



Density-dependence mediates coral assemblage structure

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Abstract. Density dependence (DD) controls community recovery following widespread mortality, yet this principle rarely has been applied to coral assemblages. The reefs of Mo'orea, French Polynesia, provide the opportunity to study DD of coral population growth, because coral assemblages in this location responded to declines in abundance with high recruitment and an increase in cover during which recruitment of pocilloporid corals was inversely associated with density. This study tests for DD in this system, first, by describing the context within which it operates: coral cover changed from 46% in 2005, to <1% in 2010 following an outbreak of a corallivorous sea star and a cyclone, and then increased to 74% by 2017, in large part through inverse density-associated pocilloporid recruitment. Second, a test for DD of recruitment was conducted by decreasing *Pocillopora* spp. cover from 33% to 19%: one year later, the density of *Pocillopora* spp. recruits was 1.65-fold higher in the low vs. high cover treatment. Finally, the effects of DD were investigated by comparing simulated and empirical distributions of pocilloporid colonies: as predicted by DD, small colonies were randomly distributed, while large colonies were uniformly distributed. Together these results demonstrate DD of population regulation for *Pocillopora* spp. corals, thus revealing the potential importance of this ecological principle in determining the resilience of coral assemblages.

Key words: coral reef; Mo'orea; *Pocillopora*; recovery; scleractinia; self-thinning; spatial distribution.

INTRODUCTION

Quantifying variation in population size is a cornerstone of ecology (Krebs 1972), but there is renewed interest in this topic because population dynamics can reveal the fundamental ways in which biomes respond to anthropogenic disturbances (Levin 1992, Hixon et al. 2002). Understanding the causes of variation in population size, however, requires measuring temporal variation in abundance, as well as experimental tests of the processes regulating population size (Murdoch 1994). Given the large changes in abundance affecting populations in virtually every ecosystem (Parmesan and Yohe 2003), time-series analyses have proliferated to quantify these effects (Goldsmith 1991), but few identify mechanisms driving changes in population size.

Slow progress in elucidating the mechanistic basis of changing population size reflects the difficulty of ascribing processes to patterns of change (McIntire and Fajardo 2009), and in terms of population size, progress has been impeded by a history of dissent over the roles of density dependence (DD) vs. density independence (Andrewartha and Birch 1954, Hixon et al. 2002). Distinguishing between these phenomena has been made difficult by conflation of “association” and “dependence,” with the latter requiring experimentation to detect cause-and-effect relationships (Sale and Tolimieri 2000, Herrando-Perez et al. 2012). Despite these issues, it is widely accepted that DD regulates population size through the dependence of demographic properties (e.g., per capita recruitment, mortality, and

growth) on density (Caley et al. 1996), in positive and negative relationships (Hixon et al. 2002).

DD regulates population sizes of many organisms (Turchin 1995, Hixon et al. 2002), but the effects are particularly well known in forests, where they modulate species coexistence and biodiversity (Guo et al. 2015). Forests also occur in the marine environment, where benthic communities dominated by sessile suspension feeders present analogues of terrestrial forests (Rossi et al. 2017), and population sizes may also be controlled by DD (Cau et al. 2016). On tropical coral reefs, DD is likely to function in dense forests of arborescent scleractinians and octocorals (Gili and Coma 1998) throughout their entire life cycle (i.e., from larvae to recruits and adult colonies). Evidences of the existence of DD can be found by studying the associations between density of adults and their early life stages (Vermeij and Sandin 2008, Bramanti and Edmunds 2016), and by observing the relationship between size and density of adult colonies (i.e., density-dependent survival).

Most ecosystems have been degraded due to anthropogenic disturbances (Murphy and Romanuk 2013), including warming (Walther et al. 2005), and in the marine realm, they also are threatened by ocean acidification (Doney et al. 2012). On coral reefs, these effects are reflected in the widespread mortality of scleractinian corals, which have promoted the use of this ecosystem as a poster child for rapid and large population declines (Aronson and Precht 2001). The aforementioned trends highlight the importance of understanding the factors controlling the size of scleractinian populations in order to increase the accuracy with which projections of future coral assemblages can be made. Arguably these effects are best studied on coral reefs subject to effective ecological time-series analyses, because legacy data provides the context necessary to interpret

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demographic trends. The reefs of Mo'orea provide an excellent choice in this regard, as they have been studied since the 1970s (Galzin and Pointier 1985, Adam et al. 2011), and have been disturbed by coral bleaching, outbreaks of the corallivorous seastar, *Acanthaster planci*, and cyclones (Adjeroud et al. 2009, Adam et al. 2011). The recovery of the coral assemblages following these disturbances has typically been rapid (i.e., in <10 yr), largely through high recruitment of *Acropora* and *Pocillopora* corals (Adjeroud et al. 2009, Holbrook et al. 2018). During the period of most recent coral recovery in Mo'orea (Holbrook et al. 2018), the density of recruits and juvenile colonies was associated with coral cover (i.e., density), in one case with a positive (*Acropora*), and in another case a negative (*Pocillopora*) relationship (Bramanti and Edmunds 2016).

The present study extends our previous analysis from the outer reefs of Mo'orea (Bramanti and Edmunds 2016), with an experimental test for DD affecting *Pocillopora* spp. recruitment, and by evaluating the role of DD, during juvenile and adult life stages, through disparity between the modeled random distribution of colonies and their empirical distribution as a function of colony size. Thirteen years of time-series analyses of changing abundance in coral assemblages are used to provide context to the analysis of DD in the population size of *Pocillopora* and for completing a year-long manipulative test of DD in this genus. Our results extend from correlational tests of DD in coral assemblages (e.g., Hughes et al. 2000, Vermeij and Sandin 2008) by establishing cause-and-effect in the role of adult density in mediating con-generic recruitment and resilience of a coral assemblage from Mo'orea.

METHODS

Dynamics of coral assemblages

A portion of the time-series analysis conducted by the Mo'orea Coral Reef, Long-Term Ecological Research (LTER) site was used to provide a historical context to the present study that was conducted from 2016 to 2017. The LTER conducts time-series analyses of coral reef communities at six outer reef sites around Mo'orea, and together these are used in Holbrook et al. (2018) to support a detailed analysis of reef recovery since 2010. The present study focuses on the coral assemblage at 10 m depth at one of these sites on the north shore (LTER 1, 17°28'29" S 149°50'13" W; Appendix S1: Fig. S1), and uses results from the photoquadrats recorded at this site by the LTER to describe the decadal history leading up to the present analysis. These photoquadrats (0.5 × 0.5 m, $n = 37\text{--}38$ photoquadrats/yr) were recorded annually (in April) from 2015 to 2017, and initially were randomly positioned along a 50-m transect on the 10-m isobath in April 2005, and thereafter were sampled in the same positions. Photoquadrats were recorded using Nikon SLR cameras (Tokyo, Japan) that provided increasing resolution from 6 to 36 megapixels as the project progressed. Cameras were fitted in a waterproof housing (Ikelite), attached to two strobes (Nikonos SB105), and supported on a framer at a fixed height above the reef.

The LTER photoquadrats were used to measure percentage cover of benthic taxa, as well as the sizes of *Pocillopora*

spp. colonies. In the LTER sampling protocol, percentage cover was determined by overlaying each image with 200 randomly placed dots that were scored for the benthic substratum on which they fell. Analyses from 2005 to 2015 were conducted using CPCe (Kohler and Gill 2006), and subsequently using CoralNet (in manual mode; *available online*),⁵ which were used to measure the cover of multiple benthic groups (Edmunds 2018), of which we report corals (pooled scleractinians and *Millepora*), *Pocillopora* spp., and macroalgae. In analyses completed for the present study, the size of *Pocillopora* spp. colonies were determined from the mean of the two major diameters of each colony, as measured using ImageJ (Abràmoff 2004) in the photoquadrats, with colonies measured if ≥50% of their area was within each photoquadrat. Given the difficulty of distinguishing among species of *Pocillopora*, colonies were measured regardless of their identity; this probably included *P. meandrina*, *P. verrucosa*, *P. eydouxi*, *P. woodjonesi*, *P. effuses*, and two other haplotypes (Edmunds et al. 2016). Although little is known about the reproduction of these corals in Mo'orea, it is likely that they broadcast spawn (Schmidt-Roach et al. 2012). While the congeneric, *P. damicornis*, is common in the back reef of Mo'orea (P. J. Edmunds, *unpublished data*), where it releases brooded larvae (Rivest and Hofmann 2014), this species is rarely encountered on the outer reefs of Mo'orea (P. J. Edmunds, *unpublished data*).

Variation in the benthic community structure over time was not analyzed with inferential statistics as these data are presented for context, and temporal variation is supported by non-overlapping SE intervals. The colony size structure of *Pocillopora* spp. was used to explore the relationship between colony size and population density (colonies/0.25 m²) over 12 yr. Although sample areas (0.25 m² quadrats) in each LTER legacy photoquadrats were smaller than the quadrats used in the present study to evaluate DD (1 m²), they provided an invaluable decadal-scale context to the 2016 analyses. The associations between mean colony density (by quadrat) and mean colony size for *Pocillopora* spp. were tested using Pearson correlations for the period of declining abundance (2005–2009, $n = 5$ yr), and the period of increasing abundance (2012–2017, $n = 6$ yr).

Manipulative test of DD

To test for an effect of density on recruitment, the density of *Pocillopora* spp. was manipulated within quadrats, with the effects evaluated after 12 months. Eighteen quadrats (1 × 1 m), marked with stainless steel pins, were haphazardly placed at 12-m depth at LTER 1 (Appendix S1: Fig. S1). Quadrats encompassed an area in which coral cover was ~30% in 2016, and was composed mostly (95%) of *Pocillopora* spp.

Quadrats were established in April 2016 and were censused for density and sizes of *Pocillopora* spp., with size recorded from two planar diameters perpendicular to one another, that were measured with a flexible tape measure (±1 cm). Planar areas were estimated geometrically assuming colonies were ellipses. Coral cover was calculated as the sum of these planar areas, which was expressed as a percentage of the area

⁵<https://coralnet.ucsd.edu>

surveyed. Quadrats were randomly assigned to either unmanipulated ($32.5\% \pm 0.5\%$ cover [mean \pm SE, $n = 9$], high density) or reduced ($19.1\% \pm 0.7\%$ cover [mean \pm SE, $n = 9$], low density) *Pocillopora* spp. density treatments, with the contrast obtained by haphazardly removing seven or eight *Pocillopora* spp. colonies from each quadrat (Appendix S1; Fig. S2). Most (>95%) coral cover was *Pocillopora* spp., and following manipulation, *Pocillopora* spp. cover differed between treatments ($t = 14.35$, $df = 16$, $P < 0.005$). After establishing the density contrast (April 2016), *Pocillopora* spp. recruits (≤ 4 cm diameter) were surveyed for density in each quadrat. The census was repeated one year later (April 2017) and densities of *Pocillopora* spp. recruits were compared between years and treatment using two-way, Model I ANOVA, with quadrats as replicates.

Mensurative test of DD

The distribution of organisms in space provides insight into the causal processes by which it is created, with a uniform distribution suggesting spatial competition (Wiegand and Moloney 2004), which is the most common driver of DD (Hixon and Johnson 2009). This approach was used in Mo'orea, because it is tractable for *Pocillopora* spp. colonies on the outer reef where they occur at high densities and form densely branched colonies that can be approximated as hemispheres. Moreover, the recent disturbances affecting this island created a clear chronology beginning with virtually no coral on the outer reef in April 2010 (Holbrook et al. 2018). With large areas of vacant space at ~ 10 m depth in 2010, it was hypothesized that recruitment initially would create a random distribution of small colonies (i.e., ≤ 4 cm diameter), which would become uniform through mortality driven by DD in which spatial competition increased as colonies increased in size. To test this hypothesis, colony distribution was investigated using nearest neighbor distances that were measured by colony size class to evaluate the effects of size on coral distributions categorized as uniform, aggregated, or random. Nearest neighbor distances were compared to expected distances that were quantified using simulations in which colonies were randomly distributed. Neighbors that are closer than expected are aggregated, while those further apart than expected are uniformly distributed (Clark and Evans 1954).

To quantify nearest neighbor distances, in April 2016, 25 quadrats (1×1 m) were haphazardly placed between 13 and 16 m depth at the LTER 1 site, with sampling points designated by the corners of each quadrat, and a total of 100 sampling points surveyed. *Pocillopora* spp. colonies from each size class located closest to each sampling point were selected to quantify the distance to their nearest congeneric neighbor of the same size class. In April 2016, colonies of *Pocillopora* spp. at 13–16 m depth on the outer reef varied in size from 2 to 29 cm diameter and, therefore, their distribution was analyzed in five size classes providing approximately equal replication by class. Size classes were defined by the greatest diameter of the colonies as 0–4.0, 4.1–8.0, 8.1–12.0, 12.1–16.0, and >16.0 cm.

Pocillopora spp. corals were randomly selected as described above, with this process repeated until 100 colonies for each size class had been identified. The distance

between nearest con-generic neighbors in the same size class was recorded in situ as the linear distance between centroids of paired colonies. As the goal was to quantify the spatial distribution of *Pocillopora* spp. colonies, nearest neighbors were defined by proximity of centroids rather than their margins (after Simberloff 1979). Analyses were completed separately for each size class, so that the spatial distribution of colonies in a single size class did not confound the results for colonies in the other size classes.

The expected distances between randomly distributed pocilloporid neighbors of the same size class were quantified using simulations in which colonies were distributed randomly. This analysis was based on additional surveys conducted over the same depth range and on the same reef in April 2016, and simulations employed the empirical colony size structure and abundance (after Simberloff 1979) that was recorded in the first part of the mensurative test for DD. The surveys to support the simulation analysis involved measuring the size of *Pocillopora* spp. colonies in 16 quadrats (1×1 m) that were randomly distributed across the reef, and were surveyed afterward (and independent of) the 25 quadrats used to determine the nearest neighbor distance. The simulations distributed colonies, which were planar circles with sizes corresponding to the empirical distribution, from nine quadrats that were randomly chosen (with replacement) from the 16 quadrats surveyed for this purpose. Corals of a known size from these quadrats were randomly assigned non-overlapping locations within a simulation grid of nine, equal-sized quadrats (1×1 m). Corals were randomly located in the entire simulation space, but the nearest neighbor distances were only calculated for corals in the central square of the grid to avoid edge effects. Nearest neighbors were calculated for the five size classes using a custom script in R, which returned the linear distance between the centroids of paired colonies in the same size class. The procedure was repeated 500 times, with each iteration providing one mean nearest neighbor distance for colonies in each of the five size classes.

The empirical distributions of *Pocillopora* spp. colonies were tested for departures from randomness by comparing the nearest neighbor distance by size class between empirical and simulated distributions (Manly 1997). A two-tailed test ($\alpha = 0.10$) distinguished among aggregated, uniform, and random distributions: if $\geq 95\%$ of the simulated mean distances were greater than the observed mean distance, the distribution was aggregated; if $< 5\%$ of the simulated mean distances were greater than the observed mean nearest neighbors distance, the distribution was uniform; all other outcomes indicated random distributions. The data and code necessary to reproduce these simulations, analyses, and figures, are available online; see *Data Availability*.

RESULTS

Dynamics of coral assemblages

Coral assemblages measured in April of every year at LTER 1 changed from 2005 to 2017 (Fig. 1), with a mean (\pm SE) coral cover of $45.8\% \pm 2.8\%$ in 2005 and $6.4\% \pm 1.5\%$ by 2009 after the coral had been consumed by *Acanthaster planci*. In February 2010, Mo'orea was impacted

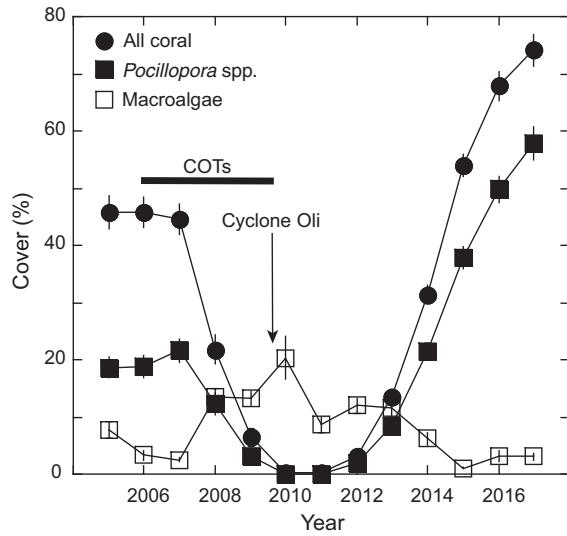


FIG. 1. Structure of the coral reef community (all coral [scleractinians and *Millepora*], *Pocillopora* spp., and macroalgae) at 10 m depth on the outer reef of Moorea from 2005 to 2017 (Appendix S1: Fig. S1). Mean cover (\pm SE) shown based on 37–38 photoquadrats recorded in April at LTER1; errors are smaller than symbols where they are not shown. *Acanthaster planci* (horizontal line) consumed corals from ~2006 to 2010 when Cyclone Oli hit (February 2010). Cover sums to $<100\%$ because crustose coralline algae (CCA), algal turf, and bare space are not shown (there is virtually no sand at this depth on the outer reef). The mean cover (\pm SE) of CCA and bare space ranged from $43\% \pm 2\%$ in 2005 to $89\% \pm 1\%$ in 2011 and $4\% \pm 1\%$ in 2017; over the same years, the cover of turf was $2\% \pm <1\%$, $2\% \pm <1\%$, and $16\% \pm 2\%$, respectively.

by Cyclone Oli, and by April 2010, mean (\pm SE) coral cover was $0.4\% \pm 0.1\%$. Thereafter, coral cover increased, reaching a mean of $74.2\% \pm 2.8\%$ (\pm SE) by 2017, with cover of hard substrata potentially available for coral settlement (i.e., the sum of macroalgae, algal turf, bare space, and crustose coralline algae) declining from 99% in 2010 to 23% in 2017. As *Pocillopora* spp. accounted for $\geq 40\%$ of coral cover prior to 2010 and $>61\%$ after 2011, *Pocillopora* spp. cover followed a similar trend to that of coral cover (Fig. 1). While the cover of macroalgae at this site increased following predation by *A. planci* and Cyclone Oli (reaching $20.0\% \pm 3.8\%$ in 2010), over the first and final three years of this study, macroalgae covered $\leq 8\%$ of the reef. During the recovery phase following Cyclone Oli, most of the macroalgae at 10 m depth on the outer reefs was *Halimeda* (5.0% cover), *Lobophora* (1.5% cover), *Asparagopsis* (1.2% cover), and *Turbinaria* (1.0% cover; Holbrook et al. 2018).

Pocillopora spp. colonies were abundant at the beginning (2005) and end (2017) of the study, but they changed in density and size over the course of the study (Fig. 2). In 2005, the biggest colony was 45 cm diameter, by 2010, there were no colonies to measure in the photoquadrats, and by 2017, colonies had increased to a maximum of 35 cm diameter. Overall, colonies were bigger in 2017 than 2005 ($t = 8.317$, $df = 708$, $P < 0.001$) and sizes were less positively skewed (Fig. 2A, B). Mean densities (\pm SE) were 7.2 ± 0.8 colonies/ 0.25 m^2 in 2005, 0 in 2010 and 2011, and 9.8 ± 0.5 colonies/ 0.25 m^2 in 2017, and the relationship between density and size reversed after the major disturbances. With predation

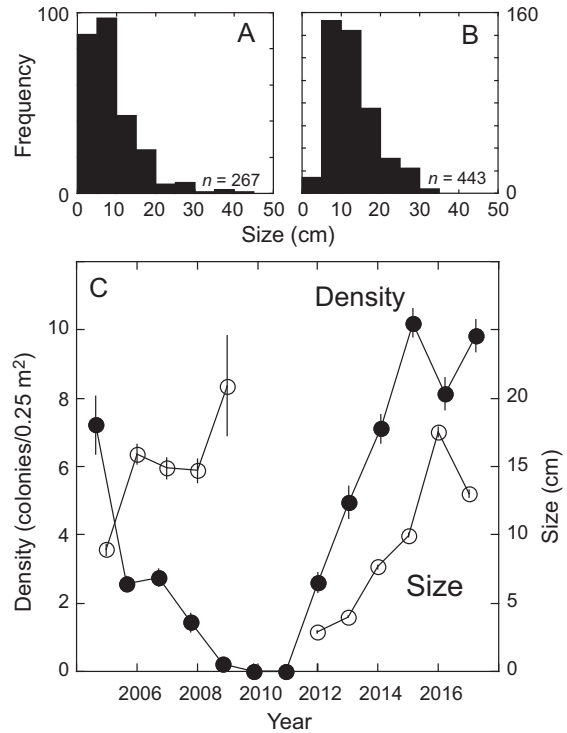


FIG. 2. Mean (\pm SE) size ($n = 8\text{--}532$) and density ($n = 37\text{--}38$ photoquadrats) of *Pocillopora* spp. at 10 m depth from 2005 to 2017; SE are smaller than symbols where they are not visible. Size–frequency distribution in (A) 2005 and (B) 2017 with (C) colony density (solid circles) and colony sizes (open circles).

by *A. planci*, before Cyclone Oli, colony density and size were inversely related ($r = -0.926$, $df = 3$, $P = 0.024$), with mean size increasing as small colonies were consumed by *A. planci*. After Cyclone Oli (2012–present), there was a trend for mean colony size to increase with colony density ($r = 0.751$, $df = 4$, $P = 0.085$) (Fig. 2).

Manipulative test of DD

When the quadrats for this portion of the study were established in April 2016 (Appendix S1: Fig. S2), the mean cover of *Pocillopora* spp. within them was $\sim 30\%$, with a mean adult density of 21.81 ± 1.56 colonies/ m^2 and a juvenile colony density of 2.56 ± 0.89 colonies/ m^2 (\pm SE, $n = 18$ quadrats); low density quadrats were downwardly manipulated to 19% cover (15.63 ± 0.94 colonies/ m^2). The quadrats were censused again in April 2017, by which time the *Pocillopora* spp. colonies had grown, increasing mean coral cover to $33.78\% \pm 0.57\%$ in the high-density quadrats and $21.15\% \pm 0.74\%$ (\pm SE, $n = 9$) in the low-density quadrats. Overall, coral cover was higher in the high-density treatment at the end of the experiment ($t = 14.5$, $df = 16$, $P < 0.005$) and, in both cases, *Pocillopora* spp. accounted for 95% of the coral cover.

The density of *Pocillopora* spp. recruits differed between treatments in a pattern that varied between years ($F_{1,28} = 4.731$, $P < 0.05$). The density of recruits was higher in the low-density compared to the high-density treatment in 2017 but not in 2016 (Tukey HSD: 2017 Low $>$ 2017 High;

2016 High = 2016 Low, $P < 0.05$). In 2016, mean densities were similar in high-density and low-density treatments, with 2.5 ± 0.31 recruits/m² vs. 2.6 ± 0.33 recruits/m², respectively (0.12 ± 0.07 recruits/colony and 0.13 ± 0.07 recruits/colony, respectively), but in 2017, they were 1.65-fold higher in low-density (4.75 ± 0.53 recruits/m², a per capita value of 0.30 ± 0.07 recruits/colony) compared to the high-density treatments (2.88 ± 0.40 recruits/m², a per capita value of 0.15 ± 0.06 recruits/colony; Fig. 3; all \pm SE, $n = 9$).

Mensurative test of DD

Comparisons of the mean distances between neighbors by size class in the empirical vs. simulated data indicated that the empirical distributions of *Pocillopora* spp. colonies

differed among size classes. For the three smallest size classes (Fig. 4A–C), 33.2–88.2% of the simulated mean distances between nearest neighbors were greater than the empirical mean distances between colonies in the same size classes, indicating that these colonies were randomly distributed (Table 1). The mean distances between centers of nearest neighboring colonies in these size classes were 23.6–28.1 cm in the empirical data and 24.7–30.2 cm in the simulated data. In contrast, for colonies in the 12.1–16 cm and >16.0 cm size classes, only 2.2% and 1.0% (respectively) of the simulated mean distances between nearest neighbors were greater than the observed mean distance (Fig. 4D, E), indicating that these colonies were uniformly distributed (Table 1). The mean distances between centers of nearest neighboring colonies in these size classes were 31.6–33.4 cm in the empirical data, but were 19.6–19.9 cm in the simulated data.

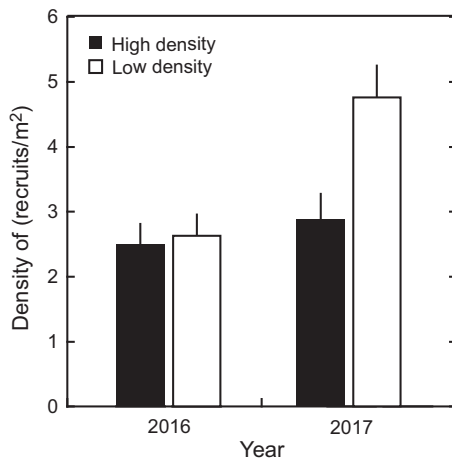


FIG. 3. Mean (\pm SE, $n = 9$) density of *Pocillopora* spp. recruits in quadrats (Appendix S1: Fig. S2) at 12 m depth in 2016 and 2017. Densities of recruits were affected by a Year \times Treatment interaction and were elevated in low-density quadrats in 2017 but not in 2016.

DISCUSSION

Biological and physical disturbances play important roles in determining the structure and function of biomes, and some of their most conspicuous effects are recorded in organism diversity and community structure (Connell 1978, Huston 1985). These principles have guided ecological investigations for decades (Petraitis et al. 1989), but their implications are particularly relevant in the Anthropocene in which the ecological ramifications of human-related disturbances are pervasive (Hughes et al. 2017a). The scale of the changes arising from these disturbances is beginning to be appreciated (Parmesan and Yohe 2003), but the approaches to studying them have favored the phenomenon (i.e., the changes) rather than exploiting ecological theory (e.g., Gaylord et al. 2015) to deepen understanding of the mechanisms causing the changes to occur. This limitation is illustrated by coral reef science, which has focused on recording declining coral cover (e.g., Hughes et al. 2017b), with less

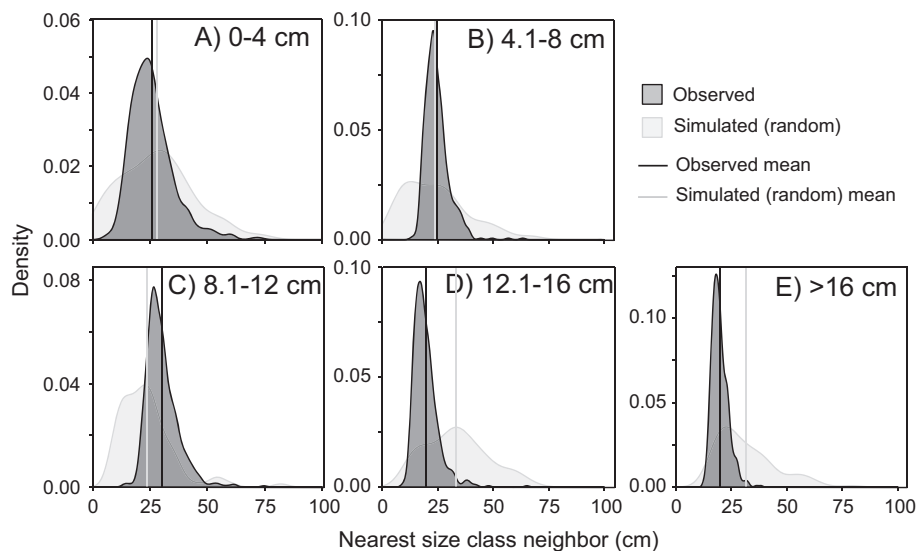


FIG. 4. Observed (dark gray) and simulated (light gray) distribution of distances between nearest size class neighbors for *Pocillopora* spp. corals by size class (A–E) at LTER1 (Appendix S1: Fig. S1). The mean observed (dark gray line) and simulated (light gray line) distance between nearest size class neighbors are shown for each size class.

TABLE 1. Results of observed ($n = 25$) and simulated ($n = 500$) distances between neighbor *Pocillopora* spp. colonies of the same size class at LTER1 (Appendix S1: Fig. S1), in 2016.

Size class (cm)	Observed distance (cm; mean \pm SE)	Simulated distance (cm)			S \geq O (%)
		Mean	5th percentile	95th percentile	
0–4.0	28.1 \pm 1.6	25.9	14.1	43.0	33.2
4.1–8	24.1 \pm 1.5	24.7	18.1	34.7	45.2
8.1–12	23.6 \pm 1.2	30.2	21.9	43.0	88.2
12.1–16	33.4 \pm 1.4	19.6	13.3	29.6	2.2
>16.1	31.6 \pm 1.3	19.9	15.2	26.9	1.0

Notes: Simulated distances are shown as mean and the 5th and 95th percentile of the distribution based on 500 trials. S > O shows the percentage of simulated (S) nearest neighbor distances that are greater than or equal to the average observed (O) nearest neighbor distance.

attention to the ecological processes driving the declines and, potentially, impeding recovery. Without knowledge of the underlying ecological processes, projections of future reef condition will remain inaccurate.

Density dependence (DD) is a general mechanism regulating population dynamics through a wide range of traits (Hixon et al. 2002, Hixon and Johnson 2009). In populations of plants and animals with sessile adults and dispersive propagules or motile juveniles, most attention to DD has addressed recruitment and spatial distribution of adults, particularly in terrestrial systems (Guo et al. 2015). Ecological analogies between terrestrial plants (i.e., trees) and “corals” (e.g., scleractinians and octocorals), as epitomized by sessile adults, arborescent morphologies, and complex life cycles, suggest that some of the principles governing plant population dynamics might also apply to corals (Rossi et al. 2017). Recruitment is associated with adult density in some corals (Bramanti et al. 2009, Bramanti and Edmunds 2016) and, in a few cases, recruitment has experimentally been shown to be density dependent (Vermeij and Sandin 2008, Doropoulos et al. 2017). However, diverse examples of DD in coral populations are lacking (but see Linares et al. 2008, Tanner et al. 2009, Cau et al. 2016) and DD is rarely considered as a mechanism to account for temporal variation in coral cover. Against this backdrop, the present study makes an important contribution by demonstrating the role of DD in the population dynamics of one of the dominant reef-building corals in the tropical Indo-Pacific.

In recent decades, the provenance, periodicity, and magnitude of the disturbances affecting coral reefs have changed compared to the 1960s and 1970s (Osborne et al. 2011). This transition has resulted in many reefs experiencing declining coral cover, rising abundance of macroalgae, and depleted fish populations (e.g., Pandolfi et al. 2003). While the coral mortality driving these changes is well known (e.g., Bellwood et al. 2004), only recently has attention turned to the possibility that some corals might be able to positively respond to disturbance once the event has past (Diaz-Pulido et al. 2009, Graham et al. 2011), thereby promoting reef recovery to increasing coral cover. The fundamental mechanisms that could mediate increases in coral cover have not been addressed in detail, even though ecological theory details key processes with generalized capacity to regulate population dynamics. Among these processes, DD is one of the most important, because population growth is directly mediated by per capita demographic rates driven by organism density (Hixon et al. 2002, Hixon and Johnson 2009).

While DD is frequently mentioned in coral reef ecology (e.g., Doropoulos et al. 2017), there are only a small numbers of studies in which it has been explicitly addressed, and these often are equivocal over the distinction between density association (i.e., correlation) and density dependence (i.e., causation) and rarely test for effects of population density on per capita demographic rates (but see Vermeij and Sandin 2008). Moreover, in coral reef ecology, studies of DD largely have been restricted to the early life stages (e.g., density-dependent recruitment), even though DD in other fields is widely accepted to act on multiple life cycle stages (Sibly and Hone 2002). By using Mo’orea as an example of a reef exhibiting high resilience of coral assemblages (Holbrook et al. 2018), our study demonstrates for *Pocillopora* spp. that population size and density are associated through (1) a density-dependent mechanism (recruitment) and (2) density-associated processes affecting the spatial arrangement of colonies.

DD of *Pocillopora* spp. recruitment corroborates our earlier analysis in which negative density-associated recruitment of *Pocillopora* spp. was recorded following mass coral mortality attributed to *A. plani* and Cyclone Oli (Bramanti and Edmunds 2016); the present experiment demonstrates causation between density and recruitment. A 37% reduction in *Pocillopora* spp. density caused a 1.65-fold increase in *Pocillopora* spp. recruitment, corresponding to a 50% increase in per capita recruitment at the low population density. This outcome is identical in relative effect, although different in magnitude, to the result of our earlier mensurative analysis of the reefs of Mo’orea (Bramanti and Edmunds 2016) in which the density of juvenile pocilloporids increased from ~ 0.25 colonies/0.25 m² at a pocilloporid cover of $\sim 15\%$, to 5.5 colonies/0.25 m² at a pocilloporid cover of $\sim 0.2\%$ (in 2011). In the present analysis, a reduction in pocilloporid cover to a value (i.e., 18%) still in excess of recent historic cover for this location (2005 and later) caused the density of juvenile pocilloporids to increase to 4.8 colonies/0.25 m². This enhanced sensitivity of pocilloporid recruitment to a reduction in pocilloporid cover (cf. Bramanti and Edmunds 2016) is consistent with the unusual effects of the El Niño year in which the study was conducted (i.e., 2016), when the supply of pocilloporid recruits in Mo’orea was substantially enhanced compared to decadal averages from this location (Edmunds 2017).

It was beyond the scope of this study to identify the proximal mechanism(s) underlying the DD of pocilloporid recruitment in Mo’orea, particularly give the diversity of

biotic interactions that could mediate DD of coral recruitment, for example, through coral–coral, coral–macroalgae, or coral–crustose coralline algal interactions. However, given the remarkably high density of coral colonies that has quickly appeared on the outer reefs of Mo’orea since the last disturbance (Holbrook et al. 2018), it is interesting to consider the possibility that density-dependent recruitment reported herein reflects the effects of a “plankton-shadow” (sensu Porter 1976) created by the “wall” of polyp mouths on adjacent coral colonies (sensu Fabricius and Metzner 2004), and coral host-specific interaction (sensu Marhaver et al. 2013; both after Bramanti and Edmunds 2016). Conceivably, high densities of branching coral colonies could create a multi-layered wall of coral mouths that effectively consumed coral planulae (Fabricius and Metzner 2004) as they descended from the plankton, and before they settled and metamorphosed, thus creating inverse density-dependent recruitment, similar to that reported here for Mo’orea. Alternatively, similar effects (i.e., inverse density-dependent recruitment) could be created by dense aggregates of adult corals through support of a unique down-current microbial consortia mediating coral recruitment success through a Janzen-Connell effect (Marhaver et al. 2013).

With establishment of causation between density and recruitment of *Pocillopora* spp., there now is motivation to conduct the experiments necessary to test for the underlying mechanisms, although our results are inconsistent with the notion of a single proximal origin. Critically, in addition to the results of the manipulative experiment, the mensurative analyses revealed three density-associated phenomena that are unlikely to have a common origin. First, from 2005 to 2009, mean colony size increased as density declined through predation by *Acanthaster planci* (Fig. 2C). Second, from 2012 to 2017, density and colony size increased in concert (Fig. 2C) to elevate coral cover and fill vacant space on the benthos (Fig. 1). And third, the distribution of *Pocillopora* spp. colonies in 2016 differed between size classes (Fig. 4) with small colonies randomly distributed, and large colonies uniformly distributed. Discordant spatial distributions by size class are a classic product of DD, with random distribution of recruits giving way to uniform distribution of adults as individuals grow and interact through spatial competition (Antonovics and Levin 1980, Fowler 1986).

The examples of density-associated phenomena described herein are each consistent with one or more parsimonious causal hypothesis. For example, *Acanthaster planci* consumes smaller corals before larger colonies (Leray et al. 2012), thus causing colony size to rise as density declines (Fig. 2C). Thereafter, while low *Pocillopora* spp. densities accentuate recruitment (Fig. 3), density increased with cover (Fig. 2C), perhaps because closely spaced branches of adjacent colonies deter fish corallivory (Wellington 1982) on recruits, thus enhancing post-settlement survival. Finally, crowding among colonies that settle at random could modify their distribution to uniform through spatial competition (Lang 1973, Antonovics and Levin 1980, Fowler 1986), and a suite of processes driving self-thinning, which is well known in terrestrial forests (Yoda et al. 1963), as well as some gorgonians (Linares et al. 2008, Cau et al. 2016).

Finally, it is valuable to place the results of the present study in the larger context of the state of coral reefs

throughout the world (Bellwood et al. 2004, Hughes et al. 2017a,b), and the poor prognosis for their future persistence (van Hooidonk et al. 2014). Present day coral reefs that are functioning as “rebound oases” (sensu Guest et al. 2018), which have experienced large declines in coral cover but have rapidly recovered because key ecological processes (e.g., coral recruitment) have remained intact, are uncommon (Graham et al. 2011, Guest et al. 2018). However, among these, the outer reef of Mo’orea has regained coral cover at a record-breaking rate of 10.5%/yr following the most recent disturbance (cf. Graham et al. 2011), and it is within this system that we report DD recruitment of the dominant coral as one feature supporting rapid recovery. The fore reef of Discovery Bay, Jamaica, provides one classic example of persistent reef degradation (Hughes 1994), where the lack of reef recovery (Jackson et al. 2014) demonstrates that strong and inverse DD recruitment for the dominant coral (*Orbicella* in Jamaica) clearly is not a universal mechanism of recovery for coral assemblages; indeed the historically low recruitment of this genus throughout the region (Edmunds et al. 2010) suggests that DD recruitment may not be feasible for this coral under any circumstance. Elucidating why coral assemblages on the outer reefs of Mo’orea are able to benefit from DD recruitment by the dominant coral clearly is an important objective for future research. While it remains uncertain which topics should be the focus of this effort, it might be particularly valuable to address the roles of cryptic diversity among spawning pocilloporids (Edmunds et al. 2016) in supporting high recruitment and the inferred prodigious supply of *Pocillopora* larvae (Tsounis and Edmunds 2016), the extent to which local vs. distantly sourced coral larvae support coral recruitment in Mo’orea (Holbrook et al. 2018), and the causes of the apparently high post-recruitment success of corals in this location (Edmunds et al. 2015).

Our study underscores the utility of applying classic ecology to present day phenomena affecting population dynamics (Gaylord et al. 2015), and the limitations of time-series analyses of community structure and mensurative experimentation in understanding why communities are changing in the Anthropocene. Coral reefs provide an excellent example of these challenges because the emphasis on describing changes in recent decades has not been matched by efforts to understand the ecological processes mediating these changes. The present study underscores the potential importance of one of these processes, and by demonstrating cause and effect of density dependence in a coral assemblage, we have shed light on one mechanism that contributes to explaining the high resilience of the outer reefs of Mo’orea (Bramanti and Edmunds 2016, Holbrook et al. 2018). These principles may have general application to other shallow coral reefs, potentially to accentuate the capacity for pre-emptive management (Hughes et al. 2013), as well as prescriptive actions to enhance the recovery of coral community assemblages (Hughes et al. 2017a). This potentially may only be realized on reefs that routinely are exposed to high densities of coral larval from local or more distant sources.

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DATA AVAILABILITY

Associated are available on the LTER Network Data Portal at <https://doi.org/10.6073/pasta/e7cbb563fc6e544bd4fd8f9c79a09681>, on GitHub at https://github.com/hrnelson/moorea_dd and on Zenodo at <https://doi.org/10.5281/zenodo.1303701>.