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## Note

Q2 Colony size–frequency distribution of pocilloporid juvenile corals along a natural  
 3 environmental gradient in the Red Sea

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## ABSTRACT

Coral colony size–frequency distributions can be used to assess population responses to local environmental conditions and disturbances. In this study, we surveyed juvenile pocilloporids, herbivorous fish densities, and algal cover in the central and southern Saudi Arabian Red Sea. We sampled nine reefs with different disturbance histories along a north–south natural gradient of physicochemical conditions (higher salinity and wider temperature fluctuations in the north, and higher turbidity and productivity in the south). Since coral populations with negatively skewed size–frequency distributions have been associated with unfavorable environmental conditions, we expected to find more negative distributions in the southern Red Sea, where corals are potentially experiencing suboptimal conditions. Although juvenile coral and parrotfish densities differed significantly between the two regions, mean colony size and size–frequency distributions did not. Results suggest that pocilloporid colony size–frequency distribution may not be an accurate indicator of differences in biological or oceanographic conditions in the Red Sea.

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## 1. Introduction

A key mechanism by which coral reef ecosystems are capable of recovering from natural or anthropogenic disturbances is their ability to replenish their populations through the successful recruitment of new individuals (Bak and Engel, 1979; Caley et al., 1996). The establishment and survival of juvenile corals are indicative of good conditions for the development and growth of corals, and consequently highlight the importance of studying demographic processes (Dunstan and Johnson, 1998; Babcock et al., 2003). Although many factors may influence recruitment and colonization patterns of reef organisms (Burt et al., 2009; Trapon et al., 2013a, 2013b; Lozano–Cortés and Zapata, 2014a), there is little information about coral reproduction and demography in the Red Sea (Berumen et al., 2013). While there are a few accounts of inferred or observed spawning patterns from the Red Sea (Shlesinger and Loya, 1985; Shlesinger et al., 1998; Hanafy et al., 2010; Bouwmeester et al., 2011a, 2011b, 2015), published literature on coral recruitment in this region is restricted to the far northern area (Gulf of Aqaba) and is focused primarily on settlement in artificial plates (Glassom et al., 2004; Abelson et al., 2005; Glassom and Chadwick–Furman, 2006).

Bak and Meesters (1998); Meesters et al. (2001) and Vermeij and Bak (2002) used colony size–frequency data and a lognormal size

distribution model of corals in the Caribbean Sea to quantify characteristics of the coral populations (e.g., coefficient of variation, mode, and skewness) and related these measurements to reef environment (e.g., degradation level). These authors used skewness to compare the proportion of small vs. large colonies as a proxy for the establishment of new juvenile corals in reefs with different degrees of pollution. They found differences in these size–frequency variables among- and within-species in different reef localities and suggested that these characters could provide a tool to more generally estimate the response of coral populations to changes in the environment. These studies reported a relationship between negative values of skewness and more degraded reefs. Similar results were found by Crabbe (2009) and Lozano–Cortés and Zapata (2014b) in other Caribbean coral reefs that had been impacted by bleaching events and tourism (Hawkins et al., 1999), as well as by Bauman et al. (2013) in reefs under extreme environmental conditions (high temperature and salinity) in the Arabian Gulf.

The Red Sea is characterized by a latitudinal gradient in physicochemical variables such as salinity (42–37 psu), temperature (20–32 °C), turbidity and primary productivity (low–high), creating distinct habitats in the north–central region from the southern region (Raitos et al., 2011, 2013, Nanninga et al., 2014). The separation between these zones occurs around 20°N where there is a notable shift in both reef development patterns and oceanographic conditions (i.e., such as a shift from clear and oligotrophic waters in the north–central region to more turbid, warmer, nutrient-rich waters with less reef development in the south [Roberts et al., 1992]). This north–south latitudinal gradient is also strongly seasonal. For example, the water temperature

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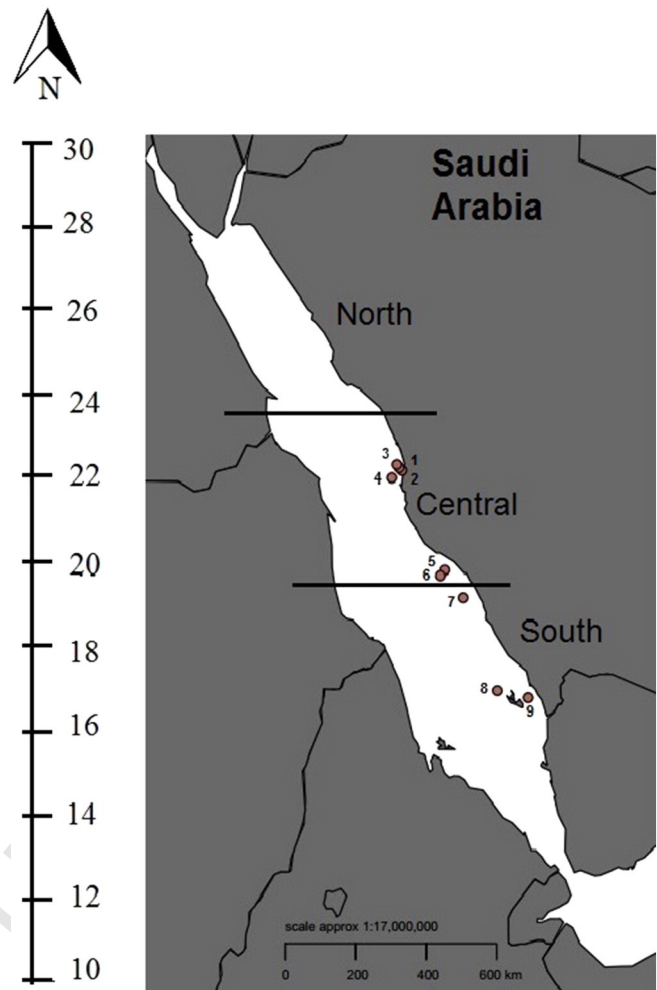
changes from 26 to 20 °C (summer–winter) in the north and from 32 to 28 °C in the south. Similarly, Raitos et al. (2013) documented a seasonal pattern for Chl-*a* with the highest concentrations during the winter and lowest during the summer. These authors attributed this seasonality to processes of vertical mixing (north) and high-nutrient water intrusion (south) during winter months, and the occurrence of strong water stratification in summer time. This marked environmental shift has also been associated with changes in biological factors of reef organisms such as abundance, community composition, and richness, as well as restrictions in gene flow between regions (Roberts et al., 1992; Froukh and Kochzius, 2007; Nanninga et al., 2014; Sawall et al., 2014a; Giles et al., in press but see Robitzsch et al., 2015). More recently, differences in zooplankton diversity and zooxanthellae density in corals have been documented along the aforementioned gradient (Pearman et al., 2014; Sawall et al., 2014b). Finally, directly inverse relationships have been reported elsewhere between juvenile coral density and fish density or algal cover (Box and Mumby, 2007; Mumby et al., 2007; Trapon et al., 2013a). Although herbivory and grazing are generally considered to be beneficial for reef health (Mumby et al., 2006; Mumby, 2009), grazing fishes may be a major source of juvenile coral mortality via incidental removal or predation while feeding (Penin et al., 2010; Doropoulos et al., 2012). On the other hand, negative interactions between algal cover and coral juvenile density are expected due to competition for space. As such, high algal cover is typically associated with low coral recruitment (Hughes et al., 2007; Mumby et al., 2007; Hoey et al., 2011).

In this study, we quantified the abundance and size of pocilloporid juvenile corals in nine coral reefs in the central and southern regions of the Saudi Arabian Red Sea. The studied reefs experience different oceanographic regimes and levels of disturbances, including biological variables such as density of grazing fishes and algal cover. By assessing the size-frequency distributions of juvenile populations, we aimed to explore the relationship, if any, between these demographic variables and reef conditions. As negatively skewed populations have been previously associated with less favorable environmental conditions, we expected to find more negative values in the southern Red Sea in comparison with the central region where coral populations are potentially under suboptimal conditions for development (e.g., reduced somatic growth and less successful reproduction). The Red Sea's natural environmental gradient represents an excellent opportunity to study the variation of juvenile colony size-frequency and its relationship with the reef environment.

## 2. Materials and methods

### 2.1. Study sites and species

A total of nine coral reefs (central and southern regions) were surveyed in the Saudi Arabian Red Sea spanning 670 km of coastline (Fig. 1, Table 1). In the central region, six reefs (one inshore, three mid-shelf, and two offshore) near Thuwal and Al Lith were surveyed between October 2013 and May 2014. Both sampling months in our study can be considered to be in the Red Sea summer season (May is early summer while October is late summer). Published studies on coral recruitment in the Red Sea using artificial settlement plates (Glassom et al., 2004; Abelson et al., 2005; Glassom and Chadwick-Furman, 2006) have reported high abundance of pocilloporid recruits in comparison with other coral species, highlighting the suitability of this family for targeted coral recruitment studies. Spawning in *Pocillopora* in the Red Sea has been reported to occur at the end of May (Bouwmeester et al., 2011a, 2015) and growth rates for pocilloporids have been reported to be between 35 to 50 mm per year (Dullo, 2005). Corals that successfully recruited and survived to the juvenile stage were probably detected at our sampling sites despite the difference in sampling dates



**Fig. 1.** Map of reefs surveyed (red circles) in the central and southern Red Sea, Saudi Arabia. The axis in the left shows the latitude. The division of the basin into northern, central and southern Red Sea is done considering marked environmental and genetical shifts previously reported (e.g., Raitos et al., 2013; Nanninga et al., 2014). Numbers indicate the nine studied reefs listed in the Table 1. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

In the southern region, three coral reefs (one mid-shelf and two off-shore) were sampled in the Farasan Banks and Farasan Islands area in February 2014. Some reefs located in the central region were affected by a major bleaching event in the summer of 2010. This bleaching event affected between 14 and 74% of the coral colonies in this region (Furby et al., 2013; Pineda et al., 2013). In the aforementioned bleaching events, pocilloporids exhibited bleaching based on their proximity to shore and depth, ranging from 0.5 to 0.7% in deeper, offshore waters to 60.9–75.0% in shallow, inshore areas. On the other hand, Riegl et al. (2012) inferred (from the state of coral communities) that the Farasan Islands were impacted by a bleaching event more than a decade ago, and regional crown-of-thorns starfish outbreaks were observed in 2006 (Riegl et al., 2013), but it is unknown if our specific study reefs were affected (Table 1).

Our study targeted pocilloporid coral species, e.g., *Pocillopora damicornis*, *Pocillopora verrucosa*, *Seriatopora hystrix*, *Stylophora pistillata*. These species utilize a brooding reproductive strategy and tend to be among the most commonly observed new recruits in coral communities in the Red Sea (cite examples from above). As such, the pocilloporids are an ideal study group in this region. While we acknowledge major taxonomic limitations associated with in-situ identification of some pocilloporid species (e.g., Keshavmurthy et al., 2013), our

**Table 1**

Juvenile coral abundance, fish density and algal cover for nine coral reefs in the Saudi Arabian Red Sea.

Reef location	Type of reef	N	Mean coral size (mm)	Coral size range (mm)	Coral density (ind/m <sup>2</sup> )	Bleaching history	Skewness	Parrotfish density (ind/m <sup>2</sup> )	Macroalgae cover (%)
<i>Central</i>									
1. Fsar	Inshore	44	31.03 ± 10.02	15–50	2.93 ± 1.03	2010	−0.2148	0.11 ± 0.04 (4)	3.50 ± 4.43 (4)
2. Al Fahal	Midshelf	54	31.81 ± 9.80	15–50	3.56 ± 1.88	2010	−0.1982	0.06 ± 0.01 (4)	1.00 ± 1.15 (5)
3. Abu Madafi	Offshore	66	26.86 ± 10.12	6–50	4.40 ± 3.92	2010	−0.9914	0.02 ± 0.02 (5)	0.50 ± 0.84 (6) <sup>c</sup>
4. Sahib Kabir	Offshore	48	26.02 ± 10.09	5–46	3.20 ± 2.21	2010 <sup>a</sup>	−0.7010	–	–
5. Manila Bay	Midshelf	58	31.63 ± 9.65	16–50	3.87 ± 1.88	No data	−0.9510	0.01 ± 0.01 (3)	–
6. Central Reef	Midshelf	58	31.55 ± 10.34	14–50	3.87 ± 1.25	No data	−0.1082	0.01 ± 0.01 (3)	0.00 ± 0.00 (3) <sup>c</sup>
<i>Southern</i>									
7. Sahib Daqua	Offshore	31	30.15 ± 11.58	14–50	2.07 ± 1.39	No data	0.2066	0.02 ± 0.01 (6)	0.00 ± 0.00 (6) <sup>c</sup>
8. Dhi Dahaya	Midshelf	32	27.27 ± 9.61	5–49	2.13 ± 1.51	No data <sup>b</sup>	−1.1088	0.42 ± 0.08 (5)	19.33 ± 5.60 (6) <sup>c</sup>
9. Zahrat Durakah	Offshore	63	28.96 ± 10.46	6–50	4.20 ± 2.70	No data <sup>b</sup>	−0.3990	0.27 ± 0.10 (3)	2.78 ± 2.03 (3) <sup>c</sup>

Mean ± standard variation is given for each variable. N (number of juvenile corals). The number in parenthesis under the category of parrotfish density and macroalgae cover indicates the number of transects surveyed in a given reef.

<sup>a</sup> Furby et al. (2013) found that the nearest two offshore reefs were affected by the 2010 bleaching event, so we assume that this reef was similarly affected.

<sup>b</sup> Riegl et al. (2012) inferred that bleaching occurred in the Farasan Islands, but it is unknown if bleaching affected these specific reefs.

<sup>c</sup> (Bouwmeester, unpublished data).

analyses only consider family-level data and are thus not impacted by species-level ambiguities.

## 2.2. Juvenile coral sampling

Surveys of juvenile pocilloporid corals were conducted on the exposed side of all sites at a 5 m depth. During the sampling, we followed the criteria proposed by Glynn et al. (1996) to differentiate between sexually originated coral recruits from remnant coral colonies. Juvenile corals ( $\leq 50$  mm maximum diameter) were surveyed systematically within 15 replicate 1 m<sup>2</sup> quadrats placed haphazardly on the reef. Each quadrat was divided into a 4 × 4 grid and the resulting 16 sub-quadrats (0.0625 m<sup>2</sup> each) were each carefully inspected to maximize the detection of juveniles. The maximum and minimum diameter of each colony was measured at the base of the colony to the nearest mm using calipers. The colony area (cm<sup>2</sup>) was estimated using the formula for a half-sphere (Area = 2 × [(maximum diameter/2 × minimum diameter/2) × π]). These area data were logarithmically transformed and the skewness (g<sub>1</sub>) was calculated for each coral reef (Meesters et al., 2001).

## 2.3. Fish density and algal cover

To determine the relationship between the abundance and size of juvenile corals with fish density, visual censuses of parrotfishes were carried out along a belt transect 50 m × 4 m (between three to six replicates) at 5–10 m depth, parallel and adjacent to the area where benthic surveys were conducted. Parrotfishes were selected for this study because their feeding activity has been documented as beneficial for coral recruitment and growth (Mumby, 2009). All of the sampling (corals, fish, and algae) was done simultaneously, but for logistical reasons and to reduce the disturbance on the fish community resulting from the divers sampling corals and algae, in some occasions the fish censuses were done deeper than 5 m depth. During the censuses all parrotfishes were counted and the mean density was estimated from the replicates per site. To estimate macroalgae cover, line intercept transects (10 m long transect, between 3 and 6 replicates per site) were done in the same area as the juvenile coral sampling along the 5 m contour and at as many of the surveyed coral reefs as possible (seven out of nine reefs, 33 replicates in total; Table 1).

## 2.4. Data analysis

Non-parametric tests were used for all analyses as the data did not meet the assumptions of normal distribution and homoscedasticity.

The analyses were performed using the computer software Statistica 7. Juvenile coral colony sizes and densities were compared among the nine reefs using a Kruskal–Wallis ANOVA (K–W). Unequal HSD Tukey post-hoc tests were used when significant differences were detected in the ANOVA. Due to the sample sizes, data for both variables were pooled into central and southern categories to explore differences between regions. Once the data was grouped, the two regions were compared using a non-parametric Mann–Whitney t-test (M–W). Following Bak and Meesters (1998), the projected surface area of each colony was estimated and size-frequency distributions were constructed from these data. As size frequencies are more informative when analyzed as geometric functions, juvenile colony area data were log-transformed to facilitate the comparison of skewness between regions (see Vermeij and Bak, 2002). A Chi-square test was carried out to compare the size-frequency distribution between the two regions (central-southern).

Fish density and algal cover data were also grouped into central and southern regions as mentioned above for the juvenile corals and compared using a Mann–Whitney test. Finally, Spearman correlations were used to explore the relationship between the variables studied (juvenile density vs fish density, juvenile density vs algal cover, and fish density vs algal cover) using the information obtained from individual reefs.

## 3. Results

### 3.1. Juvenile corals

Juvenile corals (N = 454) ranged in size from 0.5 to 50 mm maximum diameter with an overall mean diameter of 29.43 mm (SD ± 10.24 mm; Table 1). Statistical differences were detected in the size of juvenile corals among reefs (K–W,  $H_{(8, N = 454)} = 19.067$ ,  $p = 0.0145$ ), with smaller colonies in the offshore central reefs (Abu Madafi and Shib Kabir, M–W,  $U = 14,169.50$ ,  $p = 0.000973$ ; Table 1), but not between regions (M–W,  $U = 18,847.00$ ,  $p = 0.146$ ). Juvenile coral density (mean ± SD) differed significantly among reefs ( $W, H_{(8, N = 135)} = 18.426$ ,  $p = 0.0183$ ), with lower densities existing in the southern reefs (Shib Daqua and Dhi Dahaya; Table 1) and between regions (M–W,  $U = 1545.500$ ,  $p = 0.025$ ) with values higher in the central Red Sea ( $3.64 \pm 2.23$  juveniles m<sup>2</sup>) than those found in the southern Red Sea ( $2.84 \pm 2.16$  juveniles m<sup>2</sup>; Fig. 2).

The size-frequency distribution per reef shows a higher abundance of smaller individuals in the central Red Sea than in the southern Red Sea (Fig. 3). However, they were not statistically different (Chi-square  $p = 19.675$ ,  $\alpha = 0.05$ ). Reefs in both regions showed negative values of skewness (Table 1). It is notable that the more negatively-skewed size distributions came from reefs in the central region that were



recently affected by the aforementioned bleaching event while the reef from the southern region is the one with the highest parrotfish density and macroalgal cover.

### 3.2. Parrotfish density and macroalgal cover

Five species of parrotfish were recorded during the fish censuses (*Chlorurus gibbus*, *Chlorurus sordidus*, *Scarus ferrugineus*, *Scarus Niger*, *Scarus rubroviolaceus*). The comparison between the two regions for parrotfish density and macroalgal cover reveals a marked difference. The southern region possesses high values of fish density and algal cover while the central region shows an opposite pattern with lower values (Fig. 2). These differences were statistically significant for the parrotfish density (M–W,  $U = 64.50$ ,  $p = 0.016$ ) but not for the algae cover (M–W,  $U = 99.00$ ,  $p = 0.79$ ). This pattern of higher values in the southern region for fish density and algal cover is opposite to what we found for juvenile coral density. Finally, the only significant correlation was between parrotfish density and macroalgae cover showing a positive relationship along the central and southern Saudi Arabian Red Sea (Spearman,  $df = 27$ ,  $R = 0.39$ ,  $p = 0.035$ ).

## 4. Discussion

We found that the pocilloporid juvenile coral size-frequency distribution, independent of the region, was more negatively skewed for reefs under unfavorable environmental conditions (i.e., recently bleached) or under ongoing biological stress (i.e., high parrotfish density and algal cover). Coral size-frequency distribution has been used as a proxy for reef conditions and past disturbances (Bak and Meesters, 1998; Meesters et al., 2001; Vermeij and Meesters, 2002; Crabbe, 2009; Bauman et al., 2013; Lozano-Cortés and Zapata, 2014b). These

previous studies have concluded that negatively skewed corals size distributions are associated with degraded reefs and more positively skewed values with healthier ecosystems. In this study, we compared the size structure of juvenile pocilloporid corals between two regions under contrasting oceanographic conditions in the Red Sea. The central region is characterized by oligotrophic water, with temperature ranges of  $24^{\circ}\text{C}$ – $30^{\circ}\text{C}$  and salinities around 39–41 psu. In contrast, the southern region is less oligotrophic and temperatures  $26^{\circ}\text{C}$ – $32^{\circ}\text{C}$  and salinities between 36.5 and 38.5 psu (Sofianos and Johns, 2003; Raitos et al., 2013). Contrary to our expectations, the results did not show any significant juvenile size structure (number of individuals within a given size category) differences between regions. However, differences in juvenile coral size (mean colony size) and density (number of juveniles by area) among reefs with varying stress regimes were observed, suggesting that some variables of colony frequency-distribution in coral are site-specific. This study provides novel data on juvenile corals in the Red Sea that would be essential for further understanding of what is driving the unexplained patterns observed here. The juvenile coral density values reported here are lower than two previous studies in Saudi coral reefs. Jessen et al. (2014) reported a density of 110 juveniles  $\text{m}^2$  in settlement plates from a reef in the central region, while Riegl et al. (2012, 2013) found 13 juveniles  $\text{m}^2$  on natural substrata from reefs in the southern region. These differences are mainly attributed to the fact that these authors considered all scleractinia together while in this study only pocilloporids data were taken into account. Also, differences in sampling seasons among studies (affecting post-settlement survival; Glassom et al., 2004; Kuo and Soong, 2010) and the variability in settlement rates on plates versus natural substrata (e.g., Salinas-de-León et al., 2011) will result in different juvenile density estimates.

The unexpected lack of differences in size-frequency distribution between regions could be attributed to two possible causes. The first is a lack of statistical power due to insufficient sampling to detect differences in the colony size data, which might have obscured the effect size of the environmental conditions. Also, care should be taken with the nature of the data (i.e., unbalanced design and few sampled sites). The difficulty of detecting the smallest recruits ( $<20$  mm) by the naked eye during underwater observation may introduce a statistical artifact producing proportional size-frequency curves that would look identical when fitted. The second potential cause to consider is the sensitivity of pocilloporid corals to disturbances (physicochemical or biological). Previous studies have utilized skewness values to identify the level of sensitivity of particular families to changes in environmental conditions (e.g., Meesters et al., 2001). Coral families that show positive skewness values in healthy reefs and negative skewness values in degraded reefs are inferred to be sensitive to changes, while families that do not show a skewness difference between healthy and degraded reefs are inferred to be insensitive to environmental change (e.g., Meesters et al., 2001). It is possible that our sampling did not find a difference in skewness values because some frequency distribution parameters are species-specific and Red Sea pocilloporids may be robust to these environmental gradients. Similarly, the primary aim of this study was to collect juvenile coral data for the main Red Sea, as there were no data previously available. This lack of data limits our ability to compare with historical conditions or other places but we offer some suggestions for future studies to more thoroughly investigate.

As the presence of algae attracts herbivorous fishes that can cause juvenile coral mortality via incidental grazing (Bak and Engel, 1979), a considerable amount of juvenile coral mortality is expected under conditions of high algal cover and high densities of parrotfishes (Penin et al., 2010; Trapon et al., 2013a). This may be occurring in the southern region where the low density of juvenile corals compared with the central region can be associated with the ongoing conditions of algal cover and parrotfish density (5-fold and 3-fold higher than reefs in the central region respectively; Fig. 2). For the reefs in the central region, where algal cover and parrotfish densities were moderately low in comparison

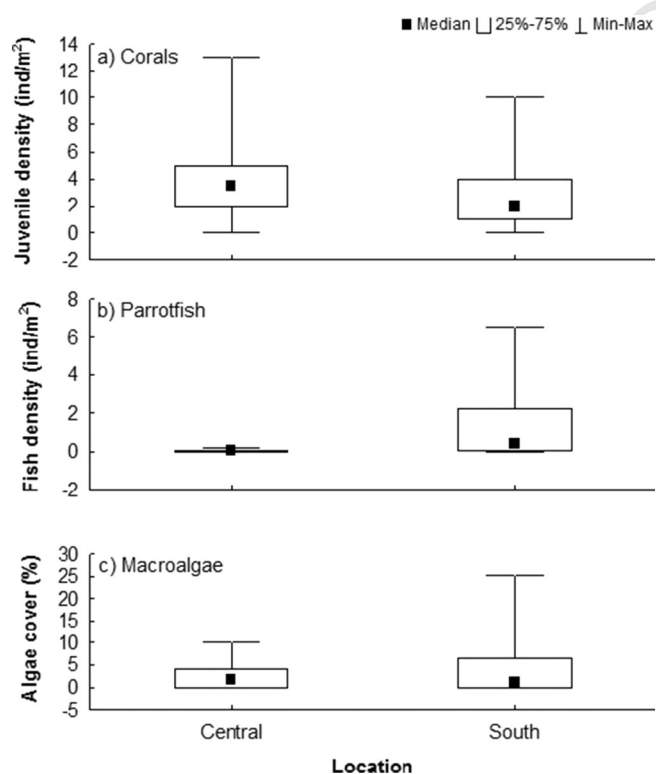
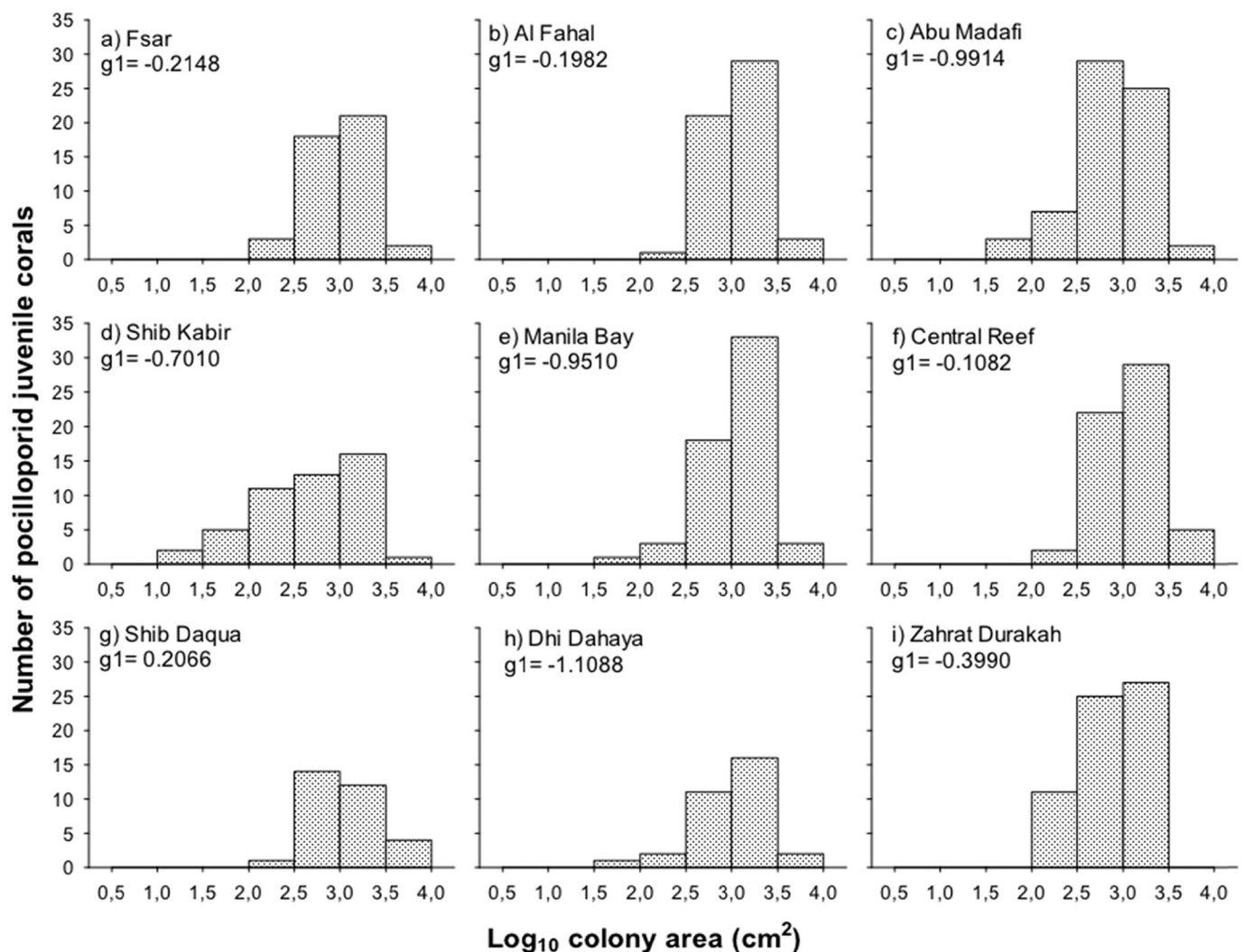


Fig. 2. Juvenile pocilloporid density (a), parrotfish density (b) and algal cover (c) for nine coral reefs grouped into two regions (central and southern) of the Saudi Arabian Red Sea. Each reef was surveyed using quadrats ( $1 \text{ m}^2$ ) for (a), visual censuses in belt transects ( $50 \text{ m} \times 4 \text{ m}$ ) for (b) and, line intercept transects ( $10 \text{ m}$ ) for (c). Differences between the two regions are statistically significant for (a) and (b), but not (c).



**Fig. 3.** Juvenile pocilloporid size frequency distribution and skewness ( $g_1$ ) for nine coral reefs in central (a–f) and southern (g–i) Saudi Arabian Red Sea. Each reef was surveyed using standardized 1 m<sup>2</sup> quadrats with 15 replicates at each reef. The y-axis shows the cumulative number of colonies in each size category. The x-axis shows the colony size categories (in 0.5 cm<sup>2</sup> bins).

347 with the southern region, the negatively skewed results may be attrib-  
 348 uted to past disturbances. These reefs were affected by a major  
 349 bleaching event three years prior to our study (summer 2010: Furby  
 350 et al., 2013; Pineda et al., 2013). Bleaching events not only can affect  
 351 coral size distributions (McClanahan et al., 2008) but also affect the  
 352 biomass of herbivorous fishes. For instance, Khalil et al. (2013) reported  
 353 a reduction of up to 2 orders of magnitude of parrotfishes and  
 354 surgeonfishes in this region after the bleaching event. Even though the  
 355 current low abundance of parrotfishes in the central region (in compar-  
 356 ison with the southern region) may be an indirect effect of this previous  
 357 disturbance, it may be related to the persistent low levels of algal cover  
 358 in this area (i.e., due to the positive correlation between parrotfish and  
 359 macroalgae). In this study and others carried out in the central Red Sea,  
 360 the macroalgal cover has varied between 3.5% to undetectable levels  
 361 (Table 1; Jessen et al., 2013) contrasting with the values of up to 19%  
 362 found in the southern region (Farasan Islands; Table 1). Nevertheless,  
 363 from our results we can conclude that algal cover and fish density are  
 364 less important than other potential factors including past bleaching  
 365 events in the size structure distribution of the juvenile pocilloporid  
 366 corals studied.

367 The Red Sea latitudinal environmental gradient is characterized by  
 368 an increase of primary productivity and turbidity towards the south,  
 369 probably as a consequence of the intrusion of nutrient-rich waters  
 370 from the Gulf of Aden, with a drastically habitat shift around the 19–

20°N. This shift coincides with the area of eddy formations in the Red 371  
 Sea and has been proposed as an environmental barrier for dispersal 372  
 and genetic flow in the southern region (Raitsos et al., 2011, 2013; 373  
 Nanninga et al., 2014; Giles et al., in press). Nanninga et al. (2014) 374  
 using *Chl-a* as a proxy for the environmental gradient found that the 375  
 patterns of gene flow in the anemonefish *Amphiprion bicinctus* followed 376  
 a stepping-stone model along the northern and central Red Sea and it 377  
 was disrupted around the aforementioned habitat shift. Giles et al. (in 378  
 press) found that the genetic isolation of the sponge *Stylissa carteri* 379  
 in the southern Red Sea was also correlated with this environmental het- 380  
 erogeneity. Similarly, simulations of coral larvae dispersal in this area 381  
 have suggested the occurrence of a barrier to northward dispersal 382  
 (Fine et al., 2013). Numerous other factors that may generate very 383  
 small-scale differences were not measured in this study, such as nutri- 384  
 ents, temperature, and light regimes, but could influence local size 385  
 structure as well. Future studies aiming to resolve the roles of all possi- 386  
 ble factors will have to carefully consider and measure these numerous 387  
 variables. The Red Sea coral reefs have developed under unique condi- 388  
 tions of salinity, temperature and isolation (Racault et al., 2015). These 389  
 conditions may have led to unique ecological adaptations within the 390  
 Red Sea and resultant differences in response to environmental stresses 391  
 compared to populations in other seas (Voolstra et al., 2015). Our data, 392  
 despite the caveats mentioned here, suggest that the Red Sea may func- 393  
 tion differently than other systems. Nonetheless, this study cannot 394

establish the causes of the patterns observed regarding the relationship between herbivorous fish and juvenile corals. Future studies should consider differences in the feeding ecology of Red Sea herbivores and the potential occurrence of mechanisms in the corals to avoid accidental predation more effectively than non-Red Sea corals. Our findings suggest that size–frequency distributions of juvenile pocilloporid corals are not sensitive to changes in biological or oceanographic factors that can present moderate stress conditions for the reef. Herein juvenile size–frequencies were not detected to act as a proxy for these potential stressors. A caveat in this study is the absence of data to compare to a “healthy” reef or prior to the bleaching event under “regular” conditions. However, the data presented here serve as an important starting point for monitoring future changes in the reef communities in these regions as a result of upcoming potential impacts.

### Submission declaration and verification

The authors have declared that the work described in this paper has not been published previously and it is not under consideration for publication elsewhere. All the authors approved the final version of this paper and its submission to Marine Environmental Research.

### Contributors

Conceived and designed the experiments: DLC MLB. Performed the experiments: DLC. Analyzed the data: DLC. Contributed reagents/materials/analysis tools: MLB DLC. Wrote the paper: DLC MLB.

### Conflict of interest

The authors have declared that no competing interests exist.

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