



# Dynamic Interplay of ENSO Events and Local Hydrodynamic Parameters Drives Demography and Health Status of Gorgonian Sea Fan Populations on a Remote Tropical Eastern Pacific Island

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Gorgonian corals occurring in shallow waters are vulnerable to changing environmental conditions and human-related pressures such as pollution, overfishing, and diseases. However, anthropogenic effects on coral systems are difficult to quantify due to the lack of base-line data of unaffected populations. In order to assess the impact of global and local environmental parameters on gorgonian populations removed from direct anthropogenic impact, we evaluated demographic parameters and the health status of *Pacificorgia cairnsi* (Gorgoniidae: Octocorallia) populations in Malpelo Island, a remote and pristine marine area in the Tropical Eastern Pacific of Colombia. Specifically, we studied *P. cairnsi* densities and population size structures under different habitat and local environmental conditions. We also studied whether ENSO events and local hydrodynamic features including locality, water depth, and upwelling conditions drive *P. cairnsi* growth rates. Finally, we evaluated the prevalence of the necrotic patch disease and rates of disease recovery. Major findings were that local hydrodynamic parameters shaped *P. cairnsi* size structures, that growth rates were affected by thermal anomalies associated to ENSO events and partly by water depth, that overall disease prevalence was low (6%) and that it did not correlate with the environmental parameters studied, and that most diseased colonies (57%) recovered via tissue breakage. The fact that *P. cairnsi*, a keystone species within the regional benthic food web, is affected by thermal anomalies remains of concern because these global events are predicted to increase in frequencies and severity in the future. Nonetheless, the low level of disease prevalence found indicates that the island's pristine conditions might facilitate disease resistance. Moreover, the findings suggest an interesting trade-off between growth rates and colony recovery in shallow waters related to tissue breakage. This study provides crucial base-line data for future investigations aiming at understanding coral responses to anthropogenic pressures and the impact of global climate change on coral communities.

**Keywords:** gorgonian corals, Tropical Eastern Pacific, disease prevalence, growth rates, ENSO

## INTRODUCTION

Gorgonian corals are among the most vulnerable reef organisms (Goldberg and Wilkinson, 2004; Sánchez et al., 2019). Being long-lived and slow-growing species, they are particularly sensitive to natural disturbances (Linares et al., 2008). Moreover, gorgonian corals are increasingly affected by disease outbreaks and abundances of many species have declined worldwide (Bourne et al., 2009; Sánchez et al., 2011, 2014). This is of great concern given that these organisms play a key ecological role in benthic communities and are considered “engineering species,” shaping the habitat and increasing its complexity by forming three-dimensional structures (Jones et al., 1994; Ballesteros, 2006; Sánchez et al., 2016). Additionally, they provide substrate and habitat for associated biota, thus increasing biomass and biodiversity of benthic communities (Buhl-Mortensen and Mortensen, 2005; Sánchez et al., 2016). Therefore, changes in gorgonian abundances in response to natural and anthropogenic disturbances may have dramatic effects on entire communities (Garrabou and Harmelin, 2002).

Anthropogenic effects on coral systems, however, are often difficult to quantify due to the lack of base-line data for unaffected populations. Thus, information from populations largely removed from human impact, such as those on the offshore Island Malpelo located in the Tropical Eastern Pacific (TEP), is particularly valuable. This uninhabited island is considered to be under pristine conditions (Zapata and Vargas-Ángel, 2003; Quimbayo et al., 2016). While gorgonians are typically diverse in the TEP (Bayer, 1953; Van Oppen et al., 2005; Sánchez, 2016), rocky reef environments of Malpelo Island are mainly dominated by species of the genera *Leptogorgia* and *Pacifigorgia* (Sánchez et al., 2011; Sánchez, 2016). Of these, *Pacifigorgia cairnsi*, which is endemic to the TEP, is considered a keystone species in Malpelo. It dominates the infralittoral seascape by forming gorgonian forests on rocky outcrops and walls up to 30 m depth (Sánchez et al., 2011; Sánchez and Ballesteros, 2014). This species also plays an important ecological role due to, for instance, strong interactions with invertebrates such as ovulid gastropods and fishes including *Oxycirrhites typus* and *Dermatolepis dermatolepis* (Sánchez et al., 2016; Sánchez, 2016). Therefore, the loss or decrease of *P. cairnsi* in Malpelo would dramatically affect the entire ecosystem; a fact that makes its study and conservation a crucial matter (*sensu* Mills et al., 1993).

These gorgonian populations cope with cold waters and high levels of suspended matter during seasonal upwelling (from December to March), as well as anomalous increases in seawater temperature during sporadic El Niño-Southern Oscillation (ENSO) events (Glynn and Colgan, 1992; Zapata et al., 2010). Moreover, in recent years, *P. cairnsi* die-offs in Malpelo have been associated to disease outbreaks (Sánchez et al., 2011; Barrero-Canosa et al., 2013), namely the “necrotic-patch disease” (NPD) (Quintanilla et al., 2018).

However, the impact of natural environmental stressors on *P. cairnsi* communities in the pristine island of Malpelo remains poorly understood, calling for coral response studies involving demographic traits such as growth rates, density, size

structure, and disease susceptibility (*sensu* Bruno et al., 2011; Rico-Esenaro et al., 2019).

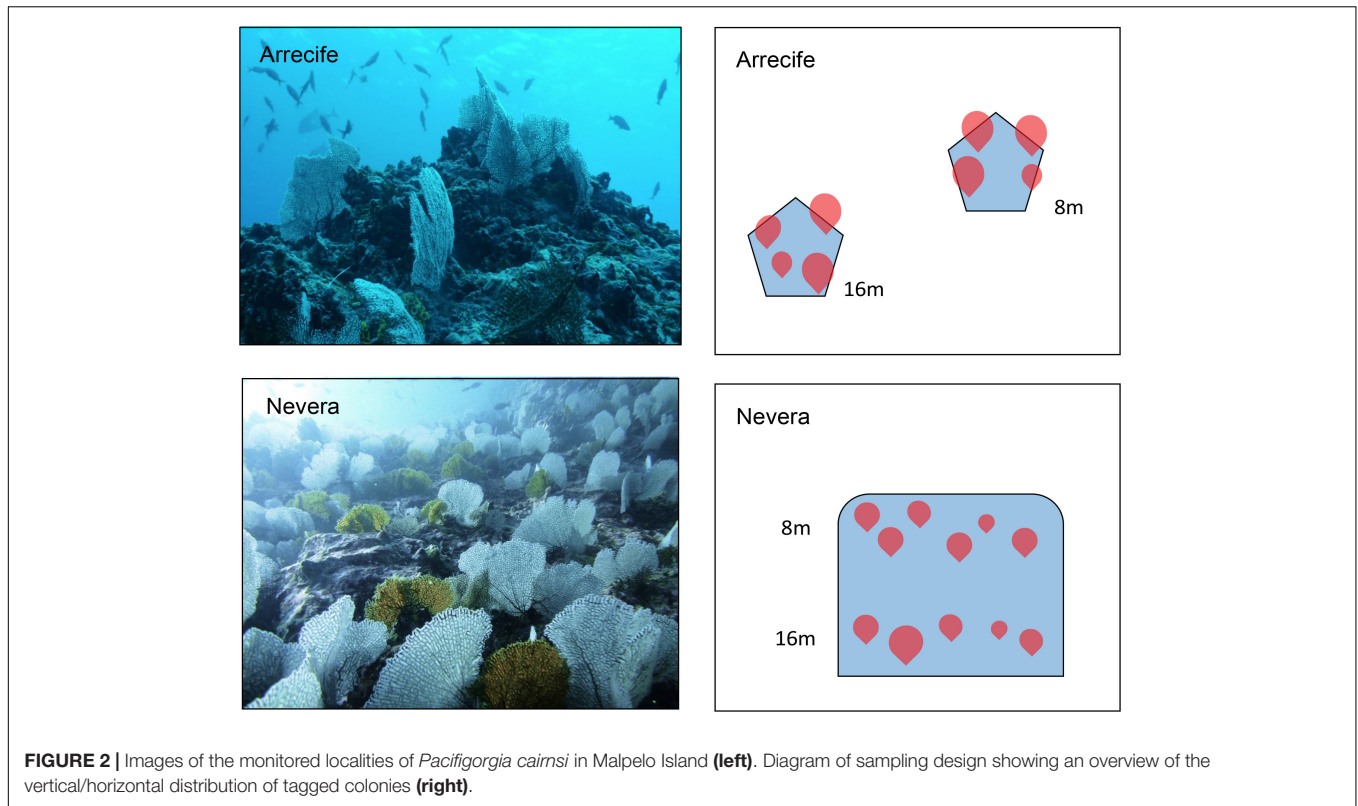
In this study, we therefore assessed the impact of ENSO events and local-scale environmental parameters on the demography and health status of gorgonian populations in the absence of direct anthropogenic pressures. First, we compared *P. cairnsi* densities and population size structures under different habitat and hydrodynamic settings to understand how local conditions drive these population parameters. We then identified the respective environmental features affecting growth rates. Finally, we evaluated NPD prevalence and colony recovery to assess their health status.

## MATERIALS AND METHODS

### Study Site and Data Collection

The study was conducted in the TEP island Malpelo, which is located about 500 km off the Colombian coast (3°58′30″N, 81°34′48″W) (Figure 1). This Fauna and Flora Sanctuary is a marine protected area and a World Heritage Site that belongs to the Marine Conservation Corridor of the TEP together with Gorgona (Colombia), Cocos (Costa Rica), Coiba (Panamá), and Galapagos Islands (Ecuador). A total of 80 *P. cairnsi* colonies of different sizes were studied in two localities exposed to leeward or windward conditions depending on dry/wet seasons and wind patterns (Velásquez-Jiménez et al., 2016). The first locality, Arrecife, is located in the northeastern part of the island, which is constantly impacted by strong waves. *P. cairnsi* colonies are patchy distributed on large stones along the rocky reef. The second locality, Nevera, is located in a sheltered





bay in the southwestern part of the island. *P. cairnsi* sea fans are continuously distributed along a wall up to depths of approximately 18–20 m (Figure 2). However, hydrodynamic conditions change considerably with water depth. Accordingly, depths of up to 10 m are influenced by strong waves and tidal movements (Velásquez-Jiménez et al., 2016). To reflect these different conditions, we studied in both sites populations in “shallow” (8 m) and “deep” (16 m) waters.

To assess the size structure, 10 quadrants each (50 × 50 cm) were randomly placed at the two depths (8 and 16 m) in the Arrecife and Nevera localities (40 quadrants in total) in June 2016. All colonies within each quadrant were counted and their total areas were registered. Underwater pictures (PowerShotG12, Canon) were taken together with an acrylic board containing a defined scale. Most underwater photographs had to be corrected for skewedness by using a standardized grid as they were taken with a deviation from the vertical plane of the colony. Total colony area was obtained by contouring the colony perimeter of each corrected photograph using Image J® software (Research Services Branch – NIMH, Bethesda, MD, United States). Colonies measuring <5 cm<sup>2</sup> were considered recruits as defined by Gomez et al. (2014) and six size classes were delimited: <5, 5–100, 101–200, 201–300, 301–400, and >400 cm<sup>2</sup>.

To study gorgonian growth rates, the total area of each tagged colony was registered by underwater pictures during eight consecutive monitoring times, covering a 3-year study period: July 2013, December 2013, March 2014, July 2014, March 2015, September 2015, March 2016, and June 2016. Growth rates for each colony were obtained by calculating the difference

in area (cm<sup>2</sup>) between two consecutive monitoring times and expressed as cm<sup>2</sup> month<sup>-1</sup>. Additionally, tissue breakage, colony recovery, and disease prevalence (% of diseased colonies) were reported over the study period.

According to the National Oceanic and Administration (NOAA)<sup>1</sup>, abnormal positive seawater temperatures associated to ENSO events ranged from +0.5 to +2.3°C during the monitoring period. As the periods July 2014–March 2015 and March 2016–June 2016 included more months with abnormal positive temperatures than with normal ones, they were considered as ENSO periods (Table 1). “La Niña” events (the cool phase of ENSO) did not occur during the study period.

<sup>1</sup><http://www.cpc.ncep.noaa.gov>

**TABLE 1 |** Upwelling conditions and ENSO events during monitoring periods.

Monitoring period	Upwelling condition	ENSO event
July 2013–December 2013	Absent	−0.4/−0.2 (ENSO absent)
December 2013–March 2014	Present	−0.2/−0.4 (ENSO absent)
March 2014–July 2014	Absent	−0.4/+0.2 (ENSO absent)
July 2014–March 2015	Present	+0.2/+0.6 (ENSO present)
March 2015–September 2015	Absent	+0.6/+1.8 (ENSO present)
September 2015–March 2016	Present	+1.8/+2.2 (ENSO present)
March 2016–June 2016	Absent	+2.2/+0.5 (ENSO present)

For each monitoring period, the oscillation range of temperatures is shown. See **Supplementary Material** for sea surface water temperature (SST) data at Malpelo Island reflecting upwelling conditions during the study period.

**TABLE 2** | Number of *Pacifigorgia cairnsi* colonies and average densities in Malpelo Island in June 2016.

Sampling site	Total number of colonies	Average density ( $\pm$ SD)
Arrecife shallow (8 m)	216	24 ( $\pm$ 6.93)
Arrecife deep (16 m)	140	14 ( $\pm$ 8.89)
Nevera shallow (8 m)	188	18.8 ( $\pm$ 6.54)
Nevera deep (16 m)	172	17.2 ( $\pm$ 6.81)
Total	716	8.5 ( $\pm$ 7.92)

Average density is expressed as number of colonies/m<sup>2</sup> ( $\pm$ SD).

### Data Analyses

Differences in size structures and densities between localities and water depths were assessed using Kruskal–Wallis and Mann–Whitney tests as implemented in PAST v3.12 (Hammer et al., 2001). The significant level was adjusted for the number of comparisons tested by Bonferroni correction. To evaluate the effect of five factors [locality, water depth, upwelling conditions (local thermal conditions), ENSO events (global thermal conditions), and colony area] on growth rates and disease prevalence, linear mixed effect (LME) models were constructed using the R v.3.1.2 (R Studio Team, 2015) package nlme (Pinheiro et al., 2009). Colony and periods were treated as random effects; locality, water depth, local and global thermic conditions, and colony area as fixed effects. Full and reduced models were fitted using a restricted maximum likelihood (REML) approach and models were compared using Akaike’s Information Criterion (AIC).

To understand site-specific effects, LME models were also applied individually to the Arrecife and Nevera datasets.

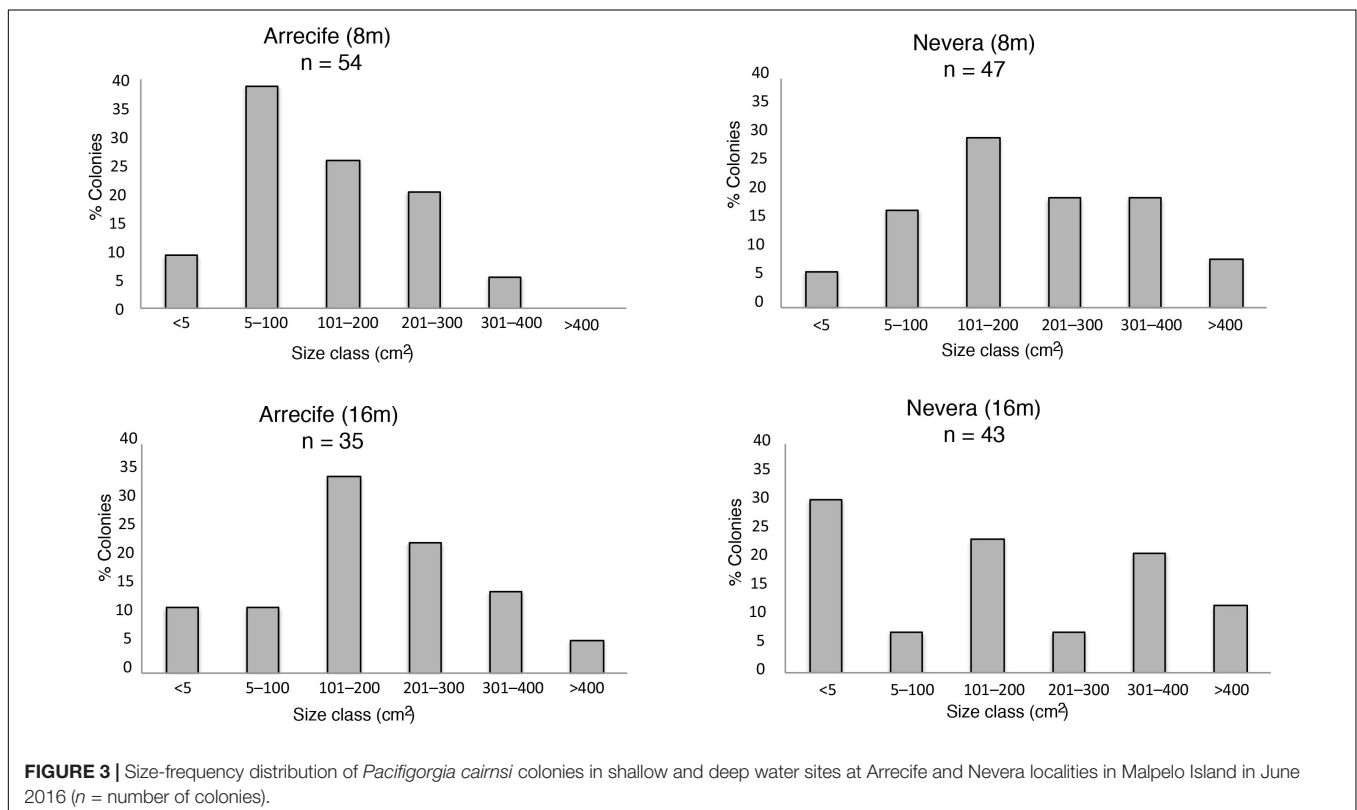
## RESULTS

### Density and Size Structure

The average *P. cairnsi* density observed was 18.5 ( $\pm$ 7.92) col m<sup>-2</sup> and did not differ between localities (Mann–Whitney test,  $P > 0.05$ ,  $P = 0.96$ ) or water depths (Mann–Whitney pairwise test,  $P > 0.008$ ,  $P = 0.93$ ) (Table 2). Images from a total of 179 *P. cairnsi* colonies were analyzed to study the size structure in June 2016. Overall, mean colony areas did not show significant differences between Arrecife and Nevera (Mann–Whitney test,  $P > 0.05$ ), but displayed significant differences between shallow sites (Mann–Whitney pairwise test,  $P < 0.008$ ). In particular, the Arrecife shallow site showed lower proportions of large colonies and higher percentage of young colonies (<100 cm<sup>2</sup>) than Nevera shallow. Additionally, the percentage of recruits (<5 cm<sup>2</sup>) and big colonies (>300 cm<sup>2</sup>) were higher in Nevera deep than in any other site (Figure 3).

### Growth Rates

The average growth rate measured for *P. cairnsi* was 6.16 cm<sup>2</sup> month<sup>-1</sup>. Visual examination of residuals of the best-fit LME models indicated that the assumptions of normality, homogeneity, and independence were all met. Global thermal conditions (ENSO events) and water depth had a significant effect on Nevera *P. cairnsi* growth rates ( $P = 0.001$  and  $P = 0.045$ ,



**FIGURE 3** | Size-frequency distribution of *Pacifigorgia cairnsi* colonies in shallow and deep water sites at Arrecife and Nevera localities in Malpelo Island in June 2016 ( $n$  = number of colonies).



**TABLE 3** | Results of the best-fitted linear mixed effect model for parameters driving *Pacifigorgia cairnsi* growth rates in Malpelo Island.

Locality/parameter	Value	Std. error	DF	t-value	p-value
<b>Arrecife</b>					
Area	0.028	0.015	18	1.843	0.082
Depth	-0.226	0.447	35	-0.505	0.617
Thermal upwelling	-3.684	2.724	18	-1.352	0.193
ENSO positive	0.082	3.197	18	0.025	0.979
<b>Nevera</b>					
Area	0.006	0.009	3	0.625	0.576
Depth	-0.945	0.453	32	-2.086	0.045*
Thermal upwelling	4.409	3.493	42	1.262	0.213
ENSO positive	-12.557	3.699	42	-3.394	0.001**
<b>Arrecife + Nevera</b>					
Area	0.01	0.007	3	1.295	0.285
Depth	-0.546	0.307	68	-1.775	0.08
Thermal upwelling	2.631	2.552	63	1.03	0.306
ENSO positive	-6.934	2.593	63	-2.674	0.009**

\* $p < 0.05$ , \*\* $p < 0.01$ .

respectively). Growth rates of colonies from Arrecife were not significantly affected by the studied parameters. Considering both localities together, only ENSO events had an effect on growth rates (Table 3).

## Disease Prevalence, Tissue Breakage, and Colony Recovery

None of the studied parameters had a significant effect on NPD prevalence. Overall, mean disease prevalence registered during the eight monitoring times was 6.02% ( $\pm 9.49\%$ ) (Table 4). Overall, 37.80% of the healthy colonies showed tissue breakage at some point during the study period. In particular, the Arrecife shallow and deep sites displayed 33.34 and 15.78% of healthy-broken colonies, respectively, and Nevera shallow and Nevera deep sites 61.12 and 42.85%, respectively. 57% of diseased colonies recovered from NPD; all of them showed signs of tissue breakage (Figure 4).

## DISCUSSION

In this study, we assessed the effects of global (i.e., ENSO events) and local hydrodynamic parameters on the demography of *P. cairnsi* populations and evaluated their health status

in a remote marine area, currently not directly affected by anthropogenic processes. Our major findings were: (i) local hydrodynamics defined *P. cairnsi* size structures, (ii) growth rates were driven by thermal anomalies and partly by water depth, (iii) disease prevalence was low and did not correlate with any of the studied environmental parameters, and (iv) most diseased colonies recovered via tissue breakage.

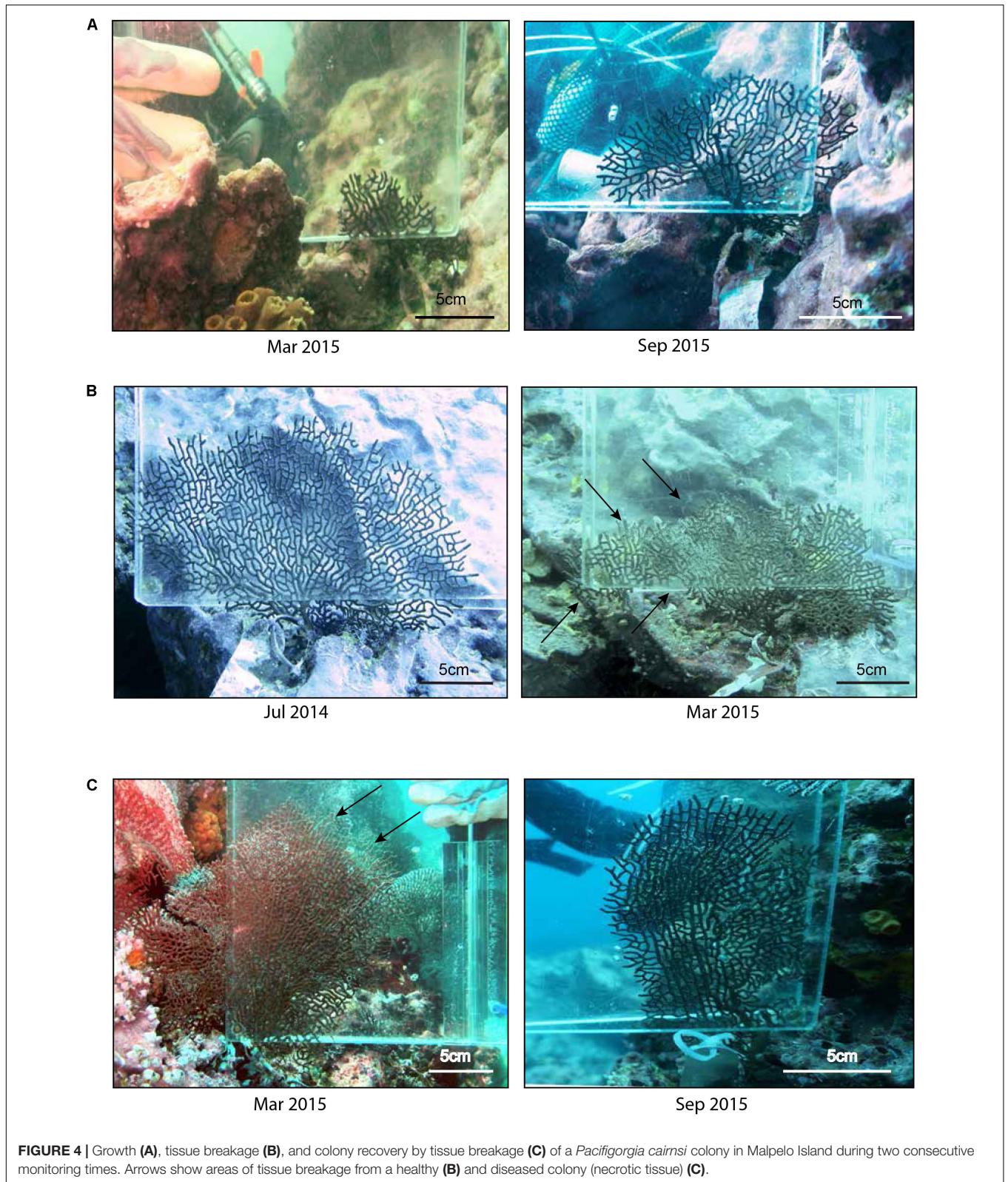
*Pacifigorgia cairnsi* densities did not differ between the localities and sites (water depth) studied. Although this pattern is consistent with those from Coiba Island (Panamanian TEP), the average density of *P. cairnsi* in Malpelo Island (18 col  $m^{-2}$ ) was considerably higher than in Coiba Island (1.2 col  $m^{-2}$ ) (Gomez et al., 2014). Patchy species distribution of gorgonians within TEP areas is attributed to variable oceanographic and environmental conditions (e.g., upwelling, freshwater and runoff sediment inputs, suspended matter, etc.) (Zapata et al., 2010; Barrero-Canosa et al., 2013; Gomez et al., 2014).

However, size structures of *P. cairnsi* colonies in Malpelo Island differed among localities and sites. Arrecife shallow showed both the highest proportion of small colonies and the lowest percentage of large colonies. As hydrodynamic forces may cause dislodgement and tissue breakage (Lasker, 1990; Chang et al., 2007), the permanent exposition of this locality to strong water motions might make local *P. cairnsi* colonies particular vulnerable. Additionally, the Nevera deep site exhibited the greatest percentage of both recruits and large colonies. Abiotic factors including light intensity, temperature, and water movement may considerably change with water depth (Garrabou et al., 2002; Mass et al., 2007) and thus modulate demographic parameters of benthic organisms such as gorgonian corals. Sheltered environments associated with deep sublittoral habitats in the Mediterranean Sea, for example, allow *Eunicella singularis* gorgonian populations to reach larger colony sizes than in shallow waters (Gori et al., 2011). Similarly, larger *Gorgonia ventalina* colonies were found at deeper environments in the Gulf of Mexico, where water motion decreases significantly with water depth (Jordán-Dahlgren, 1989). Therefore, local perturbations such as high hydrodynamic forces in shallow waters may explain the higher percentage of broken colonies both in Nevera and Arrecife shallow sites compared to Nevera deep site. Additionally, the latter site showed the highest recruitment rate, suggesting that reproductive success increases with colony size (Coma et al., 1995).

We also found that growth rates of *P. cairnsi* were affected by thermal anomalies associated with ENSO events. Average

**TABLE 4** | NPD prevalence of *Pacifigorgia cairnsi* (% diseased colonies) in Malpelo Island during eight monitoring times (July 2013, December 2013, March 2014, July 2014, March 2015, September 2015, March 2016, and June 2016).

Site	July 2013	December 2013	March 2014	July 2014	March 2015	September 2015	March 2016	June 2016
Arrecife shallow	0	3.57	0	0	11.11	8	6.67	0
Arrecife deep	0	13.33	50	7.69	0	6.25	6.67	0
Nevera shallow	0	2.7	16.67	0	9.09	8.33	0	-
Nevera deep	0	0	8	7.14	6.67	5	3.7	-
Average	0	4.9	18.67	3.71	6.72	6.90	4.26	0
(SD)	(0)	(5.82)	(21.97)	(4.29)	(4.83)	(1.56)	(3.17)	(0)



temperatures are a major factor controlling coral growth rates (Chindapol et al., 2013). Specifically, elevated seawater temperatures related to ENSO episodes exercise stress on corals

as there is a thermal optimum for coral growth (Lough and Cooper, 2011). Coral responses to thermal stress are well studied in zooxanthellate reef-building corals and include changes in



coral physiology, reduction of growth rates, up-regulation of heat-shock proteins, coral bleaching, and ultimately die-offs of entire coral reefs (Ainsworth et al., 2008; Voolstra et al., 2009; Lough and Cooper, 2011). In particular, recurrent ENSO episodes have increased thermal stress in Caribbean and Eastern Pacific reef-building corals, leading to bleaching and growth declines (Glynn et al., 2001; Manzello, 2010; Hetzinger et al., 2016). However, while thermal stress response (e.g., up-regulation of stress proteins and bleaching; Prada et al., 2009; Dias and Gondim, 2015; Löhelaid et al., 2015) has also been observed in zooxanthellate octocorals, the latter organisms seem to be more resilient to environmental stressors and show higher recovery rates after ENSO episodes than reef-building corals (Schleyer and Benayahu, 2010; Tsounis and Edmunds, 2017).

Nevertheless, responses of azooxanthellate octocorals, such as *P. cairnsi*, to thermal stress remain largely elusive. Despite the assumption that octocorals represent the most resistant coral organisms in regard to thermal stress (Tsounis and Edmunds, 2017), our findings indicate that azooxanthellate gorgonians are also vulnerable (as zooxanthellate ones) to abnormal temperatures and changes in productivity and nutrient levels associated with ENSO events (Harvell et al., 2001; Turk et al., 2011). This is of particular relevance as these global-scale events are predicted to increase in frequency and severity over the next decades (Santoso et al., 2013; Cai et al., 2014). It has also been shown that the coral recovery capacity declines with increasing frequency of ENSO episodes; exacerbated by the fact that ENSO-associated effects on coral communities may last for months or years following initial impact (Cai et al., 2014; Glynn et al., 2017). This is of great concern for benthic communities in Malpelo Island as *P. cairnsi* is a keystone species there, and its decline might have severe adverse effects on the entire benthic food web.

Apart from temperature, water motion and light are also main environmental parameters affecting coral growth (Todd, 2008; Chindapol et al., 2013). Colonies in deeper waters, for example, display decreased growth rates, minimizing metabolic demand under low-light conditions (Grigg, 2006; Kahng et al., 2010). However, *P. cairnsi* lacks zooxanthellae and light may thus not be a major limiting factor. In fact, our results suggest that hydrodynamic forces might be the main parameter affecting growth rates. Due to wave-induced tissue breakage, shallow-water colonies have to allocate considerable energy resources to tissue repair (Lartaud et al., 2016). Accordingly, the fact that depth did not contribute significantly to decreased growth rates in Arrecife deep suggests that these colonies, as the shallow ones, are probably allocating energy in tissue repair due to wave-induced tissue breakage. In contrast, deeper (and larger) colonies from Nevera deep might be able to allocate more energy to recruitment rather than to tissue repair and growth due to the sheltered environment as noted in other gorgonian corals (Coma et al., 1995; Heino and Kaitala, 1999).

Our results also showed that the prevalence of NPD affecting *P. cairnsi* in Malpelo Island was low (i.e., 6%) compared to coral diseases in other areas. For example, aspergillosis affects 6–39% of *G. ventalina* colonies throughout the Caribbean Sea

(Weil, 2004; Toledo-Hernández et al., 2007). These high levels of disease prevalence in the Caribbean Sea, compared to the TEP, have been attributed to higher levels of long-term thermal and anthropogenic stress in the former region (Barton and Casey, 2005; Ruiz-Moreno et al., 2012).

The low level of NPD prevalence observed in our study sites might thus be related to the pristine conditions of Malpelo Island. Moreover, the fact that we did not find correlations between local/global environmental parameters and NPD prevalence suggests a random and occasional behavior of the disease in *P. cairnsi*. This assumption is also supported by the fact that NPD affecting *P. cairnsi* in Malpelo Island behaves opportunistically and is likely in a state of microbial dysbiosis (Quintanilla et al., 2018). Interestingly, while tissue breakage in shallow, wave-exposed waters is energetically costly and affects growth rates, it also facilitates recovery from NPD via physical loss of affected, peripheral tissues. Overall, the NPD patterns observed in *P. cairnsi* colonies in Malpelo Island indicate that coral diseases are also present in pristine marine areas, being part of a natural population dynamic.

## CONCLUSION

Our work provides crucial base-line data on demographic and health parameters of gorgonian populations in a remote and pristine marine area removed from direct anthropogenic impact. Overall, colonies developed into mature gorgonian populations, showing high-density levels and size structures driven mostly by local hydrodynamics. However, global thermal conditions such as ENSO events negatively affected *P. cairnsi* growth rates. This is of great concern as the taxon represents a key stone species within the benthic food web and as these global-scale events are predicted to increase in frequencies and severity under conditions of climate change. Nonetheless, the low levels of disease prevalence found suggest that the island's pristine conditions might facilitate disease resistance. Moreover, our results indicate an interesting trade-off between growth rates and colony recovery in shallow waters related to tissue breakage. Finally, this study facilitates future research aimed at understanding coral responses to anthropogenic pressures and the impact of global climate change on coral communities.

## DATA AVAILABILITY STATEMENT

All datasets generated for this study are included in the article/**Supplementary Material**.

## AUTHOR CONTRIBUTIONS

EQ, TM, TW, and JS contributed to the design of the study, revised the manuscript, and approved the final text. EQ conducted the sampling, generated and analyzed the data, and wrote the manuscript. EQ and TM interpreted and discussed the data results.

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## SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2019.00694/full#supplementary-material>

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**Conflict of Interest:** The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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