

Title: Effects of tropical storms on the demography of reef corals

Andrew H. Baird^{1*}, Mariana Álvarez-Noriega^{1,2}, Vivian R. Cumbo³, Sean R. Connolly^{1,2}, Maria Dornelas⁴, Joshua S. Madin³

¹ARC Centre of Excellence for Coral Reef Studies, James Cook University, Townsville QLD, 4811, Australia

²College of Marine and Environmental Science, James Cook University, Townsville QLD, 4811, Australia

³Department of Biological Sciences, Macquarie University, Sydney, NSW, 2109, Australia

⁴Centre for Biological Diversity, Scottish Oceans Institute, University of St. Andrews, KY16 9TH, Scotland, UK

*Corresponding author email andrew.baird@jcu.edu.au; telephone: +61747814857

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 six *Acropora* spp., 3 to 40 times higher than averages rates in the five years preceding Cyclone Nathan. Fecundity was lower in three out of the four species examined following the cyclone and egg carbon content was reduced by 58-63% in the two 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 \pm 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 waves (Adjeroud et al. 2002; Connell et al. 2004; Fabricius et al. 2008; Tanner 2017). However, there are very few studies on the effect 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; Reyer et al. 2017; Cheal 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; Masel & 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 (Rodgers & Fitz 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 and P. Laboute 1986; Sheffers and Sheffers 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 and Jackson 1980; Bythell et al. 1993) and are also determined by colony shape (Madin and 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 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 1989; 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 five years 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.

METHODS

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 (105 mph) before crossing over Lizard Island on 19 March 2015.

Study location

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 five years 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 (Lyle Vail pers comm), there was no change in total coral cover at Trimodal Reef during this period (Madin et al. in press).

104

105 ***Coral assemblage structure***

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

110

111 ***Estimating whole colony mortality***

112 Thirty colonies of each of 11 scleractinian coral species were first tagged on Trimodal Reef in
 113 November 2008 and further colonies were tagged each year to keep the total number in each
 114 species at approximately 30 colonies. Based on species abundance distributions at the site
 115 (Dornelas & Connolly 2008), the species were selected to include examples of rare and abundant
 116 species representing five different growth forms: tabular (*Acropora cytherea* [Dana 1846] and *A.*
 117 *hyacinthus* [Dana 1846]), arborescent (*A. intermedia* [Brook 1891] and *A. robusta* [Dana 1846]),
 118 corymbose (*A. spathulata* [Brook 1891], *A. millepora* [Ehrenberg, 1834], and *A. nasuta* [Dana,
 119 1846]), digitate (*A. cf digitifera* [Brook 1892] and *A. humilis* [Dana, 1846]) and massive
 120 (*Goniastrea pectinata* [Ehrenberg, 1834] and *G. retiformis* [Lamarck, 1816]). In subsequent
 121 years, colonies were considered dead if either they were found without tissue on the reef or could
 122 not be found following an exhaustive search using photographs from prior years.

123

124 ***Estimating fecundity and colony size***

125 Approximately 30 additional colonies of each of the 11 species were sampled at random with
 126 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*, five *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 the *Acropora* spp., four branches were removed from near the centre of the colony, fixed and decalcified. Then, the number of eggs in each of six polyps per branch, selected at random from below the sterile zone (Wallace 1985), were counted under a dissecting microscope. For the *Goniastrea* spp., one nubbin containing approximately 20 polyps was removed from each colony and the number of eggs in six randomly selected polyps was determined as above. To estimate colony area, the sampled colonies were photographed from directly above with a scale bar and the photographs were corrected for barrel distortion. From the photographs, the contours of the focal colonies were outlined and the areas were compared to that of the scale to estimate the colonies' planar area using ImageJ.

Egg carbon content

Carbon content is often used as a proxy 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, three to six 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 placed in an outdoor flow-through aquarium on two occasions; a few days before spawning in both 2013 (pre-cyclone Nathan) and 2015 (post-cyclone Nathan). 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 μ m filtered seawater (FSW) to break apart the bundles and clean away the sperm. Five eggs from each colony were transferred individually into pre-cleaned tin capsule (ATD-1027 Tin Capsule Pre-Cleaned 6 x 4 mm; Choice Analytical) and frozen in liquid N₂. Since blank readings on each plate vary, five blank controls (capsule with no egg) for each plate were also sampled. Total carbon content of each egg was analyzed 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 function `brm()` of the package ‘brms’ (Bürkner 2017). The hurdle model first uses a binomial model to analyse zero vs. non-zero data, estimating the probability of a polyp being mature, and then uses a zero-truncated poisson or negative binomial model to analyse variation in non-zero 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 zero-truncated poisson error distribution was used for the *Acropora* spp., and a zero-truncated negative binomial error distribution was used for the *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 of $34.9 \pm 3.9\text{SE}$ % in November 2014 to $3.9 \pm 1.5\text{SE}$ % in November 2015 (Fig. 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 (Fig. 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 rate of 97% (Table 1). Indeed, only 12 colonies, either alive 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 six 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 years prior to the 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. 4- A, C, E & G, Table A1-A4 & A6). Polyp maturity was highly variable among colonies and less variable among years (grouped before and after the cyclone) (Tables A1-A4 & A6). The number of eggs per mature polyp was slightly lower after the cyclone in all species except *A. cf. digitifera* (Fig. 4- B, D, F & H, Tables A1-A4 & A6). However, this effect was small in comparison to the variation in number of eggs among polyps (Fig. 3- B, 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 A1-A4 & A6).

Changes in egg carbon content

Egg carbon content was considerably lower for both 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 (Table A5 & A6).

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 decline in fecundity in three of the four 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* & 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; Hughes et al. 2018a) suggests that these historical differences in the relative contribution 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 per polyp fecundity in three of the four 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 two 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 1989; but see Graham & van Woesik 2013) or 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 1990's 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. In particular, the intensity of tropical storms is projected to increase (Bender 2010; Cheal et al. 2017) and the return times of mass bleaching events have halved in this millennium when compared to the return times in the 20 years prior to the year 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 very low cover and diversity systems (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.

Acknowledgements: We thank the Lizard Island Research Station staff for their support, Tom Bridge for collecting the LIT data and Damaris Torres-Pulliza for producing Figure 2. Funding was provided by the Australian Research Council Centre of Excellence for Coral Reef Studies (CE140100020) and the Templeton Foundation (grant #60501, 'Putting the Extended Evolutionary Synthesis to the Test'). MD is grateful to the Scottish Funding Council (MASTS, grant reference HR09011), and the European Research Council (grant BioTIME).

REFERENCES

- Adjeroud M, Augustin D, Galzin R, Salvat B (2002) Natural disturbances and interannual variability of coral reef communities on the outer slope of Tiahura (Moorea, French Polynesia): 1991 to 1997. *Marine Ecology Progress Series* 237:121-131
- Allison GW, Gaines SD, Lubchenco J, Possingham HP (2003) Ensuring persistence of marine reserves: Catastrophes require adopting an insurance factor. *Ecol Appl* 13:S8-S24
- Álvarez-Noriega M, Baird AH, Dornelas M, Madin JS, Cumbo VR, Connolly SR (2016) Fecundity and the demographic strategies of coral morphologies. *Ecology* 97:3485-3493
- Anthony KRN, Marshall PA, Abdulla A, Beeden R, Bergh C, Black R, Eakin CM, Game ET, Gooch M, Graham NAI, Green A, Heron SF, van Hooidonk R, Knowland C, Mangubhai S, Marshall N, Maynard JA, McGinnity P, McLeod E, Mumby PJ, Nystrom M, Obura D, Oliver J, Possingham HP, Pressey RL, Rowlands GP, Tamelander J, Wachenfeld D, Wear S (2015) Operationalizing resilience for adaptive coral reef management under global environmental change. *Glob Change Biol* 21:48-61
- Aranceta-Garza F, Balart EF, Reyes-Bonilla H, Cruz-Hernandez P (2012) Effect of tropical storms on sexual and asexual reproduction in coral *Pocillopora verrucosa* subpopulations in the Gulf of California. *Coral Reefs* 31:1157-1167
- Aronson RB, Precht WF (1995) Landscape patterns of reef coral diversity - a test of the Intermediate Disturbance Hypothesis. *J Exp Mar Biol Ecol* 192:1-14
- Babcock RC (1991) Comparative demography of three species of scleractinian corals using age-dependent and size-dependent classifications. *Ecological Monographs* 61:225-244
- Baird AH, Marshall PA (2002) Mortality, growth and reproduction in scleractinian corals following bleaching on the Great Barrier Reef. *Marine Ecology Progress Series* 237:133-141
- Beeden R, Maynard J, Puotinen M, Marshall P, Dryden J, Goldberg J, Williams G (2015) Impacts and recovery from severe tropical cyclone Yasi on the Great Barrier Reef. *PLoS ONE* 10:e0121272
- Bender MA, Knutson TR, Tuleya RE, Sirutis JJ, Vecchi GA, Garner ST, Held IM (2010) Modeled impact of anthropogenic warming on the frequency of intense Atlantic hurricanes. *Science* 327:454-458
- Bürkner PC (2017) brms: An R package for Bayesian multilevel models using stan. *Journal of Statistical Software* 80:1-28
- Burns JHR, Takabayashi M (2011) Histopathology of growth anomaly affecting the coral, *Montipora capitata*: Implications on biological functions and population viability. *Plos One* 6:e28854
- Bythell JC, Gladfelter EH, Bythell M (1993) Chronic and catastrophic natural mortality of 3 common Caribbean reef corals. *Coral Reefs* 12:143-152
- Cheal AJ, Macneil MA, Emslie MJ, Sweatman H (2017) The threat to coral reefs from more intense cyclones under climate change. *Global Change Biology* 23:1511-1524
- Connell JH (1973) Population ecology of reef building corals. In: Jones OA, Endean R (eds) *Biology and Geology of Coral Reefs, Book II*. Academic Press, New York
- Connell JH (1978) Diversity in tropical rainforests and coral reefs. *Science* 199:1302-1310
- Connell JH (1997) Disturbance and recovery of coral assemblages. *Coral Reefs* 16:S101-S113
- Connell JH, Hughes TE, Wallace CC, Tanner JE, Harms KE, Kerr AM (2004) A long-term study of competition and diversity of corals. *Ecol Monogr* 74:179-210

- Done T, DeVantier L, Turak E, Fisk D, Wakeford M, van Woesik R (2010) Coral growth on three reefs: development of recovery benchmarks using a space for time approach. *Coral Reefs* 29:815-833
- Fabricius KE, De'ath G, Puotinen ML, Done T, Cooper TF, Burgess SC (2008) Disturbance gradients on inshore and offshore coral reefs caused by a severe tropical cyclone. *Limnology and Oceanography* 53:690-704
- Fisher R, Sogard SM, Berkeley SA (2007) Trade-offs between size and energy reserves reflect alternative strategies for optimizing larval survival potential in rockfish. *Marine Ecology-Progress Series* 344:257-270
- Fong P, Lirman D (1995) Hurricanes cause population expansion of the branching coral *Acropora palmata* (Scleractinia): Wound healing and growth patterns of asexual recruits. *Mar Ecol* 16:317-335
- Gotelli NJ (1991) Demographic models for *Leptogorgia virgulata*, a shallow-water gorgonian. *Ecology* 72:457-467
- Graham JE, van Woesik R (2013) The effects of partial mortality on the fecundity of three common Caribbean corals. *Mar Biol* 160:2561-2565
- Hall VR (1997) Interspecific differences in the regeneration of artificial injuries on scleractinian corals. *J Exp Mar Biol Ecol* 212:9-23
- Harmelin-Vivien ML, Laboute P (1986) Catastrophic impact of hurricanes on atoll reef slopes in the Tuamotu (French Polynesia). *Coral Reefs* 5:55-62
- Harrison PL, Wallace CC (1990) Reproduction, dispersal and recruitment of scleractinian corals. In: Dubinsky Z (ed) *Coral Reefs*, Book 25. Elsevier, Amsterdam
- Henry LA, Hart M (2005) Regeneration from injury and resource allocation in sponges and corals - A review. *Int Rev Hydrobiol* 90:125-158
- Hoeksema BW, Cairns SD (2018) World List of Scleractinia. Accessed through: World Register of Marine Species at: <http://www.marinespecies.org/aphia.php?p=taxdetails&id=1363>:accessed on 10-04-2018
- Hughes TP, Anderson KD, Connolly SR, Heron SF, Kerry JT, Lough JM, Baird AH, Baum JK, Berumen ML, Bridge TC, Claar DC, Eakin CM, Gilmour JP, Graham NAJ, Harrison H, Hobbs J-PA, Hoey AS, Hoogenboom M, Lowe RJ, McCulloch MT, Pandolfi JM, Pratchett M, Schoepf V, Torda G, Wilson SK (2018a) Spatial and temporal patterns of mass bleaching of corals in the Anthropocene. *Science* 359:80-83
- Hughes TP, Connell JH (1999) Multiple stressors on coral reefs: A long-term perspective. *Limnology and Oceanography* 44:932-940
- Hughes TP, Jackson JBC (1980) Do corals lie about their age - some demographic consequences of partial mortality, fission, and fusion. *Science* 209:713-715
- Hughes TP, Kerry JT, Álvarez-Noriega M, Álvarez-Romero JG, Anderson KD, Baird AH, Babcock RC, Beger M, Bellwood DR, Berkelmans R, Bridge TC, Butler IR, Byrne M, Cantin NE, Comeau S, Connolly SR, Cumming GS, Dalton SJ, Diaz-Pulido G, Eakin CM, Figueira WF, Gilmour JP, Harrison HB, Heron SF, Hoey AS, Hobbs J-PA, Hoogenboom MO, Kennedy EV, Kuo C-y, Lough JM, Lowe RJ, Liu G, McCulloch MT, Malcolm HA, McWilliam MJ, Pandolfi JM, Pears RJ, Pratchett MS, Schoepf V, Simpson T, Skirving WJ, Sommer B, Torda G, Wachenfeld DR, Willis BL, Wilson SK (2017) Global warming and recurrent mass bleaching of corals. *Nature* 543:373-377
- Hughes TP, Kerry JT, Baird AH, Connolly SR, Dietzel A, Eakin CM, Heron SF, Hoey AS, Hoogenboom MO, Liu G, McWilliam MJ, Pears RJ, Pratchett MS, Skirving WJ, Stella

- 378 JS, Torda G (2018b) Global warming transforms coral reef assemblages. *Nature* 556:492-
379 496
- 380 Keith SA, Woolsey ES, Madin JS, Byrne M, Baird AH (2015) Differential establishment
381 potential of species predicts a shift in coral assemblage structure across a biogeographic
382 barrier. *Ecography* 38:1225-1234
- 383 Knutson TR, McBride JL, Chan J, Emanuel K, Holland G, Landsea C, Held I, Kossin JP,
384 Srivastava AK, Sugi M (2010) Tropical cyclones and climate change. *Nature Geoscience*
385 3:157-163
- 386 Kojis BL, Quinn NJ (1985) Puberty in *Goniastrea favulus* age and size limited. *Proceedings of*
387 *the 5th International Coral Reef Congress* 4:289-294
- 388 Limbourn AJ, Babcock RC, Johnston DJ, Nichols PD, Knott B (2008) Post-settlement energy
389 reserves in *Panulirus cygnus*: experimental effects of starvation on survival and
390 nutritional condition. *Marine Biology* 153:445-456
- 391 Loya Y (1972) Community structure and species diversity of hermatypic corals at Eilat, Red Sea.
392 *Mar Biol* 13:100-112
- 393 Madin JS, Baird AH, Bridge T, Connolly SR, Zawada K, Dornelas M (in press) Cumulative
394 effects of cyclones and bleaching on coral cover and species richness at Lizard Island.
395 *Coral Reefs*
- 396 Madin JS, Baird AH, Dornelas M, Connolly SR (2014) Mechanical vulnerability explains size-
397 dependent mortality of reef corals. *Ecology Letters* 17:1008-1015
- 398 Madin JS, Connolly SR (2006) Ecological consequences of major hydrodynamic disturbances on
399 coral reefs. *Nature* 444:477-480
- 400 Reefs:submitted 02032018; minor revision 02052108; resubmitted 27062018; minor revision 19072018
401
- 402 Massel SR, Done TJ (1993) Effects of cyclone waves on massive coral assemblages on the
403 Great-Barrier-Reef - meteorology, hydrodynamics and demography. *Coral Reefs* 12:153-
404 166
- 405 Mendes JM, Woodley JD (2002) Effect of the 1995-1996 bleaching event on polyp tissue depth,
406 growth, reproduction and skeletal band formation in *Montastraea annularis*. *Marine*
407 *Ecology Progress Series* 235:93-102
- 408 Michalek-Wagner K, Willis BL (2001) Impacts of bleaching on the soft coral *Lobophytum*
409 *compactum*. I. Fecundity, fertilization and offspring viability. *Coral Reefs* 19:231-239
- 410 Pisapia C, Anderson KD, Pratchett MS (2016) Temporal consistency in background mortality of
411 four dominant coral taxa along Australia's Great Barrier Reef. *Coral Reefs* 35:839-849
- 412 Pratchett MS (2005) Dynamics of an outbreak population of *Acanthaster planci* at Lizard Island,
413 northern Great Barrier Reef (1995-1999). *Coral Reefs* 24:453-462
- 414 Reyer CPO, Adams S, Albrecht T, Baarsch F, Boit A, Trujillo NC, Carlsburg M, Coumou D,
415 Eden A, Fernandes E, Langerwisch F, Marcus R, Mengel M, Mira-Salama D, Perette M,
416 Pereznieta P, Rammig A, Reinhardt J, Robinson A, Rocha M, Sakschewski B, Schaeffer
417 M, Schleussner CF, Serdeczny O, Thonicke K (2017) Climate change impacts in Latin
418 America and the Caribbean and their implications for development. *Regional*
419 *Environmental Change* 17:1601-1621
- 420 Richmond RH (1993) Coral reefs: Present problems and future concerns resulting from
421 anthropogenic disturbance. *Am Zool* 33:524-536
- 422 Rinkevich B, Loya Y (1979) Reproduction of the Red-Sea Coral *Stylophora pistillata* 1. Gonads
423 and Planulae. *Marine Ecology Progress Series* 1:133-144

- 424 Rogers CS (1993) Hurricanes and coral-reefs - the Intermediate Disturbance Hypothesis
 425 revisited. *Coral Reefs* 12:127-137
- 426 Scheffers A, Scheffers S (2006) Documentation of the impact of Hurricane Ivan on the coastline
 427 of Bonaire (Netherlands Antilles). *J Coast Res* 22:1437-1450
- 428 Stoddart DR (1965) Resurvey of hurricane effects on the British Honduras reefs and cays. *Nat*
 429 *Insects* 207:589-592
- 430 Tanner JE (1995) Competition between scleractinian corals and macroalgae - an experimental
 431 investigation of coral growth, survival and reproduction. *J Exp Mar Biol Ecol* 190:151-
 432 168
- 433 Tanner JE (2017) Multi-decadal analysis reveals contrasting patterns of resilience and decline in
 434 coral assemblages. *Coral Reefs* 36:1225-1233
- 435 Veghel MLJv, Bak RPM (1994) Reproductive characteristics of the polymorphic Caribbean reef
 436 building coral *Montastrea annularis*. *Marine Ecology Progress Series* 109:229-233
- 437 Wolff NH, Wong A, Vitolo R, Stolberg K, Anthony KRN, Mumby PJ (2016) Temporal
 438 clustering of tropical cyclones on the Great Barrier Reef and its ecological importance.
 439 *Coral Reefs* 35:613-623
- 440 Woodley JD, Chornesky EA, Clifford PA, Jackson JBC, Kaufman LS, Knowlton N, Lang JC,
 441 Pearson MP, Porter JW, Rooney MC, Rylaarsdam KW, Tunnicliffe VJ, Wahle CM,
 442 Wulff JL, Curtis ASG, Dallmeyer MD, Jupp BP, Koehl MAR, Neigel J, Sides EM (1981)
 443 Hurricane Allen's impact on Jamaican coral reefs. *Science* 214:749-755
 444
 445

Table 1. Mortality rates of tagged colonies on Trimodal Reef following Cyclone Nathan.
Background mortality rates are the average annual mortality rates between 2008 and 2014 i.e.
pre-cyclone.

species	2010	2011	2012	2013	2014	background	Nathan
<i>Acropora cytherea</i>	15.4	16	23.8	28.6	19	20.6	100
<i>Acropora cf digitifera</i>	7.1	6.9	15.4	3.7	0	6.6	100
<i>Acropora hyacinthus</i>	6.9	10.3	34.6	32.3	8.7	18.6	100
<i>Acropora intermedia</i>	23.8	11.8	13.3	26.7	27.3	20.6	100
<i>Acropora millepora</i>	9.7	6.9	25	26.9	11.5	16.0	96.2
<i>Acropora nasuta</i>	14.3	12.5	28.6	53.3	42.9	30.3	100
<i>Acropora humilis</i>	17.5	10.8	35.3	40.7	27.3	26.3	100
<i>Acropora spathulata</i>	3.3	0	27.6	12.5	4.3	9.5	96.2
<i>Acropora robusta</i>	10.7	0	28	12.5	3.1	10.9	96.9
<i>Goniastrea pectinata</i>	3.7	0	8	0	4	3.1	92.3
<i>Goniastrea retiformis</i>	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

Figure legends

Figure 1. Representative tagged colonies before (panels A, C and E) and after (panels B, D and F) Cyclone Nathan showing a loss of tissue through injuries presumably associated with the storm. Panels A and B are *Acropora spathulata*, panels C & D are *A. humilis* and panels E and F are *Goniastrea retiformis*.

Figure 2. Representative areas of the reef crest at Trimodal Reef in November 2014 (a) and November 2015 (b).

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

Figure 4. Panels A, C, E and G: colony size (log-scale) vs. polyp maturity probability pre- and post-cyclone (in grey and blue respectively). Panels B, D, F and 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 ribbons show the 95% credible intervals. The grey and blue points correspond to the data before and after the cyclone (respectively). The sample sizes (number of colonies and number of polyps, in that order) for each species were: *A. cf. digitifera* (172, 4066), *A. hyacinthus* (151, 3612), *G. pectinata* (146, 882), and *G. retiformis* (157, 942).

Figure 5. Estimates of 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

473 sizes (number of colonies and number of eggs, in that order) for each species were: *G. pectinata*
474 (6, 29) and *G. retiformis* (7, 30).

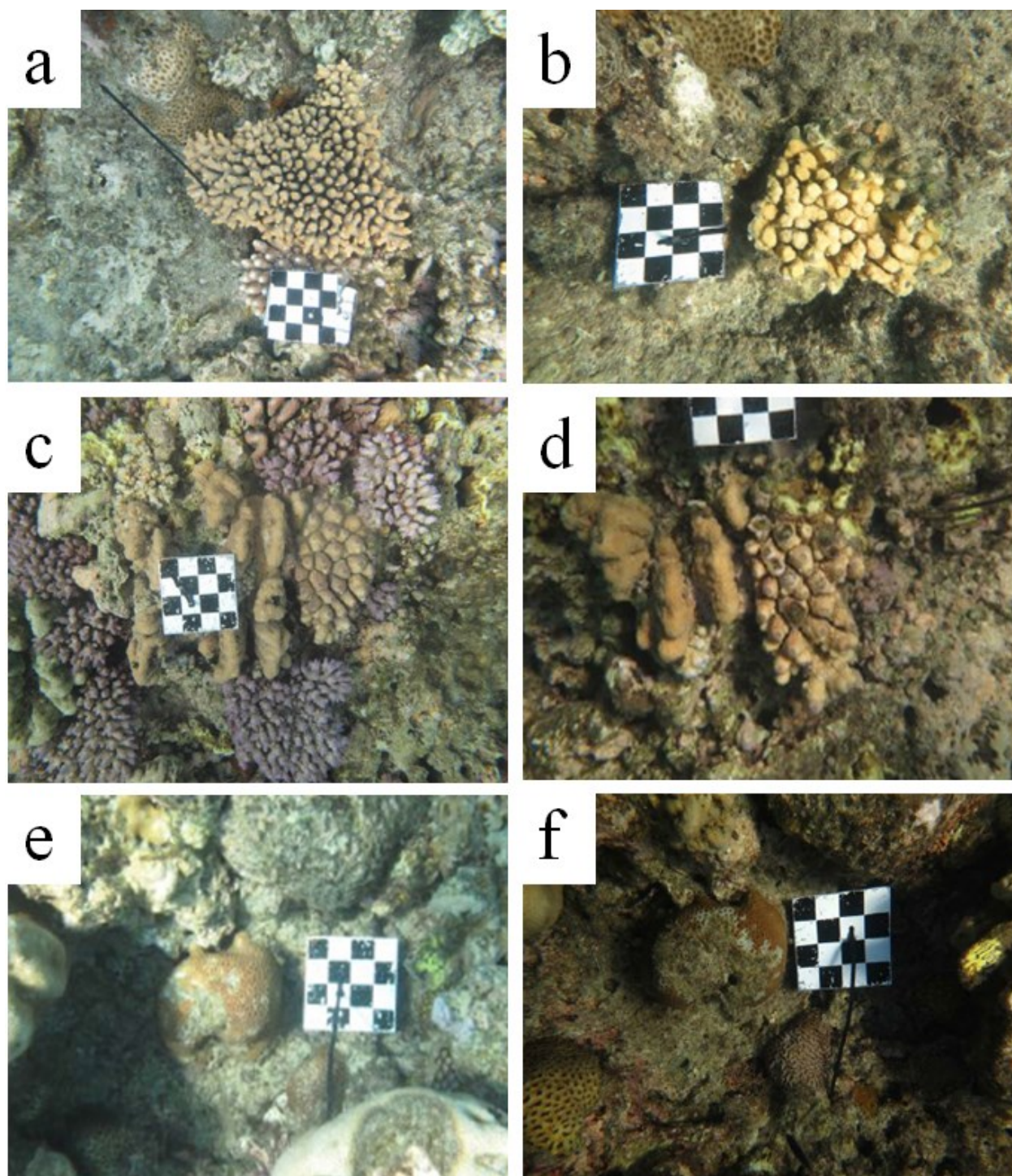
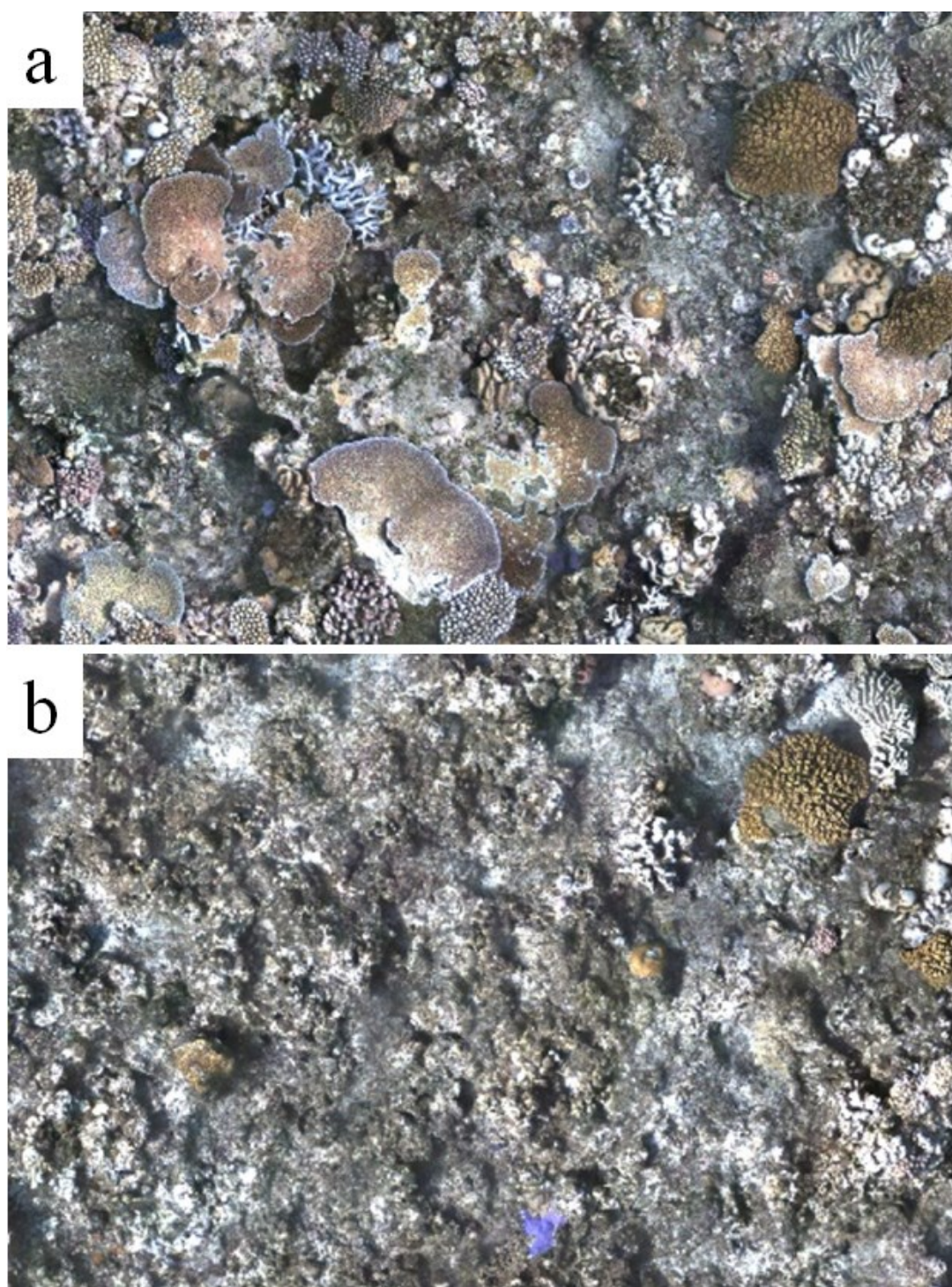


Figure 1

477



478

479

480 Figure 2

481

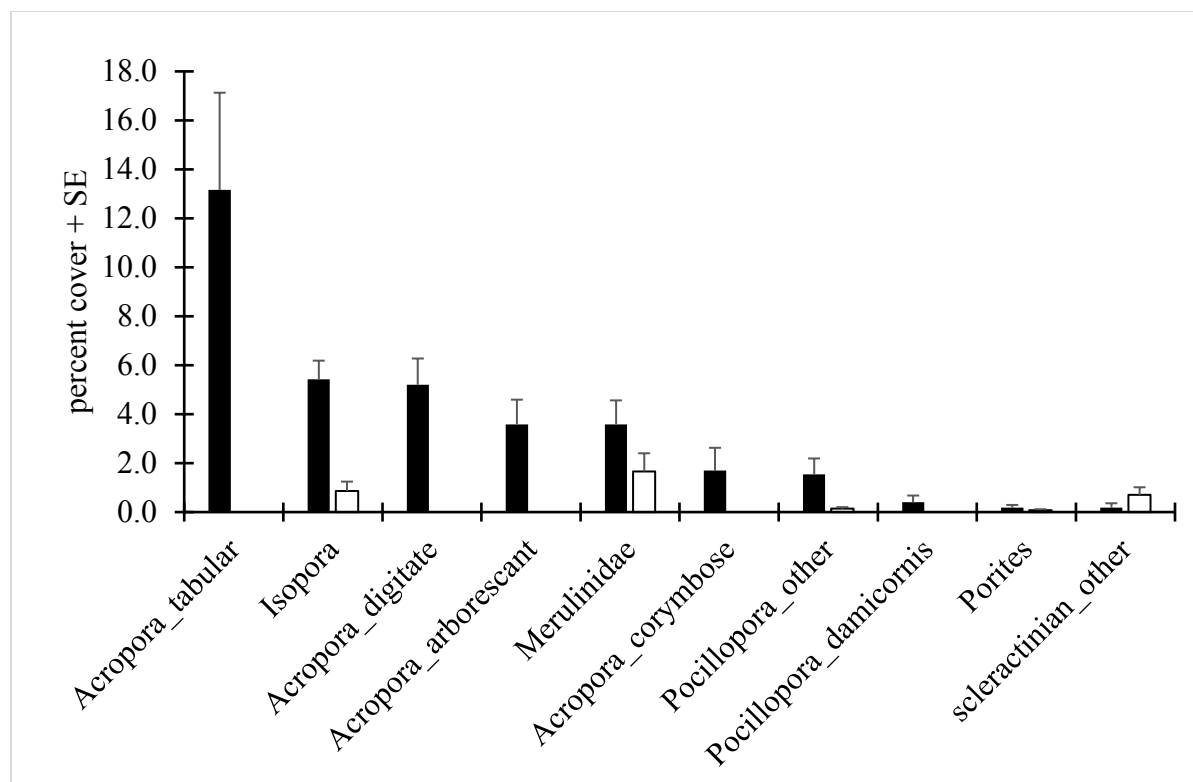
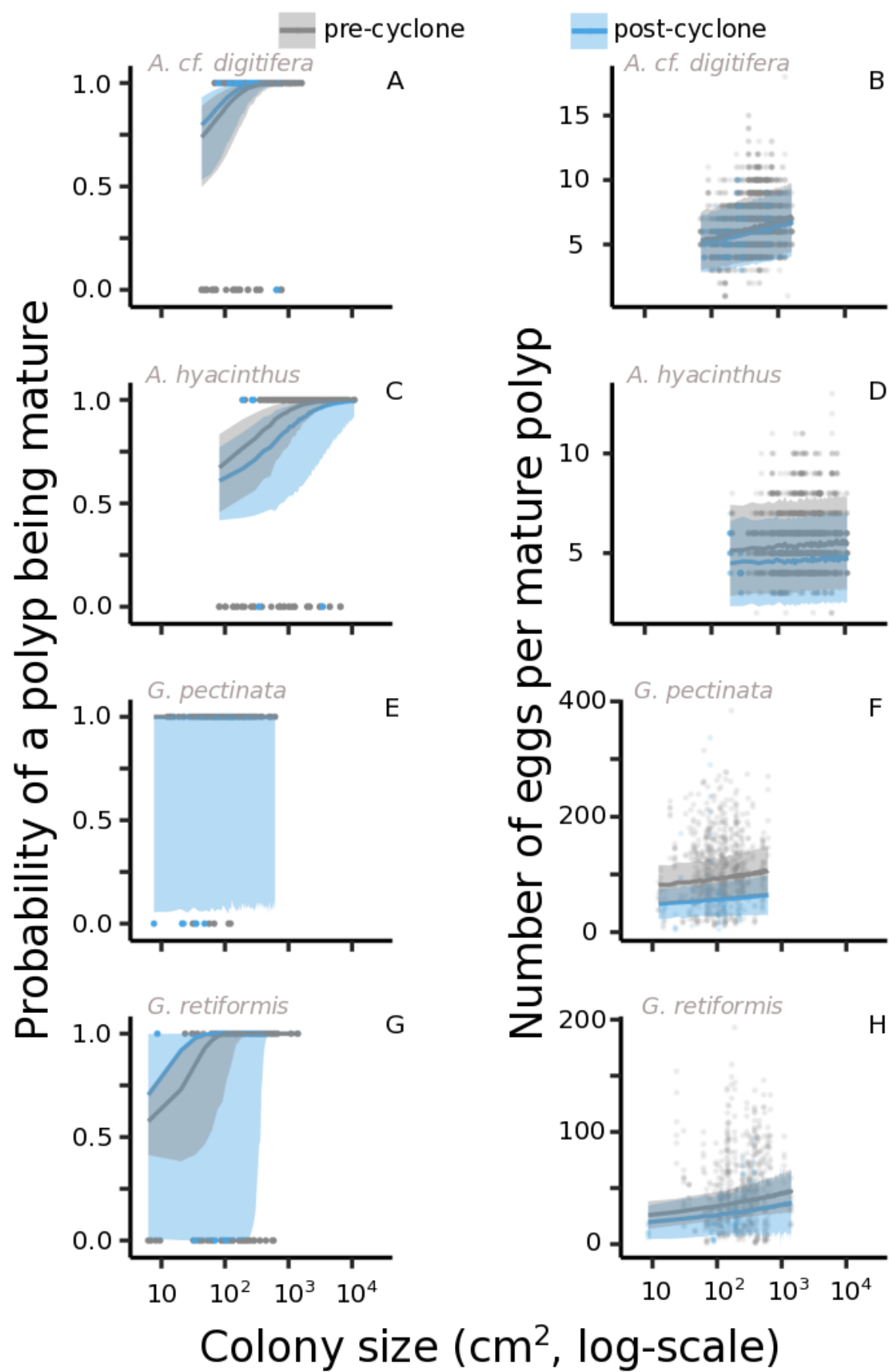
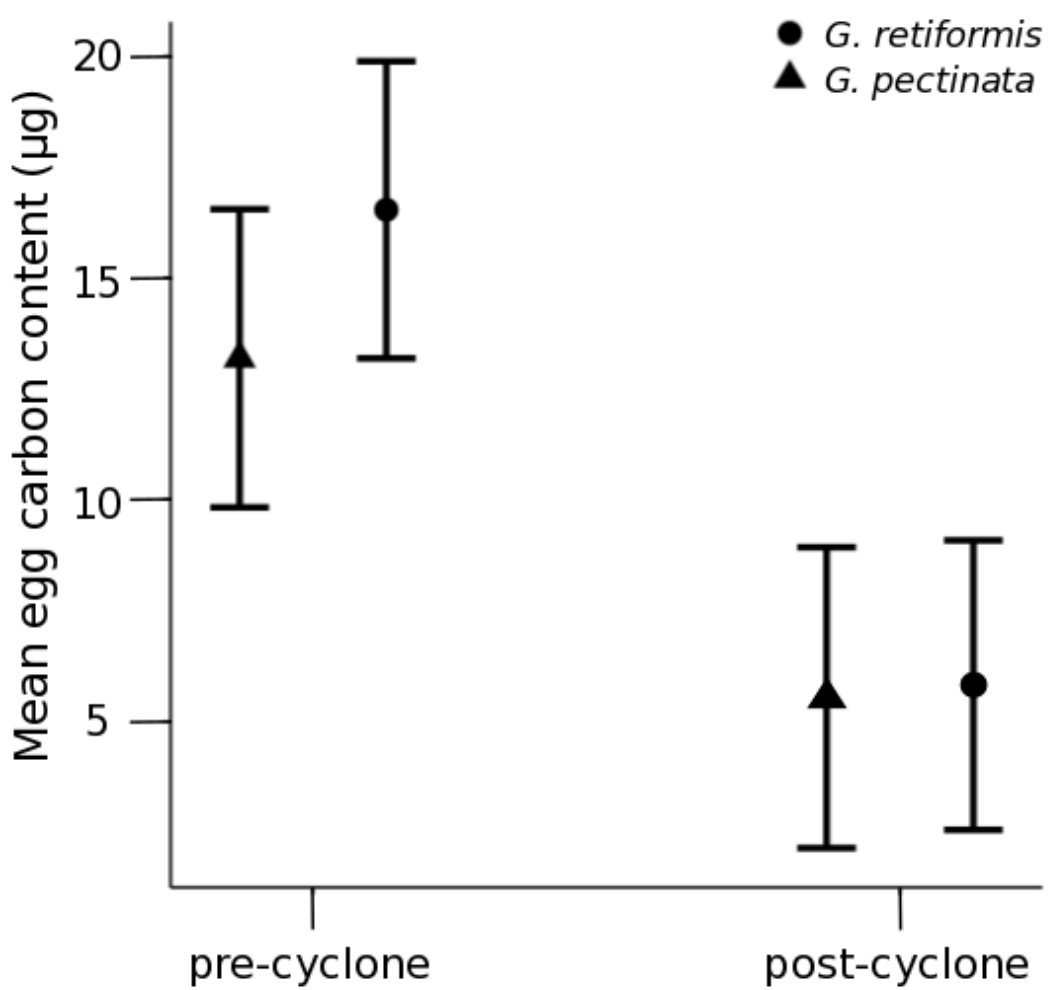


Figure 3



486 Figure 4



487

488 Figure 5.

489