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Abstract	<p>There is increased interest in understanding how stress reduces coral resistance to disturbances and how acclimatization increases the ability of corals to resist future stress. Most extreme low tides at Gorgona Island, which expose reef flats to air, do not appear to negatively affect corals because corals usually do not undergo lethal bleaching during such events. However, coral physiology and fitness may be impacted by this phenomenon. The aim of this study was to evaluate whether corals exposed to air have modified biological functions to resist bleaching. To test this, an extreme low-tide event was simulated in the field. Colonies of <i>Pocillopora damicornis</i> were exposed to air for 15 or 40 min over the course of one, two, or three consecutive days. This procedure was repeated for one to three months. Colonies of <i>P. damicornis</i> exposed to air had reduced fecundity, decreased zooxanthellae density, and changed color from darker to lighter. However, the growth rate of exposed corals was like that of non-exposed colonies. We conclude that short periods of subaerial exposure during extreme low tides are not lethal to <i>P. damicornis</i>, but negatively affect sexual reproduction, which might have deleterious effects at the population level. The periodic occurrence of extreme low tides in the tropical eastern Pacific may be one factor responsible for the high rate of asexual reproduction (e.g., fragmentation) in pocilloporid corals of this region.</p>	
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2 **Effect of short-term subaerial exposure on the cauliflower coral,**
3 ***Pocillopora damicornis*, during a simulated extreme low-tide event**

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7 **Abstract** There is increased interest in understanding how
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Keywords Growth rate · Low fecundity · Stress · Tissue damage · Trade-off · Zooxanthellae density 34 35

Introduction 36

The role and impact of natural disturbances on coral reefs **AQ2** have long been appreciated (Connell 1978; Miller 2015). 37 38 The interactions between natural disturbances and biological processes such as competition, predation, and disease 39 40 affect the structure, dynamics, and resilience of coral communities at both ecological and geological time scales 41 42 (Connell 1997; Karlson 2002; Mumby and Steneck 2011; Pandolfi 2011). While disturbance has received considerable 43 44 attention as a major force affecting coral community and reef ecosystem processes (Hughes and Connell 1999; 45 46 Riegl 2001; Connell et al. 2004), its effects on corals at the organismal level, beyond mortality, have received less 47 48 attention. Recently, there has been a surge of studies dedicated to understanding coral tolerance to different environmental 49 50 factors (Brown and Cossins 2011; Fabricius 2011; Erftemeijer et al. 2012), particularly thermal tolerance in relation to coral bleaching (Lesser 2011), yet little 51 52 is known about the sublethal physiological effects of other natural disturbances (Brown 1997). Given the increasing 53 54 deterioration of coral reefs due to natural and anthropogenic perturbations in the face of imminent climate 55 56 change, it is becoming increasingly important to understand coral thresholds to different stressors. 57 58 59

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Reef flats are the most productive and diverse zones of coral reef ecosystems (Chisholm 2003; Karlson et al. 2004); however, as the shallowest areas on reefs, they naturally exhibit high variation in environmental factors, such as temperature, salinity, water flow, and solar irradiance, and these factors can vary at multiple temporal scales. Such variation may challenge the tolerance limits of species that live on reef flats. For example, environmental variability can trigger costly acclimatization and adaptive responses that can reduce fitness (Brown 1997). Reef flats are sporadically subject to subaerial exposure (SAE) because of tidal fluctuations during spring tides and particularly when extreme low tides coincide with high barometric pressure or strong offshore winds (Loya 1976; Fadlallah et al. 1995). SAE of corals during low tides usually lasts 1–2 h but can last up to 4 h and can occur during day or night (Glynn 1976; Loya 1976; Fadlallah et al. 1995; Rosser and Veron 2011). Daily SAE can occur repeatedly for 2–5 consecutive days during a single spring tide week and during up to four consecutive months depending on location and tidal regime (Glynn 1976; Fadlallah et al. 1995; Rosser and Veron 2011). During exposure, corals and other reef organisms are unprotected from many environmental stressors such as solar radiation, wind, rain, extreme temperature, and desiccation. Exposure to these conditions may cause colony bleaching and partial or total coral death (Glynn 1968, 1976; Loya 1976; Brown et al. 1994; Eakin and Glynn 1996; Anthony and Kerswell 2007; Aguilera and Rautenberger 2010; Teixeira et al. 2013). Similar to the effects of thermal bleaching, branching corals (e.g., *Acropora* and *Pocillopora*) are the most affected by low-tide events and ongoing climate change (McClanahan 2004; Pinzón et al. 2013), whereas massive corals (faviids, mussids, poritids) are the least affected (Glynn 1976; Brown et al. 1994; Anthony and Kerswell 2007).

Pocilloporid corals are the main reef builders providing habitat and shelter for other species in tropical eastern Pacific (TEP) coral reefs (Glynn and Ault 2000; Glynn et al. 2017b). High levels of coral bleaching and mortality have been observed in coral communities following extreme low tidal events in the TEP (Glynn 1976; Eakin and Glynn 1996; Maté 2003; Zapata and Vargas-Ángel 2003). However, the available data on the impacts of SAE on TEP corals are restricted to percentages of bleaching and mortality (Glynn 1976; Eakin and Glynn 1996; Maté 2003). Glynn (1976) observed 46–100% colony tissue mortality in *Pocillopora damicornis* during simulated SAEs of 15–60 min over 4–6 consecutive days under natural solar irradiance. At Gorgona Island, Colombian Pacific, periods of >60 min of experimental SAE like those

used in this study (see below) have caused lethal bleaching, and colonies exposed for less time, with <30% of the colony bleached, recovered their coloration after a few days (IC Lemos and FA Zapata, unpublished data). In addition, Zapata and Vargas-Ángel (2003) and Zapata et al. (2010) have suggested that SAE during extreme low tides is the most probable cause of periodic loss of coral cover on coral reefs of Gorgona Island. Since not all SAE is lethal, it is important to understand its effects on growth, reproduction, and other physiological responses and how these responses might allow the coral to resist such perturbations. For instance, laboratory experiments in the coral *Stylophora pistillata* indicate that maximum gross photosynthesis is greatly reduced and calcification ceases during aerial exposure (Romaine et al. 1997).

Life-history theory postulates the existence of general trade-offs between growth, survival, and reproduction of an organism (Stearns 1992). In particular, theory predicts that an organism under stress must reallocate energy to mechanisms that maximize survival at the expense of growth, reproduction, or both. Because sexual reproduction is energetically expensive (Williams 1966), it may become compromised under stressful conditions (such as SAE) to reallocate more energy to survival. Empirical work supports the idea that corals maximize survival while compromising reproduction when they are subjected to stress (Birkeland 2015). Thus, it is expected that corals subjected to SAE will reduce reproductive processes to enhance survival. Such trade-offs will be more likely to occur when disturbances coincide with key reproductive processes such as gametogenesis. For example, at Gorgona Island, *P. damicornis* begins gamete production in February (coinciding with extreme low-tide events), but in May (when gamete maturation occurs) colonies with partial bleaching do not produce gametes (Castrillón-Cifuentes et al. 2015).

Because the effects of SAE on *P. damicornis* sexual reproduction and growth have not yet been measured, we quantified several coral vital functions including growth, reproduction, tissue damage/regeneration, and zooxanthellae density (as an important source of energy for growth, reproduction, and tissue maintenance). Overall, the aim of this study was to test whether energetically expensive functions (e.g., reproduction) are reduced to maintain normal growth rates (i.e., coral resistance) and tissue regeneration because of stress caused by environmental disturbance. Following Carilli et al. (2009), we define resistance as a coral's ability to continue normal skeletal growth under stress, and we define resilience as a coral's ability to recover normal growth rates after a stressful event.

Materials and methods

Study area

The study was carried out at Gorgona Island (Colombian Pacific), which is a Colombian natural park and therefore generally well protected from local anthropogenic pressures (no one except park officers and researchers are allowed on coral reefs of the island). The experimental coral colonies used in this study were maintained at a site known as El Hueco at La Azufrada reef, which is the island's largest and most continuous reef (Fig. 1; 2°58'10"N; 78°11'05"W). El Hueco is a natural depression, 50 m in diameter, located near the northern end of the reef flat. During high tide, El Hueco has a maximum depth of 15 m. Here corals are not exposed during extreme low tides.

The tidal regime at Gorgona Island is mixed, primarily semidiurnal, with a maximum amplitude of ~4.7 m (IDEAM 2012). Tidal amplitude varies throughout the year following predictable daily, fortnightly, monthly, annual and even longer cycles (Parker 2005); it is greater during spring tides than during neap tides every alternate week, and it is greatest once a year when the earth, the moon, and

the sun are aligned and closest to each other, causing the lowest astronomical tide. Because the shallowest corals at La Azufrada reef are located at a depth of 0.4 m below the mean lower low water tidal datum, they can be subaerially exposed during low spring tides, which can be as low as ~−0.8 m. An analysis of tidal predictions between 1966 and 1996 indicated that SAE can occur during the day (usually around mid-morning to noon) or night and can last for an hour or more. SAE events are common from January to April and less frequent from August to December. During these months, reef flats can be exposed more than twice during one spring tide series (up to five consecutive days). Furthermore, exposure can occur on average every 90 d, although intervals between two consecutive events range from 25 to 441 d (for more details, see Zapata and Vargas-Ángel 2003). However, the duration and extent that a reef is subaerially exposed cannot always be predicted accurately. This is because the predictable tidal oscillations generated by astronomical forces can be disrupted by unpredictable meteorological conditions (such as changes in barometric pressure and wind patterns) and large-scale fluctuations in mean sea level (such as those occurring by thermal expansion and contraction during El Niño/La Niña cycles; Hamlington et al. 2015; Moon et al. 2015).

Fig. 1 Map of Gorgona Island (located off the Colombian Pacific coast) showing La Azufrada reef and the site of the experiment (El Hueco). Black areas are reef formations

Experimental design

In December 2012, 81 healthy-looking (without bleaching or algal overgrowth) colonies of *P. damicornis* (following the morphospecies description by Cantera et al. 1989), with a mean diameter of 20 cm, were randomly collected from La Azufrada reef flat. The colonies were transplanted to El Hueco site, placed on plastic stretchers, and left there for 91 d to acclimatize before starting the experiment (Fig. 2a). To simulate an extreme low-tide event, the stretchers with the colonies were brought to the surface and the colonies placed on floating stretchers where the

colonies were exposed to air (Fig. 2b). The experiment lasted 103 d between March and July 2013. For the experiment, coral colonies were exposed (following a 3 × 3 factorial design) to three factors related to the duration and frequency of SAE. The first factor was the duration of SAE during a given day; this factor consisted of three levels: zero (control), 15, or 40 min. The second factor was the number of consecutive days (one, two, or three) colonies were exposed to air for the three durations of SAE. The third factor was the number of months in which combinations of levels of the first two factors were applied to colonies: 1 month (colonies exposed in March),

Fig. 2 Experimental setup to simulate an extreme low tide. **a** Colonies fastened to plastic stretchers, and stretchers anchored to substrate. **b** Colonies on floating platforms exposed to air simulating an extreme low tide. **c** Standardized photographic method with colonies placed on top of a white screen. **d** Pixelated image for color analysis

231 2 months (colonies exposed in March and May), and
232 3 months (colonies were exposed in March, May, and
233 July). Three different colonies were randomly assigned to
234 each combination of SAE treatment levels ($N = 81$).
235 Corals were exposed to air during the first week of March,
236 May, and July of 2013.

237 **Monitoring color, growth rate, and tissue loss** 238 **in colonies by digital photographic analysis**

239 Standardized underwater photographs were taken the day
240 after the colonies were exposed to air, and every month
241 until July 2013 (even though some colonies had already
242 completed their SAE treatment; for instance, the colonies
243 exposed for 1 or 2 months). In total, 243 photographs were
244 taken from 81 colonies over the course of 3 months. These
245 photographs were used to assess growth, tissue recovery,
246 and color change in the experimental units between March
247 and July 2013. Standardization consisted of placing the
248 colonies on top of a white screen; this screen had a
249 grayscale palette and a ruler attached (Fig. 2c). All pho-
250 tographs were taken at the same distance, angle, 0 expo-
251 sure, RGB mode, and white-balance manual setting, with
252 the same Nikon D3100 camera.

253 The software used for digital image analysis (ImageJ)
254 was calibrated using the ruler attached to the screen in each
255 photograph; this allowed measurement of the diameter of
256 each colony. A single estimate of growth rate (mm d^{-1})
257 was calculated for each colony using the diameter of all
258 colonies measured monthly. The effect of SAE treatment
259 combination on growth rate was tested using a factorial
260 ANOVA; growth rate data satisfied assumptions of nor-
261 mality and homoscedasticity of residuals (Kolmogorov-
262 Smirnov test $d = 0.04$, $p > 0.20$; Cochran $C = 0.11$,
263 $p = 0.40$). The percentage of net tissue loss due to SAE
264 was calculated in each colony by determining the area
265 without tissue in relation to total colony area. A three-way
266 factorial ANOVA with a repeated-measures factor was
267 used to test the effect of SAE treatment combinations on
268 tissue loss; raw data satisfied the assumption of
269 homoscedasticity (Cochran test for each sampling month,
270 $C = 0.67$, $p = 1$ for March; $C = 0.79$, $p = 1$ for May;
271 $C = 0.92$, $p = 1$ for July). Both analyses were done with
272 StatSoft Statistica v8.0.

273 Before further analyses were done, and following Sie-
274 beck et al. (2006) with some modifications, the pho-
275 tographs were pixelated by uniformly increasing the pixel
276 size $25\times$. Dark areas of the pictures that represented deeper
277 parts of the colony were removed from the image using
278 GIMP2.8 (GNU Image Manipulation program). Using the
279 histogram function in Adobe Photoshop v6.0, the hue (re-
280 flected color), saturation (proportion of gray in the hue),

and luminosity (amount of white, which is related to
zooxanthellae density and bleaching state of coral; Siebeck
et al. 2006) were determined for each of 30 pixels ran-
domly selected from each photograph (Fig. 2d). With these
three parameters, a color palette was generated to represent
the average color of the colonies for each combination of
SAE treatments (Electronic supplementary material, ESM,
Fig. S1). For statistical analyses, only hue and luminosity
were considered.

291 **Quantification of zooxanthellae density** 292 **and fecundity**

293 The day after each SAE and once every month until July
294 2013, a fragment was collected from each colony, includ-
295 ing those whose SAE treatment had already been com-
296 pleted (only one fragment was collected due to restrictions
297 by the Colombian environmental authority). In total, 243
298 fragments were taken from 81 colonies over the course of
299 3 months. A fragment consisted of a portion of a branch
300 (~ 6 cm in length) from which 2 cm of the apex (non-
301 reproductive tissue) was removed. The fragments were
302 fixed in Zenker's solution for 24 h (stock solution: 25 g
303 potassium dichromate, 50 g mercury, 10 g sodium sulfate
304 in 1000 mL of filtered water; Zenker's solution: 95 mL of
305 stock solution, 5 mL glacial acetic acid), then kept in water
306 for 24 h (with two changes), and finally decalcified in 4%
307 HCl for a few minutes until the tissue detached from the
308 skeleton. Tissue was rinsed with water to eliminate acid
309 residues and finally preserved in 70% ethanol for subse-
310 quent histological processing (Castrillón-Cifuentes et al.
311 2015).

312 Zooxanthellae density and the number of oocytes were
313 recorded by counting cells in 20 polyps randomly selected
314 from each tissue section per colony. To calculate zooxan-
315 thellae density, the area (μm^2) of the cross section of each
316 polyp, assuming it was circular, was calculated by mea-
317 suring its diameter. Then, all zooxanthellae within each
318 polyp cross section were counted, and their density was
319 calculated as the number of cells per unit area; data
320 obtained per μm^2 were extrapolated to cm^2 . Fecundity was
321 expressed as the average number of oocytes per polyp; the
322 stage of development of oocytes was not considered.

323 A three-way factorial ANOVA with repeated measures
324 was performed for zooxanthellae density, colony color
325 (luminosity and hue), and fecundity. A repeated-measures
326 ANOVA was used for this analysis because the dependent
327 variables were measured repeatedly in all the experimental
328 units (colonies) during the experiment. Raw data of lumi-
329 nosity, hue, and fecundity satisfied the assumption of
330 sphericity (Mauchly 1940), while zooxanthellae density
331 was $\log_{10}$ transformed to satisfy this assumption.

Results

Growth rate

The duration and frequency of SAE treatments (or combinations) had no effect on the growth rate of *P. damicornis* (three-way ANOVA, $p > 0.05$ for all factor main effects and interactions; Table 1). The average growth rate was 0.2 ± 0.1 (SD) mm d⁻¹. The maximum growth rate was 0.6 mm d⁻¹, and this was found in a colony exposed to air for 40 min over two consecutive days and 2 months (colonies exposed in March and May). The minimum growth rate was -0.1 mm d⁻¹, recorded for three colonies exposed to air: 1 month, 1 d, 15 min; 2 months, 3 d, 15 min; and 3 months, 2 d, 40 min. This negative value could be the result of fragmentation due to colony manipulation during the experiment, wave action, or intensive fish corallivory in the reef (Palacios et al. 2014). Although 103 d might be a short time to assess the effect of stressors on growth rate, another study in the same study location (La Azufrada) indicated that 183 d were sufficient to detect differences in pocilloporid growth rate when corals were exposed to corallivory (Palacios et al. 2014).

Tissue loss

Only the colonies exposed to air for 40 min over two and three consecutive days suffered significant tissue loss (Table 2). In addition, there was more damaged tissue in the colonies exposed for 3 months than in those exposed for 1 or 2 months (Table 2; Fig. 3a). Tissue damage was only found at the tips of the branches (Fig. 3b), but in all cases the colonies recovered the lost tissue in less than

Table 1 Results of the univariate tests of significance for a three-way factorial ANOVA to assess the effect of subaerial exposure on growth rate (mm day⁻¹) in colonies of *Pocillopora damicornis* from La Azufrada reef, Gorgona Island

Effect	DF	Growth rate			
		SS	MS	F	P
M	2	0.06	0.03	1.45	0.24
D	2	0.02	0.01	0.62	0.53
m	2	0.10	0.05	2.49	0.09
M × D	4	0.07	0.01	0.82	0.51
M × m	4	0.13	0.03	1.53	0.20
D × m	4	0.04	0.01	0.57	0.68
M × D × m	8	0.17	0.02	0.99	0.44
Error	54	1.15	0.02		

M the monthly frequency of subaerial exposure (1, 2, or 3 consecutive months), D the daily frequency of subaerial exposure within each month (1, 2, or 3 consecutive days), m the duration of subaerial exposure during any given day (0, 15, or 40 min)

4 weeks. In field observations, all colonies exposed to air produced mucus, and 37% of them (mainly those exposed to air for 40 min) produced abundant mucus, which turned into foam and accumulated at the base of the colony 20 min after the colonies were exposed to air (Fig. 3c).

Colony color

The color of *P. damicornis* colonies differed over time; in March 2013 colonies were significantly more luminous than in July 2013 (Fig. 4c; Table 2). The color hue of the colonies also changed significantly from olivaceous tones in March 2013 to browns in July 2013 (Fig. 4e; ESM Fig. S1). Changes in color due to aerial exposure indicated that the most severe treatment (40 min repeated for 3 months) generated colonies significantly lighter than the control colonies and the colonies exposed to air for 15 or 40 min during 1 or 2 months (Fig. 4d; Table 2). The high luminosity values recorded for the colonies were not evident to the naked eye during field observations (when comparing exposed to control colonies), nor were they evident during the construction of the average colony color palette (ESM Fig. S1).

Zooxanthellae density

Zooxanthellae density in the control treatments decreased during the experiment. The density of *Symbiodinium* decreased from 0.87×10^6 cells cm⁻² in March 2013 to 0.53×10^6 cells cm⁻² in July 2013 (Fig. 4a). The changes in zooxanthellae density due to aerial exposure were significant for the three factors (Table 2). In general, zooxanthellae density was lower in treatments with longer aerial exposure (frequency and duration; Table 2); colonies exposed to air for 1 month had on average 0.70×10^6 *Symbiodinium* cells cm⁻², and colonies exposed for 3 months had 0.60×10^6 *Symbiodinium* cells cm⁻². Colonies exposed for 1 d had 0.69×10^6 *Symbiodinium* cells cm⁻², and colonies exposed for 3 d had 0.58×10^6 *Symbiodinium* cells cm⁻². Conversely, 40 min of SAE seemed to increase zooxanthellae density (from 0.61 to 0.76×10^6 *Symbiodinium* cells cm⁻² in treatments of 0 and 40 min, respectively). However, this was driven by a group of colonies exposed for 40 min in March that showed an increase in zooxanthellae density in comparison with the control colonies and the colonies exposed for 15 min in the same month; these results were not representative of the experimental results as a whole (Fig. 4b).

Other significant effects of SAE on zooxanthellae density are shown in ESM Fig. S2. Zooxanthellae density was not constant throughout the study period (Fig. 4a). Environmental factors such as irradiance, nutrient availability, and temperature can modify zooxanthellae density, and

Table 2 Results of three-way analysis of variance with repeated measures on zooxanthellae density, luminosity, hue, fecundity, and tissue loss in *Pocillopora damicornis* colonies exposed to air simulating an extreme low tide

Effect	DF	Zooxanthellae density				Luminosity				Hue			
		SS	MS	F	p	SS	MS	F	p	SS	MS	F	p
Intercept	1	104,412,615	104,412,615	3018	<0.0001	1,657,182	1,657,182	11,434.6	<0.0001	141,283.1	141,283.1	16,061	<0.0001
M	2	466,704	233,352	6.7	0.002	10,638	5319	36.7	<0.0001	711.2	355.6	40.4	<0.0001
D	2	645,882	322,941	9.3	0.0003	27	13	0.1	0.9	113.4	56.7	6.4	0.003
m	2	1,345,799	672,900	19.4	<0.0001	689	345	2.4	0.1	60.2	30.1	3.4	0.03
M × D	4	345,061	86,265	2.5	0.05	894	224	1.5	0.2	92.2	23.0	2.6	0.04
M × m	4	1,083,365	270,841	7.8	<0.0001	2510	628	4.3	0.004	207.7	51.9	5.9	0.0005
D × m	4	158,748	39,687	1.1	0.3	1131	283	2.0	0.1	97.1	24.3	2.8	0.03
M × D × m	8	120,836	15,104	0.4	0.8	2234	279	1.9	0.07	126.2	15.8	1.8	0.1
Error	54												
F'	2	5,438,010	2,719,005	114.6	<0.0001	38,856	19,428	171.5	<0.0001	2030.8	1015.4	125.2	<0.0001
F' × M	4	505,271	126,318	5.3	0.0005	1986	497	4.4	0.002	754.9	188.7	23.3	<0.0001
F' × D	4	627,804	156,951	6.6	<0.0001	420	105	0.9	0.4	52.1	13.0	1.6	0.1
F' × m	4	210,967	52,742	2.2	0.07	3506	876	7.7	<0.0001	30.3	7.6	0.9	0.4
F' × M × D	8	418,249	52,281	2.2	0.03	164	20	0.2	0.9	242.3	30.3	3.7	<0.0001
F' × M × m	8	371,341	46,418	2.0	0.06	2093	262	2.3	0.02	200.4	25.1	3.1	0.003
F' × D × m	8	470,023	58,753	2.5	0.01	1475	184	1.6	0.1	68.2	8.5	1.1	0.4
F' × M × D × m	16	395,446	24,715	1.0	0.4	1743	109	1.0	0.5	181.6	11.3	1.4	0.1
Error	108	2,563,068	23,732			12,236	113			876.1	8.1		
Effect	DF	Fecundity				Tissue loss							
		SS		MS		F		p		SS	MS	F	p
Intercept	1	14,811.1		14,811.1		58.2		<0.0001		660.26		43	<0.0001
M	2	2477.4		1238.7		4.9		0.01		1311.6		42.7	<0.0001
D	2	352.3		176.2		0.7		0.5		344.17		11.2	<0.0001
m	2	153.9		76.9		0.3		0.7		216.6		7.0	0.001
M × D	4	1756.5		439.1		1.7		0.1		685.5		11.1	<0.0001
M × m	4	936.3		234.1		0.9		0.4		439		7.1	0.0001
D × m	4	1120.8		280.2		1.1		0.3		158.6		2.5	0.04
M × D × m	8	1903.8		238.0		0.9		0.5		317.7		2.6	0.01
Error	54									827.67			
F'	2	9323.7		9323.7		46.3		<0.0001		274.3		11.9	<0.0001
F' × M	4	1393.6		696.8		3.5		0.03		540.7		11.8	<0.0001
F' × D	4	86.3		43.2		0.2		0.8		152		3.3	0.01
F' × m	4	65.0		32.5		0.2		0.8		146.2		3.1	0.01

Table 2 continued

Effect	DF	Fecundity			Tissue loss		
		SS	MS	F	SS	MS	p
$F' \times M \times D$	8	1464.5	366.1	1.8	297.9	37.2	0.002
$F' \times M \times m$	8	873.4	218.3	1.1	294.5	36.8	0.002
$F' \times D \times m$	8	478.0	119.5	0.6	85.2	10.6	0.4
$F' \times M \times D \times m$	16	929.8	116.2	0.6	171.7	10.7	0.5
Error	108	10,870.3	201.3		1236.3	11.4	

Levels of aerial exposure were months (M), days (D), and minutes (m), the date of data collection (F') is the repeated measure. p values in bold denote significant effects ($p < 0.05$)

these factors can change through time (Thinh 1991; Stimson 1997). Using data from an oceanographic data logger (DST CTD, Star oddi, Iceland) deployed at La Azufrada reef (near El Hueco site, recording every 30 min), a trend was detected in which zooxanthellae density in *P. damicornis* was greater during colder and saltier conditions (ESM Fig. S3).

Fecundity

No oocytes were found in March 2013, possibly because at this time *P. damicornis* had not initiated reproduction. When reproduction was initiated, an increase in oocytes from May to July was recorded with 2.0 ± 4.8 oocytes polyp⁻¹ in May 2013 and 17.0 ± 21.4 oocytes polyp⁻¹ in July 2013. Only the monthly frequency of SAE had a significant effect on fecundity. Colonies exposed to air in three consecutive months produced 9.4 ± 8.0 oocytes polyp⁻¹, whereas colonies exposed to air in only one month produced 26.0 ± 8.1 oocytes polyp⁻¹ (Table 2; Fig. 5).

Discussion

While very prolonged SAE of corals during the most extreme low tides can cause bleaching and mortality (Glynn 1976; Eakin and Glynn 1996; Maté 2003; Zapata and Vargas-Ángel 2003), many extreme low tides at Gorgona Island, like those simulated here, which moderately expose reef flats to air, do not appear to negatively affect corals because these usually do not suffer lethal bleaching during such events. However, our results suggest that coral physiology is negatively impacted by SAE, and hence, corals modify some biological functions to resist SAE during extreme low tides. In short, colonies of *P. damicornis* exposed to air experienced decreased zooxanthellae density and reduced fecundity; however, the growth rate of exposed corals was like that of non-exposed colonies. The fact that the corals maintained normal skeletal growth (i.e., were resistant to the stress) while decreasing egg production, even when their main source of energy (zooxanthellae) was decreased, indicates that there could be a trade-off between continued growth and sexual reproduction.

Zooxanthellae density of *P. damicornis* decreased due to SAE (Fig. 4b; ESM Fig. S2); this is the expected response of corals when they are subjected to stressful conditions (Baker 2001; Ainsworth et al. 2008). However, zooxanthellae density also decreased in response to natural and temporal changes in environmental conditions at Gorgona Island (temperature and salinity; ESM Fig. S3). Stimson (1997) has shown that temporally variable environmental

Fig. 3 a Percentage of tissue loss in colonies of *Pocillopora damicornis* exposed to air for 0 min (open circles), 15 min (gray circles), and 40 min (black circles). b Apex of branches with tissue loss. c Colony with foam production. Bars are mean $\pm$ 0.95% confidence intervals

factors, not necessarily linked to stressful events, can induce changes in *P. damicornis* coloration and zooxanthellae density. Similarly, different combinations of frequency and duration of SAE resulted in the reduction in zooxanthellae density. Despite this, during the last month of the experiment (July), the zooxanthellae density of exposed colonies was not different from control colonies or exposed colonies that were recovering from 1 or 2 months of previous SAE (i.e., colonies exposed during March and May; ESM Fig. S2). A possible explanation for this lack of statistical difference in zooxanthellae density is that acute environmental changes (i.e., 15 or 40 min of non-lethal SAE) may be a mechanism for gradual acclimatization (Stambler 2010).

The high zooxanthellae density recorded for colonies exposed to air for 40 min in 1 month was an unexpected result. This could be explained by the possibility that when zooxanthellae are at low densities (as when corals are under stress), they may undergo exponential growth (Stambler 2011). Alternatively, some authors argue that loss of zooxanthellae is a high-risk ecological opportunity to quickly reject suboptimal zooxanthellae and acquire new genotypes that may be better adapted to environmental variation (Baker 2001, 2003; Baker et al. 2004; Rowan 2004; Jones et al. 2008).

As colony color is closely related to zooxanthellae density (Siebeck et al. 2006), it has traditionally been used to measure the health status of corals. Although it was not

evident to the naked eye, the luminosity and hue of the colonies changed due to SAE (Fig. 4). As expected, corals exposed for longer duration and frequency had higher values of luminosity and lower zooxanthellae density. Conversely, colonies had high values of luminosity in March (the month with highest zooxanthellae density), while colonies were less luminous in July (the month with the lowest zooxanthellae density). The hue also changed from olivaceous in March to brownish in July. These inconsistent results could indicate that the use of color alone (without other physiological parameters) is a biased indicator of the health status of corals.

There are many sublethal effects of zooxanthellae loss, including reduction in energy reserves for reproduction, tissue regeneration, and calcification (Szmant and Gassman 1990; Fitt et al. 1993; McClanahan et al. 2009). For some pocilloporid corals (Clayton and Lasker 1982; Moberg et al. 1997; Séré et al. 2010), these negative effects occur because, during optimal conditions, zooxanthellae provide 95% of the inorganic carbon and 30% of the total nitrogen that corals invest in respiration, cell division, synthesis of mucus, and formation of the skeletal matrix (Bythell 1988; Stimson 1997). The synthesized carbon surplus from these biological functions is the major source of energy for reproduction (Patton et al. 1983; Stimson 1997). Therefore, when zooxanthellae density is reduced, the coral loses its main source of energy.

Fig. 4 Changes in zooxanthellae density and color (luminosity and hue) of *Pocillopora damicornis* over time (a, c, e) and by subaerial exposure treatment (b, d, f). Bars are mean $\pm$ 0.95% confidence intervals

Another source of energy expenditure (coupled with the loss of zooxanthellae) in corals is the production of mucus (Mullen et al. 2003), which helps the organism to avoid direct contact with stressors. Specifically, mucus helps prevent drying during SAE (Romaine et al. 1997; Brown and Bythell 2005; Ritchie 2006; McClanahan et al. 2009). In our experimental colonies, no tissue loss was observed

in places where mucus or foam was deposited. In other corals, the abundance of mucocytes changes in stressful conditions. In *S. pistillata*, hyposalinity causes loss of mucocytes (Downs et al. 2009). In *Manicina areolata*, exposure to hydrocarbons increases the size of mucocytes (Peters et al. 1981). The number of mucocytes increased in bleached *Pavona clavus*, but decreased in bleached *P.*

Fig. 5 Fecundity in *Pocillopora damicornis* after subaerial exposure. Colonies were exposed for one (open circles), two (gray circles), or three months (black circles). Bars are mean $\pm$ 0.95 confidence intervals, asterisks denote significant differences

gigantea and *P. varians* (Glynn and Peters 1985). Mucus production could be interpreted as a high-cost energy investment for survival and tissue maintenance.

Given the energetically restriction for gametogenesis imposed by zooxanthellae loss and mucus production, our results demonstrate that *P. damicornis* gamete production decreased when the frequency of SAE was increased (Fig. 5). These results agree with studies that have shown that reproduction ceases during stressful events due to the high energetic cost of reproduction (Williams 1966; Ward 1995; Szmant and Gassman 1990; Omori et al. 2001; Mendes and Woodley 2002; Ward et al. 2002; Cox 2007; Birkeland 2015). Reproduction is further compromised during stressful periods because the carbon provided by the remaining zooxanthellae is needed (or relocated) for other vital functions such as maintaining growth or recovering damaged tissue (Davies 1984; Patton et al. 1977; Grottoli et al. 2004). Restricting current reproduction in favor of survival is perhaps the most prominent individual trade-off, often discussed in relation to the costs of reproduction (Stearns 1992). As coral sexual reproduction, particularly the production of eggs, is energetically expensive (Williams 1966; Ramírez-Llodra 2002) and can be inhibited by stressful conditions (like SAE), colonies tend to allocate more energy to survival (Birkeland 2015). Similarly, a

reduction in coral fecundity due to environmental disturbance can severely impact recruitment (e.g., Hughes et al. 2000; Ward et al. 2002). For example, Pengsakun et al. (2012) documented a drastic decrease in *P. damicornis* recruitment (from 4.9 and 6.8 to 0.0 and 0.6 colonies m^{-2} , respectively) during and after a bleaching event in the Gulf of Thailand. Done et al. (2010) reported a low abundance of juvenile acroporid corals on the reef flats in the GBR due to the lack of recruitment associated with reduced fecundity caused by sublethal bleaching events. Lozano-Cortés and Berumen (2016) found negatively skewed size distributions of juvenile pocilloporids on reefs that were recently impacted by a bleaching event in the central Red Sea. If the low oocyte production found in our experimental colonies of *P. damicornis* is a trend persistent in other pocilloporids in the TEP, reefs in this region are likely to be less resilient to SAE and other disturbances such as ENSO, algal overgrowth, or sedimentation.

The fact that coral growth rate was not affected by SAE (ESM Fig. S4), even with documented decreases in zooxanthellae density, mucus production, and tissue loss, suggests that *P. damicornis* at Gorgona Island is resistant to this stress (i.e., can continue normal skeletal growth during SAE; Carilli et al. 2009). Therefore, it is also possible that *P. damicornis* experiences a trade-off in which energy for sexual reproduction is reallocated to survival (specifically to maintain growth rate and tissue repair) after SAE events. Similarly, if sexual reproduction is compromised for survival, asexual reproduction (by fragmentation) could be advantageous to individual colonies and would also help to maintain reef integrity. In corals, reproductive success (gamete production, larval dispersal, recruitment, and survival) is the main mechanism for maintaining population integrity (Hughes and Tanner 2000; Vermeij 2006; Sudek et al. 2011), and both sexual and asexual reproduction are important for maintaining reef resilience and integrity. Specifically, sexual reproduction provides genetic variability and facilitates long-distance dispersal, while asexual reproduction enables well-adapted local genotypes to survive disturbances and expand to nearby localities (Aranceta-Garza et al. 2012). Additionally, fragmentation is advantageous because fragments facilitate rapid space occupation when conditions are unfavorable for sexual reproduction; hence, fragmentation reduces the risk of local genetic extinction (Chávez-Romo et al. 2013 and references therein).

Some studies indicate that asexual reproduction (mainly by fragmentation) is the dominant mode of reproduction throughout TEP reefs. Highsmith (1982) and Richmond (1985, 1987) have shown that asexual reproduction by fragmentation is a strategy that is apparently common and more successful than sexual reproduction in pocilloporids inhabiting the TEP. Glynn (1976) found that asexual

reproduction by fragmentation is a response to the environmental pressures in the TEP. In the Gulf of California (Mexico), Reyes-Bonilla (1993) found that 41% of *Pocillopora* individuals originated as settled larvae, whereas 59% grew from a fragmented branch; this indicates that asexual propagation is important in Cabo Pulmo. Similarly, Pinzón et al. (2012) reported the occurrence of coral reefs dominated by clones of *Pocillopora* at Punta Gaviotas, and Aranceta-Garza et al. (2012) documented a high degree of clonality in *P. verrucosa* from the inner coast of the Baja California peninsula.

Finally, the fact that under normal conditions *P. damicornis* has a low recruitment rate at the TEP (Birkeland 1977; López-Pérez et al. 2007; Lozano-Cortés and Zapata 2014) and that at Gorgona Island a single natural phenomenon (SAE during extreme low tides) could reduce *P. damicornis* sexual reproductive output (fecundity), highlights the vulnerability of this species to more stressful conditions. For example, during the 1997–1998 El Niño event, bleached pocilloporid corals at Gorgona Island were incapable of calcification and had reduced growth rates (Vargas-Ángel et al. 2001; Zapata and Vargas-Ángel 2003 and references therein). From this, it is possible to speculate that extreme low tides coupled with El Niño events (or even more stressful conditions) could drastically inhibit the supply of *P. damicornis* gametes or fragments (with optimal growth rates) that help to maintain population integrity and prevent local extinctions. Furthermore, the vulnerability of *P. damicornis* at other TEP reefs could be worse than at Gorgona Island reefs, given that Gorgona's reefs have exhibited a relatively high degree of resilience to past El Niño events (1982–1983 and 1997–1998) and have recovered well compared to other TEP reefs (such as those in the Galapagos Islands; Zapata 2001; Zapata and Vargas-Ángel 2003; Wellington and Glynn 2007; Glynn et al. 2017a).

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