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Experimental fragmentation reduces sexual reproductive output by the reef-building coral *Pocillopora damicornis*

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**Abstract** Natural and anthropogenic disturbances may fragment stony reef corals, but few quantitative data exist on the impacts of skeletal fragmentation on sexual reproduction in corals. We experimentally fragmented colonies of the branching coral *Pocillopora damicornis* and determined the number and size of planula larvae released during one lunar reproductive cycle. Partially fragmented colonies significantly delayed both the onset and peak period of planula release compared with intact control colonies. Most fragments removed from the corals died within 11–18 days, and released few planulae. The total number of planulae released per coral colony varied exponentially with remaining tissue volume, and was significantly lower in damaged versus undamaged colonies. However, the number of planulae produced per unit tissue volume, and planula size, did not vary with damage treatment. We conclude that even partial fragmentation of *P. damicornis* colonies (<25% of tissue removed) decreases their larval output by reducing reproductive tissue volume. Repeated breakage of corals, such as caused by intensive diving tourism or frequent storms, may lead to substantially reduced sexual reproduction. Therefore, reef management should limit human activities that fracture stony corals and lead to decreases in colony size and reproductive output.

**Key words** Fragmentation · Sexual reproduction · Planula larvae · Scleractinia · Management · Tourism

**Introduction**

The calcareous skeletons of stony reef corals may be fragmented by a variety of natural disturbances (e.g. storms, earthquakes) and anthropogenic activities (e.g. scuba diving, boat grounding, anchor drag; Rogers et al. 1988; Allison 1996; Rieg and Rieg 1996; Chadwick-Furman 1997). Breakage of stony corals reduces colony size, increases susceptibility to disease (Bak and Criens 1981; Rogers et al. 1988), and raises mortality rates (Rinkevich and Loya 1989; Ward 1995). In addition, removal of parts of the colony may adversely impact the sexual reproductive system, and reduce the total output of gametes or brooded larvae by the colony (Kojis and Quinn 1985; Szmant-Froelich 1985, Rinkevich and Loya 1989; Van Vehgel and Bak 1994). The end result of impaired sexual reproduction by corals may be a decrease in the recruitment of new young corals to the reef (Richmond 1997). Despite the potential impact of this process on reef ecosystems, little quantitative information exists on the effects of fragmentation on stony coral reproductive output. In the branching coral *Stylophora pistillata*, removal of up to 23% of the colony radius caused most colonies to become completely sterile for up to a year afterward (Rinkevich and Loya 1989). In the massive coral *Montastrea annularis*, the removal of skeleton and tissue via lesions on the coral surface led to a 50–74% decrease in the fecundity of polyps near the lesions compared with those further away (Van Vehgel and Bak 1994). Removal of half the branches of *Pocillopora damicornis* colonies caused a slight increase in the percent of remaining polyps containing gonads, but the total reproductive output of damaged colonies was not determined (Ward 1995). Finally, reduction in size lowers fecundity in colonies of the massive corals *Goniastrea faveus* (Kojis and Quinn 1985) and *M. annularis* (Szmant-Froelich 1985). The above studies assessed reproductive status mainly via histological examination of gonads, and contained limited or no information on the amount and timing of sexual products (gametes,
lakes) released by the remainder of the damaged coral colonies.

Materials and methods

We describe here the impact of three levels of experimental fragmentation on the number, timing and size of planula larvae released during a full lunar reproductive cycle by colonies of the reef-building coral *Pocillopora damicornis*.

In June 1997, we collected 20 large colonies of *P. damicornis* from 1-m depth on patch reefs in Kaneohe Bay, on the island of Oahu, Hawaii, USA. Colonies of this species are dominant components of the shallow coral community at this site, and their reproductive biology has been well-documented (Jokiel 1985; Richmond 1985). All colonies were transported to the nearby Hawaii Institute of Marine Biology, and placed in outdoor tanks supplied with running seawater. During 8 days of acclimation to the laboratory setup, all collected colonies released larvae. The total volume of each colony (skeleton plus tissue) was then determined by submerging it in a known volume of seawater and calculating the displacement volume (after Richmond 1985). The tissue volume of each colony was estimated from differences in the displacement volume of five colonies before and after tissue removal. Tissue was removed from the colonies via a high-pressure stream of sea water (range of total live colony volumes = 210–450 cm³, range of tissue volumes = 30–75 cm³, percent tissue volume = 16.3 ± 0.8% [x ± SD] of total live colony volume, n = 5 colonies).

The 20 colonies then were assigned to four experimental groups, resulting in five corals per treatment: (1) no damage (control group), (2) 25% damage, (3) 50% damage, and (4) 100% damage (completely fragmented). Pre-damage tissue volume did not vary significantly between the four experimental groups (ANOVA, F = 0.44, df = 3,16, P = 0.73). Colonies were fragmented using pressure applied by a flat board, and the remaining intact volume of each colony was then re-determined. No fragments were broken from corals in the 0% damage treatment, 20–25% of colony volume was removed from corals in the 25% damage treatment, 48–55% of volume was removed in the 50% damage treatment, and corals in the 100% damage group were completely broken into small fragments each 1–7 cm in length. Each colony, together with its fragments, was placed in a 4-l planula collector bowl supplied with unfiltered running seawater at a rate of 1 liter min⁻¹ (after Jokiel 1985; Richmond 1985). The bowls were randomly interspersed on an outdoor seawater table covered with plastic mesh net so that light intensity equaled that at 1-m depth on the adjacent reef. Water from each bowl ran into a collector cup fitted with 150-µm plankton mesh to ensure the collection of all planulae released by each colony.

The larvae released by each coral were counted daily for one lunar cycle, beginning on the new moon (5 July–2 August 1997). The dimensions (length × width) of a subsample of larvae released by the corals (n = 100 larvae treatment⁻¹) were measured. Larvae were anaesthetized in 4% MgCl₂ for 45 min, then placed in Petri dishes under a dissecting microscope connected to a computer, and their dimensions were determined using a RasterOps 24STV MediaGrabber version 2.5.2 and NIH Image version 1.4.

Results and discussion

Undamaged control colonies of *P. damicornis* began to release substantial numbers of larvae (>100 larvae colony⁻¹) at 13–16 days and peaked at 17–19 days after the new moon (Fig. 1A). In contrast, only some of the fragmented colonies produced substantial numbers of larve (>100 colony⁻¹), and these significantly delayed their onset of larval release to 15–26 days, and peak release to 18–27 days after the new moon (Fig. 1B, C; Mann-Whitney U-test, U = 25 and 26 for onset of release and peak release respectively, P < 0.05 for both).

The total number of planulae released per colony varied exponentially with remaining colony tissue volume (Fig. 2A; exponential regression test, r = 0.85, P < 0.001). Unfragmented, undamaged colonies released 10,000–38,000 planulae month⁻¹, while partially fragmented colonies released 1–10,000 planulae month⁻¹. Some of the fragmented colonies produced almost no larvae at all (Figs. 1, 2). The corals that had been completely broken into small branch fragments (100% damage group) all died by 11–18 days after the start of observations, and produced very few planula larvae per colony (range = 2–42, open triangles in Fig. 2A). The number of larvae produced per unit volume of remaining tissue did not vary significantly with experimental treatment (Fig. 2B; Kruskal-Wallis test, H = 1.28, P = 0.50), or with remaining colony size (regression test, r = 0.11, P = 0.69). Undamaged colonies produced 300–800 planulae cm⁻³ of tissue, while partially fragmented corals showed more variation, producing 1–900 planulae cm⁻³ (Fig. 2B). The sizes of larvae released did not vary significantly between the treatment groups, in terms of either larval length (x ± SD = 1.86 ± 0.23 mm, range = 1.03–2.46 mm, n = 300) or width (x ± SD = 0.78 ± 0.12 mm, range = 0.21–1.44 mm, n = 300; ANOVA, F = 0.35 and 1.00, df = 2,994 for both, P = 0.70 and 0.37 respectively).

We conclude that larval production by broken colonies of *P. damicornis* is reduced due to their smaller size and amount of remaining live tissue compared with undamaged colonies of the same pre-damage size. Larval production per unit tissue volume varies widely between individual colonies and is not significantly impacted by breakage after 1 month. Although we did not measure the larval output of fragments separately from their intact corals in all treatments, many of these fragments died before the end of the experiment.