

The effects of partial mortality on the fecundity of three common Caribbean corals

J. E. Graham · R. van Woesik

Received: 13 December 2012 / Accepted: 16 April 2013
© Springer-Verlag Berlin Heidelberg 2013

Abstract The recent intensification of human disturbances in the Caribbean has increased the prevalence of partial mortality on coral colonies. Partial mortality can change colony size by directly shrinking colonies or by splitting colonies into fragments. A reduction in colony size can also adversely affect fecundity and fitness as internal resources shift away from reproduction toward colony maintenance. This study aimed to determine whether three Caribbean coral species, *Siderastrea siderea*, *Montastraea faveolata*, and *Diploria strigosa*, along the reef tract in Puerto Morelos, Mexico (20°52'N, 86°51'W), continued to dedicate resources to reproduction when colonies were fragmented to pre-maturation size. Contrary to expectations, eggs were found in colonies that were smaller than the maturation size and had been subjected to partial mortality. The continued dedication of resources toward reproduction, even in the smallest colonies, suggests that resource trade-offs away from reproduction are not as rigid as previously suggested in stressed corals.

Introduction

Sexual reproduction is the foundation of coral population persistence. Without successful reproduction, coral populations are unable to replenish lost individuals and are destined for regional extinction. Because coral reproduction

is governed by environmental rhythms that are vulnerable to stochastic events (van Woesik 2010), reproduction is generally regarded as the most sensitive life process and is, ironically, thought to be the last life process to receive resources (Rinkevich and Loya 1985). The high intensity and frequency of recent disturbances on Caribbean reefs have increased the extent of partial coral mortality (van Woesik and Jordan-Garza 2011). As a result, many coral populations have become aggregations of small isolated fragments. Life-history theory suggests that when resources are limited it is optimal for organisms to invest in only life functions that are vital to survival (Stearns 1989; Selman et al. 2012). The application of this theory to coral biology suggests that colony shrinkage should shift resources away from reproduction (i.e., gametogenesis) toward colony maintenance (i.e., lesion repair) and growth (Hughes and Jackson 1980; Szmant-Froelich 1985; Kojis and Quinn 1985; Van Veghal and Kahmann 1994; Sakai 1998).

Evidence of resource trade-offs has been documented in corals, with injury causing a reduction in growth (Babcock 1988) and a reduction in fecundity (Kojis and Quinn 1985; Babcock 1988; Rinkevich and Loya 1985). Okubo et al. (2007) reported resorption of oocytes in small colony fragments, whereas Szmant and Gassman (1990) documented a complete failure of gametogenesis by *Montastraea annularis* following bleaching. Most evidence suggests that coral maintenance and growth take precedence over coral reproduction (Tomascik and Sander 1987; Babcock 1988; Harrison and Wallace 1990; Ward 1995; Fine et al. 2002; Okubo et al. 2007). By contrast, Rinkevich (1996) suggested that a hierarchical trade-off of resources does not exist in corals and any slowing of regeneration rates is a function of the depletion of reserve cells. Independent of whether repetitive stressors limit resources, or deplete reserve cells, the end result is often the same—a

Communicated by R. Hill.

J. E. Graham (✉) · R. van Woesik
Department of Biological Sciences, Florida Institute of
Technology, 150 West University Blvd, Melbourne,
FL 32901, USA
e-mail: graham.jessica.e@gmail.com

reduction in fecundity (Stearns 1989; Harrison and Wallace 1990; Rinkevich 1996).

By contrast, there is a general agreement that the onset of gametogenesis in corals occurs when coral colonies reach a specific size, rather than a specific age (Sakai 1998). Kojis and Quinn (1985) discovered that if coral colonies were subjected to partial mortality and were reduced below a species-specific number of polyps, colonies failed to produce gametes. Szmant-Froelich (1985) concurred and reported that fragments of *M. annularis* did not undergo gametogenesis below their maturation size. Kai and Sakai (2008) examined two corals in the western Pacific Ocean, *Favites chinensis* and *Goniastrea aspera*, and noted that the former species switched off gametogenesis upon fragmentation below maturation size, but the latter species maintained gametogenesis. Their results suggest that age rather than size determined whether polyps of *G. aspera* were reproductively active, whereas size rather than age determined whether *F. chinensis* was reproductively active. Colony fragmentation is becoming increasingly common on Caribbean reefs particularly with increases in partial mortality that results from local, regional, and global disturbances (Hughes and Jackson 1980; Hughes et al. 2003). It is important to determine whether fragmented colonies continue to devote resources to reproduction after fragmentation, or whether they are pseudopopulations that are not contributing to population persistence.

In the present study, we examined the reproductive activity of three common Caribbean species, *Siderastrea siderea*, *Montastraea faveolata*, and *Diploria strigosa*, which had been subjected to partial mortality and had undergone tissue isolation. A range of such colonies were examined to test the hypothesis that corals would continue to invest resources in gametogenesis when reduced below their maturation size. The presence of gametes in colonies that were smaller than their maturation size would suggest the continued investment of resources into reproduction, a relatively flexible exchange of resources among life processes, and age rather than size determined reproductive activity.

Materials and methods

Field methods

This study examined the fecundity of three Caribbean coral species, *S. siderea*, *M. faveolata*, and *D. strigosa*, along the reef tract located off Puerto Morelos, Mexico (20°52'24.98"N, 86°51'02.02"W). The sampling protocol was designed to obtain a population-wide estimate of fecundity of colonies that had been subjected to partial

mortality prior to sampling, including colonies that were fragmented to a size below the known size at maturity. Soong and Lang (1992) showed that ~40 % of the *D. strigosa* and *S. siderea* colonies became mature when the average colony size was between 60 and 250 cm². By contrast, *M. faveolata* delayed maturation until they reached a size of approximately 100 cm² (Van Veghal and Kahmann 1994). Therefore, the size classes (cm²) selected for the present study for *D. strigosa* and *S. siderea* were <60 cm², 60–125 cm², 126–250 cm², >250 cm², whereas the size classes for *M. faveolata* were <100 cm², 100–300 cm², 301–630 cm², and >630 cm². Similar to the protocol adopted by Soong and Lang (1992), we measured colony size directly in the field by taking maximum length (*l*) and width (90° from length) (*w*) measurements. Colony area was calculated using the equation for surface area of an ellipse (surface area = $\pi \cdot l/2 \cdot w/2$).

On August 1 2009, 40 days prior to observed spawning (September 10, 2009), 12 colonies were collected, using a hammer and chisel, from each of the four size classes from each of the four 3-m stations at Puerto Morelos, Mexico. A total of 48 colonies were sampled for each species. Two to three samples were taken from the central region of each colony, because marginal and apex polyps, generally, have lower fecundity than central polyps (Soong and Lang 1992; Sakai 1998). Each sample was placed in an individually labeled bag, transported back to the laboratory, placed in an outdoor tank, and kept at 29.5 °C—which was the temperature on the reef at the time of the study—before processing.

Laboratory methods and statistical analyses

The samples were cut and placed in 50-mL Perspex tubes containing 4 % formaldehyde in seawater solution for 12 h, and then decalcified using 10 % solution of HCl. The number of eggs was counted in four intact polyps, from each sample, using a dissecting microscope. The average number of eggs per polyp was calculated for each colony sampled, and these averages were used for statistical analyses. These averages were used to determine whether there were any differences in the number of eggs per polyp for the colonies of different sizes. The data were analyzed using a nonparametric Kruskal–Wallis test because the raw data failed tests of normality, even after transformation attempts. If the Kruskal–Wallis test was significant, a Tukey–Kramer test was used to determine which size classes supported a significantly different number of eggs than the other size classes.

Results

For all three coral species, there were no significant differences in the number of eggs per polyp among stations,

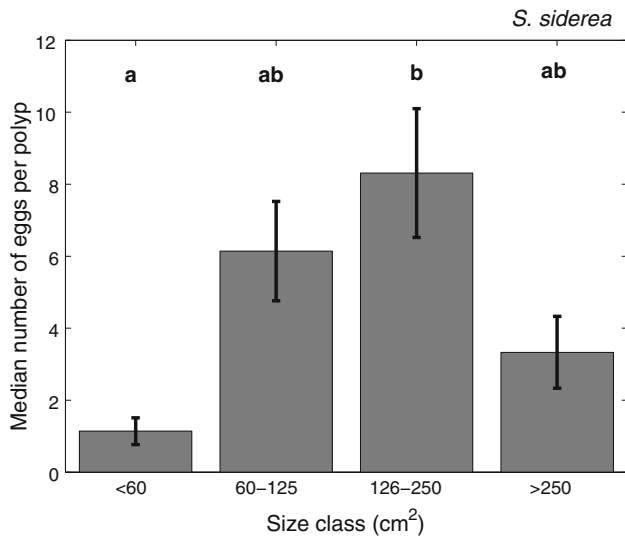


Fig. 1 The median (\pm median absolute deviation) number of eggs per polyp for each size class for *S. siderea* ($n = 48$). Letters represent results from Tukey–Kramer test where size classes with the same letter were not significantly different from each other ($H_3 = 14.58$, $p = 0.002$)

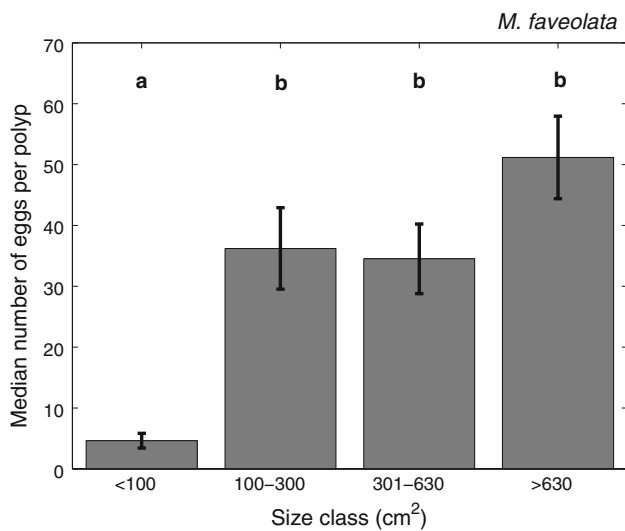


Fig. 2 The median (\pm median absolute deviation) number of eggs per polyp for each size class for *M. faveolata* ($n = 48$). Letters represent results from Tukey–Kramer test where size classes with the same letter were not significantly different from each other ($H_3 = 24.29$, $p < 0.0001$)

and therefore, the data were pooled across stations. There were, however, significant differences in the average number of eggs per polyp among different colony sizes of *S. siderea* ($H_3 = 14.58$, $p = 0.002$) (Fig. 1). The smallest colonies (<60 cm²) had significantly fewer eggs than the 126–250 cm² colonies, but the smallest colonies supported a similar number of eggs per polyp as the second and fourth size classes (60–125 cm² and >250 cm² colonies, respectively). Significant differences were also found in the

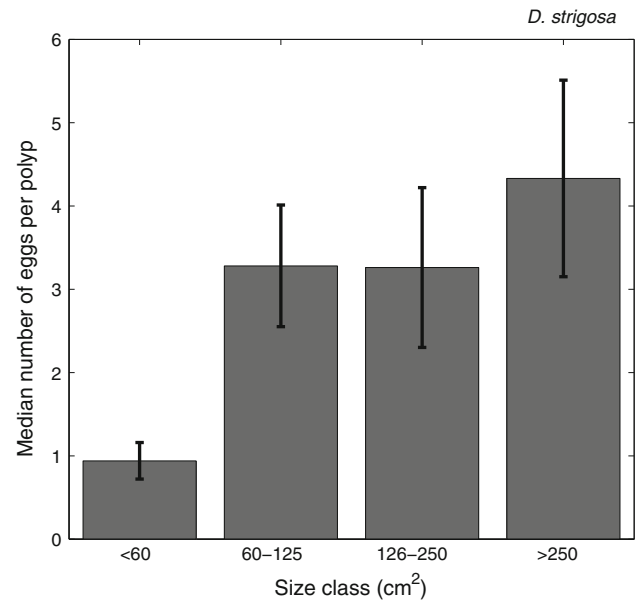


Fig. 3 The median (\pm median absolute deviation) number of eggs per polyp for each size class for *D. strigosa* ($n = 48$). There were no significant differences among size classes ($H_3 = 3.12$, $p = 0.374$)

number of eggs per polyp between the smallest colonies and all the other colonies of *M. faveolata* ($H_3 = 24.29$, $p < 0.0001$). The smallest colonies (<100 cm²) supported significantly fewer eggs than the larger colonies (Fig. 2). There were no significant differences in the number of eggs per polyp among different size classes of *D. strigosa* ($H_3 = 3.12$, $p = 0.374$) (Fig. 3). In summary, eggs were found in all large colonies, and in most of the smallest colonies that had been subjected to partial mortality and had shrunk below the species' maturation size.

Discussion

We hypothesized that the smallest colonies would still support some eggs. Although not all sampled colonies had eggs in the smallest size class, 44 % of both *D. strigosa* and *M. faveolata* and 38 % of *S. siderea* still devoted resources to the production of eggs in colonies that were smaller than their size at maturation. We also expected that the largest colonies would be fully reproductive, because colony fecundity has been found to increase with colony size for these species (Szmant-Froelich 1985; Soong 1993; Van Veghal and Kahmann 1994). Indeed, the largest *M. faveolata* colonies were fully gravid with eggs (Villinski 2003). However, the largest colonies of *S. siderea* had fewer eggs than the adjacent size class (126–250 cm²). Colonies in the adjacent, second largest size class were also not fully gravid, supporting fewer eggs than average (Wyers 1985; Soong 1993). This reduction in the number of eggs in the

largest colonies was unexpected (Szmant-Froelich 1985; Soong 1993; Van Veghel and Kahmann 1994). In the present study, sampled colonies of *D. strigosa* were not fully gravid.

The response of colonies to shrinkage, therefore, may be binary. Some coral species might switch off gametogenesis in accordance with colony size, whereas other coral species might maintain gametogenesis irrespective of colony size, once the colonies reach maturation (Kojis and Quinn 1985; Kai and Sakai 2008). In theory, a trait that involves the recognition of colony size would be particularly useful for coral species that easily and frequently fragment. Because small colonies are more likely to suffer total mortality than large colonies (Hughes and Connell 1987), self-size recognition would have several advantages, particularly if that process shunted valuable and limited resources away from gametogenesis and toward growth. Rapid growth of fragments would, in theory, allow fragments to remain in the small-size, vulnerable 'window' for the shortest amount of time. By contrast, the reduced fecundity in the largest *S. siderea* colonies might be a consequence of the loss of colony integration, compromising gametogenesis (Soong and Lang 1992). We note that colonies of *S. siderea* primarily suffer partial mortality on the central parts of colonies, whereas colonies of *M. faveolata* suffer partial mortality on the peripheral parts of colonies (Graham and van Woosik, unpublished data). Central mortality disrupts colony integration, whereas peripheral mortality simply reduces the size of the colonies while maintaining integration. Still, differences in colony integration do not explain why small *S. siderea* colonies that had shrunk below the species' maturation size still maintained their reproductive capacity, whereas large colonies showed reduced fecundity.

The present study showed that *S. siderea*, *M. faveolata*, and *D. strigosa* continued to dedicate resources to reproduction even after the colony had shrunk below their size of maturation. The continuation of growth and reproduction under stress could be an alternative, and flexible survival strategy of corals subjected to partial mortality (Banks 1997). Notably, life-history trade-off theory is generally thought to explain reductions in growth and reproductive activity in times of stress. Studies have shown that species with flexible trade-offs go extinct more rapidly than species with inflexible trade-offs, especially in response to habitat destruction (Banks 1997). Similarly, Leuzinger et al. (2011) showed that when resources were limited, reproduction received an increase in resource allocation, but reproduction was terminated beyond a critical threshold. Inflexible tradeoffs, therefore, may have both advantages and disadvantages in terms of a species' fitness. On the one hand, if coral colonies continue to reproduce while subjected to local stress, which causes chronic partial mortality and shrinkage, then there is a

chance for the genome to 'escape' the local stress via spawning (Maynard 1978; Jackson 1986; Silvertown 2008). On the other hand, ineffective allocation of resources may not be a useful survival strategy at the local level, when maintenance and survival are a priority and any resources allocated to reproduction may be costly and therefore compromise the host coral even further. Both strategies have advantages and disadvantages and are in need of further investigation. Nevertheless, the present study revealed that certain coral species may not be as effective in resource trade-offs as others, resulting in the continuation of reproduction during times of stress.

Acknowledgments We extend our thanks to Roberto Iglesias-Prieto, Anastazia Banaszak, and Robin Smith for extensive support throughout the field-sampling process. We also thank Sandra van Woosik for editorial comments. Universidad Nacional Autonoma de Mexico (UNAM), Instituto de Ciencias del Mar y Limnologia is gratefully acknowledged for logistic support, including the use of laboratory space, boats, and equipment. This research was supported by a grant from the World Bank and Global Environmental Facility (GEF) through the Coral Reef Targeted Research (CRTR) and Capacity Building for Management program and was partially supported by the Hoover Foundation.

References

- Babcock RC (1988) Age-structure, survivorship and fecundity in populations of massive corals. Proc 6th Int Coral Reef Symp 2:625–633
- Banks JE (1997) Do imperfect trade-offs affect the extinction debt phenomenon? Ecology 78(5):1597–1601
- Fine M, Oren U, Loya Y (2002) Bleaching effect on regeneration and resource translocation in the coral *Oculina patagonica*. Mar Ecol Prog Ser 234:119–125
- Harrison PL, Wallace CC (1990) Reproduction, dispersal and recruitment of scleractinian corals. Ecosyst World 25:133–207
- Hughes TP, Connell JH (1987) Population dynamics based on size or age? A reef coral analysis. Am Nat 129(6):818–829
- 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, Baird AH, Bellwood DR, Card M, Connolly SR, Folke C, Grosberg R, Hoegh-Guldberg O, Jackson JBC, Kleypas J, Lough JM, Marshall P, Nystrom M, Palumbi SR, Pandolfi JM, Rosen B, Roughgarden J (2003) Climate change, human impacts, and the resilience of coral reefs. Science 301(5635):929–933
- Jackson JBC (1986) Modes of dispersal of clonal benthic invertebrates: consequences for species' distributions and genetic structure of local populations. Bull Mar Sci 39(2):588–606
- Kai S, Sakai K (2008) Effect of colony size and age on resource allocation between growth and reproduction in the corals *Goniastrea aspera* and *Favites chinensis*. Mar Ecol Prog Ser 354:133–139
- Kojis BL, Quinn NJ (1985) Puberty in *Goniastrea favulus* age or size limited? Proc 5th Int Coral Reef Congr 4:289–293
- Leuzinger S, Willis BL, Anthony KRN (2011) Energy allocation in a reef coral under varying resource availability. Mar Biol 159:177–186
- Maynard S (1978) The evolution of sex. Cambridge University Press, Cambridge

- Okubo N, Motokawa T, Omori M (2007) When fragmented coral spawn? Effect of size and timing on survivorship and fecundity of fragmentation in *Acropora formosa*. Mar Biol 151:353–363
- Rinkevich B (1996) Do reproduction and regeneration in damaged corals compete for energy allocation? Mar Ecol Prog Ser 143:297–302
- Rinkevich B, Loya Y (1985) Intraspecific competition in a reef coral: effects on growth and reproduction. Oecologia 66:100–105
- Sakai K (1998) Gametogenesis, spawning and planula brooding by the reef coral *Goniastrea aspera* (Scleractinia) in Okinawa, Japan. Mar Ecol Prog Ser 151:67–72
- Selman C, Blout JD, Nussey DH, Speakman JR (2012) Oxidative damage, ageing, and life-history evolution: where now? Trends Ecol Evol 27(10):570–577
- Silvertown J (2008) The evolutionary maintenance of sexual reproduction: evidence from the ecological distribution of asexual reproduction in clonal plants. Int J Plant Sci 169(1):157–168
- Soong K (1993) Colony size as a species character in massive reef corals. Coral Reefs 12:77–83
- Soong K, Lang JC (1992) Reproductive integration in reef corals. Biol Bull 183:418–431
- Stearns SC (1989) The evolutionary significance of phenotypic plasticity. Bioscience 39:436–444
- Szmant AM, Gassman NJ (1990) The effects of prolonged “bleaching” on the tissue biomass and reproduction of the reef coral *Montastraea annularis*. Coral Reefs 8:217–224
- Szmant-Froelich A (1985) The effect of colony size on the reproductive ability of the Caribbean coral *Montastraea annularis* (Ellis and Solander). Proc 5th Int Coral Reef Congr 4:295–300
- Tomascik T, Sander F (1987) Effects of eutrophication on reef-building corals. Mar Biol 94:77–94
- Van Veghal MLJ, Kahmann MEH (1994) Reproductive characteristics of the polymorphic Caribbean reef building coral *Montastraea annularis*. II. Fecundity and colony structure. Mar Ecol Prog Ser 109:221–227
- van Woessik R (2010) Calm before the spawn: global coral-spawning synchronization is explained by regional wind fields. Proc R Soc B 277:715–722
- van Woessik R, Jordan-Garza AG (2011) Coral populations in a rapidly changing environment. J Exp Mar Biol Ecol 408:11–20
- Villinski JT (2003) Depth-independent reproductive characteristics for the Caribbean reef-building coral *Montastraea faveolata*. Mar Biol 142:1043–1053
- Ward S (1995) The effect of damage on the growth, reproduction and storage of lipids in the scleractinian coral *Pocillopora damicornis* (Linnaeus). J Exp Mar Biol Ecol 187:193–206
- Wyers SC (1985) Sexual reproduction of the coral *Diploria strigosa* (Scleractinia, Faviidae) in Bermuda: research in progress. Proc 5th Int Coral Reef Congr 4:301–306