

Global warming impairs stock–recruitment dynamics of corals

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Changes in disturbance regimes due to climate change are increasingly challenging the capacity of ecosystems to absorb recurrent shocks and reassemble afterwards, escalating the risk of widespread ecological collapse of current ecosystems and the emergence of novel assemblages^{1–3}. In marine systems, the production of larvae and recruitment of functionally important species are fundamental processes for rebuilding depleted adult populations, maintaining resilience and avoiding regime shifts in the face of rising environmental pressures^{4,5}. Here we document a regional-scale shift in stock–recruitment relationships of corals along the Great Barrier Reef—the world's largest coral reef system—following unprecedented back-to-back mass bleaching events caused by global warming. As a consequence of mass mortality of adult brood stock in 2016 and 2017 owing to heat stress⁶, the amount of larval recruitment declined in 2018 by 89% compared to historical levels. For the first time, brooding pocilloporids replaced spawning acroporids as the dominant taxon in the depleted recruitment pool. The collapse in stock–recruitment relationships indicates that the low resistance of adult brood stocks to repeated episodes of coral bleaching is inexorably tied to an impaired capacity for recovery, which highlights the multifaceted processes that underlie the global decline of coral reefs. The extent to which the Great Barrier Reef will be able to recover from the collapse in stock–recruitment relationships remains uncertain, given the projected increased frequency of extreme climate events over the next two decades⁷.

We examined the relationships between adult stock and the recruitment of corals in multiple years and decades before mass bleaching in 2016 and 2017, and again after the bleaching events, focusing on the abundance and taxonomic composition of two life stages: the established adult brood stock and cohorts of coral recruits on settlement panels. We show that the loss of adults is associated with a collapse in larval recruitment and a shift in the composition of the recruitment pool. The prospect of a full recovery to the original mature assemblages is uncertain, over a timeline that will almost certainly encompass further mass bleaching events⁷. Already, at 100 reef locations throughout the tropics, the interval between pairs of recurrent bleaching events has diminished from 25 years in the 1980s to only 5.9 years since 2010⁸. The Great Barrier Reef has experienced mass bleaching 4 times in the past 20 years⁸, and it is projected by climate models to bleach twice each decade from 2035, and annually after 2044, under a business-as-usual scenario for greenhouse gas emissions⁹. Corals that are ‘brooders’ release well-developed larvae that typically settle locally within a day, whereas broadcast spawning corals (spawners) release eggs and sperm that fertilize externally, followed by a peak in larval settlement 4–7 days later¹⁰. Therefore, dispersal and gene flow of brooders is more limited than spawners^{11,12}. In the Indo-Pacific, more than 90% of reef-building coral species are spawners, including the ecologically dominant genus *Acropora*¹³. Consequently, a shift in the preponderance of spawner

versus brooder recruits will alter the taxonomic and functional diversity of coral assemblages and the prevailing spatial scale of source–sink relationships, which could affect the capacity of future assemblages to cope with rapid climate change.

At the scale of the entire Great Barrier Reef, overall recruitment of corals after bleaching was reduced to 11.3% of the average levels measured repeatedly over the preceding decades (in 1996, 1997, 1998, 2004, 2015 and 2016), from 43.1 ± 1.5 (mean \pm s.e.m.) recruits per panel ($n = 1,784$ panels) to 4.9 ± 0.2 recruits per panel ($n = 977$ panels) (Fig. 1 and Extended Data Fig. 1). For spawners, recruitment dropped more steeply to 6.9% of average historical amounts, whereas brooders declined less (to 36.5% of earlier densities), shifting the taxonomic composition of recruits (Fig. 2). Previously, 41.4% of settlement panels had more than 20 spawner recruits per panel, compared to only 0.5% of panels in 2018 (Extended Data Fig. 1). From north to south in 5 latitudinal sectors, only the southernmost sector—which contained 3 of the 15 reefs that we resampled in 2018—did not show a decline (Fig. 1 and Extended Data Tables 1, 2). As expected, recruitment varied substantially from year to year (Extended Data Fig. 2) and among reef sectors (Fig. 1c and Extended Data Table 2), generating a three-way statistical interaction between recruitment in each time period (before and after bleaching), sectors (5 regions from north to south) and reproductive mode (spawner and brooder; Extended Data Tables 1, 2). Our estimates of recruitment in each latitudinal sector, based on a generalized linear mixed model that includes random effects for year and reef, indicate that recruitment of spawners fell to between 2% and 29% of the historical average in sectors 1 to 4, compared to 12% to 46% for brooders (Extended Data Table 2). This 1,400-km expanse of the Great Barrier Reef, comprising the northern two-thirds of the world's largest reef system, was severely damaged during back-to-back bleaching events^{14,15} in 2016 and 2017. The region in the far south escaped with little damage in both years. In 2018, recruitment by spawners and, especially, by brooders was higher in the south compared to historical levels—in marked contrast to elsewhere on the Great Barrier Reef (Fig. 1b, c and Extended Data Table 2).

At a more local scale, high levels of recruitment persisted over multiple decades and years at Lizard Island in the northern Great Barrier Reef (14.67° S and 145.46° E; Extended Data Fig. 2a) until severe bleaching occurred in 2016 and 2017. Although coral cover at this location was reduced sharply within the tracks of two tropical cyclones in April 2014 and March 2015, recruitment by spawners remained high afterwards in early 2016 until the subsequent, much larger-scale losses of corals that were triggered by the back-to-back bleaching events in 2016 and 2017 (Extended Data Fig. 2a). After the first regional-scale bleaching event, recruitment at Lizard Island in 2017 dropped to 1.0% of the densities recorded the previous year, and remained at 3.2% in 2018 after the second mass bleaching event in 2017¹⁴. This temporal pattern, along with the strong relationship between loss of adults

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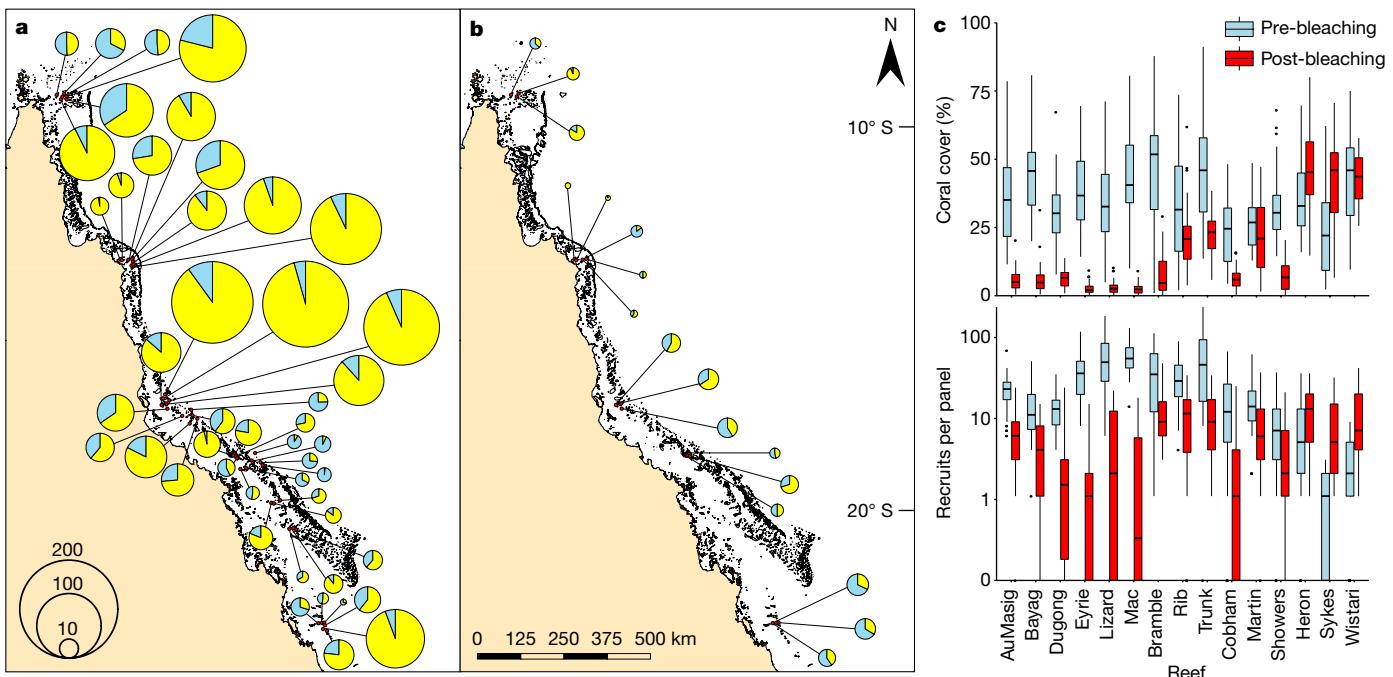


Fig. 1 | The collapse of coral recruitment along the 2,300-km length of the Great Barrier Reef. **a**, Density of recruits (mean per recruitment panel on each reef), measured over three decades, from 1996 to 2016 ($n = 47$ reefs, 1,784 panels). **b**, Density of recruits after mass mortality of corals in 2016 and 2017 due to back-to-back bleaching events ($n = 17$ reefs, 977 panels). The area of each circle is scaled to the overall recruit density of spawners and brooders combined. Yellow and blue indicate the proportion of spawners and brooders, respectively. **a, b**, The

map template is provided by Geoscience Australia under a licence from Creative Commons Attribution 4.0 International Licence. **c**, Changes over time in coral cover and recruitment density on reefs ($n = 15$) sampled in 1996 and again in 2018. Reefs are arrayed from north (left) to south (right) and their locations are mapped in **b**. Horizontal lines show the median, boxes indicate the middle two quartiles, vertical lines indicate the first and fourth quartiles, and data points show outliers.

and depletion of recruitment (Fig. 3 and Extended Data Fig. 4), suggests that recruitment after a mass bleaching event will continue to be diminished until adult brood stocks can regrow, and that recovery from bleaching may be slower than the routine decade-long recovery after a cyclone^{16,17}, owing to substantially greater and more widespread damage to the adult brood stock on upstream source reefs.

Across the entire Great Barrier Reef system, all major groups of coral recruits declined sharply in abundance in 2018 (Fig. 2a), albeit to different extents (Fig. 2b, Extended Data Fig. 3 and Extended Data Table 2). Consequently, the composition of the diminished pool of recruits changed radically on resampled reefs, which reflects marked disparities in the vulnerability of adults to bleaching⁶ and in the subsequent larval recruitment of different taxa. The largest decline in recruitment in 2018—to 7.3% of historical densities—was exhibited by the speciose and ecologically dominant acroporids, followed by *Isopora* (14.4%), other recruits (29.0%), poritids (62.4%) and pocilloporids (65.1%). As a consequence, in 2018 brooding pocilloporids replaced spawning acroporids as the predominant recruit taxon on the Great Barrier Reef (Fig. 2a). Furthermore, reefs with intact brood stocks in the south (sector 5) that escaped bleaching exhibited a markedly different trajectory in the composition of recruit assemblages compared to the northern and central regions (sectors 1–4; Fig. 2b and Extended Data Table 2).

We found a notably linear log-log relationship between the long-term changes in coral cover and recruitment on 15 resurveyed reefs (Fig. 3), which indicates that the loss of mature adults is the dominant driver of the precipitous and widespread decline in the rate of replenishment of corals (Fig. 1c and Extended Data Fig. 4). For both spawners and brooders, the slope of the stock-recruitment relationship was indistinguishable from unity ($t = 0.531, P = 0.600$ and $t = -1.880, P = 0.071$ for spawners and brooders, respectively; Fig. 3a, b), indicating that reductions in recruitment were proportional to the decline in coral cover. Coral cover increased in the southern Great Barrier Reef (Fig. 1c) on reefs that escaped bleaching in 2016 and 2017, and densities

of recruits also increased there, in contrast to the severe decline further north (Fig. 1c and Extended Data Table 2). The same linear relationship between loss or gain of adults and recruits also occurred at a larger scale, among the five sectors that we resampled along the full length of the Great Barrier Reef (Extended Data Fig. 4); this result is consistent with the maintenance of recruitment of spawners in early 2016 at Lizard Island after the local effects of two cyclones, followed by a crash in recruitment in the next two years because of the regional-scale mass bleaching and mortality of adult brood stocks. Furthermore, we observed no difference in the reproductive condition of corals immediately before mass spawning in November 2017, compared to historical levels on the same reefs two decades earlier ($t = 0.840, P = 0.412$; Extended Data Fig. 5). Therefore, we conclude that future recovery of coral recruitment on the Great Barrier Reef will be highly dependent on a gradual increase in the abundance of reproducing adults and on the resistance of surviving brood stocks to future bleaching events.

We found no evidence of mass transport of larvae northwards from unbleached southern reefs (Fig. 1), which could maintain recruitment in the northern and central sections of the Great Barrier Reef in the aftermath of the recent bleaching events. This finding is consistent with the relatively short average larval duration and limited dispersal capabilities of corals—especially brooders^{10,11,18,19}—with the dominant patterns of connectivity from north to south on the Great Barrier Reef²⁰ and with the spread southwards of repeated outbreaks of the crown-of-thorns starfish *Acanthaster solaris*²¹. Even if coral larvae could disperse northwards in demographically meaningful numbers against the prevailing currents for many hundreds of kilometres, genotypes from cooler, high latitudes in the southern Great Barrier Reef are likely to be maladapted to the warmer average and peak sea surface temperatures on northern reefs^{4,22}. Furthermore, immigration of maladapted genotypes can cause outbreeding depression and constrain adaptive capacity²³.

The strong relationship between the suppression of recruitment and the loss of adult brood stock (Fig. 3) indicates that recovery of

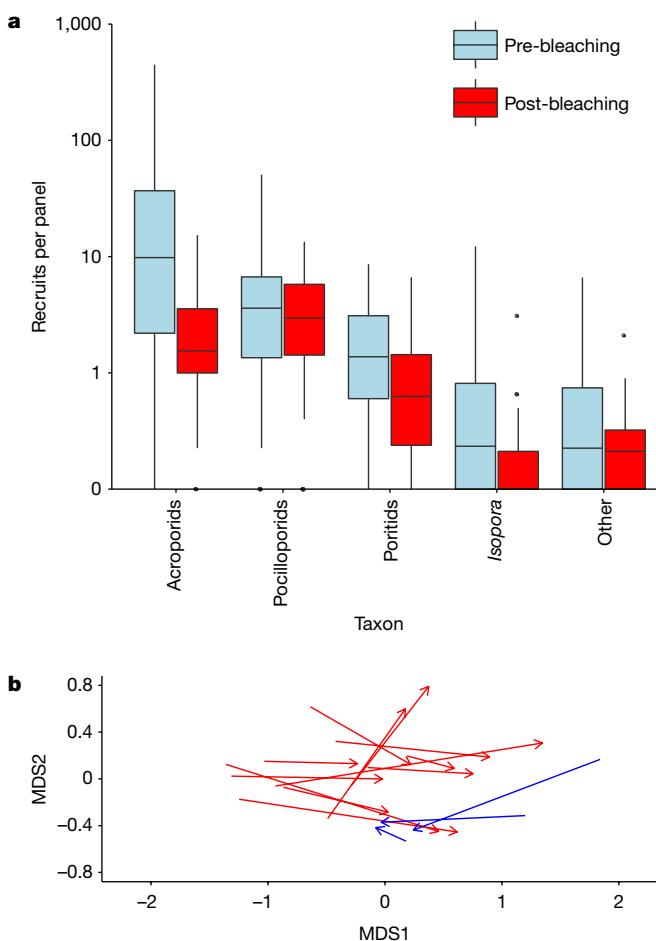


Fig. 2 | Changes in the composition of corals recruits on the Great Barrier Reef before and after mass mortality of adults. **a**, Box plots of the density of five taxonomic categories (acroporids, pocilloporids, poritids, *Isopora* and other recruits) of recruits on experimental settlement panels, measured repeatedly in 1996, 1997 and 2004 ($n = 42$ reefs) before the bleaching event, and in 2018 after mass mortality due to back-to-back bleaching ($n = 15$ reefs). Horizontal lines show the median, boxes indicate the middle two quartiles, vertical lines indicate the first and fourth quartiles, and data points show outliers. **b**, The shift in composition of coral recruits, measured by a non-metric multi-dimensional scaling analysis of recruit assemblages, on each of 15 reefs that were sampled in 1996 and 2018. The blue arrows highlight the before–after composition on three southern reefs that exhibited higher recruitment in 2018, in contrast to the other 12 central and northern reefs depicted with red arrows. Stress (a goodness-of-fit metric) = 0.079. MDS, multi-dimensional scale.

the key regenerative process of larval recruitment will be protracted, because of its reliance on the slow rebuilding of populations of sexually mature adults in coming years and decades. Furthermore, changes in the composition of the recruitment pool (Fig. 2) will also influence the configuration of recovering adult assemblages, depending on the relative survival and growth rates of individual species. The resilience of the Great Barrier Reef is often assumed to be bolstered by its sheer size and by the capacity of nearby reefs with intact adult populations to supply recruits to each other²⁴. However, the new recruitment dynamics of the Great Barrier Reef in 2018 represent a marked departure from the recent past, shifting to much lower rates of coral replenishment (Fig. 1) and an increased proportion of comparatively weedy and locally sourced recruits of brooders rather than the more widely dispersed and much more diverse larvae of spawners (Fig. 2).

In addition to future larval recruitment, one other potential source of resilience is the older cohorts of recruits—which are now juveniles—that settled before the bleaching events, which may be less susceptible to bleaching-related mortality than co-occurring adults^{25,26}. Following

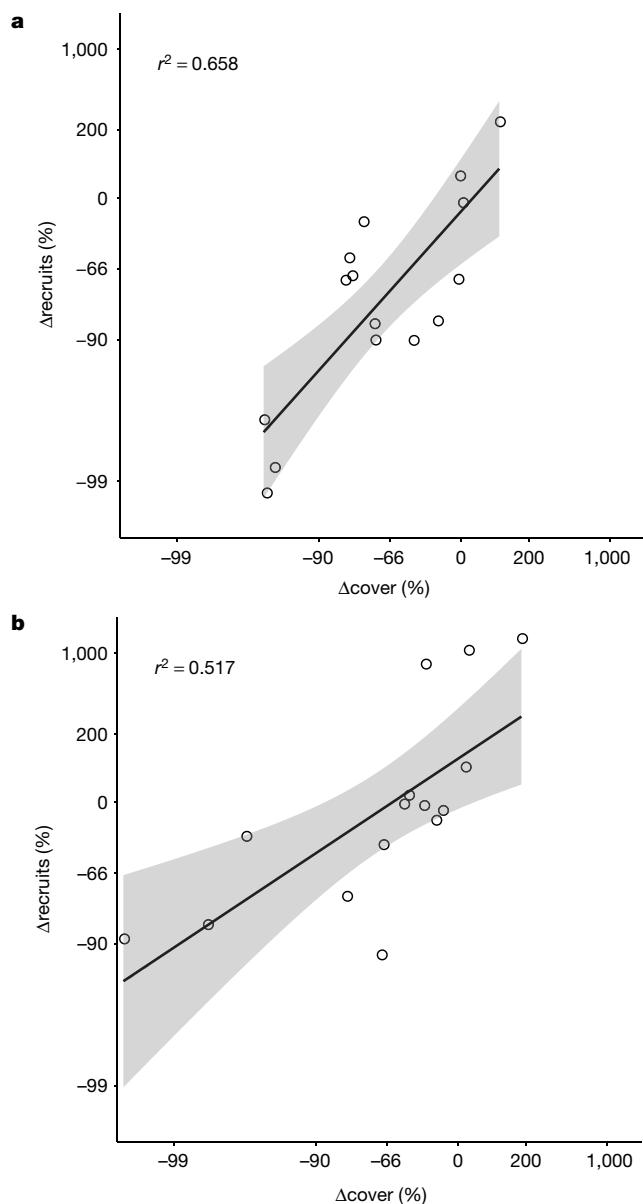


Fig. 3 | Changes in the density of coral recruits as a function of the loss or gain of adult corals. Data points represents the change in recruitment and coral cover, shown as $\log_{10}(\text{change in recruitment})$ and $\log_{10}(\text{change in cover})$, respectively, on each of the 15 individual reefs arrayed along the length of the Great Barrier Reef. Black lines represent the linear model fits and grey shading represents 95% confidence intervals. **a**, Spawners. **b**, Brooders.

mass bleaching in 1998 on Scott Reef, an isolated atoll in the Indian Ocean, a slow recovery of coral cover was driven initially by regrowth of surviving corals, and larval recruitment only recovered 5–10 years later when these remnant corals matured and bred²⁷. However, recovery of recruitment at Scott Reef was facilitated by an 18-year return time between bleaching in 1998 and another event in 2016⁸, as well as by its isolation from other stressors—such as over-harvesting, coastal development, dredging and runoff of pollutants from land—that occur in many parts of the Great Barrier Reef. Furthermore, as global temperatures continue to rise, the probability of avoiding further bleaching events on the Great Barrier Reef in the next decade or two is vanishingly small^{7–9}. According to the most recent assessment by the Intergovernmental Panel on Climate Change, 70–90% of the world's coral reefs could disappear by as soon as 2030 owing to global warming, unless decisive action is taken to reduce greenhouse gas emissions²⁸.

In conclusion, the rate of recruitment by corals on the northern and central Great Barrier Reef has been substantially diminished owing to adult mortality from global warming and other stressors, and hence the system's ecological resilience—its capacity to fully reassemble to the same species composition of mature adults before further bleaching events occur^{7,9,28}—is compromised. It will take at least a decade for the fastest growing species to recover^{16,17} and much longer for longer-lived and slow-growing species. Coral cover has already declined on the Great Barrier Reef in the majority of years since the initiation of long-term monitoring in the 1980s, reaching its lowest recorded levels in 2018²⁹. Thus, even before the mass bleaching events in 2016 and 2017, the rates of coral recruitment and growth have failed to compensate for chronic and acute mortality over the past three to four decades. Our results challenge one conventional view that the resilience of ecosystems has two distinctive elements, namely their resistance to disturbance and their recovery afterwards to the same adult assemblage³⁰. We show instead that, at a regional scale, the resistance of adult brood stocks to recurrent disturbances constrains and drives patterns of replenishment (Fig. 3 and Extended Data Fig. 4). Furthermore, our analyses suggest that thermal tolerance of established coral populations and their capacity to recover through larval recruitment are two inseparable sources of resilience to avoid the loss of dominance by corals. After three pan-tropical bleaching and mortality events since 1998 due to global warming⁸, the capacity of corals to persist, reproduce and disperse will be critical drivers of the unfolding trajectory of the world's coral reefs.

Online content

Any methods, additional references, Nature Research reporting summaries, source data, statements of data availability and associated accession codes are available at <https://doi.org/10.1038/s41586-019-1081-y>.

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Competing interests The authors declare no competing interests.

Additional information

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METHODS

To assess the effect of loss of brood stocks on the regenerative capacity of the Great Barrier Reef, we measured the abundance and composition of adult corals, and the density and composition of newly settled corals on experimental substrates (settlement panels), before and after severe back-to-back bleaching events in early 2016 and 2017. Prior to the bleaching episodes, we sampled 47 individual mid-shelf, platform reefs in five reef sectors arrayed along the length of the Great Barrier Reef. We measured recruitment at four sites on each of 18 reefs in 1996 and on 15 additional reefs in 1997, using a hierarchical sampling design with replicate reefs nested within each of five sectors stretching over 2,000 km, from approximately 10° S to 23° S. These large-scale assessments required five teams of researchers, one per sector, to synchronously deploy and retrieve sets of settlement panels along the full length of the Great Barrier Reef. In 2018, we used the same large-scale design to resample 15 of the reefs, where we had recorded recruitment and adult abundances in 1996 (Fig. 1b and Extended Data Fig. 2). In addition, we measured recruitment at 3 or 4 sites on 14 other reefs in 1996, 1997 and 1998 (sector 2), 2004 (sectors 3 and 4), 2015 and 2016 (sector 2). Our most complete recruitment records are from Lizard Island in sector 2, which was censused six times between 1996 and 2018 (Extended Data Fig. 2a).

For every year and on each reef, we timed the initial placement of settlement panels to coincide with the annual mass spawning of corals on the Great Barrier Reef in November and December³¹. We deployed eight or ten replicate settlement panels 10 days (± 1 day) before the predicted spawning, on the reef crest (1–2 m depth) at each of the replicate sites per reef. All panels at all locations and in each year were identical, 11 cm \times 11 cm, unglazed clay tiles that were attached individually to the reef by a vertical bolt drilled into the substratum. The panels were placed in the open, 1–3 m apart, parallel to the reef crest. We retrieved the panels synchronously after eight weeks (± 1 day) in January. For convenience, here we refer to each recruitment census by the year of retrieval (for example, January 2018, rather than the date of deployment of panels in November 2017). Therefore, the panels retrieved at Lizard Island in 2016 preceded the first bout of bleaching in March 2016, the 2017 panels were deployed and collected after one bleaching episode, and the 2018 census of recruitment on 15 reefs was preceded by both bleaching events. The retrieved panels were soaked in a weak solution of bleach to remove algae and soft-bodied invertebrates and subsequently all coral recruits on the tiles were counted and identified under a dissecting microscope.

To evaluate spatial and temporal changes in recruit density at the scale of the Great Barrier Reef, we used four approaches. First, we pooled all reefs from all years before bleaching, and compared the mean density of recruits in 1996–2016 versus 2017–2018 (Fig. 1a, b). A total sample size of 1,784 and 977 panels were censused before and after the bleaching events on 47 and 17 reefs, respectively. The number of recruits that settled on the panels was 76,946 and 4,763, respectively. Second, we constructed a generalized linear mixed model with a negative binomial error structure; we considered individual years and reefs to be random effects. Fixed effects were time period (before and after bleaching), latitudinal sector (1 to 5) and reproductive mode (brooder versus spawner). Reefs were modelled as random effects within sector and years as random effects within time period (Extended Data Tables 1, 2). We evaluated the support for the two random effects (year and reef) and the three-way interaction effect by comparing the fit of the full model with alternatives that omitted each of these three effects in turn, using Akaike's information criterion. Because the results of the model selection were so unambiguous (approximately 100% confidence that the full model was better

than the three alternatives that we considered), we did not fit any further models with additional terms dropped. Model selection by Bayesian information criterion yielded the same ranking of best-fitting models, and model selection by likelihood ratio testing also led to the rejection of each of the three simpler models in favour of the full model, with very high statistical significance in each case (Extended Data Table 1). Models were fitted using the function `glmer` in R³². The model estimates for mean recruitment of brooders and spawners before and after mass bleaching are shown for each sector in Extended Data Table 2. Third, we compared recruitment densities in 1996, 1997 and 2018, in all five sectors of the Great Barrier Reef, based on the same hierarchical sampling design (Extended Data Fig. 2b). Fourthly, we compared recruitment on 15 reefs in 5 sectors from 1996 that we resampled in 2018 (Fig. 1c). All of these approaches show similar temporal and geographical patterns.

We measured changes in composition of coral recruits on 15 re-sampled reefs using non-metric multi-dimensional scaling based on a Bray–Curtis dissimilarity matrix of untransformed data. The recruits—which were typically only 1–2 mm in size—had sufficient morphological features to distinguish 5 groups: pocilloporids and *Isopora* (both brooders), and acroporids, poritids and other recruits (all spawners). We measured adult abundances using eight or ten 10-m line intercept transects on the reef crest (1–2 m depth) at each of the four sites per reef, using GPS coordinates to return to the same locations. All corals were identified to species or genus, and were subsequently pooled into groups that matched the broader taxonomic categories of newly settled recruits, to reveal how changes in the abundance of adults affected the subsequent patterns of recruitment (Fig. 3). To assess whether coral recruitment in 2018 was affected by a shift in reproductive condition, we measured the proportion of colonies that contained mature oocytes in assemblages of the ecologically dominant genus *Acropora*, which accounts for more than 80% of spawned recruits. We examined corals on ten reefs in November 2017, ten days before mass spawning, following identical protocols to those we used on the same reefs in 1995. In each year, branches were broken below the apical sterile zone to reveal the presence or absence of mature oocytes in older polyps³³. On each reef, 5–149 *Acropora* colonies were sampled and measured in situ (a total of 345 corals in 1995 and 650 in 2018) (Extended Data Fig. 5).

Reporting summary. Further information on research design is available in the Nature Research Reporting Summary linked to this paper.

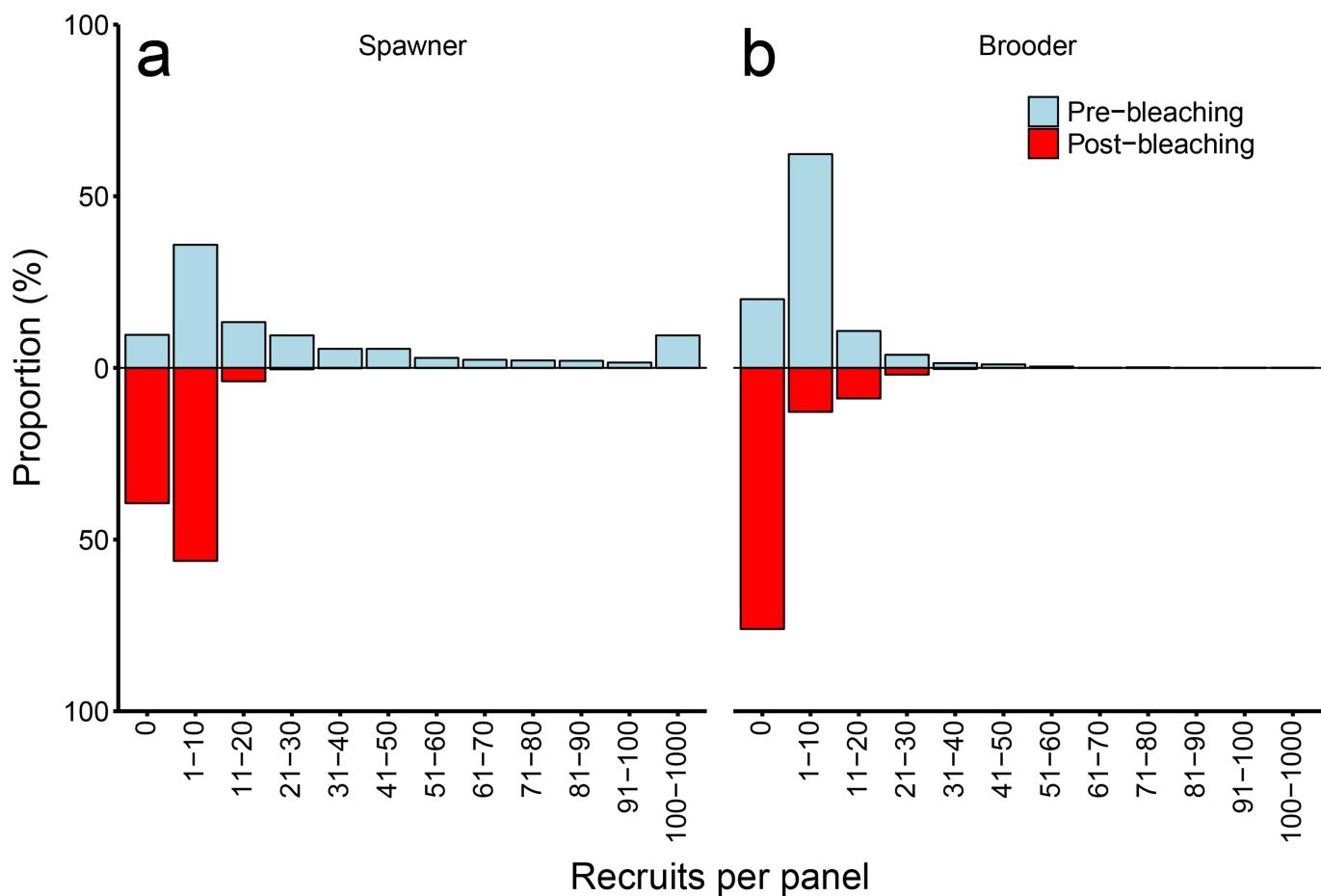
Data availability

Source data on reef locations, adult coral abundance, recruit densities and coral reproductive condition before and after bleaching are available online at the Tropical Data Hub (<https://tropicaldatahub.org/> with DOI: 10.25903/5c81fc323d129).

Code availability

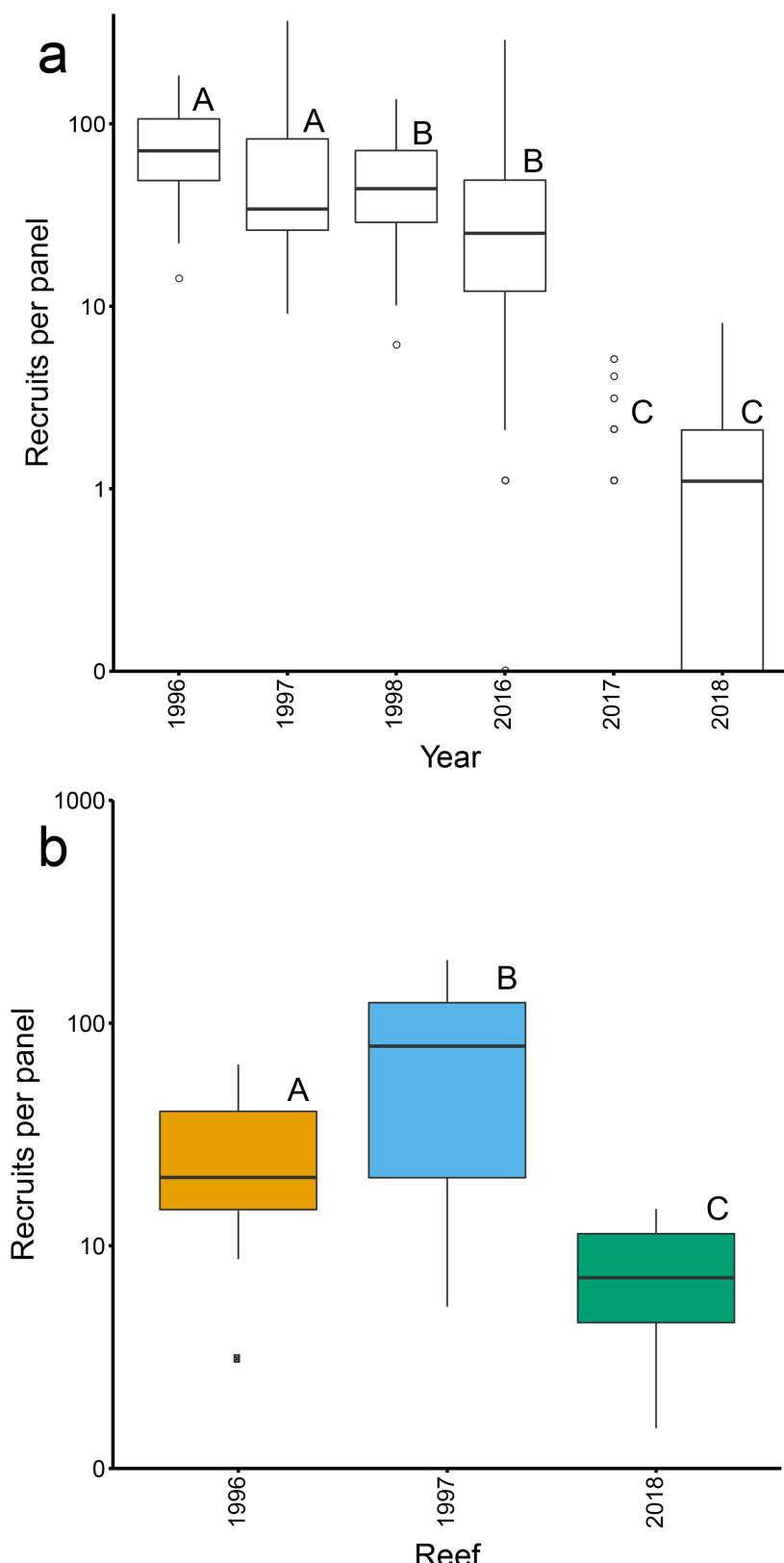
Computer code for statistical analyses is available from the corresponding author on request.

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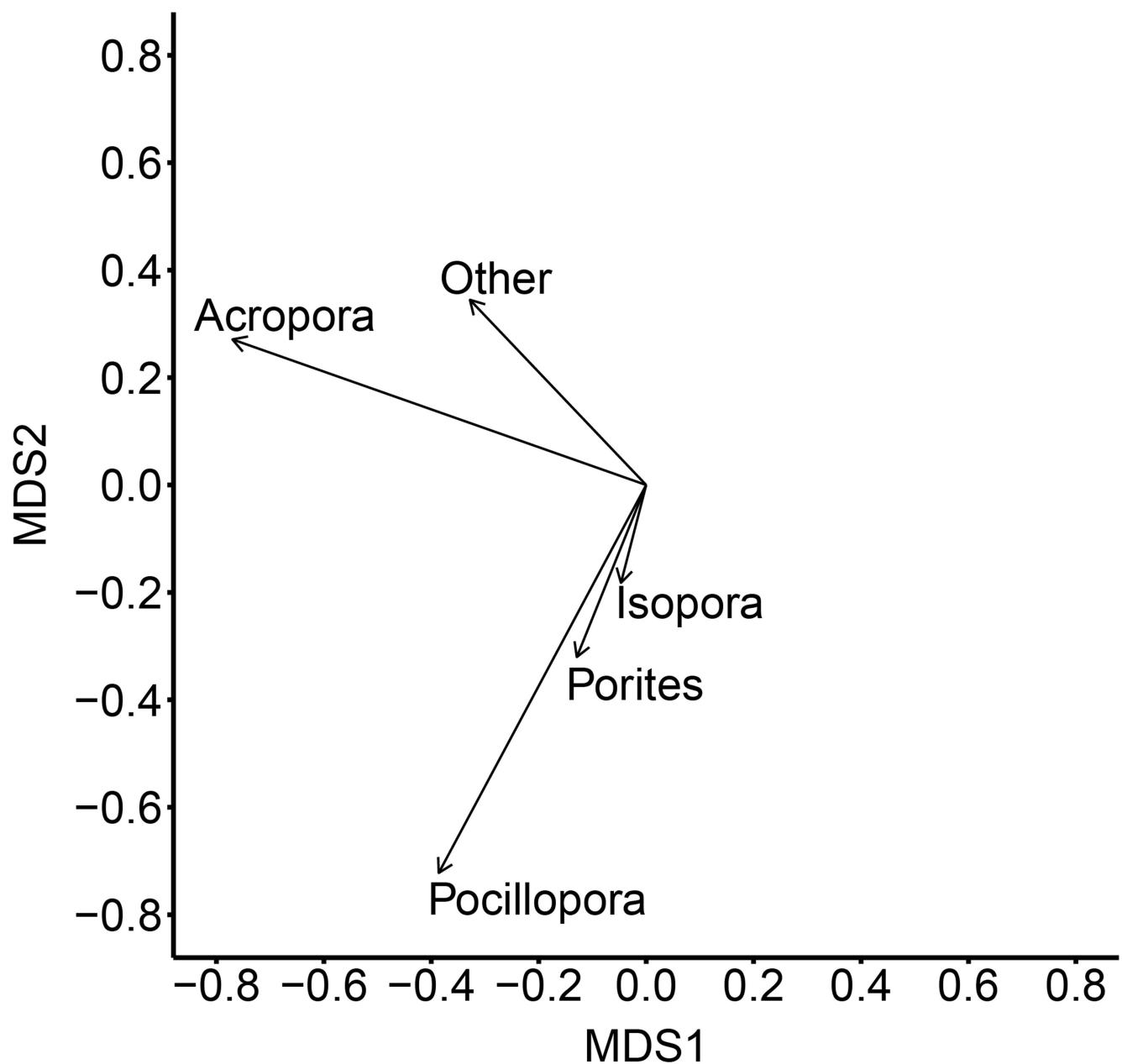
Extended Data Fig. 1 | Frequency distribution of the density of coral recruits, before and after mass bleaching in 2016 and 2017. In total, 1,784 settlement panels were deployed before mass bleaching (in 1996,

1997, 1998, 2004 and 2014–2016) on 47 reefs, and 977 panels on 17 reefs after mass bleaching in 2017–2018. Figure 1 shows the reef locations.

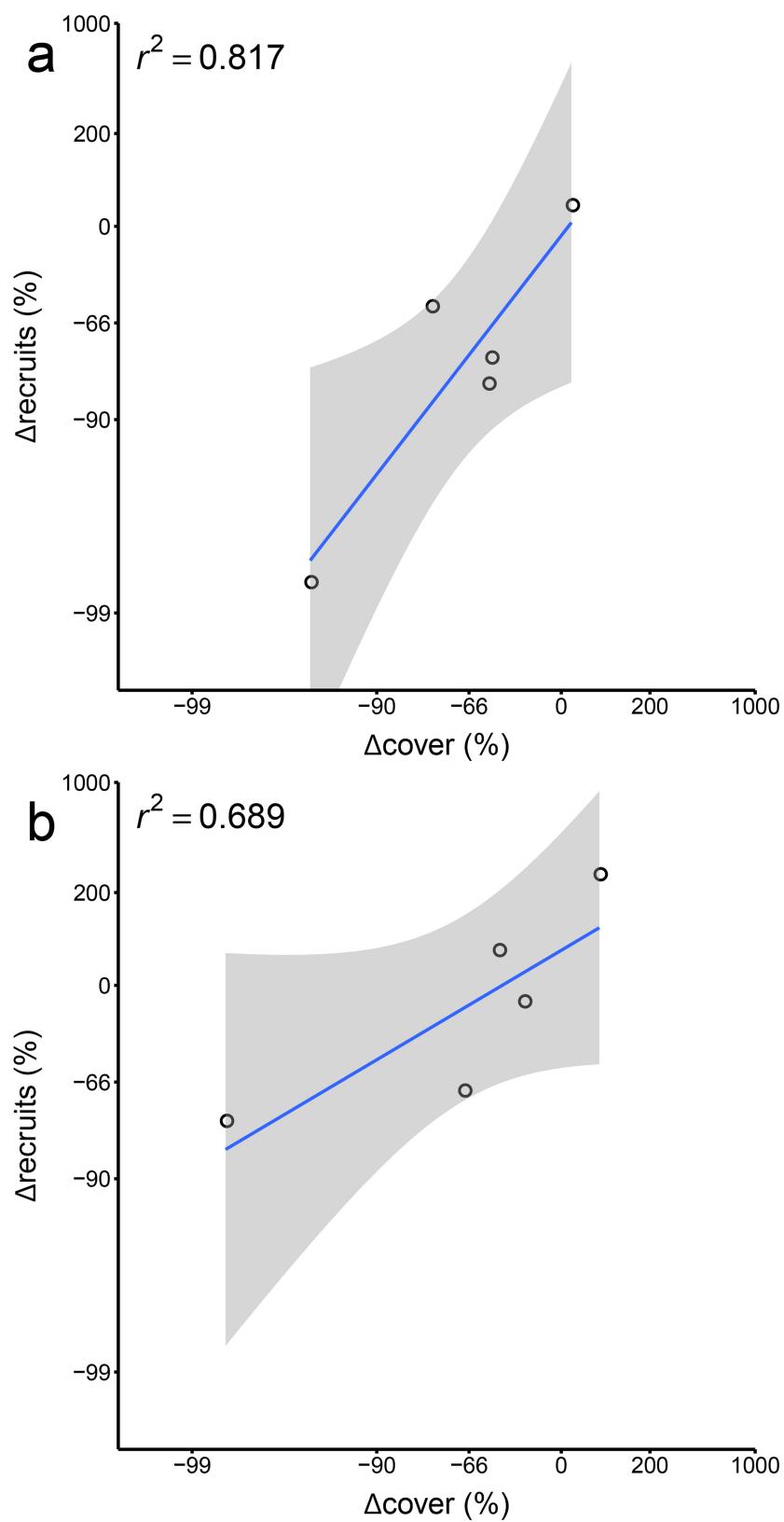


Extended Data Fig. 2 | Recruitment of corals over time. The shared lettering (A–C) indicates recruit densities in each year that are statistically indistinguishable, based on an analysis of variance with Bonferroni-corrected Tukey's post hoc test. Horizontal lines show the median, boxes indicate the middle two quartiles, vertical lines indicate the first and fourth quartiles, and data points are outliers. **a**, Box plots show recruit density per settlement panel ($n = 30, 55, 44, 125, 126$ and 118 panels in

1996, 1997, 1998, 2016, 2017 and 2018, respectively) on Lizard Island Reef in the northern Great Barrier Reef, before and after mass mortality of established corals in March 2016 (after the retrieval of settlement panels in January 2016). Most values for 2017 are zero, causing the box plots to collapse. **b**, Box plots show average recruit density per panel on the Great Barrier Reef in 1996, 1997 and 2018 ($n = 15$ reefs per year, in 5 latitudinal sectors). The same 15 reefs were resampled in 1996 and 2018; see Fig. 1c.

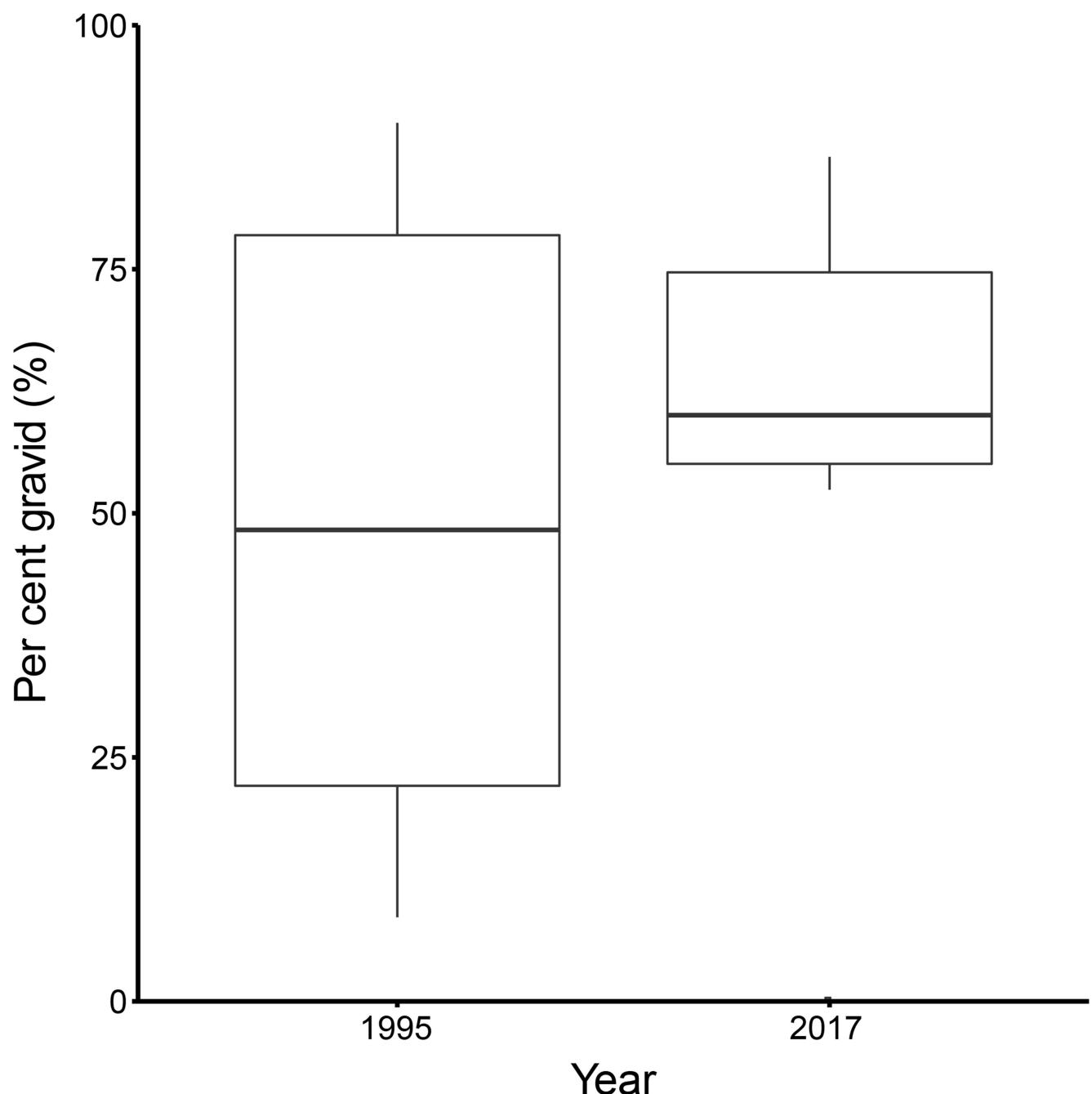


Extended Data Fig. 3 | Vectors for non-metric multi-dimensional scaling analysis. Related to Fig. 2b, showing the shift in the taxonomic composition of coral recruits.



Extended Data Fig. 4 | Changes in the density of coral recruits as a function of the loss or gain of adult corals. Data points represent the change in recruitment and coral cover, shown as \log_{10} (change in recruitment) and \log_{10} (change in cover), respectively, on each of five

sectors arrayed along the length of the Great Barrier Reef. Blue lines represent the linear model fits and grey shading represents 95% confidence intervals. **a**, Spawners. **b**, Brooders. Figure 3 shows the reef-scale relationships.



Extended Data Fig. 5 | Coral reproductive condition on the Great Barrier Reef before mass spawning in November 1995 and 2017. Data in each year were collected from the same set of ten reefs in five latitudinal sectors. Horizontal lines show the median percentage of spawning

Acropora corals that were gravid on each reef. Boxes indicate the middle two quartiles, vertical lines indicate the first and fourth quartiles. Reef locations are provided in the source data (available online at the Tropical Data Hub).

Extended Data Table 1 | Model selection results for generalized linear mixed model analysis of recruitment

Model	MLL	AIC	Akaike weight
Full Model	-15245	30897	≈ 1.000
No 3-way interaction	-15476	30991	≈ 0.000
No year effect	-15579	31201	≈ 0.000
No reef effect	-15646	31337	≈ 0.000

MLL, the maximum log-likelihood of the model; AIC, Akaike's information criterion; Akaike weight is an estimate of model-selection uncertainty: 1 indicates 100% confidence that the indicated model is the best model for inference, and 0 indicates 0% confidence.

Extended Data Table 2 | Model estimates of mean recruitment of brooders and spawners in each latitudinal sector, before and after the mass bleaching

Sector	Mean recruit density (95% CI)		Per cent change	
	Brooders			
	Pre-2016	Post-2016		
1	7.20 (3.80 – 13.67)	1.03 (0.41 – 2.60)	-85.7%	
2	3.11 (1.60 – 6.06)	0.36 (0.15 – 0.87)	-88.4%	
3	8.68 (4.53 – 16.61)	4.03 (1.69 – 9.58)	-53.6%	
4	2.57 (1.35 – 4.90)	0.95 (0.41 – 2.17)	-63%	
5	2.26 (1.08 – 4.74)	8.16 (3.20 – 20.83)	+261.1%	
Spawners				
Sector	Pre-2016	Post-2016	Per cent change	
	Pre-2016	Post-2016		
1	13.73 (7.19 – 26.24)	2.83 (1.21 – 6.66)	-79.3%	
2	32.24 (16.75 – 62.05)	0.55 (0.23 – 1.33)	-98.3%	
3	35.44 (18.31 – 68.60)	5.14 (2.25 – 11.77)	-85.5%	
4	4.62 (2.45 – 8.73)	1.35 (0.60 – 3.04)	-70.8%	
5	3.34 (1.59 – 7.04)	4.56 (1.73 – 12.01)	+36.5%	

Model estimates were based on the fixed-effect estimates from the generalized linear mixed model reported in Extended Data Table 1. The 95% confidence intervals (CI) were produced by parametric bootstrapping, using the function bootMer in R.

Life Sciences Reporting Summary

Nature Research wishes to improve the reproducibility of the work that we publish. This form is intended for publication with all accepted life science papers and provides structure for consistency and transparency in reporting. Every life science submission will use this form; some list items might not apply to an individual manuscript, but all fields must be completed for clarity.

For further information on the points included in this form, see [Reporting Life Sciences Research](#). For further information on Nature Research policies, including our [data availability policy](#), see [Authors & Referees](#) and the [Editorial Policy Checklist](#).

► Experimental design

1. Sample size

Describe how sample size was determined.

No sample size calculation was performed - the study was observational (non-manipulative).

2. Data exclusions

Describe any data exclusions.

No data were excluded

3. Replication

Describe whether the experimental findings were reliably reproduced.

The study was observational, therefore, no experimental replication was attempted

4. Randomization

Describe how samples/organisms/participants were allocated into experimental groups.

Randomization was not relevant to our study

5. Blinding

Describe whether the investigators were blinded to group allocation during data collection and/or analysis.

There were no experimental treatments. Therefore, investigators were not blinded to allocation during experiments and outcome assessment.

Note: all studies involving animals and/or human research participants must disclose whether blinding and randomization were used.

6. Statistical parameters

For all figures and tables that use statistical methods, confirm that the following items are present in relevant figure legends (or in the Methods section if additional space is needed).

n/a Confirmed

- The exact sample size (*n*) for each experimental group/condition, given as a discrete number and unit of measurement (animals, litters, cultures, etc.)
- A description of how samples were collected, noting whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
- A statement indicating how many times each experiment was replicated
- The statistical test(s) used and whether they are one- or two-sided (note: only common tests should be described solely by name; more complex techniques should be described in the Methods section)
- A description of any assumptions or corrections, such as an adjustment for multiple comparisons
- The test results (e.g. *P* values) given as exact values whenever possible and with confidence intervals noted
- A clear description of statistics including central tendency (e.g. median, mean) and variation (e.g. standard deviation, interquartile range)
- Clearly defined error bars

See the web collection on [statistics for biologists](#) for further resources and guidance.

► Software

Policy information about [availability of computer code](#)

7. Software

Describe the software used to analyze the data in this study.

R coding for statistical analysis in R-3.5.1

For manuscripts utilizing custom algorithms or software that are central to the paper but not yet described in the published literature, software must be made available to editors and reviewers upon request. We strongly encourage code deposition in a community repository (e.g. GitHub). [Nature Methods guidance for providing algorithms and software for publication](#) provides further information on this topic.

► Materials and reagents

Policy information about [availability of materials](#)

8. Materials availability

Indicate whether there are restrictions on availability of unique materials or if these materials are only available for distribution by a for-profit company.

No unique materials were used

9. Antibodies

Describe the antibodies used and how they were validated for use in the system under study (i.e. assay and species).

No antibodies were used

10. Eukaryotic cell lines

a. State the source of each eukaryotic cell line used.

No cell lines were used

b. Describe the method of cell line authentication used.

No cell lines were used

c. Report whether the cell lines were tested for mycoplasma contamination.

No cell lines were used

d. If any of the cell lines used are listed in the database of commonly misidentified cell lines maintained by [ICLAC](#), provide a scientific rationale for their use.

No cell lines were used

► Animals and human research participants

Policy information about [studies involving animals](#); when reporting animal research, follow the [ARRIVE guidelines](#)

11. Description of research animals

Provide details on animals and/or animal-derived materials used in the study.

No animals were used

Policy information about [studies involving human research participants](#)

12. Description of human research participants

Describe the covariate-relevant population characteristics of the human research participants.

Study did not involve human research participants