

<https://doi.org/10.15517/0xznfj40>

First assessment of the physiological performance of nursery corals in the Galápagos Islands: seasonal impacts on *Pocillopora* (Scleractinia: Pocilloporidae) growth

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Received 07-X I-2025. Corrected 05-V-2026. Accepted 06-VI-2026.

ABSTRACT

Introduction: Coral communities in the Galápagos Islands persist under highly variable oceanographic conditions driven by seasonal upwelling and ENSO-related thermal anomalies, which have historically constrained reef development and recovery. Following the 1982–83 El Niño event (~97 % coral mortality), recovery has been slow and fragmented. Despite this, *Pocillopora* remains the dominant reef-building genus in the central-southern archipelago and a key target for restoration. However, it remains unclear how seasonal thermal variability influences coral performance in nursery settings.

Objective: To evaluate how seasonal thermal variability affects the growth, survival, and condition of *Pocillopora* corals in nursery settings in the Galápagos, in order to inform restoration strategies.

Methods: Coral communities were assessed in Puerto Villamil Bay (Isabela Island), and 12 *Pocillopora* morphotypes were propagated in rope nurseries. Fragments were monitored using photographic records, and surface area was measured with ImageJ. Absolute, relative, and specific growth rates were calculated, along with mortality and tissue condition (% dead, bleached, and algal cover). In situ temperature data and El Niño 1+2 anomalies were incorporated to characterize thermal variability.

Results: The coral community was dominated by *Pocillopora* (73.6 %, n = 3 569 colonies). Temperatures ranged from 18.7 to 30.1 °C under La Niña conditions. Fragment size increased more than fourfold (from 6.40 ± 2.51 to 27.75 ± 15.85 cm²), with an overall survival rate of 80 %. Growth exhibited strong seasonal patterns: relative and specific growth rates were higher during the warm season, while absolute growth was greater in the cold season. However, the cold upwelling period was associated with reduced overall performance, including higher mortality, tissue loss, and algal overgrowth. Significant differences among morphotypes were observed.

Conclusions: Coral gardening is viable in the Galápagos, although seasonal cooling imposes important constraints. Restoration strategies should prioritize resilient morphotypes and account for seasonality to optimize outcomes in marginal reef systems.

Key words: coral gardening; thermal stress; La Niña, intraspecific variation; Eastern Tropical Pacific; coral physiological condition.



RESUMEN

Primera evaluación del desempeño fisiológico de corales en viveros en las islas Galápagos: efectos estacionales sobre el crecimiento de *Pocillopora* (Scleractinia: Pocilloporidae)

Introducción: Las comunidades coralinas en las islas Galápagos persisten bajo condiciones oceanográficas altamente variables, impulsadas por el afloramiento estacional y las anomalías térmicas asociadas al ENSO, que históricamente han limitado el desarrollo y la recuperación de los arrecifes. Tras el evento de El Niño de 1982–83 (~97 % de mortalidad coralina), la recuperación ha sido lenta y fragmentada. A pesar de ello, *Pocillopora* sigue siendo el género constructor dominante en el centro-sur del archipiélago y un objetivo clave para la restauración. Sin embargo, aún se desconoce cómo la variabilidad térmica estacional influye en su desempeño en viveros.

Objetivo: Evaluar cómo la variabilidad térmica estacional afecta el crecimiento, la supervivencia y la condición de corales *Pocillopora* en viveros en Galápagos, con el fin de informar estrategias de restauración.

Métodos: Se evaluaron las comunidades coralinas en la bahía de Puerto Villamil (Isabela) y se propagaron 12 morfotipos de *Pocillopora* en viveros tipo cuerda. Los fragmentos fueron monitoreados mediante registros fotográficos y su área superficial se midió con ImageJ. Se calcularon tasas de crecimiento absoluto, relativo y específico, así como mortalidad y condición del tejido (% muerto, blanqueado y cobertura algal). Se integraron datos de temperatura in situ y anomalías del Niño 1+2.

Resultados: La comunidad coralina estuvo dominada por *Pocillopora* (73.6 %, $n = 3\,569$ colonias). Las temperaturas oscilaron entre 18.7 y 30.1 °C bajo condiciones de La Niña. El tamaño de los fragmentos aumentó más de cuatro veces (de 6.40 ± 2.51 a 27.75 ± 15.85 cm²), con una supervivencia del 80 %. El crecimiento mostró patrones estacionales marcados: las tasas relativa y específica fueron mayores en la estación cálida, mientras que el crecimiento absoluto fue mayor en la estación fría. No obstante, el afloramiento frío se asoció con menor desempeño general, incluyendo mayor mortalidad, pérdida de tejido y sobrecrecimiento de algas. Se observaron diferencias significativas entre morfotipos.

Conclusiones: La jardinería de corales es viable en Galápagos, aunque el enfriamiento estacional impone limitaciones importantes. Se deben priorizar morfotipos resilientes y considerar la estacionalidad para optimizar los resultados de restauración en sistemas arrecifales marginales.

Palabras clave: jardinería de corales; estrés termal; La Niña; variación intra-específica; Pacífico Tropical Oriental; condición fisiológica del coral.

INTRODUCTION

Coral reefs are among the most biodiverse, complex, and productive ecosystems on Earth, playing a crucial role in providing ecosystem services such as shoreline protection, food security, and tourism, for millions of people in coastal and insular regions (Knowlton et al., 2021; Woodhead et al., 2019). However, in less than 50 years, approximately 40 % of global coral cover has been lost or degraded — a trend that is accelerating, with an estimated annual loss of up to 2 % (Bruno & Selig, 2007). This decline is driven by a combination of factors including ocean warming, acidification, overfishing and anthropogenic disturbances (Knowlton et al., 2021). The resulting degradation has severely impaired the productivity and resilience of coral reefs, diminishing their contributions to human well-being. These climatic

and ecological changes underscore the urgent need for active restoration practices to mitigate the severe degradation of coral reef ecosystems, at least on a local scale (Rinkevich, 2014). One of the most promising approaches to restoration is coral gardening, a strategy that involves rearing coral fragments in land-based or underwater nurseries, followed by their transplantation to degraded reef areas once they reach an appropriate size (Rinkevich, 2014). This approach has gained widespread acceptance among restoration practitioners and coral reef managers in more than 50 countries, yielding impressive results in coral restoration (Bayraktarov et al., 2020; Boström-Einarsson et al., 2020).

The Eastern Tropical Pacific (ETP) hosts coral communities that support highly complex biotic interactions, comparable to those observed in more prominent coral reef regions globally (Glynn et al., 2018). It is characterized

by extreme and fluctuating oceanographic conditions, including reduced salinity, low pH, seasonal upwelling, and significant annual and interannual changes in Sea Surface Temperature (SST), particularly caused by El Niño–Southern Oscillation (ENSO) events (Cortés et al., 2016). At the heart of the ETP lie the Galápagos Islands, the major oceanic archipelago in this marine region and a key biogeographic province (Briggs, 1974). Despite their equatorial location, these islands experience the convergence of three major water masses (Houvenaghel, 1978): the cold, nutrient-rich Equatorial Undercurrent, flowing from west to east; the cool Peruvian Coastal and Oceanic Currents, which flow more intensely from June to December (cold season); and the warmer tropical waters of the Panama Current, which dominate from January to May (warm season) (Glynn, 1984). The timing, intensity, and direction of these currents are influenced by ENSO oscillations, which intensify the Peruvian currents during “La Niña” and the Panama Current during “El Niño” (Glynn et al., 2018).

These shifts in ocean dynamics around the Galápagos Islands cause significant ecological imbalances and stress to local marine communities (Glynn & Wellington, 1983). A stark example of this occurred during the devastating 1982–1983 El Niño event, which led to the widespread collapse of Galápagos coral reefs and coral communities. Before this, the Galápagos archipelago formerly hosted numerous well-developed and healthy coral reef assemblages that had experienced continuous growth for over half a millennium (Glynn et al., 2018). However, post ENSO surveys revealed a staggering 97 % mortality due to large-scale bleaching throughout the archipelago, drastically reducing historical coral populations and eliminating most structural reefs (Glynn & Wellington, 1983). Over the past 40 years, coral recovery in the Galápagos has been slow, particularly in the central and southeastern regions of the archipelago (Feingold & Glynn, 2013). Although subsequent El Niño events of similar magnitude (1997–98, 2014–15) caused less direct damage (Glynn, 2000), evidence from

La Niña events (2007) suggests that cold-water bleaching is also a significant factor limiting coral recovery in the southern islands (Feingold & Glynn, 2013; Rhoades et al., 2023).

The remnant coral assemblages in the Galápagos now consist of isolated communities hosting several species, including *Pavona clavus*, *Pavona gigantea*, *Pavona varians*, *Pavona chiriquiensis*, *Porites lobata*, *Gardinerosis planulata*, and various Pocilloporids (Pinzón & LaJeunesse, 2010). The branching corals of the *Pocillopora* genus are key foundational species in the ETP, providing critical habitat for a diverse array of associated species (Cortés et al., 2016) and playing a significant role in coral reef formation throughout the region (Toth et al., 2012). In the Galápagos, Pocilloporids are predominantly found as scattered colonies, forming isolated patches of coral communities across the archipelago. An exception to this is “Concha y Perla” lagoon on Isabela Island, which hosts the densest *Pocillopora* aggregation in the Galápagos (Baums et al., 2014). Adjacent to this lava lagoon, we established the study site, which included a baseline survey and the installation of a pilot coral nursery. Specifically, we addressed the following questions: (1) What is the present status and health condition of coral colonies in Puerto Villamil Bay? (2) How do the climatic seasons (warm vs. cold period) influence the growth of *Pocillopora* corals cultivated in the nursery? (3) Are there differences in growth and fitness among *Pocillopora* morphotypes? (4) How do oceanographic conditions (seawater temperature and ENSO) relate to coral fitness in the nursery?

MATERIALS AND METHODS

Study area: Puerto Villamil Bay (0°57'53.6"S, 90°57'24.8"W) in Isabela Island is a topographically complex area characterized by rocky shores, islets and tidal pools (Fig. 1). It includes “Concha y Perla”, a sheltered lagoon formed by a series of islets and rocky outcrops, with a maximum depth of 6 m; “La Calera”, a tidal water body bordered by rocky shores and dominated by a sandy substrate, but

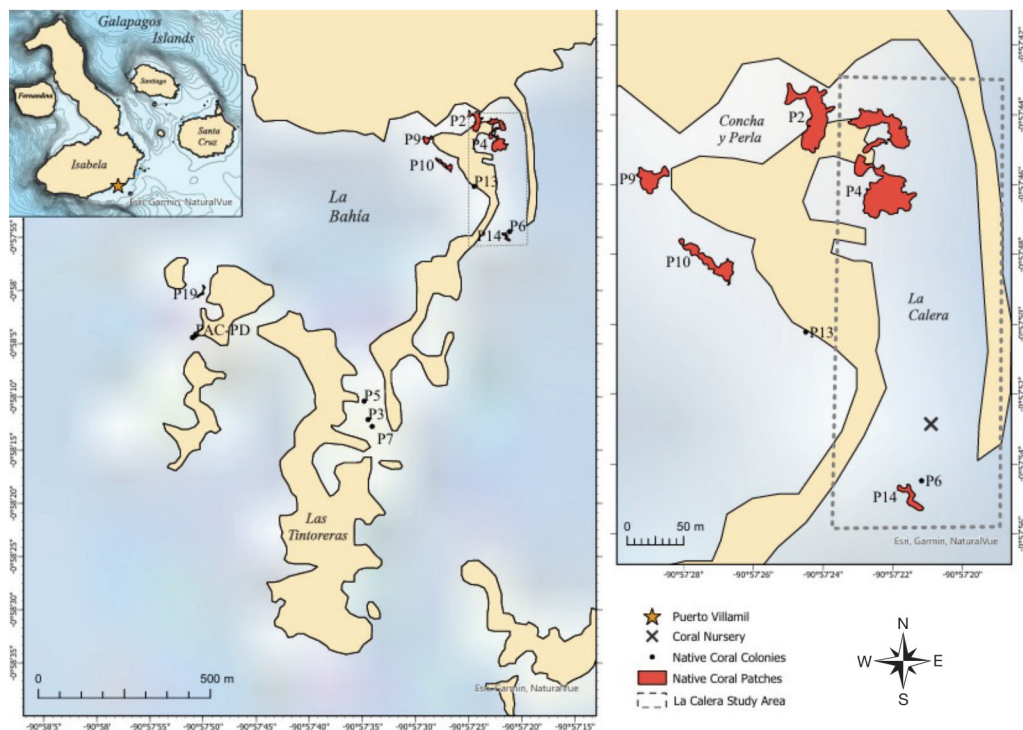


Fig. 1. Study area in Puerto Villamil Bay, Isabela Island, Galápagos Archipelago. Locations of the 12 donor colonies are shown with their respective morphotype code.

with scattered patches of hard substrate; and “La Bahía”, the main bay area, protected from waves and located near Puerto Villamil’s main pier. This area is enclosed by rocky structures that form natural boundaries with Concha y Perla, La Calera and the tourist-attracting rocky islets and channels collectively known as “Las Tintorerías”. Historically, Puerto Villamil and surrounding waters supported an extensive coral reef, however, today this area consists of isolated coral patches interspersed with rocky and sandy substrates (Baums et al., 2014; Glynn et al., 2018).

Baseline survey and establishment of coral nurseries: Between November and December 2021, we divided Puerto Villamil’s Bay into 21 quadrants of 200 x 200 m each. Inside each quadrant, coral colonies of all genera were located with a surface roving survey with snorkel equipment. Every colony

was georeferenced, measured (diameter and height), identified to the lowest taxonomic level, and its fitness scored according to the presence and degree of bleaching, disease, parasites, predation and fragmentation. Each score (based on Goergen et al., 2020) corresponded to the percentage of the surface area affected, namely: 0 = 0 %, 1 = 1–24 %, 2 = 25–49 %, 3 = 50–74 %, 4 = 75–99 %, and 5 = 100 %.

Given that the taxonomy of Pocilloporids in the ETP remains unresolved (Pinzón & LaJeunesse, 2010), with recent genomic studies revealing multiple cryptic species within previously identified taxa (Connelly et al., 2026) we used the term “morphotype” instead of species or morphospecies for this genus. We considered different morphotypes as such based on two criteria: 1) the *Pocillopora* species’ description by Hickman (2008), and a distance > 100 m between colonies, which would increase the likelihood of finding different genotypes

(Goergen et al., 2020). However, we recognize that potentially some of these colonies can be clones, according to the results of Baums et al. (2014). We selected the healthiest and most common 12 *Pocillopora* morphotypes as donors for the nurseries. For each morphotype, we aimed to collect 20 fragments while ensuring that no more than 10 % of the donor colony area was removed to minimize damage (Epstein et al., 2001). When a single colony was too small to provide 20 fragments, these were collected from 2–3 nearby colonies of the same morphotype within a maximum distance of 5 m. In cases where only one colony of a given morphotype was available, fragment

collection was restricted to the 10 % threshold, resulting in fewer than 20 fragments for some morphotypes.

At the start of the warm season (January 15, 2022) and following the methods of Shafir et al. (2010), we established two identical rope nurseries (Fig. 2) at a depth of 3 m in La Calera (Fig. 1), positioned less than 5 m apart. Each nursery consisted of six ropes, with each rope assigned to a single morphotype and supporting 7–20 fragments per morphotype. Each fragment was photographed and labeled before being attached to the rope. The nurseries were maintained weekly, by brushing off diatoms and turfing algae growing on the ropes with a synthetic

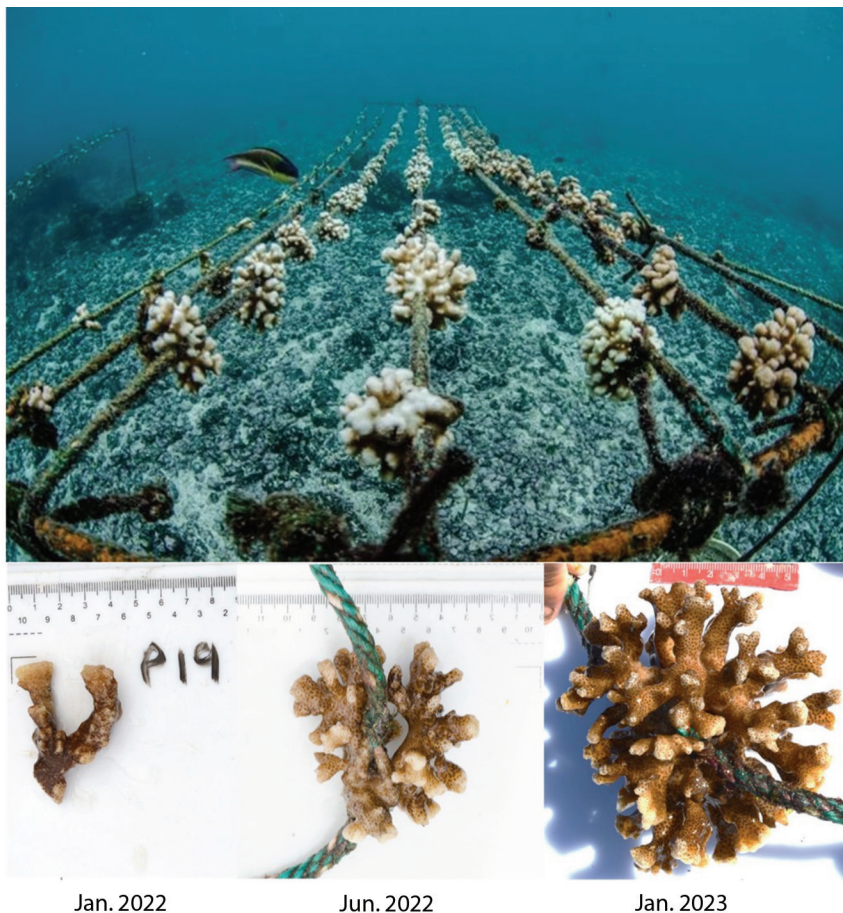


Fig. 2. Top panel: rope nurseries in Puerto Villamil, Isabela Island, Galápagos Archipelago, with *Pocillopora* coral fragments of approximately 10 months. Bottom panel: images of Morphotype P9 taken at the three sampling periods. Photo credits: Nicolás Dávalos.



bristle brush. We deployed one temperature logger (HOBO, TidbiT) at 3 m depth relative to Mean Sea Level, set at 10 min intervals for continuous temperature recordings, from mid-January 2022 to mid-December 2022. To assess whether ENSO conditions were present during the study period, we obtained El Niño Anomaly 1+2 index data. Weekly SST anomaly datasets (ENSO indices dataset wksst9120.for) were downloaded from the National Ocean and Atmospheric Administration [NOAA] Climate Prediction Center (n.d.).

Coral growth in the nursery: To study coral growth in both warm and cold seasons, we measured colony size at three time points, however we compared growth between the two seasons. We measured each colony size at the beginning of the warm season (January 2022), at the beginning of the cold season (June 2022), and at the beginning of the next warm season (January 2023). The warm season comprehended the first interval (January-May 2002), and the cold season the second (June-December 2022). Each rope was carefully removed from the nursery and placed in a bucket of seawater to minimize stress to the corals. Individual colony fragments were briefly (>1 min) exposed to air and photographed sequentially on land using a Nikon D7000 digital camera mounted on a tripod, positioned directly overhead to capture a top-down view. Each fragment was placed on a whiteboard with a measuring ruler in cm for scale. Digital photographs were processed in ImageJ (Schroeder et al., 2020), where the coral fragment's edges were traced to measure maximum length (defined as the length of the longest branch), perimeter, and coral planar area projected onto a 2D horizontal plane (House et al., 2018). We use and report coral planar area as the primary metric for evaluating growth rates, however maximum length metrics are included as supplement to ease comparison with similar studies of the region (Ishida-Castañeda et al., 2019; Manze-llo, 2010). Importantly, both metrics showed similar growth patterns, indicating that trends

observed in planar areas were consistent with those detected using maximum length.

To assess coral growth, we used three rates following the methods of Hopkins (1992). The Absolute Growth Rate (AGR) was determined as the difference in coral fragment sizes between two time points, divided by the duration of that period. The Relative Growth Rate (RGR) was calculated as the percentage increase relative to the initial fragment size, while the Specific Growth Rate (SGR) was estimated by using an exponential growth model. Relative and specific growth rates provide size-independent metrics. Growth rates were calculated by season and by morphotype within each season using the following formulas:

$$AGR = \frac{S_f - S_0}{S_0 \cdot t_{days}} (cm^2 yr^{-1} \text{ or } cm yr^{-1})$$

$$RGR = \frac{S_f - S_0}{S_0 \cdot t_{days}} (\% yr^{-1})$$

$$SGR = \frac{\ln \ln S_f - \ln \ln S_0}{t_{days}} (yr^{-1})$$

where S_f and S_0 are the final and initial sizes (measured as planar area and maximum length, ML) of each season, and t_{days} is the number of days between sampling periods. We standardized growth rates at an annual rate by multiplying the above formulas by 365 days.

Coral fitness: Mortality and coral fitness were evaluated starting in May 2022, after field assistants were retrained to standardize data collection. Monthly coral mortality was calculated for each *Pocillopora* morphotype as the ratio of dead coral fragments to the total number of coral fragments, using the formula:

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

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

To assess coral fitness, we estimated for each fragment the percentage of dead tissue,

bleached tissue and algal cover, following the Goergen et al. (2020) scoring system described above. To calculate the mean fitness indicators, we used the upper limit of each scoring range, for example for a score of 2, we reported 49 %, which likely overestimates the affected area. We then averaged these upper limits across all coral fragments per morphotype using the following formula:

$$\bar{F} = \frac{1}{N_{total}} \sum F_{max}$$

where F is the average of each health indicator, N_{total} is the total number of coral fragments, and F_{max} is the upper limit of each of the percentage range of tissue affectation. We report our results as percentages.

Statistical analyses: To assess general patterns in growth rates between seasons, we first performed paired Student's t-tests pooling all morphotypes together and calculated Cohen's d to measure effect sizes between the warm and cold seasons. Cohen's d provides a standardized measure of the magnitude of the difference between groups, allowing us to evaluate the biological relevance of seasonal effects independently of sample size. Subsequently, we conducted separate paired t-tests for each morphotype to compare growth rates between seasons, also computing Cohen's d for each case. Additionally, we assessed differences in growth rates among morphotypes within each season using Welch ANOVAs, followed by Games-Howell post-hoc tests to account for unequal variances and sample sizes. As some coral fragments died during the study period, their size measurements and growth rates (after death) were considered NA-values in our analyses. We report results for all these growth rates when evaluating all morphotypes together across seasons, however, when comparing growth rates among morphotypes we chose to only use the relative growth rates, because it provides a size-independent measure of growth that allows for direct comparison among morphotypes that differ in initial fragment size and morphology,

avoiding potential biases associated with absolute or exponential growth estimates.

Finally, to examine the relationship between coral fitness (mortality and percentage of dead tissue) and growth during the cold season (June–December 2022, when mortality data were available), we performed linear regression analyses to test whether mean coral growth rates correlated with coral mortality and/or the percentage of dead tissue per morphotype. For each analysis, we calculated both the coefficient of determination (R^2) and the associated p-value. All data and code used in the analyses presented in this study are publicly available at <https://github.com/davelascoc/galapagos-reef-revival>.

RESULTS

Coral status in Puerto Villamil Bay: We recorded a total of 3 569 hermatypic coral colonies in Puerto Villamil, belonging to Pocilloporids and four massive coral species (Appendix 1). The *Pocillopora* genus was the most abundant, representing 73.6 % of the surveyed colonies, followed by *Pavona clavus* (22.0 %), *Pavona gigantea* (2.3 %), *Porites lobata* (1.8 %), and *Pavona chiriquiensis* (0.3 %). The colonies were mainly distributed on rocky platforms between 0.5 and 7 m depths. Based on morphological descriptions in Hickman (2008), the two most common *Pocillopora* morphotypes in Concha y Perla resemble colonies historically assigned to *P. cf. damicornis* and *P. cf. capitata*, forming dense thickets near the lagoon inlet and outlet, respectively. Diameters ranged from 4 to 450 cm and heights from 2 to 300 cm, with the largest dimensions observed in *Pavona clavus* and *Pavona gigantea*, while *Pocillopora* predominated in small and medium-sized corals. Colonies of massive corals were also the tallest (Appendix 1).

In terms of their fitness, average bleaching was mild across all species, remaining below 21 %, with minimal values in *Pavona* (<2 %) and higher levels in *Pocillopora* (16 %) and *Porites lobata* (20.6 %) (Appendix 2). Diseases were higher in *P. clavus* and *P. gigantea* (29.8

and 21.5 %, respectively). All massive corals presented parasites, mainly trematodiasis (Vera & Banks, 2009), which was most prevalent in *Porites lobata* (16.1 %). Predation was also the highest in this species (5.4 %); Pocilloporids had a mild average predation and no signs of parasitism. Signs of predation and fragmentation were sporadic and of low severity in massive corals. Fragmentation scores were highest in Pocilloporids (29 %); however, in massive corals it ranged between 0 and 2.4 % (Appendix 2).

Oceanographic conditions: During our study, water temperature recorded by our HOBO loggers ranged between 18.71 and 30.15 °C, with an average of 23.12 °C. The first half of 2022 had an average water temperature of 24.90 ± 2.12 , while the second of 21.82 ± 1.13 . Warm-season months (January to May) exhibit a higher median temperature (24.54 °C) and broader interquartile range (23.29–26.59 °C), compared to the cold season months (June to December) (median = 22.05 °C, IQR = 20.90–22.72 °C). Temperature drops occurred between late April and late November and were categorized as events where water temperature fell below 20 °C. HOBO loggers revealed five significant drops (Fig. 3), indicative of the periodic shoaling of cold-water Kelvin waves

along the Galápagos shoreline (Glynn et al., 2018). The first occurred on April 26th, 2022 (Fig. 3), with an abrupt temperature drop to 19.47 °C in the second half of the warm season and with a duration of 12 hrs (14 days earlier, the temperature was 27.66 °C). Subsequent temperature minima were recorded on September 18th (18.71 °C), October 3rd (18.90 °C), November 4th (19.76 °C), and November 30th (19.09 °C, Fig. 3). El Niño index data for the 1+2 region between January 2022 and January of 2023 remained negative, with a mean of -1.02 and values ranging from 0 to -2.0, indicating persistent moderate to strong La Niña conditions throughout the study period (Appendix 3, NOAA Climate Prediction Center, n.d.)

Coral growth under seasonal variation:

In January 2022, the *Pocillopora* coral fragments had an average initial maximum length (ML) of 4.24 ± 0.95 cm and an initial planar area of 6.40 ± 2.51 cm² (mean $\pm$ SD, Table 1). Subsequent measurements clearly revealed growth over time, with mean coral areas reaching 14.41 ± 6.98 cm² in June 2022 and 27.75 ± 15.85 cm² in January 2023. During the warm season, corals exhibited an absolute growth rate of 17.85 ± 12.04 cm² yr⁻¹, corresponding to a relative growth rate of 283.61 ± 178.67 % yr⁻¹. In contrast, during the cold season, the absolute



Fig. 3. Time series of sea water temperature (°C) recorded by HOBO loggers from January to December 2022 at the nursery site in Puerto Villamil, Isabela Island, Galápagos Archipelago. The five events when temperature dropped below 20 °C are indicated with red numbers. Temperature fluctuations show seasonal variation, with higher temperatures in the first half of the year and multiple cooling events during the cold season. Note a 10-day gap in July due to logger malfunction.

Table 1

Size metrics of the 12 coral *Pocillopora* morphotypes collected and cultivated in the pilot nursery (January 2022).

Coral Morphotype	n (Jan. 2022)	n (Jun. 2022)	n (Jan. 2023)	Initial ML (cm)		Initial Area (cm ²)	
				mean	sd	mean	sd
P2	20	18	13	4.14	0.90	5.87	2.36
P3	7	7	6	3.28	0.53	4.88	1.76
P4	20	19	19	3.68	0.58	4.98	1.50
P5	20	20	18	5.21	1.16	10.54	3.51
P6	7	6	3	3.53	0.77	5.56	1.69
P7	12	12	11	4.64	0.58	6.15	1.75
P9	20	20	18	4.29	0.64	6.45	1.28
P10	12	12	8	4.48	0.96	7.27	1.30
P13	20	20	15	3.58	0.59	4.32	1.32
P14	20	20	18	4.04	0.59	5.49	1.38
P19	20	20	18	4.69	0.95	7.24	1.97
PAC.PD	13	12	7	4.69	0.99	6.89	1.03
N	191	186	154				
Overall means and SDs				4.24	0.95	6.40	2.51

n: number of coral fragments per sampling period; N: total number of coral fragments; ML: maximum length; Initial Area: planar area of coral fragments at the beginning of the cultivation period. The warm season ran from January to May 2022, and the cold season from June to December 2022.

growth rate slightly increased to 22.01 ± 18.07 cm² yr⁻¹, while the relative growth rate declined to 133.95 ± 91.95 % yr⁻¹, indicating slower proportional growth. The specific growth rate followed the same pattern as the relative growth rate, averaging 1.69 ± 0.79 yr⁻¹ during the warm season and 0.90 ± 0.59 yr⁻¹ in the cold season. Based on ML measurements, corals grew 3.36 ± 2.10 cm yr⁻¹ during the warm season and 2.49 ± 2.10 cm yr⁻¹ during the cold season (absolute growth rates). The corresponding ML-based relative growth rates were 81.17 ± 56.42 % yr⁻¹ and 41.11 ± 35.62 % yr⁻¹, whereas ML-based specific growth rates were 0.66 ± 0.40 yr⁻¹ and 0.34 ± 0.33 yr⁻¹, respectively.

Coral planar area growth rates differed significantly between seasons, although the magnitude of the differences varied with the measure of growth rate. While the absolute growth rate was higher during the cold season ($t = -2.13$, $df = 152$, $p = 0.03$, $d = -0.27$, Fig. 4), the relative and specific growth rates were twice

as high during the warm season than during the cold season (RLR: $t = 11.15$, $df = 152$, $p < 0.0001$, $d = 1.05$; SGR: $t = 13.18$, $df = 152$, $p < 0.0001$, $d = 1.12$) (Fig. 4).

Coral morphotype-specific growth rates:

When examining growth across morphotypes, significantly higher absolute growth rates of coral planar area were observed during the cold season for P5, P14, and P19 (Appendix 4), with the strongest effect in P5 and a moderate effect in P14 ($t = -7.85$, $df = 17$, $p < 0.0001$, $d = -1.40$, Fig. 5). No significant differences were detected for the remaining morphotypes, except for P13, which showed higher absolute growth rates during the warm season (Appendix 4). In contrast, 10 out of 12 morphotypes showed faster growth during the warm season when considering relative growth rates (Appendix 5). The most pronounced seasonal effects occurred for P9, P13, and P5 (Fig. 5), followed by PAC.PD and P10. Similar trends of faster growth during the warm season were found when considering

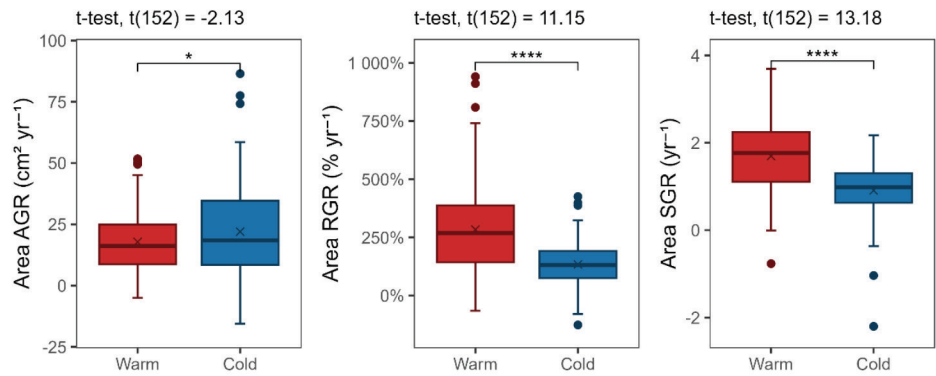


Fig. 4. Comparison of coral growth rates between warm and cold seasons for *Pocillopora* corals cultivated in the pilot nursery. The warm season ran from January to May 2022, and the cold season from June to December 2022. Boxplots illustrate differences in absolute growth rate (AGR), relative growth rate (RGR), and specific growth rate (SGR) based on coral planar area. See text for detailed descriptions on these rates. Statistical comparisons were conducted using paired t-tests, with significance levels indicated as follows: $p < 0.05 = *$, $p < 0.0001 = ****$.

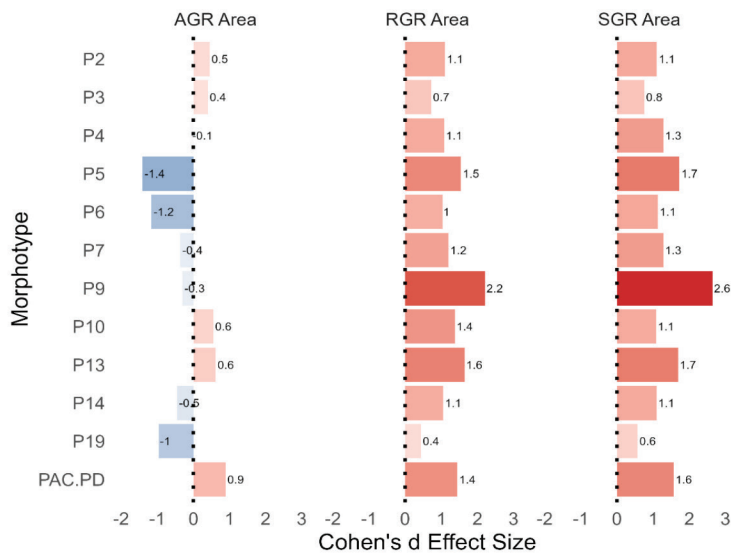


Fig. 5. Cohen's d effect sizes for differences in coral growth rates between warm and cold seasons in *Pocillopora* morphotypes cultivated in the pilot nursery. The warm season ran from January to May 2022, and the cold season from June to December 2022. Positive (red) values indicate higher growth rates during the warm season, whereas negative (blue) values indicate higher growth during the cold season. Effect sizes are shown for absolute growth rate (AGR), relative growth rate (RGR), and specific growth rate (SGR) based on coral planar area. According to standard thresholds, $d \approx 0.2$ indicates a small effect, 0.5 a moderate effect, and ≥ 0.8 a strong effect.

specific growth rates (Appendix 6, Fig. 5). Finally, ML growth was significantly faster in the warm season across all three growth rates (Appendix 7), and the effect sizes of seasonal differences per morphotype were comparable

to those obtained from coral planar area measurements (Appendix 8).

Morphotype-specific differences in relative growth rates were significant within both the warm (Welch ANOVA: $F = 6.58$, $df = 11$,

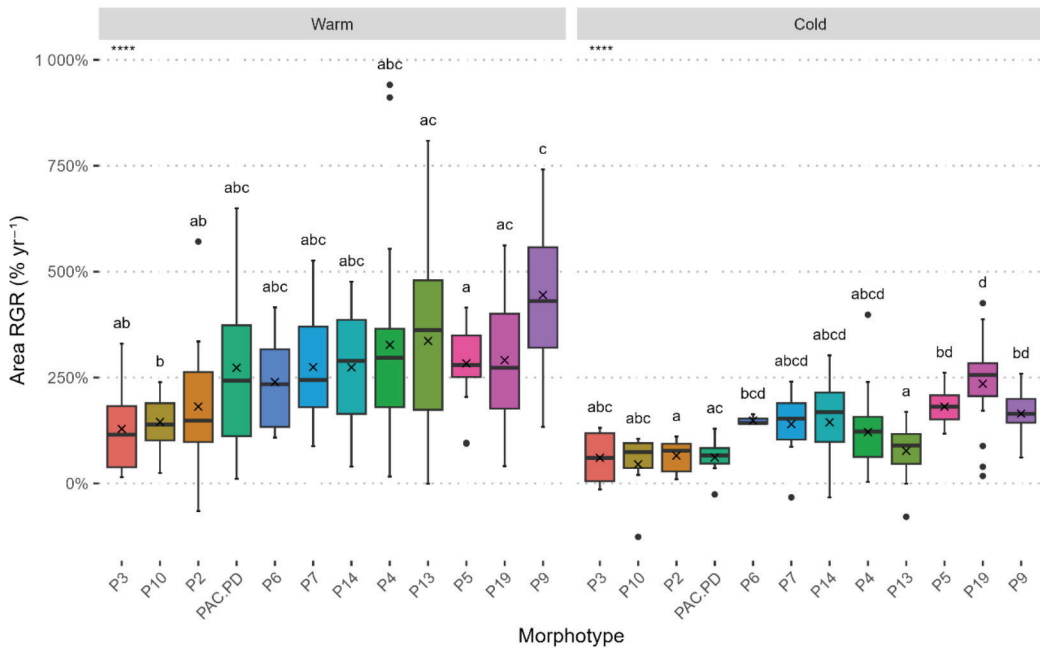


Fig. 6. Boxplots of relative growth rate (RGR) for coral planar area for the 12 *Pocillopora* morphotypes in the pilot nursery during warm and cold seasons. The warm season ran from January to May 2022, and the cold season from June to December 2022. Significant differences among morphotypes within each season were detected (****, $p < 0.0001$, Welch ANOVA). Different letters above boxplots indicate significant pairwise differences among morphotypes ($p < 0.05$, Games-Howell post-hoc test).

54.42, $p < 0.0001$) and cold (Welch ANOVA: $F = 11.74$, $df = 11$, 38.75, $p < 0.0001$) seasons. During the warm season, P9, P13, and P4 exhibited the highest values, while P3, P10, and P2 had the lowest (Fig. 6). Overall relative growth rates in the cold season were lower than those of the warm season; however, P19 maintained similar growth rates across seasons (Fig. 6).

Coral mortality patterns and fitness:

During the eight months we tracked it, mean coral mortality was 20 %, (48 of 240 fragments). Mortality remained relatively low by the end of the warm season (May 2022), reaching up to 24 % in some morphotypes, but progressively increased during the cold season, attaining values between 55 % and 74 % (Fig. 7). Similarly, bleached tissue remained below 25 % during the warm season, bleaching in most morphotypes intensified from September 2022 onwards, with some reaching nearly 50 % (Fig.

7). Dead tissue and algal cover followed similar trends, both increasing as the cold season advanced. Turf algae rapidly colonized dead tissue, reaching up to 90 % coverage in one morphotype (PAC-PD). Some corals exhibited additional symptoms of stress, such as polyp retraction, pale or pinkish pigmentation, and tissue sloughing, often culminating in complete tissue loss. Some morphotypes were more sensitive than others: P3 and PAC-PD experienced the highest mortality, as well as the greatest percentages of dead tissue and algal cover (Fig. 7). These morphotypes and other morphotypes with lower growth rates also showed higher mortality ($R^2 = 0.58$, $p = 0.004$) and higher proportions of dead tissue ($R^2 = 0.62$, $p = 0.002$, Fig. 8). Conversely, morphotypes with the highest growth rates (P5, P9, P19), displayed the lowest mortality and dead tissue percentages (Fig. 8).

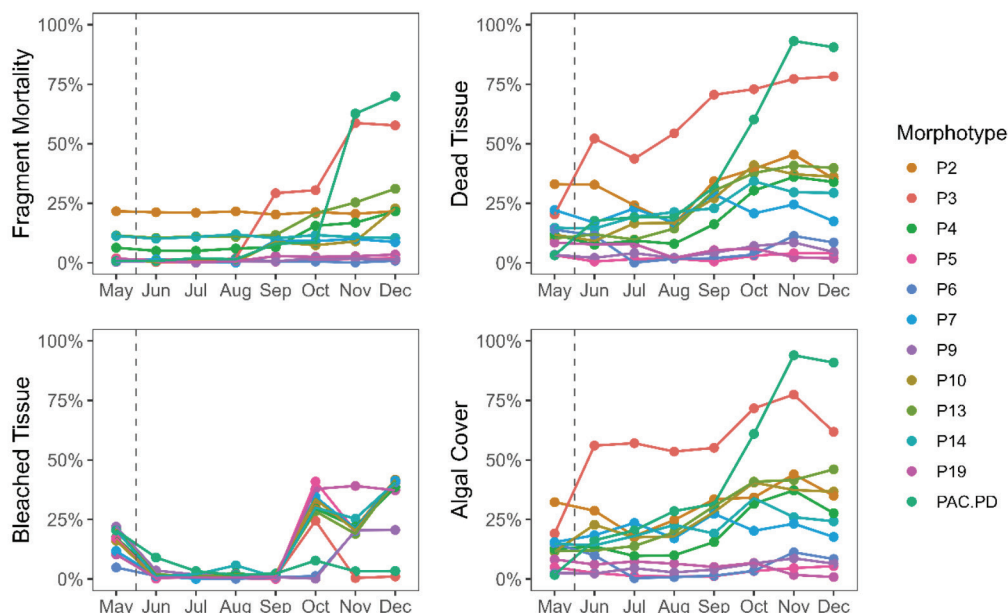


Fig. 7. Monthly fragment mortality, % of dead tissue, % of bleached tissue and % of algal cover across the 12 *Pocillopora* morphotypes growing in the pilot nursery from January to December 2022 (fitness surveys started in May 2022; see Materials & Methods). Vertical dashed lines approximate the onset of the cold season. Note that not all morphotypes are distinguishable because some color lines overlap.

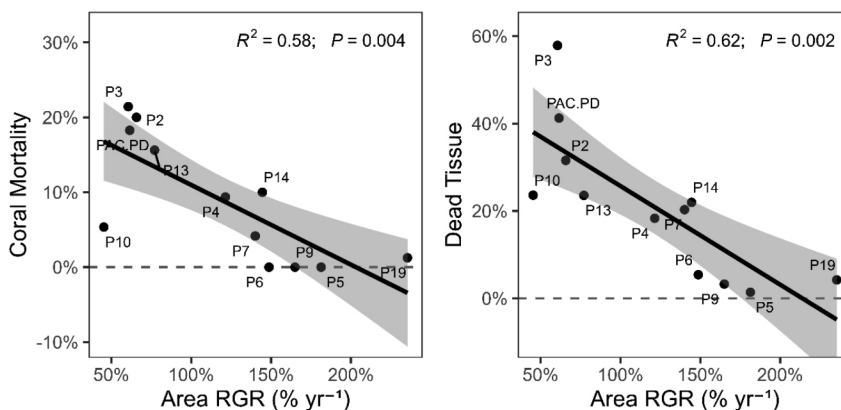


Fig. 8. Linear regressions between coral planar area relative growth rate (RGR) and coral mortality (left) and % of dead tissue (right) for the 12 *Pocillopora* morphotypes in the pilot nursery. Note the different scales on the y-axes.

DISCUSSION

Status of coral colonies in Puerto Villamil

Bay: The coral community in Puerto Villamil Bay can be characterized as a recovering post-disturbance ecosystem (Glynn et al., 2015),

currently dominated by one branching genus and a limited presence of long-lived massive corals. *Pocillopora* accounted for more than 70 % of all colonies, consistent with previous reports identifying this genus as the main reef builder in the Galápagos Archipelago (Riegl et

al., 2019). Massive corals such as *Pavona clavus*, *Pavona gigantea*, and *Porites lobata* were less frequent but larger, a pattern also reported for other marginal reefs in the region (Feingold, 2001; Glynn et al., 2015). While *Pocillopora* dominates shallow and dynamic habitats, large, massive colonies persist in deeper zones with more stable temperatures. Overall, our results from the baseline survey show good health indicators and partial regeneration; however, the *Pocillopora* dominance points to a strong reliance on clonal propagation (Baums et al., 2014), which may constrain long-term adaptive capacity. Compared with previous surveys, the larger number and size range of *Pocillopora* colonies recorded in our study may suggest continued recolonization after past ENSO disturbances, although differences in sampling effort and area should be considered. The dense thickets observed in Concha y Perla and nearby lava channels, together with morphologically uniform patches, indicate that recovery has largely occurred through asexual fragmentation (Baums et al., 2014). This strategy likely enhances short-term persistence and regrowth but may also limit genetic diversity and adaptive potential (Edmunds, 1994).

Coral fitness indicators also suggest that the Puerto Villamil community was in relatively good condition at the time of baseline sampling. Bleaching remained below 21 % across species, while predation and parasitism were generally low in *Pocillopora*. In contrast, massive corals, although rare, likely play a disproportionate role in maintaining reef structure and long-term stability. However, they also showed higher disease and parasitism levels, particularly *P. clavus*, *P. gigantea*, and *P. lobata*, consistent with previous reports for *Porites* and other massive taxa (Vera & Banks, 2009; Pisapia & Pratchett, 2014).

Environmental forcing, temperature and ENSO context: The monitoring period coincided with persistent La Niña conditions, with local water temperatures ranging from 18.7 to 30.1 °C and repeated cold-water intrusions between April and November. These cooling

events are consistent with seasonal upwelling dynamics in Galápagos (Glynn et al., 2018) and provide the environmental context for interpreting coral performance in the nursery. We note, however, that temperature likely covaried with other upwelling-related factors such as nutrient availability and turbidity, which were not measured directly in this study. Having said, our results suggest that the strong seasonality in temperature recorded by both our in-situ temperature loggers, as the ENSO index—warm conditions early in the year and pronounced cooling during the second half—influenced alternating periods of coral growth and stress.

Coral growth under seasonal variation:

Coral growth showed clear seasonal differences. Relative and specific growth rates were higher during the warm season, whereas mortality and tissue degradation increased during the cold season. These results are consistent with previous studies in the ETP showing reduced coral performance under upwelling and low-temperature conditions (Castrillón-Cifuentes et al., 2023; Combillet et al., 2022; Glynn & Stewart, 1973). In our study, growth declined by 42 % during the cold season, supporting the interpretation that cold-water upwelling was a major source of stress during the monitoring period. Seasonal upwelling in the Galapagos brings cold-water conditions, which also include changes in sea water salinity, turbidity and nutrient concentration, however these covariables were not measured during the study period and may require further research to fully understand their influence in coral stress response. Comparable findings have been reported in the ETP, where *Pocillopora* growth was reduced by 68 % during upwelling on Gorgona Island (Castrillón-Cifuentes et al., 2023), by 48 % in Costa Rica (Combillet et al., 2022) and was limited below 21 °C in Panamá (Glynn & Stewart, 1973). Hence, our findings suggest that cold-water upwelling may constrain coral growth. Like warm-water bleaching, cold stress promotes the accumulation of oxygen radicals in coral tissues, leading to bleaching, tissue



damage, reduced growth, and overall diminished fitness (Tuckett & Wernberg, 2018).

Most growth metrics showed consistent seasonal patterns. Relative and specific growth rates decreased significantly during the cold season, whereas absolute growth rates increased slightly, likely because larger colonies continued some skeletal expansion despite reduced physiological performance. Since relative and specific growth account for initial fragment size (Hopkins, 1992), they likely provide a more informative measure of seasonal coral performance in this system. Similar patterns in maximum length further suggest that both branch elongation and colony expansion were greater under warmer conditions.

Morphotype-specific growth, mortality and fitness: Growth, mortality, and tissue condition varied markedly among *Pocillopora* morphotypes, supporting substantial performance diversity within the nursery. Morphotypes such as P9 and P13 exhibited the highest relative growth, whereas P2, P3, and PAC-PD showed slower growth. Comparable genotype-dependent differences have been documented in other nursery-grown corals (Henley et al., 2022; Maneval et al., 2021; Soong & Chen, 2003). However, because several morphotypes were represented by fragments from one or a few donor colonies, these differences should be interpreted cautiously as the performance of selected donor colonies or colony groups, rather than as population-level differences for each morphotype.

Mortality patterns broadly mirrored growth responses. Fast-growing morphotypes such as P5, P9, and P19 showed the lowest mortality and algal overgrowth, whereas P3 and PAC-PD were the most affected by tissue loss and algal colonization. These results suggest that biological differences among morphotypes influenced responses to environmental stress. Bleaching increased transiently across most morphotypes during October but was not consistently associated with the highest mortality. For example, P3 and PAC-PD showed high mortality and algal cover with little bleaching,

suggesting that visible bleaching was not the only pathway of decline. Some of this discrepancy may also reflect observer limitations in detecting subtle pigmentation changes (Siebeck et al., 2006), as well as limitations in the scoring system, where the use of upper bounds of percentage ranges may overestimate the level of affectation.

Coral fitness and oceanographic influence: The main deterioration in coral condition occurred after repeated temperature drops during the second half of the year. The initial cooling event in April may have triggered early increases in dead tissue and algal cover in sensitive morphotypes such as P3, whereas stronger declines in fitness were observed after the September–November cooling events. Similar cold-water anomalies have previously been associated with coral stress and mortality in the Galápagos (Banks et al., 2009; Feingold & Glynn, 2013; Rhoades et al., 2023) and elsewhere in the ETP (Paz-García et al., 2012; Zapata et al., 2011).

Cold-water stress therefore appears to be a major constraint on coral performance in Isabela, although its effects were not uniform across morphotypes. The most susceptible morphotypes were P3, P4, P10, P13, and PAC-PD, indicating marked variability in sensitivity to cooling events. This pattern is consistent with previous studies showing differential thermal responses among colonies or cryptic taxa within *Pocillopora* (Burgess et al., 2021). In our study, several of the most susceptible morphotypes resembled colonies historically identified as *Pocillopora cf. damicornis* following Hickman (2008). However, recent genomic evidence suggests that *P. cf. damicornis* sensu stricto is absent from the ETP, and morphologically similar colonies likely belong to cryptic regional lineages (Connelly et al., 2026). Thus, the observed variation in susceptibility may reflect underlying differences in lineage identity, symbiont communities, or local environmental history. In particular, the higher sensitivity of morphotypes originating from the warmer and more sheltered Concha y Perla area may suggest local acclimatization or adaptation

to relatively higher baseline temperatures (Burgess et al., 2021; Howells et al., 2011).

Implications for coral restoration in the Galápagos: The Galápagos Archipelago represents a promising but challenging setting for coral restoration. Despite strong environmental variability and persistent La Niña conditions, coral gardening achieved 80 % survival, a value that falls within or above the range reported by regional and global restoration studies (Boström-Einarsson et al., 2020; Combillet et al., 2022; Lizcano-Sandoval et al., 2018). This suggests that coral cultivation can be feasible in the Galápagos, even under unfavorable conditions.

At the same time, our results highlight important constraints for restoration planning. Recurrent cold-water intrusions, algal overgrowth, and the apparent dependence on clonal recovery may reduce long-term resilience. Restoration efforts should therefore prioritize the propagation of fast-growing and stress-tolerant morphotypes such as P5, P9, and P19, avoid establishing nurseries during the cold upwelling season when possible, and incorporate future genetic and symbiont analyses to better identify resilient coral lineages suited to the Galápagos' highly dynamic thermal regime.

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

See supplementary material
a15v74s1-suppl. 1

ACKNOWLEDGMENTS

We are grateful to José L. Barrios Ponce and Cristopher Gómez, coral gardeners of the Galápagos Reef Revival team, who helped

during the baseline study, the assembly and maintenance of the pilot nursery, the monthly coral health monitoring, the assistance during the coral photographic sampling and many other fieldwork activities. Galápagos Reef Revival operates within the framework of the Coral Restoration and Management Plan led by the Galápagos National Park (GNP). This research was performed under GNP permit numbers PC-56-21, PC-34-22, and PC-29-23 to MB. The baseline study, pilot nursery, and monitoring activities were executed with funds of the Rufford Small Grant and Jocotoco foundation to ND, and with COCIBA and Galápagos Grants from Universidad San Francisco de Quito USFQ to MB. We also thank the editor and three anonymous reviewers for their constructive comments, which helped improve the clarity and quality of this manuscript. We acknowledge the use of ChatGPT during the manuscript revision to refine the academic language of this paper. We reviewed and edited the wording generated by ChatGPT to ensure accuracy and clarity.

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