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Coral Reef Resilience to Thermal Stress in the Eastern Tropical Pacific

Running Title: Eastern Tropical Pacific Coral Resilience

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Coral reefs world-wide are threatened by thermal stress caused by climate change. Especially devastating periods of coral loss frequently occur during El Niño-Southern Oscillation (ENSO) events originating in the Eastern Tropical Pacific (ETP). El Niño-induced thermal stress is considered the primary threat to ETP coral reefs. An increase in the frequency and intensity of ENSO events predicted in the coming decades threatens a pan-tropical collapse of coral reefs. During the 1982–83 El Niño, most reefs in the Galapagos Islands collapsed, and many more in the region were decimated by massive coral bleaching and mortality. However, after repeated thermal stress disturbances, such as those caused by the 1997–98 El Niño, ETP corals reefs have demonstrated regional persistence and resiliency. Using a 44-year data set (1970–2014) of live coral cover from the ETP, we assess whether ETP reefs exhibit the same decline as seen globally for other reefs. Also, we compare the ETP live coral-cover rate of change with data from the maximum Degree Heating Weeks experienced by these reefs to assess the role of thermal stress on coral reef survival. We find that during the period 1970-2014, ETP coral cover exhibited temporary reductions following major ENSO events, but no overall decline. Further, we find that ETP reef recovery patterns allow coral to persist under these El Niño-stressed conditions, often recovering from these events in 10–15 years. Accumulative heat stress explains 31% of the overall annual rate of change of living coral cover in the ETP. This suggests that ETP coral reefs have adapted to thermal extremes to date, and may have the ability to adapt to near-term future climate-change thermal anomalies. These findings for ETP reef resilience may provide general insights for the future of coral reef survival and recovery elsewhere under intensifying El Niño scenarios.

KEYWORDS

Climate change, coral cover, coral reefs, degree heating weeks, Eastern Tropical Pacific, ecosystem resilience, ENSO, thermal stress

ORIGINAL RESEARCH

Worldwide, coral cover is declining as reefs are affected by human activities, with compelling evidence of basin-wide coral cover decline in the Indo-Pacific (Bruno & Selig, 2007), the Great Barrier Reef (De'ath, Fabricius, Sweatman, & Puotinen, 2012) and the Caribbean (Gardner, Cote, Gill, Grant, & Watkinson, 2003). Although Hughes (2018) has suggested that returning reefs to past configurations is no longer an option, in the long-term, if local stressors such as pollution and overfishing are managed, multiple trajectories of reef recovery may still possible (Lamy, Galzin, Kulbicki, Lison de Loma, & Claudet, 2016). After extreme recurrent disturbances, coral reefs may show limited or no recovery, may undergo a phase shift from a coral-dominated state to a macroalgal or cyanobacteria-dominated alternative stable state (Mumby, 2009), or remain below a certain coral-cover threshold (e.g., 10% for Caribbean reefs; Bozec & Mumby, 2015), limiting their functionality.

El Niño Southern Oscillation (ENSO) events are naturally occurring phenomena in the Pacific Ocean consisting of two distinct states, El Niño and La Niña, with warmer and colder water in the Eastern Tropical Pacific (ETP), respectively (Clarke, 2014). ENSO events change the hydrology of the Tropical Pacific Basin and affect biological processes such as productivity and population dynamics of coral reef organisms (Glynn, Mones, Podestá, Colbert, & Colgan, 2017). During ENSO states, the sea surface temperature (SST) can exceed the upper and lower thermal limits of reef-building corals, disrupting their coral-algal symbiosis, and causing bleaching and mass mortality (Hughes, Anderson, et al., 2018). On a geological time-scale, ENSO events have been a common feature of the Pacific Ocean since 12 my ago (Zhang, Pagani, & Liu, 2014). Palaeoecological evidence suggests that permanent El Niño conditions may have occurred during the Holocene, causing the temporary collapse of ETP coral reefs (Toth et al., 2012). The last century has been characterized by fewer, but stronger, El Niño events. These events have produced the most extreme years of thermal stress on ETP coral reefs (Freund et al., 2019), and are now acknowledged to exert the primary control over coral cover changes at broad spatiotemporal scales within the ETP (Wang, Deser, Yu, DiNezio, & Clement, 2017).

Approximately 93% of the heat trapped in the atmosphere by anthropogenic greenhouse gasses is transferred directly into the ocean (Cheng, Abraham, Hausfather, & Trenberth, 2019). ENSO events are predicted to increase in frequency and intensity (Cai et al., 2018; Wang et al., 2017), potentially generating recurring thermal stress and mass bleaching events in coral reef ecosystems (Hughes, Kerry, et al., 2018). The most recent climate-change assessment therefore predicts a very high likelihood of irreversible damage to coral reefs worldwide (Heron, Maynard, van Hooidonk, & Eakin, 2016). The extreme El Niño events of 1982–83, 1997–98 and 2015–16 were characterized by exceptional warming (Oceanic El Niño Index > 2.0). Notably, the 1982–83 El Niño in the ETP triggered massive coral bleaching and mortality and caused the extirpation of coral populations in several locations such as the Galápagos Islands (Glynn, 1990). In addition to the thermal stress caused by ENSO events, ETP coral reefs experience other harsh environmental conditions in the region such as low aragonite saturation state (i.e., acidification) and high-$p\mathrm{CO}_2$ (Manzello et al., 2008), as well as high fluctuations in nutrient levels, tidal amplitude, and aerial exposure during extreme low tides (Zapata, Rodríguez-Ramírez, Caro-Zambrano, & Garzón-Ferreira, 2010).

In the ETP, coral assemblages are isolated, relatively poorly developed, and dominated by a few coral genera. They have been proposed as analogues of future environmental conditions under global warming and ocean acidification scenarios (Manzello et al., 2008). After the massive coral mortality of El Niño 1982–83, it was hypothesized that many ETP coral reefs would collapse due to slow recovery, disrupted reproductive activity, and recruitment limitations (Guzman & Cortes, 2007). However, after both the 1982–83 and 1997–98 El Niño events, coral reef recovery did occur throughout the ETP, but in a temporally and spatially heterogeneous manner (Palacios & Zapata, 2014). For example, while reefs in Colombia (Zapata, 2017), Costa Rica (Guzman & Cortes, 2007) and Panama (Glynn, Enochs, Afflerbach, Brandtneris, & Serafy, 2014) have recovered to pre-disturbance coral cover values, in an extreme scenario in the southeastern Galapagos Islands, recovery has been impaired by an initially low coral cover, limited recruitment, high rates of bioerosion by corallivores (Edgar et al., 2010), and by a reduced carbonate ion concentration which has decreased coral calcification (Manzello et al., 2015).

Time-series data on ecosystem health and productivity from habitats such as mangrove forests, seagrass beds, and coral reefs would be useful for ETP countries to quantify the economic goods and environmental services provided by them. However, unlike other coral reefs around the world, it is unknown if coral cover in the ETP is declining. This occurs, in part, because time-series data for ETP coral cover have not been collected or summarized. Identifying the factors driving reef recovery or decline is critical for defining the conservation strategies necessary to protect coral reefs in the region (Romero-Torres, Acosta, & Treml, 2017). Here, we present a 44-year live coral cover trend analysis for the ETP coral reefs from an exhaustive literature review of empirical data to test two hypotheses: 1) Whether coral reefs of the ETP are following the global trend of live coral cover decline through time, and 2) If repeated exposure to ENSO-induced heat stress is associated with regional trends in live coral cover.

MATERIALS AND METHODS

Analysis of coral cover data. To obtain the live coral cover data (defined as the percent of reef substrate covered by living scleractinian and milleporine hard corals, and hereafter referred to as coral cover), we performed a systematic search of scientific literature using several digital libraries spanning the years 1960–2018 (see SI for detailed methods).

From 1130 compiled documents, we selected 78 published studies that met our inclusion criteria for the analysis of coral cover (Table S3). We extracted the coral cover data from tables, figures, and research statements. To structure the extracted data hierarchically, we followed the definitions of Jackson, Donovan, Cramer, and Lam (2014) in the following: biogeographical provinces (3 levels), regions (16 levels), sea surface temperature regimes (4 levels), countries (8 levels), along with location (54 levels), site (177 levels), years (44), coral cover (%), algal cover (%), and sampling technique (see Fig. 1). Three time-intervals were selected, based on the onset of high-intensity El Niño events (1973–82, 1983–97, and 1998–2014). We developed a time-series of coral cover data with 568 observations, using the site as the minimum geographical unit (i.e., one or more surveys at the same coordinates on the same reef; Jackson et al., 2014). There were no data available for 1973, from the Guayaquil region, nor sufficient published coral cover data to analyse the most recent El Niño event 2015–

16, although data on this event are now starting to be published (Alvarado et al., 2020; Cruz-García, Rodríguez-Troncoso, Rodríguez-Zaragoza, Mayfield, & Cupul-Magaña, 2020). Figure S1 describes the number of surveys by region and year.

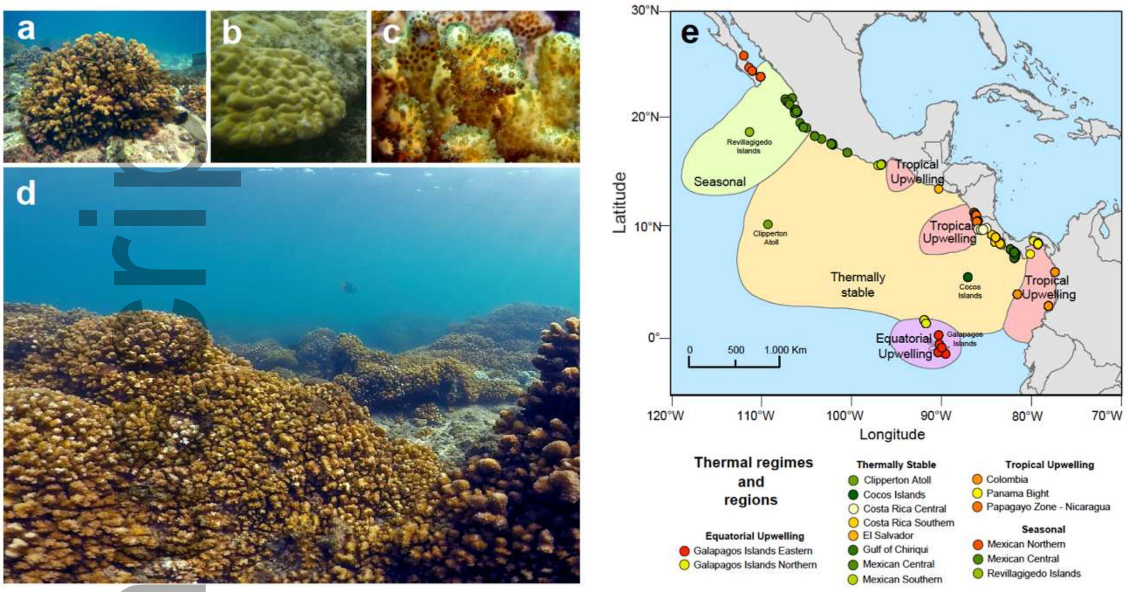

FIGURE 1 Coral assemblages in the Eastern Tropical Pacific are some of the most depauperate reefs in the tropics but include 42 species of symbiotic scleractinian corals. Coral assemblages in the ETP are dominated by dense clonal stands of *Pocillopora* and stands of massive corals in the genera *Porites*, *Pavona*, and *Gardineroseris*. **(a)** *Pocillopora* sp., **(b)** *Porites lobata,* **(c)** *Pocillopora* sp. close-up **(d)**, coral assemblages on the Gulf of California, México (images by David A. Paz-García). **(e)** Map of the study region; color shading indicates the four thermal regimes and the 16 regions (dots) of surveyed reefs.

Statistical analysis and limitations. We aggregated the coral cover data by calculating the mean coral cover per site/year, then the mean coral cover per location/year, and, finally, the mean coral cover per region/year (response variable). We added, as a factor to the coral cover data, four distinct thermal regimes (Equatorial Upwelling, Thermally Stable, Tropical Upwelling, and Seasonal). For an explanation of the thermal regimes see Romero-Torres et al. (2017) and references therein. Since the coral cover data have missing years, we tested if data were missing completely at random using IBM-SPSS Statistics version 22 (see SI). To test the hypotheses that live coral cover declined through time for each of five time-intervals (1974–82, 1983–97, 1998–2014, 1983–2014 and 1970–2014), we used generalized linear mixed models (GLMM) in R (version 3.5.1) with fixed (year and thermal regime) and random (region) effects, applying the

Statistical Package lme4 (version 3.1-137). Raw data of coral cover change proportions were used without applying any transformation.

Our coral cover analysis has three significant limitations. The first is that including different sampling techniques (e.g., chain transects, point-intercept line transects, video belt transects, and quadrat samples) could potentially increase the variance between sample groups. However, the inclusion of these different percent cover estimators provides a robust estimate for region-wide analysis of coral cover and makes our work comparable to previous studies on other coral reefs where these techniques have also been used (Moritz et al., 2018) and successfully compared (Morrison et al., 2012).

The second potential limitation stems from the inclusion of several different sampling designs used in these disparate field surveys. We did not differentiate coral cover data based on the sampling design, such as the number of replicates, the reef zones sampled (back reef, fore-reef, or reef crest) or information on species relative abundances. Many other studies have omitted these details as well. Aggregation of these surveys is justified by the broad scale nature of the questions asked and by the fact that most ETP coral reefs are homogeneous, structurally simple, low-diversity fringing reefs, concentrated in shallow (<15 m) water (Fig. 1) (Romero-Torres et al., 2017).

The third limitation derives from the fact that our time series analysis does not result from repeat sampling of the same reefs through time, but instead from sampling several different reefs, but within the same region, through time. With the exception of the four most consistently monitored sites (see Figure S3), our coral cover data do come from a variety of sources. However, given the large number of data points from each region and the homogeneity of reefs across the entire basin, our methods did successfully capture broad-scale trends that occurred there, such as widespread coral mortality following the 1982–83 El Niño, as well as prominent periods of coral recovery.

Thermal stress and annual rate of change in coral cover. We examined the relationship between the accumulated thermal stress and the annual rate of coral cover change (hereafter referred to as coral cover change) from 1982 to 2014. Ocean surface temperature satellite data began after 1982. Following Houlahan, Findlay, Schmidt, Meyer, and Kuzmin (2000), we estimated the year-on-year annual rates of coral cover change as $\log (N+1)_{t+1} - \log (N+1)_t = \Delta N$, where N is percent coral cover and t is year of study, for sites with two consecutive years of cover data and sites separated by one year (e.g., 1997 and 1999).

We estimated the accumulated thermal stress in each site based on the maximum degree heating weeks (DHW) index (Liu, Strong, Skirving, & Arzayus, 2006), that was calculated using daily SST data with 1/4° spatial resolution from the NOAA High Resolution Optimal Interpolated Sea Surface Temperature (OISST) (NOAA/OAR/ESRL PSD, Boulder, Colorado, USA; https://www.esrl.noaa.gov/psd). First, we calculated the maximum monthly mean (MMM) SST at the grid point closest to the study sites, using a long-term monthly climatology OISST data set from 1985-2012. For each site and each month of each year, we calculated the average SST and estimated the climatology for each month as the average temperature of all years' means for that month. The MMM was obtained by selecting the highest monthly mean value of the 1985–2012 climatology at each site. We used the daily OISST data for each site and their respective MMM to estimate the DHW because temperatures ~1ºC above the MMM are known to cause coral bleaching if the stress is prolonged (Liu et al., 2006); therefore, we consider appropriate the use of that DHW limit in the ETP reefs to measure the effect of thermal anomalies for this region. To do that, daily HotSpots (SST-MMM) ≥ 1ºC were summed up for 12 consecutive weeks (Liu et al., 2006), and this value divided by seven to convert degree heating days to DHW (DHW = 1/7 × sum of previous 84 daily HotSpot, HotSpot ≥ 1ºC) (DeCarlo & Harrison, 2019). Finally, the maximum DHW value reached during the year was selected to represent the maximum accumulated heat stress for the period evaluated. SST data were extracted with the package raster for R, and following climatology and DHW calculations were done in R (version 3.5.1).

To test the hypothesis that the intensity of thermal stress drives the change in coral cover across geographic and thermal regimes, we used a GLMM with random intercepts for thermal regimes with DHW as a fixed effect. GLMMs were adjusted in R (version 3.5.1) with the Statistical Package lme4 (Table S2). Raw data of coral cover change proportions was used without applying any transformation.

RESULTS

Coral Cover trends. We found a non-significant increase in the live coral cover from 1970 to 2014 in the ETP (Table S1, Fig. 2b). ETP coral cover exhibits considerable variability, regardless of the time interval or subregion of analysis (Fig. S2). From 1970 to 2014, the ETP multiannual regional coral cover fluctuated around a median of 30.3% and a mean of 30.5% (*sd* ± 20.1, including all natural and anthropic sources – see Statistical analysis and limitations, Fig. 2b). Comprehensive monitoring datasets were found in published studies for Uva Island (Glynn et al., 2014), Gorgona Island (Zapata, 2017), Costa Rica (Cortés, Jiménez, Fonseca, & Alvarado, 2010; Guzman & Cortes, 2001), and the Eastern Galapagos Islands (Fong, Smith, & Muthukrishnan, 2017). We did not locate accessible and structured datasets in other ETP locations or countries.

The 1982–83 El Niño was responsible for an abrupt decline in the mean ETP coral cover from 32.7% (*sd* ± 21.8) to 7.1% (*sd* ± 6.8) [Tukey-like test (TL): $t = -3.22$, $p < 0.01$], equivalent to a 25.6% decrease of live coral cover. During the second period following the 1982 El Niño event from 1983–1997, the mean coral cover increased significantly from 7.1% in 1983 to 33.9% (*sd* ± 19.3) in 1997 (TL: $t = 3.40$, $p < 0.01$). In contrast to the significant coral loss between the El Niño years 1982 and 1983, we did not find a difference in the mean ETP coral cover between El Niño years 1997 and 1998 (TL: $t = 1.679$, $p = 0.09$) compared to the previous period (1983-1997). The third time-interval 1998–2014, which had the highest monitoring sampling locations (more subregions and reefs surveyed per year), did not reveal an increasing or decreasing linear trend in mean coral cover (Table S1). Although coral cover increases slightly over the 44 years, this trend is not significant due to the data's high variability (Fig. 2b). Even after the catastrophic coral die-off following the 1982–83 El Niño, we did not find evidence of a coral to macroalgal phase shift. This suggests basin-wide coral recovery, except on the northern Pacific coast of Costa Rica, where macroalgae cover did increase, suggesting a phase shift there (Alvarado et al., 2018).

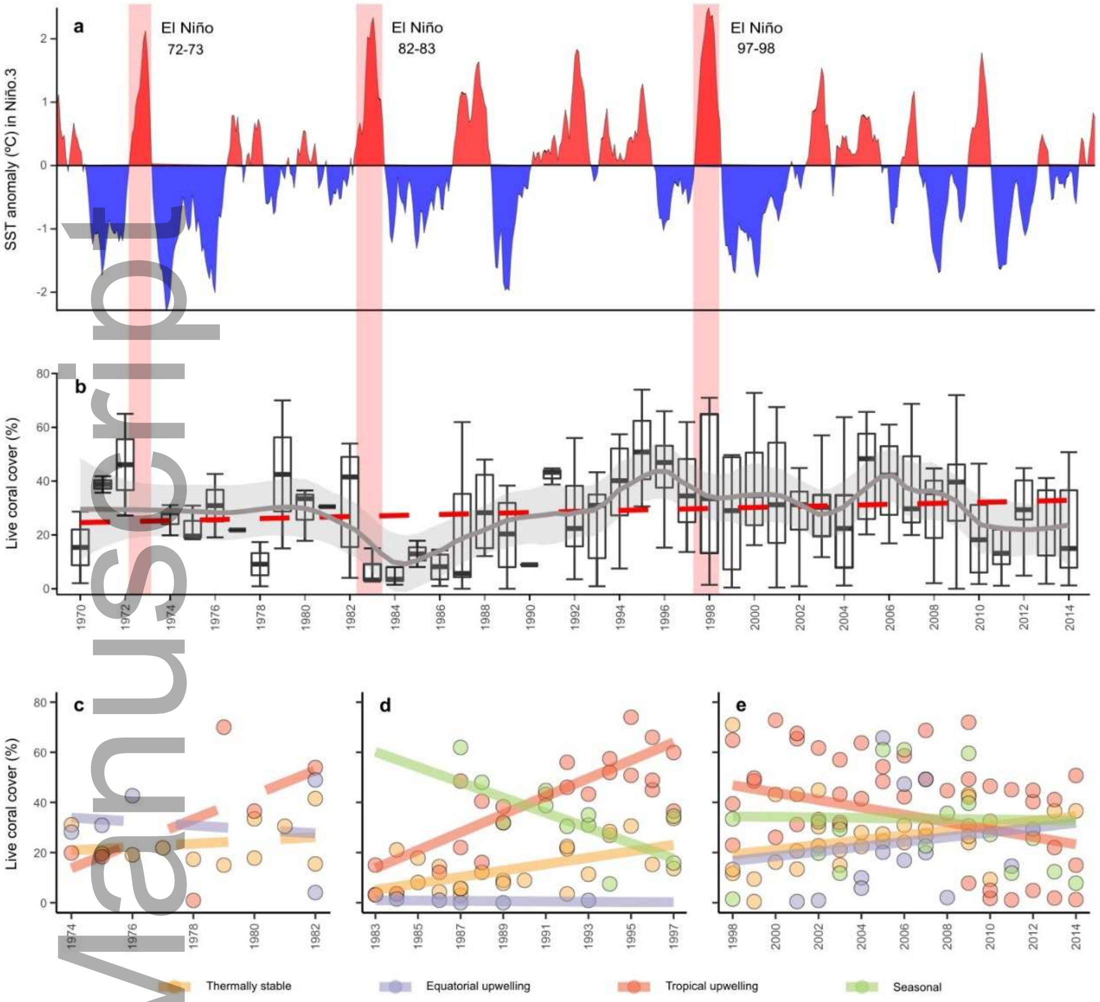

FIGURE 2 Illustration of the influence of most intense ENSO events on the coral cover in the ETP. **(a)** The upper panel indicates the positive (red) and negative (blue) SST anomalies in the Niño-3 region during 1971–2014 (NOAA Climate Prediction Center's Extended Reconstructed Sea Surface Temperature ERSSTv5). The vertical orange bars indicate the strongest El Niño events. **(b)** The panel displays, at the horizontal axis, the 44-year live-coral cover aggregated at the region scale (n = 202) for ETP coral reefs with its fitted linear trend (red dashed band). The fitted smooth line trend represents the long-term cycles of loss and recovery (grey line with the best polynomial fit with a 95% confidence level interval and a span = 0.2, *p* for year = 0.398). The vertical axis shows the live coral cover. Box plots describe the minimum, maximum, interquartile ranges and median values of live-coral cover for each year. Notice the abrupt decrease in coral cover after 1982–83 El Niño; a smaller decline occurred after 1997–98. Random intercepts and random slopes models for the time-intervals: **(c)** 1974–1982 (*p* for Thermal regime × year = 0.265), (d) 1983–1997 (*p* for

Thermal regime × year < 0.001), and (e) 1998–2014 (p for Thermal regime × year = 0.036).

Relationship between change in coral cover and heat stress. Heat stress at each site was estimated as the maximum accumulated DHW per year. Exposure beyond 8 DHWs is likely to cause massive mortality (Liu et al., 2006). Our data show that there is a weak, but significant positive linear relationship between thermal stress and the coral-cover annual rate of change in the ETP from 1982 to 2014 ($Conditional\ R^2_{GLMM} = 0.313$, $n = 133$, $p = 0.002$, Fig. 3b, Table S2).

There was considerable variability both in the distribution of heat stress across years in the ETP and the response of the coral cover changes as a function of DHW (Fig. 3a). Nineteen out of 133 observations (15.03%) of the coral-cover annual rate of change experienced four or more DHW (Fig. 3b quadrants I and IV), and 13 out of these 19 occurred during El Niño 1997–98. Ten records showed 8 or more DHW (two overlapped), and these high heat stresses occurred at the Galapagos Islands (Santa Cruz Island, DHW = 27.71 in 1982) causing a catastrophic decline in coral cover, local extirpation at many sites, and limited recovery; Gorgona Island in 1998 (DHW = 20.47) and Malpelo Island in 2010 (DHW = 13.10), the latter two produced only modest deflections in the annual rate of change in coral cover at those sites. Eighty-four percent of coral-cover annual change observations (n =113) experienced fewer than 4 DHW (Fig. 3b quadrants II and III), and 49 out of 58 of these observations are negative (Fig. 3b quadrant III). We found negative annual rates of change in the seasonal thermal regime (e.g., Mexican Northern and Mexican Central regions, green dots Fig. 3b). In the seasonal thermal regime, 5 out of 14 of the negative cover-change rates occurred during El Niño 1997–98. Between 2013 and 2015, the Gulf of California was affected by a marine heatwave (Jacox et al., 2016); however, we did not find surveys in 2015 to determine the coral cover change there.

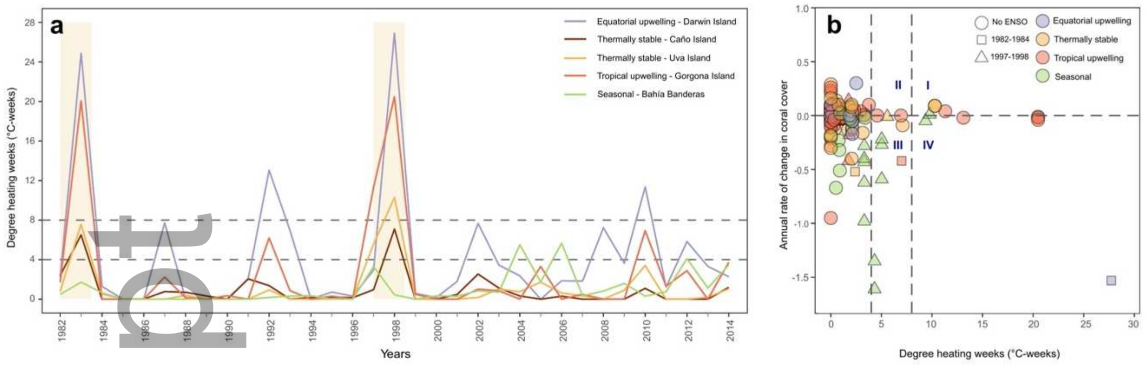

FIGURE 3 Heat stress and its effect on coral cover across the ETP. **(a)** The sequence of yearly maximum DHW experienced by the best-represented individual coral reefs sites from 1982 to 2014. When cumulative thermal stress reaches 4°C-weeks and 8°C-weeks or higher (horizontal dotted lines), bleaching is likely, as well as coral mortality from thermal stress (Liu et al., 2006), respectively. Although the thresholds were developed in seasonal systems, and are not universally applicable for equatorial regions, they are still useful for separating responses into well-defined heat-stress groups. **(b)** The association between the maximum DHW and the coral cover change at each of four thermal regimes (dot colors as Fig. 2). Each point (*n* = 133) represents the DHW and the coral cover annual rate of change per individual coral reef site. The horizontal dotted line divides the positive (≥ 0) and the negative (< 0) rate of change caused by coral growth or mortality, respectively. The vertical dotted line indicates the DHW thresholds of 4°C-weeks and 8°C-weeks, respectively. The vertical (≥ 8°C-weeks) and horizontal dotted lines create four response quadrants: I) heat stress and positive coral cover change (gain in live coral cover, 3.0% resilient response), II) no heat stress and positive coral cover change (42.85%), III) no heat stress and negative coral cover change (loss in live coral cover, 49.62%), and IV) heat stress and negative coral cover change (4.51%).

DISCUSSION

Over the past 44 years, coral cover has not declined consistently across the ETP. Instead, it exhibits long-term cycles of loss and recovery, with no consistent upward or downward trend. Even though most of the reefs in the Galapagos collapsed, and many others across the ETP were decimated after the 1982–83 El Niño, the remaining ETP reefs support the hypothesis that even high levels of heat stress did not kill them all. Between 1982 and 2014, heat stress preceded 31% of the instances of coral decline in the ETP. These localized and sporadic periods of coral loss, however, never translated into a long-term, region-wide decline. For instance, the globally severe El Niño of 1997–98 evidenced only slight declines in the ETP, and nowhere near the catastrophic response seen in the 1982-83 El Niño (Reyes-Bonilla, Carriquiry, Leyte-Morales, & Cupul-Magana, 2002). Lastly, ETP reefs also demonstrate periods of coral cover stability (1999–2014), even after taking into account high temporal and local variability.

Because we were able to successfully retrieve and analyse several quantitative archival ETP coral reef surveys, our dataset stands as a compelling example of the utility and necessity for data rescue and recovery of ecological information. We have transformed local field observations on coral cover into a much broader temporal and spatial view of coral reef dynamics. We have aligned this ecological meta-analysis precisely with physical oceanographic information on ENSO-induced heat stress. In the ETP, cycles of disturbance and recovery in live coral cover contrast strikingly with the almost monotonic decline of Caribbean coral reefs (Jackson et al., 2014); but, they bear similarities with trajectories of some reefs across the Indo-Pacific, which recovered their live coral cover after disturbances (i.e., they returned to a similar coral-dominated state) (Sheppard et al., 2017). While baseline information on ETP coral reefs demonstrates that massive coral mortalities have occurred across the region (Toth et al., 2012), our long-term analysis also shows that ETP reefs can produce coral assemblages with 30 – 50% live-coral cover within decades of the disturbance. Because of this ability to recover from thermal stress, it would be valuable to identify the factors and processes that underpin this recovery.

We hypothesize that a combination of at least four factors promotes ETP reef resilience. The first factor is growth strategies of the dominant coral species; the second is the resistance to high and low-temperature stress conferred by thermotolerant dinoflagellate symbionts; the third is the heterogeneous distribution of high-light and high-temperature stresses across the complex geography of the ETP; and the fourth factor is the possibility of ecological memory, or the degree to which present trajectory of an ecosystem is shaped by its antecedent conditions (Peterson, 2002), exhibited by other frequently stressed coral reef ecosystems (Hughes et al., 2019). These ideas are discussed below.

Our results are concordant with a 10–15 year recovery time observed for sites populated with fast-growing corals, good colonizers, and branching species such as pocilloporids and acroporids (Gilmour, Smith, Heyward, Baird, & Pratchett, 2013).

Coral assemblages in the ETP are dominated by rapidly-growing branching pocilloporids and massive to encrusting poritids. These features lead to lower coral species richness and lower functional redundancy as compared with reefs near centers of coral biodiversity, characteristics that theoretically should lead to lower resilience after disturbance events (McWilliam et al., 2018). However, pocilloporid colonies can grow at extension rates of 2.24–4.55 cm yr^{-1} (Tortolero-Langarica, Rodríguez-Troncoso, Cupul-Magaña, & Carricart-Ganivet, 2017), and can quickly recolonize, even on coarse-sediment substrates through asexual reproduction by fragmentation creating thousands of viable clones, and less frequently by sexual recruitment after disturbances (e.g., strawberry–coral model; (Williams, 1975). Rapid regrowth and recovery have been reported for several El Niño damaged reefs in the Maldives (Pisapia et al., 2016) and elsewhere in the Indian Ocean (Perry et al., 2015)**.** In both cases, this recovery was led by rapidly growing pocilloporids. Finally, a majority of survivors and new recruits on regenerating and recovering coral reefs are broadcast spawners with additional high potential for asexual growth, relatively long-distance dispersal, rapid growth rates, and a capacity for frame-work construction (Baker, Glynn, & Riegl, 2008); these are hallmark characteristics of ETP pocilloporids. Environmental conditions in the ETP produce a trade-off within the Pocilloporidae, between fast growth and low skeleton density.

Second, as is typical of other hermatypic scleractinians, corals in the ETP are reliant on endosymbiotic algae for both their growth materials and energy reserves. Over the past decades, *Durusdinium glynnii* (formerly *Symbiodinium glynnii*) (LaJeunesse et al., 2018) has come to dominate the algal symbiont communities of *Pocillopora* (Baker, Correa, & Cunning, 2017), either by differential mortality of corals hosting more temperature-sensitive symbionts (LaJeunesse et al., 2010) or by the replacement of sensitive, less tolerant symbionts with the more temperature-tolerant *D. glynnii* (symbiont shuffling) in colonies exposed to stressful conditions (Palacio Castro, 2019). These changes in the symbiont communities can increase *Pocillopora* resistance to both cold (LaJeunesse et al., 2010) and heat bleaching (Glynn, Maté, Baker, & Calderón, 2001), as well as to elevated irradiance (LaJeunesse, Reyes-Bonilla, & Warner, 2007), resulting in coral communities better suited to survive under stressful conditions. Research on the interaction between coral symbionts and harsh environments should continue to be a priority for ETP research.

Third, the coral-cover cycles of disturbance and recovery observed in this study occur under highly fluctuating environmental conditions in the ETP (1983 and thereafter). These harsh conditions are distributed stochastically in space and time across the complex geography of the ETP (Fig. 1), leading to difficulty in determining regional trends in coral cover. For example, the 1997–98 El Niño produced a major global mass-bleaching event, but whereas on several reefs bleaching and mortality were high (Bruno, Siddon, Witman, Colin, & Toscano, 2001), on others, they were minimal (Baker et al., 2008). Previously, the effect of solar insolation was noted in French Polynesia (Mumby, Chisholm, Edwards, Andrefouet, & Jaubert, 2001), where it was suggested that high cloud cover reduced radiative stress, thereby preventing mass bleaching in French Polynesia during the 1997–98 El Niño event, despite abnormally elevated water temperatures there. Even though the three major ENSO events (1982–83, 1997–98 and 2015–16) share features, such as the intensity of thermal stress throughout the ETP, each ENSO event shows unique coupled atmosphere-ocean features, temporal evolution, and physical forcing mechanisms (Capotondi et al., 2015).

Especially in the ETP, it is important to study the regional variation in naturally occurring thermal stress and the potentially synergistic relationship between cloudiness and thermal stress as a driver of coral bleaching and survival. For example, the Thermally Stable and Tropical Upwelling areas (yellow and red dots, respectively in Fig. 3b) are some of the cloudiest regions in the world (Wilson & Jetz, 2016). In contrast, the Seasonal thermal-regime area (Gulf of California; green dot) possesses among the highest levels of solar irradiance year-round (Wilson & Jetz, 2016). While we do not know if light stress influences the negative values of some coral-cover changes observed in the Seasonal regime (Fig. 3b), it could be easily argued that elevated cloudiness in the Thermally Stable area could explain why there was no mass bleaching in the last decade in the Panama Bight, despite frequent episodes of thermal stress in this same region (e.g.*,* 2009 or 2014, Fig. 3a).

Additionally, short-term temperature stress by cold water (15–18°C) can generate a physiological response similar to that of heat stress and alter the coral-algae association causing bleaching and death. Seasonal cold-water episodes are frequent in the Tropical and Equatorial upwelling thermal regimes and have caused cold-water bleaching at Malpelo Island (Hernández, Reyes-Bonilla, & Balart, 2010) and in the Gulf of California (Paz-García, Balart, & García-de-Léon, 2012). A coral bleaching indicator similar to DHW but for cold water intrusions is warranted to detect these critical negative temperature anomalies in the ETP.

Subaerial exposures during extreme low tides in 2019 caused dramatic bleaching episodes at Gorgona and Uva Island (Mejía-Rentería, Castellanos-Galindo, Osorio-Cano, & Casella, 2020), providing another factor that should be considered in the future as a potential driver of live coral cover in the ETP.

Seasonal upwelling is also common in the ETP. This can increase the chlorophyll-*a* concentration (as measured by satellite data) and elevate water turbidity protecting coral communities from radiative stress. For example, some morphological and physiological responses in pocilloporid corals in the Gulf of California coincided with a shift of environmental conditions from low to high levels of chlorophyll-*a* (i.e., from low to high turbidity) (Paz-García, Hellberg, García-De-León, & Balart, 2015). Graham et al. (2015) identified nutrient levels as a strong contra-indicator of Indo-Pacific reef recovery following bleaching. In contrast, ETP coral reefs develop under a broad range of nutrient concentrations and productivity. Given the influence of nutrients and phytoplankton on water clarity and light penetration, this aspect of ETP oceanography may be an enabling, rather than a disabling factor for ETP reef growth and survival.

Finally, growing evidence suggests that repeated exposure to heat stress conditions reduces the cumulative impact of recurrent climate extremes (DeCarlo et al., 2019; Guest et al., 2012; Hughes et al., 2019). Coral survival and the increase of resistance to recurrent stressful conditions may be the product of genetic adaptation (Dixon et al., 2015; Thomas & Palumbi, 2017) and epigenetic inheritance (Eirin-Lopez & Putnam, 2019; Putnam & Gates, 2015). Our data suggest that some of these mechanisms may be at work in the ETP, especially among the pocilloporids. For example, differential mortality of *Pocillopora* corals along the ETP in response of thermal stress seems to have selected genetically resistant coral–algal partnerships (i.e., *Durusdinium*-Clade D; LaJeunesse et al. (2010), while in areas of the Gulf of California these symbiont/host pairings are more flexible (Pettay, Wham, Pinzon, & LaJeunesse, 2011). Additionally, differential geographic connectivity pathways in dominant reef-building corals in the ETP (Romero-Torres, Treml, Acosta, & Paz-García, 2018) may create coral population isolates with resistant genetic varieties. Although epigenetic studies have not yet been performed on corals *in situ* in the ETP region, *Pocillopora* corals have shown positive responses to climate change stressors in offspring when their parents were conditioned (Eirin-Lopez & Putnam, 2019; Putnam & Gates, 2015). Thus, corals of the ETP are routinely exposed to thermal stress with a broad range of environmental conditions. This environmental heterogeneity may therefore contribute to this region's resilience and potential for near-term survival as coral reefs elsewhere succumb.

Based on our 44-year time-series analysis, coral reefs in the ETP region, when considered as a whole, have not declined in coral cover over the last 44 years despite occasional pulses of mortality, unlike elsewhere in the Caribbean and Indo-Pacific. We propose that the growth potential, algal symbiont composition, and thermal response characteristics of ETP pocilloporid corals, contribute to ETP reef resiliency. Whether or not the coral reef recovery mosaic which routinely exists across the ETP will produce full ecosystem recovery and function after every bleaching event will depend on factors such as (1) the degree of coral loss, (2) the species composition of the surviving reef, and (3) the dynamic balance of reef accumulation and bioerosion (Baker et al., 2008).

At least, for now, patterns of recovery and resilience in the ETP are likely to persist across the complex topography and high oceanographic variability of this region. Unlike the bleaching and mass mortalities that inevitably follow exceptional temperature extremes elsewhere in the tropics, frequent El Niño events in the ETP have not produced a regional oceanographic environment in which coral reefs can no longer survive.

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CONFLICT OF INTEREST

The authors declare having no conflict of interest.

DATA AVAILABILITY

All data and code generated during the current study are available at https://doi.org/10.5281/zenodo.3744864

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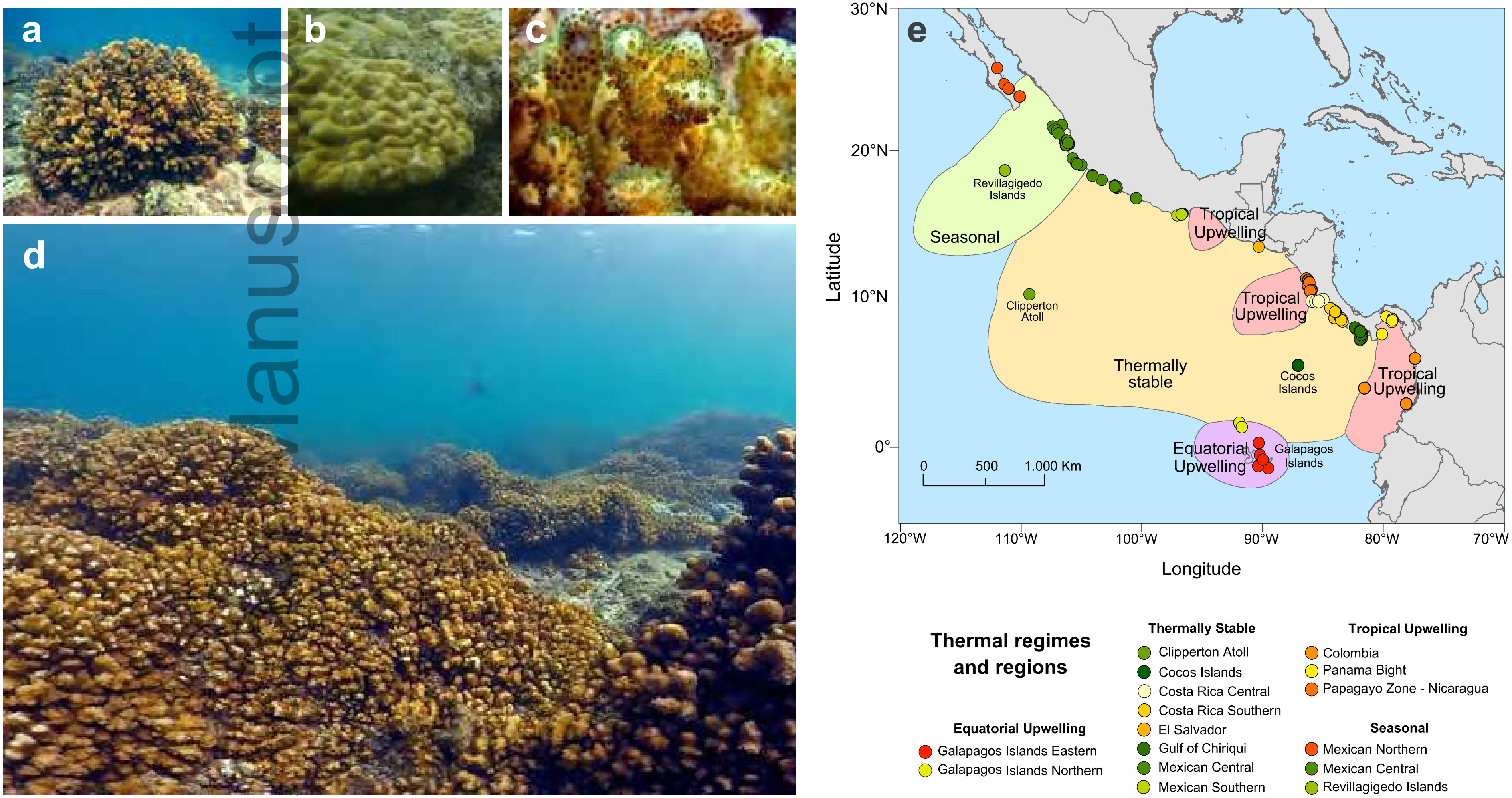
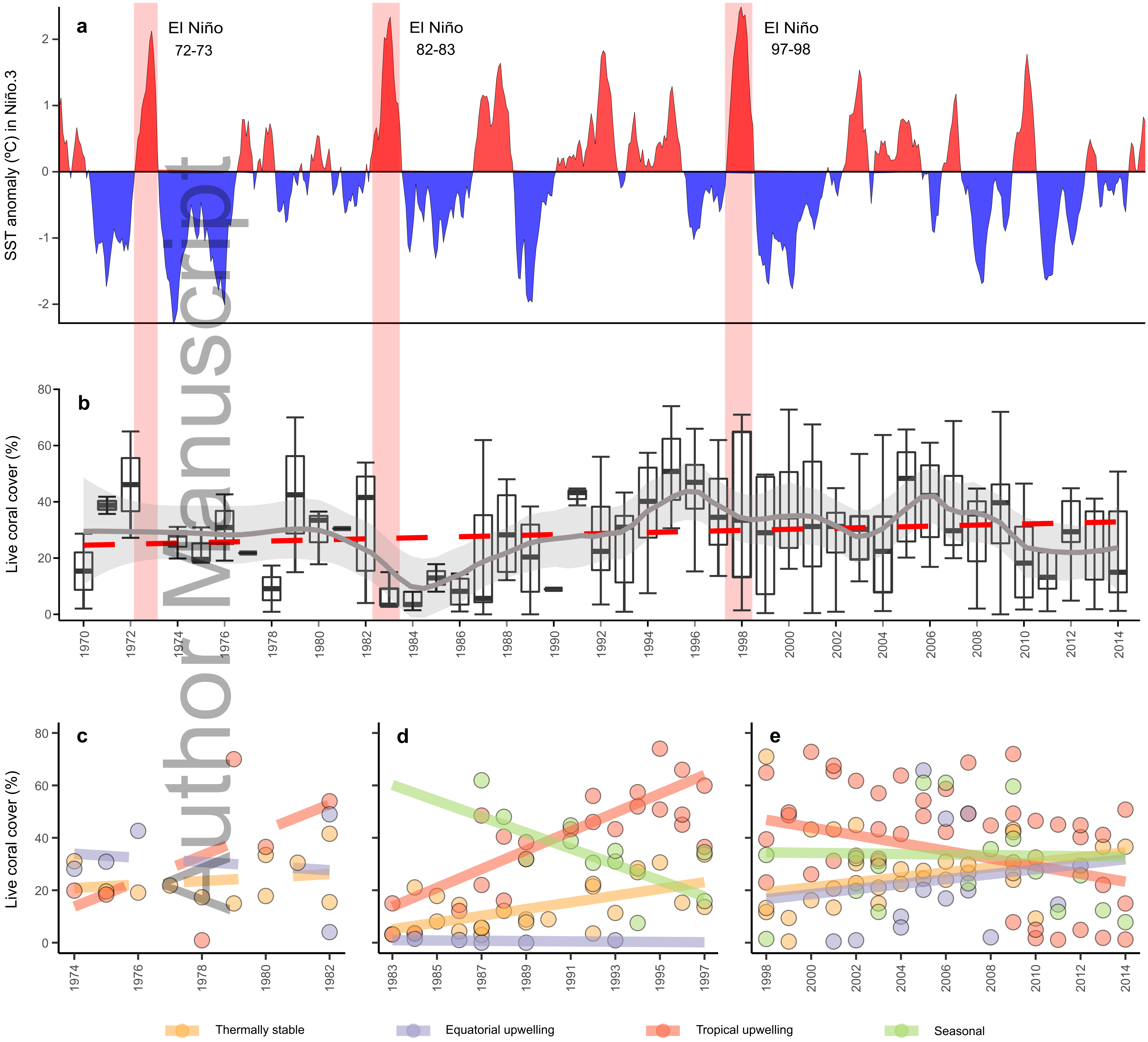
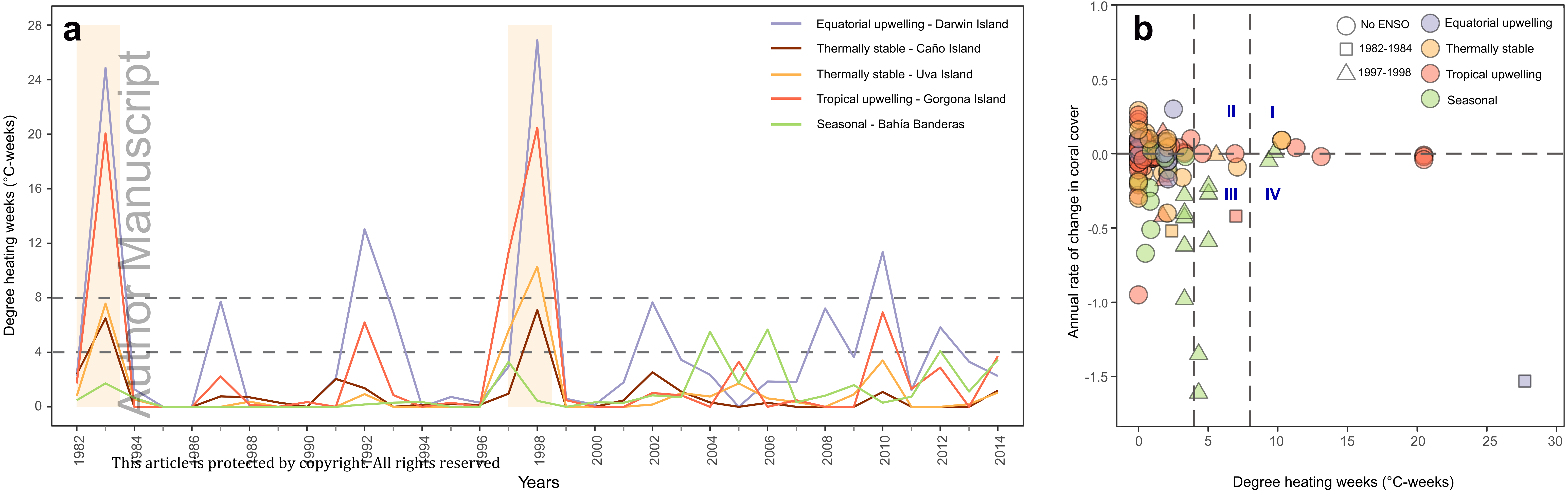

a
b
c
d
e
30°N
20°N
10°N
0°
120°W
110°W
100°W
90°W
80°W
70°W
Latitude
Longitude
Revillagigedo Islands
Seasonal
Tropical Upwelling
Clipperton Atoll
Tropical Upwelling
Thermally stable
Cocos Islands
Tropical Upwelling
Equatorial Upwelling
Galapagos Islands
0
500
1.000 Km
Thermal regimes and regions
Thermally Stable
● Clipperton Atoll
● Cocos Islands
● Costa Rica Central
● Costa Rica Southern
● El Salvador
● Gulf of Chiriqui
● Mexican Central
● Mexican Southern
Tropical Upwelling
● Colombia
● Panama Bight
● Papagayo Zone - Nicaragua
Equatorial Upwelling
● Galapagos Islands Eastern
● Galapagos Islands Northern
Seasonal
● Mexican Northern
● Mexican Central
● Revillagigedo Islands


a
El Niño 72-73
El Niño 82-83
El Niño 97-98
SST anomaly (ºC) in Niño.3
2
1
0
-1
-2
b
Live coral cover (%)
80
60
40
20
0
1970
1972
1974
1976
1978
1980
1982
1984
1986
1988
1990
1992
1994
1996
1998
2000
2002
2004
2006
2008
2010
2012
2014
c
d
e
Live coral cover (%)
80
60
40
20
0
1974
1976
1978
1980
1982
1983
1985
1987
1989
1991
1993
1995
1997
1998
2000
2002
2004
2006
2008
2010
2012
2014
Thermally stable
Equatorial upwelling
Tropical upwelling
Seasonal


a
Equatorial upwelling - Darwin Island
Thermally stable - Caño Island
Thermally stable - Uva Island
Tropical upwelling - Gorgona Island
Seasonal - Bahía Banderas
Degree heating weeks (°C-weeks)
0
4
8
12
16
20
24
28
1982
1984
1986
1988
1990
1992
1994
1996
1998
2000
2002
2004
2006
2008
2010
2012
2014
Years
b
No ENSO
1982-1984
1997-1998
Equatorial upwelling
Thermally stable
Tropical upwelling
Seasonal
I
II
III
IV
Annual rate of change in coral cover
1.0
0.5
0.0
-0.5
-1.0
-1.5
0
5
10
15
20
25
30
Degree heating weeks (°C-weeks)