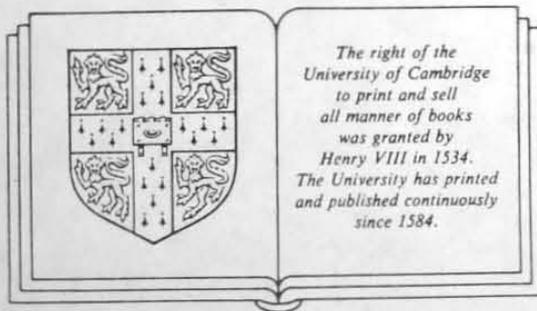


The Earth in Transition

Patterns and Processes of Biotic Impoverishment

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18 Changes in a Red Sea Coral Community Structure: A Long-Term Case History Study

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Editor's Note: Occasionally a circumstance arises in nature that, treated imaginatively by a talented scholar, allows unusual insights into cause and effect. Yossi Loya, an Israeli ecologist, recognized such an opportunity in his studies of coral communities in the Gulf of Eilat and has used the chance to gather further insights into the patterns of diversity and dominance in natural communities under various types of stress. His observations not only reveal further details of the structure and function of these communities, but reconfirm the importance of long-continued studies of specific sites to determine changes under way in response to intensified human influence, details that would otherwise be lost as the biota moves inexorably through various stages of impoverishment in response to uncontrolled chronic disturbance.

Loya offers a case history study of a coral reef exposed in different places to oil pollution and climatic anomalies. While the circumstances seem specialized, they are increasingly common, and the observations Loya makes are emergent generalities, broadly applicable to natural communities under stress.

Introduction: The Reef at Eilat

One of the central questions of ecology deals with the mechanisms that generate and maintain the diversity of organisms. There have been many varied opinions and large numbers of publications on this subject. I review here briefly our studies of community structure of corals at Eilat, Red Sea, describe changes that have occurred in coral diversity due to human versus natural disturbances, and discuss mechanisms that promote and maintain high diversity of corals on the reef-flats of Eilat.

The Gulf of Eilat is the most eastern of the two northern horns of the Red Sea, which are separated by the Sinai Peninsula. The reefs of Eilat are of the fringing type. Scleractinian corals are the most important hermatypic (reef-building) organisms (Loya and Slobodkin 1971). Hermatypic corals play a key role in forming the structure of coral reefs and in providing substrate and shelter for a wide variety of organisms. Acute damage to corals may result in a collapse of the complex community of organisms that live in close association with the corals.

In 1969 the community structure of the coral reefs at Eilat was studied in

detail by means of line transects, each 10 m long (Loya 1972). Any coral species which overlapped the line was recorded, and its projected length on the line was measured to the nearest centimeter. The line transects were surveyed from the reef-flat to 30 m depth. Only the changes that occurred in the community structure of corals on the reef-flats will be dealt with here. The data provide estimates of the number of coral species, number of colonies, percentage of total living coverage, and diversity of corals.

The average number of species per transect obtained on reef-flats not affected by human activity at the northern Gulf of Eilat was 13.5 ± 3.8 to 15.7 ± 3.4 species per 10 m transect (Loya 1972, 1976a). This diversity is high for corals measured on reef-flats (within-habitat diversity) in view of the low total number of species known from Eilat (about 100) (Loya and Slobodkin 1971). By contrast, about 330 coral species are known from the Great Barrier Reef (GBR) (Veron 1986). However, within-habitat diversity on reef-flats is lower both on Australian inshore fringing reefs and on the GBR proper than in Eilat.

A similar method suggested by Loya (1972) was used to study coral diversity on GBR reef-flats. The only difference was the length of transect lines, 30 m, used in all GBR studies. On Lizard Island the average number of coral species per transect was 11.1 ± 4.8 (data computed from Pichon and Morrissey 1981); on Heron Island, 9.8 ± 4.1 (data computed from 12 transects; Loya, Pichon, Weizman-Best, unpublished data); and on an inshore reef at Magnetic Island, 4.8 ± 3.7 (data computed from 9 transects; Pichon, Loya, and Bull, unpublished data). Clearly, if GBR data are computed for a 10 m transect as in Eilat, the average number of species per transect will decrease. Since information on community structure and species diversity of GBR corals is limited, generalization on local patterns of diversity would be premature. I would like, however, to present two hypotheses developed from our long-term studies at Eilat to help interpret causes of the high coral diversity on the reef-flats of the northern Gulf of Eilat.

Changes in Coral Community Structure Due to Natural Catastrophes and Human Disturbance

The nature reserve of the Eilat coral reefs is 3 km south of the general port of Eilat, approximately 1 km south of two major oil terminals (Figure 18.1).

Oil tankers using the port of Eilat after 1970 caused two to three major oil spills monthly, during which the nature reserve was completely blackened by oil. Between 1971 and 1973, ninety-five such spills were reported to the Israeli Ministry of Transportation. This chronic oil pollution continued until 1978–1979. From that period until the present only sporadic and minor oil

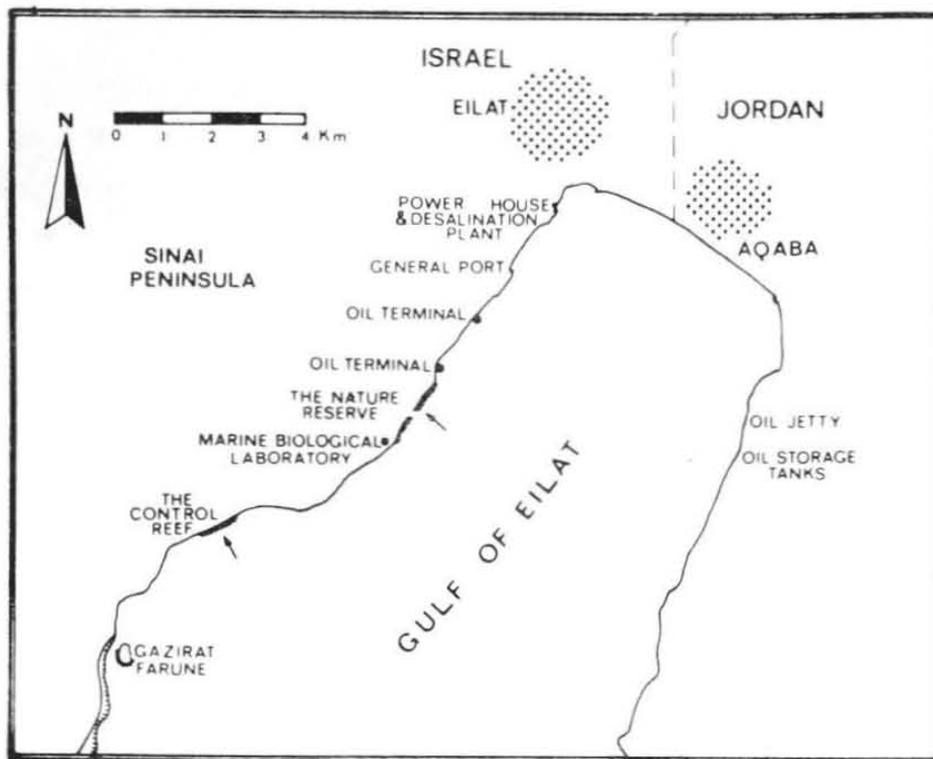


Figure 18.1. Map of the northern Gulf of Eilat showing study locations: the nature reserve and control reef (after Loya 1975).

spills have occurred, due to the drastic decrease in the number of tankers at Eilat, and the high fines inflicted by law on the shipping companies.

Since the wind direction along the Gulf of Eilat is predominantly from the north or northeast, oil spilled around the terminals is carried by surface currents toward the nature reserve. It does not, however, reach the control reef, which is further south. The "control reef" has been termed such as it was found to be free of oil pollution (Loya 1975) and served as a comparative site for studies on changes in the community structure of corals in the polluted nature reserve.

An unexpected and extremely low tide occurred at the northern part of the Gulf of Eilat between 15–20 September 1970 (Loya 1972). The water level fell approximately 20–25 cm below the reef-flat. As a result, the reef-flats were completely exposed to air and sun for three to four hours during the hottest time of the day. The air temperature ranged from a minimum of 34°C on 16 September to a maximum of 38.4°C on 18 September. The immediate consequence of the low tide was the death of approximately 80–85% of the hermatypic corals along the northern part of the Gulf (Loya 1975, 1976a). The high temperatures and desiccation were probably the direct cause of the sudden mortality. The community structure and species diversity of hermatypic corals had been studied in several reef locations along the northern Gulf of Eilat before the low tide (Loya 1972). Hence, the incident

provided a unique opportunity to study recolonization in both a chronically polluted and a clean reef.

During the low tide the corals below the lowest water level were unharmed. Since the nature reserve and the control reefs were similar in community structure (Loya 1975), it was reasonable to assume that a similar stock of coral propagules existed in both. Theoretically, providing human activities had not had a harmful effect on the coral communities at the nature reserve, a similar rate of recolonization of corals could have been expected in both localities. Twenty-one transects (each 10 m long) were surveyed on the reef-flat of the nature reserve and 12 transects on the control reef. The exact locations of the transects at both sites were carefully marked by stainless steel nails, which enabled the same transects to be resurveyed in the following years.

Figure 18.2 summarizes changes in average number of species, colonies, living coverage, and diversity ($H'h$,¹ Shannon and Weaver 1948) of corals per transect, in both reefs, between 1969 and 1982. After testing for equality of variances, *t*-tests were run on the different averages obtained. No significant difference was found between the coral community structure of the nature reserve and that of the control reef in 1969 ($P > 0.05$) when all four statistics were compared. In 1973, 1976, and 1982, however, all these factors were significantly higher ($P < 0.05$) at the control reef compared to the nature reserve. A detailed account of changes in the community structure and species diversity of corals in 1969 and 1973 is given in Loya (1975, 1976a). Although both reefs suffered similar mass mortality of corals during the low tide (85% at the nature reserve and 81% at the control reef), a marked difference was observed in recovery three years later. The extent of recruitment was twenty-three times greater at the control reef. No significant difference was found in coral community regeneration (15% at the nature reserve and 19.2% at the control reef). While the number of species, number of colonies, living coverage and $H'h$ decreased drastically at the nature reserve three years after the low tide, the control reef exhibited rapid recruitment and recovery. The significantly higher coral cover at the control reef was mainly due to massive recruitment of the most abundant species (40% more colonies per transect in 1973 as compared to 1969), and in addition, to the complete regeneration of massive colonies that had suffered partial mortality during the low tide.

Interpretation of stability in ecological systems has long been a matter of controversy among researchers (Margalef 1969; Slobodkin and Sanders 1969; Woodwell and Smith 1969; MacArthur 1972; Boesch 1974; Colwell 1974; Orians 1974; Gray 1977; Connell and Sousa 1983; King and Pimm 1983; Pimm 1984; and others). I do not seek to contribute here to the theory of stability in ecological systems. However, if we accept, as a measure of

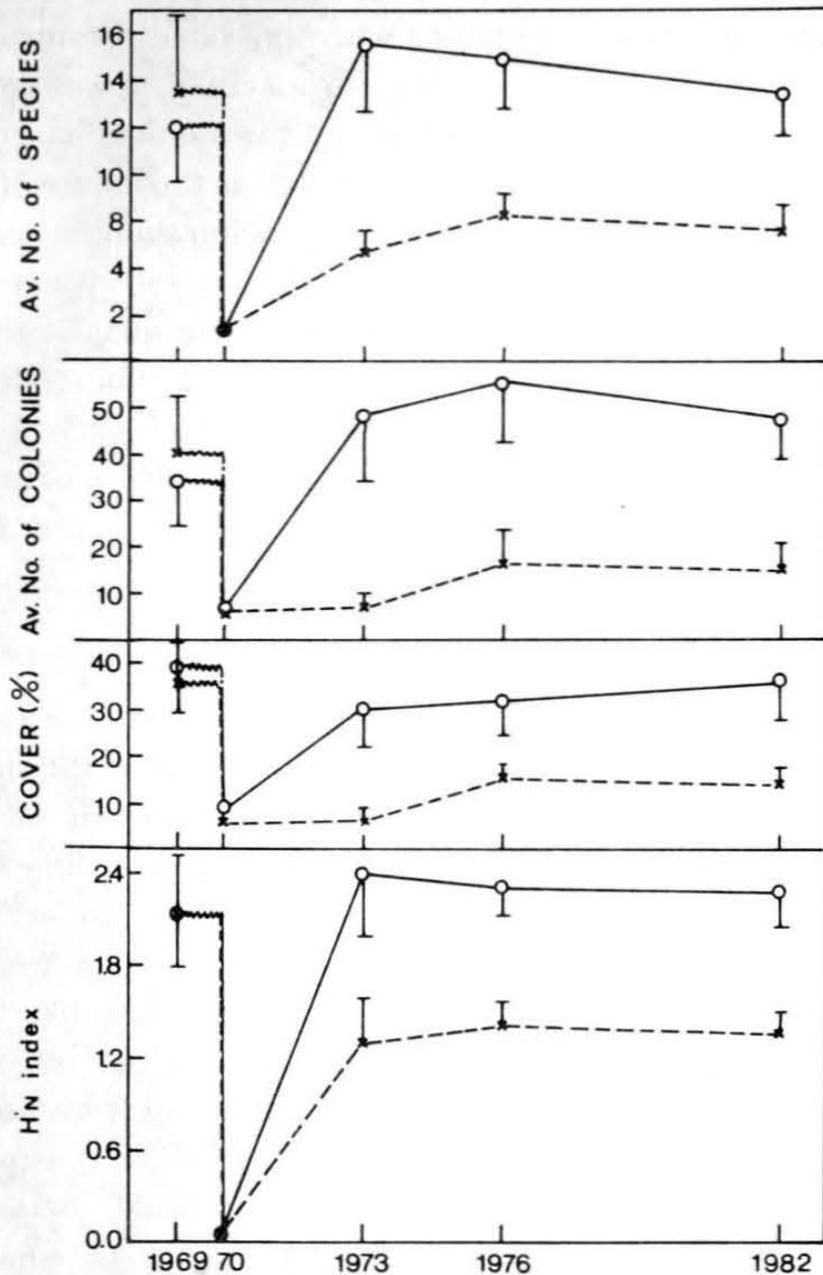


Figure 18.2. Changes in the average number of species, colonies, living coverage, and diversity of corals per transect in the reef-flats of the nature reserve and control reef between 1969 and 1982 (bars indicate standard deviations) (-x-, nature reserve; -o-, control reef).

community stability, the likelihood of return to a former configuration after external disturbance (as defined by Margalef 1969), there are marked differences between the nature reserve and the control reef. The nature reserve had not regained its former community structure and species diversity 12 years after the low tide, whereas the control reef showed remarkable resilience (as defined by Boesch 1974), and, only three years after a severe perturbation, had returned to its former configuration. A high correlation between the percentage contribution of the most common coral species to the total number of colonies and to the total living cover in the

control reef before the low tide and three years later was obtained. Non-significant correlations were obtained when the same parameters were tested at the nature reserve (see Loya 1976a for details). It was concluded (Loya 1976a) that one of the differences between the human disturbance in this instance and natural catastrophes on coral reefs is the failure of the oil-polluted environment to return to its former configuration, whereas the reconstitution of reef areas denuded by natural disturbance was mainly a function of time. There are, unfortunately, few long-term quantitative coral reef community studies to test this view (for further discussion see Johannes 1972, 1975; Endean 1973; Loya 1976a; Bak and Engel 1979; Bak and Luckhurst 1980; Dollar and Grigg 1981; Pearson 1981; Bak and Criens 1983; Brown and Howard 1985).

Oil-Pollution Effects on Eilat Corals

Until 1975 there appeared no conclusive evidence that oil floating above the reef damages the corals (Johannes 1975). Until 1975 most of the studies of the effects of oil pollution on corals were either short-term incidental observations, or laboratory experiments that did not reflect the effects on corals in nature. Our long-term quantitative studies in situ and in the laboratory have established the vulnerability and sensitivity of hermatypic corals to crude-oil and oil components (Loya 1975, 1976a; Rinkevich and Loya 1977, 1979a; Loya and Rinkevich 1979, 1980).

As indicated earlier, clear differences were shown in coral recovery between the chronically polluted nature reserve and the clean control reef. I have suggested (Loya 1975) that chronic oil pollution could damage coral communities by (a) harming the reproductive system of corals, (b) decreasing the viability of coral larvae, and (c) changing some physical properties of the reef-flat, thus interfering with normal settlement of coral larvae. Obviously, any combination of these effects is also possible, and would inhibit coral recruitment in oil-polluted reefs.

The following is a summary of our studies on the effects of oil pollution on reef corals. Our major purpose was to test the general applicability of the hypotheses outlined above. The work confirmed the sensitivity of corals to oil pollution under the circumstances that prevailed in Eilat.

We chose the coral *Stylophora pistillata* for experimentation in the field and in the laboratory, since this is the most abundant coral in the Eilat reefs (Loya 1972), and its life history has been studied in detail (Loya 1976b, c, d; Rinkevich and Loya 1979b, c). Field experiments, observations, and histological studies on two populations of *S. pistillata* in a chronically oil-polluted reef near the oil terminals (Figure 18.1) and at the pollution-free control reef revealed detrimental effects on the polluted corals. The coral population at the

polluted reef showed a higher mortality rate of colonies, a smaller number of breeding colonies, and decrease in the number of ovaria per polyp; a smaller number of planulae produced per coral head (fecundity was four times higher in the control reef), a decreased viability of planula-larvae with increased concentrations of oil, and lower success in settlement of larvae on artificial objects with increasing concentrations of oil (Rinkevich and Loya 1977).

Further studies on the effects of crude oil on the reproduction of *S. pistillata* in the laboratory, using large tanks with running sea-water, supported the field results (Rinkevich and Loya 1979c). Large and mature colonies of *S. pistillata* were cut into halves at the beginning of the reproductive period: to avoid expected variation between different colonies, one was placed in a periodically oil-polluted tank, the other in a clean tank. After two months, a significantly lower number of female gonads per polyp were recorded in 75 percent of the polluted halves, compared to the control halves. An additional effect of low concentrations of crude oil on *S. pistillata* is the immediate indication of mouth opening followed by abortion of premature larvae. Since premature extrusion of planulae occurs during an oil spill, their chances of survival or successful settlement are very low (Loya and Rinkevich 1979).

Our field and laboratory studies on the effects of oil pollution on corals may explain the lack of recolonization of corals in the chronically polluted nature reserve until 1979–1980.² However, although no major oil spills have occurred there since then, to date it has still not returned to its former community structure. It remains to be studied whether the failure of the coral community at the nature reserve to return to its former state is a result of the following: (a) a possible physical change of the reef-flat substrate (interfering with normal settlement of coral larvae), (b) algal domination of the area outcompeting corals for space and/or (c) increased tourist pressure. Rather than speculating on this issue, I prefer to address the wider question of the generation and maintenance of coral diversity.

Why Is Coral Diversity High on the Reef-Flats of the Northern Gulf of Eilat?

Hypothesis 1: Physical Disturbances

Unpredictable Midday Low Tides Act as Diversifying Forces by Preventing Monopolization of the Reef-Flat by Single or Few Competitively Superior Species. Because space for settlement and development is one of the most important limiting resources on coral reefs, overlap in the utilization of space may result in acute competition among coral populations (Lang 1973; Connell 1973, 1976, 1978; Grigg and Maragos 1974; Porter 1974; Loya 1976a; Maguire and Porter 1977) and other benthic organisms (Dayton 1971, 1975; Connell 1975;

Jackson and Buss 1975; Paine 1976; Sebens 1976, 1982; Jackson 1977; Buss and Jackson 1979; and others).

Resource monopolization by corals may take place through competitive interactions such as extracoelentric destruction, whereby the mesenterial digestive filaments of a dominant species extend onto the living tissues of an adjacent subdominant and destroy it (Lang 1973; Richardson, Dustan, and Lang 1979); rapid growth (Connell 1973); overtopping morphology (Porter 1974); or allelopathic effects (Sammarco et al. 1983). Abilities in these competitive mechanisms are species specific, and in areas of high densities on the reef have been shown to affect coral abundance and distribution patterns (Lang 1973; Grassle 1974; Grigg and Maragos 1974; Porter 1974; Connell 1976, 1978; Loya 1976a; Maguire and Porter 1977; Sheppard 1979, 1985; Porter, Battey, and Smith 1982).

Coral mass mortality on reefs may result from mechanical destruction during tropical storms, abnormally low or high seawater temperatures, floods of freshwater especially if accompanied by heavy siltation, exposure to air during midday air-temperature maxima, and *Acanthaster* predation (Glynn, Almodovar, and Gonzalez 1965; Glynn 1968, 1976, 1984; Stoddart 1969; Shinn 1972; Endean 1973; Grigg and Maragos 1974; Loya 1976a; Pearson 1981; Woodley et al. 1981; Brown and Howard 1985). The time required for recolonization and recovery of reefs after such disturbances varies from very short (two years, Shinn 1972) to prolonged periods of time (50 years or more, Grigg and Maragos 1974; Maguire and Porter 1977).

The role of disturbance on community structure and species diversity of natural communities has been documented and discussed by many investigators. (For selected bibliography and reviews, see Dayton 1971, 1975; Levin and Paine 1974; Connell 1978; Huston 1979; Paine and Levin 1981; Miller 1982; Thiery 1982; Connell and Sousa 1983; Sousa 1984; Pickett and White 1985, and others).

Grigg and Maragos (1974) proposed a model for coral community succession based on patterns of recolonization on submerged historic lava flows in Hawaii. By analyzing data sets from progressively older flows they found that diversity at first increased then gradually decreased as more and more species became established. They hypothesized that the decline in diversity in older flows was due to space limitation and competitive exclusion by dominant species, a process that took over 50 years. Glynn (1976) attributed the diversifying effect to recurrent and extreme tidal exposures of reef-flat corals off the Pacific coast of Panama. Tide-induced mortality of Pocilloporid corals, which are prime-space monopolists, resulted in increased coral species diversity.

I have suggested (Loya 1976a) that the unpredictably low tides at Eilat act

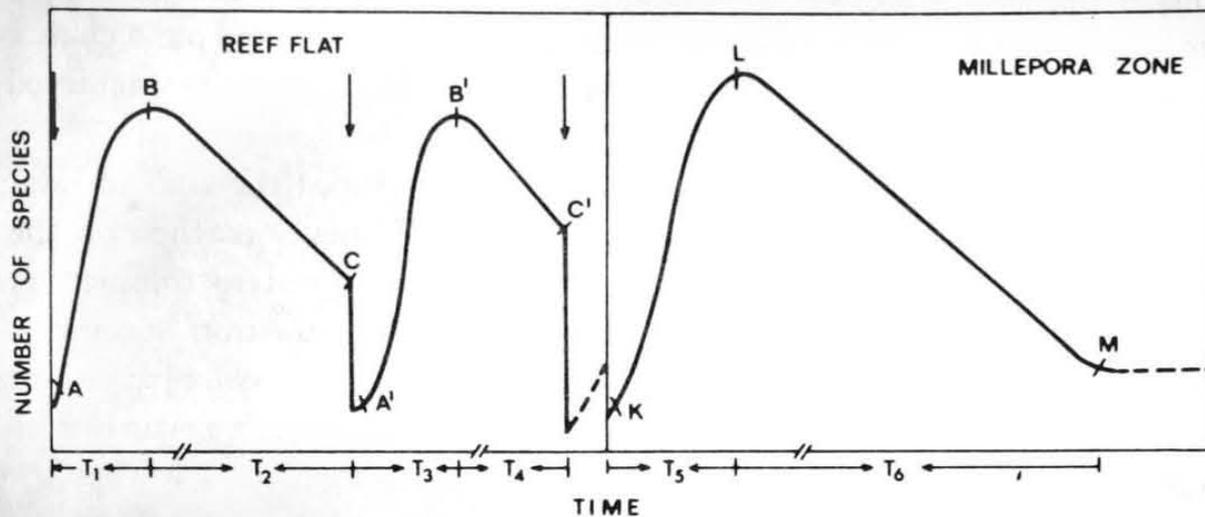


Figure 18.3. Hypothetical pattern of succession following catastrophic low tides (indicated by arrows) on the reef-flat and the undisturbed Millepora zone of the Eilat reefs. (From Loya 1976a, Copyright © 1976 *Ecology*. Reprinted with permission.)

as a diversifying force in a way similar to storm and swell damage in Hawaii (Grigg and Maragos 1974; Dollar 1982; Grigg 1983), and the Caribbean (Porter 1974; Glynn 1976). Connell's (1976) model of "the intermediate-disturbance hypothesis" best describes these examples in stating that the highest diversity of natural communities will be maintained in areas suffering disturbances intermediate on the scales of frequency and intensity.

Figure 18.3 (after Loya 1976a) presents hypothetical curves which describe the patterns of succession following disturbance on the reef-flat and the undisturbed Millepora zone (situated 0.5–2.0m below the reef-flat) at Eilat. The higher diversity recorded on the control reef three years after the low tide, compared to prior to devastation, may reflect a situation in which diversity continues to increase in time after a catastrophe (AB and $A'B'$ in Figure 18.3) until space becomes a limiting factor and competitive interactions between species may cause a decline in diversity (BC and $B'C'$). The results obtained on the average number of species recorded on the reef-flat of the control reef between 1970 and 1982 support this pattern (Figure 18.2). The time interval required to reach "species equilibrium" (as defined by Wilson 1969) is quite short (approximately 5–7 years). The time interval for full recovery and for competitive interactions to take place (T_2 and T_4) is expected to be much longer and more variable between different reefs depending on local conditions. Full recovery may be expected after 15–30 years or more (see Loya 1976a).

In contrast to the reef-flat community the Millepora zone is not exposed to air during the lowest water levels, although physical conditions are still rigo-

rous in this zone (wave action, temperature fluctuations, etc.). Here, interspecific competition is not interrupted by catastrophic low tides and has a chance to become complete. Due to space monopolization by *M. dichotoma* (achieved by fast growth), this zone has high living coverage but low diversity.

In conclusion, the frequency of extremely low tides at the Gulf of Eilat seems to be such that the "species equilibrium" is never reached on the reef-flats, and interspecific competition is not carried out to completion. Monopolization of the reef-flats by competitively superior species is interrupted, providing an opportunity for more species to colonize vacant spaces. The high diversity recorded on reef-flats which are not perturbed by human activity probably reflects early successional stages.

Hypothesis 2: Coral Reproductive Strategies

Temporal Reproductive Isolation of Eilat Corals Generates High Diversity by Decreasing Interspecific Competition. Information on sexual (see Fadlallah 1983; Harrison et al. 1984; Richmond and Jokiel 1984; Shlesinger and Loya 1985; Babcock et al. 1986; Szmant 1986; for reviews and regional patterns) and asexual (see Highsmith 1982, for review) reproduction in corals has increased considerably in recent years. However, no study has considered coral reproductive patterns in relation to coral community structure and species diversity. In trying to explain the high within-habitat diversity of hermatypic corals on reef-flats in the northern Gulf of Eilat, my second hypothesis relates to the phenomenon of temporal reproductive isolation exhibited by the most abundant coral species at Eilat (Shlesinger and Loya 1985).

We have examined the reproductive patterns of 13 ecologically important coral species at Eilat (Figure 18.4). Although these species comprise only 13% of the total known species in Eilat, they are among the most abundant, contributing approximately 60–70% of the total living cover of coral communities on the reef-flats (Loya 1972). The major reproductive activities of these species (planular shedding or gamete spawning) occur in different seasons, different months, or different lunar phases within the same month (Figure 18.4). In contrast to the temporal reproductive isolation exhibited by Red Sea corals, many corals of the Great Barrier Reef of Australia are synchronous multispecific spawners (Harrison et al. 1984; Babcock et al. 1986). The mass spawning of 105 species takes place on only a few nights of the year, between the full and last quarter moon in late spring. Synchronous spawning was observed both within and between five reefs separated by as much as 500 km.

I have mentioned that space is a major limiting resource for settlement, growth, and development of reef corals. The major reproductive activity of most of the corals studied coincides with the seasonal disappearance of

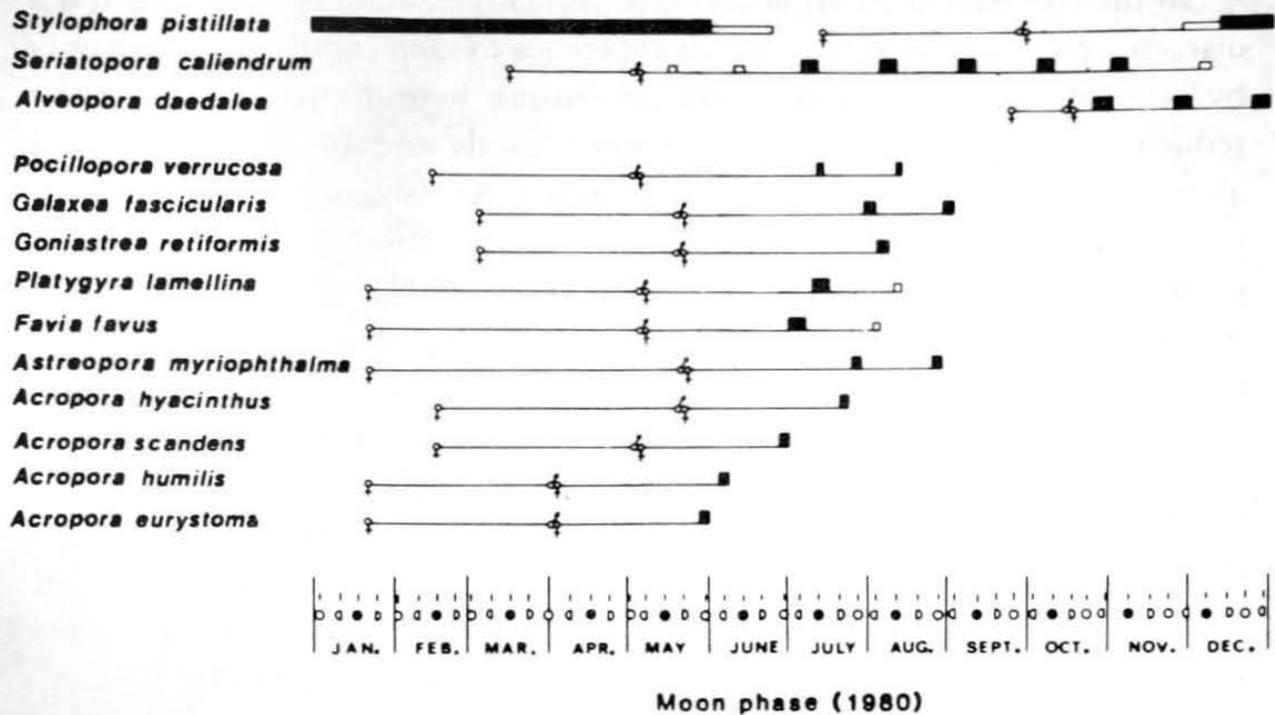


Figure 18.4. Reproductive pattern of thirteen scleractinian corals at Eilat in 1980. The first three species are brooders and the rest are broadcasting spawners. The results presented are in accordance with the lunar calendar, as follows: ●, new moon; ◐ first quarter; ○, full moon; and ◑ last quarter. The period of gonadal development is represented by a solid line with indications of the onset of oogenesis (♀), and spermatogenesis (♂). Further development of both gonads is indicated by the line following the ♂ ♀ sign. Black bars represent massive spawning (90 to 100% of the population), and blank bars represent sporadic spawning (10 to 20% of the population). (Reprinted with modifications from Loya 1985, with permission. Copyright 1985 by the AAAS.)

benthic algae, a major competitor for space on the reef-flats of Eilat (i.e., mainly during June, July, and August) (Benayahu and Loya 1977a, b, 1981). Various species of algae progressively decline in abundance during the summer months, creating more space for coral settlement. During winter, algal cover on the reef-flats is very high and space for settlement is scarce. Thus, per unit of time, space availability for settlement on the reef-flats is more predictable during summer than in winter. It seems, therefore, that a better strategy for summer breeders among the corals is to concentrate their reproductive effort in one short period of time, in order to maximize reproductive success. By contrast, winter breeders like *S. pistillata* (the only species known so far to reproduce during winter) adopt an opposite strategy, spreading the risk of reproduction over a long period of time (December to May in the case of *S. pistillata*). During the winter, the availability of space in time is random due to occasional denudation of small areas by winter storms and, to a limited degree, by grazers. A long reproductive period seems an advantageous strategy.

On the reef-flats at Eilat, intraspecific synchronization of spawning and a discrete breeding period may be advantageous to each coral species, not only by reducing gametic wastage and preventing hybridization, but also by reducing interspecific competition among corals and between corals and algae on the reef-flats. Temporal reproductive isolation may act as a mechanism that generates high coral diversity there. By contrast, mass spawning exhibited by Great Barrier Reef corals probably increases interspecific competition among corals. However, whether this may be a cause for the relatively lower within-habitat diversity of corals on the reef-flats of the GBR compared to that in Eilat remains to be shown.

The two hypotheses presented are not mutually exclusive. The net result of high coral diversity on the reef-flats along the Gulf of Eilat which are not humanly perturbed may be a cumulative effect of both external abiotic factors such as disturbance through exposure to air during midday air-temperature maxima and biotic factors such as temporal reproductive isolation.

Notes

1. $H'_n = -\sum P_i \ln P_i$; where $P_i = n_i/N$ and n_i = number individuals in the i th species and N = total number of individuals.
2. For reviews on the effects of oil pollution on coral reef communities, see Loya and Rinkevich (1980), Ray (1981), Knap et al. (1983), Fucik et al. (1984), and Bak (1987).

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