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The Red Sea coral *Stylophora pistillata* is an *r* strategist

MacArthur and Wilson[1] coined the terms *r* selection and *K* selection to describe two general kinds of selection they believed could be functioning in nature (*K* refers to carrying capacity and *r* to maximal intrinsic rate of natural increase, r_m). As originally defined, the *r* and *K* selection concepts postulated that alternative genotypes within a species possessed somewhat divergent life history characteristics: genotypes with a high r_m were suggested to have a relatively low *K* and vice versa[1]. Thus, *r* selection occurs in a fluctuating environment when there is no crowding and it is more important to increase the size of the population. *K* selection occurs in stable environments when population size is always near the maximum and increasing efficiency in resource use is required for the production of a few but extremely fit offspring. Pianka[2] extended these concepts to include comparisons of individuals of different species. He postulated that no organism is completely *r* selected or completely *K* selected, but all must reach some compromise between the two extremes. Thus, a given species could be visualised along an *r*–*K* continuum and identified by a set of *r* and *K* characteristics[2].

Stylophora pistillata (Esper), an important scleractinian coral in the Gulf of Eilat[3] has most of the *r* characteristics summarised by Pianka[2]—success in colonising unpredictable reef habitats, rapid development, great population turnover, early reproduction, high r_m, small body size, short life span, density independent mortality (often catastrophic), wide dispersal gradient and poor competitive ability. Most of the other scleractinian corals of Eilat have the opposite characteristics (K strategists), or are ranked below *S. pistillata* in their proximity to the *r* end of the *r*—*K* continuum.

The coral reefs of Eilat constitute a physically controlled coral community near the reef flat (the *r* end of the *r*–*K* continuum), existing side by side with the subtidal biologically accommodated community, increasing in diversity (and environmental predictability) to a depth of 50 m (ref. 3). The relative unpredictability of the reef flat at Eilat (in the sense of Slobodkin and Sanders[4] and Colwell[5]), compared with the deep reef, may be best demonstrated by the catastrophic and extremely low tides which occur periodically but unpredictably along the northern Gulf of Eilat. Thus, in September 1970, an unexpected and extremely low tide caused 80–90% mortality of the hermatypic coral communities on the reef flats of Eilat[6]. In spite of its small colony size[3], *S. pistillata* is among the most important

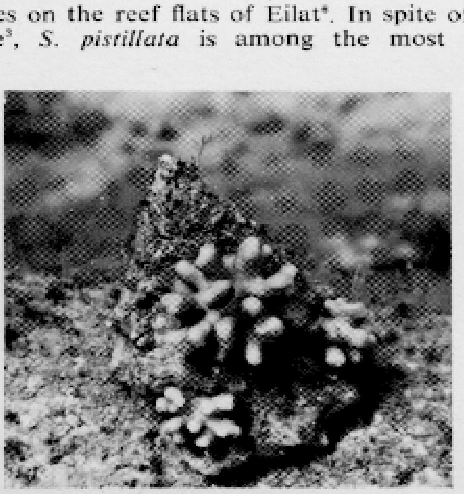

Fig. 1 *S. pistillata* colonies growing on the shell of the gastropod *Trochus dentatus*.

Table 1 Effect of initial size of colony on growth rate

Size interval of radius ($\bar{r}$)*	Number of colonies measured	$\bar{d}_1$(cm)†	$\bar{d}_2$(cm)‡	$\frac{\Delta\bar{d}}{\text{yr}}$(cm)§	$\frac{\Delta\bar{d}}{\text{yr}}$ %‖
0.01–0.50	20	0.840 (0.135)	5.104 (0.792)	1.909 (0.254)	227.26
0.51–1.00	52	1.543 (0.267)	7.170 (0.924)	2.520 (0.253)	163.32
1.01–1.50	32	2.536 (0.304)	7.800 (1.168)	2.357 (0.345)	92.94
1.51–2.00	30	3.546 (0.296)	8.958 (0.426)	2.423 (0.271)	68.33
2.01–3.00	32	4.978 (0.530)	10.682 (1.072)	2.554 (0.347)	51.30
3.01–4.00	9	6.892 (0.636)	12.510 (0.650)	2.516 (0.337)	36.50
4.01–5.00	9	8.714 (0.330)	14.055 (1.406)	2.392 (0.276)	27.45

s.d. given in parentheses.

*Geometric mean radius $\bar{r} = (l \times w \times h)^{1/3}/2$.

†Geometric mean diameter at the beginning of measurements.

‡Geometric mean diameter at the end of measurements.

§Mean increase in diameter per year $= 365\,(\bar{d}_2 - \bar{d}_1)/815$.

‖Mean % increase in diameter per year $= \left(\frac{\Delta\bar{d}}{\text{yr}}/\bar{d}_1\right) \times 100$.

frame builders of the reef flat because of its abundance[7]. Before the catastrophic low tide of 1970, it composed ~25% of the total living coverage of the reef flat of the nature reserve at Eilat. During the low tide, 98% of *S. pistillata* colonies on the reef flat were killed, while other abundant species were somewhat less affected[6].

In such uncertain conditions, the optimal strategy is to put all possible matter and energy into reproduction, and to produce as many progeny as possible[8]. Histological examination of gonads, in collections made every 2 weeks for a year, revealed that *S. pistillata* breeds during the 8 months from December to July. Colonies 4.0–5.0 cm in diameter already contained ripe eggs[8]. Three years of periodical observations of larval settlement, development and growth indicated that colonies of this size are between 2 and 3 yr old (unpublished). The only other coral species for which estimates have been made of the time required to reach sexual maturity are *Favia doreyensis* (8 yr) and *Fungia actiniformis* (10 yr) in the Great Barrier Reef[10]. In general, reduction of the age for first reproduction and an increase in progeny number tend to increase *r* (ref. 11). Envelopment of *S. pistillata* colonies with plankton nets facilitated the capture of the released planulae, and showed that a moderate-sized colony may produce 100–400 planulae within 2 h after sunset[9].

Perhaps the most important feature of *S. pistillata* as an *r* strategist is that it is usually the pioneer coral species colonising 'new environments'[1] or unexploited habitats. Such species have variously been called 'fugitive'[12], 'opportunistic'[13], 'colonising'[14], 'weedy'[15], or '*r* selected'[1]. The seawater system of the Marine Biological Laboratory at Eilat provided a good opportunity to examine the fast-colonising capabilities of this species. Ninety-five colonies of *S. pistillata* were counted in 1972 on the seawater pipe (installed in 1967, 20 m long, 30 cm in diameter), and about 100 colonies on the concrete blocks used to hold down the pipe. Other hermatypic species counted on the seawater system were *Millepora dichotoma* (ten colonies), *Favia favus* (five colonies), *Cyphastrea microphthalma* (two colonies) and *Acropora variabilis* (one colony). A new seawater pipe, installed parallel to the old pipe was colonised by 45 colonies of *S. pistillata* 8 months later. In April 1975, 92 colonies of this species were recorded, and in August 1975, 173 colonies of this species were counted

Fig. 2 Healthy colonies of *S. pistillata* (branched colony) and *F. favus* (massive colony) were brought into physical contact on October 7, 1974 (left). On January 1, 1975, the terminal tissues of the branches of *S. pistillata* which touched the *Favia* colony were seen to be killed (right). *S. pistillata* branches within a distance of 2.0–2.5 cm from the *Favia* colony were also killed, which might indicate the furthest distance the mesenterial filaments of *F. favus* can reach. Note that the differences in magnification of the two photographs are due to the use of different lenses of the Nikonos II underwater camera. The left photograph was taken with a 35-mm lens, while the right photograph was taken with a 28-mm lens.

on the same pipe. So far, no other scleractinian corals have settled on the new pipe. Another demonstration of the opportunistic colonising character of *S. pistillata* is the fact that it may be found growing in shallow lagoons attached to the roots of the mangrove tree *Avicenia maritima*, where water temperature during low tide reaches 36 °C and salinity 48‰. It may also be found attached to the shells of mobile animals, such as the gastropod *Trochus dentatus* (Fig. 1) or to any other newly introduced foreign matter on the reef.

The growth rate of *S. pistillata* is among the fastest of the scleractinian corals in the Gulf of Eilat (Y.L., unpublished and L. Fishelson, personal communication). The growth rate of 184 colonies, of various sizes, of *S. pistillata* was studied during 815 d (May 17, 1973–August 10, 1975). Each colony was numbered by a plastic tag and length, width and height were measured approximately every 3 months. Length is chosen as the distance across a coral between the tips of the branches which are furthest apart. Width is chosen as the distance perpendicular to the length axis. Height is chosen as a measure perpendicular to the length and width axes. When colonies died during the study, I tagged and measured new and healthy colonies of similar dimensions growing nearby. The shape of *S. pistillata* approximates a sphere. The colonies were, therefore, divided into size groups according to the geometric mean of their radius $(\overline{r})$. Although the range of the mean increase in diameter per year ($\Delta\overline{d}$ yr^{-1}) was very narrow (1.9–2.5 cm), among the size groups studied (Table 1), the smallest colonies increased in absolute size significantly less compared with the larger ones (t tests, $P<0.05$). The rate of growth per year of the largest size category, however, was approximately eight times slower than that of the smallest category, which might indicate that like all other organisms they grow proportionately more slowly as they age. The largest colonies of *S. pistillata* do not reach a geometric mean diameter greater than 30–35 cm (ref. 3). It is possible that when a colony reaches the size of sexual maturity (diameter of 4.0–5.0 cm) much of its energy is channelled into the production of sexual cells rather than growth, which considerably lowers the growth rate. Regeneration in this species is also very fast: some accidentally broken branches grew 5.0–7.0 cm yr^{-1}. During this study, 80–85% of the original population of *S. pistillata* died. The causes of mortality were mainly abiotic (winter storms or heavy sedimentation). Nevertheless, many new colonies settled in the same study area. Thus, *S. pistillata* has a short life span and high population turnover in comparison to the other coral species in the same area.

Although the vast majority of the hermatypic corals at Eilat are limited to the deep reef (20–50 m depth) and are rare, *S. pistillata* is very abundant and shows a wide range of dispersal, from the lagoon to the deepest point of the reef[7]. When space becomes limiting, however, *S. pistillata* is the first to be competitively excluded by the deep reef coral specialists.

The area exposed to light is one of the most important limiting factors on a coral reef. Corals compete with each other for available space in various ways[10] one of which takes the form of aggressive behaviour[16]. Observations and experiments (Fig. 2) with *S. pistillata* rank this species among the lowest in aggressive hierarchy. That is, on physical contact with most of the other hermatypic corals it is competitively excluded. Abundant species which occur together with *S. pistillata* on the reef flat proved to be more aggressive. Thus, species such as *F. favus, Platygyra lamellina, Echinopora gemmacea, Goniastrea retiformis, Pocillopora danae, M. dichotoma,* and many others can be seen to extrude their mesenterial filaments and digest away the living tissue of the neighbouring *S. pistillata*. No damaging effects have been observed, however, when several colonies of *S. pistillata* were brought into physical contact with each other.

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