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LETTER

Accounting for Life-History Strategies and Timescales in Marine Restoration

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Abstract

Understanding the drivers of restoration success is a central issue for marine conservation. Here, we explore the role of life-history strategies of sessile marine species in shaping restoration outcomes and their associated timescales. A transplantation experiment for the extremely slow-growing and threatened octocoral *Corallium rubrum* was highly successful over a relatively short term due to high survival and reproductive potential of the transplanted colonies. However, demographic projections predict that from 30 to 40 years may be required for fully functional *C. rubrum* populations to develop. More broadly, a comprehensive meta-analysis revealed a negative correlation between survival after transplanting and growth rates among sessile species. As a result, simulated dynamics for a range of marine sessile invertebrates predict that longer recovery times are positively associated with survival rates. These results demonstrate a tradeoff between initial transplantation efforts and the speed of recovery. Transplantation of slow-growing species will tend to require lower initial effort due to higher survival after transplanting, but the period required to fully recover habitat complexity will tend to be far longer. This study highlights the important role of life history as a driver of marine restoration outcomes and shows how demographic knowledge and modeling tools can help managers to anticipate the dynamics and timescales of restored populations.

Introduction

Marine coastal ecosystems host high levels of biodiversity and provide goods and services to a large proportion of the world's human population (Palumbi *et al.* 2008). The cumulative effects of multiple stressors such as overfishing, habitat destruction, and pollution together with new global threats (i.e., climate change and biological invasions) have driven compositional changes, local extinctions, and wholesale destruction of many benthic communities (Jackson *et al.* 2001; Airoldi & Beck 2007). To face this challenge, actions at both global (i.e., reduction of greenhouse gas emissions) and local levels are urgently needed (Kennedy *et al.* 2013). At local

scales, fishery regulations and marine protected areas can help to reduce or remove threats (Edgar *et al.* 2014). Even so, when the resilience of natural systems has been seriously diminished, active restoration may be necessary as a complementary tool to restore damaged populations and communities (Possingham *et al.* 2015).

Over the last few decades, the success of ecological restoration efforts in terrestrial landscapes has improved dramatically, with successful examples of enhancing ecosystem structure and function, and the provision of ecosystem services (Benayas *et al.* 2009; Perrings *et al.* 2015). In the marine realm, however, restoration approaches have generally been successful only at very small spatial scales and continue to present many

challenges (Edwards & Gomez 2007; Rinkevich 2015). Strikingly, the degree of success in marine restoration actions is not generally related to the underlying costs of the project (Bayraktarov *et al.* 2016). This is partly due to the high methodological constraints, but also due to relatively poor understanding of the drivers underlying successful actions.

Habitat-forming species such as corals and seagrasses have been the primary targets of marine restoration activities, and transplanting asexually produced units (i.e., coral fragments or seagrass shoots) has been proposed as the tool of choice for recovering habitats by bypassing sensitive early life stages (Edwards & Clark 1998). Recently, research has shown that corals display high survival rates after transplanting when compared to the dominant organisms found in seagrass beds, oyster reefs, or saltmarsh ecosystems (Bayraktarov *et al.* 2016). However, this generalization ignores the high diversity in life-history strategies of the dominant species in these benthic communities (Darling *et al.* 2012; Madin *et al.* 2014). Indeed, life-history tradeoffs between demographic rates have been observed in hard coral species, suggesting potential effects on short-term and long-term restoration success (Edwards & Clark 1998; Dizon & Yap 2006; Glassom & Chadwick 2006). Yet, quantitative evidence of how the life history of target species shapes restoration outcomes is lacking in the scientific literature. To advance the theoretical framework of marine restoration and provide tools to enhance the effectiveness of transplantation efforts, we need to go beyond habitat type toward a fuller quantitative analysis of how life-history patterns determine the best strategies or allow better prediction of the speed and eventual success of restoration efforts.

To date, most studies of transplant success in marine systems have focused on survival rates of transplanted individuals over relatively short monitoring periods (usually less than 2 years) (Bayraktarov *et al.* 2016). However, a broad goal of restoration efforts is to recover structural complexity that can provide ecosystem services at rates similar to natural ones. Thus, when planning restoration actions, managers should consider the factors affecting the time required from any transplantation action to reach the restoration goals for the target species and habitat. Long-term monitoring programs can provide suitable data to inform this issue, but funding often constrains the duration of monitoring after restoration actions and experiments (Precht & Robbart 2006; Lindenmayer & Likens 2009). Demographic modeling methods such as matrix and integral projection models (IPMs) (Morris & Doak 2002; Ellner & Rees 2006) can be used to synthesize individual data into predictions of the longer term development of transplanted populations (Linares *et al.* 2008).

In the present study, we combined demographic monitoring of transplanted and natural colonies of a temperate coral species, a comprehensive literature review of tradeoffs in the life histories of sessile marine species, and the use of population projection models to explore the dynamics of transplant efforts targeting species with different life histories. Our results support the utility of explicitly linking life-history theory to marine restoration and provide an illustrative example of anticipating the expected dynamics and timescales of restored ecosystems.

Methods

Study system

The precious red coral *Corallium rubrum* is a structural octocoral of a highly diverse coralligenous assemblage of the Mediterranean Sea and also possesses important cultural and economic value. Due to historical overexploitation, most shallow populations of *C. rubrum* can be considered functionally impaired and many are ecologically extinct (Bruckner 2009; Tsounis *et al.* 2010). To reverse this situation, an international agreement urged Mediterranean countries to strengthen their *C. rubrum* fishery regulations during the last decade (Cau *et al.* 2013). Unfortunately, the lack of enforcement of regulations on coral harvesting along with poaching is widespread across the Mediterranean basin and represents a major problem for the management of the species, hindering the effectiveness of its conservation (Linares *et al.* 2012).

Study area and transplant experiment

In 2011, the Catalan authorities intercepted 14.5 kg of illegally harvested *C. rubrum* along the Montgrí Coast (Catalonia, Spain). About 300 red coral colonies, a small portion of the intercepted colonies, were selected for a transplant experiment. These colonies were initially kept at 16 °C and fed in aquarium facilities at the Institute of Marine Sciences in Barcelona (Spain). After 1 week, the colonies were transported in coolers to the Parc Natural del Montgrí, Illes Medes i Baix Ter in the NW Mediterranean and transplanted onto a rocky wall ranging from 15 to 17 m depth using a two-component epoxy putty as glue. The site was chosen because some sparse red coral colonies were found in the vicinity, indicating its suitability for the species (Figure 1).

Demographic traits

Four transects were established within the transplanted population and surveyed through photographic sampling after transplantation, in May 2011, and again in

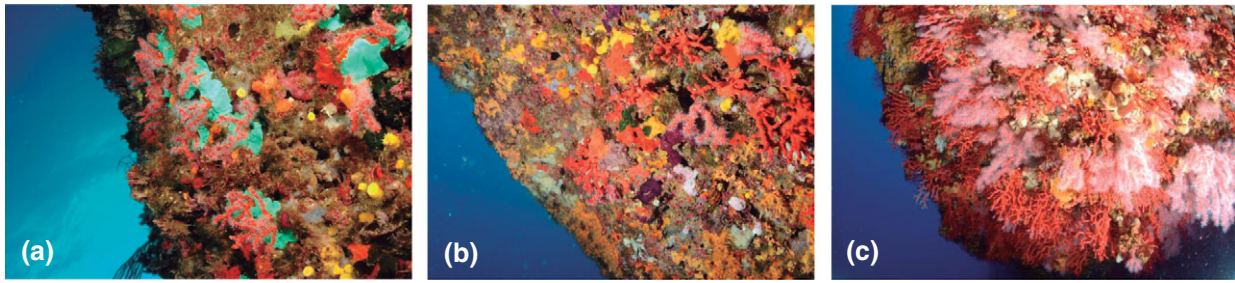


Figure 1 Restoration of *Corallium rubrum* populations. (a) A new population was transplanted in 2011; (b) most transplanted colonies survived in 2015, after 4 years of transplantation; and (c) natural well-protected *C. rubrum* populations with large colonies were used as a baseline to assess the time periods required for restoration actions. Images: J. Garrabou.

May 2015 (Figure 1). Survival rates of the transplanted colonies were quantified by individually identifying coral colonies from the photographic series from 2011 and 2015. Natural survival rates of *C. rubrum* colonies were calculated from long-term data on eight natural populations. (See Supplementary Methods for a complete description of surveys.) Reproductive potential of colonies was estimated for a sample of transplanted colonies ($n = 35$) outside the monitored transects and from a natural adjacent population ($n = 35$) in late June of 2015 by counting *C. rubrum* larvae found inside the polyps of the fertile female colonies (Tsounis *et al.* 2006). Samples were collected by SCUBA diving and fixed in 4% formaldehyde. At the laboratory, 15 polyps per sample were dissected and larvae found inside the polyps were counted.

Literature review

We explored life-history tradeoffs in marine restoration experiments following two steps. First, we systematically reviewed all transplantation experiments of marine sessile species that we could identify in a search of the literature up to November 2015. Using *Google Scholar*, we searched for a combination of the terms “restoration,” “transplantation,” or “rehabilitation” with a second term related to marine sessile taxa: “coral,” “gorgonian,” “sponge,” “macroalga,” or “seagrass.” We then selected those studies that conducted experimental transplants as a restoration technique and reported survival rates at least 1 year after transplanting.

We also compiled data on growth rates of sessile marine species since this vital, or demographic, rate is highly correlated to overall life history (Darling *et al.* 2012). We searched available studies reporting standard data on linear extension rates to approximate average species-specific growth rates for corals (Madin *et al.* 2016). In seagrasses, mean horizontal rhizome elongation rates were used as an indicator of the species growth rate (see Marbà

& Duarte 1998); thus, seagrass and sessile invertebrates were analyzed separately.

Demographic projections

Red coral

To synthesize data on growth, survival, and reproduction into predictions of population growth and increasing sizes within populations, we used IPMs parameterized with long-term demographic data from several natural red coral populations. Full description of data analysis and model construction are given in the Supplementary Material S1. Based on annual IPMs, we computed 1,000 stochastic projections assuming that all annual models can occur with equal probability at each time-step. Maximum height of transplanted colonies was measured in 2015 using photogrammetric techniques (Drap *et al.* 2013) and the distribution of heights was used to establish the starting population vector for the projections.

Linares *et al.* (2010) argue that the structural complexity of *C. rubrum* populations can be assessed by quantifying the proportion of large colonies (>100 mm), since these larger colonies provide structural complexity. Based on this parameter, we compared the outputs from our population projections to the proportion of large colonies in three relatively unimpacted *C. rubrum* populations that are located within old and well-enforced Mediterranean marine protected areas (Figure 1 & S1, Linares *et al.* 2010).

Comparative analyses

We also searched the literature for published matrix population models of other marine sessile species. We then used these models to perform deterministic population projections of 100 individuals starting at the smallest size class and computing time periods until the population reached a proportion of large individuals (largest size

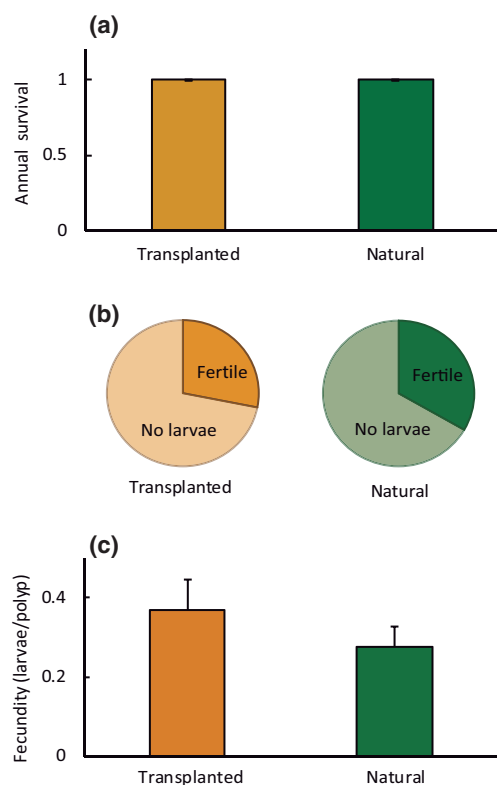


Figure 2 Demographic traits in transplanted and natural *C. rubrum* populations. (a) Mean annual survival rates; (b) proportion of fertile colonies; and (c) mean polyp fecundity, calculated as the frequency of larvae found per polyp within fertile colonies.

class) equivalent to the 20% and 80% of the expected proportion when reaching the stable stage distribution.

Results

Demographic traits of *C. rubrum* transplanted colonies

After 4 years, 99.1% of transplanted *C. rubrum* colonies were still alive. Annual survival rates of transplanted colonies did not show significant differences from control populations (Figure 2a). Transplanted colonies also had similar reproductive potential to colonies in natural populations, considering both the proportion of fertile colonies and the frequency of larvae per polyp (Figure 2b & c).

Comparative survival and growth in transplant experiments/actions

We found 50 studies that allow calculation of mean annual survival rates after at least 1 year following transplanting for a total of 59 marine structural species

(Figure 3a). These included 40 species of hexacorals, which have a mean annual survival of 60.8% (range of 6.8–98.6%); five species of gorgonians, including the present study, with mean annual survival of 48.1 (range of 30.0–99.1%); one species of sponge, with mean annual survival of 85.7%; 11 species of seagrasses, with mean annual survival of 42.5% (range of 28.9–69.2%), and two seaweeds, with mean annual survival of 43.1% (range of 25.1–80.0%). We observed a significant negative correlation between survival after transplantation and the species mean growth rates measured under natural conditions in marine sessile invertebrates (Figure 3b; $n = 35$; Pearson's $r = 0.47$, $P = 0.005$; Spearman rho = 0.37, $P = 0.046$). Seagrass species revealed a parallel pattern (Figure 3c; $n = 8$; Spearman rho = 0.81, $P = 0.022$), although the relationship was only marginally significant according to Pearson's correlation (Pearson's $r = -0.69$; $P = 0.059$). Growth data measured in natural and transplanted colonies for coral species were also highly correlated (Figure S3, $n = 17$; Pearson's $r = 0.85$; $P < 0.001$).

Demographic projections and recovery periods

Red coral

The transplanted population in 2015 was dominated by small individuals (most red coral colonies were < 35 mm in height, Figure 1 & S1), while natural red coral colonies had extremely low growth rates (Figure S2). The stochastic IPMs incorporating these traits showed that a period ranging from 30 to 40 years after transplanting is needed for populations to have a proportion of large colonies comparable to that seen in the well-preserved *C. rubrum* populations used as an ecological reference (Figure 4).

Comparative analyses

The simulated recovery periods for 41 marine sessile species were highly variable in length, ranging from years to several decades (Figure 5 & Table S3). The expected recovery length was strongly and positive associated with the species' mean survival rate regardless of the conservation goal ($n = 41$; 20% threshold: $R^2 = 0.419$; $P < 0.001$; 80% threshold: $R^2 = 0.495$; $P < 0.001$). After accounting for potential artifacts due to different matrix dimensions, mean survival rates were still a strong predictor of the expected recovery periods (Table S1).

Discussion

Marine restoration is a relatively young discipline with most efforts only operating at very small spatial scales (Bayraktarov *et al.* 2016). Filling knowledge gaps on the processes underlying restoration success is therefore

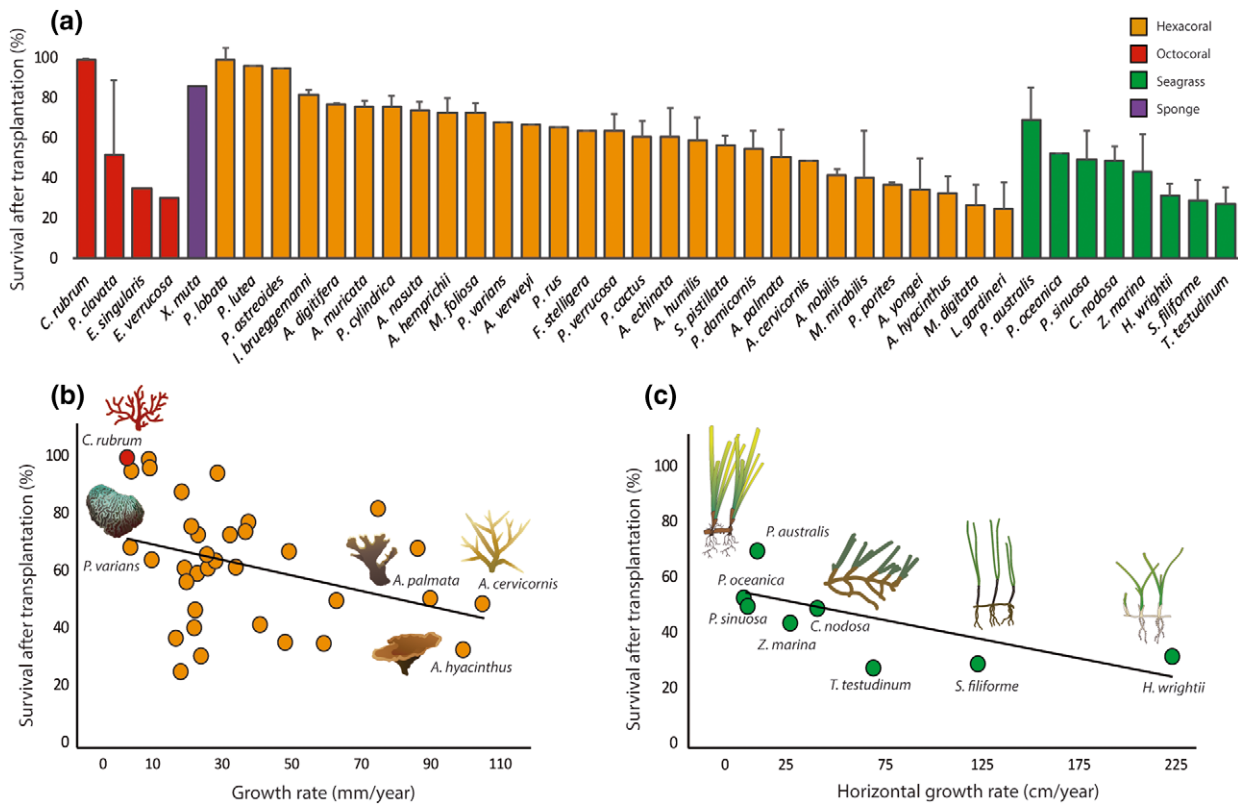


Figure 3 Survival rates of marine sessile species in transplant experiments. (a) Mean annual survival rates (Mean \pm SE). (b) Life-history tradeoff between survival after transplantation and growth rates in 35 marine sessile invertebrate species and (c) life-history tradeoff between survival after transplantation and growth rates in eight seagrass species. Each dot represents a species for which mean annual survival after transplantation and mean growth rate could be calculated from a range of published studies (see Table S1). In seagrass species, growth represents mean horizontal rhizome elongation rate (see Marbà & Duarte 1998). Images: Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/symbols/).

crucial to help further develop this field and ensure meaningful planning and success over larger spatial and temporal scales. In this study, we quantify the role of life history in shaping restoration outcomes and demonstrate a consistent tradeoff between survival and growth across different taxa with contrasting life history and functional traits, which in turn drives a tradeoff between required minimal transplantation effort at the start of a project and the minimum possible speed of ecosystem recovery.

Anticipating mortality patterns after transplantation is central to the design of any restoration action since it may determine the initial attaching effort required to achieve specific conservation goals. Here, a systematic review of transplantation experiments from tropical and temperate habitat-forming species revealed a negative tradeoff between growth and survival after transplantation that was supported in spite of differences in experimental techniques and physical properties of the environment that were not explored (Figure 3b). Slow growing massive hard corals such as *Porites*

astreoides and *P. lutea* and the sponge *Xestospongia muta* showed the highest survival after transplantation, with rates ranging from 86% to 98%. On the contrary, fast-growing corals such as *Acropora cervicornis*, *A. yongaei*, and *A. palmata* had survival rates that ranged from 35% to 44%. These results were consistent with previous transplant experiments in tropical coral species with contrasting life histories (Edwards & Clark 1989; Dizon & Yap 2006). Similarly, among seagrasses, the three slow-growing *Posidonia* species showed higher shoot survival after transplantation (from 49% to 69%) compared to faster growing *Syringodium filiforme* (29%) and *Halodule wrightii* (27%) (Figure 3c). Our findings are in agreement with allocation theory, which predicts that tradeoffs between vital rates such as growth, reproduction, and survival may arise from energetic constraints acting at physiological levels (Stearns 1989). Further, branching morphologies associated with faster life histories may increase exposure to physical damage and result in higher mortality rates (Madin et al. 2014).

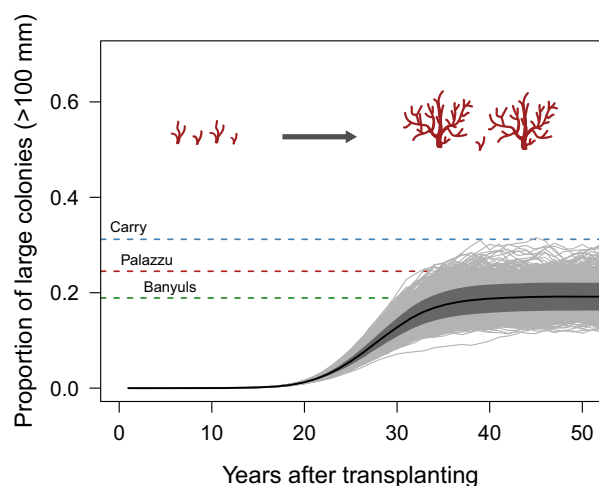


Figure 4 (a) Predicted temporal dynamics of the *C. rubrum* population size frequency distribution. Black line represents the mean and shaded area represents the standard error of 1,000 stochastic projections. The size frequency distribution of three natural and well-protected *C. rubrum* populations (dotted lines) was used as an ecological baseline (Linares et al. 2010).

There are also a number of external drivers that can strongly influence restoration success such as predation and herbivory, density of transplants, and catastrophic events (Shaish et al. 2010; Gomez et al. 2014). In spite of the clear importance of these effects, our results show that species' life histories can still provide strong predictive power concerning the outcome of trans-

plantation projects. Better understanding of both the intrinsic and extrinsic drivers of mortality patterns after transplantation would be ideal and could lead to the implementation of more successful restoration designs, since this combined approach can better define both anticipated time periods for restoration and also the relative benefits of direct transplantation effort.

There have been major international calls to ban the international trade in precious coral and to implement management regulation aimed to ensure the conservation of these species (Bruckner 2014). Yet, the feasibility of restoration actions for these emblematic species has remained uncertain and this may hinder the potential for development of future restoration plans. In the present study, we observed that the colonies of the octocoral *C. rubrum* were extremely resistant to the stress of transplantation, displaying high survival rates similar to those in natural populations (Figure 2a, Garrabou & Harmelin 2002). It is remarkable to observe this high survival rate in transplanted *C. rubrum* colonies that were subject to the stresses of being harvested, kept out of the water in the poachers' nets, transported, maintained in aquaria for 1 week, and then transplanted back into natural habitat. Yet, these transplanted *C. rubrum* colonies had a similar proportion of fertile colonies and even higher frequency of larvae per polyp after 4 years than observed for colonies in natural populations (Figure 2b & c). Assessing reproductive potential is also critical when working with most marine sessile species which, like *C. rubrum*, show limited larval dispersal and

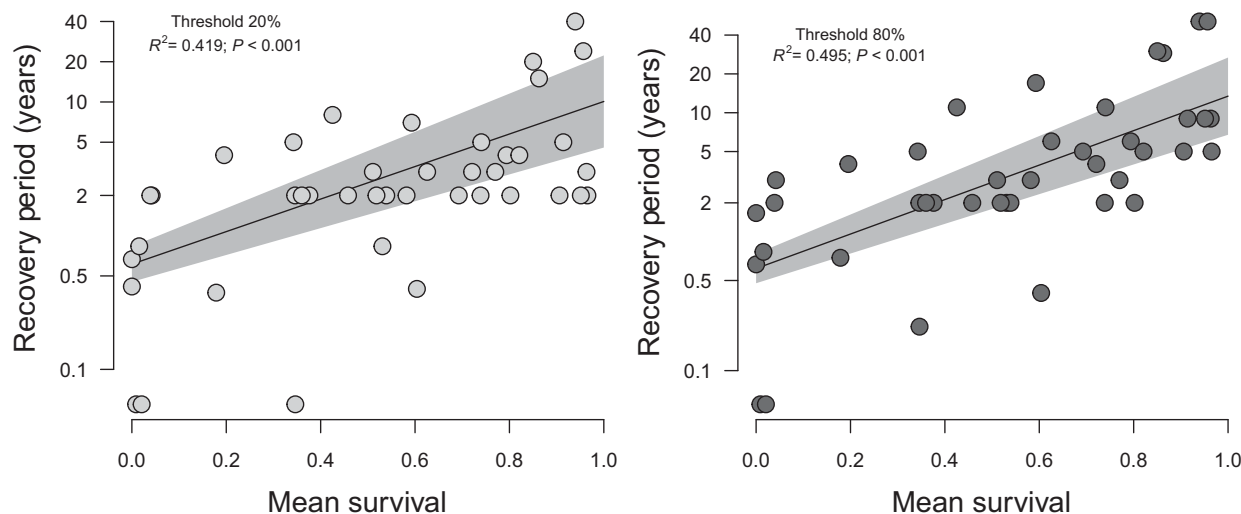


Figure 5 Projected recovery times for 41 marine sessile invertebrate species using published matrix populations models (Table S3) and setting a recovery threshold of (left) 20% and (right) 80% of the number of large colonies expected in a population at the stable stage distribution. The black lines and the shaded areas correspond to the mean and standard errors of the linear models (Table S1).

high self-recruitment rates (Ledoux *et al.* 2010). Indeed, to effectively recuperate populations through a single transplantation effort, newly restored populations must also be viable in the long term, with reproduction reaching natural rates. Here, the high survival and reproductive potential displayed by transplanted *C. rubrum* confirmed the potential success of this restoration action and strongly support the feasibility of these techniques, at least at local spatial scales, with potential applications for other long-lived precious coral species.

As important as choosing a suitable species and restoration method is considering the appropriate time scale and ecological baselines over which to evaluate restoration outcomes or to expect the restoration of ecological functions (Bull *et al.* 2014). Stochastic projections developed here revealed that periods ranging from 30 to 40 years may be necessary for newly established *C. rubrum* populations to show a colony size distribution comparable to those observed in well-preserved natural populations (Linares *et al.* 2010). These results suggest that, similar to relatively fast-growing terrestrial forest systems (Vesk *et al.* 2008), long-lived coral stands can take up to several decades to recover their functionality and to allow the development of associated organisms, such as fish and invertebrates, as may occur in tropical coral reefs (e.g., Cabaitan *et al.* 2008). More interestingly, we found that potential recovery periods can be accurately predicted by the specific mean survival, demonstrating the strong influence of the species' life histories on the temporal scales associated with restoration actions (Figure 5).

Overall, this study demonstrates a tradeoff between initial transplantation effort needed to achieve a target density of individuals and the speed of recover that may be achieved in a restoration action. For instance, targeting fast-growing species such as *A. cervicornis* or *A. hyacinthus* (with survival rates ranging from 40% to 50%) will require a twofold to threefold initial amount of attached colonies to obtain the same density of survivors compared to actions targeting slow-growing-resistant species such as the red coral *C. rubrum* or the massive coral *P. lutea*. On the other hand, life histories of the target species will also have a strong effect on the expected recovery periods that may vary as much as 20–30 years (Figure 5). Finally, because life history and functional traits are highly correlated (Adler *et al.* 2014), favoring specific strategies can have long-term consequences for habitat complexity and ecosystem responses to global change (Ortiz *et al.* 2014).

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Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's web site:

Figure S1. Population size frequency distribution of the transplanted colonies represented by the brown bars and the brown line.

Figure S2. Size-dependent growth of *C. rubrum* colonies based on data from two natural populations.

Figure S3. Growth rates in natural versus transplanted coral colonies (log-scale) for 17 coral species.

Table S1. Summary statistics for the linear model fitted to the expected recovery periods.

Table S2. Source data of survival in transplant experiments and growth references of the marine sessile species included in the comparative analysis.

Table S3. Source data of population matrix models used to project potential recovery periods.

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