SUPPLEMENT

REVISTA DE
Biología Tropical

https://doi.org/10.15517/rev.biol.trop..v71iS1.54849

The contribution of assisted coral restoration to calcium carbonate production in Eastern Pacific reefs

J. J. Adolfo Tortolero-Langarica[1,2]*; https://orcid.org/0000-0001-8857-5789
Alma P. Rodríguez-Troncoso[3]; https://orcid.org/0000-0001-6243-7679
Lorenzo Alvarez-Filip[4]; https://orcid.org/0000-0002-5726-7238
Amílcar L. Cupul-Magaña[3]; https://orcid.org/0000-0002-6455-1253
Juan P. Carricart-Ganivet[2]; https://orcid.org/0000-0001-7266-8905

1. Laboratorio de Esclerocronología de Corales Arrecifales, Unidad Académica de Sistemas Arrecifales, Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Puerto Morelos, Quintana Roo, México; adolfo.tl@bahia.tecnm.mx (*Correspondence), carricart@cmarl.unam.mx
2. Tecnológico Nacional de México / Instituto Tecnológico Bahía de Banderas, Nayarit, México; adolfo.tl@bahia.tecnm.mx (*Correspondence).
3. Laboratorio de Ecología Marina, Centro de Investigaciones Costeras, Centro Universitario de la Costa, Universidad de Guadalajara. Puerto Vallarta, Jalisco, México; pao.rodriguezt@gmail.com, amilcar.cupul@gmail.com
4. Laboratorio de Biodiversidad y Conservación de Arrecifes, Unidad Académica de Sistemas Arrecifales, Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Puerto Morelos, Quintana. Roo, México; lorenzo@cmarl.unam.mx

Received 29-VIII-2022. Corrected 27-I-2023. Accepted 10-II-2023.

ABSTRACT

Introduction: Hermatypic corals have the capacity to construct the physical reef-framework and maintain the balance of coral reef functionality. However, in the past three decades, coral communities have been menaced by natural and anthropic pressures, resulting in an abrupt coral cover decline, and slow natural recovery. To mitigate coral reef collapse, assisted restoration techniques has been implemented and improved worldwide, However, the long-term effects of such interventions on ecological attributes have been scarcely reported.

Objective: This study evaluated the effect of assisted coral intervention on calcium carbonate production (kg $CaCO_3$ m^{-2} yr^{-1}) and ecological volume (cm^3) yielded by branching and massive corals from the central Mexican Pacific.

Methods: We used colony size, extension rate, and skeletal density measurements of direct outplanted *Pocillopora* and *Pavona* coral species to calculate coral carbonate production, ecological volume, and model their long-term potential.

Results: Coral carbonate produced after one-year of outplanting increased by 42 % (1.17 kg $CaCO_3$ m^{-2} yr^{-1}), where *Pocillopora* spp. and *Pavona clavus* corals contribute with 0.97 and 0.20 kg $CaCO_3$ m^{-2} yr^{-1}, respectively. The ecological volume also increased by 384 cm^3 for *Pocillopora* and 56 cm^3 for *Pavona* after one year period. Furthermore, the results suggest that long-term coral restoration actions (10 years) have the potential to significantly increase carbonate production.

Conclusions: our data indicate that coral restoration initiatives have the potential to help mitigate the current low calcium carbonate production of Mexican Pacific reefs and may significantly contribute to the long-term maintenance of reef-framework based on ecological engineering tools, such initiatives represent essential functional properties related to reef ecosystem services provision.

Keywords: direct propagation; coral fragments; eastern tropical Pacific; branching corals; massive corals.

Revista de Biología Tropical, ISSN: 2215-2075 Vol. 71 (S1): e54849, abril 2023 (Publicado Abr. 30, 2023)

RESUMEN

El aporte de la restauración coralina asistida a la producción de carbonato calcio en arrecifes del Pacífico Oriental

Introducción: Los corales hermatípicos tienen la capacidad de construir y mantener la estructura física y mantener el equilibrio de la funcionalidad de los arrecifes coralinos. Sin embargo, en las últimas tres décadas las comunidades coralinas han sido amenazadas por presiones tanto naturales como antrópicas, resultando en una disminución abrupta en la cobertura de coral y lenta recuperación natural. Para mitigar el colapso de los arrecifes de coral, diversas técnicas de restauración asistida se han implementado y mejorado alrededor del mundo. Sin embargo, los efectos de largo plazo de dichas intervenciones en los atributos ecológicos han sido escasamente reportado.
Objetivo: Este estudio evaluó el efecto de la intervención asistida en la producción de carbonato ($kgCaCO_3$ m^{-2} yr^{-1}) y en el volumen ecológico (cm^3) producido por corales ramificados y masivos del Pacífico central mexicano.
Métodos: Utilizamos mediciones de tamaño de colonias, la tasa de extensión y densidad esquelética de especies de coral *Pocillopora* y *Pavona* trasplantadas directamente para calcular la producción de carbonato de coral, el volumen ecológico y modelar su potencial a largo plazo.
Resultados: El carbonato de coral producido después de un año de la plantación aumentó un 42 % (1.17 kg $CaCO_3$ m^{-2} yr^{-1}), donde los corales *Pocillopora* spp. y *Pavona clavus* aportaron 0.97 y 0.20 kg $CaCO_3$ m^{-2} yr^{-1}, respectivamente. El volumen ecológico también aumentó en 384 cm^3 para *Pocillopora* y 56 cm^3 para *Pavona* después de un periodo anual. Los resultados sugieren que las acciones de restauración de coral a largo-plazo (10 años) tienen el potencial de aumentar significativamente la producción de carbonato.
Conclusiones: Los datos obtenidos en este estudio indican que las iniciativas de restauración de coral tienen el potencial de ayudar a mitigar la baja producción de carbonato de calcio actual en los arrecifes del Pacífico mexicano, y pueden contribuir significativamente al mantenimiento a largo-plazo de la estructura arrecifal mediante herramientas de ingeniería ecológica. Las cuales representan propiedades funcionales esenciales relacionadas con la provisión de servicios ecosistémicos.

Palabras clave: propagación directa; fragmentos de coral; Pacífico tropical oriental; corales ramificados; corales masivos.

INTRODUCTION

The construction and stability of coral reef frameworks primarily rely on hermatypic corals, which are capable of precipitating calcium carbonate and build complex structures, which are the base of coral reef habitats (Sheppard et al., 2009). Yet, the combined impact of climate-induced factors (e.g., ocean warming, and acidification) and local human-induced pressures (e.g., marine pollution, overfishing, and nutrients load) has led to a rapid and relentless decline in coral cover and reef health. This trend poses a significant threat to the provision of reef ecosystem services in the coming decades (Hoegh-Guldberg et al., 2007; Hughes et al., 2017). While passive management measures like marine protected areas (MPAs) and marine reserve designations have been established as key conservation strategies, they appear to be insufficient in mitigating natural and anthropogenic threats (Graham et al., 2008; Selig & Bruno, 2010). As a complementary response, active human interventions, mainly through coral restoration approaches, based on adapting to changing conditions and implementing science-based improvements to mitigate coral reef degradation, have been widely performed (reviewed in Rinkevich, 2019b).

Among the various methods used to restore reef-building corals, one that has shown rapid growth rates and resilience is coral propagation through fragmentation or micro-fragmentation, which can be applied to most hermatypic morphospecies (i.e., branching, massive, columnar, and foliaceous), reducing time and costs effectively, and can be efficiently used in large-scale restoration programs (Page et al., 2018; Tortolero-Langarica et al., 2020). Small coral fragments can be produced in large quantities, and the possibility of employing multiple genotypes, which can be combined via fusion to create chimeras, can maximize the adaptive potential of corals to become more resilient to future environmental conditions (Rinkevich, 2019a). However, the biological and ecological effects of coral restoration through micro-fragmentation are still in the initial stages, thus evaluation of ecological restoration applications and development of integrative protocols are needed to accelerate coral reef resilience (Rinkevich, 2019b; Boström-Einarsson et al., 2020).

The use of ecological engineering tools in coral restoration actions (Rinkevich, 2020) represents an important aspect in the re-establishment of functional properties (e.g., calcification rates, carbonate production, and structural complexity) related to coral reef ecosystem services (i.e., habitat development, coastal protection, sand production, and track sea-level rise) at long-term scales (Perry & Alvarez-Filip, 2018). Yet, most coral restoration methods focus on biological attributes (e.g., coral growth and survival), while few interventions have been attempted to measure ecological attributes that could determine the influence of coral restoration approaches from a geo-ecological perspective (Rinkevich et al., 2019b; Rinkevich, 2020).

Coral reefs from the Eastern Tropical Pacific (ETP) region have been damaged due to repeated intensive thermal-anomalies and bleaching events, causing a coral cover decline of 50-98 % in the last two decades (Alvarado et al., 2020; Carriquiry et al., 2001; Eakin, 2001; Glynn, 2000; Reyes-Bonilla et al., 2002; Romero-Torres et al., 2020). Despite this damage, coral reef species in the ETP have revealed a high thermo-tolerance threshold, resulting in different natural recovery paths among coral reefs (Glynn et al., 2015; Glynn et al., 2017; Hueerkamp et al., 2001; Romero-Torres et al., 2020). The recovery of reef-building coral species is essential for sustaining ecological processes such as reef carbonate production and the topographical complexity of coral reef ecosystems (Lange et al., 2020; Perry & Alvarez-Filip, 2018). However, coral calcium carbonate and the three-dimensional contribution of coral species are rarely considered when determining coral restoration efficiency from an ecological perspective (Forsman et al., 2006; Tortolero-Langarica et al., 2020). This study aims to evaluate the bio-geological effect on calcium carbonate production (kg$CaCO_3$ m^{-2} yr^{-1}) and ecological space occupied (ecological volume; cm^3) by corals resulting from an active coral restoration, using the direct propagation of small fragments of branching *Pocillopora* spp. and massive *Pavona clavus* corals from the Central Mexican Pacific. The results provide us insights not only into the carbonate contribution of the most abundant coral species (Pocilloporids and Pavonids) along the ETP, but also for their long-term potential to maintain the coral reef framework in the region.

MATERIALS AND METHODS

Study area: This study was conducted between June 2018 to August 2019 at Isla María Cleofas, Islas Marías Biosphere reserve (Fig. 1), located in the north ETP at a distance of 130 km offshore of the coast (CONANP, 2010). Isla María Cleofas consists of isolated coral reef patches dominated by branching corals of the family Pocilloporidae in shallow reef areas at 2-6 m, and massive corals of the family Agariicidae and Poritidae corals at depths > 6 m (López-Pérez et al., 2015; Tortolero-Langarica et al., 2022). The annual seawater temperature (SWT) of the Islas Marías archipelago is regulated by two inter-annual ocean currents, and it varies from 18-21 °C during December to May when the California Current is dominant, and from 27-31 °C from July through November when the coastal Costa Rica current prevails (Pennington et al., 2006). The Islas Marías are also affected by frequent heatwaves associated with El Niño Southern-Oscillation (ENSO) events, seasonal upwelling, and tropical storms (Pennington et al., 2006; Wang & Feldler, 2006).

Coral propagation and coral measurements: Hermatypic corals propagation was implemented using 154 small coral fragments

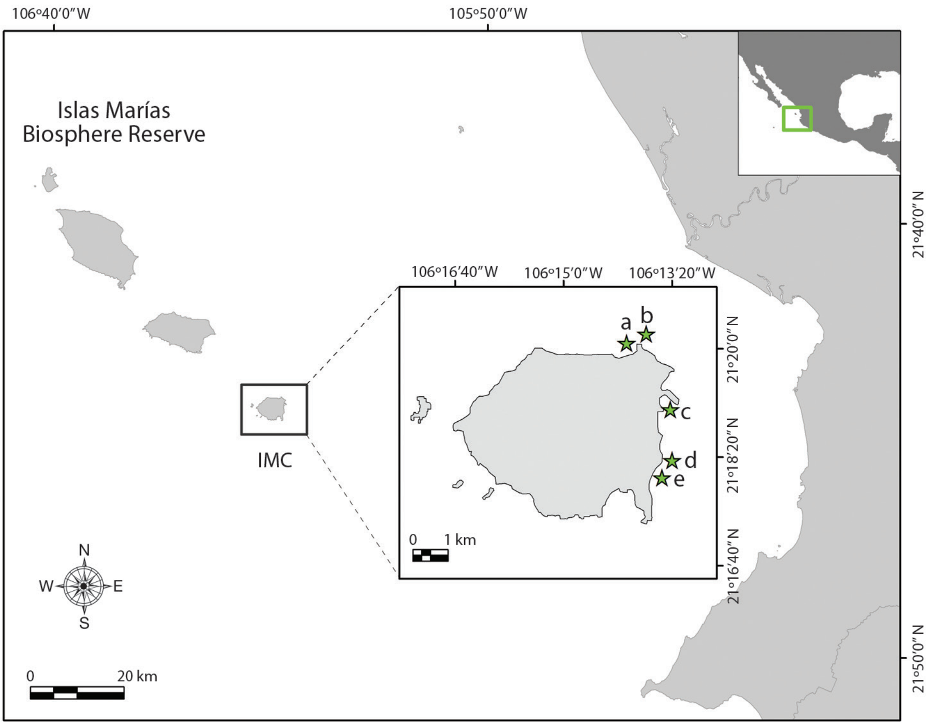

Fig. 1. Study map of the Islas Marías Biosphere Reserve in the Northeastern Tropical Pacific. The green stars indicate the surveyed reef sites on Isla María Cleofas (IMC), **a.** Regidor 1, **b.** Regidor 2, **c.** Muelas, **d.** Cleofas 1, **e.** Cleofas 2.

(sizes 3-4 cm^2) collected from corals of opportunity of *Pocillopora* spp. (n = 78), and *Pavona clavus* (n = 78), and glued using water-resistant silicon (MS-express, Fischer®) directly onto the natural limestone rock (see, Tortolero-Langarica et al., 2020). The coral fragments were placed on two coral plots of 6 m^2 at a depth of 5 m in the Regidor-2 reef site (Fig. 2). Colony size (height, length, and width) was measured using calipers (0.05 mm precision) at the beginning and end of the experimental period. Height growth (H) was calculated as the linear distances from the bottom to the uppermost growth of each coral fragment. Length growth (L) was determined as the maximum diameter of the coral fragment, while width growth (W) was obtained from the contiguous diameter perpendicular to the length growth.

The three-dimensional growth of coral fragments was estimated based on the volume of a cylinder since this most accurately expressed the total space occupied by the colony (Shafir et al., 2006). Growth metrics (H, L, and W) were used to estimate the increase in coral ecological volume (EV) of each fragment at the end of the evaluation period, EV = ϖr2H, where r = radius (L+W /4) (Rinkevich & Loya, 1983; Shafir et al., 2006). Following the exponential growth rates (%) of outplanted corals, growth rate constants (k) of ecological volumes (EV) were calculated for each *Pocillopora* and *Pavona clavus* coral using the formula $EV_t = EV_o e^{kt}$, providing $k = (\ln EV_t / EV_o)/t$, where t = time and 0 = values at initial stage of the experiment.

To compare the carbonate production of outplanted corals with that of naturally occurring corals, measurements of colony size (H, L, and W) measurements were recorded at the genus level (*Pocillopora* spp. and *Pavona* spp.) in five shallow reef sites (3-5 m depth; Fig. 1), using coral colonies found along belt transects

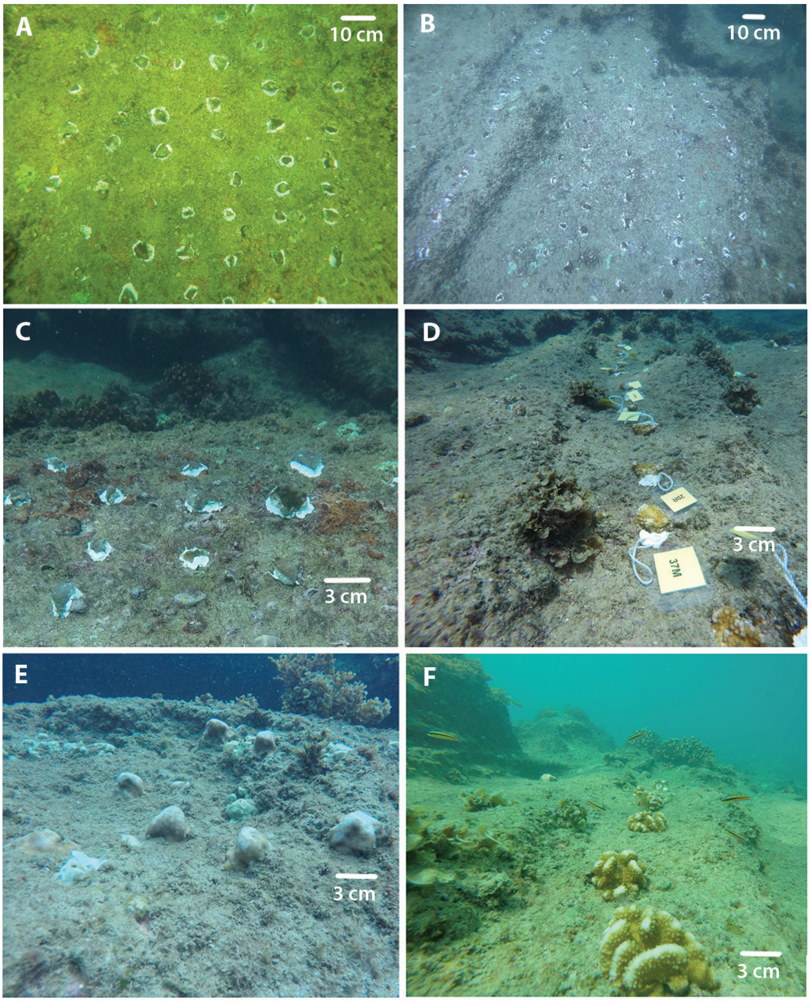

Fig. 2. Coral restoration plots were established using small coral fragments of **A**. *Pavona clavus* and **B.** *Pocillopora* spp. from Isla María Cleofas, Mexico. Panels **(C-D)** show the initial size of fragments of massive *Pavona clavus* and branching *Pocillopora* spp. respectively. Panels (**E-F**) Show the final coral sizes after one-year of growth. Scale bars in panels **(A-B)** represent the area size, while those in panels **(C-F)** indicate the size of the nearest fragment.

(n = 5) of 25 m in length. To complete the carbonate production assessment, information on coral growth (extension rate and skeletal density) was obtained from published literature for *Pocillopora* (2.74 cm^{-2} yr^{-1}, and 2.18 cm^{-3}) and *Pavona* (0.92 cm^{-2} yr^{-1}, and 1.39 cm^{-3}) corals from Islas María Cleofas (Tortolero-Langarica et al. 2020).

Colony size, extension rate and skeletal density data were used to calculate the calcium carbonate production per coral colony/transplant ($kgCaCO_3$ m^{-2} yr^{-1}), defined as the calcium carbonate produced by corals based on colony morphology following the method described by Perry et al. (2018). Annual coral carbonate production ($kgCaCO_3$ m^{-2} yr^{-1}) was estimated using both *Pocillopora* and *Pavona* coral genera at Cleofa's reef sites and coral restoration plots, by means of the census-based method (Lange et al., 2020; Perry et al., 2018). The proportion of calcium carbonate produced during the coral intervention period was also

Revista de Biología Tropical, ISSN: 2215-2075 Vol. 71 (S1): e54849, abril 2023 (Publicado Abr. 30, 2023)

calculated as CP= N_t–N_0 / t, where N_0 and N_t denote the carbonate production after outplanting and at the end of the experiment, respectively, and (t) is the time-lapse. The calcium carbonate produced by the intervention was added to the naturally produced annual coral carbonate in Cleofas and extrapolated for a ten-year period to estimate the potential of calcium carbonate production over a decade. After evaluating of normality (Shapiro-Wilk, P <0.001) and homoscedasticity (Levine, P= 0.621), differences in annual carbonate production between reef sites was assessed using a non-parametric analysis of variance (Kruskal-Wallis) with Sigma plot ver.11, using a confidence interval of 95 % (alfa = 0.05).

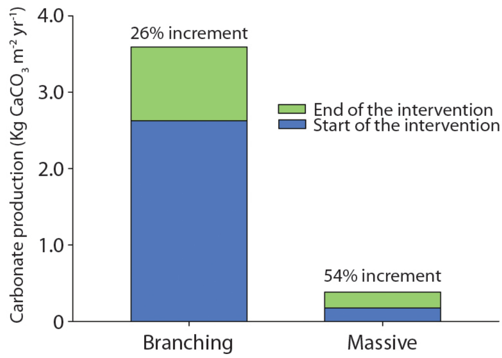

Fig. 3. The production of calcium carbonate accumulated by branching and massive corals resulted from the intervention. The colored bars indicate the proportion of carbonate production at the initial stage (blue) and after one year of growth (green).

RESULTS

Coral carbonate production after intervention: From the 154 total fragments that were outplanted, the survival rate was of 59 % (92 corals survived, including 46 *Pocillopora,* and n = 46 *Pavona*). Coral growth parameters indicated that coral height increased threefold (~ 3.52 cm), width doubled (~ 5.00 cm), and length increase twofold (~ 5.52 cm) compared with initial size of *Pocillopora*. For massive *Pavona clavus* fragments, there was an equitable increase (1.5-fold) in all growth dimensions (height ~ 1.35 cm, width ~1 .73 cm, and length ~ 1.69 cm). At the end of the study period, the mean colony calcification (± SD) for *Pocillopora* corals was of 19.58 ± 4.13 kg $CaCO_3$ m^{-2} yr^{-1}, and mean ecological volume (EV) increased more than 15-fold, accumulating to 384 cm^3 (EV initial = 25 cm^3, and EV final = 409 cm^3). For *P. clavus* fragments, the mean colony calcification was 3.97 ± 0.63 kg $CaCO_3$ m^{-2} yr^{-1}, EV increased fourfold, accumulating to a total of 56 cm^3 (EV initial = 22 cm^3, and EV final = 78 cm^3) after 13-months of intervention (Fig. 2). The total calcium carbonate at the beginning of the experiment was 2.80 kg $CaCO_3$ m^{-2} yr^{-1} compared to 3.98 kg $CaCO_3$ m^{-2} yr^{-1} at the end of the experiment, with *Pocillopora* and *Pavona* corals contributing 3.59 and 0.38 kg $CaCO_3$ m^{-2} yr^{-1}, respectively (Fig. 2). The amount of calcium carbonate produced by coral outplants was 0.97 kg $CaCO_3$ m^{-2} yr^{-1} for *Pocillopora* spp. and 0.20 kg $CaCO_3$ m^{-2} yr^{-1} for *P. clavus* coral fragments, carbonate production increased by 26 % and 54 %, respectively (Fig. 3).

The naturally carbonate production: In 2018, Isla Cleofas's sites showed a mean annual coral carbonate production of 1.78 kg $CaCO_3$ m^{-2} yr^{-1} (ranged 0.43-6.40), with significant differences among reef sites (H_4 = 11.028, P = 0.026). Among the sites, Cleofas 1 reef had the highest production (6.40 kg $CaCO_3$ m^{-2} yr^{-1}), while Las Muelas had the lowest (0.48 kg $CaCO_3$ m^{-2} yr^{-1}; Fig. 4). By including the calcium carbonate produced by coral outplants in natural Isla Cleofas' carbonate production, the potential carbonate production increased by 4.2 times for 5 years and 7.5 times for 10 years, using active coral restoration actions (Fig. 5).

DISCUSSION

The slow or absent natural coral recovery at many reef locations necessitates the implementation of reliable ecological restoration methods to mitigate local coral degradation and restore reef-associated biodiversity and ecosystem functionality (Boström-Einarsson et al.,

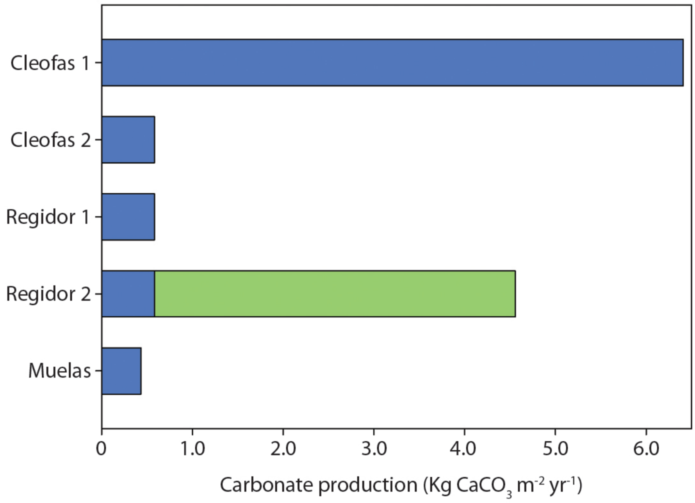

Fig. 4. The annual coral carbonate production between Cleofas´s reef sites. The blue bars represent naturally produced carbonate production, while the single green bar represents carbonate produced by outplanted corals at the intervened site.

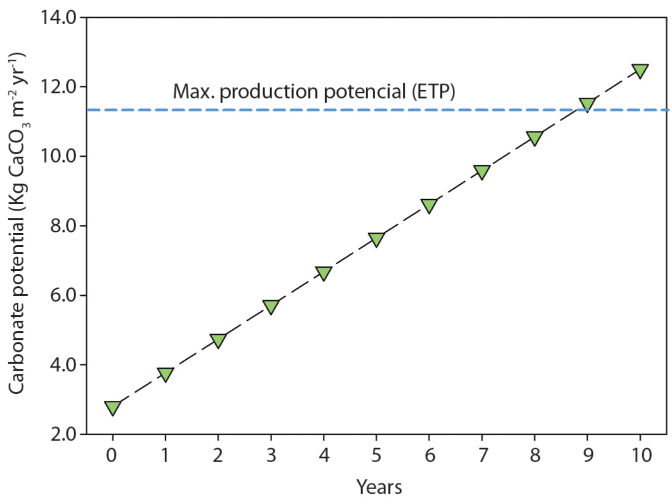

Fig. 5. The potential coral carbonate production (kg$CaCO_3$ m^{-2} yr^{-1}) estimated at the beginning of the experiment and projected over 10 years using values produced by coral intervention. The blue segmented line represents the maximum carbonate potential for Eastern Tropical Pacific Reef (*sensu* Alvarado et al., 2016; Cabral-Tena et al., 2018).

2020; Rinkevich et al., 2020). The results presented here provide an ecological insight into coral carbonate production and its response resulting from coral restoration efforts. Direct relocation of asexual recruits (corals of opportunity) is not commonly used (Rinkevich 2019b), it has been shown to be a practical and effective tool for restoring coral reef-framework and improving reef biogeochemical dynamics in terms of coral carbonate production (Tortolero-Langarica et al., 2019). This technique is both time- and cost-effective, avoiding the need for fragment transportation, over-manipulation, pre-growth, and acclimatization periods required in both the farming and nursery phases. It is, therefore, an affordable technique for restoring remote and marginal reefs (Tortolero-Langarica et al., 2020). While complementary long-term approaches are required, the direct outplanting of both branching and massive coral species used in this study facilitates the increment of ecological volume (EV) and coral carbonate production during active coral restoration actions.

The results showed an accumulated ecological volume of 384 cm^3 yr^{-1} for *Pocillopora* spp. and 56 cm^3 yr^{-1} for *Pavona clavus*, which is similar increments observeded with homologous species from other coral reef locations (Boch and Morse, 2012; Shaish et al., 2010; Tortolero-Langarica et al., 2019). *Pocillopora* spp. fragments increased more than ten-fold in EV, while *P clavus* fragments increased three-fold in contrast with their initial EV sizes in a 13-month period. This corroborates that direct propagation techniques allows the development of three-dimensional colonies and an increase in the structural complexity of coral reefs, which is critical for ecological restoration (Tortolero-Langarica et al., 2019; Rinkevich, 2020). The use of branching and massive morphologies in restoration programs benefits not only coral diversity and abundance, but also avoids morpho-specific reefs, increasing habitat types, substrata, and resource variability that promote ecosystem properties recovery (e.g., biodiversity recruitment, food webs, landscape, and soundscape) (Lamont et al., 2021; Rinkevich, 2020).

Live coral cover and carbonate production from the ETP region have both suffered a decline in the last thirty-years mainly due to multiple ENSO events (El Niño and La Niña) (Manzello et al., 2017; Romero-Torres et al., 2020; Tortolero-Langarica et al., 2022). Although coral reefs in the study area have presented slow recovery in coral accretion following thermal-stress periods, the recovery is not sufficient (Cabral-Tena et al., 2018; González-Pabón et al., 2021; Tortolero-Langarica et al., 2017); yet some Cleofas´ reefs have been resilient, acting as a nursery areas and reefs of hope. Thus, Cleofas´ coral reef has the potential to recover coral growth and carbonate production rates via active restoration (Tortolero-Langarica et al., 2022). This is congruent with coral carbonate production obtained in this study (1.78 kg $CaCO_3$ m^{-2} yr^{-1}), which is three-times higher compared the previous year (0.46 kg $CaCO_3$ m^{-2} yr^{-1}; González-Pabón et al., 2021). However, Cleofas´s carbonate production is still low compared to the carbonate potential estimated for ETP reefs (8.22-11.47 kg $CaCO_3$ m^{-2} yr^{-1}; Alvarado et al., 2016; Cabral-Tena et al., 2018, 2020) and those net values (> 5 kg $CaCO_3$ m^{-2} yr^{-1}) considered for healthy reef systems (Perry et al, 2012; Lange & Perry, 2019). This production variability can be attributed to the decrease in coral calcification during and following coral bleaching events, where coral growth rate recovery may take from months to years after organisms' functions are repaired (Allemand et al., 2011; Tortolero-Langarica et al., 2017). For a successful long-term restoration, it is important to employ coral species with a wide tolerance and resistance to local stressors, which have more opportunities to resilience to global stressors such as thermal anomalies (Guest et al., 2011; Montero-Serra et al., 2018; Tortolero-Langarica et al., 2019). It is also crucial to conduct maintenance campaigns after thermal anomalies and hurricane events to retrieve the survival of the restoration program.

Novel restoration approaches based on ecological engineering can help to accelerate the recovery of calcium carbonate production in damaged and degraded coral reefs (Rinkevich, 2019b; Rinkevich, 2020). These approaches include the direct relocation of coral fragments, which promotes optimal effects on coral carbonate production with a high potential of success in long-term and large-scale interventions, relatively low-cost and less-labor (Tortolero-Langarica et al., 2019; Tortolero-Langarica et al., 2020). This idea is consistent with the coral carbonate production rates observed in this study, which showed higher annual values than those naturally produced (3.98 kg $CaCO_3$ m^{-2} yr^{-1} vs 1.78 kg $CaCO_3$ m^{-2} yr^{-1}) over the same period (Fig. 4, Fig. 5). This assertion can be also corroborated with the potential forcarbonate production resulting from this study, where the specific values for *Pocillopora* and *Pavona* values (Fig. 5) are similar to the carbonate production modeled for future coral assemblage in the ETP (*sensu* Cabral-Tena et al., 2018). Therefore, the continued effect of human intervention through active coral restoration, in conjunction with an integrative conservation strategy (i.e., management, self-sustainability, outreach, government, and community ownership) may be a cornerstone of effective coral community conservation and the prevention coral degradation in the current and future states of coral reef ecosystems (Boström-Einarsson et al., 2020; Suding et al., 2015).

The direct relocation of reef-building species, such as massive *P. clavus* and branching *Pocillopora* spp. from the central Mexican Pacific, has resulted in reliable and effective ecological restoration. This is due to the positive effect on coral ecological volume and carbonate production, which may contribute significantly to coral recovery and the persistence of the reef-framework (Tortolero-Langarica et al., 2019; Tortolero-Langarica et al., 2020). The use of small coral fragments is an alternative practical ecological engineering technique that has proved to be a long-term intervention initiative in the Isla Marías archipelago, and a promising tool to be adopted in other ETP coral reef localities. Moreover, the development and scale-up of active restoration programs are imperative to both, short- and long-term maintenance and functionality of reef ecosystems, as remediation and a complementary strategy under the current global coral reef crisis.

Ethical statement: the authors declare that they all agree with this publication and made significant contributions; that there is no conflict of interest of any kind; and that we followed all pertinent ethical and legal procedures and requirements. All financial sources are fully and clearly stated in the acknowledgements section. A signed document has been filed in the journal archives.

ACKNOWLEDGMENTS

The present work was supported by the Consejo Nacional de Ciencia y Tecnología (CONACYT) postdoctoral fellowship (CVU 410380) to JJATL, and the project PAPIIT IN200420 to JPCG. We thank to the Mexican authorities of Reserva de la Biosfera Islas Marias (SEMARNAT/CONANP), and Secretaría de Gobierno (SEGOB) for the permits and facilities provided. We especially loke to thank to the organization Protección y Restauración de Islas y Zonas Naturales (PROZONA AC), La Punta Outdoors SA de CV, and Grupo Cleofas "Maria Cleofas vessel" and their crew for their accommodations and assistance during field expeditions.

REFERENCES

Allemand, D., Tambutté, E., Zoccola, D., & Tambutté, S. (2011). Coral calcification, cells to reefs. In Z. Dubinsky, & N. Stambler (Eds.), *Coral reefs: an ecosystem in transition* (pp 119–15). Springer.

Alvarado, J. J., Sánchez-Noguera, C., Arias-Godínez, C. G., Araya, T., Fernández-García, C., & Guzmán, A. G. (2020). Impact of El Niño 2015-2016 on the coral reefs of the Pacific of Costa Rica: the potential role of marine protection. *Revista de Biología Tropical, 68*(Suppl. 1), S271–S282.

Alvarado, J. J., Cortes, J., Guzman, H., Reyes-Bonilla, H. (2016) Bioerosion by the sea urchin *Diadema mexicanum* along Eastern Tropical Pacific coral reefs. *Marine Ecology*. *37*, 1088–1102. https://doi.org/10.1111/maec.12372.

Boch, C. A., & Morse, A. N. C. (2012). Testing the effectiveness of direct propagation techniques for coral restoration of *Acropora* spp. *Ecological Engineering*, *40*, 11–17. https://doi.org/10. 1016/j.ecoleng.2011.12.026.

Boström-Einarsson, L., Babcock, R. C. Bayraktarov, E. Ceccarelli, D., Cook, N., Ferse, S. C., Hancock, B., Harrison, P., Hein, M., Shaver, E., Smith, A., Suggett, D. A., Stewart-Sinclair, P., Vardi, T., & McLeod, I. M. (2020). Coral restoration—A systematic review of current methods, successes, failures and future directions. *PLoS ONE*, *15*, e0226631

Cabral-Tena, R. A., López-Pérez, A., Alvarez-Filip, L., González-Barrios, F. J., Calderon-Aguilera, L. E., & Aparicio-Cid, C. (2020). Functional potential of coral assemblages along a typical eastern tropical Pacific reef tract. *Ecological Indicators*, *119*, 106795. https://doi.org/10.1016/j.ecolind.2020.106795.

Cabral-Tena, R. A., López-Pérez, A., Reyes-Bonilla, H., Calderon-Aguilera, L. E., Norzagaray-López, C. O., Rodríguez-Zaragoza, F. A., Cupul-Magaña, A., Rodríguez-Troncoso, A. P., & Ayala-Bocos, A. (2018). Calcification of coral assemblages in the eastern Pacific: Reshuffling calcification scenarios under climate change. *Ecological Indicators, 95*, 726–734. https://doi.org/10.1016/j.ecolind.2018.08.021.

Carriquiry, J. D., Cupul-Magaña, A., Rodríguez-Zaragoza, F., & Medina-Rosas, P. (2001). Coral bleaching and mortality in the Mexican Pacific during the 1997-98 El Niño, and prediction from a remote sensing approach. *Buletin of. Marine Science, 69*, 237–249.

CONANP (Comisión Nacional de Áreas Naturales Protegidas) (2010). *Programa de Conservación y Manejo Reserva de la Biosfera Islas Marías, México*. Secretaria de Medio Ambiente y Recursos Naturales, México.

Eakin, C. M. (2001). A tale of two ENSO events: carbonate budgets and the influence of two warming disturbances and intervening variability, Uva Island, Panama. *Bulletin of Marine Science, 69*, 171–186.

Forsman, Z. H., Rinkenvich, B., & Hunter, C. L. (2006). Investigating fragment size for culturing reef-building corals (*Porites lobata* and *P. compressa*) in ex situ nurseries. *Aquaculture*, *261*, 89–97.

Glynn, P. W. (2000). Effects of the 1997-98 El Niño Southern-Oscillation on Eastern Pacific corals and coral reefs: An overview. *Proceedings 9th International Coral Reefs Symposium, Bali, Indonesia, 2*, 169–174.

Glynn, P. W., Alvarado, J. J., Banks, S., Cortés, J., Feingold, J. S., Jiménez, C., Maragos, J. E., Martínez, P., Maté, J. J., Moanga, D. A., Navarrete, S., Reyes-Bonilla, H., Riegl, B., Rivera, F., Vargas-Ángel, B., Wieters, E. A., & Zapata, F. A. (2017). Eastern Pacific coral reef provinces, coral community structure and composition: an overview. In P. Glynn, D. P. Manzello, & I. Enochs (Eds.), *Coral Reefs of the Eastern Tropical Pacific* (pp. 107–176). Springer.

Glynn, P. W., Riegl, B., Purkis, S., Kerr, J. M., & Smith, T. B. (2015). Coral reef recovery in the Galápagos Islands: the northernmost islands (Darwin and Wenman). *Coral Reefs*, *34*, 421–436. https://doi.org/10.1007/s00338-015-1280-4.

Graham, N. A., McClanahan, T. R., MacNeil, M. A., Wilson, S. K., Polunin, N. V., Jennings, S., Chabanet, P., Clark, S., Spalding, M. D., Letourneur, Y., Bigot, L., Galzin, R., Öhman, M. C., Garpe, K. C., Edwards, A. J., & Sheppard, C. R. C. (2008). Climate warming, marine protected areas and the ocean-scale integrity of coral reef ecosystems. *Plos One*, *3*(8), e3039.

González-Pabón, M. A., Tortolero-Langarica, J. J. A., Calderon-Aguilera, L. E., Solana-Arellano, E., Rodríguez-Troncoso, A. P., Cupul-Magaña, A. L., & Cabral-Tena, R. A. (2021). Low calcification rate, structural complexity, and calcium carbonate production of *Pocillopora* corals in a biosphere reserve of the central Mexican Pacific. *Marine Ecology*, *42*(6), e12678. https://doi.org/10.1111/maec.12678

Guest, J. R., Dizon, R. M., Edwards, A. J., Franco, C., & Gomez, E. D. (2011). How quickly do fragments of corals "self-attach" after transplantation? *Restoration Ecology*, *19*, 234–242. https://doi.org/10.1111/j.1526-100X.2009.00562.x.

Hoegh-Guldberg, O., Mumby, P. J., Hooten, A. J., Steneck, R. S., Greenfield, P., Gomez, E., Harvell, C. D., Sale, P. F., Edwards, A. J., Caldeira, K., Knowlton, N., Eakin, C. M., Iglesia-Prieto, R., Muthiga, N., Bradbury, R., Dubi, A., & Hatziolos, M. E. (2007). Coral reefs under rapid climate change and ocean acidification. *Science, 318*, 1737–1742. https://doi.org/10.1126/science.115250.

Hueerkamp, C., Glynn, P. W., D'Croz, L., Maté, J. L., & Colley, S. B. (2001). Bleaching and recovery of five eastern Pacific corals in an el Niño-related temperature experiment. *Bulletin of Marine Science*, *69*, 215–236.

Hughes, T. P., Barnes, M. L., Bellwood, D. R., Cinner, J. E., Cumming, G. S., Jackson, J. B. C., Kleypas, J., van de Leemput, I. A., Lough, J. M., Morrison, T. H., Palumbi, S. R., van Nes, E. H., & Scheffer, M. (2017). Coral reefs in the Anthropocene. *Nature*, *546*, 82–90. https://doi.org/10.1038/nature22901.

Lamont, T. A. C., Williams, B., Chapuis, L., Prasetya, M. E., Seraphim, M. J., Harding, H. R., May, E. B., Janetski, N., Jompa, J., Smith, D. J., Radford, A. N., & Simpson, S. D. (2021). The sound of recovery: Coral reef restoration success is detectable in the soundscape. *Journal of Applied Ecology*, *59*(3), 742–756. https://doi.org/10.1111/1365-2664.14089.

Lange, I. D., Perry, C. T., & Álvarez-Filip, L. (2020). Carbonate budgets as indicators of functional reef "health": A critical review of data underpinning census-based methods and current knowledge gaps. *Ecological Indicators, 110*, 105857. https://doi.org/10.1016/j.ecolind.2019.105857.

Lange, I. D., & Perry, C. T. (2019). Bleaching impacts on carbonate production in the Chagos Archipelago: influence of functional coral groups on carbonate budget trajectories. *Coral Reefs, 38*(4), 619–624. https://doi.org/10.1007/s00338-019-01784-x.

López-Pérez, A., Cupul-Magaña, A., Ahumada-Sempoal, M. A., Medina-Rosas, P., Reyes-Bonilla, H., Herrero-Pérezrul, M. D., Reyes-Hernández, C., & Lara-Hernández, J. (2015). The coral communities of the Islas Marias archipelago, Mexico: structure and biogeographic relevance to the Eastern Pacific. *Marine Ecology*, *37*(3), 679–690. https://doi.org/10.1111/maec.12337

Manzello, D. P., Eakin, C. M., & Glynn, P. W. (2017). Effects of global warming and ocean acidification on carbonate budgets of Eastern Pacific coral reefs. In

P. Glynn, D. P. Manzello, & I. Enochs (Eds.), *Coral Reefs of the Eastern Tropical Pacific* (pp. 517–533). Springer.

Montero-Serra, I., Garrabou, J., Doak, D. F., Figuerola, L., Hereu, B., Ledoux, J. B., & Linares, C. (2018). Accounting for Life-history strategies and timescales in marine restoration. *Conservation Letters*,*11*(1), e12341. https://doi.org/10.1111/conl.12341.

Page, C. P., Muller, E. M., & Vaughan, D. E. (2018). Microfragmenting for the successful restoration of slow growing massive corals. *Ecological Engineering*, *123*, 86–94.

Pennington, J. T., Mahoney, K. L., Kuwahara, V. S., Kolber, D. D., Calienes, R., & Chavez, F. P. (2006). Primary production in the eastern tropical Pacific: a review. *Progress in Oceanography*, *69*, 285–317. https://doi.org/10.1016/j.pocean.2006.03.012

Perry, C. T., & Alvarez-Filip, L. (2018). Changing geo-ecological functions of coral reefs in the Anthropocene. *Functional Ecology, 33*(6), 976–988. https://doi.org/10.1111/1365-2435.13247, 1-13.

Perry, C. T., Edinger, E. N., Kench, P. S., Murphy, G. N., Smithers, S. G., Steneck, R. S., & Mumby, P. J. (2012). Estimating rates of biologically driven coral reef framework production and erosion: a new census-based carbonate budget methodology and applications to the reefs of Bonaire. *Coral Reefs*, *31*, 853–868. https://doi.org/10.1007/s00338-012-0901-4.

Perry, C. T., Lange, I. D., & Januchowski-Hartley, F. A. (2018). *ReefBudget Indo-Pacific: online resource and methodology*. University of Exeter. http://geography.exeter.ac.uk/reefbudget/.

Reyes-Bonilla, H., Carriquiry, J. D., Morales, G. E., & Cupul-Magaña, A. L. (2002). Effects of the 1997-99 El Niño and anti El Niño events on coral communities of the Pacific coast of México. *Coral Reefs*, *21*, 368–372. https://doi.org/10.1007/s00338-002-0255-4

Rinkevich, B. (2019a). Coral chimerism as an evolutionary rescue mechanism to mitigate global climate change impacts. *Global Change Biology*, *25*, 1198–1206.

Rinkevich, B. (2019b). The active reef restoration toolbox is a vehicle for coral resilience and adaptation in a changing world. *Journal of Marine Science and Engineering*, *7*, 201.

Rinkevich, B. (2020). Ecological engineering approaches in coral reef restoration. *ICES Journal of Marine Sci*ence, *78*(1), 410–420. https://doi.org/10.1093/icesjms/fsaa022

Rinkevich, B., & Loya, Y. (1983). Short-term fate photosynthetic products in a hermatypic coral. *Journal of Experimental Marine Biology and Ecology*, *73*, 175–184. https://doi.org/10.1016/0022-0981.

Romero-Torres, M., Acosta, A., Palacio-Castro, A. M., Treml, E. A, Zapata, F. A, Paz-García, D. A, & Porter, J. W. (2020). Coral reef resilience to thermal stress in the Eastern Tropical Pacific. *Global Change Biology*, *26*(7), 3880–3890. https://doi.org/10.1111/gcb.15126.

Selig, E. R., & Bruno, J. F. (2010). A global analysis of the effectiveness of marine protected areas in preventing coral loss. *Plos One, 5*(2), e9278.

Shaish, L., Levy, G., & Rinkevich, B. (2010). Employing a highly fragmented, weedy coral species in reef restoration. *Ecological Engineering*, *38*, 1424–1432. https://doi.org/10.1016/j. ecoleng.2010.06.022.

Sheppard, C. R. C., Davy, S. K., & Pilling, G. M. (2009). *The Biology of Coral Reefs*. Oxford University Press.

Suding, K., Higgs, E., Palmer, M., Callicott, J. B., Anderson, C. B., Baker, M., Gutruch, J. J., Hondula, K. L., LaFevor, M. C., Larson, B. M. H., Randall, A., Ruhl, J. B., & Schwartz, K. Z. S. (2015). Committing to ecological restoration. *Science*, *348*, 638–640. https://doi.org/10.1126/science.aaa4216.

Tortolero-Langarica, J. J. A., Rodríguez-Troncoso, A. P., Carricart-Ganivet, J. P., & Cupul-Magaña, A. L. (2017). Calcification and growth rate recovery of the reef-building *Pocillopora* species in the northeast tropical Pacific following an ENSO disturbance. *PeerJ*, *5*, e3191. https://doi.org/10.7717/peerj.3191.

Tortolero-Langarica, J. A. Rodríguez-Troncoso, A. P. Cupul-Magaña, A. L. Alarcón-Ortega, L. C., & Santiago-Valentín, J. D. (2019). Accelerated recovery of calcium carbonate production in coral reefs using low-tech ecological restoration. *Ecological Engineering*, *128*, 89–97. https://doi.org/10.1016/j.ecoleng.2019.01.002

Tortolero-Langarica, J. J. A., Rodríguez-Troncoso, A. P., Cupul-Magaña, A. L., Morales-de-Anda, D. E., Caselle, J. E., & Carricart-Ganivet, J. P. (2022). Coral calcification and carbonate production in the eastern tropical Pacific: the role of branching and massive corals in the reef maintenance. *Geobiology*, *20*, 533–545. https://doi.org/10.1111/gbi.12491

Tortolero-Langarica, J. J. A., Rodríguez-Troncoso, A. P., Cupul-Magaña, A. L., & Rinkevich, B. (2020). Micro-fragmentation as an effective and applied tool to restore remote reefs in the Eastern Tropical Pacific. *International Journal of Environmental Research and Public Health*, *17*(18), 6574. https://doi.org/10.3390/ijerph1718657.

Wang, C., & Fiedler, P. C. (2006). ENSO variability in the Eastern tropical Pacific: a review. *Progress in Oceanography*, *69*, 239–266. https://doi.org/10.1016/j.pocean.2006.03.004.