Lesion regeneration in the branching coral *Acropora palmata*: effects of colonization, colony size, lesion size, and lesion shape

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ABSTRACT: The regeneration of lesions caused by the fragmentation of *Acropora palmata* colonies was examined in the northern Florida Reef Tract, USA. The recovery of *A. palmata* lesions followed a negative exponential model. Lesion regeneration was influenced by the initial size and perimeter of lesions, but was not affected by the presence of colonizers or the size of the colonies or fragments bearing the lesions. Significant differences in regeneration rates were found among small (0–5 cm^2), medium (5–10 cm^2), and large (10–20 cm^2) lesions. The largest lesions (>20 cm^2) did not show a significant recovery over time. When the total area recovered during the first 30 d was normalized to initial perimeter length, both small and large lesions regenerated similar amounts of tissue. However, closure rates (the rate of movement of the growing lip towards the center of the lesion) were significantly faster for small lesions (7.3 [SE = 1.3] mm mo^{-1}) compared to medium (4.9 [0.4] mm mo^{-1}) and large (4.3 [0.3] mm mo^{-1}) lesions. Results of this study support previous studies suggesting that the regeneration process is sustained by a limited, initial amount of energy that may be determined by the extent of damage experienced by the colony.

KEY WORDS: Coral lesions · Lesion regeneration · *Acropora palmata* · Coral fragmentation · Lesion size and shape

INTRODUCTION

Coral colonies experience frequent, small-scale disturbances that result in the partial loss of tissue. Injuries or lesions on corals can be created by physical and biological agents such as storms, sedimentation, diseases, high temperature, predation, competition for primary space, human activities, and pollution (Connell 1973, Glynn 1973, Loya 1976, Bak & Van Es 1980, Bak & Criens 1981, Knowlton et al. 1981, 1988, Rogers et al. 1982, Bak 1983, Hutchings 1986, Hawkins & Roberts 1992, Bythell & Sheppard 1993, Guzmán et al. 1994). The regeneration of lesions can represent a significant drain on the energetic resources available for coral maintenance, growth and reproduction, and can

have long-lasting effects on the composition and survivorship of reef communities (Loya 1976, Gladfelter et al. 1977, Bak 1983, Wahle 1983, Kobayashi 1984, Liddle & Kay 1987, Meesters et al. 1992, 1994, 1996, Guzmán et al. 1994, Van Veghel & Bak 1994, Lirman 1997).

Previous research on the regeneration of experimentally inflicted coral lesions has shown that several factors can influence the recovery process, including lesion size and shape, overall extent of damage, position of lesions within a colony, and size of the colonies bearing the lesions (Loya 1976, Bak et al. 1977, Bak & Van Es 1980, Bak 1983, Chadwick & Loya 1990, Meesters et al. 1992, 1994, 1997, Oren et al. 1997, van Woesik 1998). The fragmentation of *Acropora palmata* colonies by storms and boat impacts provided an excellent opportunity to test the effects of these and some additional factors on the regeneration of lesions created by the detachment of coral branches.

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Acropora palmata (elkhorn coral) is a dominant species in the shallow, exposed areas of reefs throughout the Caribbean (Wells 1988). The dominance of this coral species in high-energy zones has been attributed to its plastic morphology, strong skeleton, rapid growth, and ability to form new colonies from fragments (Graus et al. 1977, Chamberlain 1978, Gladfelter et al. 1978, Schuhmacher & Plewka 1981, Highsmith 1982, Gladfelter 1991, Lirman & Fong 1997). *A. palmata* has also good regenerative capabilities, as evidenced by the rapid recovery of small, circular experimental lesions (Bak 1983, Meesters & Bak 1995). Colonies of *A. palmata* on the Florida Reef Tract undergo periodic fragmentation (Lirman 1997), and the resulting lesions can be colonized by algae and other organisms (Rogers et al. 1982, Bak 1983). Since linear extension of broken *A. palmata* branches can be delayed or slowed down until the resulting lesions are completely recovered, and the colonization of lesions by bioeroders can weaken colonies (Hernandez-Ávila et al. 1977, Mitchell-Tapping 1983), it is of great importance for *A. palmata* colonies to recover these lesions rapidly.

Although large scale, acute events such as hurricanes, disease or predator outbreaks, and bleaching concentrate scientific attention due to their often catastrophic effects; smaller scale, chronic disturbances may also have considerable impacts on coral populations. The regeneration of lesions caused by the periodic fragmentation of *Acropora palmata* by storms or boat impacts may represent a significant energetic drain for damaged colonies and, considering that lesion regeneration can affect other vital processes such as growth and sexual reproduction, it may play a significant role in the long-term survivorship of *A. palmata* populations in the Florida Reef Tract. The objectives of this study were to test if regeneration of *A. palmata* lesions caused by fragmentation is affected by: (1) the size of the colonies or fragments bearing the lesions; (2) the size and shape of lesions; and (3) the colonization of lesions by algae and other organisms.

METHODS

The recovery of lesions on *Acropora palmata* colonies and fragments was examined at Elkhorn Reef (25° 21.766′ N, 80° 09.961′ W) in the northern Florida Reef Tract, USA. This reef has a well-developed *A. palmata* coral population that undergoes periodic fragmentation (Lirman & Fong 1995, 1996). The lesions monitored in this study were all produced by the detachment of *A. palmata* branches from adult colonies as a result of storms or boat impacts.

Elkhorn Reef was surveyed at weekly intervals during the summers of 1994 and 1995. Whenever boat or storm damage was detected (as evidenced by the appearance of coral lesions showing a bright, white skeleton devoid of significant algal colonization), lesions were labeled and subsequently photographed at different time intervals with a Nikonos V camera equipped with a 28 mm lens and close-up lens outfit. Outlines for all lesions were scanned and surface area and perimeter for each lesion were estimated with NIH Image Software.

The recovery process was evaluated by calculating: (1) regeneration rates (change in lesion size with time; $cm^2 \ d^{-1}$), (2) linear closure rates (rate of movement of the growing lip towards the center of the lesion; mm mo^{-1}), and (3) total amount of tissue regenerated during the first 30 d (cm^2). To determine closure rates, 12 radial measurements were taken for each lesion from the edge of the growing lip towards the center of the lesion along 6 axes drawn on acetate paper and placed over the photographs. Measurement were taken at each time interval and averaged for small, medium, and large lesions.

Effects of colonizers. Thirty lesions created by a boat grounding in June 1994 were tagged and assigned to 1 of 2 groups at random. Lesions in the experimental group were brushed free of any filamentous algae at bi-weekly intervals using a plastic denture brush. The algal removal was done with extreme care to avoid damaging the coral polyps developing along the growing edge of the lesions. To minimize any differences between groups resulting from the stress caused by brushing, the brush was passed very lightly over the control lesions without removing any of the colonizing algae.

Effects of lesion size and shape. Seventy *Acropora palmata* lesions caused by Tropical Storm Gordon were marked in November 1994, less than a week after the storm, and their recovery followed through time. Lesions were grouped into 4 size categories: small (0–5 cm^2), medium (5–10 cm^2), large (10–20 cm^2), and extra-large (>20 cm^2).

Recovery of lesions on colonies and fragments. In August 1995, a boat impacted the *Acropora palmata* population on Elkhorn Reef and many of the fragments produced could be found resting on top of their colony of origin or on the bottom nearby. Newly created fragments were chosen so that their lesions matched those on their colonies of origin, and lesions were tagged on both colonies and fragments. The fragments were tied with monofilament line to large pieces of coral rubble and placed on the bottom near the standing colonies. Maximum linear diameter of colonies bearing the lesions and surface area of the fragments were estimated to evaluate the effects of colony and fragment size on the regeneration of lesions.

Statistical methods. Size of lesions was regressed against time since injury. To normalize the data, lesion size was logarithmically transformed ($\ln(x+1)$; Sokal & Rohlf 1981). Data for each lesion were fitted to the exponential model: lesion size = $a \cdot e^{(-b \cdot days)}$ using a least squares procedure. Regression parameters (slope and intercept) were averaged within groups (Meesters et al. 1997). Differences among regeneration rates were tested among all groups with ANCOVA (Sokal & Rohlf 1981). The relationships between lesion size, perimeter, shape (perimeter/area ratio), colony and fragment size, and the amount of tissue regenerated during the first 30 d were tested with regression.

RESULTS

A thick, growing lip developed within 2 wk around the edges of the lesions (Fig. 1). New polyps could be observed behind this growing lip as it moved towards the center of the lesion. Regeneration rates of lesions on *Acropora palmata* decreased exponentially with time as shown by a good fit to the exponential model (Table 1). An exception to this pattern are the extra-large lesions (<20 cm^2) that did not show a significant recovery over the time of the study. Regeneration rates were strongly size-dependent (Table 1, Fig. 2), and significant differences in regeneration rates were found among all 3 groups tested (i.e., small, medium, and large; ANCOVA, p < 0.05). Given the lack of regeneration, extra-large lesions were excluded from the analysis.
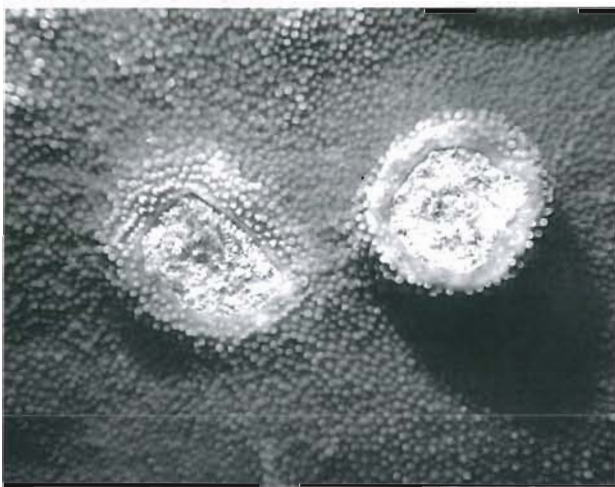

Fig. 1. *Acropora palmata*. Close-up photograph of a lesion caused by the detachment of a branch during Tropical Storm Gordon (November 1994) showing the formation of the growing lip that moves towards the center of the lesion as regeneration proceeds

Linear closure rates decreased exponentially with time for all lesion sizes (Fig. 3) and were influenced by initial lesion size. Mean closure rates for the first 30 d were significantly faster for small lesions (7.3 [SE = 1.3] mm mo^{-1}) compared to medium (4.9 [0.4] mm mo^{-1}) and large (4.3 [0.3] mm mo^{-1}) lesions (ANCOVA, p < 0.05, Tukey *a posteriori* comparisons test). No significant differences in closure rates were found between medium and large lesions.

For the lesions created by Tropical Storm Gordon on Elkhorn Reef, lesion perimeter and initial area were positively correlated (r = 0.90). In contrast, the complexity of lesion shape, as estimated by the perimeter/area-ratio, was negatively correlated with lesion size (r = -0.91). The total amount of tissue regenerated during the first 30 d was significantly affected by lesion size (Fig. 4A, r^2 = 0.59, p < 0.01) and perimeter (Fig. 4B, r^2 = 0.50, p < 0.01). When the area recovered during this period was normalized to initial perimeter length, although large lesions appeared to recover a larger amount of tissue, no significant relationships were established (Fig. 4C, r^2 = 0.08, p > 0.1).

Control lesions that were heavily colonized by algae shortly after fragmentation recovered faster than brushed lesions devoid of colonizers (Table 1, ANCOVA, p < 0.05). At the end of this experiment (138 d), control colonies had recovered a larger percentage of their initial lesion area (94%) compared to brushed lesions (81%).

Although standing colonies regenerated lesions of equal size slightly faster than fragments placed on the bottom, this difference was not statistically significant (Table 1, ANCOVA, p > 0.1). After 3 mo, colonies recovered a larger percentage of their original lesion area (89%) compared to fragments (70%). No significant relationships were found between either colony or fragment size and the total amount of tissue regenerated during the first 30 d (regression, p > 0.1).

Table 1. Regression parameters for the regression between lesion size and regeneration time. Regression parameters for each group represent means (±1 SE) of individual lesions fitted to the model: lesion size = $a \cdot e^{(-b \cdot days)}$. ns = not significant, p_{reg} = probabiltiy of regression

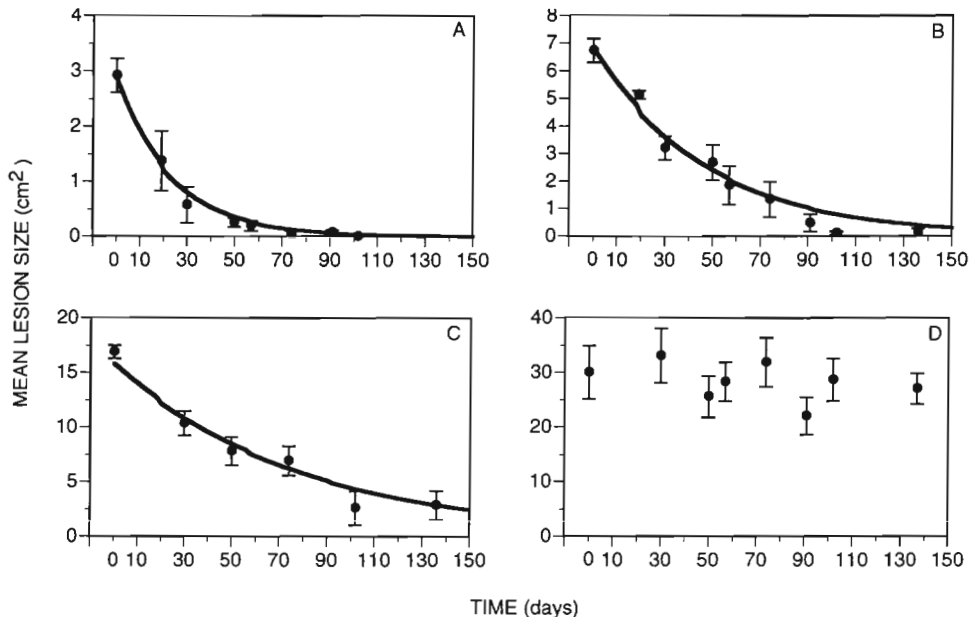| Lesions	N	Intercept	Reg. coeff.	r^2	p_{reg}
Small	20	3.1 (0.4)	−0.040 (0.007)	0.86	<0.01
Medium	20	7.1 (0.5)	−0.021 (0.002)	0.77	<0.01
Large	12	16.2 (0.7)	−0.012 (0.002)	0.73	<0.01
Extra-large	12	31.3	ns	ns	ns
Controls	15	6.2 (1.3)	−0.032 (0.002)	0.73	<0.01
Brushed	15	6.7 (1.1)	−0.024 (0.003)	0.66	<0.05
Colonies	15	7.8 (1.3)	−0.018 (0.004)	0.73	<0.01
Fragments	15	7.3 (1.3)	−0.013 (0.004)	0.50	<0.05

Fig. 2. *Acropora palmata*. Change in mean size (±1 SEM) with time for (A) small (<5 cm², n = 20), (B) medium (5–10 cm², n = 20), (C) large (10–20 cm², n = 12), and (D) extra-large (>20 cm², n = 12) lesions. Regression lines are averaged for individual lesions within groups fitted to the model: lesion size = $a \cdot e^{(-b \cdot days)}$. Regression coefficients can be found in Table 1

DISCUSSION

Lesion regeneration on corals has been studied extensively using mainly small (<5 cm²), experimentally-created lesions. In this study, it is shown that several previous findings can also be applied to the regeneration of a wide range of lesion sizes caused by fragmen-

Fig. 3. *Acropora palmata*. Mean closure rates (movement of the growing lip towards center of lesion, ±1 SEM). Small = <5 cm², medium = 5–10 cm², large = 10–20 cm². Given the lack of recovery observed for lesions >20 cm², these were excluded from the analyses

tation of *Acropora palmata* colonies. For *A. palmata* lesions created by storms or boat groundings, regeneration rates were dependent on initial lesion size and decreased exponentially with time. Whereas more than half of small lesions (<5 cm²) recovered completely during the first 30 d, the largest lesions (>20 cm²) did not show any significant recovery over time. Similar effects of initial lesion size on recovery rates has been documented for experimental lesions (e.g., Bak & van Es 1980, Oren et al. 1997, van Woesik 1998).

The exponential decrease in both lesion size and the movement rate of the growing lip with time observed here support the hypothesis that the regeneration of coral lesions is fueled by an initial, limited supply of energy drawn from the undamaged tissue on the colony bearing the lesion as proposed by Bak (1983) and Meesters et al. (1992, 1994, 1997). The faster initial closure rates of small lesions indicate that the regeneration process and the amount of resources available for regeneration may be related to the extent of the damage experienced by the fragmented colonies. In *Acropora palmata*, the size of a lesion is determined by the cross section of the broken branch. The detachment of a large branch results in a significant biomass loss and a potential drain of resources, resulting in the slower closure rates recorded for larger lesions.

The recovery of *Acropora palmata* lesions was influenced by lesion size and shape. The total amount of tissue recovered during the first month of regeneration was proportional to lesion size and perimeter. How-
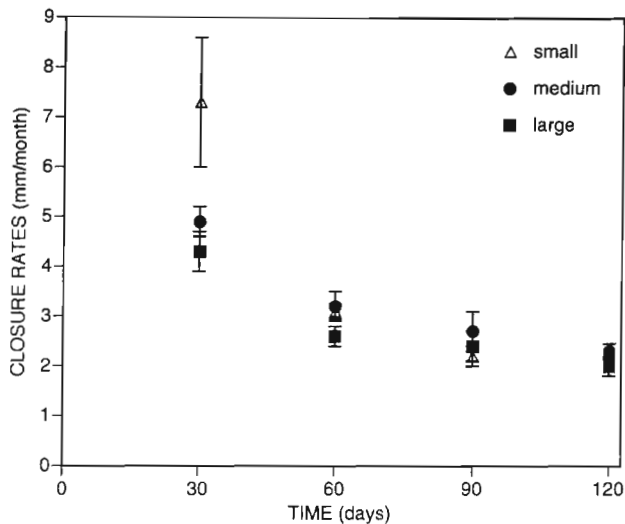
ever, when the amount of tissue recovered was normalized to initial perimeter length, small and large lesions recovered similar amounts of tissue. Similar results were obtained by Meesters et al. (1997) who concluded that perimeter length is the most important variable affecting lesion regeneration. In contrast, Oren et al. (1997) found that lesions with longer perimeters recovered relatively more tissue than lesions with shorter perimeters. Although these reports highlight the influence of perimeter length and lesion shape, the faster closure rates documented here for

lesions with small initial areas and short perimeters suggest that size effects cannot be dismissed. Further studies such as those by Oren et al. (1997) that manipulate both size and shape are needed to fully understand the role of lesion size and perimeter on regeneration.

Another factor that may influence the recovery of lesions is their location within the damaged colonies. Meesters & Bak (1995) documented a regeneration-potential gradient along *Acropora palmata* branches that decreases as distance from the branch tips increases. This regeneration gradient was attributed to the younger age of polyps at the branch tips, and the general mobilization of energy from basal portions towards the ends of branches where linear extension takes place (Pearse & Muscatine 1971). The role of lesion position on regeneration of lesions created by fragmentation was not tested in this study but merits further investigation.

Previous studies suggest that *Acropora palmata* fragments and colonies may have different resource allocation strategies after fragmentation. Since lesions on colonies have to heal completely before linear extension of the damaged branches can resume (Lirman 1997), the rapid regeneration of lesions on colonies is crucial for the continued growth of damaged colonies. In contrast, newly-formed fragments direct most of their energy initially towards cementation to the bottom, and new growth was found to be delayed until this process is complete (Lirman & Fong 1997). Based on this, it was hypothesized that lesions on colonies would recover faster than on fragments. Results presented here did not support the differential resource allocation hypothesis; although colonies regenerated a larger percentage of their initial lesion area compared to fragments, no significant differences in recovery rates were detected, suggesting that lesion recovery may be an important process for both *A. palmata* colonies and fragments.

The effects of colony size on lesion regeneration have been studied previously with differing results. Connell (1973) and Loya (1976) showed reduced regeneration capabilities in small coral colonies (8 to 80 cm^2), whereas Bak & Van Es (1980) and Wahle (1983) did not find any relationship between colony size and regeneration rates. Moreover, Chadwick & Loya (1990) found that small solitary corals can recover faster than larger corals with similar amounts of damage. In this study, no significant relationship was found between regeneration of lesions and fragment or colony size, indicating that even small colonies (50 cm in diameter) and fragments (50 cm^2) are capable of regenerating lesions at rates similar to those of larger units. This supports the concept that the resources required for regeneration can be drawn from the tissue
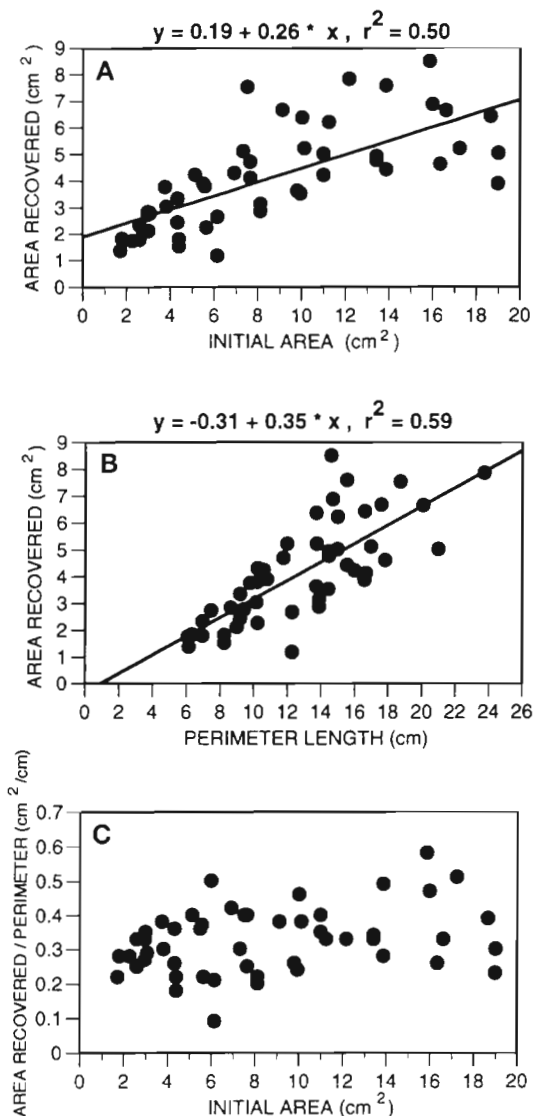

Fig. 4. *Acropora palmata*. Relationships between area recovered during the first month and (A) initial lesion size, (B) initial perimeter length, and (C) between area recovered per perimeter length and initial lesion size. Given the lack of recovery observed for lesions >20 cm^2, these were excluded from the analyses

found in the vicinity of the lesion, and that if the ratio of damaged to undamaged polyps within a certain area of the colony is low enough to support regeneration, lesions may recover independently of colony size (Meesters et al. 1994).

The colonization of skeletal lesions can be rapid, and a dense community of filamentous algae can develop within 2 to 3 wk. Bak & Van Es (1980) and Van Woesik (1998) observed that the regeneration of coral lesions can proceed even in the presence of colonizing organisms. In fact, Rogers et al. (1982) showed that the recovering coral tissue can grow right over the algal community. In the algal removal experiment, control lesions grew faster and recovered a higher percentage of their initial lesion area than lesions that were scraped free of colonizers, confirming that lesion regeneration can take place normally even in the presence of colonizers. Although extreme care was exercised to avoid damaging coral polyps along the periphery of the lesions, the slower regeneration of brushed lesions may be attributed to the stress created by the removal of colonizers.

The recovery of *Acropora palmata* lesions caused by fragmentation provided a test for several hypotheses proposed by previous studies based on the regeneration of experimental lesions. Results presented here show that, as was the case for the recovery of small (1–5 cm^2) circular lesions on several coral species, recovery can be affected by lesion size, shape, and the extent of the initial damage. Similarly, the recovery of *A. palmata* lesions of a wide size range (1–20 cm^2) was found to be dependent on a limited amount of energy that results in an initial burst of regeneration, followed by an exponential response in recovery rates with time.

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