Coral population dynamics across consecutive mass mortality events

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Abstract

Annual coral mortality events due to increased atmospheric heat may occur regularly from the middle of the century and are considered apocalyptic for coral reefs. In the Arabian/Persian Gulf, this situation has already occurred and population dynamics of four widespread corals (*Acropora downingi*, *Porites harrisoni*, *Dipsastrea pallida*, *Cyphastrea micropthalma*) were examined across the first-ever occurrence of four back-to-back mass mortality events (2009–2012). Mortality was driven by diseases in 2009, bleaching and subsequent diseases in 2010/2011/2012. 2009 reduced *P. harrisoni* cover and size, the other events increasingly reduced overall cover (2009: −10%; 2010: −20%; 2011: −20%; 2012: −15%) and affected all examined species. Regeneration was only observed after the first disturbance. *P. harrisoni* and *A. downingi* severely declined from 2010 due to bleaching and subsequent white syndromes, while *D. pallida* and *P. daedalea* declined from 2011 due to bleaching and black-band disease. *C. microphthalma* cover was not affected. In all species, most large corals were lost while fission due to partial tissue mortality bolstered small size classes. This general shrinkage led to a decrease of coral cover and a dramatic reduction of fecundity. Transition matrices for disturbed and undisturbed conditions were evaluated as Life Table Response Experiment and showed that *C. microphthalma* changed the least in size-class dynamics and fecundity, suggesting they were 'winners'. In an ordered 'degradation cascade', impacts decreased from the most common to the least common species, leading to step-wise removal of previously dominant species. A potentially permanent shift from high- to low-coral cover with different coral community and size structure can be expected due to the demographic dynamics resultant from the disturbances. Similarities to degradation of other Caribbean and Pacific reefs are discussed. As comparable environmental conditions and mortality patterns must be expected worldwide, demographic collapse of many other coral populations may soon be widespread.

Keywords: climate change, coral reef, demographics, mass mortality, population dynamics

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Introduction

Coral reefs are among the most sensitive ecosystems to excursions from mean environmental conditions, such as temperature, UV irradiation, and nutrient levels and suffer heavy mortality from consequent bleaching and diseases (Hoegh-Guldberg *et al.*, 2007; Selig *et al.*, 2010; Wiedenmann *et al.*, 2013; D'Angelo & Wiedenmann, 2014; Riegl *et al.*, 2015). Rising global temperatures and alterations in nutrient dynamics are predicted to further increase the frequency of coral bleaching and mortality events that have already increased dramatically since the 1980s (Donner *et al.*, 2005; Baker *et al.*, 2008). Forecasts predict worst-case scenarios of annual bleaching variably between 2040 and 2100 as well as increased severity of disease outbreaks with associated concerns for the future persistence of coral reef ecosystems (Sheppard, 2003; Donner, 2009; Van Hooidonk *et al.*, 2013; Logan *et al.*, 2014; Maynard *et al.*, 2015).

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Precise description of population-level effects of such annual bleaching and mass mortality on corals reefs is already possible today. The SE Arabian/Persian Gulf, no stranger to extreme temperatures and frequent coral bleaching (Coles & Fadlallah, 1991; Burt *et al.*, 2011; Purkis *et al.*, 2011; Riegl *et al.*, 2011; Bauman *et al.*, 2013a), recently experienced four significant coral mortality events back-to-back. Three were caused by bleaching and subsequent diseases (2010, 2011, and 2012), one only by a disease outbreak (2009). Thus, annual coral mortality associated with bleaching and diseases, as forecast by Van Hooidonk *et al.* (2013) and Maynard *et al.* (2015), seems to already be a reality in the world's warmest sea with coral reefs (Feary *et al.*, 2010; Bauman *et al.*, 2011; Burt *et al.*, 2011; Riegl & Purkis, 2012), and the first recorded four consecutive mass mortalities may allow a glimpse into the future of coral population dynamics in a highly disturbed world.

We present here the results of a detailed monitoring program of coral populations across said four disturbances with special reference to flow among size classes, because size distributions in the Gulf have been

shown to be shaped by environmental extremes (Bauman *et al.*, 2013b). This provides baseline information about dynamical processes required for further modeling. We use matrix models (Caswell, 2001) to explore aspects of population dynamics and persistence (Hughes & Tanner, 2000). As the Gulf harbors a depauperate, yet typical, Indo-Pacific fauna (Coles, 2003), these results can serve as direct analog to the future of reefs across the Indo-Pacific.

Material and methods

Coral communities and population dynamics were monitored in the area of Ras Ghanada (UAE). From 2007 onward, 40 phototransects were obtained at two sites, three times per year. A probabilistic sampling approach (Smith *et al.*, 2010) was employed, and transects were placed haphazardly near sampling areas defined by GPS points, within a radius of about 50 m. Overlapping photographs created 0.75 × 5 m photocorridors. Images of each transect were merged and gridded to unit pixel size, where 1 pixel = 1 mm². All corals were identified to species, their outlines digitized and assigned a unique color code. Individual colonies were defined as any autonomous, freestanding coral colonies, or parts thereof with living tissue (Bauman *et al.*, 2013a), a definition allowing colonies to undergo fission by partial tissue mortality. Coral areas, measured as projected surface area, were assigned to five size bins that corresponded to five coral life stages, defined by radius: size class 1 (=SC1, <5 cm), SC2 (<10 cm), corals entering sexual maturity above a puberty size (=SC3, 10–20 cm; but variability can exist in minimum size at puberty; Soong, 1993), SC4 (20–30 cm), and SC5 (>30 cm). These size classes are justified by life-history traits (citations in Riegl *et al.*, 2012). SC3 corals truncated at edges of the transect image were included if they measured >30 cm diameter at any point or had areas equivalent to 15 cm radius, automatically including them in SC3. Only very few SC4 corals were encountered in transects and were treated identical to SC3 corals. Otherwise, most large corals would have had to be excluded, leading to bias against the large size classes. SC5 corals were encountered so rarely that SC4 and SC5 were amalgamated for all analyses. Small truncated corals (i.e., that only partially fell within the phototransect) were ignored because inclusion might have artificially bolstered smaller size classes than the truncated corals actually belonged to (Riegl *et al.*, 2012).

Recruits, colonies of <2 cm diameter, were counted whenever possible and concentrated efforts were made in 2009, 2011, and 2012. Recruitment was highly variable in space and time (see also Bauman *et al.*, 2011, 2014). Most recruitment was observed in areas of caprock or artificial substrata (see also Burt *et al.*, 2009) outside the dense coral area, within which recruits were frequently found in close proximity to larger corals – making unequivocal distinction from asexual propagules difficult. As consistent and defensible recruit counts proved elusive, we excluded this size class from quantitative analysis.

Over time, the size-class distributions of the measured corals represented a sequence of population vectors from which transition matrices (*T*) containing survival, growth, and shrinkage probabilities could be inverted using Wood's method as implemented in Caswell (2001). The resulting size-class transition models were verified by hindcasting (see Supplemental Information). Test model runs were begun by multiplying the inversely solved size-class transition matrices by the first (oldest) monitoring population vector, running for as many time steps as available from the monitoring effort (max. *N* = 19), and comparing results (Figs S1, S3, S6, S9, S12, S15).

As recruitment was not explicitly measured (i.e., number of newly settled recruits), the solved matrices (*T*) contained primarily juvenile and adult life-history events and the full life cycle was best considered as expressed by two matrices where

$$A = T + F \tag{1}$$

The full transition matrix *A* is the sum of the known life-history event matrix (*T*), which expresses the flow among the measured size classes, and a matrix (*F*) of size-class-specific fertilities. *F* was unknown due to spatial and temporal variability of coral recruitment and difficulty of assigning parentage (whether from within or outside the populations) to observed coral recruits. *T* was known as it could be solved inversely by Wood's method.

Thus, fertility was only indirectly assessed via the frequency of small corals. Recruits, which would be required for reliable fertility estimates, were not visible in phototransects. As the dynamics of the evaluated coral populations depend on a combination of shrinkage and largely unquantified recruitment, and the true value of matrix *F* (eq. 1) was unobtainable, the derivation of an asymptotic population growth rate from the matrices (dominant eigenvalue) could not be expected to yield all information required to understand potential future trajectories. Nonetheless, the matrices solved from the undisturbed period could still be treated against those from the disturbed period as a Life Table Response Experiment (LTRE; Hughes & Tanner, 2000; Caswell, 2001) to explore what changes in life stages (i.e., survival/growth/ shrinkage probabilities of individual SCs) had the greatest influence on the dominant eigenvalue of matrix *T*. The dominant eigenvalue *λ* of a transition matrix is the population's asymptotic growth rate (if >1 the population will grow), and its associated eigenvector, if scaled to proportional contribution of each element, is the stable size-class distribution (SsD; Fig. S1) at which the population will settle, if an equilibrium is attained. Whether an equilibrium, and thus SsD, can be reached at all depends on patterns of recruitment. Strong local retention of larvae (i.e., recruitment of the population into itself) will favor SsD, strong connectivity (import and export) can make attaining SsD unlikely. Thus, the distance of observed population vectors from theoretical SsD can give insight into levels of connectivity vs. local recruitment (see also Supplemental Information).

Not all results of population analyses are shown here. Results from analyses for different species are repetitive and therefore are mostly shown in the Supplemental Information and described in detail there.

As phototransects were of a fixed, relatively small size, any growth occurring in the enclosed coral populations was

faithfully reproduced. Sizes of corals were evaluated as their projected area and if considered circular, then a 10% increase in radius would lead to 21% increase in area at each step. For example, an arbitrary population of 100 corals consisting of 70% SC 1, assuming that all are at 5 cm diameter, will increase in cover in 1 year from 14% of a 500×75 cm phototransect to 21%. All massive corals grow in the range of 1–2 cm radius per year, *Acropora* grows up to 10 cm per year (Coles & Fadlallah, 1991; Riegl, 2002; Burt *et al.*, 2010; Vajed Samiei *et al.*, 2012; Bauman *et al.*, 2013a,b). Thus, the observed rapid changes in cover were indeed realistic (Fig. 1), and they also coincided with short-term variability as observed by Burt *et al.* (2010).

To calculate fecundity, we used data from Bauman *et al.* (2011) and Shlesinger *et al.* (1998) for number of oocytes per polyp or mesentery in Gulf or Red Sea corals, where information from the study area was not available. Using generalizations based on measurements of skeletons following numbers cm^{-2} were assigned: 12 polyps*14 oocytes cm^{-2} in *Acropora downingi*, 60 polyps (30 female)*10 oocytes cm^{-2} in *Porites harrisoni* (as this coral is gonochoric and sex ratios in the examined population were unknown, we assumed an even distribution with a ratio of 1; Soong, 1991), 1 polyp*700 oocytes cm^{-2} in *Dipsastrea pallida*, 15 polyps*78 oocytes cm^{-2} in *Cyphastrea microphthalma*, and 20 mesenteries*14 oocytes cm^{-2} in *Platygyra daedalea*. Fecundity was calculated as number of polyps/mesenteries cm^{-2}*number of oocytes per polyp/mesentery * projected surface area of colony. It was then expressed as 'standard fecundity', the

summed oocyte output of 100 colonies apportioned into observed fecund size classes (i.e., SC3, SC4 which included SC5), thus accounting for size dependencies of life processes. These 100 corals were assigned a space cover of '1'. As disturbances decreased coral space cover and therefore per-spatial-unit reproductive output, 'per unit' fecundity was projected by multiplying 'standard fecundity' by the decline in space cover (Table S2). Thus, a given fecundity value (e.g., 1000 oocytes in 100 corals with a cover value 1) would be decreased if fewer individuals and thus less reproductive surface area were available (e.g., 1000 oocytes in 100 corals*0.5*0.5, if cover had declined by half and of that cover, that of the fertile SCs had also decreased by half).

Results

Monitored coral system

In the monitored coral system near Ras Ghanada in eastern Abu Dhabi, 29 of the southern Gulf's regularly occurring 35 species existed (Table S1). Five species accounted for >50% space cover and are known (Riegl, 1999; Riegl & Purkis, 2009, 2012) as keystone species in southern Gulf reefs due to their common occurrence, and/or importance as frame builders (Purkis *et al.*, 2005). Following analyses concentrate on these species:
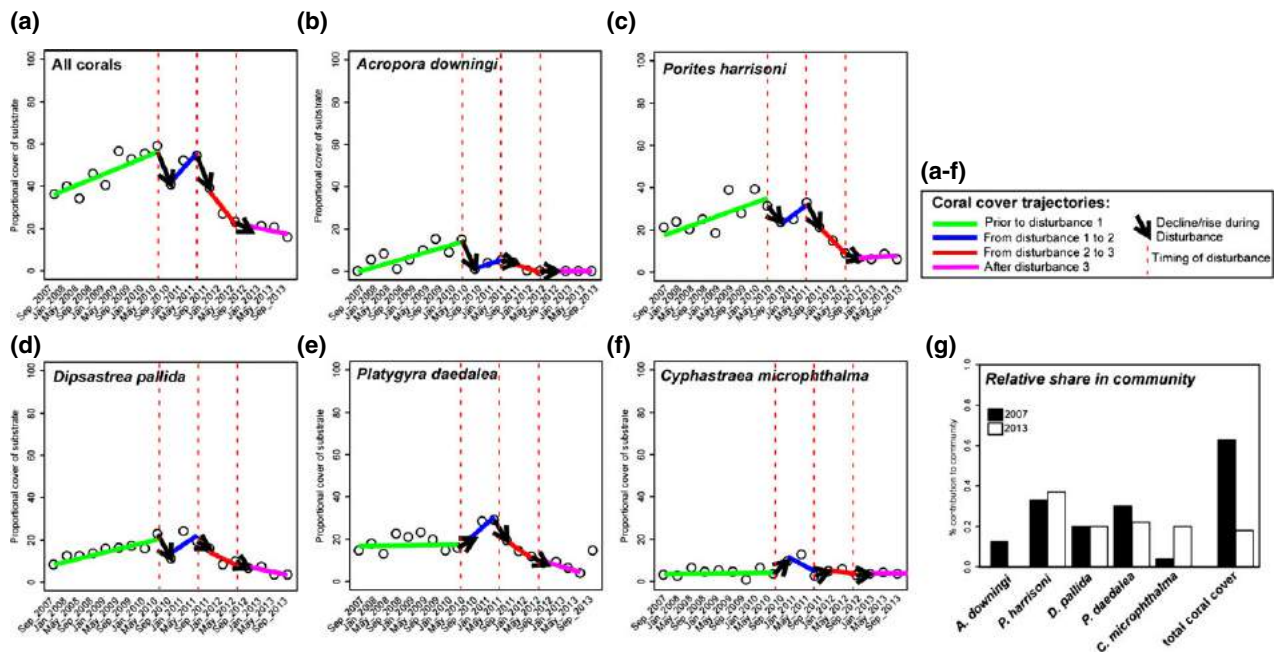
Fig. 1 (a-f) Trajectory of coral cover. Coral cover trajectories are linear regressions over coverage values *P. harrisoni* shows three episodes of cover declines (September 2009/2010/2011), *A. downingi* crash after two events, *D. pallida* and *P. daedalea* cover declined after September 2011, *C. microphthalma* cover remained essentially unchanged. Note that *y*-axis is proportional substrate cover, not share in total coral cover. (g) Changes in the % contribution to the community, as share in the space covered by all corals. *A. downingi* virtually disappeared, and *C. micropthalma* gained in importance, changes in the other species are not significant. Total cover by these five species fell to about a quarter of predisturbance levels.

Acropora downingi (2007: 15% of coral cover; prior to dieback in 1996/1998 cover was >70%, almost disappeared in many areas but strong regeneration until 2010; a fast-growing and aggressive species that rapidly monopolizes space and builds framework). *Porites harrisoni* (2007: 39% of coral cover; dominant frame builder since decline of *Acropora* in 1996/1998), *Dipsastrea* (formerly: *Favia*; Budd *et al.*, 2012); *pallida* (2007: 9% of coral cover; ubiquitous and key colonizer of new substrates); *Platygyra daedalea* (2007: 28% of coral cover; common everywhere); *Cyphastrea microphthalma* (2007; 9% of coral cover; most heat-tolerant of all Gulf corals; common in most habitats and often the last coral to persist after mass mortalities).

Diseases and temperatures as drivers of mortality events

Mortality events are shown in Table 1 and responded to temperatures reaching or exceeding the bleaching threshold of 35.7 °C (Riegl *et al.*, 2011) during peak temperatures at the end of August. Except in 2009, coral bleaching preceded diseases. Not all corals were equally affected (Table 1). Except in 2009, onset of events was sharp, in the last week of August or first of September, and epidemic mortality lasted until November. The 2009 event was poorly defined with elevated, but nonepidemic, mortality only in *P. harrisoni* from June to November. During winter, coral diseases always recess (Riegl, 2002). While some nearby areas also bleached in 2013, the study area escaped renewed bleaching apparently due to strong winds that caused cooling of the shallow water column.

Over the study period, coral cover declined in response to the mass mortalities, but effects and subsequent regeneration differed among species and events (Fig. 1). From September 2007 to September 2010, there was either increase in cover (*P. harrisoni*, *D. pallida*, *A. downingi*) or stasis (*P. daedalea*, *C. microphthalma*). The 2010 event reduced overall coral cover by about 20%. While some species experienced cover reduction (*P. harrisoni* and *A. downingi*, with steepest decline; and *D. pallida*), others were not affected (*C. microphthalma*, *P. daedalea*). Regeneration of space cover or continuous growth was observed in all species, but in *A. downingi*, it was slower than predisturbance growth (Fig. 1).

Regeneration was interrupted again in 2011 with a comparable decline (−20%) of total cover. Also cover by *P. harrisoni* declined as much as in the previous year. *P. daedalea* also declined strongly, with less drastic decline in *D. pallida* and *A. downingi* (already at ~5% cover). Following this event, cover per species as well as total cover showed a persistent decline, which reflected the continuous negative effects of coral diseases. The 2011 event caused significant cover reductions across all species (Table 1) and decline in cover continued over the entire next year.

The 2012 event caused the least decline (−15%), but cover was already low (Fig. 1). Except *C. microphthalma*, which remained at essentially steady cover, and *A. downingi*, which had all but disappeared, all other species continued to decline. Over the following year, declines in cover slowed, *C. microphthalma* remained steady, while *P. harrisoni* increased slightly. *A. downingi* remained at zero level.

In sum, cover in these four species declined over the four events and subsequent years by 72%. This was more than the 65% decline of coral cover in total (Table 1), which suggests that some of the rarer species, not studied in detail here, suffered relatively less mortality (Fig. 1g). Importance (relative contribution) of *C. micropthalma* quintupled (the 'winner'), while *A. downingi* disappeared from the dataset (the 'loser';

Table 1 Characterization of mortality events at Ras Ghanada, Abu Dhabi. Reduction in coral cover refers to all species present, not only the four studied in detail in this study. These suffered higher losses than shown in this table (72%, see text). Bleaching level refers to percentage of bleached corals observed across the entire community: B, bleached; PB, partially bleached; NB, not bleached

Year of event	Months	Cause	Bleaching level	Species most affected	Overall coral cover reduction, %
2009	May–September	White Syndrome, Cyanobacteria	B = 0 PB = 0 NB = 0	*Porites harrisoni*	10
2010	September–November	Moderate bleaching, White Syndrome, Cyanobacteria	B = 0.1 PB = 0.11 NB = 0.78	*Acropora downingi*	20
2011	August–November	Strong bleaching, Black-band disease, Cyanobacteria	B = 0.39 PB = 0.35 NB = 0.15	*Platygyra daedalea*, *Dipsastrea pallida*, *Porites harrisoni*	20
2012	August–November	Strong bleaching, Black-band disease	B = 0.82 PB = 0.17 NB = 0.01	*Platygyra daedalea*, *Dipsastrea pallida*, *Porites harrisoni*	15

however, *A. downingi* did not disappear from the region, colonies remained at nearby sites that fell without the sampled area). While the other three species shrank, their relative contribution to the community did not change significantly (*t*-test, *P* = 0.7).

Size-class distribution across three subsequent mortality events

Size-class distribution clearly reflected the disturbance events by an overall shrinkage of average coral size (Figs 2b and S2). At the beginning of monitoring, ~70% of corals were in the smallest SC, which increased to 85% by September 2013 (Fig. S2). Most drastic changes were seen in the major framework-building species. *A. downingi* changed from 72% in the smallest size-class predisturbance to 95% after two disturbances and then completely disappeared. *P. harrisoni* increased from 55% to 86% in the smallest SC. *D. pallida* lost primarily small colonies across the first two events, while the third event reduced large colonies. *P. daedalea* changed little across the first event (smallest SC changed from 50 to 52%; Fig. S2), but colonies clearly shrank across the next two events. *C. microphthalma* suffered the smallest changes in size distribution and cover across all three mortality events (Figs 1, 2 and S2), but also suffered loss in the big SCs.

Fecundity reduction due to tissue loss

The reductions in coral size and cover had repercussions on fecundity, and significant reproductive potential was lost in all species, with smallest changes in *C. micropthalma* (Table 2). The severely reduced remnant population of *A. downingi* lost all fecundity prior to complete disappearance from the sampling area. This made recovery from a local population highly unlikely and suggested that this species can only persist if connected to another, still fertile, population. Also *P. harrisoni, D. pallida,* and *P. daedalea* fecundity had declined to a level that, coupled with the shrinkage in live cover, would suggest a declining trajectory (Table 2). *C. microphthalma* was a clear 'winner' in the situation: not only had it suffered little cover reduction and therefore increased its total share of cover in the overall community (Fig. 1g), it also had suffered the least size-based fecundity reductions. This would suggest increasing importance of *C. microphthalma* in future community composition (Fig. S18).

Dynamics based on projection matrices

Availability of sufficient time series of size distributions allowed inverse solution of transition matrices containing survival, growth, and shrinkage probabilities of size classes for each of the investigated species (details in Supplemental Information). This allows explicit definition of altered growth/mortality dynamics of the survivors of the bleaching/disease outbreaks. For all species, at least one 'undisturbed' and one 'disturbed' matrix could be solved prior to and across the consecutive mass mortalities (see also Supplemental Information) and compared as a Life Table Response Experiment (LTRE; Caswell, 2001).

Undisturbed scenarios identified all species except *A. downingi* and *D. pallida* near theoretical stable-stage distribution (Fig. 2). Undisturbed *A. downingi* showed strong flow into the large SCs and strong retention there, as would be expected from a fast-growing species. This is concordant with populations tending toward forming closed canopies of large tables in undisturbed systems (Riegl, 1999; Baird & Hughes, 2000; Purkis & Riegl, 2004). Under disturbance, there was a strong tendency toward shrinkage into the smallest SC and retention there. The largest SC disappeared (Fig. 2c).

All other species showed strong flow from the large SCs into the smallest SC, even in the undisturbed scenario. This partial mortality is indicative of constant low-level tissue loss (predation, diseases, competition, etc.) in a generally stressful environment. This dynamics, despite strong growth into larger SCs, maintain a large proportion of small corals, even in the expected SsD (Fig. 2b). The net effect of disturbance across all species was a stronger retention in the smallest two size classes (=absence of growth) and loss of retention in the largest size classes. This was caused by shrinkage due to partial tissue mortality. Prior to disturbance, all species had loops in either SC3 or 4. Due to the disturbances, none ended with any loops in larger than SC2 and severe shrinkage, predominantly from SC3 and SC4 into SC1, was observed. Prior to disturbances, shrinkage was in many cases only by a single size class (Fig. 2a,b). The overall tendency toward shrinkage due to partial tissue loss was also clearly reflected by less/more deviation of observed size distributions from the theoretical SsD before/after disturbance (Fig. 2b; see also Supplemental Information).

The LTRE confirmed stronger retention in SC1 and SC2 and the various shrinkages into smaller SCs as the major differences in life-history characteristics prior to and after the disturbances in all species (see Supplemental Information). Among the most important contributions to changes in λ in all species were modifications in SC1 dynamics (greater retention). All λ were below 1, which is due to matrices emphasizing asexual (=fission due to partial tissue mortality) over sexual reproduction (see Supplemental Information)
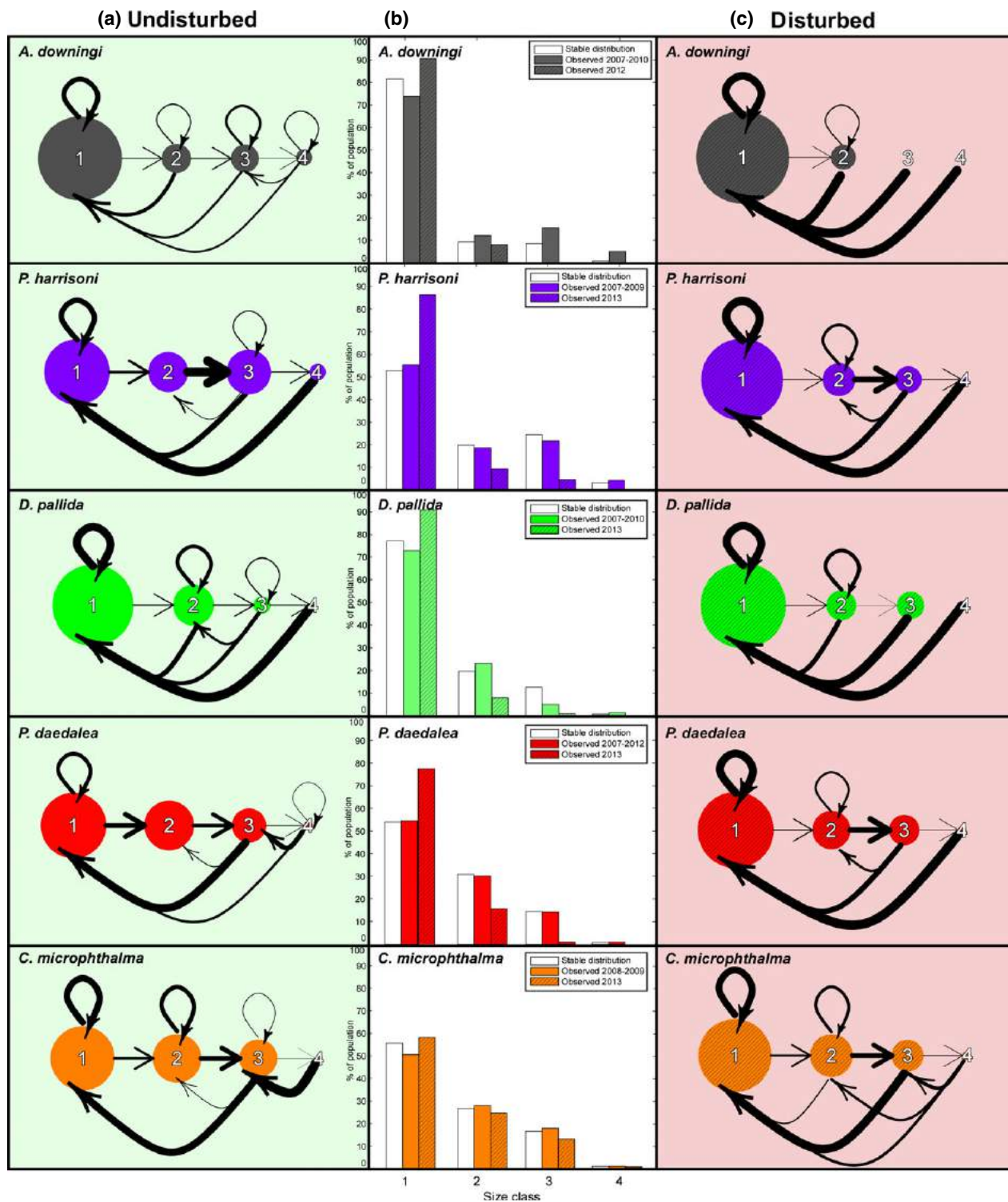
Fig. 2 Species-specific dynamics and expected stable size-class distributions (SsD) under undisturbed (columns a and b) and disturbed (column c) conditions. Life cycle graphs show transition probabilities among size classes (bubble size shows frequency at SsD, arrows scale 0–1, matrices shown in Supplemental Information). Columns (b) and (c) show deviation of observed size distributions (period in legends) from the expected SsD in undisturbed conditions (for further quantification see Supplemental Information). Note that values in b are means over different periods than in Fig. S2

Table 2 Standard fecundity (expressed as oocytes per 100 colonies) prior to, and after, the significant coral cover reduction of 2010–2013. The changed size distributions reduce fecundity (column 4), which is acerbated by reduced overall coral cover (column 5). 'standard fecundity' is relative to 100 fertile (SC3-5) colonies, standard fecundity was multiplied by the proportion of space cover (planar coral area) remaining after the disturbances and the proportion of corals in SC3-5 (see Material and Methods and Table S2)

	Standard fecundity of 100 corals 2007–2010 prior to demographic change	Standard fecundity of 100 corals 2013 after demographic change	Remainder after demographic change only, %	Remainder after demographic plus cover changes, %
Acropora downingi	562 096	0	0	0
Porites harrisoni	1 658 101	241 313	15	4
Dipsastrea pallida	683 966	55 270	8	3
Platygyra daedalea	1 276 738	331 620	26	8
Cyphastrea microphthalma	4 896 132	3 187 107	65	65

and reflect the importance of shrinkage into small (<5cm) but presumably infertile tissue remnants (Fig. S18a). In *A. downingi* and *P. harrisoni*, λ were greater in the disturbed matrices, a result of SC1 having been boosted by shrinkage and colony fission, which increases the number of individuals, but not the expected space cover (Fig. S18b). In the LTRE for *P. harrisoni*, changes in SC1 and SC2 dynamics had the greatest absolute effect on λ (Figs S3 and S6). In *A. downingi*, it was the loss of SC3 and SC4. Further evaluation of ramet survival (asexually produced, genetically identical propagules, i.e., tissue fragments) is needed to assess whether shrinkage events can indeed be considered successful asexual recruitment events, potentially mitigating the effects of greatly decreased space cover and fertility and thus truly raising λ. In *D. pallida* and *P. daedalea*, λ decreased after disturbance as did expected cover at SsD (Fig. S18b). The severe reductions after 2012 may be evidence of lost resilience in most species due to decimation of the bigger SCs and, consequently, fertility (Fig. S2). The LTRE suggested that *C. micropthalma* was the only species not suffering major life-dynamic changes. *C. micropthalma* was the only species that additionally did not even decline in cover and was expected to decline the least at SsD (Fig. S18b). Except for *C. microphthalma*, population resilience appears severely challenged in all species, latest after three back-to-back disturbances.

Under the assumption that populations would again approach SsD, the coral community composition obtained from the undisturbed vs. disturbed matrix models (Fig. 2) would differ and be dominated by *C. microphthalma* and *P. daedalea* (Fig. S18).

Discussion

This study provides a glimpse into future coral population dynamics. Annual bleaching events coupled with disease outbreaks, such as described herein, are expected as a potentially lethal endpoint of present climate warming between 2040 and 2100 (Donner, 2009; Van Hooidonk *et al.*, 2013; Maynard *et al.*, 2015). Gulf corals already exist at temperatures predicted for that interval (Riegl *et al.*, 2011), and disturbance frequencies are apparently also attaining the predicted values (Van Hooidonk *et al.*, 2013).

One main effect of these disturbances was shrinkage into smaller size classes and increased retention there, causing significant loss of coral cover. Thus, as predicted for fish communities (Cheung *et al.*, 2012), future corals will be smaller and therefore less fecund, with consequent lower regeneration potential of populations. Also, the linkage between bleaching and disease outbreaks is again clearly demonstrated (Miller *et al.*, 2009; Selig *et al.*, 2010; Maynard *et al.*, 2015). Degradation dynamics, which led to ~65% reduction of overall coral cover was species-specific. The previously dominant species *A. downingi* was a clear 'loser' (Loya *et al.*, 2001) and declined primarily by whole-colony mortality. A previously not dominant but nonetheless common species, *C. microphthalma*, suffered the least changes due to partial mortality and ended as a 'winner'. The other studied species showed comparable declines (Table S2). In all species except *C. microphthalma*, disturbances changed primarily growth-oriented population dynamics (growth transitions stronger than shrinkage) into such dominated by shrinkage. This mirrors predictions by Darling *et al.* (2013) that coral decline is linked to life histories.

A. downingi had dominated the undisturbed community prior to 1996/1998 (Riegl, 1999), can be classified as 'competitive' (Darling *et al.*, 2013; McClanahan, 2014) and had proven highly susceptible to disturbances but capable of strong recovery (Burt *et al.*, 2008). After this disturbances quadruplet, these corals disappeared from the study site, albeit not from the entire

region, where variably sized populations persist (Riegl B, Purkis S, Burt J, Bauman A, Howells E, personal observation). *A. downingi* has previously disappeared regionally and required restocking (larvae influx) from connected populations (Riegl, 2002; Burt *et al.*, 2008). However, even if some corals survived, shrinkage would have significant negative implications for fertility, especially because *Acropora* also have peripheral sterile zones (Wallace, 1999). Thus, it remains to be seen whether surviving connected populations will be fecund enough to sustain a comeback in this species.

P. harrisoni had dominated space cover in the study area since the original decline of *A. downingi* in 1996/1998 (Riegl & Purkis, 2012). It suffered significant partial mortality and vestigial ramets, not connected by tissue bridges, were the sad remnants of most colonies. As in *A. downingi*, this caused a life cycle shift (Fig. 1) favoring shrinkage transition over growth with significantly depressed fecundity (Table 2), creating an obstacle to recovery also in this species.

Within the merulinids, a hierarchy in resistance to damage existed from *D. pallida* to *P. daedalea* and *C. microphthalma*. The latter was the only coral that maintained almost undisturbed coral cover and only minor changes in growth dynamics across all events. *D. pallida* and *P. daedalea* lost much tissue area, partial mortality was widespread and many corals shrank. Due to the smaller size of colonies, more whole-colony mortality was observed than in *P. harrisoni*. But populations maintained higher fertility, especially *P. daedalea* (Table 2) and growth dynamics (Figs 1 and S9) suggest that the species may be able to recover. *P. daedalea* may grow into larger colonies (stronger growth transition from SC2 into SC3 in disturbed model, Fig. 2) and thus yet again obtain higher relative cover. While also *C. microphthalma* suffered elevated partial mortality, this had no clear effect on population dynamics or cover (Figs 1 and S15) and it is expected to be increasingly dominant in the future (Fig. S18). It is therefore clearly a 'stress-tolerant' species (Darling *et al.*, 2013).

Thus, a 'degradation cascade' existed with declining impacts from the originally dominant species (*A. downingi*, the 'loser') to an intermediate community that may persist until disturbances become too frequent (alternate dominance by *P. harrisoni*, or the merulinids *D. pallida* and *P. daedalea*), until finally a 'stress-tolerant' community (Darling *et al.*, 2013; McClanahan, 2014) is characterized by a 'winner' that was previously a less predominant species, *C. microphthalma*. This observation is consistent with previous descriptions of mortality and degradation events in the region (Riegl, 1999; Burt *et al.*, 2008; Riegl *et al.*, 2011; Bauman *et al.*, 2013a,b) and other Caribbean, Indo-Pacific, and Pacific reefs (Berumen & Pratchett, 2006; Perry *et al.*, 2014;

McClanahan, 2014; Glynn *et al.*, 2015; and many others).

The existence of such a degradation cascade is not unique to the Gulf and has been observed in other regions as well, most famously on Caribbean reefs (Perry *et al.*, 2014). The formerly dominant *Acropora* (*A. palmata*, *A. cervicornis*) were depleted by bleaching and diseases to give way to dominance by *Orbicella*, especially *O. annularis*, ecologically equivalent to the Gulf's *P. harrisoni*. Later, *Orbicella* also declined to give way to the stress-tolerant *P. astraeoides* and *Undaria agaricites* (Green *et al.*, 2008; Vermeij *et al.*, 2011; Perry *et al.*, 2014; Edmunds, 2015). The Gulf equivalent is dominance by small merulinids, and a degradation series from *Acropora* to *Platygyra* and *Dipsastrea* to *Cyphastrea* dominance. In the most degraded and most frequently disturbed Gulf coral systems, only *C. microphthalma* remains. Thus, wordwide, *Acropora* suffer the greatest losses and are considered to be in widespread decline (Carpenter *et al.*, 2008).

The proximity to stable-stage distribution (SsD) may be a useful indicator for connectivity dynamics. SsD is best reached by closed populations or such with little or infrequent import of recruits. *A. downingi* was furthest from SsD, and its dynamics under disturbance (mortality of large parts, or of entire local populations; Riegl, 2002; Burt *et al.*, 2008) suggest a strong connectivity requirement. Merulinids had converged toward SsD at comparable rates and distance (as expressed by Keyfitz's Δ, see Supplemental Information), a potential indication of strong local recruitment dynamics. *P. harrisoni*, the only gonochoric species, was closest to SsD, suggesting highest reliance on local recruitment. These findings suggest disadvantages for *A. downingi* and *P. harrisoni*. *A. downingi* disadvantages stem from increasingly few connected populations, with shrinking fecundity due to more small, less fecund, corals (Table 2, Fig. 2). Also local recruitment, apparently characteristic for *P. harrisoni*, will decrease for the same reasons (Table 2). Frequent disturbances should thus increasingly favor merulinid dominance, ending in communities of mainly *C. micropthalma*, which seem to suffer less shrinkage than the other species and retain the most fecundity (Table 2).

The observation of a 'degradation cascade' suggests a pathway and potential basins of stability. Such dynamics can be visualized as a weighted digraph, and by applying the Quirk-Ruppert criteria of qualitative stability (Edelstein-Keshet, 2005). Drawn as a strongly simplified *Acropora-Porites*-Merulinidae (i.e., *Dipsastrea*, *Platygyra*, and *Cyphastrea*) system (that can be complicated and expanded at will), we find stability in the undisturbed system (trace < 0), instability in the moderately disturbed system (trace > 0), and stability again

(trace < 0) in the disturbed system (Fig. 3). The instability of the moderately disturbed system is caused by positive (i.e., amplifying) feedbacks to the death of the previously aggressive competitor *A. downingi*, the denuded skeletons of which form preferred settling substrate for recruits of all, but most particularly their own, species (hence '+' in Fig. 3). Also, dead *Porites* form preferred settlement substrate for both merulinids and *Porites*. This mechanism allows return to the undisturbed state, in which live *A. downingi* colonies disadvantage their own and recruits of others, while aggressing on other corals, thus maintaining the *A. downingi* dominated state. If, however, no *A. downingi* recruits are available, denuded skeletons will rapidly disintegrate (Purkis & Riegl, 2004) and the species will play no more role in the competitive network (hence '0' in Fig. 3). While merulinids and poritids maintain their own competitive interactions (with merulinids disadvantaging *Porites*, hence '−'), the system is yet again stable (trace < 0). Further degradation to a merulinid-only (*Cyphastrea* dominated) system is possible and also stable, as merulinid larvae will not settle on their own live tissue (thus, trace < 0).

The described mechanism is, of course, akin to a shift from a high-coral to a low-coral stable state. Progressive loss of species can be quantified by changes in population dynamics described above: corals suffer significant tissue loss which shrinks colonies but frees up dead skeleton as settlement substrate, provided enough grazers keep algae at bay. But shrinkage also reduces fecundity, and there exists a minimum size for colonies to remain fertile. Therefore, a sequence of disturbances, each leading to increased shrinkage of remnant coral tissue, can lead to the eventual disappearance of corals from the system due to loss of fertility (Hughes & Tanner, 2000; Edmunds, 2007; Vermeij *et al.*, 2011). Stability of the degraded state can be achieved by purely demographic means (shrinkage into infertility, which, especially in case of dependence on local recruitment, hinders regeneration), even without superior competitors. In the Caribbean, this situation was famously exacerbated by herbivore loss that favored a capable, unchecked, competitor (macro-algae; Hughes, 1994). In the Gulf, macroalgae are held in check by high urchin densities (John & George, 2001), thus, demographic parameters and settlement dynamics (Bauman *et al.*,
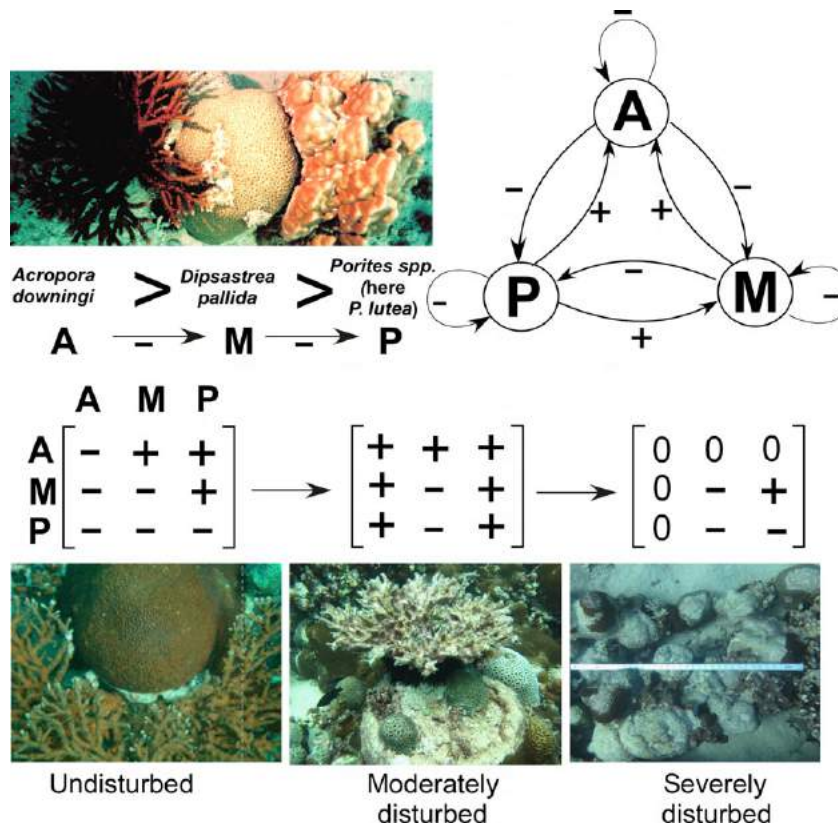
Fig. 3 Strongly simplified community dynamics (A, *Acropora*; P, *Porites*; M, Merulinidae) in Arabian/Persian Gulf expressed as a weighted digraph. '+' signifies an interaction benefitting the species at the head of the arrow, '−' disadvantages the species at the head of the arrow, and '0' signifies absence of interaction, because a species is dead and most skeletons gone. The graph can be expressed as an adjacency matrix (middle row). Signs in the main diagonal can be summed to obtain the trace.

2014) are the key determinants of coral regeneration after disturbances. However, in the Eastern Pacific (southern Galápagos), corals were so severely reduced by the 1982 ENSO (El Niño Southern Oscillation) that skeletons as well as reef frameworks were removed by urchin grazing, which subsequently also disadvantaged coral settlement (Glynn *et al.*, 2015). Thus, these reefs never recovered from a state of sparse, widely spaced coral heads (mainly *Pavona clavus*). Depensatory (Allee) effects clearly have come into play in Galápagos and maybe also Gulf coral dynamics, where shrinkage into the infertile SCs has depressed relative population growth rate, thus maintaining corals in a low-cover/small colony size state (Knowlton, 1992).

Another few disturbances and the remaining vigorous Gulf reefs may also reach such a permanently degraded ecological state. The same fate awaits all reefs that harbor species with comparable population dynamics. Many reefs across the Indo-Pacific are in immediate peril.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Flow of analyses for results presented in the following text.

Figure S2. Size distribution of corals at Ras Ghanada in the intervals surrounding the three subsequent bleaching and mortality events that influenced all corals as shown in Fig. 1 and also indicated by fat arrows here.

Figure S3. Growth model for *A. downingi*.

Figure S4. (a) Sensitivity and elasticity of dominant eigenvalue (λ) to changes in matrix entries of disturbed and undisturbed models in *A. downingi*.

Figure S5. (a) Stable size-class distribution from undisturbed model and proximity of observed size-distributions prior to (grey columns) and after (white colums) disturbances, after which the deviation is increasing.

Figure S6. Growth model for *P. harrisoni*.

Figure S7. (a) Sensitivity and elasticity of dominant eigenvalue (λ) to changes in matrix entries of disturbed and undisturbed models in *P. harrisoni*.

Figure S8. (a) Stable size-class distribution from undisturbed model and proximity of observed distribution prior to and after disturbances.

Figure S9. Growth model for *D. pallida*.

Figure S10. (a) Sensitivity and elasticity of dominant eigenvalue (λ) to changes in matrix entries of disturbed and undisturbed models of *D. pallida*.

Figure S11. (a) Stable size-class distribution from undisturbed model and proximity of distribution prior to (grey columns) and after (white colums) disturbances, when deviation increased.

Figure S12. Growth models for *P. daedalea*.

Figure S13. (a) Sensitivity and elasticity of the dominant eigenvalue (λ) to changes in matrix entries of disturbed and undisturbed models of *P. daedalea*.

Figure S14. (a) Stable size-class distribution from undisturbed model and the proximity of the observed size-class distribution prior to (grey columns) and after (white colums) disturbances, when deviation is increasing.

Figure S15. Growth models for *C. micropthalma*.

Figure S16. (a) Sensitivity and elasticity of the dominant eigenvalue (λ) to changes in matrix entries of disturbed and undisturbed models of *C. microphthalma*.

Figure S17. (a) Stable size-class distribution from undisturbed model and the proximity of the observed size-class distribution prior to (grey columns) and after (white colums) disturbances, when deviation is increasing.

Figure S18. Differences in (a) dominant Eigenvalue λ (=asymptotic population growth-rate) prior to and after disturbances, corresponding to life-cycle graphs in Fig. 1 in the main text.

Table S1. Coral species encountered at Ras Ghanada.

Table S2. Reduction of space cover per species.