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Impact of the 2023–2024 ENSO Event of the North Pacific Coral Reefs of Costa Rica

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Abstract

Coral reefs are increasingly impacted by marine heatwaves and global warming, with the 2023–2024 El Niño–Southern Oscillation (ENSO) event causing unprecedented thermal stress across the Eastern Tropical Pacific. This study assessed the effects of this event on coral reefs in the Gulf of Papagayo, Costa Rica. Sea surface temperatures exceeded the bleaching threshold for seven months, reaching a record 10.2 Degree Heating Weeks—twice the levels recorded during the 1997–1998 ENSO. Benthic and fish community surveys revealed severe coral mortality, particularly in *Pocillopora*-dominated reefs, with some sites losing over 90% of live coral cover. Resilience varied across sites, likely influenced by factors such as local water circulation, coral genetic diversity, symbiont type, and heterotrophic capacity. Reefs with higher genetic diversity and thermally tolerant *Durusdinium* symbionts showed partial recovery. Seasonal upwelling appeared to buffer thermal stress in some areas, potentially acting as a natural climate refuge. Bleaching also impacted reef fish communities, with a notable decline in invertebrate-feeding species on degraded reefs. These findings highlight the interplay between prolonged thermal stress, coral biology, and local oceanographic processes in shaping reef resilience. Identifying and protecting such climate refugia will be critical for coral conservation under future climate change scenarios.

Keywords: bleaching; *Pavona clavus*; *Pocillopora*; resilience; sea surface temperature; upwelling; El Niño

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Academic Editor: Alma Paola Rodríguez-Troncoso

Received: 5 September 2025
Revised: 4 October 2025
Accepted: 8 October 2025
Published: 11 October 2025

Citation: Alvarado, J.J.; Quesada-Perez, F.; Solano, M.J.; Calvo-Fong, M.; Mena, S. Impact of the 2023–2024 ENSO Event of the North Pacific Coral Reefs of Costa Rica. *Diversity* **2025**, *17*, 0. https://doi.org/

1. Introduction

Corals are among the most sensitive organisms to elevated temperatures [1], largely due to their close relationship with symbiotic algae [2]. This relationship is disrupted when temperatures exceed the coral's physiological thresholds, causing the coral to expel its symbiotic microalgae—a phenomenon known as coral bleaching. During bleaching, corals depend on stored energy reserves and residual heterotrophic feeding to survive. If the thermal stress persists over time, the corals may die [2,3].

These bleaching events have become more frequent over the past three decades due to both the El Niño-Southern Oscillation (ENSO) and global climate change [4]. ENSO is an oceanographic-atmospheric pattern that occurs on average every 4–7 years with varying intensities. It causes large volumes of warm water to move and remain across the Pacific Ocean, disrupting the water column's mixed layers and lowering the thermocline and nutricline [5,6]. This phenomenon has severely impacted both marine and terrestrial ecosystems [7,8]. In coral reefs, a significant loss of live coral cover has been recorded in several regions, affecting reproductive patterns and ecological succession [4–9].

Anthropogenic global warming has elevated Earth's mean temperature, causing El Niño events to become more intense and frequent [10–16]. As global warming continues, coral bleaching events are expected to occur more frequently and intensify. Climate models predict that rising average sea temperatures may surpass critical thresholds for corals, leading to more severe bleaching events like those observed in recent decades [17]. Moreover, the increased frequency of extreme climate events, such as El Niño, will place greater stress on coral ecosystems, diminishing their resilience and raising mortality rates [2].

El Niño events have consistently influenced the structure and dynamics of coral reef ecosystems in the Eastern Tropical Pacific (ETP), exerting long-term ecological consequences on reef-building corals (mainly corals of the genera *Pocillopora* and *Porites*) and associated biota. The 1982–1983 event caused unprecedented mortality, with losses of up to 90% of live coral cover and extensive framework erosion. Although the 1997–1998 event also generated substantial disturbance, overall mortality was lower, highlighting regional variability and providing evidence of partial resilience within ETP coral assemblages [9].

Recently, coral reef ecosystems experienced their fourth major bleaching event [18]. This event was a direct result of the 2023–2024 El Niño phenomenon [1]. The 2023–24 global warming event was the largest ever recorded, exceeding pre-industrial levels by 1.45 °C, a value dangerously close to the 1.5 °C threshold identified by the Paris Climate Agreement [19]. Over the past 15 years, the global average surface temperature has entered a phase of accelerated warming [19]. The 2023 event saw the Pacific and Caribbean waters of Central America classified as the regions with the highest mortality rates due to bleaching, a result of significant thermal stress accumulation. Costa Rica's Pacific coast was identified as a bleaching hotspot, reaching over 18 Degree Heating Weeks [19]. The impact of this event was drastic in several regions of the planet including Florida [20], Australia [21] and Mexico [22].

El Niño events have historically impacted Costa Rica's Pacific coast since the 1980s [23–25]. The most significant impacts occurred during the 1982–83 [23,26,27] and 1997–98 events [28]. During the 2016 event, a differential impact was observed, with the southern part of the country (Caño Island and Golfo Dulce) being the most affected [29].

By March 2023, early signs of coral bleaching were observed in Golfo Dulce and other regions of the Mexican Pacific (Tatiana Villalobos and Omar Valencia, pers. comm.). In response, a rapid ecological assessment protocol was developed to monitor coral health along Costa Rica's northern Pacific coast. This study aimed to evaluate the condition of coral reefs over a one-year period, from the onset of thermal anomalies to the return of baseline temperatures, providing insights into the spatial and temporal dynamics of bleaching under extreme ENSO conditions. We aim to test whether the 2023–2024 El Niño event significantly altered coral cover and bleaching severity along Costa Rica's northern Pacific coast. We hypothesize that the 2023–2024 El Niño event significantly increased coral bleaching severity and mortality along Costa Rica's northern Pacific coast, with spatial variability in impact intensity reflecting differential thermal stress accumulation and historical exposure to ENSO events.

2. Materials and Methods

2.1. Study Area

The Gulf of Papagayo includes the reefs and coral communities found below the Santa Elena Peninsula, including the Murcielago Islands, Culebra Bay, and Punta Gorda (Figure 1). The area has been extensively studied since the 1980s, and at least 16 species of reef-building corals have been reported, with reefs and coral communities dominated by the *Pocillopora* genus at depths of up to 10 m [30]. The gulf is in one of the three seasonal upwelling areas in the Eastern Tropical Pacific (ETP) [31], which affects the region from December to April [32,33], and brings colder (18–20 °C), acidic (pH 7.8) and nutrient-rich waters [34–36].

Figure 1. Sampling sites in the Papagayo Gulf in the North Pacific of Costa Rica.

2.2. Temperature and Thermal Stress Data

Sea surface temperature (SST) and Degree Heating Weeks (DHW) data for each surveyed site were obtained from NOAA's Coral Reef Watch (CRW) 5 km resolution virtual station products [37]. Historical data from 1985 to 2024 were used to calculate the Maximum Monthly Mean (MMM) baseline following standard CRW methodology. The MMM is defined as the highest long-term average of monthly SST at a given location and serves as the basis for identifying anomalous warming events. Corals typically begin to experience stress and bleaching when temperatures exceed this MMM by approximately 1 °C [38]. Accordingly, the bleaching threshold was set at MMM + 1 °C. These metrics were used to quantify the intensity and duration of thermal stress conditions during the 2023–2024 ENSO event and to compare them with previous strong ENSO events (1997–1998 and 2015–2016), with particular focus on periods when DHW values surpassed CRW Alert Levels 1 ($\geq$4 DHWs) and 2 ($\geq$8 DHWs), which indicate increasing risk and severity of coral bleaching events.

2.3. Field Assessments

Reef surveys were conducted at five sites in the Gulf of Papagayo between July 2023 and November 2024 (Figure 1). Three sites—Sombrero (3 m), Jicaro (7 m), and Matapalo (7 m)—were coral reefs dominated by *Pocillopora* spp. The remaining two sites included Güiri-Güiri (6 m), a reef dominated by *Pavona clavus*, and Zapotillal (6 m), a coral community growing on basaltic substrate. Surveys were carried out during five periods: July 2023, October–November 2023, January 2024, July–August 2024, and November 2024. Due to logistical constraints, not all sites were visited during every monitoring period; however, each site was surveyed on at least three occasions. On each reef survey, benthic and fish community data were collected via SCUBA using standard methodologies.

All surveys were conducted at fixed geographic coordinates to ensure consistency across sampling events. Although permanent transects were not established, the fringing configuration of the reef, together with its relatively small size and shallow depth, restricted the available working area. These characteristics allowed fieldwork to be consistently carried out within the same zones, minimizing spatial variability in the observations. The sites were chosen based on the historical presence of coral reefs and coral communities in the area.

In the present study, when coral growth occurred on a basaltic structure formed primarily by coral skeletons it was considered a coral reef, but when this basaltic structure was absent and the substrate consisted of sand or rock it was considered a coral community [39,40]. Through this important distinction it is possible to know the contribution of corals to the construction of the topographic characteristics and to determine the vitality of the coral formations over time [41].

2.3.1. Benthic Cover

Benthic community data were collected using a photo-quadrat methodology along three 20 m transects at each site. Along each transect, 20 photographs of 50 × 50 cm quadrats were taken—one every meter as the diver advanced. Images were analyzed using PhotoQuad software v1.4 [42]. Substrate cover was estimated by overlaying 50 stratified random points on each photograph and identifying the substrate beneath each point to the lowest possible taxonomic level. Each substrate was then assigned to one of the following functional groups: live coral, pale coral, bleached coral, recently dead coral, crustose coralline algae (CCA), macroalgae, turf algae, or others. The "others" category included cyanobacteria, sponges, ascidians, anemones, sand, rubble, rock, and other unclassified substrates.

2.3.2. Fish Community

Fish community data were collected using three belt transects per census, each measuring 20 m in length, 5 m in width, and 2 m in height. Within each transect, all fish observed were counted, identified to species level, and assigned to a total length category: <5, 5–10, 10–15, 15–20, 20–25, 25–50, 50–100, 100–150, 150–200, 200–250, and 250–300 cm [43,44]. Size frequency data for each species were then converted to biomass using species-specific length–weight relationships, following the equation $W = aLb$, where W is weight (g), L is total length (cm), and a and b are constants obtained from FishBase [45].

2.4. Statistical Analysis

Prior to statistical analyses, data distributions were assessed using the Shapiro–Wilk test for normality and Levene's test for homogeneity of variances. Because several datasets deviated from these assumptions, we applied non-parametric approaches. To assess differences in mean coverage of healthy, pale, bleached and overall live coral across monitoring dates, Kruskal–Wallis tests were performed. When significant differences were detected, post hoc pairwise comparisons were conducted using Mann–Whitney U tests.

Non-metric multidimensional scaling (NMDS) analyses were conducted to assess variations in benthic cover and fish community composition across sites and monitoring periods during the 2023–2024 ENSO event. Prior to analysis, both benthic cover (%) and fish biomass (kg m^{-2}) data were log-transformed using the formula $\log_{10}(x + 1)$. Sites were categorized into three reef types: *Pocillopora*-dominated reefs, *Pavona*-dominated reefs, and coral communities. Analysis of Similarities (ANOSIM) tests were used to evaluate differences in benthic cover and fish community composition among reef types. Additional ANOSIM tests were performed to assess differences based on reef condition, classifying sites into three status categories: healthy (≥90% of live coral cover classified as healthy), bleached (≥30% of live coral cover classified as bleached), and severely degraded (live coral cover—including healthy, pale, and bleached—declined by at least 50% relative to the initial estimate).

Reef fish species were classified into six functional groups based on feeding habits: detritivorous herbivores, macroalgae herbivores, invertebrate feeders, omnivores, planktivores, and piscivores. To assess differences in overall fish biomass and biomass per functional group across reef status categories, Kruskal–Wallis tests were performed. When significant differences were detected, post hoc pairwise comparisons were conducted using Mann–Whitney U tests. At last, we used Procrustes analysis to assess the concordance between trajectories of benthic cover and fish community composition, with statistical significance evaluated through permutation tests.

3. Results

3.1. Temperature and Thermal Stress

NOAA's Coral Reef Watch satellite data show that the surveyed reefs in the Papagayo Gulf experienced abnormally high sea surface temperatures (SSTs) and thermal stress during several months in 2023 and 2024. SSTs exceeded 30 °C from May to October 2023 and again in May 2024, surpassing the estimated bleaching threshold of 29.9 °C (calculated as the maximum monthly mean from 1985 to 2024 + 1 °C) (Figure 2A). Degree Heating Weeks (DHWs) exceeded eight from July to August 2023 and again from October to November, reaching Alert Level 2, which indicates a high risk of widespread coral bleaching (Figure 2B). A maximum of 10.2 DHWs was recorded at the end of July 2023—the highest ever observed for the region and over two times greater than the previous maximum of 4.1 DHWs recorded during the 1997–1998 ENSO event.

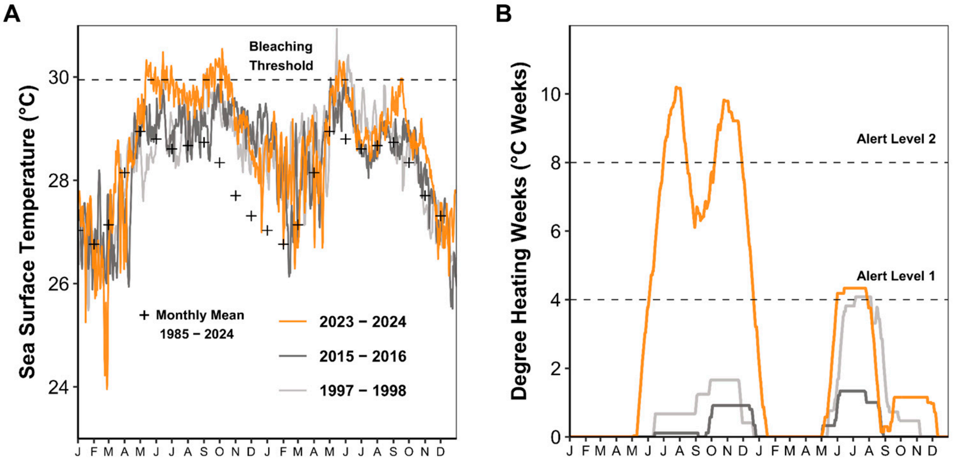

Figure 2. Dynamics in (**A**) mean sea surface temperature and (**B**) degree heating weeks at the surveyed reef sites in the Papagayo Gulf, North Pacific of Costa Rica, retrieved from the NOAA/CRW time series. The orange lines show the values throughout the 2023–2024 ENSO event. The other colored lines refer to previous warming events.

3.2. Benthic Cover

The 2023–2024 ENSO event had a significant impact on live coral cover across some reefs in the Papagayo Gulf. Mean live coral cover (±95% CI), including healthy, pale, and bleached corals, declined across the five surveyed sites declined from 42 (±37) % to

13 (±11) % between July 2023 and the July–November 2024 monitoring period (Figure 3A). However, these differences were not statistically significant (Kruskal–Wallis; $p = 0.11$), as trajectories of coral cover varied substantially among sites. While some reefs experienced near-total coral mortality, others showed relative stability in live coral cover throughout the event (Figure 3B).

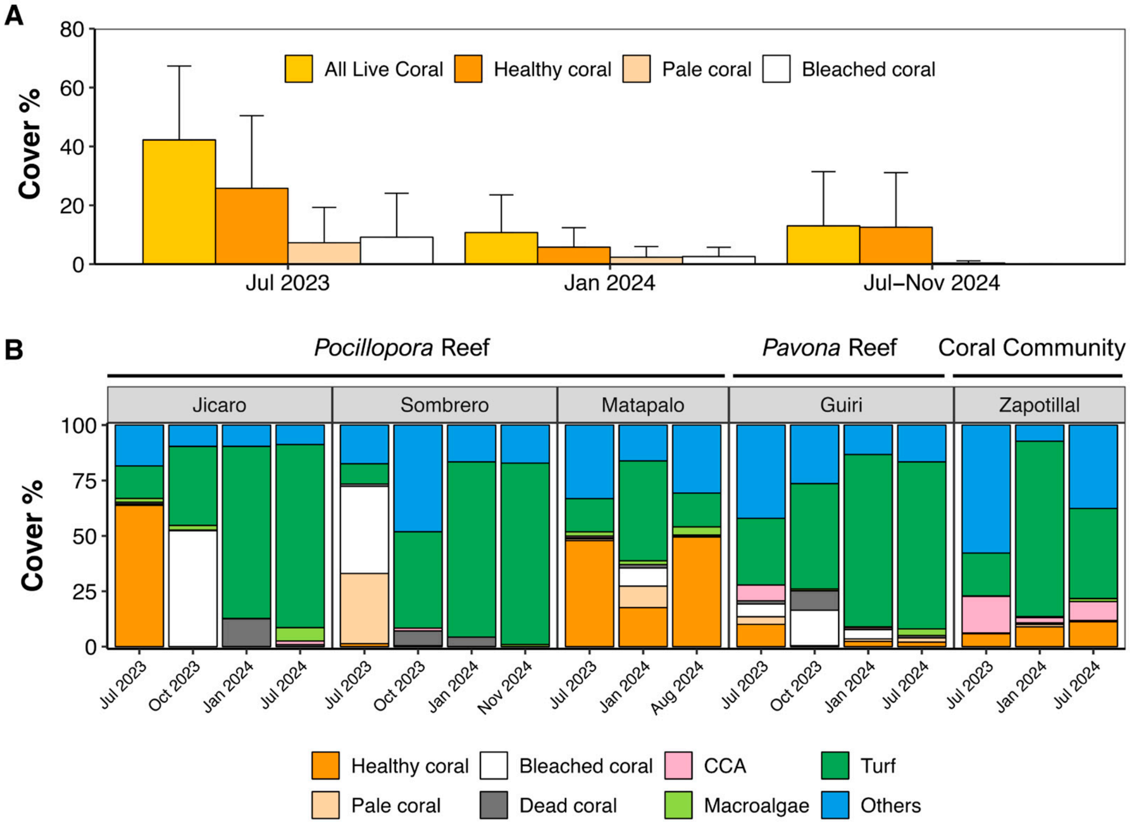

Figure 3. Change in the cover of the major benthic categories during the 2023–2024 ENSO event. (**A**) Change in mean coral cover (±95% CI) across all surveyed sites. (**B**) Change in the mean cover of the major benthic categories at each site.

The reefs of Sombrero and Jícaro, where *Pocillopora* was the dominant reef-building coral, experienced near-total coral mortality by October 2023 and January 2024, respectively (Appendices A and B). At Matapalo, another *Pocillopora*-dominated reef, healthy coral cover was approximately 48% in January 2023. By January 2024, healthy coral cover had declined to 18%, with 23% and 27% of the remaining live coral categorized as bleached and pale, respectively. By July 2024, however, signs of recovery were observed, with healthy coral cover rebounding to around 49% (Figure 3B; Appendix C).

At Guiri, a *Pavona*-dominated reef, signs of thermal stress and bleaching were already apparent by July 2023, and by October, nearly all corals had bleached (Appendix D). Overall, live coral cover at this site declined from 19% in July 2023 to just 4% by August 2024. By contrast, minimal signs of bleaching were observed at Zapotillal—a coral community growing on basalt substrate—in July 2023, January 2024, and July 2024, and the estimated mean live coral cover even showed a slight increase over the course of the monitoring period. (Figure 3B).

As expected, the reefs where most corals had died by the end of the monitoring period—Jicaro, Sombrero, and Guiri—exhibited the most pronounced changes in benthic cover composition during the 2023–2024 ENSO event (Figure 4A). Benthic cover trajectories varied among *Pocillopora*-dominated reefs, *Pavona*-dominated reefs, and coral communities

(ANOSIM; $p < 0.001$). Although the NMDS analysis showed a clear separation in benthic community composition by reef type at the beginning of the monitoring period, this distinction diminished over time. As bleaching progressed and widespread coral mortality occurred at several sites, benthic compositions converged, particularly between Güiri (*Pavona*-dominated) and Jicaro and Matapalo (both *Pocillopora*-dominated). Consequently, a significant difference in benthic composition was also detected when reefs were grouped by status—healthy, bleached, or severely degraded—rather than by reef type (Figure 4A; ANOSIM, $p < 0.001$).

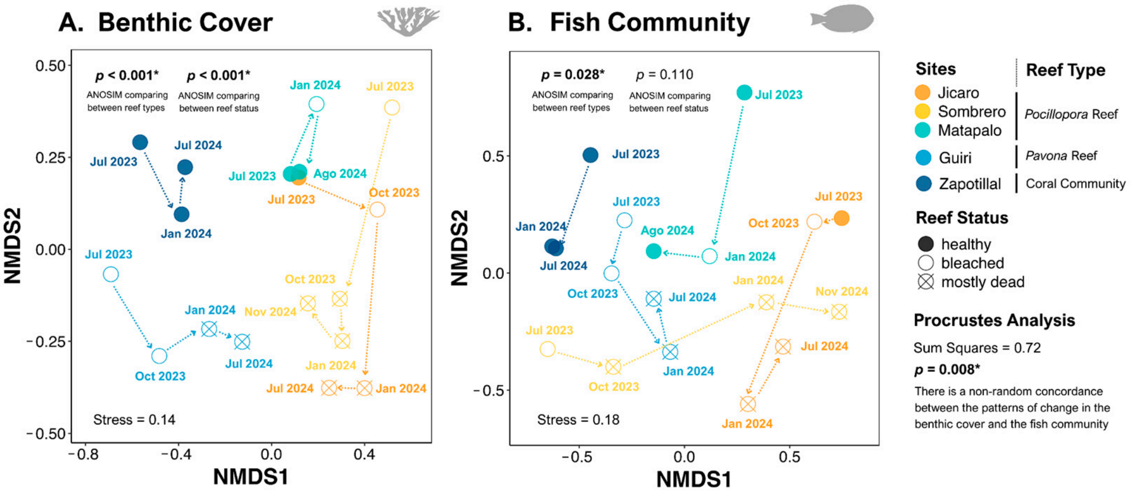

Figure 4. Non-metric multidimensional scaling (NMDS) plots showing changes in (**A**) benthic cover composition and (**B**) fish community composition during the 2023–2024 ENSO event. NMDS stress values and ANOSIM *p*-values comparing between reef types and reef status are shown. The results of a Procrustes analysis, assessing the concordance between changes in benthic and fish community composition, are also presented. Asterisks (*) indicate statistically significant differences ($p < 0.05$).

3.3. Fish Community

Similarly to the benthic cover, the trajectories of fish community composition during the 2023–2024 ENSO event varied among reef types (Figure 4B; ANOSIM, $p = 0.028$). In Zapotillal—a coral community—fish community composition remained relatively stable throughout the monitoring period. In contrast, at other reefs, fish communities changed as bleaching progressed and widespread coral mortality occurred. NMDS plots indicated a trend toward separation in fish community composition between healthy and severely degraded reefs; however, high variability within groups was observed, and the ANOSIM comparing reef types was not statistically significant ($p = 0.101$). Procrustes analysis showed moderate concordance between the trajectories of benthic cover and fish community composition, indicating a co-association between these ecological components (Figure 4; Sum of Squares = 0.72, $p = 0.008$).

In reefs where *Pocillopora* was the dominant reef-building coral, overall fish biomass per square meter showed a decreasing trend as corals bleached and died (Figure 5A). Despite this tendency, mean fish biomass did not differ significantly across reef statuses (Kruskal–Wallis; $p = 0.09$), which may be reflecting the limited time frame covered in this study instead of an ecological effect. Among the fish functional groups considered, invertebrate feeders consistently exhibited the highest biomass across all reefs. However, their biomass was significantly greater in healthy reefs compared to bleached or severely degraded reefs (Figure 5B). Other functional groups, such as piscivores and macroalgae-feeding herbivores, displayed trends of higher and lower biomass, respectively, in healthy reefs relative to severely degraded reefs, although these differences were not statistically significant.

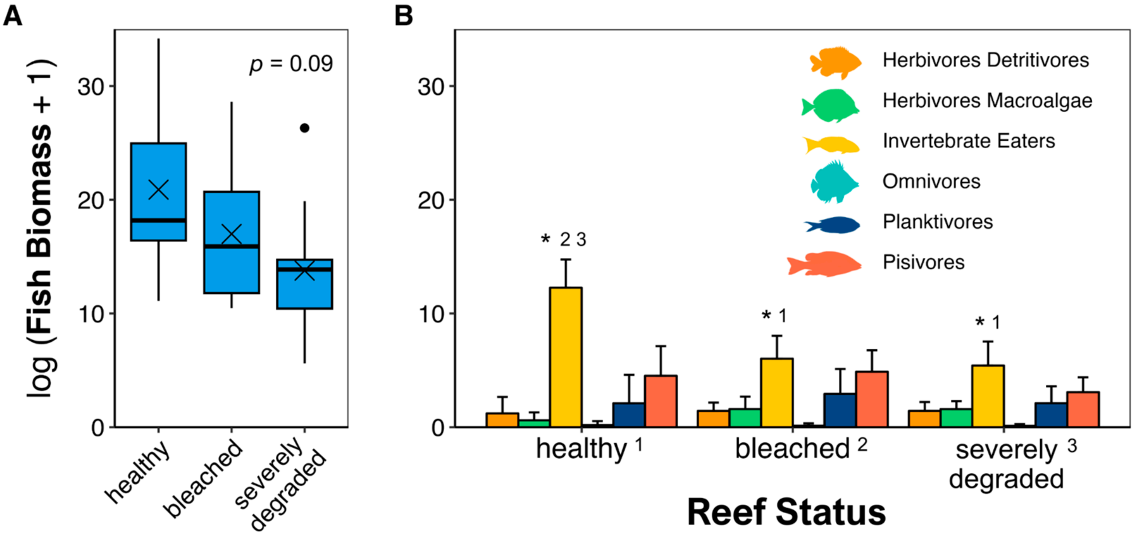

Figure 5. Comparison of fish biomass per square meter among reefs with different health statuses (healthy, bleached, and severely degraded), where *Pocillopora* was the dominant reef-building coral. (**A**) Total fish biomass across reef conditions. The X symbol denotes the mean. The p-value from the Kruskal–Wallis test assessing differences among reef statuses is shown. (**B**) Mean fish biomass (±95% CI) per functional group. Asterisks (*) indicate statistically significant differences ($p < 0.05$) between reef statuses. Numbers (1, 2, 3) indicate which reef statuses differ significantly based on pairwise Mann–Whitney U tests: (1) healthy, (2) bleached, (3) severely degraded.

4. Discussion

The 2023–2024 ENSO event stands out as the most intense marine heatwave ever recorded in the Gulf of Papagayo. It not only reached the highest levels of thermal stress observed in the region to date but was also marked by an unprecedented duration, with sea surface temperatures (SSTs) exceeding 30 °C continuously from May to October 2023 (Figure 2). This prolonged exposure to elevated temperatures resulted in the complete loss of live coral cover on the Jícaro and Sombrero reefs, both located in the inner bay. In contrast, reefs situated in the outer bay, such as Matapalo, Güiri, and Zapotillal, demonstrated greater resistance and partial recovery from bleaching, experiencing less severe impacts compared to the inner bay sites.

Cambronero-Solano et al. [46] analyzed the water mass behavior in both the inner and outer parts of Culebra Bay between 2017 and 2019. Their findings indicated that the inner part of the bay remained warmer than the outer parts during the negative ENSO phase. This may be due to less circulation in the inner part, and the fact that water is retained for longer periods of time. These conditions could help explain why reefs in the inner part of the bay suffered more from the impacts of the 2023–2024 ENSO than those located in other regions.

Another key factor in coral response is the genetic diversity and connectivity that may exist between different populations. In 2023, Hidalgo-Sánchéz et al. [47] determined that the Jícaro coral reef had very low genetic diversity of *Pocillopora* corals, which were the only reef builders present. The results showed that this reef supported a highly clonal population, possibly due to strong asexual reproduction. Furthermore, the Matapalo reefs and the Zapotillal coral community were found to have greater genetic diversity and higher connectivity between them. The fact that the Jícaro reef was composed almost entirely of clones made it more vulnerable to the impact of high temperatures, as it lacked intra-population variability to support a broader stress response. In contrast, Zapotillal and Matapalo reefs, with greater population diversity and a greater presence of sexual reproduction, were better acclimatized and therefore more resilient than Jícaro. This could also explain the death of the Sombrero reef, which, although it did not undergo the same population genetic analysis, is located even further inside the Bay and shares similar conditions with Jícaro.

Likewise, a recent assessment of the diversity of symbiotic microalgae associated with four coral genera (*Pavona*, *Porites*, *Pocillopora*, and *Psammocora*) at several sites in Bahía Culebra showed that most corals have flagellated endosymbionts associated with the genus *Cladocopium* [48]. This genus of flagellated endosymbiont is known to occur in cooler environments with lower turbidity [49]. In addition, the presence of the genus *Durusdinium* was identified in corals of the genus *Pocillopora* at locations such as Matapalo [48]. *Durusdinium* has been identified as a genus of flagellated endosymbiont tolerant to thermal stress [50–52]. Therefore, this may also represent a factor in the recovery of the Matapalo reef, compared to other sites in the Bay. In Panama and Ecuador, it has been observed that after El Niño events, corals hosting this type of endosymbiont showed greater tolerance to bleaching [53].

Now the question arises as to what other mechanisms could be involved in the recovery of corals under such an intense water warming event. An interesting example is the Güiri reef, which was visited monthly throughout the El Niño event as part of a coral restoration project [54,55]; Alvarado et al. prep. At this location, bleaching was intense, with several colonies remaining pale for at least six months (Figure 3). During our field visits, we observed bleached coral colonies with open polyps during the day, which could be interpreted as a possible feeding action by the organism. Hughes & Grottoli [56] determined that coral heterotrophy may function as a mechanism to withstand prolonged thermal stress. The acquisition of diverse food sources by corals is vital for resilience and recovery, which under thermal stress events remains dependent on heterotrophy [57]. Likewise, the type of endosymbiont that the coral possesses, whether *Cladocopium* or *Durusdinium*, will affect its trophic strategy. Corals dominated by *Cladocopium* may have a greater autotrophic capacity than those possessing *Durusdinium*. This heterotrophic capacity in corals hosting *Durusdinium* is greater in summer, when temperatures are warmer [58].

Culebra Bay is in an area of coastal upwelling, where from December to April, because of the trade winds, the surface layers of the sea are replaced by cold waters rich in nutrients [33]. The warmest months in Culebra Bay are from May to September, when the trade winds are absent and the intertropical convergence zone shifts northward. By October, sea temperatures begin to drop as the trade winds become more intense, and the intertropical convergence zone shifts southward. The coldest temperatures are reached in February and March. The difference in average temperature between the upwelling and non-upwelling seasons can be as much as 4 °C.

The impact of the onset and presence of the upwelling period was also evident in 2023, when temperatures begin to gradually drop after October, reaching below 28 °C by December, indicating that this ocean-atmospheric phenomenon is a factor that will help corals recover from bleaching. During the Papagayo upwelling, the entry of cold waters [36] and the presence of greater cloudiness probably help to compensate for marine heat waves [28], which could indicate that these reefs function as thermal refuges [59]. Randall et al. [60], based on historical data on sea surface temperature and coral cover and growth rate on coral reefs in the Gulf of Panama, where upwelling occurs, versus the more thermally stable Gulf of Chiriquí, propose that upwelling is buffering the impacts of climate change, as well as thermal stress events during El Niño. They propose that the presence of upwelling zones can serve as climate refugia. Such refuge effects provided by upwelling systems from bleaching have also been observed in southern China [61] and the Galapagos [62].

The results of this study reveal that fish community composition responded variably to the 2023–2024 ENSO event, depending on reef type. Reefs dominated by *Pocillopora* showed a general decline in fish biomass as coral died. In contrast, the fish community at Zapotillal—a relatively stable coral community—remained consistent throughout the monitoring period. As the *Pocillopora* reef undergoes bleaching, it gradually loses the diversity of fauna associated with live coral, which serves as a food source for other organisms, including fish. In contrast, the coral community at Zapotillal is developing on a basaltic rocky reef with intermediate structural complexity, providing refuges for various organisms, promoting algal growth on the substrate, and supporting a more diverse array of food sources (e.g., algae and invertebrates). This difference may explain the contrasting impacts of ENSO at the two sites. Although coral bleaching also occurs at Zapotillal, the fish community relies on alternative food sources that are less affected. In more coral-dependent systems like Jícaro, the loss of live coral has a more pronounced effect on associated fish communities. The moderate concordance between benthic and fish community trajectories underscores the importance of benthic structural complexity in maintaining reef fish resilience and suggests that widespread coral mortality likely led to the degradation of critical fish habitat—a pattern widely documented in response to thermal disturbances [63,64].

Fish communities' responses to coral bleaching and mortality are known to vary over time [65,66], and are more likely to be extensive when there are changes in the reef structural complexity [65]. These modifications happened due to changes in fish species fitness, habitat loss and dependency on living corals (e.g., obligated corallivores). The specific trend experimented by each species is determined by their tolerance to disturbances and functionality [67]. Among the fish functional groups assessed, invertebrate feeders exhibited significantly higher biomass in healthy reefs than in bleached and dead reefs, underscoring their reliance on live coral shelter and foraging resources [68]. Past research in the northern Pacific of Costa Rica has shown that dead coral reefs host significantly different fish communities than live coral reefs, with lower biomass across most functional groups [69]. In our study, apart from invertebrate feeders, no statistically significant differences were observed among the other groups.

Even though no statistical differences were detected, a slight increase in both types of herbivores was observed in both bleached and severely degraded reefs (Figure 5). After coral cover depletions, immediate increases in herbivorous fish abundance have been reported due to greater algal cover, but these tend to decline as the coral framework erodes or there is redistribution of individuals [65]. At the same time, piscivores also did not show any statistical differences across reef states, but a slight decline in their biomass was detected in severely degraded reefs (Figure 5). This pattern may be related to the overall stability in fish biomass regardless of the health status, given that piscivore abundances tend to decrease when prey availability is reduced [66]. Lastly, it is relevant to point out that in species without obligate feeding behaviors, shifts in their prey may occur; however, long term declines can still be expected as their food availability is reduced [67]. Altogether, the obtained results suggest that while the effects of coral mortality on fish communities may already be emerging, the time frame of this study may have been too short to fully capture long-term changes in community composition. Thus, continued monitoring is necessary, particularly in reefs where most corals have died, as fish communities are likely to undergo further shifts over time.

The changes in fish composition and the decline of certain functional groups may signal trophic vulnerability and reflect a broader loss of ecosystem services provided by reef fishes. These services include regulating functions such as algal control and parasite removal [70,71], supporting functions like nitrogen fixation and sediment processing [71–73], and provisioning services tied to fisheries and tourism, including the ornamental trade [74,75]. Ecosystem services frameworks help capture the full social–

ecological role of reef fishes, encompassing not only their ecological functions but also their cultural significance, economic value, and conservation importance as recognized by IUCN listings [76–78]. The decline in key fish groups following bleaching events may therefore not only affect biodiversity but also compromise critical services essential for ecosystem functioning and human wellbeing. Overall, these findings highlight the functional vulnerability of certain reef fish groups to thermal disturbances and underscore the need for conservation strategies that integrate both benthic and fish community structure, as well as the ecosystem services they support, to strengthen reef ecosystem resilience.

5. Conclusions

The 2023–2024 ENSO event represented an unprecedented episode of thermal stress for coral reefs in the Gulf of Papagayo, surpassing previous events in both duration and intensity. Coral responses to this event were highly heterogeneous, highlighting the critical role of both intrinsic factors—such as genetic variability, the type of endosymbionts present, and the ability to shift toward heterotrophic feeding—and extrinsic factors, including reef location within the bay, prevailing ocean current systems, and the presence of seasonal coastal upwelling, in shaping coral resistance and resilience to bleaching. Notably, recovery observed at sites like Matapalo and Zapotillal underscores the importance of conserving areas with high biodiversity and genetic connectivity. Furthermore, the buffering effect of seasonal upwelling suggests that such regions may serve as natural climate refugia under future warming scenarios.

These findings emphasize the urgency of incorporating ecological and oceanographic insights into reef management and conservation strategies. In a context where global pressures such as ocean warming remain beyond immediate control, the effective management of local stressors—including intensive tourism, overfishing, and coastal development—is essential to support coral recovery following bleaching events [17]. Prioritizing the protection of resilient reef areas and promoting measures that enhance the adaptive capacity of coral ecosystems will be vital to safeguard biodiversity and ecosystem services (tourism and artisanal fishing) in the face of ongoing climate change.

Author Contributions: All authors had significant contributions to this study. Conceptualization, J.J.A.; methodology, J.J.A., F.Q.-P. and M.J.S.; software, J.J.A., F.Q.-P., M.J.S., M.C.-F. and S.M.; validation, J.J.A., F.Q.-P., M.J.S., M.C.-F. and S.M.; formal analysis, J.J.A., F.Q.-P., M.J.S., M.C.-F. and S.M.; investigation, J.J.A., F.Q.-P., M.J.S., M.C.-F. and S.M.; resources, J.J.A.; data curation, J.J.A., F.Q.-P., M.J.S., M.C.-F. and S.M.; writing—original draft preparation, J.J.A., F.Q.-P., M.J.S., M.C.-F. and S.M.; writing—review and editing, J.J.A., F.Q.-P., M.J.S., M.C.-F. and S.M.; visualization, J.J.A. and F.Q.-P.; supervision, J.J.A.; project administration, J.J.A.; funding acquisition, J.J.A. All authors have read and agreed to the published version of the manuscript.

Funding: The study was funded by the Vice-Rector for Research at the University of Costa Rica, the University of Costa Rica Research Foundation, and Peninsula Papagayo.

Institutional Review Board Statement: Not applicable.

Data Availability Statement: All data can be available upon request.

Acknowledgments: We are very grateful to the administrative staff of CIMAR, as well as the team from Marina Papagayo and Ecodesarrollo Papagayo, the German international cooperation agency GIZ and SINAC-ACLAC. The support in the field of B/A Divers and ALMACO was vital to carry out a safe and efficient operation. We want to give a special thanks to the Sustainability team from Peninsula Papagayo and the members of LECAN. The project has research permit resolutions ACT-OR-DR-038-19, ACT-OR-DR-100-20, ACT-OR-DR-124-2021 and is registered at the University of Costa Rica under the code B9089.

Conflicts of Interest: Authors were employed by the company BlueSeeds. The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Abbreviations

The following abbreviations are used in this manuscript:

ANOSIM	Analysis of similarities
CCA	Crustose coralline algae
CRW	Coral reef watch
DHW	Degree heating weeks
ENSO	El Niño-Southern Oscillation
ETP	Eastern Tropical Pacific
NMDS	Non-metric multidimensional scaling
NOAA	National Oceanographic and Atmospheric Administration
SST	Sea surface temperature

Appendix A

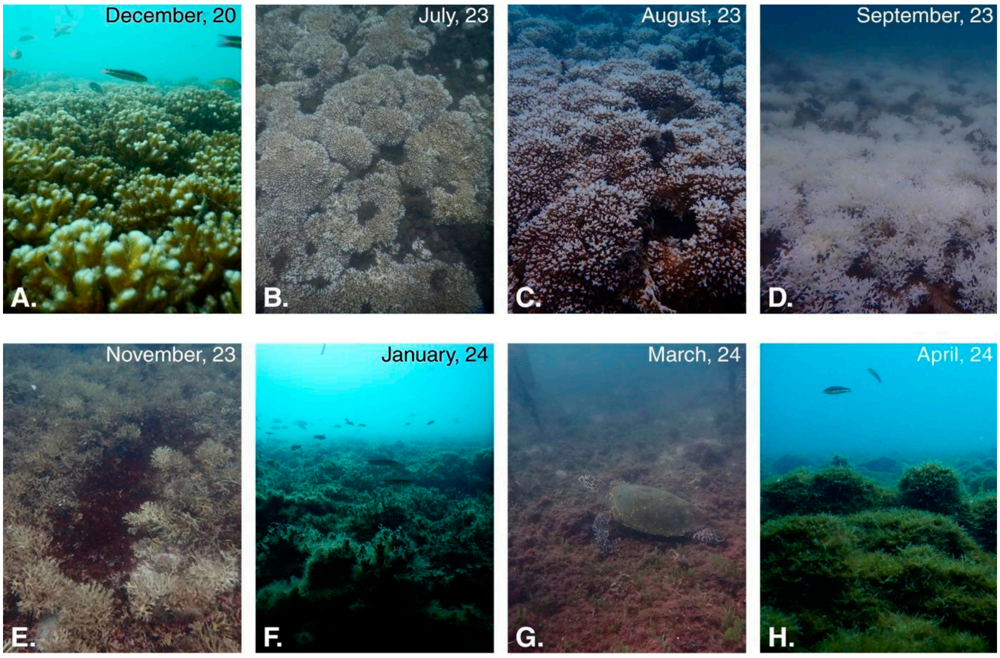

Figure A1. Progress of the impact of the El Niño phenomenon 2023–2024 on the Jicaro reef, Culebra Bay. (**A**) December, 2020; (**B**) July, 2023; (**C**) August, 2023; (**D**) September, 2023; (**E**) November, 2023; (**F**) January, 2024; (**G**) March, 2024; (**H**) April, 2024.

Appendix B

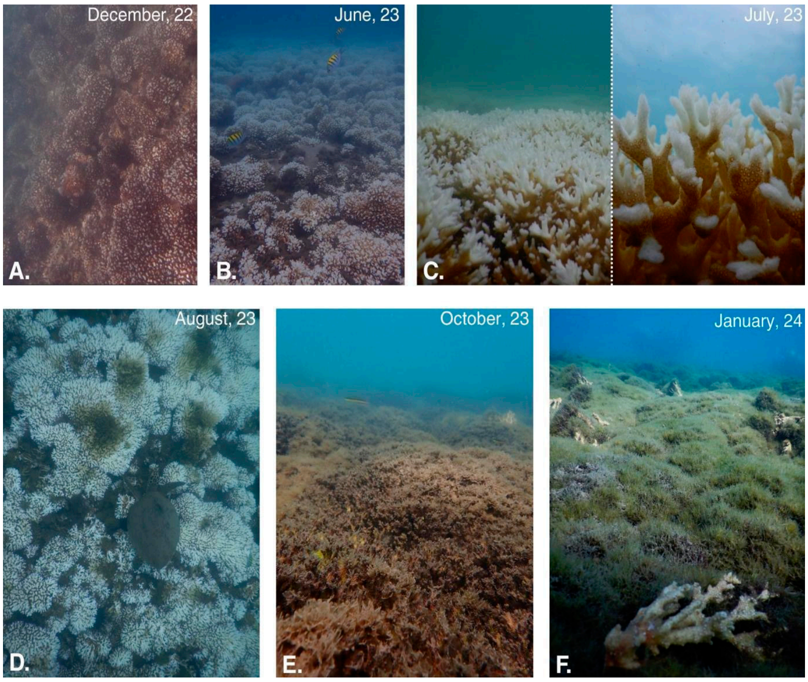

Figure A2. Progress of the impact of the El Niño phenomenon 2023–2024 on the Sombrero reef, Culebra Bay. (**A**) December, 2022; (**B**) June, 2023; (**C**) July, 2023; (**D**) August, 2023; (**E**) October, 2023; (**F**) January, 2024.

Appendix C

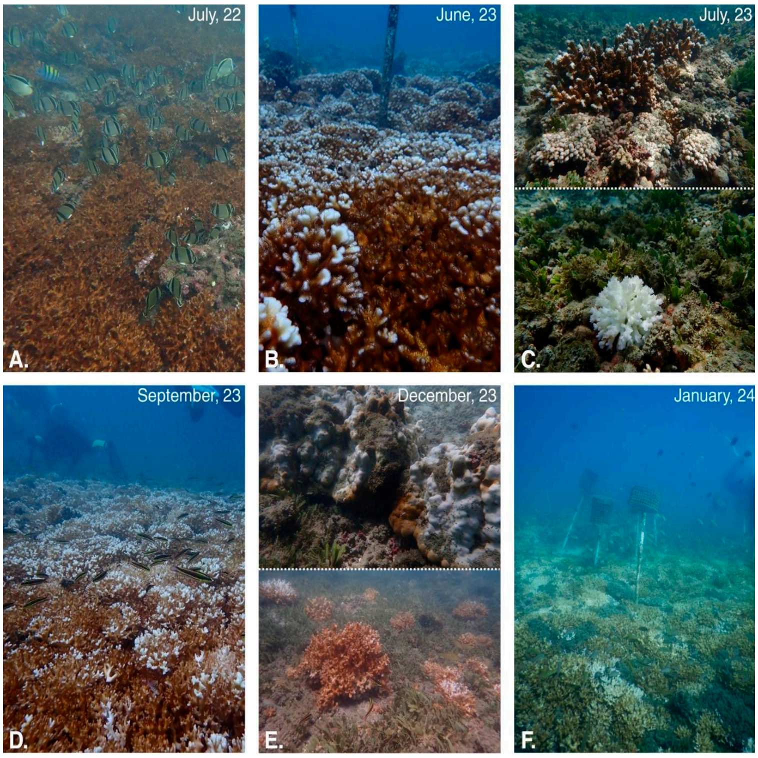

Figure A3. Progress of the impact of the El Niño phenomenon 2023–2024 on the Matapalo reef, Culebra Bay. (**A**) July, 2022; (**B**) June, 2023; (**C**) July, 2023; (**D**) September, 2023; (**E**) December, 2023; (**F**) January, 2024.

Appendix D

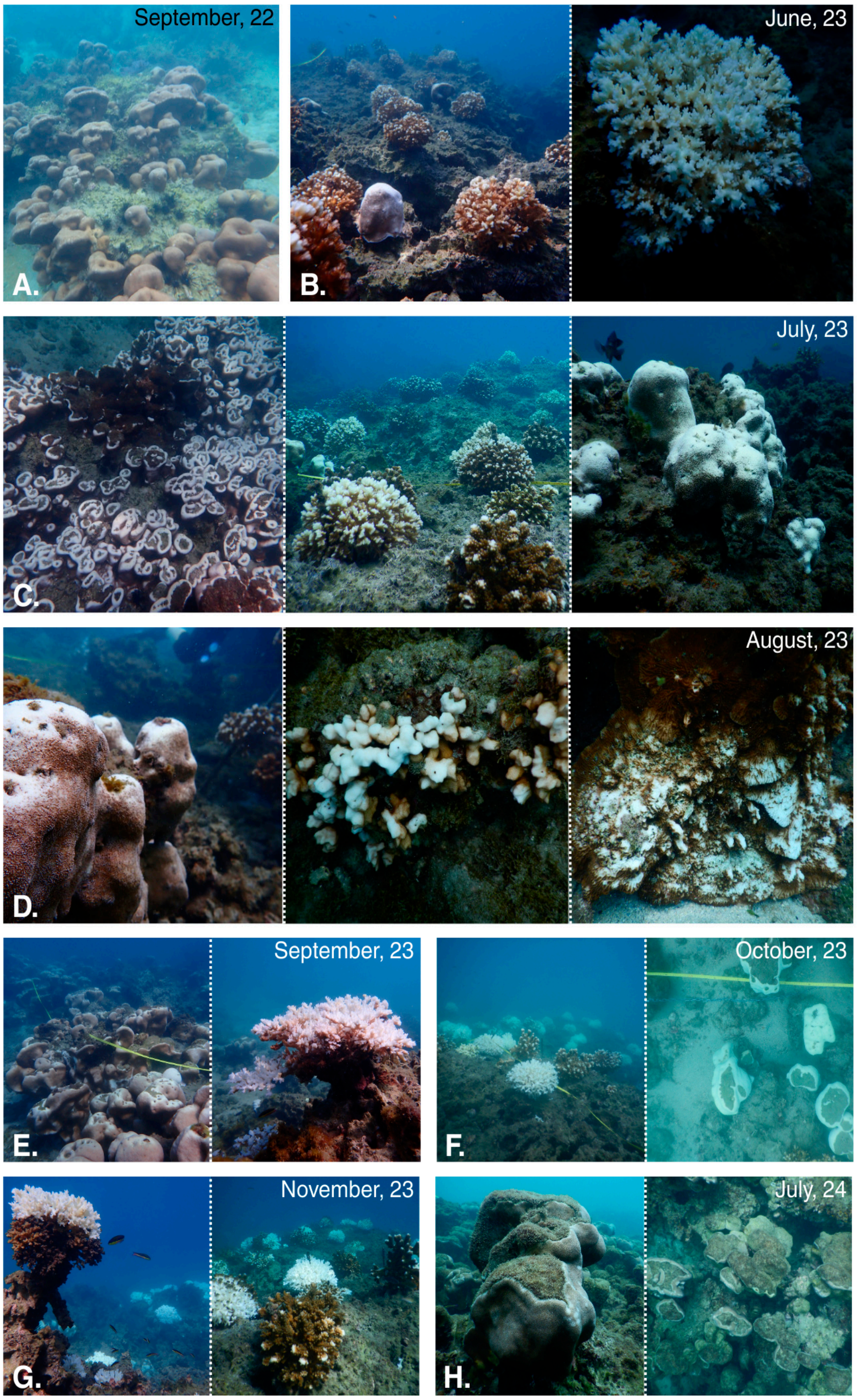

Figure A4. Progress of the impact of the El Niño phenomenon 2023–2024 on the Güiri-Güiri reef, Culebra Bay. (**A**) September, 2022; (**B**) June, 2023; (**C**) July, 2023; (**D**) August, 2023; (**E**) September, 2023; (**F**) October, 2023; (**G**) November, 2023; (**H**) July, 2024.

References

1. Goreau, T.J.F.; Hayes, R.L. 2023 Record marine heat waves: Coral reef bleaching HotSpot maps reveal global sea surface temperature extremes, coral mortality, and ocean circulation changes. *Oxf. Open Clim. Change* **2024**, *4*, kgae005. [CrossRef]
2. Hoegh-Guldberg, O. Climate change, coral bleaching and the future of the world's coral reefs. *Mar. Freshw. Res.* **1999**, *50*, 839–866. [CrossRef]

3. Hughes, T.P.; Anderson, K.D.; Connolly, S.R.; Heron, S.F.; Kerry, J.T.; Lough, J.M.; Baird, A.H.; Baum, J.K.; Berumen, M.L.; Bridge, T.C.; et al. Spatial and temporal patterns of mass bleaching of corals in the Anthropocene. *Science* **2018**, *359*, 80–83. [CrossRef]
4. Claar, D.C.; Szostek, L.; McDevitt-Irwin, J.M.; Schanze, J.J.; Baum, J.K. Global patterns and impacts of El Niño events on coral reefs: A meta-analysis. *PLoS ONE* **2018**, *13*, e0190957. [CrossRef]
5. Philander, S.G.H. El Niño southern oscillation phenomena. *Nature* **1983**, *302*, 295–301. [CrossRef]
6. McPhaden, M.J.; Zebiak, S.E.; Glantz, M.H. ENSO as an integrating concept in earth science. *Science* **2006**, *314*, 1740–1745. [CrossRef]
7. Barber, R.T.; Chavez, F.P. Biological consequences of El Niño. *Science* **1983**, *222*, 1203–1210. [CrossRef] [PubMed]
8. Holmgren, M.; Scheffer, M.; Ezcurra, E.; Gutiérrez, J.R.; Mohren, G.M.J. El Niño effects on the dynamics of terrestrial ecosystems. *Trends Ecol. Evol.* **2001**, *16*, 89–94. [CrossRef] [PubMed]
9. Glynn, P.W.; Mones, A.B.; Podestá, G.P.; Colbert, A.; Colgan, M.W. El Niño–Southern Oscillation: Effects on Eastern Pacific coral reefs and associated biota. In *Coral Reefs of the Eastern Tropical Pacific*; Glynn, P.W., Manzello, D., Enochs, I., Eds.; Coral Reefs of the World; Springer: Dordrecht, The Netherlands, 2017; pp. 251–290. [CrossRef]
10. Baker, A.C.; Starger, C.; McClanahan, T.; Glynn, P.W. Corals' adaptive response to climate change. *Nature* **2004**, *430*, 741. [CrossRef]
11. Baker, A.C.; Glynn, P.W.; Riegl, B. Climate change and coral reef bleaching: An ecological assessment of long-term impacts, recovery trends and future outlook. *Estuar. Coast. Shelf Sci.* **2008**, *80*, 435–471. [CrossRef]
12. Freeman, L.A.; Kleypas, J.A.; Miller, A.J. Coral reef habitat response to climate change scenarios. *PLoS ONE* **2013**, *8*, e82404. [CrossRef]
13. Munday, P.L.; Jones, G.P.; Pratchett, M.S.; Williams, A.J. Climate change and the future for coral reef fishes. *Fish Fish.* **2008**, *9*, 261–285. [CrossRef]
14. Harley, C.D.G.; Hughes, A.R.; Hultgren, K.M.; Miner, B.G.; Sorte, C.J.B.; Thornber, C.S.; Rodriguez, L.F.; Tomanek, L.; Williams, S.L. The impacts of climate change in coastal marine systems. *Ecol. Lett.* **2006**, *9*, 228–241. [CrossRef]
15. Shanks, A.L.; Rasmuson, L.K.; Valley, J.R.; Jarvis, M.A.; Salant, C.; Sutherland, D.A.; Lamont, E.I.; Hainey, M.A.H.; Emlet, R.B. Marine heat waves, climate change, and failed spawning by coastal invertebrates. *Limnol. Oceanogr.* **2020**, *65*, 627–636. [CrossRef]
16. Dalton, S.J.; Carroll, A.G.; Sampayo, E.; Roff, G.; Harrison, P.L.; Entwistle, K.; Huang, Z.; Salih, A.; Diamond, S.L. Successive marine heatwaves cause disproportionate coral bleaching during a fast phase transition from El Niño to La Niña. *Sci. Total Environ.* **2020**, *715*, 136951. [CrossRef] [PubMed]
17. Hughes, T.P.; Kerry, J.T.; Álvarez-Noriega, M.; Álvarez-Romero, J.G.; Anderson, K.D.; Baird, A.H.; Babcock, R.C.; Beger, M.; Bellwood, D.R.; Berkelmans, R.; et al. Global warming and recurrent mass bleaching of corals. *Nature* **2017**, *543*, 373–377. [CrossRef]
18. Reimer, J.D.; Peixoto, R.S.; Davies, S.W.; Traylor-Knowles, N.; Short, M.L.; Cabral-Tena, R.A.; Burt, J.A.; Pessoa, I.; Banaszak, A.T.; Winters, R.S.; et al. The fourth global coral bleaching event: Where do we go from here? *Coral Reefs* **2024**, *43*, 1121–1125. [CrossRef]
19. Jiang, N.; Zhu, C.; Hu, Z.-Z.; McPhaden, M.J.; Lian, T.; Zhou, C.; Qian, W.; Chen, D. El Niño and sea surface temperature pattern effects lead to historically high global mean surface temperatures in 2023. *Geophys. Res. Lett.* **2025**, *52*, e2024GL113733. [CrossRef]
20. Neely, K.L.; Nowicki, R.J.; Dobler, M.A.; Chaparro, A.A.; Miller, S.M.; Toth, K.A. Too hot to handle? The impact of the 2023 marine heatwave on Florida Keys coral. *Front. Mar. Sci.* **2024**, *11*, 1489273. [CrossRef]
21. Byrne, M.; Waller, A.; Clements, M.; Kelly, A.S.; Kingsford, M.J.; Liu, B.; Reymond, C.E.; Vila-Concejo, A.; Webb, M.; Whitton, K.; et al. Catastrophic bleaching in protected reefs of the Southern Great Barrier Reef. *Limnol. Oceanogr. Lett.* **2025**, *10*, 340–348. [CrossRef]
22. López-Pérez, A.; Granja-Fernández, R.; Ramírez-Chávez, E.; Valencia-Méndez, O.; Rodríguez-Zaragoza, F.A.; González-Mendoza, T.; Martínez-Castro, A. Widespread coral bleaching and mass mortality of reef-building corals in Southern Mexican Pacific reefs due to 2023 El Niño warming. *Oceans* **2024**, *5*, 196–209. [CrossRef]
23. Guzman, H.M.; Cortés, J.; Richmond, R.H.; Glynn, P.W. Efectos del fenómeno de "El Niño-Oscilación Sureña" 1982–83 en los arrecifes coralinos de la Isla del Caño, Costa Rica. *Rev. Biol. Trop.* **1987**, *35*, 325–332.
24. Jiménez, C.; Cortés, J. Effects of the 1991–1992 El Niño on scleractinian corals of the Costa Rican central Pacific coast. *Rev. Biol. Trop.* **2001**, *49*, 239–250.
25. Jiménez, C.E.; Cortés, J. Coral cover change associated to El Niño, eastern Pacific, Costa Rica, 1992–2001. *Mar. Ecol.* **2003**, *24*, 179–192. [CrossRef]
26. Guzman, H.M.; Cortés, J. Cocos Island (Pacific of Costa Rica) coral reefs after the 1982–83 El Niño disturbance. *Rev. Biol. Trop.* **1992**, *40*, 309–324.
27. Guzman, H.M.; Cortés, J. Reef recovery 20 years after the 1982–83 El Niño massive mortality. *Mar. Biol.* **2007**, *151*, 401–411. [CrossRef]
28. Jiménez, C.; Cortés, J.; León, A.; Ruiz, E. Coral bleaching and mortality associated with the 1997–98 El Niño in an upwelling environment in the eastern Pacific (Gulf of Papagayo, Costa Rica). *Bull. Mar. Sci.* **2001**, *69*, 151–169.

29. Alvarado, J.J.; Sánchez-Noguera, C.; Arias-Godínez, G.; Araya, T.; Fernández-García, C.; Guzman, A.G. Impact of El Niño 2015–2016 on the coral reefs of the Pacific of Costa Rica: The potential role of marine protection. *Rev. Biol. Trop.* **2019**, *68*, S271–S282. [CrossRef]
30. Cortés, J.; Jiménez, C.E. Corals and coral reefs of the Pacific of Costa Rica: History, research and status. In *Latin American Coral Reefs*; Cortés, J., Ed.; Elsevier: Berlin, Germany, 2003; pp. 361–385. [CrossRef]
31. Romero-Torres, M.; Acosta, A.; Palacio-Castro, A.M.; Treml, E.A.; Zapata, F.A.; Paz-García, D.A.; Porter, J.W. Coral reef resilience to thermal stress in the Eastern Tropical Pacific. *Glob. Change Biol.* **2020**, *26*, 3880–3890. [CrossRef]
32. Jiménez, C.; Bassey, G.; Segura, A.; Cortés, J. Characterization of the coral communities and reefs of two previously undescribed locations in the upwelling region of Gulf of Papagayo (Costa Rica). *Rev. Cienc. Mar. Costeras* **2010**, *2*, 95–108. [CrossRef]
33. Alfaro, E.J.; Cortés, J.; Alvarado, J.J.; Jiménez, C.; León, A.; Sánchez-Noguera, C.; Nivia-Ruiz, J.; Ruiz, E. Clima y variabilidad climática de la temperatura subsuperficial del mar en Bahía Culebra, Guanacaste, Costa Rica. *Rev. Biol. Trop.* **2012**, *60*, 159–171. [CrossRef]
34. Rixen, T.; Jiménez, C.; Cortés, J. Impact of upwelling events on the sea water chemistry in the Gulf of Papagayo (Culebra Bay), Costa Rica. *Rev. Biol. Trop.* **2012**, *60*, 187–195. [CrossRef]
35. Stuhldreier, I.; Sánchez-Noguera, C.; Rixen, T.; Cortés, J.; Morales, A.; Wild, C. Effects of seasonal upwelling on inorganic and organic matter dynamics in the water column of Eastern Pacific coral reefs. *PLoS ONE* **2015**, *10*, e0142681. [CrossRef]
36. Sánchez-Noguera, C.; Stuhldreier, I.; Cortés, J.; Jiménez, C.; Morales, A.; Wild, C.; Rixen, T. Natural ocean acidification at Papagayo upwelling system (North Pacific Costa Rica): Implications for reef development. *Biogeosciences* **2018**, *15*, 2349–2360. [CrossRef]
37. Liu, G.; Heron, S.F.; Eakin, C.M.; De La Cour, J.L.; Geiger, E.F.; Tirak, K.V.; Skirving, W.J.; Strong, A.E. NOAA Coral Reef Watch (CRW) daily global 5-km (0.05 Degree) satellite coral bleaching heat stress monitoring product suite. NOAA National Centers for Environmental Information: Asheville, NC, USA, 2018. Available online: https://doi.org/10.25921/6jgr-pt28 (accessed on 2 April 2025).
38. Glynn, P.W.; D'Croz, L. Experimental Evidence for high temperature stress as the cause of El Niño coincident coral mortality. *Coral Reefs* **1990**, *8*, 181–191. [CrossRef]
39. Harriott, V.J.; Banks, S.A. Latitudinal variation in coral communities in Eastern Australia: A qualitative biophysical model of factors regulating coral reefs. *Coral Reefs* **2002**, *21*, 83–94. [CrossRef]
40. Kleypas, J.A.; McManus, J.W.; Meñez, L.A.B. Environmental limits to coral reef development: Where do we draw the line? *Am. Zool.* **1999**, *39*, 146–159. [CrossRef]
41. Glynn, P.W.; Wellington, G.M. *Corals and Coral Reefs of the Galápagos Islands*; University of California Press: Berkeley, CA, USA, 1983; p. 330. [CrossRef]
42. Trygonis, V.; Sini, M. photoQuad: A dedicated seabed image processing software, and a comparative error analysis of four photoquadrat methods. *J. Exp. Mar. Biol. Ecol.* **2012**, *424–425*, 99–108. [CrossRef]
43. Alvarado, J.J.; Beita, A.; Mena, S.; Fernández-García, C.; Guzmán, A.G. Ecosistemas coralinos del Área de Conservación Osa, Costa Rica: Análisis estructural y necesidades de conservación. *Rev. Biol. Trop.* **2015**, *63*, 219–259. [CrossRef]
44. Alvarado, J.J.; Beita, A.; Mena, S.; Fernández-García, C.; Guzmán, A.G.; Cortés, J. Ecosistemas coralinos del Parque Nacional Isla del Coco, Costa Rica: Análisis estructural y temporal. *Rev. Biol. Trop.* **2016**, *64*, 153–175. [CrossRef]
45. Froese, R.; Pauly, D. FishBase. World Wide Web Electronic Publication. 2016. Available online: http://www.fishbase.org/ (accessed on 16 October 2016).
46. Cambronero-Solano, S.; Tisseaux-Navarro, A.; Vargas-Hernández, J.M.; Salazar-Ceciliano, J.P.; Benavides-Morera, R.; Quesada-Ávila, I.; Brenes-Rodríguez, C. Hydrographic variability in the Gulf of Papagayo, Costa Rica during 2017–2019. *Rev. Biol. Trop.* **2021**, *69*, S74–S93. [CrossRef]
47. Hidalgo-Sánchez, R.; Alvarado, J.J.; Araya-Valverde, E.; Díaz-Ferguson, E. Genetic diversity and structure of *Pocillopora* spp. corals in the Gulf of Papagayo, Costa Rica. *Discov. Ocean.* **2025**, *2*, 16. [CrossRef]
48. Alfaro-Monge, B.C. Diversidad genética de los endosimbiontes dinoflagelados (Dinophyceae: Symbiodiniaceae) de los corales hermatípicos en Bahía Culebra, Pacífico de Costa Rica. Licenciatura Thesis, Universidad de Costa Rica, San José, Costa Rica, 2025.
49. Millán-Márquez, A.M.; Velasco-Montoya, D.A.; Terraneo, T.I. Symbiodiniaceae diversity in *Pocillopora* corals in different environments of the Colombian Eastern Pacific: Symbiont specificity in spite of coral-host flexibility. *Coral Reefs* **2024**, *43*, 1581–1597. [CrossRef]
50. Thornhill, D.J.; LaJeunesse, T.C.; Kemp, D.W.; Fitt, W.K.; Schmidt, G.W. Multi-year, seasonal genotypic surveys of coral–algal symbioses reveal prevalent stability or post-bleaching reversion. *Mar. Biol.* **2006**, *148*, 711–722. [CrossRef]
51. Goulet, T.L.; LaJeunesse, T.C.; Fabricius, K.E. Symbiont specificity and bleaching susceptibility among soft corals in the 1998 Great Barrier Reef mass coral bleaching event. *Mar. Biol.* **2008**, *154*, 795–804. [CrossRef]

52. Kemp, D.W.; Hoadley, K.D.; Lewis, A.M.; Wham, D.C.; Smith, R.T.; Warner, M.E.; LaJeunesse, T.C. Thermotolerant coral–algal mutualisms maintain high rates of nutrient transfer while exposed to heat stress. *Proc. R. Soc. B* **2023**, *290*, 20231403. [CrossRef] [PubMed]
53. Glynn, P.W.; Maté, J.L.; Baker, A.C.; Calderón, M.O. Coral bleaching and mortality in Panama and Ecuador during the 1997–1998 El Niño–Southern Oscillation event: Spatial/temporal patterns and comparisons with the 1982–1983 event. *Bull. Mar. Sci.* **2001**, *69*, 79–109.
54. Fabregat-Malé, S.; Mena, S.; Alvarado, J.J. Nursery-reared coral outplanting success in an upwelling-influenced area in Costa Rica. *Rev. Biol. Trop.* **2023**, *71*, e54879. [CrossRef]
55. Fabregat-Malé, S.; Mena-González, S.; Quesada-Perez, F.; Alvarado, J.J. Testing the feasibility of coral nurseries in an upwelling area in the North Pacific of Costa Rica. *Front. Mar. Sci.* **2024**, *11*, 1400026. [CrossRef]
56. Hughes, A.D.; Grottoli, A.G. Heterotrophic compensation: A possible mechanism for resilience of coral reefs to global warming or a sign of prolonged stress? *PLoS ONE* **2013**, *8*, e81172. [CrossRef]
57. Martinez, S.; Grover, R.; Ferrier-Pagès, C. Unveiling the importance of heterotrophy for coral symbiosis under heat stress. *mBio* **2024**, *15*, e01966-24. [CrossRef]
58. Wang, Q.; Zheng, X.; Zhou, X.; Zhang, H.; Cai, L.; Leung, J.Y.S.; Huang, L. Symbiont genus determines the trophic strategy of corals: Implications for intraspecific competition for energy sources in coral reefs. *Ecol. Indic.* **2024**, *158*, 111477. [CrossRef]
59. Palmer, C.; Jimenez, C.; Bassey, G.; Ruiz, E.; Villalobos-Cubero, T.; Chavarria-Diaz, M.M.; Harrison, X.A.; Puschendorf, R. Cold water and harmful algal blooms linked to coral reef collapse in the Eastern Tropical Pacific. *PeerJ* **2022**, *10*, e14081. [CrossRef]
60. Randall, C.J.; Toth, L.T.; Leichter, J.J.; Maté, J.L.; Aronson, R.B. Upwelling buffers climate change impacts on coral reefs of the eastern tropical Pacific. *Ecology* **2020**, *101*, e02918. [CrossRef] [PubMed]
61. Zhu, W.; Ren, Y.; Liu, X.; Huang, D.; Xia, J.; Zhu, M.; Yin, H.; Chen, R.; Li, X. The impact of coastal upwelling on coral reef ecosystems under anthropogenic influence: Coral reef community and its response to environmental factors. *Front. Mar. Sci.* **2022**, *9*, 888888. [CrossRef]
62. Riegl, B.; Glynn, P.W.; Banks, S.; Keith, I.; Rivera, F.; Vera-Zambrano, M.; D'Angelo, C.; Wiedenmann, J. Heat attenuation and nutrient delivery by localized upwelling avoided coral bleaching mortality in northern Galapagos during 2015/2016 ENSO. *Coral Reefs* **2019**, *38*, 773–785. [CrossRef]
63. Wilson, S.K.; Graham, N.A.; Pratchett, M.S.; Jones, G.P.; Polunin, N.V. Multiple disturbances and the global degradation of coral reefs: Are reef fishes at risk or resilient? *Glob. Change Biol.* **2006**, *12*, 2220–2234. [CrossRef]
64. Graham, N.A.; Cinner, J.E.; Norström, A.V.; Nyström, M. Coral reefs as novel ecosystems: Embracing new futures. *Curr. Opin. Environ. Sustain.* **2014**, *7*, 9–14. [CrossRef]
65. Garpe, K.C.; Yahya, S.A.S.; Lindahl, U.; Öhman, M.C. Long-term effects of the 1998 coral bleaching event on reef fish assemblages. *Mar. Ecol. Prog. Ser.* **2006**, *315*, 237–247. [CrossRef]
66. Williamson, D.H.; Ceccarelli, D.M.; Evans, R.D.; Lamb, S.D.; Russ, G.R. Habitat dynamics, marine reserve status, and the decline and recovery of coral reef fish communities. *Ecol. Evol.* **2014**, *4*, 337–354. [CrossRef]
67. Pratchett, M.S.; Hoey, A.S.; Wilson, S.K.; Messmer, V.; Graham, N.A.J. Changes in biodiversity and functioning of the reef fish assemblages following coral bleaching and coral loss. *Diversity* **2011**, *3*, 424–452. [CrossRef]
68. Pratchett, M.S.; Munday, P.L.; Wilson, S.K.; Graham, N.A.; Cinner, J.E.; Bellwood, D.R.; Mcclanahan, T.R. Effects of climate-induced coral bleaching on coral-reef fishes—Ecological and economic consequences. In *Oceanography and Marine Biology: An Annual Review*; CRC Press: Boca Raton, FL, USA, 2008; Volume 46, pp. 257–302. [CrossRef]
69. Mena, S.; Quesada-Perez, F.; Sánchez-Noguera, C.; Salas-Moya, C.; Alvarado, J.J.; López-Garro, A.; López, L.F. Estructura comunitaria de ecosistemas coralinos en sitios de importancia para la conservación de la biodiversidad marina del Pacífico Norte de Costa Rica. *Rev. Biol. Trop.* **2025**, *73*, e63715. [CrossRef]
70. Edwards, C.B.; Friedlander, A.M.; Green, A.G.; Hardt, M.J.; Sala, E.; Sweatman, H.P.; Williams, I.D.; Zgliczynski, B.; Sandin, S.A.; Smith, J.E. Global assessment of the status of coral reef herbivorous fishes: Evidence for fishing effects. *Proc. R. Soc. B* **2014**, *281*, 20131835. [CrossRef]
71. Tebbett, S.B.; Chase, T.J.; Bellwood, D.R. Farming damselfishes shape algal turf sediment dynamics on coral reefs. *Mar. Environ. Res.* **2020**, *160*, 104988. [CrossRef]
72. Alvarado, J.J.; Grassian, B.; Cantera-Kintz, J.R.; Carballo, J.L.; Londoño-Cruz, E. Coral reef bioerosion in the eastern tropical Pacific. In *Coral Reefs of the Eastern Tropical Pacific: Persistence and Loss in a Dynamic Environment*; Glynn, P.W., Manzello, D.P., Enochs, I.C., Eds.; Springer: Dordrecht, The Netherlands, 2017; pp. 369–403. [CrossRef]
73. Perry, C.T.; Salter, M.A.; Lange, I.D.; Kochan, D.P.; Harborne, A.R.; Graham, N.A. Geo-ecological functions provided by coral reef fishes vary among regions and impact reef carbonate cycling regimes. *Ecosphere* **2022**, *13*, e4288. [CrossRef]
74. Quimbayo, J.P.; Mendes, T.C.; Kulbicki, M.; Floeter, S.R.; Zapata, F.A. Unusual reef fish biomass and functional richness at Malpelo, a remote island in the Tropical Eastern Pacific. *Environ. Biol. Fishes* **2017**, *100*, 149–162. [CrossRef]

75. Gijón-Díaz, D.; Reyes-Bonilla, H.; Guerrero-Izquierdo, T.P.; Fernández-Rivera Melo, F.J. Potencial económico de la captura de peces de ornato bajo protección federal en México. *Rev. Biol. Trop.* **2017**, *65*, 195–210. [CrossRef]
76. Reyes-Bonilla, H.; Morello, G.; Calderon-Aguilera, L.E.; Velasco-Lozano, M.; Ramírez-Ortiz, G.; Morales-MontesDeOca, E. Ecosystem services offered by fishes in shallow and mesophotic reefs of the southern Gulf of California. *Biodivers. Conserv.* **2025**, *34*, 1903–1928. [CrossRef]
77. Costanza, R.; de Groot, R.; Braat, L.; Kubiszewski, I.; Fioramonti, L.; Sutton, P.; Farber, S.; Grasso, M. Twenty years of ecosystem services: How far have we come and how far do we still need to go? *Ecosyst. Serv.* **2017**, *28*, 1–16. [CrossRef]
78. Holstein, D.M.; Fletcher, P.; Groves, S.H.; Smith, T.B. Ecosystem services of mesophotic coral ecosystems and a call for better accounting. In *Mesophotic Coral Ecosystems*; Loya, Y., Puglise, K.A., Bridge, T.C.L., Eds.; Springer: Cham, Switzerland, 2019; pp. 943–956. [CrossRef]