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Effect of Colony Size, Polyp Size, and Budding Mode on Egg Production in a Colonial Coral

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Abstract. The factors that influence egg production in the massive coral *Goniastrea aspera* were examined in colonies of various sizes collected before the first spawning of the year. Particular attention was given to polyp size, measured in three dimensions as volume.

Although a polyp in a colony containing as few as 13 polyps produced eggs, colonies with fewer than 60 polyps had fewer eggs per unit volume of polyp. The relationship between colony size and colony fecundity suggested that 60 polyps is the minimum size at which a colony can achieve active maturity. Polyp volume of small colonies before maturation was also smaller than that of the larger colonies, suggesting that colony size, as well as polyp size, is crucial for sexual maturity.

The position of a polyp in the colony (and thus its mode of budding) also affects its maturity (and thus its egg production). Marginal polyps (those on the edge of the colony) usually exhibited extratentacular budding, and the resulting polyps were initially immature. Consequently, egg production by such polyps is a function of their age, calculated from the time of their formation by extratentacular budding. In contrast, non-marginal polyps always exhibited intratentacular budding. Moreover, in the non-marginal areas of large colonies (>84 polyps), the polyps produced by intratentacular budding were always mature. In all colonies, marginal polyps were smaller in volume and had a lower number of eggs for each unit of volume than did non-marginal ones. This suggests that polyps play different roles according to their position in a colony: marginal polyps contribute to defense and expansion of the area of attachment, whereas the role of non-marginal polyps is reproductive. The fecundity of mature colonies increased linearly with colony size, and large colony size cannot be attained without expansion of the attachment area.

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Introduction

Recent studies on reproduction of colonial, scleractinian corals have revealed that polyps in small colonies produce no eggs or few eggs, and that in large, fecund colonies polyps at or near the margin of the colony produce fewer eggs than those in central positions (Harriott, 1983; Chornesky and Peters, 1987; Harrison and Wallace, 1990; Szmant, 1991; Soong and Lang, 1992; Van Veghel and Kahmann, 1994; Hall and Hughes, 1996). A coral colony is usually derived from a single polyp by budding, so that the polyps in the colony are usually genetically identical (Jackson and Coates, 1986) and likely to have the same structure and the same potential for any physiological function (Meester and Bak, 1995). Thus, the recent work has demonstrated that coral polyps may differ in reproductive activity even though they share the same structure and genetic identity.

In colonial corals, colony size is considered to be important for the maturation of polyps (reviewed in Harrison and Wallace, 1990), but the size of a coral has another aspect, *i.e.*, polyp size. Although the polyp is the basic unit for physiological activities, its size has not often been studied. Two exceptions are the studies by Harriott (1983) and Van Veghel and Kahmann (1994). Harriott (1983) investigated sexual reproduction in four scleractinian coral species, and suggested that polyp size rather than colony size limits gonad production in the mussid coral *Lobophyllia corymbosa*; she presented no data on polyp size. Van Veghel and Kahmann (1994) studied reproduc-

tion in three morphotypes of the faviid coral *Montastrea annularis*, measuring polyp size two-dimensionally at the base. They found that the fertility (measured as the percentage of polyps with eggs) of polyps from 27 colonies was less than 40% in small polyps (<1.5 mm) and increased with polyp diameter.

To date, however, no study of coral reproduction has quantitatively examined the relationship between the size of a polyp and its egg production. Furthermore, polyp size has previously been measured in two dimensions, even though it is the space within a polyp that limits gamete volume. Thus, I measured the three-dimensional size of polyps in the faviid coral *Goniastrea aspera*.

I examined the effect of colony size, polyp size, and location of polyps on egg production. I show that not only colony size but also polyp size is related to egg production, and further suggest that fertility in *G. aspera* is also affected by polyp age, determined as the time since formation by extratentacular budding.

Materials and Methods

Collection, colony size, and egg count

I collected specimens of *G. aspera* at the lowest low tide level on the fringing reef of Sesoko Island, Okinawa, southern Japan (26° 38′N, 127° 52′E). This coral is a simultaneous hermaphrodite; in Okinawa it has one or two spawning peaks per year, in June and July (Heyward *et al.*, 1987; Hayashibara *et al.*, 1993; Sakai, 1997). To assess egg production by polyps, 23 *G. aspera* colonies of various sizes were collected on 21 May 1991, 10 days before the predicted date of the first spawning of the year. Before collection, the length, width, and height of the colony were measured to the nearest 1 mm. Since egg production may be affected by disease or injury and by contact with large benthic organisms such as neighboring corals, I chose colonies without such features.

The collected colonies were fixed in 10% formalin in seawater for at least 24 h, and decalcified in a solution of 5% formalin + 5% acetic acid. I counted the number of polyps in the colony after decalcification and used this value as a measure of colony size, because the polyp number is highly correlated with colony somatic biomass (Sakai, 1998). Then, randomly selected polyps (n ranged from 1 to 20 according to colony size) were cut from the decalcified colony after the maximum and minimum diameters of the oral side were measured to the nearest 0.1 mm. Polyp height was measured after the polyps were excised from the colony. I estimated the volume of each polyp from its diameter and height. While non-marginal polyps (in polyp row 2 or higher, away from the colony margin; Fig. 1) were always cylindrical, marginal polyps (in the row at the colony edge) were frequently more

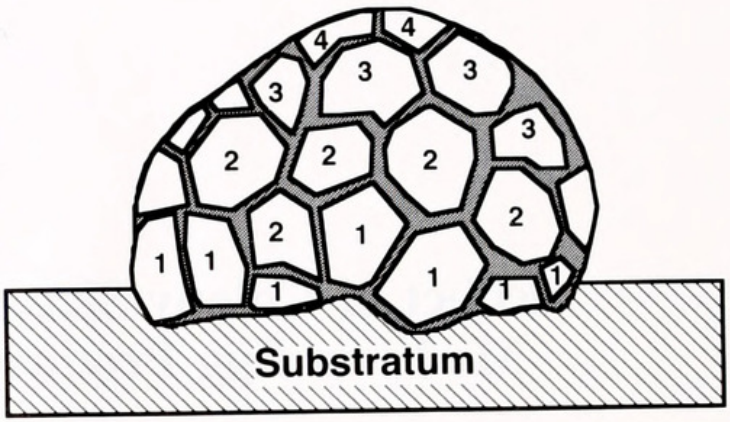

Figure 1. Diagram showing position classification of polyps in a colony. Each white polygon represents a polyp, and the number inside the polygon indicates the row number of that polyp. Row number was determined as the next highest number to the lowest number in adjacent polyps. 1 = marginal polyps; ≥2 = non-marginal polyps.

conical. Hence, I estimated the polyp volume as $k \times \pi \times [(\text{maximum diameter} + \text{minimum diameter})/4]^2 \times \text{height}$, where k ranged from $^1/_3$ (conical) to 1 (cylindrical). The value of k was subjectively determined for each polyp according to its shape. Each polyp was dissected under a stereoscopic microscope, and all the eggs within a polyp were counted. I measured the diameter of five eggs, randomly selected from each of four polyps in each of ten fecund colonies. The overall mean of the egg diameter in the polyps was 310 ± 30 μm (Mean ± SD, n = 200). There was no significant colony effect on the egg diameter (Model III nested ANOVA, df = 9, SS = 9663.98, F = 0.99, P = 0.5; when polyps were nested in the colonies). Thus, egg production can be compared in terms of number of eggs per polyp volume (NE/PV, see below).

Preliminary examination of the effect of polyp position on egg production in four fecund colonies showed that marginal polyps had significantly lower NE/PV than non-marginal polyps (Table I). NE/PV of polyps in row 2 or higher did not differ significantly ($P > 0.05$). In subsequent analyses I therefore grouped polyps in a colony into marginal and non-marginal sets. Polyp-group fertility, as percentage of polyps with eggs to total number of sampled polyps, was calculated separately for marginal and non-marginal polyps in each colony.

Budding mode and polyp biomass

To examine the relationship between estimated polyp volume and polyp biomass, I collected 11 colonies of *G. aspera* of various sizes (from 40 to 420 polyps) in October 1993, when reproductive tissue was negligible (Sakai, 1997). These colonies were fixed and decalcified as described for the egg-count specimens. When I counted the number of polyps in the decalcified colonies, I also re-

Table I

Intracolonial variation in NE/PV (number of eggs per polyp volume, mm^{-3}) in four fecund colonies

Colony size (number of polyps)	Kruskal-Wallis test among polyp rows (P value)	Tukey-type multiple comparison
84	<0.01	1st <<< 2nd ≈ 3rd+
85	<0.01	1st < 2nd, 1st <<< 3rd+, 2nd ≈ 3rd+
167	<0.01	1st << 2nd, 1st < 3rd, 1st << 4th+, 2nd ≈ 3rd ≈ 4th+
349	<0.001	1st << 2nd, 1st < 3rd, 1st << 4th, 2nd ≈ 3rd ≈ 4th+

Note: Ordinals in the multiple comparison (Zar, 1996) represent polyps of the ith row from the colony edge; 3rd+ and 4th+ indicated polyps more central than 2nd and 3rd rows, respectively (Fig. 1). Probability in multiple comparison: ≈, $P > 0.05$; <, $P < 0.05$; <<, $P < 0.01$; <<<, $P < 0.001$. Number of polyps examined in each row ranged from 5 to 10.

corded the mode of budding (*i.e.*, intratentacular or extratentacular) for marginal and non-marginal polyps separately. Formation of a new bud outside the polyp wall was recorded as extratentacular budding, and formation of a new polyp wall dividing the original polyp was recorded as intratentacular budding.

Four polyps, two marginal and two non-marginal, were randomly selected from each colony after decalcification. These 44 polyps were measured and excised from the colonies as described for egg-count polyps, and then rinsed in distilled water and dried at 60°C to constant weight. Each polyp was weighed to the nearest 0.1 mg. The estimated polyp volume showed a strong linear correlation with the somatic biomass, both in marginal ($r^2 = 0.87$, $P < 0.0001$, $n = 22$) and non-marginal ($r^2 = 0.84$, $P < 0.0001$, $n = 22$) polyps, with no significant difference between the two regression lines (ANCOVA, df = 1, SS = 0.29, $F = 0.17$, $P = 0.7$). Therefore, assuming that the polyp volume represents the somatic biomass, I calculated the average number of eggs per polyp volume (NE/PV, mm^{-3}) for marginal and non-marginal polyps in each colony.

Colony fecundity

Egg production by a whole colony (colony fecundity) was estimated as the sum of egg production by marginal and non-marginal polyps. The total egg production for each polyp type was calculated as the mean number of eggs per polyp multiplied by the number of polyps of that type in the colony.

Statistical analyses

I examined the relationship between colony size (polyp number) and fertility and mean NE/PV, fitting a curve using the logistic equation, since egg production by coral polyps over colony size is expected to be sigmoidal (Babcock, 1991). For the remaining regression analyses, I examined linear, exponential, power, and logarithmic functions, and used the one with the highest correlation coefficients after examining the residuals (Zar, 1996). I used Model III ANOVA, nesting random-effects such as individual colonies within fixed-effects such as colony size classes (Zar, 1996). The assumptions for ANOVA (*i.e.*, normality and homogeneity of variance) were examined with the Shapiro-Wilk W test and O'Brien's tests. Logarithmic transformation was made if necessary; when the assumptions were severely violated even after the transformation, a nonparametric analysis such as the Wilcoxon paired-sample test was performed using means from colonies. Statistical analyses were performed with computer software packages (Data Desk, Data Description Inc., Ithaca, NY; JMP, SAS Institute, Cary, NC; Kaleida Graph, Synergy Software, Reading, PA).

Results

Marginal and non-marginal polyps

Six of twenty-three colonies smaller than 2 cm in diameter (9 polyps) had only marginal polyps. Hence, the comparisons between marginal and non-marginal polyps were conducted for the 17 colonies that had both polyp types. Values for mean polyp volume, fertility, and mean NE/PV of non-marginal polyps were significantly greater than those of marginal polyps from the same colony (Wilcoxon paired-sample test, all $P < 0.01$; Fig. 2A–C). The mode of budding was also significantly different between the two groups (Fisher exact test, $P < 0.0001$). All the budding (total = 58) in non-marginal polyps was intratentacular, and 96% of the budding (total = 53) in marginal polyps was extratentacular.

Colony size, polyp size, and egg production by polyps

To examine the relationships among colony size, polyp size, and egg production, I grouped the colonies into three size classes: small (S; ≤60 polyps, or ≤4.5 cm in mean colony diameter), medium (M; 60–150 polyps, or 4.5–9 cm), and large (L; >150 polyps, or >9 cm). The classification was made because (1) below 60 polyps, NE/PV was extremely small; and (2) after 150 polyps, the fitted curve using the logistic equation between the colony size and NE/PV leveled off (Table II; Fig. 2C).

No eggs were found in colonies with marginal polyps only or with marginal polyps and one non-marginal polyp

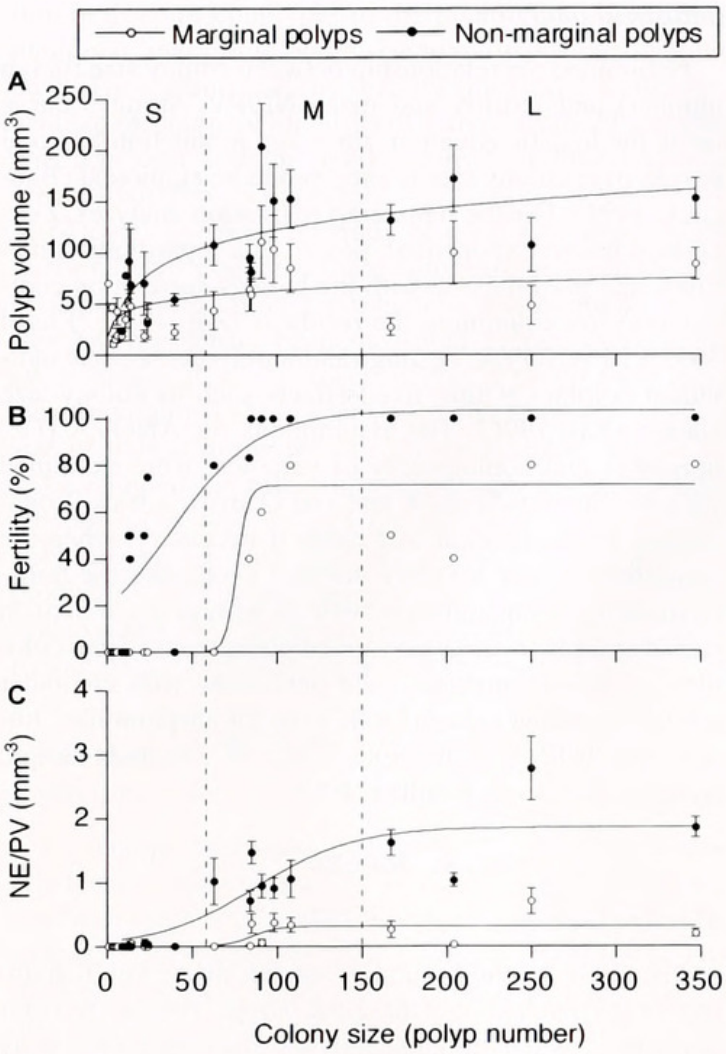

Figure 2. Relationship between colony size (polyp number) and mean polyp volume (A), fertility (B), and mean NE/PV (number of eggs per polyp volume, C) of marginal and non-marginal polyps in a colony. Bars show the standard error. The borders of the colony size classes (S, M, and L) are shown with broken lines. The models and the parameters for curve fits are given in Table II.

Table III

ANOVA results for mean polyp volume and mean NE/PV (number of eggs per polyp volume) among the colony size classes (S = small, M = medium, L = large)

Source	df	Sum of squares	*F*	*P*
A. Mean volume of marginal polyps				
Colony size class (S, M, & L)	2	2.81	5.05	0.02
Colony [Colony size class]	19	5.28	2.00	0.01
B. Mean volume of non-marginal polyps				
Colony size class (S, M, & L)	2	1.62	7.14	0.007
Colony [Colony size class]	14	1.59	1.62	0.08
C. Mean NE/PV of marginal polyps				
Colony size class (M, & L)	1	0.01	0.50	0.5
Colony [Colony size class]	8	0.24	3.92	0.001
D. Mean NE/PV of non-marginal polyps				
Colony size class (M, & L)	1	0.34	6.37	0.04
Colony [Colony size class]	8	0.43	3.44	0.002

Note: Analyses for all dependent variables (Model III ANOVA) contain colonies nested within the colony size class. The S size class was excluded from the NE/PV analyses because of a severe violation of ANOVA assumptions. Logarithmic transformation was used in all the cases, and the assumptions for ANOVA were satisfied, excepting normality in D.

(<13 polyps, or <3 cm in colony diameter; $n = 8$). The smallest colony that produced eggs had 13 polyps (≈3 cm colony diameter), two of which were non-marginal and the only polyps with eggs.

Model III nested ANOVAs showed significant among-class differences in mean polyp volume for both marginal and non-marginal polyps (Table IIIA, B). *Post-hoc* tests (Scheffé test) showed that the S class colonies had smaller mean polyp volume than the M class colonies for both marginal and non-marginal polyps (Table IV; Fig. 2A). The S class colonies had smaller non-marginal polyp volume than the L size class colonies, but this was not true

Table II

Curve fits for Figure 2

Curve	Polyp type	Model used	Parameters a	Parameters b	Parameters c	r^2	*P*
A. Volume	Marginal	Logarithmic	19.2	21.7	—	0.26	0.01
	Non-marginal	Logarithmic	−21.0	71.6	—	0.52	0.001
B. Fertility	Marginal	Logistic	71.4	$2.31 \cdot 10^{-9}$	0.315	0.81	<0.0001
	Non-marginal	Logistic	103	19.2	0.0391	0.70	<0.0001
C. NE/PV	Marginal	Logistic	0.317	$3.44 \cdot 10^{-6}$	0.134	0.54	<0.0001
	Non-marginal	Logistic	1.86	0.0843	0.0348	0.78	<0.0001

Note: The models and the parameters: Logarithmic, $Y = a + b \cdot \log X$; Logistic, $Y = a/(1 + ((a - b) \cdot e^{(-c \cdot X)}/b))$.

Table IV

Mean polyp volume, polyp fertility, and mean NE/PV (number of eggs per polyp volume) among the colony size classes

Colony size class	Mean polyp volume (mm^3)	Fertility (%)	Mean NE/PV (mm^{-3})	n
Marginal polyps				
S	33.2 ± 4.8	3.1 ± 3.1	0.004 ± 0.004	13
M	77.4 ± 10.9	63.3 ± 15.8	0.19 ± 0.07	6
L	65.6 ± 17.0	62.5 ± 10.3	0.30 ± 0.14	4
Non-marginal polyps				
S	59.7 ± 9.3	32.1 ± 11.8	0.02 ± 0.01	7
M	131.5 ± 18.7	93.9 ± 3.9	1.02 ± 0.10	6
L	140.7 ± 13.9	100	1.82 ± 0.36	4

Note: The size classes: S, ≤ 60; M, 62–150; L, >150 polyps. Mean ± SE calculated from means of individual colonies are shown. Number of colonies = n. Bars connect means that were judged not significantly different ($P > 0.05$) by Scheffé test (for mean polyp volume of marginal and non-marginal polyps after nested ANOVA), Tukey-type test (for fertility of marginal and non-marginal polyps after Kruskal-Wallis test), and nested ANOVA (for mean NE/PV of marginal and non-marginal polyps between the M and the L size classes).

for marginal polyps. The M and the L class colonies did not differ in mean polyp volume for either marginal or non-marginal polyps.

Fertility (Fig. 2B) was significantly lower in the S size class than in the M and L size classes for both marginal and non-marginal polyps (Table IV; $P < 0.001$; Kruskal-Wallis test). As with mean polyp volume, fertility did not differ significantly between the M and the L size classes (Table IV). Fertility of non-marginal polyps was 100% in all the colonies that were larger than 84 polyps. The complete fertility of the non-marginal polyps was not due to large polyp volume. Although the volume was significantly larger in non-marginal polyps than in marginal polyps within a colony, small non-marginal polyps were fertile, whereas some of marginal polyps within the same volume range were not (Fig. 3). The overall fertility of these marginal polyps was 66.7% ($n = 57$), and polyp volume was positively associated with fertility.

ANOVA could not be performed for mean NE/PV among colonies in all the size classes, because the many 0 scores in mean NE/PV in the S size class (Fig. 2C) was a severe violation of ANOVA assumptions. However, mean NE/PV of both marginal and non-marginal polyps in the S size class was an order of magnitude smaller than those in the M and the L size classes (Table IV). I performed Model III nested ANOVAs excluding colonies in the S size class. Mean NE/PV of marginal polyps was not significantly different between the L and the M size classes (Table IIIC); in contrast, the difference was significant for non-marginal polyps (Table IIID).

Colony fecundity

Some colonies in the S size class produced eggs, but their colony fecundity was less than 60 eggs. In contrast, the fecundity of colonies in the M and the L size classes was more than 4500 eggs, and it increased linearly with colony size (Fig. 4). The X intercept of colony size *vs.* colony fecundity in the regression line for the M and L size class colonies was 58.3 polyps. Hence I considered the colony size for active maturation to be 60 polyps. Marginal polyps contributed less than 1% to the fecundity of colonies in the M size class. The contribution by marginal polyps decreased with colony size, and it was less than 0.1% in the L size class (>150 polyps).

Discussion

The results suggest that the sexual maturation of a polyp is less a function of its size than of the mode of

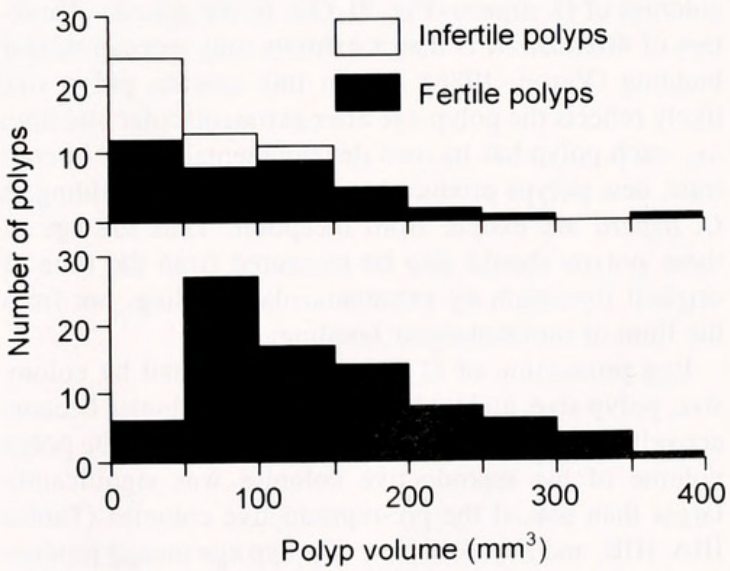

Figure 3. Polyp size distribution for marginal (top) and non-marginal (bottom) polyps from colonies larger than 84 polyps. All the polyps from eight colonies were pooled. Infertile and fertile polyps are shown separately.

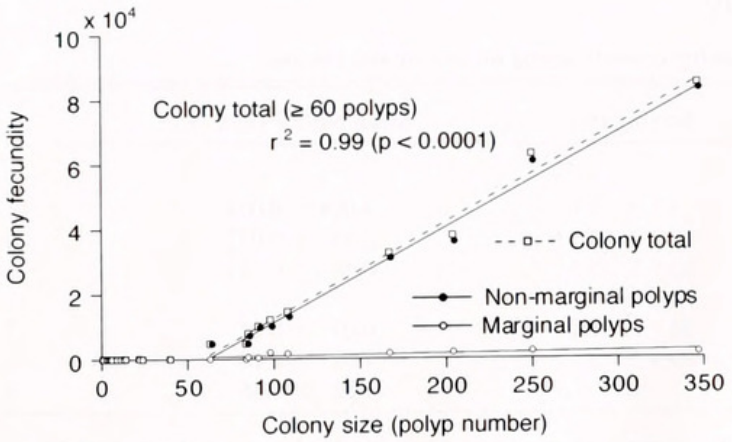

Figure 4. Relationship between colony size (number of polyps) and colony fecundity. The total colony fecundity and the contribution of marginal and non-marginal polyps to colony fecundity are presented separately. Linear regressions were conducted for colonies larger than 60 polyps.

budding that produced it. In large colonies of mature *G. aspera* (>84 polyps), the non-marginal polyps, which showed intratentacular budding, always contained eggs regardless of polyp size, but less than 70% of the marginal polyps were fertile (Fig. 3). New polyps produced by intratentacular budding of mature non-marginal polyps appear to share the developmental stage of their parent polyps, whereas new small polyps produced by extratentacular budding are rarely fertile and may be regarded as developmentally "young" polyps. In the Caribbean massive faviid coral *Montastrea annularis,* not all the polyps in the central area are fertile, and polyp fertility is positively correlated with polyp size (Van Veghel and Kahmann, 1994), as in marginal polyps from the large colonies of *G. aspera* (Fig. 3). One of the generic characters of *Montastrea* is that it exhibits only extratentacular budding (Veron, 1986). So for this species, polyp size likely reflects the polyp age after extratentacular budding; *i.e.,* each polyp has its own developmental clock. In contrast, new polyps produced by intratentacular budding in *G. aspera* are mature from inception. Thus the age of these polyps should also be measured from the time of original formation by extratentacular budding, not from the time of intratentacular budding.

Egg production of *G. aspera* was affected by colony size, polyp size, and budding mode. The colonies became actively reproductive at a size of 60 polyps, and the polyp volume of the reproductive colonies was significantly larger than that of the pre-reproductive colonies (Tables IIIA, IIIB, and IV). An effect of polyp age on egg production has been suggested by Kojis and Quinn (1985). They divided mature colonies of *Goniastrea favulus* into fragments smaller than the minimum size at maturity observed in naturally growing colonies, and found that some of the fragments produced gametes. In *G. aspera,* non-marginal polyps were formed in colonies with more than eight polyps, which then began intratentacular budding. All non-marginal polyps in colonies larger than 84 polyps were fertile, presumably because all the polyps have attained maturity upon extratentacular budding.

This study demonstrates that polyps within a mature colony of *G. aspera* play different roles according to their position, even though all the polyps in a colony share the same structure and are likely to be genetically identical and physiologically connected to each other. Significant differences in polyp volume, NE/PV, and mode of budding were detected between marginal and non-marginal polyps within a colony. Moreover, NE/PV of marginal polyps was relatively constant in mature colonies, whereas NE/PV of non-marginal polyps was significantly higher in the larger mature colonies (>150 polyps) than in smaller mature colonies (60–150 polyps; Tables IIIC, IIID and IV). This implies that marginal polyps function as a buffer for the non-marginal polyps, which produce the bulk of the gametes (Fig. 4), against external perturbations such as competition and grazing, which are likely to be heavier at the colony edge (Jackson, 1979; Hughes and Jackson, 1985; Chornesky and Peters, 1987; Soong and Lang, 1992). In addition, marginal polyps may also contribute to the expansion of the attachment area of the colony (Chornesky and Peters, 1987). In a massive coral colony, polyps in the central area contribute to colony growth, increasing the surface area of the colony. However, large colony size cannot be attained without expansion of the attachment area as well. As a colony becomes larger, its total fecundity becomes greater with an increase in the number of fecund, non-marginal polyps. Thus, the differences between the marginal and the non-marginal polyps play a role in promoting high colony fecundity.

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