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Reproductive Integration in Reef Corals

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Abstract. The extent of colonial integration in structurally simple animals like scleractinian corals is poorly understood. We have used sexual reproductive characters (location of fertile polyps and colony size at maturation) to assess colony-level individuality, *i.e.*, the development, in coral colonies, of characters above the polyp level. Ten morphologically-diverse species of reef corals were used: *Acropora cervicornis, A. palmata, Diploria clivosa, D. strigosa, Favia fragum, Montastrea cavernosa, Porites astreoides, P. furcata, Siderastrea radians,* and *S. siderea.*

In no species were equally fertile polyps homogeneously distributed throughout a colony. Most inhomogeneities of fertile polyps could be attributed to intra-colony position or ontogenetic effects. The results of simple manipulations simulating natural wounds in three massive species strengthen the evidence that the position of polyps within a colony determines fertility.

Small colonies are not reproductive. Puberty size (colony size at maturation) could be explained by the infertility pattern along the colony margin, which does not require colony-level integration. Shape-related growth constraints could also produce the puberty size patterns found in massive corals. Infertility in the short radial polyps of *A. palmata* and in the axial polyps of *A. cervicornis* provided the only clear evidence of reproductive integration in this study: both are related to a morphological characteristic (polyp dimorphism) commonly associated with integration in colonial invertebrates.

Introduction

Colonial organisms are composed of iterated units that usually originate from a single zygote. The degree of integration of colonial animals has long been the focus of scientific interest (Beklemishev, 1969; Hubbard, 1973; Sandberg, 1973; Rosen, 1979; Ryland, 1979; Shelton, 1979; Chapman, 1981; Mackie, 1986; Harvell, 1991). The objective of this study is to understand the extent to which the modules (*e.g.*, zooids, polyps, *sensu* Chapman, 1981) of a colony are interdependent and act as one unit; *i.e.*, how much individuality a colony has attained. Increasing individuality at the colony or genet level sets a higher stage at which selection could operate directly (Schopf, 1973; Buss, 1987).

Colonies of hydrozoans, bryozoans, and some other marine invertebrates are polymorphic, with two or more kinds of modules, each of which is capable of some vital functions (Hyman, 1940). A certain degree of integration is necessary in polymorphic colonies since differentiated modules cannot exist on their own. Indeed, an evolutionary tendency towards higher integration exists in colonial organization, at least in some lineages (Beklemishev, 1969; Boardman and Cheetham, 1973; Coates and Oliver, 1973; Coates and Jackson, 1985).

When modules are isomorphic and presumably have the same ability to perform all necessary living functions (Hyman, 1940), the level of individuality achieved by a colony is less obvious. For example, most colonial species of the highly successful scleractinian reef corals are composed of morphologically similar polyps. Differentiation of polyps does occur in some species (Veron, 1981; Foster, 1985), such as acroporids, which show a considerable degree of morphological variation between the axial polyps at their branch tips and the radial polyps that develop on their walls (Veron and Wallace, 1984).

Morphologically identical polyps that are produced by extratentacular budding in some colonies have been termed individuals (Duerden, 1902; Wells, 1973). Most colonial corals are classified as aggregates of independent polyps, since polypal (or rather its skeletal counterpart, the corallite) attributes constitute most of the taxonomic

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characters of scleractinian species (Vaughan and Wells, 1943; Wells, 1956). This line of thinking—*i.e.,* that coral colonies are merely aggregates of polyps—would appear to be justified by the plasticity of gross colony shape (Barnes, 1973; Foster, 1979; Veron and Pichon, 1982) and the indeterminate growth (Sebens, 1987) of most reef coral colonies.

However, a certain degree of functional integration may occur even within the structurally simple reef corals. For example, polyp retraction is coordinated within colonies of some species (Shelton, 1982); soluble organic compounds and Ca^{++} are translocated among polyps (Pearse and Muscatine, 1971; Taylor, 1977), and skeletal regeneration tends to restore symmetry of colony shape (Stephenson and Stephenson, 1933; Connell, 1973; Loya, 1976). One might conclude that colonies act as individuals. Moreover, ecologists tend to treat whole colonies as individuals (Connell, 1973; Hughes, 1984; Chornesky, 1989).

The above contrasting views about whether a coral colony is an aggregation of polyps or an integrated unit have yet to be reconciled. In comparing species, inferences of integration have been based on morphological characters, because function and structure are often correlated. In reef corals, branching colony shapes, dimorphic polyps, intratentacular budding (especially when it is incomplete, as in the meandroid condition), common (cerioid) walls, perforations in walls, and a well-developed coenosarc (soft tissues not belonging to individual polyps) are all thought to provide evidence of integration (Table I). Few data are available to test these assumptions. However, Hubbard (1973) found sediment-shedding ability, an expression of behavioral integration, to be greater in meandroid corals than in other corals which are considered less integrated morphologically.

In this study sexual reproductive characters were used to assess the nature of coloniality in reef corals. From an evolutionary point of view, the integration of sexual reproductive (hereafter called reproductive) activities within a coral colony should present no conflict among polyps, since all the constituent polyps are presumably of the same genotype [but see Buss (1982) for a discussion of the likely effects of somatic mutations]. Reproduction has been studied for many years in scleractinian corals (Duerden, 1902; Vaughan, 1909), but most research has concentrated on population level characteristics, *e.g.,* sexuality, reproductive mode, and spawning time (see reviews by Fadlallah, 1983; Harrison and Wallace, 1990; Richmond and Hunter, 1990). In some species, fertile polyps are distributed unevenly within the colony (Harrigan, 1972; Wallace, 1985; Kojis, 1986; Chornesky and Peters, 1987). Moreover, colony size, rather than age, is the primary factor determining reproductive status in two species (Kojis and Quinn, 1985; Szmant-Froelich, 1985). These two phenomena (fertile polyp location and fertile colony size) might be used as evidence for reproductive integration since, in each case, a reproductive character appears to be expressed beyond the level of single polyps.

In each of the ten morphologically diverse species of reef corals studied, we found uneven distribution of fertile polyps in the colony, and colony size-related maturation. Nonetheless, we argue that, except for the dimorphic polyps of *Acropora,* each of these patterns could have a simpler explanation. Indeed, at present there is little unamunambiguous evidence for reproductive integration in the isomorphic genera of reef corals.

Materials and Methods

Within colony infertility—observations

Ten species of shallow water corals (Table I) were monitored for reproductive activities along the Caribbean coast

Table I

Characteristics postulated to reflect potentially higher levels of morphological integration

Species	Branching	Dimorphic	Extratentacular budding	Meandroid	Common wall	Perforate walls	Coenosarc
Acropora cervicornis (Lamarck)	Y	Y	Y	N	N	Y	Y
Acropora palmata (Lamarck)	Y	Y	Y	N	N	Y	Y
Porites furcata Lamarck	Y	N	Y	N	Y	Y	N
Porites astreoides Lamarck	N	N	Y	N	Y	Y	N
Diploria clivosa (Ellis and Solander)	N	N	N	Y	Y	N	N
Diploria strigosa (Dana)	N	N	N	Y	Y	N	N
Siderastrea radians (Pallas)	N	N	Y	N	Y	N	N
Siderastrea siderea (Ellis and Solander)	N	N	Y	N	Y	N	N
Montastrea cavernosa (Linnaeus)	N	N	Y	N	N	N	N
Favia fragum (Esper)	N	N	N	N	N	N	N

"Y" implies higher integration than "N" (Wells, 1973; Jackson, 1979; Oliver and Coates, 1987). Species are ranked according to the number of "Y"s.

of Panama between July, 1987, and August, 1988. During their respective reproductive seasons, whole colonies (in the case of species of small size), or samples from various parts of large colonies were collected at random, preserved, and decalcified by means of standard techniques (Soong, 1991).

Except for *Favia fragum,* fecundity was estimated after dissection by directly counting eggs, or measuring the size of gonads with a dissecting microscope or, for species with small gonads, by histological preparations. In *F. fragum,* planulae are easier to observe than eggs, so the number of planulae per polyp were counted under the dissecting microscope as an estimate of brood size or fecundity. For all species, the identity of ovaries, spermaries, and planulae (if present) were confirmed by histology (Soong, 1991).

Owing to numerous instances of partial colony mortality, edge zones in *Siderastrea siderea* can occur virtually everywhere over the surface. Therefore, data for this species were collected separately for colony margins on both vertical and horizontal surfaces. Variations in tissue thickness within colonies were noticed in five species; those in *Siderastrea* spp. and *Porites furcata* were measured under a dissecting microscope.

Within colony infertility—manipulations

A series of field experiments was initiated to determine the possible causes of the infertile colony margins found in three species of massive corals. The scheme basic to all the manipulations was to create artificial margins across the centers of healthy, undamaged colonies (*Siderastrea siderea*—20–70 cm in diameter; *Porites astreoides*—15–25 cm; and *S. radians*—3.5–8 cm). A cut about 1 cm deep and 2 mm wide was made across the entire mid-region of each colony with a hacksaw, effectively severing all soft tissue connections between the two sides of the cut. In one group consisting of 10 specimens per species, ("tissue cut"), the two halves remained connected by dead skeletal material. In a second group of 10 colonies ("cut and fill"), underwater epoxy (Birkeland, 1976) was used to fill and cover the open wounds and to fill the gaps created by sawing. A third group of 10 colonies ("total cut;" 20 colonies were used in *S. radians*) were separated into halves when the skeletal connection was completely severed. After manipulation, all colonies remained larger than the estimated puberty size (see below) for the species. This experiment was initiated in February–March 1988, before the start of gametogenesis in *S. siderea.* The other two species reproduce year round in Panama (Soong, 1991). Patterns of fertile polyp distribution were determined by dissection or histology four to five months later, at the end of July, and were compared with undisturbed colonies collected in the same habitat. The reverse experiment—tying two marginal pieces together to create an artificial "central condition"—was not employed, because preliminary trials showed that the trimming necessary to fit the pieces together removed the original marginal polyps.

Relationship between colony size and maturation

When a species was in reproductive condition (Soong, 1991), one sample of tissue (about 5 × 5 cm) was collected from the center of healthy-looking colonies of various known sizes. All specimens were examined after fixation, decalcification, and dissection. In species with small, inconspicuous gonads (*P. furcata, P. astreoides* and *Diploria clivosa*), histological slides were prepared from each specimen; in the remainder, histological confirmation of reproductive condition was limited to some randomly chosen specimens. For brooding species, reproductive data were collected during various months throughout the year. Fertility in the broadcasting species was assessed within one to two months of their annual spawning periods. Each sample was rated qualitatively as either infertile (no gonads), or fertile (gonads or planulae present in the sample). If colony size data were available, samples collected for study of colony infertility were also used to assess maturation.

Colonies of each species were ranked, from smallest to largest, and the size at which most colonies become mature was then assessed. Colony size was calculated as the surface area: the product of the maximal length and width of the living tissue (both dimensions measured in the field). In *A. palmata,* colony size was estimated by summation of the surface area of all the branches and the base. In the ramose *Acropora cervicornis* and *P. furcata,* the lengths of the living branches were taken as a measure of size. Puberty size was defined operationally as equal to the surface area or live-branch length of the smallest colony (or branch) in the first group of 20 consecutively ranked colonies (or branches) of which 90% or more were fertile.

Sample sizes in these studies ranged from 41 in *D. strigosa* (relatively rare) to 501 in *S. radians.*

Results

Within colony infertility—observations

Marginal areas. In no species were equally fertile polyps homogeneously distributed, and infertile polyps were generally associated with colony margins (summary in Table II). *Favia fragum* was the only massive species studied in which marginal polyps were fertile. These marginal polyps also carried planulae (average 73% of marginal polyps, n = 77 colonies, each colony large enough to have five central polyps), although their mean brood size was significantly lower than that of the central polyps (Wilcoxon's signed-ranks test, $T_s = 55$, $P < 0.01$, n = 77

Table II

Location of infertile polyps in fecund colonies of ten species of reef corals

Species	Colony shape	Location of infertile polyps	No. of colonies
Favia fragum	Massive	none, but 27% of marginal polyps lack planulae (*vs.* 7% of central polyps lacking planulae)	77
Siderastrea radians	Massive	0 to 0.25–0.5 cm from margin (one to two rows of polyps)	65
Porites astreoides	Massive	0 to 0.5–1.5 cm from margin (three to 10 rows of polyps)	10
Montastrea cavernosa	Massive	0 to 0.5–1 cm from margin (one row of polyps)	16
Siderastrea siderea	Massive	0 to 0.7–2 cm from margin on horizontal surface (at least two rows of polyps); 0 to 1–4 cm from margin on vertical surface (more than three rows of polyps)	17
Diploria strigosa	Massive	0 to 1–3.5 cm from margin (meandroid and lacks distinct polyps)	12
Diploria clivosa	Encrusting	0 to 1–4 cm from margin (meandroid and lacks distinct polyps)	9
Acropora cervicornis	Branching	0 to 2–6 cm from tip, 0 to 1–4.5 cm from base; and any shaded areas along branches	26; 11
Acropora palmata	Branching	0 to 3–10 cm from tip at spawning; 0 to 2–3.5 cm from basal margin at spawning, shorter infertile zone earlier in the year	23; 8
Porites furcata	Branching	0 to 0.5 cm from tip, 0 to 1–3 cm from base (>50% of whole branch length)	178

colonies, Fig. 1). Regardless of how fertility was measured, all other massive corals had an infertile marginal area equivalent to the width of at least one polyp (Table II), as exemplified in *S. radians* (Fig. 2).

In *Siderastrea radians,* the frequency of fertile polyps showed no significant correlation with colony size, either in the marginal row (Spearman's r = 0.08, $P > 0.05$, n = 20), or in the penultimate row (Spearman's r = 0.40, $P > 0.05$, n = 20) of polyps. The infertile area of large colonies of *S. siderea* was significantly wider on vertical surfaces than on the corresponding horizontal surfaces of the same specimens (Sign test, n = 13, t = 0, $P < 0.01$). The width of these infertile areas, however, showed no significant correlation with colony size (vertical margin, Spearman's r = −0.15, $P > 0.05$, n = 21 colonies; horizontal margin, Spearman's r = −0.15, $P > 0.05$, n = 18 colonies). A gradient of increased fecundity was observed in the first few centimeters of the fertile region for horizontal surfaces (Fig. 3).

In branching species, the distribution of fertile polyps was clearly related to the growth axis of the branches. For example, in *Porites furcata,* fertile polyps were concentrated in the distal half of the branches, but their abundance decreased again near the growing tip (Fig. 4). Usually the basal margin of the branches was lighter in color,

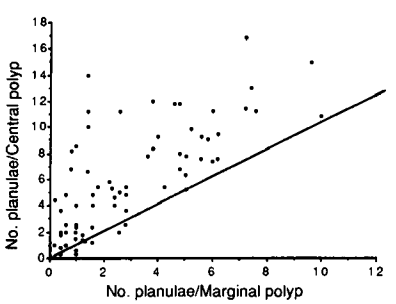

Figure 1. Brood sizes of central *versus* marginal polyps in *Favia fragum.* Mean number of planulae per polyp based on five marginal polyps per colony and (depending upon colony size) up to five central polyps per colony; each point represents one colony. The diagonal line indicates equal brood size in marginal and central polyps.

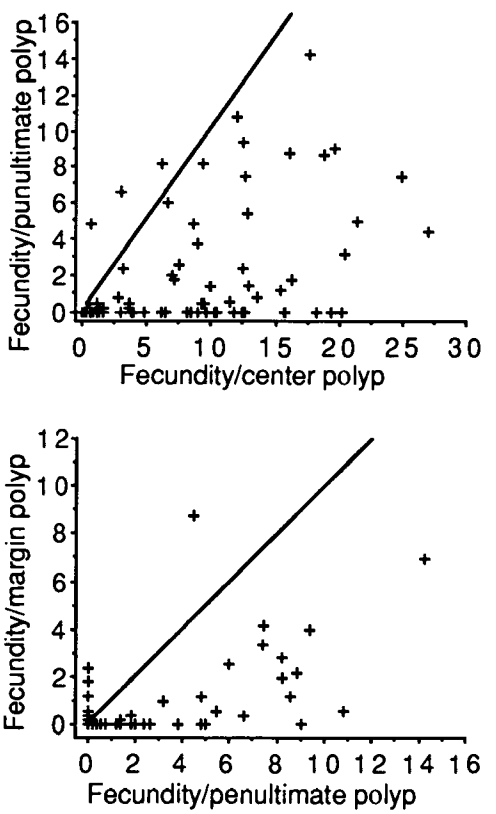

Figure 2. Fecundity of polyps within colonies of *Siderastrea radians.* Fecundity: mean number of eggs per polyp, based on five polyps per location in each colony. Penultimate polyp: row of polyps immediately adjacent to margin polyps. Difference significant among the three groups (Friedman test, T = 102.8, $P < 0.01$; pair-wise tests between any two groups also significant using Wilcoxon's signed-ranks test).

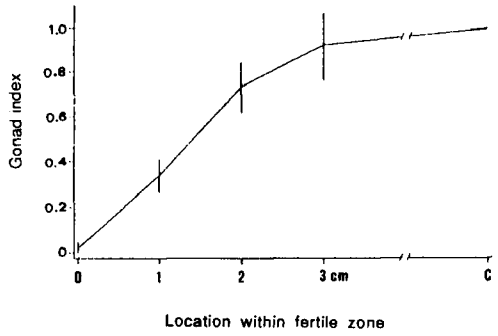

Figure 3. Fecundity gradient on horizontal surface of *Siderastrea siderea.* Gonad index: mean gonad length × frequency of gonads (ovaries or spermaries), based on two randomly chosen mesenteries per polyp in each of ten randomly chosen polyps) at any given location relative to that in the center of the horizontal surface of the colony. Vertical bars represent the standard errors of the mean. 0: beginning of fertile zone, C: center of the horizontal surface. n = 8 male and 8 female colonies.

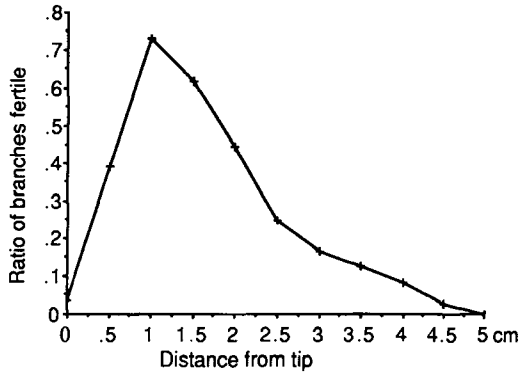

Figure 4. Probability of gonad occurrence along the branches of fertile, female *Porites furcata.* At any position (at one cm intervals) along the branch, probability of gonad occurrence, *i.e.,* number of female branches having ovaries at that position relative to the total number of fertile, female branches checked; n = 178 branches.

presumably due to fewer endosymbiotic zooxanthellae. Soft tissue thickness also tapered toward the base, and the internal mesenterial filaments were degenerate.

In *Acropora cervicornis,* the large axial polyps and the basal tissues (1–4.5 cm from the base) of the branches were infertile, whereas gonads located within 2 to 6 cm of the branch tips always had smaller eggs than those in the mid-region of the branches (n = 21 branches).

In *A. palmata,* the pattern apparently changed with the annual reproductive cycle. When oogenesis was first noticed in February, small eggs were found in the whole colony. No gonads were present in the polyps that we presumed to have been produced after the onset of oogenesis. Infertile areas were observed in the encrusting bases (n = 5 colonies, end of July) and along the growing edges of branches (n = 3 colonies, shortly before the presumed spawning event in September).

Non-marginal areas. Relatively fine-scale variations were found within the fertile regions of some species. The few polyps of *F. fragum* undergoing intratentacular division (each with two discrete mouths enclosed by a common body wall) contained significantly more planulae than did five adjacent non-dividing polyps (Wilcoxon's signed-ranks test, $T_s = 2$, $P < 0.01$, n = 17 comparisons from 11 colonies). What are presumed to be young polyps within the non-marginal areas of *S. radians, S. siderea* and *P. furcata* could be identified in the colony, both from their fewer cycles of septa and their conical vertical profiles ("old" polyps have full cycles of septa and cylindrical vertical profiles). These young polyps were usually infertile, whereas intermediate-sized polyps carried some gonads, but were less fecund than adjacent, fully developed, cylindrical polyps (for *S. radians,* Table III; for *S. siderea,* Table IV; in both species, Wilcoxon's signed-ranks test, $T_s = 0$, $P < 0.01$). Small polyps carried eggs after reaching a tissue thickness of about 3.2 mm, and were estimated to be about eight months old, since the average skeletal increment of *S. siderea* in Panama is about 5 mm per year (H. Guzman, pers. comm.). The age of the infertile margins was more than 2 years old in *S. siderea,* judging from skeletal thicknesses (about 2 cm) at their vertical edges.

As described for Indo-Pacific acroporids (Wallace, 1978; Veron and Wallace, 1984), radial polyps on the upper surfaces of *A. palmata* could be classified into two types—ones with long polyp walls (thus exert), and others which have almost no walls. The frequency of fertile polyps was significantly higher in long polyps than in adjacent short polyps (5 large and 5 small polyps from each of 15 colonies, pooled, G = 66.2, $P < 0.01$). When only fertile

Table III

Fecundity of young and old polyps within the fertile area of Siderastrea radians

	Number of eggs per polyp (sample size)	
Colony	Old polyp	Young polyp
1	6.2 (5)	1.6 (5)
2	15.8 (5)	5.0 (5)
3	13.6 (5)	3.8 (5)
4	19.6 (5)	0 (5)
5	20.4 (5)	6.8 (5)
6	27.0 (5)	0 (5)
7	17.6 (5)	5.0 (5)
8	24.8 (5)	1.6 (5)
9	15.4 (5)	1.7 (5)
10	18.2 (5)	3.4 (5)
11	21.4 (5)	4.6 (5)

Table IV

Relative fecundity of polyps within fertile colonies of Siderastrea siderea

	Relative fecundity		
Colony	Large polyp	Medium polyp	Small polyp
1	100% (10)	1% (5)	0% (2)
2	100% (10)	56% (2)	1% (7)
3	100% (10)	15% (4)	9% (5)
4	100% (10)	10% (4)	1% (4)
5	100% (10)	0% (7)	—
6	100% (10)	0% (1)	0% (4)
7	100% (10)	40% (6)	1% (9)
8	100% (10)	0% (3)	0% (11)
9	100% (10)	—	3% (3)
10	100% (10)	0% (3)	—

Number in parenthesis indicates sample size.

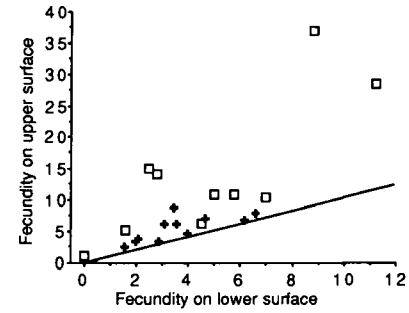

Figure 5. Comparison of fecundity between the upper and the lower surfaces of *Acropora palmata.* Mean area fertility (square): mean number of fertile polyps per cm^2, based on 2-32 cm^2/colony. Mean fertile polyp fecundity (cross): mean number of eggs per fertile polyp, based on 10 to 166 polyps per colony. The diagonal line indicates equal numbers on both surfaces.

polyps were compared, the number of eggs per fertile polyp was also significantly higher in the long polyps (Wilcoxon's signed-ranks test, $T_s = 0$, $P < 0.05$, n = 6 colonies, 6–14 polyps/colony). Short polyps, however, were more than 50% of the polyps on the upper surfaces (n = 5 colonies). Along the mid-branch regions, gonads were absent in areas where polyp density was low and the soft tissues were relatively thin, possibly as a result of shading (n = 11 colonies). Regenerated portions, where live tissues lack polypal mouths, were also infertile.

The upper surfaces of branches of *A. palmata* had a much higher fecundity than lower surfaces, as there were more fertile polyps per unit surface area (Wilcoxon's signed-ranks test, $T_s = 0$, $P < 0.01$, n = 10 colonies, Fig. 5), and larger numbers of eggs within fertile polyps (Wilcoxon's signed-ranks test, $T_s = 0$, $P < 0.01$, n = 11 colonies, Fig. 5). In addition, the soft tissues on the upper surfaces of *A. palmata* were at least twice as thick as those of the lower surfaces (measured from decalcified soft tissues), and their corresponding rate of vertical skeletal increment was about twice as great, as evidenced by growth bands revealed by X-ray of skeletal slabs from seven colonies. Central polyps on the horizontal surfaces of *S. siderea* also had thicker tissues (unpub. data) and longer gonads, and a proportionately larger number of mesenteries were carrying gonads than those on vertical surfaces. Thus the fecundity of horizontal polyps was significantly higher than that of the vertical polyps (Wilcoxon's signed-ranks test, $P < 0.01$, n = 16 colonies, Fig. 6).

Within colony infertility—manipulations

One month after the initiation of each experiment, colonies were checked for possible adverse responses to manipulations. Except for one colony of *S. siderea* which showed some discoloration and had become pink along its new artificial margin, all others looked normal, with no visible wound-related necroses. (This marginal discoloration also occurs naturally in some colonies of *S. siderea*). Seven specimens of *S. radians* were collected, and dissection revealed that the severed polyps still contained gonads.

Success retrieving the experimental colonies varied among species and treatments 5–6 months after manipulation. In *S. siderea,* only some (n = 8) of the "tissue cut" and "total cut" specimens were recovered, so the data for all the manipulated colonies were pooled. In *P. astreoides,* the only species with notable new growth, the wounds of simple "tissue cut" specimens were covered by a thin layer of regenerating tissues, and the "total cut" specimens showed some new growth along the margin.

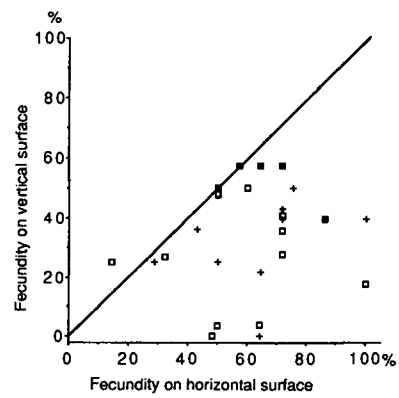

Figure 6. Comparison of fecundity between vertical and horizontal surfaces of *Siderastrea siderea.* For each surface on each colony, relative gonad lengths (cross): mean gonad length based on two randomly chosen mesenteries per polyp in 10 randomly-chosen polyps per sample, relative to the largest estimate of mean gonad length from any location in any colony. Relative fecundity (square): fecundity (see gonad index in Fig. 3 legend) relative to largest estimate of fecundity in any colony.

As an artificial margin was not successfully maintained in the above treatments, only the "cut and fill" specimens were checked for gonads. Seven "cut and fill," eight "tissue cut" and 15 "total cut" specimens were retrieved for *S. radians* and lumped together, since all three treatments showed the same trend, *i.e.*, the fecundity of the artificial margins was intermediate between that of the centers and the natural margins (significant differences with Wilcoxon's signed-ranks test: center > artificial margin, $T_s = 0$, $P < 0.01$, n = 29 colonies; artificial margin > natural margin, $T_s = 3.5$, $P < 0.01$, n = 11 colonies).

Except in *S. radians,* an infertile zone was found along every artificial margin. In *S. siderea,* the width of this newly generated infertile zone was comparable to the horizontal margins in natural colonies (difference insignificant, Wilcoxon's two-sample test, $U_s = 195$, $P > 0.05$, $n_1 = 18$, $n_2 = 16$, two-tail), and most (16/18) of the artificial margins had more than one row of infertile polyps. In the "cut and fill" specimens of *P. astreoides,* no significant difference was found between the infertile widths of the natural and manipulated margins (Wilcoxon's two-sample test, $U_s = 69.5$, $P > 0.05$, $n_1 = 10$, $n_2 = 10$, $P > 0.05$, two-tail). In *S. radians,* the polyps along the artificial margins remained fertile, although their fecundity was significantly lower than that of centrally located polyps in the same colonies (Wilcoxon's signed-ranks test, $T_s = 0$, $P < 0.01$, Table V).

Table V

Fecundity of polyps after manipulation in Siderastrea radians

	Number of eggs per 20 mesenteries						
Colony #	Center	Natural margin	Artificial margin	Colony #	Center	Natural margin	Artificial margin
1	20	13	—	16	12	6	—
2	20	7	0	17	12	3	—
3	20	2	2	18	11	5	7
4	18	2	—	19	10	1	0
5	17	17	—	20	9	—	0
6	17	8	—	21	9	3	—
7	17	3	—	22	8	8	0
8	16	15	—	23	8	3	—
9	16	6	0	24	8	3	—
10	15	14	—	25	8	0	—
11	15	2	—	26	7	3	—
12	15	2	0	27	6	2	0
13	14	7	0	28	3	3	—
14	13	6	—	29	3	2	0
15	13	5	—	30	3	0	—

Relationship between colony size and maturation

All ten species of western Atlantic reef corals studied showed size-correlated reproductive activities, with larger colonies having much higher fertility rates (Table VI).

Estimates of puberty size ranged from 2.3 cm^2 to 195 cm^2 in the seven species of massive reef corals (Table VII). The puberty size estimate of the massively branching *A. palmata* was very large (1600 cm^2). Puberty size estimated as branch length was 17 cm in *A. cervicornis,* and 1.4 cm in *P. furcata.*

Discussion

An integrated colony with polyps specialized for various roles would seem to be adaptive in reef environments, even in the absence of obvious morphological differentiation. Caution should be exercised in inferring integration, however, as exemplified by the clonal sea anemone, *Anthopleura elegantissima,* where an individual clonemate may have a different size, division rate, defensive tissues, and fertility according to its position in a patch (Francis, 1976). Since clonemates of *A. elegantissima* are separated, these differences develop in the absence of any connections after the polyps have divided. In a coral colony with morphologically connected polyps, heterogeneous patterns may similarly represent developmental stages or the independent responses of polyps to their own surroundings. Colony-level integration should be invoked only if inhomogeneities in form or function cannot be explained by microenvironmental or ontogenetic effects.

In the following sections, patterns of reproductive unevenness found in different species of colonial corals are discussed in relation to presumptive environmental or ontogenetic factors or, in the two acroporids, used as evidence for integration (Table VIII).

Within colony infertility patterns—marginal areas

Regardless of colony size and shape, the results for these ten species clearly indicate that the marginal polyps differ reproductively from the central polyps of the same colonies. What is the reason for this marginal pattern? Chornesky's (1989) observations may offer a good environmental explanation. Her study of natural encounters between colonies of *Porites* and *Agaricia,* showed that the margins of certain corals are in a dynamic state of temporary advances and retreats. Not only is the energy requirement for these confrontations potentially high (Rinkevich and Loya, 1985), but the continuing physical presence of the tissues themselves is less certain. In addition to competition, encroaching predators, such as snails, sea stars, and fire worms are more likely to attack at colony margins (J. Hayes, pers. comm.). An investment in somatic tissues, which can expand or fight along the margin, is presumably more important than one in reproductive tissues, which only increases the stake upon losing (Hughes and Jackson, 1985).

In the manipulated specimens of *S. siderea, S. radians,* and *P. astreoides,* some form of reduced fertility appeared in all artificially generated margins (see Results). Polyps

Table VI

Frequency of fertile colonies in each collected size class

Species		Size class (surface area of live colony; cm^2) 0–4	4–15	15–60	60–250	250–1000	1000–4000	>4000
Favia fragum	% fertile	63	93	94	—	—	—	—
	n	38	74	17	—	—	—	—
Siderastrea radians	% fertile	50	86	97	100	—	—	—
	n	64	206	208	23	—	—	—
Porites astreoides	% fertile	0	9	19	79	94	100	—
	n	4	12	26	47	55	11	—
Diploria clivosa	% fertile	0	0	40	57	93	100	100
	n	1	5	5	14	29	23	3
Diploria strigosa	% fertile	—	—	20	42	100	100	100
	n	—	—	5	12	9	6	9
Montastrea cavernosa	% fertile	—	0	100	92	100	94	100
	n	—	1	6	13	20	18	5
Siderastrea siderea	% fertile	0	0	0	47	96	100	96
	n	3	4	7	19	27	13	23
Acropora palmata	% fertile	—	0	0	7	31	43	88
	n	—	4	9	14	16	7	33
		Size class, branch length (cm) <1	1–2	2–7	5–9	9–13	13–17	>17
Porites furcata	% fertile	0	77	94	—	—	—	—
	n	5	39	252	—	—	—	—
Acropora[1] *cervicornis*	% fertile	—	—	—	0	38	59	89
	n	—	—	—	4	13	17	18

"n" is the number of colonies examined.
[1]: Only thick branches (>1 cm diameter).

along the artificial margins originally had been in the center of colonies, and would be expected to be fully fertile had there been no manipulations. Alternatively, these results could be attributed to wounding caused by the operation itself, rather than the changed location of the polyps. Polyps not operated upon but close to the artificial margins, however, also became infertile in *P. astreoides* and *S. siderea*. Thus, regardless of its causes, the experimentally-induced infertile marginal response was not simply due to the age of the polyps.

The infertile bases of the branching *A. cervicornis* and *P. furcata* are subject to adverse environments, due to reduced access to water flow and sunlight. Encroachment by fouling organisms is a constant threat here, particularly to *P. furcata* which has compact colonies. The nearly infertile bases in branches of *P. furcata* make up more than 50% of the live tissue cover (Fig. 5), and all are older polyps, raising the alternative possibility of polyp senescence (Palumbi and Jackson, 1983). In *P. furcata* the fate of individual polyps may be predetermined. Live branches of *P. furcata* average 3.5 cm in length (pers. obs.), and their annual extension in the study area is about 2.0–3.7 cm (Meyer and Birkeland, 1975); hence the life expectancy of an individual polyp is about one to two years. Since oogenesis and embryogenesis are lengthy processes, basally located polyps should not be able to complete their investment in reproduction before dying. But the microenvironment near the branch bases may also deteriorate to the point that developing gonads can no longer be supported in the polyps.

The infertile tips of three branching species (*P. furcata, A. cervicornis* and *A. palmata*) could be the result of a time constraint, since all the polyps (except the terminal axial polyps in *Acropora*) are young, and oogenesis takes at least six months in the two acroporids (Soong, 1991).

The prominent, non-reproductive axial polyps of *A. cervicornis* indicate colony-level integration. Axial polyps are not young since they give rise to the radial polyps in the branch. They have less chlorophyll and lower photosynthetic rates, yet higher rates of skeletal deposition, than the radial polyps (Goreau, 1963). The nutrients that axial polyps receive from radial polyps (Pearse and Muscatine, 1971; Taylor, 1977; Gladfelter, 1983) presumably contribute to the fast rates of branch extension in

Table VII

Reproductive characters of ten species of reef corals in Panama

Species	No. of colonies	Size range of samples (cm^2)	Puberty size:area (length)	Smallest reproductive colony l × w (cm)	Width of infertile margin: median; range (cm)
Non-branching					
Favia fragum	129	0.25–19.6	2.3 (1.5)	0.6 × 0.6	none
Siderastrea radians	501	0.2–128	4.0 (2)	1.3 × 1.1	0.25; 0.25–0.5
Porites astreoides	155	4–2,530	70 (8.4)	3 × 2	1; 0.5–1.5
Montastrea cavernosa	63	12–10,000	20 (4.5)	5 × 4	1; 0.5–1
Diploria clivosa	79	4–5,400	12 (11)	7 × 5	2; 1–4
Siderastrea siderea	117	2–20,164	156 (12.5)	9 × 7	1; 0.7–2 (horizontal surface) 2; 1–4 (vertical surface)
Diploria strigosa	41	36–62,500	195 (14)	7 × 6	2; 1–3.5
Branching					
Acropora palmata	84	9–40,000	1600	16 × 8	tip: 5; 3–10 base: 3; 2–3.5
Acropora cervicornis	52	5–29	17*	9 (length)	tip: 4; 2–6 base: 3; 1–4.5
Porites furcata	296	0.6–6	1.4*	1 (length)	~50% branch length

* Size measured in cm^2 of surface area of live colonies, except for *A. cervicornis* and *P. furcata*, for which branch length in cm is given.

acroporids (Shinn, 1976; Oliver *et al.*, 1983; Tunnicliffe, 1983). Apparently, the differentiation of axial polyps is not terminal, since non-growing axials do reproduce (Oliver, 1984).

Within colony infertility patterns—non-marginal areas

New polyp generation, whether by intra- or extra-tentacular budding, may take a long time to complete in scleractinian corals (Stephenson and Stephenson, 1933), since skeletal development underlying the soft tissues is involved (Goreau, 1963; Barnes, 1973). But in *F. fragum*, which buds intratentacularly, reproductive ability is not compromised during polyp multiplication and colony growth. Extratentacular budding, occurring in most of the other corals of this study, produces a mosaic of polyps of various sizes and developmental stages. Young polyps are infertile, and we suspect that their other functions, *e.g.*, feeding, may also be rudimentary.

The short polyps on the upper surface of *A. palmata* have a diminished morphology and a lower fertility than the long polyps due, perhaps, to crowding. On the under surfaces, where polyp density is less than 50% of that on the upper surfaces, polyp size is much more homogeneous (pers. obs.). Small polyps on the upper surfaces do not appear to be young: they are scattered throughout the upper surface of the branch, and parallel corallite growth revealed by X-radiographs indicates that they are unlikely to have been generated later than the long polyps (pers. obs.). Although their function has not been determined, the infertility of the short radial polyps in *A. palmata*

Table VIII

Explanations for uneven distribution of fertile polyps within colonies

Explanations	Based on	Phenomenon
Environmental effects	Observations and Manipulations	1. infertile colony margins: most species 2. low-fertility on vertical surface of colonies: *S. siderea* 3. low-fertility on shaded surfaces of colonies: *A. palmata*
Ontogenetic effects	Observations	1. juvenile polyps budded extratentacularly 2. juvenile polyps along colony margins 3. juvenile polyps at tips of branching corals
Integration	Observations	1. short radial polyps: *A. palmata* 2. axial polyps: *A. cervicornis*

presumably represents a second example of reproductive integration in acroporid corals.

Relationship between colony size and maturation

Colony size acts as another colony-level reproductive character. As a simple example, young polyps estimated at one to two years old (see Table III, IV) in a large colony of *S. siderea* carry eggs, but much older polyps in a small colony below puberty size for its species are infertile. But how do individual polyps "know" the size of their colony?

After reaching a certain minimum colony size, corals may start reproducing due to microenvironmental changes imposed upon each polyp. The polyps in a large colony simply experience a different environment from those in a small colony, and the combined effect on many polyps produces what appears to be a colony-level character. For example, as colonies of the marine hydroid *Podocoryne carnea* become larger and their zooids become denser, elevated levels of CO_2 in the center of the colony may induce the development of generative zooids which are responsible for sexual reproduction (Braverman, 1962; Braverman, 1963).

The distribution of fertile polyps provides a model for explaining puberty size. Small colonies may fail to reproduce, not because of their small sizes *per se,* but because virtually all of their polyps are marginally located. Hence no colony-level integration would exist. The above hypothesis would be falsified if: (1) no marginal infertility existed in large reproductive colonies; (2) the critical size at which a colony becomes reproductive is much larger than that predicted from the extent of the marginal infertility pattern; or (3) only specialized polyps are reproductive.

Of the seven massive corals studied here, six species have infertile margins, whereas marginal polyps in the small *F. fragum* are fertile but have a lower fecundity than the corresponding central polyps (Table VII). For each species, the smallest fertile colonies were recorded and its dimension compared to the width of its infertile margin (Table VII). If marginal infertility is directly additive, we would expect a colony with a radius greater than that of the width of the infertile margin to be reproductive, since (as in two *Siderastrea* spp.) there is no relationship between the width of the infertile margin and colony size. In most species, however, the smallest reproductive colonies are a little larger than is expected from this simple extrapolation of infertile margins. The additional infertility may be explained as follows.

In a small colony, any polyp is likely to be subject to marginal influences from all directions, whereas in a large colony marginal polyps at any location are less likely to be affected by environmental perturbations on the opposite margins of the colony. Moreover, as indicated by the gradient of increasing fecundity found in the first few centimeters of the fertile region, marginal effects on polyp fertility extend beyond the infertile marginal area. To be reproductive, therefore, a colony should be larger than the size obtained by simple extrapolation from its infertile margins.

In addition to the proposal about environmental and ontogenetic effects, at least one other hypothesis can explain the reproductive size effect without invoking colony integration. Using an idealized hemispherical, massive colony as a model, the number of polyps is directly proportional to the square of the radius of the colony, since all the polyps are on the surface of the colony; *i.e.,*

$$N = c \cdot r^2 \tag{1}$$

where N is the number of polyps, r is radius of the colony, and c is a constant. The number of polyps in the following year is approximately

$$N_{(t+1)} = c \cdot (r + a)^2 \tag{2}$$

where "a" is annual vertical skeletal increment, *i.e.,* the increase in radius of the hemispherical colony. The annual increase per polyp would be

$$\frac{c \cdot (r + a)^2 - c \cdot r^2}{c \cdot r^2} = \frac{2 \cdot r \cdot a + a^2}{r^2} \tag{3}$$

According to Equation (3), if the annual skeletal increment, "a" remains constant and is small relative to r, the per polyp growth rate will be decreasing as colony size (or r) increases (Fig. 7). In other words, if a colony increases in diameter at the same linear rate, and its shape remains the same, the investment of each polyp in somatic growth (polyp proliferation) would decrease with increasing colony size. Assuming energy intake per polyp is independent of colony size, the excess energy available to polyps in large colonies could be used in reproduction. The critical point, *i.e.,* whether skeletal increment "a" is constant, or at least does not increase throughout a coral's life span, is supported by numerous studies (Connell,

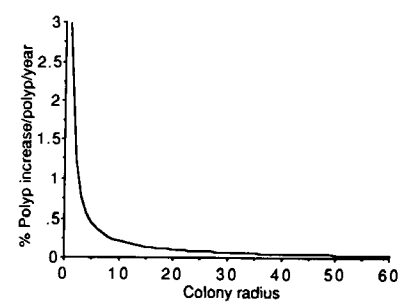

Figure 7. Model of the increase in polyp number as a function of the colony radius in a hemispherical colony. Unit of colony radius in terms of average annual skeletal increment.

1973; Nazaki *et al.*, 1978; Druffel, 1982; Hudson, 1985; Hughes and Jackson, 1985).

A closer look at the above hypothesis indicates that the curvature of the skeletal surface (Barnes, 1973), rather than colony size *per se*, is important in determining reproductive status. Given the same absolute vertical increment (or radial increase), a polyp in a colony of high curvature (usually a small colony) can invest more energy in growth since relatively more space will be available to add new polyps, whereas a polyp in a colony of low curvature (and usually large) would have little room for the addition of new polyps. (For the same reason, the lumpy surfaces present in large colonies of some species (Barnes, 1973; Isdale, 1977; Hughes and Hughes, 1986) effectively change the curvature of their surface and increase their surface area, presumably thereby maintaining the high growth rate of individual polyps.) Therefore, all of the observed patterns of uneven fertile polyp distribution in massive species are explicable without invoking integration.

In branching species, two factors are obviously important in the distribution of fertile polyps. The infertile tips in the three species studied are all young polyps (except for the axial polyps of acroporids). The infertile basal part of *A. cervicornis* and *P. furcata* are both associated with some degree of environmental degradation. The infertility of short branches in these two species could be explained by considering both an ontogenetic effect at the tips and an environmental effect at the bases. A branch would have to be long enough to have mid-regional polyps devoid of both effects to be reproductive.

Environmental and ontogenetic effects, however, cannot satisfactorily explain the size effect in *A. palmata*. Colonies with encrusting bases only (no standing branches) generally are small and non-reproductive, but none of the 13 medium sized (100–625 cm^2) encrusting colonies were fertile, and only one of nine colonies with small branches (100–644 cm^2) carried gonads. In large colonies with several fully developed branches (>3000 cm^2), however, marginal polyps along encrusting bases and growing edges of branches have been observed to carry eggs at the beginning of oogenesis. Obviously, the difference in fertility between a small and large colony of *A. palmata* is more than a simple combination of environmental and ontogenetic effects acting on individual polyps. Reproductive integration in colonies of *A. palmata* is likely.

Morphology and integration

As mentioned in the Introduction, many morphological characters have been proposed as being correlated with integration (see Table I). Summarizing these characters, the species studied here seem to constitute a gradient, with the two acroporids having the highest potential for being morphologically integrated, and *F. fragum* having the lowest potential. We will assess the extent to which these characters appear to relate to reproductive integration.

Colony shapes. Although relationships between colony shape and extent of integration have often been proposed (Jackson, 1979; Silen, 1981; Oliver and Coates, 1987; McKinney and Jackson, 1989), shape itself does not necessarily imply any given level of organization, as exemplified below.

Graus and Macintyre (1976, 1982) found that realistic growth forms of *Montastrea annularis* can be simulated simply by programming polypal growth rates to vary as a function of the intensity and distribution of light, which itself varies with location on a colony and depth. In these simulations different colony shapes are generated as a result of individual polyps responding independently to environmental gradients across a colony. A simple "rule change" at the module level, or some environmental variation, can easily produce various complex colony shapes without invoking higher levels of integration (see also Harper and Bell, 1979; Bell, 1986; Gottlieb, 1986, for modular plants).

In branching species, new polyps are concentrated at the growing tips, and polypal age increases down the branch from the tip. The segregation of young and old polyps in these colonies could easily initiate the development of colony integration through temporally differentiated life history traits of individual modules (Bonner, 1965). For example, the translocation of materials to the growing tips in *Acropora* (Pearse and Muscatine, 1971), a clear case of colony integration, could have evolved as a character of individual polyps, in which polypal age or developmental stage is the factor determining whether to export or import nutrients. Similarly, polyps could be genetically programmed to grow when young, to reproduce later, and to engage in defense when old. At any rate, the persistent developmental gradient along the branch, corresponding to predictable environmental (selective) gradients, could facilitate the development of temporal differentiation in polypal functions. The same effect in a massive species, where young and old polyps are more evenly distributed within the colony, would be more difficult to develop, since environmental gradients are imposed upon heterogeneously-aged polyps. The view that branching corals have a higher potential to develop integration concurs with Jackson's (1979) general argument, that branching colonial animals should be more integrated because their basal attachment is critical to the survival of the whole colony.

Polyp dimorphism. In this study, dimorphism of polyps (Table I) is associated with reproductive integration. Both acroporids have polyps of divergent morphology and both

species appear to be reproductively integrated. Direct inference of integration from morphology is supported here.

Budding types. Conflicting inferences about integration can be drawn from an examination of the modes of budding in corals. Duerden (1902) and Wells (1973) noted that polyps produced intratentacularly lack directive mesenterial couples (but see Matthai, 1926); daughter polyps, therefore, differ morphologically from the original polyp. Based on this morphological difference, they suggested that the entire colony formed by intratentacular budding should be regarded as an individual, whereas extratentacular budding produces many identical individuals (polyps) aggregated as a colony. The observations in this study, however, suggest just the opposite from a reproductive perspective. A colony produced by complete intratentacular budding (*F. fragum*) is homogeneous with respect to the fertility of its polyps (and by inference, other functions as well); an extratentacularly budded colony, in contrast, is a mosaic of large, old, fertile polyps intermixed with small, young, infertile or less fertile polyps. Integration should be higher in the latter, since at any moment, the young developing polyps are presumably more dependent on other polyps.

Other morphological characters. None of the reproductive data gathered during this study provided support for any of the other morphological characters (Table I) that are commonly used to imply integration. For example, reproductive fertility patterns in the two meandroid *Diploria* spp. resembled those of the extratentacularly budded *Montastrea cavernosa* and *Siderastrea siderea.*

Adaptiveness of integration

The ability to conduct signals, either through a primitive colonial nervous system, or through excitable epithelia is an important attribute of a true colony. In addition, the ability to share resources should set colonies clearly apart from mere aggregates of individually-acting polyps (Mackie, 1986). Judging by these non-reproductive criteria, reef corals do possess a certain extent of integration (see Introduction).

Many other marine invertebrates are also colonial, and some (including cnidarians) have developed much higher levels of integration. Why are colonial reef corals different? There are several possible reasons:

(1) Reef corals are sessile. Highly coordinated behavior among polyps may not be as important as it is in pelagic colonial organisms (*e.g.,* siphonophorans), for which locomotory activity is necessary (Mackie, 1986).

(2) Unlike many soft-bodied polymorphic species, most reef corals settle on hard substrata, and each polyp deposits calcium carbonate as it grows, hence no other differentiated supporting mechanism is necessary.

(3) One possible advantage of most polyps potentially being able to reproduce is that a "mutant polyp" would be less likely to reap all the reproductive success of the colony (Buss, 1982). Considering that a large, massive coral colony may live for centuries or even millennia, the occurrence of somatic mutations would appear to be inevitable, and the low level of integration might be adaptive after all.

(4) Ecologically, coral colonies are often separated into ramets (Hughes and Jackson, 1980). A less integrated colony with totipotent polyps may be better able to adjust to new conditions after environmental changes or damage (Chornesky, 1989).

(5) Most reef corals harbor zooxanthellae and are therefore less dependent upon external feeding for their carbon (Edmunds and Davis, 1989). The more homogeneous distribution of sunlight relative to the more patchily distributed zooplankton may allow less colony integration than in sedentary colonial animals lacking photosymbionts.

(6) Developmental constraints may be a non-selectionist's explanation for low integration in these corals.

In conclusion, a coral colony is an individual, in the sense that it is genetically homogeneous, and the constituting polyps are coordinated physiologically by their physical connections. Evolutionarily, a coral colony cannot be considered an individual, in the sense that the genet is a better unit of selection (Janzen, 1977), whereas the polyp characters are what is directly controlled by genetics.

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Literature Cited

Barnes, D. J. 1973. Growth in colonial scleractinians. *Bull. Mar. Sci.* **23:** 280–298.

Beklemishev, W. N. 1969. *Principles of Comparative Anatomy of Invertebrates.* University Chicago Press, Chicago, IL.

Bell, A. D. 1986. Evolutionary and non-evolutionary theories of senescence. *Phil. Trans. R. Soc. Lond.* **B313:** 143–159.

Birkeland, C. 1976. An experimental method of studying corals during early stages of growth. *Micronesica* **12:** 319–322.

Boardman, R. S., and A. H. Cheetham. 1973. Degrees of colony dominance in stenolaemate and gymnolaemate bryozoa. Pp. 121–220 in *Animal Colonies: Development and Function Through Time,*

R. S. Boardman, A. H. Cheetham, and W. A. Oliver, eds. Dowden, Hutchinson and Ross, Inc., PA.

Bonner, J. T. 1965. *Size and Cycle: An Essay on the Structure of Biology.* Princeton University Press, Princeton, NJ.

Braverman, M. H. 1962. Studies in hydroid differentiation. I. *Podocoryne carnea* culture methods and carbon dioxide induced sexuality. *Exp. Cell Res.* **26:** 301–306.

Braverman, M. H. 1963. Studies on hydroid differentiation. II. Colony growth and the initiation of sexuality. *J. Embryo. Exp. Morph.* **11:** 239–253.

Buss, L. W. 1982. Somatic cell parasitism and the evolution of somatic tissue compatibility. *Proc. Natl. Acad. Sci. USA* **79:** 5337–5341.

Buss, L. W. 1987. *The Evolution of Individuality.* Princeton University Press, Princeton, NJ.

Chapman, G. 1981. Individuality and modular organisms. *Biol. J. Linn. Soc.* **15:** 177–183.

Chornesky, E. A. 1989. Repeated attack and retaliation during spatial competition between corals. *Ecology* **70:** 843–855.

Chornesky, E. A., and E. C. Peters. 1987. Sexual reproduction and colony growth in the scleractinian coral *Porites astreoides. Biol. Bull.* **172:** 161–177.

Coates, A. G., and J. B. C. Jackson. 1985. Morphological themes in the evolution of clonal and aclonal marine invertebrates. Pp. 67–106 in *Population Biology and Evolution of Clonal Organisms,* J. B. C. Jackson, L. W. Buss, and R. E. Cook, eds. Yale University Press, New Haven, CT.

Coates, A. G., and W. A. J. Oliver. 1973. Coloniality in zoantharian corals. Pp. 3–27 in *Animal Colonies: Development and Function Through Time,* R. S. Boardman, A. H. Cheetham and W. A. J. Oliver, eds. Dowden, Hutchinson and Ross, Inc., PA.

Connell, J. E. 1973. Population ecology of reef building corals. Pp. 205–245 in *Biology and Geology of Coral Reefs,* O. A. Jones and R. Endean, eds. Academic Press, London.

Druffel, E. M. 1982. Banded corals: changes in oceanic carbon-14 during the little ice age. *Science* **218:** 13–19.

Duerden, J. E. 1902. The significance of budding and fission. *Ann. Mag. Nat. Hist. ser. 7.* **10:** 382.

Edmunds, P. J., and P. S. Davis. 1989. An energy budget for *Porites porites* (scleractinia), growing in a stressed environment. *Coral Reefs* **8:** 37–43.

Fadlallah, Y. H. 1983. Sexual reproduction, development and larval biology in scleractinian corals, a review. *Coral Reefs* **2:** 129–150.

Foster, A. B. 1979. Phenotypic plasticity in the reef corals *Montastraea annularis* (Ellis and Solander) and *Siderastrea siderea* (Ellis and Solander). *J. Exp. Mar. Biol. Ecol.* **39:** 25–54.

Foster, A. B. 1985. Variation within coral colonies and its importance for interpreting fossil species. *J. Paleontol.* **39:** 1359–1381.

Francis, L. 1976. Social organization within clones of the sea anemone *Anthopleura elegantissima. Biol. Bull.* **150:** 361–376.

Gladfelter, E. H. 1983. Circulation of fluids in the gastrovascular system of the reef coral *Acropora cervicornis. Biol. Bull.* **165:** 619–636.

Goreau, T. F. 1963. Calcium carbonate deposition by coralline algae and corals in relation to their roles as reef builders. *Ann. N.Y. Aca. Sci.* **109:** 127–167.

Gottlieb, L. D. 1986. The genetic basis of plant form. *Phil. Trans. R. Soc. Lond.* **B313:** 197–208.

Graus, R. R., and I. G. Macintyre. 1976. Light control of growth form in colonial reef corals: computer simulation. *Science* **193:** 895–897.

Graus, R. R., and I. G. Macintyre. 1982. Variation in growth forms of the reef coral *Montastrea annularis* (Ellis and Solander): A quantitative evaluation of growth response to light distribution using computer simulation. Pp. 441–464 in *The Atlantic Barrier Reef Ecosystem at Carrie Bow Cay. Belize. I. Structure and Communities,* K. Rutzler and G. Macintyre, eds. Smithsonian Institute Press, Washington, DC.

Harper, J. L., and A. D. Bell. 1979. The population dynamics of growth form in organisms with modular construction. Pp. 29–52 in *Population Dynamics,* R. M. Anderson, B. D. Turner, and L. R. Taylor, eds. Blackwell Sci. Pub., London.

Harrigan, J. F. 1972. The planula larva of *Pocillopora damicornis:* Lunar periodicity of swarming and substratum selection behavior. Ph.D. Dissertation, University of Hawaii.

Harrison, P. L., and C. C. Wallace. 1990. Reproduction, dispersal and recruitment of scleractinian corals. Pp. 133–207 in *Coral Reefs, Ecosystems of the World 25,* Z. Dubinsky, ed. Elsevier, New York.

Harvell, C. D. 1991. Coloniality and inducible polymorphism. *Am. Nat.* **138:** 1–14.

Hubbard, J. A. E. B. 1973. Sediment-shifting experiments: A guide to functional behavior in colonial corals. Pp. 31–42 in *Animal Colonies: Development and Function Through Time,* R. S. Boardman, A. H. Cheetham, and W. A. J. Oliver, eds. Dowden, Hutchinson and Ross, Inc., PA.

Hudson, J. H. 1985. Long-term growth rates of *Porites lutea* before and after nuclear testing: Enewetak Atoll (Marshall Islands). *Proc. 5th Int. Coral Reef Symp.* **6:** 179–185.

Hughes, D. J., and R. N. Hughes. 1986. Metabolic implications of modularity: studies on the respiration and growth on *Pilosa electra. Phil. Trans. R. Soc. Lond.* **B313:** 28–37.

Hughes, T. P. 1984. Population dynamics based on individual size rather than age: a general model with a reef coral example. *Am. Nat.* **123:** 778–795.

Hughes, T. P., and J. B. C. Jackson. 1980. Do corals lie about their age? Some demographic consequences of partial mortality, fission and fusion. *Science* **209:** 713–715.

Hughes, T. P., and J. B. C. Jackson. 1985. Population dynamic and the life histories of foliaceous corals. *Ecol. Mono.* **55:** 141–166.

Hyman, L. H. 1940. *The Invertebrates: Protozoa Through Ctenophora.* McGraw-Hill, New York.

Isdale, P. 1977. Variation in growth rate of hermatypic corals in a uniform environment. *Proc. 3rd Int. Coral Reef Symp.* **2:** 403–408.

Jackson, J. B. C. 1979. Morphological strategies of sessile animals. Pp. 499–555 in *Biology and Systematics of Colonial Animals.* G. Larwood and B. R. Rosen, eds. Academic Press, London.

Janzen, D. H. 1977. What are dandelions and aphids? *Am. Nat.* **111:** 586–589.

Kojis, B. L. 1986. Sexual reproduction in *Acropora (Isopora)* species (Coelenterata: Scleractinia). I. *A. cuneata* and *A. palifera* on Heron Island reef, Great Barrier Reef. *Mar. Biol.* **91:** 291–309.

Kojis, B. L., and N. J. Quinn. 1985. Puberty in *Goniastrea favulus,* age or size limited? *Proc. 5th Int. Coral Reef Symp.* **4:** 289–294.

Loya, Y. 1976. Skeletal regeneration in a Red Sea scleractinian coral population. *Nature* **261:** 490–491.

Mackie, G. O. 1986. From aggregates to integrates: physiological aspects of modularity in colonial animals. *Phil. Trans. R. Soc. Lond.* **B313:** 175–196.

Matthai, G. 1926. Colony-formation in astraeid corals. *Phil. Trans. R. Soc. Lond.* **B214:** 313–356.

McKinney, F. K., and J. B. C. Jackson. 1989. *Bryozoan Evolution.* Allen and Unwin, London.

Meyer, D. L., and C. Birkeland. 1975. Biological monitoring data. Pp. 358–370 in *Environmental Monitoring and Baseline Data,* D. M. Windsor, eds. Smithsonian Institute, Washington, DC.

Nazaki, Y., D. M. Rye, K. K. Turekian, and R. E. Dodge. 1978. A 200 year record of carbon-13 and carbon-14 variations in a Bermuda coral. *Geop. Res. Let.* **5:** 825–828.

Oliver, J. K. 1984. Intra-colony variation in the growth of *Acropora formosa:* extension rates and skeletal structure of white (zooxanthellae free) and brown-tipped branches. *Coral Reefs* **3:** 139–147.

Oliver, J. K., B. E. Chalker, and W. C. Dunlap. 1983. Bathymetric adaptations of reef building corals at Davis Reef, Great Barrier Reefs, Australia. I. Long-term growth responses of *Acropora formosa*. *J. Exp. Mar. Biol. Ecol.* **73:** 11–35.

Oliver, W. A. J., and A. G. Coates. 1987. Phylum Cnidaria. Pp. 140–193 in *Fossil Invertebrates,* R. S. Boardman, A. H. Cheetham, and A. J. Rowell, eds. Blackwell Scientific Publication, London.

Palumbi, S. R., and J. B. C. Jackson. 1983. Aging in modular organisms: ecology of zooid senescence in *Steginoporella* sp. (Bryozoa, Cheilostomata). *Biol. Bull.* **164:** 267–278.

Pearse, J. S., and L. Muscatine. 1971. Role of symbiotic algae (zooxanthellae) in coral calcification. *Biol. Bull.* **141:** 350–363.

Richmond, R. H., and C. L. Hunter. 1990. Reproduction and recruitment of corals: comparisons among the Caribbean, the tropical Pacific, and the Red Sea. *Mar. Ecol. Prog. Ser.* **60:** 185–203.

Rinkevich, B., and Y. Loya. 1985. Intraspecific competition in a reef coral: effects on growth and reproduction. *Oecologia* **66:** 100–105.

Rosen, B. R. 1979. Modules members and communes. A postscript introduction to social organisms. Pp. XIII–XXXV in *Biology and Systematics of Colonial Animals,* G. Larwood and B. R. Rosen, eds. Academic Press, London.

Ryland, J. S. 1979. Structural and physiological aspects of coloniality in bryozoa. Pp. 211–242 in *Biology and Systematics of Colonial Animals,* G. Larwood and B. R. Rosen, eds. Academic Press, London.

Sandberg, P. A. 1973. Degree of individuality in cheilostome bryozoa: skeletal criteria. Pp. 305–316 in *Animal Colonies: Development and Function Through Time,* R. S. Boardman, A. H. Cheetham, and W. A. J. Oliver, eds. Dowden, Hutchinson and Ross, Inc., PA.

Schopf, T. J. M. 1973. Ergonomics of polymorphism: its relation to the colony as the unit of natural selection in species of the phylum ectoprocta. Pp. 247–294 in *Animal Colonies: Development and Function Through Time,* R. S. Boardman, A. H. Cheetham, and W. A. Oliver, eds. Dowden, Hutchinson and Ross, Inc., PA.

Sebens, K. P. 1987. The ecology of indeterminate growth in animals. *Ann. Rev. Ecol. Syst.* **18:** 371–407.

Shelton, G. A. B. 1979. Co-ordination of behavior in cnidarian colonies. Pp. 141–154 in *Biology and Systematics of Colonial Animals,* G. Larwood and B. R. Rosen, eds. Academic Press, London.

Shelton, G. A. B. 1982. Anthozoa. Pp. 141–154 in *Electrical Conduction and Behavior in 'Simple' Invertebrates,* G. A. B. Shelton, ed. Glarendon Press, Oxford.

Shinn, E. A. 1976. Coral reef recovery in Florida and the Persian Gulf. *Environ. Geol.* **1:** 241–254.

Silen, L. 1981. Colony structure in *Flustra foliacea* (Linnaeus). *Acta Zoologica* **62:** 219–232.

Soong, K. 1991. Sexual reproductive patterns of shallow-water reef corals in Panama. *Bull. Mar. Sci.* **49**(3): 832–846.

Stephenson, T. A., and A. Stephenson. 1933. Growth and asexual reproduction in corals. *Great Barrier Reef Exp. 1928–1929.* **3:** 168–217.

Szmant-Froelich, A. 1985. The effect of colony size on the reproductive ability of the Caribbean coral *Montastrea annularis* (Ellis and Solander). *Proc. 5th Int. Coral Reef Symp.* **4:** 295–300.

Taylor, D. L. 1977. Intra-colonial transport of organic compounds and calcium in some Atlantic reef corals. *Proc. 3rd Int. Coral Reef Symp.* **1:** 432–436.

Tunnicliffe, V. 1983. Caribbean staghorn coral population—Pre-hurricane Allen conditions in Discovery Bay, Jamaica. *Bull. Mar. Sci.* **33:** 131–151.

Vaughan, T. W. 1909. Geology of the keys, the marine bottom deposits, and recent corals of southern Florida. *Carnegie Inst. Wash. Yearbook* **8:** 140–144.

Vaughan, T. W., and J. W. Wells. 1943. Revision of the suborders, families, and genera of the Scleractinia. *Geol. Soc. Amer. Spec. Paper* **44:** 1–363.

Veron, J. E. N. 1981. The species concept in scleractinia of eastern Australia. *Proc. 4th Int. Coral Reef Symp.* **2:** 183–186.

Veron, J. E. N., and M. Pichon. 1982. Scleractinia of Eastern Australia. Part IV Poritidae. *Aust. Inst. Mar. Sci. Mono. Ser.* **5:** 1–159.

Veron, J. E. N., and C. C. Wallace. 1984. Scleractinian of Eastern Australia. Part V. Family Acroporidae. *Aust. Inst. Mar. Sci. Mono. Ser.* **6:** 1–485.

Wallace, C. C. 1978. The coral genus *Acropora* (Scleractinia: Astrocoeniina: Acroporidae) in the central and southern Great Barrier Reef Province. *Mem. Qd. Mus.* **18:** 273–319.

Wallace, C. C. 1985. Reproduction, recruitment and fragmentation in nine sympatric species of the coral genus *Acropora*. *Mar. Biol.* **88:** 217–233.

Wells, J. W. 1956. Scleractinia. Pp. 328–444 in *Treatise on Invertebrate Paleontology, pt. F. Coelenterata,* R. C. Moore, ed, Geol. Soc. Amer., and University Kansas Press, Lawrence, KS.

Wells, J. W. 1973. What is a colony in anthozoan corals? P. 29 in *Animal Colonies: Development and Function Through Time,* R. S. Boardman, A. H. Cheetham, and W. A. J. Oliver, eds. Dowden, Hutchinson and Ross, Inc., PA.