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COLONY INTEGRATION DURING REGENERATION IN THE STONY CORAL *FAVIA FAVUS*

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Abstract. Modular organisms consist of repeated building blocks. An important consequence of modularity may be reflected in the ability of a colony to continually reallocate priority of resource transport among its units in response to stress. Hermatypic corals, the main organisms constructing tropical reefs, are prone to damage by a multitude of agents. Since colonization of lesions by competitors is a potent threat to colonial organisms, fast recovery is an important component of colony survival. Previous regeneration studies have claimed that the energy requirements of this essential process are fueled only by the polyps directly bordering the injured area. This ''localized regeneration hypothesis'' rejects the necessity for wide colony integration during regeneration and sees no advantage to large colony size. The objective of the present study was to test an alternative regeneration hypothesis that argues, in contrast, that injury repair (i.e., closure of lesions by newly formed tissues) in corals may require extended colony integration (i.e., internal translocation of resources from sites of acquisition to sites of maximal demand). To test our hypothesis we examined: (1) the relationship between colony size and percentage recovery of lesions differing in size and shape; and (2) the effect of different sized lesions on the fecundity of polyps located at increasing distances from the lesion site. Both experiments were conducted on the common, spherically shaped coral *Favia favus* in the Red Sea near Eilat, Israel. The relatively small lesions (<1 cm^2) were the only ones to support the localized regeneration hypothesis, since their recovery was unaffected by colony size. However, the two larger lesion types (approximate sizes of 2 cm^2 and 3 cm^2) confirmed the importance of large colony size for achieving fast recovery. In the second experiment we found that small lesions, repeated monthly, caused only a localized reduction in fecundity, while larger monthly repeated lesions caused significant reductions in fecundity up to a distance of 15 cm away from their site. Both experiments indicate that regeneration from injury may require an extended magnitude of energy integration throughout the colony, and that the extent of this integration is regulated by the colony in accordance with lesion characteristics. It is also concluded that in long-lived organisms such as corals, there is a priority of energy allocation to recovery rather than to reproduction. Our findings reveal the existence of injury thresholds within a colony that determine energy allocation and intra-colonial translocation of energy products toward regions of maximal demand. We suggest that such injury thresholds may characterize many other coral species and that colony integration during stress is a basic life-preserving ability and one of the most important advantages of clonal and colonial organisms.

Key words: artificial lesions; clonal organisms; colony integration; coral regeneration; energy allocation; Favia favus*; fecundity; Israel; Red Sea.*

INTRODUCTION

Modular organisms consist of repeated building blocks (modules, ramets, polyps, zooids), that are asexually derived by vegetative growth (Harper 1977, Hughes 1989, Hughes et al. 1992). A fundamental characteristic of modular repeated units (polyps of corals and hydrozoans, zooids of bryozoans, and colonial ascidians), and one that distinguishes them from modules at lower levels of organization, is their ability to function, survive, and reproduce sexually, alone or in small groups, if separated from each other by injury or fission (Jackson 1979, Hughes and Jackson 1980, Hughes et al. 1992).

Hermatypic corals, the main organisms constructing tropical reefs, suffer damage from a multitude of agents, such as storms (Scoffin 1993), sedimentation (Loya 1976*a*, Rogers 1990), temperature fluctuations (Jokiel and Coles 1990), emersion at low tide (Loya 1972, 1976*b*), predation (Cameron et al. 1991), diseases (Gladfelter 1982, Peters 1984, Brown 1997), bleaching (Glynn 1993), competitive interactions (Chornesky 1989), and humans (Brown and Howard 1985). Because of their modular organization, corals,

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like many plants, may sustain partial mortality (Hughes and Jackson 1985). Natural lesions in stony corals are frequent and appear in a broad range of shapes and sizes (Loya 1972, Bythell et al. 1993, Genin et al. 1995). Since colonization of lesions by competitors (mainly algae and excavating sponges) is a potent threat, recovery from such disturbances is an important component of colony survival (Loya 1976*c*, Palumbi and Jackson 1982, Brown and Howard 1985, Jokiel and Coles 1990, Cameron et al. 1991, Rogers 1993, Meesters et al. 1994, Van Veghel and Bak 1994, Ward 1995).

Convergence of form and function has accompanied the evolution of modular growth in terrestrial plants and colonial aquatic invertebrates (Dyrynda 1986). Part of this convergence is related to exploitation of resources (space and light), and the ability to translocate energy from sources to sinks (Ryland and Warner 1986). In modular organisms such as plants, studies on resource allocation and carbon budgets have revealed the importance of an internal balance of carbon use in determining rates of translocation (Lang and Thorpe 1983, Bloom et al. 1985, Chapman et al. 1990, Marshall 1990). Furthermore, clonal plants can redistribute resources internally from sites of acquisition to sites where such resources are scarce (Hester et al. 1994, Kemball and Marshall 1995, Hutchings and Wijesinghe 1997). In colonial invertebrates, zooidal responses to localized stress, caused by grazing, are highly variable, and are modified at times in very localized regions of a colony by both intrinsic and extrinsic stimuli (Hughes and Cancino 1985, Harvell and Grosberg 1988, Harvell 1991). For example, localized injury of the growing edge in a marine bryozoan induces energy transport (i.e., carbon) toward the damage (Palumbi and Jackson 1983, Best and Thorpe 1985, Harvell and Padilla 1990, Harvell 1991, 1992, Harvell and Helling 1993). In hydrozoan colonies, injuries accelerate the onset of reproduction due to elevated CO_2 concentrations in the injury site (Braverman 1974).

In this paper we experimentally characterize the scale of dynamics of colony integration during injury repair in the coral *Favia favus.* One hypothesis regarding regeneration in colonial corals argues that the resources required for this process are derived only from those polyps directly bordering the lesion area (Bak et al. 1977, Bak and Steward-Van Es 1980, Bak 1983, Meesters et al. 1994, 1997*a*). In other words, regeneration (i.e., closure of a lesion by newly formed tissues) requires minor integration of only a restricted and localized portion of the colony, since ''a minimal area would be needed for optimum regeneration'' (Bak and Steward-Van Es 1980). Meesters et al. (1994) further claimed that successful regeneration depends on the amount of tissue bordering a lesion and not on colony size. In contrast, we recently suggested that lesions with a relatively long perimeter receive a higher energetic allocation from the colony compared with smaller lesions, probably due to the larger colony area associated with their recovery (Oren et al. 1997*a*). We tested this hypothesis by examining intra-colonial translocation of ^{14}C-labeled products in experimentally injured colonies of three Red Sea scleractinians, *F. favus*, *Platygyra lamellina* (Oren et al. 1997*b*), and *Porites* sp. (Oren et al. 1998). These studies indicated that injuries may induce significant translocation of photosynthetic products from polyps located up to a distance of 10 cm. Moreover, these studies were the first to show that the extent of this integration is regulated by the size and shape of the injury.

Because the energy available to an organism is often limited, and must be allocated among competing biological functions, such as maintenance, somatic growth, and reproduction (Kozlowski and Wiegert 1986), energy trade-offs between regeneration and reproduction may also reflect the degree of colony integration. This pattern has been examined in many coral species including: *Stylophora pistillata* (Loya 1976*c*, *d*, 1985, Rinkevich and Loya 1989), *Acropora cervicornis, A. palmata, Diploria clivosa, D. strigosa, Favia fragum, Montastrea cavernosa, Porites astreoides, P. furcata, Siderastrea radians, S. siderea* (Soong and Lang 1992), *Montastrea annularis* (Van Veghel and Bak 1994), *Pocillopora damicornis* (Ward 1995), *Acropora hyacinthus, A. gemmifera*, and *Goniastrea retiformis* (Hall 1997). These studies suggest that the negative effect exerted by one process on the other results from the energy link between the two; however, the extent of the association is as yet unknown.

In this study we examine a new regeneration hypothesis, which suggests that the process of lesion regeneration in colonial corals may require different magnitudes of colony integration (i.e., internal translocation of resources from sites of acquisition to sites of maximal demand). To test this hypothesis, we designed two experiments. (1) We tested the relationship between colony size and regeneration of tissue lesions differing in size and shape. If the resources necessary for the repair of damaged polyps come only from polyps adjacent to the lesion, then no relationship is expected between colony size and percentage recovery of lesions differing in size and shape (i.e., the localized regeneration hypothesis). If, however, a significant positive relationship is found between these variables, then the alternative hypothesis is more likely (i.e., that injury repair in corals requires extended coral integration). Furthermore, larger corals are expected to heal faster than smaller corals, when they suffer similar damage. (2) We examined the extent of the energetic link between injury regeneration and sexual reproduction. If an increasing magnitude of trade-off is found between reproduction and regeneration (i.e., ''prioritizing'' energy allocation to injury recovery rather than to gonad production) in colonies with increasing lesion sizes, it will indicate that an extended magnitude of energy integration throughout the colony is required

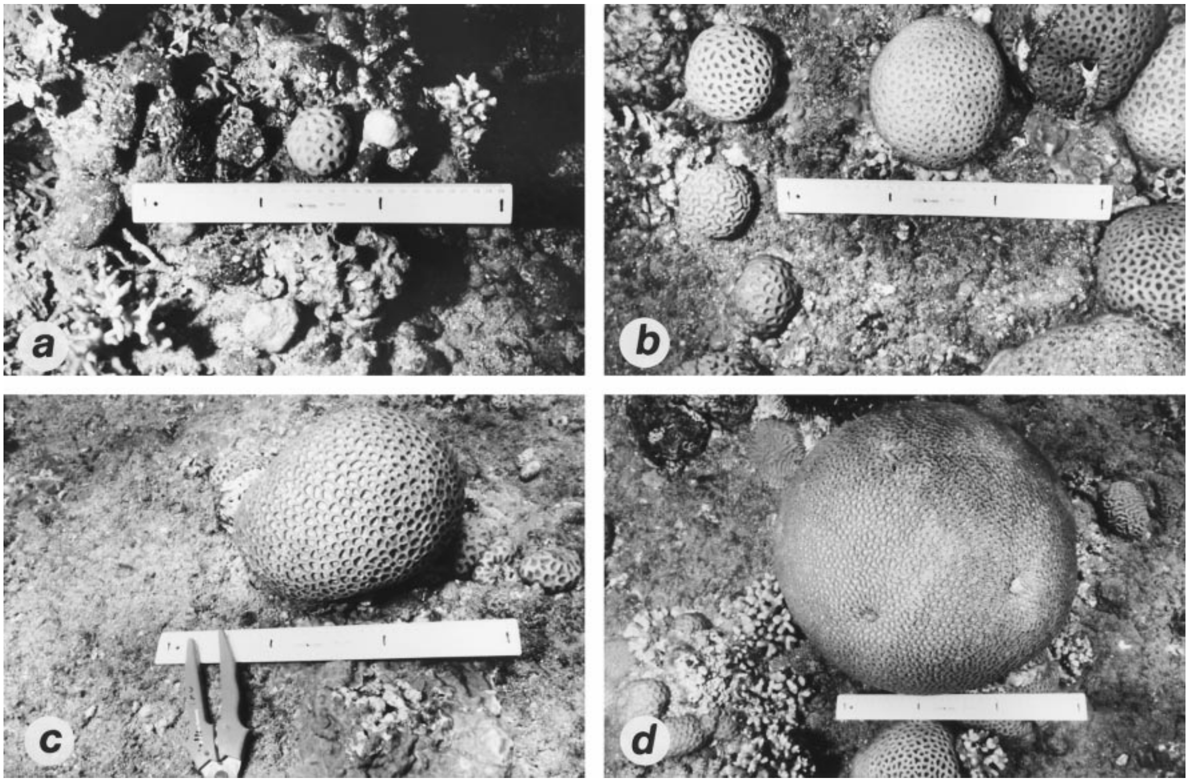

FIG. 1. Representative colonies of *Favia favus* from each of the four size classes examined in the study: (a) small, (b) intermediate, (c) large, and (d) very large. Length of ruler = 30 cm; distances between the black lines marked on the ruler = 10 cm.

during the healing process. The different lesion sizes inflicted on the surface of *F. favus* colonies, in both experiments, were designed to induce an increasing scale of injury stress, and reveal possible increasing magnitudes of intra-colonial energy integration.

METHODS

Spherical colonies of *Favia favus* are common in the shallow reef (0.5–4 m) in front of the Marine Biology Laboratory (MBL) in the Red Sea at Eilat, Israel. Although most *F. favus* colonies in this region are healthy and uninjured, they are occasionally subject to surface injuries (i.e., partial mortality) resulting from predation by parrot fish (Torovezky 1997) and gastropods (Gur and Loya 1996) as well as from southern storms (Y. Loya, *personal observations*). Such injuries may range from <1 cm^2 (i.e., a single polyp) up to 100 cm^2. Small injuries are characterized by a circular shape, while the larger ones vary in shape and size from a rounded patchy appearance to elongated and narrow.

Lesion recovery vs. colony size

Uninjured colonies of *F. favus* in the shallow reef (2–3 m) of the Marine Biology Laboratory in Eilat were tagged and photographed during November 1994, using a Nikonos-V camera (Nikon Corporation, Tokyo, Japan) with 20-mm lens. After measuring the surface area of each colony with a computerized image analyzer (Olympus CUE-3; Data Translation, Incorporated, 100 Locke Drive, Marlboro, Massachusetts USA), 72 healthy intact colonies (ranging in size from 6 to 24 cm in diameter) were selected and divided into three size classes, each comprising 24 similar-sized colonies: small (surface area = 71 ± 20 cm^2, Fig. 1a), intermediate (431 ± 176 cm^2, Fig. 1b), and large (1204 ± 313 cm^2, Fig. 1c).

The relationship between the surface area of the colony and its ability to regenerate was tested for three different types of tissue lesion: (1) single polyp lesions (SP, Fig. 2a); (2) elongated lesions of two neighboring polyps (E-2, Fig. 2b); and (3) elongated lesions of three neighboring polyps in a row (E-3, Fig. 2c). We inflicted one lesion type (either SP, E-2, or E-3) on the upper surface of each colony using an air-pick jet (i.e., an air tube connected to the scuba regulator, which removes soft tissue causing only minor damage to the underlying skeleton). Within each size class, SP lesions were inflicted on eight colonies, eight with E-2 and eight with E-3 lesions. The average projected area (square millimeters ± SD) and perimeter length (millimeters ± SD) of these lesion types are presented in Table 1. The E-3 lesions were additionally inflicted on another size class of six very large colonies (surface area = 1569

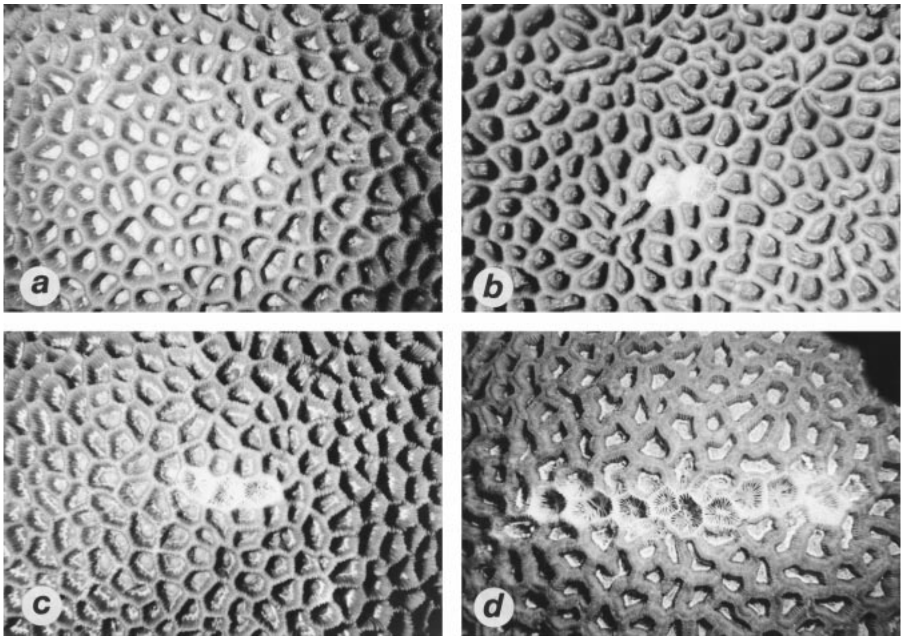

FIG. 2. Photographs (70% actual size) of the lesion types: (a) single polyp lesion (SP), (b) elongated lesion of two neighboring polyps in a row (E-2), (c) elongated lesion of three neighboring polyps in a row (E-3), and (d) elongated lesion of 10 neighboring polyps in a row (E-10).

± 228 cm^2, Fig. 1d) that were significantly larger than the large size class colonies ($P < 0.01$, *t* test).

Recovery of all lesion types (i.e., percentage reduction of the projected lesion area) was monitored monthly from early December 1994 to February 1995 by calibrated underwater photography (Nikonos-V with an 80-mm lens and close-up outfit). The first series of photographs was taken immediately after lesions were inflicted (early December 1994), and then at three consecutive monthly intervals. The percentage recovery of each lesion type, in the course of the monthly intervals, was analyzed from the photographs by image analyzer and then transformed into arcsine square root of *p* for further statistical analysis. Recovery of the various lesions as a function of time (first, second, and third month) was tested by ANOVA with repeated measures.

A decreased rate of regeneration (i.e., closure of the lesion by newly formed tissues) over time is a well known phenomenon in coral regeneration (Bak et al. 1977, Bak and Steward-van Es 1980, Bak 1983, Meesters et al. 1992, 1997*a*, Van Woesik 1998), also recently recorded in *F. favus* (Oren et al. 1997*a*). We therefore focused on the relationship between colony size and lesion recovery during the first month of regeneration (i.e., rapid regeneration phase). The effects of both lesion type (SP, E-2, or E-3) and colony size (small, intermediate, or large) on percentage recovery of the various lesions were tested by two-way ANOVA.

TABLE 1. Average dimensions (± 1 SD) of the experimentally inflicted lesions (see Fig 2 for description of lesion type).

Lesion type	Projected surface area (mm^2)	Perimeter (mm)
SP	87 ± 14	35 ± 5
E-2	182 ± 16	59 ± 8
E-3	274 ± 35	83 ± 8
E-10	958 ± 93	282 ± 23

Polyp fecundity vs. injury

F. favus is a broadcast spawner in which reproduction begins at four years when colony diameter is ~3.5 cm (Shlesinger 1985). Oogenesis in mature *F. favus* colonies starts in January and spawning takes place during June (Shlesinger 1985). The effects of injury on reproduction in *F. favus* colonies were characterized in terms of polyp fecundity (number of oocytes per polyp septum) and oocyte diameter. We tested the effect of three different lesion types (either SP, E-3, or E-10) on fecundity of 40 colonies, each ~40 cm in diameter, as follows: 16 colonies were inflicted with one SP lesion (Fig. 2a); 8 colonies with one E-3 lesion (Fig. 2c); and 16 colonies with one E-10 lesion (Fig. 2d). This experiment was initiated in February 1996, during the initial stages of *F. favus* oogenesis. It was expected that during the initial stages of oogenesis an increasing demand for resources would be required by the colony; hence, a trade-off between reproduction and regeneration would be most apparent. All lesions were inflicted on the upper central part of the spherical colonies. During this experiment, we injured the colonies in two ways: (1) one-time lesions, SP and E-10 (each $n = 8$)

TABLE 2. Average percentage (± 1 SD) lesion recovery during three consecutive monthly intervals (see Fig. 2 for description of lesion type).

		Recovery rates (%)		
Colony size	Lesion type	0–30 d	31–60 d	61–90 d
Small	SP	48.3 ± 7.3	19.8 ± 5.6	3.7 ± 3.2
	E-2	20.6 ± 4.0	2.70 ± 2.5	0.4 ± 2.3
	E-3	17.3 ± 4.2	−0.1 ± 2.3	−1.1 ± 1.9
Intermediate	SP	50.6 ± 7.0	17.1 ± 3.7	2.9 ± 2.2
	E-2	34.3 ± 5.4	17.6 ± 6.0	4.1 ± 2.8
	E-3	27.2 ± 3.9	9.50 ± 3.8	1.4 ± 2.7
Large	SP	52.0 ± 7.8	24.3 ± 4.1	4.2 ± 3.0
	E-2	32.5 ± 5.6	7.80 ± 3.0	1.2 ± 2.6
	E-3	37.8 ± 5.0	11.3 ± 3.4	1.2 ± 3.0

that were allowed to heal without any further interference until June 1996 (i.e., 5 mo between injury and polyp sampling); and (2) monthly repeated lesions, SP, E-3, and E-10 (each $n = 8$) that were also inflicted in February 1996 and thereafter re-inflicted monthly (i.e., the newly formed tissues surrounding each lesion were removed every month) throughout oogenesis. For controls, we tagged another group of 10 intact colonies of the same size. These colonies were used to determine the fecundity of intact colonies of *F. favus.*

In June 1996, (approximately two weeks before spawning), we sampled three pairs of polyps from each of the experimentally injured colonies, using a round stainless-steel corer with a cross section of 1 cm^2. Polyp samples were taken from opposite sides of the different lesions, at distances of 1, 7, and 15 cm from the center of the lesion. In the colonies bearing the E-3 and E-10 lesions, these samples were taken from the two opposite sides perpendicular to the elongated axis of the lesion. In addition, three pairs of polyps were similarly sampled from each of the 10 intact control colonies, at equal sampling distances (1, 7, and 15 cm) away from the central polyp of each colony. In the laboratory, the polyps were decalcified and five septa within each polyp were examined under a binocular microscope to determine their reproductive state. Because mature oocytes of *F. favus* are large (380 μm, Shlesinger 1985), this enabled direct measurement and total count of the oocytes. The effects of both lesion type (SP, E-3, and E-10) and sampling distances (1, 7, and 15 cm) on polyp fecundity were tested by two-way ANOVA. It should be noted that no samples were taken from marginal polyps located at the growing edges of *F. favus,* where fecundity often declines (Hughes and Jackson 1985, Chornesky and Peters 1987, Harrison and Wallace 1990).

RESULTS

Lesion recovery vs. colony size

All lesions exhibited their highest percentage recovery during the first month after injury ($P < 0.001$, repeated-measures ANOVA). During the second month, the E-2 and E-3 lesions in the small colonies had already begun to exhibit lower recovery rates, while in the larger size groups they continued to heal (Table 2). During the third month, recovery from all lesion types was negligible (Table 2).

The percentage recovery of the experimental colonies during the first month after injury is presented in Fig. 3 a–c. Lesion recovery was significantly affected by colony size and lesion type (for each factor $P = 0.0001$, two-way ANOVA, Table 3). However, there was a significant interaction between the main effects ($P = 0.019$, Table 3).

An a posteriori analysis shows that lesion recovery in the large-colony class and in the intermediate-colony class was significantly higher than in the small-colony class (Student-Newman-Keuls test [SNK], $P < 0.05$). However, there was no significant difference between the intermediate- and large-colony classes (SNK, $P > 0.05$). In addition, there were significant differences between the SP and the E-2 lesions (SNK, $P < 0.05$), and between the SP and E-3 lesions (SNK, $P < 0.05$). The recovery rates of the SP lesions do not appear to be affected by colony size (Fig. 3a). The larger E-2 lesions healed more slowly among small colonies compared to both intermediate and large colonies (Fig. 3b), accounting for part of the significant interaction between lesion type and colony size ($P < 0.019$, Table 3). In contrast to the E-2 lesions, recovery rates of the E-3 lesions varied significantly (SNK, $P < 0.05$) in each of the colony size classes (Fig. 3c). Recovery rates for E-3 lesions were highest in the large colonies (37.8 ± 5%, $n = 8$, Fig. 3c) and lowest among the small colonies (17.3 ± 4.2%, $n = 8$, Fig. 3c). This difference also contributes to the significant interaction between lesion type and colony size. When we inflicted E-3 lesions on six very large *F. favus* colonies (Fig. 1d), the average percentage recovery did not differ significantly after 1 mo from the average recovery recorded in the large colonies (t test, $P > 0.05$, Fig. 3c).

Polyp fecundity vs. injury

The mean diameter of the oocytes in the intact *F. favus* colonies was 400 ± 25 μm (mean ± 1 SD, $n = 10$). Neither lesion type, nor sampling location affected

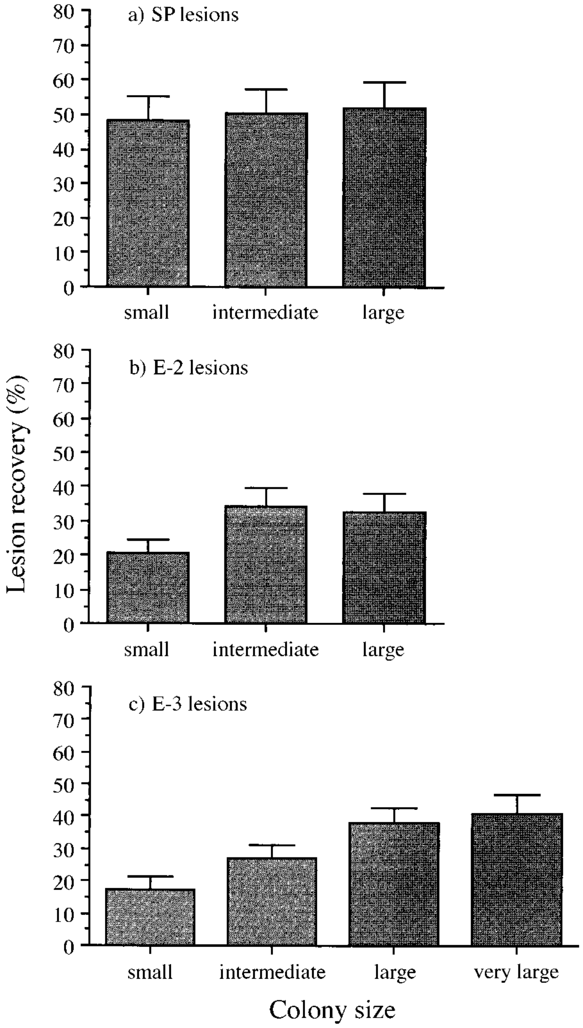

FIG. 3. Average percentage recovery rates recorded for the small, intermediate, and large *Favia favus* colonies during the first month after injury: (a) colonies inflicted with SP lesions ($n = 8$), (b) colonies inflicted with E-2 lesions ($n = 8$), and (c) colonies inflicted with E-3 lesions ($n = 8$). Error bars represent the upper range of the 95% confidence interval for the mean deduced from the calculated percentage data (arcsine square-root p transformation for percentage data).

TABLE 3. Two-way analysis of varience examining the effect of *Favia favas* colony size and lesion type on percentage recovery of the lesions (for details see Fig. 3).

Source	df	Sum of squares	Mean square	F	P
Colony size (A)	2	877.1	438.5	15.2	0.0001
Lesion type (B)	2	3281.4	1640.7	56.8	0.0001
Interaction (AB)	4	364.7	91.1	3.2	0.019
Error	72	2079.7	28.9		

the diameters of the oocytes (two-way ANOVA, $P > 0.05$). The mean fecundity of polyps in intact control colonies was 14.2 ± 2 oocytes/septum (mean ± 1 SD) and the mean fecundity of these colonies did not vary with respect to distance (1, 7, and 15 cm) from the colony center (14.1 ± 1.8, 14.4 ± 1.9 and 14.4 ± 2.3 oocytes/septum, respectively, one-way ANOVA, $P > 0.05$).

Polyp fecundity in colonies with one-time lesions

The SP and E-10 lesions (each $n = 8$) inflicted in February 1996 and allowed to heal without any further interference until June 1996 (Fig. 4) did not affect polyp fecundity at any of the sampling distances ($P > 0.05$, two-way ANOVA). That is, the average number of oocytes per septum recorded in polyps sampled at distances of 1, 7, and 15 cm from the SP lesions (14.5 ± 1.5, 13.6 ± 1.8 and 14.3 ± 2.4 oocytes/septum, respectively) and E-10 lesions (13.3 ± 1.3, 14.5 ± 2.3 and 14.1 ± 1.5 oocytes/septum, respectively) did not differ significantly from the fecundity values of the intact control colonies ($P > 0.05$, two-way ANOVA).

Polyp fecundity in colonies with monthly repeated injury

In contrast to the nonsignificant reduction in fecundity in colonies with one-time lesions (Fig. 4), monthly repetition of lesions (SP, E-3, and E-10, each $n = 8$)

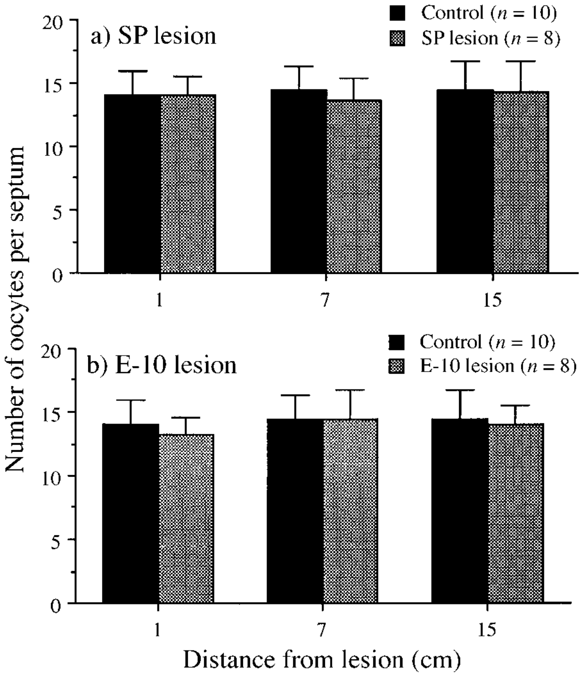

FIG. 4. Gray bars depict fecundity in terms of average oocytes per septum (+1 SD) recorded in *Favia favus* polyps sampled at distances of 1, 7, and 15 cm away from: (a) one-time SP lesions ($n = 8$), and (b) one-time E-10 lesions ($n = 8$). Black bars represent the fecundity of polyps sampled from intact control colonies ($n = 10$), at distances of 1, 7, and 15 cm away from the colony center. The lesions were inflicted on the upper surface of the colonies in February 1996 (initial oogenesis phase). Polyps for fecundity examination were sampled in June 1996.

TABLE 4. Two-way analysis of variance examining the effect of lesion type and the distance from the lesion on polyp fecundity of *Favia favus* (for details see Fig. 5).

Source	df	Sum of squares	Mean square	*F*	*P*
Lesion type (A)	2	1050.5	525.3	168.1	0.0001
Distance from lesion (B)	2	901.5	450.8	144.2	0.0001
Interaction (AB)	4	446.8	111.7	35.7	0.0001
Error	63	196.8	3.1		

significantly reduced fecundity. Both lesion type and the distance from the lesion reduced fecundity, and there was a highly significant interaction between these main effects (Table 4).

Multiple comparisons tests indicate that each of the repeated lesion treatments (SP, E-3, and E-10) differed significantly in their effect on fecundity (SNK, $P < 0.05$). We also found that each sampling distance (1, 7, and 15 cm from the lesion) differed significantly in its effect on fecundity (SNK, $P < 0.05$). The SP lesions reduced the fecundity of polyps located 1 cm away from them (3.1 ± 1.9 oocytes/septum, Fig. 5a); however, this lesion did not reduce the fecundity of polyps located at 7 and 15 cm (14.5 ± 2.3 and 14.1 ± 2.4 oocytes/septum, respectively, Fig. 5a). In contrast to the SP lesions, the repeated E-3 lesions reduced fecundity up to 7 cm (1 cm = 1 ± 1 oocytes/septum, 7 cm = 7.9 ± 2 oocytes/septum, Fig. 5b) without affecting the fecundity of polyps located at 15 cm (14 ± 2 oocytes/septum, Fig. 5b). This difference between the SP and E-3 lesions may explain part of the interaction between lesion type and distance from lesion ($P < 0.0001$, Table 4). An additional part of this interaction may be explained by the marked fecundity reductions caused by the E-10 lesions only (1 cm = 0.9 ± 1.1 oocytes/septum, 7 cm = 1.6 ± 1.2 oocytes/septum, and 15 cm = 1.75 ± 1.2 oocytes/septum, Fig. 5c).

DISCUSSION

Lesion recovery vs. colony size

The ability to regenerate is essential for coral survival. Rapid regeneration precludes settlement and subsequent overgrowth by competing organisms or total disruption of the physiological integrity of the colony (Loya 1976*c*, Wahle 1983, Brown and Howard 1985, Jokiel and Coles 1990, Cameron et al. 1991, Rogers 1993, Ward 1995). Previous studies of coral regeneration indicated that lesion recovery is a localized process, fueled energetically only by the polyps directly bordering the injured area (Bak et al. 1977, Bak and Steward-Van Es 1980, Bak 1983, Wahle 1983, Meesters et al. 1994, 1997*a*). This localized regeneration hypothesis assumes that colony-wide integration is not necessary for lesion healing, and assumes no interaction between colony size and rate of healing. The localized regeneration hypothesis is based on experiments that focused mainly on healing of small, circular lesions of ∼1 cm^2 (Wahle 1983, Lester and Bak 1985, Meesters et al. 1992, Meesters and Bak 1993, Meesters et al. 1994, Van Veghel and Bak 1994). The results of our study show that small lesions do not elicit the full regenerative potential of *F. favus* colonies, since the lesions require a minor energy investment for their recovery. The relatively small SP lesions examined in our study (∼1 cm^2) were the only ones to support the localized regeneration hypothesis, since their recovery was unaffected by colony size (Fig. 3a). However, the larger E-2 and E-3 lesions confirmed the significance

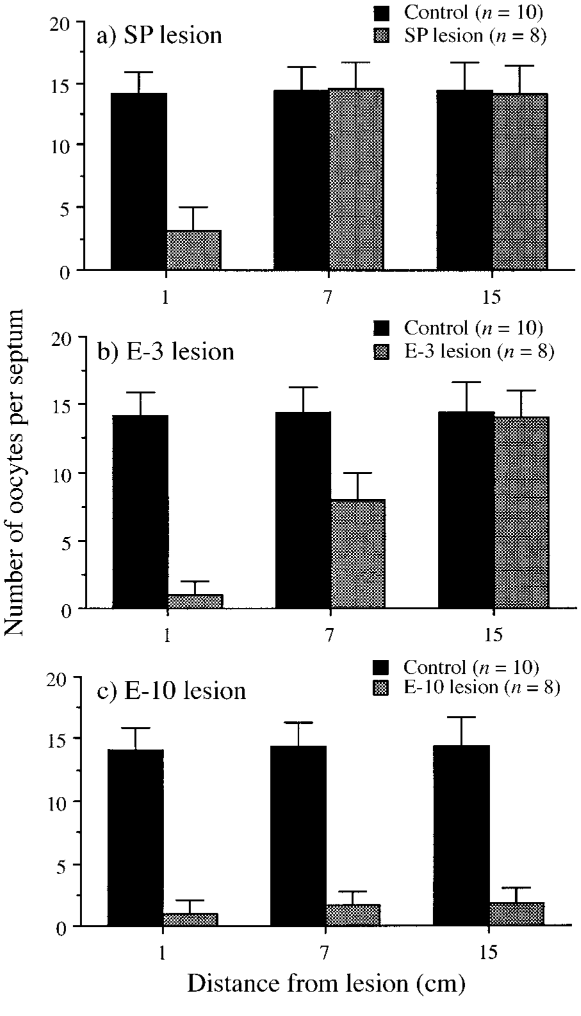

FIG. 5. Gray bars depict fecundity in terms of average oocytes per septum (± 1 SD) recorded in *Favia favus* polyps sampled at distances of 1, 7, and 15 cm away from: (a) monthly repeated SP lesions ($n = 8$), (b) monthly repeated E-3 lesions ($n = 8$), and (c) monthly repeated E-10 lesions ($n = 8$). The lesions were inflicted on the upper surface of the colonies in February 1996 (initial oogenesis phase) and then re-inflicted monthly throughout the entire oogenesis phase. Black bars present the fecundity of polyps sampled from intact control colonies ($n = 10$), at distances of 1, 7, and 15 cm away from the colony center. Polyps for fecundity assessment were sampled in June 1996.

of colony size in recovery (Fig. 3b, c). This suggests that regeneration of major injuries depends upon colony integration, and indicates that lesion characteristics (i.e., size and shape) regulate the extent of this integration.

The various recovery rates exhibited by the different lesion types indicate that *F. favus* colonies distinguish between different injuries and respond in accordance with the magnitude of the injured area. Such an ability was previously demonstrated in other colonial invertebrates, such as bryozoans (Palumbi and Jackson 1983, Harvell 1991), compound ascidians (Mackie and Singla 1983), sponges (Ayling 1981), and clonal plants suffering from localized injury or stress (Shea and Watson 1989, Jackson et al. 1990, Evans 1991, Landa et al. 1992, Hutchings and Wijesinghe 1997). Harvell and Helling (1993) suggested that the mechanisms underlying the extent of resource translocation in bryozoans and other colonial invertebrates are based on a change in the strength of the carbon sink. In clonal plants, the level of carbohydrate translocation has been suggested to serve a number of potential functions such as storage and maintenance of old roots and reserve meristems (Ho 1988, Landa et al. 1992). These functions of translocation may be important in allowing clonal plants to monopolize a local area or to explore a patchy environment (Landa et al. 1992, Wijesinghe and Handel 1994, Hutchings and Wijesinghe 1997). Thus, Hutchings and Wijesinghe (1997) and Landa et al. (1992) have shown that in clonal plants physiological integration can redistribute resources internally from sites of acquisition to areas where resources are scarce. Shea and Watson (1989) found that damaged fireweed plants (i.e., artificial leaf and flower herbivory) move assimilates throughout the plant, despite the strongly sectorial pattern of assimilate movement in undisturbed plants.

Life history traits of most colonial organisms are generally size- rather than age-dependent (Connell 1973, Hughes and Jackson 1985, Sebens 1987, Babcock 1991, Soong 1991, Hughes et al. 1992, Ward 1995, Hall and Hughes 1996). Previous studies have suggested that large size may benefit sedentary colonial organisms in maximizing their feeding capabilities and gas exchange by increasing the drag imposed by water movement (Connell 1973, Hughes and Jackson 1985, Ryland and Warner 1986, Babcock 1991, Hall and Hughes 1996). Colonial organisms exhibit considerable morphological plasticity, and the particular growth form assumed by a colony is often a function of the flow regime it inhabits (Jackson 1979, McFadden 1986). In bryozoan colonies faster ambient flow velocities were found to reduce feeding of zooids of small colonies but not of large colonies (Okamura 1984). However, McFadden (1986) noted that some soft corals undergo continual asexual fission as they grow, thereby forming aggregations of small, physiologically discrete daughter colonies. She showed that this growth strategy may be an effective means of maximizing nutrient intake per unit biomass of the genotype, in the absence of other selective forces acting on colony size. In our study, the significantly higher recovery rates attained by the large *F. favus* colonies compared to the smaller ones, reveal an additional benefit of being large.

Polyp fecundity vs. injury

Partial mortality occurs naturally in many modular organisms (Hughes and Jackson 1985, Bythell et al. 1993, Meesters et al. 1997*b*). It has been suggested for a variety of solitary and colonial taxa that regeneration and sexual reproduction compete for the available energy resources (Kojis and Quinn 1985, Szmant-Froelich 1985, Chapman et al. 1990, Harrison and Wallace 1990, Babcock 1991, Hall and Hughes 1996, Rinkevich 1996). The negative effect of injury on reproduction has already been demonstrated in many clonal organisms (bivalves, Trevaillion et al. 1970; ectoprocts and sponges, Jackson and Palumbi 1979; zoanthids, Karlson 1983) including corals (Rinkevich and Loya 1989, Van Veghel and Bak 1994, Ward 1995, Hall 1997). However, in contrast to previous studies in corals, which concluded that injury reduces coral fecundity only in the vicinity of the lesion (Wahle 1983, Van Veghel and Bak 1994, Hall 1997), our results show that the negative effect of injury on fecundity in *F. favus* may extend up to a distance of 15 cm from the injured area (Fig. 5c). This discrepancy may be explained by differences between our study and previous ones in terms of sampling intervals. For example, Van Veghel and Bak (1994) examined the fecundity of *Montastrea annularis* 2.5 mo after injury, and Hall (1997) examined fecundity in *Goniastrea retiformis, Acropora hyacinthus,* and *A. gemmifera* 9 mo after injury. Such delays between injury and measurements of fecundity may mask the full extent of the energetic link between regeneration and reproduction, as supported by the insignificant effect of the 5-mo old injuries on fecundity in *F. favus* (Fig. 4). The size of the experimentally inflicted lesions also influences the strength and persistence of this link. We found that relatively small lesions caused only localized reduction in fecundity (Fig. 5a), whereas the large lesions caused extensive reduction in fecundity up to 15 cm from the injury site (Fig. 5c). These findings indicate that small lesions induce only a localized energetic involvement for their healing, while larger ones elicit a much higher level of colony integration.

A decrease in regeneration rate over time is well known in scleractinian corals (Bak et al. 1977, Bak and Steward-van Es 1980, Bak 1983, Meesters et al. 1992, 1997*a*, Van Woesik 1998), including *F. favus* (Oren et al. 1997*a*). Our findings support this observation and in addition highlight the possibility that repeated injuries prolong the process of regeneration in its initial phase (i.e., rapid recovery phase typifying the first month after injury, Table 2). More interestingly, healing of repeated injuries in *F. favus* is favored over

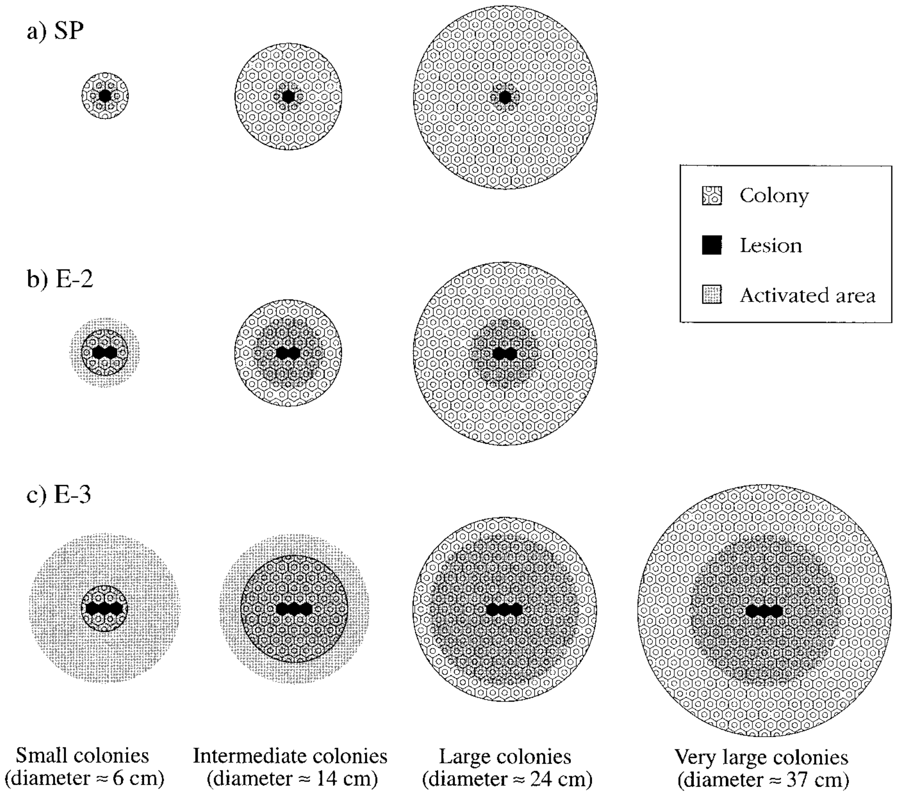

FIG. 6. Extent of colony integration during lesion recovery in *Favia favus*. Panels (a)–(c) illustrate the extent of colony integration "activated" by the SP, E-2, and E-3 lesions, respectively. The lesion types are in black; the colony portion (i.e., number of intact polyps) required for the rapid recovery of each lesion type is in transparent gray; the area containing the hexagons presents the actual surface area of the colony.

reproduction in the colony. In clonal organisms with shorter lives, this phenomenon is rare, and normally the energetic investment in reproduction does not decrease during lesion recovery (e.g., hydrozoans, Braverman 1974, Stebbing 1980; bryozoans, Harvell 1991, 1992, Harvell and Helling 1993; weedy plants, Lang and Thorpe 1983, Bloom et al. 1985, Chapman et al. 1990, Marshall 1990). Our fecundity data support the previous conclusion of Harrison and Wallace (1990), who claimed that in long-living organisms, such as corals, there is a priority of energy allocation to recovery rather than to reproduction.

Extent of colony integration during regeneration

Transport of organic compounds within hermatypic corals is well documented (Pearse and Muscatine 1971, Muscatine and Porter 1977, Taylor 1977, Muscatine et al. 1981). Pearse and Muscatine (1971) have already suggested that symbiont photosynthates are translocated throughout the coral tissue to the region of maximal demand. Recently, we have shown oriented intra-colonial transport of ^{14}C-labeled products toward regenerating areas in the massive stony corals *F. favus*, *Platygyra lamellina* (Oren et al. 1997*b*), and *Porites* sp. (Oren et al. 1998). These studies indicated that the products required for lesion recovery are supplied not only by polyps directly bordering the injured area, but also by polyps located farther away (up to 10 cm from the injured area), and that the extent of this translocation is regulated by the size and shape of the injury. The results of the present study further support and extend these findings, since both experiments (i.e., colony size vs. lesion recovery and lesion recovery vs. polyp fecundity) reveal extensive colony integration during the regeneration process. We presume that integration following injury is attained by translocation and utilization of photosynthetic energy sources, rather than translocation of stem cells as suggested by Rinkevich (1996). The fact that ^{14}C-labeled products are also incorporated into recovering skeletons of *F. favus* (Oren et al. 1997*b*) supports this contention. Furthermore, *F. favus* cells experimentally labeled with ^{3}H-thymidine at restricted sites located 3–5 cm from the injury site failed to show any significant cell translocation toward recuperating areas (U. Oren, *unpublished data*).

The similar recovery rates elicited by the small SP lesions (average lesion size = 87 ± 14 mm^2, Table 1) in each of the coral size classes (Fig. 3a) indicate that their rapid recovery requires a low extent of colony integration: the number of intact polyps necessary for their healing is very small and is confined within the actual surface area of the small colonies (Fig. 6a). The localized reduction in fecundity caused by the SP lesions (Fig. 5a) further indicates that they activate a small colony area for their recovery. It is possible, in the specific case of the small SP lesions, that the bordering polyps are the only ones to be involved in regeneration, as previously suggested (Bak et al. 1977, Bak and Steward-Van Es 1980, Bak 1983, Wahle 1983, Meesters et al. 1994, 1997*a*).

The E-2 lesions exhibited low recovery rates in the small colonies, and relatively high and similar recovery rates in both intermediate and large colonies (Fig. 3b). This indicates that the number of intact polyps required for their recovery is greater than the actual surface area of the small colonies, but is still confined to within the actual surface area of both the intermediate and large colonies, as illustrated in Fig. 6b.

The E-3 lesions (Table 1) recovered more quickly in the large-colony size class compared to the intermediate and small ones (Fig. 3c), suggesting that the colony portion of the surface area required for their rapid recovery is larger than the actual surface area of the small and intermediate colonies, as illustrated in Fig. 6c. The similar recovery rates exhibited by the E-3 lesions in the two largest size classes (Fig. 3c) suggest that the colony portion of surface area required for their rapid recovery is smaller than the actual surface area of the large colonies. The extended reduction in fecundity (up to the distance of 7 cm, Fig. 5b) caused by the E-3 lesion compared to the localized fecundity reduction caused by the SP lesions (only at a distance of 1 cm, Fig. 5a) further indicates that larger lesions activate larger portions of the colony surface area for their recovery. Our contention of increasing levels of colony energy involvement with larger lesion size was reinforced by the high extent of reduction in fecundity (up to the distance of 15 cm, Fig. 5c) caused by the E-10 lesions.

An important consequence of modularity may be reflected by the ability to reprioritize pathways of resource transport among the units of a colony, in response to environmental changes and various stresses caused by biotic and abiotic factors. The present study highlights the advantages of a larger colony size in achieving faster recovery from injuries, and that the extent of energy reallocation by a colony is dictated by the injury size. We suggest that the existence of injury thresholds, which determine energy allocation and intra-colonial translocation of energy products within a colony toward regions of maximal demand, is a basic life-preserving ability and one of the most important advantages of clonal and colonial organisms.

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