oceans

*Article*

# Widespread Coral Bleaching and Mass Mortality of Reef-Building Corals in Southern Mexican Pacific Reefs Due to 2023 El Niño Warming

**Andrés López-Pérez [1,*], Rebeca Granja-Fernández [2,3], Eduardo Ramírez-Chávez [4], Omar Valencia-Méndez [5], Fabián A. Rodríguez-Zaragoza [3], Tania González-Mendoza [5] and Armando Martínez-Castro [6]**

1 Laboratorio de Arrecifes y Biodiversidad (ARBIOLAB), Departamento de Hidrobiología, Universidad Autónoma Metropolitana Unidad Iztapalapa, Ciudad de México 09340, Mexico
2 Programa de Maestría en Biosistemática y Manejo de Recursos Naturales y Agrícolas (BIMARENA), Centro Universitario de Ciencias Biológicas y Agropecuarias, Universidad de Guadalajara, Zapopan 45200, Mexico; beckygranja@gmail.com
3 Laboratorio de Ecología Molecular, Microbiología y Taxonomía (LEMITAX), Departamento de Ecología, Centro Universitario de Ciencias Biológicas y Agropecuarias, Universidad de Guadalajara, Zapopan 45200, Mexico; fabian.rzaragoza@academicos.udg.mx
4 Instituto de Recursos, Universidad del Mar. Ciudad Universitaria, Puerto Ángel 70902, Mexico; eduardo@angel.umar.com
5 Centro de Investigación y Educación Superior de Ensenada, Ensenada 22860, Mexico; ovalencia@cicese.mx (O.V.-M.); taniamaribel.gonzalez.mendoza@gmail.com (T.G.-M.)
6 Parque Nacional Huatulco, Santa María Huatulco 70989, Mexico; armando.martinez@conanp.gob.mx
* Correspondence: alopez@xanum.uam.mx

**Abstract:** In May 2023, oceanic and atmospheric anomalies indicated El Niño conditions in the eastern Pacific, followed by coral bleaching in coral communities and reefs of Huatulco. We conducted surveys and sampled coral reef communities from late June to mid–August of 2023 to evaluate the intensity and extent of the changes associated with the warming event. From January of 2023, Huatulco experienced positive sea surface temperature (SST) anomalies; however, beginning in June, the high-temperature anomalies became extreme (>31 °C; ~2 °C above historical records). These high temperatures resulted in extensive coral bleaching in middle–late June and mortality from middle–late July (>50–93%). In addition, the area experienced significant reductions in echinoderm abundance and fish biomass. In 2023, severe bleaching affected coral systems in the Central Mexican Pacific, Gulf of Mexico, and Mexican Caribbean, making this the most devastating marine heatwave event, simultaneously impacting coral reefs across Mexico's Pacific and Atlantic coasts.

**Keywords:** ENSO; coral bleaching; coral mortality; Huatulco; echinoderms; fish

check for updates

**Citation:** 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. https://doi.org/10.3390/oceans5020012

Academic Editors: Michael W. Lomas and Marco Taviani

Received: 15 November 2023
Revised: 8 March 2024
Accepted: 1 April 2024
Published: 4 April 2024



## 1. Introduction

The El Niño Southern Oscillation (ENSO) is a global-scale climatic event, with consistent records dating back to the early Holocene period in the eastern Pacific [1]. ENSO is an interannual and irregular event that alternates between two phases, El Niño and La Niña, leading to changes in sea surface temperature (SST) in extensive ocean areas compared to average conditions. While El Niño results in positive anomalies (warming), La Niña causes negative anomalies (cooling) in the ocean [2]. Both climatic anomalies can significantly stress terrestrial and aquatic ecosystems, including coral reefs [1].

Depending on various factors—such as their relative strengths, onset seasons, maturity, overall duration, and the spatial extent of maximum SST anomalies—in synergy with local and regional stressors [3,4], ENSO events may lead to coral bleaching. Under adequate environmental conditions, reef-building corals fix calcium and carbonate ions in seawater to secrete a white calcium carbonate skeleton [5]. As coral tissue is translucent, coral bleaching occurs when there is a partial to complete loss of dinoflagellate algae population within the coral host (70 to >90% reduction in algal density) or a degradation of algal pigments [6]. Under mild thermal stress, the coral host can survive and recover the algal symbionts when seawater temperatures decrease over several weeks to months; however, acute and prolonged thermal stress can lead to severe coral bleaching, regardless of whether it is associated with warm or cold phases, causing extensive coral mortality and concomitant degradation of coral reef ecosystems [7,8]. The first extensive coral bleaching and mortality in the eastern Pacific associated with an ENSO event was reported by Glynn [9], who observed bleaching and mortality in the Gulf of Chiriquí and the Galapagos Islands during early 1983 but also signaled widespread bleaching and mortality in several other localities in the Pacific and Caribbean [9]. Numerous studies have addressed coral bleaching and mortality linked to both positive and negative moderate-to-strong ENSO anomalies in the eastern Pacific, extending from the Gulf of California [10–13] to the central Mexican Pacific [14,15], the southern Mexican Pacific [16,17], and Central America from Costa Rica to Ecuador (see [8,18,19] and the references therein).

On the Pacific coast of Mexico, coral bleaching events were associated with the ENSO event in 1982–1983 [20], as well as during subsequent ENSO events in 1987 [10], 1997–1998 [11,12,14], 2009–2010 [16], and 2015–2016 [15,17]. Contrary to Central America, where ENSO has had catastrophic effects from Costa Rica to Ecuador [8], coral mortality in Mexico has ranged from 15 to 60% of coral colonies [10–12] in the Baja Peninsula area. In other areas, the impact has been different. In the central area [14] and in some parts of the southern Mexican Pacific reef track (specifically, the westernmost Puerto Ángel reefs), 96% of corals died during the 1997–1998 ENSO event [21]; however, during the 2009–2010 ENSO event, mortality remained modest [16].

The Climate Prediction Center of the National Oceanic and Atmospheric Administration: https://www.cpc.ncep.noaa.gov/products/CDB/CDB_Archive_html/CDB_archive.shtml (accessed on 20 September 2023) reported that during early 2023, there was a transition from negative to positive anomalies in the Pacific. However, it was not until May that the oceanic and atmospheric anomalies were consistent with El Niño conditions: https://www.cpc.ncep.noaa.gov/products/CDB/CDB_Archive_html/bulletin_052023/ (accessed on 20 September 2023). Since mid–June 2023, multiple reports on social media emerged regarding disturbances in coral communities and reefs in the southern Mexican Pacific and other areas of Central America, indicating mild to severe coral bleaching associated with El Niño conditions. In this study, we document the impact of the current 2023 El Niño bleaching event on coral communities and reefs located on the central coast of Oaxaca in the Southern Mexican Pacific. The data indicate that bleaching caused significant mortality on Huatulco reefs by early-to-mid August. Concurrently, bleaching and mortality also occurred in the Central Mexican Pacific, the Gulf of Mexico, and the Mexican Caribbean [22].

## 2. Materials and Method

The Huatulco reef area is located on the western margin of the Gulf of Tehuantepec in the southern Mexican Pacific (Figure 1). The Eastern Pacific warm pool (SST > 28 °C) influences these coastal waters; this oceanographic feature is centered off Guatemala and the southwestern coast of Mexico and is characterized by high temperatures, small annual thermal oscillations (<2 °C), an average surface salinity of 34, and the presence of a shallow (20–40 m) and relatively stable thermocline [23]. Seasonally (November through March), the area is under the influence of intense wind bursts called Tehuanos, which produce substantial changes in the structure of the water column and complex coastal circulation [24]. ENSO events, which have a frequency of 4–5 years between phases, are the predominant cause of interannual oceanographic fluctuations within the southern Mexican Pacific [23].

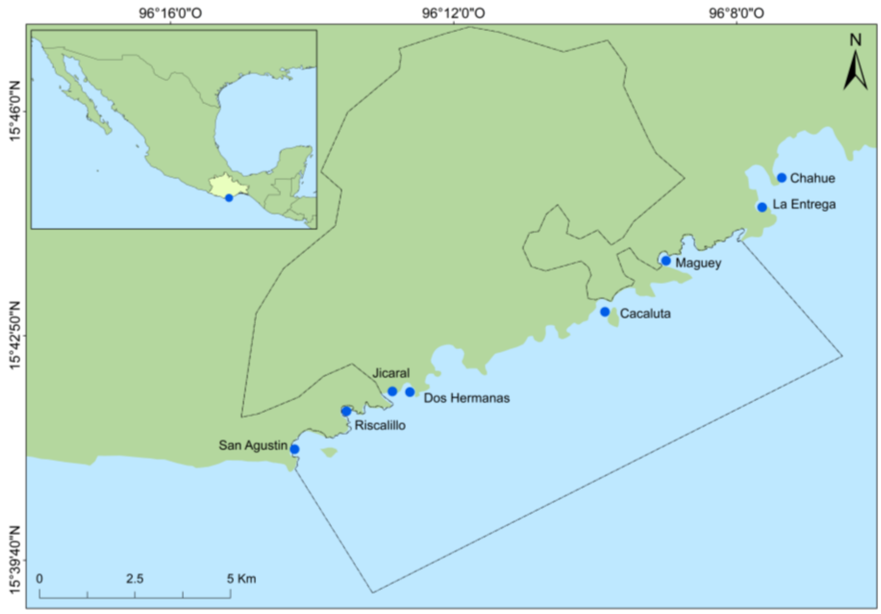


**Figure 1.** Studied localities in Huatulco, southern Mexican Pacific.

Monthly historic sea surface temperature (SST) records of the study area were gathered from the Hadley Centre Sea Ice and Sea Surface Temperature data set: https://www.metoffice.gov.uk/hadobs/hadisst/ (accessed on 28 July 2023). Satellite images were also gathered; daily SST records for each surveyed reef locality were obtained from January to September 2023: Aqua/MODIS, level 3 processing, 4 × 4 km resolution, http://oceancolor.gsfc.nasa.gov (accessed on 1 October 2023). Monthly pooled satellite-derived temperature data from January to September 2023 were calculated and plotted alongside historical data from 1870 to 2023. Concurrently, we obtained the daily 5 km satellite coral bleaching heat stress Degree Heating Weeks (DHW) for 1 January to 31 December 2023 from the NOAA Coral Reef Watch: https://coralreefwatch.noaa.gov/product/5km/index_5km_dhw.php (accessed on 12 January 2024). We employed the DHW product as it is directly related to the timing and intensity of coral bleaching, given that it accumulates instantaneous bleaching heat stress during the most recent 12-week period [25].

From 27 June to 2 July 2023, a rapid survey was conducted on the Riscalillo, Jicaral, Dos Hermanas, Cacaluta, Maguey, and Chahué reefs using SCUBA and free-diving techniques to identify coral species and depth-based bleaching and mortality patterns (Figure 1, Table 1).

**Table 1.** Sites, dates, and survey type.

| Site | Drone | Transect |
|---|---|---|
| San Agustín | June–July 2017, 27 June–2 July, 14–18 August | 27 June–2 July, 17–22 August |
| Riscalillo | June–July 2017, 27 June–2 July, 14–18 August | 27 June–2 July, 17–22 August |
| Jicaral | June–July 2017, 27 June–2 July, 14–18 August | 27 June–2 July, 17–22 August |
| Dos Hermanas | June–July 2017, 27 June–2 July, 14–18 August | 27 June–2 July, 17–22 August |
| Cacaluta | June–July 2017, 27 June–2 July, 14–18 August | 27 June–2 July, 17–22 August |
| Maguey | June–July 2017, 27 June–2 July, 14–18 August | 27 June–2 July, 17–22 August |
| La Entrega | June–July 2017, 27 June–2 July, 14–18 August | 27 June–2 July, 17–22 August |
| Chahué | June–July 2017, 27 June–2 July, 14–18 August | 27 June–2 July, 17–22 August |

The substrate was characterized via the use of a lightweight uncrewed aerial vehicle (UAV) that conducted flights over the studied area before (June–July 2017) and twice during the current 2023 El Niño bleaching event (27 June–2 July and 14–18 August 2023). The UAV flights followed a reticular pattern over the San Agustín, Riscalillo, Cacaluta, Maguey, and La Entrega reefs (Figure 1, Table 1). Structure-from-motion (SfM) algorithms were implemented to recreate the substrate [26]. The substrate was identified—using a support vector machine (SVM) algorithm for each time frame, with a segmentation scale of 50—as live coral, bleached coral, dead coral, sand, and rocks. Substrate characteristics represent the percentage change in live, bleached, and dead corals before and during the heat stress event. However, only the first three substrates were visually depicted.

Belt transects were used to record the echinoderm (echinoids) density (20 × 2 m, 40 $m^2$) and fish abundance and size (20 × 4 m, 80 $m^2$) three times before the 2023 El Niño bleaching event (February 2020, September–October 2021, and February 2023) and during the event (August 2023); see Table 1. All sampling transects were haphazardly placed on each locality, running parallel to the coastline in shallow (0–5 m) and deep waters (>5 m) within the bathymetric range where reefs occur (2–18 m) [20].

The trophic level for each fish species was retrieved from FishBase [27]. The trophic level index categorizes adult fish species based on their position within the food web. Herbivores and detritivores have a trophic level below 2.20. Omnivores (low-trophic-level omnivores) who consume plant matter and other prey (e.g., sponges, isopods, and amphipods) have a level ranging from 2.20 to 2.80, while omnivores (high-trophic-level omnivores) with a preference for animals but feed on diverse prey (e.g., algae, bivalves, isopods, and fish larvae) have a value of 2.81–3.70. Piscivores and carnivores, with a preference for large decapods, cephalopods, and fish (carnivores), have a value above 3.70 [27,28].

Finally, data analyses on substrate characteristics, sea urchin density, fish biomass, and trophic level before and during the 2023 El Niño bleaching event were conducted via parametric or non-parametric two-independent sample tests [29]. The analysis, graphing, and hypothesis testing were conducted in R studio [30].

## 3. Results

Positive SST anomalies occurred in Huatulco from January of 2023. Notably, anomalies were relatively higher in January (1.4 °C) but were more modest from February to April 2023 (0.2–0.48 °C). SST anomalies increased in May (0.76 °C) and, starting in June 2023, the area experienced abnormally high temperatures (>31 °C since early June; approximately 2 °C above historical records) along with calm and clear waters (Figure 2). Consequently, this situation led to severe bleaching in the coral communities and reefs located in the Huatulco area.

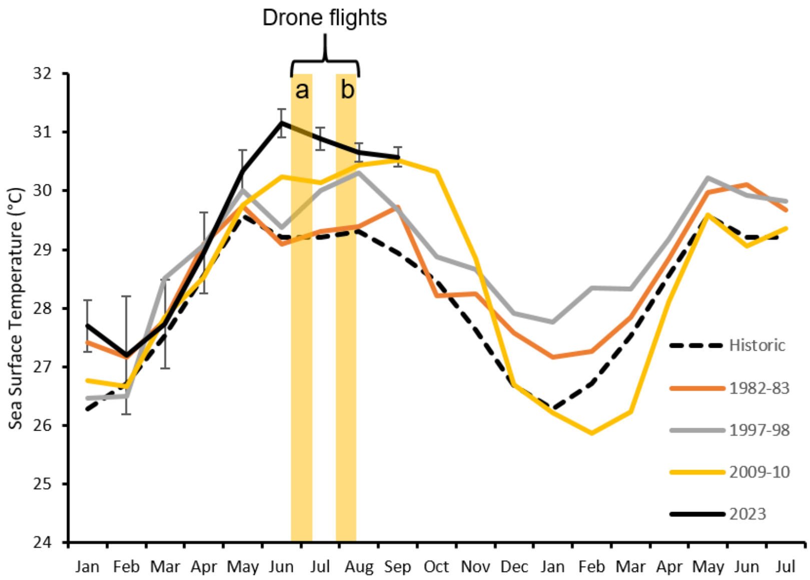


**Figure 2.** Historical monthly average sea surface temperature (SST) records (1870–2022) and satellite-derived (Aqua/MODIS, level 3 processing, resolution of 4 × 4 km, http://oceancolor.gsfc.nasa.gov accessed on 20 September 2023) SST (January–September 2023) from Huatulco. Color lines refer to previous ENSO events in the Huatulco area. Drone flights: (a) late June–early July 2023; (b) early August 2023. For exact dates, see Table 1.

Bleaching started in the Huatulco vicinity by mid–June 2023. According to a rapid survey, bleaching was widespread by late June–early July from San Agustín (15.686320°, −96.230536°) to Chahué reef (15.751882°, −96.119355°). The coral species *Porites panamensis* and *Pavona gigantea* were the most affected by bleaching, as they were entirely white across all depths (0–17 m) at all reef sites. *Pocillopora* spp. bleaching was particularly severe in shallow water (<5 m depth), with >95% of *Pocillopora* cover bleached; however, there was a slight reduction, to 75–80% of *Pocillopora* cover bleached, at mid-depths (5–7 m). As the depth increased (>7 m), bleaching decreased to 50–60% of the total *Pocillopora* cover. Even though the percentage and bleaching severity decreased with depth, all of the *Pocillopora* spp. colonies were pale in color, including at the base of the coral branches. In some cases, corals presented yellow, pink, or blue fluorescence. By July 2023, we had already observed the start of coral mortality and some algal overgrowth in *Pocillopora* spp. colonies, independent of their depth (Figure 3).

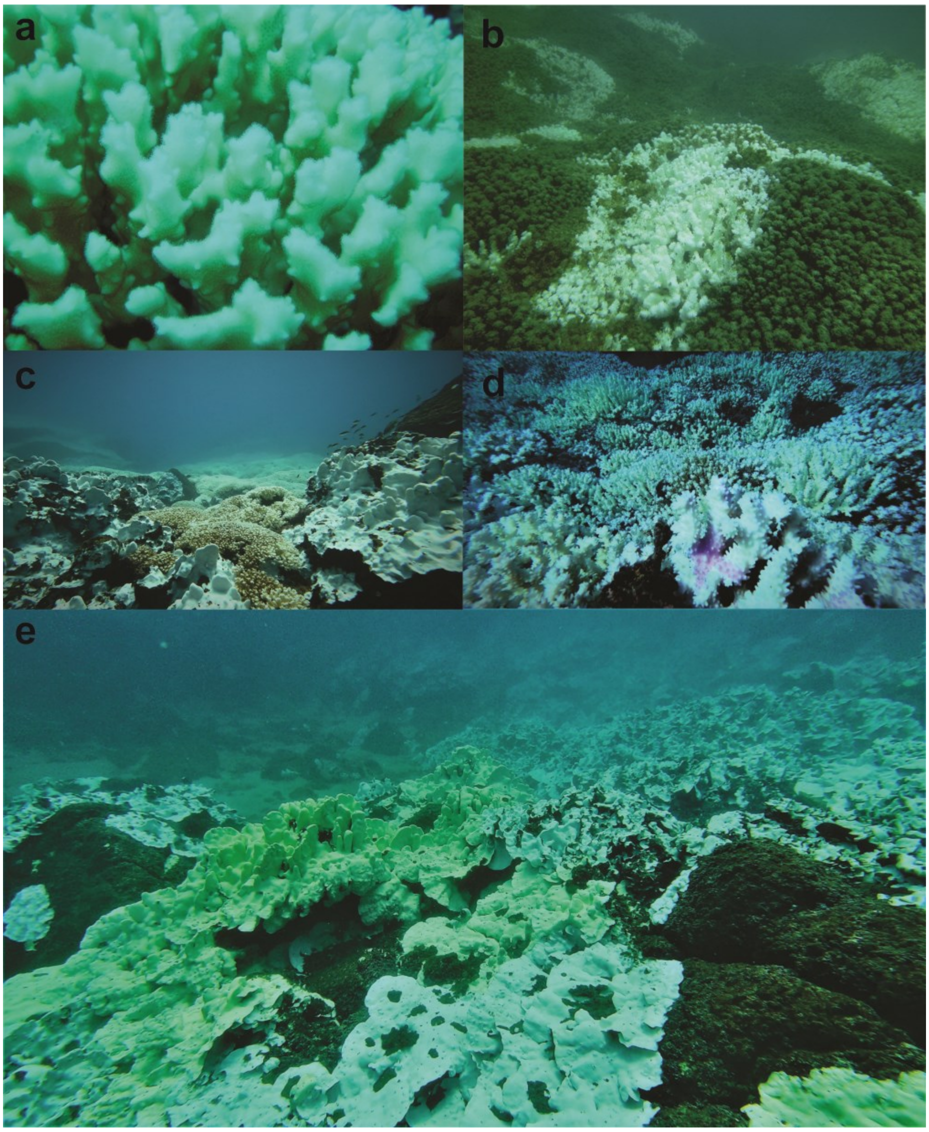


**Figure 3.** Coral bleaching in Huatulco, southern Mexican Pacific: (**a**) detail, bleached *Pocillopora verrucosa*, San Agustín reef, 5 m depth, 20 August 2023; (**b**) bleached and recently dead corals, Cacaluta island, 5 m depth, 21 August 2023; (**c**) bleached reef landscape, Cacaluta island, 5 m depth, 21 August 2023; (**d**) bleached and fluorescent *Pocillopora* spp. reef landscape, Cacaluta island, 5 m depth, 21 August 2023; (**e**) bleached and fluorescent *Pavona gigantea* landscape, Violín reef, 9 m depth, 23 August 2023. Photo credits: Andrés López Pérez (**a**,**b**); Virgilio Antonio Pérez, Buceo Huatulco (**c**–**e**).

Following the initial rapid survey, UAV flights rendered striking images of the area's extent and severity of coral bleaching. During El Niño conditions, extremely clear waters allowed the UAVs to obtain imagery down to the reef base (12–17 m). The results from orthomosaic classification analysis revealed that, by late June to early July, the average coral bleaching of the entire coral area of Huatulco reached 76.85% (±12.27%). We observed moderate mortality in La Entrega (~12.31%; dead/bleached ratio [d/b] = 0.18) and San Agustín (~8.29%, d/b = 0.26), whereas it was low in Riscalillo (0.06%, d/b = 0.08), resulting in average mortality of 6.59% (±12.27%, d/b = 0.3) for the whole coral area associated with the ENSO.

Significant changes in coral communities and reefs were observed by early-to-mid August 2023 (Table 1). Across all sites, the average bleaching prevalence had declined to 30% (±19.11%), and mean mortality increased from 6.59% to 70% (19.11%; d/b = 2.33), with substantial variations observed among reefs. Cacaluta (d/b = 1.05) and Maguey (d/b = 0.98) reefs showed mortality values of approximately 50%, whereas Riscalillo (d/b = 2.81), San Agustín (d/b = 4.74), and La Entrega reefs experienced coral mortalities exceeding 70%. Notably, La Entrega experienced catastrophic mass mortality (92.82%, d/b = 12.93; Figure 4).

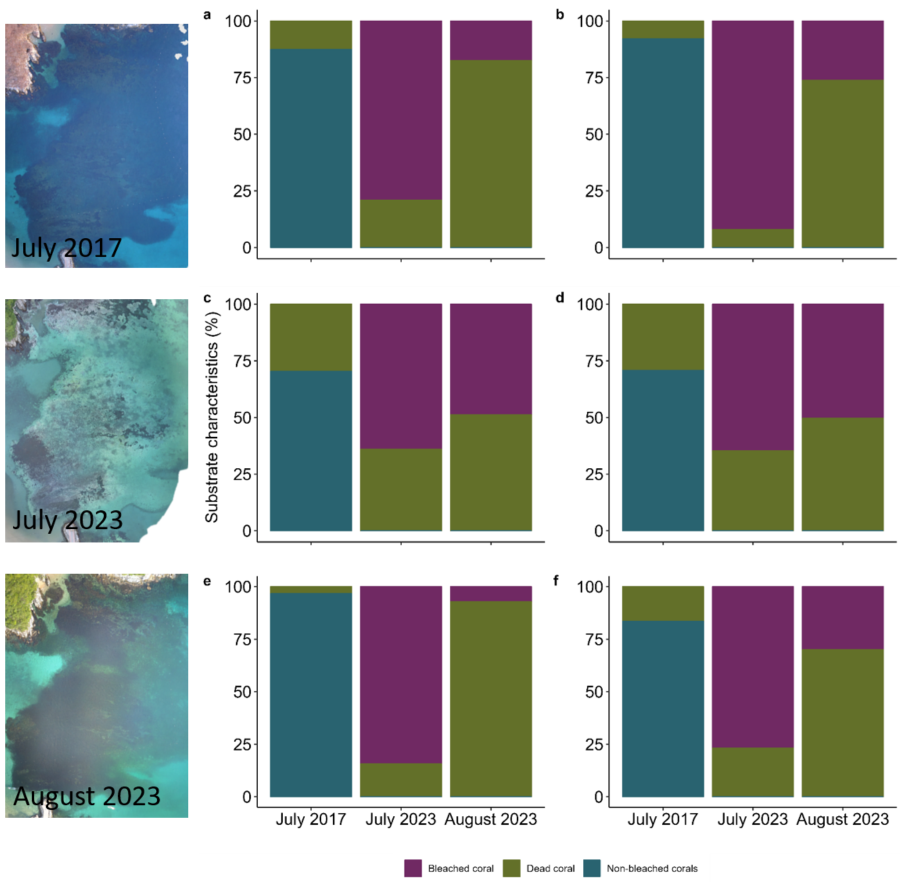


**Figure 4.** Drone-derived substrate characteristics (%) during non-bleaching (July 2017, left panel above) and 2023 El Niño bleaching (early July, left panel middle; early–middle August 2023, left panel below) in Huatulco, southern Mexican Pacific: (**a**) San Agustín; (**b**) Riscalillo; (**c**) Cacaluta island; (**d**) Maguey; (**e**) La Entrega; (**f**) Huatulco.

Data analysis revealed significant changes in substrate characteristics over time in the study area. Bleaching was not observed during the non-bleaching periods (February 2020 and September 2021) but increased rapidly and significantly in the summer of 2023 (29.9%, Mann–Whitney U-test = −7.28, $n$ = 132, $p$ = 0.0001). Additionally, dead coral coverage remained relatively invariable during non-bleaching periods (19.7–24.7%) but peaked sharply during 2023 El Niño bleaching (70 ± 23.5%, Mann–Whitney U-test = −6.81,

$n$ = 132, $p$ = 0.0001). Non-bleached live coral coverage remained relatively stable during non-bleaching periods (75.3–80.2%) but dropped to zero by July 2023 (Mann–Whitney U-test = 8.58, $n$ = 132, $p$ = 0.0001). In summary, the live coral coverage in the Huatulco area was approximately 75–80% during non-bleaching periods, with dead coral coverage ranging within 20–25% with no signs of bleaching. However, by July 2023, all corals at all sites had bleached entirely, and by August, 50–93% of the total coral cover had died (Figures 4 and 5).

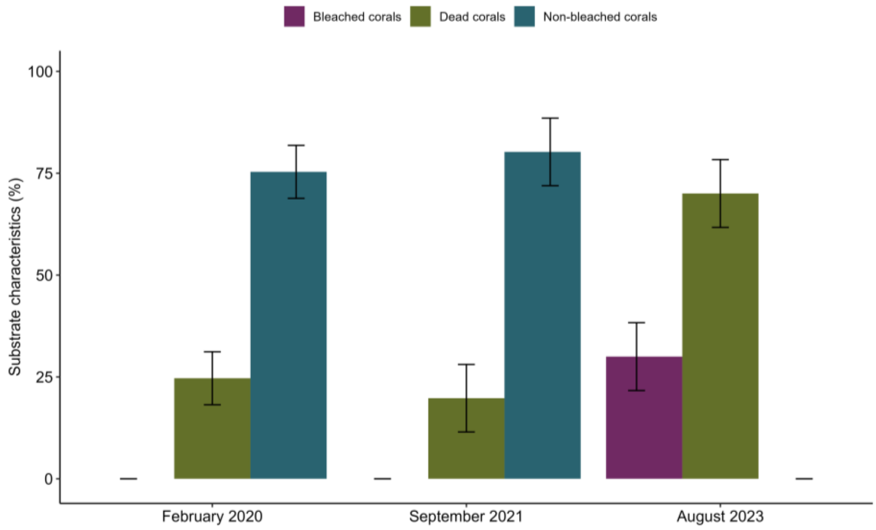


**Figure 5.** Census-derived substrate characteristics during non-bleaching (2020–2021) and 2023 El Niño bleaching event in Huatulco, southern Mexican Pacific.

Corals experienced no heat stress in the Huatulco area from 1 January to 16 May 2023 (Figure 6). Reef surveys conducted during February 2023 resulted in non-bleached corals; however, from 17 May 2023 (day 137), the coral bleaching heat stress increased rapidly. By 21 June 2023 (day 172), DHW showed values over 5 in concordance, with a video being posted on social networks showing the coral bleaching. From 2 to 6 July 2023 (days 183–187), reef surveys presented massive coral bleaching and modest coral mortality associated with heat stress. Between 17 and 21 August 2023 (days 229–233), DHW reached values around 15–16, and reef surveys revealed massive coral mortality (Figure 6). Echinoderm abundance and fish biomass also experienced significant declines. Declines in abundance were observed in both of the sea urchins *Eucidaris thouarsii* (Student-t = 2.24, $n$ = 147, $p$ = 0.0001; Figure 7a) and *Diadema mexicanum* (Student-t = 2.01, $n$ = 147, $p$ = 0.0001; Figure 7b) in August 2023, when compared to the previous non-bleaching sampling periods. There was also a significant decrease in fish biomass during the 2023 bleaching event (Mann–Whitney U-test = −6.9, $n$ = 147, $p$ = 0.0005; Figure 8) in the Huatulco area reefs.

During La Niña and ENSO-neutral periods, we recorded 80 fish species, whereas this richness decreased significantly to 36 species during the 2023 El Niño. The majority of the decreased biomass belonged to corallivorous species (non-bleaching biomass: *Pseudobalistes naufragium*, 79.25 $g \cdot m^{-2}$; *Cantherhines dumerilii*, 67.42 $g \cdot m^{-2}$, *Arothron hispidus*, 64.60 $g \cdot m^{-2}$) and carnivorous species (non-bleaching biomass: e.g., *Diodon holocanthus*, 139.22 $g \cdot m^{-2}$; *Haemulon scudderii*, 49.08 $g \cdot m^{-2}$; *Caranx caninus*, 41.50 $g \cdot m^{-2}$). The omnivorous species (19 species) with a trophic range of 2.8–3.7 and super-carnivorous species (20 species) with a trophic level greater than 3.8 exhibited the most significant declines. Prior to the El Niño event, the average trophic level was 3.43 while, during El Niño, it dropped slightly (3.28), indicating a shift toward fish with omnivorous feeding habits in the systems (Figure 9).

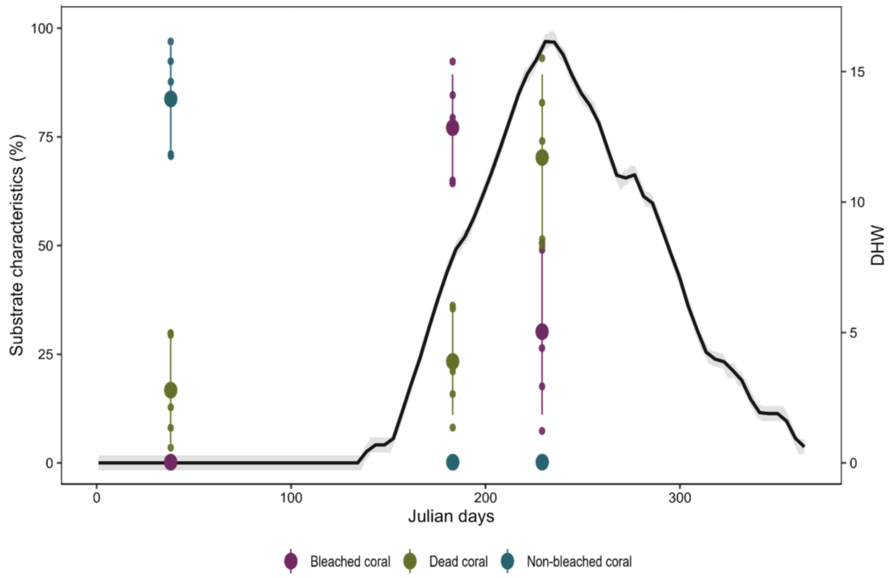


**Figure 6.** Changes in substrate characteristics (%) and degree heating weeks (DHW, black line) daily data for 2023 in the southern Mexican Pacific. DHW and substrate characteristics (average ± 95% confidence interval).

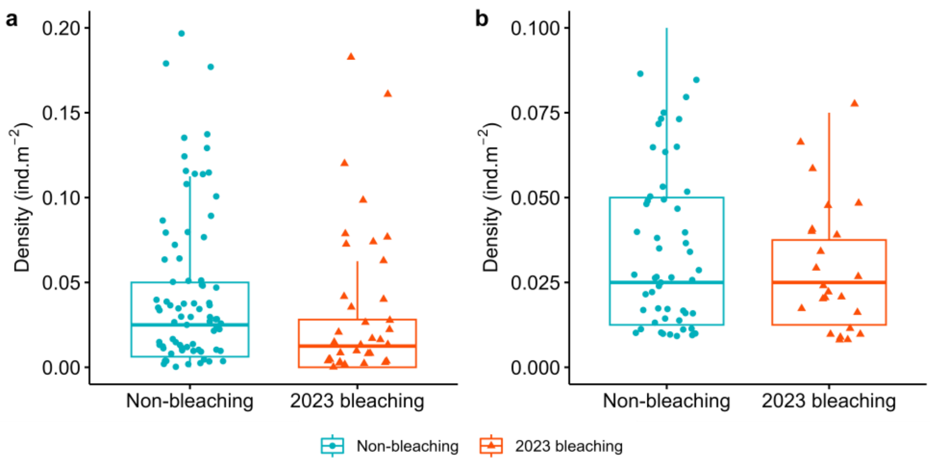


**Figure 7.** Sea urchin density during non-bleaching (2020–2021) and 2023 El Niño bleaching time frames in Huatulco, southern Mexican Pacific: (**a**) *Eucidaris thouarsii*; and (**b**) *Diadema mexicanum*.

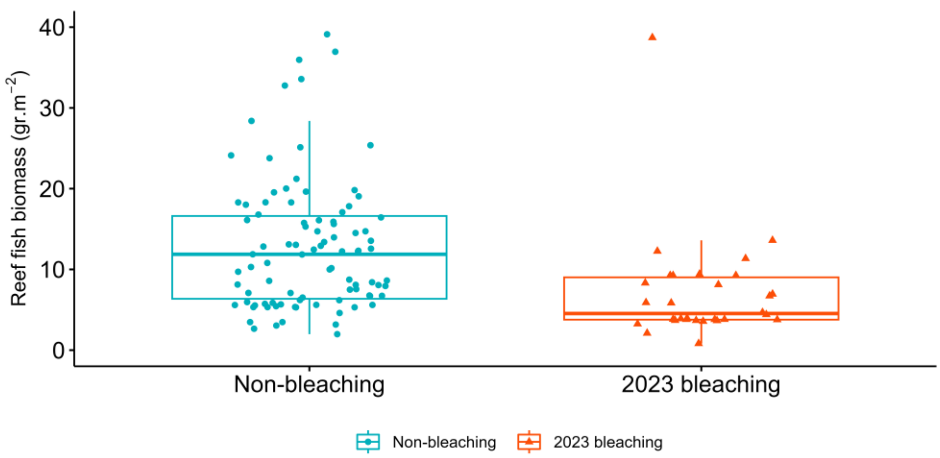


**Figure 8.** Fish biomass during non-bleaching (2020–2021) and 2023 El Niño bleaching time frames in Huatulco, southern Mexican Pacific.

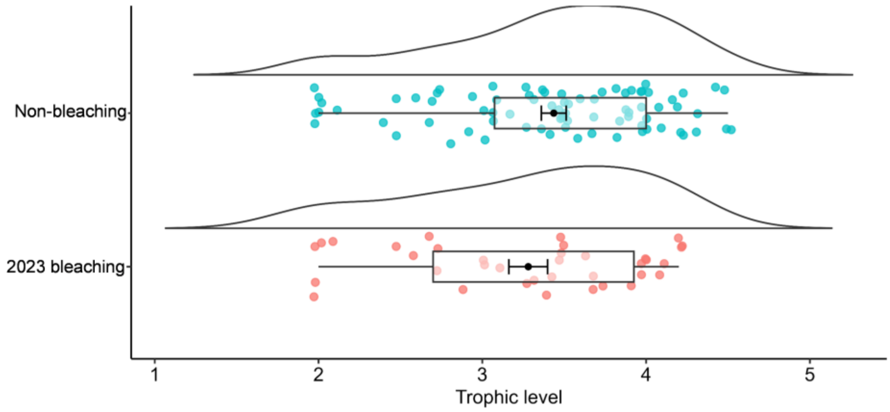


**Figure 9.** Trophic level during non-bleaching (2020–2021) and 2023 El Niño bleaching. Inside the boxplot is graphed mean + se.

## 4. Discussion

In Huatulco, the 2023 El Niño event led to a positive thermal anomaly of +1.6 °C above the historical average from June to September. Furthermore, it was 0.5 to 0.7 °C warmer than the previous (2009–2010) El Niño in the area. Consequently, the 2023 El Niño event is presently the warmest event documented in the Huatulco area. The initial observations of coral bleaching in Huatulco occurred during mid-to-late June, approximately four to six weeks after the announcement of the El Niño condition in the eastern Pacific: https://www.cpc.ncep.noaa.gov/products/CDB/CDB_Archive_html/bulletin_052023/ (accessed on 20 September 2023), and also when DHW index reached values around 3.7 to 5.6. The 2023 El Niño event is part of a sequence of strong El Niño anomalies affecting coral systems in the Mexican Pacific (Figure 2) [14,16,20,21]. In 2023, coral bleaching was also reported in the central Mexican Pacific (pers. comm. Rodríguez-Troncoso, Cupul-Magaña, and Rodríguez-Zaragoza) and Baja California Sur entrance (pers. comm. Reyes-Bonilla), illustrating that bleaching is widespread in the Mexican Pacific. Concurrently, there are also reports of coral bleaching from the Gulf of Mexico [22] and the Mexican Caribbean (pers. comm. Álvarez-Filip). These reports indicate that the current El Niño event may correspond with the most devastating bleaching event ever striking coral systems in Mexico.

The Oaxaca reef track has experienced three bleaching events associated with ENSO events, one in 1997–1998 during La Niña [21] and the other two in 1982–1983 and 2009–2010 during El Niño conditions [16,20]. Indirect evidence suggests that the 1982–1983 ENSO event resulted in unquantifiable mortality at La Entrega reef, as indicated by the colony-size patterns of *Pavona gigantea* [20]. In the 1997–1998 cooling event, only the westernmost sites of the Puerto Ángel reef area experienced high (>90%) coral mortality [21]. Meanwhile, the 2009–2010 El Niño event caused only moderate (18%) mortality in the Huatulco reef area [13]. Conversely, the current overall mortality in Huatulco is above 50%, with numerous cases reaching values exceeding 73.8% and La Entrega experiencing unprecedented mass mortality (>92%) as heat stress values (according to DHW) reached 15.5–16.5. However, the current mortality percentages may be understated, as positive SST anomalies and El Niño conditions are predicted to persist through the first several months of 2024: https://www.cpc.ncep.noaa.gov/products/analysis_monitoring/enso_advisory/ensodisc.html (accessed on 12 January 2024). In the southern Mexican Pacific, the first news of massive coral bleaching (21 June 2023) occurred when the product reached an average of 5.4 (±0.24). However, incipient mortality occurred when the value rose to an average of 7.8 (±0.31). Nevertheless, massive coral mortality (>50%) occurred by earlier to mid–August, when DHW values reached average values of 13.2 to 15.7.

The coral genus most impacted by rising temperature in Huatulco is unquestionably *Pocillopora* due to its shallower distribution compared to *Pavona* and *Porites*, making it more vulnerable to the synergy between heat shock and increasing solar radiation [7]. Due to elevated temperature and irradiance, the primary disruptive mechanism causing bleaching is suggested to be damage to and reduction in the D1 protein in the photosystem II reaction center of dinoflagellate cells, as well as disruption of the Calvin cycle (which mediates photosynthetic carbon dioxide fixation) [31–33]. The bleaching sensitivity of *Pocillopora* spp. varies as a function of the dinoflagellate species, with *Pocillopora*—which hosts *Durusdinium glynnii*—exhibiting the highest heat tolerance in the eastern Pacific [34]. We suggest that the intensity of the current El Niño could surpass the thermal tolerance of those corals hosting *D. glynnii*, as corals are dying regardless of species identity and depth. Nevertheless, future research on holobionts surviving the 2023 El Niño event may elucidate whether organism survival in the area relates to symbiont recombination or natural selection (sensu [35]).

The 2023 El Niño event has resulted in changes to holobiont physiology and affected several biological organization levels. Reductions in density and biomass were observed in echinoderms (Figure 6) and fish (Figure 7), respectively, alongside mass coral bleaching and mortality (Figures 4 and 5) when compared with non-bleaching periods. For instance, in early to mid–August 2023, the density of the sea urchins *D. mexicanum* and *E. thouarsii* decreased by around 50%, while fish biomass decreased by 45.7%.

Previous heatwave events in Huatulco have significantly impacted the echinoderm population, particularly *D. mexicanum* and *E. thouarsii* [16]. The density of *D. mexicanum* in the tropical Eastern Pacific is relatively low (0.008–14.04 ind·m$^2$; [36,37]) compared to that of other *Diadema* species from different regions [38]. Huatulco's densities range from 0.26 to 6.8 ind·m$^2$ [39]. Generally, during El Niño events, *D. mexicanum* populations tend to increase due to low predation and the availability of algal turf as a food source [36,40]. Nonetheless, Huatulco populations were reduced during the 2009–2010 and 2023 El Niño events (average density: non-bleaching = 0.03 ind·m$^2$ vs. bleaching = 0.01 ind·m$^2$) [16]. The population reduction during the 2009–2010 El Niño was likely due to the combination of warming events and the previous mass mortality caused by a pathogen [16,41]. This mass mortality event resulted in many loose spines and hundreds of bare tests scattered throughout the Huatulco reefs [41]. In contrast, only a few were observed during the 2023 El Niño. On the other hand, densities of *E. thouarsii* in Huatulco have been reported to be as high as 1.14 ind·m$^2$, exceeding those observed in the present study. It is worth noting that a population increase in *E. thouarsii* was recorded during the El Niño 2009–2010 event [16]. However, the opposite was observed during the 2023 El Niño, with an average non-bleaching density of 0.07 ind·m$^2$ compared to the 2023 El Niño density of 0.03 ind·m$^2$. No skeletons or spines of either sea urchin species were observed on the reefs during the survey, which suggests the possibility that the organisms moved to deeper or adjacent areas rather than perishing. Both species feed primarily on algal turf and macroalgae, but they may also consume scleractinian corals [42,43]. The observed displacement in a vertical direction could be attributed to the rise in herbivorous fish, with which the sea urchins may be competing for food (algal turf), as well as coral reduction and mortality. Further surveys and analyses are necessary to address this hypothesis.

Over the past four decades, coral bleaching events have significantly reduced live coral cover in concert with local chronic stressors, resulting in a regime shift from coral to macroalgal dominance on coral reefs worldwide [44]. According to our data, the 2023 El Niño bleaching event severely reduced the live coral cover in Huatulco and proportionally increased the coverage of turf and fleshy macroalgae. This regime shift has impacted the communities that rely on the reef for food and shelter to the point of reducing the trophic level of the fish-associated community. According to data, two elements may have contributed to the observed pattern: the dramatic reduction in fish richness and abundance—particularly of super-carnivorous taxa and corallivores—and the increases in biomass at the base trophic level. Recent studies have indicated that the reef fish community becomes increasingly dissimilar between alternative reef ecosystem states. For instance, following the 1998 El Niño disturbance in Seychelles, mid-trophic level species—including specialists such as corallivores—declined with the loss of coral habitat. However, there was an increase in biomass at base trophic levels, as herbivorous species benefitted from increased algal resources [45]. Notably, following the reef fish community and their associated changes in trophic level in Huatulco reef systems may render information for understanding the link between habitat structure, fish communities, and the concomitant trophic level changes during ecosystem recovery in impoverished eastern Pacific coral reef systems.

In summary, the ENSO disturbances in the eastern Pacific have resulted in species elimination, displacement, or recruitment beyond the coral [46,47]. For instance, if the 2023 El Niño-related mortality persists, *Pavona varians* populations in Huatulco reefs may face local extinction, as these are the only populations in the southern Mexican Pacific [20]. Their loss would join the documented cases of species elimination in the Huatulco area (*Leptoseris papyracea*, *Psammocora stellata*, and *Cycloseris distorta*) [48], resulting in an overall decrement in range distribution throughout the eastern Pacific and, consequently, in the regional richness of coral species. On the other hand, echinoderms and fish experienced horizontal or vertical displacements in response to seasonal and interannual warming and cooling in the area, resulting in decreases or increases in the abundance and density of these species [16,49,50]. At present, the observed decrease in abundance is altering both density (sea urchins) and biomass (fish) metrics in the area, possibly due to the vertical displacement of individuals to deeper areas, as observed in the Central Mexican Pacific (pers. comm. Galván-Villa). Other researchers have reported that ENSO events can impact the abundance and distribution of invertebrates, primarily corallivores (e.g., mollusks and macrocrustaceans) [8,51]. Our rapid survey revealed the absence of macrocrustacean species, including *Stenorhynchus debilis* and *Trapezia* spp., which are typically associated with *Pocillopora* spp. corals. In addition, sponges (*Amphimedon texotli*), ascidians, and gorgonians (*Leptogorgia* spp.) experienced tissue and associated fauna (e.g., brittle star *Ophiothela mirabilis* and microcrustaceans) loss, implying that ENSO has had physiological impacts on different species, highlighting the need for future work to investigate this point further.

The rapid decline in stony coral coverage in the Huatulco area will likely impact the ecosystem's carbonate budgets and reef architecture. Carbonates fixed in coral skeletons could also be lost, which has been observed in Caribbean reef-building corals affected by stony coral tissue loss disease [52,53]. Coral mortality can have far-reaching effects on reef biodiversity and socio-ecosystem functioning [54,55]. Therefore, future area monitoring can provide valuable information for estimating the extent of carbonate and functional losses [56] in southern Mexican Pacific reefs. Additionally, it can provide a baseline for local and large-scale coral reef management procedures.

The documented mass mortality of corals off Huatulco may impede reef recovery in the short- and medium-term at the regional scale, as mass mortality may profoundly alter connectivity patterns across the tropical eastern Pacific, where Huatulco is a pivotal stepping stone for reef-associated fauna from El Salvador and Costa Rica toward northwestern Pacific reefs located in areas such as Ixtapa-Zihuatanejo and those located at the entrance of the Gulf of California [57]. In this context, it is necessary to implement regional initiatives for designing and managing a network of natural protected areas to address the increasingly severe and frequent future bleaching events predicted with simulation models utilizing the latest data on bleaching incidence and projected climate change [58].

Finally, the impacts of coral bleaching, mortality, and ecosystem recovery patterns in response to the ENSO disturbance in the eastern Pacific offer essential lessons for envisioning future recovery following the 2023 El Niño disturbance. Overall, aside from holobiont differences in bleaching associated with thermally sensitive symbionts [13], differences in the extent of bleaching, mortality, and recovery among sites may be attributed to various factors, including chronic pollution, distance from human settlements and, where applicable, the age of the protective area and the efficacy of the application of management strategies [7,19]. Regarding mortality, the 2023 El Niño event has bleached the entire live coral cover in the Huatulco area. Notably, the mortality was higher in chronically polluted and heavily visited tourist areas, such as the San Agustín and La Entrega reefs [pers. comm. Díaz-Díaz]. In contrast, less extensive mortality occurred in relatively isolated reef sites.

Relatively isolated coral systems have recovered within several months of the ENSO events in the central Mexican Pacific following mild bleaching [15]. Reefs in the Huatulco area that experienced massive coral mortality in 2000 have recovered after 8–12 years following bleaching. The live coral cover on Isla del Coco, Costa Rica, experienced a fivefold increase over 20 years after the 1987 bleaching event [59]. Additionally, reefs with pH levels below 8.0 and an aragonite saturation state (Ωarag) of ≤3 in the Galapagos Archipelago have not yet recovered following the 1982–1983 warming event [18]. As noted, both mortality and recovery patterns relate to the persistence of human and environmental disturbances. Therefore, management should prioritize reducing and eliminating disturbances as an immediate and large-scale strategy. On a smaller scale, recovery efforts can be enhanced by adopting a social–ecological system perspective to identify context-specific actions for managing local stressors, such as small-scale fisheries, pollution, and mechanical destruction [60].

**Author Contributions:** Conceptualization, A.L.-P., R.G.-F. and E.R.-C.; Data curation, A.L.-P., R.G.-F., E.R.-C., O.V.-M., T.G.-M. and A.M.-C.; Formal analysis, A.L.-P., R.G.-F., E.R.-C. and O.V.-M.; Funding acquisition, A.L.-P. and O.V.-M.; Investigation, A.L.-P., R.G.-F., E.R.-C., O.V.-M., F.A.R.-Z., T.G.-M. and A.M.-C.; Methodology, A.L.-P.; Resources, A.L.-P. and E.R.-C.; Visualization, A.L.-P., E.R.-C. and O.V.-M.; Writing—original draft, A.L.-P.; Writing—review and editing, A.L.-P., R.G.-F., E.R.-C., O.V.-M., F.A.R.-Z., T.G.-M. and A.M.-C. All authors have read and agreed to the published version of the manuscript.

**Funding:** This research was funded by Consejo Nacional de Humanidades Ciencias y Tecnologías (funding number 86397), and the Universidad Autónoma Metropolitana (funding number 14705007).

**Institutional Review Board Statement:** Not applicable.

**Informed Consent Statement:** Not applicable.

**Data Availability Statement:** The data presented in this study are available upon request from the corresponding author.

**Acknowledgments:** The authors wish to extend their gratitude to Parque National Huatulco authorities and Buceo Huatulco for logistic support. Numerous colleagues and students provided invaluable support during field campaigns, for which we are grateful. We are especially grateful with Derek Manzello (Center for Satellite Applications and Research, NOAA) who kindly provide Degree Heating Weeks (DHW) data. We would also like to thank the reviewers and editorial staff.

**Conflicts of Interest:** The authors declare no conflicts of interest. The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript; or in the decision to publish the results.

## References

1. Carré, M.; Sachs, J.P.; Purca, S.; Schauer, A.J.; Braconnot, P.; Falcón, R.A.; Julien, M.; Lavallée, D. Holocene history of ENSO variance and asymmetry in the eastern tropical Pacific. *Science* **2014**, *345*, 1045–1048. [CrossRef]
2. Clarke, A.J. El Niño physics and El Niño predictability. *Annu. Rev. Mar. Sci.* **2014**, *6*, 79–99. [CrossRef]
3. Mumby, P.J.; Chisholm, J.R.; Edwards, A.J.; Andrefouet, S.; Jaubert, J. Cloudy weather may have saved Society Island reef corals during the 1998 ENSO event. *Mar. Ecol. Prog. Ser.* **2001**, *222*, 209–216. [CrossRef]
4. Zhang, N.; Feng, M.; Hendon, H.H.; Hobday, A.J.; Zinke, J. Opposite polarities of ENSO drive distinct patterns of coral bleaching potentials in the southeast Indian Ocean. *Sci. Rep.* **2017**, *7*, 2443. [CrossRef]
5. Allemand, D.; Tambutté, É.; Zoccola, D.; Tambutté, S. Coral calcification, cells to reefs. In *Coral Reefs: An Ecosystem in Transition*; Dubinsky, Z., Stambler, N., Eds.; Springer: Dordrecht, The Netherlands, 2011; pp. 119–150. [CrossRef]
6. Fitt, W.K.; McFarland, F.K.; Warner, M.E.; Chilcoat, G.C. Seasonal patterns of tissue biomass and densities of symbiotic dinoflagellates in reef corals and relation to coral bleaching. *Limnol. Oceanogr.* **2000**, *45*, 677–685. [CrossRef]
7. Douglas, A.E. Coral bleaching—-how and why? *Mar. Poll. Bull.* **2003**, *46*, 385–392. [CrossRef] [PubMed]
8. 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: Persistence and Loss in a Dynamic Environment*; Glynn, P.W., Manzello, D.P., Enoch, I.C., Eds.; Springer: Dordrecht, The Netherlands, 2017; pp. 251–290. [CrossRef]
9. Glynn, P.W. Widespread coral mortality and the 1982–83 El Niño warming event. *Environ. Conserv.* **1984**, *11*, 133–146. [CrossRef]
10. Reyes-Bonilla, H. 1987 coral reef bleaching at Cabo Pulmo reef, Gulf of California, Mexico. *Bull. Mar. Sci.* **1993**, *52*, 832–837.

11. Reyes-Bonilla, H. Effects of the 1997–1998 El Niño–Southern Oscillation on coral communities of the Gulf of California, Mexico. *Bull. Mar. Sci.* **2001**, *69*, 251–266.
12. Iglesias-Prieto, R.; Reyes-Bonilla, H.; Rodríguez, R.R. Effects of 1997-1998 ENSO on coral reef communities in the Gulf of California, Mexico. *Geofís. Int.* **2003**, *42*, 467–471.
13. LaJeunesse, T.C.; Reyes-Bonilla, H.; Warner, M.E. Spring "bleaching" among *Pocillopora* in the Sea of Cortez, eastern Pacific. *Coral Reefs* **2007**, *26*, 265–270. [CrossRef]
14. Carriquiry, J.D.; Cupul-Magaña, A.L.; Rodríguez-Zaragoza, F.; Medina-Rosas, P. Coral bleaching and mortality in the Mexican Pacific during the 1997–98 El Niño and prediction from a remote sensing approach. *Bull. Mar. Sci.* **2001**, *69*, 237–249.
15. Cruz-García, R.; Rodríguez-Troncoso, A.P.; Rodríguez-Zaragoza, F.A.; Mayfield, A.; Cupul-Magaña, A.L. Ephemeral effects of El Niño–Southern Oscillation events on an eastern tropical Pacific coral community. *Mar. Freshw. Res.* **2020**, *71*, 1259–1268. [CrossRef]
16. López-Pérez, A.; Guendulain-García, S.; Granja-Fernández, R.; Hernández-Urraca, V.; Galván-Rowland, L.; Zepeta-Vilchis, R.; López-López, D. Reef community changes associated with the 2009–2010 El Niño in the southern Mexican Pacific. *Pac. Sci.* **2016**, *70*, 175–190. [CrossRef]
17. Nava, H.; López, N.; Ramírez-García, P.; Garibay-Valladolid, E. Contrasting effects of the El Niño 2015–16 event on coral reefs from the central pacific coast of Mexico. *Mar. Ecol.* **2021**, *42*, e12630. [CrossRef]
18. Manzello, D.P.; Enochs, I.C.; Bruckner, A.; Renaud, P.G.; Kolodziej, G.; Budd, D.A.; Carlton, R.; Glynn, P.W. Galápagos coral reef persistence after ENSO warming across an acidification gradient. *Geophys. Res. Lett.* **2014**, *41*, 9001–9008. [CrossRef]
19. Alvarado, J.J.; Sánchez-Noguera, C.; Arias-Godínez, G.; Araya, T.; Fernández-García, C.; Guzmán, 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.* **2020**, *68*, 271–282. [CrossRef]
20. Glynn, P.W.; Leyte-Morales, G.E. Coral reefs of Huatulco, West Mexico: Reef development in upwelling Gulf of Tehuantepec. *Rev. Biol. Trop.* **1997**, *45*, 1033–1047. Available online: https://revistas.ucr.ac.cr/index.php/rbt/article/view/21114 (accessed on 20 September 2023).
21. Reyes-Bonilla, H.; Carriquiry, J.; Leyte-Morales, G.; Cupul-Magaña, A. Effects of the El Niño-Southern Oscillation and the anti-El Niño event (1997–1999) on coral reefs of the western coast of México. *Coral Reefs* **2002**, *21*, 368–372. [CrossRef]
22. Horta-Puga, G.; Gutiérrez-Martínez, J.; Morales-Aranda, A.A.; Victoria-Muguira, M. Mass bleaching in SW Gulf of Mexico. *Reef Encount.* **2023**, *38*, 59–63.
23. Fiedler, P.C.; Talley, L.D. Hydrography of the eastern tropical Pacific: A review. *Prog. Oceanogr* **2006**, *69*, 143–180. [CrossRef]
24. Trasviña, A.; Barton, E.D.; Brown, J.; Velez, H.S.; Kosro, P.M.; Smith, R.L. Offshore wind forcing in the Gulf of Tehuantepec, Mexico: The asymmetric circulation. *J. Geophys. Res. Oceans* **1995**, *100*, 20649–20663. [CrossRef]
25. Skirving, W.; Marsh, B.; De La Cour, J.; Liu, G.; Harris, A.; Maturi, E.; Geiger, E.; Eakin, C.M. CoralTemp and the Coral Reef Watch Coral Bleaching Heat Stress Product Suite Version 3.1. *Remote Sens.* **2020**, *12*, 3856. [CrossRef]
26. Westoby, M.J.; Brasington, J.; Glasser, N.F.; Hambrey, M.J.; Reynolds, J.M. 'Structure-from-Motion'photogrammetry: A low-cost, effective tool for geoscience applications. *Geomorphology* **2012**, *179*, 300–314. [CrossRef]
27. Froese, R.; Pauly, D. FishBase. 2019. Available online: http://www.fishbase.org (accessed on 20 September 2023).
28. Lin, H.Y.; Costello, M.J. Body size and trophic level increase with latitude, and decrease in the deep-sea and Antarctica, for marine fish species. *PeerJ* **2023**, *11*, e15880. [CrossRef] [PubMed]
29. Zar, J.H. *Biostatistical Analysis*, 5th ed.; Prentice Hall: Upper Saddle River, NJ, USA, 2010; p. 944.
30. RStudio Team. *RStudio: Integrated Development for R. RStudio*; PBC: Boston, MA, USA, 2020; Available online: http://www.rstudio.com/ (accessed on 20 September 2023).
31. Jones, R.J.; Hoegh-Guldberg, O.; Larkum, A.W.D.; Schreiber, U. Temperature-induced bleaching of corals begins with impairment of the $CO_2$ fixation mechanism in zooxanthellae. *Plant Cell Environ.* **1998**, *21*, 1219–1230. [CrossRef]
32. Warner, M.E.; Fitt, W.K.; Schmidt, G.W. Damage to photosystem II in symbiotic dinoflagellates: A determinant of coral bleaching. *Proc. Natl. Acad. Sci. USA* **1999**, *96*, 8007–8012. [CrossRef] [PubMed]
33. Lesser, M.P.; Farrell, J.H. Exposure to solar radiation increases damage to both host tissues and algal symbionts of corals during thermal stress. *Coral Reefs* **2004**, *23*, 367–377. [CrossRef]
34. Palacio-Castro, A.; Smith, T.; Brandtneris, V.; Snyder, G.; van Hooidonk, R.; Mate, J.; Manzello, D.P.; Glynn, P.; Fong, P.; Baker, A. Increased dominance of heat-tolerant symbionts create resilient coral reefs in nearterm ocean warming. *Proc. Natl. Acad. Sci. USA* **2023**, *120*, e2202388120. [CrossRef]
35. LaJeunesse, T.C.; Smith, R.; Walther, M.; Pinzón, J.; Pettay, D.T.; McGinley, M.; Aschaffenburg, M.; Medina-Rosas, P.; Cupul-Magaña, A.L.; Pérez, A.L.; et al. Host–symbiont recombination versus natural selection in the response of coral–dinoflagellate symbioses to environmental disturbance. *Proc. R. Soc. B Biol. Sci.* **2010**, *277*, 2925–2934. [CrossRef]
36. Alvarado, J.J.; Reyes-Bonilla, H.; Benítez-Villalobos, F. *Diadema mexicanum*, erizo de mar clave en los arrecifes coralinos del Pacífico Tropical Oriental: Lo que sabemos y perspectivas futuras (Diadematoida: Diadematidae). *Rev. Biol. Trop.* **2015**, *63*, 135–157.
37. Zamorano, P.; Leyte-Morales, G. Densidad poblacional de cuatro especies de erizo (Echinodermata: Echinoidea) en el arrecife de La Entrega, Oaxaca. *CICIMAR Oceánides* **2005**, *20*, 65–72. [CrossRef]
38. Alvarado, J.J.; Cortés, J.; Guzman, H.; Reyes-Bonilla, H. Density, size, and biomass of *Diadema mexicanum* (Echinoidea) in Eastern Tropical Pacific coral reefs. *Aquat. Biol.* **2016**, *24*, 151–161. [CrossRef]

39. Herrera-Escalante, T.; López-Pérez, R.A.; Leyte-Morales, G.E. Bioerosion caused by the sea urchin *Diadema mexicanum* (Echinodermata: Echinoidea) at Bahías de Huatulco, Western Mexico. *Rev. Biol. Trop.* **2005**, *53*, 263–273. [PubMed]
40. Glynn, P.W. El Niño warming, coral mortality and reef framework destruction by echinoid bioerosion in the eastern Pacific. *Galaxea* **1988**, *7*, 129–160.
41. Benítez-Villalobos, F.; Díaz-Martínez, J.P.; Martínez-García, M. Mass mortality of the sea urchin *Diadema mexicanum* in La Entrega at Bahias de Huatulco, Western Mexico. *Coral Reefs* **2009**, *28*, 1017. [CrossRef]
42. Hickman, C.P., Jr. *A Field Guide to Sea Stars and Other Echinoderms of Galápagos*; Sugar Spring Press: Lexington, KY, USA, 1998; p. 83.
43. Glynn, P.W.; Wellington, G.M.; Birkeland, C. Coral reef growth in the Galapagos: Limitation by sea urchins. *Science* **1979**, *203*, 47–49. [CrossRef] [PubMed]
44. Hoegh-Guldberg, O.; Mumby, P.J.; Hooten, A.J.; Steneck, R.S.; Greenfield, P.; Gomez, E.; Harvell, C.D.; Sale, P.F.; Edwards, A.J.; Caldeira, K.; et al. Coral reefs under rapid climate change and ocean acidification. *Science* **2007**, *318*, 1737–1742. [CrossRef] [PubMed]
45. Hempson, T.N.; Graham, N.A.; MacNeil, M.A.; Hoey, A.S.; Wilson, S.K. Ecosystem regime shifts disrupt trophic structure. *Ecol. Appl.* **2018**, *28*, 191–200. [CrossRef]
46. Glynn, P.W.; De Weerdt, W.H. Elimination of two reef-building hydrocorals following the 1982-83 El Niño warming event. *Science* **1991**, *253*, 69–71. [CrossRef]
47. Lluch-Belda, D.; Lluch-Belda, D.B.; Lluch-Cota, S.E. Changes in marine faunal distributions and ENSO events in the California Current. *Fish. Oceanogr.* **2005**, *14*, 458–467. [CrossRef]
48. Leyte-Morales, G.E.; Reyes-Bonilla, H.; Cintra-Buenrostro, C.E.; Glynn, P.W. Range extension of *Leptoseris papyracea* (Dana, 1846) to the west coast of Mexico. *Bull. Mar. Sci.* **2001**, *69*, 1233–1237.
49. Osland, M.J.; Stevens, P.W.; Lamont, M.M.; Brusca, R.C.; Hart, K.M.; Waddle, J.H.; Langtimm, C.A.; Williams, C.M.; Keim, B.D.; Terando, A.J.; et al. Tropicalization of temperate ecosystems in North America: The northward range expansion of tropical organisms in response to warming winter temperatures. *Glob. Chang. Biol.* **2021**, *27*, 3009–3034. [CrossRef] [PubMed]
50. Sánchez-Velasco, L.; Beier, E.; Godínez, V.M.; Barton, E.D.; Santamaría-del-Angel, E.; Jiménez-Rosemberg, S.P.A.; Marinone, S.G. Hydrographic and fish larvae distribution during the "Godzilla El Niño 2015–2016" in the northern end of the shallow oxygen minimum zone of the Eastern Tropical Pacific Ocean. *J. Geophys. Res. Oceans* **2017**, *122*, 2156–2170. [CrossRef]
51. Engle, J.M.; Richards, D.V. New and unusual marine invertebrates discovered at the California Channel Islands during the 1997–1998 El Niño. *Bull. South. Calif. Acad. Sci.* **2001**, *100*, 186–198.
52. Medellín-Maldonado, F.; Cruz-Ortega, I.; Pérez-Cervantes, E.; Norzogaray-López, O.; Carricart-Ganivet, J.P.; López-Pérez, A.; Alvarez-Filip, L. Newly deceased Caribbean reef-building corals experience rapid carbonate loss and colonization by endolithic organisms. *Commun. Biol.* **2023**, *6*, 934. [CrossRef]
53. Alvarez-Filip, L.; Dulvy, N.K.; Gill, J.A.; Côté, I.M.; Watkinson, A.R. Flattening of Caribbean coral reefs: Region-wide declines in architectural complexity. *Proc. R. Soc. B Biol. Sci.* **2009**, *276*, 3019–3025. [CrossRef]
54. Perry, C.T.; Alvarez-Filip, L. Changing geo-ecological functions of coral reefs in the Anthropocene. *Funct. Ecol.* **2019**, *33*, 976–988. [CrossRef]
55. Williams, G.J.; Graham, N.A. Rethinking coral reef functional futures. *Funct. Ecol.* **2019**, *33*, 942–947. [CrossRef]
56. González-Barrios, F.J.; Álvarez-Filip, L. A framework for measuring coral species-specific contribution to reef functioning in the Caribbean. *Ecol. Indic.* **2018**, *95*, 877–886. [CrossRef]
57. Lequeux, B.D.; Ahumada-Sempoal, M.A.; López-Pérez, A.; Reyes-Hernández, C. Coral connectivity between equatorial eastern Pacific marine protected areas: A biophysical modeling approach. *PLoS ONE* **2018**, *13*, e0202995. [CrossRef] [PubMed]
58. Suggett, D.J.; Smith, D.J. Coral bleaching patterns are the outcome of complex biological and environmental networking. *Glob. Chang. Biol.* **2020**, *26*, 68–79. [CrossRef] [PubMed]
59. Guzman, H.M.; Cortés, J. Reef recovery 20 years after the 1982–1983 El Niño massive mortality. *Mar. Biol.* **2007**, *151*, 401–411. [CrossRef]
60. Valdez-Rojas, C.; Beas-Luna, R.; Lorda, J.; Zepeda-Domínguez, J.A.; Montáño-Moctezuma, G.; Medellín-Ortíz, A.; Torre, J.; Micheli, F. Using a social-ecological systems perspective to identify context specific actions to build resilience in small scale fisheries in Mexico. *Front. Mar. Sci.* **2022**, *9*, 904859. [CrossRef]