

Ephemeral effects of El Niño southern oscillation events on an eastern tropical Pacific coral community

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Abstract. Coral-reef ecosystems of the central Mexican Pacific have been routinely affected by both moderate and severe El Niño Southern Oscillation (ENSO) events over the past 20 years. Such conditions are associated with abnormally high (1997–1998, 2002–2003, 2009–2010, and 2015–2016; ‘El Niño’) and low (1999–2000, 2008–2009, and 2010–2011; ‘La Niña’) seawater temperatures. Because few studies have documented how ENSO events affect both corals and key coral competitors such as macroalgae, we evaluated the short- and long-term changes in the cover of three reef coral genera, namely, *Pocillopora*, *Pavona* and *Porites*, as well as four coral competitors, namely, macroalgae, turf algae, coralline algae (CCA) and sponges, over a multi-year period that encapsulated two strong ENSO events: the 2010–2011 La Niña and the 2015–2016 El Niño. Such temperature anomalies caused a short-lived decrease in coral cover, alongside a concomitant increase in CCA. The communities eventually returned to their coral-dominated states within several months of the ENSO events, suggesting that these reef habitats can recover from such episodes of anomalous seawater temperatures.

Additional keywords: benthic ecology, coralline algae, coral reefs, ENSO, Mexican Pacific, thermal stress.

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Introduction

Coral-reef ecosystems harbour a high biodiversity (Sheppard *et al.* 2010), and the skeletons of the reef-building corals on which they are based contribute to a benthic complexity that, in part, drives such diversity by providing substrata and refugia (Steele 1999; Bruno and Bertness 2001; Idjadi and Edmunds 2006). Over the past few decades, these ecosystems have been affected by numerous stressors, including global climate change (GCC, namely the associated warming), diseases, and more direct anthropogenic pressures, such as seawater pollution (Brown 1997; Hughes and Connell 1999; Hughes *et al.* 2018). As a consequence, mass coral mortality has been recorded in many areas, and this has resulted in a reduction in coral cover

and coincident increases in the abundance of other benthic taxa (e.g. algae and sponges; Aronson and Precht 2001; Gardner *et al.* 2003; Hughes *et al.* 2003).

Hermatypic corals maintain an endosymbiotic relationship with dinoflagellates of the family *Symbiodinaceae* (Muscatine and Porter 1977) in which the corals (hosts) are nourished by photosynthetically fixed organic carbon translocated by the dinoflagellates; meanwhile, the metabolic wastes from the hosts are exploited by these microalgae (Davies 1984). This relationship may be compromised during ENSO events, because abnormal increases in temperature may result in *Symbiodinaceae* photoinhibition and, in the case of long exposure, expulsion known as coral bleaching (Podestá and Glynn 1997; Glynn and

Ault 2000; Glynn *et al.* 2017), with a consequent dead, if the coral does not recover, which can be observed as tissue necrosis (Gates *et al.* 1992), leaving the calcareous skeleton exposed and subject to colonisation or recruitment by coral competitors such as microscopic filamentous algae, macroalgae, crustose coralline algae and sponges (Glynn 1984; Hughes 1985). Many of these taxa are (1) important in the habitat structure of coral-reef ecosystems and (2) important competitors with corals for space and resources (Cortés *et al.* 1984; Robinson 1985; Tribollet and Golubic 2011).

Fleshy macroalgae are among the most potent competitors of coral, and, in extreme cases, they may influence coral physiology (e.g. growth and fecundity) and ability to recover from stress events (Hughes 1985; Smith *et al.* 2006; Rasher and Hay 2010). Turf algae are among the first organisms to recruit to recently available coralline substrata because this group can settle on rock, coral rubble, and even on live coral tissue (Robinson 1985; Smith *et al.* 2006), as can massive and encrusting sponges (Schönberg and Wilkinson 2001). Although coralline algae (CCA) can also colonise calcareous coral substrate and compete with corals for space and light, they are critical for reef integrity and are the preferred settlement substrate for myriad coral larvae (Harrington *et al.* 2004).

Historically, coral-reef ecosystems of the tropical eastern Pacific (TEP) have been affected by El Niño Southern Oscillation (ENSO) events, which have caused mass coral-bleaching episodes (Podestá and Glynn 1997; Glynn and Colley 2001). The central Mexican Pacific (CMP) has been one of the most affected regions; for instance, the 1997–1998 El Niño elicited a bleaching episode that culminated in the mortality of 96% of all corals. Carriquiry *et al.* (2001) found that branching species (*Pocillopora* sp.) were compromised more so than were massive and submassive corals, such as *Porites* spp. and *Pavona* spp., during this event. Subsequent ENSO events have since occurred, with no considerable negative effects being documented; this is remarkable, given that the 2010–2011 La Niña and 2015–2016 El Niño events were associated with temperatures at least 4°C lower and more than 3°C higher than the average respectively, for >3 weeks. These events led to mass coral bleaching and mortality on a global scale (Glynn *et al.* 2017; Hughes *et al.* 2018), and 99% of the corals at certain sites of the CMP bleached. However, 97% of these corals recovered in the interim 20 years; given that subsequent ENSO events occurred, it is likely that this is evidence for coral acclimatization (Rodríguez-Troncoso *et al.* 2014, 2016). These prior works were predominantly focussed on coral colony dynamics, although these framework-constructing invertebrates are not the only organisms affected by temperature anomalies, nor are they the sole drivers of ecosystem recovery.

Other benthic fauna that compete with corals for space and resources, such as filamentous and fleshy algae, can dramatically increase in abundance and temporally during coral bleaching and mortality events (Glynn *et al.* 2017); however, these peaks in macroalgal abundance tend to be ephemeral, because corals can ultimately recover (either via tissue regrowth from bleached colonies or larval recruitment from elsewhere; Nava and Carballo 2013; Corado-Nava *et al.* 2014). Despite such resilience being documented in these two studies, other works have hypothesised that repeated ENSO events

could eventually lead to coral → algae phase shifts (McManus and Polsenberg 2004; Roff *et al.* 2015), especially on marginal reefs that are more susceptible to losses in coral cover (Cruz *et al.* 2018). Because coral mortality provides calcareous substrata for the settlement of other benthic groups, we hypothesised that coral assemblages might shift to being dominated by coral competitors, namely algae and sponges, after CMP ENSO events; this shift could then affect the collective ability of the corals to recover from disturbance. To test this idea, we evaluated short- and long-term temporal changes in the live cover of pocilloporid, poritid and pavonid corals, as well as their algal and sponge competitors, in response to both La Niña and El Niño events that occurred over a 5-year period (2011–2015) in the CMP. It was hypothesised that the ensuing results would provide critical information on how these reefs respond to, and potentially recover from, environmental disturbance.

Materials and methods

Study area

Surveys were performed twice monthly (see details below) between 2011 and 2015 at Islas Marietas National Park (IMNP; 20°40'35"N–20°41'45"N, 105°33'30"W–105°38'10"W), which consists of two small islands (Isla Larga and Isla Redonda) of volcanic origin (CONANP 2007) and is ~8 km off the coast (Fig. 1). This natural protected area harbours one of the most important coral-reef ecosystems of the TEP (Glynn *et al.* 2017), and has, as has the entirety of the region, been severely affected by ENSO events that have caused both abnormal decreases and increases in sea-surface temperature (SST; Pantoja *et al.* 2012), which then led to coral bleaching and consequent mortalities (Carriquiry *et al.* 2001; Reyes-Bonilla *et al.* 2002).

The coral cover of the patch reefs of the two islands averages ~17%, and ~20 species of hermatypic corals can be found across the *Pocillopora*, *Porites* and *Pavona* genera (Reyes-Bonilla *et al.* 2010; Cupul-Magaña and Rodríguez-Troncoso 2017). The coral distribution differs across islands; however, in general, branching *Pocillopora* sp. corals are most abundant at 1–8 m, whereas massive and submassive species such as *Pavona* sp. and *Porites* sp. are mostly distributed from 5 to 12 m (Cupul-Magaña and Rodríguez-Troncoso 2017); this distribution pattern is common of reefs of the TEP. The area is influenced by the following three primary oceanographic currents: (1) the cold, low-salinity California Current, (2) the warm, low-nutrient Costa Rica Current, and (3) warm, high-salinity water from the Gulf of California (Wyrtki 1965). Consequently, temperature and salinity fluctuate greatly over time (Álvarez-Arellano and Gaitán-Morán 1994) in this oceanographic transition zone, which experiences two seasons, namely, the cold dry season from November to April (hereafter 'cold') and the warm rainy season (hereafter 'warm') from May to September (Palacios-Hernández *et al.* 2010). During certain points in the year, upwelling occurs (De La Lanza-Espino and Cáceres Martínez 1994), and runoff can influence the reefs during the rainy season (Rouzé *et al.* 2015). Finally, IMNP is popular with tourists, although their number is controlled to reduce potential environmental impacts (Cupul-Magaña and Rodríguez-Troncoso 2017).

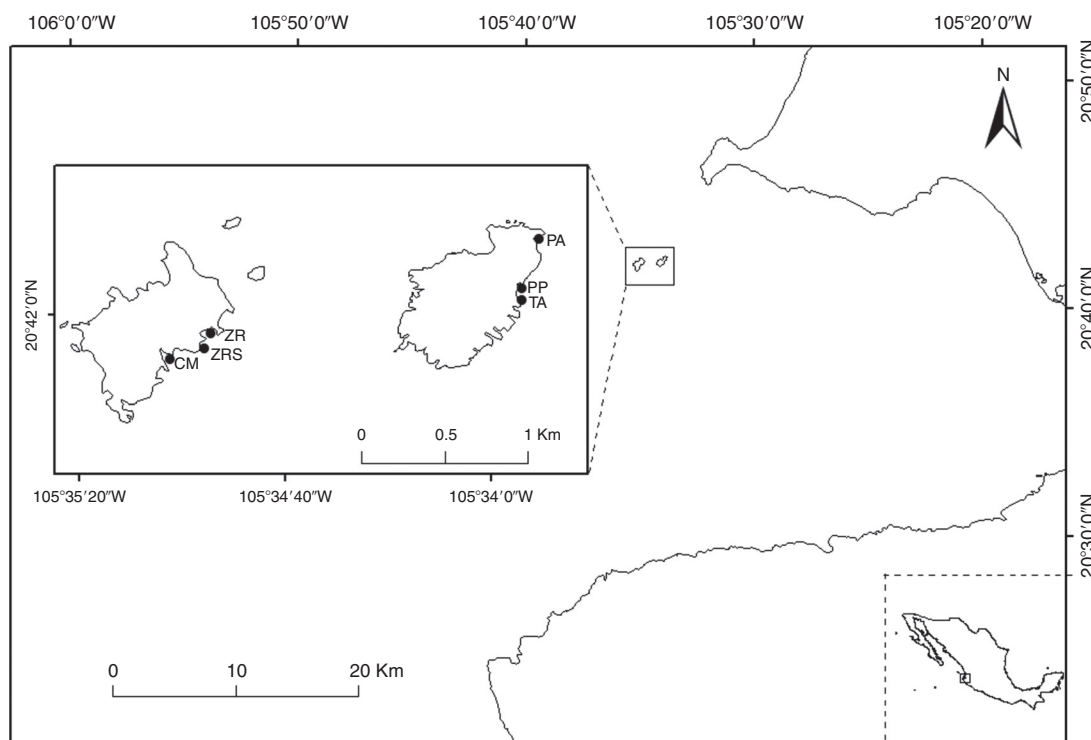


Fig. 1. Study area at Islas Marietas National Park (Nayarit, Mexico). The sampling sites at Isla Larga were Cueva del Muerto (CM), Zona de Restauracion (ZR) and Zona de Restauracion Sur (ZRS), whereas those of Isla Redonda were Plataforma Pavonas (PP), Playa del Amor (PA) and Tunel-Amarradero (TA).

Data collection

Benthic surveys were performed from February 2011 to November 2015 at six sites (three per island; Fig. 1); there was a bias towards those sites with (1) the highest coral cover and (2) all three major coral genera present. Every 2 months from 2011 to 2015, six square frames (1 m^2) at each site were evenly distributed across each of five 25-m permanent transects ($n = 30$ transects per site) placed parallel to the island at a depth of 3–12 m following the benthonic structure of each site. Within each frame, cover of coral and non-coral benthic key taxa were visually identified *in situ* and classified into one of the following groups: (1) coral (subdivided into healthy, pale, bleached or dead), (2) coralline algae on dead coral (CAC), (3) sponges on dead coral (SC), (4) turf algae on dead coral (TC), (5) macroalgae on dead coral (MC), (6) turf algae on non-coral substrate (TA), or (7) coralline algae on non-coral substrate (CA). Details on how distinctions were made can be found in Table 1. Sea surface-temperature data were obtained from (1) the NOAA satellite service hosted on the International Research Institute for Climate and Society website (<http://iri.columbia.edu/>) and (2) HOBO Pendant® loggers (15-min logging interval; changed every 2 months) placed at the average survey depth (7 m). A bi-monthly temperature mean (\pm standard error) was calculated and used in the analyses described below. We also collected oceanic Nino-index (ONI) data from NOAA to determine the periods at which thermal anomalies were occurring. Briefly, we defined thermal anomalies as periods in which the average temperature deviated significantly from the mean for that time

Table 1. Coral-health classifications ($n = 4$) and non-coral benthic groups ($n = 4$) considered in the analyses in the present paper

Classification	Characteristics
Healthy	Heavily pigmented tissues
Pale	Lightly pigmented tissues
Bleached	Live tissue evident, albeit without any pigmentation (owing to the absence of endosymbionts or endosymbiont pigments)
Dead	Coral skeletons lacking live tissue
Coralline algae on dead coral (CAC) (CAC) (CAC)	Coralline algae on dead coral (calcareous substrate)
Sponge on dead coral	Sponge on dead coral (calcareous substrate)
Turf algae on dead coral	Turf algae on dead coral (calcareous substrate)
Macroalgae on calcareous substrata (MC)	Macroalgae on dead coral (calcareous substrate)

period in prior years in both La Niña and El Niño events, according with NOAA database obtained.

Data analysis

So as to determine the effect of time on coral-community parameters, data were pooled across sites. There was a particular focus on assessing short-term (cold vs warm seasons) and long-term (inter-annual variation, with an emphasis on the

effects of ENSO events) changes. The variation in cover of the coral (divided into the four aforementioned health categories) and coral competitors (Table 1) were evaluated for each of the three genera (*Pocillopora*, *Porites* and *Pavona*). The community composition and cover changes were analysed using a two-way (time \times season), fixed-factor, Type I multivariate permutational analysis of variance (PERMANOVA). Prior to PERMANOVA, similarity percentage (SIMPER) analysis and non-metric multidimensional scaling (nMDS) were performed and Bray–Curtis similarity matrices were created from square root-transformed data with PRIMER® v6.1.11, with the PERMANOVA plug-in (Clarke and Gorley 2006; Anderson *et al.* 2008). The statistical significance was tested with 10 000 permutations and the sum of squares Type III model. Two-way SIMPER analysis was performed to compare the cover of (1) corals of the four health classifications and (2) the coral competitors for each coral genus. This was undertaken to estimate the contribution of each biological parameter to the average dissimilarity over time. The similarity among coral-health classifications and coral competitors growing on colonies of each coral genus was observed over survey year and season.

A canonical redundancy analysis (RDA) was performed to assess the relationship among cover of all coral-health classification groups (as live coral cover, LCC) and non-coral benthic functional groups (TA and CA only) and environmental variables (SST and ENSO events, thermal anomalies), over time. The data were square root-transformed to reduce the influence of overly dominant groups. Multi-collinearity was evaluated among variables before RDA, and environmental variables with (1) Pearson correlation coefficients (r) of >0.90 and (2) variance inflation factors (VIF) of >10 were omitted. Statistical significance was calculated using Monte Carlo tests (9999 permutations) with CANOCO® v 4.5 (ter Braak and Smilauer 2002).

Results

Pocilloporids were most dominant at the two study sites ($\sim 4\text{--}5\%$; Fig. 2c), followed by *Pavona* (3–5%; Fig. 2e) and *Porites* (1–2%; Fig. 2a). Each genus was colonised differently by competitors, and *Pocillopora* skeletons were more likely to be overgrown by turf algae and CCA (Fig. 2d). Colonies of all three genera paled at higher temperatures (Fig. 2a, c, e), an observation that is discussed in more detail below when presenting the RDA. PERMANOVA showed significant temporal differences in (1) the relative proportion of different coral-health classifications and (2) the assemblage of non-coral benthic functional groups settling on coralline substrata for both *Porites* and *Pocillopora* (Table 2). The main differences in the cover of *Porites* and *Pocillopora* (see Supplementary material table S1, available at the journal's website) were observed across seasons (cold vs warm) in 2011, 2014 and 2015 (Fig. 3a, b). In contrast, *Pavona* health did not vary significantly over time (Tables 2, table S1), despite some temporal differences evident in Fig. 3c. SIMPER analysis showed that the variation in coral pigmentation, as well as the abundance of CAC, contributed 90% to the average dissimilarity at the genus level (table S2). There was a slight decrease in the cover of healthy poritids in the 2014 warm season, corresponding to the beginning of an ENSO event (Fig. 2a). Coralline algae tended to overgrow poritids in the cold seasons (Fig. 2b, table S3).

During the winter of 2011, as well as the warm seasons of 2014 and 2015, there was a higher cover of pale and bleached pocilloporids, and, consequently, a lower cover of healthy colonies (Fig. 2c, d). Coralline algae and sponges were more prone to overgrow available skeletons of pocilloporid corals in the warm seasons of 2011 and 2015, and the highest level of macroalgal settlement on dead pocilloporid skeletons occurred during the cold season of 2011 (Fig. 2d).

SIMPER analysis indicated that the variables that cumulatively contributed 90% of the dissimilarity in the *Pavona* dataset were healthy corals, pale corals, bleached corals, and CAC cover (table S4), and the cover of healthy colonies varied substantially over the study period (Fig. 2e). That being said, in 2014 there was an increase in the cover of pale and bleached corals, and the CAC cover was higher in 2013 (Fig. 2f). The RDA documented marginally significant temporal variation ($R^2_{\text{adjusted}} = 0.421$, $P = 0.0152$) in coral pigmentation and cover of benthic groups settled on coral substrata for each target coral genus. Of note, increases in temperature (warm seasons of 2014 and 2015, in particular) were associated with the highest values of pale and bleached corals for all coral genera analysed (Fig. 2). Also, during the 2011 cold season, there was an increase in MC on pocilloporid corals, coinciding with the highest values of cover of dead corals for this genus; there was also an increase in turf algae throughout the reef systems at this time. The presence of SC on pavonid and pocilloporid corals was negatively correlated with temperature, whereas the covers of CAC and TC (*Pavona* only) were positively associated with it (Fig. 4).

Discussion

The 1997 El Niño event caused both a massive bleaching and mortality of 96% of the coral colonies along the CMP, affecting all genera, although with a greater effect on *Pocillopora* sp. coverage (Carriquiry *et al.* 2001), and resulted in a shift from the once-common genus *Pocillopora* to the presumably more resilient genus *Pavona* (Cupul-Magaña 2008). We also documented increases in cover of dead, bleached and pale corals as a result of the 2011, 2014 and 2015 ENSO events. The availability of tissue-free coral skeleton provided an opportunity for settlement or recruitment by a variety of benthic taxa. However, these changes were not permanent, and the communities were once again coral-dominated by the end of the study period (2015). Our observations are in line with those in previous studies, which found that macroalgae, CCA and filamentous algae are the first benthic groups to colonise newly barren coralline substrata (Cortés *et al.* 1984; Glynn 1993; Tribollet and Golubic 2011); however, in many cases, they are later outcompeted by corals. In contrast, some other sessile organisms, such as boring sponges, can permanently colonise partially dead corals (Bell *et al.* 2013; Glynn *et al.* 2017), resulting in long-term decreases in coral cover. Such phase shifts not only affect the corals themselves, but also other reef inhabitants (e.g. sea urchins; Sotelo-Casas *et al.* 2018).

The presence of macroalgae can affect the growth, fertility, settlement and recovery of corals after a bleaching event (Hughes 1985; Smith *et al.* 2006; Rasher and Hay 2010) and can be permanent (Wilkinson 2000; McClanahan *et al.* 2002; Gardner *et al.* 2003; Hughes *et al.* 2003; Pandolfi *et al.* 2003; Bellwood *et al.* 2004). However, macroalgae did not always

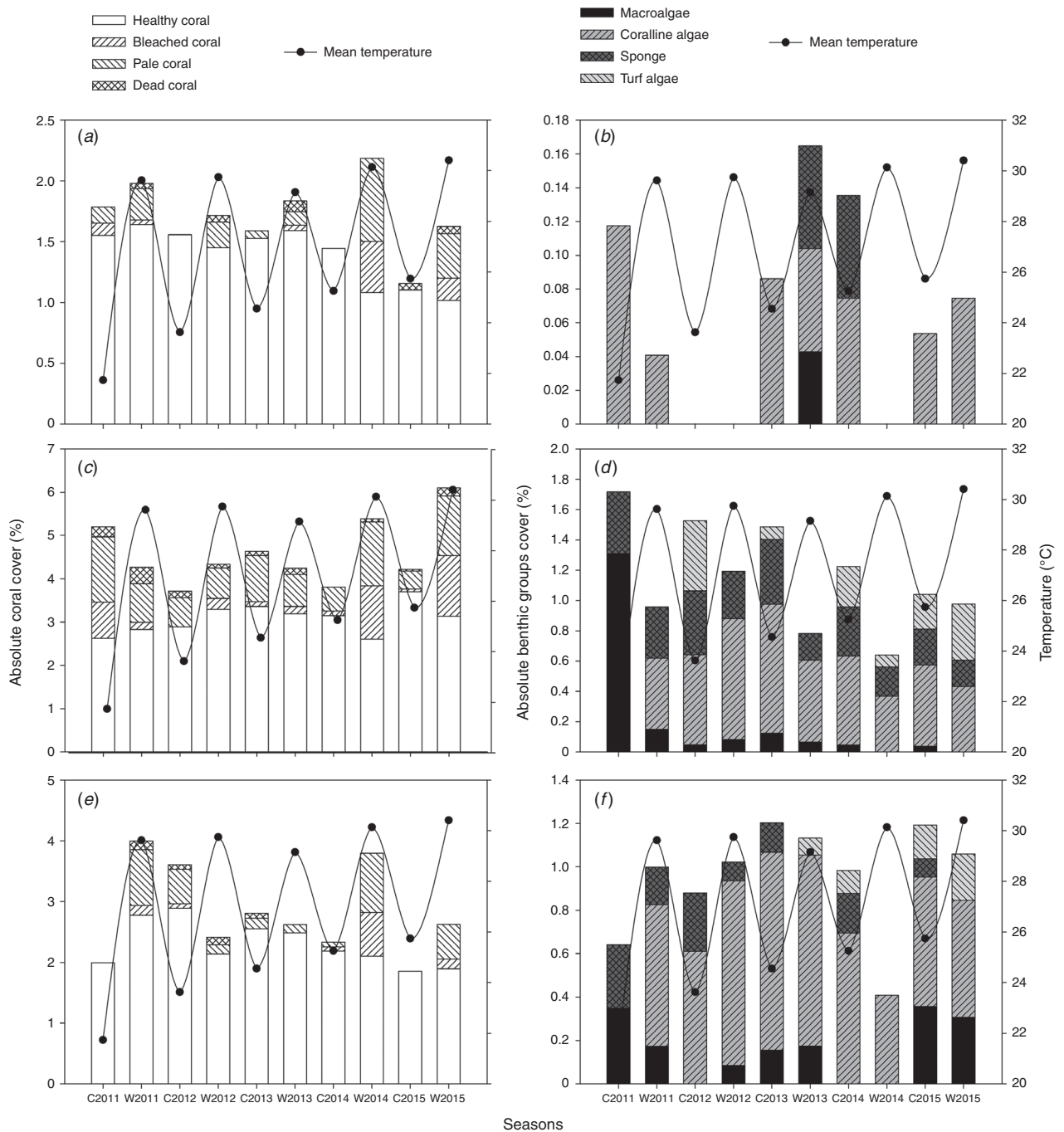


Fig. 2. Graph showing (a, c, e) a relative cover of coral tissue of varying health or (b, d, f) non-coral benthic taxa (macroalgae, coralline algae, sponges, and turf algae) over-growing coral skeletons in the cold (C) and warm (W) seasons of 2011 through 2015 for (a, b) *Porites*, (c, d) *Pocillopora* and (e, f) *Pavona*. Temperature records (lines and right y-axis) depict mean seasonal values.

increase in abundance after coral colonies were compromised by high temperatures herein, even when calcareous substrate was readily available. During the low-temperature La Niña event of 2011, in contrast, their presence on the skeletons of *Pocillopora* spp. increased, albeit only ephemerally. Coralline algae were more likely to fluctuate seasonally on coral skeletons at IMNP, and their abundance tended to peak after high-temperature

events (2014 and 2015), especially on *Porites* spp. skeletons. Given their capacity for bioconstruction through deposition of aragonite and calcite (Hernández-Zulueta *et al.* 2017), such competition with corals in the CMP is not necessarily of net detriment to the overall health of the reef. Sponges preferred the skeletons of *Pocillopora* spp. and *Pavona* spp. when temperatures dropped as a result of the 2011 La Niña event. Although it

Table 2. PERMANOVA results for the effects of time (season or year) on coral-colony appearance (relative frequency of the following eight categories (Table 1): healthy coral, pale coral, bleached coral, dead coral (bare skeleton), macroalgae, turf algae, coralline algae or sponges) for the following three coral genera: *Porites*, *Pocillopora* and *Pavona*
 Statistically significant ($P < 0.001$) differences are indicated in bold

Coral genus	Source of variation	Pseudo- <i>F</i>	<i>P</i>
<i>Porites</i>	Year	11.5	<0.001
	Season	24.1	<0.001
	Year × season	7.60	<0.001
<i>Pocillopora</i>	Year	4.76	<0.001
	Season	2.87	0.032
	Year × season	5.85	<0.001
<i>Pavona</i>	Year	2.28	0.021
	Season	1.54	0.197
	Year × season	1.39	0.187

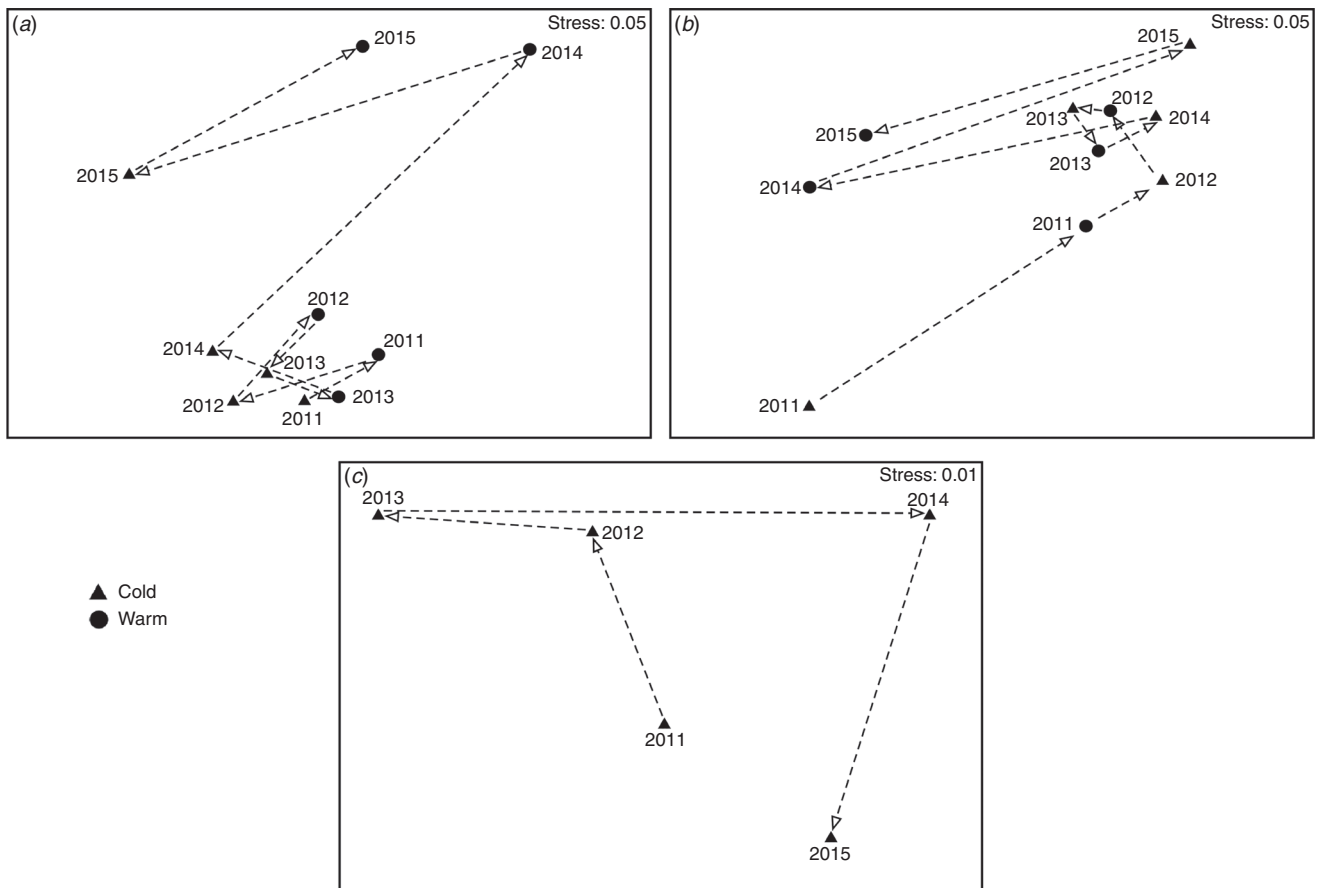


Fig. 3. Non-metric multidimensional scaling (nMDS) ordinations of cover data for corals and competitors that settled on dead coral substrata (macroalgae, turf algae, coralline algae and sponges) for the genus (a) *Porites*, (b) *Pocillopora* and (c) *Pavona* over seasons and (a, b) years and (c) years only.

is tempting to attribute the differential cover of macroalgae, CCA and sponges to thermal stress-induced decreases in coral health, and, therefore, increases in availability of dead coral skeleton on which to grow, such ENSO-driven temperature changes may also affect these coral competitors (Lindquist 1986); whether the coral-health changes or the temperature

effects on these coral competitors are more important in driving the abundance of the sessile benthonic groups remains to be determined.

Different coral species have different responses to environmental changes (McClanahan *et al.* 2009; Rodríguez-Troncoso *et al.* 2014; Baker *et al.* 2017), and such was documented herein.

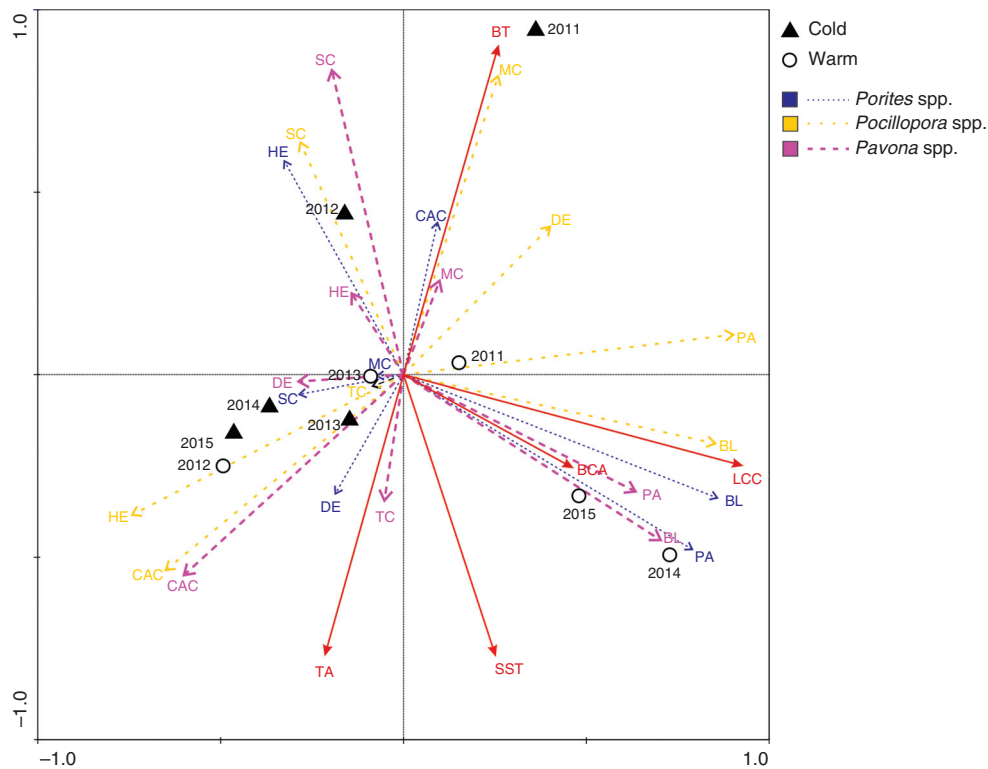


Fig. 4. Redundancy analysis (RDA) of the seasonal and annual variation in the cover of corals (*Porites* spp., *Pocillopora* spp. and *Pavona* spp.) and the following coral competitors: macroalgae on coral (MC), turf algae on coral (TC), coralline algae on coral (CAC) and sponges on coral (SC). Coral-health abbreviations: HE, healthy; PA, pale; BL, bleached; and DE, dead. The following predictive variables are represented by solid red arrows: ENSO events = thermal anomalies, sea-surface temperature (SST), live coral cover (LCC), benthic coralline algal (BCA) cover, and benthic turf algal (BT) cover.

Historically, *Pocillopora* spp. have been considered the least resistant to thermal stress of the eastern Pacific coral genera (Baker *et al.* 2017; Glynn *et al.* 2017); however, at the same time, they have a greater capacity for recovery than do *Pavona* spp. and *Porites* spp. (Carriquiry *et al.* 2001). Although Cortés *et al.* (1984) found thermal stress-challenged pocilloporids to be more likely to be overgrown by algae, we documented this only after anomalously low temperatures (i.e. after the 2011 La Niña event). Otherwise, CCA, sponges and turf algae were more likely to overgrow corals. It is worth noting that a greater diversity of taxa settled on these branching coral skeletons than on the massive and submassive poritids and pavonids, on which CCA were more likely to settle. This may be due to the higher structural complexity of branching corals (Crowder and Cooper 1982). Given the differences in (1) morphology and (2) environmental sensitivity of the three target coral genera, it is unsurprisingly, then, that the assemblage of coral competitors differed temporally in a distinct manner for each coral genus; these findings are discussed in more detail below.

Massive corals, such as *Porites* spp., are considered to be more resistant to thermal stress (Loya *et al.* 2001; McClanahan 2004), and the El Niño event of 1997–1998 resulted in the mortality of only 30% of the poritids (Carriquiry *et al.* 2001; Reyes-Bonilla *et al.* 2002). At our six study sites at IMNP, *Porites* spp. were the least affected by the positive thermal

anomalies that occurred in 2014 and 2015, and, as mentioned above, only the cover of CCA on colonies of this genus changed significantly over time. This contrasts with observations made by Glynn (1984) and Robinson (1985) who found turf algae to be the first colonisers of barren poritid skeletons. This lack of turf on poritids observed herein could be attributed to (1) the massive, exposed nature of the colonies, which permitted frequent herbivory (data not shown), or (2) strong wave energy (not quantified).

Pavonids also proved to be resilient to negative and positive thermal anomalies associated with La Niña and El Niño events respectively, and few bleached or dead pavonids were observed. This is in agreement with McClanahan (2004), who found massive and submassive species (such as all pavonids of the CMP) to possess a high capacity for thermal acclimatization. That being said, some pavonid colonies paled after the 2014–2015 high-temperature El Niño event, but tissues did not disintegrate; those tissues that did die, were settled on by CCA after the 2014 El Niño, although this coral → CCA shift was ephemeral.

Changes in the coral cover, and the ecological implications resulting from such changes, depend on the intensity and duration of the stress event (Cortés *et al.* 1984), as well as the degree of organismal acclimatization (Connell 1997; Hughes and Connell 1999). In the present study, the increase in CCA at

the expense of corals appeared to be related to anomalous temperatures (2011, 2014 and 2015 ENSOs); however, this shift was ephemeral, because coral tissues later out-competed the CCA. This could be attributed not only to the biology of the corals, but also the fact that CCA is a food source for fish and echinoderms (Díaz-Pulido *et al.* 2009). Regardless, our results showed that this insular coral-reef community is resistant to thermal stress, especially when compared with other reef communities in the region (e.g. the Islas Mariás Biosphere Reserve; López-Pérez *et al.* 2016). This is noteworthy because the IMNP, in addition to being frequently affected by anomalous temperatures, is a popular tourist destination and, therefore, appears to be resilient to both thermal-stress events and intense, local anthropogenic pressures.

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Conflicts of interest

The authors declare that they have no conflicts of interest.

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