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Skeletal regeneration in a Red Sea scleractinian coral population

CORALS may be harmed by their natural enemies or by environmental conditions. The ability of scleractinian corals to regenerate damaged parts has been documented qualitatively by many investigators[1–10], but detailed quantitative data on the rate of regeneration have not been reported. Most reports dealing with the destruction of coral reefs have emphasised the long time required for recovery[11]. I have found, however, that the rate of skeletal regeneration in a population of the branched coral *Stylophora pistillata* (Esper) is surprisingly fast. During the first 2 months of regeneration, damaged colonies grew twice as fast as intact control colonies. Within the same colony, damaged branches grew faster than intact branches, which resulted in a tendency to regain symmetry lost through breakage. Larger colonies showed a better capacity to resist damage than smaller colonies.

Stylophora pistillata is one of the most important scleractinian corals in the Gulf of Eilat[12] because of its abundance and major contribution to the reef framework[13]. Seventy colonies of *S. pistillata*, growing in shallow water (3–4 m deep) at Eilat, were damaged by breaking some of their branches with a diver's knife. All damaged colonies were numbered by means of plastic tags and photographed before and after breakage, as well as during recovery. The growth rate of approximately 200 intact colonies studied previously in the same area[14] served as a control for comparative analysis. The study lasted from August 11 1974 to October 12 1975. The length, width and height of each colony were measured under water every 2–3 months. Length is defined as the distance across a coral between the tips of branches which are farthest apart; width is a measure perpendicular to the length axis; height is orthogonal to the width and length axes. Since the shape of *S. pistillata* approximates a sphere, the colonies were divided into size groups, according to the geometric mean of their radius, $\bar{r}$ (Fig. 1).

The initial response of the coral to breakage was to cover the exposed areas rapidly with living tissue to prevent settlement of fouling organisms. Fishelson[8] found that after a catastrophic low tide that caused partial desiccation or death of many colonies of Red Sea scleractinian corals, regeneration in branched colonies started with reorganisation and reactivation of the peripheral soft tissue along the line of destruction. The regenerated tissue grew over fouling algae, which had settled on the dead coral skeleton, resulting in a "sandwich structure", in which the old skeleton and newly deposited skeleton engulfed the algae. According to Connell[15], if tissue damage on a coral surface is sufficiently large, recovery may not be rapid enough to exclude colonisation by fouling organisms, that may ultimately kill the coral. Fifty-one out of seventy damaged colonies survived throughout the study (Fig. 1). Most of the smallest colonies ($\bar{r}$ < 1.00 cm), however, were covered by filamentous algae within a few days of being broken, and shortly afterwards they were dead. This confirms Connell's[15] conclusions that larger colonies have a better capacity to resist invasion and damage than smaller ones of the same species.

Figure 1 presents the extent of skeletal damage caused to each size category and the rate of regeneration and growth.

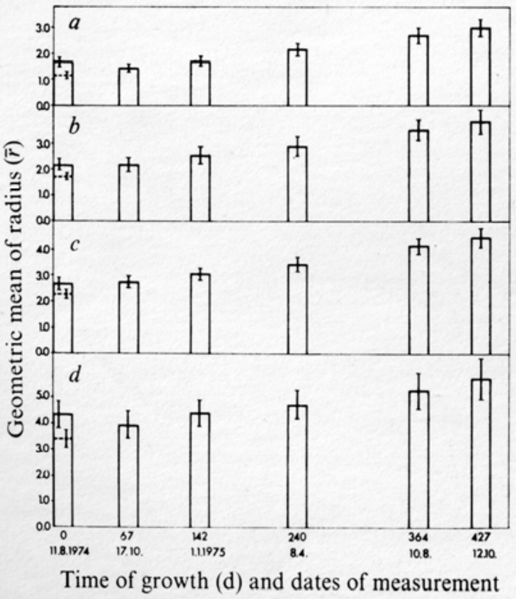

Fig. 1 Skeletal growth rate in damaged colonies of *S. pistillata*. The corals were divided into size groups according to their geometric mean radius ($\bar{r}$) after breakage. ($\bar{r} = (l \times w \times h)^{1/3}/2$ where l is length, w is width, and h is height (cm).) The $\bar{r}$ of each size group is given (in cm) by the height of the bars. The vertical lines in the middle of the bars represent the standard deviations. The horizontal broken line in the left bar of each size group represent $\bar{r}$ after breakage. The percentage decrease in $\bar{r}$ after breakage for each size group was 29.08, 19.46, 14.20 and 21.74 in order of smallest to largest size group. The estimated number of days of growth (±s.d.) required to regain original $\bar{r}$ were 122±17, 67±7, 51±5 and 116±15 in order of smallest to largest size group. The expected number of days of growth required to regain original $\bar{r}$ after 25% breakage are 104±14, 86±10, 90±9 and 133±17 in order of smallest to largest size category. N, number of colonies measured. *a*, $N = 11$, $\bar{r} = 1.00–1.50$; *b*, $N = 14$, $\bar{r} = 1.51–2.00$; *c*, $N = 16$, $\bar{r} = 2.01–3.00$; *d*, $N = 10$, $\bar{r} = 3.01–4.00$.

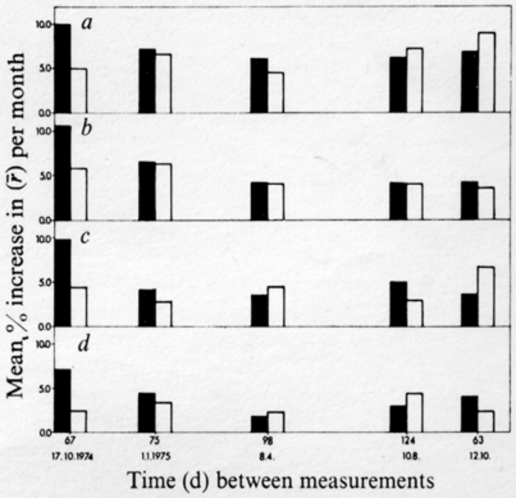

Fig. 2 Comparison between the mean percentage increase in geometric mean of radius ($\bar{r}$) per month ($\Delta\bar{r}$ %/month) of damaged corals (black bars) and intact control corals, belonging to the same size interval (blank bars). Average values of $\bar{r}$, in the different dates of measurements are given in Fig. 1.

$$\Delta\bar{r}\ \%/\text{month} = \frac{30}{\Delta t}\,\frac{(\bar{r}_t - \bar{r}_{t-1}) \times 100}{\bar{r}_{t-1}}$$

where Δt is time (d) between measurements.

N_1, Number of colonies measured in regenerating groups; N_2, number of colonies measured in intact control groups. *a*, $\bar{r} = 1.00–1.50$, $N_1 = 11$, $N_2 = 23$; *b*, $\bar{r} = 1.51–2.00$, $N_1 = 14$, $N_2 = 19$; *c*, $\bar{r} = 2.01–3.00$, $N_1 = 16$, $N_2 = 17$; *d*, $\bar{r} = 3.01–4.00$, $N_1 = 10$, $N_2 = 9$.

The percentage decrease in $\bar{r}$ of different size groups varied from 14% to 29%. Assuming linear growth between the periods when measurements were taken, and taking into account the different standard deviations of $\bar{r}$, within each size category (Fig. 1), I estimated the number of days of growth required by the damaged corals to attain their size before breakage (see legend to Fig. 1). To compare the different size groups with respect to their capacity for skeletal regeneration, the expected average number of days of growth to regain original size after 25% breakage was calculated for each group (see legend to Fig. 1). The largest size group ($\bar{r} = 3.01$–4.00 cm) required a significantly longer time to attain its original size than did any of the other groups (t tests, $P < 0.05$), which strengthens the assertion that this species grows more slowly as it ages[14].

Figure 2 compares the mean percentage increases in $\bar{r}$ per month ($\Delta\bar{r}$ %/month) in the damaged corals and the intact control groups. During the first 2 months of regeneration, all damaged corals grew twice as fast as the intact control corals. After the damaged colonies had regained their original size, no significant differences were observed between the average growth rate of damaged and intact colonies (t tests, $P > 0.05$). In general, the growth of both regenerating and intact colonies slowed down during the winter (December to April).

Ninety per cent of the population exhibited accelerated growth at the damaged portions of the colony (compared with intact branches) as well as a tendency to regain symmetry lost by breakage. Similar observations have been reported before[3–6]. This phenomenon suggests some integrated response between the parts of a single colony[15]: individual polyps act synergistically to differentiate tissue and create edge zones of proliferation[16], and locally to accelerate skeletogenesis. The idea of integrated response is strengthened by evidence of transfer of energy-rich organic products between adjacent parts of a colony[17]. Thus, Pearse and Muscatine[17] suggested that translocated products of zooxanthellae may enhance calcification rates in corals, by serving either as specific substrates in the organic matrix or as general energy sources.

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