UNIVERSIDAD SAN FRANCISCO DE QUITO USFQ

Colegio de Ciencias Biológicas y Ambientales

Coral Restoration in the Galápagos: Tracking Mortality and Health of Hermatypic Corals in Nurseries and Outplants

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Coral Restoration in the Galápagos: Tracking Mortality and Health of Hermatypic Corals in Nurseries and Outplants

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“The natural world is a symphony, and every creature plays a part in the harmony of existence.”

— Alexander von Humboldt

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RESUMEN

Las Islas Galápagos sufrieron una pérdida catastrófica de corales durante el evento El Niño de 1982–1983, con un 97% de cobertura coralina desaparecida. Cuatro décadas después, la recuperación aún no se ha completado. La restauración coralina se presenta como una estrategia prometedora para recuperar y mejorar la resiliencia de estos ecosistemas. Este estudio evaluó la mortalidad y salud de corales cultivados y trasplantados en el sureste de Isabela, Galápagos, entre octubre de 2023 y junio de 2024, durante condiciones de El Niño, analizando la influencia de variables ambientales—temperatura, pH, salinidad, sólidos disueltos totales y oxígeno disuelto—en su desempeño. Se monitorearon mensualmente más de 2,300 fragmentos de coral en viveros y sitios de trasplante. Los resultados mostraron una alta supervivencia y bajos porcentajes de tejido muerto, blanqueamiento y cobertura algal en *Pocillopora*, y mayor afectación en corales masivos. No encontramos tendencias importantes en la mortalidad y salud de corales a lo largo del tiempo. No encontramos influencias significativas de la mayoría de las variables ambientales en el desempeño de los corales *Pocillopora* durante las condiciones térmicas moderadas asociadas al evento El Niño registrado durante el período de estudio. Pero sí encontramos un leve efecto de la salinidad, los sólidos disueltos totales y la temperatura en la mortalidad y salud en corales *Porites*. El éxito de estos esfuerzos iniciales de restauración resalta el potencial de la siembra de corales como una herramienta de conservación en Galápagos. Comprender las respuestas de los corales a la variabilidad ambiental contribuirá a mejorar las estrategias adaptativas de restauración, especialmente ante la intensidad de los eventos El Niño.

Palabras Clave: corales, siembra de coral, restauración coralina, eco-fisiología, mortalidad de coral, salud coralina, El Niño

ABSTRACT

The Galápagos Islands suffered a catastrophic loss of corals during the 1982–1983 El Niño event, with 97% of coral cover gone. Four decades later, recovery is still not complete. Coral restoration is presented as a promising strategy to recover and improve the resilience of these ecosystems. This study evaluated the mortality and health of cultivated and transplanted corals in southeastern Isabela, Galápagos, between October 2023 and June 2024, during El Niño conditions, analyzing the influence of environmental variables—temperature, pH, salinity, total dissolved solids, and dissolved oxygen—on their performance. More than 2,300 coral fragments were monitored monthly in nurseries and outplant sites. The results showed high survival rates and low percentages of dead tissue, bleaching, and algal cover in *Pocillopora* corals, while massive corals were more affected. There were no significant changes in coral mortality and health over time. We found no significant influence of most environmental variables on the performance of *Pocillopora* corals under the moderate thermal conditions associated with the El Niño event recorded during the study period. However, we observed a slight effect of salinity, total dissolved solids and temperature on mortality and health in *Porites* corals. The success of these initial restoration efforts highlights the potential of coral nurseries as a conservation tool in Galápagos. Understanding coral responses to environmental variability will contribute to improving adaptive restoration strategies, especially in the face of intense El Niño events.

Keywords: corals, coral nursery, coral restoration, eco-physiology, coral mortality, coral health, El Niño

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INTRODUCTION

Coral reefs are one of the most iconic tropical marine ecosystems, which form complex habitats that offer crucial ecosystem services, including coastal protection, support for fisheries, and opportunities for ecotourism (Harborne et al., 2006; Woodhead et al., 2019). Hermatypic corals build reefs, and are made of colonial organisms that, by secreting calcium carbonate, create the structural foundation of coral reefs (Hickman, 2008; Schuhmacher & Zibrowius, 1985). Coral colonies, composed of identical polyps, rely on mutualistic endosymbiotic algae, known as zooxanthellae, which supply most of the nutrients necessary for coral growth and survival (Hickman, 2008; Yamashita et al., 2014). Despite their ecological and socioeconomic importance, coral ecosystems are increasingly threatened by environmental disturbances and human activities, jeopardizing their long-term survival (Eddy et al., 2021; Edgar et al., 2010). The worldwide degradation of coral reefs generates cascading effects on ecosystems and on the human communities that depend on the services coral reefs provide (Woodhead et al., 2019).

One of the most well-known threats to corals is bleaching, which has become more frequent and severe due to rising ocean temperatures (Mellin et al., 2024). Elevated temperatures accelerate zooxanthellae metabolism, leading to an overproduction of reactive oxygen species (Nielsen et al., 2018; Szabó et al., 2020). This oxidative stress causes corals to expel their symbionts, reducing calcification rates, increasing nutrient stress, and ultimately leading to coral death if thermal stress persists (Hill & Ralph, 2007; Jones, 2008). Corals are also sensitive to cool water exposures, which triggers a different physiological mechanism of bleaching. In such cases, photosynthetic efficiency decreases, and pigment concentrations are altered (Gates et al., 1992; Higuchi et al., 2015; Pontasch et al., 2017; Saxby et al., 2003).

Either way, corals without zooxanthellae lose access to vital nutrients, compromising their ability to grow, defend against disease, and recover from injury (Davies, 1984).

Beyond temperature, other environmental parameters critically influence coral physiology. Acidic pH disrupts cellular functions and microbial communities, lowering calcification rates and skeleton formation (Hoegh-Guldberg et al., 2007; Meron et al., 2011; Venn et al., 2013). Salinity fluctuations and dissolved solids in water impact osmotic balance and nutrient absorption; low salinity can reduce photosynthetic efficiency and lead to bleaching, tissue swelling, and necrosis (Downs et al., 2009). High levels of dissolved solids often correlate with sedimentation and turbidity, which smother, abrade, and shade corals, inhibiting recruitment and growth (Flores et al., 2012; Rogers & Ramos-Scharrón, 2022). Finally, oxygen availability, in conjunction with water flow, is vital for coral metabolism. Optimal oxygen concentrations support respiration and calcification, whereas hypoxia or hyperoxia impair these processes, causing tissue loss (Haas et al., 2014; Osinga et al., 2017; Wijgerde et al., 2012). Together, these environmental factors highlight the complex nature of coral vulnerability, emphasizing the need to address multiple stressors to study the health of coral ecosystems.

These environmental threats are particularly evident in the Eastern Tropical Pacific (ETP), a marine bioregion that has suffered frequent and severe coral loss, including reefs along the coast of mainland Ecuador and within the Galápagos Islands (Glynn et al., 2001). Hermatypic coral species in the ETP are dominated by the Genera *Pavona*, *Porites* and *Pocillopora* (Cortés et al., 2017). They all have demonstrated relative resilience, despite facing challenging environmental conditions in the region like ocean temperature fluctuations, increased nutrients and acidic waters (Castrillón-Cifuentes et al., 2023; Glynn et al., 2017). In contrast to other tropical coral ecosystems, environmental conditions in the ETP are influenced by cold ocean currents and climatic phenomena like El Niño Southern Oscillation (ENSO), which limit coral reef growth (Rhoades et al., 2023).

Corals in Galápagos have bleached both by heat (1982-83 and 1997-98; Glynn et al., 2001, 2018) and cold waves (e.g., 2008-10; Rhoades et al., 2023), caused by severe El Niño and La Niña events, respectively. The most severe bleaching event occurred in El Niño of 1982-1983, which led to the loss of around 97% of coral cover in the Galápagos Islands, due to the anomalous and prolonged warming of the Pacific's surface waters (Glynn, 1984). Today, 40 years later, coral reefs in the Galápagos have not fully recovered from that loss (Glynn et al., 2018).

Coral restoration initiatives have become a crucial tool for mitigating coral loss, promoting coral recovery in affected areas and increase coral adult offspring resilience (Humanes et al., 2024; Westoby et al., 2020). Coral nurseries enable the growth of coral fragments under optimized conditions before they are transplanted into degraded reef areas. Examples of coral restoration projects in the ETP with promising results are in Gorgona Island, Colombia (Ishida-Castañeda et al., 2020); Bahía Culebra, Costa Rica (Fabregat-Malé et al., 2024) and the Central Mexican Pacific (Tortolero-Langarica et al., 2014). There are some coral nursery programs along the coast of Ecuador, fighting against the strong damage that the reefs of this region have suffered, due to the same ENSO conditions and pollution from abandoned fishing gear (Figueroa-Pico et al., 2020; Glynn et al., 2001). The Galápagos Reef Revival project works with nurseries in coral stocks around the southeast of Isabela Island, in the Galápagos, as a key approach to restore degraded coral communities (Dávalos et al., *in prep.*).

Considering the oceanographic background of Galápagos —upwelling processes and ENSO— and coral restoration as a novel conservation practice in the archipelago, it is essential to evaluate the viability of large coral nurseries and the influence of environmental factors on coral cultivation. This knowledge can help researchers and conservationists optimize nursery conditions, improving coral survival and growth before transplantation (Fabregat-Malé et al., 2024; Merck et al., 2022). This study aimed to assess mortality and health of coral fragments in nurseries and outplants on Isabela Island, Galápagos, during the 2023-24 El Niño event. Additionally, it evaluated how different environmental variables such as temperature, pH, salinity, total dissolved solids (TDS) and dissolved oxygen (DO) affected coral performance over time. Our research questions were: 1) How do coral fragment mortality and health vary over time? And 2) What environmental variables have a significant effect on them?

METHODS

Study Area

The Galápagos Islands —a volcanic archipelago in the ETP, located 1000 km from the South American coast— experiences contrasting regimes with significant differences in temperature, nutrients, and phytoplankton productivity (Vinueza et al., 2014). Coral ecosystems in Galápagos are crucial for biodiversity, hosting several animal species, including uncommon and endemic ones (Dawson et al., 2009). Notably, the far-northern island of Darwin hosts Wellington Reef, the last remaining structural coral reef in the archipelago. This ecosystem is dominated by massive corals of the genera *Pavona* and *Porites* (Glynn et al., 2015, 2018). In contrast, the central/south-eastern region presents reduced scattered coral patches, forming small coral communities (Glynn et al., 2018). This north-south gradient in coral presence is shaped by variations in temperature, pH and nutrient availability (Riegl et al., 2019).

Despite its equatorial location, Galápagos experiences substantial geographic and seasonal temperature variability driven by the convergence of three major ocean currents: the cold, nutrient-rich Equatorial Undercurrent flowing from west to east; the cool Peruvian Coastal and Oceanic Current from the southeast, which intensifies between June and November (cool season); and the warmer tropical waters of the Panamá Current from the northeast, dominating from January to May (warm season; Glynn & Wellington, 1983).

The southeastern coast of Isabela, the largest island in the Galápagos Archipelago, host high densities of *Pocillopora* colonies, especially in the coastal lagoon "Concha de Perla", where asexual-originated coral aggregations thrive across lava pools (Baums et al., 2014). Since 2022, the "Galápagos Reef Revival" restoration initiative has established coral nurseries in southeast Isabela to cultivate coral fragments (Dávalos et al., *in prep.,* Figure 1). This initiative is located about 300 m southeast of Puerto Villamil's dock, the island's main maritime entry point. The nursery and outplant sites are distributed across two proximal water bodies. The coral nursery and one outplant site are located in "La Bahía" (0°57'53.6"S, 90°57'24.8"W), the main bay bordered by the island shores and rocky islets, and most of the transplanted corals are in "La Calera" (0°57'53.4"S, 90°57'21.1"W), a rocky tidal channel that connects the open ocean with "Concha de Perla". Like most marine ecosystems in Galápagos, this coral restoration area experiences significant seasonal temperature fluctuations (Glynn & Wellington, 1983). A previous study in 2022 reported monthly temperatures between 19 and 28°C during La Niña conditions (Dávalos et al., *in prep.*).

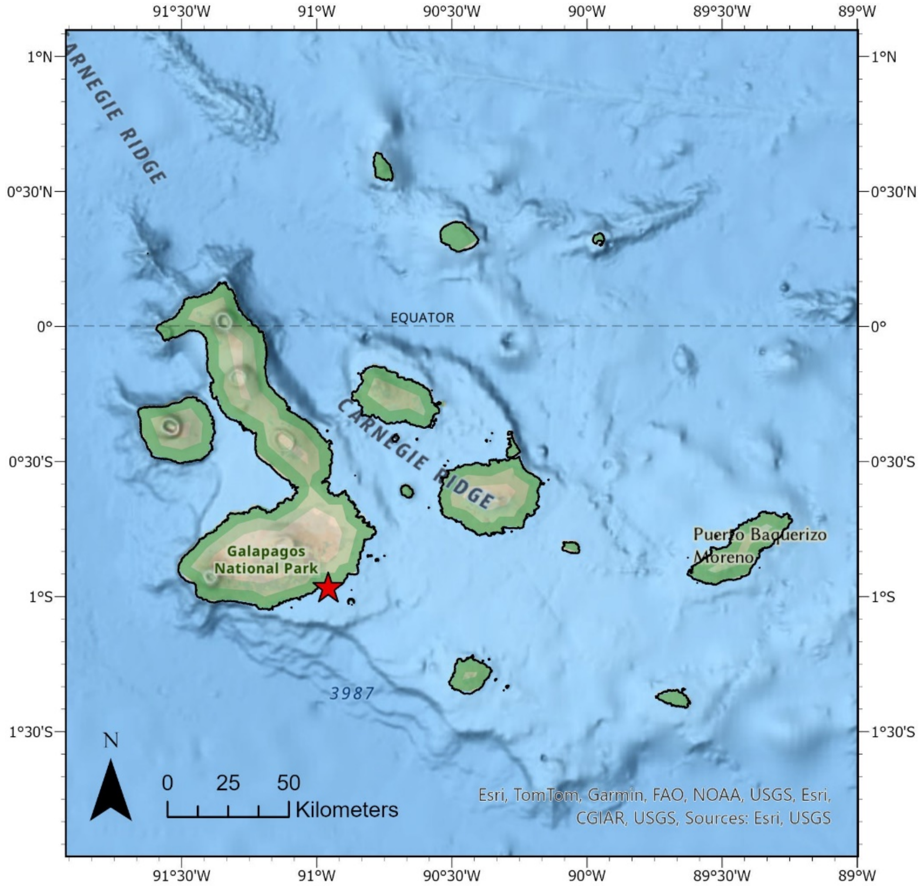

Figure 1. Map of the Galápagos Islands and the location of the restoration area in Isabela.

Coral Gardening and Transplantation

We performed a baseline survey and a pilot coral nursery which were essential to evaluate the feasibility of coral cultivation in Puerto Villamil. In 2021, a thorough assessment of coral communities in Puerto Villamil Bay and the southern sites of Isabela Island identified >3,600 hermatypic coral colonies, primarily of the *Pocillopora* Genus (Dávalos et al., *in prep.*). This baseline study recorded and identified corals up to species level based on Hickman's Cnidarian ID Guide (2008). In addition, each colony was classified as a "morphotype", based on traditional morphological characteristics (Hickman, 2008) and a minimum distance of 100 m between colonies to ensure origin distinction (Goergen et al., 2020). This survey yielded nine hermatypic coral species and 57 morphotypes; although we recognize that Pocilloporids taxonomy is not resolved (Pinzón et al., 2013; Pinzón & Lajeunesse, 2011) and the actual number of *Pocillopora* species might be reduced to two, and the total number of coral hermatypic species in our site to seven (Dávalos et al., *in prep.*). In addition to the baseline study, we performed further surveys to explore other sites around southeast Isabela and Isla Tortuga (1°0'34.8"S, 90°52'22.8"W), a rugged crescent-shaped islet located 7 km southeast of Isabela's shoreline.

The pilot nursery consisted of selecting the healthiest colonies of each morphotype identified in the baseline study (n=12) and fragmenting them into n=20 pieces of 4.29 cm ± 0.94 (mean ± sd) of length. In this pilot nursery, 240 fragments were attached to a nursery rope at 3 m depth in La Calera in January 2022 (Figure 2). Rope nurseries are structures where coral fragments are attached to horizontal ropes, forming parallel series lines over a metal structure (Levy et al., 2010; Shafir et al., 2010). When the coral fragments were big enough to survive on the sea floor (after around one year in the nursery), they were physically relocated and attached with small amounts of cement to the degraded reef area in "La Calera" in March 2023 (Figure 2; Clark & Edwards, 1995).

A second nursery of bigger scale was established in September 2023 (Figure 2) and included three gardening techniques: ropes, tables and trees at a depth range of 3-6 m. The ropes contained most of *Pocillopora* morphotypes selected in the 2021 baseline survey and pilot nursery (Dávalos et al., *in prep.*). Tables are submerged platforms with flat, horizontal mesh boards separated from the seabed, where corals are attached to a stable surface to grow (Shaish et al., 2008). These structures hosted the massive corals (*Pavona* and *Porites*). Tree nurseries are vertical tree-like structures with horizontal branches where coral fragments are attached (Nedimyer et al., 2011). These assemblies hosted *Pocillopora* morphotypes from some donor colonies sampled around Puerto Villamil and the east slope of Isla Tortuga. The coral fragments that are analyzed in this study correspond to those in the second and larger-scale nursery, and those transplanted in La Calera in March 2023 (which were previously cultivated in the pilot nursery; Figure 2).

Data Collection

Environmental Variables: Oceanic Physical Conditions.

We measured oceanic physical conditions from two sources: temperature loggers (HOBO TidbiTs and iButtons) and a multiparameter probe (HANNA HI98194), which measured sea surface temperature (SST), pH, salinity, total dissolved solids (TDS) and dissolved oxygen (DO). HOBO loggers were configured to record every 10 min from July 28, 2022, to September 5, 2023, while iButtons recorded hourly from July 5, 2023, to June 23, 2024. Both were deployed at La Bahía and La Calera. Monthly multiparameter measurements were taken from December 2022 to December 2023 (Figure 2), with some exceptions due to logistical issues. Starting in January 2024, calibration issues prevented further use of the multiparameter device. For each measurement, we placed the multiparameter probe underwater at a depth of 1 to 2 m for approximately 5 min.

To analyze El Niño and La Niña oceanographic events, weekly data for the El Niño 1+2 Index were obtained from the Climate Prediction Center (CPC) of NOAA. This index represents sea surface temperature anomalies (SSTA) in the region between 0°-10°S and 80°W-90°W (NOAA Climate Prediction Center, n.d.).

Biological Variables: Surveys of Coral Mortality and Health.

We conducted monthly surveys between October 2023 and June 2024 in the nurseries, and between October 2023 and May 2024 in the outplant zones (Figure 2). We recorded the amount of present and dead fragments per morphotype to quantify coral mortality. On the other hand, health assessments involved evaluating three physiological indicators: % of dead tissue, % of bleached tissue and % of algal cover. Following protocols in Goergen et al., (2020), these variables were measured in each coral fragment using a scale from 1 to 5, where each level corresponded to a percentage range of the surface affected: 1 = 1-24%, 2 = 25-49%, 3 = 50-74%, 4 = 75-99%, and 5 = 100%.

Data Management

Temperature Profiles.

We combined temperature measurements from the HOBOs and iButtons into a single dataset. For this study, we used the temperature measured in La Bahía as a reference for the project area, since at this site the measurements have greater temporal continuity. One of the iButtons located in La Calera got lost, generating a gap in information about this water body between September 2023 and January 2024. The HOBO device uncalibrated, so we adjusted its temperature measurements by subtracting 1.2°C, the average difference between the HOBO and iButton data during the time overlap of data from both devices, between July and September 2023.

Biological Variables Calculations.

For each morphotype, we calculated monthly coral fragment mortality as the ratio between the number of dead corals and the total number of corals, applying the following formula:

$$M = \frac{N_{dead}}{N_{total}}$$

where M is the coral fragment mortality, N_{dead} is the number of dead corals and N_{total} is the total number of initial corals.

To calculate the averages of coral health indicators (% of dead tissue, % of bleached tissue and % of algal cover), the upper limits of the health range of each fragment were averaged.

$$\overline{H} = \frac{1}{N_{total}} \sum H_{max}$$

where $\overline{H}$ is the average of the health indicator, N_{total} is the total number of corals and H_{max} is the upper limit of each of the percentage range of affectation of each coral.

Data Analysis

Statistical Analyses.

To analyze trends in the biological variables over time, we applied quasi-binomial logistic regressions, calculating the McFadden coefficient of determination (McFadden R^2) and corresponding p-values. Given the high prevalence of zero values in our data, this model was chosen as it accounts for overdispersion, which is not handled adequately by standard models (Lindén & Mäntyniemi, 2011; Ver Hoef & Boveng, 2007). To evaluate and quantify the effect of the environmental variables on coral fragment mortality, % of dead tissue, % of bleached tissue and % of algal cover, we also performed quasi-binomial logistic regressions for all biological and environmental variables interactions. In addition, we ran a Principal Component Analysis (PCA) to visualize how the environmental and biological variables interacted with each other. To analyze the interactions between variables we used data corresponding to the period between October and December 2023, as this period was the only period with overlapping data from the multiparameter with that of coral surveys. All the statistical analyses and graphs were performed in RStudio 4.2.1.

RESULTS

Environmental Variables

Temperature Profiles.

During the study period (between October 2023 and June 2024), SST averaged 26°C, with a range from 21°C to 30°C (Figure 2). The transition to El Niño conditions began in February 2023, as indicated by sustained positive anomalies in the El Niño 1+2 Index. SSTs remained above 24°C and reached values of 29°C and 30°C during the warmest months (Figure 2).

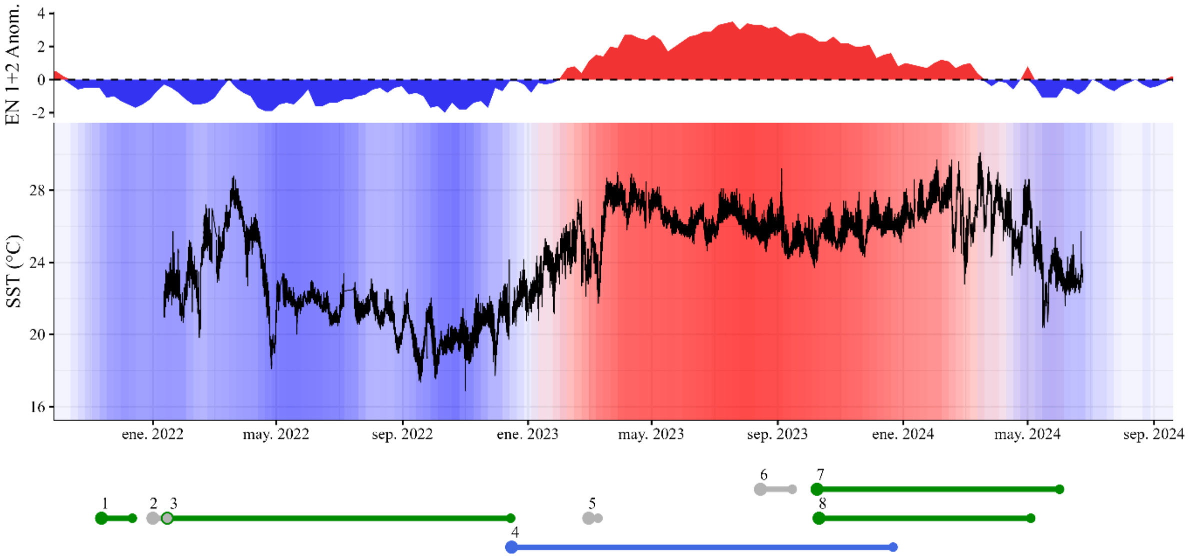

Figure 2. El Niño 1+2 anomalies (NOAA), Sea Surface Temperatures (SSTs) derived from HOBBO and iButtons, and timeline with the key activities of the project. Blue and red coloration represents cold (La Niña) and warm (El Niño) periods, respectively, while the black line shows SST fluctuations of temperature loggers deployed in La Bahía in Isabela Island. Numbers at the bottom of the figure represent key moments of the project: 1: Baseline Survey, 2: Assemble of Pilot Nursery, 3: Pilot Nursery Monitoring, 4: Multiparameter Surveys, 5: Pilot

Nursery Outplanting, 6: Assemble of Bay Nursery, 7: Bay Nursery Monitoring, and 8: Pilot Outplants Monitoring. and 8: Pilot Outplants Monitoring.

Multiparameter Measurements.

The environmental conditions measured with the multiparameter in Puerto Villamil showed stable values throughout the study period. The mean pH was 8.08 (range: 8.02–8.15), while salinity averaged 26.26 psu (range: 21.37–33.91). Dissolved oxygen remained high, with a mean of 91.10% (range: 85.66–95.19), and total dissolved solids averaged 20.26 ppt (range: 16.57–25.77; see Appendix A).

Biological Variables

Coral Mortality and Health in the Bay Nursery and Pilot Outplants.

Our data consisted of a total of 2,104 coral fragments from the Bay Nursery that belonged to 46 morphotypes, and of 256 coral fragments from the outplants belonging to 24 morphotypes (Appendix B). The ropes hosted 1,600 fragments, while 360 and 144 coral fragments were placed on the tables and in the trees, respectively.

After 236 days (from October 2023 to June 2024), we recorded a total mortality of 5.25% in the Bay Nursery **Figure** *3*and after 206 days (from October 2023 to May 2024), just one colony of one morphotype died in the Pilot Outplants, representing a total mortality of 0.39%**Figure** ***4***. Massive corals presented the highest variability, with mortality, % of dead tissue and % of algal cover ranging from 0% to 100%, while % of bleached tissue from 0% to almost 80% (Figure 3; Appendix C). The morphotypes with the highest mortalities belonged to *Porites* (75%) and *Pavona* (25%). These taxa also had high affection levels related to % of dead tissue and % of algal cover (Figure 3). Additionally, *Pavona* corals bleached the most (up to 75%). Conversely, mortality did not exceed 20% in *Pocillopora* corals from ropes and trees.

Also, % of dead tissue and % of algal cover fluctuated between 0% and 30%, with some exceptions extending to 83% of dead tissue and 72% in algal cover. The % bleached tissue reached 28 and 32% in two morphotypes, and the rest kept below 15% (Figure 3; Appendix C). On the other hand, *Pocillopora* corals at the Pilot Outplants exhibited an extremely low % of dead tissue, not exciding 7% most of time, with one exception of one morphotype reaching 19% in late 2023 (Figure 4). Similarly, % of algal cover was low (less than 20% throughout the time). However, some morphotypes reached 37.5% of bleached tissue (Figure 4; Appendix C).

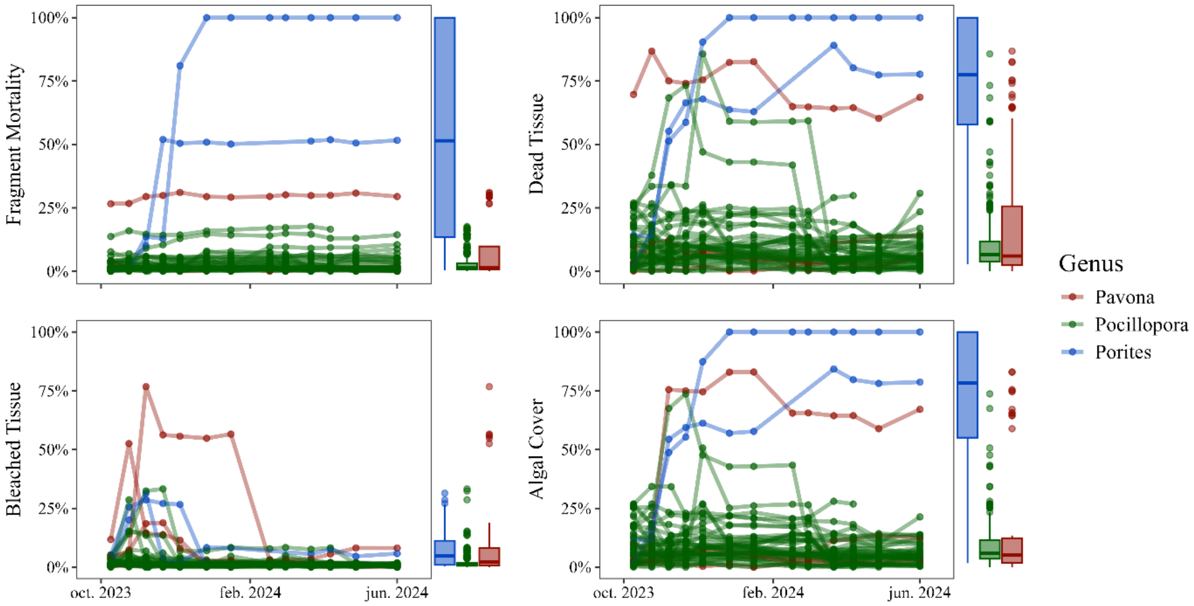

Figure 3. Monitoring of coral fragment mortality and health in the Bay Nursery from October 2023 to June 2024. Lines represent individual morphotype trajectories over time, while boxplots summarize the data distribution during the study period.

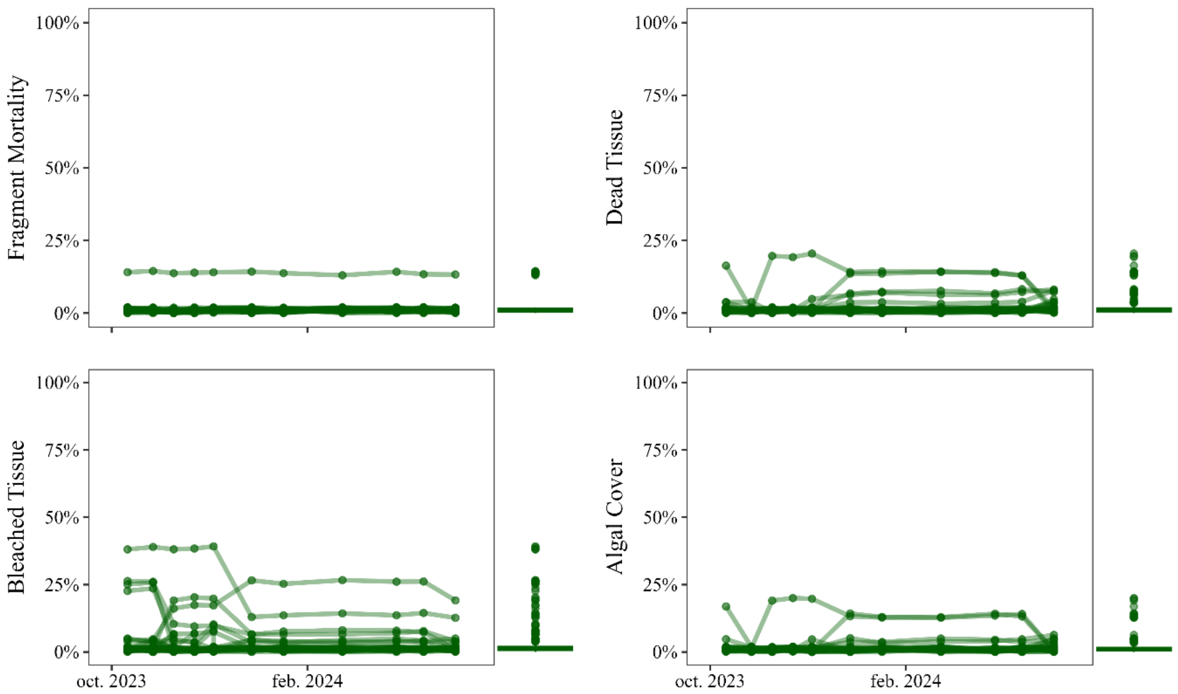

Figure 4. Monitoring of *Pocillopora* coral fragment mortality and health in the Pilot Outplants from October 2023 to May 2024. Lines represent individual morphotype trajectories over time, with boxplots summarizing the data distribution during the study period. All monitored fragments belonged to the *Pocillopora* Genus.

Coral Mortality and Health Across Time.

The quasi-binomial logistic regression model indicated a significant positive association between time and coral mortality, but with a minimal explained variance (McFadden R^2 = 0.04, p = 0.01). The quasi-binomial analyses for coral health indicators revealed no significant trend over time for % of bleached tissue (McFadden R^2 = 0.00, p = 0.075), while the % of dead tissue (McFadden R^2 = 0.08, p = 0.020) and % of algal cover (McFadden R^2 = 0.22, p = 0.003) showed significant results, however, the variation explained by the model is almost negligible. The regression results for each Genus in nurseries and outplants showed that mortality, % of dead tissue and % of bleached tissue significantly changed through time in *Porites* corals, with a higher variation explained (Appendix D). In contrast, *Pocillopora* and *Pavona* corals only presented increasing bleaching through time (Appendix D).

Influence of Environmental Variables on Coral Mortality and Health.

In general, the environmental variables had little effect on coral mortality and health. However, *Porites* corals seem to be the most sensitive to most of these variables, as we found significant relationships between salinity, TDS and temperature with mortality, % of dead tissue and % of algal cover (Appendix E).

In the PCA for *Pocillopora*, the first two principal components (Dim1 and Dim2) explained 59.2% of the variance in the data (Figure 5). Dim1 was primarily characterized by the environmental variables and accounted for 37.2% of the total variance, while Dim2, was characterized by % of dead tissue and algal cover, explaining 22.0%. Overall, for *Pocillopora*, there were no strong correlations between the environmental variables and coral mortality or health metrics, which is consistent with the results from the quasi-binomial model (Appendix E). A subtle negative correlation between pH and bleaching is observed, which again is consistent with the quasi-binomial model. In the case of massive corals, the first two components accounted for 71.9% of the variance (Figure 5), with Dim1 explaining 47.4% of the variance and Dim2 24.5%. Dim1 was more influenced by mortality, dead tissue, algal cover, TDS, salinity and DO; while bleaching is the most strongly related to Dim2. Higher temperature and pH were related to mortality, dead tissue and algal cover. Nevertheless, bleaching did not show clear relationships with other variables. In both PCAs, coral mortality, % of dead tissue, and % of algal cover showed correlations among themselves, as did salinity, TDS, and DO.**Figure 5**

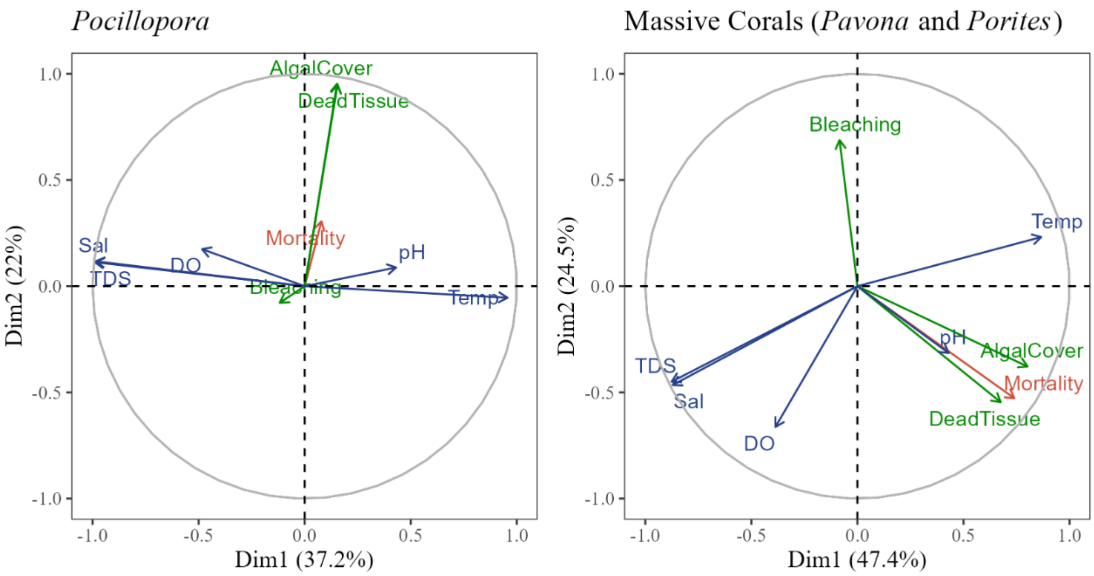

Figure 5. Principal Component Analysis (PCA) loading plots showing the relationships between the environmental variables (blue), fragment mortality (red), and health indicators (green) for *Pocillopora* corals (left panel) and *Pavona* and *Porites* massive corals (right panel). Axes represent the first two principal components (Dim1 and Dim2) and the percentage of total variance explained by each.

DISCUSSION

Environmental Variables

Temperature Profiles.

The warm season of 2023 was characterized by higher-than-average SSTs that extended through what is normally the cold season (June to November), eliminating the expected seasonal cooling. In 2022, La Niña conditions dominated, resulting in cooler temperatures and a pronounced cold season, during which SSTs frequently dropped below 24°C. In contrast, 2023 experienced persistently elevated temperatures throughout the year, with no evident cold season observed, a direct consequence of the El Niño event. This prolonged warming period disrupted the typical oceanographic cycle in the Galápagos, potentially amplifying thermal stress on marine organisms, including corals (Rivera, 2023).

Multiparameter Measurements.

The environmental variables measured in Puerto Villamil showed dynamic conditions typical of shallow coastal environments. Salinity (mean 26.26 psu) is lower in comparison with measurements in the region (32-34 psu; Delcroix & Hénin, 1991). During El Niño, sea surface salinity in the ETP decreases significantly, primarily due to increased precipitation, reduced upwelling of deep salt water and the eastward advection of fresher waters from the central Pacific (Delcroix & Hénin, 1991; Vialard et al., 2002). In addition, the study area, being surrounded by mangroves, estuarine environments, and coastal lava pools, could be susceptible to fluctuations in salinity, as these ecosystems are influenced by tidal exchanges, evaporation, and localized freshwater inputs (Lugo & Snedaker, 1974). Dissolved oxygen (mean 91.10%) reflected well-mixed, oxygen-rich waters (O'Boyle et al., 2009), while pH occasionally peaked at 8.47 due to tidal dynamics and photosynthetic activity from algae, likely reducing dissolved carbon levels (Gattuso et al., 1998). TDS averaged 20.26 ppt, consistent with other marine environments (Adjovu et al., 2023).

Biological Variables

Coral Mortality and Health.

The mortality and health indicators remained low and stable in *Pocillopora* fragments from both nurseries and outplants (Figure 3 & Figure 4). In contrast, massive corals experienced higher levels of affectation (Figure 3). Overall, coral gardening efforts in Isabela have been successful, as most morphotypes exhibited low mortality and maintained good health throughout the study.

Many coral restoration study cases conducted in the ETP have highlighted significant progress and comparable outcomes (with similar strategies and species). Nevertheless, the presence and different intensity of certain ecological processes and interactions require caution when comparing results. The closest coral restoration study to Galápagos is in Gorgona Island, Colombia, where *Pocillopora damicornis* achieved a survival rate of up to 66.9% in nurseries and 100% post-transplantation (Ishida-Castañeda et al., 2020). In Costa Rica, *Pocillopora* spp. exhibited 100% survival on the seabed, while massive corals such as *Pavona gigantea*, *Pavona clavus*, and *Porites lobata* experienced mortality rates of 52.5%, 28.6%, and 80%, respectively, due to greater susceptibility to factors such as predation, sedimentation, and tissue loss (Fabregat-Malé et al., 2024). In Mexico, *Pocillopora* spp. and *Pavona clavus* directly transplanted in the Marías Islands achieved survival rates of 58% and 61%, respectively, although extreme climatic events like Hurricane Willa significantly contributed to losses (Tortolero-Langarica et al., 2014). In that case, mortality was higher in *Pocillopora* due to its branching structure, which makes it more susceptible to breakage during extreme events like hurricanes, unlike massive corals, which are more resistant due to their flatter and more compact structure. In the rest of the study cases, the higher affectation in massive species and the role of sedimentation on tissue loss are consistent with the results of our monitoring and the correlation between TDS and % of dead tissue, respectively (Fabregat-Malé et al., 2024; Liñán-Cabello et al., 2011).

These studies also underscore the importance of controlling algal cover and leveraging the positive impact of grazer species such as sea urchins (e.g., *Diadema mexicanum*), which act as a natural biological controller (Fabregat-Malé et al., 2024). When a coral tissue is weak or dies, turf algal colonization and overgrowth begins, impacting coral capacity of regeneration (De Carvalho & Villaça, 2021; Diaz-Pulido & McCook, 2002). While mixed-species algal turfs may not directly cause coral mortality, certain species can actively overgrow killing coral tissue (Jompa & McCook, 2003; Smith et al., 2006). In the ETP, unconsolidated accumulations of dead coral debris are related to colonizing cryptic macroalgae (Fong et al., 2017). These ecological processes may explain the observed association between biological variables, such as mortality and % of algal cover. Such interactions emphasize the importance of maintaining low algal cover during restoration efforts to improve coral survival. Other species with a critical impact are corallivores that limit coral growth and recovery (e.g., *Arothron meleagris* in Gorgona; Ishida-Castañeda et al., 2020). Overall, these findings reinforce the need to consider local environmental factors, ecological interactions and adaptive strategies to ensure the success of restoration efforts for massive corals.

Our results indicate that coral mortality and health indicators in Galápagos nurseries and transplants were not significantly impacted by the measured environmental variables. This lack of association suggests that these coral morphotypes, particularly within the *Pocillopora* genus, were not affected by the environmental conditions, which we consider moderate, during the “cold season” of 2023, dampened by the ongoing El Niño event. de la Torre (2023) compared the thermal tolerance of *Pocillopora* fragments from the same nursery in Isabela and their donor colonies, measuring photosynthesis and respiration rates under different temperatures. The experimental results showed that nursery corals had high thermal tolerance, with optimal performance at temperatures exceeding 32°C, suggesting resilience to high temperatures and El Niño events (de la Torre, 2023). The slight influence of pH on coral bleaching matches with previous knowledge about their physiology. In *ex situ* experiments, low pH states impact coral development and recovery in *Pocillopora* and massive corals (Hall et al., 2015; Viyakarn et al., 2015). The surface waters of the ETP have relatively low pH, so further study of the role of pH in the physiology of corals in the region may be valuable (Fiedler & Lavín, 2017).

We recorded and quantified coral mortality and tissue loss but did not evaluate their causes at a histological resolution. Despite their vulnerability, research on coral mortality and health in the ETP is limited (Galloway et al., 2009), leading to a relatively low number of coral diseases compared to other regions (Rodríguez-Villalobos & Reyes-Bonilla, 2019). In other parts of the world, scientific research has deeply studied more than 30 diseases that affect coral survival, health, growth and regeneration (Galloway et al., 2009). *Pocillopora* corals in the ETP suffer various health issues, including white band-like diseases (Garzón Ferreira & Pinzón C., 2016) and tissue loss lesions caused by predation (Rodríguez-Villalobos et al., 2015). Other cases include atrophy, zooxanthellae depletion, and tissue ablation, often combined with bleaching, algal and sponge overgrowth, bioerosion, and unexplained tissue loss (Alvarado et al., 2017; Rodríguez-Villalobos et al., 2014). In addition, anthropogenic factors, such as pollution, coastal development, and destructive fishing practices, contribute to mortality emergence and spread (Figueroa-Pico et al., 2020; Ponti et al., 2016; Susmaa et al., 2024). The wide variety of factors that influence coral physiology indicates the need for further studies that examine coral health in Galápagos at a histopathological level.

Another factor that can influence the mortality and health of *Pocillopora* corals in nurseries is the initial size of the fragments. Larger fragments tend to have higher survival rates and faster recovery from stress compared to smaller ones (Ishida-Castañeda et al., 2020). This relationship is likely due to the greater energy reserves and structural integrity in larger fragments, which make them more resilient to environmental stressors such as temperature fluctuations, sedimentation, and predation (Fabregat-Malé et al., 2024; Ishida-Castañeda et al., 2020). Therefore, considering fragment size in nursery-based restoration efforts is essential to improve the effectiveness of transplantation and long-term survival.

One limitation of this study was the relatively short duration of the multiparameter measurements, as the equipment required frequent recalibration, reducing the amount of environmental data collected. Future research should aim to increase the frequency and duration of environmental monitoring, particularly during key climatic events such as La Niña, to better understand the interactions between environmental conditions and coral health. Additionally, establishing new nurseries with a wider range of environmental conditions and fragment sizes would provide more robust insights into the factors affecting coral survival and resilience.

CONCLUSIONS

This study reinforces the potential of *Pocillopora* as a resilient genus for coral restoration programs in the Galápagos and the broader ETP region. The observed welfare of *Pocillopora* morphotypes under the moderate environmental conditions of the 2023 El Niño event suggests their adaptability to fluctuating oceanographic conditions. However, the challenges faced by massive corals like *Pavona* and *Porites* highlight the need for species-specific approaches in restoration efforts. Future initiatives should prioritize adaptive strategies that integrate long-term environmental monitoring with active management of the nurseries. As climatic anomalies like El Niño may become more frequent, understanding species-specific responses and developing tailored interventions will be critical to ensuring the resilience and recovery of coral ecosystems in this vulnerable region.

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APPENDIX A: SUMMARY OF ENVIRONMENTAL VARIABLES FROM MULTIPARAMETER

Environmental Variable	Mean	Min	Max	SD
DO [%]	91.10	85.66	95.19	4.02
pH	8.08	8.02	8.15	0.06
Sal [psu]	26.26	21.37	33.91	5.49
TDS [ppt]	20.26	16.57	25.77	3.98
Temp [°C]	25.29	22.18	27.50	1.64

DO: dissolved oxygen, pH: alkalinity, Sal: salinity, TDS: total dissolved solids, Temp: temperature.

APPENDIX B: CORAL MORPHOTYPES IN NURSERIES AND OUTPLANTS

Origin Site	Genus	Species	Morphotype	N of Fragments			
				Bay Nursery			Pilot Outplants
				Ropes	Trees	Tables	
Calera & Concha Perla	*Pocillopora*	*Pocillopora capitata*	P9	100			24
			PDY		15		
			PX2	100			8
		Pocillopora cf. meandrina	PM		15		8
		Pocillopora damicornis	P10	100			8
			P13	100			8
			P14	100			
			P4	100			8
			PD1		15		
			PD1-2		15		8
			PDB		15		8
			PDI				8
			PDX		15		
			PMIX		15		
		Pocillopora inflata	PINF		15		8
		Pocillopora spp.	Mix				32
	Pavona	*Pavona chiriquiensis*	PCH5			24	

		Pavona gigantea	PAG3			24	
	Porites	*Porites lobata*	POL13			24	
Hortensia	*Pocillopora*	*Pocillopora capitata*	PX9	20			
		Pocillopora damicornis	PX10	100			8
Islote El Faro	*Pocillopora*	*Pocillopora damicornis*	P19	100			24
Las Tablas	*Pocillopora*	*Pocillopora capitata*	PX4	100			8
			PX5	100			8
		Pocillopora damicornis	PX7		60		
		Pocillopora verrucosa	PX6	100			8
			PX8	100			8
Lobería Chica	*Pavona*	*Pavona clavus*	PAC7			24	
			PACE			24	
	Porites	*Porites lobata*	POL18			24	
Lobería Grande	*Pocillopora*	*Pocillopora damicornis*	PLG3		15		8
			PLG4		15		8
			PLG5		15		8
			PLG6		15		
Punta El Faro	*Pocillopora*	*Pocillopora capitata*	PX3	100			8
Tintoreras	*Pocillopora*	*Pocillopora capitata*	P?5	100			16
			P5				8
		Pocillopora damicornis	P?7	80			
		Pocillopora verrucosa	PX1	100			8
Tortuga	*Pocillopora*	*Pocillopora damicornis*	PT2		12		
			PT4		12		

	Pocillopora verrucosa	PT5		12		
		PT6		12		
		PT9		12		
		PT1		12		
		PT10		12		
		PT3		12		
		PT7		12		
		PT8		12		
Total			1600	360	144	256

APPENDIX C: SUMMARY OF BIOLOGICAL VARIABLES

Restoration Phase	Technique	Genus	Fragment Mortality (%)			% of Dead Tissue			% of Bleached Tissue			% of Algal Cover		
			mean	**min**	**max**	**mean**	**min**	**max**	**mean**	**min**	**max**	**mean**	**min**	**max**
Bay Nursery	Rope	*Pocillopora*	3.63	0.00	16.00	6.08	0.00	28.72	0.34	0.00	5.27	5.64	0.00	26.21
	Tree	*Pocillopora*	0.15	0.00	6.67	10.36	0.00	83.83	0.95	0.00	31.67	9.01	0.00	72.20
	Table	*Pavona*	7.21	0.00	29.17	20.70	0.00	86.46	9.30	0.00	76.67	17.59	0.00	81.29
		Porites	54.69	0.00	100.00	69.76	1.04	100.00	8.09	0.00	31.38	67.68	1.04	100.00
Pilot Outplants	Transplant	*Pocillopora*	0.39	0.00	12.50	0.91	0.00	18.88	2.52	0.00	37.50	0.73	0.00	18.88

APPENDIX D: TENDENCIES OF BIOLOGICAL VARIABLES ACROSS TIME

Restoration Phase	**Genus**	**Fragment Mortality**			**% of Dead Tissue**			**% of Bleached Tissue**			**% of Algal Cover**		
		McFadden R^2	**p value**	**signif**	**McFadden R^2**	**p value**	**signif**	**McFadden R^2**	**p value**	**signif**	**McFadden R^2**	**p value**	**signif**
Bay Nursery	*Pavona*	0.00	0.95		0.00	0.79		0.19	0.01	**	0.01	0.49	
	Pocillopora	0.00	0.18		0.04	0.00	***	0.13	0.00	***	0.05	0.00	***
	Porites	0.37	0.00	***	0.54	0.00	***	0.32	0.01	**	0.56	0.00	***
Pilot Outplants	*Pocillopora*	0.00	1.00		0.02	0.10		0.03	0.03	*	0.01	0.27	

McFadden R^2 and p-values correspond to the results of logistic regression models used to assess trends in biological variables over time. McFadden R^2 is a measure of model fit that ranges from 0 to 1, where higher values indicate a better fit. P-values indicate the statistical significance of the models, with a threshold of $p < 0.05$ considered statistically significant. Asterisks indicate the level of statistical significance for p-values: *** corresponds to $p < 0.001$, ** corresponds to $p < 0.01$ and * corresponds to $p < 0.05$.

APPENDIX E: CORRELATION BETWEEN ENVIRONMENTAL AND BIOLOGICAL VARIABLES

Ocean Variable	Restoration Phase	Genus	Fragment Mortality			% of Dead Tissue			% of Bleached Tissue			% of Algal Cover		
			McFadden R^2	p	signif	McFadden R^2	p	signif	McFadden R^2	p	signif	McFadden R^2	p	signif
DO	Bay Nursery	*Pavona*	0.00	0.96		0.00	0.98		0.07	0.41		0.05	0.51	
		Pocillopora	0.00	0.95		0.00	0.78		0.01	0.55		0.00	0.90	
		Porites	0.00	0.92		0.17	0.40		0.45	0.13		0.15	0.43	
	Pilot Outplants	*Pocillopora*	0.00	1.00		0.00	0.93		0.00	0.80		0.00	0.78	
pH	Bay Nursery	*Pavona*	0.00	0.99		0.00	0.98		0.01	0.72		0.01	0.83	
		Pocillopora	0.00	0.56		0.00	0.61		0.07	0.06		0.00	0.53	
		Porites	0.47	0.15		0.17	0.40		0.57	0.10		0.17	0.39	
	Pilot Outplants	*Pocillopora*	0.00	1.00		0.01	0.53		0.00	0.71		0.01	0.66	
Sal	Bay Nursery	*Pavona*	0.00	0.95		0.00	0.99		0.04	0.55		0.14	0.32	
		Pocillopora	0.01	0.52		0.01	0.40		0.02	0.34		0.01	0.44	
		Porites	0.86	0.05	*	0.85	0.01	**	0.01	0.89		0.83	0.02	*
	Pilot Outplants	*Pocillopora*	0.00	1.00		0.02	0.45		0.01	0.51		0.03	0.44	
TDS	Bay Nursery	*Pavona*	0.00	0.95		0.00	0.99		0.04	0.56		0.14	0.32	
		Pocillopora	0.01	0.52		0.01	0.40		0.02	0.32		0.01	0.43	
		Porites	0.86	0.05	*	0.85	0.01	**	0.00	0.93		0.84	0.02	*
	Pilot Outplants	*Pocillopora*	0.00	1.00		0.02	0.44		0.01	0.50		0.03	0.44	
Temp	Bay Nursery	*Pavona*	0.00	0.95		0.00	0.99		0.03	0.62		0.13	0.33	
		Pocillopora	0.01	0.49		0.01	0.38		0.03	0.24		0.01	0.41	
		Porites	0.85	0.04	*	0.87	0.01	**	0.00	0.91		0.85	0.02	*

Pilot Outplants	*Pocillopora*	0.00	1.00	0.02	0.41	0.01	0.49	0.03	0.43

DO: dissolved oxygen, pH: alkalinity, Sal: salinity, TDS: total dissolved solids, Temp: temperature. McFadden R^2 and p-values correspond to the results of logistic regression models used to assess the relationship between environmental and biological variables. McFadden R^2 indicates the proportion of variance explained by the model, ranging from 0 to 1, with higher values suggesting a better model fit. p-values reflect the statistical significance of the models, with a threshold of $p < 0.05$ considered statistically significant. Asterisks indicate the level of statistical significance for p-values: *** corresponds to $p < 0.001$, ** corresponds to $p < 0.01$ and * corresponds to $p < 0.05$.