of larvae (larval dispersion hubs) (Shafir 2006a; Horoszowski-Fridman 2011).

Reef restoration still has some shortcomings. The lack of critical analysis of the long-term, ecosystem-level effectiveness of restoration has been widely criticized (reviewed in Hein et al. 2017). Experimental studies typically only assess the success of restoration efforts by measures of the growth and survivorship of transplanted corals. Some argue against active restoration, stating that it is no substitute for preserving original habitat and that the success of active restoration intervention is difficult to determine due to insufficient monitoring (Gomez and Edwards 2007). Indeed, it is evident that restoration cannot be effective for some species until the global stressors of ocean warming and acidification are resolved (Garrison 2008; Cruz 2015). Additionally, because local stressors like overfishing and tourism directly damage reefs while also

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making them more susceptible to stressors from global climate changes (Knowlton and Jackson 2008), properly implemented and managed MPAs are a necessary aspect of reef protection. However, in many cases reefs are not capable of recovering sufficiently without active human intervention to replace some of what was lost (Goreau and Hilbertz 1996; Rinkevich 2008, 2014).

While active restoration of coral reefs is now considered a viable option for restoring some of the biodiversity and ecosystem function of coral reefs (Rinkevich 2005; Benayas et al. 2009), the field is still very young. There is a great deal of variation in methods and species used. The newness of the field also means that there are comparatively few published studies of restoration projects. For this reason, some reviews of reef restoration have mined information from websites, though I chose not to do so in this paper. While websites for organized restoration efforts such as the Coral Restoration Foundation (CRF) provide ample information on their methods, they often lack detailed data on response variables with which to quantify the success of their efforts. Additionally, many restoration efforts are not set up as formal studies for publication, and typically lack rigor and critical evaluation of their effectiveness (Hein et al. 2017). While several reviews and meta-analyses of reef restoration methodologies have already been conducted (Rinkevich 2005; Yeemin et al. 2006; Chou et al. 2009; Young et al. 2012), most of these studies do not directly compare quantitative and qualitative data of methods and the results those methods produce or are regionally limited in scope.

Because of the rapid expansion of this field of study and limitations of earlier reviews, I have critically examined reef restoration methods in current use worldwide. I compared different methods in terms of how they affect the survival of corals, as this is one of the most commonly used indicators of restoration success (Hein et al. 2017; this study). I do so by asking several supporting questions: (1) Are some methodologies (outplanting or nurseries) more effective than others in terms of producing high survivorships? (2) Does the method of attaching coral transplants to the reef site affect survivorship? (3) Does rearing frags in a nursery prior to outplanting impact survivorship relative to frags and/or colonies that are outplanted without a nursery phase? (4) Do some species experience overall higher success rates than others? (5) Within a species, do different methodologies have an effect on survivorship? To answer these questions, I propose the following hypotheses: (1) Some methodologies for nurseries and for outplanting will produce higher survivorships than others. (2) Method of attachment is a significant factor in the survivorship of frags, both in nurseries and transplantation sites. (3) Rearing frags in a nursery prior to outplanting has a significant positive effect on the survivorship of frags. I also examine and report on the qualitative data, and I identify trends, gaps, and shortcomings in the existing research. My ultimate goal with this paper is to provide a comprehensive understanding of current restoration efforts and use it to provide suggestions for advancing the field in the future.

Background

Coral Biology

Scleractinian corals first appeared in the fossil record about 240 million years ago and have evolved into their modern reef building forms over the last 60-70 million years (Wood 1999). Today coral reefs are one of the most biodiverse and productive ecosystems on the planet, rivaling that of tropical rain forests (Turgeon 2002, Sale 2008). Reefs are the largest biogenic structures on earth, the most well-known example of which is the Great Barrier Reef (GBR) which is vast enough to be visible from space (NOAA 2014). A single reef is composed of many hundreds to many millions of colonies of polyps. A new colony is initiated when a coral planula larva settles out of the plankton onto hard substratum and begins to bud into polyps. An individual polyp is very small, typically ~1-3mm in diameter, but a single mature colony may consist of thousands to hundreds of thousands of physiologically linked individuals, and some species may grow the be size of a small car (NOAA 2014). The "true" corals or scleractinian corals (sclero- meaning "hard") compose the largest order (Scleractinia, ~1400 species) in the class Anthozoa. Scleractinian corals secrete calcium carbonate exoskeletons, and it is their skeletons together with coralline algae, sponges, and calcium carbonate precipitation (cementation) which create the hard foundation and physical structure of the reef. Reef building (hermatypic) corals provide the primary structural foundation of a reef. As corals die, their calcium carbonate skeletons contribute to the underlying foundation of the reef and gaps between corals are filled in by reef rubble, sediment, and other debris (Collins 2011). The reef foundation is further

cemented together by coralline algae and by invertebrates like shelled mollusks, tube dwelling polychaetes, bryozoans, and sponges (Veron 2000). Hermatypic corals may contribute as much as 75% of the CaCO₃ budget of modern reefs through building their skeletons (Cantin et al. 2010)

Corals come in a wide variety of growth forms that are typically grouped into five major categories (Veron 2000). Corals may be *massive* (solid and similar in shape in all dimensions), *encrusting* (adheres to the substrate), *branching* (forms branches and usually arborescent or tree-like), *columnar* (forming columns), or *laminar* (plate-like). Nearly all coral growth forms can reproduce by asexual fragmentation in addition to sexual reproduction (Highsmith 1982).

While the kinds of corals are many and diverse, they all share a few basic features. Each polyp has a large central gastrovascular cavity for digesting food with a single opening at the top (referred to as the mouth) for both ingesting food and expelling waste. The mouth is ringed by rows of tentacles loaded with stinging cells called nematocytes which capture prey and act as the polyp's primary defense mechanism. The tissues of each polyp are comprised of three layers; an outer ectodermis, an inner gastrodermis which lines the gastrovascular cavity, and a middle layer called the mesoglea (Veron 2000). Hermatypic corals also have vital relationships with photosynthetic algae called zooxanthellae. These modified dinoflagellates live intracellularly in the gastrodermis of the coral at concentrations of ~1–5 million cells per square centimeter and provides its host with the products of photosynthesis, such as the sugars glucose and glycerol, fatty acids, lipids, and amino acids. Zooxanthellae give up to 90% of their photosynthetic product to their host, allowing corals to grow in the

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oligotrophic waters of the tropics (Veron 2000). In return, the zooxanthellae have access to carbon dioxide and nitrogenous compounds that are produced as metabolic waste by their host and that are essential for the alga to photosynthesize and grow. They also gain protection from herbivores and are provided with a place to live that is stable yet exposed to sunlight (Veron 2000; Berkelmans and van Oppen 2006). Although corals are carnivores, they rely heavily on their zooxanthellae for nutrition. Calcification rates are up to two times higher on sunny days than on cloudy days and this difference is attributed to the zooxanthellae, though the physiological mechanism by which they influence growth is not confirmed (NOAA 2014). Because of their partnership with the zooxanthellae, hermatypic corals are usually only found in the clear, oligotrophic waters of the tropics within the euphotic zone, as these conditions allow the zooxanthellae to receive ample sunlight for photosynthesis. Corals and their symbionts also require warm water; they do best in temperatures of 23°- 29°C but can survive at temperatures as low as 18°C and as high as 40°C for short time periods. Because of this, coral reefs are usually only found in a belt around the equator between 30° north and 30° south (Figure 1).

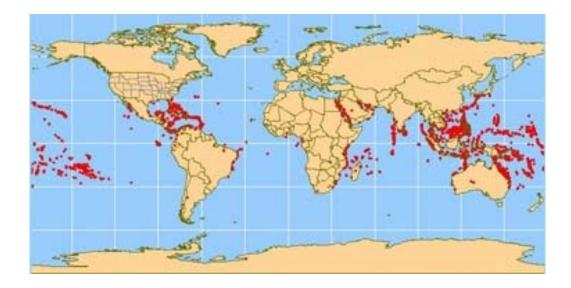


Figure 1. Major coral reef sites Major coral reef sites are seen as red dots on this world map. Most of the reefs, with a few exceptions, are found in tropical and semitropical waters between 30° north and 30° south latitudes. Figure from the National Oceanic and Atmospheric Administration Coral Reef Information System, 2014.

Why We Need Reefs and the Threats They Face

Coral reefs provide humans with food, drugs, protection from waves, and other services (Goreau and Trench 2013; Jompa et al. 2013). One of the most easily visible services that coral reefs provide to coastal human populations is protection of shorelines from both normal wave action and larger waves generated by storms. Reefs are a far more effective wave barrier than any human made sea wall. They provide "soft shore protection"; their permeable, open structure dissipates wave energy as the water passes through the corals, refracting the wave instead of reflecting it (Goreau et al. 2013). This means that by the time the waves reach the shore, they are much less forceful and can deposit sand rather than erode it. Healthy reefs effectively dissipate the energy of even large ocean swells and if they are broken by heavy storm waves, they grow back on their own without needing repair (Goreau et al. 2013). When a reef dies or coral cover is reduced, rates of bioerosion of the reef exceed accretion and so its ability to dissipate the force of waves is greatly reduced, allowing heavier wave action to fall on sandy beaches. Many beaches worldwide are shrinking due to the decreased protection from their deteriorating barrier reefs, as well as rising sea levels and sand mining (Goreau et al. 2013). Beaches in tropical areas face an additional threat; as reefs disappear, they contribute less new beach sand while wave action falling on the beach increases simultaneously as the protective barrier reef shrinks, both of which contribute to increased coastal erosion. (Goreau and Hilberts 1996).

Anthropogenic impacts are the cause of severe declines observed in coral reef habitats in recent decades. Human-caused climate change is producing rising sea levels and ocean temperatures, which in turn causes these ecosystems to decline. (Goreau and Trench 2013). Severe reef degradation is also occurring due to more localized threats, such as destructive fishing practices that use dynamite and cyanide on the reef, overfishing to supply both food and the aquarium trade, coral mining, elevated nutrient runoff, pollution, sedimentation, and direct physical damage from boats, anchors, tourists, and coral diseases. The combination of so many threats has led to rapid declines in coral populations (Gardner et al. 2003; Bruno and Selig 2007). Corals in the Indo-Pacific have also been devasted by outbreaks of the crown-of-thorns starfish *Acanthaster planci*, a species of sea star native to the region that feeds on corals (Veron 2000). Roughly every 17 years since the 1960s, normal populations of the sea star have increased to plague-like densities that eat the coral faster than it can grow, causes changes in the species composition, trophic structure, and topography of reef communities (Birkeland and Lucas 1990; Hoey et al. 2016). While there is some debate about whether these outbreaks are normal or are a biproduct of anthropogenic influence, it is certain that corals have a much harder time coping with them when they are already exposed to many other threats (Hoey et al. 2016).

With so many stressors, reefs cannot recover on their own and most are in a continuous state of decline. One result of this is that the sustainability of many reef fisheries, the primary source of income for small scale fishermen, is in jeopardy. In many tropical nations like Indonesia, these fishermen provide most of the coastal population's food protein. (Jompa et al. 2013). Many reefs no longer function as vital ecosystems; the coral-dominated vertical structure of the reef is turning into benthic ecosystems where isolated corals are a minor component because the corals are being eroded faster than they can grow. These ecosystems are at such a severe point of degradation that they are now defined as coral communities rather than coral reefs because biodiversity is seriously reduced. The corals themselves have eroded so much that their ability to protect shorelines, keep pace with rising sea levels, or provide food, shelter, and spawning and nursery grounds is significantly reduced (Goreau and Trench 2013; Jompa et al. 2013).

In addition to the more localized threats listed above, corals are also suffering the effects of ocean-wide changes in water temperature and acidity, and there is substantial evidence to suggest that reefs already under stress from local factors are more vulnerable to global change (Pandolfi et al. 2005). Under normal circumstances, a small proportion of the symbiotic zooxanthellae will become damaged and be expelled by the coral. However, because the corals' zooxanthellae live near the upper limit of

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their thermal tolerance, increases in temperature of just 1-2°C are enough to cause significant stress (Veron 2000). Higher temperatures damage the photosynthetic pathways of the zooxanthellae, so the coral polyp actively expels the damaged algae (Fujise et al. 2014). Because the algae give the corals their color, expelling the algae causes their soft tissues to become transparent, showing the white limestone skeleton beneath; this is the phenomenon known as coral bleaching. Depending on the severity of the bleaching, the corals may be able to recover an algal population and survive, but if the bleaching is extensive or if high temperatures persist, the bleached coral will eventually die and macroalgae will overgrow their skeletons, resulting in a phase shift of the reef environment (Figure 2). Tropical oceans have already warmed by nearly 1°C in the last century and continue to warm, making mass bleaching events much more common (Veron 2000). Widespread coral bleaching events caused by increases in water temperature, once a rare phenomenon, have been increasing in severity and frequency and have become the largest threat to reefs worldwide (Veron 2000).



Figure 2. Coral bleaching

Increased ocean water temperatures cause bleaching that can devastate healthy reefs in just a few months. Image composite from R. Vevers, XL Catlin Seaview Survey.

The burning of fossil fuels and other anthropogenic activities have increased the amount of atmospheric CO_2 by as much as 39 gigatons (Sabine et al. 2004). This has caused the atmosphere to warm, though the high thermal capacity of the world's oceans has prevented a more drastic atmospheric temperature increase (Rixen M. et al. 2005). The ocean has also absorbed much of the heat trapping carbon dioxide, causing the ocean to acidify by the reaction of CO_2 with water to form carbonic acid. Since pre-industrial times, the pH of the oceans has decreased (become more acidic) by 0.1 units (Albright et al. 2015). Because the pH scale is logarithmic, this equates to about a 30% increase in acidity, and pH is predicted to drop another 0.3 to 0.5 units by the end of the century. Models currently estimate that by this time, all coral reefs will cease to grow

and start to dissolve (Silverman et al. 2009). This is because corals use calcium carbonate to build their skeletons, so greatly increased acidity increases rates of bio erosion while simultaneously reducing the amount of CaCO₃ available (Albright et al. 2015).

Methods

Literature Search

I made my literature search as comprehensive as possible by accessing online reference inventories (e.g., Google Scholar and Research Gate), library catalogs, and relevant reference lists and bibliographies. I used multiple data sources including journal articles, book chapters, and reports to gather quantitative and qualitative data on a variety of methodologies for restoring degraded reefs or for growing corals for outplanting to degraded reefs. To locate relevant articles, I used the search terms "coral reef restoration", "coral tree nurseries", "coral nurseries", "coral reef restoration metaanalysis", "gardening the reef", and "artificial reef restoration". Additionally, I screened the reference lists from all retrieved articles and used the "Cited By" feature on Google Scholar to search for relevant articles. I looked for articles which gave detailed accounts of the methods used and of the response variables which indicated the success of their methods.

Because I wanted to determine the effect of different restoration methodologies on the success of the restoration project, I recorded all information pertaining to how the projects were conducted. I recorded geographic location, methodology type (as listed in Table 1), means used to attach coral fragments or colonies to a degraded reef site or nursery, depth of restoration site or nursery, duration of the study, coral species used, number of coral fragments installed in the nursery or outplanted to the degraded reef site, whether the fragments were naturally generated or were cut from intact coral for the purpose of the study, and whether the fragments were exposed to air at any

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point. For nursery studies I additionally recorded whether the nursery methodologies used kept the fragments fixed (immobile), floating (fixed to the nursery structure, the entirety of which is floating in the water column), or allowed them to swing (fragment attached to nursery structure by a length of line and can therefore move with the current), as each of these variations allow for a different flow regime, which has been found to be an important factor in coral growth (Rinkevich 2014). I recorded data reported by each study for the response variables of percent survivorship and growth rate, as these were the most commonly used measures of success with 43 out of 44 studies examined using either one (13 studies) or both (30 studies) of these indicators. Percent survivorship was understood to be the percent of living corals that remained at the end of the study, with mortality including both the corals that had completely died and those that had become detached from the restoration site and subsequently lost. Growth and survivorship are fundamental indicators that are crucial to determining the success of any restoration effort and the efficacy of the methods used. I also recorded any effects of fragment size, depth, or high temperature events severe enough to cause bleaching. If a study provided additional information that was relevant to their methods or which they deemed important to the level of success of their restoration experiment but did not fall within the above listed categories for methods and response variables, I made additional notes of these. Nearly all studies lacked information in at least one of the above categories (for some methods this was sometimes simply because not all categories were applicable to the methods used), therefore studies were selected which reported data in the majority of the described categories of methods and which reported on at least one of the described response variables. This resulted in a preliminary total

of 44 studies from which data was used, 19 of which focused solely on the nursery phase of restoration. A small number of the 44 studies used in this research could only be used to gather information on the kinds of methods that are in use and not for how their methods affected the response variables as they did not provide response variable data in a format that could be compared with data from other studies (i.e. response variables like growth or survivorship were presented as an average across multiple species or were only presented relative to other experiments within the study). However, in cases where survivorship was averaged across multiple species or experiments, but had a very small standard deviation, the average was used for each of the included species or experiments.

Through my literature search I identified three main types of restoration strategies: "gardening the reef", direct transplantation, and planulae (*see Glossary*) settlement. The "gardening the reef" concept (Rinkevich 1995) was inspired by terrestrial silviculture. It involves collecting fragments of coral colonies (hereafter referred to as "frags") that have either been naturally generated by heavy wave action or that are harvested from healthy colonies and culturing them for a period of months to years in a coral nursery. After growing in the nursery, cultured colonies are then outplanted to a degraded reef site. Direct transplantation also uses frags that have been created either naturally or intentionally but does not involve a nursery phase; frags are instead outplanted directly to the degraded reef site. Planulae settlement uses sexually produced coral planulae rather than frags and usually involves allowing the planulae to settle *ex situ* and then moving settlement plates to a degraded reef site, though field settlement projects have also been performed. These three general categories can be further broken down into a total of 10 different outplanting methodologies. I also identified 12 distinct types of coral nurseries. Both nursery and outplanting methods are described in detail in Table 1 and illustrated in Appendices 1 and 2.

Table 1. Su	mmary of all nursery an	nd outpla	nting methodologies.
	Method	Code	Description
	Midwater nets tied to bottom	N1	Trays holding a few dozen frags are attached to rope nets, anchored at a fixed distance above the bottom and suspended in the water column by floats. Frags are attached to trays by either gluing them to plastic pins or inserting the base of the frag into a short length of hose inserted into the tray to keep the frag in place.
	Floating midwater nets	N2	Similar to N1, except that the rope nets are suspended at a fixed distance beneath the surface by floats and anchored at one or two points to prevent the nursery from drifting away. This allows the nursery to move with tidal variations while keeping the frags at a constant depth.
nurseries	Mesh-top table	N3	Also called a fixed leg nursery, this keeps the frags at a fixed distance above the sea floor. A metal or PVC frame table is attached to the substrate and plastic mesh with small mesh size forms the top of the table. Frags are either glued to plastic pins or inserted into a short length of hose, which is then inserted into the mesh to keep the frags in place.
	Culturing settlement plates <i>in</i> <i>situ</i>	N4	Planulae are collected <i>in situ</i> with planulae traps in place over spawning colonies with planulae traps. Mailer's paper is cut to fit within a petri dish and placed in a seawater flowthrough table to "precondition" for at least two months and develop a natural biofilm. The papers are then attached to the inside of both halves of the petri dish. Several dozen planulae are then inserted into the prepared petri dishes. Settled planulae are later transferred to plastic pins and moved to an <i>in situ</i> nursery to grow larger.
	Rack nursery	N5	Racks are constructed by pounding steel rods vertically into the substrate and connecting them with a horizontal rod or PVC pipe. Frags are then hung from the horizontal bar with monofilament line. This allows frags to swing freely in the current.
	Coral Tree Nursery	N6	A long PVC pipe is tethered to the sea floor and buoyed with a subsurface floatation device, such that the entire nursery floats and is able to move with tides and waves. Fiberglass rods are placed horizontally through the PVC pipe every few feet in an "x" shape and frags are

			average ded from the reds by several inches of
			suspended from the rods by several inches of
			monofilament line, allowing them to swing freely.
	A frame anna an	N7	Large pieces of construction wire mesh are bent in the
	A-frame nursery	11/	middle to create an "A" shape. Frags are fixed to the mesh with cable ties.
	Cement disk		
		N8	Frags are fixed to cement disks, which are then attached to a frame or table nursery.
	nursery		Ropes are untwisted enough to allow a frag to be
			inserted between the coils of the rope so that the frag
	Dono numori	N9	· · ·
	Rope nursery	19	will be held in place. The ropes are then suspended between poles embedded in the sea floor to keep frags
			off of the substrate.
			Lines are strung between poles embedded in the sea
			floor and frags are suspended from them with several
	Line nursery	N10	inches of monofilament line, allowing the frags to swing
			freely.
			Frequently used for encrusting species. Colonies are
			fragmented into very small pieces (about >1 cm ² to
	Microfragmentation	N11	3 cm^2) and glued to ceramic tiles. Tiles are cultured in
	interorragmentation	1111	flowthrough tanks until colonies have grown enough to
			fuse and cover the tile.
			Cinder blocks with vertical cement cylinders attached
			are deployed to sandy or hard substrate. Frags are
			attached to cement pucks with adhesive and the puck is
	Block nursery	N12	outplanted to the top of a cement cylinder. This design is
			intended to allow transplantation at the end of the
			nursery stage without directly handling the coral.
	Outplanting nursery		After growing in a nursery to a size deemed large
	raised colonies to	01	enough for transplantation, colonies are removed from
	natural substrate	01	the nursery and attached directly to the substrate of the
			restoration site.
	Outplanting nursery		After growing in a nursery to a size deemed large
	raised colonies to	O2	enough for transplantation, colonies are removed from
	frame		the nursery and attached to a metal frame anchored to
			the substrate of the restoration site.
	Outplanting	~~~	After planulae have settled and been grown to an
	cultured sexual	03	appropriate size <i>ex situ</i> , colonies are transplanted to the
	recruits		restoration site. Collected planulae are placed in settlement traps on the
	<i>In situ</i> planula	04	degraded reef to encourage settlement onto natural
outplanting	settlement	04	substrate.
outplaining			Collected frags are scattered onto coral rubble substrate
			without any kind of attachment. This method is meant to
			mimic the natural asexual reproduction of many
	Frag scattering	05	branching coral species; when colonies are naturally
	8 8		broken by storms and heavy wave action, the resulting
			frags can often reattach to the substrate and create a new
			colony.
	Transplanting wild	O6	Whole colonies from healthy reefs are removed from the
	colonies	00	substrate and moved to the restoration site.
	Transplanting	07	Frags are transplanted and attached to the degraded reef
	uncultured frags		site without first being cultured in a nursery.
	Reattaching frags at	08	Broken frags and colonies are reattached to the substrate
	source site		or to standing coral skeletons. Primarily used when

		incidents like ship groundings have significantly damaged the reef.
Outplanting settlement plates	09	Tiles that have been colonized by newly settled corals <i>ex situ</i> are outplanted to the degraded reef site. Outplanted tiles may or may not be protected from corallivores by a plastic or metal mesh cage.
Biorock with transplants	O10	Biorock is an open structure metal frame constructed from a conductive metal to which frags are attached. A low voltage is used to charge the structure, thereby turning it into the cathode of an electrolysis reaction. This causes dissolved calcium and magnesium minerals (mostly aragonite (CaCO3) and brucite (Mg(OH)2)) to precipitate out of the seawater and create a limestone coating on the surface of the metal very similar to the limestone skeletons of scleractinian corals.

I used Excel (Microsoft Office 365) to organize and record all of the information I took from studies (Excel file is Appendix 3). Growth and survivorship data sometimes had to be extrapolated from graphs. When studies did not report growth data as percent increase per unit time, the available data was converted to this form when possible. The calculated percents are included in Appendix 3 rather than the initial and final sizes.

Data Analysis

Within a single study, experiments varied by location, species used, attachment type, depth, fragment size, genotype, or density of fragments. Often there were multiple kinds of experiments within a single study, or subcategories within each experiment (e.g. a study may have transplanted both asexually and sexually produced corals to multiple locations with outplants placed at multiple depths at each location). Due to this large degree of variability in experimental design, I counted every observation from each study as an individual data point. For the purposes of this paper, "observation" is used to mean an experiment within a study that does not have any lower levels of variability and can be recorded as a single data point. For example, if a study outplanted 10 different species of coral to two different locations, then each species and its associated response variables at each site were taken as individual observations, meaning that there were 20 total observations from that study. When data for survivorship or detachment was presented by a study as an average with a standard deviation without providing the data from which these values were derived, only the average was used for graphing and calculating statistics; similarly, when it was presented as a range, only the median was used. For assessing survivorships, I adopted the assertion of Thornton et al. (2000) that survivorships ranging from 50% to 100% indicate success.

SigmaPlot 12.5 was used to graph the survivorship data. Nursery or outplanting methodologies that were used by very few studies (< 3 studies per method) were not included in graphs. I ran three separate nonparametric 2-way ANOVAs on ranks using Statistical Analysis Software (SAS), one on survivorship data from nurseries and one on survivorship data from outplanted frags, to determine if the species and the methodology used affected their survivorship, and another on survivorship data from outplanted frags to determine if culturing frags in a nursery significantly affected survivorship after outplanting relative to frags outplanted without a nursery period. I used ranks to replace the data because of the large variability in experimental procedures, species, and sample size made the data extremely non-normal. I used the standard level of statistical significance (p < 0.05) in assessing the results of these tests.

I constrained my analysis of growth data to species of corals with branching morphologies. Growth cannot be meaningfully compared between different morphologies (e.g. branching and massive) because they grow in fundamentally different ways. A branching coral and a massive coral of similar size may occupy the same ecological volume, but the open structure of a branching corals means that has accrued a much lower mass of calcium carbonate to achieve that size. Similar principles apply when trying to make comparisons of growth between other morphology types. I therefore focused on a single morphology for analysis. I chose branching corals because they are the most commonly used. Due to their naturally fast growth rates and ability to reproduce via asexual fragmentation, they are a popular choice for restoration. Growth rates were measured by multiple metrics over varying time periods. Among the different metrics, growth rates were given as either a percent increase, a fold increase, or as absolute growth over a given time period. I standardized these measures to reflect the amount of growth that occurred over a one-year time period. I converted units of absolute growth to cm, cm^2 , or cm^3 as was appropriate.

Results

Qualitative

Several of the studies I used in this research offered findings that were not assessed quantitatively due to the limited number of studies that presented them. These findings are important to keep in mind as they may be sources of some of the variation in the quantitative data I evaluate below. A few studies found that the initial size of the frag had significant effects on survival, with larger frags tending to have higher survivorship (Garrison 2008, Raymundo et al. 2004, Garrison & Ward 2012, Bruckner & Bruckner 2001, Bruckner & Bruckner 2006, Epstein 2001). Depth of the outplanting site was also found to be a significant factor, with shallower outplanting sites producing higher growth rates than deeper sites (Shafir et al. 2006B, Jompa et al. 2013, Zamani et al. 2013, Levy et al. 2010, Soong and Chen 2010).

All observations of frags transplanted to Biorock were highly successful with survivorships all greater than 85% (Figure 4B). Corals growing on Biorock were much more resilient to severe high temperature events with survival rates 16–50 times higher than those of corals growing on natural substrate (Goreau et al. 2013). In addition to uncommonly high survivorships, Biorock provides several other benefits to restoration efforts. Corals and other calcifying organisms that settle on Biorock grow 2 to 8 times faster than those growing on natural substrate, depending upon species and other environmental factors (Goreau et al. 2013). Biorock also has recruitment rates of new corals that are hundreds or even thousands of times higher than those in literature for recruitment to natural substrates (Zamani et al. 2013). These last two effects alone allow

new reefs to form very rapidly. Such rapid growth and recruitment mean that these reefs may be able to keep pace with rising sea levels (Goreau and Hilbertz 1996). The electrical current not only stimulates the growth of corals directly on the Biorock, but up to 3 meters around it as well (Nitzsche 2013). As more corals grown on the Biorock structure, the complexity they add makes it an increasingly effective at dissipating wave energy, thereby protecting shorelines from erosion (Goreau et al. 2013). One study found that densities of reef associated fishes were 6 times greater around a Biorock reef than the control (Bakti et al. 2013). Although this method has existed since the 1970s, its implementation has been limited to a few studies in Indonesia and the Caribbean. With such promising results, this method merits further study across a broader geographic range, especially when high degree of variability of success rates among other methods is considered.

Frag shape may be an important consideration in choosing the attachment method, orientation of the fragment, and location of the outplanting site. Shafir et al. (2006a) observed that frags from species with longer, narrower branching morphologies had the highest rates of detachment and hypothesized their shape exposed them to more shearing force. The age of frags at collection may also be important; lower survival rates were observed among older frags taken from proximal regions of donor colonies relative to frags that were more distal in origin (Bowden-Kirby 2001). Ladd (2016) found that concentrating outplants at 3 per square meter optimized survival while higher densities had lower survival.

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Quantitative Analyses

In total, 76 species of coral were used across the 44 studies, 26 of which are in the genus *Acropora* (Table 2). Of the 76 species, 50 were used by only a single study, while 11 were used by more than three studies. The most commonly used species overall was *A. cervicornis* (12 studies), followed by *A. palmata* (9 studies) and *P. damicornis* (8 studies). Nursery-only studies hosted the highest diversity of species (n = 42) while outplanting-only studies used 16 different species. Some species (n = 5) appeared in both nursery-only studies and in outplanting-only studies. Studies which implemented a nursery phase prior to outplanting used 23 species.

Table 2. List of coral species used in restoration efforts worldwide, in outplanting and/or in nurseries. Restoration projects are pooled by region: Caribbean C (Jamaica, Puerto Rico, British Virgin Islands, Belize), East Africa EA (Mauritius, Zanzibar), Florida and the Florida Keys FFK, Hawaii H, Indonesia I, Japan J, Palau P, Red Sea RS, South China Sea SCS (Thailand, Singapore, Taiwan, Philippines), Yemen Y. Number of studies refers to the number of studies which were found to use a given species.

Species	С	EA	FFK	Н	Ι	J	Р	RS	SCS	Y	# of studies
Acropora		Х									1
austera											
Acropora	Х		Х								12
cervicornis											
Acropora					Х						1
cytherea							37		37		2
Acropora							Х		Х		2
digitifera								v			1
Acropora								Х			1
eurystoma Acropora									Х		5
formosa									Λ		5
Acropora									Х		1
grandis											1
Acropora		Х									1
hemprichi											
Acropora								Х			1
humilis											
Acropora							Х		Х		2
hyacinthus											
Acropora						Х					1
intermedia											
Acropora								Х			1
lamarcki											
Acropora									Х		1
millepora											

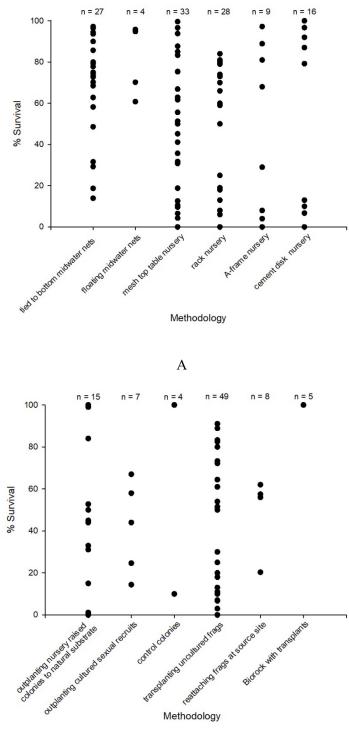
Acropora muricata		Х					Х	2
Acropora nasuta		Х						1
Acropora nobilis				Х				1
Acropora	Х		Х					9
palmata Acropora						Х		1
pharonis	37							
Acropora prolifera	Х							4
Acropora						Х		1
pulchra								
Acropora selago		Х				V		1
Acropora squarrosa						Х		1
Acropora tenuis				Х	Х			4
Acropora				Х				1
valenciennesi						v	V	4
Acropora valida Acropora						X X	Х	4 1
variabilis						Л		1
Caulastrea							Х	1
furcata Cyphastrea							Х	1
serailia							Λ	1
Dendrogyra			Х					1
cylindrus Disploastrea							Х	1
helipora							Α	1
Echinopora							Х	4
lamellosa						Х		1
Favia favus						7	Х	1
Favia speciosa Favites abdita							X	1
Galaxea		Х					Х	2
fascicularis								_
Goniastrea minuata							Х	1
Goniastrea							Х	1
<i>pectinata</i>							V	1
Goniopora lobata							Х	1
Heliopora							Х	2
coerulea							V	1
Hydnophora exesa							Х	1
Hydnophora							Х	2
rigida Merulina							Х	4
scabricula							1	т
Millepora			Х					1
complenata								

Millepora dichotoma						Х			1
Millepora spp.		Х							1
Montipora aequituberculata							Х		2
Montipora				Х					1
capitata									-
Montipora digitata		Х					Х		6
Montipora							Х		1
sabricula Orbicella			Х						1
annularis									
Orbicella			Х	Х					2
faveolata Orbicella			Х						1
franksi			А						1
Pavona cactus		Х						Х	2
Pavona danai		Х							1
Pavona		Х							1
decussata Platygyra								Х	1
daedalea									
Platygyra							Х		1
sinensis Do cillino un				\mathbf{v}					1
Pocillipora meandrina				Х					1
Pocillopora		Х				Х	Х		8
damicornis									
Pocillopora		Х							1
verrucosa Porites				\mathbf{v}					1
asteroidea				Х					1
Porites				Х					1
compressa									-
Porites		Х							1
cylindrica				37			37	37	2
Porites lobata				Х			Х	Х	3
Porites lutea							Х	Х	3
Porites palmata		Х							1
Porites porites	Х								3
Porites rus							Х		2
Porites							Х		2
sillmaniana									•
Psammocora digitata							Х		2
digitata Psammocora							Х		1
obtusangula							••		·
Pseudodiploria clivosa				Х					1
Seriatophora						Х			1
hystrix									

Solenastrea	Х		1
bournoni			
Stylophora		Х	4
pistillata			
Turbinaria		Х	1
pelata			

Survivorship

A wide variety of methods were used for both constructing nurseries and outplanting frags. All methods displayed a wide variation in survivorships and no single method appears superior in its ability to produce consistently successful results (Figure 3A, B). Nursery studies provided 148 observations in total, 103 of which had survivorships greater than 50%. A nonparametric 2-way ANOVA by ranks on data from nurseries revealed that survivorship was strongly affected by the methods used (p < 0.0001), and also by the species used (p < 0.05), indicating that methods were the main influencer of survivorship. Differences in survivorship between species were fairly, but not entirely, consistent between the different nursery methods (interaction term, p = 0.0768). As shown in Figure 4A, several species that did well in cement disk nurseries or tied to bottom midwater net nurseries had lower survival rates in A-frame, floating midwater net, and rack nurseries. Some species that perform poorly with other methods have increased survivorship in mesh top table nurseries; other species have the lowest survival in this same nursery method.



В

Figure 3. Comparison of survivorship across different methodologies for (A) nurseries and (B) outplanting. The *n* values given above each column indicate the number of observations in each category. Some dots overlap and are not distinct, so the number of visible points may differ from the *n*.

Outplanting studies provided 72 observations in total, 37 of which had survivorships greater than 50%. For outplanting, methods (p < 0.0001) and species (p =0.0358) again had a significant effect on the survival of outplanted corals. There was also significant interaction between methods and survivorship (p = 0.044) and there are no consistent trends in the effects of methods on survivorship between different species (Figure 4B). For some species, cultured frags that were outplanted to natural substrates survived better relative to natural growing "control" colonies at a given outplanting site, while other species experienced the opposite effect in the same nursery method. Similarly, some species had higher survivorships when transplanted to natural substrate if they had first been cultured in a nursery, while others performed better without the nursery period. Frags from seven species were transplanted to Biorock, and all had survivorships above 85%. The 19 studies that focused on the nursery stage of restoration provided 148 observations, and of these, 103 observations had survivorships \geq 50%. A smaller fraction of observations from the 25 outplanting studies were successful, where 37 of the 72 total observations had survivorships $\geq 50\%$.

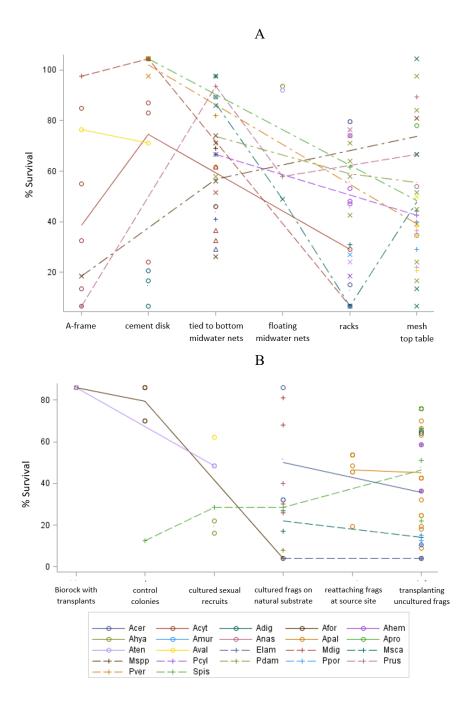


Figure 4. Survivorship as a function of species and methods used in (A) nurseries and (B) outplanting. Survivorship of frags in nurseries was primarily dependent upon the nursery methods used, while in outplanting there was no consistent variation. Species names have been shortened to the first letter of the genus and the first 3 letters of the species. Lines track variances in mean survivorship for species used with multiple methods.

Of the 25 outplanting studies, nine outplanted colonies that had first been cultured in a nursery while 14 others directly outplanted frags without a nursery phase. Another 3 studies utilized larval settlement, either onto settlement plates in lab that were later transplanted, or onto natural substrate. For both outplanting preceded by a nursery phase and direct outplanting, the majority of observations had survivorships above 50%. Although there was a slightly larger fraction of observations from cultured colonies than uncultured frags that did so (17 out of 30 cultured observations and 23 out of 45 uncultured observations), there was no significant difference in survivorship between the two (p > 0.05) (Figure 5), indicating that implementation of a nursery phase does not have any effect on the survivorship of outplants.

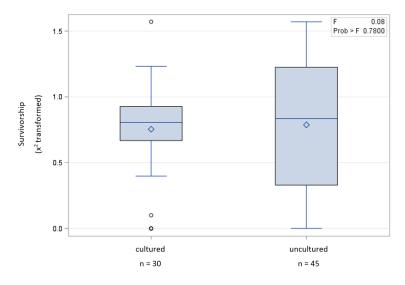


Figure 5. The effect of culturing frags in a nursery before outplanting on the survivorship of each observation. The interquartile ranges (IQR, shown by the boxes) completely overlap, demonstrating that implementing a nursery period has no significant effect on the survivorship of frags post-outplanting. The smaller box and shorter whiskers of the "cultured" plot indicates that there is less variation in the survivorships of these observations. The diamonds in the IQR indicate the mean, the bars indicate the median, the ends of the whiskers show the range of the data, and the circles past the end of the whiskers on the "cultured" plot indicate outliers. The means are nearly identical (49% average survivorship in cultured, 50% % average survivorship in uncultured), as are the medians (52% in cultured, 55% in uncultured).

Out of the 25 outplanting studies, 22 provided data on both attachment type and survivorship. From these, I determined 6 primary attachment types that were used for outplanting corals: adhesives, cable ties, wire, wedging, frag scattering, and natural settlement (Figure 6).

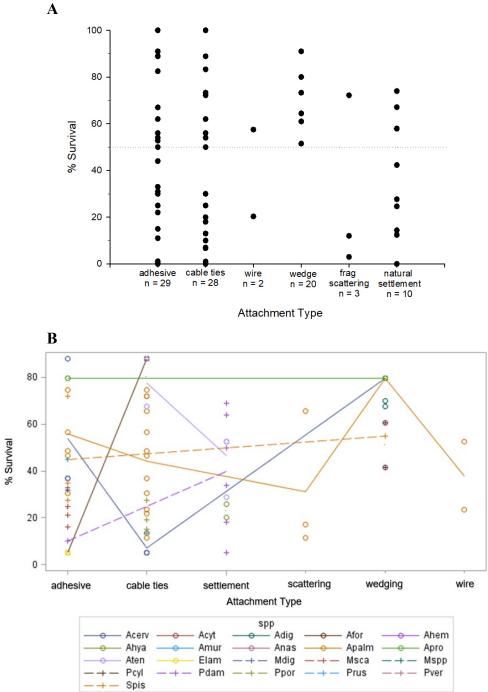


Figure 6. Survivorship as a function of attachment type across all species. (A) Some observations within a given attachment type have completely overlapping survivorship values, so the number of observations *n* for each attachment type is provided for clarity. The dotted line at 50% survivorship makes clear that all the wedge observations had survivorships above 50%. (B) Species names have been shortened to the first letter of the genus and the first 3-4 letters of the species. Lines connect points indicating the mean survivorship of species that appear in multiple method types (e.g. the solid orange line connects between the mean survivorships of *A. palmata* in each method; the observations for this species are represented by the orange circles).

Adhesives (which included marine epoxy, cement, glue, and putty) were combined because they all provide the same kind of attachment of coral to substrate (i.e. coral is "stuck" to substrate) and studies that used multiple kinds of adhesive found no significant differences in their effects on response variables. Adhesives were used in 8 studies and 12 of the 27 observations within these studies showed survivorship >50%. Nylon and plastic cable ties were also grouped into "cable ties". Cable ties had 15 out of 31 observations with >50% survivorship, a proportion slightly greater than survival with adhesives. Wedging describes any attachment method involving inserting a frag into a tight space to keep it in place, whether it is into a hole or crack directly in the substrate, the mesh frame of artificial substrate, or a short piece of hose that is subsequently inserted into mesh. Attachment by wedging (used by 4 of the 25 outplanting studies) was the only method which produced greater than 50% survivorship in every observation (n = 21). Frag scattering does not actually involve directly attaching frags to substrate, but rather is a means of "outplanting" frags to a restoration site in a way that attempts to replicate the natural processes by which branching corals asexually

reproduce. Only three studies used this method and only 1 observation of 3 total reported a survivorship above 50%. Natural settlement includes both planulae that were allowed to settle onto ceramic settlement plates or plastic pushmounts in laboratory conditions before being outplanted and planulae that were allowed to settle onto cleaned natural substrate *in situ*. This method was used by 3 studies and 4 observations of 10 total showed survivorship greater than 50%. Wire was used to reattach broken corals to standing coral skeletons and was the only attachment type that caused damage to the coral itself; tissue mortality was observed in the area immediately around the wire (Bruckner and Bruckner 2001, 2006). There were only two observations that used this attachment type, one of which reported survivorship >50%.

A two-way nonparametric ANOVA by ranks showed that both attachment type (p = 0.0001) and species (p < 0.0001) had a significant effect on survival, and that some species, though not all, survived significantly better by one method than another (interaction: p < 0.0001). As shown in Figure 6B, both *A. cervicornis* and *A. palmata* had their highest survivorships when outplanted via wedging, while *A. formosa* and *A. tenuis* performed the best when cable ties were used. *A. prolifera* performed equally well across all attachment types in which it was used. *P. damicornis* survived significantly better when sexually produced planulae settled onto substrate than when frags were outplanted with adhesive. Survivorship for each attachment method varied among different species (Figure 7).

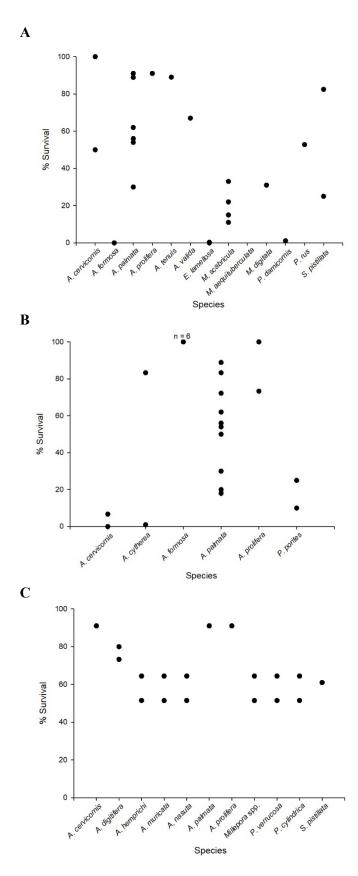




Figure 7. Survivorship by species for (A) adhesive, (B) cable ties, and (C) wedging. Wire, frag scattering, and natural settlement were not graphed due to very low numbers of observations.

Growth

Studies which reported growth rates for branching corals did so by a wide variety of metrics. Nursery-only studies reported the growth of branching species by six different metrics (Table 3). Linear extension was used by seven studies; all other metrics were used by only one study each (Shaish et al (2008) provided both the "height" and "width" metrics).

Table 3. Diversity of growth metrics used to measure the amount of growth of branching corals growing in nurseries. The average, standard deviation SD, and range are given in the units of their respective methods.

are given in the unit	s of their respect	ve methods.		
Growth Metric	No. of observations	Average	SD	Range
Linear extension (cm per yr)	39	21.87	21.60	89
Area (cm2, % per year)	6	157.54	110.57	303.36
Height (% per yr)	6	297.47	60.11	146
Width (% per yr)	6	484.60	405.08	960.68
Ecological volume (% per yr)	7	461.073	245.17	573.25
Ecological growth rate constant (% per yr)	5	626.34	48.07	116.8

The study that provided growth rates as increases in "height" and "width" did not define what is meant by these terms or what dimensions of the colony were measured. Some studies provided the amount of the growth over a unit of time other than one year; this data was scaled accordingly. Seven different metrics were used to measure the growth of branching coral species after they had been outplanted (Table 4). Only a few studies used each of the metrics given below, so sample size is limited. In the case of the linear extension metric, 6 of the 10 observations came from a single study using Biorock, which had much higher growth rates than those from other studies and likely caused bias. Because of the low sample sizes, I did not attempt to analyze how nursery or outplanting methods affected coral growth rates.

No. of **Growth Metric** Average SD Range observations Height 5 23.98 20.48 52.78 (% per year) Linear extension 10 2882.00 2396.76 5724.1 (% per year) Mass increase 5 318.14 392.01 961.09 (% per year) Linear extension 6 7.73 5.69 12.74 (cm per year) Diameter 2 5.6 11.20 119.40 (% per year) Ecological volume 2 3804 3385.75 6771.5 (% per year) Ecological volume 12 7.21 3.45 14 (fold increase)

Table 4. Diversity of growth metrics used to measure the amount of growth of outplanted branching corals. The average, standard deviation SD, and range are given in the units of their respective methods.

Some studies provided the amount of the growth over a unit of time other than one year; this data was scaled accordingly.

Growth in both nursery-living and outplanted corals (Tables 3 and 4, respectively) displays a large degree of variation regardless of the metric used to measure it. In nearly all cases, the SD is nearly as large or larger than the average.

Growth rates could not be compared between different methodologies within a single metric because either sample sizes were insufficiently large to produce confident results, all observations within a metric came from only 1-2 studies, or all observations of growth given by a particular metric were also all used by the same methodology (or some combination thereof).

Discussion

Overall, my analysis provides substantial evidence for the need to tailor restoration methodologies to the specific species being used. Understanding exactly how the survivorship of different species is affected by methods is somewhat limited, as many species have only been used with one or two method types. Yet all the species which were used across multiple methodologies showed that survival was heavily dependent upon methods. My analysis also provides support for the usefulness of restoration in general, as the majority of observations in both nurseries and outplanting sites have survival greater than 50% and securing frags to degraded reef sites improves survivorship over the natural processes of frag scattering and larval settlement.

Although the average survivorships between nursery and outplanting observations were not significantly different (t-test: p = 0.80), a higher percentage of nursery observations (69.6%) than outplanting observations (51.4%) had survivorships \geq 50%. This is as expected, as nurseries are meant to provide a safe, stable environment for the frags to grow. In general, cement disk and tied to bottom midwater net nurseries produced the highest success rates for commonly used species, though there is still some non-significant species-level variation. Many species are represented in only a single methodology. Therefore, more research is needed to determine the optimal method for these less frequently used species and whether they are viable options for restoration, specifically in projects attempting to restore a higher level of biodiversity to the degraded reef site.

While most methods of attachment produced highly variable survival rates, all wedging observations showed survivorships above 50%. It is possible that wedging

provides a more secure attachment so that fewer frags are lost, however this could not be confirmed from the available data. Generally, adhesives, cable ties, and wedging are the means of attachment most likely to produce successful results, and all are more effective in achieving higher rates of survival than natural propagation methods (e.g. frag scattering and larval settlement). My analysis shows that regardless of the attachment type used, the attachment method must be carefully considered because some species experience significantly different survival rates when different attachment methods are used. Other species experience little to no variation in survival between different attachment types. Restoration efforts must act accordingly and use an attachment method shown to produce the highest survival rates for a given species. As with the methods of outplanting, some species are represented by only a single attachment type and more research is needed on these species to determine what effects they experience when different methods of attachment are used.

Direct transplantation without a nursery phase has been criticized for its inconsistency in producing high rates of survival and its limitations in restoring coral cover (Guzman, 1991; Yap,2004; Forrester et al., 2012; Cabaitan et al., 2015; Cruz 2015). My analysis showed that culturing frags in a nursery in fact had no effect on survival after outplanting relative to frags that did not have a nursery period. However, this does not necessarily mean that the nursery phase should be eliminated. Nurseries provide benefits to restoration efforts outside of effects on the survivorship of frags which provide strong support for the efficacy of the "gardening the reef" approach. Multiple studies found that frags which had been cultured in a nursery experienced a variety of reproductive benefits after they were outplanted. Rearing frags in nurseries

improves their recruitment abilities; Okubo et al. (2010) found that although wild colonies had more oocytes, colonies cultured in nurseries had larger oocytes and were able to produce more gametes, such that cultured colonies had reproductive rate similar to or higher than wild colonies. Additionally, crossing a wild colony with a cultured colony improved the survival of the offspring above that of a purely wild cross (Okubo et al. 2010). For Stylophora pistillata, Amar (2007) reported that nursery-borne larvae are larger, equipped with higher numbers of endosymbionts, contain more chlorophyll per planula, and grew into colonies with higher growth rates than larvae from colonies of natural origin. Once transplanted, nursery-raised colonies may also release planulae more frequently than natural colonies (Horoszowski-Fridman 2011). Nurseries themselves may act as larval dispersion hubs and attract large numbers of reef fish (Amar and Rinkevich 2007), creating a kind of pseudo-reef habitat where none previously existed. Additionally, once frags have grown to sufficient size in the nursery, they may become donor colonies for new frags, thereby removing harvesting pressure from neighboring healthy reefs (Rinkevich 1995). Yet nurseries have their drawbacks as well. They add a considerable amount of expense and time to restoration projects, potentially making them unfeasible in poorer countries. Therefore, restoration efforts with limited funding need to evaluate several factors in determining whether a nursery is needed: Can the local reef support large and/or multiple frag harvests? What is the natural recruitment rate to the restoration site, and would having the added larval dispersion hub provided by a nursery positively improve natural recruitment, thereby accelerating restoration efforts? Answers to such questions can help determine whether the added benefits of a nursery outweigh the additional cost. Where possible however,

the evidence suggests that implementation of coral nurseries has the potential to increase the long-term success of restoration.

Reef restoration has been critiqued for its practice of harvesting frags from healthy colonies rather than using naturally produced frags, with critics stating that doing so damages the corals and serves to weaken a healthy reef ecosystem. However, Lirman et al. (2010) found that pruning branches actually promoted growth; when the growth of the surviving transplanted branch tips was added to the regrowth of donor branches, the new coral produced (measured by linear extension) is 1.4–1.8 times more than the amount produced by the same number of branches in control colonies in 3-4months. Decreases in linear extension of the fragmented donor branches were only temporary, and donor branches grew faster than control branches after the initial recovery period of 3–6 weeks, indicating a shift of resources toward recovery. If too many branches are taken from a single colony, it can have negative effects; Epstein (2001) found that harvesting more than 10% of a colony's branches resulted in significantly higher colony mortality. Yet if done correctly, frag harvesting appears to be a viable means of stocking nurseries. This may depend on the species of coral used and more research is needed to determine whether 10% per colony is an appropriate maximum harvest size across species. The long-term effects of frag harvesting on donor colonies also needs to be evaluated, as the above findings were concluded after relatively short time periods.

I was unable to compare the effect that different methods had on the growth of outplanted corals due to multiple issues in the data. Due to fundamental differences in the way corals with different morphologies grow, it would not have been meaningful to

compare the amount of growth between different growth forms, such as between branching and massive forms. Yet even when I focused solely on branching species, the most commonly used growth form in the studies examined, the data were still incomparable for several reasons discussed previously. The wide variety of metrics used and the consequently low sample sizes of observations, as well as the bias created when all observations within a metric were taken from only one or two studies meant that any comparisons of the effect that different methods had on growth rates could not be made with confidence. This is a serious deficiency of reef restoration as a whole. Growth ought to be a fundamental indicator of the success of a restoration effort; if corals in a restored site are not growing well, the system has not truly been restored. The ability to meaningfully and confidently compare the effect that different methods have on growth rates is critical to the future of the field in order to hone techniques to be as efficient as possible, thereby maximizing the impact that restoration efforts make toward rehabilitating the biodiversity and ecosystem function of a degraded reef ecosystem. Additionally, consistent and standardized reporting of growth rates may be a useful tool for determining the effects that climate change is having on restored corals and whether restoration is and effective tool for counteracting its effects.

Based on the findings and problematic data discussed above, I propose several changes to how future restoration studies are conducted so that synthetic questions such as the ones examined in this thesis can be answered. There needs to be a standard framework for reporting information on methods and results if meaningful comparisons are to be made between different studies, methods, and regions. The current lack of such a framework inhibits development of guidelines for what is and is not effective.

For example, if a significant proportion of restoration studies do not report data on the biotic and abiotic factors present at an outplanting site, or whether the frags used were broken by naturally processes or harvested by humans, it cannot be determined whether these environmental and methodological factors have an impact on the survival of frags. Similarly, if some studies do not report survivorship data, it becomes much more difficult to accurately determine the effect of different methods. For growth to be compared, it is necessary to use a standardized method of measuring corals and a single metric for reporting that is appropriate for the given coral's morphology. Using a profusion of varied metrics for a single morphology, as observed here in branching corals, makes comparisons of growth between different methods extremely difficult, if not impossible. Detailed records of the abiotic conditions of the restoration site should also be included which specifically include salinity, water temperature, depth, and water quality and clarity, as these are factors know to influence the growth and survival of corals (Rinkevich 1995). In studies where both multiple species and multiple experimental variations are used, survivorship and growth cannot be grouped only by experiment, as doing so may mask important variations in responses at the species level to the methods used. Additionally, standards must be set for the maximum number of frags that can be harvested from a single colony in order to minimize damage to donor colonies and ensure that healthy reefs remain healthy, though more research is needed to determine if the 10% maximum reported by Epstein (2001) is a valid standard.

The time scale over which projects are monitored after outplanting also has the potential to strongly influence observations of survivorship and growth. Herlan and Lirman (2008) noted that mortality of frags was highest in the first 8 weeks after

harvesting and mortality rates decreased after that point. There have been multiple cases of coral transplants that appear highly degraded, even dead, eventually showing signs of recovery if given enough time (Yap 2003). Although some means of restoration have been found to accelerate the growth of transplanted frags well above those natural colonies (Zamani et al. 2013, Bakti et al. 2013, Jompa et al. 2013, Forsman et al. 2015), corals are still relatively slow growing animals with extremely long lifespans (Jaap 2000). Continued long-term monitoring is therefore necessary to determine the true "success" of a restoration project and to avoid reporting misleading survivorship trends. However only six of the studies examined in my research spanned more than 2 years, with most lasting between 6 and 24 months.

Knowing the efficacy of different reef restoration methods would greatly help those who are working to reduce the rapid loss of coral reef habitats worldwide. Restoration must therefore be carried out as precisely and efficiently as possible in order to have the largest impact towards repairing degrading ecosystems and preventing further loss of biodiversity, as well as avoid wasting time and resources. Doing so requires detailed information on all the biotic and abiotic factors that influence the health of corals and effect the success of outplants. It also necessitates an understanding of how various methodologies perform under varying abiotic parameters and the responses of different species of coral to these regionally and locally fluctuating parameters. It must also be known how the effects of the methods used interact with the effects of abiotic factors. While this research addresses some of the necessary information, it is limited in the questions that can be effectively answered due to the large inconsistencies in how data are reported. More consistent and detailed reporting of both methods used and the results they produce will facilitate better understanding of how the many aspects of reef restoration interact. This is why the changes I here propose for more rigorous and critical evaluation of the effectiveness of restoration studies are needed. If they are implemented on a broad scale, it would allow future meta-analyses to determine the methods that are the most likely to produce high success rates for different regions and coral species. While there is still significant site-specific variation in both biotic and abiotic factors that will also influence the success of any given restoration project (Yap 2000), providing the necessary information to allow existing efforts to be evaluated on a broad scale will enable future restoration projects to be planned with higher efficiency.

Conclusion

Reef restoration is a very new field that has proliferated rapidly to include a wide variety of methodologies and species. Based on the literature from both experimental restoration studies and previous reviews of the field, I saw a need to quantitatively compare the effect that different methodologies had on the survivorship of corals used in restoration. This quantitative approach reinforced the viability of active restoration of reefs, as my research showed that active restoration methods improved the survival of frags above that of methods that emulate natural coral propagation (e.g. frag scattering and natural settlement). It simultaneously highlights the need to tailor the methods used to the species involved in a given restoration effort due to the significant effect I found methods to have on the survival of corals. Reefs worldwide continue to decline sharply, and so this field must continue to advance rapidly if it is to be effective in slowing or even reversing the damage done to reefs by anthropogenic agents. Changing how future restoration studies are conducted to include more detailed reporting of environmental factors, methods, and response variables by standardized metrics as I propose may help in the development of guidelines for what is and is not effective. It is my hope that both the data presented by this research and the changes I propose will be useful tools in the continued improvement of this field.

Glossary

ex situ – Outside, off site, or away from the natural location (e.g. an experiment conducted in a lab)

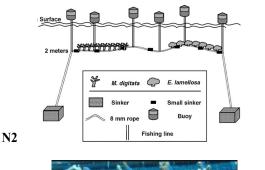
in situ – in the natural or normal place (e.g. an experiment conducted in the natural environment)

planula(e) – free-swimming or crawling larval type with a more or less cylindrical or egg-shaped body that bears numerous cilia (tiny hairlike projections), which are used for locomotion.

pushmount – a small screw-like plastic device approximately 4 cm in length with a small cavity in the head that can be inserted into a hole in the substrate. A frag can be inserted into the cavity in the head of the pushmount to keep it in place, or planulae can settle onto the pushmount in lab so that they may be easily transplanted to an *in situ* nursery.

recruitment – when juvenile organisms survive to be added to a population, by birth or immigration, usually a stage whereby the organisms are settled and able to be detected by an observer

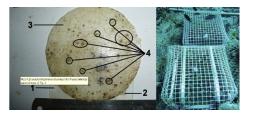
Appendix







N3 a



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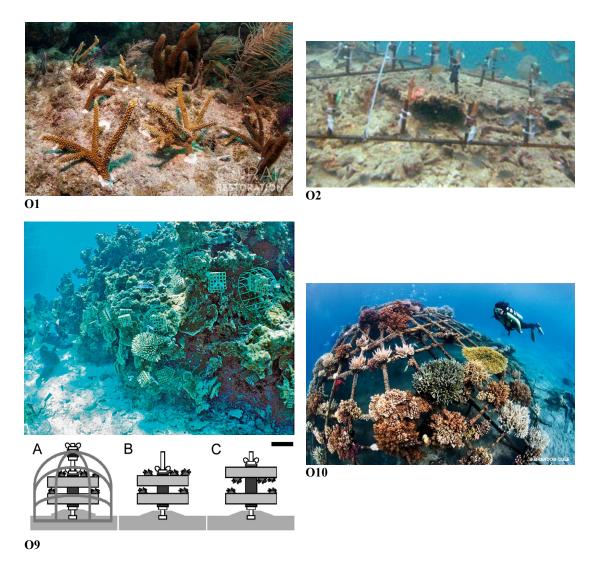
Appendix 1. Images illustrating several nursery methods. Labels refer to codes given in Table 1, which provides detailed descriptions of each method. Image sources are as follows: (N2) Levy et al. 2010; (N3 a) <u>https://www.marinethemes.com/artificial-reefs/;</u> (N3 b) Mbije et al. 2010; (N4) Linden 2011; (N6) Coral Restoration Foundation; (N10) <u>http://www.coralrestoration.org/staghorn-coral/</u>; (N11) Mote Marine Laboratory; (N12) <u>https://www.rsmas.miami.edu/</u>

N6

N11

N3 b





Appendix 2. Images illustrating some outplanting methods. Labels refer to codes given in Table 1, which provides detailed descriptions of each method. Image sources are as follows: (O1) http://coralrestoration.org/outplanting-methods/; (O2) Putchim et al. 2008; (O9) Nakamura et al. 2011; (O10)

 $http://www.alertdiver.com/Biorock_Electric_Reefs.$

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