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PRACTICAL ARTICLE

Optimizing industrial-scale coral reef restoration: comparing harvesting wild coral spawn slicks and transplanting gravid adult colonies

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Accelerating coral reef restoration is a global challenge that has been attempted around the world. Previous attempts show varying levels of success at localized scales, but comparisons of cost and benefits to evaluate large-scale reef restoration approaches are lacking. Here, we compare two large-scale restoration approaches: the harvesting, development, and release of wild coral spawn slicks onto a target reef, with the transplantation of gravid coral colonies to provide a seed population and local source of larvae. Comparisons incorporate the best available information on demographic rates to estimate population growth, beginning at embryo production to colony maturity 4 years following deployment. Cost-effectiveness is considered in a coarse manner. The harvesting, development, and controlled release of coral spawn slicks is anticipated to achieve large-scale restoration of coral communities with low-impact technology at low cost per colony. Harvesting wild spawn slicks has the potential to (1) transport billions of larvae up to thousands of kilometers that (2) are relevant to coral restoration efforts at vast geographical scales while (3) benefitting from the use of technology with extremely low impact on wild populations and (4) retaining natural genetic and species diversity needed to enhance the resilience of restored communities. Transplanting colonies is most useful from reefs designated to be impacted by infrastructural development by providing an opportunity for transfer to high value zones, from dedicated nurseries, and for brooding species. Our contribution provides insights into critical elements of both concepts, and we highlight information gaps in parameter uncertainties.

Key words: corals of opportunity, harvest, restoration, spawn slicks, transplant

Implications for Practice

- When using vessel-based storage facilities for reef restoration, higher quantities of coral embryos can be obtained from pumping wild coral spawn slicks than from transplanted reproductively mature colonies at similar levels of cost-effectiveness.
- Harvesting approaches could be implemented on large vessels such as commercial trailer suction hopper dredgers to collect reproductive material from healthy reefs with minimal impact to wild populations and transport them over long distances for deployment onto target reefs in need of rehabilitation at ecologically relevant scales.
- Before full-scale efforts are attempted, empirical experiments are necessary to test feasibility and optimize the industrial-scale applications of the coral spawn slick harvesting technology.

Introduction

Coral reef restoration projects have traditionally been small in scale (i.e. <1 ha), expensive (i.e. average $5,411,993 US per hectare), and limited as a tool for coral reef conservation (Edwards & Gomez 2007; Mumby & Steneck 2008; Bayraktarov et al. 2016). Yet, in light of large-scale disturbances (Hughes et al. 2018), strategies for ecosystem-scale reef conservation are currently being reevaluated. Renewed interest in active coral restoration techniques for conservation is escalating (Fig. 1) because even the best-practice management approaches cannot protect coral reefs in a global warming context (Anthony et al. 2017).

Despite over 20 years of research and applied effort examining transplant, gardening, and seeding approaches, seascape-scale restoration remains the critical technical challenge for coral reef ecosystems (e.g. Rinkevich 1995; Heyward et al. 2002; Horoszowski-Fridman et al. 2011; Guest et al. 2014; Edwards et al. 2015; De La Cruz & Harrison 2017).

Author contributions: all authors conceived, designed, and interpreted the study; CD, MvK, RCB collected the data; CD created the model, analyzed the predictions, and wrote the first draft; all authors contributed to the final version of the paper.

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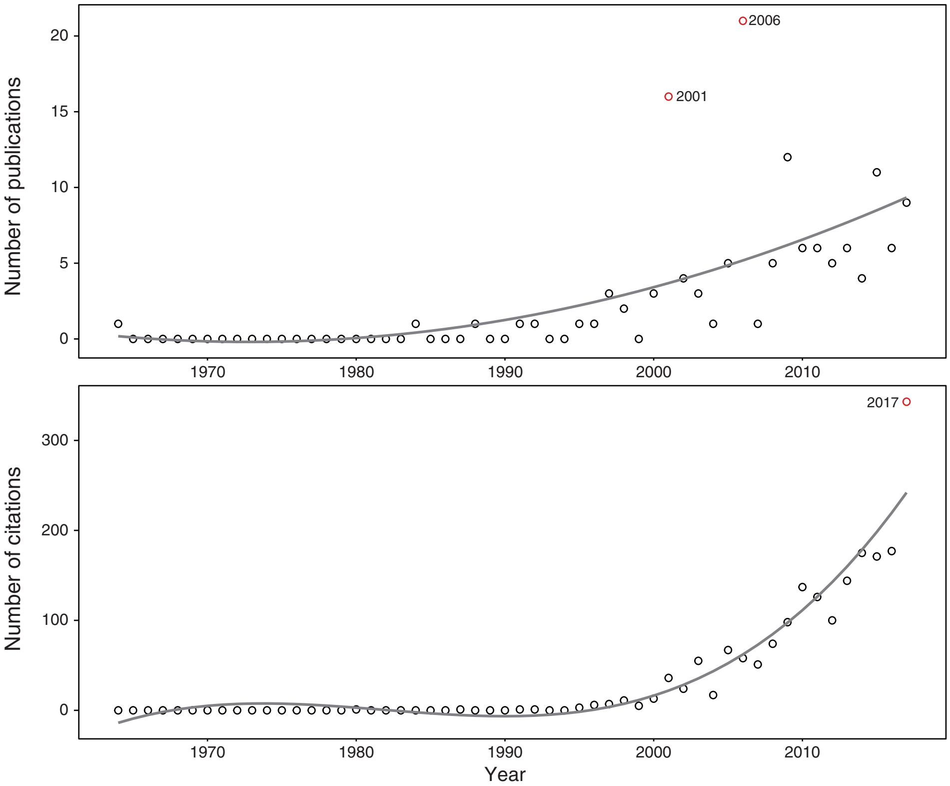

Figure 1. Number of publications (top) investigating coral restoration and number of citations of those publications (bottom) from 1964 to 2017. Data were retrieved from the Web of Science on 28 June 2018 using "coral" AND "restor*" in the title. A total of 136 publications were retrieved, with a total of 1,902 citations retrieved from those publications. The number of publications was best fit using a second order polynomial (adj. $R^2 = 0.43$) and the number of citations using a third order polynomial (adj. $R^2 = 0.92$). Red dots represent outliers with their corresponding year.

Currently, reef restoration initiatives are being planned on the world's largest coral reef system, the Great Barrier Reef (GBR), so potential methods to achieve large-scale restoration are receiving critical evaluation (e.g. Reef Restoration and Adaptation Program 2018).

Applications of mass seeding have proven to be effective for the large-scale restoration of terrestrial forests (Broadhurst et al. 2008) and seagrass beds (Busch et al. 2010), so similarly supplying reefs with sexually derived coral larvae may provide a viable approach for coral reef restoration. Coral restoration experiments have previously trialed two approaches to engineer larval supply to degraded reefs in small-scale experiments (14–96 m^2): outplanting gravid colonies onto reefs to promote local recruitment (Horoszowski-Fridman et al. 2011; Ferse et al. 2013) and "mass seeding" approaches using wild (Heyward et al. 2002) and laboratory-raised larvae (Edwards et al. 2015; De La Cruz & Harrison 2017). In those studies, outplanting gravid colonies increased planulae production compared to output from resident colonies in Horoszowski-Fridman et al. (2011) but not Ferse et al. (2013). Positive effects from mass settlement through to production of mature colonies have been observed (De La Cruz & Harrison 2017), although population effects have also been found to be negligible despite successful larval seeding (Heyward et al. 2002; Edwards et al. 2015).

The vast supply of coral larvae following annual spawning events (Babcock et al. 1986; Oliver & Willis 1987), the benefits of using genetically diverse communities for restoration (Broadhurst et al. 2008), plus the somewhat positive results from the aforementioned experiments suggest further examination of techniques to capture or produce coral larvae for large-scale restoration activities is worthwhile. Hence, in this work we examine the possible application of two approaches that aim to take advantage of sexually produced coral gametes for large-scale restoration on the GBR. One approach investigates the use of harvesting wild coral spawn slicks, whereas the other approach investigates the transplantation of gravid adult coral communities providing an initial population and a local source of larvae (Fig. 2).

Methods

Vessel

The approaches aim to take advantage of using a medium-sized trailer suction hopper dredger (TSHD) for the large-scale restoration of coral reefs. While not previously tested, it is anticipated that TSHDs offer an already existing facility with which to harvest coral slicks or colonies, retain them on the vessel in the large hopper (14,000 m^3), and transport the

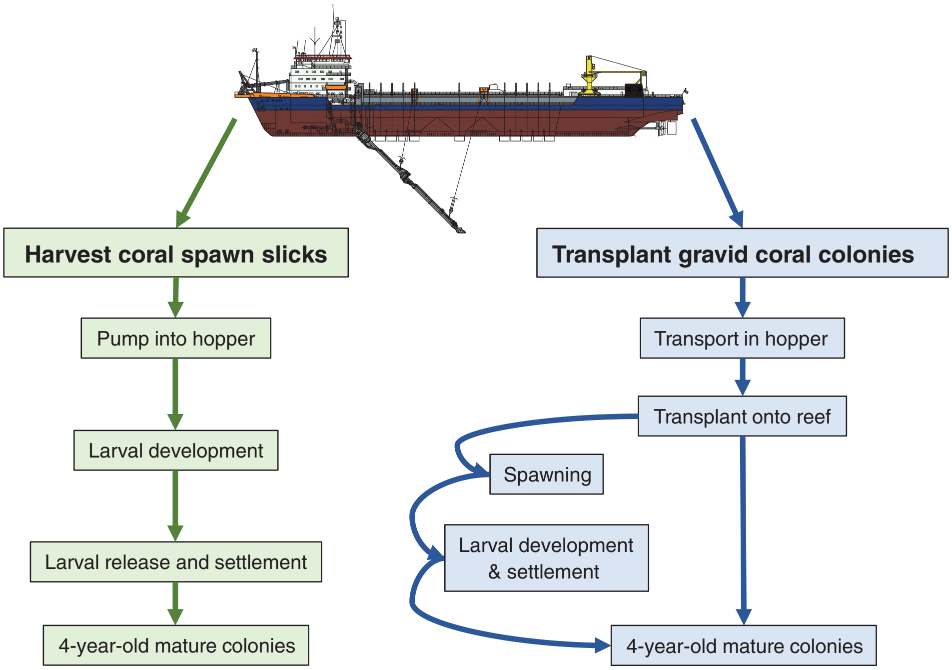

Figure 2. Conceptual diagram comparing the (left) coral spawn slick harvesting approach and (right) gravid coral colony transplantation approach for industrial-scale restoration on the Great Barrier Reef, Australia.

resources to locations necessary for release onto targeted reefs. Laboyrie et al. (2018) define a TSHD as a river- or sea-going self-propelled vessel, with one or two suction pipes, that are trailed over an area to be dredged. Excavated material is sucked up in the vessel's well or hopper, for storage and transport, until later discharge at the placement location. Emptying of the hopper functions by depositing the dredged material through doors or valves on the bottom of the vessel, or by using pumps and jets to pump it to the desired site directly or through a pipeline.

Model Functioning

The two approaches function differently in the way that coral embryos are either harvested from wild release or produced from transplanted colonies for recruitment onto a reef targeted for restoration (nominally defined as 1 ha). First, the "coral spawn slick harvest" approach aims to take advantage of the dense coral spawn slicks that are produced following annual coral spawning events (Oliver & Willis 1987). It is anticipated that surface slicks of coral spawn will be harvested the morning following spawning events, by which time fertilization of eggs has already occurred and dead sperm drifted away from the slick (Oliver & Willis 1987). Dense concentrations of embryos are collected from surface slicks and pumped into the hopper of the TSHD for development to larvae competent to settle, followed by passive release onto the target reef (Fig. 2).

Second, the "gravid coral colony transplant" approach aims to take advantage of the preservation of corals that are threatened by permanent destruction from marine construction works (e.g. dredging for port access) (Pollock et al. 2014; Ter Hofstede et al. 2016). It is anticipated that gravid coral colonies are collected, transported in the hopper of the TSHD, and transplanted onto the target reef prior to spawning. Following spawning, they release their gametes into the water column that develop until competency and settlement onto the target reef (Fig. 2).

Mechanistic models were developed to estimate the effectiveness of the two approaches for coral restoration. In essence, the models track reproductive particles beginning from a simulated mass spawning event, applying stochastic and probabilistic functions of spawning rates, fecundity, colony and propagule survival, and failure risk at different life-history stages (Fig. 3). The models estimate costs for the two approaches in USD, as well as according to three scenarios of daily retention rates, to compare effectiveness in the production and costs of coral larvae to mature colonies using the different approaches under different environmental settings. Data are produced from 9,999 simulations to incorporate variability around model parameters, which differ for each approach (Table 1).

Model Parameterization

Model parameters, values, rationale, and sources are fully detailed in Table 1. Biological values were informed by lab measurements where references could not be sourced (i.e. polyp density, eggs per polyp). A very coarse cost estimate has been anticipated for employing a medium-sized TSHD for the applications presented. Important components of the cost estimate are mobilization of the vessel (depends on its actual location just before mobilization), time the vessel is active on site (depends on the rehabilitation method used), and demobilization of the vessel (depends on the location the vessel needs to be

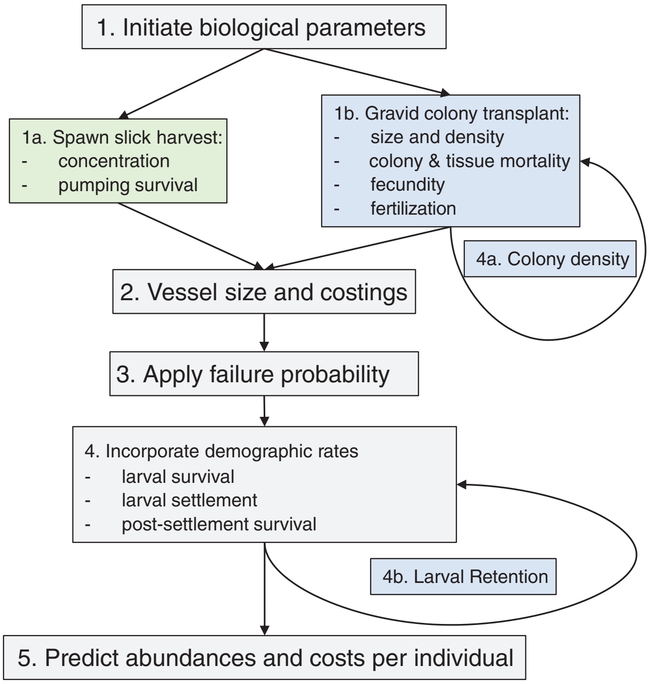

Figure 3. Work flow diagram of the slick harvesting and colony transplantation modeling approaches for industrially scaled coral reef restoration.

demobilized to). The cost of each component can be estimated by taking the envisaged duration of that component and multiplying it by an estimated day or weekly rate. The day rate of a vessel is normally situation and vessel specific. Important components that make up the day rate of a vessel are "depreciation and interest," "maintenance and repair," "consumables such as fuel," "crew," and any support vessels and crew that are needed beyond those that can be delivered by the vessel itself. Estimated costs for modifications of the vessel have been incorporated.

For our work, we assumed a mobilization and demobilization period of 2 weeks each. The "time on site" varies with the rehabilitation concept that is used—harvesting larvae should require less time on site than transplanting coral colonies—however, we have assumed 2 weeks for each approach to incorporate redundancy. In terms of daily or weekly rates, we took the normal dredging day rate as a starting point. Since the coral transplantation as well as the slick harvesting concepts mainly pump water, rather than sand and rock, it is safe to assume that the maintenance and repair cost will probably be lower than assumed under normal dredging conditions. However, when a larger part of the crew needs to consist of scientists, e.g. the crew-related part of the day rate could in fact be higher than currently used. In a more detailed design phase prior to application, precise costs would need to be determined. Overall, the costs used for our calculations have been estimated quite conservatively.

Differences in particle retention rates and colony transfer layers are estimated by modeling different scenarios. The estimated values of embryo pumping survival (0.70–0.80) and failure risk rates are identified as key components that require field testing due to their potential nonlinear impacts to the viability of the approaches. Failure risk rates are estimated to be higher for the harvest than the transplant approach (Table 1), due to the reliance on locating coral spawn slicks during a narrow time frame following a periodic event, as well as complications associated with slick formation and vessel operations under suboptimal weather conditions. Overall, the estimated values applied are all highly conservative.

Early survival rates are applied every 24 hours to release propagules. Larval settlement is instantaneous and occurs once larvae achieve competency, estimated at 5 days following release (Babcock & Heyward 1986). Settlement rates are derived from De La Cruz and Harrison (2017) and Edwards et al. (2015), to capture lower and upper limits, respectively. Presumably the lower rates of settlement are related to the state of substrata—that is, high algal competition in De La Cruz and Harrison (2017) and low algal competition in Edwards et al. (2015). Finally, post-settlement survival rates were applied in annual time-steps, using the ranges provided for different size-classes (Table 1), based on annual growth rates set to 1 cm/year (Doropoulos et al. 2015).

Transplanting techniques of coral colonies are based on Ter Hofstede et al. (2016). Two scenarios compare using two layers or one layer of coral colonies in the hopper of the TSHD during colony transfer from donor reefs to the focal reef. A coral mortality rate of 3–9% and tissue mortality rate of 15–25% for transplanted colonies due to handling stress and damage were incorporated (Ter Hofstede et al. 2016). It is estimated that five trips can be achieved in a 2-week period, inclusive of colony collection and transplantation (Ter Hofstede et al. 2016), resulting in 10,639 (1.1 colonies/m^2) and 5,320 (0.5 colonies/m^2) transplanted colonies on the 1 ha reef by using two layers or one layer of coral colonies in the TSHD per trip (Table 1). Daily particle retention rates for larvae produced by the transplantation approach vary from 100% (reference), 92% (upper), and 74% (lower) because spawning and larval development occurs in the water column at the focal reef (Table 1). In contrast, daily particle retention rates are fixed at 100% for the coral spawn slick harvesting approach due to larval containment within the TSHD hopper (Table 1).

All modeling was conducted using R version 3.4.4 (R Development Core Team 2018).

Results

Simulation modeling predicted that harvesting wild coral spawn slicks into a 14,000 m^3 hopper resulted in a median abundance of 2.2×10^9 coral embryos (Fig. 4). In comparison, the transplantation of 10,639 (two layers, 1.1 colony/m^2) and 5,320 (one layer, 0.5 colony/m^2) gravid coral colonies to a 1 ha focal reef resulted in 6.9×10^8 and 3.4×10^8 fertilized embryos released into the water column, respectively (Fig. 4). After 5 days of larval development, the median abundance of competent coral larvae remained highest using the slick harvest approach with 5.0×10^8 larvae in the vessel hopper. The transplantation approach using two layers of coral colonies during transportation and assuming 100% daily retention following spawning resulted in

Table 1. Parameterization for coral restoration models using different approaches and scenarios. Rows in italics emphasize key components that require field testing.

Variable	*Range*	*Explanation*	*Source*
1. Biological			
1a. Slick harvesting			
Embryos in slick	203–253/L	Concentration of live embryos in center of spawn slick	Oliver and Willis (1987)
Pumping survival	*0.70–0.80*	*Proportion of surviving embryos following pumping from surface slick into vessel*	*Estimated*
1b. Colony transplanting			
Colony diameter	30–40 cm	Coral colony size for transplantation	Anticipated
Polyp density	72–88/cm^2	Density of coral polyps per cm^2 of each colony	Measured using *Acropora digitifera* Heron reef
Polyp maturity	0.35–0.45	Proportion of mature polyps based on 30–40 cm diameter colonies	Álvarez-Noriega et al. (2016)
Eggs per polyp	3–10 eggs	Abundance of eggs per mature polyp	Measured using *A. digitifera* Heron reef
Transplant coral colony mortality	0.03–0.09	Proportion whole coral colony mortality following coral removal, transport, and transplanting	Ter Hofstede et al. (2016)
Transplant coral tissue mortality	0.15–0.25	Proportion of coral tissue mortality following colony removal, transport, and transplanting	Ter Hofstede et al. (2016)
Colonies spawning	0.65–0.75	Proportion of transplanted colonies spawning	Babcock et al. (1994)
Egg fertilization	$\mu = 0.55$; $\sigma = 0.14$	Proportion of spawned eggs fertilized in the water column	Oliver and Babcock (1992)
2. Vessel size and cost			
Vessel volume	14,000 m^3	Volume of a medium-sized TSHD	Van Oord
Vessel surface area	1,330 m^2	Surface area within a medium-sized TSHD	Van Oord
Vessel weekly rate	580,000 USD	Weekly rate of medium-sized TSHD	Anticipated
Mobilization	2 weeks	Time needed to mobilize vessel to working location	Anticipated
Demobilization	2 weeks	Time needed to demobilize vessel from working location	Anticipated
3. Failure risk rates			
Slick harvest	*1 in 4*	*Failure due to unanticipated risk (e.g. bad weather)*	*Estimated*
Colony transplant	*1 in 10*	*Failure due to unanticipated risk (e.g. predator outbreak)*	*Estimated*
4. Demographic rates			
Larval survival	24 h: 0.72–0.88 48 h: 0.69–0.85 72 h: 0.47–0.57 96 h: 0.31–0.38 120 h: 0.21–0.25	Proportional survival rates (hours) since embryo collection into vessel or fertilization in water column	Pollock et al. (2017)
Larval settlement	0.008–0.050	Lower and upper limits of larval settlement from water column to reef	Edwards et al. (2015) and De La Cruz and Harrison (2017)
Post-settlement survival	0–1 cm: 0.0063–0.02 1–2 cm: 0.77–0.94 2–5 cm: 0.80–1.00 >5 cm: 0.86–1.00	Proportional survival rates (size-based) since larval settlement onto the reef	Doropoulos et al. (2015); Ter Hofstede et al. (2016); De La Cruz and Harrison (2017)
4a. and 4b. Scenarios			
Slick harvesting		Harvest slicks for larval rearing and release onto reef	
Time needed	2 weeks	Variability of exact spawning times, slick collection over consecutive mornings, larval rearing prior to release	Anticipated
Extra costs	870,000 USD	E.g. wages, infrastructure, etc.	Anticipated
Embryo conc.	203–253/L	Concentration of live embryos in center of spawn slick	Oliver and Willis (1987)
Colony transplanting		Transplant gravid adult colonies onto focal reef	
Time needed	2 weeks	1 trip per day with hopper full of coral colonies	Anticipated
Extra costs	2,325,000 USD	E.g. wages, support teams, infrastructure, etc.	Anticipated
Transfer layers	1|2	Colony layers in hopper → 1.1 or 0.5 colonies/m^2 on reef	Anticipated
Daily retention %	100|87–97|69–79	Control, upper limit, lower limit modeled for GBR	Black et al. (1990)

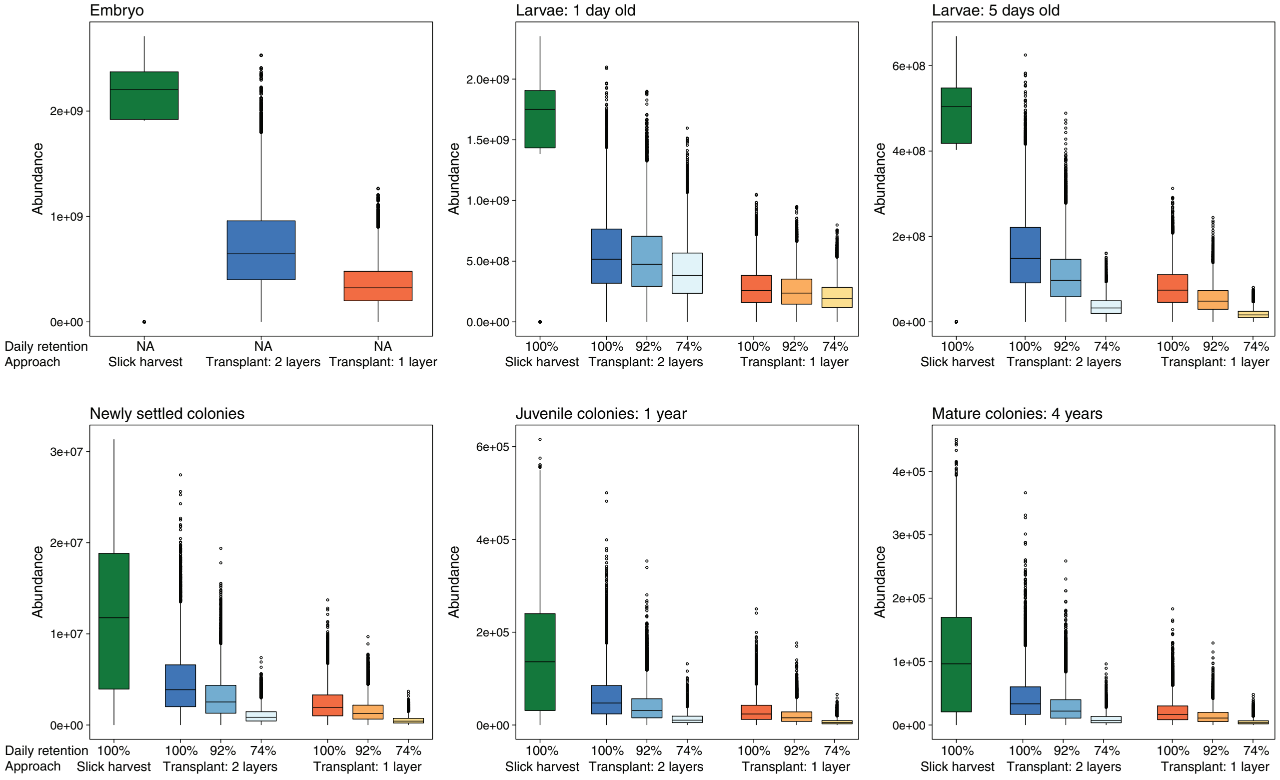

Figure 4. Abundances of embryos to mature coral colonies using different restoration approaches and scenarios. The approaches compare harvesting wild coral spawn slicks with transplanting gravid coral colonies to a 1 ha focal reef. The middle line of each boxplot indicates the median value, upper and lower hinges indicate the 75 and 25% quantiles, upper and lower whiskers represent the maximum and minimum observations +1.5× the inter-quartile range, and individual dots represent outliers.

1.5×10^8 larvae, followed by the scenario with 92% daily retention that resulted in 9.7×10^7 larvae remaining at the focal reef after 5 days. All other scenarios had less than 75 million competent larvae at the focal reef 5 days following spawning (Fig. 4). The abundance of newly settled corals on the reef ranged from 1.2×10^7 to 4.2×10^5 individuals, with the highest values predicted for the slick harvesting approach. Following 4 years of growth and survival, the slick harvest approach was predicted to have a median of 9.6×10^4 mature colonies, with the transplantation approach using two layers during transfer and 100 and 92% daily retention predicted to develop a single cohort of 3.3×10^4 and 2.2×10^4 mature colonies, respectively (Fig. 4).

Costs associated with all scenarios and daily retention rates have been calculated for each life-history stage to provide cost–benefit information for any particular strategy implemented. Costs associated with the production of coral embryos were similar using the slick harvesting and transplant approach with two layers of coral colonies during transportation, costing a median of US$0.002–0.010 per individual embryo. The transplant approach using one layer of coral colonies during transportation was double the cost, at US$0.020 per individual embryo (Fig. 5). At 5 days larval development, the cost of competent larvae remained lowest for the slick harvesting approach at a median price of US$0.01 per individual, followed by the transplantation approach using two layers during transportation at 100 and 92% daily retention, at $0.04 and $0.07, respectively. The transplantation approach using one layer during transportation with 74% daily retention was the most expensive, costing US$0.39 per 5-day-old larvae (Fig. 5). Ultimately, the median cost of 4-year-old mature coral colonies was cheapest using the slick harvesting approach at US$55 per colony. For the transplantation approach using two layers of colonies during transportation and assuming 100% daily retention of released particles, the median cost was US$206 per 4-year-old mature colony. All other scenario combinations ranged from US$314 to 1,875 per colony (Fig. 5).

Overall, harvesting wild coral spawn slicks into a 14,000 m^3 hopper to produce 500 million competent larvae would access less than 0.03% of gametes produced during a single mass spawning event from a single reef with 30% *Acropora* cover (Appendix S1, Supporting Information). A conceptual diagram of the harvesting, development, and release process is illustrated in Figure 6.

Discussion

Our study suggests the harvesting of wild coral spawn slicks provides a promising approach for boosting coral abundances

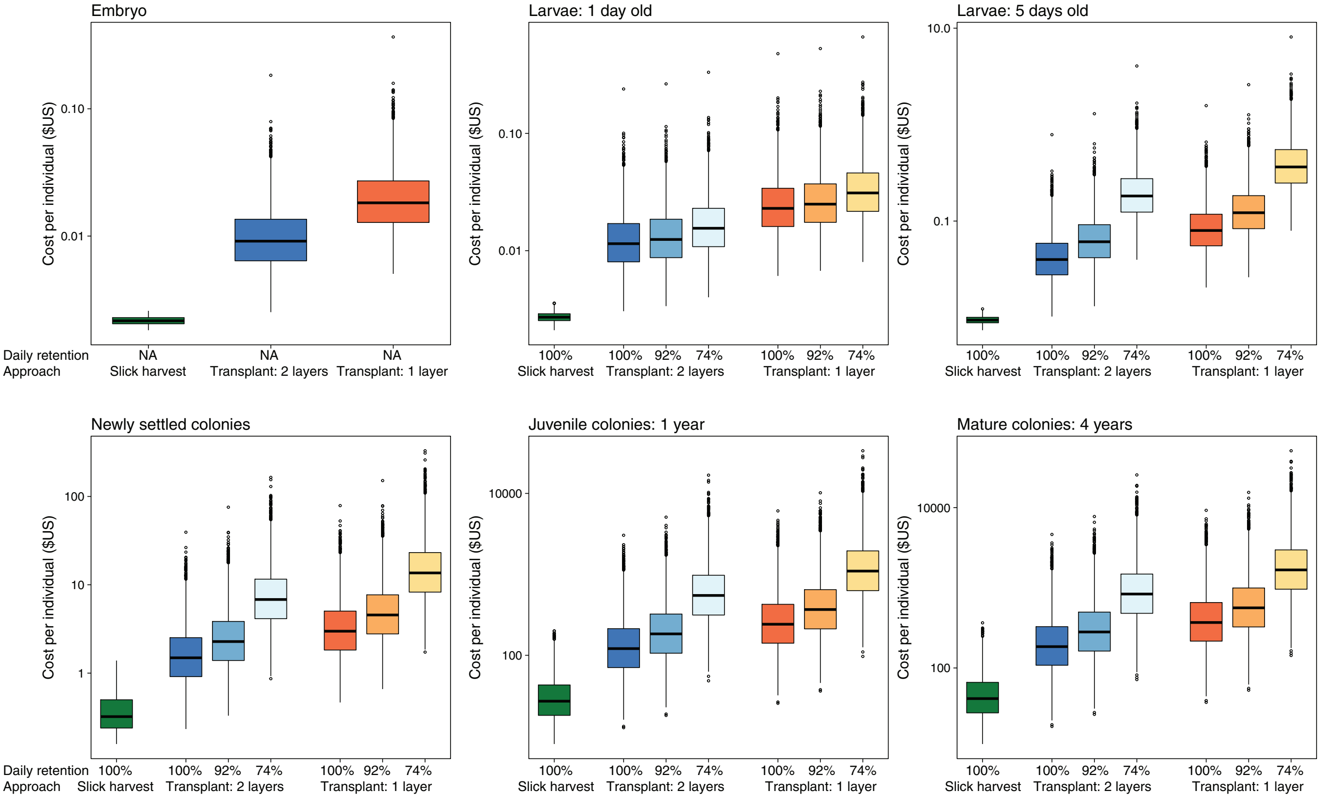

Figure 5. Cost per individual (US$) from new embryos to mature coral colonies using different restoration approaches and scenarios. Note log scale on *y*-axis. See Figure 2 legend for details.

on disturbed coral reefs at industrial-scales relevant to the GBR, and other large Indo-pacific coral reef provinces where synchronous spawning events are prominent (Baird et al. 2009) and live coral cover is high. Based on parameters from the literature and assumptions we have applied, the slick harvesting approach has better outcomes than the transplantation approach in terms of production and cost per unit of a single cohort of corals—producing billions of larvae and circa 100,000 mature colonies—with minimal impact to natal sources. Even though the gravid coral transplantation approach may not produce as many larvae to a targeted reef in a single spawning event, it has the additional benefit of instantly increasing coral cover, spawning in consecutive years with ongoing recruitment, and is more appropriate for corals with brooding reproductive modes and/or asynchronous spawning—such as those most common on Caribbean coral reefs (Baird et al. 2009). So while slick harvesting appears optimal in terms of risks to the source reef, biodiversity benefits, and cost-effectiveness, both approaches are appropriate in particular circumstances and could possibly even be combined when appropriate.

The slick harvesting and colony transplanting approaches presented in our study can achieve the scale of restoration necessary for current coral restoration targets at prices that are affordable, while removing the need for any land-based aquaculture and excessive labor costs. For example, Guest et al. (2014) showed it is feasible to produce mature corals on a reef for US$60 per colony, though it should be taken into account that the work was conducted in a developing country. Another study estimated the cost of US$160 for a substrate containing several 10-month-old juvenile colonies (Nakamura et al. 2011). Thus, even though the cost estimates used in this study are coarse and can likely be reduced through optimization, they are still predicted to be slightly cheaper than current estimates based on detailed empirical trials.

Harvesting wild coral spawn slicks is ecologically advantageous because it minimizes impacts to coral colonies while maintaining natural biodiversity. Slick harvesting would have minimal effects on the maintenance of natural coral populations because it accesses an insignificant fraction released by a coral community. Moreover, no direct interactions occur with adult coral colonies when harvesting slicks, alleviating any physical loss of coral skeleton resulting from breakage or stress. Biodiversity benefits of harvesting coral spawn slicks stem from the fact that mass spawning provides a community of larvae that reflect the genetic and species diversity of the adult coral communities from where they are released. Inclusion of genetic and species diversity are key to long-term success of restoration activities for the recovery and resilience of restored communities (Broadhurst et al. 2008; Van Oppen et al. 2017). On the GBR, mass coral spawning generally takes place over 3–4 consecutive nights following the October, November, or December

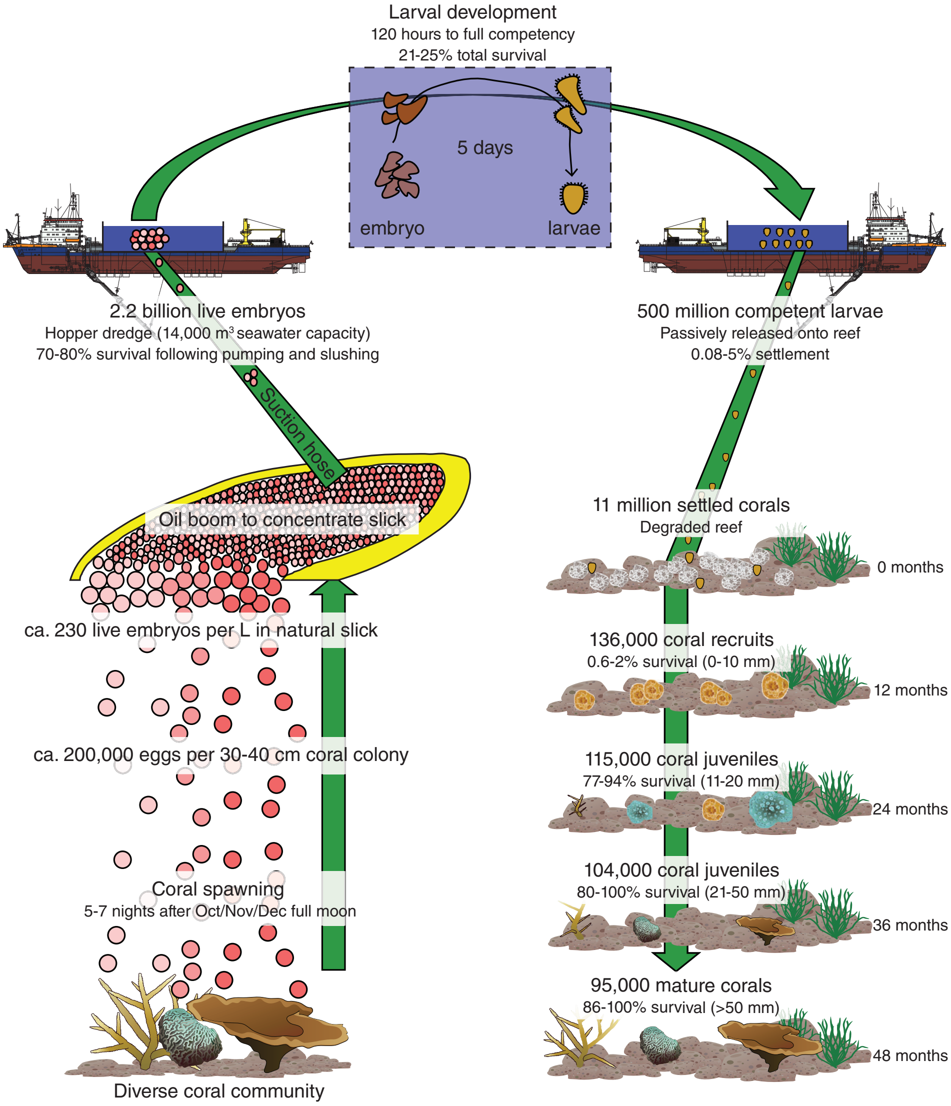

Figure 6. Operationalization of the slick harvesting approach for large-scale coral reef restoration on the Great Barrier Reef, Australia.

full moons, with different corals participating in spawning each night (Harrison et al. 1984; Babcock et al. 1986). Harvesting could, therefore, aim to occur over two or three consecutive days to optimize diversity.

Conventional transplanting techniques do incur damage or stress to adult coral colonies, which can be associated with transplantation (e.g. Ter Hofstede et al. 2016) or fragmentation (e.g. Feliciano et al. 2018). Colonies can also abort gametes, resorb or delay release following collection-induced stress, so care during handling would need to be maximized. However, transplantation of coral colonies is of value in many contexts, especially when areas of live coral are designated to be impacted by infrastructural developments such as dredging (Pollock et al. 2014; Ter Hofstede et al. 2016). Using such "corals of opportunity" presents a valuable resource that can be strategically transplanted on permanent or transportable structures to act as a "coral engine" (sensu Van Oord 2017) for larval production in a given area. For example, if a reef is designated as having high connectivity to many nearby degraded reefs that require external larval supply (Doropoulos & Babcock 2018), the coral engine can be transferred to that location prior to reproduction. Moreover, larvae from corals that use a brooding reproductive strategy will not be captured when harvesting coral spawn slicks because they do not participate in synchronous mass spawning events or release positively buoyant gametes. The relative abundance of corals that spawn or brood their offspring also varies regionally, with the Caribbean containing relatively more brooding than spawning corals, in contrast to Indo-Pacific reefs (Baird et al. 2009). Therefore, the optimal approach is also related to local settings, and transplanting corals of opportunity can be used to target particular functional groups and in particular reef environments that complement those sourced using the harvesting approach.

While our modeling has used the best available data for parameterization, our evaluation of the approaches is contingent on some key, untested assumptions that require empirical investigation before full-scale implementation can take place. First, embryo survival rates following pumping from the water into a vessel were estimated at 0.70–0.80. This estimate requires testing to improve model predictions, and pumping configuration development and trialing could aim to improve survival. Second, embryo concentrations in wild coral spawn slicks have only been reported in the literature in a single study and with no replicate samples (Oliver & Babcock 1992). The concentration of live embryos in wild slicks will have massive natural variability, so actual concentrations encountered at the time of harvesting are likely to be both higher and lower than this reported value, with direct impacts to the efficiency of the harvesting approach. Third, the risk and cost terms incorporated into both scenarios are conservative best-guess estimates; we have modeled the harvest approach with 2.5 times more failures than the transplant approach, and costs for vessels will in practice vary with factors such as re-location costs and context-specific requirements for operations on particular reefs. From an execution perspective, harvesting coral spawn slicks appears riskier as the entire operation depends on a periodic event, and the formation of slicks can be highly dependent on weather conditions, whereas the transplantation of gravid colonies prior to spawning is not restricted by the same narrow timeframe. However, spawning generally occurs at low-intermediate wind speeds (Keith et al. 2016), and the use of helicopters to spot and oil booms to concentrate slicks can help alleviate risk, in addition to mass spawning occurring over multiple nights within a given region. Importantly, factors such as water quality and exposure to external stressors (e.g. high risk of thermal anomaly, crown-of-thorns outbreak) would also need to be considered prior to application of any transplantation or reseeding (Doropoulos & Babcock 2018; Gilby et al. 2018; Ladd et al. 2018). Furthermore, while we accounted for the effects of benthic state on larval settlement rates, ranging from optimal (Edwards & Gomez 2007) to suboptimal (De La Cruz & Harrison 2017), competition effects have not explicitly been incorporated in this work for post-settlement growth and survival. Consideration of ecological processes on the benthos is critical for the long-term success of active coral restoration (Ladd et al. 2018); e.g. macroalgal removal is suggested to be labor-intensive and should be coupled with natural processes such as enhanced herbivory to optimize restoration (Ceccarelli et al. 2018).

Our study has found that harvesting wild coral spawn slicks provides an opportunity for industrial-scale reef restoration under rapidly changing environmental conditions. One full execution of slick harvesting could result in the production of circa 100,000 mature colonies on targeted reefs 4 years following harvesting, rearing, and release. Yet prior to full-scale execution, smaller-scale trials are needed for test harvesting and husbandry methodologies to refine logistics and parameters. The approach could also be combined with complementary techniques to restore impacted reefs, including transplanting adult corals, especially for brooding species, or as part of efforts to increase the potential of coral populations to resist bleaching. Experimental techniques include translocating larvae released from heat tolerant corals to reefs at risk of bleaching, “heat hardening” of larvae during translocation, and adding heat tolerant *Symbiodinium* to the larvae during development (Anthony et al. 2017; Van Oppen et al. 2017). In addition to, and not in replacement of, best management practices that aim to conserve optimal reef state (Mumby & Steneck 2008), this study provides a foundation for industrial-scale coral reef restoration aimed to restore reef state and function under anthropogenic stress.

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Supporting Information

The following information may be found in the online version of this article:

Appendix S1. Estimating impact of slick harvesting relative to amount released from a single mass spawn event.

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