Rebuilding Coral Reefs: How tourism can be a driver behind solutions in a changing ocean

Tourism catalyzing solutions for coral reefs

Johanna Calle-Triviño[1], Daniela Rojas-Cano[2,3], Laura Angélica Niño-Torres[2,3], Norberto Colín-García[4], Roberto Hernández-Landa[4], Macarena Blanco-Pimentel[5], Jesús Ernesto Arias-González[6], Camilo Cortés-Useche[1], Rodolfo Rioja-Nieto[3]

[1] Wave of Change, Iberostar Hotels and Resorts, Quintana Roo, México

[2] Posgrado en Ciencias del Mar y Limnología, UNAM, Instituto de Ciencias del Mar y Limnología, Circuito Exterior s/n Ciudad Universitaria, 04510, México.

[3] Laboratorio de Análisis Espacial de Zonas Costeras (COSTALAB), Facultad de Ciencias, UMDI-Sisal.

[4] Escuela Nacional de Estudios Superiores, Unidad Mérida, Universidad Nacional Autónoma de México

[5] Wave of Change, Iberostar Hotels and Resorts, Bávaro, Dominican Republic

[6] Department of Marine Resources, Center for Research and Advanced Studies, National Polytechnic Institute of Mexico, Mérida, Mexico

Abstract

Coral reefs are threatened by multiple stressors that have driven a decline in the cover of reef-building coral species, resulting in a loss of reef structure and function. Restoration reef science provides useful conservation tools to preserve and restore the key species and ecological functions of these ecosystems. However, gaps remain in restoring ecosystem functions at large scales. This study provides a guide of how to invest and apply innovative solutions and immediate action strategies from the tourism-hotel sector in alliance with academia and key stakeholders, Throught development and implementation of a multi-species restoration program at two sites in the Mexican Caribbean: Manchoncitos Reef, Riviera Maya and La Francesita Reef, Cozumel. Where we have identified effective propagation and outplanting techniques for key critically endangered species, as well as genotypes resistant to temperature stress and Stony Coral Tissue Loss Disease (SCTLD). We include a comparative analysis over time (2020-2022) showing positive ecological processes and recovery of ecological functions reflected in increased coral cover, structural complexity and fish biomass. We have genetic stock available in two nurseries to develop education, research, technological innovation, recreation and tourism activities. Baseline assessment of the study areas will make it possible to adapt repopulation techniques not only for hard corals, but also to advance in the comprehensive restoration of the ecosystem to incorporate new elements to the reef, such as fish, crab or sea urchin postlarvae that accelerate herbivory functions and in turn improve the natural processes of the coral reefs, allowing for a return to equilibrium. The project will improve the understanding of the use of restoration as a tool for climate change adaptation especially in collaboration with the private sector.

Keywords: Assisted translocation Coral Reef Restoration, Ecological Functions, Mesoamerican Reef

INTRODUCTION

For decades, coral reefs have faced complex and additive interactions with risk drivers, which have generated important modifications in their structure and functions, such that they have undergone relatively rapid changes among ecological states of equilibrium [1]. Their conservation has created major challenges for communities, researchers, governments and those involved in coral reef work.

Caribbean reefs have experienced significant losses of key species such as Acroporids since the 1970s [2, 3, 4], and more recently, the loss of coral communities and populations due to bleaching [5, 6, 7], increased intensity of storm and hurricane frequency [8, 9], phase shifts [10, 11] and the prevalence of emerging diseases [12, 13, 14], such as the case of Stony Coral Tissue Loss Disease (SCTLD), first reported in Florida in 2014 [15].

In the Mexican Caribbean, SCTLD has been observed since 2018, and to date has caused the mortality of over 80% of the most susceptible coral populations, mainly of the Meandrinadae family and the Faviinae subfamily, affecting important reef-building species [16]. In the Puerto Morelos region, between 2020 and 2021, reefs were also exposed to extreme events, such as storms and hurricanes, causing physical and physiological damage to coral species (Tropical Storm Cristobal, June 2020; Hurricane Gamma Category 1, Hurricane Delta Category 2, and Hurricane Zeta Category 1, all three in October 2020; and Hurricane Grace Category 1, August 2021). Hurricanes Delta and Grace caused coral bleaching after their impact, possibly due to the low temperatures generated after these natural phenomena (unpublished data).

Considering that disturbances on Caribbean coral reefs will increase in the foreseeable future, it is necessary to improve conservation strategies at the local level (i.e. planning urban development, reducing sedimentation, water pollution, and overfishing, establishing no-take protected areas, etc.) and effectively implement active restoration actions in the coming decades [17, 18]. With these interventions, widespread coral reef degradation under increasingly adverse conditions might be mitigated. .

Currently, most coral reef restoration programs in the Caribbean focus on tissue production, generally using fast-growing species such as *Acropora palmata* and *Acropora cervicornis*. Few programs consider the sexual reproduction of other mass-growing type species, where in most cases the projects have a duration of one or two years with no baseline data available, gaps in knowledge of the identity of the genotypes of the corals being used, information on water quality and absent long-term monitoring [19, 20]. In most projects the metrics to determine the "effectiveness" of the programs do not generally contemplate ecological aspects such as the recovery of ecosystem functions [19, 21]. Also, there is a need to implement coral reef restoration projects that include science, policy, governance and investment to achieve scientific commitment to develop novel research to address the challenges of climate change, as well as beyond the reef interventions to promote environmental education and training of community leaders advocating solutions that facilitate best practices in local communities [18, 22, 23, 24, 25, 26, 27].

The tourism industry is adopting responsible tourism practices through regenerative leadership, although gaps remain between sustainability initiatives and comprehensive coral reef conservation and restoration. Iberostar Group is strategically scaling up these efforts, using solid scientific investment, by hiring researchers within its staff and establishing alliances with academia in each of the destinations where they operate [20, 24, 25; 28; 29]. Here we present the results of ecological assessments of the coral reef restoration program in Mexico, from 2020 to date, showing increases in percentage of coral cover and slight increases in the Reef Functional Index (RFI). We also show an outline of the program, integrating academia, local communities and government authorities. In the program we include activities to catalyze coral biodiversity for resilience, including the selection of appropriate reefs for restoration, the selection of coral species to maximize functional diversity, the use of heat stress resistant coral material, monitoring water quality and the assessment of ecological changes over time as a result of coral reef restoration strategy.

RESULTS

The results obtained from the monitoring analysis using the AGRRA methodology (Figure 1), at the outplanting sites of both reefs over time, showed an increasing trend in the scleractinian coral cover, along with a decrease in macroalgae and abiotic substrate. In Francesita reef, for 2020, macroalgae cover (53 ± 10.01%) was predominant, followed by other invertebrates (19 ± 11.40%), corals (11.33 ± 3.44%) and abiotic substrate (8.83 ± 10.06%). In 2021, there was a decrease in macroalgae cover (45.33 ± 7.71%) and an increase in coral (14.33 ± 2.58%) and abiotic substrate cover (10 ± 12.11%). Finally, in 2022 there was a substantial increase in coral cover (33.66 ± 20.02%), which contrasts with the decrease in the percentage of macroalgae cover (24.33 ± 14.73%). In the case of Manchoncitos, in 2020 abiotic substrate cover predominated (46.33 ± 0.19%), followed by macroalgae (21.50 ± 13.27%), other invertebrates (12.16 ± 5.45), and coral cover (15.83 ± 4.57%), with minor contributions of CCA (3.66 ± 3.07%) and cyanobacteria (0.5 ± 1.22%). In 2021, there was an increase in coral cover (31.16 ± 7.16%) and a considerable decrease in abiotic substrate (17.33 ± 10.07%). In 2022, the percentage coral cover (30.16 ± 14.49%) and the other benthic categories remained the same as the previous year, except for cyanobacteria with no observations in 2022.

Figure 1. Changes in benthic community structure at Francesita reef and Manchoncitos reef over time.

Based on the results obtained from the analysis of photomosaics, turf algae was the most abundant benthic component in Manchoncitos reef in both 2020 and 2021. Invertebrates and fleshy macroalgae were the next most abundant benthic organisms. The live coral cover was less than 10% in both years (Figure 2). The coral composition was dominated by some of the main Caribbean reef building species, including *Orbicella annularis*, *O. faveolata* and *M. cavernosa* —totaling 65.0% in 2020 and 70.9% in 2021; this reef was affected by SCTLD (*O. faveolata* in 2020 and 2021; and *Siderastrea siderea* in 2021).

Figure 2. Benthic reef cover (%) for Manchoncitos reef (Mexico) for 2020 (black bars) and 2021 (white bars). Benthic category codes are LC: live coral, FMA: fleshy macroalgae, TA: turf algae, CMA: calcareous macroalgae, CCA: crustose coralline algae, AINV: aggressive invertebrate, OINV: other invertebrate, CYAN:

cyanobacteria, ABIO: abiotic substrate, UNK: unknown/unidentifiable substrates, N/A: no data for that point intercept.

The main benthic components of Francesita reef were turf algae, aggressive invertebrates and fleshy macroalgae. Benthic cover (%) was similar between years (2020 and 2021), as can be observed in Figure 3. Live coral cover was 7.8% in 2020 and 9.2% in 2021. Brooders are the primary coral species in Francesita reef (>90% in 2020 and >85% in 2021), with *A. agaricites* being the most abundant, followed by *Porites porites* and *P. furcata*. Caribbean reef building species (e.g., *Orbicella* genus) cover less than 5% of all coral cover in both 2020 and 2021. Although more species were identified in 2021, the coral species covered by the most abundant species was similar between years, with the highest change occurring with *P. furcata*, which shifted from 2.9% in 2020 to 15.1% in 2021. The species affected by SCTLD in Francesita were *A. agaricites* in 2020 and *Siderastrea siderea* in 2021.

Figure 3. Benthic reef cover (%) for Francesita reef (Mexico) for 2020 (black bars) and 2021 (white bars). Benthic category codes are LC: live coral, FMA: fleshy macroalgae, TA: turf algae, CMA: calcareous macroalgae, CCA: crustose coralline algae, AINV: aggressive invertebrate, OINV: other invertebrate, CYAN: cyanobacteria, ABIO: abiotic substrate, UNK: unknown/unidentifiable substrates, N/A: no data for that point intercept.

At Manchoncitos Reef 35 coral species and 54 fish species were registered, while at Francesita reef 26 coral species and 69 fish species were observed

(Supplementary Table 3). At both reefs, the Haemulidae family presented the highest abundance.

Kruskal-Wallis tests showed significant differences ($p<0.05$) in coral cover and total fish biomass. Significant differences between years were also observed for the RFI (Figure 4 a and d), with an increase of ~0.10 at Manchoncitos Reef (x^2= 13.556, df= 2, p-value= 0.00113) and an increase of ~0.09 at Francesita reef from 2020 to 2022 (x^2=11.275, df= 2, p-value= 0.0035). Post-hoc pairwise comparisons between years revealed significant differences in RFI at Francesita reef between 2020/2022 (Bonferroni test, p-value=0.0065), and between every year monitored (Bonferroni test, p-value=0.045, 0.0065 and 0.013) at Manchoncitos reef.

and increased reef function between 2020-2022 in the study areas, which seem to be related to the ecological benefits of transplantation at both reefs.

Figure 4. Ecological benefits due to outplanting. Considering date as a descriptive variable. Reef Functional Index (RFI) (a and d); Coral cover (b and e); Total fish biomass (c and f).

Live coral cover was significantly different over time at the two reefs. Manchoncitos reef showed an increase of ~15% (x=8.1238, df= 2, p-value= 0.01722) in hard coral cover over time, between 2020 and 2021 (Bonferroni test, p-value=0.038), while at Francesita reef there was a ~22% increase in hard coral cover (x^2= 8.0819, df= 2, value p= 0.01758) (Figure 4 b and e) presenting a significant gain in 2022, compared to 2020 and 2021 (Bonferroni test, p-value=0.013, 0.031).

No significant differences were observed between years for the total fish biomass at Manchoncitos reef (x^2= 2.24, df= 2, p-value= 0.3263), unlike Francesita where there were significant differences (x^2= 9.62, df= 2, p-value= 0.008148) (Figure 4 c and f) between 2021/2022 and 2020/2022 (Bonferroni test, p-value=0,024).

Results of the genetic analysis showed that the main Cozumel nursery contained seven genotypes in the 24 ramets of the study (Figure 5).

Figure 5. Clustering dendrogram of *Acropora palmata* ramets in the Cozumel nursery.

Temperature and light at both reefs during 2020-2022 presented similar data, as did mean dissolved oxygen (DO), pH, salinity, nitrites, nitrates, phosphates and enterococci (Supplementary Table 2). However, in 2020, after Tropical Storm Cristobal and Hurricanes Gamma, Delta and Zeta, in the second half of the year there was a strong decrease in sea temperature, which was more evident at Manchoncitos reef (Figure 6a). This caused a strong mass bleaching event, mainly affecting *Orbicella faveolata* colonies (Figure 6b-c).

Figure 6. Temperature (ºC) and luminosity (Lux) trend at Manchoncitos Reef in 2020. **a)** Temperature and luminosity decreases in October during hurricanes Gamma, Delta and Zeta **b)** *Orbicella faveolata* colonies before Hurricane Delta **c)** bleached *O. faveolata* colonies after Hurricane Delta.

DISCUSSION

This study demonstrates how active restoration actions positively influence 1) the recovery of ecological functions, reflected in an increase in coral cover, structural complexity and fish biomass, and 2) the maintenance of a good representation of the adaptive alleles of the selected species in the coral nurseries, incorporating improvements in local conditions to rebuild these ecosystems.

In the case of Mexico, collaborative work with different stakeholders has allowed the incorporation of innovative techniques for its restoration program, such as molecular biology, analysis of spectral signatures, among others. Molecular biology has been one of the most useful tools for understanding coral reefs, generating information that helps to improve coral adaptation to climate change [36]. The genetic diversity of coral reef species varies considerably between species and even between individuals of the same species. This information can be used to detect more suitable genetic variants that may be applied in restoration programs [37, 38]. For this reason, the current research has been carried out in collaboration with research centers and universities in Mexico to identify the organisms genetically more adapted to environmental stressors and use them for reef restoration.

Challenges remain in achieving results towards comprehensive ecological restoration. Hence the importance of continuing to consolidate multidisciplinary collaborations and catalyze solutions for future reef restoration, incorporating research, passive and active restoration actions, local support and long-term monitoring (Figure 7). If humanity were to succeed in reducing greenhouse gas emissions, it is still necessary to continue investing and working on these types of strategies and solutions that can be a possible model to replicate and implement in different locations where coral reef restoration is needed [39,40,41].

Figure 7. Outline for rebuilding coral reefs through the organizational capacity of the private sector to invest in research, active restoration, improve local considerations and long-term engagement.

Based on the results obtained, both reefs are degraded, Francesita reef has low coral cover (%) and species richness, and Manchoncitos reef has high algal cover (turf and fleshy) and cyanobacteria. Despite the degraded conditions, a remarkable result is the increase in coral cover from 2020 to 2022 at both reefs. This increase is mainly due to the decrease in macroalgae cover at Francesita reef and the low cover of abiotic substrate at Manchoncitos reef, at least in the areas of active intervention. Furthermore, despite the impact of four hurricanes in these areas in 2020, coral cover increased or was maintained, and could be considered a positive indicator of active restoration efforts.

Both photomosaics and AGRRA analyses for Francesita indicated that there was an increase in coral cover in 2021. However, for Manchoncitos the photomosaic analysis indicated a decrease in coral cover, while AGRRA analysis showed an increase. These contradictory results suggest that the difference is directly related to the sampling method used. It seems that there is an overestimation of the data when using traditional methods, in this case AGRRA as reported by Barrera-Falcon et al. 2021 [42].

In the case of Francesita, as a reef with a smaller area (0.0048 km^2) and taking into account the ideal sampling area using photogrammetric techniques (0.00038

km^2) proposed by Hernández-Landa et al. 2020 [43], the restoration efforts carried out in the intervened area (0.001 km^2) are probably sufficient to represent changes for the entire reef. However, at Manchoncitos (0.15 km^2), with an intervened area of 0.0015 km^2, active restoration efforts should be increased to cover a larger area in order to see results for the rest of the reef. It is possible that these changes will be reflected in the long term in ecological succession processes, where demographic monitoring of populations is evaluated to determine changes in population growth rates (λ) or sexual recruitment rates [44].

The results suggest that the approach and actions proposed here may accelerate the ecological succession processes needed to scale up restoration [27, 45, 46, 47, 48].

To date, these results also show the ecological benefits of outplanted colonies, mainly manifested in an increase in coral cover and greater structural complexity reflected in the RFI, a fact also reported by Calle-Triviño et al. (2021), in an area of the Arrecifes del Sureste Marine Sanctuary in Dominican Republic.

Periodic active restoration actions can influence the decrease in the cover of opportunistic species [49], as well as in the processes of herbivory and corallivory. Furthermore, including massive corals is also favorable because they have shown higher outplanted survival, influencing the repair and maintenance of ecological services and functions [50]. Therefore, human assistance is necessary in restoration programs to safeguard coral reefs [51].

The ecology and structural functionality of Caribbean coral reefs have undergone severe ecological changes due to the abrupt mortality of massive and large corals as a consequence of bleaching events and the presence of SCTLD. Álvarez-Filip *et al.,* (2022) [16] described a 30% reduction in the ability of coral communities in the Mexican Caribbean region to produce calcium carbonate. If this scenario of coral cover loss continues and additionally in the absence of natural recovery process, the structural complexity will be modulated only by destructive forces, representing a high risk for coastal protection. Because of this, hard coral cover needs to be increased as a step towards increasing reef resilience. Not only with active calcification processes by building corals [52], but also forming a protective surface layer on reef framework [53], using different restoration techniques.

Obtaining the greatest possible quantity and quality of data from the area will allow us to adapt outplanting techniques, incorporate new elements to the system, such as the introduction of fish postlarvae [25], crabs or urchins that could accelerate herbivory functions and in turn improve the natural processes of the coral reefs, allowing an increasing return to equilibrium. It will be fundamental to continue building relationships between government, academia, tourism and local communities to increase restoration efforts and expand watershed-based approaches to make rehabilitation and restoration processes more efficient, as well as to promote nature-based solutions.

MATERIALS AND METHODS

The study was conducted at Manchoncitos reef in Riviera Maya (20º45'34 "N 86º57'00 "W) and Francesita reef in Cozumel (20º21'47" N 87º01'36 "W), which are part of the Mesoamerican Reef System (MAR), the second largest barrier reef in the world (Figure 8). Although there are well-studied reefs for these two areas in the Mexican Caribbean, there is an absence of historical data in both peer reviewed and non-peer reviewed literature for these two reefs. Therefore, to our knowledge the data provided in this manuscript constitute the first scientific report of baseline records for these two reefs.

Figure 8. Location of Manchoncitos reef and Francesita reefs in the Mexican caribbean.

Manchoncitos is an area with reef patches between five and 13 m deep. It has an approximate length of 500 m and an area of 0.15 km^2. It presents elevated bottom formations between one and seven m high, mainly due to the presence of colonies of *Orbicella* spp. that reach between six and seven m in diameter and which dominate in this reef zone along with colonies of *Montastraea cavernosa*. There are still colonies of *Diploria labyrinthiformis*, *Colpophyllia* spp. and *Pseudodiploria* spp. that survived SCTLD and other conditions that have occurred in these two years of study. There are a few isolated colonies of *Acropora cervicornis* and *A. palmata*, where the eroded skeletons of the latter remain. Most of the year mobile invertebrates of commercial and ecological importance are present, such as lobsters (*Panulirus argus*) and sea cucumbers (*Holothuria* ssp.) and vertebrates such as green turtles (*Chelonia mydas*). In 2022 two juvenile specimens of top predators (sharks *Ginglymostoma cirratum* and *Carcharias taurus*) were recorded.

Francesita is a smaller fringe reef formation located in the west side of Cozumel island. This reefs is approximately 200 m long with an estimated area of 0.0048 km^2 and located between seven and 10 m deep. This reef is influenced by strong currents most of the year, as is the case for the rest of the reefs belonging to the Cozumel Reefs National Park. The reef is surrounded by sand, followed by an extensive area of approximately 0.06 km^2 of seagrass (*Thalassia testudinum* and *Syringodium filiforme*). It is common to observe hosting rays (*Hypanus americanus*, *Urobatis jamaicensis*), queen conch (*Lobatus gigas*) and cucumbers (*Holothuria* spp.). The reef is dominated by opportunistic coral species such as *Porites* spp. and *Agaricia* spp. and most of the coral skeletons that died recently due to SCTLD (*M. cavernosa*, *D. labyrinthiformis*, *Pseudodiploria* spp., *O. annularis*, *O. faveolata*, *O. franksi* and *Eusmilia fastigiata*). In addition, it has been colonized by excavating sponges and macroalgae. During the study, one *G. cirratum* and three large adult >40 cm *Sphyraena barracuda* specimens were recorded. This site is a popular snorkeling spot, where c.a. 600 people visit per day (unpublished data).

In the middle of 2020, two coral nurseries were installed on each reef. Each one of them has 20 structures of three different types with a capacity of 25 to 30 fragments each (Supplementary Figure 1).

Two outplantings were performed in May and July 2021 on each of the reefs, and a third one in August 2021, just after Hurricane Grace (this was done with opportunity coral fragments), and two more in May and July 2022. (Supplementary Table 1).

All criteria and steps used in the design and implementation of the program are described in detail in the Planning and design guide for coral reef restoration programs [30].

The ecological assessment was carried out through annual monitoring of both reefs at the outplanted sites between 2020 and 2022. Based on the Atlantic and Gulf Reef Rapid Reef Assessment, protocol (AGRRA) Version 5.4 [31], six permanent transects of 10 m were randomly located at the outplanted sites to carry out the assessments. For the benthos survey, the point intercept methodology was used with measurements collected every 10 cm along each of the transects, recording the category corresponding to the substrate observed just below each point. The benthic community was grouped into six categories: Coral (scleractinian coral), CCA (crustose coralline algae), cyanobacteria, other invertebrates, macroalgae and abiotic substrate.

To measure the fish abundance at each of the outplanted sites, six transects were performed (30 m long × 2 m wide) in the same habitat as the permanent transects. The number of individuals corresponding to the reef fish species of commercial and ecological importance covered by the AGRRA protocol was recorded, as well as their sizes in the class size ranges proposed in the protocol. This was complemented by a survey of coral and fish species richness at each of the reefs.

In addition, data for photomosaic analysis were collected from both reefs at the same time for 2020 and 2021. Data for 2022 are still under analysis, with the aim of having data that included a bigger area and obtaining a larger scale ecological assessment to understand if ongoing restoration actions were having an impact on the entire reef or only in the area where outplanted sites were initiated and where the permanent transects for the AGRRA are located. Photos were taken with two parallel GOPRO Hero 8 cameras separated by approximately 1m. Images were taken at a 0.5 second interval, making several tracks in a determined area of approximately 250 m^2 [32]. For each reef survey, photos were imported into Agisoft Metashape (Professional Edition, version 1.7) and organized into the same layout. Each section was processed separately using a standardized processing pipeline. This entailed first aligning the photos, then manually inspecting and correcting alignment errors and finally optimizing the camera distortion modeling to achieve a scene model with the greatest degree of accuracy possible. Once the photomosaics and points had been uploaded into QGIS, AGRRA codes were used to identify and categorize all points distributed across the photomosaics into living and non-living benthic categories. All corals were identified to the lowest level possible (species and genus). If the genus or species could not be determined, corals were identified as unidentifiable live coral (LC). Coral health status was noted when there was visual evidence of disease, bleaching, paleness, or predation at the colony level. Sponges and gorgonians were characterized into one of two categories, upright and encrusting. Other benthic organism groupings included: encrusting ascidians, anemones, zoanthids, annelids, and corallimorphs. Abiotic factors were divided into the descriptive codes: sand, rock, rubble, mud, and hole. All unidentifiable points, due to image quality (blurriness/distortion/artifacts) or the presence of something blocking clear sight to the benthic floor (ie. a fish, sea fan, scale bars, etc), were marked as unknown (UNK). For instances in which points fell within holes in the photomosaic itself (white space due to no image overlay), the points were marked as having no data (No_Data or N/A). Point count data files were exported from QGIS and compiled in RStudio (version 4.0.5) before summary statistics were acquired using Excel.

To determine the positive effects due to active restoration and outplanting efforts, ecological indicators were estimated. Three main variables considered as coral indicators were calculated: 1) coral cover, obtained directly from the benthos percentage cover data, 2) Reef Functional Index (RFI), calculated considering the values and equation presented by González-Barrios & Álvarez-Filip (2018) [33], which quantifies the structural complexity of the coral based on parametric models of coral growth and complexity of morphology, and 3) total fish biomass, obtained using the abundance and size class data,considering the length-weight relationship equation $W = aLb$ described by Bonsack & Harper (1988) [34]. Constants (a and b) for length-weight relationships for each species were obtained from Froese & Pauly (2019) [35]; a logarithmic transformation was performed to improve the visualization of the data.

Kruskal-Wallis tests were performed to compare the values of the three indicators between years for each reef, followed by Bonferrioni's post-hoc tests for pairwise comparisons. All analyses were performed at significance of $\alpha = 0.05$ and carried out with the statistical program R, using customized scripts.

For genetic characterization, 1 cm^2 tissue samples were collected from 24 colonies of *A. palmata* and three colonies of *A. cervicornis* from Cozumel to be genotyped. Samples were placed in vials with 95% ethanol, stored, and were sent to Eurofins BioDiagnosis laboratory (WI, USA) for DNA extraction and Single Nucleotide Polymorphisms (SNPs) analysis. Galaxy framework web-based software was used for statistical analysis.

To obtain temperature and light measurements, four HOBO Pendant data loggers were deployed, three in Manchoncitos and one in Francesita. Two were programmed every five minutes and two every two hours to measure in situ light and temperature variations. In October 2021 and 2022 water quality data were collected for the two reefs (Supplementary Table 2).

As an approach to integrate assisted translocation into the restoration program, 13 of the 24 colonies of *A. palmata,* which had been maintained and adapted >1ºC during 23 months in Francesita's nursery, were translocated to the Manchoncitos outplanting site.

Finally, in order to have a comprehensive restoration program, as part of the efforts led by the Government of the State of Quintana Roo in compliance with the SEMA-Zone 4 project under the parametric insurance, and with the collaboration of INAPESCA and UNAM (Spanish acronyms), 43 individuals of Caribbean King Crab (*Maguimithrax spinosissimus*) were released at the same transplant site in Manchoncitos.

Acknowledgments

We would like to thank the Iberostar Group, Dressel Divers for aquatic and logistical support, Centro de Investigación y de Estudios Avanzados del Instituto Politécnico Nacional (National Polytechnical Institute Research and Advanced Studies Center, CINVESTAV), students from the National Autonomous University of Mexico (UNAM-ENES, Merida), The National Commission of Natural Protected Areas (CONANP), Mexican Caribbean Biosphere Reserve (MCRB) and Cozumel Reefs National Park (CRNP), Perry Institute for photomosaic analysis, Iliana Baums and Sheila Kitchen for SNPs analysis. Handling of species and development of research activities were possible thanks to the Iberostar-Cinvestav alliance.

References

1. Nyström M, Folke C, Moberg F. Coral reef disturbance and resilience in a human-dominated environment. Trends Ecol Evol. 2000;15(10):413-417. doi: 10.1016/s0169-5347(00)01948-0. PMID: 10998519.

2. Davis GE. A century of natural change in coral distribution at the Dry Tortugas: A comparison of reef maps from 1881 and 1976. Bull Mar Sci. 1982; (32): 608-623.

3. Miller mw, Bourque AS, Bohnsack JA. An analysis of the loss of acroporid corals at Looe Key, Florida, USA: 1983-2000. Coral Reefs. 2002; (21): 179-182. doi: 10.1007/s00338-002-0228-7.

4. Aronson R, Bruckner A, Moore J, Precht B, Weil E. *Acropora cervicornis*. The IUCN Red List of threatened species. 2008. e.T133381A3716457. doi: 10.2305/IUCN.UK.2008.RLTS.T133381A3716457.en.

5. Eakin CM, Morgan JA, Heron SF, Smith TB, Liu G, Alvarez-Filip L, et al. Caribbean corals in crisis: record thermal stress, bleaching, and mortality in 2005. PLoS One. 2010; 5(11):e13969. doi: 10.1371/journal.pone.0013969. PMID: 21125021.

6. Levas S, Schoepf V, Warner ME, Aschaffenburg M, Baumann J, Grottoli AG. Long-term recovery of Caribbean corals from bleaching. J Exp Mar Biol Ecol. 2018; 506:124–134. doi: 10.1016/j.jembe.2018.06.003.

7. Bellwood DR, Pratchett MS, Morrison H, Gurney GG, Hughes TP, Álvarez-Romero JG, et al. Coral reef conservation in the Anthropocene: confronting spatial mismatches and prioritizing functions. Biol Conserv. 2019; 236 604-615. doi: 10.1016/j.biocon.2019.05.056.

8. Przeslawski R, Ahyong S, Byrne M, Wörheide G, Hutchings P. Beyond corals and fish: the effects of climate change on noncoral benthic invertebrates of tropical reefs. Glob Chang Biol. 2008; (14): 2773–2795. doi: 10.1111/j.1365-2486.2008.01693.x.

9. Jokiel PL, Jury CP, Kuffner IB. 2016. Coral calcification and ocean acidification. In: Hubbard DKCS, Rogers JH, Lipps GD, Stanley Jr, editors. Coral reefs at the crossroads. Coral reefs of the world. Netherlands: Springer; 2016. p. 7–45.

10. Aronson RB, Macintyre IG, Precht EF, Murdoch TJT, Wapnick CM. The expanding scale of species turnover events on coral reefs in Belize. Ecological Monographs. 2002; 72(2): 233-249.

11. Arias-González JE, Fung T, Seymour RM, Garza-Pérez JR, Acosta-González G, Bozec YM, et al. A coral-algal phase shift in Mesoamerica not driven by changes in herbivorous fish abundance. PLoS One. 2017;12(4):e0174855. doi: 10.1371/journal.pone.0174855. PMID: 28445546

12. Antonius A & Ballesteros E. Epizoism: a new threat to coral health in Caribbean reefs. Rev Biol Trop. 1998; 46: 5. doi: 10.15517/rbt.v46i5.29375.

13. Harvell CD, Kim K, Burkholder JM, Colwell RR, Epstein PR, Grimes DJ, et al. Emerging marine diseases--climate links and anthropogenic factors. Science. 1999;285(5433):1505-10. doi: 10.1126/science.285.5433.1505. PMID: 10498537.

14. Hughes TP, Anderson KD, Connolly SR, Heron SF, Kerry JT, Lough JM, et al. Spatial and temporal patterns of mass bleaching of corals in the Anthropocene. Science. 2018; 359(6371):80-83. doi: 10.1126/science.aan8048. PMID: 29302011.

15. Precht WF, Gintert BE, Robbart ML, Fura R, Van Woesik R. Unprecedented disease-related coral mortality in Southeastern Florida. Scientific Reports. 2016; 6(1), 1-11. doi: 10.1038/srep31374

16. Álvarez-Filip L, González-Barrios FJ, Pérez-Cervantes E, Molina-Hernández A, Estrada Saldívar N. Stony coral tissue loss disease decimated Caribbean coral populations and reshaped reef functionality. Communications Biology. 2022; 5(1):440. doi: 10.1038/s42003-022-03398-6. PMID:35681037.

17. Kennedy EV, Perry CT, Halloran PR, Iglesias-Prieto R, Schönberg CH, Wisshak M, et al. Avoiding coral reef functional collapse requires local and global action. Curr Biol. 2013; 23(10):912-8. doi: 10.1016/j.cub.2013.04.020. PMID: 23664976.

18. Setter RO, Franklin EC, Mora C. Co-occurring anthropogenic stressors reduce the timeframe of environmental viability for the world's coral reefs. PLoS Biol. 2022; 20(10):e3001821. doi: 10.1371/journal.pbio.3001821. PMID: 36219619.

19. Boström-Einarsson L, Babcock RC, Bayraktarov E, Ceccarelli D, Cook N, Ferse SCA, et al. Coral restoration - A systematic review of current methods, successes, failures and future directions. PLoS One. 2020;15(1): e0226631. doi: 10.1371/journal.pone.0226631. PMID: 31999709; PMCID: PMC6992220.

20. Bayraktarov E, Banaszak AT, Montoya-Maya P, Kleypas J, Arias-González JE, Blanco M, et al. Coral reef restoration efforts in Latin American countries and territories. PLoS One. 2020 Aug 5;15(8):e0228477. doi: 10.1371/journal.pone.0228477. PMID: 32756569.

21. Calle-Triviño J, Muñiz-Castillo AI, Cortés-Useche C, Morikawa M, Sellares-Blasco R, Arias-González JE. Approach to the Functional Importance of Acropora cervicornis in Outplanting Sites in the Dominican Republic. Front Mar Sci. 2021; 8:668325. doi: 10.3389/fmars.2021.668325.

22. Calle-Triviño J, Cortés-Useche C, Sellares-Blasco RI, Arias-González JE. Assisted fertilization of threatened Staghorn Coral to complement the restoration of nurseries in Southeastern Dominican Republic. Reg Stud Mar Sci. 2018; 18, 129–134. doi: 10.1016/j.rsma.2018.02.002.

23. Calle-Triviño J, Rivera-Madrid R, León-Pech MG, Cortés-Useche C, Sellares-Blasco RI, Aguilar-Espinosa M, et al. Assessing and genotyping threatened staghorn coral *Acropora cervicornis* nurseries during restoration in southeast Dominican Republic. PeerJ. 2020;8: e8863. doi: 10.7717/peerj.8863. PMID: 32337099.

24. Cortés-Useche C, Hernández-Delgado EA, Calle-Triviño J, Sellares Blasco R, Galván V, Arias-González JE. Conservation actions and ecological context: optimizing coral reef local management in the Dominican Republic. PeerJ. 2021a; 9:e10925. doi: 10.7717/peerj.10925. PMID: 33854832.

25. Cortés-Useche C., Reyes-Gamboa W, Cabrera-Pérez JL, Calle-Triviño J, Cerón-Flores A, Raigoza-Figueras R, et al. Capture, Culture and Release of Postlarvae Fishes: Proof-of-Concept as a Tool Approach to Support Reef Management. Front Mar Sci. 2021b; 8:718526. doi: 10.3389/fmars.2021.718526.

26. Kleypas J, Allemand D, Anthony K, Baker AC, Beck MW, Hale LZ, et al. Designing a blueprint for coral reef survival. Biol Conserv. 2021; 257, 109107. doi: 10.1016/j.biocon.2021.109107.

27. Quigley KM, Hein M, Suggett DJ. Translating the 10 golden rules of reforestation for coral reef restoration. Conserv Biol. 2022; 36(4):e13890. doi: 10.1111/cobi.13890. PMID: 35075743.

28. Schmidt-Roach S, Duarte C, Hauser CA, Aranda M. Beyond reef restoration: next-generation techniques for coral gardening, landscaping, and outreach. Front Mar Sci. 2020; 7:672. doi: 10.3389/fmars.2020.00672.

29. Blanco M, Evensen NR, Cortés-Useche C, Calle-Triviño J, Barshis DJ, Galvan V, et al. All-inclusive coral reef restoration: How the tourism sector can boost restoration efforts in the caribbean. Front Mar Sci. 2022 (9):931302. doi: 10.3389/fmars.2022.931302.

30. Calle-Triviño J, Niño-Torres LA, D. Rojas-Cano, K. Flores-Quintal, A. Ruiz-Flores, E. Cortés-Martínez, M. Soto-Alonso & C. Cortés-Useche. Manual planificación y diseño de programas de restauración de arrecifes coralinos. Wave of Change. 2022.

31. Lang JC, Marks W, Kramer, P, Richards-Kramer PA, Ginsburg, RN. AGRRA Protocols Version 5.4. 2010 [Cited 2023 May 15]. Available from: http://www.agrra.org/method/AGRRA-V5.4_2010.pdf.

32. Neufeld AM, Fundakowski G. Coral Restoration Foundation Photomosaic Manual. Florida: Coral Restoration Foundation; 2019, 30 p.

33. González-Barrios, FJ, Álvarez-Filip L. A framework for measuring coral species-specific contribution to reef functioning in the Caribbean. Ecol Indic. 2018; 95, 877–886. doi: 10.1016/j.ecolind.2018 .08.038

34. Bonsack JA, Harper DE. Length-Weight Relationships of Selected Marine Reef Fishes from the Southeastern United States and the Caribbean. 1988; NOAA. NOAA Tech Memo NMFS-SEFC: 215.

35. Froese R, Pauly D. FishBase. 2019 [Cited 2023 May 15]. Available from: http://www.fishbase.org

36. Knowlton N. Molecular genetic analyses of species boundaries in the sea. Hydrobiologia. 2000; 420:73–90. doi: 10.1023/A:1003933603879.

37. Vollmer SV, Palumbi SR. Hybridization and the evolution of reef coral diversity. Science. 2002; 296(5575):2023-5. doi: 10.1126/science.1069524. PMID: 12065836.

38. Wright R, Correa AMS, Quigley LA, Santiago-Vázquez LZ, Shamberger KEF, Davies SW. Gene Expression of Endangered Coral (Orbicella spp.) in Flower Garden Banks National Marine Sanctuary After Hurricane Harvey. Front Mar Sci. 2019; 6-672. doi: 10.3389/fmars.2019.00672.

39. Duarte CM, Agusti S, Barbier E, Britten GL, Castilla JC, Gattuso JP, et al. Rebuilding marine life. *Nature.* 2020; 580, 39–51.

40. Schmidt-Roach S, Duarte C, Hauser CA, Aranda M. Beyond reef restoration: next-generation techniques for coral gardening, landscaping, and outreach. Front. Mar. Sci. 2020; 7. doi: 10.3389/fmars.2020.00672

41. Bowden-Kerby A. Coral-Focused Climate Change Adaptation and Restoration Based on Accelerating Natural Processes: Launching the "Reefs of Hope" Paradigm. Oceans. 2023; 4(1), 13-26; https://doi.org/10.3390/oceans4010002

42. Barrera-Falcon E, Rioja-Nieto R, Hernández-Landa RC, Torres-Irineo E. Comparison of Standard Caribbean Coral Reef Monitoring Protocols and Underwater Digital Photogrammetry to Characterize Hard Coral Species Composition, Abundance and Cover. Front Mar Sci. 2021. doi: 10.3389/fmars.2021.722569.

43. Hernández-Landa RC, Barrera-Falcon E, Rioja-Nieto R. Size-frequency distribution of coral assemblages in insular shallow reefs of the Mexican Caribbean using underwater photogrammetry. PeerJ. 2020;8: e8957. doi: 10.7717/peerj.8957. PMID: 32337105.

44. Baums IB, Baker AC, Davies SW, Grottoli AG, Kenkel DC, Kitchen SA, et al. Considerations for maximizing the adaptive potential of restored coral populations in the western Atlantic. Ecol Appl. 2019; 29(8): e01978. doi: 10.1002/eap.1978. PMID:31332879.

45. Shaver EC, Courtney CA, West JM, Maynar J, Hein M, Wagner C, et al. A Manager's Guide to Coral Reef Restoration Planning and Design. NOAA Coral Reef Conservation Program. NOAA Technical Memorandum CRCP 36. 2020; 128 p. doi: 10.25923/vht9-tv39.

46. Shaver E, McLeod E, Hein MY, Palumbi SR, Quigley K, Vardi T, et al. A roadmap to integrating resilience into the practice of coral reef restoration. Glob Chang Biol. 2022; (16):4751-4764. doi: 10.1111/gcb.16212. PMID: 35451154.

47. Bhattacharya D, Stephens TG, Tinoco HAI, Richmond RH, Cleves PA. Life on the edge: Hawaiian model for coral evolution. Limnol Oceanogr. 2022; 67 (9). doi:10.1002/lno.12181.

48. Suggett DJ, van Oppen MJH. Horizon scan of rapidly advancing coral restoration approaches for 21st century reef management. Emerg Top Life Sci. 2022; 6(1):125-136. doi: 10.1042/ETLS20210240. PMID: 35119476.

49. Yap HT. Coral reef ecosystems. In: Orcutt j, editors. Earth System Monitoring. NY: Springer. 2013. doi: 10.1007/978-1-4614-5684-1_5.

50. Page CA, Vaughan DE. The cultivation of massive corals using “micro-fragmentation” for the “reskinning” of degraded coral reefs. Conference: Benthic Ecology Meeting; 2014 [Cited 2022 October 30]; University of North Florida, Jacksonville Florida. Available from: https://www.researchgate.net/publication/287204400_The_cultivation_of_massive_corals_using_micro-fragmentation_for_the_reskinning_of_degraded_coral_reefs.

51. Wagner M. Coral Reef Restoration Methods in the Caribbean and Florida Keys. OUR Journal: ODU Undergraduate Research Journal. 2022; 9:11. doi: 10.25778/g9x4-5w95.

52. Perry CT, Steneck RS, Murphy GN, Kench PS, Edinger EN, Smithers SG. Regional-scale dominance of non-framework building corals on Caribbean reefs affects carbonate production and future reef growth. Glob Chang Biol. 2015; 21 (3): 1153–1164. doi: 10.1111/gcb.12792.

53. Kuffner IB, Toth LT, Hudson JH, Goodwin WB, Stathakopoulos A, Bartlett L, et al. Improving estimates of coral reef construction and erosion within situ measurements. Limnology and Oceanography. 2019; 64(5), 2283–2294. doi: 10.1002/lno.11184.

FIGURE FILES

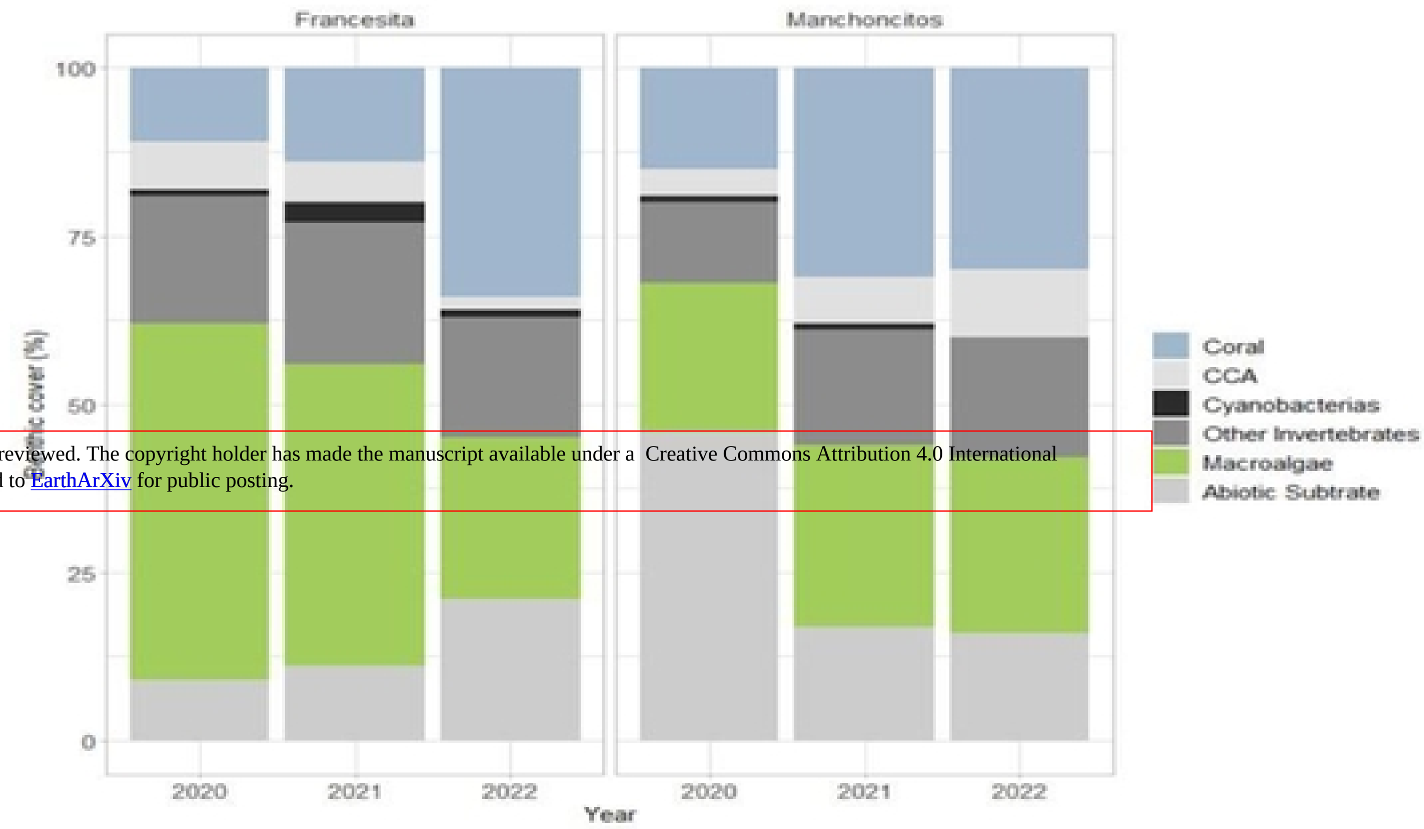

Figure 1. Changes in benthic community structure at Francesita reef and Manchoncitos reef over time.

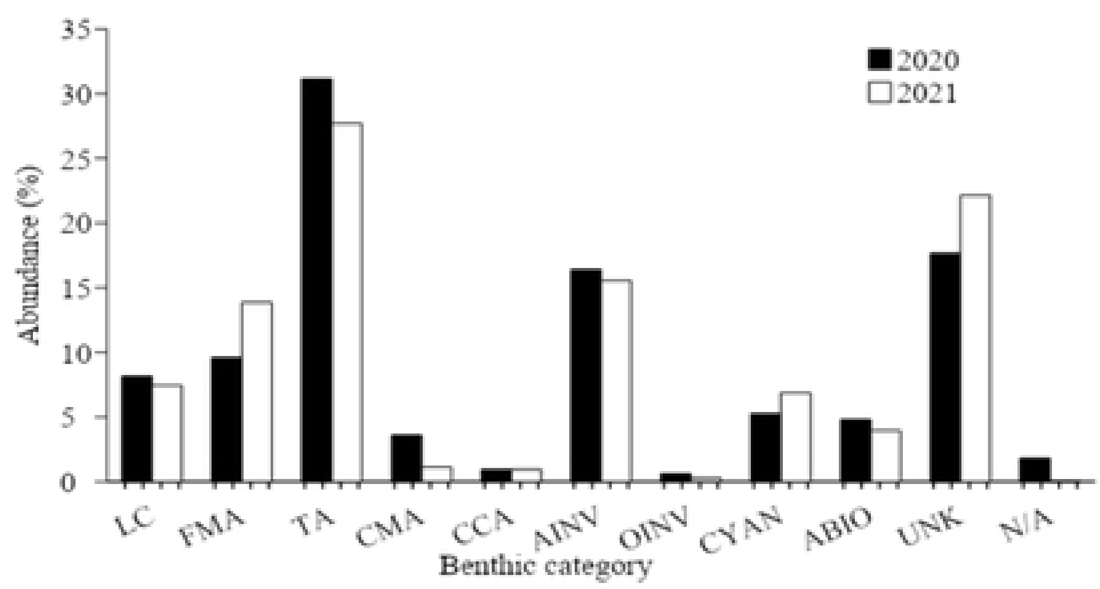

Figure 2. Benthic reef cover (%) for Manchoncitos reef (Mexico) for 2020 (black bars) and 2021 (white bars). Benthic category codes are LC: live coral, FMA: fleshy macroalgae, TA: turf algae, CMA: calcareous macroalgae, CCA: crustose coralline

algae, AINV: aggressive invertebrate, OINV: other invertebrate, CYAN: cyanobacteria, ABIO: abiotic substrate, UNK: unknown/unidentifiable substrates, N/A: no data for that point intercept.

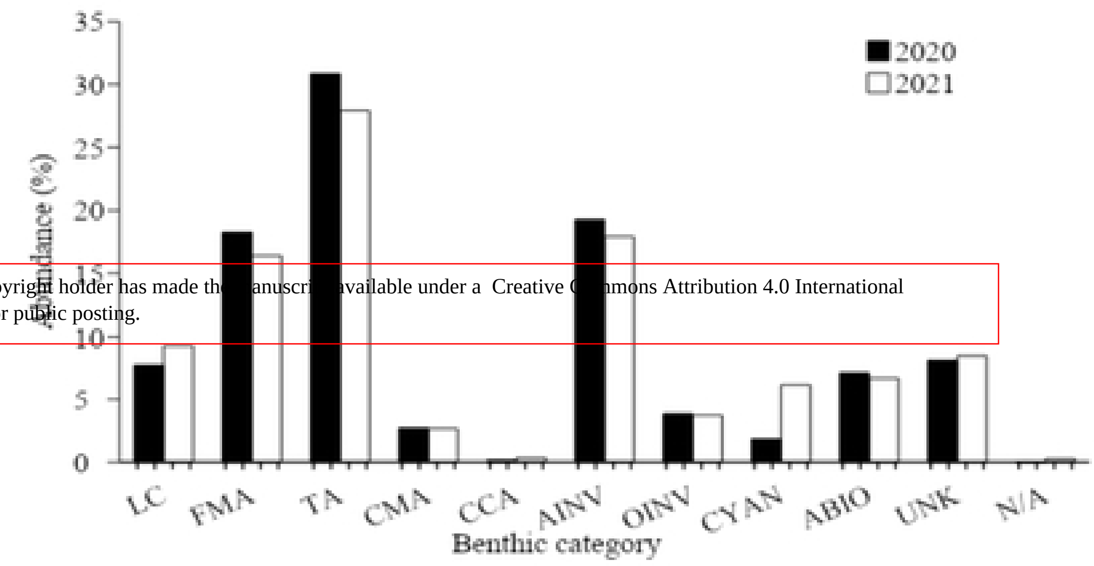

Figure 3. Benthic reef cover (%) for Francesita reef (Mexico) for 2020 (black bars) and 2021 (white bars). Benthic category codes are LC: live coral, FMA: fleshy macroalgae, TA: turf algae, CMA: calcareous macroalgae, CCA: crustose coralline algae, AINV: aggressive invertebrate, OINV: other invertebrate, CYAN: cyanobacteria, ABIO: abiotic substrate, UNK: unknown/unidentifiable substrates, N/A: no data for that point intercept.

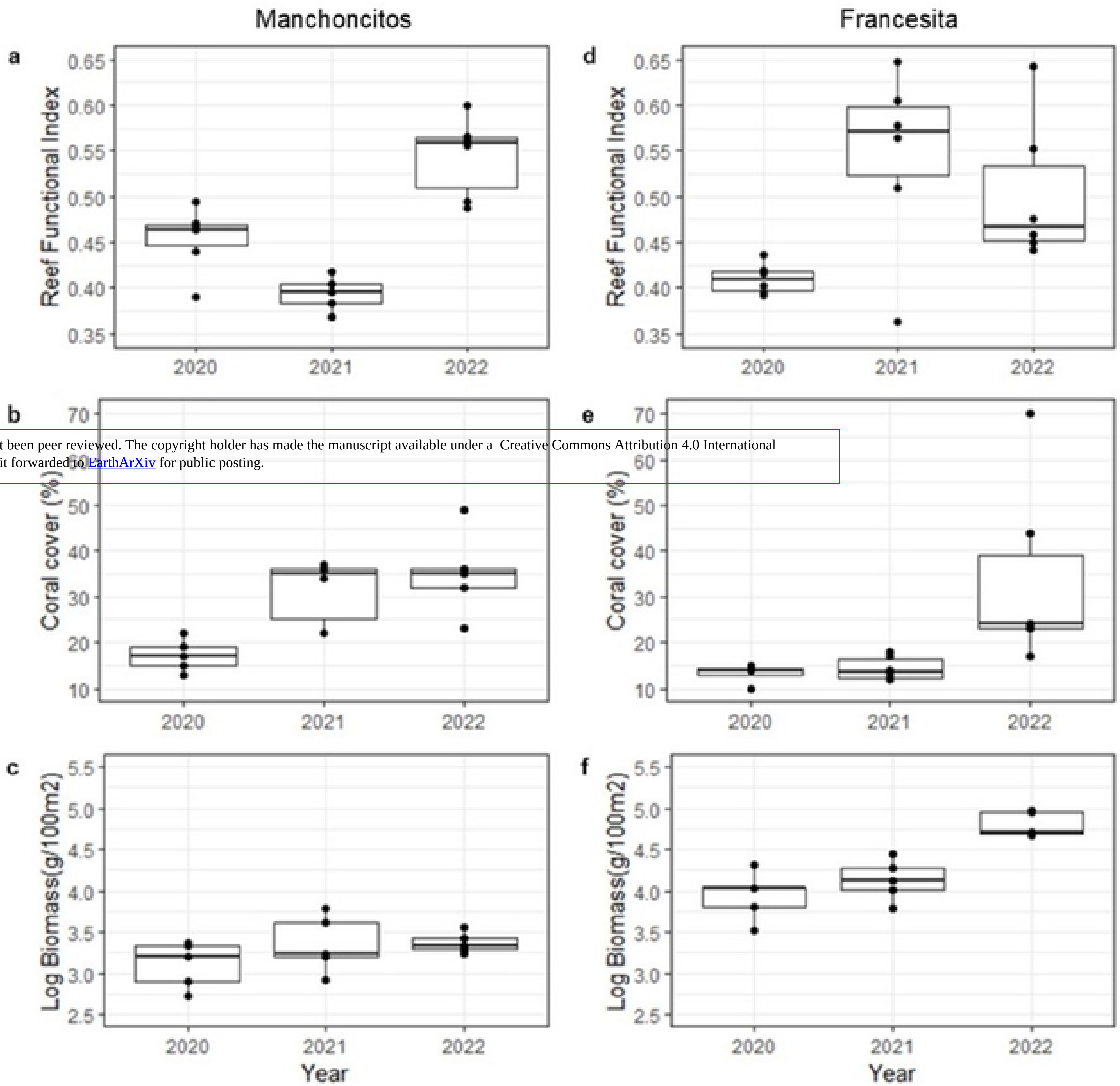

Figure 4. Ecological benefits due to outplanting. Considering date as a descriptive variable. Reef Functional Index (RFI) (a and d); Coral cover (b and e); Total fish biomass (c and f).

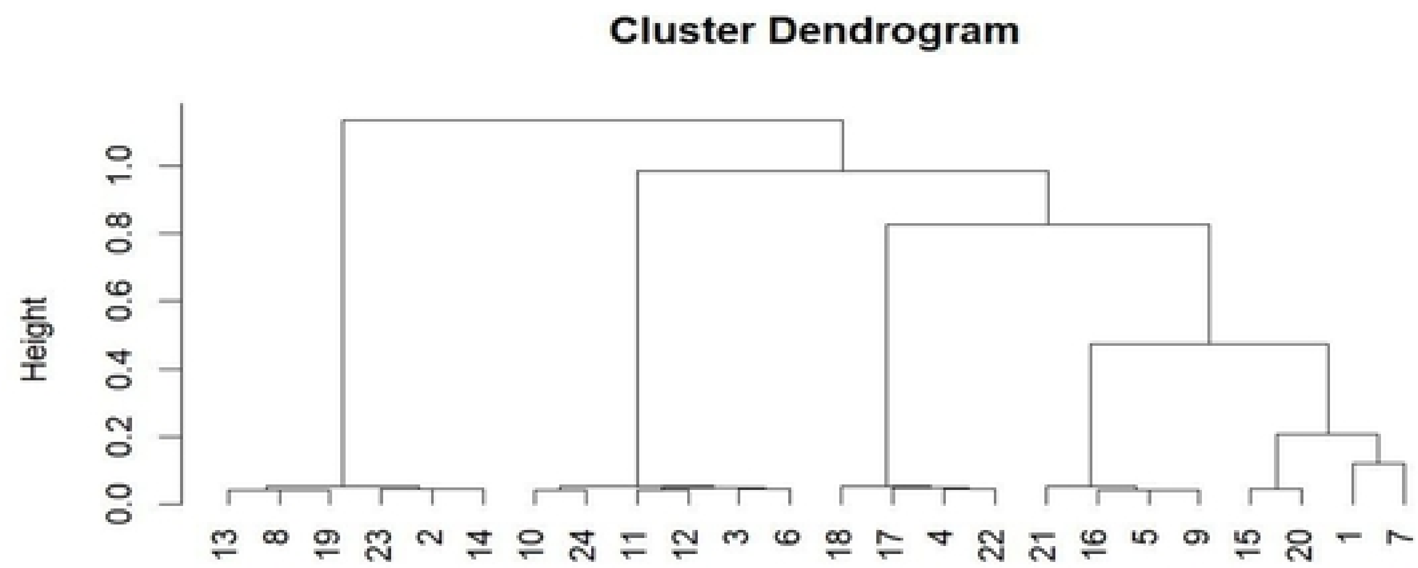

Figure 5. Clustering dendrogram of *Acropora palmata* ramets in the Cozumel nursery.

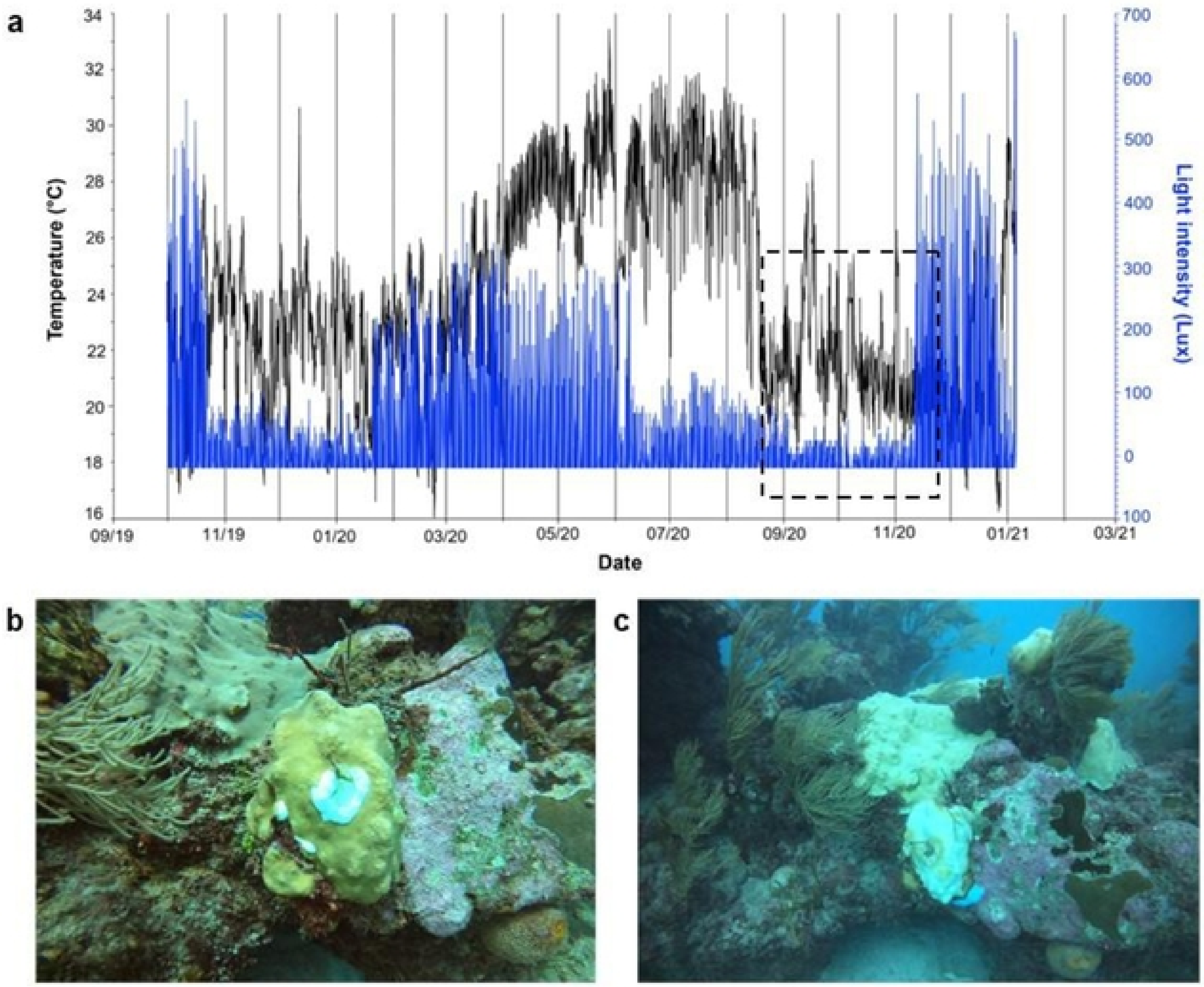

Figure 6. Temperature (ºC) and luminosity (Lux) trend at Manchoncitos Reef in 2020. **a)** Temperature and luminosity decreases in October during hurricanes Gamma, Delta and Zeta **b)** *Orbicella faveolata* colonies before Hurricane Delta **c)** bleached *O. faveolata* colonies after Hurricane Delta.

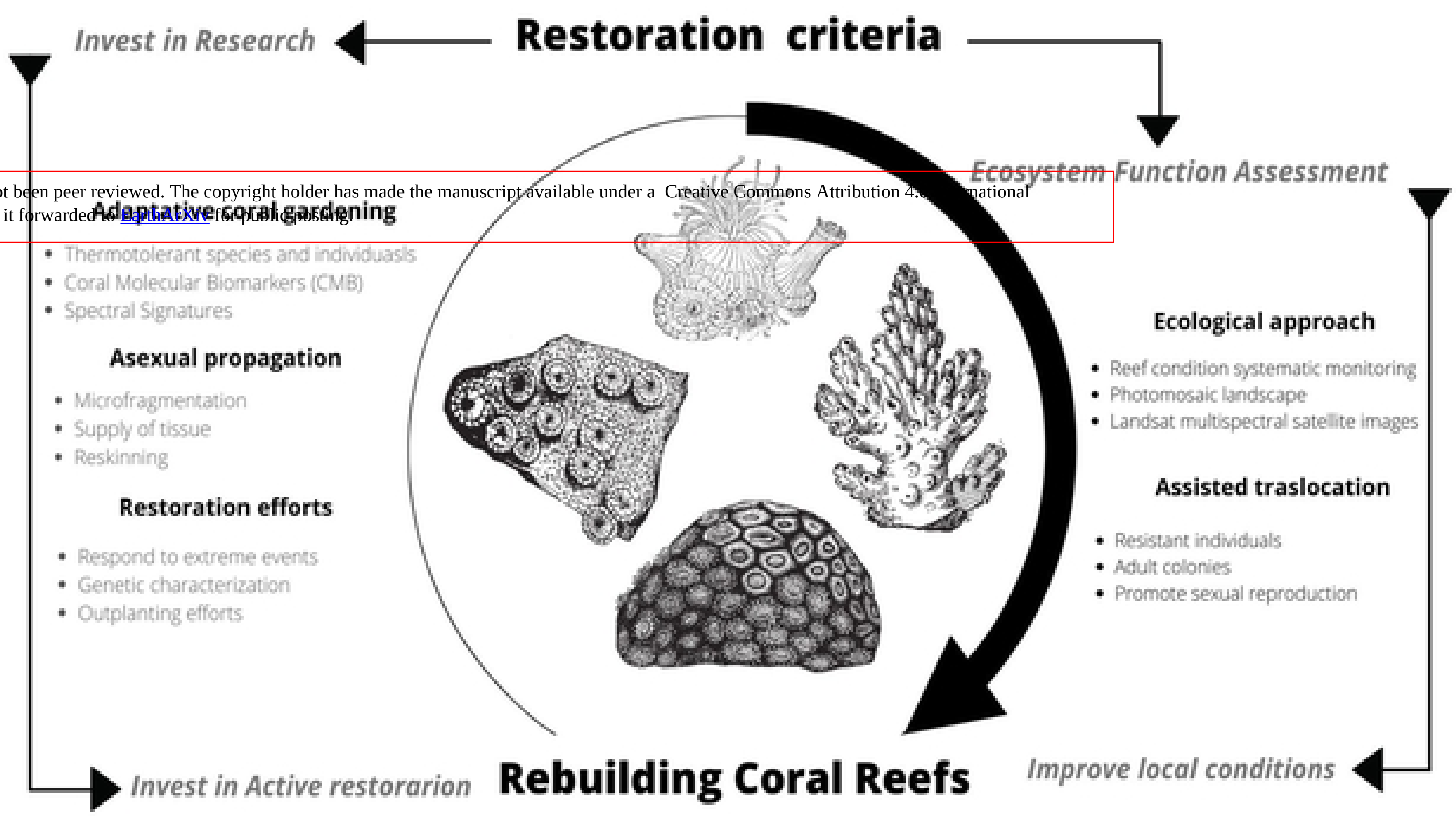

Figure 7. Outline for rebuilding coral reefs through the organizational capacity of the private sector to invest in research, active restoration, improve local considerations and long-term engagement.

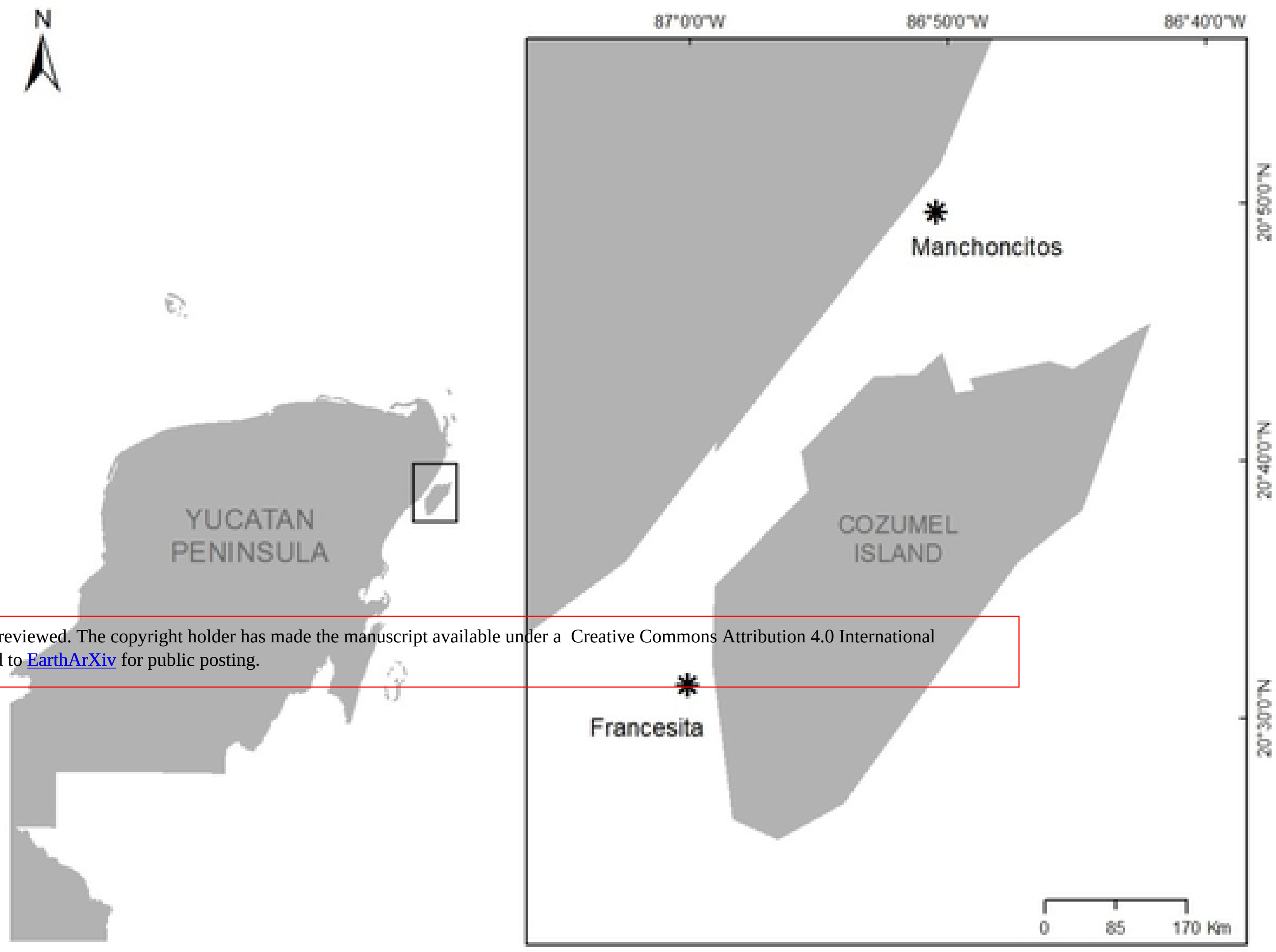

Figure 8. Location of Manchoncitos reef and Francesita reefs in the Mexican caribbean.