Egg production by colonies of a gorgonian coral

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ABSTRACT: Reproductive success, the production and fertilization of gametes, is a key component of fitness. Among many colonial marine invertebrates, the production of gametes by a colony is a function of both gamete production per module (e.g., polyp, zooid) and the number of modules in the colony (i.e., colony size). We examined variance in gamete production per polyp and egg production per colony over a range of colony sizes, and the relationship between egg production and growth in the common Caribbean gorgonian *Plexaura flexuosa*. The number of polyps per colony and the average number of mature eggs per polyp both were greater among larger female colonies (>70 cm in height) than among smaller colonies (<70 cm), resulting in a 1 to 2 order of magnitude increase in whole colony egg release for the larger colonies. In a group of 24 colonies, 98% of the 9.2×10^6 eggs produced in one spawning event came from the 12 colonies taller than 70 cm. Branch extension rates showed no relationship to colony size, but whole colony relative growth appears to decrease as colony size increases. This suggests that proportionately less energy is used for growth as a colony gets larger, and thus may be available for reproduction.

KEY WORDS: Reproduction · Growth · Invertebrates · Modular animals · *Plexaura flexuosa*

INTRODUCTION

An array of studies has examined the reproductive biology of benthic marine invertebrates in the context of life history strategies (e.g., Vance 1973, Harvell & Grosberg 1988, Levitan 1995). Factors such as fertilization success and larval mortality have been considered important determinants of reproductive success (i.e., the production and fertilization of gametes). However, for the many marine invertebrates that exhibit clonal growth, the highly variable size of mature colonies can also lead to large differences in numbers of gametes produced. This in turn can have a tremendous effect on estimates of reproductive success among colonies and populations. To date, only a few studies have estimated egg production of whole colonies, and they have noted high levels of variance based on colony size (e.g., Babcock 1984, 1991, Coma et al. 1995, Hall & Hughes 1996). Variance in gamete production among

colonies can decrease effective population size because effective population size is inversely proportional to variance in reproductive success (e.g., Hughes et al. 1992). Furthermore, 2 studies have indicated that large colonies contribute disproportionately to egg production by whole populations (Babcock 1984, Coma et al. 1995).

Variance in the reproductive output of clonal taxa is primarily a function of the iterative production of modules, each of which may be capable of reproduction. Additional variability is associated with the integration of modules into physiologically connected colonies. For example, in many corals and other colonial animals all modules in a colony delay reproduction until the colony reaches a minimum size (e.g., Karlson 1986, Harvell & Grosberg 1988, Coma et al. 1995). Additionally, gamete production per polyp increases as colony size increases among some coral species (e.g., Babcock 1991, Coma et al. 1995, Hall & Hughes 1996). Delay in reproduction and increases in egg production per polyp with colony size may reflect greater availability of energy in general among larger colonies or a change in the allocation of energy from growth to reproduction (e.g., Hughes & Jackson 1985, Kinzie & Sarmiento

1986, Hall & Hughes 1996). Thus life history analyses of clonal organisms should incorporate data on the fecundity of modules and colonies, as well as the manner in which resources are distributed between fecundity and growth of the colonies.

The objectives of this study were (1) to document the reproductive cycle of *Plexaura flexuosa*, a common Caribbean gorgonian coral, and (2) to examine variance in gamete volume per polyp, egg production by whole colonies, and growth of branches and colonies. Using measurements of egg production per polyp, polyp density, and colony surface area within and across colonies, we (3) quantified the relationship between colony size and egg production, and (4) compared the relative contributions of colonies of various sizes to egg production by a population. Using measurements of branch extension and estimates of relative growth in whole colonies over a range of colony heights, we (5) examined the relationship between reproductive output and growth. Although we present data on the timing of both egg and spermary development, most of our discussion about reproductive output focuses on egg production. Eggs are more readily quantified than sperm, and although sperm density sometimes limits gorgonian reproductive success (Lasker et al. 1996), the number of eggs produced sets an upper limit for reproductive success.

MATERIALS AND METHODS

We assessed reproductive output and growth of *Plexaura flexuosa* colonies on patch reefs in the San Blas Islands, Panama. *P. flexuosa* is a gonochoric branching gorgonian coral common throughout the Caribbean (Bayer 1961, Goldberg 1973, Lasker & Coffroth 1983). Unless otherwise stated, all samples were collected from colonies on Korbiski Reef, a patch reef 2 to 4 m deep (Korbiski-1 in Robertson 1987, Fig. 1). All *P. flexuosa* samples were preserved in 10% formalin in seawater immediately after collection, then rinsed in freshwater for ~16 h and transferred to 70% ethanol before examination.

Reproductive cycle. A number of plexaurids, including *Pseudoplexaura* spp., *Plexaurella* sp., and the congeners *Plexaura homomalla* and *Plexaura kuna*, spawn shortly after the summer full moons (Brazeau & Lasker 1989, Coma & Lasker 1997, pers. obs.). In order to determine the spawning cycle of *Plexaura flexuosa*, gamete volumes in polyps from 6 male and 6 female colonies were followed over 5 lunar cycles during the 1994 summer. One growing tip (i.e., 1° branch) from each colony was taken approximately biweekly from May 29, 1994 to October 3, 1994, and more frequently (every 3 to 4 d) during July and August when we suspected spawning would occur.

Average gamete volume per polyp for each branch was determined by counting and measuring the diameters of all eggs (or spermaries) in 10 polyps using a binocular dissecting microscope fitted with an eyepiece micrometer. Polyps were chosen randomly from a segment of the branch between 2 and
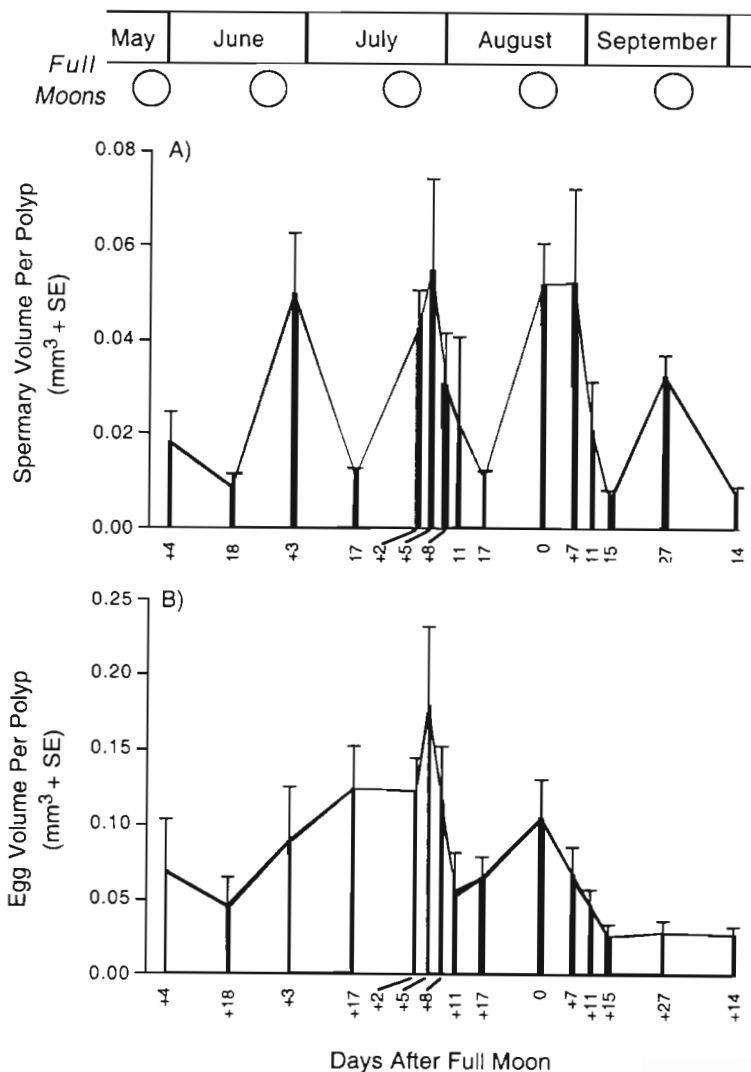

Fig. 1. *Plexaura flexuosa*. Average gamete volume (mm³) per polyp (+SE) over 5 lunar cycles of the 1994 reproductive season for (A) 6 male and (B) 6 female colonies. Samples were taken on all dates labeled. Full moons were May 25, June 23, July 22, August 21, and September 19

3 cm from the branch tip. Gamete diameters were converted to volumes (assuming gametes were spherical), summed within each polyp, then averaged over the 10 polyps in each sample. Eggs were pink and up to ~750 μm in diameter; spermaries were gray to beige, and up to ~450 μm in diameter. Female polyps seldom contained more than 4 large (≥400 μm) eggs, while male polyps contained as many as 22 spermaries.

Variability in egg production. Egg production by a polyp may vary depending on the polyp's location within a colony or on the size of the colony itself. To examine within-colony variability, average egg volume per polyp was determined for branches at different distances from the branch tips. Branches were classified according to branch order (sensu Brazeau & Lasker 1988), and 10 polyps were dissected from the central 1 cm portion of 1° source, 1° tributary, 2° and 3° branches, and from pieces of the colony base. One branch of each type was sampled from each of 8 female colonies (50 to 81 cm tall). Samples were collected 1 to 2 d after the July 1994 full moon (~4 to 5 d before spawning). Egg volume data were heteroscedastic and could not be transformed to normality; therefore differences among branch orders were tested using Friedman's 2-way (colony × branch order) ANOVA by ranks.

To examine variability in egg production per polyp among colonies of different sizes, one 1° branch was taken from each of 24 female colonies ranging from 33 to 107 cm in height. Samples were collected 4 to 5 d before the July 1994 full moon (~10 to 11 d before spawning). Egg volume per polyp for each branch was determined by counting and measuring all eggs in 10 polyps, converting egg diameters to volumes, summing the egg volumes within each polyp, then averaging the total volume across the 10 polyps. Polyps were chosen randomly from a segment of the branch between 2 and 3 cm from the branch tip. Regression analysis was used to test the relationship between egg volume per polyp and colony height.

Release of eggs. The total number of eggs released during a spawning event was calculated for 24 female colonies using counts of mature eggs per polyp, estimates of the percent of mature eggs released per spawning event, and estimates of the number of polyps per colony of a given size, as described below.

Size and number of mature eggs per polyp: To determine the size of mature eggs (i.e., those that could be spawned), 1 clump of primary and secondary branches was collected from each of 2 female colonies and kept in separate running-seawater aquaria during the August 1995 spawning. Over 200 eggs spawned from these branches on August 19 and 20 were collected, preserved in 5% formalin, and their diameters measured.

The average number of mature eggs per polyp was determined for primary branches from 24 female colonies ranging from 33 to 107 cm tall (see 'Variability in egg production' above). Because these samples were collected ~10 to 11 d before spawning, eggs had not yet reached their maximum size. To correct for this, a comparison was made of egg sizes from branches of 6 colonies collected ~10 and ~1 d before spawning (10 polyps per colony per sampling event).

Eggs released during spawning: The percent of mature eggs released during a spawning event was estimated by comparing the average number of mature eggs per polyp in branches that were collected from 6 female colonies before and after spawning events in both July and August 1994 (1 branch per colony per sampling event; 10 polyps per branch). Samples for 'before spawning' were collected 0 to 5 d after the full moon. Samples for 'after spawning' were collected 15 to 17 d after the full moon.

Polyps per colony: Polyp densities on branches of 8 female colonies (50 to 81 cm tall) were determined from counts of the number of polyps within measured areas of 5 branch orders (1° source, 1° tributary, 2° and 3° branches, and a piece from the colony base). For 1°, 2°, and 3° branches, the measured areas were approximately 1 cm long and located at the center of each branch; branch diameter at the ends of the 1 cm section was measured and surface area computed using the average diameter (range for all branches was 0.99 to 2.26 cm²). Polyp density within an area of approximately 1×2 cm (range 1.64 to 3.33 cm²) was measured at the base of the colony. Polyp densities were compared using a 2-way ANOVA without replication.

In order to estimate the number of polyps in an entire colony, the polyp density measures were multiplied by the total surface area of branches of each order. Total surface areas for the different branch orders were estimated for 10 colonies (33 to 107 cm in height) from Tiantupo Reef (Tiantupo-1 in Robertson 1987). All branches on each colony were counted and categorized by branch order. Length (to nearest mm using a flexible clear ruler) and diameter (to nearest 0.1 mm using calipers) were measured on ten 1°, 2°, and 3° branches and on all higher order branches. Surface area (SA, cm²) of each branch was calculated (πdh). Average SA and polyp density for each branch order were used to calculate whole colony polyp number.

For purposes of prediction, a regression was fitted between number of polyps and colony volume (i.e., the volume of a box fitted around the colony calculated from colony maximum height, width, and depth measured to nearest cm) for these 10 colonies. Because this relationship was highly significant, the resulting regression equation was used to estimate the number of polyps on another group of 24 female colonies using
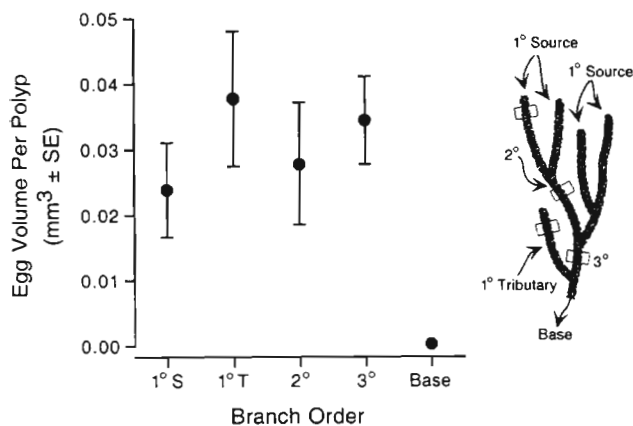
Fig. 2. *Plexaura flexuosa*. Average egg volume (mm³) per polyp (±SE) across 5 branch orders in 8 colonies (10 polyps per branch order per colony). S: source, T: tributary
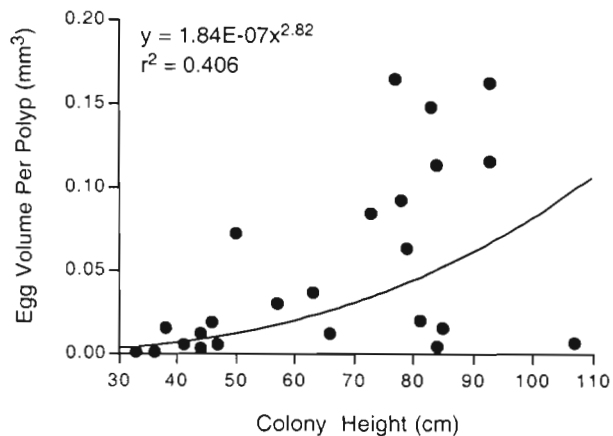

Fig. 3. *Plexaura flexuosa*. Average egg volume (mm³) per polyp as a function of colony height in 24 colonies (10 polyps per colony)

measurements of their volume (i.e., height × width × depth). The number of eggs released during spawning by each of the 24 colonies was estimated by multiplying (1) the number of polyps in the colony by (2) the number of mature eggs produced per polyp by (3) the percentage of mature eggs in a polyp released during a spawning event.

Growth rates. Growth rates were determined for 29 colonies on 3 patch reefs (Tiantupo-1, Porvenir-17, and Aguadargana-1 in Robertson 1987). Our measure of growth was the change in length of primary branches. On each colony, a section of 11 to 21 primary branches was identified and sketched to allow relocation. The length of each primary branch was measured (±1 mm) in 1995 and again in 1996 (297 to 355 d). Because the branches measured on each colony were adjacent to one another, their growth rates may not have been independent. Therefore, we used averages for each colony in our statistical analyses.

RESULTS

Reproductive cycle

Plexaura flexuosa spawning events during the summer of 1994 can be identified by precipitous drops in gamete volume per polyp that occurred after the full moons (Fig 1). Evidence of spawning was particularly striking among male colonies (Fig. 1A). All 6 male colonies spawned after the June 23, July 22, August 21, and September 17, 1994, full moons. Four of the 6 males also may have spawned after the May 25 full moon. Fine-scale sampling after the July 22 and August 21 full moons indicated that spawning started 6 or 7 d after the full moon and ended 11 to 15 d after the full moon.

Changes in the average number of mature eggs (≥500 µm; see below) per polyp over time showed that 5 of the 6 females spawned heavily during only 1 or 2 lunar cycles (after the July and/or August full moons; results not shown), in contrast to the male colonies, each of which spawned 4 or 5 times over the 5 lunar cycles.

Our sampling scheme was based on our familiarity with the spawning of other plexaurids, and it is possible that *Plexaura flexuosa* spawned outside of our summer sampling period. However, the shape of the egg volume per polyp curve (Fig. 1B), with its peak in July, indicates that there is seasonality to *P. flexuosa* spawning, and that if spawning occurs outside this time period, it is likely to be light. Furthermore, average egg volumes of samples taken on February 2, 1995 (4 d before the full moon), were similar to those of postspawning samples from October 3, 1994, again suggesting that spawning did not occur outside the summer months.

Variability in egg production per polyp

There was no significant difference in average egg volume per polyp among 1°, 2°, and 3° branches (Fig. 2; Friedman's X^2 = 4.95; p = 0.176). There was a virtual absence of gametes in polyps from the bases of colonies, however, which resulted in a significant difference when these samples were included in the analysis (Fig. 2; Friedman's X^2 = 19.3; p = 0.0007).

Colony height had a significant effect on egg volume per polyp (Fig. 3; r^2 = 0.406; $F_{1, 22}$ = 15.1; p = 0.0008). Although every polyp examined except 1 contained at least 1 egg, there were differences in the percentage of polyps bringing eggs to maturity. Of the 120 polyps examined
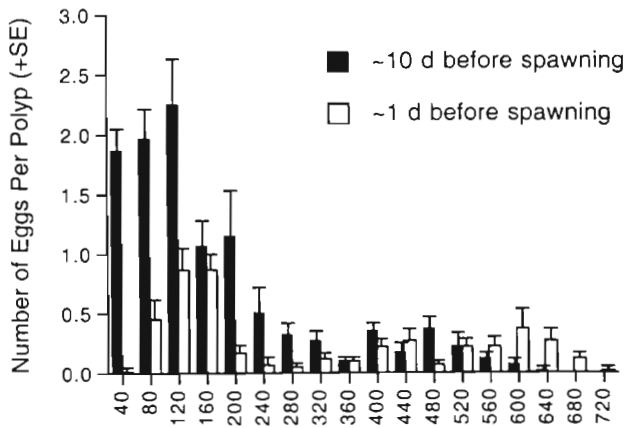
Fig. 4. *Plexaura flexuosa.* Comparison of egg size class distributions in 6 colonies ~10 and ~1 d before spawning (10 polyps per colony per sampling date)

from the 12 small colonies (<70 cm), only 13% contained large (≥400 μm) eggs, with an average of 1.3 large eggs per polyp among these polyps. Of the 120 polyps from the 12 large colonies (>70 cm), 55% contained at least 1 large egg, with an average of 1.9 polyp^{-1}.

Release of eggs

Size and number of mature eggs per polyp

Spawned eggs ranged in size from 533 to 667 μm in diameter, with an average of 597 ± 27 μm (±SD). A comparison of egg sizes from ~10 and ~1 d before spawning in 6 female colonies showed that the number of eggs ≥400 μm on the earlier date roughly corresponded to the number of eggs ≥500 μm on the later date (Fig. 4). Therefore, for samples collected ~10 d before spawning, we counted all eggs ≥400 μm as 'mature eggs' that could be released that month. The number of mature eggs per polyp in samples from 24 colonies collected ~10 d before spawning ranged from 0 to 2.2, and increased with increasing colony size (Fig. 5A).

Eggs released during spawning

Branches collected prior to spawning contained an average of 1.09 ± 0.73 mature eggs per polyp (±SD; range among branches 0.1 to 2.6; data not shown). Branches collected after spawning had an average of 0.17 ± 0.24 mature eggs per polyp (±SD; range 0.0 to 0.8; data not shown). This observation indicates that 84% of the mature eggs present in pre-spawning samples were released.
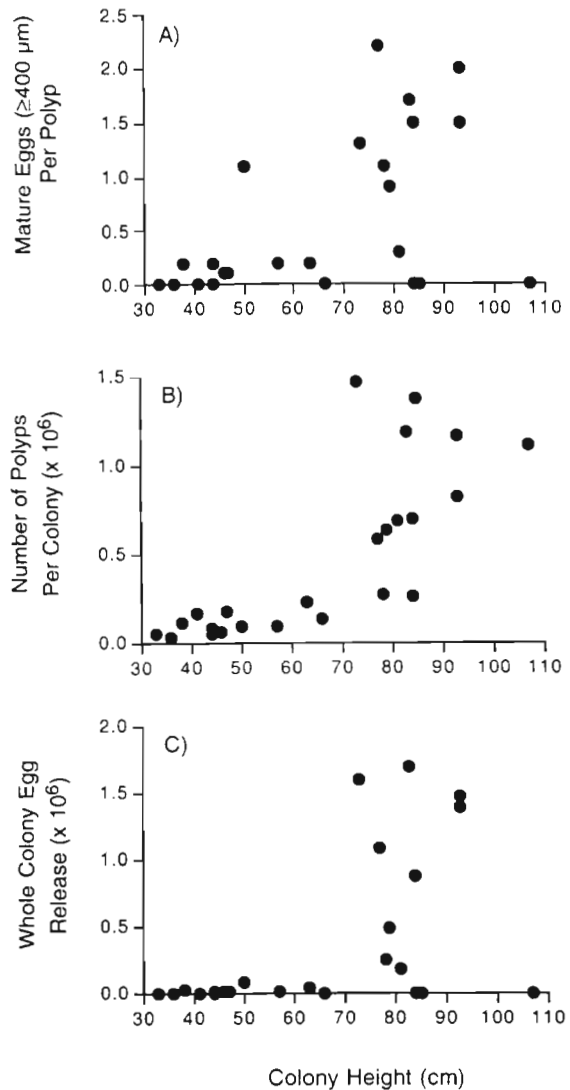
Fig. 5. *Plexaura flexuosa.* (A) Per polyp fecundity, (B) whole colony polyp count, and (C) whole colony egg release by colony height for 24 colonies

Polyps per colony

Total branch counts (all branch orders) of 10 colonies ranged from 117 branches for a 37 cm tall colony to 3861 branches for a 107 cm tall colony (Table 1). Total surface area ranged from 0.104 to 6.73 m^2 (Table 1). Primary, 2°, and 3° branches together accounted for an average of 92% of total colony surface area (range 87 to 97%; Table 1).

Polyp density did not differ across branch orders (ANOVA without replication, $F_{4, 28} = 2.36$, p = 0.078) and averaged 50 ± 8 polyps cm^{-2} (±SD). Using this density, the total number of polyps per colony ranged from 5.18 × 10^4 (37 cm tall colony) to 3.36 × 10^6 (107 cm tall colony; Table 1). Colony volume (colony height × width ×

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Table 1 Surface area and polyp number estimates for 10 *Plexaura flexuosa* colonies. Volume given as colony width × depth × height. Total number of polyps calculated using 50 polyps cm⁻² (see text). Total number and % of total surface area given for each branch order

Col-ony	Height (cm)	Volume (m³)	Total branch length (cm)	Surface area (m²)	Total no. of polyps	No. of branches (% of total surface area) for each branch order						
						1°	2°	3°	4°	5°	6°	7°
1	33	0.0203	861	0.114	56800	103 (52)	33 (27)	9 (18)	3 (3)	0	0	0
2	37	0.0178	638	0.104	51800	78 (45)	29 (35)	8 (12)	2 (7)	0	0	0
3	42	0.0194	782	0.129	64300	95 (51)	36 (27)	9 (15)	3 (7)	0	0	0
4	42	0.0464	1040	0.167	83500	171 (42)	58 (32)	15 (12)	6 (10)	2 (3)	0	0
5	52	0.0598	1940	0.307	154000	173 (65)	48 (18)	14 (10)	5 (6)	1 (2)	0	0
6	66	0.247	6830	1.06	528000	760 (52)	225 (31)	65 (9)	21 (4)	7 (3)	3 (1)	1 (0.03)
7	70	0.549	6010	1.13	566000	506 (61)	132 (23)	37 (8)	11 (4)	4 (2)	1 (1)	0
8	85	0.495	7110	1.28	642000	540 (61)	153 (27)	44 (6)	14 (4)	5 (2)	2 (1)	0
9	96	0.288	3890	0.755	377000	444 (51)	134 (16)	39 (20)	9 (4)	4 (4)	2 (4)	0
10	107	2.25	36200	6.73	3360000	2681 (65)	834 (18)	245 (10)	78 (4)	15 (1)	6 (1)	2 (1)

depth) was a good predictor of total number of polyps ($r^2 = 0.988$; $F_{1,8} = 685$; $p = 0.0001$), yielding the equation:

Polyp number = 1.46×10^6 colony volume (m³) + 3960

$$(1)$$

Whole colony egg release

Colony volume, and therefore polyp count (estimated using Eq. 1), rose dramatically after a colony reached ~70 cm in height (Fig. 5B) The average number of polyps in colonies less than 70 cm tall was 104 000 ± 58 900 (mean ± SD); the average number of polyps in colonies greater than 70 cm was 852 000 ± 403 000 (mean ± SD) — over an 8-fold increase. Similarly, the number of mature eggs per polyp (Fig. 5A) increased in colonies greater than 70 cm, with colonies less than 70 cm averaging 0.18 ± 0.30 mature eggs per polyp (mean ± SD), and colonies greater than 70 cm

averaging 1.0 ± 2.2 (mean ± SD) — a 6-fold difference. Consequently, whole colony egg release (number of polyps multiplied by number of mature eggs per polyp) increased dramatically after colony height reached 70 cm, and ranged from 0 to 1.69×10^6 eggs per colony per spawning event (Fig. 5C).

Growth rates

Average branch growth rates varied tremendously among colonies, ranging from –13.3 to +37.3 mm yr⁻¹ (Fig. 6). Negative growth rates reflect loss of tissue, most likely due to predation by the gastropods *Cyphoma* spp. and the polychaete *Hermodice carunculata*. (*Plexaura flexuosa* is not known to fragment like its congener *P. kuna* [pers. obs.].) There was no relationship between colony size and branch growth rate (Tiantupo: $r^2 = 0.198$, $F = 1.97$, $p = 0.20$; Porvenir-17: $r^2 = 0.007$, $F = 0.056$, $p = 0.82$; Aguadargana: $r^2 = 0.028$, $F = 0.204$, $p = 0.67$). There also was no difference in branch growth rate among the 3 reefs ($F_{2,26} = 0.506$; $p = 0.61$). Branch growth rate across all colonies was 7.7 ± 3.4 mm yr⁻¹ (average ± SE).

As in other gorgonians (Coma 1994), most growth in *Plexaura flexuosa* probably occurs in 1° branches. Because there appears to be no difference in 1° branch growth rate across colony size for *P. flexuosa*, the number of 1° branches divided by total linear length of a colony represents its relative growth rate. Plotting this ratio against colony height for the 10 colonies in Table 1 shows that there are significantly fewer growing tips per linear cm of colony tissue as colony height increases (Fig. 7; $r = -0.636$, $p = 0.049$). Assuming that there are no systematic differences in 1° branch
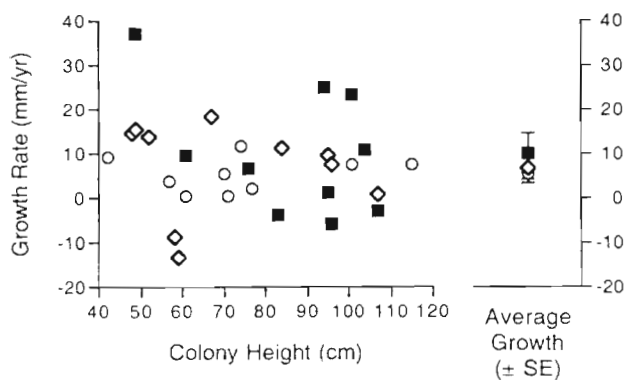
Fig. 6. *Plexaura flexuosa*. Average branch growth rate (mm yr⁻¹) by colony height for 29 colonies on 3 reefs and average growth rate per reef (±SE)

growth rates throughout a colony (but see Kim 1996), relative growth decreases as colonies get larger.

DISCUSSION

Colony size and consequences for populations

Large *Plexaura flexuosa* colonies (>70 cm in height) produced on average 6 times more mature eggs per polyp than smaller colonies (Fig. 5A), and they had on average 8 times more polyps than smaller colonies (Fig. 5B). These differences in colony size and egg production per polyp resulted in a dramatic increase in whole colony egg release for colonies over 70 cm tall (Fig. 5C). Among colonies with mature eggs, those that were 33 to 66 cm tall released 10^3 to 10^4 eggs per colony per spawning event, while those that were 73 to 107 cm tall released 10^5 to 10^6 eggs per colony per spawning event. Of the estimated 9.2×10^6 eggs released by these 24 females during 1 spawning event, 9.0×10^6 came from the 12 colonies over 70 cm tall. In other words, 98% of the eggs were produced by only half of the colonies.

On 3 other reefs in the San Blas region, female colonies taller than 70 cm comprised 23, 38, and 49% of the female populations (Beiring 1997). Using average colony egg production values from the 24 colonies discussed above (15500 eggs for colonies <70 cm and 749000 eggs for larger colonies), large colonies produce 93 to 98% of the eggs released on these 3 reefs. Therefore, the vast majority of eggs from these reefs are produced by a relatively small subset of the population.

In the 2 other studies where whole population egg production has been estimated, similar results have been reported. Coma et al. (1995) found that colonies of the Mediterranean gorgonian *Paramuricea clavata* taller than 40 cm comprised only 3% of the population yet contributed approximately 40% of the female gametes and 33% of the male gametes. For the scleractinian *Goniastrea aspera*, Babcock (1984) reported that colonies greater than 6 cm in mean radius comprised less than 22% of the population but contributed approximately 80% of total annual egg production. Although they did not measure egg production, Potts et al. (1985) found similar results for living surface area; of 65 colonies of 7 *Porites* species measured, 50% of the living surface area came from only 6 colonies.

These results indicate that population size alone, without reference to colony size structure, may be a poor predictor of population egg production and reproductive success. The huge variance in egg production among coral colonies leads to a much lower effective population size than predicted by a simple census of colonies (Hughes et al. 1992).
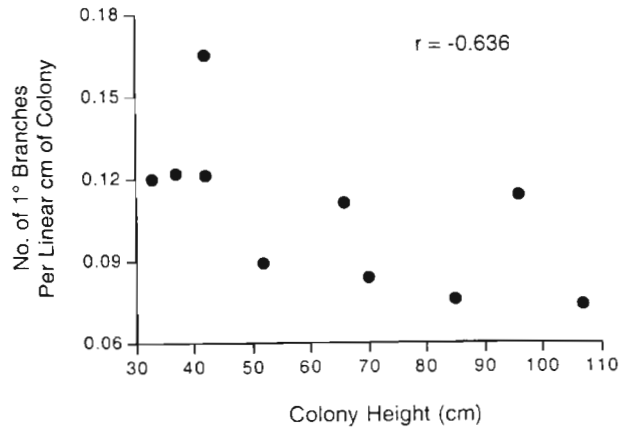
Fig. 7. *Plexaura flexuosa*. Relationship between colony height and the number of 1° branches per linear cm of colony for 10 colonies

Reproduction, growth, and colony size

Reproduction and growth are commonly represented as processes competing for limited resources (e.g., Jackson & Hughes 1985). The relationship is considerably more complex among clonal animals, where clonal growth can enhance reproduction by generating additional reproductive modules.

Delay in reproduction until a minimum colony size is reached is a trait common to many colonial invertebrates (e.g., Harvell & Grosberg 1988, Brazeau & Lasker 1989, 1990, Keough 1989, Babcock 1991, Soong & Lang 1992, Van Veghel & Kahmann 1994, Coma et al. 1995, Fan & Dai 1995, Hall & Hughes 1996; see also review by Harrison & Wallace 1990). Most *Plexaura flexuosa* colonies become reproductive between 20 and 30 cm in height (Beiring 1997). Once reproduction began, reproductive output of individual *P. flexuosa* polyps increased with increasing colony size (Figs. 3 & 5A). Similar findings have also been reported among hard corals (Rinkevich & Loya 1979, Kojis & Quinn 1981, 1985, Babcock 1984, 1991, Van Veghel & Kahmann 1994, Hall & Hughes 1996) and other soft corals (Brazeau & Lasker 1990, Coma et al. 1995).

The relationship between reproductive output and growth rate is ambiguous. Absolute linear growth rates (i.e., branch extension rates) did not change with colony size (Fig. 6), similar to many other anthozoans (e.g., Kinzie & Sarmiento 1986, Hughes & Connell 1987, Babcock 1991, Yoshioka & Yoshioka 1991, Coma 1994, Goh & Chou 1995, but see Chornesky & Peters 1987). However, there were fewer growing tips, and presumably less annual extension, per linear cm of colony with increasing colony height (Fig. 7), and therefore, on a relative or per polyp basis, less energy is invested in growth as a colony gets bigger (Connell

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