Regeneration after experimental breakage in the solitary reef coral *Fungia granulosa* Klunzinger, 1879

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Abstract: As a result of experimental breakage, polyps of the solitary reef coral *Fungia granulosa* Klunzinger, 1879 formed fragments that fractured either radially along the septa, or perpendicular to the septal edges. Recovery was strongly dependent on fracture orientation, fragment size, and percent breakage. Corals with 51-90% breakage either regenerated very slowly or lost mass and died during the 8 months of the study. In those with 10-50% breakage, both tissue and skeletal regeneration increased with the proportion of the fracture perpendicular to the septa. It appears that only the septal edges at the outer polyp margin and the inner mouth area are able to add skeletal mass, while the sides of the septa are unable to initiate regrowth. Small corals (<50 g) with 10-40% breakage recovered much more rapidly than did larger (>50 g) individuals (calculated time to regain initial size = 4-10 months for small corals). These rates were at least twice as slow as those known for a colonial coral in the same reef area. Regeneration of the fragments also depended upon the presence of a mouth. Skeletal regrowth began as a fan of septa that radiated from the mouth area and spread along the septal sides. It is concluded that, when broken by disturbance, small individuals can rapidly recover from 10-40% skeletal loss. The ability to regenerate is exhibited by many members of the family Fungiidae, and has developed into autotomy and asexual maintenance of populations in some species.

Key words: Coral; Fragmentation; *Fungia*; Growth; Regeneration; Skeleton

INTRODUCTION

Coral reefs are damaged by a variety of disturbances. Tropical storms may reduce reefs to rubble (Highsmith et al., 1980; Woodley et al., 1981; Dollar, 1982; Rogers et al., 1982), and predators, disease, and low tides may remove the live tissues of scleractinian corals while leaving their skeletons intact (Loya, 1976a; Bak & Criens, 1981; Pearson, 1981). Two major processes contribute to the recovery of reef areas damaged through disturbance: colonization by planktonic coral larvae, and regeneration of remaining coral fragments (Loya, 1976a). Much documentation of reef recovery has focussed on the influx of larvae (Grigg & Maragos, 1974; Loya, 1976a; review by Pearson, 1981). However, coral regrowth from existing fragments may contribute substantially to the
reestablishment of coral communities (Highsmith et al., 1980; Dollar, 1982; Highsmith, 1982).

All scleractinian corals thus far examined can regenerate at least partially after breakage (Highsmith, 1982), and the colonies of at least one species may recover fully in only 2–5 months (Loya, 1976b). Regeneration occurs in two distinct steps. First, coral tissue regrows over the wound. If this does not occur rapidly, boring organisms and pathogenic bacteria may invade the exposed skeleton and retard or prevent regrowth (Bak & Criens, 1981; Highsmith et al., 1983). Some corals can grow tissue over the colonizing organisms that settle on wounds (Bak et al., 1977; Rogers et al., 1982). Second, the new tissue secretes calcium carbonate to replace lost skeletal parts. Skeletal growth may be oriented toward the damaged areas, resulting in the eventual recovery of coral symmetry (Loya, 1976b; Yamashiro et al., 1989). If detached, the regenerating coral fragment also may recement to the substratum and thus regain stability (Bak & Criens, 1982; Highsmith, 1982).

In some scleractinian corals, fragmentation and regeneration are a natural means of asexual reproduction. Several colonial and solitary corals spread by breakage and regrowth of fragments (Highsmith, 1982; Nishihira & Poung-In, 1989). Most corals in the family Fungiidae detach early in life from stalks, which then may regenerate new polyps or colonies (Wells, 1966; Yamashiro & Yamazato, 1987; Hoeksema, 1989). However, quantitative data are scanty concerning rates and processes of coral regeneration after experimental breakage. Microarchitectural changes after breakage have been described in Acropora hawaiiensis (Isa, 1987). Regeneration after lesion formation (Bak et al., 1977) and after experimental breakage (Bak & Criens, 1981) have been examined in some Caribbean corals. Kawaguti (1937) and Abe (1940) observed regeneration in fungiid corals, but their studies were qualitative and short-term. The only long-term detailed studies of scleractinian regrowth after experimental breakage have focussed on a single colonial species (Loya, 1976b; Rinkevich & Loya, 1989).

No quantitative data exist on rates and processes of experimental regeneration in solitary scleractinian corals. Regrowth in solitary corals is fundamentally different from that in colonial corals, in that the former must restore the lost parts of a single polyp, while the latter asexually bud new polyps. In addition, little is known about size–growth relationships in solitary reef corals (Abe, 1940; Bablet, 1985).

Solitary free-living corals of the family Fungiidae are common on many Indo–Pacific coral reefs (Wells, 1966; Loya & Slobodkin, 1971; Sheppard, 1981; Veron & Hodgson, 1989). They are among the few scleractinian corals able to survive on soft substrata (Highsmith, 1982; Nishihira & Poung-In, 1989), and may serve as nuclei for the formation of new patch reefs, as well as extend existing reefs onto adjacent sandy areas (Sheppard, 1981). Due to their relatively thin, disk shape, solitary fungiids are susceptible to fragmentation by water motion or other disturbances (Wells, 1966; Hoeksema, 1989). Thus their ability to regenerate after breakage may be important to the establishment and extension of certain coral reefs.

This paper examines regeneration and size–growth relationships in Fungia granulosa.
REGENERATION IN A SOLITARY CORAL

Klunzinger, 1879, a common solitary coral on the Red Sea reefs of Eilat. We show that regrowth after experimental breakage strongly depends on fragment size, percent breakage, and the orientation of the fracture area. Complete recovery is estimated to take at least twice as long as in a colonial branching coral from the same reef area.

MATERIALS AND METHODS

This study was conducted on the fringing coral reef adjacent to the H. Steinitz Marine Biology Laboratory, Eilat, Gulf of Eilat, Red Sea. At least 6 species of free-living fungiid corals occur on the reefs of Eilat (Loya & Slobodkin, 1971; Hoeksema, 1989). We used a common solitary species, Fungia (Wellsofungia) granulosa, as identified by Hoeksema (1989).

In March 1989, undamaged polyps of F. granulosa were collected from the reef and transported to the laboratory. The live wet mass of each coral was obtained by placing it on a paper towel for a few minutes to remove excess moisture, then weighing it in air on an electronic balance to the nearest 0.01 g. We then photographed each coral and traced its outline onto paper. The polyps were divided into two size classes by live wet mass: small (4-50 g) (= 30-60 mm polyp length) and large (51-150 g) (= 61-90 mm polyp length). Then they were broken into fragments with the aid of a hammer and chisel. We broke the corals into fragment shapes that mimicked those found in the natural population. In each size class, 7-14 corals were subjected to each of the following treatments: (1) 10-50% breakage (= 10-50% mass removed), (2) 51-90% breakage (= 51-90% of mass removed), and (3) undamaged, intact controls. Immediately after breakage, the corals were remeasured and returned to the reef. The control and broken corals were interspersed at 10 m depth in an area where abundant fungiids naturally occur. At 2, 4, and 8 months after breakage, the corals were recollected and remeasured in the laboratory. The corals were kept continually submerged in flowing seawater while in the laboratory, and did not appear to suffer damage associated with handling. All corals were returned to the reef within a few days after each sampling period. Individuals were identifiable throughout the study by their unique features, such as nicks and septal irregularities. Data in the text are presented as $\bar{x} \pm SD$. Arcsine transformations were performed to normalize the percentage data for all parametric statistical tests.

RESULTS

MORPHOLOGY OF THE FRACTURES

Two types of fractures were created during breakage of the polyps. One type occurred along the radiating septa, and produced wedge-shaped fragments (Fig. 1A,B). The other occurred perpendicular to the septa, across the septal edges (Fig. 1C). Some fragments
possessed both types of fractures, or a gradation between the two (Fig. 1D,E). Each fragment was scored according to the percent of its total fracture area that occurred perpendicular to the septa (examples in legend to Fig. 1).

Fig. 1. Morphology of fractures and regeneration in *F. granulosa*. Scale bars = 1 cm. (A) Wedge-shaped skeletal fragments created by fractures along the septa (= 0% perpendicular to the septa). (B) Regenerating fan of septa radiating from the mouth area of a live fragment, at 8 months after breakage. Note that none of the fractures is oriented perpendicular to the septa, and that regeneration has occurred only at the mouth area. (C) Live fragment with fracture oriented across the septal edges (= 100% perpendicular to the septa). (D,E) Live fragments with mixed fractures. Note that fracture areas perpendicular to the septa have regenerated, while areas parallel are dead. 30 and 60% of the total fracture areas are perpendicular to the septa, respectively. (F) Naturally regenerating live polyp in the field (mouth is at center).
TISSUE REGENERATION

Some broken corals completely covered their fractures with living tissue in < 1 month, while others did not during the entire 8 months of the study. In the corals with 10–50% breakage (Fig. 1C,E), tissue regeneration was related to fracture orientation: the percent fracture area covered by regenerated tissue correlated positively with the percent of the fracture area perpendicular to the septa (product–moment correlation test, $r = 0.96$, $P < 0.001$) (Fig. 2). Fracture areas along the septal edges healed, while those parallel to the septa did not (Fig. 1). Corals with 51–90% breakage ($n = 25$) regenerated tissue over significantly less of their fracture areas than did corals with 10–50% breakage (Mann–Whitney $U$ test, $U = 356$, $P < 0.01$), and this amount did not correlate with fracture orientation (product–moment correlation test, $r = 0.277$, $P = 0.181$).

The fracture areas that remained exposed became covered with fouling organisms (Fig. 1B,D,E), including algae, tunicates and sponges. A bivalve settled on and grew over one fracture. Fouling organisms were observed on the fractures within 2 wk, and persisted on exposed areas for at least 8 months.

Skeletal breakage also affected the tissue covering the unbroken parts of the corals. The level of tissue necrosis varied significantly among the three breakage categories (Fig. 3) (Kruskal–Wallis test, $H = 9.215$, $P < 0.01$), and was highest in the corals with 51–90% breakage. The amount of tissue necrosis decreased with coral size in all breakage categories (Fig. 3).

All of the intact control corals ($n = 21$) survived throughout the study, while 88% of the broken corals ($n = 43$) survived. All of the corals that died were small (< 5 g each) and had suffered 80–90% breakage.
SKELETAL REGENERATION

Skeletal growth in both small and large corals decreased significantly with percent breakage (product-moment correlation tests, \( r = 0.646, P < 0.001 \), \( r = 0.871, P < 0.001 \), respectively), and at > 80\% breakage, most corals lost mass (Fig. 4). For corals with 10–40\% breakage, small individuals regenerated their skeletons significantly faster than did large polyps; however, at > 40\% breakage this difference disappeared (Mann–Whitney \( U \) tests, \( U = 42, P < 0.01 \), \( U = 159, P > 0.01 \), respectively). The skeletal growth rates of intact control corals did not differ significantly from those of corals with 10–50\% breakage, in both small and large size classes (Mann–Whitney \( U \) tests, \( U = 87, P = 0.37 \), \( U = 33, P = 0.56 \), respectively). The growth of intact corals corresponded to linear extension rates of 0–10 mm yr\(^{-1}\) and mass changes of - 1.7 (some specimens lost weight) to 16.2 g yr\(^{-1}\).
Skeletal growth rate decreased exponentially with size in both intact controls and corals with 10–50% breakage (Fig. 5), but not in those with 51–90% breakage.

Assuming linear growth between sampling periods, the estimated time to regain original size after 10–40% breakage in small corals is calculated as 6.74 ± 2.47 months (range = 4–10 months). Large corals, and corals with >40% breakage grew very little, or not at all (Fig. 4), and so their time to regain initial size was not calculated.

The corals that added skeletal mass directed their growth toward the missing parts of the polyp. Regenerated areas were clearly visible due to their lighter colored tissue, and septa oriented non-parallel to those of the original fragment (Fig. 1). This redirection of growth toward damaged areas resulted in the eventual restoration of polyp symmetry (Fig. 1).
Skeletal regeneration also varied with the size and orientation of the fractures. Corals with 10–50% breakage decreased regeneration rate exponentially with fracture size (product–moment correlation test, $r = 0.712, P < 0.001$) (Fig. 6), while corals with 51–90% breakage showed no significant correlation (product–moment correlation test, $r = 0.149; P = 0.478$). In addition, skeletal growth increased with the percent of the fracture perpendicular to the septa, both in corals with 10–50% breakage (product–moment correlation test, $r = 0.743, P < 0.001, n = 18$) (Fig. 7), and in corals with 51–90% breakage (product–moment correlation test, $r = 0.531, P < 0.01$). This interaction of healing and fracture orientation is similar to that observed for tissue regeneration (Fig. 2).
The presence of a mouth appeared to be important for regrowth. A significantly higher percentage of fragments possessing mouths regenerated (89.3%, n = 28) than did those lacking mouths (6.7%, n = 15) (G test of independence, G = 15.64, P < 0.01). New growth often began as a fan of septa radiating from the mouth area, in both naturally (Fig. 1F) and experimentally broken corals (Fig. 1B). All skeletal growth originated at either the inner septal edges that form the mouth (Fig. 1B), or at the outer septal edges that form the polyp margin (Fig. 1C), never along the septal sides (Fig. 1D).

![Diagram](image1)

Fig. 6. Skeletal growth (% mass change · 8 months⁻¹) vs. surface area of fractures (mm²) in damaged polyps (n = 18) of *F. granulosa* with 10–50% breakage.

![Diagram](image2)

Fig. 7. Correlation of skeletal growth and fracture orientation in damaged polyps (n = 18) of *F. granulosa*. Only corals with 10–50% breakage are shown. See Fig. 1 for explanation of fracture orientation.
Tissue Regeneration

The regrowth of live tissue over exposed fractures is the first step to recovery in broken scleractinian corals (Loya, 1976b; Bak et al., 1977; Rogers et al., 1982; Rinkevich & Loya, 1989). In damaged polyps of *F. grunulosa*, the sides of the septa appeared unable to regenerate tissue (Figs. 1,2). This may be explained by the normal growth pattern of these corals. During normal growth, solitary fungiid corals add new tissue and skeleton almost entirely at the outer edges of the septa, along the margin of the disk (Yamashiro et al., 1989). Growth does not usually occur along the sides of the septa, and in fact these areas may be unable to grow.

Moreover, the morphology of the tissue–skeletal relationship in these corals may determine the sites at which tissue regrowth can occur. Because the skeleton is narrow at the septal edges, when the polyp is broken, the ratio of surface area of tissue/skeleton is much higher and wounds can heal more rapidly here than along the septal sides. Similarly, branching corals may cover rapidly their wounds at the tips of narrow broken branches, because only a small skeletal area is exposed on each branch (Loya, 1976b). In massive colonial corals, small lesions heal more rapidly than do large lesions, due to the smaller skeletal area exposed (Bak et al., 1977).

A combination of factors may have led to the weight loss and eventual death (Figs. 3,5) of the corals that did not regenerate tissue over their fractures. Boring organisms may have invaded the coral skeleton through the exposed area, and excavated the interior of the coral (Highsmith et al., 1983). Physical abrasion also may have occurred at the exposed skeletal surfaces (Woodley et al., 1981). Finally, pathogenic bacteria such as white band disease may have entered the surrounding coral tissue through the wound, and eventually killed the remainder of the fragment (Bak & Criens, 1981; Gladfelter, 1982). As in other broken corals, the survivorship of fragments was size-dependent (Fig. 3; Loya, 1976b; Highsmith et al., 1980).

Skeletal Regeneration

The estimated recovery time of 4–10 months for small corals (30–60 mm length) of *F. grunulosa* with 10–40% breakage was about twice that for small colonies (30–45 mm diameter) of the branching coral *Stylophora pistillata* (2–5 months) from the same reef area (Loya, 1976b). However, large corals (61–90 mm length) of *F. grunulosa* appeared to regenerate much more slowly, if at all (Fig. 4b), in contrast to large (50–90 mm diameter) *S. pistillata* (Loya, 1976b). In both species, the most rapid growth occurred in small corals with <40% breakage (Fig. 4; Loya, 1976b). These solitary corals behaved similarly to the colonial coral *S. pistillata* (Loya, 1976b) in that they redirected growth toward damaged areas to regain lost symmetry. However, the regenerating solitary corals did not shown accelerated growth in comparison with intact controls (Fig. 4), as found in *S. pistillata* (Loya, 1976b).
The relatively long regeneration time of *F. granulosa* compared with *S. pistillata* reflects the generally slower growth rates of solitary and massive corals (linear extension rates = 4–20 mm yr\(^{-1}\)) versus branching species (100–200 mm yr\(^{-1}\)) (reviewed by Buddemeier & Kinzie, 1976). *S. pistillata* in an r-strategist in that it recruits and grows rapidly, but is a poor competitor (Loya, 1976c). In contrast, solitary fungiid corals grow (Abe, 1940; Buddemeier et al., 1974) and recruit (Schuhmacher, 1977) comparatively slowly, but are superior in terms of competition for living space (Chadwick, 1988, and references therein).

The observed exponential decrease in relative growth rate with size in this solitary coral (Fig. 5) also has been documented for many colonial reef corals (Goreau & Goreau, 1960; review by Buddemeier & Kinzie, 1976; Hughes & Connell, 1987) and for an aposymbiotic cold-water coral (Fadlallah, 1983). Slower growth in large vs. small individuals of *F. granulosa* suggests diversion of energy into sexual reproduction rather than into somatic growth later in life, as discussed by Loya (1976c, 1985).

The expression of growth as mass gained per unit mass of coral (Figs. 4–7) does not reveal the absolute growth rate of each individual. However, these units are ecologically meaningful because they express the amount of calcification per unit of coral size. Units of relative or percent growth have been adopted in many studies on coral growth (Goreau & Goreau, 1960; Loya, 1976c; Fadlallah, 1983; Hughes & Connell, 1987). Buddemeier & Kinzie (1976), however, have argued cogently for the use of absolute growth units, which have been included here for comparison (see Results).

The orientation of the breakage site on *F. granulosa* polyps appeared to greatly affect skeletal regeneration. This phenomenon has not been reported to occur in broken colonial corals. This may be due to the nature of skeletal regeneration in solitary vs. colonial corals. Whereas a colonial coral regenerates by budding new polyps, a broken solitary coral regrows the lost parts of a single polyp, and certain areas of the polyp may be physiologically unable to regenerate new skeleton. In *F. granulosa*, all skeletal regeneration commenced at the outer edges of the septa, or at the mouth area along the inner septal edges, and never along the septal sides (Figs 1,2,7). After new septa were produced, they deposited calcium carbonate along the sides of the original, damaged septa (Fig. 1). It may be that the lateral sides of the septa in scleractinian corals are incapable of active skeletal growth. This possibility needs to be investigated in other coral species.

Yamashiro et al. (1989) found that in the solitary coral *Diaseris fragilis* (= *Fungia/Cycloseris* fragilis in Hoeksema, 1989) growth occurred almost exclusively at the septal edges, in both intact and autotomized corals. Cessation of growth at several points along the polyp margin led to the formation of slits in the polyp wall that facilitated fragmentation. In *D. fragilis*, all fragments retained part of the mouth area (= the inner septal edges), and regrowth began here and proceeded along the septal sides (Yamashiro et al., 1989). Thus, the morphology of regeneration appears to be very similar in both autotomized (Yamashiro et al., 1989) and experimentally (Fig. 1B) and naturally broken (Fig. 1F) solitary funguids.
The present study is the first to experimentally demonstrate the importance of the mouth area in coral regeneration. These results, together with those on natural regrowth (Yamashiro et al., 1989), support the idea that the mouth is a central organizing area for regeneration and probably for normal development in scleractinian polyps.

REGENERATION IN NATURALLY BROKEN CORALS

The ability to regenerate lost parts appears to be widespread in fungiid corals. Kawaguti (1937) documented regrowth after experimental breakage in F. actiniformis, and the present paper in an additional species. In addition, all fungiids thus far studied can regenerate new polyps or colonies from the stalk left after the normal detachment of juveniles (Wells, 1966; Yamashiro & Yamazato, 1987; Hoeksema, 1989). Most members of the subgenus Fungia (Cycloseris) (= Diaseris) appear to actively autotomize as a means of asexual reproduction (Hoeksema, 1989). In this subgenus, the ability to regenerate after fragmentation has allowed the asexual maintenance and spread of populations on soft substrata, where larval propagules cannot survive (Nishihira & Poug-In, 1989).

The development of radial slits in F. fragilis (= Diaseris fragilis) allows polyps to cover the sides of the septa almost entirely with tissue prior to breakage (Yamashiro et al., 1989). This avoids the exposure of bare skeleton which may lead to skeletal erosion and tissue necrosis in experimentally broken corals (Figs. 1,3,4). Thus, slit formation probably increases the survival rate of regenerating fragments, especially of small fragments that often die when artificially fractured (Fig. 3).

Broken and regenerated polyps often are found in field populations of fungiids (Hoeksema, 1989). The flat, relatively thin disk shape and free-living existence of many fungiid corals makes them particularly vulnerable to skeletal breakage from human interference and storms. Their capacity for regeneration thus may be important to their survival in areas subject to frequent disturbances, or on soft substrates where fragmentation is the only viable means of population growth (Nishihira & Poug-In, 1989).

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