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Reef Community Changes Associated with the 2009–2010 El Niño in the Southern Mexican Pacific¹

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Abstract: We surveyed coral reefs communities before (September 2007–March 2009) and during (September 2009) the 2009–2010 El Niño event on the coast of Oaxaca, southern Mexican Pacific to evaluate community changes associated with the warming event. From May 2009 to December 2010, we recorded positive deviations from the historical in situ sea surface temperature values. There were differences among the coral species *Pocillopora damicornis*, *Porites panamensis*, and *Porites panamensis* with significant reductions in chlorophyll *a* and *Symbiodinium* density during El Niño, resulting in bleaching (>13%) and increase in algal coverage (mainly geniculate coralline algae). Concurrently, echinoderm and fish assemblages also experienced significant modifications; abundances of the sea urchins *Eucidaris thouarsii* and *Centrostephanus coronatus* increased during the warming event, whereas *Diadema mexicanum* declined; meanwhile, fish species such as *Thalassoma lucasanum* declined in favor of *Stegastes acapulcoensis* and *Haemulon maculicauda* during the warming event. During the El Niño event, changes in composition and abundance of echinoderms and fish may have been due to horizontal and/or vertical redistribution of species rather than species mortality or recruitment. The observed changes in coral physiology and consequent modifications in coral, echinoderm, and fish communities highlight that the 2009–2010 El Niño event impacted several levels of biological organization in the coral reefs of southern Mexico, beyond the actual corals themselves. The observed changes add to local stressors associated with coastal development and ultimately threaten the health of the once considered best-developed reef system in the Eastern Pacific.

INCREASES IN SEA WATER temperature associated with El Niño–Southern Oscillation (ENSO) events have resulted in the widespread degradation of coral reef ecosystems worldwide (Glynn 1993, Hoegh-Guldberg 1999). Degradation is associated with massive coral

reef bleaching during which reef-building stony corals lose their dinoflagellate algal symbionts (genus *Symbiodinium*) as a result of long-lasting positive anomalies in sea surface temperatures (SST). Along with triggering coral bleaching and subsequent mass mortality,

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ENSO events have also resulted in turnover of long-term symbiotic relationships between *Symbiodinium* clades and their coral hosts (Baker et al. 2004, LaJeunesse et al. 2010), phase shifts from coral to algal dominance (McClanahan, Muthiga, and Mangi 2001; Aronson et al. 2002), reduction in reproductive output and recruitment (Ward, Harrison, and Hoegh-Guldberg 2000; Booth and Beretta 2002), changes in composition and abundance of invertebrates and vertebrates in coral communities and reefs (Hernández, Reyes-Bonilla, and Balart 2010; Glynn et al. 2014), and alterations in ecosystem functioning (Bellwood et al. 2004).

ENSO has had a long-lasting impact history in Eastern Pacific coral reef frameworks (Toth et al. 2012). During the last three decades, high (El Niño) and low (La Niña) sea temperatures associated with ENSO have caused bleaching and ultimately coral mortality in the Gulf of California (Reyes-Bonilla 1993, 2001; Reyes-Bonilla et al. 2002; Iglesias-Prieto, Reyes-Bonilla, and Riosmena-Rodríguez 2003; LaJeunesse, Reyes-Bonilla, and Warner 2007; LaJeunesse et al. 2010; Paz-García, Balart, and García-de-León 2012), the Mexican Pacific (Carriquiry et al. 2001, Reyes-Bonilla et al. 2002), and Central America (Glynn 1984, 1990; Feingold 2001; Glynn et al. 2001; Guzmán and Cortés 2001; Jiménez et al. 2001). In particular, Panamanian gulfs (Chiriquí and Panama) and Galapagos Islands experienced bleaching and coral mortality during the 1982–1983 El Niño (Glynn 1988), but widespread bleaching and coral mortality was also recorded from the Gulf of California (Reyes-Bonilla 2001) to Colombia (Jiménez et al. 2001) and Ecuador during the 1997–1998 El Niño (Glynn et al. 2001).

Eastern Pacific ENSO-related studies have focused on addressing coral bleaching and its associated mortality (Glynn 1990; Reyes-Bonilla 1993, 2001; Munguía-Vega and Reyes-Bonilla 1999; Carriquiry et al. 2001; Feingold 2001; Glynn et al. 2001; Jiménez et al. 2001; Reyes-Bonilla et al. 2002; Iglesias-Prieto, Reyes-Bonilla, and Riosmena-Rodríguez 2003; Paz-García, Balart, and García-de-León 2012), its bioerosive effect (Scott, Risk, and Carriquiry 1988; Glynn 1990; Eakin 1996, 2001;

Reaka-Kudla, Feingold, and Glynn 1996), historical and ecological long-term responses (Colgan 1990, Glynn and Colgan 1992, Guzmán and Cortés 2001, Toth et al. 2012), and recently the bleaching susceptibility of *Symbiodinium* clades in the area (LaJeunesse, Reyes-Bonilla, and Warner 2007; LaJeunesse et al. 2010; Paz-García et al. 2012).

Despite extensive research into the coral bleaching phenomena in the Eastern Pacific, there are few studies examining the population biology of affected species or communities (Glynn 1988; Hernández, Reyes-Bonilla, and Balart 2010; Glynn et al. 2014) and there is a lack of studies addressing the effect of ENSO at several levels of biological organization. These data are not only needed to evaluate the effect of ENSO beyond corals themselves, but they are also required to predict the capacity of corals and reefs to respond to environmental changes. Considered as a strong El Niño warm pool (*sensu* Ashok et al. 2007), the 2009–2010 El Niño exerted coral bleaching and disturbances at several levels of biological organization in reef communities from southern Mexico. In this paper, we evaluate the influence of the strong 2009–2010 El Niño (WonMoo et al. 2011) at several levels of biological organization, from coral physiology up to echinoderms and fish communities that live in or are associated with coral reef communities in the coast of Oaxaca, western Mexico.

MATERIALS AND METHODS

Study Area

To evaluate the influence of the 2009–2010 El Niño event at several levels of biological organization, we compared surveys of coral reef communities before (September 2007–March 2009) and during (September 2009) El Niño in the Mazunte–Montosa Island area in the coast of Oaxaca, southern Mexico (Figure 1).

The study area (Figure 1) is typical of the Eastern Tropical Pacific. The region experiences a dry season that extends from November to April, and a rainy season (800–1,500 mm yr⁻¹) from May to October. The Eastern Pacific warm pool (SST >28°C) influences

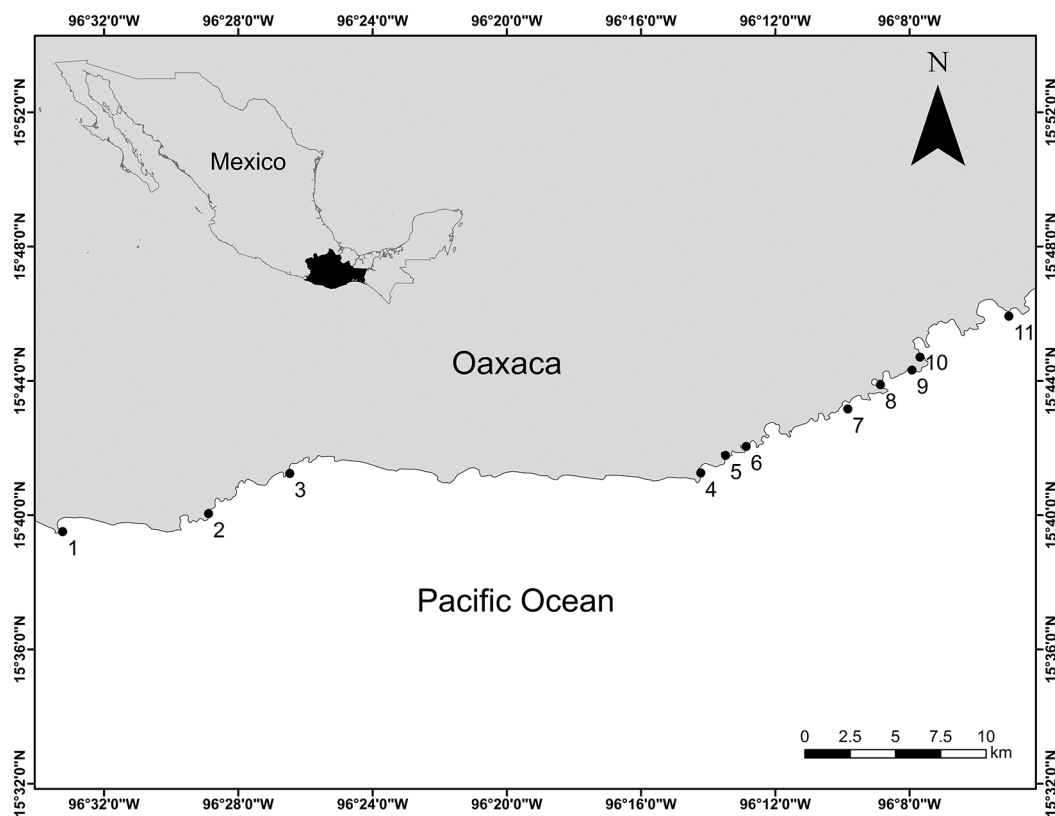


FIGURE 1. Location of studied reefs from the coast of Oaxaca, southern Mexico. 1=Mazunte, 2=Estacahuite, 3=Tijera, 4=San Agustín, 5=Riscalillo, 6=Jicaral, 7=Cacaluta Island, 8=Maguey, 9=Violín, 10=La Entrega, 11=Montosa Island.

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 ($<2^{\circ}\text{C}$), an average surface salinity of 34 practical salinity units, and the presence of a shallow (20–40 m) and quite stable thermocline (Fiedler and Talley 2006).

The most important source of interannual oceanographic variability along the coast of Oaxaca is the development of the ENSO event every 4 to 5 yr (Fiedler and Talley 2006), characterized by a deepening of the thermocline and nutricline, which negatively impacts primary productivity. When ENSO changes to its cold phase (La Niña), the conditions reverse, resulting in reduced depth of the thermocline. Consequently, nutrient-rich waters can

come close to the ocean surface, enhancing regional productivity (Pennington *et al.* 2006).

Temperature

Monthly historic SST records of the studied area were gathered from the Hadley Centre Sea Ice and Sea Surface Temperature data set (<http://www.metoffice.gov.uk/hadobs/hadisst/>; retrieved December 2013). In situ temperature was measured at 1-hr intervals with temperature data loggers (HOBO Data Logger UA-002-64; precision $\pm 0.53^{\circ}\text{C}$) deployed in 11 localities of Oaxaca, from Mazunte to Montosa Island (Figure 1). Monthly pooled data of the 2009–2010 El Niño were calculated and plotted against historical (1870–2008) data.

Corals

Five samples (10 cm²) from random colonies of *Pocillopora damicornis*, *Porites panamensis*, and *Pavona gigantea* were collected per locality, before (September 2007; San Agustín, Jicaral, Cacaluta Island, La Entrega) and during (September 2009; San Agustín, Riscalillo, Cacaluta Island, Maguey) the 2009–2010 El Niño event. To determine *Symbiodinium* densities, fragments (2 cm²) of each sample were fixed in formalin (4%) and the tissue was disrupted by sonication (60 min); subsamples of the solution were counted in a hemocytometer (Piniak, Lipschultz, and McClelland 2003). Chlorophyll *a* (Chl *a*) was extracted in acetone (90%) from an extra piece (2 cm²); the concentrations were determined spectrometrically using the equations of Jeffrey and Humphrey (1975). Extra nubbins (2 cm²) were fixed in formalin (4%) and decalcified using 10% acetic acid; the biomass was obtained by weighting the tissue after drying at 60°C for 24 hr (Edmunds and Davies 1986). Finally, biomass samples were used for total lipid extraction according to Folch, Lees, and Sloan (1957).

Because no significant differences among localities were detected in the data before the El Niño event or among localities during the El Niño event (after one-way analysis of variance [ANOVA]), sites were merged to estimate mean values ($\pm 95\%$ confidence interval) for each variable (i.e., *Symbiodinium* density, Chl *a* concentration, Chl *a* cell⁻¹, biomass, and total lipids) and species (*P. damicornis*, *P. panamensis*, *P. gigantea*), for both before ($n=20$) and during ($n=20$) the El Niño event. We tested the effect of the 2009–2010 El Niño warming event by looking for meaningful changes before and during the event, in each variable and species, using a Student *t* analysis after checking for normality and homogeneity deviations.

Coral Reef Communities

Substrate characteristics were gathered before (November–December 2008) and during (September 2009) the El Niño event for Riscalillo, Violín, and Montosa Island reefs, using 25 m long point-intersect transects (data every 25 cm). Along each transect, all underlying

coral species at each intersect-point were recorded. Additionally, substrate characteristics such as rocks, sand, algal mat, rubble, or cemented coral cover (dead coral) were recorded.

Echinoderm assemblages were sampled using a belt-transect (25 \times 1 m, echinoids; 25 \times 2 m, asteroids), quantifying in detail all echinoderms present in any cavity or hollow and without removing any rock or coral (Alvarado and Chiriboga 2008). Echinoderms were sampled before (November–December 2008) and during (September 2009) the El Niño event in Riscalillo, Cacaluta Island, Maguey, La Entrega, and Montosa Island. Meanwhile, fish assemblages were sampled along a belt-transect (25 \times 2 m) (Brock 1954). Duration of the fish counts was standardized to <20 min per transect. Fish censuses were conducted before (November–December 2008) and during (September 2009) the El Niño event at San Agustín, Cacaluta Island, La Entrega, and Montosa Island. All surveyed transects were randomly placed in the reefs, running parallel to the coastline at random depths but inside the bathymetric interval where reefs occur. All surveys were conducted during daytime (1000 to 1600 hr).

We used an ordination procedure (principal coordinates analysis, PCO) to graphically determine whether before and during El Niño samples could be grouped based on their overall assemblages. In addition, vector overlays (Spearman correlation >0.5) between PCO axis and original variables were drawn (Anderson, Gorley, and Clarke 2008). PCO was conducted on Bray-Curtis similarity matrices of square-root transformed data (Clarke and Warwick 2006). Furthermore, we tested the effect of the 2009–2010 El Niño on substrate characteristics, echinoderms, and reef-related fish assemblages in Oaxaca, through one-way permutational ANOVA (PERMANOVA) of fixed effects. PERMANOVA were conducted on Bray-Curtis similarity matrices of square-root transformed data, and 9,999 permutations were performed in all cases. Finally, to identify the major changes in echinoderms or fish communities in terms of composition and species abundance linked to the warming event, we used the similarity percentages routine (SIMPER). Multidimensional scaling,

PERMANOVA, and SIMPER were computed using Primer 6 (Clarke and Warwick 2006).

RESULTS

Temperature

SST historical values showed lower values occurred during January ($\sim 26.2^{\circ}\text{C}$), steadily increased from January to May ($\sim 29.5^{\circ}\text{C}$) and steadily declined toward January. Compared to the historic pattern, in situ recorded temperature remained very close to the historic data from January 2009 to April 2009 (Figure 2), but from May 2009 to December 2010 positive deviations from the historic values were evident. Compared to the historical trend, in situ data during May 2009 showed an increase of $\sim 0.2^{\circ}\text{C}$, but during June 2009 this difference increased to $\sim 1.03^{\circ}\text{C}$, and in October 2009, it was as large as 1.85°C above historical data. During November 2009, the difference between historical and in situ data became smaller, and during December 2009 no difference was detected. From January 2010 to May 2010, temperature was lower than the historical values, the largest difference occurred during March 2010 when in situ data were $\sim 1.28^{\circ}\text{C}$ lower than the historical value. From May to July 2010, in situ

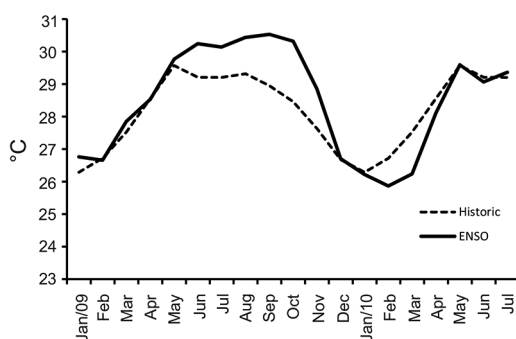


FIGURE 2. Historic (1870–2008) and in situ recorded sea surface temperature during the 2009–2010 El Niño in southern Mexico. In situ temperature was measured at intervals of 1 hr with HOBO pendant temperature data loggers (precision $\pm 0.53^{\circ}\text{C}$) deployed in 11 localities of the Mazunte to Montosa Island reef track. ENSO = El Niño–Southern Oscillation.

recorded temperatures were close to the historical means.

Corals

Coral bleaching was first observed by early/middle August 2009 mainly affecting *P. panamensis* and *P. gigantea* irrespective of depth (0 to 15 m) at all reef sites. During September 2009, bleaching was mild and widespread in patch reefs from Mazunte to Montosa Island, but bleaching of whole colonies irrespective of species was also observed. Bleaching ranged from 3% to 13.3% (mean 7.7 ± 5.2) but was particularly large at Montosa Island.

Bleaching of *P. damicornis*, *P. gigantea*, and *P. panamensis* colonies in the studied area resulted from the significant reductions in Chl *a* and *Symbiodinium* densities as the 2009–2010 El Niño developed in the region (Figures 3A, B). *Symbiodinium* decline was highly variable among taxa, while *P. damicornis* and *P. gigantea* experienced higher losses ($\sim 82.7\%$ to 67.4%), *P. panamensis* declines were relatively minor ($\sim 22.9\%$). The same trend was observed regarding Chl *a* concentration, while *P. panamensis* experienced a decline of $\sim 29\%$, *P. damicornis* experienced declines up to $\sim 70.1\%$.

During the El Niño event, *P. damicornis* and *P. gigantea* experienced significant reductions in Chl *a* cell^{-1} (*P. damicornis*, $\sim 61.8\%$; *P. gigantea*, $\sim 48.6\%$) (Figure 3C), but they showed meaningful increments in biomass (*P. damicornis*, $\sim 38.4\%$; *P. gigantea*, $\sim 110.2\%$) (Figure 3D), whereas, *P. gigantea* was the only species that experienced significant reductions in lipid content ($\sim 41.1\%$) (Figure 3E). *Porites panamensis* remained invariable to changes associated with 2009–2010 El Niño event in Chl *a* cell^{-1} (Figure 3C), biomass (Figure 3D) and lipid content (Figure 3E).

Coral Reef Communities

Associated with the 2009–2010 El Niño event, substrate characteristics in the studied area experienced modifications (Figure 4). During the warming event, there was a slight increase (2.4% to 6.1%) in algal cover (mainly turf algae), but by September 2009 algae (mainly geniculate coralline algae belonging to genus

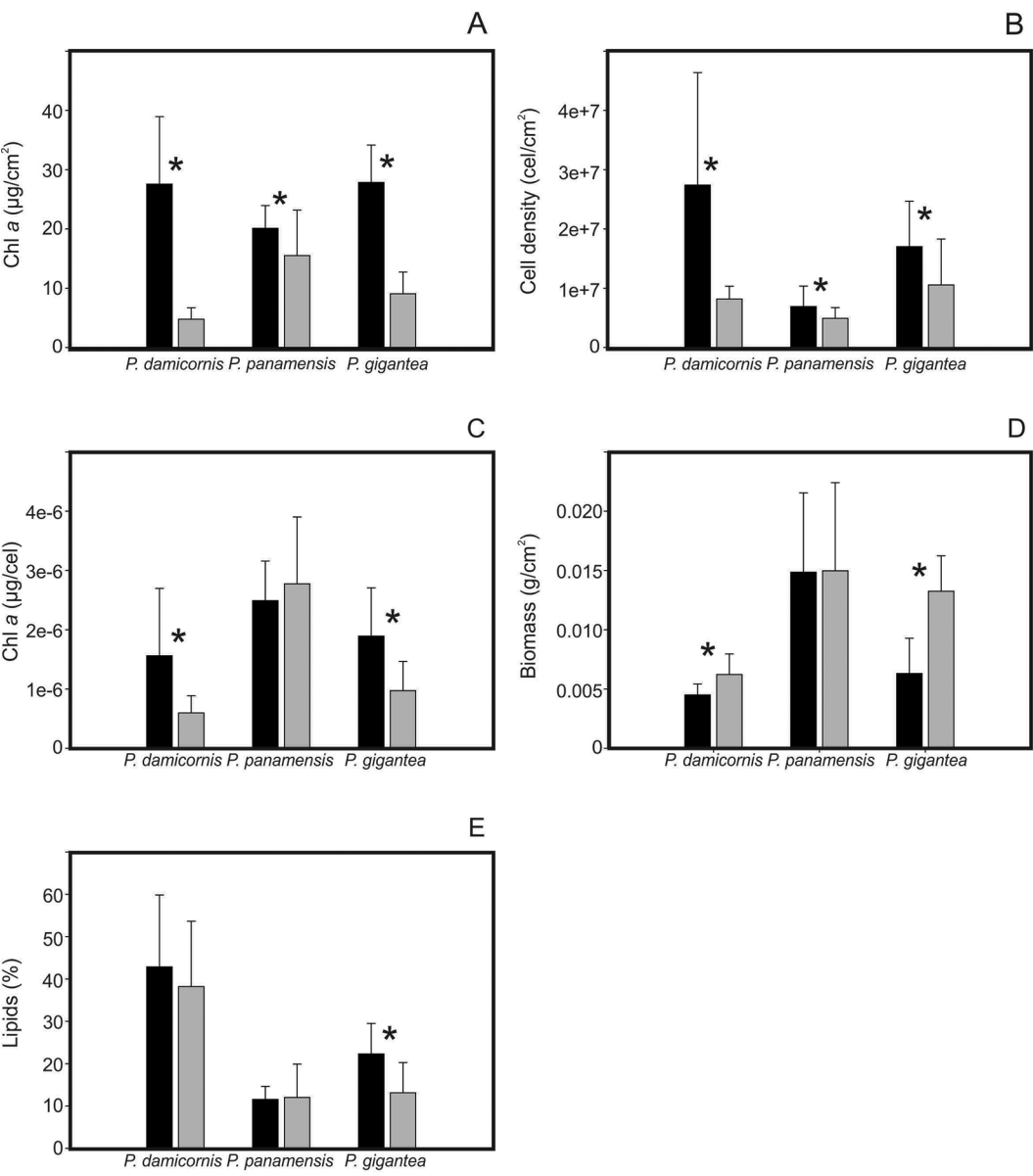


FIGURE 3. Chlorophyll *a* (Chl *a*), *Symbiodinium* density, Chl *a* cell⁻¹, biomass, and lipids before (September 2008, black) and during (September 2009, gray) the 2009–2010 El Niño in southern Mexico. Coral species are noted on each graph. Data are expressed as mean ± SD. Asterisks (*) indicate significant differences.

Amphiroa) overgrew live corals. Coral coverage experienced decline (6.5% to 19.4%), while bleaching up to 13% was recorded. Vector overlays (Spearman correlation >0.5) showed that coral bleaching and algal coverage experi-

enced the largest modifications. Permutational analysis demonstrated that changes associated with the warming event resulted in significant differences in substrate characteristics (PERMANOVA; pseudo-*F*=5.01, *P*=.0018).

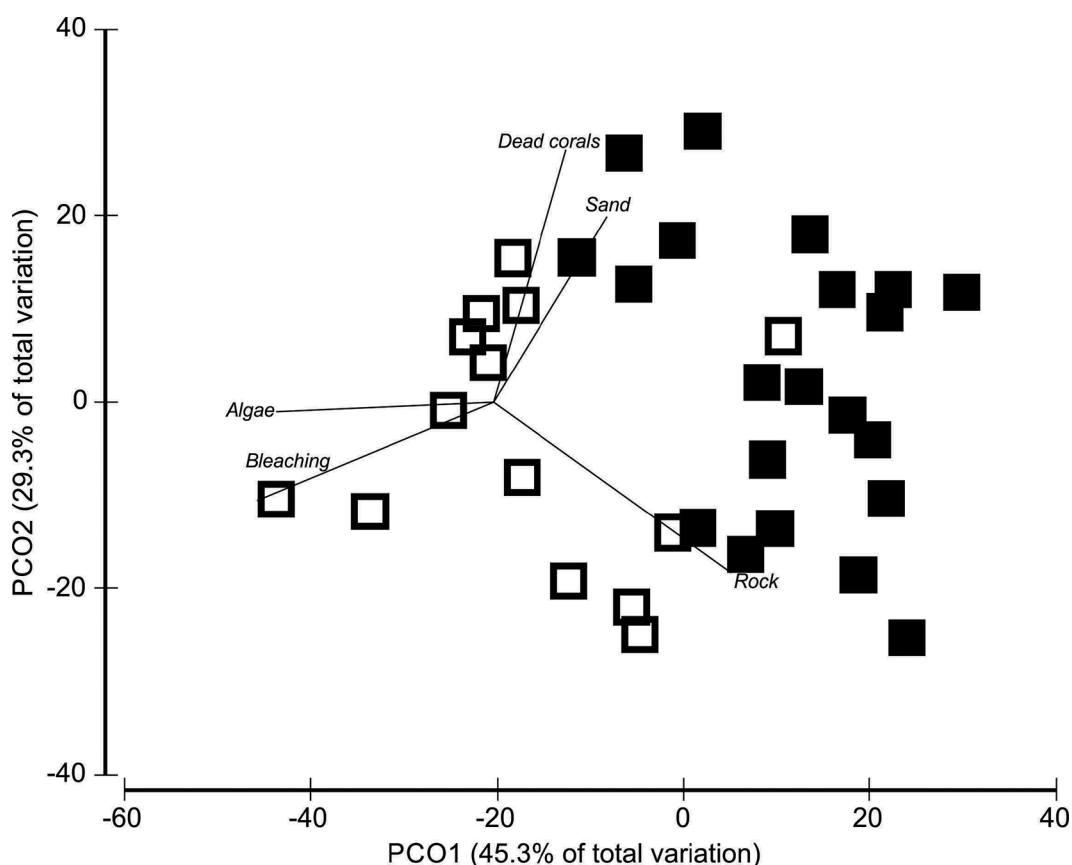


FIGURE 4. Principal coordinates analysis (PCO) ordination of substrate characteristics of coral reefs before (closed squares) and during (open squares) the 2009–2010 El Niño in southern Mexico. Vector overlays among PCO axis and original variables; only Spearman correlation >0.5 are shown.

Along with substrate characteristics, echinoderm communities inhabiting the studied areas (Riscalillo, Cacaluta Island, Maguey, Violín, La Entrega, Montosa Island) were significantly (PERMANOVA; pseudo- $F=12.02$, $P=.0001$) modified by the 2009–2010 El Niño event (Figure 5). Analysis of the composition and abundance of species (SIMPER) reveals that as El Niño developed in southern Mexico, there was a decline in the abundance of the sea urchin *Toxopneustes roseus* (100%), *Diadema mexicanum* (95.8%), and the sea star *Pharia pyramidatus* (43.4%), but an increase in the sea urchin *Eucidaris thouarsii* (140%), *Centrostephanus coronatus* (69.5%) and the sea star *Phataria unifascialis* (50.7%). Vector overlays (Spearman correlation >0.5) showed that the

sea urchins *E. thouarsii*, *D. mexicanum*, and *C. coronatus* experienced the largest modifications during the warming event.

Fish assemblages inhabiting the studied area (San Agustín, Cacaluta Island, La Entrega, Montosa Island) experienced significant modifications (PERMANOVA; pseudo- $F=5.38$, $P=.0001$) associated with 2009–2010 El Niño (Figure 6). Abundance analysis (SIMPER) demonstrated that during the 2009–2010 El Niño event, there were increases in *Diodon hystrix* (2,600%), *Abudefduf troschelii* (1,750%), *H. maculicauda* (666%), *Johnrandallia nigrirostris* (610%), *Plagiotremus azaleus* (585%), *Halichoeres nicholsi* (377%), *T. lucasanum* (302%), *Microspathodon dorsalis* (211%), *Halichoeres chierchiae* (184%), *Microspathodon bairdii* (183%),

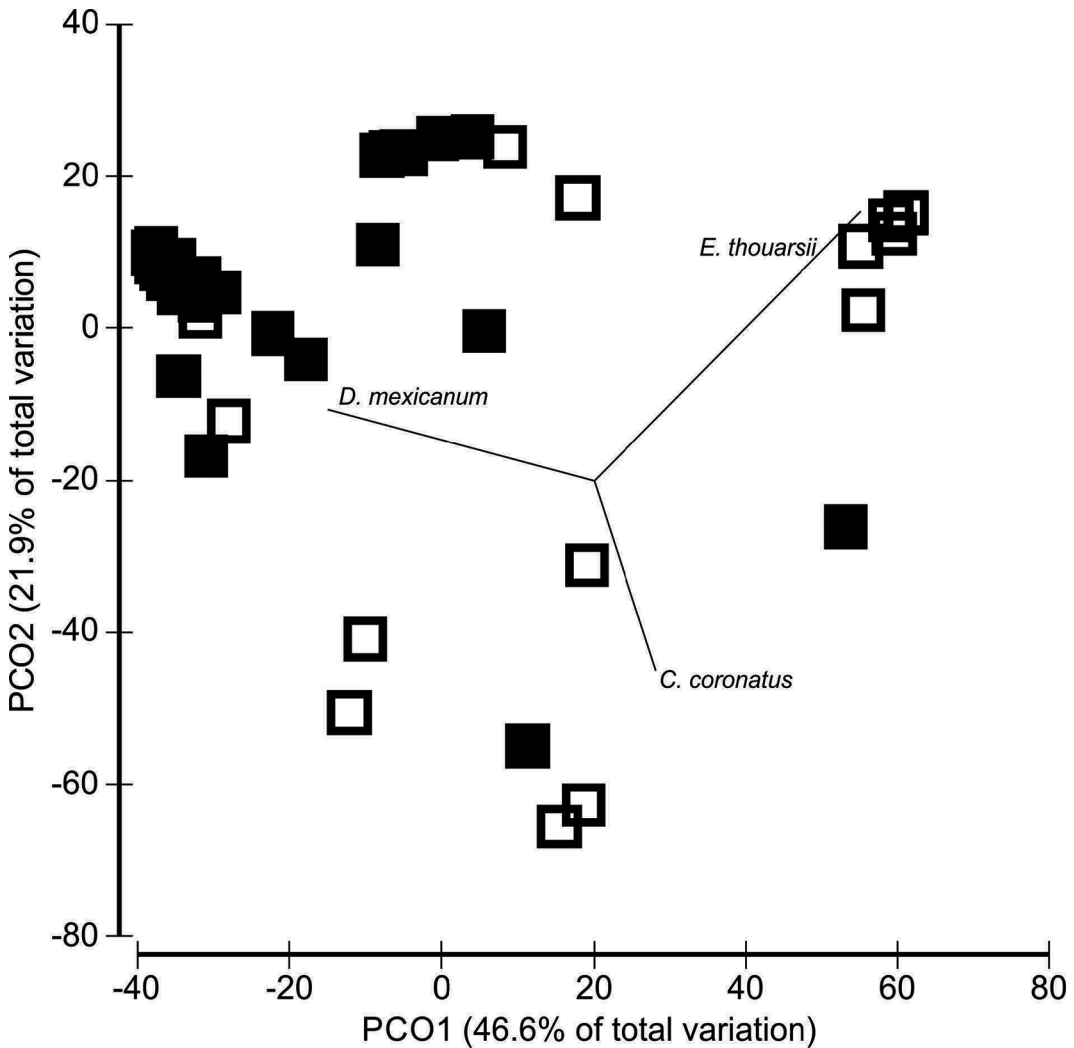


FIGURE 5. Principal coordinates analysis (PCO) ordination of reef-associated echinoderm assemblages before (closed squares) and during (open squares) the 2009–2010 El Niño in southern Mexico. Vector overlays among PCO axis and original variables; only Spearman correlation >0.5 are shown.

S. acapulcoensis (163%), *Chaetodon humeralis* (158%), *Stegastes rectifraenum* (127%), *Cephalopholis panamensis* (121%), and *Lutjanus argentiventris* (118%) relative to the prewarming condition. Meanwhile, the species *Dermatolepis dermatolepis*, *Harengula thrissina*, *Cantharhines dumerilii*, *Malacoctenus hubbsi*, *Zanclus cornutus*, *Scarus rubroviolaceus*, *Ophioblennius steindachneri*, *Caranx caballus*, and *Cirrhitichthys oxycephalus* practically disappear during

El Niño. In addition, there were declines in the species *Bodianus diplotaenia* (93%), *Chromis atrilobata* (81%), *Stegastes flavilatus* (78%), *Cirrhitus rivulatus* (68%), *Halichoeres dispilus* (45%), and *Halichoeres notospilus* (42%). Vector overlays (Spearman correlation >0.5) showed that the fish species *T. lucasanum*, *S. rubroviolaceus*, *C. dumerilii*, *H. maculicauda*, and *S. acapulcoensis* experienced the largest modifications during the warming event.

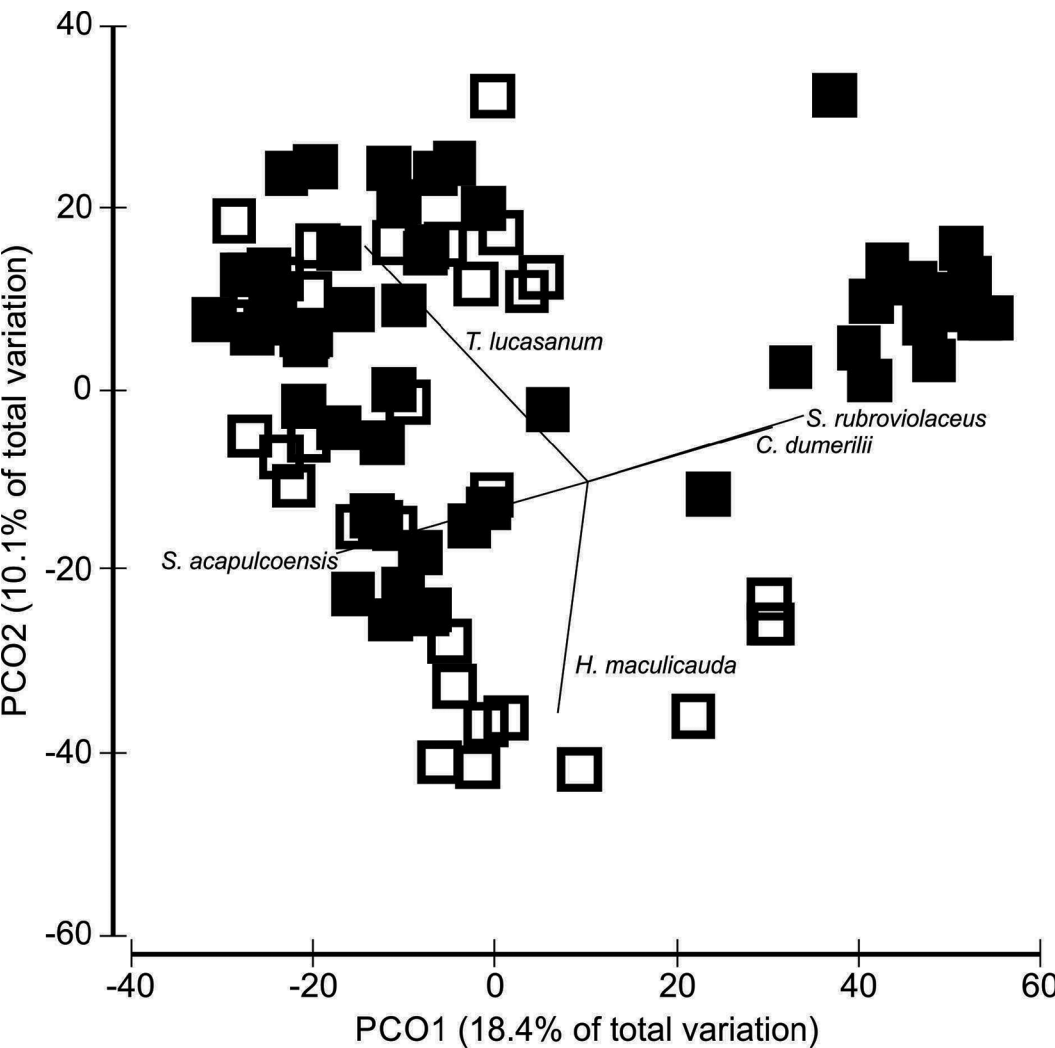


FIGURE 6. Principal coordinates analysis (PCO) ordination of reef-associated fish assemblages before (*closed squares*) and during (*open squares*) the 2009–2010 El Niño in southern Mexico. Vector overlays among PCO axis and original variables; only Spearman correlation > 0.5 are shown.

DISCUSSION

The 2009–2010 El Niño event influenced several biological and/or organizational levels in coral reef communities from the southern Mexican Pacific. SST increments affected coral physiology, but also stressed coral communities, while altering invertebrate (echinoderms) and vertebrate (fish) communities that live in or are associated with coral reef communities in southern Mexico.

The 2009–2010 El Niño was detected by temperature data loggers in southern Mexico as early as May 2009, when an increase of $\sim 0.2^{\circ}\text{C}$ with respect to the historical average was recorded. At that time, however, visual signs of stress (i.e., bleaching) were not observed in any of the patch reefs located in the surveyed area. By June 2009, temperature was $\sim 1.03^{\circ}\text{C}$ above historical records and by October 2009 it was $\sim 1.86^{\circ}\text{C}$ higher than the

average historical temperature. Bleaching was first observed by early/middle August 2009 (1.1°C above) in southern Mexico, but by early September 2009 (1.57°C above) it was widespread, though mild, in patch reefs of the area. The visual signs of bleaching detected during September 2009 were related to algal symbiont physiological alterations associated with an increase in the sea water temperature. The influence of temperature in the observed reduction of Chl *a*, *Symbiodinium*, and Chl *a* cell⁻¹ most likely involved irreversible photosystem damage caused by thermal stress (Hoegh-Guldberg and Smith 1989; Glynn 1993; Fitt and Warner 1995; Warner, Fitt, and Schmidt 1996). Heat stress has been recurrently invoked as the main cause of bleaching during El Niño events (Hoegh-Guldberg and Smith 1989, Glynn 1993) in the Caribbean, Indian Ocean, South Pacific, and Eastern Pacific (Jones et al. 2000, Glynn et al. 2001, Reyes-Bonilla et al. 2002, Riegl 2003, Eakin et al. 2010) and was also reported as being responsible for the coral bleaching during the 2009–2010 ENSO in the Central Pacific (Vargas-Ángel et al. 2011), Venezuela (del Mónaco et al. 2012), Indian Ocean (Guest et al. 2012, Marimuthu et al. 2013), and Brazil (Miranda, Cruz, and Leão 2013).

We observed an agreement among the decrease of the total lipids and the reduction of Chl *a*, *Symbiodinium*, and Chl *a* cell⁻¹ during the 2009–2010 warming event in the studied area, meanwhile tissue biomass values were inversely correlated with bleaching. Reductions in coral tissue biomass are commonly linked to increases in seawater temperatures (Fitt et al. 2000), because higher temperatures lead to increasing respiratory metabolism and decline of energy reserves in the coral tissue. While total lipid reduction during the 2009–2010 warming event is in agreement with the depletion of energy reserves in coral tissue, the increase (*P. damicornis*, *P. gigantea*) or stability (*P. panamensis*) in tissue biomass suggest that these species may have obtained energy from heterotrophic feeding (Grottoli, Rodríguez, and Palardy 2006; Palardy, Rodríguez, and Grottoli 2008), absorption of dissolved organic matter (Houlbrèque et al. 2004), a

combination of genotypic and physiological variation among coral colonies and/or their endosymbionts (i.e., overall performance of the holobiont) (Thornhill et al. 2011), or a combination of these. The relative importance of any of these sources of energy in the gain or maintenance of coral tissue biomass in the studied species during the 2009–2010 El Niño event in southern Mexico is unknown, but future research may investigate the role of heterotrophic carbon ingestion as a relevant source of energy for corals in the area.

Physiological responses of algae and coral hosts to the 2009–2010 El Niño in the studied area were species-specific. It has been proposed that species-specific responses may be related to a combination of genotypic and physiological variation among coral colonies (Edmunds 1994), their endosymbionts, or the overall performance of the holobiont (LaJeunesse et al. 2010). In the studied area, *Pocillopora* spp. colonies harbor the *Symbiodinium* D1 clade (LaJeunesse et al. 2010), whereas *Pavona* spp. and *P. panamensis* harbor clade C (Walther-Mendoza et al. 2016). The *Symbiodinium* D1 clade is thermally tolerant; indeed corals containing these symbionts were more abundant on reefs after episodes of bleaching and mortality in western Mexico (LaJeunesse et al. 2010) and Central America (Baker et al. 2004) or unaffected during bleaching elsewhere in the Eastern Pacific (Glynn et al. 2001). On the contrary, *Symbiodinium* C types are more susceptible to bleaching (Glynn et al. 2001, Baker et al. 2004). The presence of D and C *Symbiodinium* clades in *Pocillopora*, *Pavona*, and *Porites* in the southern Mexican Pacific (LaJeunesse et al. 2010, Walther-Mendoza et al. 2016) suggest that these combinations of holobionts may tolerate the seasonally stressful environmental conditions that pervade in the area (i.e., regional upwelling) and to some extent, extraordinary events such as El Niño. In the near future, studies monitoring the genetic identity of *Symbiodinium* before, during, and after environmental perturbation may help to evaluate the performance of the holobionts in the area and their ability to cope with future stressful environmental events.

Warming not only altered coral physiology in southern Mexican reefs, but also the reef community itself. By February 2010, bleaching resulted in mortality not only in the sampled localities (Riscalillo, Violín, Montosa Island), but it was also widespread from Mazunte to Montosa Island (A.L.P., pers. obs.), along a coastal stretch of ~55 km in Oaxaca, southern Mexican Pacific. Previous ENSO-related stressful events in the studied area were observed during 1998 in Mazunte and Tijera patch reefs, but they were probably associated with cold stress (Reyes-Bonilla et al. 2002); those authors estimate that as much as 90% of the live coral cover was lost in the area. Also, Glynn and Leyte-Morales (1997) showed that the size distribution of *P. gigantea*, and the presence of large dead or eroded coral framework areas at La Entrega, may be indicative of perturbations caused by the 1987 ENSO event. So far, there are no published reports addressing coral bleaching associated with the 2009–2010 ENSO event in the entire Eastern Pacific, but mortality associated with bleaching was reported in the Indian Ocean (5% to 94% bleaching, Guest et al. 2012; 2% to 10%, Marimuthu et al. 2013), Central Pacific (35% bleaching, Vargas-Ángel et al. 2011), Caribbean (12% bleaching, Bayraktarov et al. 2013), and Atlantic (Brazil, Miranda, Cruz, and Leão 2013; Venezuela, 34%, Bastidas et al. 2012, and 62% bleaching, del Mónaco et al. 2012). Compared with these reports, the studied area experienced bleaching levels similar to those observed in Indonesia (Guest et al. 2012), but larger than values recorded elsewhere. Similarly, bleaching was associated with heat stress but compared to bleaching reported during 2010 in other areas, reefs in the central southern Mexican Pacific preceded bleaching elsewhere by almost a year (Vargas-Ángel et al. 2011, Bastidas et al. 2012, Guest et al. 2012, del Mónaco et al. 2012, Marimuthu et al. 2013, Miranda, Cruz, and Leão 2013).

Ordination and PERMANOVA analysis demonstrated that echinoderm communities were significantly modified by the 2009–2010 El Niño event in the studied area. Variables associated with El Niño are able to cause several disturbances to coral reef-associated

organisms (Glynn 1990), most of them associated with changes in abundance of a few key grazing species of sea urchins (Glynn 1988; Haley and Solandt 2001; McClanahan, Muthiga, and Mangi 2001; Aronson et al. 2002; Attrill and Kelmo 2007). An increase of *Diadema* spp. has been commonly noted following warming events in the Eastern Pacific (Glynn 1988) and the Atlantic (Attrill and Kelmo 2007) as a consequence of high recruitment, low predation, and the increase of benthic algae in reef systems. Changes in the echinoderm community have also been related to local extinction of species as recorded in northern Bahia, Brazil (Attrill, Kelmo, and Jones 2004), colonization of the reef environment by opportunistic echinoids (Attrill, Kelmo, and Jones 2004), and vertical migration of individuals (Glynn 1988). We hypothesize that the observed decline in the abundance of the sea urchin *D. mexicanum* and the sea star *P. pyramidatus*, but the increase in the sea urchin *E. thouarsii*, resulted from the widespread mortality of the former in Oaxaca reefs during May 2009 (Benítez-Villalobos, Díaz-Martínez, and Martínez-García 2009), coupled with the vertical migration of *P. pyramidatus* and *E. thouarsii*. The latter authors observed a high number of loose spines and hundreds of bare tests of *D. mexicanum* scattered over La Entrega reef and as far as 80 km away and suggest disease as the cause. When *D. mexicanum* mortality occurred during May 2009, temperature was ~0.2°C above the historical record, with an accumulation of no more than 2–3 weeks of heat stress; it is uncertain whether *Diadema* mortality was due to a physiological temperature-related breakdown of the species. A microbial-mediated outbreak linked to warmer sea water temperature (Webster and Bourne 2012) may have played a role. On the other hand, sea stars and urchins move intermittently to search for food (Mueller et al. 2012) or to avoid physical stress (Broszeit et al. 2013). Vertical movement of *E. thouarsii* toward shallow waters was already suggested by Glynn (1988) to explain its density increase on Galapagos reefs following the 1982–1983 El Niño disturbance. *Pharia pyramidatus*, on the other hand, is abundant (2.43 individuals 50 m⁻²) in

shallow, relatively cold waters (mean 25°C) of the Gulf of California (Reyes-Bonilla, González-Azcárraga, and Rojas-Sierra 2005), but rather rare (0.1 individuals 50 m⁻², unpubl. data) in warmer (mean 28°C) tropical reefs from Oaxaca; therefore, it is likely that the species may have moved toward deeper, cooler waters to avoid physical stress.

Along with changes in composition and abundance in echinoderm communities, we observed modifications in reef-related fish assemblages associated with the 2009–2010 El Niño in southern Mexico. Many fish species experienced increases or decreases during the warming event (see Results section) similar to the observed changes in abundance and composition in response to physical stress (i.e., upwelling) observed in the studied area (López-Pérez et al. 2013) and elsewhere in Central America (Glynn et al. 2014). In particular, acute increases (Spearman correlation >0.5) were observed in the planktivorous *T. lucasanum*, the herbivorous *S. acapulcoensis*, and piscivorous *H. maculicauda*, whereas acute declines were recorded in the herbivorous *S. rubroviolaceus* and the omnivorous *C. dumerilii*. Contrary to the observed changes, longer-term impacts of bleaching such as degradation of reef framework and loss of structural integrity might be more dramatic to fish assemblages than the sudden increase of turf algae and loss of coral tissue during bleaching (Garpe et al. 2006, Graham et al. 2013, Glynn et al. 2014, and references therein). Nonetheless, we notice that the changes in corals, the coral community itself, and physical stress (~1.85°C above historic data) associated with the 2009–2010 warming event exerted a rapid response of fish assemblages. Rather than being associated with local extinction, mortality, or recruitment (Glynn et al. 2014), the observed changes in fish species composition and abundance may have been largely due to horizontal and/or vertical redistribution of species in the area. Similar processes were invoked to explain short-term fish response to bleaching in Tanzania reefs during the 1997–1998 ENSO (Garpe et al. 2006); in particular, roving herbivores should be able to benefit from sudden increases in turf algae following coral mortality (Hart, Klumpp, and Russ 1996).

The observed changes in coral physiology and modifications in coral, echinoderm, and fish communities highlight that the 2009–2010 El Niño event impacted several levels of biological organization in coral communities and reefs of southern Mexico beyond the actual corals themselves. Future studies may investigate whether the geographic setting of the coral reef track in southern Mexico may enhance heterotrophic carbon ingestion, resulting in higher survival (Thornhill et al. 2011) and potential recovery following bleaching and other stressors. Similarly, future studies monitoring the genetic identity of *Symbiodinium* before, during, and after environmental perturbation may help to evaluate the performance of the holobionts in the area and their ability to cope with future stressful environmental events.

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