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Cite this article: Dietzel A, Bode M, Connolly SR, Hughes TP. 2020 Long-term shifts in the colony size structure of coral populations along the Great Barrier Reef. *Proc. R. Soc. B* **287**: 20201432.

<http://dx.doi.org/10.1098/rspb.2020.1432>

Received: 17 June 2020

Accepted: 21 September 2020

Subject Category:

Ecology

Subject Areas:

ecology

Keywords:

colony size-frequency distribution, disturbance, recruitment, population viability, reef recovery, size structure

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Electronic supplementary material is available online at <https://doi.org/10.6084/m9.figshare.c.5136040>.

Long-term shifts in the colony size structure of coral populations along the Great Barrier Reef

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The age or size structure of a population has a marked influence on its demography and reproductive capacity. While declines in coral cover are well documented, concomitant shifts in the size-frequency distribution of coral colonies are rarely measured at large spatial scales. Here, we document major shifts in the colony size structure of coral populations along the 2300 km length of the Great Barrier Reef relative to historical baselines (1995/1996). Coral colony abundances on reef crests and slopes have declined sharply across all colony size classes and in all coral taxa compared to historical baselines. Declines were particularly pronounced in the northern and central regions of the Great Barrier Reef, following mass coral bleaching in 2016 and 2017. The relative abundances of large colonies remained relatively stable, but this apparent stability masks steep declines in absolute abundance. The potential for recovery of older fecund corals is uncertain given the increasing frequency and intensity of disturbance events. The systematic decline in smaller colonies across regions, habitats and taxa, suggests that a decline in recruitment has further eroded the recovery potential and resilience of coral populations.

1. Introduction

Population biology is fundamentally concerned with changes in population size and structure, and with rates of birth and death that depend on sex, size and/or age. Shifts in population structure arise from temporal and spatial variation in the underlying demographic processes. Human demographers have long used the age structure of populations to reveal the impact of past mortality events such as wars or famines, and to forecast future population growth or declines [1,2]. Changes in the population structure of keystone taxa not only affect their demographic performance but can also have cascading effects on community composition and ecosystem functioning. The global decline in large, old trees [3], for instance, implies a loss of critical habitat, food and carbon storage [4]. Such detailed demographic data are, however, rarely available for populations of wild animal and plant species, which limits our ability to identify the processes underlying population decline and to assess long-term population viability.

Reef-building corals resemble trees in their pivotal role as primary habitat providers, and in the importance of the size of individuals for population dynamics [5–7]. Consequently, changes in the size structure of coral colonies have major implications for demographic performance, and for the structural complexity of the reef environment, which in turn affects fish abundance and the productivity of coral reef fisheries [8]. The size structure of coral colonies often differs markedly between species [9] and is sensitive to environmental conditions [10] and disturbances [11,12]. However, the size structure of local populations rarely attains a stable equilibrium due to stochastic pulses of

recruitment and disturbance [13,14]. Non-equilibrial, transient dynamics are particularly likely to be prevalent in long-lived species with highly persistent life stages [15].

Coral population biology and demography is commonly based on measurements of recruitment and of the size-specific survivorship, growth, fecundity and mortality of colonies [5,6]. While declines in coral cover have been well documented on many reefs [16,17], trends in the size structure of coral populations, particularly over long temporal and large spatial scales, are rarely examined. There has been some support [18] for an early hypothesis that coral populations will be likely to respond to changing disturbance regimes with shifts towards relatively more large colonies due to reduced recruitment [12]. Shifts towards relatively more small colonies driven by post-disturbance pulses of recruitment have, however, also been reported [19,20]. Differences in disturbance history, assemblage structure and connectivity all shape the trajectory of populations and communities. These studies have, however, been constrained in their spatial scale [18,20] or taxonomic scope [19]. A better understanding of long-term and regional shifts in the colony size structure of coral taxa with different life-history strategies is urgently needed. Declines in the abundance of large, highly fecund colonies [6] would compromise a population's fecundity, reducing its viability and ability to provide structurally complex reef habitat for other reef organisms. Conversely, a reduced abundance of small colonies may indicate declines in recruitment [13,18] or high post-settlement mortality [21].

Here, we document decadal changes in the colony size structure of coral populations in 2016 and 2017 relative to their historic baselines in 1995 and 1996, on reef crests and slopes along the 2300 km length of the Great Barrier Reef (GBR). Any observed changes will be the result of long-term dynamics such as ocean warming, as well as a series of substantial mortality events, including several cyclones, four mass bleaching events (1998, 2002, 2016 and 2017) and two major outbreaks of the crown-of-thorns starfish *Acanthaster cf. solaris*. We examine changes in colony size structure as changes in size-class abundances and as changes in the mean, standard deviation and 10th and 90th percentiles of colony size on a logarithmic scale, to allow for comparison with similar studies in other regions [12,18–20]. We explore these shifts in latitudinal regions along the GBR with different disturbance histories, and in all major coral taxa. We place particular emphasis on changes in the abundance of large, fecund colonies and of very small colonies, as indicators of declines in reproductive output and recruitment.

2. Material and methods

(a) Survey locations

We assessed coral communities and their colony size structure on the reef crest and reef slope using a nested sampling design, on replicate sites and reefs in five sectors along the length of the GBR (figure 1a). Crest assemblages were surveyed at 1–2 m depths on 15 mid-shelf reefs, three per sector, in 1995 and again in 2017. Reef slope communities were assessed at 6–7 m depths on 15 different mid-shelf reefs in 1996 and in 2016. At each of the 30 reefs, we ran eight to ten 10 m line-intercept transects at each of four sites. We measured the length of the intercept of each physically discrete colony (i.e. contiguous colony tissue) with the transect tape to the nearest cm. Separate intercepts of the same colony were summed. We identified all intercepting colonies

using the following 12 morpho-functional benthic groups of hard corals, predominantly composed of the species listed in parentheses: *Isopora* (*I. palifera*, *I. cuneata*), *Montipora* (*M. foliosa*, *M. grisea*, *M. hispida*, *M. tuberculosa*, *M. montasteriata*), tabular *Acropora* (*A. hyacinthus*, *A. cytherea*, *A. paniculata*), other *Acropora* (*A. gemmifera*, *A. humilis*, *A. millepora*, *A. tenuis*, *A. valida*, *A. loripes*, *A. nasuta*, *A. secale*, *A. danaei*, *A. florida*, *A. formosa*, *A. intermedia*, *A. microphthalma*, *A. robusta*), favids (species and genera from the formerly recognized family Faviidae, now mostly reclassified as merulinids [22], predominantly of the genera *Favia*, *Cyphastrea*, *Goniastrea*, *Favites*, *Echinopora*, *Montastrea*, *Leptastrea*), Poritidae (*P. annae*, *P. cylindrica*, *P. lobata*), *Pocillopora damicornis*, *Stylophora* (mostly *S. pistillata*), *Seriatopora* (mostly *S. hystrix*), Mussidae (*Acanthastrea*, *Symphyllia*, *Lobophyllia*), other *Pocillopora* (*P. eydouxi*, *P. verrucosa*) and other scleractinians. Benthic groups were chosen to comprise ecologically similar species based on shared taxonomy, growth form and life history, and to ensure sufficient sample sizes. The presented size distributions are thus representative of the size distribution at the taxonomic group level and are not necessarily indicative of the constituent species-level distributions. We recorded a total of 40 105 intercepts across all years, habitats, taxa and sectors. Elsewhere, we have examined spatial patterns in the taxonomic composition of these coral assemblages [23] and long-term shifts in coral recruitment onto settlement panels on the 30 reefs [24].

(b) Statistical analyses

To examine trends in colony size structure, we used colony intercept lengths as a proxy for colony size (see also [19,20]). We examined trends in the colony size structure of individual taxa and entire communities (i.e. pooled across all taxa), both in terms of changes in size-class abundances and as changes in the mean and standard deviation, as well as the 10th and 90th percentile of colony size as indicators of changes in the relative abundance of small and large colonies (figure 1b). Notably, an increase in the 10th percentile of colony size indicates a decline in the relative abundance of small colonies. Frequency distributions of colony sizes [11], and line-intercept lengths [20], typically follow a lognormal distribution. To formally test for lognormality in our data, we ran Shapiro–Wilk tests on log-transformed intercept lengths. Because sample sizes of some taxa were small at the scale of individual reefs and sectors, we pooled data and analysed taxon-specific trends at the scale of the GBR. To examine changes in size-class abundances, we binned log-transformed intercept lengths into quintiles (1st quintile: small; 2nd to 4th quintile: medium-sized; 5th quintile: large) (figure 1b). Colony size structures often vary widely between taxa, habitats and regions [9]. Bin boundaries were therefore allowed to vary between taxa, habitats and sectors, but fixed across survey years (electronic supplementary material, table S1). We used bootstrap resampling ($n = 1000$) to assess uncertainties in size-class abundances.

To examine changes in the mean (μ), standard deviation (σ) and the 10th and 90th percentile of colony size, both in communities and individual coral taxa, we fitted multi-level multiple linear regression models to the log-transformed intercept data, in which μ and σ of size structure were modelled as functions of year, habitat and sector (and their interactions) for community-level analyses, and as functions of year, habitat and taxon (and their interactions) for taxon-specific analyses (pooled across sectors). All modelling analyses were carried out in a Bayesian framework with brms [25]. Previous studies reported changes in the moments of the colony size-frequency distributions (i.e. mean, variance, skewness and kurtosis; e.g. [11,12,20]). Our procedure also reported the first two moments of the distribution, but also allowed us to statistically examine the effects of year, sector, habitat and taxon on colony size

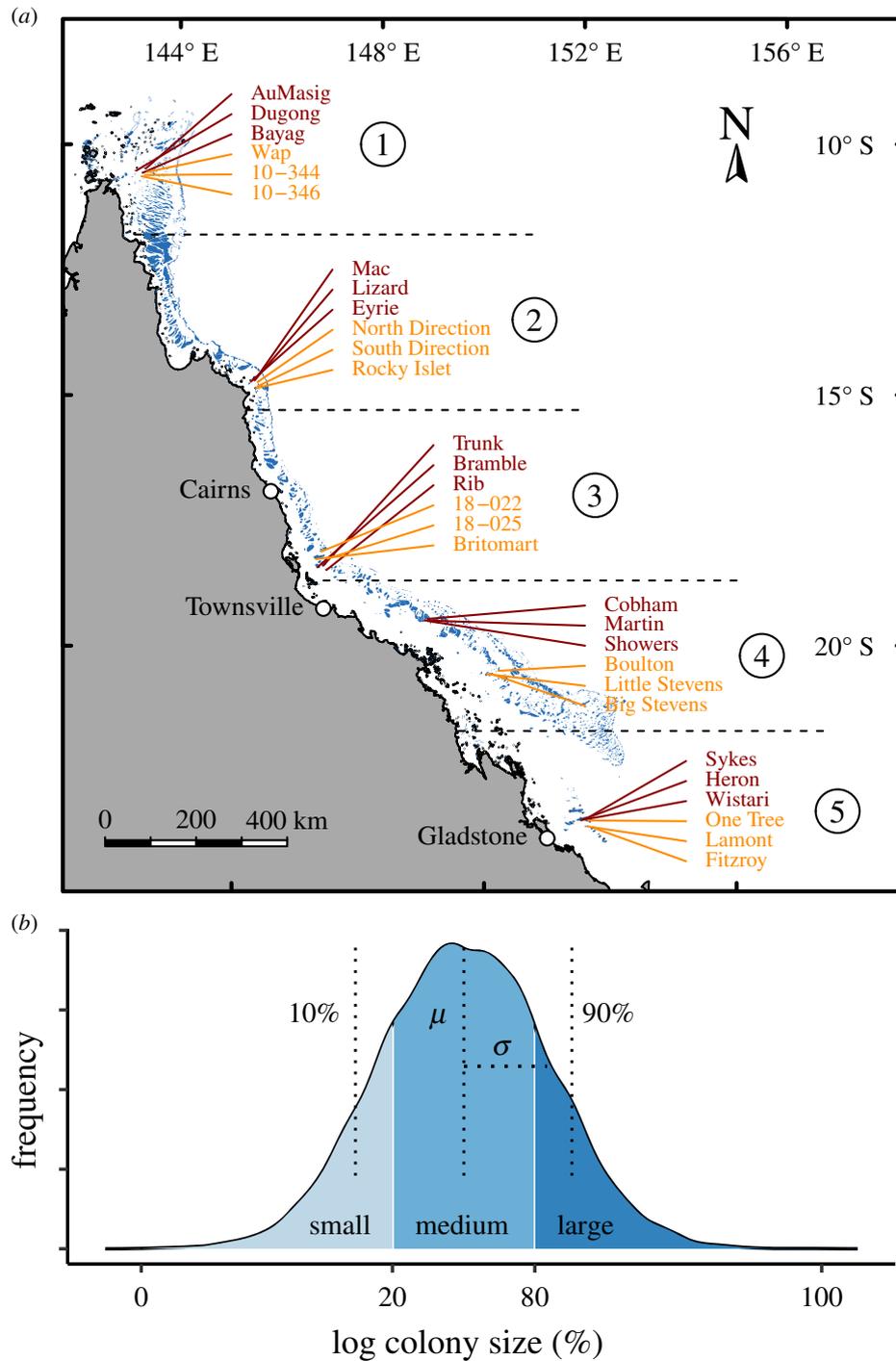


Figure 1. Map of survey locations and colony size metrics. (a) Map showing locations of reefs on which crest (red) and slope (orange) communities were surveyed in five sectors along the length of the GBR. Blue polygons show the locations of individual reefs. (b) Size structure metrics used to measure changes in size-class abundances (small, medium, large: based on quintiles) and changes in the moments of colony size structure (mean (μ), standard deviation (σ), 10th percentile, 90th percentile).

structure. We chose a Bayesian approach over a frequentist linear model because (i) it makes it convenient to quantify uncertainty of μ and σ , as well as uncertainty of the 10th and 90th percentile, by sampling from the posterior distributions, and (ii) uncertainty estimates are more robust because they can account for asymmetrically distributed uncertainty distributions. We report parameter uncertainties as 95% highest posterior density intervals (HPDI). All models were run with weakly informative priors, 2000 iterations (warmup=200) in each of three chains and with a thinning rate of 5. We examined chain mixing, carried out posterior predictive checks to examine model fit, and we used the Gelman–Rubin convergence statistic (R-hat) to examine model convergence.

3. Results

(a) Changes in size-class abundances

Abundance of coral colonies declined sharply across all size classes, on both the reef crest and slope, in almost all taxa and in all sectors, with the exception of the far south (figures 2 and 3). These declines were accompanied by declines in total coral cover, on average (mean \pm s.d., $n = 15$ reefs), from 41.0% ($\pm 15.6\%$) to 16.3% ($\pm 15.3\%$) on reef crests and from 34.6% ($\pm 12.5\%$) to 22.3% ($\pm 13.8\%$) on reef slopes (table 1). At the scale of the GBR, the abundance of small colonies (number of intercepts in the first quintile in 1995 or 1996) declined by 76.1%

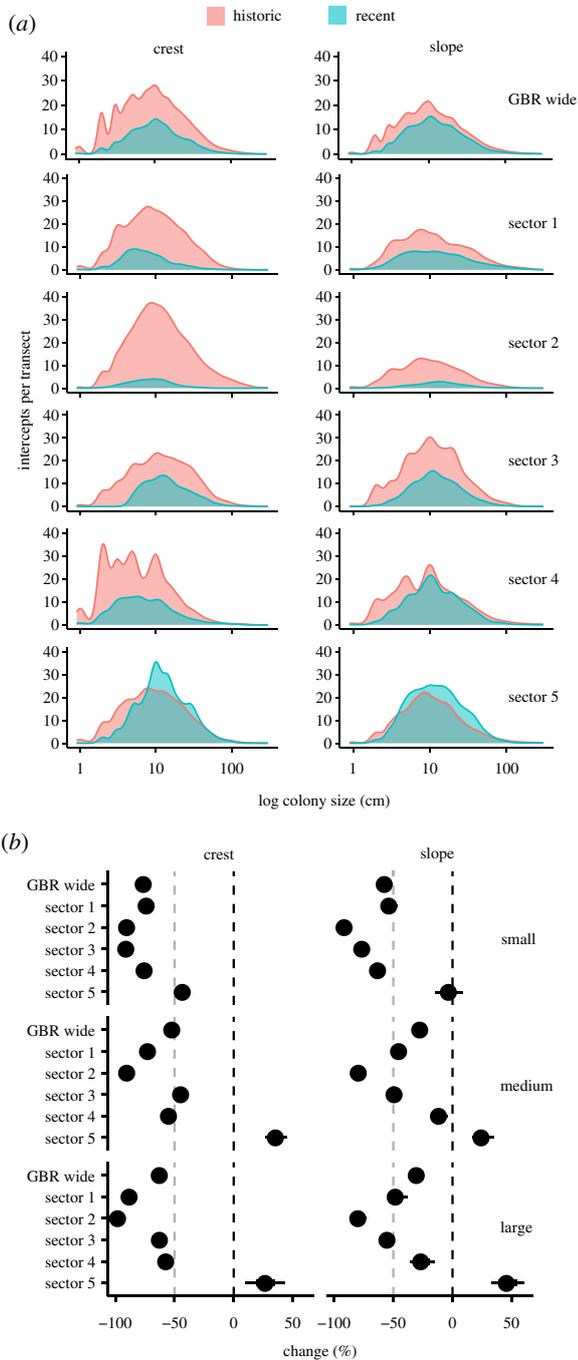


Figure 2. Changes in the colony size structure of crest (left) and slope (right) communities by sector. (a) Coral colony size structure of historic (1995/1996) and recent surveys (2016/2017) are shown for each of five sectors (1: far north to 5: far south) and pooled across all sectors (top). (b) Changes in the abundance of small, medium-sized and large colonies by sector and habitat. Percentage changes in reef-level abundances are defined as changes in the number of intercepts in the 1st quintile (small), 2nd to 4th quintile (medium) and 5th quintile (large) of colony size. All estimates are shown as 95% highest posterior density intervals. The point indicates the median, the thick line the 66% credible interval and the thin line the 95% credible interval. (Online version in colour.)

(95% CI: 74.3%–77.7%) on the crest and 57.2% (54.2%–60.1%) on the slope (figure 2b). The overall abundance of large colonies (in the 5th quintile) also decreased sharply, by 62.7% (59.9%–65.1%) on the crest and 30.7% (26.3%–35.6%) on the slope. The overall abundance of medium-sized corals (in the 2nd to 4th quintile) also declined, on crests by 52.2% (50.4%–54.0%) and on slopes by 27.5% (24.4%–30.2%) (figure 2b).

Declines in size-class abundances were most pronounced on all reefs in sectors 1–3 in the northern half of the GBR (figure 2a), which experienced extreme thermal stress in 2016 and 2017. In these three sectors, the abundance of large colonies (in the 5th quintile) on the crest dropped by 88.2% (95% CI: 85.1%–91.1%), 97.9% (96.7%–98.9%) and 62.0% (55.0%–68.1%), respectively, and by 48.1% (38.6%–56.6%), 86.4% (73.9%–86.4%) and 55.3% (47.4%–61.4%) respectively on the slope (figure 2b). The declines were less severe on reefs in sector 4 where large colonies declined by 57.1% (50.5%–62.7%) on the crest and by 24.5% (14.3%–35.5%) on the reef slope. In marked contrast, on southern reefs in sector 5 the abundance of large colonies increased by 25.8% (10.1%–41.1%) on the crest and by 46.9% (28.4%–66.4%) on the slope (figure 2b). Geographic patterns of changes in the abundance of large colonies were largely reflective of geographic changes in coral cover (table 1).

Similar geographic patterns emerged in trends in the abundances of small colonies (in the 1st quintile). On the reef crest, the abundances of small colonies declined consistently across all sectors. In sectors 1 to 4, the abundance of small colonies dropped by 74.3% (95% CI: 69.5%–78.5%), 90.1% (87.8%–92.2%), 91.0% (88.5%–93.4%) and 75.2% (71.9%–78.5%), respectively (figure 2b). Although reefs in the far south recorded the lowest declines, small colonies in sector 5 were still 43.6% (36.2%–50.1%) less abundant on crests in 2016 than in 1996. On the reef slope, the abundances of small colonies declined by 54.3% (95% CI –46.7%–61.6%) in sector 1, 91.5% (87.6%–94.5%) in sector 2, 76.1% (71.8%–79.9%) in sector 3 and 62.7% (57.6%–67.1%) in sector 4 (figure 2b), and remained stable in sector 5 (–15% to +9.1%).

Changes in community composition and in the mean colony size of individual taxa accompany these geographic patterns in the colony size structure of coral communities. Most taxa increased in mean size in sectors 3 to 5, on both the reef crest and reef slope, but marked shifts towards larger sized taxa were not recorded (electronic supplementary material, figure S1). By contrast, crest communities in sectors 1 and 2 experienced shifts towards smaller sized taxa and more taxa decreased in mean colony size than increased. Declines in the mean colony size and relative abundance of acroporid corals, the largest sized taxa in our surveys, were particularly pronounced (electronic supplementary material, figure S1). Notably, several taxa were not recorded in recent surveys, particularly in sector 1.

The decline in numbers of small, medium and large colonies was remarkably consistent across all major taxa, on both crests and slopes (figure 3). The abundance of small colonies on the reef crest declined by at least 50% in 11 of the 12 major taxa, with half of them losing greater than 75% of their small colonies (figure 3b). The exception was other *Pocillopora*, which lost 28.0% (1.7%–52.0%) of its small colonies. Declines were less severe on the reef slope, where 9 out of 12 taxa lost at least half of their small colonies. Small colonies of tabular *Acropora* and other *Pocillopora* were comparatively less affected, but still declined, on average, by 12.2% (–32.9% to +13.6%) and 30.2% (–71.6% to +18.9%), respectively (figure 3b).

Changes in the abundances of large colonies (in the 5th quintile) varied between taxa. Numbers of large colonies declined by greater than 50% in 8 out of 12 of the taxa on the crest and in 5 taxa on the reef slope (figure 3b). Slow-growing, long-lived groups like Poritidae and Mussidae

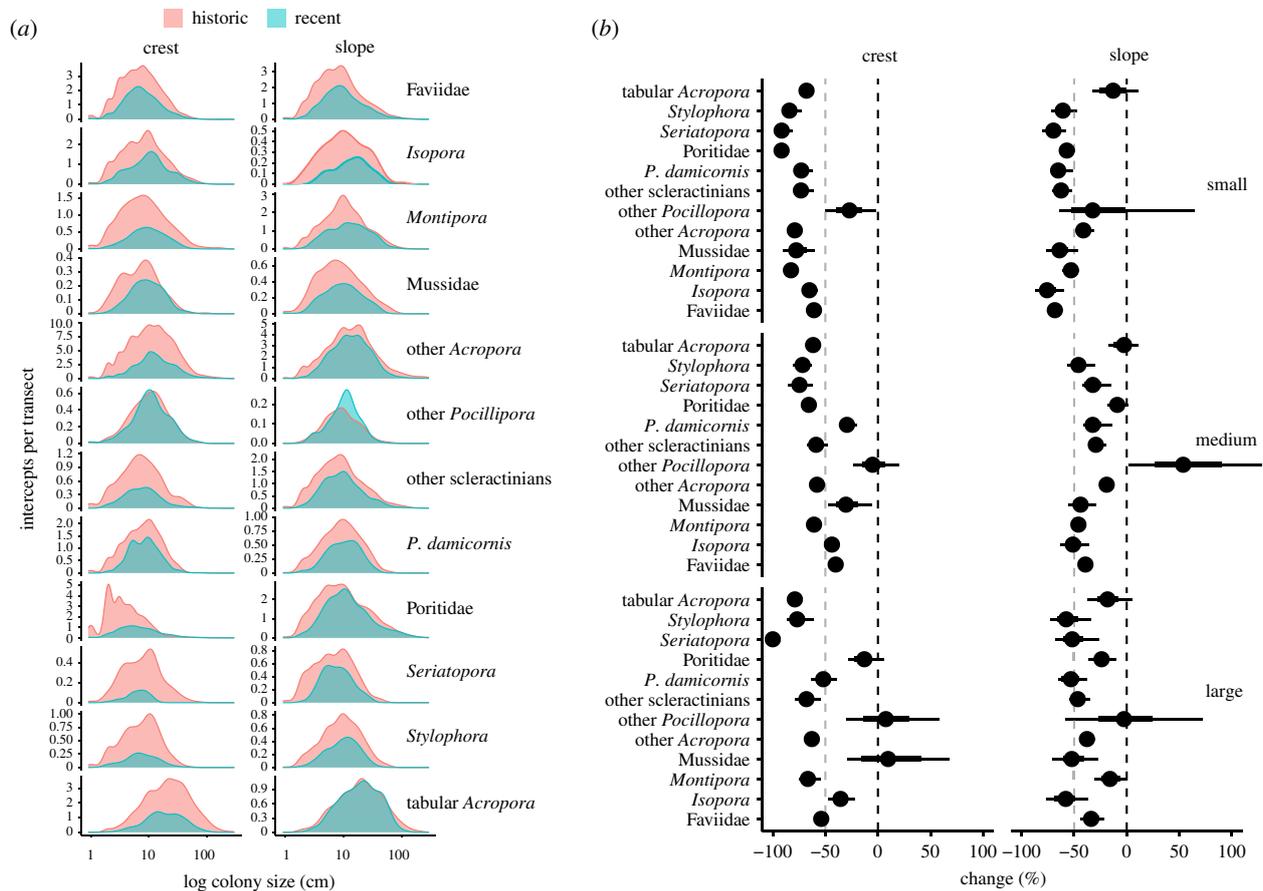


Figure 3. Changes in the colony size structure of major coral taxa. (a) Colony size structure of historic (red, 1995/1996) and recent surveys (blue, 2016/2017) are shown for each of 12 coral taxa on reef crests (left) and reef slopes (right). (b) Changes in the abundance of small, medium-sized and large colonies by taxa and habitat. Percentage changes in absolute abundances are defined as changes in the number of intercepts in the 1st quintile (small), 2nd to 4th quintile (medium) and 5th quintile (large) of intercept lengths. All estimates are shown as 95% highest posterior density intervals. The point indicates the median, the thick line the 66% credible interval and the thin line the 95% credible interval.

Table 1. Changes in the percentage benthic cover of communities (in each sector) and of each taxon (at the scale of the GBR) on the reef crest and reef slope.

| taxon | crest | | | slope | | |
|--------------------------|----------|--------|----------|----------|--------|----------|
| | historic | recent | % change | historic | recent | % change |
| community sector 1 | 36.4 | 6.3 | −82.7 | 34.1 | 19.4 | −43.2 |
| community sector 2 | 63.7 | 2.8 | −95.6 | 19.1 | 4.0 | −79.0 |
| community sector 3 | 41.6 | 17.4 | −58.1 | 42.8 | 18.5 | −56.8 |
| community sector 4 | 28.1 | 12.1 | −57.0 | 39.0 | 24.9 | −36.0 |
| community sector 5 | 34.9 | 42.8 | 22.5 | 37.0 | 40.3 | 8.8 |
| Faviidae | 3.1 | 1.6 | −46.5 | 3.9 | 2.3 | −39.8 |
| <i>Isopora</i> | 2.7 | 1.6 | −38.5 | 0.8 | 0.4 | −52.5 |
| <i>Montipora</i> | 2.2 | 0.6 | −72.1 | 3.5 | 2.3 | −35.3 |
| Mussidae | 0.3 | 0.2 | −27.7 | 0.8 | 0.4 | −50.0 |
| other <i>Acropora</i> | 15.6 | 5.8 | −62.7 | 11.8 | 6.3 | −46.1 |
| other <i>Pocillopora</i> | 0.6 | 0.6 | −2.1 | 0.2 | 0.2 | 17.9 |
| other scleractinians | 1.0 | 0.4 | −64.4 | 2.8 | 1.6 | −41.0 |
| <i>P. damicornis</i> | 1.7 | 1.0 | −42.1 | 1.0 | 0.5 | −45.0 |
| Poritidae | 1.6 | 0.9 | −45.0 | 5.1 | 4.3 | −15.4 |
| <i>Seriatopora</i> | 0.4 | 0.0 | −90.0 | 0.7 | 0.4 | −44.4 |
| <i>Stylophora</i> | 0.7 | 0.2 | −76.2 | 0.8 | 0.4 | −53.6 |
| tabular <i>Acropora</i> | 11.1 | 2.9 | −74.0 | 3.1 | 2.5 | −19.1 |

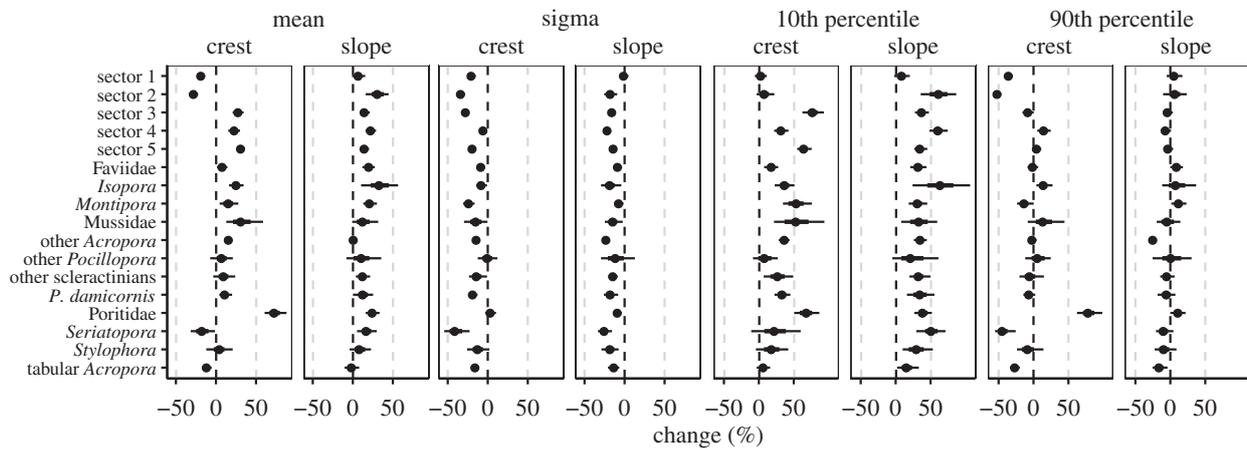


Figure 4. Changes in the mean, standard deviation (sigma) and 10th and 90th percentile of the colony size structure of crest and slope communities in five sectors and of individual taxa (pooled across sectors). Percentiles are indicators for the relative abundance of small (10th) and large (90th) colonies, where an increase in the 10th percentile indicates a decrease in the relative abundance of small colonies. All estimates are shown as 95% highest posterior density intervals (HPDI) where the point indicates the median, the thick line the 66% credible interval and the thin line the 95% credible interval.

suffered comparatively minor losses of large colonies. Large colonies of Poritidae declined by 14.9% (−30.6% to +1.6%) on crests, and by 23.8% (10.3%–35.2%) on slopes. Large Mussidae increased by 8.8% (−41.4% to +81.3%) on crests, but declined by 50.5% (28.1%–71.1%) on slopes. Large colonies (in the top quintile) of the genus *Seriatopora* declined by 100% on the reef crest and by 49.6% (29.6%–87.9%) on the reef slope.

The abundance of medium-sized colonies (2nd to 4th quintile) also declined in most taxa and habitats. On the crest, 7 of the 12 examined taxa lost at least half of their medium-sized colonies. Medium-sized colonies of the genera *Seriatopora* (−63.9% to −86.1%) and *Stylophora* (−62.5% to −78.5%) were the most affected. On the slope, the abundance of medium-sized colonies approximately halved in 4 of the 12 taxa, remained stable in tabular *Acropora* (−17.5% to +11.3%) and Poritidae (−17.6% to +0.8%), and increased by 55.1% (−6.2% to +134.3%) in other *Pocillopora* (figure 3b).

(b) Changes in the mean, standard deviation and percentiles of colony size

While before–after coral abundances on both the reef crest and reef slope declined across all size classes (figures 2 and 3), colonies in the 10th percentile were larger in 2016 and 2017 (figure 4), due to the disproportionate loss of small colonies. By contrast, colonies in the 90th percentile of colony size remained stable in size. The disproportionate decline in small colonies resulted in a systematic narrowing of colony size structures, across habitats, sectors and taxa (figure 4), as indicated by declines in the standard deviation (sigma) of colony size. For both crest and slope communities, the standard deviation of colony size was remarkably similar between sectors in 1995 and 1996, but was consistently lower across all sectors and more variable between sectors in the recent surveys. Increases in the 10th percentile of colony size, indicating declines in the relative abundance of small colonies, were particularly pronounced in the central and southern regions of the GBR (sectors 3 to 5), and changed comparatively little in crest communities of sectors 1 and 2 (figure 4).

The size of the largest colonies (90th percentile) remained stable on reef slopes in all sectors and on crest communities in sectors 3 to 5 (figure 4). Combined with the disproportionate loss of small colonies, this resulted in consistent increases in mean colony size across all sectors and habitats, with the exception of crest communities in sectors 1 and 2, where mean colony size decreased by 20.0% (14.7%–24.7%) and 27.7% (21.9%–32.9%), respectively. On the crests in sectors 3 to 5, mean colony size increased by 23.3% (16.5%–29.8%), 21.0% (14.5%–28.2%) and 30.4% (24.6%–36.3%) (figure 4). On the reef slope, mean colony size increased consistently across sectors, by up to 32.1% (17.5%–48.2%) (sector 2). A north–south gradient was particularly evident on the reef crest, where size structures shifted more in the south towards larger mean colony sizes, with relatively fewer small and more large colonies (figure 4). By contrast, shifts in colony size structure were consistent across sectors on the reef slope.

The size structure of individual taxa also changed markedly (figure 4). The size of the smallest colonies (10th percentile) increased consistently across all taxa and habitats (figure 4), while the size of the largest colonies (90th percentile) remained comparatively stable except for crest populations of tabular *Acropora* and *Seriatopora* (figure 4). As a result, mean colony size increased, and the standard deviation of colony size (sigma) decreased in most taxa and habitats. Changes were particularly pronounced in corals of the genus *Seriatopora* and the family Poritidae. The colony size structure of Poritidae shifted towards larger colonies, indicated by increases in mean colony size (crest: 72.7% (60.6%–88.9%), slope: 24.1% (15.3%–32.2%)), increases in the size of large colonies (90th percentile, crest: 78.2% (60.2%–95.8%), slope: 11.0% (−0.8% to +20.9%)), and by marked increases in the size of small colonies (10th percentile, crest: 67.5% (49.5%–85.9%), slope: 38.0% (26.2%–51.3%)). Corals of the genus *Seriatopora* suffered sharp declines in the relative abundance of both small and large colonies, as indicated by increases in the 10th percentile of colony size (crest: 21.5% (−10.8% to +54.2%), slope: 50.2% (28.2%–70.0%)) and decreases in the 90th percentile (crest: 44.8% (29.1%–57.4%), slope: 9.8% (−20.7% to +4.1%)), resulting in a pronounced narrowing of their colony size structure (figure 4). Large colonies of tabular *Acropora* declined in size by 26.7% (19.3%–33.2%) on the reef crest and by 16.0% (4.7%–25.5%) on the reef slope (figure 4).

4. Discussion

Our study documents the systematic decline of absolute coral abundances across size classes, habitats, sectors and taxa on the GBR over the last two decades. Sharp declines in the abundances of medium-sized and, in particular, highly fecund large colonies signal the depletion of coral brood stock required to replenish diminished populations (figures 2 and 3). The simultaneous, disproportionate decline in the abundance of small colonies, by 76.1% on the crest and 57.2% on the slope (figures 2–4) corroborates findings that the depletion of coral brood stocks impaired coral recruitment rates on the GBR following mass coral bleaching in 2016 and 2017 [24].

Here, we used colony line-intercept lengths as a proxy for colony size to estimate shifts in colony size structure (see also [19,20]). This quantity is not a direct measure of colony size, however, we believe that our conclusion that the colony size structure of coral populations has fundamentally shifted along the GBR over the last decades is robust because (i) we followed a consistent sampling protocol; (ii) we examined relative changes in size-class abundances and size structure rather than seeking to infer absolute changes in colony areal extent or similar (which would have been sensitive to a calibrated relationship between intercept length and size); (iii) while short intercepts may stem from both small and large colonies, long intercepts will only be produced by large colonies, and therefore shifts in intercept distributions will reflect qualitative changes in the underlying colony size structure; and (iv) for studies of this kind, sampling biases are unlikely to vary systematically between taxa, or over space and time, given sufficient sample size [20]. We acknowledge, however, that using line intercepts can be a poor proxy of the areal extent or volume of colonies, particularly for thicket-forming species like staghorn *Acropora*, for species with frequent partial mortality events and for colonies with irregular shapes like encrusting corals. Novel survey technologies such as photo-mosaics will help alleviate these shortcomings in future work. The long legacy of line-intercept transect data, however, makes it an irreplaceable source of historical demographic data in corals, covering time periods and regions in which photo-mosaics are unavailable.

Our results support the hypothesis that, in deteriorating reef environments, coral populations can exhibit a disproportionate loss of small coral colonies due to the depletion of adult brood stocks and the resulting decline in recruitment rates, as witnessed on reefs in the Caribbean [12,18]. By contrast, our findings are inconsistent with alternative suggestions that naturally higher recruitment rates on many Indo-Pacific reefs (compared with Caribbean reefs [26]) may instead boost the relative abundance of small colonies, as reefs recover, as well as reducing mean colony size and the relative abundance of large colonies, as found in the Red Sea [19] and Kenya [20]. In the Red Sea, recruitment rates remained constant following coral mass bleaching [19] but declined by 89% compared with historic baselines on Australia's GBR in the aftermath of back-to-back mass bleaching events in 2016 and 2017 [24]. In demographically open populations, the relationship between brood stocks and recruitment may be obscure at local scales but emerges at the scale of larval dispersal [24,27]. Discrepancies in post-disturbance changes in recruitment between reefs in the Red Sea and on the GBR may reflect differences in the severity, extent

or patchiness of disturbance impact. However, attributing shifts in size structure to disturbances and post-disturbance recovery processes is challenging. Prognoses of future trends in colony size structures of coral populations on the GBR, in particular regarding post-bleaching recovery of populations and communities, will require further spatially extensive surveys.

Geographic patterns in trends in size-class abundances are likely to reflect the history of recent reef disturbances on the GBR. Changes were most pronounced in the northern and central sectors of the Reef, which experienced extreme thermal stress in 2016 and 2017. Size-class abundances on reefs in the far south, which escaped mass bleaching in 2016 and 2017, remained comparatively unchanged (figures 2 and 3). Although crest communities in sectors 1 and 2 shifted towards relatively more small colonies, declines in their absolute abundances of 74.3% and 90.1%, respectively, (figure 2*b*) indicate that this outcome should not be misconstrued as signs of resilience or recovery. Shifts towards smaller colonies may be attributable to the lower bleaching susceptibility of recruits [28] and juveniles [29], and to the partial mortality of medium-sized and large colonies.

As reef disturbance regimes continue to change and escalate [30], with virtually all reefs in the world projected to experience annual severe bleaching conditions before the end of the century under current emission trajectories [31], the window for the recovery of populations and assemblages between consecutive mass mortality events is shrinking. Populations, in particular of slow-growing and late-maturing taxa, may no longer be afforded sufficient time to recover pre-disturbance brood stocks and population-levels of reproductive output [6]. Allee effects at low densities of sexually mature conspecific colonies may further impair the successful fertilization of eggs, particularly in rare and severely depleted species [32,33]. Lower mortality rates of large individuals may provide a temporary refuge from population decline and recruitment failure, but may mask the erosion of population viability if trends in the decline in smaller colonies, which, individually, contribute comparatively little to overall benthic cover, are overlooked [13].

The implications of shifts in colony size structure extend beyond demography because they also affect the ability of corals to perform ecological functions. Most notably, the largest colonies in a population or community contribute disproportionately to reproduction [6], and therefore to the genetic make-up of future generations [34], but also provide essential habitat for other reef organisms like fish [35]. Declines in the abundance of large colonies thus reduce the productivity of reef ecosystems, and fisheries [8], both directly, through declines in the availability of coral gametes, larvae and recruits, which constitute important sources of food for fish [36] and other reef organisms including corals [37], and indirectly, through the loss of structural complexity and habitat. In the Caribbean, the abundance of *Acropora cervicornis* and *Acropora palmata*, two branching coral species with complex morphology, has declined steeply, especially since the 1980s [16,38], indicating that the historical baseline of what constitutes the colony size structure of an 'undisturbed' population or assemblage has probably shifted on many reefs for decades, if not centuries or millennia [39]. Large-scale long-term trends in the abundance of large old corals and their unique ecological roles remain largely under-explored, compared with similar studies in trees [3,4,40].

5. Conclusion

Our study demonstrates the importance of moving beyond a traditional focus on coral cover, to examine the abundance of colonies with different sizes [41]. Cover is a valuable overall measure of reef health, but size structure offers insights into the demographic processes that underlie declines in coral cover, and which hold crucial clues about future population trajectories. Detecting demographic shifts that may indicate, for instance, recruitment failure or the depletion of brood stock will be critical to our ability to predict recovery or continued decline. As the depletion of coral populations and the erosion of the structural complexity of reef habitat continue, and the frequency of reef disturbances

increases [30], we urgently need better data on demographic trends in corals [42].

Data accessibility. Data and code are available from the Dryad Digital Repository: <https://doi.org/doi:10.5061/dryad.ncjxksrq> [43].

Authors' contributions. A.D. and T.P.H. conceived the study. T.P.H. and A.D. collected the data. M.B. and S.R.C. assisted with statistical analyses. A.D. wrote the paper with input from all authors.

Competing interests. We declare we have no competing interests.

Funding. This study received support from the Australian Research Council's Centre of Excellence Program (grant no. CE140100020) and a Laureate Fellowship (to T.P.H.).

Acknowledgements. We thank the many volunteers who participated in field studies.

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