

**Ecological implications of marine silviculture: The use of nursery-grown coral
transplants as ecological engineering tools for reef restoration**

Yael Bina Horoszowski-Fridman

A THESIS SUBMITTED FOR THE DEGREE

“DOCTOR OF PHILOSOPHY”

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University of Haifa

Faculty of Natural Sciences

Department of Evolutionary and Environment Biology

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Ecological implications of marine silviculture: The use of nursery-grown coral transplants as ecological engineering tools for reef restoration

Yael Bina Horoszowski-Fridman

Abstract

Coral reefs create major biodiversity ‘hotspots’ that provide human populations with vital ecosystem goods and services. Unfortunately, coral reefs around the world are experiencing rapid degradation as a result of anthropogenic activities and intensifying global changes. The limitations of traditional management efforts to avert reef loss raises an urgent need for new active restoration approaches that will enable reef reconstruction capable of supporting sustainable coral and reef-associated species adaptation despite the growing surrounding threats. The marine silviculture approach ‘*gardening coral reefs*’ is an emerging reef restoration methodology centered on ecological engineering tools. Inspired by forest restoration rationales, this two-phase practice consists of (a) farming numerous new coral colonies to plantable size in underwater coral nurseries, and (b) transplanting the farmed colonies onto degraded reefs. Due to the novelty of this marine silviculture approach, the second phase of the gardening methodology has not yet been fully explored. This dissertation aims to advance the nascent field of active reef restoration through the research of farmed-coral transplants performance, and through the study of silviculture rationales applicable for coral reef restoration purposes. It explores the theory and practice of using nursery-grown coral transplants as ecological engineering tools to enhance biodiversity, resilience, and overall sustainability of restored reefs. The first part of the dissertation focuses on reproductive features of farmed coral transplants, providing two studies that examine the ability of nursery-bred corals to reproduce after transplantation onto damaged reefs. In the first study, the reproductive outputs of nursery-farmed *Stylophora pistillata* colonies from three transplantation trials and naturally-grown colonies at the restoration site were studied and evaluated during three reproductive seasons post transplantation in Eilat (Red Sea, Israel; Study 1). The transplanted colonies not only reproduced at their new resident site, but showed better reproductive capacities than the natal *S. pistillata* colonies. A higher percentage of nursery-bred colonies released planula larvae and gravid transplants

also shed more planulae per colony compared to natal colonies, yielding significantly higher total planulae figures in the transplanted vs. the naturally developed *S. pistillata* colonies. In order to evaluate if this enhanced reproductive performance is limited to the initial reproductive seasons or can sustain over a longer period of time at the degraded reef, the study of the reproductive outputs of farmed transplants was extended to eight reproductive seasons (7.5 years) following transplantation (Study 2). Although natal and transplanted corals grew side by side at the disturbed environment, the nursery-grown transplants continued to show enhanced larval release (2.6-22.5 times more planulae/colony; 11.6 ± 1.8 planulae/transplant vs. 1.5 ± 0.3 planulae/natal colony; multiyear average of 8 reproductive seasons) and higher percentages of gravid colonies ($91 \pm 2.1\%$ transplants vs. $34 \pm 7.6\%$ natal colonies) throughout the 7.5 years study period. The inveterate heightened larval production of transplants maintained for such a long period of time post transplantation reveals a possible enduring impact of nursery conditions on fitness and ecological traits of transplants. Moreover, the research highlights the ecological engineering capacity of nursery-bred transplants to enhance the larval pool and reseed degraded reefs. The second part of the dissertation explores the first time use of a novel transplantation approach named '*Reef Carpets*', which resembles the commercially available turf grass units used in terrestrial lawn-gardening (Study 3). Preset coral units of three branching species, *Acropora variabilis* (N=132), *Pocillopora damicornis* (N=212) and *S. pistillata* (N=364), were cultured at the coral nursery and deployed along with the annexed reef biota accumulated during nursery-period on a sandy bottom substrate in Eilat. The *Reef Carpets* coral performance was monitored during 17 months following their transfer from the protective nursery conditions to a rather hostile environment. The research included the study of transplants' survival rates, partial mortality, self-attachment, damage from fish and gastropod corallivores, and the reproductive outputs of *S. pistillata*. Additionally, the transplants' ecosystem engineering effect on reef-associated species was studied by monitoring the natural recruitment of the reef-associated fauna and analyzing the structure and species diversity of the developing fish and invertebrate communities in the Reef carpeted areas. The transplantation of the *Reef Carpets* resulted in an immediate reef structure that supported coral recruitment and provided ecological niches for coral-associated invertebrates and fish. The 17 month monitoring of the *Reef Carpet* corals revealed high species specific survival rates (50-65%), a dynamic partial mortality pattern similar in the three transplanted coral species, and a significant increase of transplants' self-attachment. The moderate fish corallivory

documented at the restoration site was more intense for *A. variabilis* and *S. pistillata* as compared to *P. damicornis*, and corallivorous gastropods showed a significantly higher attraction to the two pocilloporid species. Similarly to the results of the two first studies presented in the dissertation, the farmed Reef Carpeted *S. pistillata* transplants showed a higher reproductive performance than the natal colonies at the study site (4.6 ± 1.7 planulae/transplant vs. 1.6 ± 0.6 planulae/natal colony), despite of the harsh environmental conditions. The *Reef Carpet* corals stimulated the development of diverse fish and invertebrate communities (183 taxa recorded by visual censuses) that showed dynamic and complex biological interactions. The 3D properties of the coral species used reveal different ecological engineering consequences in structuring the fish and invertebrate communities. The moderate *Reef Carpets* corals' mortality resulted in dead skeletons becoming hubs for reef biota, sustaining over 80% of associated species diversity. Shifting reef restoration focus from coral cover to biodiversity, this new transplantation approach could be used to scale up restoration activity, providing an effective ecosystem engineering tool to generate new reef zones and support biodiversity of degrading reefs. The last study in the dissertation offers a synthesis of recent advances in farmed coral transplantation and discusses the influence of active reef restoration on biodiversity outcome (Study 4). In particular, it focuses on diversity estimates of the population genetics, species, and ecosystem levels through study of forest restoration rationales, tools, and recommendations that can be applied in the marine silviculture approach. This study highlights theoretical and practical considerations to advance current active reef restoration practices. Together, the above studies provide management implications that can accelerate the recovery of damaged coral reefs, enhancing biodiversity and reef resilience. They explore the ecological engineering properties of farmed coral transplantation in which the novel instruments of *enhanced nursery-bred coral reproduction* and *Reef Carpets* can be customized through the application of forest restoration rationales, and be used to effectively restore degraded reefs in an era of changing climate conditions and intensifying anthropogenic pressure.

Chapter 1

Organization of Dissertation Format

The following dissertation focuses on the emerging marine silviculture approach for active coral reef restoration. More specifically, it aims to advance the nascent discipline of farmed coral transplantation as many of its theoretical and practical aspects are still largely unrevealed. This dissertation begins with an integrative introductory chapter that provides the theoretical background, research objectives and motivation of this PhD work. Four articles then follow, which study nursery-bred coral performance and ecosystem engineering capacity ensuing their transplantation onto degraded reefs. Each of the articles reveals the ability to use nursery-grown coral transplants as ecosystem engineering tools for coral reef restoration. The first two articles focus on reproductive features of farmed coral transplants and their capacity to increase natural reef resilience by contributing to the local coral reproduction. In the first study, the near-term ability of nursery-bred corals to reproduce after their transplantation onto damaged reefs was explored. Following the surprising findings that nursery-grown transplants are not only capable of reproducing after transplantation, but also show enhanced reproductive performance compared to natal coral colonies, the reproductive outputs of the farmed transplants were further examined over the long term. To this end, the second study followed the reproductive capacity of the farmed transplants over eight reproductive seasons post transplantation (7.5 years), revealing that the enhanced reproductive ability is maintained over time and can constitute an ecological engineering tool to enhance the larval pool of degraded reefs. The third study presents a new coral transplantation approach named the '*Reef Carpets*'. It followed the *Reef Carpet* corals acclimation in the degraded reef, their reproductive outputs, and their ecosystem engineering effect on reef-associated species. This study confirms once again the enhanced reproductive performance of nursery-grown transplants and reveals the ability of farmed transplants to thrive on degraded reefs and be also used as an ecological engineering tool to restore reef biodiversity. The fourth study offers a synthesis of recent advances in farmed coral transplantation and discusses the influence of active reef restoration on biodiversity outcome. Literature on forest restoration by tree implantation, a parallel terrestrial discipline, was surveyed in order to glean insights and uncover important

transplantation rationales and considerations that could advance farmed coral transplantation and enhance biodiversity of restored reefs. The general discussion section provides an integrative examination of all four studies' findings mentioned above. It provides management implications and highlights how the theoretical and practical aspects of using nursery-grown corals as ecological engineering tools for reef restoration could all be collectively harnessed to form a diversified and effective restoration toolbox to confront the current coral reef crises.

Chapter 2

General introduction

Coral reefs: a valuable and threatened ecosystem

Coral reefs, one of the most diverse and productive ecosystems on earth, provide human populations with vital goods and services, including coastal protection, cultural activities and recreational possibilities (Woodhead *et al.* 2019). Additionally, they serve as the major source of income, seafood and protein for tens of millions of people. Despite occupying less than 1% of the seabed, coral reefs are often portrayed as “the rainforests of the sea” as they are centers of marine biodiversity and support one of the most diverse natural communities of the planet. They function as crucial sites for spawning, nursery, breeding and feeding for a myriad of marine organisms and their overwhelming biodiversity represent a still largely undiscovered source for medical, pharmaceutical and aquaculture potentialities (Reaka-Kudla 1997; Burke *et al.* 2011;). The numerous goods and services provided by reefs rely on the existence of reef-building, hermatypic corals (phylum Cnidaria, class Anthozoa), that are responsible for building the massive biogenic structures that span entire reefs, islands and barrier reefs over the past 200 million years. Hermatypic corals are colonial animals that precipitate calcium-carbonate exoskeletons and live in association with dinoflagellate unicellular algae of the genus *Symbiodinium* (zooxanthellae), situated in their gastrodermic tissue. The coral biogenic structures and architectures form the complex topographic relief crucial for the existence of the multitude of reef dwelling animals (Bozec *et al.* 2013).

Despite the long history and geological persistence of coral reefs, overexploitation of reef resources and human-amplified global changes have significantly altered reef’s ability to cope with natural disturbances and maintain themselves (Kleypas 2019). Increased load of sedimentation and reclamation of reefs associated with coastal development, anchor damage, coral mining, pollution, agricultural runoff, recreational activities, destructive fishing methods, overfishing and collection of animals for ornamental trade (Tun *et al.* 2010; Burke *et al.* 2011) are only a partial list of the anthropogenic threats that have guided reefs beyond their adaptive capacity. Alarmingly, 20% of the world’s coral reefs have already been destroyed and show no immediate prospects of recovery, 24% are under impending risk of

collapse through human pressures, and a further 26% of the world's reefs are under a longer term threat of collapse (Edwards & Gomez 2007). The worldwide massive degradation documented over the past few decades has led in many cases to permanent shifts in reef communities, modifications of the abiotic environmental conditions and substantial loss of reef areas (IPCC 2019; Kleypas 2019). Not only are the biological communities of coral reefs threatened, but reef degradation affects millions of people in more than 100 countries who depend on this ecosystem for food and income (Burke *et al.* 2011).

Conservation and restoration of coral reefs

Degraded reefs rarely recover naturally from human induced changes without an intervention (Rinkevich 2005b; Huntington *et al.* 2011; Young *et al.* 2012). Ecological restoration is defined by *the Society of Ecological Restoration* as: "the process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed". Ecological restoration aims to transition a degraded ecosystem into "a trajectory of recovery that allows adaptation to local and global changes, as well as persistence and evolution of its component species" (*SER International principles and standards for the practice of ecological restoration*, Gann *et al.* 2019). Assisting recovery may be guided either by passive-indirect measures, or by means of active-direct interventions (Edwards & Gomez 2007). Passive-indirect measures are actions that do not directly interfere with reef organisms but concentrate on imposing management efforts and legislation in order to create appropriate conditions for reef self-healing through natural processes (e.g., implementation of Marine Protected Areas, fisheries management). These measures are helpful in reducing localized anthropogenic pressure (provided that good management and enforcement exist; see Mora *et al.* 2006) but are insufficient to alleviate the threats faced by contemporary coral reefs (Burke *et al.* 2011; Huntington *et al.* 2012; Mouillot *et al.* 2016). For example, they are unable to counter current-carried pollution and poor to no natural coral recruitment (example of Eilat's "no-use zone", Epstein *et al.* 1999; Epstein *et al.* 2005), or cope with large scale perturbations such as massive coral bleaching events (Graham *et al.* 2007; Mumby & Steneck 2008; Mcleod *et al.* 2019). Furthermore, in highly affected reefs, regaining pre-disturbance levels of live coral cover, species diversity and framework complexity requires decades to centuries (Baker *et al.* 2008) and recovery needs to be accelerated in order to protect threatened biodiversity. With the anticipated increase in climatic perturbations frequency (Hughes *et al.* 2017) and the high pressure exerted on reefs by human

populations, reef managers and policy makers need to expand current conservation efforts (Mouillot *et al.* 2016) and supplement traditional measures with active restoration tools (Rinkevich 2008).

Early active restoration initiatives focused on direct coral transplantation of whole coral colonies or coral fragments that were taken from healthy localities and transferred to denuded sites (Clark & Edwards 1995; Yap *et al.* 1998). However, several disadvantages are associated with these methodologies. Removing numerous corals from healthy reefs harms those areas and consequently contributes to the overall damage. Facing today's wide decline, too many localities are threatened, leaving too few undamaged reefs capable of supplying enough source material for direct transplantation. Since the number of colonies that can be sampled from the reef is limited, direct coral transplantations of whole colonies are restricted to small scale interventions. Therefore, using fragments instead of colonies as the source material for direct transplantation could overcome some of these drawbacks. Excised branches, fragments and portions of corals have the ability to grow and regain the initial spatial complexity, allowing for a new colony to be established (Shaish *et al.* 2006). Indeed, fragmentation results in a much higher number of "units" to begin with, but also has obvious downfalls. First, the survival capacity of fragments directly transplanted onto a degraded reef is reduced (Van Treeck & Schuhmacher 1997; Yap *et al.* 1998; Dizon *et al.* 2008). Only a few studies, such as Guzmán (1991) have shown high survival of directly transplanted ramets, indicating that only a few sites are adequate for this methodology. Most of the studies investigating the relationship between fragment size and survivorship have come to the conclusion that survival is size dependent: The larger the fragment, the better chances it has to survive (Smith & Hughes 1999; Lindahl 2003; Soong & Chen 2003; Bruckner & Bruckner 2006; Latypov 2006; Garrison & Ward 2008); however more stress is inflicted to the donor colony, affecting donor colony's survival and reproduction (Epstein *et al.* 2001). In addition, small fragments are more susceptible to threats encountered in natural reefs, such as predation (e.g., when a corallivorous fish/gastropod attacks a small fragment, the resulting damage in comparison to its surface area is much higher than in the case of a colony). Fragmentation may also compromise reproductive activities and outputs (Zakai *et al.* 2000; Guest *et al.* 2007), affecting corals for several reproductive seasons following breakage (Rinkevich & Loya 1989).

In order to overcome these problems, Rinkevich (1995, 2006, 2008, 2015) proposed to apply forest rehabilitation guidelines for active coral reef restoration, as forests and reefs

share numerous ecological, functional and physiological traits. The main building blocks of these two ecosystems, trees and corals respectively, are ecosystem engineers that are responsible for the structural arrangement of the habitat (Epstein *et al.* 2003). Ecosystem engineers are organisms that modify, maintain or create habitats by regulating, directly or indirectly, the availability of resources to other species. By doing that, they profoundly affect the communities and ecosystems they inhabit and impact the abundance and distribution of other species (Jones *et al.* 1994). Ecosystem engineers' disappearance results in profound changes of the biological diversity and lead to the loss of species that depend on their presence/absence (Schiel 2006). In addition to these common features, trees and corals also share similar rules of growth and pattern formation, and are capable of both sexual and vegetative propagation. Similarly to reefs, forests are subject to chronic anthropogenic pressure and their inability of self-recovery has led to the development of efficient restoration tools. The rationales guiding silviculture principles concentrate on preserving the key characteristics of the ecological system in order to maintain critical ecosystem functions and services (Epstein *et al.* 2003). The tree species cultured in nurseries and planted for restoration, promote the recreation of forest communities and commonly show the best restoration performance. The transplantation of trees on a denuded site prevents takeover by other species and allows to jump-start and accelerate successional processes as the presence of the transplants modify the site conditions and microclimate (Parrotta 1992; Lugo 1997). Even though planted forests are usually less diverse than natural forests, they are regarded as an important tool for terrestrial biodiversity conservation as they provide a valuable habitat for endangered species and increase the stability and the productivity of denuded areas (Hartley 2002; Rinkevich 2008).

'Gardening coral reefs' – a marine silviculture approach

Based on silviculture rationales, the "*gardening coral reefs*" approach adopt ecological engineering tools (Rinkevich 2014, 2015, 2019) and is composed of two phases: The first phase consists of generating a pool of farmed coral colonies, reared in underwater coral nurseries to plantable size, which is then followed by a second phase of transplanting these colonies onto degraded reefs. Due to the protected environmental conditions of nurseries, the new pool of coral colonies can originate from any source material, as minute fragments (nubbins, 1-10 polyps) or sexual recruits (Shafir *et al.* 2006; Shaish *et al.* 2008; Levy *et al.* 2010; Mbije *et al.* 2010; Linden & Rinkevich 2011). The employment of nubbins

eliminates any stress inflicted to donor colonies (thus, also suitable for rare or endangered species; Lirman *et al.* 2010) and enables the fast establishment of a large stock of corals that can be used for restoration (Shafir *et al.* 2006). The transplantation of large farmed colonies, rather than coral fragments, can increase the transplants' ability to acclimate on degraded reef and potentially contribute to the local coral reproduction. The addition of transplants onto collapsing reefs can help maintain the ecosystem's function and homeostasis, prevent phase shifts or other species loss, and reinforce natural reef recovery.

Research motivations and overview

The first step of the gardening concept has been successfully practiced in several reef localities in the world (Young *et al.* 2012; Rinkevich 2014) and the several coral nursery prototypes established enabled to acquire the skills to rear the growing of thousands of new colonies of numerous coral species (Mbije *et al.* 2010; Lirman *et al.* 2014; Lirman & Schopmeyer 2016; Rinkevich 2019). Research on the transplantation of the nursery-bred corals has so far primarily explored the feasibility aspects and methodological issues, such as the attachment of transplanted corals to substrates, the choice of coral species, and their survival (Putchim *et al.* 2009; Edwards *et al.* 2010; Shaish *et al.* 2010; Muko & Iwasa 2011; Bowden-Kerby & Carne 2012; Villanueva *et al.* 2012; Young *et al.* 2012; Mbije *et al.* 2013; Gomez *et al.* 2014; Guest *et al.* 2014; Rinkevich 2014; Horoszowski-Fridman *et al.* 2015). This emerging discipline of farmed-coral transplantation is still in its infancy. Until sufficient advances in the nursery stage are achieved, the ecological engineering properties associated with the transplantation phase are still largely unrevealed and unconsolidated. This dissertation focuses on the second phase of the gardening concept. It analyzes the impact of transplantation on farmed coral performance, ecosystem engineering capacity, and the reproductive outputs of nursery-grown transplants in the near and long term. Existing literature was surveyed in order to glean insights of forest restoration by tree implantation to uncover similar restoration approaches that could benefit active reef restoration and enhance biodiversity.

Chapter three of the dissertation examines the reproductive outputs of *Stylophora pistillata* naturally-grown colonies and nursery-farmed transplants from three coral-transplantation trials, studied for the duration of three reproductive seasons. This allowed to test the assumption that nursery-bred corals are capable of reproducing after their transplantation on damaged reefs and contribute to the local coral reproduction.

Chapter four of the dissertation further explores reproductive features of coral transplants and their capacity to increase natural reef resilience. This work was built off the findings in Chapter three stating that *S. pistillata* transplants showed better reproductive capacities than the natal colonies along the three studied post-transplantation reproductive seasons and as a result of this finding, the observation was extended to eight reproductive seasons following transplantation. The extended observation period allowed to test the hypothesis that this enhanced reproductive performance will be limited in time, and thus, the transplants reproductive outputs will eventually level off with that of the natal colonies at the degraded reef.

Chapter five focuses on the first time employment of a new coral reef restoration approach named the ‘Reef Carpets’. Similar to the commercially available turf grass units used in terrestrial lawn-gardening, I cultured preset coral units of three branching species at the coral nursery and deployed them (along with the annexed reef biota accumulated during nursery-period) on a sandy bottom substrate. I tested the prediction that the Reef Carpet corals could be used to restore highly modified reef areas (such as soft degraded reef substrates) and provide ecological niches for coral-associated invertebrates and fish. I followed the transplants’ ecosystem engineering effect on reef-associated species by monitoring the natural recruitment of the reef-associated fauna on the Reef Carpets, analyzing the structure and species diversity of the developing fish and invertebrate communities.

Chapter six offers a synthesis of recent advances in farmed coral transplantation and discusses the influence of active reef restoration on biodiversity outcome. In particular, my work focuses on diversity estimates of the population genetics, species, and ecosystem levels, through study and transference of forest restoration rationales, tools, and recommendations that can be applied in the gardening approach for active reef restoration. This chapter highlights theoretical and practical considerations to advance current practices employed in coral reef rehabilitation. It provides management implications that can help accelerate the recovery of damaged coral reefs.

Research objectives

The main objectives of this research are:

- 1) Evaluate nursery-grown corals’ ability to enhance reef resilience by contributing to the larval pool after their transplantation onto degraded reefs

- 2) Test a new transplantation approach – *Reef Carpets*
- 3) Study the performance of *Reef Carpet* coral transplants and their ecosystem engineering effect on reef-associated species at the degraded reef
- 4) Identify silviculture rationales to be harnessed in the transplantation phase of the *gardening coral reefs* methodology in order to enhance biodiversity of restored reefs

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Chapter 3

Engineering of coral reef larval supply through transplantation of nursery-farmed gravid colonies

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Contribution to the Paper	Conceived and designed the experiment, performed the experiment, analyzed the data, prepared figures and table, drafted the paper and led the writing of the manuscript.		
Certification:	This paper reports on original research I conducted during the period of my Higher Degree by Research candidature and is not subject to any obligations or contractual agreements with a third party that would constrain its inclusion in this thesis. I am the primary author of this paper.		
Name and Signature		Date	24 November 2019

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By signing the Statement of Authorship, each author certifies that:

- i. the candidate's stated contribution to the publication is accurate (as detailed above);
- ii. permission is granted for the candidate to include the publication in the dissertation

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Name and Signature	Ido Izhaki 	Date	24 November 2019

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Contribution to the Paper	Conceived and designed the experiment, acquired funding and revised the manuscript.		
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Engineering of coral reef larval supply through transplantation of nursery-farmed gravid colonies

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ABSTRACT

The continuous worldwide degradation of coral reefs raises an urgent need for novel active restoration techniques as traditional conservation practices have failed to impede the incessant reefs' decline. While applying the "gardening coral reefs" methodology in Eilat (Red Sea, Israel), we examined reproductive outputs of naturally-grown and outplanted, nursery-farmed *Stylophora pistillata* colonies from three coral-transplantation trials (November 2005, May 2007, and September 2008), along three reproductive seasons. Surprisingly, transplanted colonies showed better reproductive capacities than the natal *Stylophora* colonies during >4 post-transplantation years. A higher percentage of nursery-farmed colonies released planula larvae as compared to naturally-grown colonies. Gravid transplants also shed more planulae per colony, yielding significantly augmented numbers of total planulae over naturally developed *S. pistillata* colonies. Our results indicate that nursery-grown corals may be used to enhance reef resilience by contributing to the larval pool, forming an engineered larval dispersal instrument for reef rehabilitation.

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1. Introduction

Coral reefs are declining at an alarming pace as increasing human activities, local stressors and global changes act in unison to shift numerous sites of this delicate ecosystem into different configurations (Hughes et al., 2003; Hoegh-Guldberg et al., 2007). Careful literature assessments foretell a dismal fate for coral reefs (Rinkevich, 2008), leading to the suggestion for a new geological epoch, the Anthropocene (Bradbury and Seymour, 2009). As a myriad of reef species depend on corals for their survival, the future of reef communities rests on the abilities of the reefs to respond adequately to increasing climate changes and growing pressure by human activities. The ominous consequences of the continuous reef deterioration worldwide have raised awareness of the urgency in promoting efficient management measures. Unfortunately, most of the current conservation practices (known as "passive restoration"; [Rinkevich, 2008]) are insufficient for averting reef degradation as they are often slow, suffering from numerous biotic/abiotic limitations and leading to highly stochastic outcomes. Active restoration instruments can therefore complement current management tools and effectively cope with reef degradation (Rinkevich, 2008).

Recently, the two-step method inspired by silviculture rationales known as "gardening coral reef" (Rinkevich, 1995, 2005a, 2006, 2008) has drawn intense scientific investigation. The first phase concen-

trates on generating a pool of farmed colonies, reared in underwater nurseries to a size sufficiently large enough to transplant. The second phase consists of transplanting these new adult colonies onto degraded reefs. Like in terrestrial forestation, transplantation of nursery-grown corals can be used as a sustainable tool that carries ecological engineering benefits, such as the construction of rehabilitated coral reefs with particular coral coverage, associated species' compositions and emerged seascape (Rinkevich, 2008; Shafir and Rinkevich, 2008).

This study is part of the work evaluating the state of restored experimental knolls (Dekel Beach, Eilat, Israel). Nursery-farmed colonies of seven scleractinian species (*Stylophora pistillata*, *Pocillopora damicornis*, *Acropora pharaonis*, *Acropora variabilis*, *Acropora valida*, *Acropora humilis*, and *Millepora dichotoma*) were transplanted in three different years (November 2005, May 2007, and September 2008; T1–T3, respectively). The colonies showed high survivorship, fast growth rates, attracted invertebrates and fish that recruited on, within, and between the branches (unpublished). To further evaluate post-transplantation performances we monitored reproductive efforts of one of the transplanted species, *S. pistillata*, a hermaphroditic brooding species with long reproduction seasonality (Rinkevich and Loya, 1987). Planula larvae were collected *in situ* from transplants and naturally growing, healthy colonies, representing reproduction of the resident *S. pistillata* population, during the peaks of three reproductive seasons (2007, 2009 and 2010), along >4-year post transplantation. In this paper, we ask if outplanted nursery-reared corals can also enhance reef resilience by contributing to the corals' larval pool, thus be used as engineered dispersal nuclei for reef rehabilitation.

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2. Materials and methods

2.1. Study site

The reef at Eilat (Red Sea, Israel; 29°30'N; 34°57'E) has been declining for the past four decades due to the rapid expansion of Eilat city, recreational and tourist activities, and pollution (Rinkevich, 2005b). By applying the "gardening" concept, 1400 nursery-farmed colonies of six branching coral species (*S. pistillata*, *P. damicornis*, *A. pharaonis*, *A. variabilis*, *A. valida*, and *A. humilis*) and a scleractinian hydrozoan (*M. dichotoma*) were transplanted onto five bare knolls at the Dekel Beach, Eilat. These colonies had first been reared for eight to twenty-four months in a floating nursery at a depth of 6 m (which is 14 m above the sea bottom) in the northern Gulf of Eilat, away from the reef, coral predators and recreational activities (Shafir et al., 2006). The restoration site is located 2.7 km south of the nursery, between a navy base and the commercial port of Eilat and in front of a diving center. The first 18-m depth of this reef is sandy and slopes moderately with scattered knolls exhibiting declining coral coverage (completely bare to well covered knolls, though the latter are rare). The farmed colonies were secured to the knolls during three transplantation sessions (November 2005, May 2007, and September 2008; T1–T3, respectively) by attaching devices (plastic pegs [Shafir et al., 2006] and masonry anchors) that were inserted into pre-drilled holes, further secured with minuscule epoxy glue (AquaMend).

2.2. Larval collection

S. pistillata is a brooding coral species, which, in Eilat, used to release planulae larvae from December to July (Rinkevich and Loya, 1987), but has recently shifted its reproductive seasonality (Amar et al., 2007), from January to August peaking in April to June. Transplanted and naturally growing colonies (6–24 cm diameter; Table 1) situated between 7- and 13-m depth were examined for larval release at peak-spawning months during June 2007, May–June 2009 and April–May 2010 (Fig. 1A, B). Larval release was quantified over several nights at each sampling period, not considering the unalike moon phase changes (Rinkevich and Loya, 1987). Similar size resident colonies in good state of health (without broken branches or damaged tissue parts), growing on the transplanted knolls or in their close proximity, were chosen in each reproductive season. In 2007, we examined 30 *S. pistillata* colonies, 10 from November 2005 transplants, 10 from May 2007 transplants and 10 naturally growing. Ninety-four colonies were examined in 2009, 15 transplants from each of the above two transplantation groups, 14 from the 2008 group and 40 naturally growing colonies. Seventy-three colonies were examined in 2010, 18 transplants from each of the transplantation groups and 19 resident colonies. Planulae-collection devices (Amar et al., 2007; Fig. 1B) were placed over each one of the

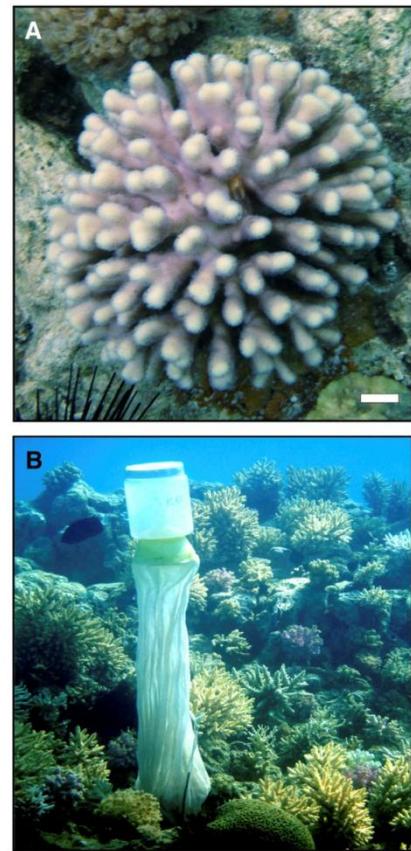


Fig. 1. Reproductive efforts of nursery-farmed and resident *Stylophora pistillata* colonies. (A) A gravid transplant, 3.5 years after transplantation. White bare = 2 cm (B) planulae-collection device placed over a transplanted colony in the restored knoll.

Table 1

Larval collection during reproductive seasons 2007, 2009 and 2010. Planulae were collected from natal *Stylophora pistillata* colonies and transplants, following 3 transplantation sessions (November 2005, May 2007, and September 2008; T1–T3 transplants, respectively).

Year	Sampled months	Colonies	Colony diameter (cm)	Reef dwelling period (years)	Colonies examined (n)	Planulae-releasing colonies (%)	Planulae collected	
							Total (n)	Range/colony
2007	June	Natal	6–9	3–5	10	0	0	0
		T1	8–9	1.5	10	80	37	0–15
		T2	6–7	0.15	10	100	225	1–96
2009	May–June	Natal	8–24	4–12	40	32	57	0–17
		T1	22–24	3.5	15	93	275	0–46
		T2	10–14	2.15	15	100	153	2–55
		T3	8–11	0.67	14	100	164	1–28
2010	April–May	Natal	9–24	5–12	19	47	41	0–17
		T1	22–24	4.5	18	100	216	1–42
		T2	10–16	3.15	18	89	148	0–29
		T3	9–14	1.67	18	89	103	0–45

colonies from sunset to sunrise and brought to the laboratory. The planulae were gently washed with seawater into wide Petri dishes and counted under a stereomicroscope.

2.3. Statistical analysis

Data analyses were performed using SPSS software for Windows version 16.0. Since no transformation succeeded to yield normality, the non-parametric Mann–Whitney test was used in order to compare the average numbers of planulae per colony between the different groups and cohorts. Bonferroni adjustment was used to account for multiple testing in order to maintain 5% Type I error. For group comparisons within a reproductive season, our Bonferroni-adjusted alpha levels were <0.016 for 2007 and <0.008 for 2009 and 2010. For cohort comparison, our Bonferroni-adjusted alpha level was <0.007 .

3. Results

Only a small percentage of examined resident colonies released planulae over the monitored period (0%, 32% and 47% at 2007, 2009 and 2010 censuses, respectively; Table 1), as compared to the vast majority of the studied transplants (80–100% during the three reproductive seasons; Table 1). Surprisingly, 100% of the studied colonies from T1 released larvae, even 4.5 years after their transplantation to the knolls, demarcating their high fecundity from the low reproductive activities represented by the same size naturally growing corals (Table 1). The recorded number of released planulae per colony varied greatly (0–96) in all experimental groups (Table 1). However, during the three reproductive seasons, significantly more larvae were released from T1 and T2 transplants than from the residing colonies (Mann–Whitney, $p<0.05$ after Bonferroni adjustment; Fig. 2). Larval release by T3 transplants was also higher than that of the natal colonies during the studied periods (11.7 ± 2.3 vs. 1.4 ± 0.5 in 2009; 5.7 ± 2.4 vs. 2.2 ± 0.9 in 2010), though, in 2010, the difference was not significant following the high variation recorded in larval release ($p>0.05$ after Bonferroni adjustment; Fig. 2). Variations between yearly larval collections of the same group of colonies were recorded as well. In 2007, T1 colonies (at the sizes of 8–9 cm diameter) released, on average, 3.7 ± 1.4 (mean \pm

SE) planulae (1.5 years after transplantation) and in 2009 18.3 ± 2.9 planulae (22–24 cm diameter, Table 1; $p<0.05$ after Bonferroni adjustment, Fig. 2). These results could be associated with increased colonial sizes. The average number of planulae released by T1 colonies in 2010 (22–24 cm diameter, Table 1) was 12 ± 2.7 planulae per colony, an average that did not differ significantly from the two previous years ($p>0.05$ after Bonferroni adjustment, Fig. 2). However, T2 colonies (at the sizes of 6–7 cm) released 22.5 ± 9.1 planulae two months after transplantation (they were transplanted as gravid colonies), versus 10.2 ± 3.5 and 8.2 ± 1.9 planulae, two and three years later, respectively (10–14 cm and 10–16 cm colony diameter; Table 1; Fig. 2). We recorded a decrease in the average number of planulae released by this group of colonies during 2009 and 2010 compared to 2007, but this decrease was not significant ($p>0.05$ after Bonferroni adjustment, Fig. 2). T3 colonies exhibited a considerable decrease in planulae yield as they released, on average, 11.7 ± 2.3 planulae in 2009, eight months following transplantation (8–11 cm colony diameter; Table 1) and 5.7 ± 2.4 planulae in 2010 (9–14 cm diameter, Table 1; $p<0.05$ after Bonferroni adjustment, Fig. 2).

As time elapsed, impressive differences were recorded in larval release between transplants and natal colonies. During the 2007 reproductive season, T1 and T2 transplants released 37 and 225 more planulae, respectively, than the same number of natal colonies (0 planulae; Table 1). The transplants' enhanced reproductive capacity was maintained two years later as 4.8, 2.6 and 2.8 times more planulae were collected from colonies of T1, T2 and T3, respectively, in 2009 (total of 275, 153 and 164 planulae), than from the residing colonies (57 planulae; Table 1). This enhanced performance was further maintained, as during 2010 reproductive season 5.3, 3.6 and 2.5 times more planulae were collected from T1, T2 and T3 colonies, respectively (216, 148 and 103 planulae), than from the resident colonies (41 planulae; Table 1).

4. Discussion

This study constitutes one of the first works to demonstrate positive long-term impacts of coral transplantation. The results present coral transplantation as an ecological engineering instrument

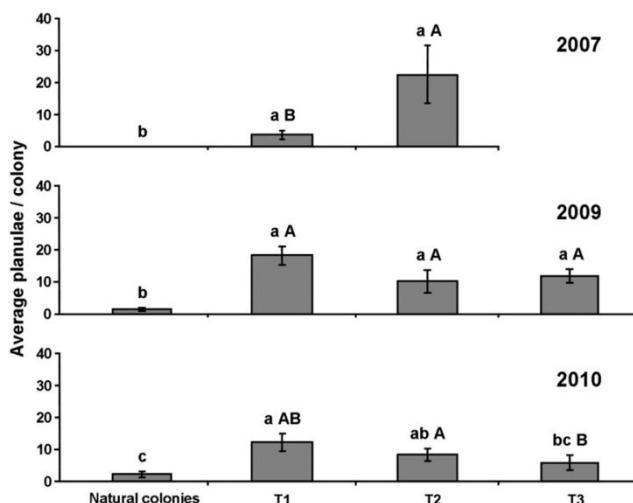


Fig. 2. Average numbers of planulae per colony collected from natural and transplanted *Stylophora pistillata* colonies (mean \pm SE). Small letters denote statistically significant differences within years (Mann–Whitney U test after Bonferroni adjustment, $p<0.05$). Capital letters denote statistically significant differences within the same cohort between years (Mann–Whitney U test after Bonferroni adjustment, $p<0.05$).

that subsidizes local planulae production. These results, together with Amar and Rinkevich (2007) results, demonstrating the ability of a mid-water coral nursery to act as a larval dispersion hub, signify the "gardening" concept (Rinkevich, 1995, 2005a, 2006, 2008) as an applied tool for coral reef restoration. Certainly, it should be demonstrated that these larvae recruit successfully; nevertheless, the enhanced pool of planulae provides the initial stimulation step of natural reef recovery. As such, it constitutes an essential milestone for the initiatives of forestalling the precipitous decline of reef ecosystems worldwide. These outcomes, therefore, support the assumption that coral reefs' goods and services are potentially recoverable through engineering manipulations, and that the "gardening" approach may serve as an applied tool for mitigating human and environmental destructive impacts (Rinkevich, 2008). While the methodology employed in this study is adequate for brooding species, future work should examine reproductive outputs of transplanted broadcasting species. Altogether, active restoration measures powered by ecological engineering tools provide novel incite, substantial for balancing coral reef conservation and exploitation.

Previous restoration interventions usually focused on translocating coral material, mostly coral colonies or coral fragments, from healthy localities to degraded areas (reviewed in Rinkevich, 2005a). The fragmentation of coral colonies and the direct transfer of colonies to damaged reefs often caused stress, which reduced reproduction capacities (Rinkevich, 2005a; Guest et al., 2007). Aiming to avert species loss in the face of current and predicted reef degradation (Hughes et al., 2003; Hoegh-Guldberg et al., 2007, 2008; Bradbury and Seymour, 2009), reef recovery by outplanting of gravid coral material has not been considered as a management tool even in cases of extreme suggestions, such as the "assisted colonization" notion (Hoegh-Guldberg et al., 2008).

By examining the reproductive performance of one brooding coral species, the present study demonstrates the effectiveness of using adult transplants reared in coral nurseries, not only to reinforce local coral community but also to potentially enhance natural reef resilience by contributing to the larval pool. Results also revealed that most of natal colonies did not participate in larval release during the sampling dates, along the three studied reproductive seasons. Further work is needed to elucidate the whole spectrum of reasons for these outcomes, but clearly, as the study site is located in front of a busy diving center, natal coral populations are directly impacted by intense anthropogenic stressors. These stressful conditions may consume available energy sources that otherwise would be diverted to coral growth and reproduction (Oren et al., 2001; Guest et al., 2007). To our surprise, most of the transplants demonstrated high levels of fecundity, years after their transplantation, following a relatively short period (about one year; unpublished) of idyllic conditions in the coral nursery. A coral nursery aims at creating favorable environments for corals to survive and thrive, including reducing the threats of coral predators and competition with other sedentary organisms (Shafir and Rinkevich, 2008). Furthermore, the recorded differences in reproductive outputs between natal colonies and transplants cannot be referred to as genetically disparate source populations since donor *Stylophora* colonies used to establish the nursery-farmed coral stock were collected from an adjacent location (Shafir et al., 2006) about 900 m north of the restoration site.

Restoring the biological communities of complex ecosystems such as coral reefs constitutes a challenge as the type and extent of the biological, physical and chemical processes, controlling the characteristics and persistence of the habitat, are not always straightforward and may vary in space and time. Integrating reproduction considerations into active coral reef restoration planning could potentially enhance the restoration's success, sustainability and scale. Transplantation of farmed gravid corals, prior to their reproductive season, might surface as an efficient applied tool for reseeding degraded reefs. For example, 10,000 nursery-reared *S. pistillata* transplants releasing

20 planulae per colony per night (Table 1; Fig. 2) during eight months of reproductive season may yield >20 million planulae. This is a significant larval import, which could sustain local populations. The above estimation is comparable to using the floating mid-water coral nursery as larval dispersion hub, where 10,000 *S. pistillata* colonies in the nursery release approximately >20 million larvae during each reproductive season (Amar and Rinkevich, 2007). Using either approach provides ample numbers of coral larvae for improved recruitment, a multi-year supply of planulae. Consequently, reef resilience could increase and reef restoration may occur through the natural self-seeding process rather than an act of rehabilitation. Furthermore, previous studies that utilized sexually produced propagules as a source material for reef restoration were costly, single year tools that required elaborate *ex situ* and *in situ* practices (i.e., Okamoto et al., 2005; Petersen et al., 2005; Nozawa, 2008; Omori and Iwao, 2009). Rearing colonies from larvae is time consuming and too costly to be performed in large restoration measures.

If nursery-reared colonies are transplanted just at the onset of the reproductive season, larvae released at transplantation sites will clearly benefit from the advantageous conditions during growth stages at the nursery, revealing another ecological engineering facet of the nursery phase. Ecological engineering in restoration is widely used in terrestrial habitats to reverse or lessen the environmental degradation caused by human activities (Benayas et al., 2009). However, while restoration of terrestrial ecosystems has been applied for nearly two centuries (Rinkevich, 2006), the concept of active reef restoration is less than two decades old. Therefore, the theoretical and empirical aspects of active reef restoration are still in their nascent stages, waiting for further work. Restoration actions, like transplantation of gravid coral colonies to a restored reef, can also provide insights into the dynamics and functioning of coral reef systems, as this form of ecological engineering manipulation directly affects coral reef population genetics. Moreover, former suggestions (e.g., Cowan et al., 2006) have advocated that sustainable reef population require larvae imported from outside the local area. The results of this study and those of Amar and Rinkevich (2007) may otherwise encourage using the strategy of improved reproduction of nursery-reared coral colonies in limited connectivity sites or when it is needed to increase corals' genetic diversity, to enhance provision of ecosystem services.

The results of the present work further demonstrate that reef restoration based on the "gardening" rational (Rinkevich, 1995, 2005a, 2006, 2008) is a legitimate approach, aiming to reconstruct self-sustaining coral communities; therefore, this rationale no longer sees restoration as a deterministic process. The rehabilitation of degraded coral reefs to diverse ecosystems is feasible, though depending on the strategies and tools applied. Active restoration should be enforced when coral reef ecosystem fails to naturally recover from disturbances or when this process may take over centuries to be accomplished.

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Chapter 4

Long-term heightened larval production in nursery-bred coral transplants

Statement of Authorship

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Principal author

Name of Principal Author (Candidate)	Yael Bina Horoszowski-Fridman		
Contribution to the Paper	Conceived and designed the experiment, performed the experiment, analyzed the data, prepared figures and table, drafted the paper and led the writing of the manuscript.		
Certification:	This paper reports on original research I conducted during the period of my Higher Degree by Research candidature and is not subject to any obligations or contractual agreements with a third party that would constrain its inclusion in this thesis. I am the primary author of this paper.		
Name and Signature		Date	24 November 2019

Co-Author Contributions

By signing the Statement of Authorship, each author certifies that:

- i. the candidate's stated contribution to the publication is accurate (as detailed above);
- ii. permission is granted for the candidate to include the publication in the dissertation

Name of Co-Author	Prof. Ido Izhaki
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Contribution to the Paper	Analyzed the data and revised the manuscript.		
Name and Signature	Ido Izhaki 	Date	24 November 2019

Name of Co-Author	Prof. Baruch Rinkevich		
Contribution to the Paper	Conceived and designed the experiment, acquired funding and revised the manuscript.		
Name and Signature	Buki Rinkevich 	Date	23 11 2019



Long-term heightened larval production in nursery-bred coral transplants



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Abstract

The ‘gardening coral reefs’ method is part of the approaches proposed for counteracting the substantial impacts of global climate change on the survival of coral reefs. It incorporates ecosystem engineering strategies for coral nursery farming and coral colonies out-planting. This study explores the reproductive output of three sets of nursery-grown *Stylophora pistillata* colonies along eight reproductive seasons following transplantation, as compared to that of native corals. When native and transplanted corals grew side by side in a disturbed environment, the nursery-grown transplants showed enhanced larval release (2.6–22.5 times more planulae/colony; multiyear average: 11.6±1.8 planulae/transplant vs. 1.5±0.3 planulae/native colony) with higher percentages of gravid colonies (91±2.1% transplants vs. 34±7.6% native colonies). The inherently enhanced larval production of transplants, maintained for such a long period of time post-transplantation, reveals a possible enduring impact of the nursery conditions on future fitness and ecological traits of transplants. This is further supported by the emerging documentation regarding the enhanced growth of corals under nursery conditions, which continues to be detected even years after transplantation was conducted on the natural reef. The above enhancement of coral reproduction can be harnessed as a human intervention tool for countering global climate change impacts.

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Keywords: Gardening approach; Reef rehabilitation; Coral nursery; Coral transplantation; Reproduction; Planulae output

Introduction

Global climate change (GCC) threatens the structure and functioning of the world's ecosystems (Scheffers et al., 2016). In the marine realm, coral reefs are among the most vulnerable to GCC drivers following decades of anthropogenic pressure that already compromised reef resilience (Kleypas, 2019). GCC stressors impair the reefs' ability to remain in a coral-dominated state (Graham, Jennings, MacNeil, Mouillet,

& Wilson, 2015), and include global warming, ocean acidification, shifts in climatic regimes, enhanced storm severity and frequencies, and rising sea-level (Scheffers et al., 2016; van Oppen et al., 2017). Such threats not only lead to the direct mortality of coral reef populations followed by the loss of habitat and ecosystem goods and services, but also have profound and sometimes long-lasting impacts on coral reproduction by lowering fecundity, fertilization success and pre/post-settlement survival (Harrison, 2011; and literature therein). These non-lethal, indirect effects hamper genetic diversity and decelerate coral recruitment, further slowing or preventing recovery of degrading reefs.

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The literature documents cases of natural adaptation in corals in response to GCC drivers, via hitherto-ignored mechanisms of soft inheritance (including epigenetic and trans-generational acclimatization; Putnam & Gates, 2015; Putnam, Davidson, & Gates, 2016; Torda et al., 2017; Liew et al., 2018; Eirin-Lopez & Putnam, 2019; and literature therein). Yet, given the forecasted rapid rates of climate change, it is questionable whether corals would be able to adapt quickly enough (Torda et al., 2017; van Oppen et al., 2017) and withstand both GCC and anthropogenic challenges. Thus, new approaches of reef restoration that steer away from the conventional wisdom of reconstructing historical reef populations are urgently needed in order to create novel and self-sustaining reefs, capable of maintaining key ecological functioning and ecosystem processes in a changing world. Taking into account the projected GCC threats, several new approaches have been discussed, including assisted migration, assisted evolution (comprising assisted gene flow, epigenetic programming and the manipulation of the coral microbiome; Damjanovic, Blackall, Webster, & van Oppen, 2017; van Oppen et al., 2017; and literature therein), ecological engineering of the coral symbionts (Levin et al., 2017) or the coral colonies (e.g. ‘genetic rescue’; Whiteley, Fitzpatrick, Funk, & Tallmon, 2015; van Oppen et al., 2017), and the increasingly explored ‘Gardening Coral Reefs’ methodology (Rinkevich, 1995) that harnesses ecosystem engineering tactics (Shaish, Levi, Katzir, & Rinkevich, 2010; Horoszowski-Fridman, Izhaki, & Rinkevich, 2011; Schopmeyer et al., 2012; Horoszowski-Fridman, Brêthes, Rahmani, & Rinkevich, 2015; Rinkevich, 2015a; Afiq-Rosli et al., 2017; Horoszowski-Fridman & Rinkevich, 2017; Linden & Rinkevich, 2017; Rachmilovitz & Rinkevich, 2017; Taira, Toh, Sam, Ng, & Chou, 2017).

The ‘Gardening Coral Reefs’ approach for active reef restoration is based on silviculture principles, concepts and theories (Rinkevich, 1995) and comprises two steps. The first involves the development of large new stocks of coral colonies and their mariculture in mid-water floating nurseries under optimal conditions for coral survival and growth. The second consists of transplanting the nursery-farmed corals, once they have grown into fully developed colonies, onto degraded reef areas. In addition to the success of farming large stocks of numerous coral species in a variety of locations worldwide (Rinkevich 2014; Schopmeyer et al., 2017), the nursery phase has also surfaced as an ecological engineering tool to augment coral reproduction (Amar & Rinkevich, 2007; Baria, Villanueva, & Guest, 2012; Guest, Baria, Gomez, Heyward, & Edwards, 2014; Rinkevich, 2015a; Linden & Rinkevich, 2017). For example, increased numbers of oocytes and planulae were documented in farmed *Stylophora pistillata* colonies in an underwater coral nursery in the Red Sea compared to corresponding reef residing colonies (Amar & Rinkevich, 2007), and significantly higher percentages of gravid *Acropora millepora* colonies were recorded in a coral nursery in the Philippines compared to naturally-growing colonies on the reef (Baria et al., 2012;

Guest et al., 2014). However, it is still unclear whether nursery-rearing can have positive effects beyond the farming stage or beyond the short term following transplantation. Growing in nursery-improved conditions could lead to ill-adapted, un-acclimated corals that could prove detrimental when facing the harsh conditions of the natural reef post-transplantation. Conversely, growing in improved conditions with abundant resources could provide the coral a higher energy allocation to mechanisms such as stress tolerance or defense and thus confer an advantage in coping with the natural reef conditions. A flow-on effect of the nursery phase, increasing reproduction of coral transplants, could reinforce the genetic diversity of restored reefs enhancing their capability to adapt to wider environmental fluctuations, and further assist in mitigating some of the indirect impacts of GCC mentioned above. To explore the long-term impacts of nursery rearing on the reproductive features of coral transplants, we followed three sets of colonies from the brooding hermatypic coral *Stylophora pistillata*, (n=567), each reared for up to 24 months in an underwater coral nursery. The nursery-bred colonies were transplanted onto a degraded reef during three consecutive (18 months apart) transplantation sessions (Fig. 1A,B) and their reproductive outputs were studied over a 7.5-year period (Fig. 1C), comparing their performance to native *S. pistillata* colonies.

Materials and methods

Experimental setup

The study was conducted on a degraded reef area at the northern edge of the Red Sea (Eilat, Israel; 29°30'N; 34°57'E), a marine ecosystem suffering extensive anthropogenic pressure as a result of recreational activities, the rapid urban development of the city of Eilat, and pollution (Rinkevich, 2005b). A new stock of the brooding hermaphroditic coral *Stylophora pistillata* was generated asexually at Eilat’s underwater coral nursery, floating at a depth of 6 m (14 m above the seafloor). The maricultured *S. pistillata* were cloned from adult donor colonies (10–20 cm diameter) that were completely fragmented (Shafir et al. 2006); three donor colonies originated from artificial substrates at Eilat’s navy port (adjacent to the future transplantation site; Shafir et al., 2006) and >10 donor colonies originated from artificial substrates from the proximity of the coral nursery. The newly-generated colonies were randomly positioned in the nursery and their placement was periodically shuffled. Occasionally, as part of nursery maintenance and stock enhancement, the newly developing nursery-bred colonies were partially re-fragmented to generate additional colonies (Shafir et al., 2006; Shafir & Rinkevich, 2010). Due to the distance between the nursery and the natural reef, the intensive care during nursery rearing (e.g., removal of coral competitors and predators and spacing colonies in conjunction with growth), and the nursery characteristics (e.g., reduced

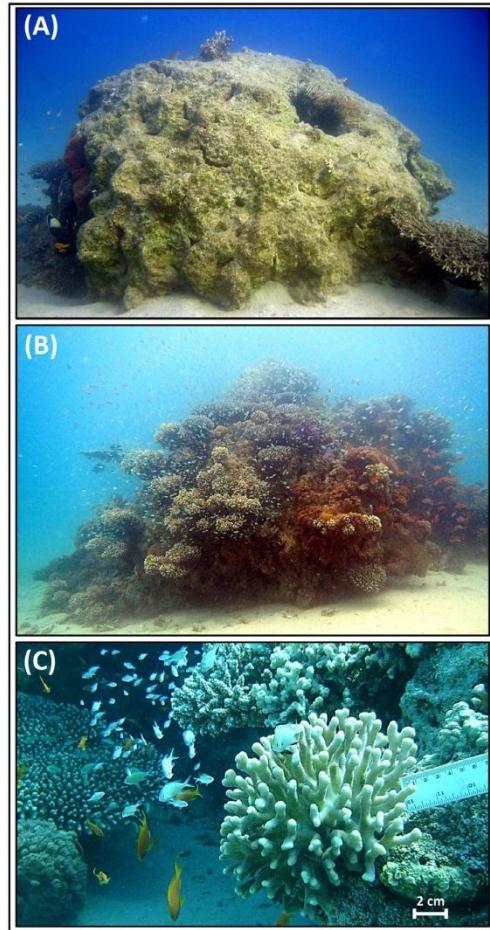


Fig. 1. Nursery-grown coral transplantation as part of the “Gardening Coral Reefs” approach at the Dekel Beach (Eilat, Israel). (A) One of five degraded bare knolls selected for coral transplantation (B) A restored knoll, 11 years after transplantation of nursery-farmed corals originating from the Eilat *in situ* coral nursery (C) A gravid *Stylophora pistillata* transplant, residing for 8 years on the restored knoll. White bar = 2 cm.

sedimentation, enhanced water flow; Rinkevich, 2006), the new colonies developed in favorable conditions for coral survival and growth exhibiting two- to threefold faster growth rates (Shafir et al., 2006; Shafir & Rinkevich, 2010; Linden & Rinkevich, 2017) and higher survival rates than natural colonies on the reef (Horoszowski-Fridman et al., 2015). Three sets of maricultured *S. pistillata* colonies ($n=567$), each set reared in the nursery for 8–24 months from 1–2 cm fragments until regrown into fully developed

branching colonies, were randomly selected out of the nursery stock for three consecutive transplantation sessions [November 2005 ($n=265$), May 2007 ($n=122$) and September 2008 ($n=180$) – TS1, TS2 and TS3, respectively; Horoszowski-Fridman et al., 2011, 2015; Horoszowski-Fridman & Rinkevich, 2017]. At each of the transplantation sessions, the farmed colonies were transferred 2.7 km south of the coral nursery to the experimental site at ‘Dekel Beach’, situated just offshore of a popular diving center between the commercial and naval ports of Eilat. They were transplanted, among other nursery-bred coral species, onto five denuded knolls scattered on a 200-m-long sandy bottom at a depth of 7–13 m (Fig. 1A,B; see Horoszowski-Fridman et al., 2015 for a map of the study site). The farmed transplants were randomly divided between the experimental knolls and individually tagged with a numbered plastic strip for future monitoring (Horoszowski-Fridman et al., 2015).

Larva collection

In each of the studied reproductive seasons, planula larvae were collected simultaneously from nursery-grown transplants and control colonies of similar sizes (Table 1; minimum 6 cm diameter, reflecting gravid colonies), naturally settled and growing among the transplants on the experimental knolls, or in close proximity (i.e., reference knolls located a few meters away of the transplanted knolls; Horoszowski-Fridman et al., 2015). The sampled colonies were randomly selected anew at each reproductive season. Only colonies with no partial mortality or any visual sign of damage or stress were used as native controls. A total of 290 transplants and 126 native controls were examined for their output of larvae throughout the peak spawning months (April to June; Amar, Chadwick, & Rinkevich, 2007; Shefy, Shashar, & Rinkevich, 2018) of 6 reproductive seasons within a duration of 7.5 years following transplantation (2007, 2009, 2010–2013; 8 reproductive seasons following TS1). Larval release was quantified over 5 to 8 nights irrespective to the lunar cycle (Linden, Huisman, & Rinkevich, 2018) at each sampling period. Planulae were collected *in situ* using planula traps that were placed on each *S. pistillata* colony from sunset until sunrise. They were then gently flushed with filtered seawater into wide Petri dishes and counted under a stereomicroscope, following Horoszowski-Fridman et al. (2011).

Statistical analyses

Data analysis was performed using the SPSS v.21 software for Windows. The reproductive output of residents and transplanted *S. pistillata* colonies (average of three transplanted sets, TS1–TS3) was analyzed using a paired-samples t-test, subsequent to the Shapiro-Wilk test performed in order to assess normal distribution of the differences between transplants and native colonies.

Table 1. *In situ* planula collection from native and nursery-grown *Stylophora pistillata* colonies, transplanted during three consecutive transplantation sessions (November 2005, May 2007, September 2008; TS1, TS2, TS3, respectively).

Year	Group	Reproductive seasons following transplantation	Examined colonies		Planulae collected		
			N (releasing larvae)	Diameter range (cm)	Total (n)	Average/c colony (\pm SE)	Range/c colony
2007	Native	-	10 (0)	6-9	0	0	0
	TS1	2	10 (8)	8-9	37	3.7 \pm 1.4	0-15
	TS2	1	10 (10)	6-7	225	22.5 \pm 9.1	1-96
2009	Native	-	40 (13)	8-24	57	1.4 \pm 0.5	0-17
	TS1	4	15 (14)	22-24	275	18.3 \pm 2.9	0-46
	TS2	3	15 (15)	10-14	153	10.2 \pm 3.5	2-55
	TS3	1	15 (15)	8-11	164	11.7 \pm 2.3	1-28
2010	Native	-	19 (9)	9-24	41	2.2 \pm 0.9	0-17
	TS1	5	18 (18)	22-24	216	12.0 \pm 2.7	1-42
	TS2	4	18 (16)	10-16	148	8.2 \pm 1.9	0-29
	TS3	2	18 (16)	9-14	103	5.7 \pm 2.4	0-45
2011	Native	-	22 (9)	10-25	45	2.0 \pm 0.7	0-13
	TS1	6	22 (22)	16-25	256	11.6 \pm 1.8	2-34
	TS2	5	22 (19)	10-16	138	6.3 \pm 1.8	0-37
	TS3	3	22 (17)	10-18	173	7.9 \pm 2.0	0-33
2012	Native	-	20 (6)	10-24	41	2.1 \pm 1.1	0-17
	TS1	7	20 (20)	14-24	448	22.4 \pm 4.2	5-77
	TS2	6	20 (20)	10-20	363	18.2 \pm 3.9	3-57
	TS3	4	20 (17)	11-24	319	16.0 \pm 4.7	0-64
2013	Native	-	15 (8)	10-25	18	1.2 \pm 0.3	0-4
	TS1	8	15 (14)	15-23	88	5.9 \pm 1.0	0-13
	TS2	7	15 (12)	11-18	173	11.5 \pm 3.4	0-45
	TS3	5	15 (12)	11-22	62	4.1 \pm 0.9	0-14

The average numbers of planulae per colony shed by *S. pistillata* residents and the three groups of transplants, as well as the multiyear averages, were analyzed during each reproductive season with the non-parametric Mann-Whitney test, as no transformation successfully yielded normality. A multiple-comparison Bonferroni adjustment was used to account for multiple testing in order to maintain the 5% Type I error.

The yearly comparisons between the planula distribution of native and nursery-grown *S. pistillata* colonies were analyzed using the chi-square test.

Results

Higher reproductive outputs were recorded for the transplanted *S. pistillata* colonies at the Dekel Beach (Fig. 1C), as compared to native colonies, and throughout the 7.5-year study period. Only 0-53% of the 126 healthy-looking native colonies, of reproductive size, released larvae during all of the examined seasons, compared to 77%-100% larval releasing colonies from the 290 transplants sampled (TS1-TS3 groups; Range reflects differences between years; Fig. 2A; Table 1). These numbers reveal an overall significant difference between the reproductive efforts of transplants and their control counterparts of similar size, naturally growing *S.*

pistillata colonies (paired t-test, $t_3=6.83$, $p=0.001$; multiyear average: $34\pm7.64\%$ [mean \pm SE] planulae-releasing native colonies vs. $91\pm2.06\%$ planulae-releasing transplants; TS1-TS3 pooled across transplantation cohorts; Fig. 2A).

Numbers of planulae per colony, for the native and transplanted groups, varied greatly in each year throughout the study period (Fig. 3A,B, χ^2 , $p<0.001$ for each year). Results revealed 0-17 planulae per colony for the native colonies and 0-77, 0-96 and 0-64 for TS1, TS2 and TS3 colonies, respectively (Table 1), showing a significantly higher annual larval release per colony in the nursery-grown transplants (Mann-Whitney, $p<0.05$ after Bonferroni adjustment; Table 1; Fig. 2B). The reproductive output of nursery-grown *S. pistillata* transplants did not align with the performance of native colonies even 7.5 years after first transplantation (2013), where 93.3% of the TS1 colonies produced 5.9 ± 1.0 planulae/colony, compared to 53.3% of native colonies, releasing 1.2 ± 0.3 planulae/colony (a total of 88 planulae from TS1 transplants vs. 18 from residents; Figs. 2A,B, 3A, B; Table 1). The same was found for TS2 (6.2 years post transplantation) and TS3 (4.7 years) cohorts, where in both $\sim 80\%$ of the colonies released larvae (11.5 ± 3.4 and 4.1 ± 0.9 planulae/colony, respectively; Fig. 2B), 9.6 and 3.4 times more than the number of larvae released from the naturally growing colonies (173 and 62 planulae vs. 18, respectively; Table 1). Collectively, during years 2007-2013, $11.6\pm$

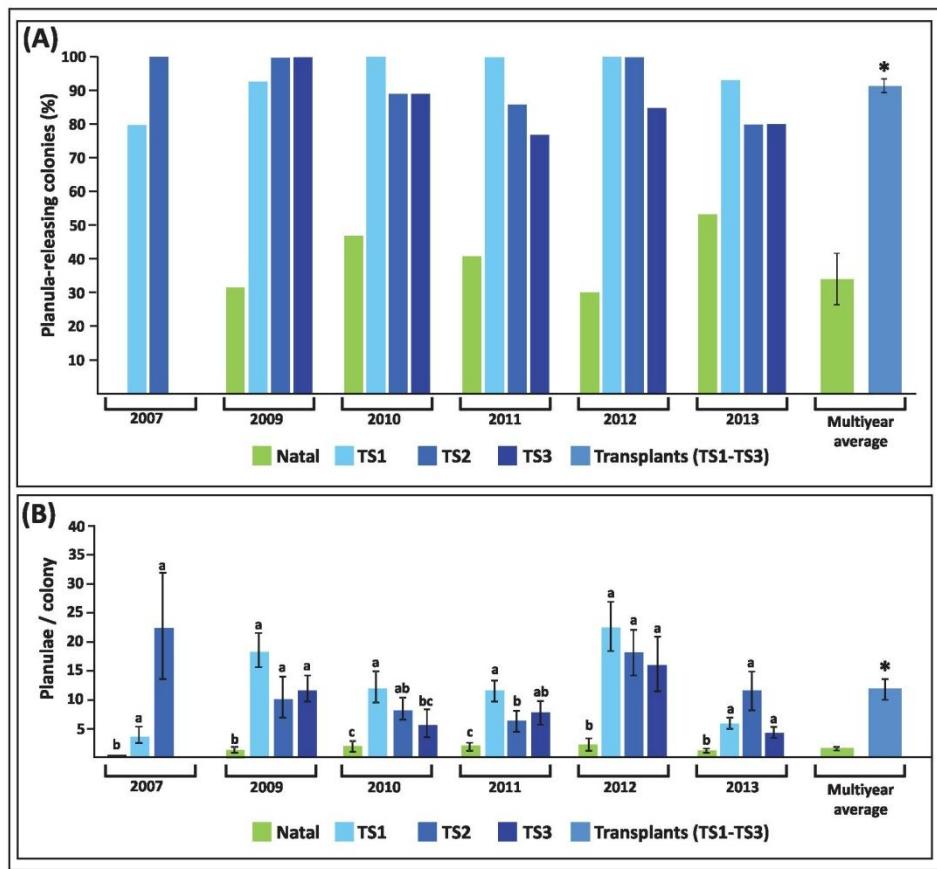


Fig. 2. Reproductive efforts of *Stylophora pistillata* colonies at the Dekel Beach. (A) Percentages of planula-releasing native and transplanted colonies per transplantation session. * denotes a significant difference between native colonies and transplants (multiyear mean \pm SE, average of three transplanted cohorts TS1-TS3; Paired t-test, $t_5=6.831$ $p=0.001$). (B) Average numbers of planulae per colony collected from native and transplanted colonies (mean \pm SE) per transplantation session. Letters denote significant differences within years (Mann-Whitney U test after Bonferroni adjustment, $p<0.05$). * denotes a significant difference between native colonies and transplants (multiyear mean \pm SE, average of three transplanted cohorts TS1-TS3; Mann-Whitney U test, $p=0.002$).

1.8 planulae/colony were collected from TS1-TS3 transplants vs. 1.5 ± 0.3 planulae/colony from native *S. pistillata* colonies (Mann-Whitney, $p=0.002$; Fig. 2B).

Discussion

Coral reproduction traits are affected by anthropogenic impacts that are further amplified by GCC effects (Rinkevich & Loya, 1987; Harrison, 2011; Hartmann, Marhaver, & Vermeij, 2017). While it may still go unnoticed, a phenomenon of gradual weakening in reproduction and changes in coral reproductive traits are already recorded in the coral reef in

Eilat (Zakai, Dubinsky, Avishai, Caaras, & Chadwick, 2006; Shefy et al., 2018). It is thus interesting to find that when growing native and transplanted corals side by side in a disturbed environment, the formerly nursery-grown *S. pistillata* transplants show increased performance compared to native colonies. Extending our early results (Horoszowski-Fridman et al., 2011), this high performance had been maintained throughout the 7.5-year study period (8 reproductive seasons following the first transplantation act) and did not level off with time, as expected if it was merely due to resource accretion during the nursery period. A large proportion (47%–100%) of native *S. pistillata* colonies examined over the years did not release larvae (0–33% of corresponding transplants),

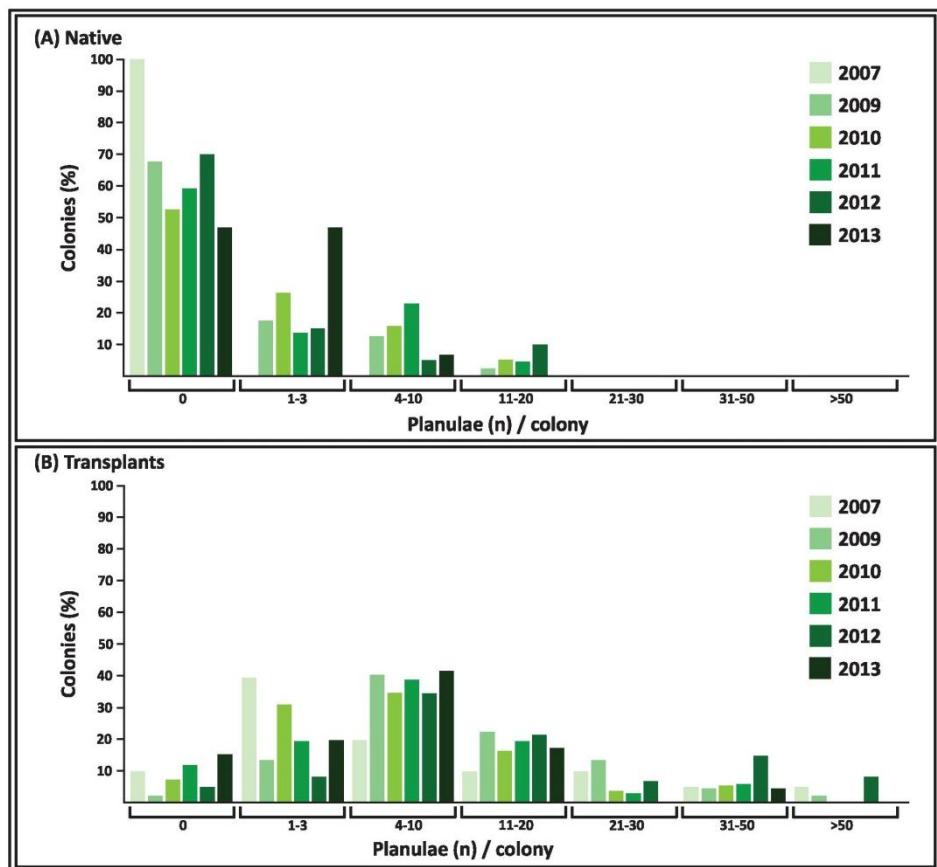


Fig. 3. Distribution of planula larvae. The significantly different overall distributions (χ^2 test for each year, $p < 0.001$) of the released planulae/*Stylophora pistillata* colony throughout the six reproductive seasons during 7.5 years post-transplantation. (A) Native colonies, (B) nursery-farmed transplants, pooled across transplantation cohorts.

and the average numbers of planulae released were low (multiyear average of 1.5 ± 0.3 vs. 11.6 ± 1.8 planulae/colony from transplants). In contrast, transplants released between 2.6 to 22.5 times more planulae/colony over the study years ($34 \pm 7.6\%$ vs. $91 \pm 2.1\%$ of planulae-releasing native and transplanted colonies, respectively). Using the above figures to calculate the output of 20 reproductive seasons of an *S. pistillata* adult (Rinkevich & Loya, 1987), and considering 120 days of peak larva release per year (March-June; Amar et al., 2007), 1000 transplants will produce about 28 million larvae as compared to 3.5 million from the same number of native colonies.

Using coral transplants with enhanced reproductive capacity could assist in countering population decline while local breeding stocks recover, especially in places where settlement is highly dependent on local sources (e.g., Hughes &

Tanner, 2000; van Oppen, Lutz, De'ath, Peplow, & Kininmonth, 2008). This is also true in brooding populations where the size of the adult stocks determines their resilience and their chances of recovery (Doropoulos, Ward, Roff, González-Rivero, & Mumby, 2015). Recent studies provide evidence that degraded reef areas may suffer from limited rates of natural recruitment as a result of the reduced number of breeding corals and following the dwindling of coral populations (dela Cruz & Harrison, 2017). Transplants with inherently enhanced larval production could help mitigate the long-term effects of sub-lethal bleaching that decreases the reproductive outputs of surviving corals (Szmant & Gassman, 1990; Ward, Harrison, & Hoegh-Guldberg, 2000; Omori, Fukami, Kobinata, & Hatta, 2001), lasting several years following the onset of recovery from the bleaching

event (Mendes & Woodley, 2002). High fecundity may increase the pace of genetic adaptation to changing environments (Torda et al., 2017) and thus, reef resilience. Combining such an approach with additional management efforts should aid in supplementing the genetic diversity of restored populations due to the reinforced breeding stock and the extensive larval addition. Nonetheless, the relationships between the planula surplus and the settlement and recruitment on restored reefs are important aspects that are yet to be determined.

While the poor performance of native colonies documented in this study likely reflects the reduced health of the reef in a highly impacted location (Hartmann et al., 2017), the question remains as to why the nursery-grown transplants' reproductive performance was persistently high and long-lasting. The recorded differences between native colonies and transplants cannot be attributed to genetically disparate source populations as part of the donor *S. pistillata* colonies used to establish the nursery-bred coral stock originated from the restoration site (Shafir et al., 2006). It is also highly unlikely that the differences in fecundity are attributable to genotypic diversity; the used number of donor colonies is assumed to represent a wide range of the populations' genetic diversity (Shearer, Porto, & Zubillaga, 2009; Afiq-Rosli et al., 2019), preventing genotypes to play an over-riding influence role on the reproductive output. The literature shows that coral nursery conditions positively influence reproductive traits, both in brooding and in broadcasting corals (Amar & Rinkevich, 2007; Okubo, Yamamoto, Nakaya, & Okaji, 2010; Horoszowski-Fridman et al., 2011; Baria et al., 2012; Guest et al., 2014). For example, almost 90% of *Acropora millepora* colonies in the nursery were gravid as compared to only 25% of reef-residing colonies (Baria et al., 2012; Guest et al., 2014). Likewise, cultured *S. pistillata* colonies had 35% higher numbers of oocytes/polyp and shed higher numbers of planulae/colony than similarly sized naturally-growing colonies on the natural reef (Amar & Rinkevich, 2007). These outcomes are directly linked to the improved conditions in the coral nurseries as compared to natural habitats (Rinkevich, 2005a; Shafir et al., 2006; Levy, Shaish, Haim, & Rinkevich, 2010), but do not explain the present study's results of augmented reproductive output in such a long term. The effects of resource accumulation during rearing would have surely dissipated long before they were still observed 7.5 years post-transplantation on the reef. Likewise, coral nurseries positively modulate growth rates of cultured corals (Shafir et al., 2006; Lirman et al., 2010; Bongiorni et al., 2011; Baria et al., 2012; Guest et al., 2014; Linden & Rinkevich, 2017) and the augmented growth rates of nursery-farmed transplants continue to be detected for up to 4 years after being transplanted on the natural reef (Horoszowski-Fridman et al., 2015; Afiq-Rosli et al., 2017). Conjointly, the above documentations of prolonged nursery-rearing effects on both reproduction and growth rates may imply, although not yet verified, an epigenetic signature.

Epigenetic changes (including methylation, histone modifications, small RNAs, and phenotypic plasticity) can come into play not only under stress conditions (Bräutigam et al., 2013; Pértille et al., 2017) but may also be induced by various nurturing circumstances such as parental care and improved nutrition (Champagne et al., 2006; Cropley, Suter, Beckman, & Martin, 2006). In respect to coral adaptation, epigenetic modifications have already been suggested to occur in coral clones subject to different environmental conditions (Dixon, Bay, & Matz, 2014; Putnam & Gates, 2015; Putnam et al., 2016; Liew et al., 2018; Dimond & Roberts, 2020). Therefore, rearing corals in nurseries with improved biological and environmental conditions (such as enhanced plankton supply, lack of competition, reduced sedimentation loads, decreased predation, optimal light conditions, increased water flow; Rinkevich, 2005a; Shafir et al., 2006; Levy et al., 2010; Afiq-Rosli et al., 2017) may have a continued epigenetic impact on their future fitness and ecological traits (reproduction, growth), enhancing their ability to counter harsh environmental situations. This may also be achieved under field scenarios: a reciprocal transplantation experiment in the Philippines (Raymundo, 2001) has shown that fragments of *Porites attenuata* originating from a pristine reef location grew significantly faster than fragments from a degraded reef area, regardless of the different treatments to which they were subjected. Interestingly, an epigenetically controlled linkage between reproductive performance and environmental stressors, including lifestyle factors (stress, physical activity, diet, toxin exposure, etc.) has already been shown in mammals (Palmer, Bakos, Fullston, & Lane, 2012; Stuppia, Franzago, Ballerini, Gatta, & Antonucci, 2015; Hart, 2016;). An enhanced larval production in reef-transplanted corals due to epigenetic-associated coral nursery conditions could have far-reaching implications for coral reef restoration, particularly as an adaptation tool for reef corals to counter GCC impacts, and especially if these epigenetic impacts are vertically transferred to nursery-farmed progenies. The study of epigenetic effects in corals is still in its infancy, and whether it is the mechanism underlying the observed performance of coral transplants in this study, merits further experimental investigation.

This study is the first report of extended higher reproductive performance of nursery-grown and outplanted coral colonies in comparison to wild stocks. The accumulated research on the 'gardening tenet' discovers additional facets of coral nurseries aside from the classical use as a source of stock material for coral transplantation (Rinkevich, 2014; Schopmeyer et al., 2017). A coral nursery may serve as a genetic repository for coral and reef-associated species (Schopmeyer et al., 2012); a 'larval dispersion hub' to enhance natural reseeding of impacted reefs (Amar & Rinkevich, 2007; Rinkevich, 2015a); as a tool to establish large stocks of sexually-derived coral colonies (Baria et al., 2012; Toh, Guest, & Chou, 2012; Guest et al., 2014; Linden & Rinkevich, 2017); as the first step for the 'tiling the reef' approach (Rachmilovitz & Rinkevich, 2017); as an

accelerator of coral growth (Afiq-Rosli et al., 2017); as a novel tradable instrument in the conservation of coral reefs (Rinkevich, 2015b); as an enhancer of selected genotypes of interest and reef associated fauna (Shafir & Rinkevich, 2010; Horoszowski-Fridman & Rinkevich, 2017; Taira et al., 2017); and in the establishment of connectivity (stepping stones) between biologically unconnected reefs (Rinkevich, 2015a). The long-term observations described here reveal an additional and unexpected prolonged effect of the nursery phase, the enhancement of transplants' reproductive outputs, which provides a potential tool to aid mitigating the direct and indirect effects of GCC.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Chapter 5

Reef Carpets: Shifting reef restoration mission from live coral cover to biodiversity enhancement

Statement of Authorship

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Reef Carpets: Shifting reef restoration mission from live coral cover to biodiversity enhancement

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ABSTRACT:

In the marine silviculture approach for active reef restoration, new coral colonies are farmed in underwater nurseries and then transplanted onto degraded reefs. In an attempt to augment coral transplantation benefits and accelerate the scale of restoration practice, a new farmed coral transplantation approach termed '*Reef Carpets*', resembling the commercial turf grass sod units used in terrestrial lawn-gardening, is presented and explored. Preset coral units of three branching species, *Acropora variabilis*, *Pocillopora damicornis* and *Stylophora pistillata*, were cultured at the coral nursery in Eilat (Red Sea) and deployed along with the accompanying reef biota that accumulated during nursery-period on a sandy bottom substrate. The transplantation of the Reef Carpets resulted in an immediate reef structure that supported coral recruitment and provided ecological niches for coral-associated invertebrates and fish. The Reef Carpets coral performance was monitored during a 17 month period following the transfer from the protective nursery conditions to the rather hostile new environment. Despite some adverse impact of moveable sediment underneath the Reef Carpets that led to a significant increase in partial mortality rates, the transplants exhibited high species-specific survival rates (50-65%) and a significant increase of their self-attachment to the Reef Carpet structure. Fish corallivory was more intense for *A. variabilis* and *S. pistillata* as compared to *P. damicornis*, and corallivorous gastropods showed a significantly higher attraction to the two pocilloporid species. The farmed *S. pistillata* transplants showed a higher reproductive performance than the natal colonies at the study site (4.6 ± 1.7 planulae/transplant vs. 1.6 ± 0.6 planulae/natal

colony), despite the harsh environmental conditions. The Reef Carpet corals stimulated the development of diverse fish and invertebrate communities (183 taxa recorded by visual censuses) that showed dynamic and complex biological interactions. The 3D properties of the coral species used revealed different ecosystem engineering consequences in structuring the reef-associated communities and harboring fish and invertebrate species diversity. The transplants' dead colonies emerged as an important habitat for reef biota, sustaining over 80% of the Reef Carpets associated species diversity. Shifting reef restoration focus from live coral cover to biodiversity enhancement, the Reef Carpets new transplantation approach can be leveraged to scale up restoration activity, and provide an effective ecological engineering tool for generating new reef zones and supporting biodiversity in degrading reefs.

Introduction

Coral reef ecosystems provide livelihood, food, and socio-cultural services to hundreds of millions of people around the world (Woodhead *et al.* 2019). These marine 'hotspots' also support one of the highest concentrations of biological diversity (Glynn 2011; Plaisance *et al.* 2011). Yet, adverse global climatic changes together with the rise in anthropogenic stressors (such as pollution, coastal development, overexploitation of reef resources, destructive fishing methodologies) are impeding coral reefs' resilience and natural adaptive capacities (IPCC 2019; Kleypas 2019), and make them one of the most endangered habitats on the planet (Young *et al.* 2016). Since traditional management methodologies (including MPAs and fishing restriction) are not effective enough to avert the alarming worldwide reef degradation and threat of extinction (e.g., Rinkevich 2008; Mouillot *et al.* 2016; Bates *et al.* 2019; Bruno *et al.* 2019), active restoration became central to reef conservation and various approaches have just recently been developed (Rinkevich 2019).

One such recently emerging methods, 'gardening coral reefs', was inspired by forest restoration rationales (Rinkevich 1995, 2005a, 2014, 2015; Young *et al.* 2012; Schopmeyer *et al.* 2017). Coral reefs are often referred to as the 'rain forests of the sea', but moreover, the two ecosystems, reefs and forests, also share numerous ecological and functional properties (Epstein *et al.* 2003; Horoszowski-Fridman & Rinkevich 2017). Hence, the marine silviculture approach incorporated various forest restoration principles and theories, forming a coral restoration toolbox that is centered on ecological engineering tools (Linden & Rinkevich

2011, 2017; Horoszowski-Fridman *et al.* 2011, 2015; Rinkevich 2014, 2015; Chou 2016; Horoszowski-Fridman & Rinkevich 2017; Rachmilovitz & Rinkevich 2017; Linden *et al.* 2019; Rosado *et al.*, 2019). The ‘Gardening coral reefs’ approach is based on two successive phases: 1) Farming of new stocks of coral colonies originating from sexual/aseexual propagation in underwater nurseries, followed by 2) Transplantation of the nursery-bred corals onto degraded reefs once they have reach suitable size. The first phase of the gardening approach has benefited from prolonged research (Soong & Chen 2003; Omori 2005; Shafir *et al.* 2006; Amar & Rinkevich 2007; Okamoto *et al.* 2008; Shaish *et al.* 2008; Levy *et al.* 2010; Lirman *et al.* 2010; Mbije *et al.* 2010; Shafir & Rinkevich 2010; Bongiorni *et al.* 2011; Linden & Rinkevich 2011, 2017; Schopmeyer *et al.* 2012, 2017; Iwao *et al.* 2014; Drury *et al.* 2017), revealing the capacity to farm new coral colonies of over 86 species in different nursery prototypes worldwide (Rinkevich 2014). In comparison, study of the transplantation phase of the gardening methodology is still limited, and many of the applicable theoretical and practical aspects have yet to be illuminated.

The most commonly used coral transplantation method to date, is individual transplantation of nursery-grown coral colonies, requiring manual attachment of each colony, one at the time. First, such a practice requires hard substrates to which the individual colonies can be secured. However, in many degraded reef localities, the reef substrate is no longer suitable for coral attachment, for example, areas previously subjected to dynamite fishing, sediment-covered zones following land reclamation activities, or following phase shift events (Hughes *et al.* 2010; Bongiorni *et al.* 2011; Fox *et al.* 2019). Second, the individual transplantation of each farmed-colony is more labor intensive and time consuming, limiting this method to small scale efforts only. Additionally, coral nurseries have surfaced as platforms for the recruitment of reef-associated organisms (Shafir & Rinkevich 2010; Taira *et al.* 2017; Sam *et al.* 2018; Wee *et al.* 2019), which could be transplanted in tandem with the farmed colonies to restore and enhance transplanted reefs biodiversity. However, transplantation methods that allow to incorporate the nursery-annexed reef biota are not yet available. As part of the effort to overcome the above mentioned drawbacks and enhance the active reef restoration toolbox, this study explores a novel transplantation approach termed ‘*Reef Carpets*’ after the commercially available turf grass sod units used in terrestrial new lawn or lawn repair application. Preset coral units of three branching species were generated and cultured at the coral nursery in Eilat (Gulf of Aqaba, Red Sea). The units were deployed, along with the annexed biota accumulated during the nursery-rearing period, on a sandy bottom substrate.

We monitored the performance of the Reef Carpet corals during a 17 month period following their transfer from the protective nursery conditions to the rather hostile new environment, recording their survival, partial tissue loss and damage from fish and gastropod corallivores. Additionally, we examined the ability of the Reef Carpet corals to provide refugia for the reef fauna and stimulate the development of coral-associated communities.

Materials and Methods

Study sites

The study was conducted at the northern part of the Gulf of Eilat, Red Sea, Israel, an area subjected to extensive anthropogenic pressures, including recreational activities, pollution, intermittent municipal sewage outflow, industrial installations and the heedless development of the city of Eilat, amongst others (Zakai & Chadwick-Furman 2002; Rinkevich 2005b). The coral colonies were reared in the Eilat's underwater floating coral nursery ($29^{\circ}32'28.04''N$, $34^{\circ}58'23.99''E$), floating at a depth of 6-8 m (12-14 m above the seafloor) where corals were maintained under favorable conditions (Rinkevich 2006; Shafir *et al.* 2006; Shafir & Rinkevich 2010).

The transplantation site, Kisuski Beach, is located 2 km south-west of the coral nursery amid an intense recreational zone, adjacent to a diving center, a water sport center and an underwater restaurant. The sea floor at this location is unstable, made of well-sorted, medium to small-grained mobile sand that is constantly in motion due to winds, southern storms and sand-inhabiting organisms. Hard corals are scarce at this site and are limited to a few scattered knolls with less than 10% coral cover, and a small number of corals growing on artificial objects.

Generating Reef Carpet subunits at the coral nursery

The Reef Carpet (RC) idea was inspired by the commercially available turf grass units (also called sod) used in terrestrial gardening for fast lawn formation. The RCs were constructed from subunits carrying preset corals that were farmed at the coral nursery. In this experiment we used a total of 708 nursery-bred colonies of three branching corals, *Stylophora pistillata*, *Pocillopora damicornis* and *Acropora variabilis*, fragmented from adult colonies collected at the natural reef (Shafir *et al.* 2006; Shafir & Rinkevich 2010 for methodological details), and from additional genotypes that settled naturally on the coral

nursery's infrastructure. The coral fragments were glued on top of plastic nails and were cultured on nursery-rearing trays (RC subunits; each consisting of a plastic net mesh 0.25 cm² in size stretched over a 40X60 cm PVC frame) for a period of 8-36 months until developing 3D branching colonial structures. Each RC subunit possessed coral genotypes of a single species, along with the biota community that had developed on the tray during the nursery phase. The number of colonies per tray varied (1-30) according to their sizes (5-50 cm in diameter). Colonies that accidentally detached from the plastic nails during or after the preparation (ca. 20%) were directly attached to the nursery-rearing tray's net using plastic cable ties. Upon maturation, the subunits were placed in plastic containers filled with seawater and transferred from the nursery to the transplantation site by boat.

Reef Carpet Deployment on a soft bottom substrate

Three Reef Carpets of 8.4m² each (3X2.8m) were placed 24m to 33m apart, each comprised of 194 to 294 farmed colonies that were assembled by joining the RC subunits on the sandy sea bed at a depth of 10.7-13.3m (Fig. 1a1,2; Table S1). SCUBA divers randomly distributed the subunits between the 3 RCs and positioned them in accordance to a pre-planned scheme that maintained the relative proportion of colonies per species, with random distribution of the corals (Fig. S1). The 35 subunits per RC were arranged in seven columns and five rows, and were placed directly on the sand, attached to each other with plastic cable ties. Each RC was secured to the sand with 50 cm U-shaped iron bars, fully inserted within the sediment.

Monitoring

SCUBA diving surveys were conducted every 2 to 3 months throughout a period of 17 months from the onset of RC deployment. In each survey all transplanted colonies were examined for the following parameters: 1) survival; 2) colony self-attachment: tissue/skeletal spread beyond initial attachment onto the plastic nail/net; 3) partial tissue death (i.e., partial mortality): appearance of bare skeleton areas, estimated visually at 5% intervals; 4) fish bites: typical lesions inflicted by the removal of tissue, exposing the underlying skeleton (Rotjan & Lewis 2008); 5) presence of the gastropod predators, *Drupella cornus* and *Coralliophila sp.*; 6) disappearance from the RC. Additional visual censuses and underwater digital photography were used to record the reef-associated communities developing on the RCs. All fish and invertebrate specimens spotted above, on, within and between the branches of each transplanted colony were recorded, counted (when possible), and identified *in situ* to the lowest taxonomic level possible. Similar censuses were applied throughout the experiment duration to each nursery-rearing tray, including the PVC frames

and plastic nets of the trays, and on sedimentation loads on the trays. Species identification was subsequently confirmed or modified using digital photographs and the World Register of Marine Species (WoRMS) database and by consultations with taxonomists, where applicable. Boring and within coral biota (e.g., gall crabs, *Lithophaga* bivalves) could only be included when the small openings they typically form at the coral surface were observed. Whenever ambiguity arose (e.g., identifying boring bivalves to species level under field conditions), specimens were assigned to a higher taxonomic levels. Permits restricted sampling collections.

Planula larvae collection

In order to evaluate the potential contribution of RC to the local reproduction, the reproductive outputs of transplanted *S. pistillata* colonies (a brooding coral species) were compared to the naturally-growing natal colonies. Planula traps were simultaneously placed (5 randomly selected nights, January – August, the reproductive season of *S. pistillata*; Shefy *et al.* 2018) from sunset to sunrise over 16 sexually mature (>8cm diameter; Rinkevich & Loya 1979) natal colonies and 20 randomly selected intact colonies from each RC. The trapped larvae were then gently flushed with filtered seawater into wide Petri dishes and counted under a stereomicroscope, as described (Horoszowski-Fridman *et al.* 2011).

Data analyses

Data analysis was performed using the SPSS v.21 software for Windows. Mixed-model ANOVA was used to analyze experimental effects on dependent variables, with time (17 months) as within-subjects factors and coral species as a between-subjects factor. The dependent variables were coral survival, disappearance, self-attachment, partial mortality, fish attacks, and the presence of gastropod predators. The arcsine square root transformation was applied for survival, self-attachment, partial mortality, and the proportion of colonies attacked by fish and gastropods. Mauchly's test of sphericity was used to test the assumption of sphericity. Huynh-Feldt correction was used when the assumption of sphericity was violated. Tukey post-hoc tests were used to compare differences among the three coral species' survival, self-attachment, and the proportion of colonies attacked by fish and gastropods. The Kaplan–Meier analysis was used to generate the curve of survival time for the three transplanted species, followed by the Mantel–Cox *log-rank* test for the survival curves comparison. The reproductive output of natal and transplanted *S. pistillata* colonies was analyzed using one sample *t*-test, comparing natal colonies output with the

average output of the three RCs pooled together (RC1-RC3), after normal distribution was confirmed.

In order to study community development on the RCs, a Canonical Correspondence Analysis (CCA) was performed with the CANOCO version 4.5 (Ter Braak & Smilauer 2002). We investigated the composition of reef-associated species in relation to environmental factors attributed to the coral species, the state of the coral colonies (alive/dead), time since RC transplantation and spatial considerations (location on the RC: center or periphery, associated with the substrate or with corals). This unimodal method of ordination allowed for visualization of the correlations between the environmental variables and the taxon in a two dimensional ordination diagram, where the RC taxa are represented by triangles, and the environmental variables are expressed by arrows outgoing from the origin (the arrow's length reflects the importance of the variable). The statistical significance of the relationships between the species and the environmental variables was tested by the Monte Carlo permutation test, using 499 permutations under a reduced model (Ter Braak & Smilauer 2002). The analysis was initially done on all the RC-related taxa, followed by a separate examination of the fish community, the invertebrate community, and the subgroup that appear to have the most intimate association with coral hosts, crustaceans (estimated to constitute 35% of the coral-associated invertebrates; Stella *et al.* 2011).

In order to explore the diversity of the developing community at the RC, we used EstimateS version 9.1.0 (Colwell 2013) to calculate the non-parametric abundance-based (Chao 1) and incidence-based (Chao 2) estimators of species richness. The analysis was conducted separately for the fish fauna, the total invertebrate fauna, and the crustaceans only, based on 100 randomizations without Replacement. Chao 1 was calculated for the fish and crustacean community, whereas Chao 2 was computed for the invertebrate community (based on presence/absence data), as counting organisms under field conditions was not always possible in this group (like boring organisms, such as *Lithophaga* sp., colonial ascidians, etc.). To compare the diversity in each group, one-way ANOVAs were performed followed by Tukey HSD Post-hoc tests using the web-based statistical calculator resource Statpages (<https://statpages.info/anova1sm.html>).

Results

A flash reef instantly flourishing with life in the middle of a sandy seabed “reef desert”

The Reef Carpets transplantation in the middle of a vast sandy area (Fig. 1a2-4) instantly generated new lively reef activity. Despite the moveable sediment underneath the reef carpets leading to a dynamic pattern of partial colony mortality that was repaired and repeated, many of the corals survived, thrived, and contributed to the local coral reproduction. The ecosystem engineering effects of the transplants became quickly evident as the transplants stimulated the development of a diverse reef-associated community in each of the carpets (183 fish and invertebrate taxa recorded by the visual censuses). The new reef plots provided settlement sites: numerous new coral recruits were observed among the RCs during the survey and coral-obligate crustaceans (e.g., *Cymo*, *Trapezia* and *Tetralia* species) settled in colonies of their specific coral hosts. The RCs also became nursery sites: juvenile fish cohorts aggregated between the branches of the RC corals and several egg masses (of unknown origin) were spotted during the survey. These new transplanted reefs enabled the formation of trophic webs and complex biological interactions, such as the establishment of multiple ‘cleaning stations’ by *Labroides dimidiatus* in each of the RC plots and predators such as *Pterois* lurking for newly settled fish aggregates. Additionally, the transplants’ dead colonies resulting from the moderate coral mortality transformed into hubs for reef biota hosting a variety of usually cryptic, well camouflaged specimens in the fouling of the carbonate skeletons.

Coral attributes during the study period

In total, 132 *A. variabilis*, 212 *P. damicornis* and 364 *S. pistillata* transplants were inserted in the three RCs. Following the 17-month monitoring period, the three coral species exhibited different survival rates as indicated from the significant interaction between species and time (mixed-model ANOVA, $F_{12,36} = 4.076$, $P=0.001$; Fig. 1b). *A. variabilis* demonstrated the highest survival rate (Tukey post-hoc tests, $P<0.05$), and first mortality was only detected eight months after the RC transplantation. No significant difference in survival was observed between the two pocilloporid species (Tukey post-hoc tests, $P>0.05$). The median post transplantation lifespan of *A. variabilis*, *P. damicornis* and *S. pistillata* was 17, 13 and 11 months, respectively, and the probability of survival was significantly different for each of the three species (Kaplan-Meier analysis, Mantel-Cox log-rank test, $\chi^2=7.087$, $df=2$, $P=0.029$;

Table S2; Fig S2). In the final survey, the survival rate averaged $65.3 \pm 6.2\%$ (mean \pm SE) in *A. variabilis*, $54.6 \pm 8.6\%$ in *P. damicornis*, and $48.7 \pm 6.5\%$ in *S. pistillata* (Fig. 1b).

The number of colonies disappearing from the RCs after 17 months was marginal, overall ranging from $4.2 \pm 1.3\%$ (*S. pistillata*) to $6.2 \pm 3.4\%$ (*P. damicornis*), and did not differ significantly between the three species (mixed-model ANOVA, $F_{12,36}=0.746$, $P=0.698$; Fig S3). Partial mortality (the loss of tissue resulting from physical or biological traumas such as sedimentation and predation) was commonly observed during the study period in all three coral species and steadily increased over time. Since partial mortality is a natural and a common occurrence among scleractinian corals (also reflecting cases of aging processes; Rinkevich & Loya 1986), a number of transplants showed various levels of partial mortality at the onset of transplantation ($32.3 \pm 12.2\%$ of *A. variabilis* colonies, $37.8 \pm 7.0\%$ of *P. damicornis* and $45.3 \pm 13.2\%$ of *S. pistillata* suffered $6.4 \pm 2.0\%$, $9.6 \pm 1.0\%$ and $19.3 \pm 4.7\%$ partial mortality/colony, respectively). Partial mortality may compromise coral performance (Cumming 2002; Mercado-Molina *et al.* 2018) and therefore, we first explored if the initial level of partial mortality impacted the subsequent colony survival. No significant difference was found between the colonies with and without partial mortality at onset of transplantation (mixed-model ANOVAs - *A. variabilis*: $F_{2,035,8,139}=3.755$, $P=0.069$; *P. damicornis*: $F_{4,173,16,690}=0.882$, $P=0.499$; *S. pistillata*: $F_{4,582,18,330}=1.753$, $P=0.176$; Fig. S4). After the RC deployment in the sandy seabed, some sand (the unstable substrate) moved through the trays' nets (Fig. 1a2-4) causing partial mortality. Consequently, the percentage of colonies with partial mortality increased significantly over time (mixed-model ANOVA, $F_{2,739,16,432}=79.304$, $P<0.001$) affecting all three species similarly ($F_{5,477,16,432}=1.863$, $P=0.152$; Fig. 1c). After 17 months, partial mortality was observed in 96% -100% of the colonies, its extent, which also increased significantly over time (mixed-model ANOVA, $F_{3,505,21,028}=80.021$, $P<0.001$) averaged $41.0 \pm 6.0\%$, $52.1 \pm 4.1\%$ and $63.7 \pm 1.7\%$ in *A. variabilis*, *P. damicornis* and *S. pistillata*, respectively, at the end of observations ($F_{7,009,21,028}=1.728$, $P=0.156$; Fig. 1d).

Despite the adverse impact of the moving sediment, colonies continued to grow and spread on the RC structure. Self-attachment of transplants to the RC frames increased significantly over time (mixed-model ANOVA, $F_{6,36}=95.994$, $P<0.001$; Fig. 1e) and was observed at a higher rate in *A. variabilis* ($F_{12,36}=7.424$, $P<0.001$; Tukey post-hoc tests, $P<0.05$), whereas the two pocilloporid species had comparable rates (Tukey post-hoc tests, $P>0.05$). After 17

months, $58.0\pm3.3\%$ of *A. variabilis*, $16.2\pm5.1\%$ of *P. damicornis* and $12.5\pm4.5\%$ of *S. pistillata* permanently attached to the RC sub frame.

Corallivory by fish and gastropod snails was dynamic at the RCs. Throughout the 17-month monitoring period, the extent of fish attacks on the corals' tissue varied over time (mixed-model ANOVA, $F_{3.904,23.424}=6.932$, $P=0.001$; Fig. 2a). *A. variabilis* and *S. pistillata* were more prone to fish attacks than *P. damicornis* ($F_{7.808,23.424}=3.945$, $P=0.005$; Tukey post-hoc tests, $P<0.05$), nevertheless, the number of colonies that showed fish bites did not exceed $24.1\pm12.7\%$ (recorded in *A. variabilis* at the last observational point). The number of fish bites per colony was comparable among the three species throughout the survey, fluctuating between 0.7 ± 0.3 to 5.1 ± 3.0 bites/attacked colony (mixed-model ANOVA, $F_{5.982,17.946}=1.523$, $P=0.227$; Fig. 2b). Foraging by corallivorous gastropods *Drupella cornus* and *Coralliophila sp.* further inflicted damages on the transplants affecting all three species (Fig. 2c), yet significantly more impact was recorded on pocilloporid colonies (mixed-model ANOVA, $F_{12,36}=5.000$, $P<0.001$; Tukey post-hoc tests, $P<0.05$), with no difference between the pocilloporid species (Tukey post-hoc tests, $P>0.05$). The combined average number of these gastropods in foraged colonies varied between 0.3 ± 0.3 to 5.9 ± 2.9 gastropods/colony in *A. variabilis*, 0.8 ± 0.4 to 3.0 ± 0.8 gastropods/colony in *P. damicornis*, and 1.0 ± 0 to 3.4 ± 0.6 gastropods/colony in *S. pistillata* (Fig. 2d). Mixed-model ANOVA analysis indicated a significant interaction between time and species ($F_{4.459,13.375}=3.991$, $P=0.022$), nonetheless, the Tukey post-hoc tests showed that no pair of species was significantly different from each other.

The reproductive output of *S. pistillata*

The RC transplants had higher reproductive outputs than the natal colonies at the study site. Planulae were obtained from 50% of natal and 68.3% (mean of RC1-RC3) of transplanted *S. pistillata* colonies examined (Table 1; Fig. S5). Although the proportion of colonies participating in the reproduction did not significantly differ between these groups (One sample t-test, $t_2=4.16$, $P=0.053$), significantly more planulae/colony were released by the RC transplants when compared with the natal colonies (RC1-RC3, 4.6 ± 1.7 planulae/transplant vs. 1.6 ± 0.6 planulae/natal colony; mean \pm SE; One sample t-test, $t_2=4.45$, $P=0.047$; Fig. S5).

The reef-associated community that developed in the Reef Carpet units

The presence of the RC corals has stimulated the formation of fish and invertebrate communities at each of the RC plots. The RC biota list revealed 66 fish taxa (Table S3) and 123 invertebrate taxa, out of which 39 were crustacean (Table S4). Most fish taxa (71.2%;

N=44) were identified to the species level, 9.1% (N=6) to genus, and 18.2% (N=12) were assigned to the family level, altogether representing 47 species from 39 genera belonging to 19 fish families. The identification of the invertebrate specimens under field conditions required an extensive effort; only 32.5% (N=40) invertebrate taxa were identified to the species level, 12.2% (N=15) to the genus level, 16.3% (N=20) to families, and the remaining invertebrate taxa were classified to lower taxonomic ranks [Infraorder: 14.6% (N=18); Order: 4.9% (N=6); Subclass: 0.8% (N=1); Class: 6.5% (N=8); Phylum: 12.2% (N=15)], representing 40 species, 50 genera and 51 families. For the 39 crustacean taxa, 35.9% (N=14) were identified to the species level, 5.1% (N=2) to genus, 7.7% (N=3) to family, 46.2% (N=18) to Infraorder, and 5.1% (N=2) to the order level, representing 14 species from 13 genera belonging to 14 families of crustaceans.

The transplantation of the three coral species, each unique in its 3D structure, had created several new habitats for reef dwelling organisms (live colonies, dead colonies, and the substrate underneath the colonies of each of the coral species) that were each characterized by specific associated fish and invertebrates taxa. These new ecological niches had varying influence on the structure of the fish and invertebrate communities that developed at the RCs over the study period, as revealed by the CCA analysis. Since neither the RC nor the location within the RC (RC center or periphery) contributed to the structuring of the RCs communities (Fig. S6), the three environmental variables (plot, center, and periphery) were excluded from subsequent analyses. Considering the fish community structure (Fig. 3a), the horizontal axis of the ordination was primarily affected by the coral species in the RC and the substrate underneath the colony (understory), with a strong effect of live *A. variabilis* colonies (left side of X-axis), live *P. damicornis*, and the tray (right side of X-axis). Dead colonies of the three coral species demonstrated a comparable weight on the fish community structure (right side of the X-axis, arrows of same direction and length). The vertical axis was influenced by the time scale since RC deployment (lower part of Y-axis). The distribution of fish taxa along the ordinates was not random; the two axes accounted for 70.5% of the variance in the species-environment relation (Monte Carlo test, $F=7.250$, $P=0.002$). Three groups of fish species emerged: 1) those associated with live *A. variabilis* colonies, mostly coral-specialist species found among live corals (e.g., *Gobiodon reticulatus*, *Dascyllus aruanus*, *Dascyllus trimaculatus*); 2) species related to live *P. damicornis* colonies and the understory substrate, including species with strong habitat association with live corals (e.g., *Pseudochromis olivaceus*) and bottom-dwelling species (*Muraenidae*); 3) fish

species associated with live *S. pistillata* colonies and dead coral skeletons (e.g., *Amblyglyphidodon*, *Ecsenius*, and *Pterois* species).

In the invertebrate community (Fig. 3b), live colonies of the three coral species had a substantial impact on the horizontal axis of the ordination, with a strong effect of live *A. variabilis* (right side of X-axis), followed by *P. damicornis* and *S. pistillata* (left side of the X-axis). Like in the fish community, the vertical axis was strongly impacted by the time scale (upper part of Y-axis), and it was also affected by the dead coral colonies and the understory environment. Here again, taxa distribution along the ordinates were not random, and the two axes accounted for 60.9% of the variance in the species-environment relation (Monte Carlo test, $F=25.563$, $P=0.002$). Three groups of species emerged: invertebrate species associated with live *A. variabilis* colonies (e.g., *Tetralia cavimana*), species associated with live pocilloporid colonies (e.g., *Trapezia cymodoce*), and species associated with dead coral skeletons or the RC framework underneath the colonies (e.g., *Mycale fistulifera*, and most ascidians and sponge morphospecies recorded).

We then focused on the crustacean community (Fig. 3c). The horizontal axis was mainly affected by live *A. variabilis* colonies (right side of X-axis), followed by live *P. damicornis* and *S. pistillata* colonies (left side of the X-axis). As with the fish and invertebrates (all), the vertical axis was strongly impacted by time (upper part of Y-axis) with a similar effect of dead coral colonies and the understory substrate. Taxa distribution was not random and the two axes accounted for 71.2% of the variance in the species-environment relation (Monte Carlo test, $F=35.251$, $P=0.002$). Four groups of crustacean species were defined, reflecting the preferences of many coral-dependent crustaceans for a specific coral host (Stella *et al.* 2010; Wee *et al.* 2019): species attracted to live *A. variabilis* colonies (e.g., *Tetraloides nigrifrons*, *Tetralia cavimana*), to live *P. damicornis* colonies (e.g., *Alpheus lottini*), to live *S. pistillata* colonies (e.g., *Hapalocarcinus marsupialis*), and species associated with dead coral skeletons or the RC underlying substrate (e.g., *Lysmata amboinensis*).

The new habitats created by the RC corals provided different shelter and living space opportunities and thus, harbored different levels of the RCs biota's species diversity. After 17 months, the fish community diversity differed significantly between the three coral species (one-way ANOVA, $F_{2,5768}=271.711$, $P<0.001$; Fig. 4a; Table S5). Fish diversity was highest in *S. pistillata* RC subunits, with the Chao 1 prediction of 77 ± 30 (mean \pm SD) fish species associated with *Stylophora*, followed by *A. variabilis* and *P. damicornis*, harboring 68 ± 7 and 62 ± 11 fish species, respectively (Tukey HSD Post-hoc tests, $P<0.001$). We then

extended the analysis, looking at the specific habitats generated by the RCs, i.e., subdividing the fish taxa associated with live colonies, dead colonies, and the substrate underneath the colonies, for each of the coral species. Again, the diversity of the fish community differed significantly between these habitats (one-way ANOVA, $F_{8,5762}=853.435$, $P<0.001$; Fig. 4b; Table S6). The highest fish diversity was assigned to live *A. variabilis* colonies (76 ± 18 species), followed by the understory environments of the three coral species (60 ± 48 , 49 ± 14 , and 41 ± 5 fish species for *P. damicornis*, *S. pistillata* and *A. variabilis* understories, respectively; Tukey HSD Post-hoc tests, $P<0.001$). *Acropora* understory had comparable diversity to live *P. damicornis* (39 ± 3 species) and *S. pistillata* (38 ± 9 species) colonies (Tukey HSD Post-hoc tests, $P>0.05$). Similarly, the dead coral heads of the two pocilloporid species did not significantly differ in their estimated species richness (23 ± 17 and 22 ± 10 fish species for *S. pistillata* and *P. damicornis*, respectively; Tukey HSD Post-hoc tests, $P>0.05$), and the lowest diversity was attributed to the dead *A. variabilis* heads (8 ± 1 fish species; Tukey HSD Post-hoc tests, $P<0.001$).

Observing the invertebrate community species diversity (Figs. 4c-f; Tables S7-S10), *P. damicornis* contained the highest diversity and *A. variabilis* the lowest, either for the total community (Chao 2) or crustaceans only (Chao 1; 126 ± 13 , 121 ± 2 and 106 ± 2 invertebrate species, and 40 ± 2 , 39 ± 0.1 and 35 ± 3 crustacean species, expected for *P. damicornis*, *S. pistillata* and *A. variabilis*, respectively; one-way ANOVAs, invertebrates: $F_{2,5768}=2885.123$, $P<0.001$, crustaceans: $F_{2,5768}=3665.725$, $P<0.001$; Figs. 4c,e; Tables S7,S9). Species diversity analyses for the different habitats (live colony/dead colony/understory) yielded comparable patterns for the invertebrate and crustacean biodiversity as well, that differed significantly between the various habitats (one-way ANOVAs, invertebrates: $F_{8,5762}=4302.382$, $P<0.001$, crustaceans: $F_{8,5762}=4571.741$, $P<0.001$; Figs. 4d,f; Tables S8,S10). The highest diversity for the whole invertebrate community was estimated in the live colonies of the three coral species, with maximum of 110 ± 1 invertebrate species for *S. pistillata* colonies, 107 ± 5 species for *P. damicornis* and 105 ± 4 species for *A. variabilis* (Tukey HSD Post-hoc tests, $P<0.001$). For the crustacean community, a maximum of 38 ± 6 crustacean species was estimated for live *A. variabilis* colonies (Tukey HSD Post-hoc tests, $P<0.001$), while species diversity for live *S. pistillata* and *P. damicornis* colonies was 36 ± 1 species (Tukey HSD Post-hoc tests, $P>0.05$). The highest diversity of the live coral colonies was followed by the dead pocilloporid corals together with the substrate underneath *Pocillopora*: 95 ± 7 , 87 ± 19 and 86 ± 7 invertebrates species were estimated in dead *S. pistillata*, *P. damicornis* understory and dead *P.*

damicornis, respectively (Tukey HSD Post-hoc tests, $P<0.001$ except for *P. damicornis* understory and dead *P. damicornis*, $P>0.05$) and 30 ± 8 , 24 ± 2 and 18 ± 10 crustaceans species were computed for dead *P. damicornis*, dead *S. pistillata*, and *P. damicornis* understory, respectively (Tukey HSD Post-hoc tests, $P<0.001$). Lower species diversity was associated with dead *A. variabilis* colonies (64 ± 13 invertebrate species and 14 ± 4 crustacean species; Tukey HSD Post-hoc tests, $P<0.001$ for both cases). The *Acropora* and *Stylophora* understories had the lowest associated invertebrates/crustaceans diversity (61 ± 4 and 58 ± 5 invertebrate species, respectively; Tukey HSD Post-hoc tests, $P<0.001$; 8 ± 0.1 and 7 ± 1 crustacean species, respectively; Tukey HSD Post-hoc tests, $P>0.05$).

Interestingly, the dead Pocilloporid colonies harbored a substantial fraction of the invertebrate species diversity, their species diversity reached 80-86% (invertebrate) and 66-83% (crustacean) of that estimated in the live Pocilloporid corals. While obligate symbionts that depend on coral hosts for food and shelter such as *Trapezia guttata* and *Hapalocarcinus marsupialis* were only observed on live corals, the dead colonies supported generalist species such as the omnivorous cleaner shrimps *Saron marmoratus* and *Stenopus hispidus*. Moreover, three of the invertebrate taxa recorded were only present in dead colonies (Phyllodocida, Porifera and Mollusca specimens).

Dead coral heads, thus, emerged as an important habitat for reef-associated fauna, with estimated species richness reaching as much as 11% to 86% of the estimated live coral diversity (Figs. 4b,d,f).

Discussion

The massive coral reef degradation documented over the last decades on a worldwide scale requires innovative active restoration approaches to support and expand present reef restoration initiatives. The ‘coral gardening’ methodology, a two-phase practice adapted from terrestrial silviculture, has proven to be efficient in propagating large stocks of various coral species amenable for restoration, in numerous locations around the world (Rinkevich 2014; Schopmeyer *et al.* 2017). However, one of the big challenges of this marine silviculture approach is the development of a large scale, new coral stock transplantation methodology that can be used to restore large areas of severely degraded reefs where the underlying hard substrate is highly modified to non-existent. In response to this pressing need, this study presents a new ecological engineering approach for coral reef restoration named ‘Reef

'Carpet' (RC), which mimics the turf grass sod units' application in commercial lawn-gardening. Like the terrestrial counterpart application, the RC methodology consists of generating and farming preset coral units in a coral nursery and when ready, assembling and outplanting the units in degraded reef zones. This new method creates an efficient alternative to the labor intensive individual coral colonies transplantation practice, which is most commonly used to date (e.g., Drury & Lirman 2017; Rinkevich 2019).

In order to test this new approach, preset coral units of *A. variabilis*, *P. damicornis*, and *S. pistillata* were cultured at the coral nursery in Eilat and later relocated along with the accompanying reef biota that accumulated during nursery period, to a new hostile sandy-bottom substrate area and followed for 17 months. The Reef Carpets transplantation established flash reef structures in the middle of the vast sandy area. They supported coral recruitment and provided ecological niches for invertebrates and fish, instantly demonstrating lively reef activity. Despite some adverse impact of moveable sediment underneath the Reef Carpets that led to a significant increase in partial mortality rates along the study period, as well as corallivory by fish and gastropods, the transplants exhibited high species-specific survival rates (50% - 65%). These results are comparable with the 17 month survivorship of nursery-grown colonies transplanted on a rocky reef substrate in Eilat 1.5 km south of current site (Horoszowski-Fridman *et al.* 2015), where 78% and 52% survival rate were assigned to *P. damicornis* and *S. pistillata*, respectively. The corallivory activity of the fish and the Muricid gastropods documented at the RCs during the study was generally moderate (e.g. half the rate of fish corallivory recorded in the above mentioned transplantation on a rocky reef; Horoszowski-Fridman *et al.* 2015). Muricid gastropods such as the *Drupella* and *Coralliophila* that were present at the RCs, are increasing in abundance in the northern Red Sea over the last decades (Schoepf *et al.* 2010) and can cause extensive coral mortality (Morton *et al.* 2002; Baums *et al.* 2003; Rotjan & Lewis 2008; see Shafir *et al.* 2008 for an outbreak report 700m away from the RCs). Their observed density at the RCs was mostly below 4 gastropods/colony and the presence of predator fish such as *Coris aygula* and *Thalassoma lunare* contributed to their 'top-down' abundance regulation. Their significant higher appearance in the pocilloporid colonies over their preferred *Acropora* prey at the RCs may indicate a more effective gastropod removal by fish from *A. variabilis* colonies or a differential stress-related attraction (Morton *et al.* 2002, and literature therein; Al-Horani *et al.* 2011). Interestingly, the decline in *A. variabilis* survivorship and the increase in partial mortality, first observed after eight months, coincided with the appearance of the

corallivorous snails in the *Acropora* colonies. Despite the harsh environmental conditions, high reproductive efforts were recorded for transplanted *S. pistillata* colonies (ca. 3 times higher) when compared to natal colonies. These results add to previously documented long term enhanced larval production in nursery-bred transplants (Horoszowski-Fridman *et al.* 2011), highlighting an important effect of the nursery rearing phase.

One of the clear outcomes of this study, is the recruitment of reef associated biota (usually less discussed in coral transplantation sessions; but see Mbije *et al.* 2013; dela Cruz *et al.* 2014; Horoszowski-Fridman *et al.* 2015), that occurred similarly in all three RCs. This represents the ecological engineering impacts of transplants on the surrounding environment. During the 17 months period, we recorded, by visual censuses, 183 fish and invertebrate taxa that showed dynamic and complex biological interactions (e.g., the formation of multiple 'cleaning stations' by *Labroides dimidiatus*). The 3D properties of the used coral species reveal different ecological engineering consequences in structuring the fish and invertebrate communities. Each of the used coral species, and the various segregated microhabitats they generated, had a distinctive contribution to the communities' composition that developed at the RCs, harboring different fractions of species diversity. The ecological niches created by live colonies, and the coral species, emerged as important elements in influencing community composition and species diversity. Indeed, the literature attests that *Acropora* and *Pocillopora* corals contribute the most to fish habitat and are favored by many coral-dwelling species (Pratchett *et al.* 2008; Coker *et al.* 2014; Pratchett *et al.* 2014). Furthermore, many coral-dependent crustaceans, including *Cymo*, *Trapezia* and *Tetralia* species recorded at the RCs, exhibit specific preference for the species of their coral host (Stella *et al.* 2010; Wee *et al.* 2019). In the case of the RC fish community composition, live colonies of *S. pistillata* had a comparable effect to the dead coral skeletons of the three coral species, probably reflecting their contribution to the RC structural complexity, rather than influencing fish community structure by specific associations with coral-specialist species. Nonetheless, topographic complexity has been acknowledged as important as live coral cover in structuring fish assemblages since some coral reef fish rely more on the structural relief than on live coral (Chabanet *et al.* 1997; Jones & Syms 1998; Lindahl *et al.* 2001; Pratchett *et al.* 2008; Pratchett *et al.* 2014).

The results further signify the overlooked issue of the ecological engineering impacts and the ecological importance of dead coral colonies. In most reef restoration acts, coral survival is one of the major success criteria, whereas high rate of dead colonies implies failures

(Edwards 2010). However, dead coral colonies construct specific habitat types in the coral reef that host a wide range of reef dwelling organisms, sustaining up to 86% of the associated species diversity recorded in this study. Plaisance *et al.* (2011) revealed substantial reef biodiversity in dead coral heads of four coral families (Pocilloporidae, Meandrinidae, Poritidae, Agariciidae). In a study of epifaunal invertebrate communities associated with live and dead nursery-grown corals during nursery culture, Wee *et al.* (2019) found a higher abundance and taxonomic richness on dead fragments of *Pocillopora acuta* and *Platygyra sinensis*, the latter also supported a higher diversity than the live coral fragments. Additionally, the epifaunal communities established on live and dead *P. acuta* varied significantly. Coles (1980) studied decapod communities associated with live and dead *Pocillopora meandrina* colonies and found the species diversity of non-symbiont communities on dead colonies to be substantially higher than diversity of symbiont communities on live corals. He concluded that the community on live colonies is markedly impoverished compared to the species assemblage residing in the corals after their death. Similarly, Enochs & Manzello (2012) discovered that contrary to the paradigm that live corals are the apex of biodiversity, the species richness of motile cryptofauna (i.e., taxa inhabiting intra/inter-skeletal spaces) was higher among dead coral substrates. Similar patterns were observed in reef fish; within areas of high coral cover, moderate levels of coral mortality increase habitat heterogeneity and associated fish diversity (Jones & Syms 1998; Wilson *et al.* 2009; Coker *et al.* 2014). Live and dead corals offer different resources for reef fauna (Coles 1980; Enochs 2012; Enochs & Manzello 2012; Coker *et al.* 2014; Wee *et al.* 2019): live corals provide nutritional sources such as coral tissue, mucus, fat bodies, particulate organic matter, and concentrate pray and plankton abundance whereas micro/filamentous algae and detritus are abundant on dead coral surfaces, which also provide a greater assortment of food resources. The live and dead coral colonies offer different shelter and camouflage opportunities (Jones & Syms 1998; Coker *et al.* 2014). Live corals provide settlement cues for reef-associated species (Pratchett *et al.* 2008; Wee *et al.* 2019), their skeleton is used by specialized burrowers and gall-forming species (Stella *et al.* 2011), while dead colonies constitute a settlement substrate for encrusting and sessile non-coral, less competitive organisms. The surface covered by coral tissue is homogenous and rather simplified compared with the spatial heterogeneity of microhabitats provided by dead corals (Coles 1980; Stella *et al.* 2010). Together with live coral cover, dead colonies increase the spectrum of reef habitats available, not only for the limited subset of coral-specialist residing among

living corals that often benefit from a competitive advantage (Stella *et al.* 2010; Enochs & Manzello 2012; Pratchett *et al.* 2014), but also for generalist and non coral-obligate taxa (Coles 1980).

In terrestrial silviculture, the importance of dead habitat elements has already been recognized (e.g., dead trees, logs, and coarse woody debris), as they constitute important components for some forest species and contribute to the planted forests' structural diversity (Franklin *et al.* 2002; Lindenmayer & Hobbs 2004; Carnus *et al.* 2006; Manning *et al.* 2013). Likewise, the diversity and abundance of the whole spectrum of reef organisms are strongly linked to habitat diversity and complexity (Chabanet *et al.* 1997; Pratchett *et al.* 2014) and when increased by niche diversification, reef heterogeneity could provide a larger variety of habitats, supporting ecosystem services and resilience (Bozec *et al.* 2013; Pratchett *et al.* 2014). Incorporating biodiversity considerations in the restoration scheme is indispensable (Drury & Lirman 2017; Horoszowski-Fridman & Rinkevich 2017). Associations between reef-dwelling species and corals not only benefit the reef fauna, but can also increase coral persistence (Stella *et al.* 2011), including interactions with herbivorous invertebrates and fish (Enochs 2012; Lefcheck *et al.* 2019) and mutualist invertebrates (Stella *et al.* 2010). Therefore, coral transplantation plans should consider the wider needs of the reef fauna by providing specific species composition for habitat specialists while enhancing niche diversity for less dependent species.

Further research is needed to elaborate and develop the concept of Reef Carpets in reef restoration. The characteristics of the target transplantation site should be considered when planning the RC units, in order to reduce potential adverse effects such as the sand-mediated partial mortality observed in this study. Some of the additional aspects that will need to be clarified, are the effects of interspecific vs. intraspecific corals competition within the RC units and the combination effects of species with different characteristics (colony morphology, life-history traits, growth rates etc.) for biodiversity enhancement. Additionally, it should be examined how different RC types could be configured to maintain ecosystem functions and supply specific services (e.g., attraction/transplantation of target associated species, nursery sites for reef fauna, reproduction enhancement, connectivity, fishery enhancement, and diversion of recreational activities from natural reefs). Nonetheless, this new RC transplantation methodology can enhance restoration scale, since large zones, including areas unsuitable for natural regeneration by coral recruitment (e.g., following blast fishing, land reclamation siltation, phase shifts, etc.), can be quickly covered by preplanned

coral assemblages (including bleaching tolerant and stress-resistant stocks; Drury & Lirman 2017; van Oppen *et al.* 2017) with their already present associated biota. Additionally, the enhanced reproductive capacity of nursery-bred transplants can bolster coral reproduction at restored reefs and amplify restoration outcome, increasing degraded populations' genetic diversity and capacity to face future changes. Our success in the hard task of combating reef decline relies on the development of new approaches for generating well-conceived, self-perpetuating reef zones designed to maintain a variety of ecological flows, supply habitats for a wide range of reef biodiversity, and provide various ecosystem services to reef organisms and human populations alike.

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Table

Table 1: *In situ* planulae collection from 2 groups of *Stylophora pistillata* colonies: a) naturally-growing colonies at the experimental site; b) nursery-bred transplanted colonies composing three Reef Carpets (RC1-RC3).

Colonies examined (n)	Planulae-releasing colonies (%)	Range of planulae collected		Total planulae collected	Average planulae/colony ± SE
		Min	Max		
Natal	16	50	0	9	26
RC 1	20	70	0	16	82
RC 2	20	60	0	24	75
RC 3	20	75	0	38	118

FIGURE LEDGENDS

Figure 1: The deployment of Reef Carpets on a soft-bottom substrate and the performance of the Reef Carpet corals over 17 months. (a) A Reef Carpet at: 1) construction; 2) immediately after deployment; 3) 7 months following deployment; 4) 17 months following deployment. (b) Survivorship of transplants. (c) The percentage of transplants suffering from partial mortality. (d) The average magnitude of tissue loss/colony due to partial mortality. (e) Self attachment. Mean ± SE. In each panel, a mixed-model ANOVA was performed. Letters denote statistically significant groups (Tukey post-hoc tests, $P<0.05$).

Figure 2: Corallivory by fish and the gastropod predators *Drupella sp.* and *Coralliophila sp.* (a) The percentage of transplants damaged by fish. (b) The average number of damaged sites per attacked colony (c) The percentage of transplants in which *Drupella sp.* and *Coralliophila sp.* were recorded. (d) The average number of gastropod predators in attacked colonies. Mean ± SE. In each panel, a mixed-model ANOVA was performed. Letters denote statistically significant groups (Tukey post-hoc tests, $P<0.05$).

Figure 3: Species-environment b-plots based on a canonical correspondence analysis (CCA) for the effect of environmental factors (arrows) on RC community structure (associated species/taxa represented by triangles). (a) Fish species/taxa. Eigenvalues: axis 1 = 0.530; axis 2 = 0.228. The variance explained by each axis (%) is shown. (b) Invertebrate species. Eigenvalues: axis 1 = 0.466; axis 2 = 0.375. The variance explained by each axis (%) is shown. For clarity, only environmental variables (arrows) are shown (see Fig. S7 for the complete diagram also showing the 123 taxa). (c) Crustacean species. Eigenvalues: axis 1 = 0.651; axis 2 = 0.353. In each ordination diagram, the variance explained by each axis (%) is shown. Environmental variables: time in months since RC transplantation (**Date**); spotted in a live A.

variabilis, *P. damicornis* or *S. pistillata* colony (**Ac Alive**, **Pd Alive** and **Sp Alive**, respectively), or in a dead colony of the before mentioned species (**Ac Dead**, **Pd Dead** and **Sp Dead**, respectively), or substrate-associated (seen on the tray/sediment covering the tray; **Tray**). For list of species abbreviations – see Tables S3 and S4.

Figure 4: The diversity, based on Chao 1 and Chao 2 richness estimators, of the reef-associated communities developing over 17 months at RCs made of three coral species: *A. variabilis*, *P. damicornis* and *S. pistillata*. The fish diversity associated with (a) *A. variabilis*, *P. damicornis* and *S. pistillata* transplants, and (b) live colonies, dead colonies and the understory substrate of the former species. The invertebrate diversity associated with (c) *A. variabilis*, *P. damicornis* and *S. pistillata* transplants, and (d) live colonies, dead colonies and the understory substrate of the former species. The crustacean diversity associated with (e) *A. variabilis*, *P. damicornis* and *S. pistillata* transplants, and (f) live colonies, dead colonies and the understory substrate of the former species. Mean \pm SD. In each panel, diversity was compared with one-way ANOVAs. Letters denote statistically significant groups (Tukey HSD Post-hoc tests $P<0.05$).

Fig.1

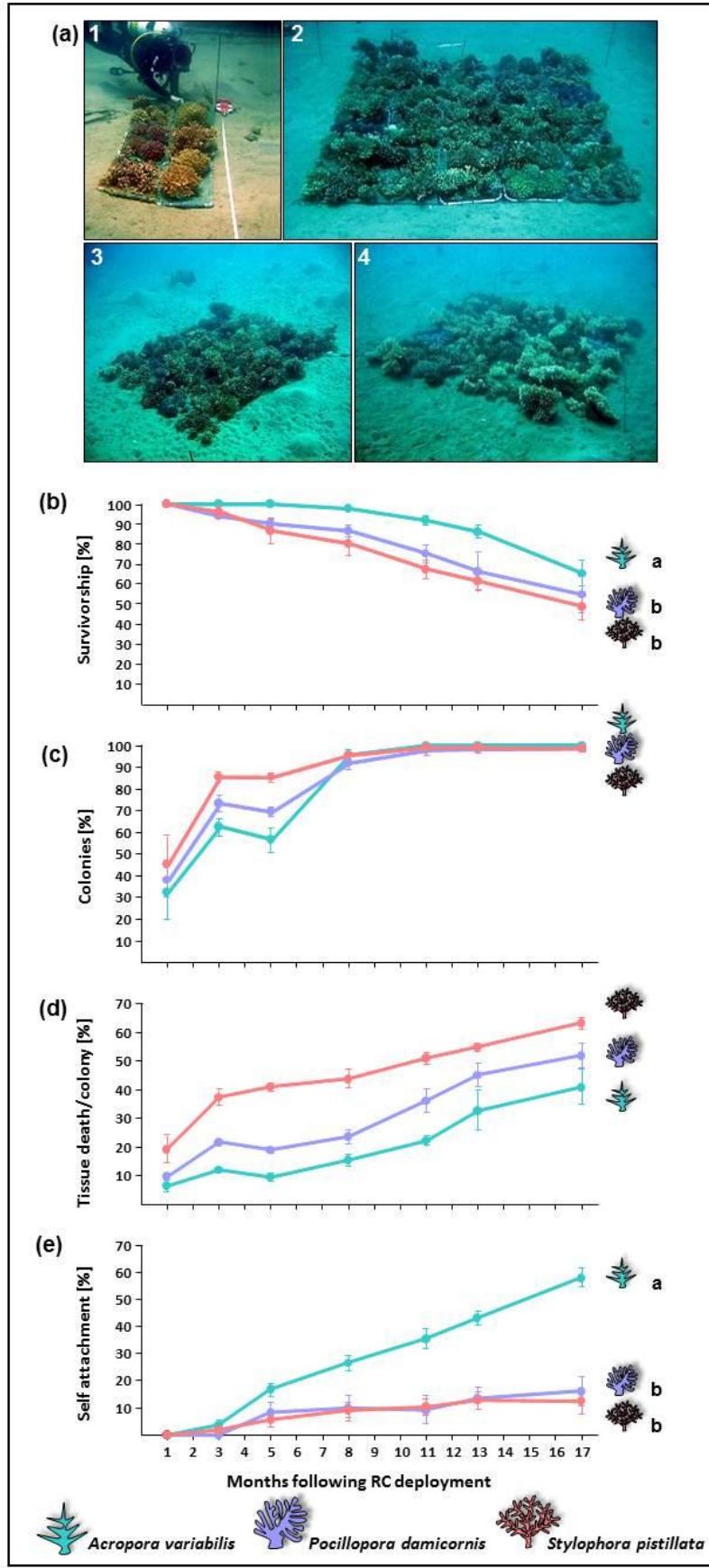
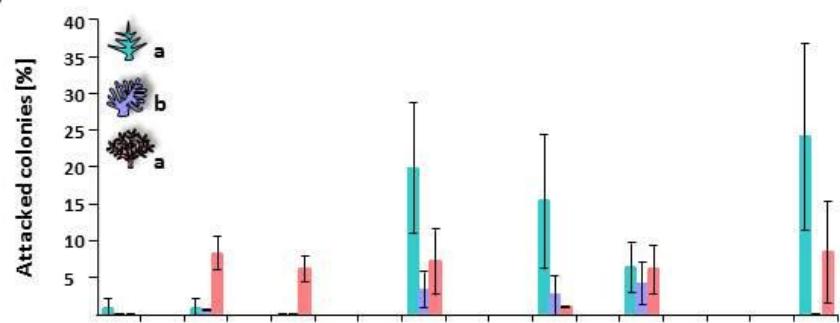
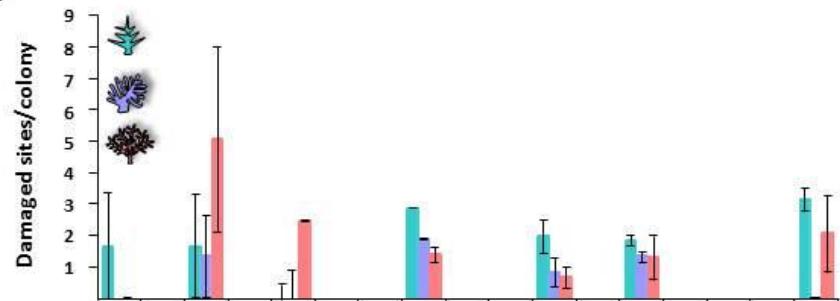


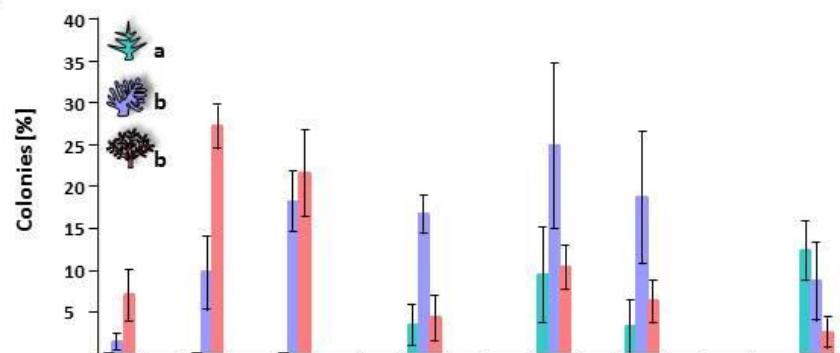
Fig.2 (a)



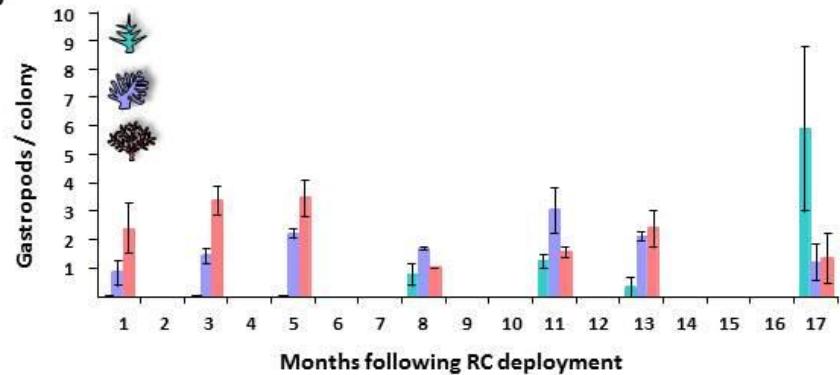
(b)



(c)



(d)



Acropora variabilis

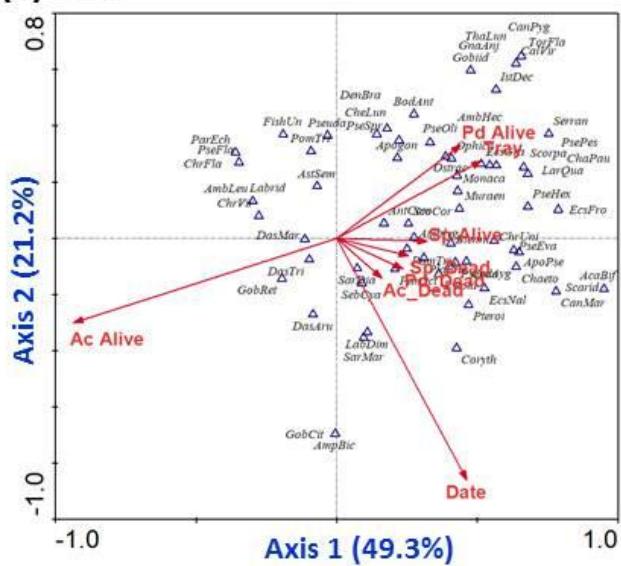


Pocillopora damicornis

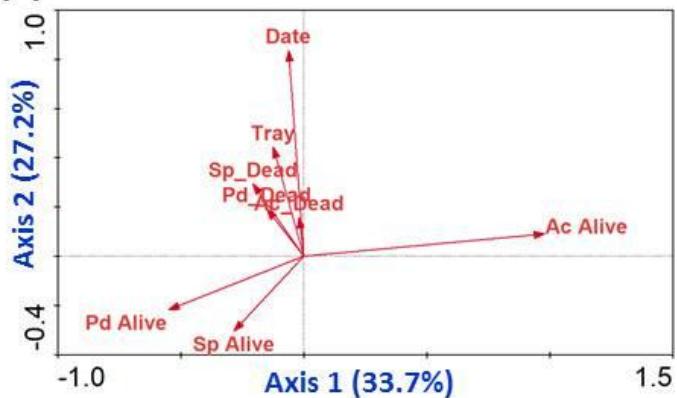


Stylophora pistillata

Fig.3 (a) Fish



(b) Invertebrates



(c) Crustacean

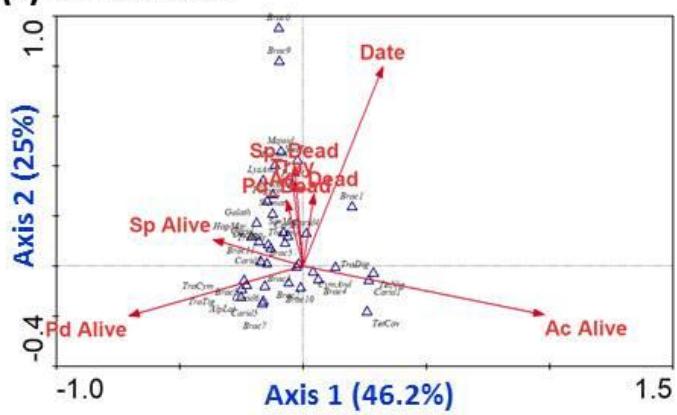
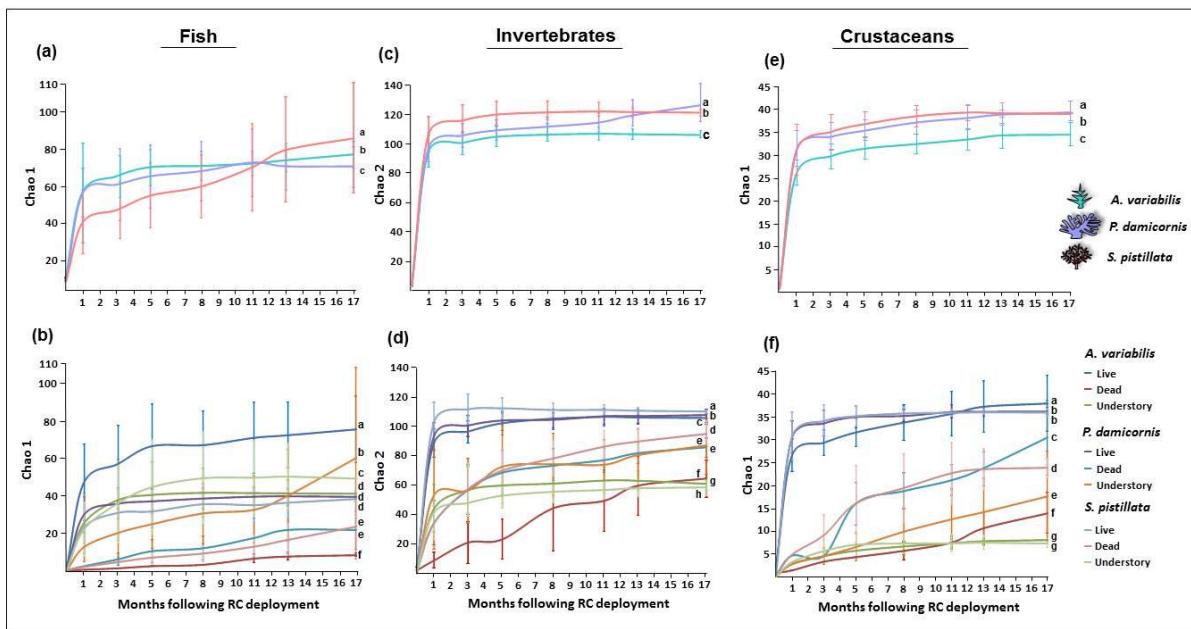


Fig.4



Supplementary Materials

Tables

Table S1. Experimental design of three Reef Carpets deployed on a soft-bottom substrate at Kisuski Beach (Red Sea, Eilat, Israel).

(a)	Reef Carpet 1		Reef Carpet 2		Reef Carpet 3	
	# sub-units	# colonies	# sub-units	# colonies	# sub-units	# colonies
<i>Stylophora pistillata</i>	10	92	11	155	11	117
<i>Pocillopora damicornis</i>	12	63	12	90	12	59
<i>Acropora variabilis</i>	13	39	12	49	12	44
Total	35	194	35	294	35	220

(b)	Distance between Reef Carpets (m)	
	RC2	RC3
RC1	29.15	33.05
RC2		24.05

Table S2: Statistical comparison of mean survival times, estimated by the Kaplan-Meier analysis, for the three coral species transplanted as Reef Carpets during 17 months post-transplantation.

	Median (months)			
	Estimate	Std. Error	95% Confidence Interval (months)	
			Lower Bound	Upper Bound
<i>Acropora variabilis</i>	17	0.221	16.567	17.433
<i>Pocillopora damicornis</i>	13	0.535	11.952	14.048
<i>Stylophora pistillata</i>	11	0.514	9.992	12.008

	Chi-Square	df	P
Log Rank (Mantel-Cox)	7.087	2	0.029

Table S3: List of fish taxa census at the Reef Carpets over 17 months.

Phylum	Family	Genus	Species	Abbreviation
Chordata	Antennariidae	<i>Antennarius</i>	<i>Antennarius commerson</i>	AntCom
	Apogonidae	<i>Apogon</i>	<i>Apogon psefion</i>	ApoPse
	Apogonidae*	-	-	Apogon
	Blenniidae	<i>Plagiotremus</i>	<i>Plagiotremus rhinorhynchos</i>	PlaRhi
	Blenniidae	<i>Ecsenius</i>	<i>Ecsenius nalolo</i>	EcsNal
	Blenniidae	<i>Ecsenius</i>	<i>Ecsenius frontalis</i>	EcsFro
	Blenniidae	<i>Ecsenius</i>	<i>Ecsenius gravieri</i>	EcsGra
	Blenniidae*	-	-	Blenni
	Chaetodontidae	<i>Chaetodon</i>	<i>Chaetodon paucifasciatus</i>	ChaPau
	Chaetodontidae*	-	-	Chaeto
	Gobiidae	<i>Gobiodon</i>	<i>Gobiodon reticulatus</i>	GobRet
	Gobiidae	<i>Gobiodon</i>	<i>Gobiodon citrinus</i>	GobCit

Phylum	Family	Genus	Species	Abbreviation
	Gobiidae	<i>Paragobiodon</i>	<i>Paragobiodon echinocephalus</i>	ParEch
	Gobiidae	<i>Eviota</i>	-	Eviota
	Gobiidae	<i>Asterropteryx</i>	<i>Asterropteryx semipunctatus</i>	AstSem
	Gobiidae	<i>Istigobius</i>	<i>Istigobius decoratus</i>	IstDec
	Gobiidae	<i>Gnatholepis</i>	<i>Gnatholepis anjerensis</i>	GnaAnj
	Gobiidae	<i>Amblygobius</i>	<i>Amblygobius hectori</i>	AmbHec
	Gobiidae*	-	-	Gobiid
	Holocentridae	<i>Sargocentron</i>	<i>Sargocentron diadema</i>	SarDia
	Holocentridae	<i>Sargocentron</i>	<i>Sargocentron marisrubri</i>	SarMar
	Labridae	<i>Paracheilinus</i>	<i>Paracheilinus octotaenia</i>	ParOct
	Labridae	<i>Labroides</i>	<i>Labroides dimidiatus</i>	LabDim
	Labridae	<i>Larabicus</i>	<i>Larabicus quadrilineatus</i>	LarQua
	Labridae	<i>Coris</i>	<i>Coris aygula</i>	CorAyg
	Labridae	<i>Pseudocheilinus</i>	<i>Pseudocheilinus evanidus</i>	PseEva
	Labridae	<i>Pseudocheilinus</i>	<i>Pseudocheilinus hexataenia</i>	PseHex
	Labridae	<i>Bodianus</i>	<i>Bodianus anthoides</i>	BodAnt
	Labridae	<i>Cheilinus</i>	<i>Cheilinus lunulatus</i>	CheLun
	Labridae	<i>Thalassoma</i>	<i>Thalassoma lunare</i>	ThaLun
	Labridae*	-	-	Labrid
	Monacanthidae*	-	-	Monaca
	Muraenidae*	-	-	Muraen
	Ophichthidae*	-	-	Ophich
	Ostraciidae*	-	-	Ostrac
	Pomacentridae	<i>Dascyllus</i>	<i>Dascyllus marginatus</i>	DasMar
	Pomacentridae	<i>Dascyllus</i>	<i>Dascyllus trimaculatus</i>	DasTri
	Pomacentridae	<i>Dascyllus</i>	<i>Dascyllus aruanus</i>	DasAru
	Pomacentridae	<i>Chromis</i>	<i>Chromis viridis</i>	ChrVir
	Pomacentridae	<i>Chromis</i>	<i>Chromis flavaxilla</i>	ChrFla
	Pomacentridae	<i>Pomacentrus</i>	<i>Pomacentrus trichourus</i>	PomTri
	Pomacentridae	<i>Pomacentrus</i>	<i>Pomacentrus trilineatus</i>	PomTri
	Pomacentridae	<i>Chrysiptera</i>	<i>Chrysiptera unimaculata</i>	ChrUni
	Pomacentridae	<i>Amphiprion</i>	<i>Amphiprion bicinctus</i>	AmpBic
	Pomacentridae	<i>Amblyglyphidodon</i>	<i>Amblyglyphidodon leucogaster</i>	AmbLeu
	Pomacentridae	<i>Amblyglyphidodon</i>	-	Amblyg
	Pseudochromidae	<i>Pseudochromis</i>	<i>Pseudochromis springeri</i>	PseSpr
	Pseudochromidae	<i>Pseudochromis</i>	<i>Pseudochromis olivaceus</i>	PseOli
	Pseudochromidae	<i>Pseudochromis</i>	<i>Pseudochromis pesi</i>	PsePes
	Pseudochromidae	<i>Pseudochromis</i>	<i>Pseudochromis flavivertex</i>	PseFla
	Pseudochromidae*	-	-	Pseudo
	Scaridae	<i>Calotomus</i>	<i>Calotomus viridescens</i>	CalVir
	Scaridae*	-	-	Scarid
	Scorpaenidae	<i>Scorpaenodes</i>	<i>Scorpaenodes corallinus</i>	ScoCor
	Scorpaenidae	<i>Sebastapistes</i>	<i>Sebastapistes cyanostigma</i>	SebCya
	Scorpaenidae	<i>Scorpaenopsis</i>	-	Scorpa
	Scorpaenidae	<i>Pterois</i>	-	Pteroi
	Scorpaenidae	<i>Dendrochirus</i>	<i>Dendrochirus brachypterus</i>	DenBra
	Serranidae	<i>Pseudanthias</i>	-	Pseuda
	Serranidae*	-	-	Serran
	Sparidae	<i>Acanthopagrus</i>	<i>Acanthopagrus bifasciatus</i>	AcaBif

Phylum	Family	Genus	Species	Abbreviation
	Syngnathidae	<i>Corythoichthys</i>	-	Coryth
	Tetraodontidae	<i>Canthigaster</i>	<i>Canthigaster pygmaea</i>	CanPyg
	Tetraodontidae	<i>Canthigaster</i>	<i>Canthigaster margaritata</i>	CanMar
	Tetraodontidae	<i>Torquigener</i>	<i>Torquigener flavimaculosus</i>	TorFla
	FishUnidentified	-	-	FishUn

*= lowest taxonomic rank identified when not recognized to genus or species level.

Table S4: List of invertebrate taxa census at the Reef Carpets over 17 months.

Phylum	Subphylum	Class	Subclass	Order	Infraorder	Family	Genus	Species	Abbreviation
Annelida	NR	Polychaeta	Sedentaria	Sabellida	NR	Serpulidae	<i>Spirobranchus</i>	-	Spirob
	NR	Polychaeta	Sedentaria	Sabellida	NR	Serpulidae*	-	-	Serpul
	NR	Polychaeta	Sedentaria	Sabellida	NR	Sabellidae*	-	-	Sabell
	NR	Polychaeta	Sedentaria	Terebellida	NR	Terebellidae*	-	-	Terebe
	NR	Polychaeta	Errantia	Phyllodocida*	-	-	-	-	Phylio
Arthropoda	Crustacea	Malacostraca	Eumalacostraca	Decapoda	Brachyura	Trapeziidae	<i>Trapezia</i>	<i>Trapezia cymodoce</i>	TraCym
	Crustacea	Malacostraca	Eumalacostraca	Decapoda	Brachyura	Trapeziidae	<i>Trapezia</i>	<i>Trapezia tigrina</i>	TraTig
	Crustacea	Malacostraca	Eumalacostraca	Decapoda	Brachyura	Trapeziidae	<i>Trapezia</i>	<i>Trapezia digitalis</i>	TraDig
	Crustacea	Malacostraca	Eumalacostraca	Decapoda	Brachyura	Trapeziidae	<i>Trapezia</i>	<i>Trapezia guttata</i>	TraGut
	Crustacea	Malacostraca	Eumalacostraca	Decapoda	Brachyura	Tetraliidae	<i>Tetraloides</i>	<i>Tetraloides nigritrons</i>	TetNig
	Crustacea	Malacostraca	Eumalacostraca	Decapoda	Brachyura	Tetraliidae	<i>Tetralia</i>	<i>Tetralia cavimana</i>	TetCav
	Crustacea	Malacostraca	Eumalacostraca	Decapoda	Brachyura	Xanthidae	<i>Cymo</i>	<i>Cymo andreossyi</i>	CymAnd
	Crustacea	Malacostraca	Eumalacostraca	Decapoda	Brachyura	Cryptochiridae	<i>Haplocarcinus</i>	<i>Haplocarcinus marsupialis</i>	HapMar
	Crustacea	Malacostraca	Eumalacostraca	Decapoda	Brachyura	Majoidea*	-	-	Majoid
	Crustacea	Malacostraca	Eumalacostraca	Decapoda	Brachyura	Portunidae*	-	-	Portun
	Crustacea	Malacostraca	Eumalacostraca	Decapoda	Brachyura1*	-	-	-	Brac1
Crustacea	Malacostraca	Eumalacostraca	Decapoda	Brachyura2*	-	-	-	-	Brac2
	Malacostraca	Eumalacostraca	Decapoda	Brachyura3*	-	-	-	-	Brac3
	Malacostraca	Eumalacostraca	Decapoda	Brachyura4*	-	-	-	-	Brac4
	Malacostraca	Eumalacostraca	Decapoda	Brachyura5*	-	-	-	-	Brac5
	Malacostraca	Eumalacostraca	Decapoda	Brachyura6*	-	-	-	-	Brac6
	Malacostraca	Eumalacostraca	Decapoda	Brachyura7*	-	-	-	-	Brac7
	Malacostraca	Eumalacostraca	Decapoda	Brachyura8*	-	-	-	-	Brac8
	Malacostraca	Eumalacostraca	Decapoda	Brachyura9*	-	-	-	-	Brac9
	Malacostraca	Eumalacostraca	Decapoda	Brachyura10*	-	-	-	-	Brac10
	Malacostraca	Eumalacostraca	Decapoda	Brachyura11*	-	-	-	-	Brac11

Phylum	Subphylum	Class	Subclass	Order	Infraorder	Family	Genus	Species	Abbreviation
	Crustacea	Malacostraca	Eumalacostraca	Decapoda	Caridea	Alpheidae	Alpheus	<i>Alpheus lottini</i>	AlpLot
	Crustacea	Malacostraca	Eumalacostraca	Decapoda	Caridea	Palaemonidae	Periclimenes	-	Pericl
	Crustacea	Malacostraca	Eumalacostraca	Decapoda	Caridea	Palaemonidae	Urocaridella	<i>Urocaridella antonbruuni</i>	UroAnt
	Crustacea	Malacostraca	Eumalacostraca	Decapoda	Caridea	Stenopodidae	Stenopus	<i>Stenopus hispidus</i>	SteHis
	Crustacea	Malacostraca	Eumalacostraca	Decapoda	Caridea	Hippolytidae	Saron	<i>Saron marmoratus</i>	SarMar
	Crustacea	Malacostraca	Eumalacostraca	Decapoda	Caridea	Thoridae	Thor	<i>Thor amboinensis</i>	ThoAmb
	Crustacea	Malacostraca	Eumalacostraca	Decapoda	Caridea	Lysmatidae	Lysmata	<i>Lysmata amboinensis</i>	LysAmb
	Crustacea	Malacostraca	Eumalacostraca	Decapoda	Caridea1*	-	-	-	Carid1
	Crustacea	Malacostraca	Eumalacostraca	Decapoda	Caridea2*	-	-	-	Carid2
	Crustacea	Malacostraca	Eumalacostraca	Decapoda	Caridea3*	-	-	-	Carid3
	Crustacea	Malacostraca	Eumalacostraca	Decapoda	Caridea4*	-	-	-	Carid4
	Crustacea	Malacostraca	Eumalacostraca	Decapoda	Caridea5*	-	-	-	Carid5
	Crustacea	Malacostraca	Eumalacostraca	Decapoda	Caridea6*	-	-	-	Carid6
	Crustacea	Malacostraca	Eumalacostraca	Decapoda	Caridea*	-	-	-	Carid
	Crustacea	Malacostraca	Eumalacostraca	Decapoda	Anomura	Paguroidea*	-	-	Paguro
	Crustacea	Malacostraca	Eumalacostraca	Decapoda	Anomura	Galatheidae	Galathea	-	Galath
	Crustacea	Malacostraca	Eumalacostraca	Decapoda*	-	-	-	-	Decapo
	Crustacea	Malacostraca	Hoplocarida	Stomatopoda*	-	-	-	-	Stomat
Bryozoa	NR	Gymnolaemata	NR	Cheilostomatida	NR	Bugulidae	Bugula	-	Bugula
Chordata	Tunicata	Asciidiacea	NR	Phlebobranchia	NR	Asciidiidae	Phallusia	<i>Phallusia nigra</i>	PhaNig
	Tunicata	Asciidiacea	NR	Phlebobranchia	NR	Asciidiidae	Phallusia	<i>Phallusia arabica</i>	PhaAra
	Tunicata	Asciidiacea	NR	Phlebobranchia	NR	Corellidae	Rhodosoma	<i>Rhodosoma turicum</i>	RhoTur
	Tunicata	Asciidiacea	NR	Stolidobranchia	NR	Pyuridae	Halocynthia	<i>Halocynthia spinosa</i>	HalSpi
	Tunicata	Asciidiacea	NR	Stolidobranchia	NR	Pyuridae	Pyura	<i>Pyura gangelion</i>	PyuGan
	Tunicata	Asciidiacea	NR	Stolidobranchia	NR	Pyuridae	Boltenia	<i>Boltenia yosiiyoya</i>	BolYos
	Tunicata	Asciidiacea	NR	Stolidobranchia	NR	Pyuridae	Herdmania	<i>Herdmania momus</i>	HerMom
	Tunicata	Asciidiacea	NR	Stolidobranchia	NR	Styelidae	Botryllus	<i>Botryllus eilatensis</i>	BotEil
	Tunicata	Asciidiacea	NR	Stolidobranchia	NR	Styelidae	Polycarpa	<i>Polycarpa cryptocarpa</i>	PolCry
	Tunicata	Asciidiacea	NR	Stolidobranchia	NR	Styelidae	Polycarpa	<i>Polycarpa mytiligera</i>	PolMyt
	Tunicata	Asciidiacea	NR	Aplousobranchia	NR	Diazonidae	Rhopalaea	-	Rhopal

Phylum	Subphylum	Class	Subclass	Order	Infraorder	Family	Genus	Species	Abbreviation
	Tunicata	Asciidiacea	NR	Aplousobranchia	NR	Didemnidae	Diplosoma	-	Diplos
	Tunicata	Asciidiacea	NR	Aplousobranchia	NR	Didemnidae	Didemnum	-	Didemn
	Tunicata	Asciidiacea1*	-	-	-	-	-	-	Ascid1
	Tunicata	Asciidiacea*	-	-	-	-	-	-	Ascid
Cnidaria	NR	Anthozoa	Hexacorallia	Actiniaria*	-	-	-	-	Actini
	NR	Anthozoa	Octocorallia	Alcyonacea	NR	Xeniidae*	-	-	Xeniid
	NR	Scyphozoa	Discomedusae	Rhizostomeae	NR	Cassiopeidae	Cassiopea	<i>Cassiopea andromeda</i>	CasAnd
Echinodermata	Echinozoa	Echinoidea	Euechinoidea	Diadematoida	NR	Diadematidae	Diadema	<i>Diadema setosum</i>	DiaSet
	Echinozoa	Echinoidea	Euechinoidea	Diadematoida	NR	Diadematidae	Echinothrix	<i>Echinothrix calamaris</i>	EchCal
	Echinozoa	Echinoidea	Euechinoidea	Echinothurioida	NR	Echinothuriidae	Asthenosoma	<i>Asthenosoma marisrubri</i>	AstMar
	Echinozoa	Echinoidea	Euechinoidea	Camarodonta	Echinidea	Echinometridae	Echinometra	<i>Echinometra mathaei</i>	EchMat
	Echinozoa	Echinoidea	Euechinoidea	Camarodonta	Echinidea	Echinometridae	Heterocentrotus	<i>Heterocentrotus mammillatus</i>	HetMam
	Echinozoa	Echinoidea	Euechinoidea	Camarodonta	Echinidea	Echinometridae	Echinostrephus	<i>Echinostrephus molaris</i>	EchMol
	Echinozoa	Echinoidea	Euechinoidea	Camarodonta	Echinidea	Toxopneustidae	Tripneustes	<i>Tripneustes gratilla elatensis</i>	TriGra
	Echinozoa	Echinoidea	Cidaroidea	Cidaroida	NR	Cidaridae*	-	-	Cidari
Asterozoa	Ophiuroidea	Myophiuroidea	Amphilepidida	NR	Ophiotrichidae	Ophiothrix	-	-	Ophiot
	Asterozoa	Ophiuroidea	Myophiuroidea	Ophiacanthida	NR	Ophiocomidae	Ophiocoma	-	Ophioc
	Asterozoa	Ophiuroidea	Myophiuroidea	Ophiurida*	-	-	-	-	Ophiu1
	Asterozoa	Astroidea*	-	-	-	-	-	-	Astero
	Echinozoa	Holothuroidea*	-	-	-	-	-	-	Holoth
Crinozoa	Crinoidea*	-	-	-	-	-	-	-	Crinoi
Foraminifera	NR	Tubothalamea	NR	Miliolida	NR	Soritidae*	-	-	Soriti
Mollusca	NR	Bivalvia	Pteriomorphia	Mytilida	NR	Mytilidae	Lithophaga†	-	Lithop
	NR	Bivalvia	Pteriomorphia	Mytilida	NR	Mytilidae*	-	-	Mytili
	NR	Bivalvia	Pteriomorphia	Ostreida	NR	Pteriidae	Pteria	-	Pteria
	NR	Bivalvia	Pteriomorphia	Ostreida	NR	Pteriidae	Pinctada	-	Pincta
	NR	Bivalvia	Pteriomorphia	Ostreida	NR	Pinnidae	Streptopinna	<i>Streptopinna saccata</i>	StrSac
	NR	Bivalvia	Pteriomorphia	Ostreida	NR	Pinnidae	Pinna	<i>Pinna muricata</i>	PinMur
	NR	Bivalvia	Pteriomorphia	Ostreida	NR	Ostreidae1*	-	-	Ostre1
	NR	Bivalvia	Pteriomorphia	Ostreida	NR	Ostreidae2*	-	-	Ostre2

Phylum	Subphylum	Class	Subclass	Order	Infraorder	Family	Genus	Species	Abbreviation
	NR	Bivalvia	Pteriomorpha	Ostreida	NR	Ostreidae3*	-	-	Ostre3
	NR	Bivalvia	Pteriomorpha	Arcida	NR	Arcidae*	-	-	Arcida
	NR	Bivalvia	Pteriomorpha	Pectinida	NR	Pectinidae*	-	-	Pectin
	NR	Bivalvia	Heterodonta	Cardiida	NR	Cardiidae (Subfamily Tridacnidae*)	-	-	Tridac
	NR	Bivalvia1*	-	-	-	-	-	-	Bival1
	NR	Bivalvia*	-	-	-	-	-	-	Bivalv
	NR	Gastropoda	Caenogastropoda	Littorinimorpha	NR	Cypraeidae*	-	-	Cyprea
	NR	Gastropoda	Caenogastropoda	Littorinimorpha	NR	Vermetidae	Serpulorbis	Serpulorbis inopertus	Serlno
	NR	Gastropoda	Caenogastropoda	Neogastropoda	NR	Muricidae	Drupella	Drupella cornus	DruCor
	NR	Gastropoda	Caenogastropoda	Neogastropoda	NR	Muricidae	Coralliphila	-	Corall
	NR	Gastropoda	Caenogastropoda	Neogastropoda	NR	Muricidae*	-	-	Murici
	NR	Gastropoda	Caenogastropoda	Neogastropoda	NR	Conidae	Conus	-	Conus
	NR	Gastropoda	Caenogastropoda	Neogastropoda	NR	Nassariidae*	-	-	Nassar
	NR	Gastropoda	Patellogastropoda*	-	-	-	-	-	Patell
	NR	Gastropoda	Heterobranchia	Nudibranchia*	-	-	-	-	Nudibr
	NR	Gastropoda*	-	-	-	-	-	-	Gastro
Porifera	NR	Demospongiae	Heteroscleromorpha	Poecilosclerida	NR	Podospongidae	Negombata	Negombata magnifica	NegMag
	NR	Demospongiae	Heteroscleromorpha	Poecilosclerida	NR	Mycalidae	Mycale	Mycale fistulifera	MycFis
	NR	Demospongiae	Heteroscleromorpha	Clionida	NR	Clionaidae*	-	-	Clioni
	NR	Demospongiae	Heteroscleromorpha	Clionida	NR	Clionaidae	Cliona	Cliona viridis	CliVir
	NR	Calcarea	Calcaronea	Leucosolenida	NR	Grantidae	Grantia	-	Granti
Porifera1*	-	-	-	-	-	-	-	-	Pori1
Porifera2*	-	-	-	-	-	-	-	-	Pori2
Porifera3*	-	-	-	-	-	-	-	-	Pori3
Porifera4*	-	-	-	-	-	-	-	-	Pori4
Porifera5*	-	-	-	-	-	-	-	-	Pori5
Porifera6*	-	-	-	-	-	-	-	-	Pori6
Porifera7*	-	-	-	-	-	-	-	-	Pori7
Porifera8*	-	-	-	-	-	-	-	-	Pori8
Porifera9*	-	-	-	-	-	-	-	-	Pori9

Phylum	Subphylum	Class	Subclass	Order	Infraorder	Family	Genus	Species	Abbreviation
Porifera10*	-	-	-	-	-	-	-	-	Pori10
Porifera11*	-	-	-	-	-	-	-	-	Pori11
Porifera12*	-	-	-	-	-	-	-	-	Pori12
Porifera13*	-	-	-	-	-	-	-	-	Pori13
Porifera14*	-	-	-	-	-	-	-	-	Pori14
Porifera*	-	-	-	-	-	-	-	-	Porife
Xenacoelomorpha	Acoelomorpha	NR	NR	Acoela	Crucimuschulata	Convolutidae	Waminoa	Waminoa brickneri	WamBri

*= lowest taxonomic rank identified when not recognized to genus or species level.

NR= No rank

† The boring bivalves commonly associated with *S. pistillata* colonies in Eilat are *Leiosolenus lessepsianus* (formerly *Lithophaga lessepsiana*). However, due to the difficulty to surely identify boring species under field conditions, we assigned all boring *Lithophaga/Leiosolenus* species to *Lithophaga* genus.

Table S5: Results of ANOVA test, followed by Tukey HSD Post-hoc tests, of the fish diversity recorded in the 3 Reef Carpet coral species, *A. variabilis*, *P. damicornis* and *S. pistillata*.

Source of Variation	Sum of Squares	df	Variance	F	p
Between Groups	262509.3	2	131254.6	271.7107	<0.001
Within Groups	2786334	5768	483.0676		
Total	3048843	5770			

Tukey HSD Post-hoc Tests

	Mean difference	95% confidence interval		p
		Lower bound	Upper bound	
<i>A. variabilis</i> vs. <i>P. damicornis</i>	-6.3800	-8.3227	-4.4373	<0.001
<i>A. variabilis</i> vs. <i>S. pistillata</i>	8.9800	7.2067	10.7533	<0.001
<i>P. damicornis</i> vs. <i>S. pistillata</i>	15.3600	13.7856	16.9344	<0.001

Table S6: Results of ANOVA test, followed by Tukey HSD Post-hoc tests, of the fish diversity recorded in live colonies, dead colonies, and on the substrate of *A. variabilis*, *P. damicornis* and *S. pistillata* composing the 3 Reef Carpets.

Source of Variation	Sum of Squares	df	Variance	F	p
Between Groups	1559540	8	194942.5	853.4352	<0.001
Within Groups	1316161	5762	228.4209		
Total	2875701	5770			

Tukey HSD Post-hoc Tests

	Mean difference	95% confidence interval		p
		Lower bound	Upper bound	
<i>A. variabilis</i> Alive vs. <i>A. variabilis</i> Dead	-67.2700	-72.6307	-61.9093	<0.001
<i>A. variabilis</i> Alive vs. <i>A. variabilis</i> Tray	-34.4500	-37.7761	-31.1239	<0.001
<i>A. variabilis</i> Alive vs. <i>P. damicornis</i> Alive	-36.1000	-38.2265	-33.9735	<0.001
<i>A. variabilis</i> Alive vs. <i>P. damicornis</i> Dead	-53.7300	-56.7895	-50.6705	<0.001
<i>A. variabilis</i> Alive vs. <i>P. damicornis</i> Tray	-15.6100	-18.9713	-12.2487	<0.001
<i>A. variabilis</i> Alive vs. <i>S. pistillata</i> Alive	-37.5000	-39.4245	-35.5755	<0.001
<i>A. variabilis</i> Alive vs. <i>S. pistillata</i> Dead	-52.2600	-54.6588	-49.8612	<0.001
<i>A. variabilis</i> Alive vs. <i>S. pistillata</i> Tray	-26.1800	-29.7060	-22.6540	<0.001
<i>A. variabilis</i> Dead vs. <i>A. variabilis</i> Tray	32.8200	26.9342	38.7058	<0.001
<i>A. variabilis</i> Dead vs. <i>P. damicornis</i> Alive	31.1700	25.8689	36.4711	<0.001
<i>A. variabilis</i> Dead vs. <i>P. damicornis</i> Dead	13.5400	7.8006	19.2794	<0.001
<i>A. variabilis</i> Dead vs. <i>P. damicornis</i> Tray	51.6600	45.7542	57.5658	<0.001
<i>A. variabilis</i> Dead vs. <i>S. pistillata</i> Alive	29.7700	24.5467	34.9933	<0.001
<i>A. variabilis</i> Dead vs. <i>S. pistillata</i> Dead	15.0100	9.5939	20.4261	<0.001
<i>A. variabilis</i> Dead vs. <i>S. pistillata</i> Tray	41.0900	35.0890	47.0910	<0.001
<i>A. variabilis</i> Tray vs. <i>P. damicornis</i> Alive	-1.6500	-4.8790	1.5790	0.8133
<i>A. variabilis</i> Tray vs. <i>P. damicornis</i> Dead	-19.2800	-23.1871	-15.3729	<0.001
<i>A. variabilis</i> Tray vs. <i>P. damicornis</i> Tray	18.8400	14.6923	22.9877	<0.001
<i>A. variabilis</i> Tray vs. <i>S. pistillata</i> Alive	-3.0500	-6.1497	0.0497	0.0579

<i>A. variabilis</i> Tray vs. <i>S. pistillata</i> Dead	-17.8100	-21.2245	-14.3955	<0.001
<i>A. variabilis</i> Tray vs. <i>S. pistillata</i> Tray	8.2700	3.9878	12.5522	<0.001
<i>P. damicornis</i> Alive vs. <i>P. damicornis</i> Dead	-17.6300	-20.5837	-14.6763	<0.001
<i>P. damicornis</i> Alive vs. <i>P. damicornis</i> Tray	20.4900	17.2247	23.7553	<0.001
<i>P. damicornis</i> Alive vs. <i>S. pistillata</i> Alive	-1.4000	-3.1514	0.3514	0.2422
<i>P. damicornis</i> Alive vs. <i>S. pistillata</i> Dead	-16.1600	-18.4223	-13.8977	<0.001
<i>P. damicornis</i> Alive vs. <i>S. pistillata</i> Tray	9.9200	6.4854	13.3546	<0.001
<i>P. damicornis</i> Dead vs. <i>P. damicornis</i> Tray	38.1200	34.1828	42.0572	<0.001
<i>P. damicornis</i> Dead vs. <i>S. pistillata</i> Alive	16.2300	13.4182	19.0418	<0.001
<i>P. damicornis</i> Dead vs. <i>S. pistillata</i> Dead	1.4700	-1.6855	4.6255	0.8803
<i>P. damicornis</i> Dead vs. <i>S. pistillata</i> Tray	27.5500	23.4714	31.6286	<0.001
<i>P. damicornis</i> Tray vs. <i>S. pistillata</i> Alive	-21.8900	-25.0275	-18.7525	<0.001
<i>P. damicornis</i> Tray vs. <i>S. pistillata</i> Dead	-36.6500	-40.0989	-33.2011	<0.001
<i>P. damicornis</i> Tray vs. <i>S. pistillata</i> Tray	-10.5700	-14.8796	-6.2604	<0.001
<i>S. pistillata</i> Alive vs. <i>S. pistillata</i> Dead	-14.7600	-16.8336	-12.6864	<0.001
<i>S. pistillata</i> Alive vs. <i>S. pistillata</i> Tray	11.3200	8.0067	14.6333	<0.001
<i>S. pistillata</i> Dead vs. <i>S. pistillata</i> Tray	26.0800	22.4705	29.6895	<0.001

Table S7: Results of ANOVA test, followed by Tukey HSD Post-hoc tests, of the invertebrate diversity recorded in the 3 Reef Carpet coral species, *A. variabilis*, *P. damicornis* and *S. pistillata*.

Source of Variation	Sum of Squares	df	Variance	F	p
Between Groups	305715.4	2	152857.7	2885.123	<0.001
Within Groups	305596.4	5768	52.9813		
Total	611311.8	5770			

Tukey HSD Post-hoc Tests

	Mean difference	95% confidence interval		p
		Lower bound	Upper bound	
<i>A. variabilis</i> vs. <i>P. damicornis</i>	20.3900	19.7466	21.0334	<0.001
<i>A. variabilis</i> vs. <i>S. pistillata</i>	15.0500	14.4627	15.6373	<0.001
<i>P. damicornis</i> vs. <i>S. pistillata</i>	-5.3400	-5.8614	-4.8186	<0.001

Table S8: Results of ANOVA test, followed by Tukey HSD Post-hoc tests, of the invertebrate diversity recorded in live colonies, dead colonies, and on the substrate of *A. variabilis*, *P. damicornis* and *S. pistillata* composing the 3 Reef Carpets.

Source of Variation	Sum of Squares	df	Variance	F	p
Between Groups	1299313	8	162414.1	4302.382	<0.001
Within Groups	217514.5	5762	37.7498		
Total	1516827	5770			

Tukey HSD Post-hoc Tests

	Mean difference	95% confidence interval		p
		Lower bound	Upper bound	
<i>A. variabilis</i> Alive vs. <i>A. variabilis</i> Dead	-41.0800	-43.2593	-38.9007	<0.001
<i>A. variabilis</i> Alive vs. <i>A. variabilis</i> Tray	-44.2800	-45.6321	-42.9279	<0.001
<i>A. variabilis</i> Alive vs. <i>P. damicornis</i> Alive	2.0500	1.1855	2.9145	<0.001
<i>A. variabilis</i> Alive vs. <i>P. damicornis</i> Dead	-19.5700	-20.8138	-18.3262	<0.001
<i>A. variabilis</i> Alive vs. <i>P. damicornis</i> Tray	-18.5100	-19.8765	-17.1435	<0.001
<i>A. variabilis</i> Alive vs. <i>S. pistillata</i> Alive	4.7900	4.0077	5.5723	<0.001
<i>A. variabilis</i> Alive vs. <i>S. pistillata</i> Dead	-10.2000	-11.1752	-9.2248	<0.001
<i>A. variabilis</i> Alive vs. <i>S. pistillata</i> Tray	-47.0100	-48.4434	-45.5766	<0.001
<i>A. variabilis</i> Dead vs. <i>A. variabilis</i> Tray	-3.2000	-5.5927	-0.8073	0.001
<i>A. variabilis</i> Dead vs. <i>P. damicornis</i> Alive	43.1300	40.9750	45.2850	<0.001
<i>A. variabilis</i> Dead vs. <i>P. damicornis</i> Dead	21.5100	19.1768	23.8432	<0.001
<i>A. variabilis</i> Dead vs. <i>P. damicornis</i> Tray	22.5700	20.1692	24.9708	<0.001
<i>A. variabilis</i> Dead vs. <i>S. pistillata</i> Alive	45.8700	43.7466	47.9934	<0.001
<i>A. variabilis</i> Dead vs. <i>S. pistillata</i> Dead	30.8800	28.6782	33.0818	<0.001
<i>A. variabilis</i> Dead vs. <i>S. pistillata</i> Tray	-5.9300	-8.3696	-3.4904	<0.001
<i>A. variabilis</i> Tray vs. <i>P. damicornis</i> Alive	46.3300	45.0173	47.6427	<0.001
<i>A. variabilis</i> Tray vs. <i>P. damicornis</i> Dead	24.7100	23.1216	26.2984	<0.001
<i>A. variabilis</i> Tray vs. <i>P. damicornis</i> Tray	25.7700	24.0839	27.4561	<0.001
<i>A. variabilis</i> Tray vs. <i>S. pistillata</i> Alive	49.0700	47.8099	50.3301	<0.001
<i>A. variabilis</i> Tray vs. <i>S. pistillata</i> Dead	34.0800	32.6919	35.4681	<0.001
<i>A. variabilis</i> Tray vs. <i>S. pistillata</i> Tray	-2.7300	-4.4708	-0.9892	<0.001
<i>P. damicornis</i> Alive vs. <i>P. damicornis</i> Dead	-21.6200	-22.8208	-20.4192	<0.001
<i>P. damicornis</i> Alive vs. <i>P. damicornis</i> Tray	-20.5600	-21.8874	-19.2326	<0.001
<i>P. damicornis</i> Alive vs. <i>S. pistillata</i> Alive	2.7400	2.0280	3.4520	<0.001
<i>P. damicornis</i> Alive vs. <i>S. pistillata</i> Dead	-12.2500	-13.1697	-11.3303	<0.001
<i>P. damicornis</i> Alive vs. <i>S. pistillata</i> Tray	-49.0600	-50.4562	-47.6638	<0.001
<i>P. damicornis</i> Dead vs. <i>P. damicornis</i> Tray	1.0600	-0.5406	2.6606	0.5053
<i>P. damicornis</i> Dead vs. <i>S. pistillata</i> Alive	24.3600	23.2169	25.5031	<0.001
<i>P. damicornis</i> Dead vs. <i>S. pistillata</i> Dead	9.3700	8.0872	10.6528	<0.001
<i>P. damicornis</i> Dead vs. <i>S. pistillata</i> Tray	-27.4400	-29.0981	-25.7819	<0.001
<i>P. damicornis</i> Tray vs. <i>S. pistillata</i> Alive	23.3000	22.0245	24.5755	<0.001
<i>P. damicornis</i> Tray vs. <i>S. pistillata</i> Dead	8.3100	6.9079	9.7121	<0.001
<i>P. damicornis</i> Tray vs. <i>S. pistillata</i> Tray	-28.5000	-30.2520	-26.7480	<0.001
<i>S. pistillata</i> Alive vs. <i>S. pistillata</i> Dead	-14.9900	-15.8330	-14.1470	<0.001
<i>S. pistillata</i> Alive vs. <i>S. pistillata</i> Tray	-51.8000	-53.1469	-50.4531	<0.001
<i>S. pistillata</i> Dead vs. <i>S. pistillata</i> Tray	-36.8100	-38.2774	-35.3426	<0.001

Table S9: Results of ANOVA test, followed by Tukey HSD Post-hoc tests, of the crustacean diversity recorded in the 3 Reef Carpet coral species, *A. variabilis*, *P. damicornis* and *S. pistillata*.

Source of Variation	Sum of Squares	df	Variance	F	p
Between Groups	21079.05	2	10539.52	3665.725	<0.001
Within Groups	16583.89	5768	2.8752		
Total	37662.94	5770			

Tukey HSD Post-hoc Tests

Mean difference	95% confidence interval		p	
	Lower bound	Upper bound		
<i>A. variabilis</i> vs. <i>P. damicornis</i>	5.0000	4.8501	5.1499	<0.001
<i>A. variabilis</i> vs. <i>S. pistillata</i>	4.5000	4.3632	4.6368	<0.001
<i>P. damicornis</i> vs. <i>S. pistillata</i>	-0.5000	-0.6215	-0.3785	<0.001

Table S10: Results of ANOVA test, followed by Tukey HSD Post-hoc tests, of the crustacean diversity recorded in live colonies, dead colonies, and on the substrate of *A. variabilis*, *P. damicornis* and *S. pistillata* composing the 3 Reef Carpets.

Source of Variation	Sum of Squares	df	Variance	F	p
Between Groups	523877	8	65484.63	4571.741	<0.001
Within Groups	82533.64	5762	14.3238		
Total	606410.7	5770			

Tukey HSD Post-hoc Tests

Mean difference	95% confidence interval			p
	Lower bound	Upper bound		
<i>A. variabilis</i> Alive vs. <i>A. variabilis</i> Dead	-33.5300	-34.8724	-32.1876	<0.001
<i>A. variabilis</i> Alive vs. <i>A. variabilis</i> Tray	-30.0000	-30.8329	-29.1671	<0.001
<i>A. variabilis</i> Alive vs. <i>P. damicornis</i> Alive	-1.7500	-2.2825	-1.2175	<0.001
<i>A. variabilis</i> Alive vs. <i>P. damicornis</i> Dead	-7.5400	-8.3062	-6.7738	<0.001
<i>A. variabilis</i> Alive vs. <i>P. damicornis</i> Tray	-20.3300	-21.1717	-19.4883	<0.001
<i>A. variabilis</i> Alive vs. <i>S. pistillata</i> Alive	-2.0000	-2.4819	-1.5181	<0.001
<i>A. variabilis</i> Alive vs. <i>S. pistillata</i> Dead	-14.2200	-14.8207	-13.6193	<0.001
<i>A. variabilis</i> Alive vs. <i>S. pistillata</i> Tray	-30.6800	-31.5630	-29.7970	<0.001
<i>A. variabilis</i> Dead vs. <i>A. variabilis</i> Tray	3.5300	2.0561	5.0039	<0.001
<i>A. variabilis</i> Dead vs. <i>P. damicornis</i> Alive	31.7800	30.4525	33.1075	<0.001
<i>A. variabilis</i> Dead vs. <i>P. damicornis</i> Dead	25.9900	24.5528	27.4272	<0.001
<i>A. variabilis</i> Dead vs. <i>P. damicornis</i> Tray	13.2000	11.7211	14.6789	<0.001
<i>A. variabilis</i> Dead vs. <i>S. pistillata</i> Alive	31.5300	30.2220	32.8380	<0.001
<i>A. variabilis</i> Dead vs. <i>S. pistillata</i> Dead	19.3100	17.9537	20.6663	<0.001
<i>A. variabilis</i> Dead vs. <i>S. pistillata</i> Tray	2.8500	1.3473	4.3527	<0.001
<i>A. variabilis</i> Tray vs. <i>P. damicornis</i> Alive	28.2500	27.4414	29.0586	<0.001
<i>A. variabilis</i> Tray vs. <i>P. damicornis</i> Dead	22.4600	21.4816	23.4384	<0.001
<i>A. variabilis</i> Tray vs. <i>P. damicornis</i> Tray	9.6700	8.6314	10.7086	<0.001
<i>A. variabilis</i> Tray vs. <i>S. pistillata</i> Alive	28.0000	27.2238	28.7762	<0.001
<i>A. variabilis</i> Tray vs. <i>S. pistillata</i> Dead	15.7800	14.9249	16.6351	<0.001
<i>A. variabilis</i> Tray vs. <i>S. pistillata</i> Tray	-0.6800	-1.7523	0.3923	0.5668

<i>P. damicornis</i> Alive vs. <i>P. damicornis</i> Dead	-5.7900	-6.5297	-5.0503	<0.001
<i>P. damicornis</i> Alive vs. <i>P. damicornis</i> Tray	-18.5800	-19.3977	-17.7623	<0.001
<i>P. damicornis</i> Alive vs. <i>S. pistillata</i> Alive	-0.2500	-0.6886	0.1886	0.7034
<i>P. damicornis</i> Alive vs. <i>S. pistillata</i> Dead	-12.4700	-13.0365	-11.9035	<0.001
<i>P. damicornis</i> Alive vs. <i>S. pistillata</i> Tray	-28.9300	-29.7901	-28.0699	<0.001
<i>P. damicornis</i> Dead vs. <i>P. damicornis</i> Tray	-12.7900	-13.7759	-11.8041	<0.001
<i>P. damicornis</i> Dead vs. <i>S. pistillata</i> Alive	5.5400	4.8359	6.2441	<0.001
<i>P. damicornis</i> Dead vs. <i>S. pistillata</i> Dead	-6.6800	-7.4702	-5.8898	<0.001
<i>P. damicornis</i> Dead vs. <i>S. pistillata</i> Tray	-23.1400	-24.1614	-22.1186	<0.001
<i>P. damicornis</i> Tray vs. <i>S. pistillata</i> Alive	18.3300	17.5443	19.1157	<0.001
<i>P. damicornis</i> Tray vs. <i>S. pistillata</i> Dead	6.1100	5.2463	6.9737	<0.001
<i>P. damicornis</i> Tray vs. <i>S. pistillata</i> Tray	-10.3500	-11.4292	-9.2708	<0.001
<i>S. pistillata</i> Alive vs. <i>S. pistillata</i> Dead	-12.2200	-12.7393	-11.7007	<0.001
<i>S. pistillata</i> Alive vs. <i>S. pistillata</i> Tray	-28.6800	-29.5097	-27.8503	<0.001
<i>S. pistillata</i> Dead vs. <i>S. pistillata</i> Tray	-16.4600	-17.3639	-15.5561	<0.001

Figures

Figure S1: The experimental design of three Reef Carpets (8.4m² each; 3X2.8m) constructed from preset subunits that were prepared and nursed at the coral nursery. Each Reef Carpet subunit is made of a nursery-rearing tray (plastic nets of 0.25 cm² mesh size, stretched over 40X60cm PVC frames) and includes coral colonies of the same species. The corals are distributed randomly; the relative proportion of colonies per species is maintained for each Reef Carpet. The 35 subunits per Reef Carpet are arranged in seven columns and five rows. The orientation and depth are shown above each Reef Carpet schematic diagram.

Figure S2: Kaplan–Meier curve of survival time of Reef Carpet *Acropora variabilis*, *Pocillopora damicornis* and *Stylophora pistillata* colonies transplanted on a soft-bottom substrate and monitored over 17 months.

Figure S3: The percentage of *Acropora variabilis*, *Pocillopora damicornis* and *Stylophora pistillata* colonies that disappeared from the Reef Carpets over 17 months (Mean ± SE). A mixed-model ANOVA performed on the proportion of new missing colonies of every observation point indicates no significant effect of time and no significant difference between the three coral species ($F_{6,36}=1.131$, $P=0.364$ and $F_{12,36}=0.746$, $P=0.698$, respectively).

Figure S4: Comparison of 17 months survival rates of colonies without, or with some extent of partial tissue death at the time of transfer to the Reef Carpets deployed on a soft-bottom substrate. (a) *Acropora variabilis*. (b) *Pocillopora damicornis*. (c) *Stylophora pistillata*.

Figure S5: The reproductive effort of *Stylophora pistillata* colonies at Kisuski Beach. (a) Average numbers of planulae per colony collected from natal and transplanted colonies (mean ± SE). * denotes statistically significant differences between natal colonies and transplants (One sample t-test; average of three Reef Carpet colonies, RC1-RC3). (b) Percentages of planulae-releasing natal and transplanted colonies (One sample t-test; average of three Reef Carpet colonies, RC1-RC3).

Figure S6: Species-environment b-plot based on a canonical correspondence analysis (CCA) for the effect of environmental factors (arrows) on RC community structure (associated species/taxa represented by triangles). (a) The ordination diagram showing both environmental variables and species. (b) For clarity, only the environmental variables are shown. Eigenvalues: axis 1 = 0.507; axis 2 = 0.371. The variance explained by each axis (%) is shown. Environmental variables: time in months since RC transplantation (**Date**); spotted on RC1, RC2 or RC3 (**Plot**); located at the center (**C**) or at the periphery (**P**) of the RC; spotted in a live *Acropora variabilis*, *Pocillopora damicornis* or *Stylophora pistillata* colony (**Ac Alive**, **Pd Alive** and **Sp Alive**, respectively), or in a dead colony of the before mentioned species (**Ac Dead**, **Pd Dead** and **Sp Dead**, respectively), or substrate-associated (seen on the tray/sediment covering the tray; **Tray**). For list of species abbreviations – see Tables S3 and S4 in the supplementary materials.

Figure S7: Species-environment b-plot based on a canonical correspondence analysis (CCA) for the effect of environmental factors (arrows) on the invertebrate community structure (associated species/taxa represented by triangles). Eigenvalues: axis 1 = 0.466; axis 2 = 0.375. The variance explained by each axis (%) is shown. Environmental variables: time in months since RC transplantation (**Date**); spotted in a live *Acropora variabilis*, *Pocillopora damicornis* or *Stylophora pistillata* colony (**Ac Alive**, **Pd Alive** and **Sp Alive**, respectively), or in a dead colony of the before mentioned species (**Ac Dead**, **Pd Dead** and **Sp Dead**, respectively), or substrate-associated (seen on the tray/sediment covering the tray; **Tray**). For list of species abbreviations – see Table S4 in the supplementary materials.

Fig.S1

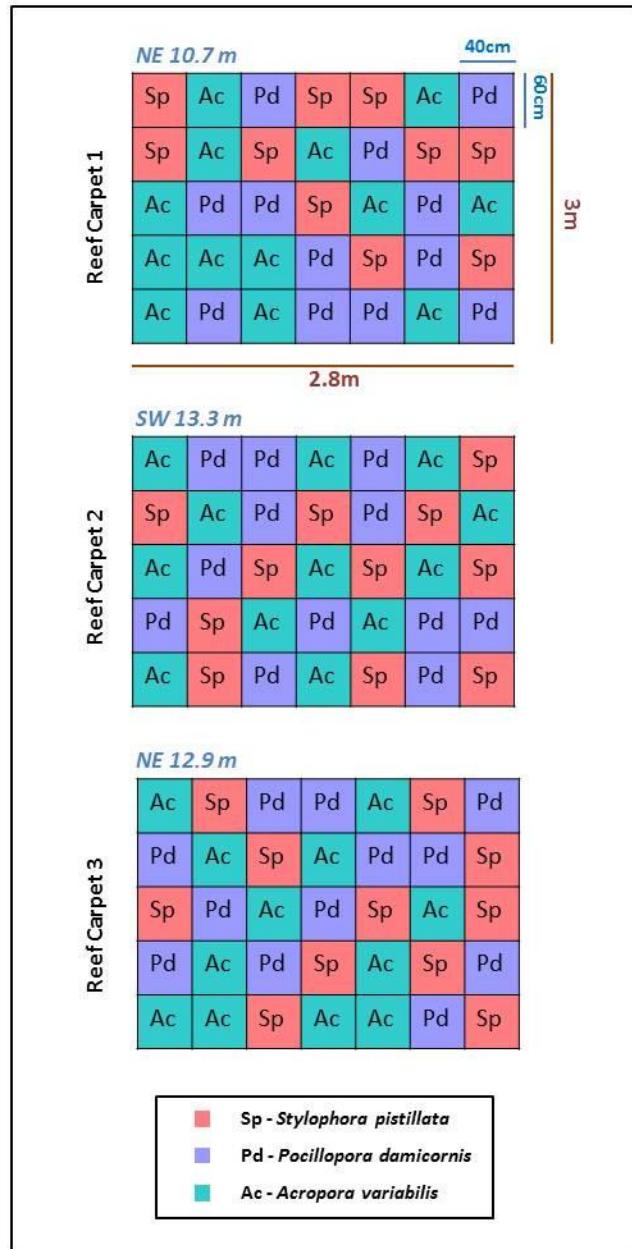


Fig.S2

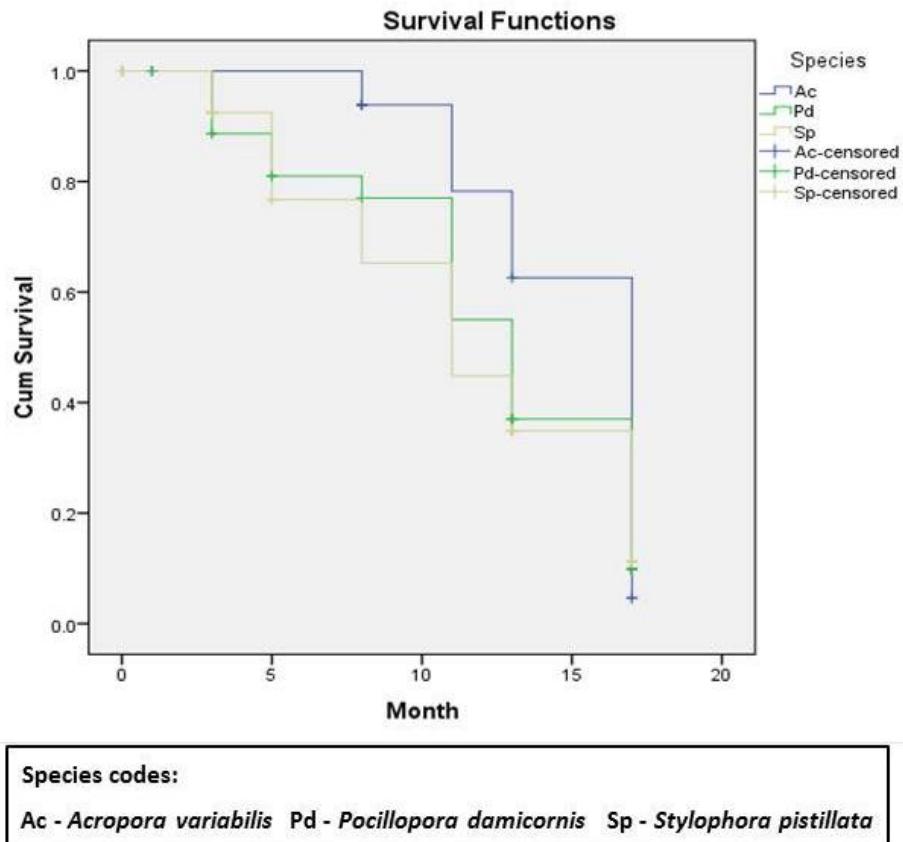


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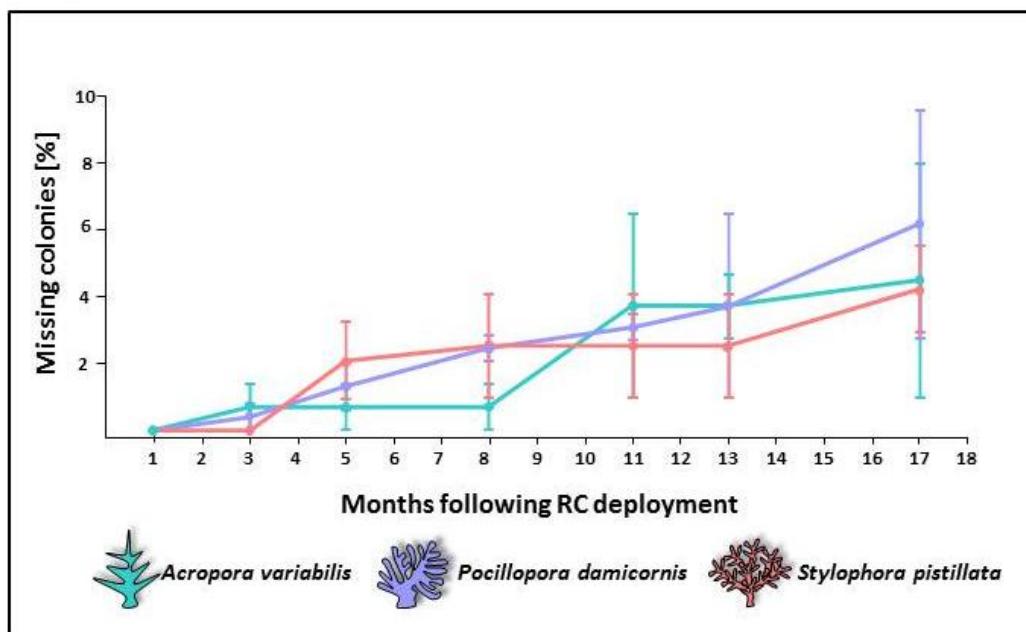


Fig.S4

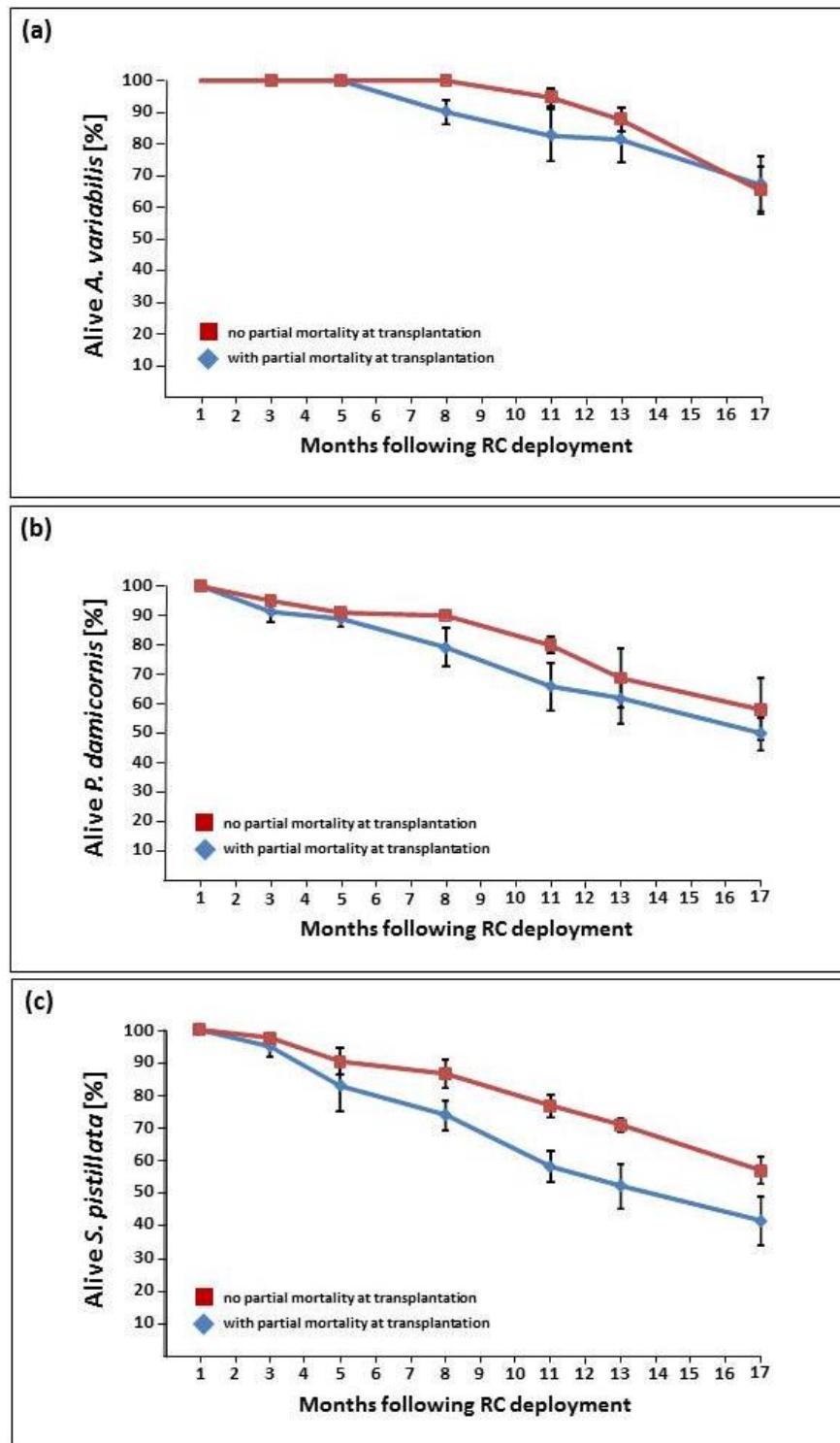


Fig.S5

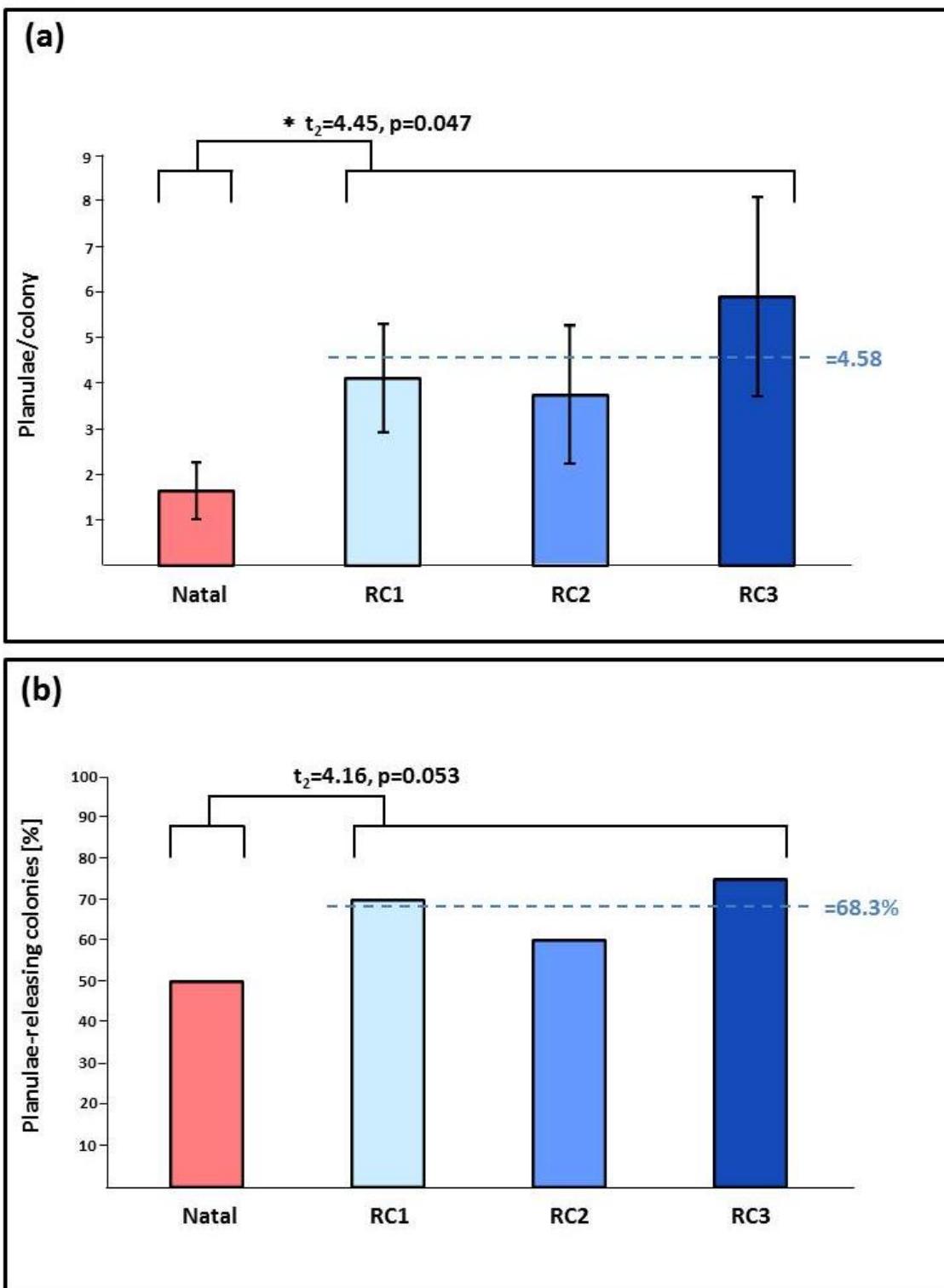


Fig.S6

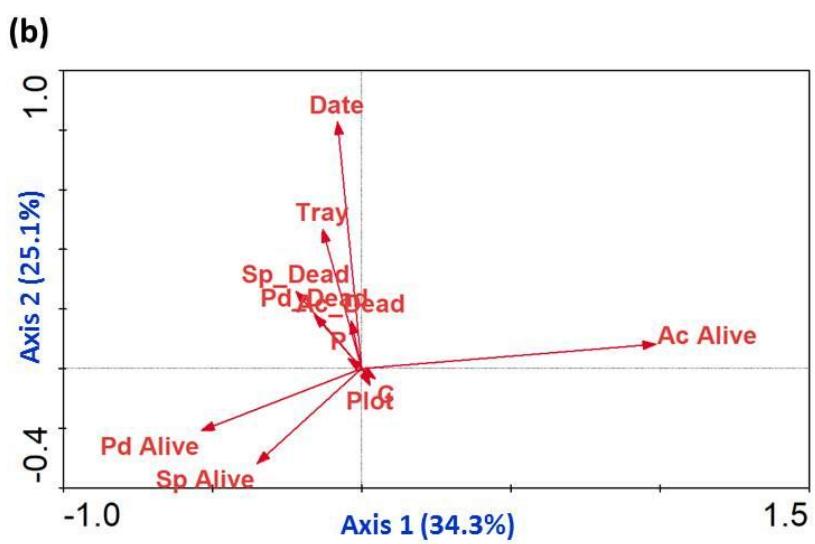
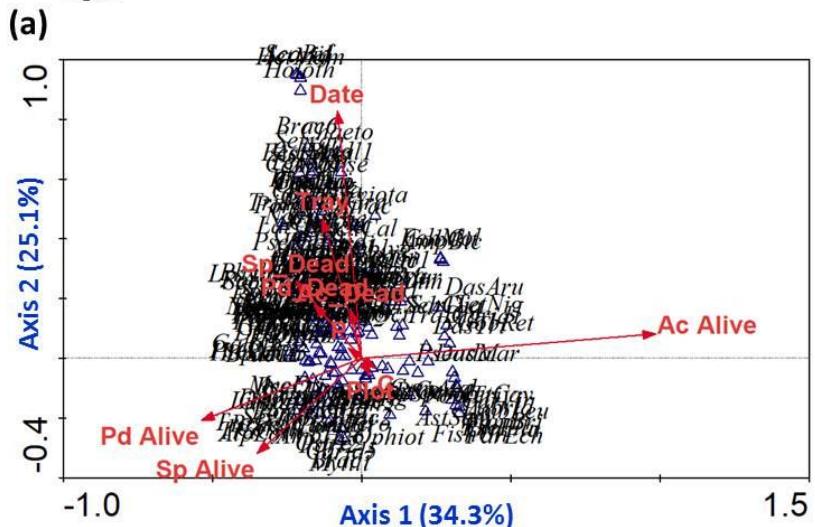
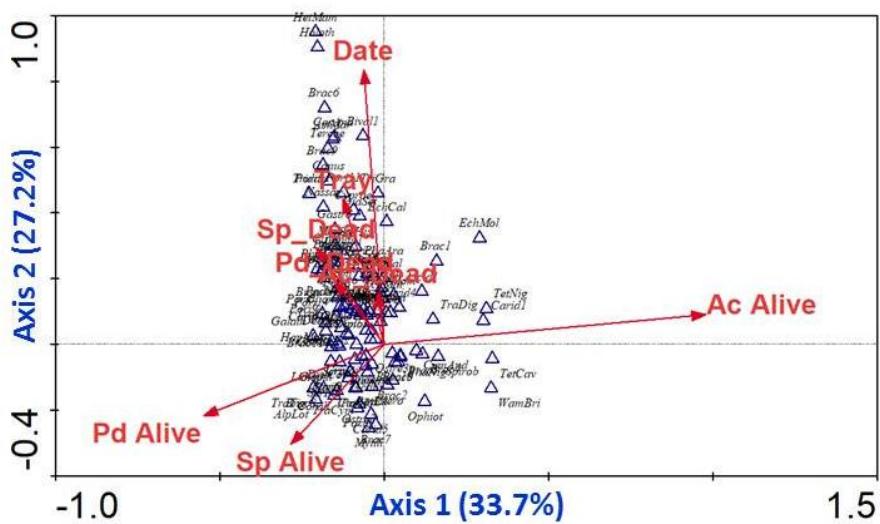


Fig.S7



Chapter 6

Restoration of the Animal Forests: Harnessing Silviculture Biodiversity Concepts for Coral Transplantation

Statement of Authorship

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By signing the Statement of Authorship, each author certifies that:

- i. the candidate's stated contribution to the publication is accurate (as detailed above);
- ii. permission is granted for the candidate to include the publication in the dissertation

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Contribution to the Paper	Developed the ideas and structure of the paper, revised the manuscript.		
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Restoration of the Animal Forests: Harnessing Silviculture Biodiversity Concepts for Coral Transplantation

Yael B. Horoszowski-Fridman and Baruch Rinkevich

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Abstract

Coral reefs and rain forests are among the most diverse and productive ecosystems on earth, sharing numerous ecological and functional properties. Decades of anthropogenic activities and the overexploitation of reef/forest resources have led to a worldwide rapid degradation of both ecosystems, threatening the continued function of these habitats and their ability to provide numerous goods and services. Inspired by silviculture, an emerging approach to reef restoration is the gardening coral reefs tenet, in which numerous new coral colonies are farmed *in situ* in mid-water coral nurseries and are subsequently available for transplantation on degraded reefs. As in forestation, transplantation of corals can be used as

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a sustainable tool that carries ecological engineering benefits, such as the reconstruction of rehabilitated coral reefs with a particular coral coverage and associated species' compositions, increased rugosity (3-d structural complexity), and enhanced biodiversity.

Forest restoration initiatives have been underway for over a century, leading to the development of consolidated silviculture rationales. In contrast, many theoretical aspects have yet to be elucidated in the newly emergent discipline of active reef restoration. Due to the numerous similarities between coral reef and forest ecosystems, as well as between their restoration approaches, insights regarding the use of tree plantations for forest restoration could substantially advance the restoration of coral reefs. Here, we synthesize recent advances in farmed coral transplantation and discuss the influence of active reef restoration on biodiversity outcomes. We particularly focus on diversity estimates at the population genetics, species, and ecosystem levels, consulting forest restoration literature for rationales, tools, and recommendations that can be harnessed in the gardening approach for active reef restoration.

Keywords

Biodiversity • Gardening approach • Active reef restoration • Marine silviculture • Tree plantation • Forest restoration • Coral transplantation

1 Introduction

Coral reefs and rain forests are two ecosystems that share numerous ecological and functional properties (Connell 1978). They are among the most diverse biomes on earth, and they provide vital goods and services to human populations, including food, livelihood, cultural values, and monetary fluxes from recreational activities. Forests also supply fiber, timber, and wood for fuel, while reefs protect adjacent coastal areas from erosion and provide important sources of protein to hundreds of millions of people (Chazdon 2008; Rinkevich 2008). The numerous goods and services supplied by forests and reefs rely on the existence of their building blocks, which are trees and hermatypic corals, respectively – sessile ecosystem engineering organisms that follow similar architectural patterns (Epstein et al. 2003; Lartaud et al., this volume). These habitat constructors alter the physical characteristics of the environment and create new living spaces and a surplus of ecological niches. The three-dimensional complex topographic reliefs that trees and hermatypic corals create are crucial for the existence of the multitude of associated fauna and flora and provide essential breeding, nursing, and feeding sites for a myriad of organisms (Graham and Nash 2013).

Regrettably, decades of anthropogenic activities, overexploitation of forest/reef resources, and intensifying climate changes have led to a worldwide rapid degradation of both ecosystems, threatening their continued functioning. On land, the conversion of forest areas into farmlands, forest fragmentation, extensive logging,

cattle grazing activities, and the enhanced frequencies and magnitudes of perturbations (e.g., fire, floods) have substantially impacted soil quality and hydrological processes, leading to habitat and biodiversity losses (Chazdon 2003, 2008; Rodrigues et al. 2009, 2011; Bullock et al. 2011; Latawiec et al. 2015). Likewise, the chronic impacts of overfishing and pollution, coupled with major coral bleaching events and the outbreaks of diseases, have led to extensive coral mortalities, changes in species composition and recruitment failures (Graham et al. 2014), the loss of reef resilience, and irreversible phase-shift scenarios (Rinkevich 2015a).

In response to these outcomes, forest restoration initiatives have been underway for over a century (Rodrigues et al. 2009), supported by numerous silviculture concepts and practices (Lindenmayer and Hobbs 2004; Lamb et al. 2005; Carnus et al. 2006; Brockerhoff et al. 2008; Chazdon 2008; Rodrigues et al. 2011). An increasingly sanctioned approach to the reforestation of degraded forest areas is the use of tree plantations (also referred to as “plantation forests/planted forests”, cultured forest habitats established for afforestation/reforestation purposes using planting, seeding, or both; Carnus et al. 2006). The planted trees reshape the altered physical and chemical conditions of the degraded sites, enabling the return of the original communities of the forest habitat through natural succession or human-assisted processes. According to Chazdon (2008), plantations constitute 4 % of the world’s forested area, and their planting rates are increasing by 2.8 million ha/year (~2 %). Although many of the world’s plantations are established for commercial production, considerable areas are set aside for the conservation of endangered species and biodiversity (Lindenmayer and Hobbs 2004; Carnus et al. 2006; Brockerhoff et al. 2008), and they evolve with time and through succession processes into “natural forests” (Chazdon 2003; Rodrigues et al. 2009), even though they represent biologically depleted ecosystems (Latawiec et al. 2015). Using plantations in restoration acts enables the mitigation of many hindrances to ecological succession, while indirectly supporting natural recovery, averting ecological phase shifts and ultimately restoring ecosystem services and biodiversity (Brockerhoff et al. 2008; Paquette and Messier 2010).

Reef restoration, in contrast, is a novel ecological discipline that has been receiving increasing attention over the past two decades, though many of its theoretical and practical aspects have yet to be elucidated. Following the realization that passive rehabilitation measures are providing insufficient outcomes, much effort is being devoted to the development of effective active reef restoration tools (Lirman et al. 2010; Young et al. 2012; Rinkevich 2014, 2015a). One of these emerging tools is the marine silviculture approach, also known as gardening coral reefs (Rinkevich 1995, 2005, 2006, 2008, 2014, 2015a, b). Inspired by silviculture rationales and methodologies, this practice has two phases. In the first phase, numerous new coral colonies are farmed in designated underwater coral nurseries, which are made available in the second phase for transplantation onto degraded reef areas (Fig. 1). As in terrestrial forestation, coral transplantation incorporates ecological engineering tools, for example, the use of specific coral species and various genotypes, sizes and compositions of transplants, emerged seascapes, and more.



Fig. 1 The gardening coral reefs approach, a two-phase methodology (coral farming and coral transplantation) inspired by silviculture rationales, was tested first in the Red Sea (**a–c**) and then in reef sites worldwide, including the Philippines (**d–f**). Two nursery types and two transplantation methodologies are shown: (**a**) new coral colonies of various species cultured in the mid-water coral nursery at Eilat (Israel, Red Sea), showing small farmed fragments (*right side*) and adult colonies ready for transplantation (*left side* and tray held by the scuba diver). (**b**) Transplantation of a nursery-grown *Acropora valida* colony on a degraded knoll at Dekel Beach, Eilat. The colony has been reared in the nursery on a plastic peg that is inserted into a drilled hole within the rocky substrate. (**c**) A transplanted knoll at the Dekel Beach, completely covered by nursery-grown coral transplants of various coral species, 1.5 years after transplantation. This figure depicts the recruitment of coral-dwelling fish that reside in the restored knoll. (**d**) New coral colonies of *Montipora digitata*, *Porites rus*, and *Pavona frondifera* cultured at the rope coral nursery of Bolinao (Philippines). Each rope holds colonies (various genotypes) of a single species that was initiated from small inserted fragments that grew and developed into large colonies. (**e**) Transplantation of the rope nursery of *Montipora digitata* colonies on a degraded sandy substrate in Santiago lagoon, Bolinao. The ropes, which are covered with the farmed corals, are secured individually with cable ties to iron bars anchored into the substrate. (**f**) Another case of rope nursery transplantation on the soft bottom of a degraded area in Santiago lagoon, covered by parallel rows of *Montipora digitata* (Photographs **d–f** by Gidi Levy)

Due to the numerous structural and functional similarities between the rain forest and the coral reef ecosystems, as well as between the restoration approaches (Epstein et al. 2003; Rinkevich 2006), insights gathered over decades regarding the use of plantations in forest restoration could substantially advance the restoration of coral reefs (animal forests). Below, we will discuss the rationales for farmed coral transplantation and review the current knowledge on transplanting nursery-grown corals. By reviewing the use of tree plantations for forest restoration and by identifying key issues related to biodiversity conservation, we will attempt to highlight tools, rationales, and lessons of silviculture that can be harnessed in the “gardening coral reefs” approach.

2 Farmed Coral Transplantation: Aims and Recent Advances

Changes to the physical and biological properties of an ecosystem (e.g., changes to the light intensity that reaches substrates following tree clearing in forests or loss of branching corals in coral reefs; Fig. 2) are a major barrier to the natural rehabilitation of degraded areas (Lugo 1997). Furthermore, the natural recruitment of coral larvae in the coral reefs, like of tree propagules in the forests, depends on larval/seed survival, which are processes that rely on the right substrates' physical and biological properties and are also characterized by large post-settlement mortalities (Rinkevich 2005). Thus, the transplantation of adult coral colonies on degraded reefs allows (i) the reshaping of local environmental conditions (Rinkevich 2008; Fig. 2) and (ii) the augmentation of degraded biodiversity while bypassing mortalities characteristic to early stages (Rinkevich 2005). While the latter is more straightforward, the remodeling of the local conditions of impacted reef areas via coral transplantation is not clear, as it is rooted in silviculture rationales (which have yet to be studied in coral reefs).

In forest restoration, the ecological engineering tool of tree plantations is often used in order to recreate suitable conditions for the initiation of native communities via natural processes (Lugo 1997; Lamb et al. 2005; Chazdon 2008). In these cases, plantations are composed of monocultures or mixed stands of native, sometimes even exotic, species, selected based on ecological engineering criteria and their ability to adapt to the new and modified conditions of the degraded site (Kelty 2006). Following tree transplantation, canopies alter the understory environmental settings, such as light intensity, temperature, and humidity, while the planted trees further stabilize the soil, improving nutrient and organic matter contents as the aboveground litter accumulates (Brockhoff et al. 2008), lessening the likelihood of takeover by opportunistic plants (Chazdon 2003) and negating phase-shift scenarios. Such plantations generate a foster ecosystem with microclimates that facilitate the recruitment of ecosystem biodiversity (Chazdon 2003; Carnus et al. 2006; Brockhoff et al. 2008), creating a tool that can be harnessed to reef restoration by transplanting large numbers of nursery-grown adult corals (Fig. 2). Thus, farmed corals could be used not only to reinforce poor local coral populations or to support coral-associated species but also to change the seascape and prevent phase shifts to non-coral-dominated structures, alleviating ecological barriers to reef regeneration (Rinkevich 2014).

Research in the newly emerged discipline of farmed coral transplantation has explored feasibility aspects and methodological issues, such as the attachment of transplanted corals to substrates (Edwards et al. 2010; Shaish et al. 2010a, b; Bowden-Kerby and Carne 2012; Villanueva et al. 2012; Young et al. 2012; Mbije et al. 2013; Guest et al. 2014; Rinkevich 2014; Horoszowski-Fridman et al. 2015; and unpublished; Fig. 1), the choice of coral species, and their survival (Putchim et al. 2009; Muko and Iwasa 2011; Villanueva et al. 2012; Young et al. 2012; Mbije et al. 2013; Guest et al. 2014; Shaish et al. 2010a, b; Gomez et al. 2014; Horoszowski-Fridman et al. 2015). One third (26/86; Table 1) of the coral species cultured in coral nurseries worldwide (Rinkevich 2014) was used in transplantation,

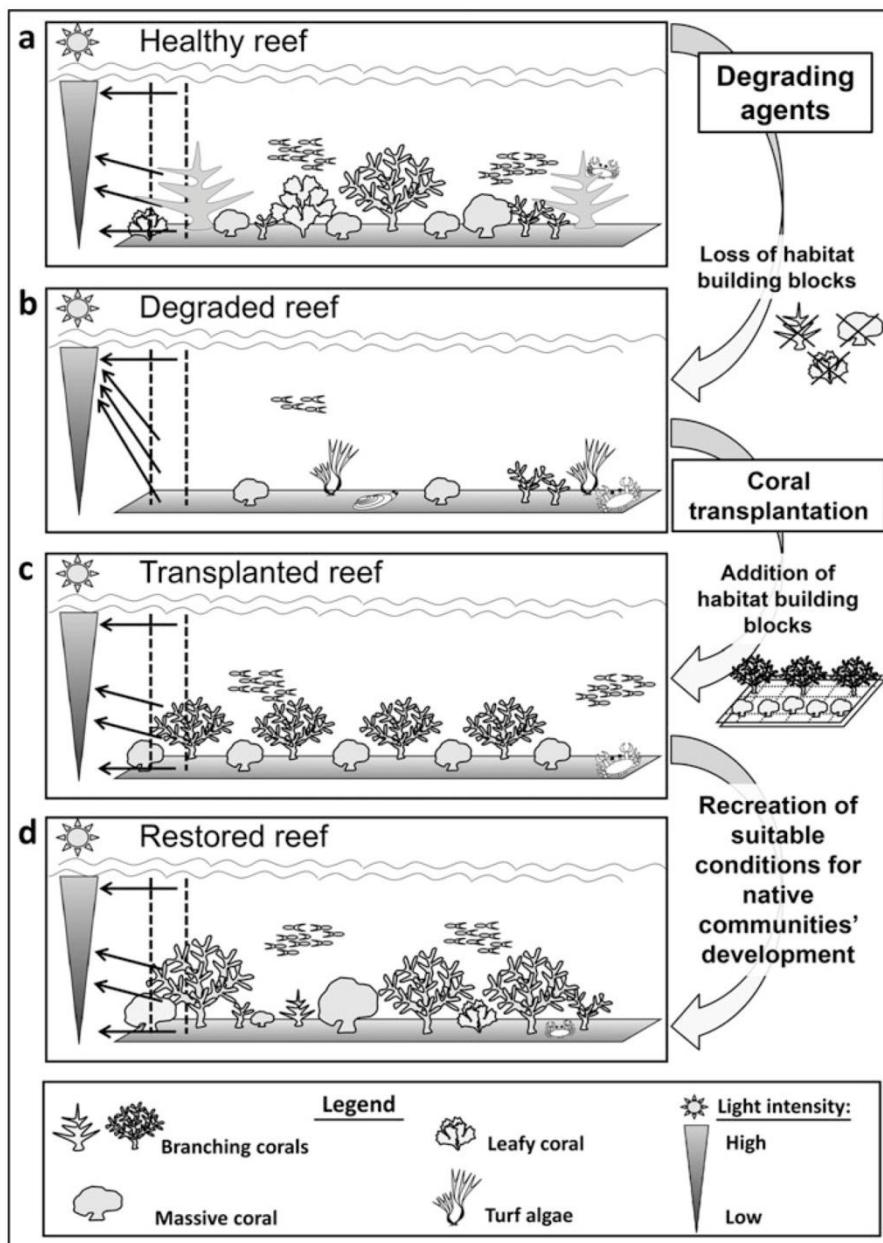


Fig. 2 Reshaping local environmental conditions in a degraded reef via coral transplantation – an example of changes in light intensity. (a) An illustration of light intensity (indicated by black arrows) at four levels along a healthy reef's water column: below water surface, upper colonial plane, mid-colonial plane, and substrate. (b) Caused by the loss of coral coverage, the irradiation level on the substrate and mid-colonial/upper colonial planes was modified by the removal of coral

and those species revealed variable yet remarkable abilities to acclimate and thrive on degraded reefs. Nursery-grown transplants grew on restored reefs (Putchim et al. 2009; Edwards et al. 2010; Shaish et al. 2010b; Nakamura et al. 2011; Bowden-Kerby and Carne 2012; Villanueva et al. 2012; Young et al. 2012; Mbije et al. 2013; Guest et al. 2014), in some cases maintaining the augmented growth rates recorded in the coral nursery (Horoszowski-Fridman et al. 2015) even while directly affected by seasonality and environmental conditions (Shaish et al. 2010a) or by the appearance of corallivorous organisms (Horoszowski-Fridman et al. 2015). Transplanted corals also contributed to reef reproduction by broadcasting gametes (Guest et al. 2014) or by larval release (Horoszowski-Fridman et al. 2011).

The successful integration of coral transplants into degraded reefs has resulted in the provision of new ecological niches for reef-dwelling fauna (Fig. 1c). Nursery-grown *Stylophora pistillata* and *Pocillopora damicornis* transplants in the Red Sea created new living spaces for a range of reef-associated invertebrate species, such as boring and surface inhabitants (e.g., *Trapezia* crabs, *Alpheus* shrimps, *Spirobranchus* worms, and *Lithophaga* bivalves; Horoszowski-Fridman et al. 2015). The transplantation of *Montipora digitata* and *Porites cylindrica* corals on damaged sites in the Philippines resulted in the return of reef fish communities (Shaish et al. 2010b; Gomez et al. 2014). In Tanzania, fish- and coral-associated invertebrates were recruited to the presence of transplanted *Acropora muricata*, *Acropora nasuta*, *Acropora hemprichii*, *Pocillopora verrucosa*, *P. cylindrica*, and *Millepora* sp. (Mbije et al. 2013).

Recent studies conducted in several countries worldwide also evaluated economic aspects of farmed coral transplantation, revealing that expenditure vary depending on the source of the coral transplants (e.g., sexually vs. asexually propagated colonies), the distance between the restoration sites and the coral nurseries, the transplantation methodology, and the labor/local economy of the concerned country (Edwards et al. 2010; Nakamura et al. 2011; Villanueva et al. 2012; Young et al. 2012; Mbije et al. 2013; Guest et al. 2014; Horoszowski-Fridman et al. 2015; Rinkevich 2015b). Concentrating on the more recently developed methodologies, the costs of farmed coral transplantation (including the nursery culture phase) can be minimized to 0.5US\$ per each asexually propagated coral colony, equaling the costs of silviculture practices (Rinkevich 2015b; see also Rodrigues et al. (2011) for an example of forest restoration costs).

Fig. 2 (continued) colonies following reef degradation. (c) The transplantation of coral colonies is used to modulate the local physical conditions of restored reefs. (d) The light intensity at the substrate, mid-colonial, and upper colonial planes is adjusted to pre-degradation levels. Once the physical characteristics of the impacted reef are reinstated, the development of native reef communities through natural processes as time progresses is made possible

Table 1 A list of the farmed coral species used in transplantation acts

No.	Coral species	Location	References
1	<i>Acropora cervicornis</i>	C&WA	Young et al. (2012)
2	<i>Acropora digitifera</i>	S	Edwards et al. (2010)
3	<i>Acropora formosa</i>	P	Shaish et al. (2010a)
4	<i>Acropora grandis</i>	TH	Putchim et al. (2009)
5	<i>Acropora hemprichii</i>	TA	Mbije et al. (2013)
6	<i>Acropora humilis</i>	I	Horoszowski-Fridman et al. (2011)
7	<i>Acropora hyacinthus</i>	S	Edwards et al. (2010)
8	<i>Acropora millepora</i>	P	Guest et al. (2014)
9	<i>Acropora muricata</i>	F, S, TA, TH	Putchim et al. (2009), Edwards et al. (2010), Mbije et al. (2013)
10	<i>Acropora nasuta</i>	S, TA	Edwards et al. (2010), Mbije et al. (2013)
11	<i>Acropora palmata</i>	C&WA	Young et al. (2012)
12	<i>Acropora pharaonis</i>	I	Horoszowski-Fridman et al. (2011)
13	<i>Acropora tenuis</i>	J	Nakamura et al. (2011)
14	<i>Acropora valida</i>	I, P	Villanueva et al. (2012), Horoszowski-Fridman et al. (2011)
15	<i>Acropora variabilis</i>	I	Horoszowski-Fridman et al. (2011)
16	<i>Acropora samoensis</i>	S	Edwards et al. (2010)
17	<i>Echinopora lamellosa</i>	P	Shaish et al. (2010a)
18	<i>Favia favus</i>	I	Horoszowski-Fridman (unpublished), Edwards et al. (2010)
19	<i>Merulina scabricula</i>	P	Shaish et al. (2010a)
20	<i>Millepora dichotoma</i> and <i>Millepora sp.</i>	I, TA	Horoszowski-Fridman et al. (2011), Mbije et al. (2013)
21	<i>Montipora digitata</i>	P	Shaish et al. (2010a, b)
22	<i>Pocillopora damicornis</i>	I, P	Shaish et al. (2010a), Horoszowski-Fridman et al. (2011, 2015)
23	<i>Pocillopora verrucosa</i>	TA	Mbije et al. (2013)
24	<i>Porites cylindrica</i>	P, TA	Mbije et al. (2013), Gomez et al. (2014)
25	<i>Porites rus</i>	P	Shaish et al. (2010a)
26	<i>Stylophora pistillata</i>	I	Horoszowski-Fridman et al. (2011, 2015)

C&WA Caribbean and Western Atlantic, F Fiji, I Israel (Red Sea), J Japan, P Philippines, S Seychelles, TA Tanzania, TH Thailand

3 Addressing Biodiversity Concerns in Coral Transplantation: A Take-Home Lesson from Silviculture

Biological diversity, at all organizational levels, is adversely affected by habitat degradation (Carnes et al. 2006; Bullock et al. 2011). The impoverishment of coral reef biodiversity impacts the habitat's ability to withstand stressors, respond to changing conditions, and sustain ecosystem services (Pratchett et al. 2014). Active reef restoration attempts to reverse these diminution trends in biodiversity. In

particular, the diversity estimates at the population genetics, species, and ecosystem levels are relevant to discussions regarding the impacts of active reef restoration on biodiversity outcomes, features that are discussed below.

3.1 Genetic Diversity

A growing number of studies employ genetic analyses at the population level to better understand the processes involved with human activities and restoration activities (Shearer et al. 2009; Schopmeyer et al. 2012). The genetic diversity of each single population has profound impacts on disease resistance and the ability to stand environmental perturbations, including global change impacts (Carnus et al. 2006). Thus, whereas coral populations worldwide are genetically diverse (Shearer et al. 2009), the repopulation of degraded reefs with nursery corals grown from a limited number of clonal genotypes (the most rapid and cost-effective practice for the production of a large pool of nursery-grown corals; Rinkevich 1995, 2015a, b) could result in restored populations with a diminished genetic diversity compared to the original populations, lowering their adaptability capacities and ability to face unexpected stressors. That is the reason why consideration on the genetic diversity of farmed corals is given at the coral nursery stage so as to maintain the capacities and resilience of the reconstructed reefs (Rinkevich 1995, 2014, 2015a; Baums 2008; Shearer et al. 2009 Bowden-Kerby and Carne 2012). Thus, concerns for reduced population genetics have emerged following the use of transplants generated from asexual propagation (Baums 2008; Table 2).

Similar concerns were implied in silviculture, where selection programs have gradually decreased the genetic diversity of planted tree stocks, and, together with the generation of clonal plantations from a reduced number of genotypes, have impacted the forests' capacity to withstand environmental changes and perturbations of both biotic and abiotic nature (Carnus et al. 2006). In order to reduce the threats associated with clonal plantations, it is now recommended to use clonal mixtures of 30–40 genotypes of the planted tree species. In the same way, Shearer et al. (2009) have suggested using 10–35 coral colonies so as to retain 50–90 % of the allelic diversity of these populations. Quantifying levels of species-specific allelic diversity and preserving the genetic integrity of damaged populations should become a part of reef restoration goals, integrated into restoration strategies and management (Table 2).

The reduced genetic heterogeneity in transplanted coral colonies may also hamper reproductive efforts and fecundity due to reduced fertilization rates, following self-fertilization sterility phenomena and inbreeding depression (Shearer et al. 2009; Iwao et al. 2014; Table 2), processes that are of particular relevance in genetically isolated populations. A recent study (Iwao et al. 2014) has suggested using more than six donor colonies in order to optimize the fertilization rates once cultured colonies reach reproductive stages. Another approach that has been successfully tested in silviculture acts and can be easily adapted to reef restoration is “enrichment planting” (Lamb et al. 2005; Paquette and Messier 2010), the improvement of

Table 2 Concerns, opportunities, and silviculture tools related to the genetic diversity of nursery-farmed corals

Concerns associated with the use of clonal coral transplants
1. Decreased adaptability to environmental (e.g., temperature increase), anthropogenic (e.g., sedimentation), and biological (e.g., competition, diseases) challenges
2. Hampered reproductive efforts, fecundity and success rates, inbreeding depression
3. Modification of coral population genetic structures due to (a) the use of a restricted number of genotypes, (b) the provenance of the donor colonies, (c) genetic bottleneck, (d) genetic drift, (e) gene flow over geographic scales
4. Impacts on associated reef fauna
Opportunities associated with farmed coral transplants
1. Selection of genotypes of interest, primarily those that can better withstand global change impacts
2. Integration of resilient varieties into degraded reefs
3. Counteracting the occurrence of ill-adapted local populations in degraded reefs
4. Enhancement of the genetic diversity of remnant natal populations on degraded reefs
5. Increasing the density of sexually mature adults for the purpose of enhancing local reproduction on degraded reefs
6. Using coral nursery and transplant pools as genetic repositories for reintroducing lost alleles
Silviculture tools and recommendations to be applied in the transplantation of farmed coral colonies
1. Determination of the minimal (and optimal) number of donor colonies used for the generation of clonal transplants, alleviating the risks associated with genetic diversity
2. Determination of the minimal (and optimal) number of donor colonies used for the generation of clonal transplants, offering optimization of reproductive efforts
3. Complementing transplantation of asexually produced colonies with sexually generated transplants
4. Using ecosystem engineering tools that enhance/assist local coral reproduction (e.g., employing coral nursery as “planulae hubs,” transplantation of gravid colonies, etc.)
5. Using the native populations of degraded reefs (or as similar as possible) to generate transplant pools
6. To ensure that the genotypes used to generate clonal transplants can cope with the emerging environmental/biological conditions
7. Maintaining landscape connectivity in order to allow the expansion of adapted genotypes in the face of altered environmental conditions

biodiversity or the percentage of desirable species/genotypes in a forest by increasing the planting density in an already growing forest stand. In addition, other ecosystem engineering tools that support an enhanced sexual propagation of transplanted coral colonies at degraded reef sites (Table 2), such as the use of coral nurseries as planulae hubs (Rinkevich 2015a) or the transplantation of gravid corals at the onset of the reproductive season (Horoszowski-Fridman et al. 2011), would result in enhanced genetic diversity in the restored reefs.

The modification of restored reef coral population genetics is an additional issue of concern. The transplantation of colonies with low genetic heterogeneity could lead to situations of bottlenecks and genetic drifts (Table 2), where local genotypes

could be lost. Furthermore, transplanting corals that originate from coral populations that are genetically disparate from those of the transplanted sites (a potential constraint imposed by the scarcity of donor colonies at damaged sites) could lead to “anthropogenic”-guided gene flow, which would modify the genetic structure of local coral populations or replace local genotypes altogether, a phenomenon that may result in the loss of local micro-adaptations or in reduced phenotypic responses to various environmental challenges. To meet these threats, forest restoration approaches recommend using stocks of local species and natal genotypes, so as to avoid genetic modification and preserve the genetic structures of the local populations (Carnus et al. 2006; Brockerhoff et al. 2008; Rodrigues et al. 2009; Table 2). Plant studies have also revealed that the population genetics of plant species directly affect the diversity of the associated biota (Whitham et al. 2003). For example, increasing the transplants’ genotypic diversity from monocultures to eight genotypes (Johnson et al. 2006) in evening primrose, *Oenothera biennis*, and from monocultures to 12 genotypes in tall goldenrod, *Solidago altissima* (Crutsinger et al. 2006), resulted in a significant increase in arthropod species richness, remodeling the associated communities and trophic webs. In *Zostera marina* seagrass-transplanted plots, a comparison of single vs. six genotype compositions revealed that enhanced genotypic diversity increased the abundance of the associated epifauna (Reusch et al. 2005), supporting the concept of the “minimum viable interacting population” (Whitham et al. 2003). Whether such effects exist in coral reefs (Table 2) is yet to be determined, since to our knowledge, the relationship between the intraspecific diversity of corals and the diversity of their related communities has not been studied in detail.

Nursery-farmed coral transplants may otherwise positively impact reef biodiversity outcomes (Table 2). First, coral nurseries can be used for the selective amplification of genotypes of interest and for creating cohorts of transplants that are resistant to future threats, including global change impacts (e.g., bleaching-resistant coral colonies; Bowden-Kerby and Carne 2012), as recommended in silviculture (Tepe and Meretsky 2011). Like in silviculture strategies (Carnus et al. 2006), coral nurseries can also be used to generate resilient varieties of corals through approaches such as assisted evolution (i.e., the acceleration of naturally occurring evolutionary processes like selection, mutations, acclimatization, symbiont community change, etc.), assisting with their integration into degraded coral communities. The transplantation of nursery-grown coral colonies can also alleviate constraints of local sexual reproduction repression that result from the reduced densities of remnant corals on degraded reefs. This may be further supported by floristic evidence showing that densely planted populations have a reproductive advantage over sparsely planted populations of the same size (Morgan and Scacco 2006). It should be noted that transplanting large farmed colonies rather than small colonies or coral fragments increases the capability of the transplants to participate in the local corals’ reproduction at their new resident reefs (Horoszowski-Fridman et al. 2011), further improving the restored reefs’ natural resilience. Additionally, coral nurseries can function as genetic repositories (Table 2) that preserve genetic material lost as a result of natural catastrophes (Schopmeyer et al. 2012). Then, the lost alleles and

species can be reintroduced back into degraded populations, including those of other reef-associated species that are constantly recruited to the nurseries (Shafir and Rinkevich 2010); the simultaneous transplantation of farmed corals together with the recruited reef biota is a phenomenon not recorded in the transplantation of trees that are farmed in nurseries under sterile conditions.

3.2 Species Diversity

The loss of species diversity is a major threat to ecosystem functioning and resilience, as it supports many of the habitat's ecological processes, goods, and services (Paquette and Messier 2010; Bullock et al. 2011). Active reef restoration carries impacts on species diversity in the restored reefs through several pathways, some of which are discussed below.

The attributes of transplanted corals: The ability to modify the damaged site, to provide living space, and to facilitate the establishment of both native and dependent reef species can vary according to the corals' species-specific characteristics, including the autogenic and allogegenic ecological engineering properties. Therefore, the attributes of the selected transplanted species may disparately influence the reef's biodiversity, a notion well established in silviculture, where diverse and even contrasting understory conditions are achieved according to the tree species' features (Lugo 1997). As an example, different leaf size and branching patterns may create understories with different light intensity and quality (Lemenih et al. 2004), resulting in microenvironments that support or contain the existence of other forest-associated species. Likewise, the autogenic and allogegenic ecological engineering properties of transplanted coral species may impose differential impacts on reef fauna abundance and diversity, also leading to different reef physiognomy. For example, compared to massive colonial forms, branching species contribute enhanced three-dimensional complexities for reef-dwelling invertebrates and fish. Branching coral species have vaster impacts on the reef's relief complexity (Pratchett et al. 2014), a quality that promotes the attraction of grazers and in turn facilitates coral spat recruitment and their survivorship by reducing competitive macroalgae (Bozec et al. 2013).

Diversity of transplanted coral species: The number of farmed coral species used for transplantation is expected to influence the coral species diversity and the reef-associated species diversity in restored reefs. As in forest restoration (Lamb et al. 2005), two strategies can be employed in order to reestablish coral biodiversity on denuded reefs using farmed coral colonies. The first uses the transplantation of a small number of fast-growing, early successional pioneering coral species in order to quickly cover a vast area of the degraded reef, forestalling community phase-shift developments. While this was not tested yet in reef restoration practices, evidence from silviculture studies attests to the ability of this approach to positively impact biodiversity (Lamb et al. 2005; Brockerhoff et al. 2008). The success of such a strategy in reestablishing species diversity depends mainly on the ability of organisms to recruit to the restored zone from the surrounding areas (Lamb et al. 2005).

When using this approach, one can predict stochastic outcomes, leading to a significantly modified biodiversity compared to that of the original population.

The second approach uses the transplantation of a large number of coral species to bypass the natural succession sequence and to increase species diversity while also contributing to the habitat's niche diversity. This enables the generation of a buffer effect in the face of environmental variations, caused by a differential responses of different species to fluctuating environmental conditions (e.g., different bleaching susceptibilities; see also "the insurance hypothesis of biodiversity" in Dizon and Yap 2005 and references therein). This approach has been studied in silviculture, where it is highly recommended to use a high number of tree species when planning forest restoration activities (Kelty 2006). This approach has also led to an enhanced abundance and diversity of ecological niches (Rodrigues et al. 2011). The species mixtures chosen for transplantation together with inter-/intra-competitive interactions determine the final community assembly and species diversity. It is also postulated that, as in forests (Kelty 2006; Paquette and Messier 2010), the larger the variety of transplanted coral species, the lower the risks for diseases and corallivory incidents.

As coral mariculture is a relatively young practice, the limited ecological knowledge that is available regarding the nursery rearing and transplantation of numerous coral species is a hindrance for transplanting an increased number of coral species. Therefore, under certain circumstances, it would be beneficial to combine these two approaches in order to enhance the outcomes of farmed coral transplantation on reef biological diversity while at the same time optimizing the use of restoration resources.

Functional diversity: In silviculture, it is now becoming evident that the composition of particular faunal assemblages can have a major impact on restored habitats, and in some cases, the presence of such assemblages can be of greater importance for biodiversity conservation than the number of planted species (Lindenmayer and Hobbs 2004; Lamb et al. 2005). Therefore, integrating into farmed coral transplantation functional considerations, such as the use of species that present disparate ecological characteristics (e.g., allogeic and autogenic ecosystem engineers species), species that share similar effects on ecosystem processes, or species that respond to environmental fluctuations in various ways, could improve the impacts of restoration on reef biodiversity. Reef restoration, as in forestry (Carnus et al. 2006; Rodrigues et al. 2009; Paquette and Messier 2010), can make use of ecological considerations in order to enhance functional diversity, including the choice of species, transplants morphologies (massive, branching, encrusting), and biological traits (e.g., *r* vs. *K* selection strategies, semelparous vs. iteroparous species). The enhancement of functional diversity can also be supported by adopting the consideration of various ecological processes such as inter-/intraspecific competitive interactions, transitive vs. nontransitive hierarchies, leading to the formation of more stable ecosystems, as was confirmed in silviculture practices when species that have a complementary use of habitat resources were used (Carnus et al. 2006; Kelty 2006; Paquette and Messier 2010). Thus, in coral reef restoration, harnessing facilitative interactions between coral species or between corals and reef-dwelling organisms

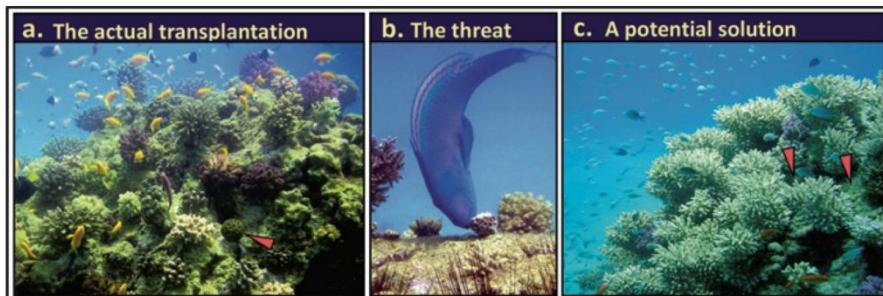


Fig. 3 Can facilitative interaction improve the survival of farmed transplants on degraded reefs? An example from Dekel Beach, Eilat (Red Sea, Israel), where colonies were transplanted directly onto bare knolls. (a) An overview of a transplanted knoll immediately following the transplantation of nursery-grown coral colonies of various species, including *Favia favus* colonies (massive form; red arrow). (b) Two days after transplantation, a *Favia* transplant is attacked by a parrot fish, who removed tissues and substantial parts of the colony's skeleton. (c) The integration of *Favia* transplants among previously planted dense plots of Acroporid branching coral species (red arrows) generates a physical barrier to fish attacks

(Dizon and Yap 2005; Bozec et al. 2013) could also contribute to the augmentation of functional diversity. An example of a case where facilitative interactions were used to ameliorate the integration of transplanted coral colonies into a restored reef can be seen in the restoration act performed in Eilat (Red Sea, Israel). Horoszowski-Fridman et al. (2015 and unpublished results) followed nursery-grown *Favia favus* colonies that were transplanted among other farmed coral species on bare substrate plots (Fig. 3a). The massive shaped *Favia* transplants were attacked within a few hours to a few days post transplantation by scarid fish that grazed on coral tissues, removing substantial parts of the peripheral corals' skeletons (Fig. 3b). Transplanting these massive corals among canopies of previously planted dense plots of branching Acroporid species (Fig. 3c) has significantly reduced fish attacks due to the limited accessible spaces between the new and the older transplants, which enhanced the survival rates of the *Favia* colonies.

Connectivity: When transplantation sites are isolated, the natural reintroduction of lost species native to the regenerating area may be restricted. As illustrated by forest restoration studies, the diversity (and abundance) of forest-associated plant and animal species are higher when tree plantations are located near remnant forests that serve as a source of propagules of native species (Lindenmayer and Hobbs 2004). Selecting coral transplantation sites that are connected to other reefs, capable of acting as local seeding sources of reef species and as hubs of “biocontrol” species (e.g., natural enemies of corallivorous and competing sessile organisms), could enhance the diversity of both the corals and their associated species.

The inclusion of coral-dwelling species naturally recruited to coral nurseries: Contrary to terrestrial nurseries, where the trees are farmed under sterile conditions, an *in situ* coral nursery is an open-to-the-environment site (Shafir and Rinkevich 2010; Rinkevich 2015a). As a result, substantial numbers of reef taxa larvae are

attracted to the farmed coral colonies, including fish and invertebrates (thousands of specimens of more than 100 morphologically large species were recruited in the first five operational years in a nursery situated at Eilat, Red Sea; Shafir and Rinkevich 2010, and personal observations). Many of these species were transferred to the degraded reef together with the coral transplants, increasing the diversity and abundance of other reef-associated species in the restored area (unpublished). Clearly, the “free” use of reef-associated assemblages that are established in coral nurseries can enhance the biodiversity of transplanted areas, accelerating the recovery toward a self-sustaining reef ecosystem.

3.3 Ecosystem Diversity: Structural Complexity and Habitat Diversity

In forest restoration, the spatial and structural diversity of plantations are as vital to the ecosystem biodiversity as the chosen planted species are (Lindenmayer and Hobbs 2004; Carnus et al. 2006; Brockerhoff et al. 2008). The same holds true for restored reefs, where the diversity and abundance of the whole spectrum of reef organisms are strongly linked to habitat complexity (Chabanet et al. 1997; Pratchett et al. 2014). As complexity is increased at the ecosystem level, reef heterogeneity provides a larger variety of ecological niches and habitats, supporting ecosystem services and resilience (Bozec et al. 2013; Pratchett et al. 2014). As is recommended for silviculture practices (Lindenmayer and Hobbs 2004; Carnus et al. 2006), reef ecosystem diversity should be considered on two spatial scales: a local level, i.e., the structural complexity of the transplanted reef, and a regional level, i.e., how restored reefs are ordered, arranged, and integrated into the ecosystem’s landscape.

On a local scale, the reef’s structural complexity can be strengthened by transplanting species of various coral morphologies (e.g., branching, massive, or encrusting forms; Table 3), as is practiced in silviculture with different tree forms (Lindenmayer and Hobbs 2004). In the same way, the spatial arrangement of the coral transplants in the restored reefs and the variable spacing designs have direct bearings on topographic complexity and reef heterogeneity (Fig. 4). In plantations established for restoration purposes, spatial heterogeneity is increased by planting trees in variable spacing designs that combine dense and spaced plots (Carnus et al. 2006). Plantation heterogeneity is also augmented by using transplants of different size-classes and spatially dispersing them within the restored plots, as tree-associated organisms favor properties allied to different age-classes of trees (e.g., hollows, large branches, bark accumulation; Lindenmayer and Hobbs 2004; Carnus et al. 2006; Brockerhoff et al. 2008). Additionally, when plantations are managed for biodiversity purposes, structures like horizontal and vertical dead trees, logs, and snags are also given importance as they constitute important components for some forest species (Carnus et al. 2006). Canopy gaps are also used as an applied tool to influence the understory’s microclimate (e.g., soil temperature and moisture, the amount and quality of light that reaches the forest floor), modulating the colonization, survival, and growth of the regenerating forest biota (Lemenih et al. 2004). The

Table 3 Coral transplantation measures that allow the advancement of habitat diversity on local and regional scales, inspired by silviculture practices and rationales

Coral transplantation strategies for enhanced habitat diversity	
Local scale	Using various coral colony morphologies simultaneously
	Considering the site-specific variable spacing of coral genotypes/species within and between planted plots
	Using variable size-classes of coral transplants
	Integration of coral skeletons
	Inclusion of bare substrate patches
	Considering various typographic arrangements of transplants (e.g., in aggregates, in order, or in random)
	Development of planting strategies that favor high reef biodiversity (e.g., functional groups, island planting design)
Landscape scale	Creation of buffer and transition zones
	Increasing landscape connectivity by forming biological corridors/stepping stones
	Provision of enlarged or supplementary habitats
	Increasing the structural and functional complexity of the landscape

Lemenih et al. (2004), Lindenmayer and Hobbs (2004), Lamb et al. (2005), Carnus et al. (2006), Brockerhoff et al. (2008), Chazdon (2008), Rodrigues et al. (2009, 2011), Paquette and Messier (2010), Holl et al. (2011), Latawiec et al. (2015)

rationales of these practices can also be adapted for reef restoration (Table 3), as coral-related features such as colonial sizes and architectural complexity affect the presence, abundance, and diversity of the associated fauna, including fish and invertebrates (Chabanet et al. 1997).

As the use of coral colonial structures, sizes, and positioning may lead to discrete topographies, structural complexities, habitat diversity, and whole ecosystem diversity changes (Fig. 4), these lessons ascertained from silviculture should be taken into consideration when performing active reef restoration. Two strategies developed for silviculture, the “functional group design” (Rodrigues et al. 2009, 2011) and the “island planting” design (Holl et al. 2011), could be of particular interest to coral transplantation schemes. Following the first transplantation design (Rodrigues et al. 2009, 2011), farmed coral species would be divided into two functional groups, “filling” and “diversity.” The “filling” group consists of coral species that exhibit fast growth and high coverage capabilities (i.e., branching species), allowing a quick reef recovery while providing structural heterogeneity and an unfavorable, challenging environment for competing macroalgae and other sessile coral competitors while at the same time generating improved microclimatic conditions for the “diversity” group. The “diversity” group consists primarily of slow growth/low structural complexity coral species, which represent a wide range of colonial forms (e.g., massive, leafy, encrusting). The transplantation of this coral species assemblage is meant to enhance species diversity and functional diversity at the restored reef, while also augmenting the perpetuation probabilities of the reconstructed reef. As with tree transplantation, the transplantation design of planted corals should start with a large

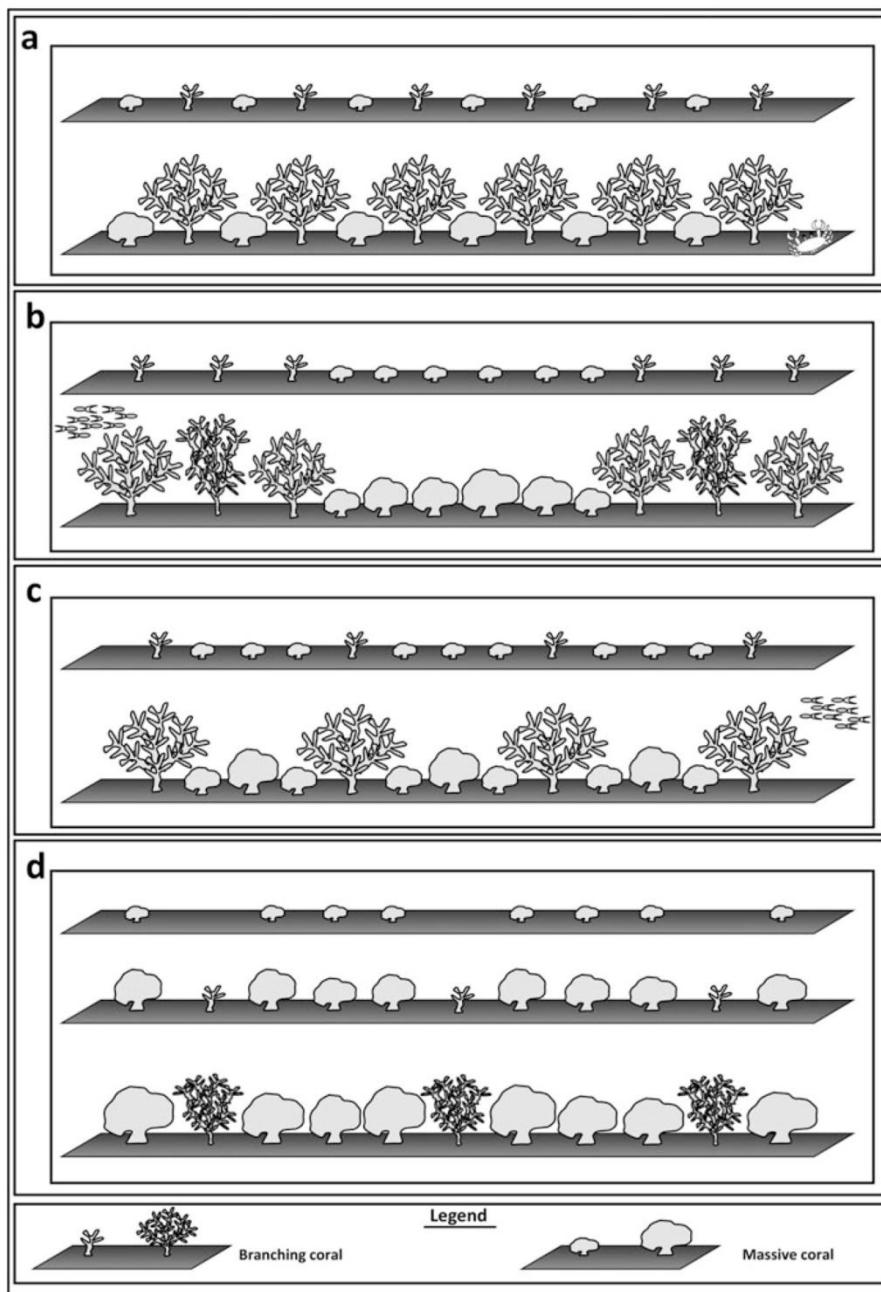


Fig. 4 Schematic illustrations of four transplantation designs, each containing two coral species (one branching and one massive), leading to discrete reef topographies. Each case (a–d) reveals arrangements at the transplantation stage (*upper line*) as well as expected topographical reef complexity scenarios (*lower line*), based on the biological features of the transplant species, i.e.,

number of individuals from the “filling” group species and few individuals from each species of the “diversity” group. The initial recovery that follows the growth of the “filling” species would foster the growth and establishment of the “diversity” species.

The “island planting” transplantation design (Holl et al. 2011) argues for a transplantation layout in small patches (i.e., islands) in order to stimulate recovery by nucleation. Following results from silviculture, this planting design would promote a reduced long-term effect of planted corals on final species composition compared to the “functional groups design,” creating restored reefs with a higher resemblance to the surrounding reefs. Determining the optimal patch size of each island is of importance in order to decrease possible edge effects on coral growth and survival, increase facilitating interactions, and maximize the ability of transplanted “coral island” plots to spread. Such a design could further facilitate coral recruitment by augmenting the grazing levels around the dense patches (Bozec et al. 2013).

An additional avenue for influencing reef biodiversity through the enhancement of spatial heterogeneity is to envisage coral transplantation in the context of the landscape. As in silviculture (Carnus et al. 2006), transplanted reefs can be positioned within the landscape mosaic according to various scenarios, and like in forests (Lamb et al. 2005), the ability of the separately restored reef patches to complement each other on a regional scale can further impact reef restoration outcomes for biodiversity. Given the wide spatial scale at which reef degradation is taking place, performing coral transplantation acts at the entire landscape level is not always a realistic goal. Therefore, designing site-based operations within regional contexts and managing them within the consideration of the whole heterogeneous mosaic landscape may provide opportunities to meet the restoration goals while maintaining ecological functioning, services, and biodiversity. Numerous take-home lessons can be drawn from silviculture, ameliorating the abilities of coral transplantation to increase heterogeneity on the landscape level and consequently increase reef biodiversity (Table 3). Plantations are often located at forest margins, where they constitute a transition zone between woodlands and open landscapes (Brockerhoff et al. 2008). They are also used to create buffer zones and biological corridors/stepping stones, with the purpose of increasing landscape connectivity (Lindenmayer and Hobbs 2004; Carnus et al. 2006; Brockerhoff et al. 2008; Chazdon 2008; Latawiec et al. 2015). Plantations are also managed with the purpose of increasing the landscape’s structural and functional complexity by juxtapositioning different plantation types, sizes, and shapes within and between the degraded zones and remnant forests (Brockerhoff et al. 2008; Paquette and Messier 2010). Correspondingly,

Fig. 4 (continued) the faster growth and significantly larger ecological volumes of the branching species compared to the massive species. **(a and b)** Equal numbers of colonies from each species, transplanted **(a)** alternately or **(b)** in aggregations. Colonial growth and reef structural complexity can also be modulated by varying the ratios between the species, for example, **(c)** reducing the amount of fast-growing, voluminous branching species compared to the massive, slow growth species or **(d)** delaying their transplantation

farmed coral transplants could also be used to extend the margins of still functioning reefs in areas of intense human impact, offering a transit area with some buffering effects between adverse anthropogenic influences and the remnant reefs (Table 3). Following some silviculture rationales, coral transplants can also be used to create margins around marine protected areas, forming a gradient in the environmental conditions that preserves an artificial and permanent stage of natural succession as well as a supplementary habitat for edge-specialist and reef-generalist species. Nursery-grown coral transplants can further be used to alleviate connectivity limitations between sites, as they can alter the landscape's permeability (Table 3). Like trees in plantations (Lindenmayer and Hobbs 2004), even if the coral species selected are not suitable for the settlement of certain coral-associated species and will not create the original reef species composition, they may still enable or facilitate animal movement and migration between remnant reef patches. Combining the transplantation of farmed corals with the additional ecosystem engineering tools of the coral gardening approach, such as serially positioning mid-water coral nurseries to create novel biological corridors through stepping stone mechanisms (Rinkevich 2015a), could substantially alter the restricted connectivity between reef sites. Additionally, transplanted zones of different types, sizes, and shapes could be planned and integrated within and between remnant reefs, in order to increase the structural and functional diversity of the reef's landscape (Table 3).

4 The Reefs of Tomorrow: Successful Restoration in an Uncertain Future

An increasing number of terrestrial and marine ecosystems are being inevitably transformed due to anthropogenic influences and global change (Hobbs et al. 2009; Graham et al. 2014). In such a reality, one must deliberate whether the recovery and conservation of coral reef biodiversity should focus primarily on reinstating the primeval reef configuration. As the global degradation of coral reefs continues and environmental conditions are being affected by climatic variations, the recreation of past reefs will probably necessitate increasing inputs of energy and money and may even lead to unsustainable reefs that are ill adjusted to the current environmental conditions and unable to support species adaptation following global change impacts and anthropogenic outcomes. Rather than aiming for a static ecosystem state, a portfolio of different future ecosystem trajectories could be set as a reference system (Rodrigues et al. 2011), allowing for the selection and preservation of the desired biodiversity attributes. In human-impacted terrestrial landscapes, new reconstructed forests do not always have species compositions that are similar to old-growth forests, but they do recover many elements and features of their former ecological services and biodiversity (Lindenmayer and Hobbs 2004; Brockerhoff et al. 2008; Chazdon 2008). It is even becoming legitimate to integrate non-native species into new habitats if they support important ecosystem functions that would otherwise be lost in the degraded systems, for the purpose of protecting biodiversity (Hobbs et al. 2009; Walther et al. 2009). In human-impacted tropical marine landscapes, the

predicted future threats of ocean acidification, elevated water temperatures, and disease outbreaks should be taken into account when planning the transplantation of farmed corals, in order to accommodate large fractions of threatened biodiversity. Coral nurseries could be used as a tool for maintaining stocks from a wide variety of sources (i.e., genetic and species repositories; Schopmeyer et al. 2012), especially if they are to become major suppliers of coral material for reef rehabilitation (as in silviculture). If reef restoration is to move from damage control to ecosystem engineering, the transplantation of denuded areas with farmed corals will allow the shifting species composition to be adjusted according to the new resulting conditions (as discussed in forestry; Tepe and Meretsky 2011).

As no single conservation action can benefit all species, the reef restoration toolbox should be capable of providing a portfolio of various rationales and methodologies tailored to different restoration goals, financial limitations, and local ecosystem conditions. Of the major challenges emerging in farmed coral transplantation, the most urgent are harnessing biodiversity goals and the need to increase the scale of the transplantation operations in order to draw alongside the pace and scale of reef degradation. At the same time, further consultation of forest restoration protocols may continue to advance reef restoration rationales and generate new ideas for coral reef rehabilitation. Our success in the hard task of preserving the invaluable biodiversity of coral reefs relies on the development of new approaches for generating well-conceived, self-perpetuating reef zones, designed to maintain a variety of ecological flows, supply habitats for a wide range of reef biodiversity, and provide various ecosystem services to reef organisms and human populations alike.

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5 Cross-References

► Growth Patterns in Long-Lived Coral Species

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Chapter 7

General Discussion

During the last decades coral reefs have been rapidly degrading worldwide. Their ability to sustain biological populations, provide numerous ecosystem goods and services and persevere can no longer be taken for granted. Similar to the effect on other marine and terrestrial ecosystems, the negative implications of human activity is intensified by climatic shifts, forming a new harsher reality for coral reefs in the Anthropocene (Williams *et al.* 2019). The limitation of traditional management to avert reef loss and alleviate threats faced by coral reefs requires disciplined preventative measures and the development of innovative intervention and reef restoration strategies. Conventional active reef restoration has focused on returning degraded reefs to historical, pre-disturbance conditions. However, global climate changes and the increased dependency of the growing world population on reef resources are challenging past reefs' sustainability and their future maintenance will probably require permanent intervention and a growing investment. Similar to terrestrial restoration and forestation (Chazdon 2008; Hobbs *et al.* 2009, 2010; Hobbs 2016; Mori *et al.* 2017), reef restoration should harness climate change scenarios. Past reef conditions should be used as benchmarks for developing new coral reef communities that retain desired ecosystem attributes and maintain the provision of goods and services (Graham & Hicks 2015; van Oppen *et al.* 2017; Rinkevich 2015, 2019). In order to reconstruct sustainable reefs capable of supporting species adaptation despite global changes and anthropogenic outcomes, reef restoration rationales are shifting from damage control to ecological engineering (*sensu* Mitsch 2014; Rinkevich 2015).

The marine silviculture approach (also known as 'gardening coral reefs'), a two-phase practice inspired by silviculture rationales, is an emerging reef restoration methodology centered on ecological engineering tools (Rinkevich 2014). In the first phase, numerous new coral colonies are farmed in coral nurseries, which in turn are used in the second phase for transplantation onto degraded reef areas. The transplantation of nursery-bred corals holds promise for rebuilding Anthropocene reefs. However, in order to form a meaningful intervention, the new approach for reef restoration should incorporate theory-based studies and their underlying principles of biological and ecological consideration. This should be

reflected in the development of a coral transplantation toolbox with techniques that enable to achieve location specific, well-defined restoration goals. Through the study and application of forest restoration rationales, and by researching the performance of farmed transplants, this dissertation aims to advance the nascent field of farmed coral transplantation. It explores the theory and practice of using nursery-grown coral transplants as ecological engineering tools to enhance reef resilience and improve its adaptation under ever changing marine and climate conditions.

Harnessing biological and ecological considerations in coral transplantation

Biological diversity sustains and regulates many of the habitat's ecological processes, goods and services (Paquette & Messier 2010; Bullock *et al.* 2011; Mace *et al.* 2012). High level of biodiversity supports the ecosystem's ability to endure environmental changes, retain its functionality and maintain its resilience (Mori *et al.* 2016). Coral reef degradation has strong negative effects on reef biodiversity (Pratchett *et al.* 2014). Farmed coral transplantation provides an opportunity to cope with these trends at three different levels of biological diversity: (a) within species (genetic and population levels), (b) between species, and (c) within ecosystems (habitat and landscape levels; Chapter 6).

Farmed coral transplantation as an ecological engineering tool to restore the genetic diversity of degraded reefs

In the first level, taking into account genetic aspects of degraded reef populations, nursery-grown transplants can be used as an ecological engineering tool for the selection and amplification of genotypes of interest (e.g., bleaching tolerant genotypes). It allows to repopulate reefs with colonies that have higher resistance to environmental threats and counteract the occurrence of ill-adapted local populations on degraded reefs. The farmed transplants can also be used to enhance the genetic diversity of remnant populations on degraded reefs and increase the density of sexually mature colonies to alleviate constraints of reproduction repression following reduced adults' density (the Allee effect; Petersen & Levitan 2001). Additionally, farmed grown transplants provide a tool to integrate resilient varieties developed in coral nurseries through approaches such as assisted evolution (van Oppen *et al.* 2017) into degraded reefs. The nursery-bred colonies can also help maintain, reproduce and then reintroduce lost alleles or species decimated from the reef following catastrophic events (e.g., Schopmeyer *et al.* 2012; also valid for coral-associated species recruited to nurseries during rearing phase).

In order to protect and reinstate the genetic diversity of restored coral populations using farmed coral transplantation, two concerns should also be addressed (Chapter 6). The first is the risk associated with reduced genetic diversity of farmed transplants repopulating degraded reefs, especially if they are of clonal origin. The second is the modification of coral population genetics at restored reefs due to low genotype numbers, donor colonies provenance, genetic bottlenecks and drifts, and gene flow over geographic scales. These risks could lead to decreased adaptability and reduced phenotypic responses to environmental, biological, and anthropogenic challenges, loss and replacement of local genotypes and micro adaptations, and additionally compromise coral reproductive efforts. A potential effect of the genetic heterogeneity of transplanted corals on the diversity of related biota also exists, as shown from plant studies (Whitham *et al.* 2003; Reusch *et al.* 2005; Crutsinger *et al.* 2006; Johnson *et al.* 2006), but is not yet confirmed in coral reefs. Following silviculture guidelines (Chapter 6), it is important to identify both the minimal and the optimal number of donor colonies needed to generate clonal transplants' pool to preserve genetic integrity and optimize reproduction of damaged populations, and complement clonal transplantation with sexually-generated farmed transplants. Additionally, farmed transplants should be generated from local species and natal genotypes (or as close as possible to native populations) with periodic checks performed to ensure the ability of used genotypes to cope with emerging conditions. Landscape connectivity should be strengthened to allow expansion of genotypes adapted to altered conditions.

An additional avenue for increasing genetic diversity of degraded reefs and countering the above mentioned risks is the use of nursery-farmed transplants as ecosystem engineering tools to increase or subsidize local coral reproduction as discovered and studied in Chapters 3 and 4 and further illustrated in Chapter 5. Following the larval outputs of naturally-growing and farmed *Stylophora pistillata* colonies transplanted onto a degraded reef and on a sandy bottom area, revealed that nursery-bred colonies display increased reproductive performance compared to natal colonies, having higher proportions of planulae releasing colonies as well as higher numbers of planulae (2.6-22.5 times more) shed per colony. This inveterate heightened reproductive capacity is maintained over time, still detected after eight reproductive seasons post transplantation (7.5 years) while growing side by side with natal colonies at the disturbed areas (Chapter 4). While the direct effect of abundant resources during the farming rearing stage has terminated after the transplantation, the prolonged high reproductive capacity was possibly induced by an

epigenetic effect at the nursery because of the beneficial pampering conditions during the rearing time. Epigenetic changes are not only promoted by stress but also by various pampering situations and can affect reproductive traits (Cooney *et al.* 2002; Champagne *et al.* 2006; Cropley *et al.* 2006; Palmer *et al.* 2012; Stuppia *et al.* 2015; Hart 2016; Fullston *et al.* 2017). They have already been detected in coral clones subject to different environmental conditions (Dixon *et al.* 2014; Putnam & Gates 2015; Putnam *et al.* 2016; Liew *et al.* 2018). This assumption is further reinforced by the observations of a similar enhanced and prolonged effect of nursery-rearing phase on farmed corals' growth rates, maintained for years following transplantation (Horoszowski-Fridman *et al.* 2015; Afiq-Rosli *et al.* 2017); yet additional investigation is required for the confirmation of the mechanism responsible for this ecological engineering tool.

These outcomes, in addition to providing one of the first records of both positive long-term impact of coral transplantation and higher reproductive effort of farmed specimens compared to wild stocks, also support the assumption that reefs good and services are potentially recoverable through ecological engineering manipulations. The transplantation of farmed gravid colonies just prior to the reproduction season could be used to reseed degraded reefs and sustain local populations (Chapter 3). Employing transplantation methodologies such as *Reef Carpets* (Chapter 5) could allow scaling up such reseeding initiatives from an area coverage, ease of transfer and application point of view. Moreover, the transplantation of nursery-bred colonies with increased reproductive capacity onto degraded reefs can be used as an ecosystem engineering tool to counter population declines in limited connectivity reefs where settlement is highly dependent on local sources. It can also assist to counter declines in brooding populations where resilience is determined by the size of adult pool and in locations where the reduced number of breeding corals leads to limited larval supply. The transplantation of nursery-bred gravid colonies can also be used to mitigate long-term effects of sub-lethal coral bleaching that can reduce coral reproduction for several post-bleaching years. The high fecundity of transplants may increase the pace of genetic adaptation to changing environments and the extensive larval additions, together with the reinforced breeding stocks, aid supplementing the genetic diversity of restored populations. However, the relationship between the planulae surplus and the coral recruitment and settlement in restored reefs still needs to be explored.

Farmed coral transplantation as an ecological engineering tool to restore the species diversity of degraded reefs

Nursery-grown coral transplantation can also be used as an ecosystem engineering tool to influence a second level of biodiversity: the species diversity of restored reefs (Chapter 6). Different reef states and configurations support different species and processes (Woodhead et al. 2019). The number of farmed coral species transplanted, whether restricted or large, will have a direct effect on coral species diversity of reconstructed areas and will also affect the abundance and diversity of reef associated species. Transplanting a small number of pioneering, fast growing species can be used to avert phase shifts in threatened reefs and cover vast areas for the protection of biodiversity and ecosystem functioning, while transplanting a large number of farmed coral species can be used to immediately increase coral species diversity and ecological niches for reef fauna, bypassing natural succession sequence. In the first case, the reestablishment of species diversity will depend on recruitment and due to its stochastic nature or priority effects (Young et al. 2001), the resulting biodiversity may differ from the original population. The second approach may lower the risks of disease and corallivory, provide a buffer effect due to differential species response to fluctuations, and allow a more controlled community assembly. Additionally, the choice of transplanted coral species may have different effects on reef associated species (Stella et al. 2011), as emerged from the census of *Reef Carpets* fauna (Chapter 5) where the importance of *Acropora* colonies as fish habitat and pocilloporid colonies as invertebrate habitat was noticeable, as well as the differential effects of *Acropora variabilis*, *Pocillopora damicornis* and *S. pistillata* transplants on the structure and diversity of the fish and invertebrate communities.

Specific characteristics of coral species used for transplantation can also be manipulated to create variable microenvironments and generate different reef layouts, to differentially affect reef fauna abundance and diversity (Chapter 6). For example, colony morphological traits can be selected to enhance the complexity of the restored reef's relief which should increase the attraction of grazer species; that, in turn, will facilitate coral recruitment and enhance new spats' survival. Considering functional diversity, functional redundancy and facilitative interactions between coral species and between corals and reef-associated species can also amplify farmed corals' ability to be used as ecological engineering tool for impacting species diversity in reef restoration. Functional diversity provides the capacity for a differential response to environmental fluctuations while

functional redundancy secures the maintenance of ecosystem processes. Together they provide the opportunity to integrate ecological processes such as competition, facilitation, and complementary resource use in coral transplantation. Connectivity considerations also impact transplanted reefs' species diversity. The selection of sites for farmed corals transplantation and those sites connectivity to other reefs may allow the latter to be local sources of natural reintroduction of both corals and associated fauna in the restored reefs. Finally, we can take advantage of the recruitment of reef associated fauna in the coral nursery during rearing phase in order to supplement the biodiversity of transplanted reefs by transplanting them together with the farmed colonies (Chapters 5 and 6).

Farmed coral transplantation as an ecological engineering tool to restore the ecosystem diversity of degraded reefs

Nursery-grown coral transplantation can further be used as an ecological engineering tool at the third level of biodiversity, the ecosystem level, for enhancing the habitat complexity and diversity on a local and regional scale (Chapter 6). Merely increasing live coral cover by transplanting vast homogeneous areas of nursery-bred colonies will most likely not accommodate large fractions of reef biodiversity (Chapter 5). Combining the use of different coral morphologies and size classes, variable spacing of genotypes and species within and between transplanted plots, as well as variable typographic arrangements (random, orderly, aggregates, etc.) in the restoration planning enables increasing the structural complexity of restored reefs. Integrating coral skeletons and bare substrate patches will also increase reef heterogeneity, providing a larger variety of ecological niches and habitats (Chapter 5). Similarly to the recognition of the importance of dead habitat elements (dead trees/logs/woody debris, etc.) in restored forests, dead corals are substantial habitat components for reef biodiversity (Enochs & Manzello 2012), capable of sustaining up to 80% of the species diversity of the *Reef Carpets* plots, in addition to providing different resources to reef biota than live corals (Chapter 5). All of the above strategies affect the presence, abundance and diversity of restored reefs' biodiversity. These reef-specific restoration plans and techniques allow to create and change reef topography, structural complexity and habitat diversity, overall projecting on the whole ecosystem diversity. Additionally, nursery-grown coral transplants can be used as ecosystem engineering tool to design site-base transplantation within regional context, considering the landscape heterogeneous mosaic (Chapter 6). The order, arrangement and integration of

transplanted areas within the reef landscape can be used to create buffer zones and transition zones around pristine or heavily exploited reefs. It enables to generate an enlarged or supplementary habitat and establish biological corridors and steppingstones to improve landscape connectivity.

Biodiversity-focused transplantation approaches

Developing farmed coral transplantation strategies that stimulate reef biodiversity is an important next step for increasing restoration outcomes on reef fauna. Methodologies employed in parallel disciplines, such as the silviculture functional groups and island planting designs (Chapter 6) should be tested and adjusted for reef restoration, as well as innovative avenues specifically tailored for coral reefs, as presented in *Reef Carpets* (Chapter 5) of this dissertation. In this transplantation methodology, pre-made coral mat units are created and farmed in the coral nursery and outplanted together with the reef associated biota that had accumulated during the rearing phase. Testing this approach for the first time on a hostile environment of a sandy bottom in the northern Red Sea has demonstrated the capability of nursery-bred coral units to initiate reef regeneration. The transplantation of *Reef Carpets* resulted in an immediate reef structure in the middle of a sandy “reef desert”. It instantly formed a new lively reef that bolsters coral reproduction, supports coral recruitment as well as development of diverse fish and invertebrate communities. It enabled the formation of trophic webs, complex and dynamic biological and ecological interactions and the moderate *Reef Carpets* corals’ mortality resulted in dead skeletons becoming hubs for reef biota. Moreover, this new methodology provides an alternative to the most commonly used practice of transplanting individual colonies; it reduces transplantation costs and increases restoration area coverage scale, which is one of the more pressing challenges in the emerging field of reef restoration. The coverage of large zones becomes feasible with such a technique, including areas where reef regeneration could not have occurred through natural recruitment. In addition, the heightened inveterate reproductive performance characteristic of nursery-bred transplants (Chapters 3 and 4) strengthens reef resilience, promoting reef growth and regeneration through natural processes. This new transplantation approach further presents an applied ecological engineering tool that impacts the three levels of reef biodiversity explored in this dissertation.

Active reef restoration is still in its infancy and many of its theoretical and practical aspects are yet to be explored to build up its capacity to confront the challenges faced by reefs today. Using nursery-grown coral transplants as ecological engineering tool for reef restoration present numerous opportunities to address biodiversity concerns of degrading reefs. The hard task of preserving the invaluable biodiversity of these tropical treasures relies on our ability to create a diversified and effective restoration toolbox for inducing well-conceived, self-perpetuating reef zones designed to maintain a variety of ecological flows, supply habitats for a wide range of reef biodiversity, and provide ecosystem services to reef organisms and human populations under a range of future environmental conditions.

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**עקרונות אקולוגיים במערכות ימיות:
שתיות אלמוגים מושתלה - כלי הנדסה סביבתית לשיקום שונות אלמוגים**

על בינה הורושובסקי-פרידמן

תקציר

שוניות אלמוגים מתאפיינות בעושר רב של מגוון ביולוגי ומשמעות לאוכלוסיית האדם שירותים שונים ומשאבים חיוניים. למרבה הצעיר, מבחן של שוניות האלמוגים ברחבי העולם מדרדר במהירות כתוצאהם מפעילות האדם ושינויי אקלים עולמיים ההולכים וגוברים. כתוצאה מוגבלותיהם ויכולתן הולקה של פעולות הניהול והשימור שננקטו עד כה לבסוף את הרס השוניות, ישנו ביום צורך דחוף לפתח שיטות שיקום פעיל (אקטיבי) על מנת שיובילו ליצירתן מחדש המוחודשת של שוניות אלמוגים המסוגלות לתמוך בהתקפות בת-קיימא של מיini אלמוגים ומיני יצורים שכני שונית נלוים, על אף איומי הסביבה הגוברים. שיטתה הירנות הימית, המכונה גם "גינון שוניות אלמוגים", הינה גישה חדשה לשיקום שוניות אלמוגים הבוססת על כלים מתחום ההנדסה הסביבתית. שיטה זו פותחה בהשראת עקרונות שיקום פעיל של חברות יער (ירנות יבשתית) ומורכבת שני שלבים: א) ייצור מושבות אלמוגים חדשות במשתלה אלמוגים וגידולן שם עד הגיען לגדים המתאימים לשטילה; ב) העתקת מושבות חדשות אלו וشتילתן בשוניות פגעות. בשל חישונתה של שיטת הירנות הימית, היבטים רבים של השלב השני (שתיות אלמוגים מושתלה) טרם נחשפו ונלמדו. מטרתנה של עבודה דוקטורט זו הינה לקדם תחום ידע חדש ומתפתח זה של שיקום שוניות אלמוגים פעיל, הן על ידי מעקב אחר שגשוש של אלמוגים מושתלה שנשתלו בשוניות פגעות, והן על ידי מחקר והבנה של עקרונות הירנות היבשתית תוך הטענתם והתאמתם לצרכי שיקום שוניות. בעבודה זו מוצגים ארבעה מחקרים הובננים היבטים תיאורתיים ומעשיים של שימוש בשיטתה אלמוגי מושתלה ככלי להנדסה סביבתית המאפשר להעצים את המגוון הביולוגי של שוניות משוקמות, את **כושר עמידתן והთואשותן**, וכן את **יכולת הקיום** שלהן.

חלוקת הראשון של עבודה זו מתמקד במאפיינים של בית אלמוגי מושתלה לאחר שתילתן בשונית, ומציג שני מחקרים המתקנים אחר יכולתם של אלמוגים מושתלה להתרבות ולשחרר פגעות (לרווות) לאחר שתילתם בשוניות פגעות. המחקר הראשון בוחן את תוצריו הרבייה המינית של אלמוגים מושתלה מהסוג *Stylophora pistillata*, שנשתלו במהלך שלושה אירופי שתילה באתר פגוע בשונית אילת, במשך שלוש עונות רבייה לאחר השטילה. כמו כן, המחקר עקב אחר תוצריו הרבייה של אלמוגי שיכון מקומיים שהתרפתחו וגדלו באתר שונית פגעה זו באופן טבעי. המושבות השתוולות לא רק שהתרבו במקום מחייתם החדש, אלא אף הראו יכולות רבייה מוגברות ביחס למושבה נאסף ממושבות אלו. שתוולות שחרר פגעות בהשוואה למושבות הטבעיות ומספר רב יותר של פגיפות למושבה נאסף ממושבות אלו. אי לכך, כמוות הפגיפות הכלילית שנאספה מקבוצת המושבות השתוולות הייתה גבוהה באופן משמעותי מזו שנאספה מקבוצת מושבות האלמוגים שגדלו באופן טבעי בשונית. על מנת להעריך האם יכולת רבייה מושבת זו של מושבות האלמוגים השתוולים מוגבלת לתקופה הסמוכה לשטילה, או שביבולתן של המושבות להמשך ולשחרר פגיפות לטווח זמן ארוך בשונית הפגעה, הוארך המקבב אחר תוצריו הרבייה לכדי שמונה עונות רבייה, המהוות שבע וחצי שנים לאחר השטילה (מחקר 2). על אף שהמושבות הטבעיות והשתיולות גדלו זו לצד זו בסביבה מופרעת, מושבות המשתלה המשיכו לשחרר מספר גבוה יותר של פגיפות למושבה (פ"י 2.6-22.5 יותר פגיפות למושבה, 11.6±1.8 פגיפות למושבת מושתלה לעומת 1.5±0.3 פגיפות

למושבה טبيعית, ממוצע רב שנתי של 8 עונות רבייה). כמו כן, בקרוב אלמוגים המשטלה נצפו יותר מושבות מעוברות (בממוצע, $91 \pm 2.1\%$ ממושבות המשטלה שחררו פגיות לעומת $34 \pm 7.6\%$ מהמושבות הטבעיות) לארוך כל 7.5 שנים מחקר. יכולת רבייה מוגברת ומושרשת זו, הנמשכת אצל אלמוגים המשטלה השתוילים לאורך תקופה כה ארוכה, מרמזת על השפעה ארוכת טווח של תנאי המשטלה המיטביים על מצבן, יכולותיהם ומאפייניהם האקולוגיים של המושבות השתוילות. יתרה מזו, המחקר חושף את יכולות ההנדסה הסביבתית של אלמוגים משטלה שתוילים בהගרים באופן משמעותי את מאגר הפגיות בשינויים פגועות, וביכולתם ליצור מחדש מושבות אלמוגים אלו בפגיות אלמוגים.

בחלקו השני של[U]בבודת[/U] המחקר נבחנה בפעם הראשונה שיטה של שתילת אלמוגים חדשנית בשם "מרבדשא אלמוגים". שיטה זו מתחילה אחר הרעיון של שימוש מסחרי ביחסות דשא מוקן (המכונה "מרבדשא") בפועלות הגינון של מדאות יבשתיות (מחקר 3). מושבות אלמוגים שלושה מינים מעוניינים, שיטתית *S. pistillata*; N=212; (*Acropora variabilis*; N=132), שיחית (*Pocillopora damicornis*; N=364), שגודלו במשטלה, שימשו לייצור מבועד מועד של יחידות שתילה. בתום תקופת הגידול במשטלה הועתקו יחידות אלו במלואן, יחד עם חברות החיה הנלוות שהתוספה ליחידות במהלך תקופת המשטלה, ונפרשו על מצח חולי באילת. התאקלמותן של מושבות אלמוגים המרבדשא נוטרה במהלך 17 חודשים מרגע העברתם מתנאי המשטלה המוגנים לסביבה הזורה. המחקר כלל מעקב אחר שרידות, תמונת העברתם ומאפיינים רביתיים של אלמוגי השיחן. כמו כן, לאחר שאלמוגי אבן הינים מינים מהנדסי-סביבה, ובכך גם מאפיינים רביתיים של אלמוגי השיחן. במחקר נוכחותם ועל שיישוגם של צוריכים שונים נבחנה יכולת זו של מושבות האלמוגים במרבדשא להשביע על אוכלוסיית השונית במרבדשא-האלמוגים נוטרה, ונבחנו המבנה ומגוון המינים שמרכזים את חברות הדגים וחסרי החוליות שהפתחו ביחסות המרבדשא. שתילת מרבדשא-האלמוגים יצירה באופן מיידי מבנה שוני, שתמך בגישות והתיישבות אלמוגים חדשים וספק גומחות מרחביות ואקוולוגיות חדשות עבור דגים וחסרי חוליות. כפי שהתגלה במהלך 17 חודשים הניטור של השונית החדשה שהזיפה במרכזו של "מדבר שונית", שרידות האלמוגים הייתה תלות מין ונעה בין 50% ל-65%. התמונת החליקת שנכפתה במושבות האלמוגים במרבדשא הייתה במוגמת עלייה זהה בשלושת מיני האלמוגים, וכך על פי כן נרשמה אליה מובהקת בהתקפות המושבות על מבנה המרבדשא לאורך תקופת הניסוי. טריפת הדגים שנרשמה באתר הניסוי הייתה נמוכה יחסית, אך הייתה יותר משמעותית עבור אלמוגי השיטית והשיחן לעומת אלמוגי השיחית. חלזונות טורפי-אלמוגים נמשכו יותר לשני מיני השיחניים (שיחן ושיחית) של מרבדשא האלמוגים. בדומה לתוצאותיהם של שני המחקרים הראשונים המוצגים בעבודה זו, מושבות המשטלה מהסוג שיחן הפגינו יכולות רביה מוגברות ביחס למושבות הטבעיות באתר הניסוי (נאספו בממוצע 4.6±1.7 פגיות למושבת משטלה לעומת 1.6±0.6 פגיות למושבות טבעית), על אף תנאי הסביבה המתגרים. נוכחות מושבות האלמוגים במרבדשא הותה תמריץ להתקפותן וונגשון של חברות מגוונות (183 טקסונים נוכחות בתכיפות שדה), הן של דגים והן של חסרי חוליות, בהן נצפו יחסית גומלי מורכבים ודינאמיים. למאפיינים התלת מימדיים של מיני האלמוגים שנשתלו במסגרת הניסוי היו השפעות הנדסה-סביבתיות שונות וכטזאה מכך, תרומותם לבניה חברות הדגים וחסרי החוליות היו שונות. שלדי האלמוגים שנכחו בניסוי כתוצאה מההתמונת של אלמוגי מרבדשא האלמוגים הפכו למוקדי מחייה של מינים שכני שונית, ואף הכילו מעל 80% מ מגוון המינים הנלוים שתועדו. תכיפות אלו וושפota את חטיבתן של גומחות אקוולוגיות שונות ומגוונות עבור חברות היוצרים שכני השונית. שיטת שתילה זו מהווה חלופה לעפולות השיקום لكنה מידה גדולה. מלבד הרצון להגדיל את כיסוי כל מושבה בנפרד, ומאפשרת את הרחבת פעולות השיקום לכמה מידה גדולה. האלמוגים החים, שיטת שתילה זו מסיטה את המוקד של שיקום פעיל של שינויי אלמוגים לכל נושא

המגון הביוווגי של השוניות ומהוועה על כן כלי הנדסה-סביבתית יעיל על מנת לייצר שטחי שונות חדשות שימושים את המגון הביוווגי של שוניות פגעות.

המחקר הריבעי המוצע בעבודה זו מציג את כל הידע עד כה בתחום שתילת אלמוני משטלה ודן בהשפעת שיקום שוניות על חברות שוניות האלמוניים הפגעות. בפרט, הוא מתמקד ברבדים השונים של המגון הביוווגי - המגון הגנטי, מגון המינים, והmagicן בرمת בית הגידול, ובווען עקרונות והמלצות מתחום הייענות היבשתית שיכוליםקדם את שיטת הייענות הימית ולהתמעב בה. מחקר זה מדגיש שיקולים תיאורתיים ומעשיים שיש לנקח בחשבון במסגרת פעילות השיקום של שוניות אלמוניים הנהוגות כיום. יחדיו, ארבעת מחקרים אלו מספקים הבנה וניהול מושכל של שיקום שוניות פגעות, יגבירו את המגון ובהתבטים הכרחיים לבניית תנאי ממשק שייאיצו את התאוששותן של שוניות פגעות, יגבירו את המגון הביוווגי בהן, ויתרמו ליכולת הקיימות שלן. הם חושפים את יכולות ההנדסה הסביבתית הטמונה עצם שימוש באלמוני משטלה המהווים מינים מהנדסי סביבה לצורך שיקום שוניות אלמוניים, הכוללים מאפיינים וכליים חדשים שהוצגו בעבודה זו – יכולות רבייה מוגברות של אלמוני משטלה ושיטת השטילה החדש "מרבדשא-אלמוניים". ככלים אלו, בשילוב עקרונות הלקוויים מתחום הייענות היבשתית, יכולים להוביל לשיקום בר-קיימה של שוניות פגעות בעידן של שינוי אקלים ולחץ אנושי החולך וגובר.

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שתיילת אלמוגים משטלה - כלי הנדסה סביבתית לשיקום שוניות אלמוגים**

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דוקטורט פרסומיים

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