

Switch between Morphospecies of *Pocillopora* Corals

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ABSTRACT: *Pocillopora* corals are the main reef builders in the eastern tropical Pacific. The validity of *Pocillopora* morphospecies remains under debate because of disagreements between morphological and genetic data. To evaluate the temporal stability of morphospecies in situ, we monitored the shapes of individual colonies in three communities in the southern Gulf of California for 44 months. Twenty-three percent of tagged colonies of *Pocillopora damicornis* changed to *Pocillopora inflata* morphology during this time. This switch in identity coincided with a shift to a higher frequency of storms and lower water turbidity (i.e., lower chlorophyll *a* levels). Seven months after the switch, *P. inflata* colonies were recovering their original *P. damicornis* morphology. All colonies of both morphospecies shared a common mitochondrial identity, but most *P. damicornis* colonies undergoing change were at a site with low-flow conditions. This is the first in situ study to document switching between described morphospecies, and it elucidates the influence of temporal shifts in environmental conditions on morphologically plastic responses.

Keywords: morphological plasticity, *Pocillopora* type 1, eastern tropical Pacific, *Pocillopora damicornis*, *Pocillopora inflata*, morphospecies.

Introduction

Scleractinian corals are traditionally described according to differences in their skeletal morphology (i.e., as morphospecies; Best et al. 1984; Veron 2013). However, corals can modify their morphology to cope with variation among habitats and environmental shifts over time (Prada et al. 2008; Pfennig et al. 2010). This morphological plasticity can be extensive, often generating skeletal features that overlap between species (Veron 2000; Todd 2008), which has led to considerable confusion in the taxonomy and systematics of scleractinian corals (Fukami et al. 2008).

Pocillopora corals are the main reef builders in the eastern tropical Pacific, despite growing under environmental conditions that are generally unfavorable for reef development and that can become worse still during broad interannual changes (Kleypas et al. 1999; Glynn and Ault 2000; Halfar et al. 2005; Manzello et al. 2008). Associated with these fluctuating conditions, *Pocillopora* corals exhibit high variation in their skeletal morphology (Glynn and Ault 2000; Ketchum and Reyes-Bonilla 2001; Rodriguez-Ramirez and Zapata 2011). This variation has led to confusion and debate over the taxonomic validity of *Pocillopora* species defined by morphology in the region (Glynn and Ault 2000; Ketchum and Reyes-Bonilla 2001; Veron 2002).

Much of the confusion in *Pocillopora* taxonomy is due to species descriptions that rely on colony and branch traits known to be highly plastic in the environmentally variable eastern tropical Pacific. For example, Pinzón and LaJeunesse (2011) found that five morphologically defined *Pocillopora* species were not congruent with differentiation among three mitochondrial lineages. Colonies bearing just one of these haplotypes (*Pocillopora* type 1) show several morphologies throughout their range (Pinzón et al. 2013; Marti-Puig et al. 2014). The high morphological variation seen within a single mitochondrial lineage thus seems especially pronounced in the eastern tropical Pacific (Pinzón and LaJeunesse 2011; Paz-García et al. 2015).

Five *Pocillopora* morphospecies (*P. capitata*, *P. damicornis*, *P. eydouxi*, *P. meandrina*, and *P. verrucosa*) have been reported from the Gulf of California (Glynn and Ault 2000; Reyes-Bonilla et al. 2005). *Pocillopora inflata*, in particular, is an uncommon morphospecies found mainly in Central America (Costa Rica, Panama, and the Galapagos Islands) and along the southwest coast of Mexico (La Entrega, Oaxaca), although occasionally reported from the Gulf of California (Glynn 1999; Glynn and Ault 2000).

All *Pocillopora* morphospecies in the Gulf of California possess mitochondrial haplotypes from a single lineage,

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Pocillopora type 1 (sensu Pinzón and Lajeunesse 2011). This observation, along with patterns of morphological variation between morphospecies seen under different flow regimes (Paz-García et al. 2015), suggests that these recognizable morphospecies result from morphological plasticity. If so, then shifts in environmental conditions may trigger morphological changes between morphospecies. Although corals are known to change their morphology following transplantation to a new environment (Hoogenboom et al. 2008; Prada et al. 2008; Todd 2008), such morphological changes have not been documented under natural conditions. In this study, we followed a morphological plasticity event that occurred from *P. damicornis* to *P. inflata* morphospecies in the south of the Gulf of California after a period of regime shift of environmental conditions in storm frequency and lower water turbidity (i.e., lower chlorophyll *a* levels). To characterize the changing colonies genetically, we determined the mitochondrial lineage identity of individuals that did and did not undergo the morphological switch.

Methods

Locations and Gross Morphology Condition

We followed gross morphological changes in *Pocillopora* colonies for 44 months (from March 2011 to November 2014) at three locations in the southern Gulf of California (fig. 1). Three hundred colonies were tagged along permanent linear transects of 50 m in March 2011 at depths of 2–5 m. Each colony was identified to the species level according to taxonomic descriptions based on skeleton morphology (Glynn 1999; Veron 2000; Ketchum and Reyes-Bonilla 2001), and identification of *Pocillopora inflata* morphospecies from underwater pictures was confirmed by the taxonomist who originally described it (Glynn 1999). Colonies were monitored every 3–6 months and were initially re-tagged annually; they were re-tagged more frequently as the study progressed. Despite these efforts, approximately 16% of the tags were lost each year (50% total by the end of the study). All remaining colonies were monitored and included in this study (150 colonies: *Pocillopora damicornis*, $n = 63$; *Pocillopora meandrina*, $n = 41$; *Pocillopora verrucosa*, $n = 46$). The morphology of tagged colonies was monitored using underwater pictures (Canon D10 and Canon Power Shot A630 with housing).

A subset of changed (*P. inflata*, $n = 14$) and unchanged (*P. damicornis*, $n = 6$; *P. verrucosa* $n = 5$; *P. meandrina*, $n = 5$) colonies were selected randomly to verify the host lineage identity using two mitochondrial regions (an open reading frame [ORF] of as-yet-unknown function and the putative control region [CR] following protocols described in Paz-García et al. 2015). Sequences generated in this study were deposited in GenBank, and accession numbers are KF985973 and KF985980.

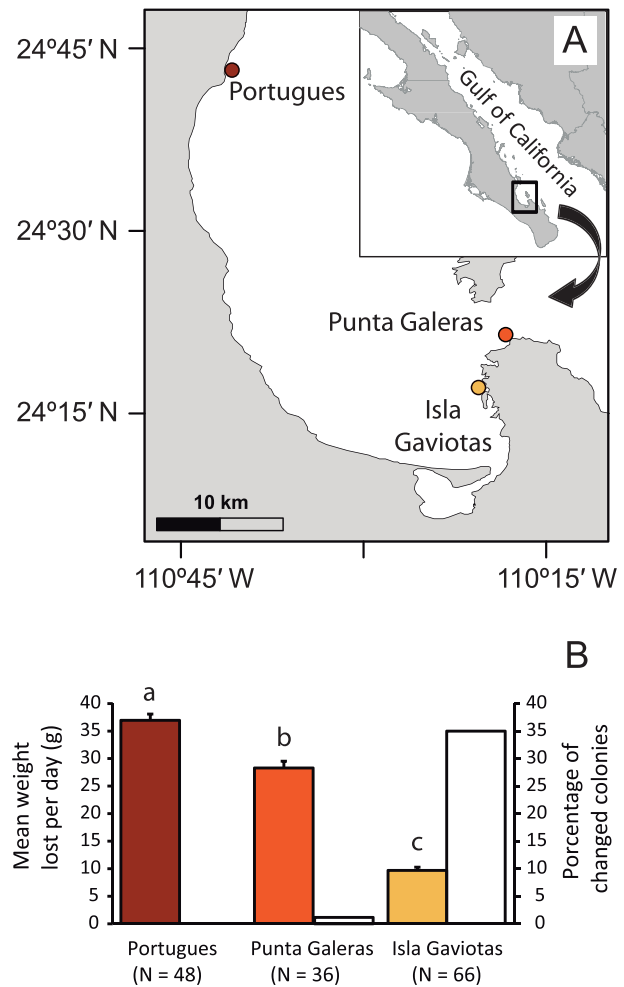


Figure 1: A, Location of studied coral communities in the southern Gulf of California. B, Flow conditions (as determined by mean rate of dissolution of gypsum; solid bars) and percentage of colonies changed to *Pocillopora inflata* morphospecies (open bars) at the surveyed sites. Error bars indicate SE. All sites were significantly different ($P < .005$, by post hoc Tukey tests). The number of tagged colonies at each location is given in parentheses.

Water Flow, Frequency of Storms, and Satellite Data

In an earlier study (Paz-García et al. 2015), we showed that the Punta Galeras and Isla Gaviotas locations had different water flow conditions, regardless of the method of flow estimation (rate of dissolution of gypsum vs. dye release) or season (winter vs. summer). Thus, differences in water flow among the three locations were assessed using the rate of dissolution of gypsum (Muus 1968) as in Paz-García et al. (2015). Nine molds were deployed at each location and retrieved after 5 days during winter (February 2013). After log transformation, the total weight loss over the 5 days was used to calculate the mean weight loss per day among sites and compared using ANOVA. Post

hoc Tukey tests were used to evaluate significant pairwise differences after ANOVA.

To test for an association between environmental conditions and the phenotypic change of coral colonies, we retrieved environmental data for the period from January 2010 through December 2014 from different websites. The frequency of storms was addressed from data on the occurrence and strength of storms. Data were obtained from the National Oceanic and Atmospheric Administration Historical Hurricane Tracks website (<http://csc.noaa.gov/hurricanes>) and from the National Hurricane Center's Tropical Cyclone Reports (<http://www.nhc.noaa.gov/2010epac.shtml>). Using this data set, a storm was counted if it entered a buffer zone of 200 km around the reef location (Chávez-Romo et al. 2013). Values for monthly sea surface temperatures (SSTs), photosynthetically active radiation (PAR), and chlorophyll *a* were acquired from the Giovanni online data system developed by the Goddard Earth Sciences Data and Information Services Center (<http://disc.sci.gsfc.nasa.gov/giovanni>; Acker and Leptoukh 2007). Monthly measurements were averaged over approximately 4 km² from the waters adjacent to Isla Gaviotas (24.271°N, 110.354°W). To test whether storm frequency was associated with similar morphological changes in coral colonies used for the original description of *P. inflata* (Glynn 1999), storm data were retrieved for between January 1994 and December 1998 for the type locality (La Entrega, Oaxaca, hereafter referred to as the southwest coast of Mexico) and compared with our data from the Gulf of California.

Detection of Regime Shifts

We used a sequential regime shift detection approach (Rodionov 2004) to determine whether a regime shift in environmental conditions was associated with morphological changes in coral colonies. A regime shift is defined as rapid change in environmental conditions from one relatively stable state to another (Rodionov and Overland 2005). Thus, a regime shift is detected if there is a significant change in the mean of an environmental variable between regimes. Equally weighted arithmetic means of the regimes were calculated using Sequential Regime Shift Detector software, version 3.4 (<http://www.climatologic.com>). This approach was set to 12 and 24 months in length of proposed regimen to detect interannual shifts, and all environmental values that were higher than three standard deviations were treated as outliers (i.e., three in Huber weight parameter; see Rodionov 2004 for more information). Thus, equally weighted arithmetic means of the regimes detected were used to represent significant regime shifts in our environmental data set.

Results

During the first 2 years of the study, no major morphological changes were observed in the branch or colony morphology of the tagged colonies. In March 2013, 35 of the 63 *Pocillopora damicornis* colonies showed signs of swollen node growth (<1.5 cm in width) in the bifurcation of branches at Isla Gaviotas (fig. 2A, 2B). Beginning in No-

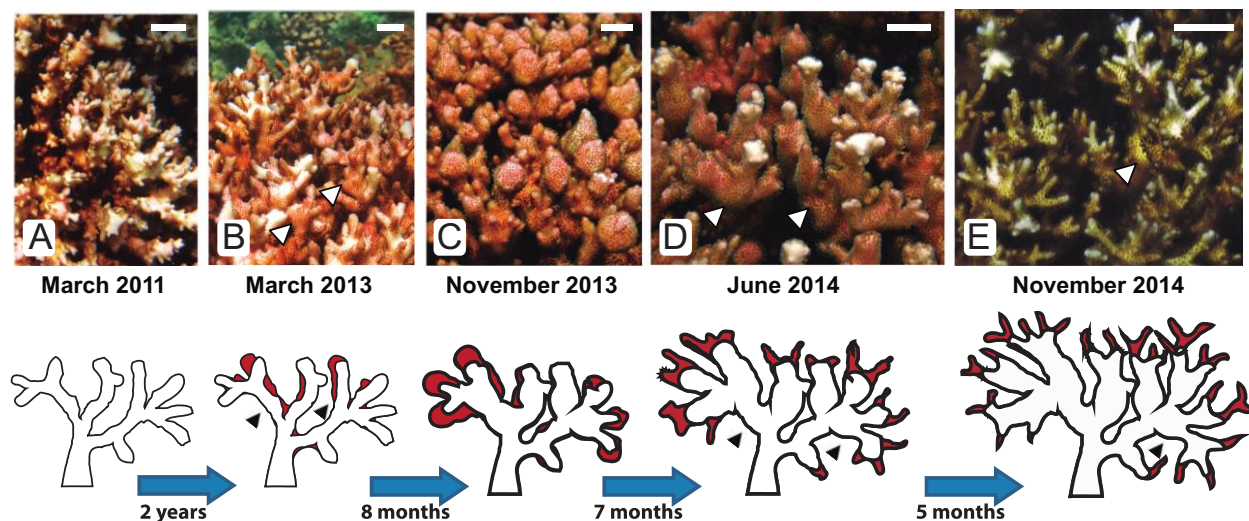


Figure 2: Tagged colony at Isla Gaviotas, showing the change from *Pocillopora damicornis* (A, B) to *Pocillopora inflata* (C) morphospecies. The same colony is shown as it begins to recover *P. damicornis* morphology (D) and when *P. damicornis* morphology is fully recovered (E). The diagrams below illustrate the morphological changes, which were primarily swollen branch tips. Arrowheads in 2B indicate emerging swollen nodes, a diagnostic branch trait used for the identification of the *P. inflata* morphospecies. Arrows in 2D and 2E indicate the remnants of the swollen branch tips. Scale bars indicate 1 cm.

vember 2013, these 35 colonies had changed from *P. damicornis* to *Pocillopora inflata* morphospecies (fig. 2C; hereafter referred to as changed colonies). These changes were evident at both the branch and colony level in the shape of swollen terminal and subterminal branches (fig. A1; figs. A1, B1, available online). Most of the changed colonies were located in a small area (~200 m² of surveyed area of 1,300 m²) of the reef at Isla Gaviotas. With the exception of one colony at Punta Galeras (figs. 1B, A1), no signs of morphological changes resembling changes to *P. inflata* morphospecies were seen in tagged or other colonies at Portugues or Punta Galeras during surveys made between November 2013 and February 2014 (hereafter referred to as unchanged colonies). The frequency of changed colonies was significantly higher at Isla Gaviotas than at the other two sites ($\chi^2 = 43.79$, $df = 2$, $P < .001$) and coincided with the lowest flow rates in the studied locations (fig. 1B). Seven months after the morphological switch, *P. inflata* colonies were recovering their original *P. damicornis* morphology (fig. 2D). This recovering progressed by the growth of small branches or extensions over distal parts of the swollen branches (see video 1, available online). Finally, in November 2014, the colonies had recovered the morphology of *P. damicornis* (fig. 2E).

Two mitochondrial regions (ORF and CR) were analyzed in 30 individuals. All the sequences were identical, and their identities were confirmed as being from the *Pocillopora* type 1 mitochondrial lineage.

A regime of high frequency of storms and high concentration of chlorophyll *a* occurred between 2012 and 2013 in the south of the Gulf of California ($P < .001$; figs. 3A, B1A). Colonies of *P. inflata* were first observed just after four strong and closely spaced storms and coincided with a subsequent shift to lower concentrations of chlorophyll *a* in early November 2013. No significant regime shift was detected in monthly SSTs or PAR (fig. B1B, B1C). A similar shift in the pattern of storm frequency occurred along the southwest coast of Mexico in autumn of 1997 (fig. 3B), 6 months before the collections for the original description of *P. inflata*.

Discussion

Here we report the direct observation of a phenotypic switch from one morphospecies (*Pocillopora damicornis*) to a different morphospecies (*Pocillopora inflata*) and recovery to its original morphology (*P. damicornis*) that occurred following an environmental regime shift in the



Video 1: Still photograph from a video (video 1, available online) that shows morphological switch and recovery of lace coral (*Pocillopora*) morphospecies following a shift in environmental conditions.

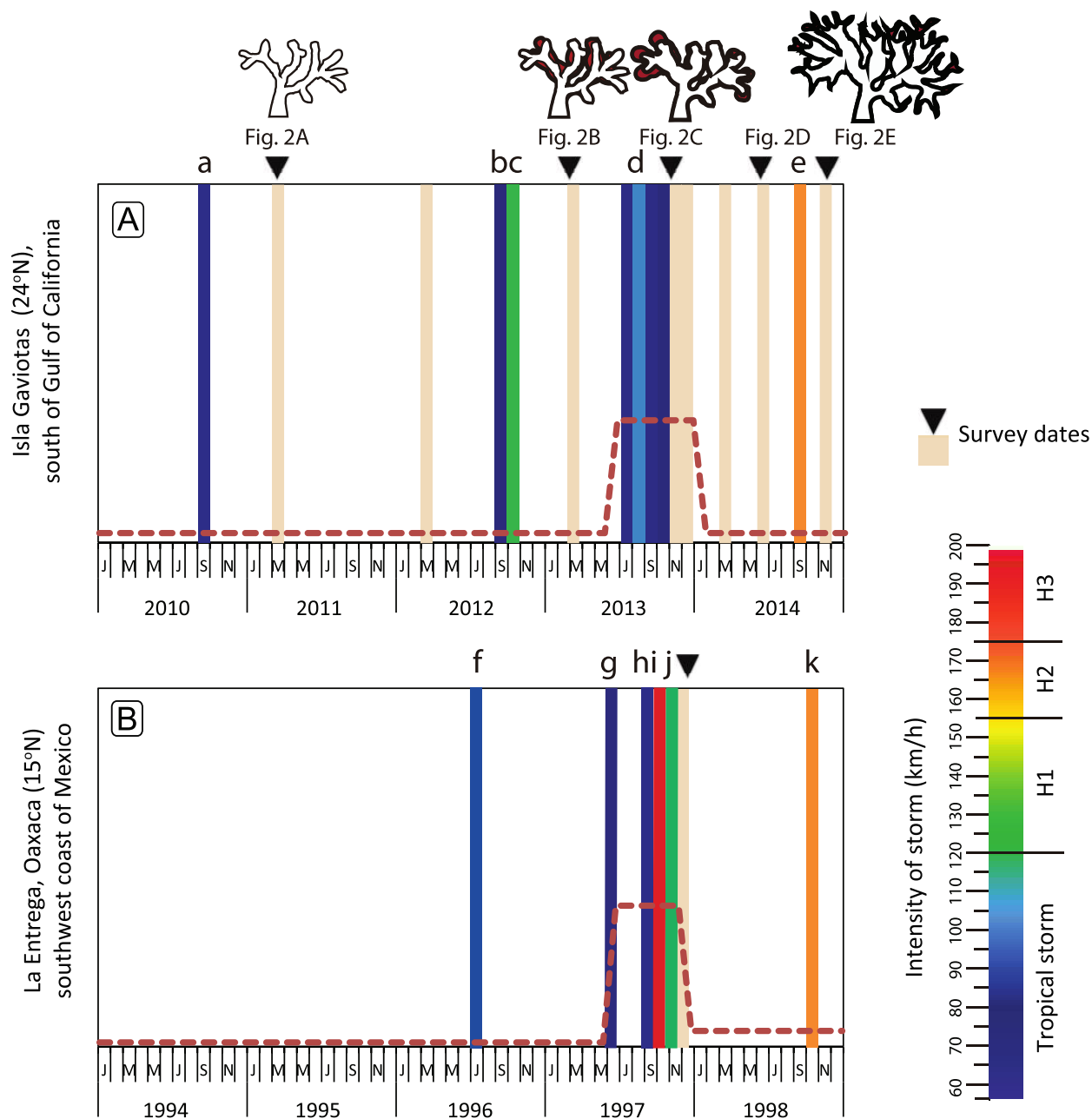


Figure 3: Storm frequency in the southern Gulf of California from 2010 to 2014 and on the southwest coast of Mexico (collection site from Glynn 1999) from 1994 to 1998. Colored bars indicate the monitoring dates and the incidence and intensity of storms (H = hurricane category). Arrowheads indicate the date when the photographs in figure 2 were taken (A) and when collections were made for Glynn 1999 (B). Dashed lines indicate the equally weighted arithmetic means and represent a significant regime shift ($P < .05$). Lowercase letters *a-k* indicate the names of the storms as follows: *a* = Georgette; *b* = Norman; *c* = Paul; *d* = Erick; *e* = Norbert; *f* = Cristina; *g* = Andres; *h* = Olaf; *i* = Pauline; *j* = Rick; *k* = Lester. Data are also presented in table B1, available online.

southern Gulf of California. The branch morphology, low abundance, and restricted distribution of the corals that underwent the morphological change all agreed with the species description and ecological features of *P. inflata* (Glynn 1999; Glynn and Ault 2000). A similar switch be-

tween these morphologies may have previously gone unnoticed due to the small size of the swollen node growth (<1.5 cm of width) during the morphological transition (fig. 2B). The relatively short time to morphological recovery of this coral (which began to return to its original

shape after about 6 months; figs. 2, A1) may explain why *P. inflata* has been observed in some surveys, only to be absent after 1–3 years in subsequent surveys (Glynn 1999). In addition, a few studies that have monitored the morphology of *Pocillopora* corals for 9–24 months have reported similar changes in swollen branches (Nakamura and Yamasaki 2006; Mass et al. 2011; see below). Our findings show that some coral colonies can maintain their morphology over long periods (unchanged colonies over more than 3 years, fig. A1), whereas others at the same location show fast and remarkable morphological changes at the branch and colony level over short periods (8 months). If other such events of morphological plasticity occur along the Eastern Pacific, these may be responsible for the marked interannual fluctuations of abundance in these and other morphospecies that have been noted previously (Guzmán and Cortés 2001).

Our observations of plasticity in the southern Gulf of California led us to ask whether the southwest Mexican type locality of *P. inflata* had experienced similar environmental conditions before those samples were collected. Indeed, a similar and significant increase in the number of storms occurred both in the autumn of 1997 at the southwest coast of Mexico and in the autumn of 2013 in the Gulf of California (fig. 3). Our field observations also indicate that an initial morphological change of swollen node growth occurred in March 2013, perhaps in response to the storms that occurred in autumn 2012 (1 year before). Similarly, a storm impacted on the southwest coast of Mexico 1 year before the collections described in Glynn 1999 (in summer of 1996; fig. 3B). Thus, we suggest that the *P. inflata* shape is a morphotype that develops in response to storm events occurring during the summer and autumn periods of 2 previous years. Other stresses may trigger this same morphological response. For example, *P. inflata* was reported in the Galapagos Islands for the first time during a period of coral recovery from disturbances produced by the 1982–1983 El Niño Southern Oscillation event (Glynn 1999).

The swollen branch response that we saw in changed colonies was not found in all morphotypes, nor was it found at all studied sites, but it was most frequent at the site with low-flow conditions. *Pocillopora* corals in low-flow environments are more liable to morphological plasticity (Paz-García et al. 2015), so the *P. inflata* morphology may be a coping response prompted by the increase in water flow during storm events. Similar morphological responses under enhanced flow have been reported elsewhere. For example, transplanted fragments of *P. damicornis* began to develop thicker, more swollen branches after 9 months of constant high (20 cm/s) flow (Nakamura and Yamasaki 2006). *Pocillopora verrucosa* also developed short but swollen branches after 2 years in higher flow (Mass et al. 2011). Models also predict that thicker, swollen branches will be induced by high water flow and light availability (Filatov et al.

2010; Chindapol et al. 2013). In contrast to experimental studies, where constant water flow is provided, our observations indicate that (1) the short, swollen branch response does not necessarily occur in all individuals under natural conditions and (2) similar changes in morphology may be triggered by pulses of high flow caused by storms.

Association of host coral with different algal symbiont types may confer a physiological advantage during environmental shifts or under stressful conditions (Mieog et al. 2009; LaJeunesse et al. 2010). Although we did not verify the type of symbiont here, previous studies in the Gulf of California show that *Pocillopora* morphospecies display an association with two *Symbiodinium* types (C1b-c and D1; Pettay et al. 2011; McGinley et al. 2012). Additional integrative studies should test whether changes to the host-symbiont combination and their synergistic effects could be related to the morphological plasticity reported here.

Pocillopora corals display a high number of morphospecies in the Tropical Eastern Pacific within only three mitochondrial lineages (Pinzón and LaJeunesse 2012; Paz-García et al. 2015), especially in the Gulf of California, where five morphospecies cooccur and share a single mitochondrial lineage (type 1). Here, we directly observed plastic changes between two morphospecies under natural conditions. On the basis of this evidence, we suggest that *P. inflata* shape is an artificial group triggered by stressful conditions and that at least some of the morphological diversity seen in *Pocillopora* in the Tropical Eastern Pacific is driven by shifts in environmental conditions.

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Appendix A from D. A. Paz-García et al., “Switch between Morphospecies of *Pocillopora* Corals” (Am. Nat., vol. 186, no. 3, p. 000)

View of Unchanged and Changed Corals

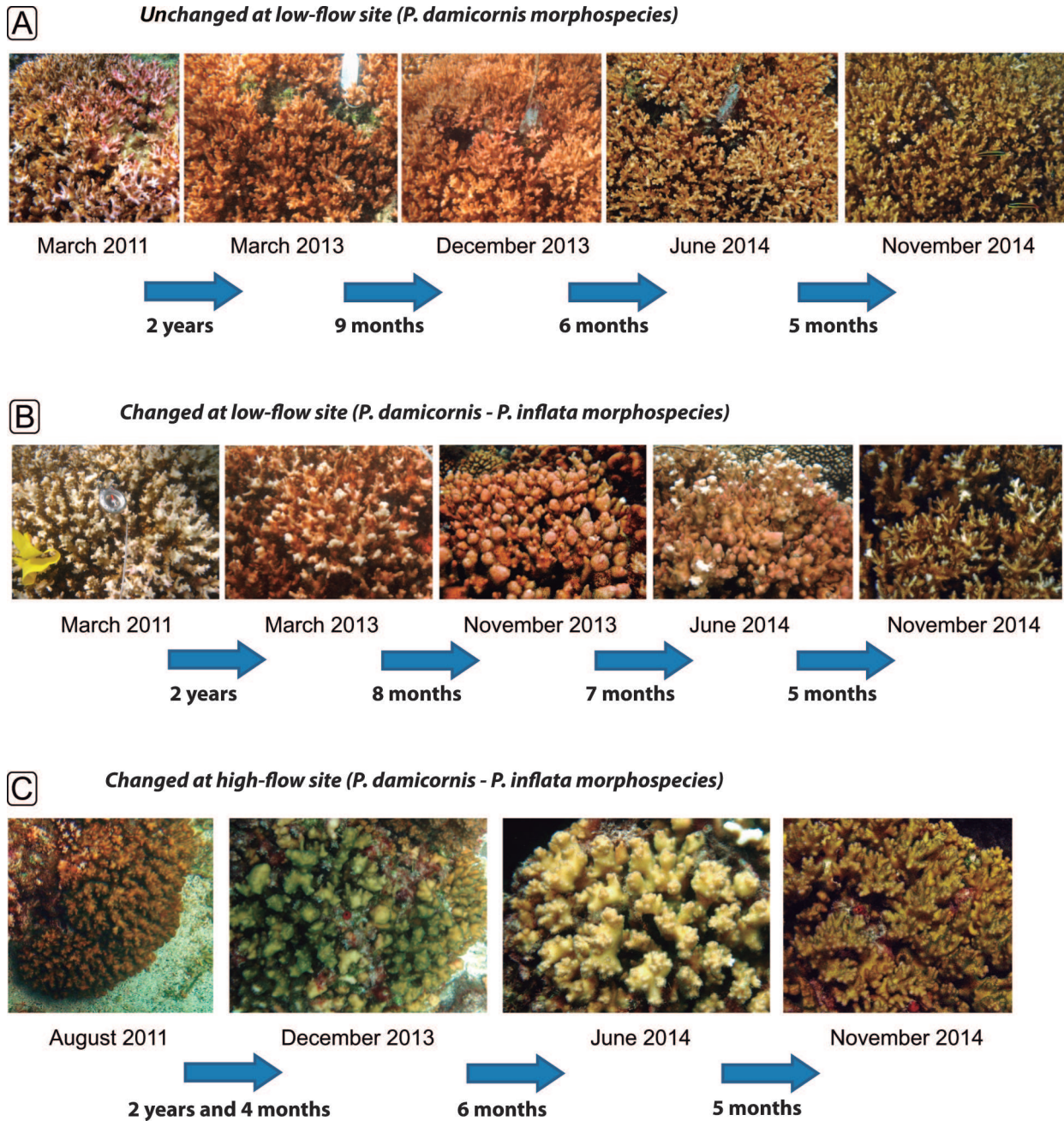


Figure A1: View of unchanged (A) and changed (B, C) colonies at low-flow and high-flow sites south of the Gulf of California, March 2011–November 2014.

**Appendix B from D. A. Paz-García et al., “Switch between
Morphospecies of *Pocillopora* Corals”
(Am. Nat., vol. 186, no. 3, p. 000)**

Storm Information and Environmental Monthly Averages

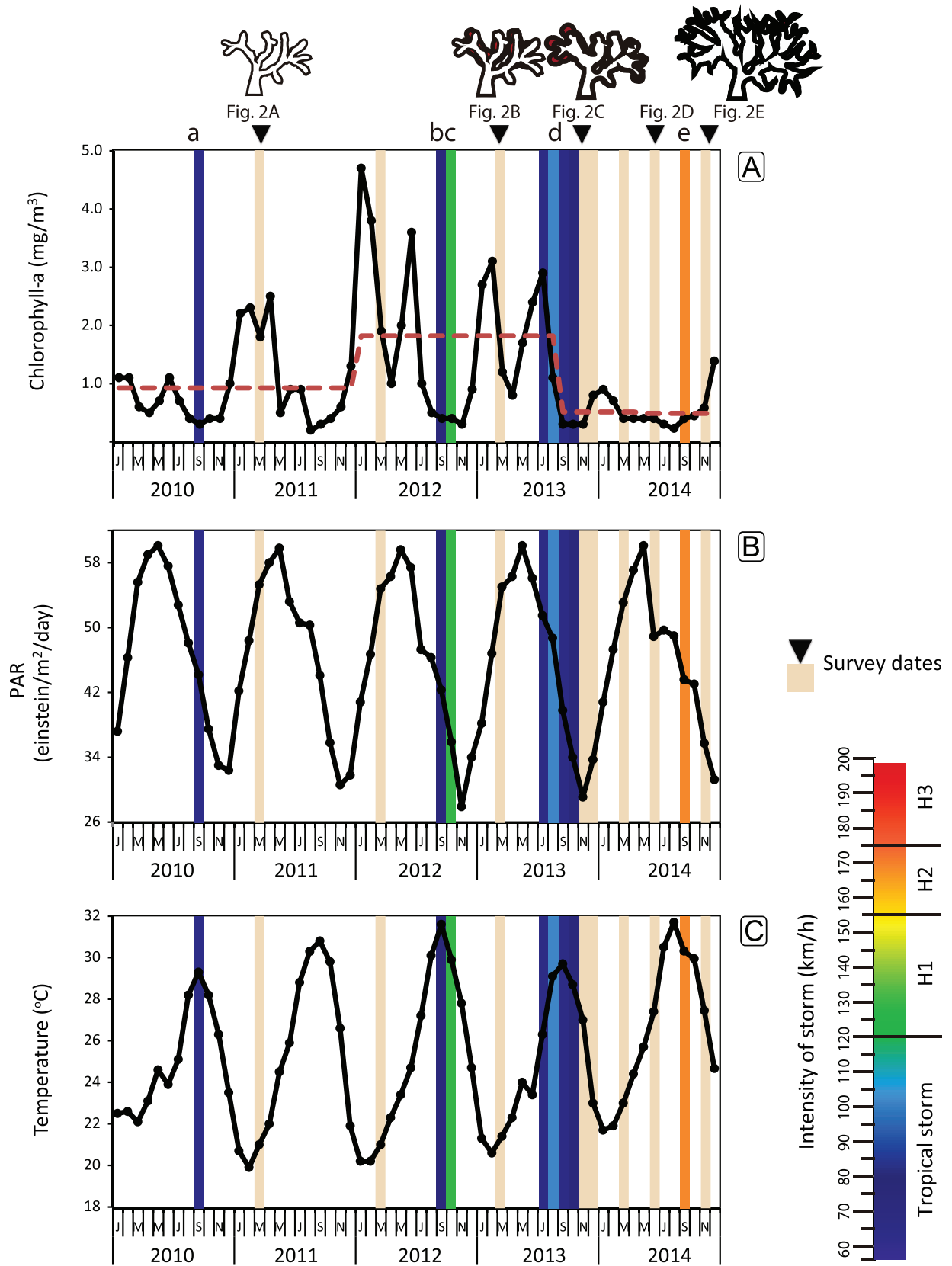


Table B1: Storm frequency in the southern Gulf of California, 2010–2014, and on the southwest coast of Mexico, 1994–1998

Location, date	Name of storm	Category	Intensity (km/h)	Minimum distance to location (km)
Isla Gaviotas, Gulf of California (24°N):				
09/22/2010	Georgette	Tropical storm	56	23
09/28/2012	Norman	Tropical storm	74	160
10/16/2012	Paul	Hurricane category 1	130	200
07/09/2013	Erick	Tropical storm	65	176
08/29/2013	Juliette	Tropical storm	102	86
09/07/2013	Lorena	Tropical storm	65	154
10/15/2013	Octave	Tropical storm	74	189
09/05/2014	Norbert	Hurricane category 1	148	190
09/15/2014	Odile	Hurricane category 2	167	56
La Entrega, Oaxaca, southwest coast of Mexico (15°N): ^a				
07/03/1996	Cristina	Tropical storm	90	20
06/03/1997	Andres	Tropical storm	72	120
06/10/1997	Blanca	Tropical storm	72	70
09/29/1997	Olaf	Tropical storm	63	20
10/08/1997	Pauline	Hurricane category 3	200	33
11/10/1997	Rick	Hurricane category 1	119	10
10/17/1998	Lester	Hurricane category 2	165	150

Note: Data are also presented in figure 3.

^a Collection site from Glynn 1999.

Figure B1: Average monthly values of chlorophyll *a* concentrations (*A*), photosynthetically active radiation (*B*), and sea surface temperatures (*C*) in the southern Gulf of California from 2010 to 2014. Colored bars indicate monitoring dates and the incidence and intensity of storms (H = hurricane category). Arrowheads indicate the date when the photographs in figure 2 were taken. Dashed lines indicate the equally weighted arithmetic means and represent a significant regime shift ($P < .001$). Lowercase letters *a–e* indicate the names of the storms as follows: *a* = Georgette; *b* = Norman; *c* = Paul; *d* = Erick; *e* = Norbert.