Effects of tropical storms on the demography of reef corals

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ABSTRACT: Disturbances, such as cyclones, have a major effect on the structure and dynamics of coral reef assemblages. However, the effect of cyclones on demographic traits, such as fecundity, has rarely been quantified, and direct estimates of mortality at the species level are rare. Here, we document the effect of Severe Tropical Cyclone Nathan on the demography of corals on the reef crest at Trimodal Reef in the northern Great Barrier Reef. Mortality rates based on tagged colonies were very high, ranging from 85.2% in *Goniastrea retiformis* to 100% in 6 *Acropora* species, 3 to 40 times higher than averages rates in the 5 yr preceding Cyclone Nathan. Fecundity was lower in 3 out of the 4 species examined following the cyclone, and egg carbon content was reduced by 58–63% in the 2 species examined. These results suggest that energy normally invested in reproduction was diverted to other processes such as injury repair and demonstrate that cyclones have important sub-lethal effects in addition to high rates of whole colony mortality. Coral cover was reduced from 34.9 ± 3.9% (mean ± SE) to 3.4 ± 1.5%, with reductions in the cover of all taxa except those with predominantly massive morphologies such as the Poritidae. A projected increase in the frequency of tropical storms as a result of global warming, combined with an increase in the frequency and scale of coral bleaching, suggest a fundamental shift in mortality regimes on reefs which has the potential to threaten their long-term persistence.

KEY WORDS: Coral reefs · Climate change · Demography · Disturbance · Recovery

INTRODUCTION

Tropical storms are common on coral reefs (Stoddart 1965, Connell 1997, Allison et al. 2003, Anthony et al. 2015). Many aspects of the effects of storms on reef-building coral assemblages are well established. In particular, the loss of coral cover following tropical storms is often dramatic but usually patchy (Woodley et al. 1981, Bythell et al. 1993, Beeden et al. 2015). Similarly, tropical storms cause an abrupt change in coral assemblage structure, with a decrease in the relative and absolute abundance of species with morphologies most susceptible to wave damage (Adjeroud et al. 2002, Connell et al. 2004, Fabricius et al.

2008, Tanner 2017). However, very few studies have investigated the effects of tropical storms on demographic rates such as mortality, growth and fecundity. Such data are required in order to project the likely effect of changes in the intensity of tropical storms as a consequence of global warming (Bender et al. 2010, Cheal et al. 2017, Reyer et al. 2017).

The high wind speeds characteristic of tropical storms produce waves of sufficient size to fracture or dislodge coral colonies from the substratum (Woodley et al. 1981, Massel & Done 1993, Madin & Connolly 2006). Colonies that are not dislodged by waves can be injured through collisions with the dislodged colonies as they are transported across the reefs by

waves (Rogers et al. 1983, Fong & Lirman 1995). Coral tissue is also blasted or abraded by the force of water movement or through sand mobilised by waves (Woodley et al. 1981). The forces generated by tropical storms can be sufficiently large to change reef geomorphology, resulting in long-term changes to coral assemblage structure and patterns of zonation on reefs (Harmelin-Vivien & Laboute 1986, Scheffers & Scheffers 2006, Cheal et al. 2017).

The loss of coral cover following cyclones generally scales positively with wind speeds (Fabricius et al. 2008, Beeden et al. 2015). Loss of coral cover is also related to reef aspect, with sites in the lee of storm-generated waves generally less affected (Fabricius et al. 2008). Mortality rates following tropical storms are generally size specific (Hughes & Jackson 1980, Bythell et al. 1993) and are also determined by colony shape (Madin & Connolly 2006). For example, the probability of dislodgement in response to storms increases above a certain size in some morphologies, such as tabular species, producing bath-tub shaped mortality curves (Madin et al. 2014).

The effects of tropical storms on variables other than coral cover and assemblage structure are poorly understood. For example, there is almost no research into the effect of tropical storms on coral growth or reproduction (but see Aranceta-Garza et al. 2012) and surprisingly few direct estimates of mortality at the species level. Previous research into the effects of injury in corals suggests that a reduction in fecundity is likely. For example, reproductive output is often reduced in injured colonies (Kojis & Quinn 1985, Rinkevich & Loya 1979, but see Graham & van Woesik 2013) or areas of a colony adjacent to injury (Van Veghel & Bak 1994, Hall 1997), presumably because energy is directed to the repair of injured tissue rather than towards reproduction (Henry & Hart 2005). Similarly, reproductive output is also reduced by competition (Tanner 1995) and bleaching (Baird & Marshall 2002, Mendes & Woodley 2002). Harrison & Wallace (1990) predicted that vital functions of corals, such as regeneration and maintenance, were less likely to be affected by stress than non-vital functions, such as growth and reproduction. Similarly, Tanner (1995) argued that growth and maintenance should be favoured over reproduction because the fitness of long-lived colonial organisms with high fecundity and indeterminate growth, such as most corals, is influenced more by size transitions and survival probabilities than fecundity (e.g. Gotelli 1991). Thus, a coral colony should theoretically achieve greater lifetime fitness if it sacrifices current fecundity when a temporary demand for resources is placed upon it, such as

would occur following injury. Testing these hypotheses and clarifying the relationship among traits is critical for our understanding of coral life histories.

Here, we use demographic data from 5 yr pre-cyclone and observations post-cyclone to test the effects of Tropical Cyclone Nathan on coral assemblage structure, mortality, fecundity and egg carbon content of reef corals on the reef crest of Trimodal Reef, in the northern Great Barrier Reef.

MATERIALS AND METHODS

Study location and severe Tropical Cyclone Nathan

Tropical Cyclone Nathan began as a tropical low pressure system on 9 March 2015, and intensified into a Category 4 system with maximum wind speeds of 165 km h^{-1} before crossing over Lizard Island on 19 March 2015.

The data were collected from Trimodal Reef in the northern Great Barrier Reef, from 2009 to 2015. Trimodal Reef is located on the northern section of the reef surrounding Lizard Island between Palfrey Island and South Island (14.6998° S, 145.4486° E). The coral assemblage at Trimodal Reef is typical of semi-exposed mid-shelf reefs the length of the Great Barrier Reef. The 5 yr preceding Cyclone Nathan were largely free from disturbances such as cyclones and bleaching. The only exception was a crown of thorns *Acanthaster planci* outbreak between approximately 2012 and 2013. While this outbreak reduced coral cover at some sites around Lizard Island (L. Vail pers. comm.), there was no change in total coral cover at Trimodal Reef during this period (Madin et al. 2018).

Quantifying coral assemblage structure and estimating whole colony mortality

Coral assemblage structure at Trimodal Reef was quantified using 5 replicate 10 m line intercept transects (Loya 1972) at 1 m depth in November 2014 and 2015. The intercepts of coral colonies >5 cm maximum diameter were measured to the nearest 1 cm. Colonies were identified to genera or morphological groups of *Acropora* following Veron (2000).

Thirty colonies of each of 11 scleractinian coral species were first tagged on Trimodal Reef in November 2008, and further colonies were tagged each year to keep the total number in each species at approximately 30 colonies. Based on species abundance distributions at the site (Dornelas & Connolly

2008), the species were selected to include examples of rare and abundant species representing 5 different growth forms: tabular, *Acropora cytherea* and *A. hyacinthus*; arborescent, *A. intermedia* and *A. robusta*; corymbose, *A. spathulata*; *A. millepora* and *A. nasuta*; digitate, *A.* cf. *digitifera* and *A. humilis* and massive, *Goniastrea pectinata* and *G. retiformis*. In subsequent years, colonies were considered dead if they either were found without tissue on the reef or could not be found following an exhaustive search using photographs from prior years.

Estimating fecundity and colony size

Approximately 30 additional colonies of each of the 11 species were sampled at random with respect to size from the same area of the reef crest each year to avoid potential effects of fragment collection on subsequent colony growth estimates from 2009 to 2014. Due to very high mortality as a result of Cyclone Nathan, only 16 *G. pectinata*, 13 *G. retiformis*, 5 *A. hyacinthus* and 12 *A.* cf. *digitifera* were sampled in 2015. Cyclone Nathan killed all colonies of the other species. All species are broadcast-spawning hermaphrodites, and sampling for fecundity occurred in the week before the predicted date of spawning in all years. For *Acropora* spp., 4 branches were removed from near the centre of the colony, fixed and decalcified. The number of eggs in each of 6 polyps branch^{-1}, selected at random from below the sterile zone (Wallace 1985), were then counted under a dissecting microscope. For the *Goniastrea* spp., 1 nubbin containing approximately 20 polyps was removed from each colony, and the number of eggs in 6 randomly selected polyps was determined as above. To estimate colony size, a scale of known area was placed upon each colony, which was then photographed from directly above. These images were corrected for barrel distortion, then the colonies were outlined and the planar area of each colony was estimated by comparison to the scale using ImageJ.

Egg carbon content

Carbon content is often used as a proxy for energy content, and lower energy in eggs is correlated with reduced larval survivorship in the plankton (Fisher et al. 2007) and post-settlement mortality (Limbourn et al. 2008). To test for an effect of the cyclone on egg carbon content, 3 to 6 colonies of each of *A. hyacinthus*, *A. baeodactyla*, *G. pectinata* and *G. retiformis*

were collected from the reef crest at Trimodal Reef adjacent to the tagged colonies and were placed in an outdoor flow-through aquarium a few days before spawning in 2013 (pre-cyclone) and again in 2015 (post-cyclone). Prior to the expected night and time of spawning, the colonies were isolated in individual buckets. Colonies of the *Acropora* spp. did not spawn in 2015. Gamete bundles from each of the colonies of *G. pectinata* and *G. retiformis* that spawned were collected and washed in 0.2 μm filtered seawater to break apart the bundles and clean away the sperm. Five eggs from each colony were transferred individually into pre-cleaned tin capsules (ATD-1027 Tin Capsule Pre-Cleaned 6 × 4 mm; Choice Analytical) and frozen in liquid N$_2$. Since blank readings on each plate vary, 5 blank controls (capsule with no egg) for each plate were also sampled. Total carbon content of each egg was analysed on a solid sample combustion unit (Shimadzu) at the Australian Institute of Marine Science.

Statistical analyses

To estimate polyp fecundity, we used a hurdle model with the package brms in the software program R (Bürkner 2017). The hurdle model first uses a binomial model to analyse 0 vs. non-0 data, estimating the probability of a polyp being mature, and then uses a 0-truncated Poisson or negative binomial model to analyse variation in non-0 data, estimating the number of eggs per mature polyp. Since polyp maturity and the number of eggs per mature polyp often increase with colony size (Kojis & Quinn 1985, Babcock 1991, Álvarez-Noriega et al. 2016), we used colony size (log-scale) and cyclone status (pre- or post-cyclone) as fixed effects, and colony identity and year (nested within cyclone status) as random effects. Year nested within cyclone status could not be included in the model estimating maturity probability for *G. pectinata* because all polyps were mature in 2010, 2011 and 2013, causing problems with convergence. A 0-truncated Poisson error distribution was used for *Acropora* spp., and a 0-truncated negative binomial error distribution was used for *Goniastrea* spp. due to overdispersion.

To estimate egg carbon content, we fitted a linear mixed effects model with the function brm from the brms package (Bürkner 2017). Species, cyclone status and an interaction between them were used as fixed effects, and colony identity as a random effect. All statistical analyses were performed in R version 3.2.3 (R Core Team 2015) in a Bayesian framework.

RESULTS

Change in coral cover and assemblage structure

Coral cover was reduced by 90% following Cyclone Nathan, from a mean ± SE of 34.9 ± 3.9% in November 2014 to 3.9 ± 1.5% in November 2015 (Figs. 1 & 2). Cover was reduced in all taxa with the exception of *Porites* and other scleractinians (Fig. 3). Loss of cover was higher in branching taxa, such as *Acropora* and *Pocillopora*, and lower in taxa with predominantly encrusting and massive morphologies, such as the Merulinidae, *Porites* and other scleractinians (Figs. 1–3).

Mortality as result of Cyclone Nathan

Mortality from Cyclone Nathan was extremely high in all species. Only 9 of the 241 colonies alive in 2014 were alive in 2015 (Fig. 2), an overall mortality of 97% (Table 1). Indeed, only 12 colonies, either alive
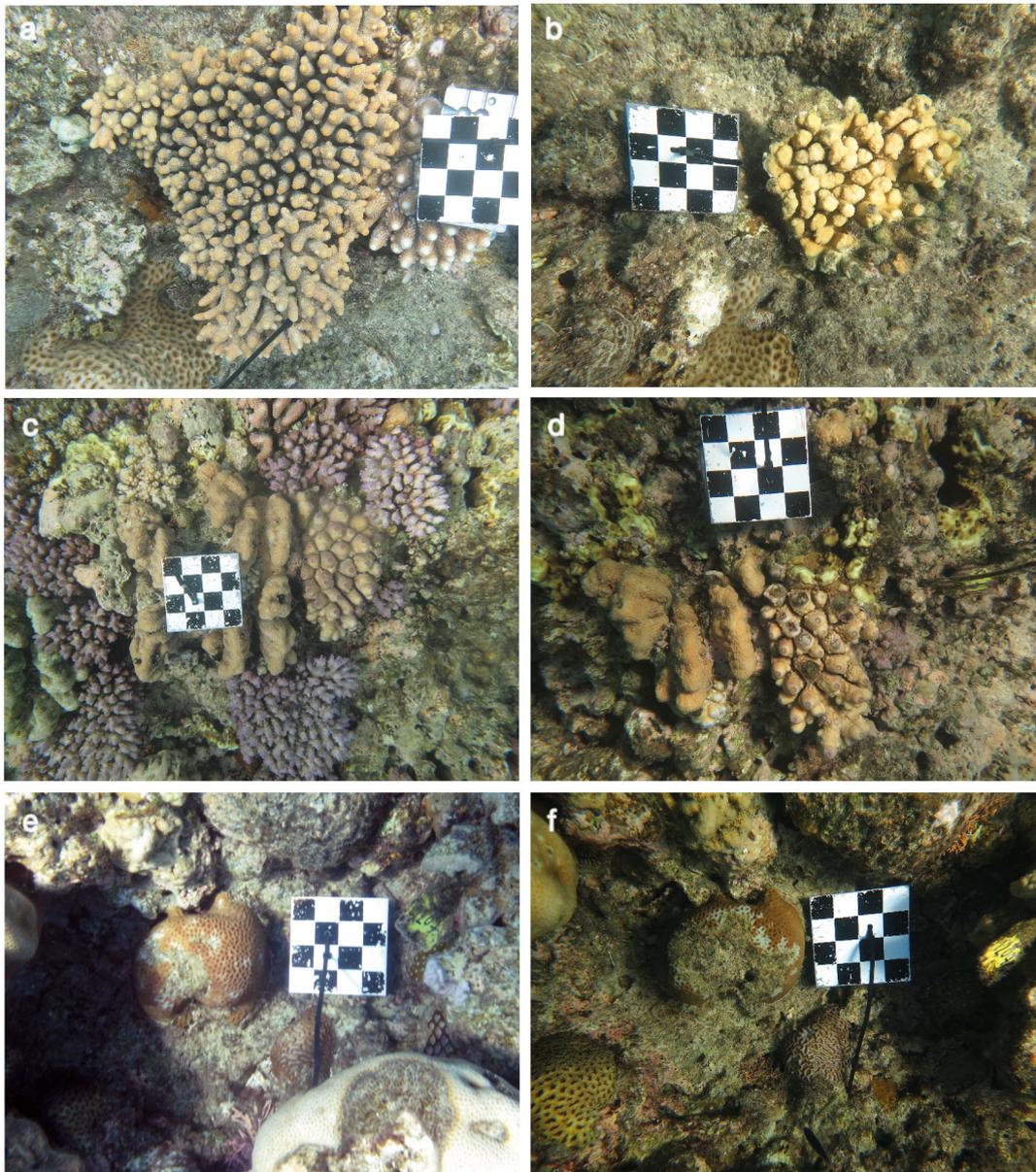

Fig. 1. Representative tagged coral colonies (a,c,e) before and (b,d,f) after Cyclone Nathan showing a loss of tissue through injuries presumably associated with the storm. (a,b) *Acropora spathulata*; (c,d) *A. humilis*; (e,f) *Goniastrea retiformis*. Scale grid is 10 × 10 cm
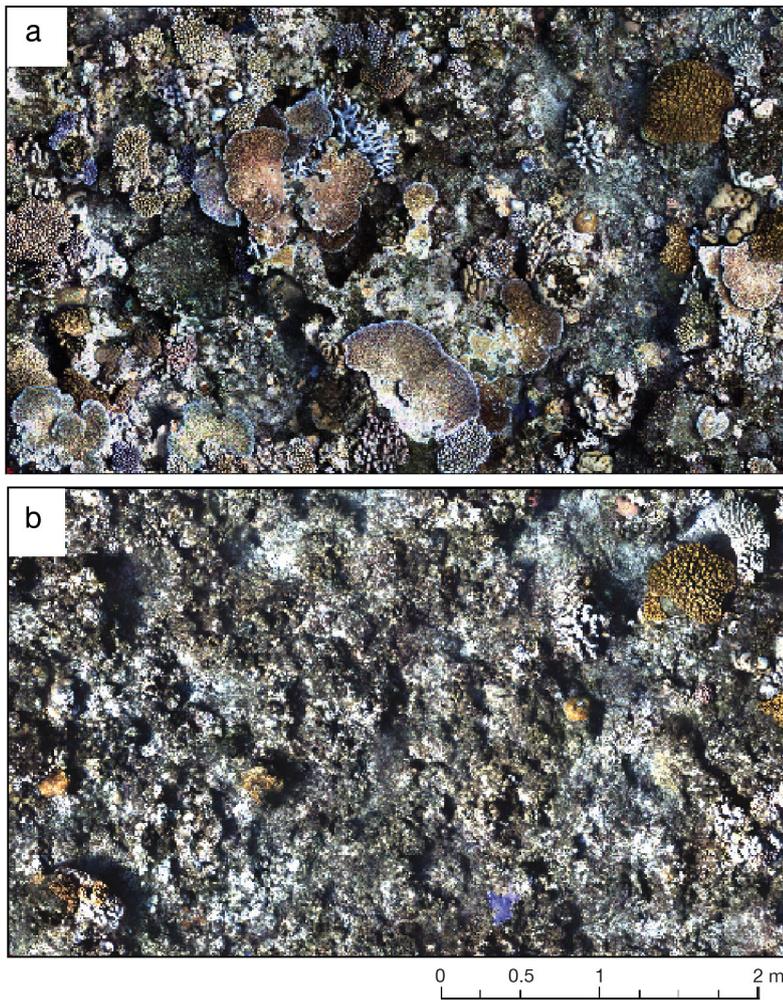
Fig. 2. Representative areas of the reef crest at Trimodal Reef in (a) November 2014 and (b) November 2015
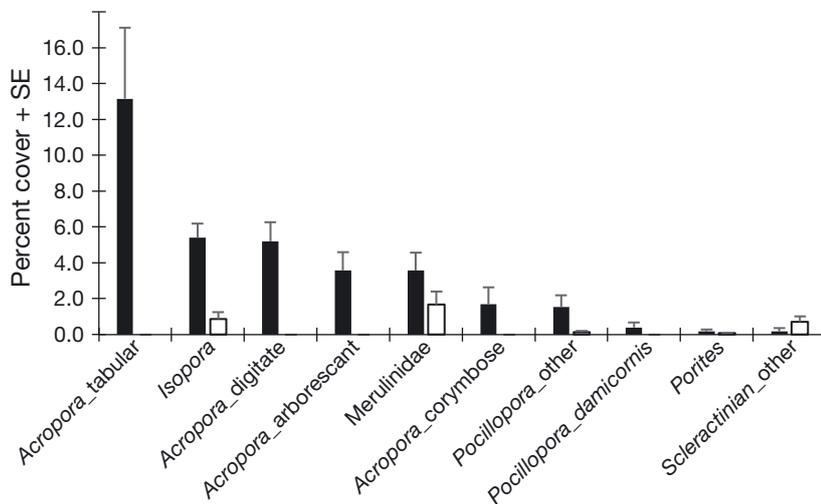

Fig. 3. Coral assemblage structure at Trimodal Reef before (November 2014, black bars) and after (November 2015, white bars) Severe Tropical Cyclone Nathan

or dead, could be found in 2015, suggesting that as many as 229 colonies had been dislodged by waves or debris during the storm. Mortality rates in 6 of the tagged *Acropora* spp. were 100% (Table 1). Mortality was lowest in *Goniastrea retiformis* where 85.2% of colonies were killed. The rates of mortality following the cyclone were 3.5 to 40 times higher than the average annual mortality rates for each species in the 5 yr prior to Cyclone Nathan (Table 1).

Changes in reproductive output in response to Cyclone Nathan

Polyp maturity was not overly affected by Cyclone Nathan, and increased with colony size for all species except for *G. pectinata* (Fig. 4a,c,e,g; see Tables S1–S4 & S5 in the Supplement at www.int-res.com/articles/suppl/m606p029_supp.pdf). Polyp maturity was highly variable among colonies and less variable among years (grouped before and after the cyclone) (Tables S1–S4 & S5). The number of eggs per mature polyp was slightly lower after the cyclone in all species expect *A.* cf. *digitifera* (Fig. 4b,d,f,h; Tables S1–S4 & S5). However, this effect was small in comparison to the variation in number of eggs among polyps (Fig. 4b,d,f,h). In contrast to polyp maturity, there was little variation in eggs per mature polyp among colonies and almost negligible variation among years (grouped before and after the cyclone) (Tables S1–S4 & S5).

Changes in egg carbon content

Egg carbon content was considerably lower for both *Goniastrea* species following Cyclone Nathan (58% lower in *G. retiformis* and 64% lower in *G. pectinata*) (Fig. 5). Egg carbon content was slightly higher for *G. retiformis* than for *G. pectinata* before the cyclone but not after (Tables S5 & S6).
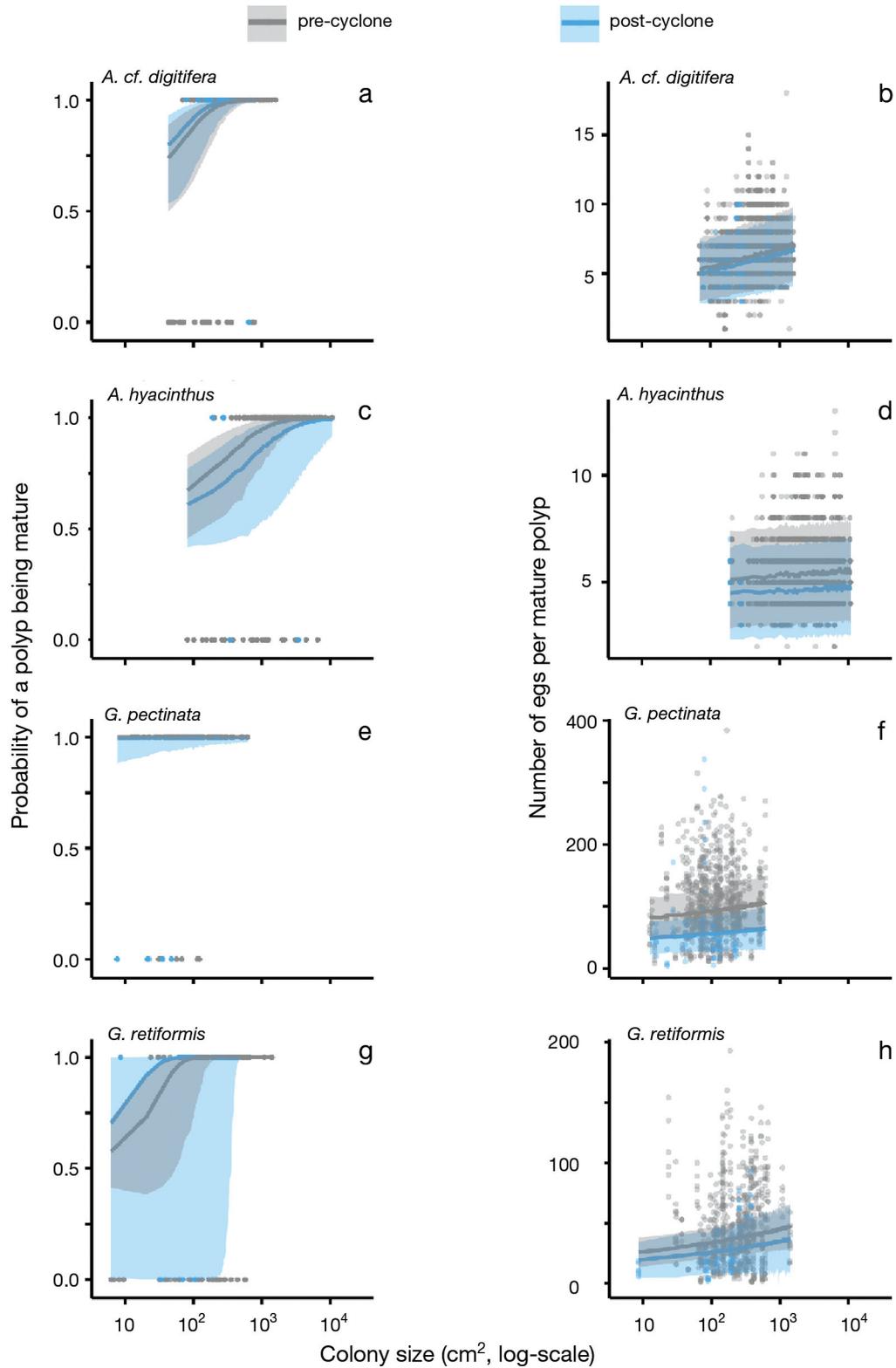
Fig. 4. (a,c,e,g) Colony size (log-scale) vs. polyp maturity probability pre- and post-cyclone (in grey and blue, respectively). (b,d,f,h) Colony size (log-scale) vs. the number of eggs per mature polyp pre- and post-cyclone (in grey and blue, respectively). The solid lines show estimates and the shaded areas show the 95% credible intervals. Sample sizes (number of colonies and number of polyps, in that order) for each species were: *Acropora* cf. *digitifera* (172; 4066), *A. hyacinthus* (151; 3612), *Goniastrea pectinata* (146; 882) and *G. retiformis* (157; 942)

Table 1. Mortality rates (%) of tagged colonies on Trimodal Reef from 2010 to 2014, i.e. pre-cyclone, and following Cyclone Nathan. Background: average annual mortality rates between 2010 and 2014

Species	2010	2011	2012	2013	2014	Back-ground	Na-than
Acropora cytherea	15.4	16	23.8	28.6	19	20.6	100
Acropora cf. *digitifera*	7.1	6.9	15.4	3.7	0	6.6	100
Acropora hyacinthus	6.9	10.3	34.6	32.3	8.7	18.6	100
Acropora intermedia	23.8	11.8	13.3	26.7	27.3	20.6	100
Acropora millepora	9.7	6.9	25	26.9	11.5	16.0	96.2
Acropora nasuta	14.3	12.5	28.6	53.3	42.9	30.3	100
Acropora humilis	17.5	10.8	35.3	40.7	27.3	26.3	100
Acropora spathulata	3.3	0	27.6	12.5	4.3	9.5	96.2
Acropora robusta	10.7	0	28	12.5	3.1	10.9	96.9
Goniastrea pectinata	3.7	0	8	0	4	3.1	92.3
Goniastrea retiformis	3.4	0	7.1	0	0	2.1	85.2
Total	10.5	6.8	22.4	21.6	13.5	15.0	97.0

DISCUSSION

Cyclone Nathan had a profound effect on the coral assemblage on Trimodal Reef. Mortality rates were extremely high in all tagged coral species, although mortality was slightly lower in species with a massive morphology than in branching species. Most mortality was presumably due to dislodgement during the storm, although some colonies could have been killed by other factors, such as sand-blasting, prior to dislodgement. This high mortality resulted in a large decline in coral cover. In addition, there was a small

Fig. 5. Estimates of the effect of cyclone status on the mean carbon content (µg) per egg for *Goniastrea pectinata* and *G. retiformis*. Error bars show the 95% credible intervals. The sample sizes (number of colonies and number of eggs, in that order) for each species were: *G. pectinata* (6; 29) and *G. retiformis* (7; 30)

decline in fecundity in 3 of the 4 species examined and a large decline in egg carbon content in the few colonies that survived the cyclone.

Cyclone Nathan had a dramatic effect on coral assemblage structure, including a 90% decline in coral cover and reductions in the abundance of all taxa except for other scleractinians. Similarly, there was a shift in the relative abundance of taxa caused by differential susceptibility to cyclonic disturbance, with taxa dominated by species with massive morphologies (e.g. Merulinidae, *Porites* and other scleractinians) less affected than taxa composed mostly of branching species (e.g. *Acropora*, *Pocillopora* and *Stylophora*). Such shifts in the relative abundance of taxa following disturbance might have a role in the maintenance of species richness (Connell 1978, Rogers 1993, Aronson & Precht 1995).

The rates of mortality recorded on the reef crest at Trimodal were exceptionally high when compared to most previous estimates of cyclone-induced mortality (e.g. Connell 1973, Bythell et al. 1993, Connell et al. 2004). Until the turn of the century, and despite the frequency of disturbance events on reefs, background mortality from predation, competition and sedimentation typically exceeded mortality from catastrophic disturbances (Connell 1973, Done et al. 2010, Pisapia et al. 2016). For example, between 1963 and 1993, mortality attributed to catastrophic disturbance accounted for less than one-third of the whole colony mortality in coral assemblages on Heron Island (Hughes & Connell 1999). Similar patterns were evident at St Croix, in the Caribbean (Bythell et al. 1993). The scale of the damage caused by Cyclone Nathan, when considered along with the increasing frequency of catastrophic mortality following mass bleaching events (Hughes et al. 2017, 2018a), suggests that these historical differences in the relative contributions of catastrophic and background mortality to population dynamics are changing in response to increasing anthropogenic sources of disturbance, and that reefs are transitioning into novel coral assemblages that differ greatly from the assemblages of the recent past (Hughes et al. 2018b).

The mortality of tagged colonies (97%) was greater than the loss of coral cover (90%), because approximately 80% of the tagged colonies were *Acropora* spp. (Table 1), compared to about 60% of the coral
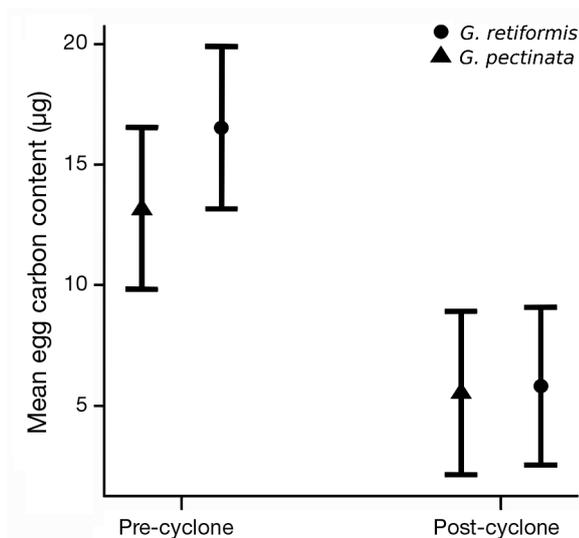
assemblage (Fig. 3). *Acropora* spp. are generally more susceptible to hydrodynamic disturbances, such as storms, due to their branching morphology (Madin et al. 2014; Table 1).

Cyclone Nathan reduced the per polyp fecundity in 3 of the 4 species examined; however, these declines were small in comparison to the pre-cyclonic variation in fecundity among polyps. In contrast, egg carbon content was considerably reduced in the 2 species examined. This was almost certainly a result of injuries sustained by surviving colonies (Fig. 1), because reproductive output is often reduced in injured colonies (Kojis & Quinn 1985, Rinkevich & Loya 1979, but see Graham & van Woesik 2013) or in areas of a colony adjacent to injury (van Veghel & Bak 1994, Hall 1997). This suggests that there might be a trade-off in energy allocation between maintenance and fecundity; that is, injury repair is favoured over reproduction as hypothesised by Harrison & Wallace (1990) and Tanner (1995). Fecundity is also often reduced in response to competition (Tanner 1995), disease (Burns & Takabayashi 2011) and bleaching (Michalek-Wagner & Willis 2001, Mendes & Woodley 2002). Declines in reproductive output following Nathan highlight sub-lethal effects of cyclones that might further impede population recovery. Nonetheless, the high rates of whole-colony mortality will have a much greater effect on the reproductive output of these populations than the often minor declines in fecundity.

Corals have evolved to cope with a high frequency and intensity of disturbance (Richmond 1993). Indeed, coral assemblages at Trimodal Reef have been affected by catastrophic disturbances in the past, in particular an *Acanthaster planci* outbreak in the late 1990s that reduced coral cover to less than 10% (Pratchett 2005) and other cyclones in the more distant past (Wolff et al. 2016). Nonetheless, coral assemblages at Trimodal Reef had recovered to moderate levels of cover and diversity by 2011 (Keith et al. 2015) if not before. However, the frequency and intensity of disturbance on reefs appears to be increasing. The intensity of tropical storms is projected to increase (Bender et al. 2010, Cheal et al. 2017), and the return times of mass bleaching events have halved in this millennium when compared to the return times between 1980 and 2000 (Hughes et al. 2018a). Indeed, back to back mass bleaching events on the Great Barrier Reef in 2016 and 2017 have further transformed reefs in the region surrounding Lizard Island, including Trimodal Reef, to systems with very low cover and diversity (Hughes et al. 2018b). Furthermore, global warming is projected to increase the intensity of tropical storms in the near future (Knutson et al. 2010, Cheal et al. 2017), suggesting the potential for a fundamental shift in mortality regimes on reefs that might threaten their long-term persistence.

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