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RECOLONIZATION OF RED SEA CORALS AFFECTED BY NATURAL CATASTROPHES AND MAN-MADE PERTURBATIONS¹

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Abstract. The recovery patterns of hermatypic corals following an unpredicted catastrophic low tide were studied on two reef flats in the northern Gulf of Eilat, Red Sea: (a) the nature reserve of Eilat, Israel which is chronically polluted, and (b) a control reef which is pollution-free. The coral community structure and species diversity in both reefs were studied in 1969 and served as a base line for comparing the extent of mortality during the low tide (1970), and the extent of recovery 3 years later (1973).

In 1969 no significant differences were found ($p > 0.05$) between the coral community structure of the nature reserve and the control reef when the average number of species, number of colonies, living coverage, and diversity (H'_x) per transect were taken into account. During the low tide both reefs suffered mass mortalities of corals (85% at the nature reserve and 81% at the control reef). Although the extent of mortality in both reefs did not differ significantly ($p > 0.05$), a marked difference was observed in their recovery 3 years later. The extent of coral recolonization was 23× greater at the control reef, but no significant difference ($p > 0.05$) was found in the extent of coral community regeneration in both places (15% at the nature reserve and 19.2% at the control reef). While the number of colonies, number of species, living coverage, and H'_x are drastically decreased at the nature reserve 3 years after the catastrophic low tide, the control reef exhibited an outstanding fast recovery (full recovery is expected 5-6 years from the low tide). The commonest species on the control reef in 1969 showed the highest rates of recruitment in 1973, which might indicate the opportunistic life history of these species. I conclude that one of the differences between man-made polluting activities and natural catastrophes on coral reefs, is the possibility that the human-perturbed environment will not return to its former configuration, while reconstitution of reef areas denuded by natural disturbances is mainly a function of time.

The higher coral diversity recorded on the control reef in 1973 ($H'_x = 2.403$) as compared to 1969 ($H'_x = 2.206$) may reflect a succession pattern in which diversity continues to increase in time after a catastrophe, until space becomes limiting and competitive interactions between species cause a decline in diversity. The unpredictable and extremely low tides at the Gulf of Eilat seem to interfere with this scheme and prevent monopolization of the reef flat by competitively superior species. I suggest that catastrophic low tides act as an important diversifying force on the reef flats of Eilat, in a similar way as other biological and physical disturbances affect coral communities (Porter 1974).

Key words: *Community; coral; diversity; hermatypic; Israel; opportunistic species; pollution; recolonization; Red Sea; succession.*

INTRODUCTION

Environmental predictability and environmental stability are gaining increasingly important weight in theoretical considerations of organization and species diversity of natural communities (Pianka 1966, Levins 1968, Sanders 1968, Slobodkin 1968, Odum 1969, Woodwell and Smith 1969, MacArthur 1972, May 1973, and others). Colwell (1974) has greatly contributed in simplifying and clarifying some of the wide variety of meanings associated with these concepts by defining three parameters (predictability, constancy, and contingency) which are sufficient aspects in describing periodic phenomena. Coral reefs are ideal places for observing processes in-

involved with fluctuating physical and biological phenomena on a small areal scale because they consist of several clear-cut zones which differ greatly in environmental predictability. Thus, the reef flats along the Gulf of Eilat, Red Sea, are unpredictable to a much larger extent than the deep-water reefs (25-50 m depth) since physical parameters such as water temperature, salinity, wave action, and (mainly) tides fluctuate more widely and irregularly around their means compared to the same parameters in the deep reefs (Loya 1972).

Moore (1972) reviewed different aspects of physical and biological stress in the tropical marine environment. The effects of physical and biological disturbances, especially competition and predation, on the maintenance of hermatypic coral communities have been extensively studied only in recent years

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(Lang 1971, 1973; Porter 1972a, 1972b, 1974; Connell 1974; Grigg and Maragos 1974). As in other benthic communities (Paine 1966, Dayton 1971, Dayton et al. 1974, Levin and Paine 1974), physical or biological disturbances on coral communities interrupt the local succession towards climax or "species equilibrium" (*sensu* Wilson 1969) and often act as diversifying forces (Porter 1972a, 1974; Grigg and Maragos 1974). The present work provides additional evidence of physical disturbances (unpredictable catastrophic low tides) promoting hermatypic coral diversity.

Catastrophic coral mortality on reefs often results from various unpredictable events, some of which have been reviewed by Stoddart (1969). The major causes for such coral mortality seem to be mechanical destruction during tropical storms (Moorhouse 1936, Stephenson et al. 1958, Stoddart 1963, Glynn et al. 1965, Ball et al. 1967, Shinn 1972), floods of freshwater especially when accompanied by heavy siltation and long exposure to air during heavy rains (Hedley 1924, Mayor 1924, Rainford 1925, Crossland 1928, Slack-Smith 1959, Goodbody 1961, Banner 1968, Taylor 1968), unseasonal low temperatures (Dana 1874, Verrill 1902, Shinn 1972), and exposure to air during midday air-temperature maxima (Wood-Jones 1910, Edmonson 1928, Moorhouse 1936, Hiatt 1951, Glynn 1968).

Loya (1972) reported midday exposure of the Eilat reef flats during an unexpected and extremely low tide that occurred 15–20 September 1970. The low water level was 40 cm lower than predicted for that period (Fishelson 1973a). During the low tide the corals on the reef flats were fully exposed to the sun (and air temperature of 34°C–38.4°C), 3–4 h every day. Approximately 80%–90% of the hermatypic corals on the reef flats were killed. Inasmuch as the community structure and species diversity of hermatypic corals were studied in 1969 in several reef locations along the northern Gulf of Eilat (Loya 1972), it was a unique opportunity to study the process and rates of coral recolonization in different reef ecosystems.

Recovery of denuded reefs has been shown by many workers to be a prolonged process (Guppy 1889; Mayor 1918, 1924; Tandy and Coleman 1931; Crossland 1939; Brock et al. 1966; Banner 1968; Stoddart 1969, 1974; McVey 1970; Maragos 1972; Endean and Stablum 1973; Connell 1974; Grigg and Maragos 1974). Grigg and Maragos (1974) estimated that recovery time for recolonization of hermatypic corals on submerged lava flows at Hawaii was in the order of 20 yr in exposed areas, while at sheltered stations more than 50 yr might be required for complete recovery. Conversely, a potential for rapid recovery of coral communities following

devastation by *Acanthaster planci* has been indicated by Pearson (1973) on the Great Barrier Reef off the Queensland, Australia coast. An outstandingly fast recovery of a reef was reported by Shinn (1972) who noted that live fragments of *Acropora cervicornis* littering a reef after a storm were responsible for the complete reconstruction of a reef tract within 2 yr.

This paper compares the recovery patterns of hermatypic coral communities on two reef flats: one at the coral nature reserve of Eilat, Israel (at a location locally called "The Japanese Gardens"), and the other located 5 km further south and referred to in the text as the control reef. Unfortunately, the nature reserve neighbors the general port of Eilat and two major oil terminals, and has been continuously perturbed in the last few years by chronic oil pollution and mineral pollution (Fishelson 1973b, Loya 1975). The control reef, on the other hand, has been free from any form of man-made perturbations, and therefore was a good location for comparing the extent of coral recolonization and regeneration with that of the nature reserve.

During the catastrophic low tide no harm was done to corals situated deeper than the lowest water level. It was thus reasonable to assume that a similar stock of coral propagules existed in the nature reserve and the control reef. Hence, a theoretically similar rate of recolonization of corals could have been expected in both localities, provided that man's activities have no harmful impact on the coral communities at the nature reserve. Those species that can rapidly respond to newly open or unexploited habitats have variously been called fugitive (Hutchinson 1951), opportunistic (MacArthur 1960, Hutchinson 1967), colonizing (Lewontin 1965), weedy (Baker 1965, Harper 1965), or *r*-selected (MacArthur and Wilson 1967). This study attempts to relate the fast recovery of the control reef to opportunistic life histories of the commonest corals on the reef flats of the Gulf of Eilat.

METHODS

A review of different methods used in quantitative studies of coral reefs and the problems involved at the level of sampling unit and field recording is given by Stoddart (1969). Loya (*in press*) reviewed possible uses of plotless and transect methods for quantitative studies of coral communities. In the present study 10-m line transects were used to study the community structure of corals, as described by Loya and Slobodkin (1971) and Loya (1972). Any coral species that underlay the line was recorded and its projected length onto the line was measured to the nearest centimeter. Porter (1972b) used a similar method with a 10-m chain, where the number of

chain links covering each species of living coral was recorded.

During the summer of 1969, 21 transects were surveyed on the reef flat of the nature reserve and 12 transects at the control reef. The exact location of the transects was carefully marked by stainless steel nails. This enabled the resurvey of the same transects during the 1970 catastrophic low tide and 3 years later. Series of photographs were taken along the line transects before, during, and after the low tide.

As a result of the catastrophic low tide, some coral species were separated by the death of intervening parts. In these cases the separate parts were still considered together as one individual colony. Otherwise, an individual colony was defined as any colony growing independently of its neighbors, i.e., whenever an empty space was recorded between two adjacent colonies. The hydrozoans *Millepora dichotoma* and *M. platyphylla* were included in this study because they are important frame-builders of the reef flat.

Different diversity indices were used for the study of the community structure and species diversity of the hermatypic corals of Eilat (Loya 1972). In the present study, Shannon and Weaver's (1948) index of diversity is used: $H'_N = -\sum_{i=1}^s p_i \ln p_i$, where p_i is the proportion of individuals of the i th species ($i = 1, 2, \dots, s$), and $H'_c = -\sum_{i=1}^s p_i \ln p_i$, where p_i is the proportion of living coverage of the i th species.

RESULTS

The nature reserve

A major perturbation on a reef resulting in the mortality of corals will normally start a localized succession. If such a disturbance did not permanently change the physical properties of the region, one may expect that it will cause the system to revert to an earlier state in the sequence of succession. It is very interesting to observe the repeatability of species lists and species abundance in this process of reversion. Yet, the rate of reconstruction of damaged coral assemblages depends upon many factors, and a marked difference was observed in the recolonization rate of the nature reserve and the control reef by hermatypic corals.

Figures 1 and 2 compare the total number of colonies and the living coverage of hermatypic corals on the nature reserve in 1969 and 1973. The names of the corals corresponding to the species code numbers are given in Appendix I. In both histograms the total number of colonies and the living coverage are almost always higher in 1969. Chi-square contingency tests bear out these results, showing a significantly larger number of colonies and amount of living coverage in 1969 ($p < 0.05$).

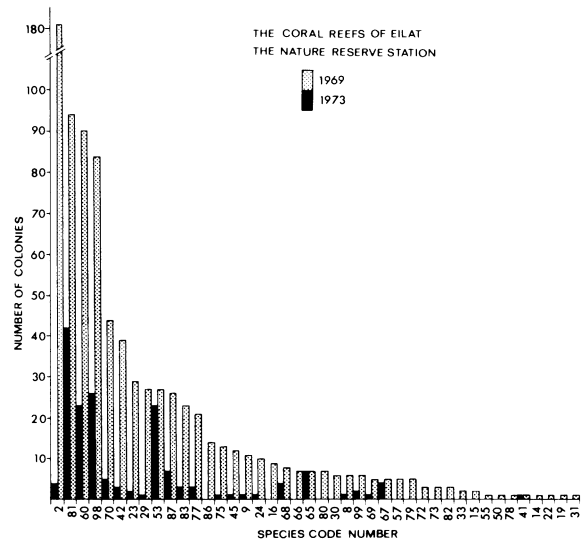


FIG. 1. A comparison between the total number of colonies of each coral species in 1969 and 1973 over 21 transects of the nature reserve.

Three years after the catastrophic low tide, the numbers of all the commonest coral species at the nature reserve were drastically reduced. Nineteen coral species that were recorded in 1969 were missing (= extinct) in 1973. The decrease in the number of colonies of the 12 most abundant species (Fig. 3) ranged from 15% (*Porites lutea*) to 98% (*Stylophora pistillata*). The decrease in the living coverage of the same two species ranged from 55% to 98%. The marked decrease in the total number of species recorded, as well as in living coverage and number of colonies, is a direct result of the 1970 catastrophic low tide.

During the low tide, 128 partially killed coral colonies were counted over 21 transects. Most of these corals fully regenerated within 6–12 months (see Fishelson 1973a). In the 1973 census, 166 colonies were counted in the same 21 transects. The increase in the number of colonies was due to sparse and almost negligible recolonization (compared to the control reef) by *P. lutea* (16 colonies) *M. dichotoma* (8 colonies), *Cyphastrea microphthalma* (7 colonies), *Favia fava* (5 colonies) and *Acanthastrea echinata* (2 colonies). The data concerning specific mortality rates and slight recolonization of different corals at the nature reserve served as the basis for estimates of the extent of recovery due to regeneration vs. recolonization in both reefs.

The control reef

The reef flats of the nature reserve and the control reef fall into two of the three categories suggested by Slobodkin and Sanders (1969) for "low

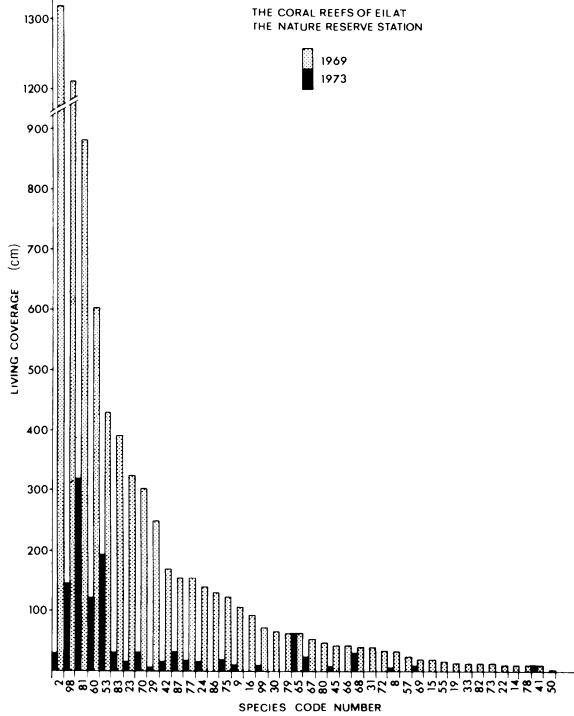


FIG. 2. A comparison between the total living coverage of each coral species in 1969 and 1973 over 21 transects of the nature reserve.

diversity environments." Immediately after the catastrophic low tide, one may look on these reefs as "new environments" in which the number of species is increasing (MacArthur and Wilson 1967, Patrick 1967, Wilson 1969, Simberloff 1969, Simberloff and Wilson 1969, 1970, Schoener 1974). They also fit in the category of unpredictable environments, in which the variances of environmental properties

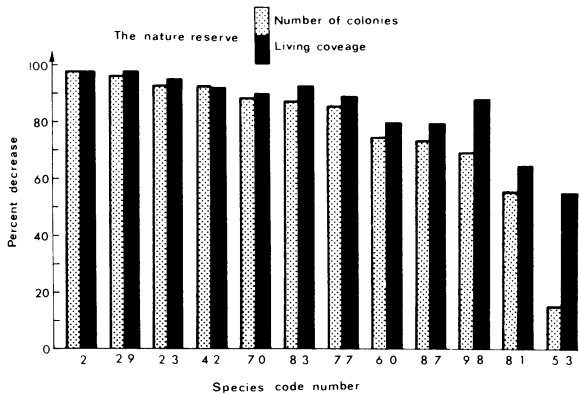


FIG. 3. The percent decrease in abundance and living coverage of the commonest coral species on the nature reserve in 1973, as compared to 1969.

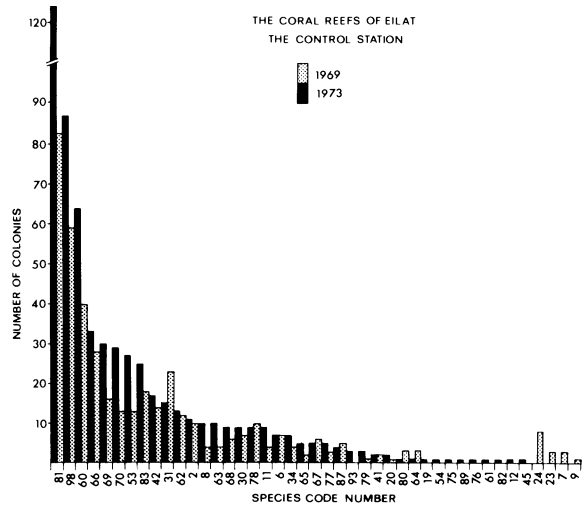


FIG. 4. A comparison between the total number of colonies of each coral species in 1969 and 1973 over 12 transects of the control reef.

among successive periods are relatively high and irregular both spatially and temporally (Slobodkin and Sanders 1969, Colwell 1974).

Figures 4 and 5 compare the total number of colonies and the living coverage of hermatypic corals, respectively, on the control reef in 1969 and 1973. The four single dotted bars at the right end of Fig. 4 represent coral species that were present in 1969

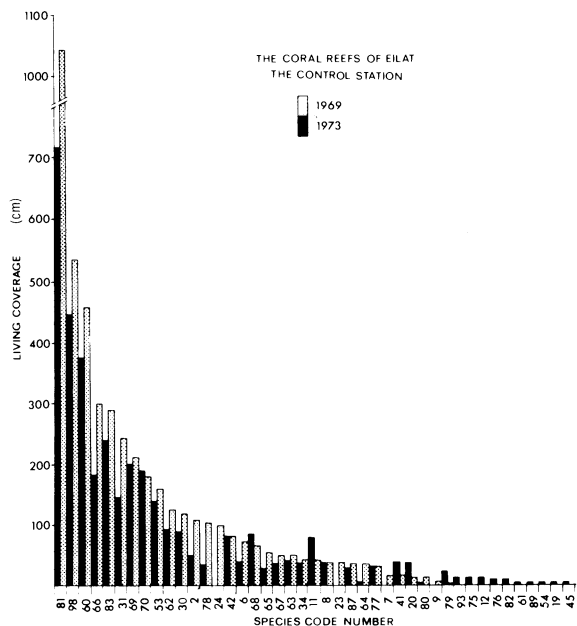


FIG. 5. A comparison between the total living coverage of each coral species in 1969 and 1973 over 12 transects of the control reef.

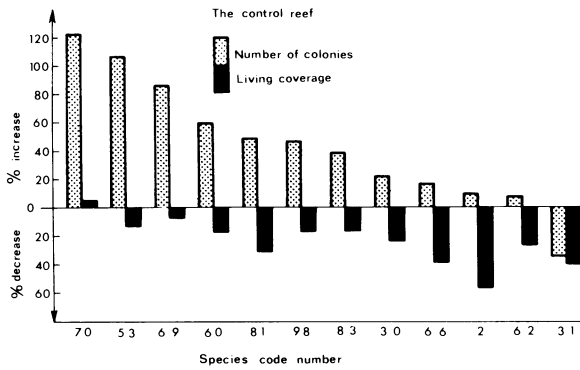


FIG. 6. The percent decrease or increase in abundance and living coverage of the commonest coral species on the control reef in 1973, as compared to 1969.

but missing in 1973. The 10 single black bars represent new species that colonized the control reef after the catastrophic low tide. Figure 4 shows that, within species, the 1973 values are almost always higher than the 1969 values, and that the general picture is of a higher number of coral colonies in 1973. However, Fig. 5 indicates smaller living coverage per species in 1973. Chi-square contingency tests run on the data presented in Figs. 4 and 5 confirm the general impression given by the histograms, i.e., a significantly larger number of colonies were recorded on the control reef in 1973 than in 1969 ($p < 0.05$), while a significantly lower living coverage was obtained in 1973 as compared to 1969 ($p < 0.05$).

Figure 6 presents the percent increase or decrease in the total number of colonies and the living coverage of the 12 commonest coral species at the control reef in 1973, as compared to 1969. Most of the species showed a considerable population increase in 1973. In some cases, such as *Platygyra lamellina* and *P. lutea*, the increase in number of colonies was $> 100\%$. The significantly lower living coverage obtained for almost all the species in 1973,

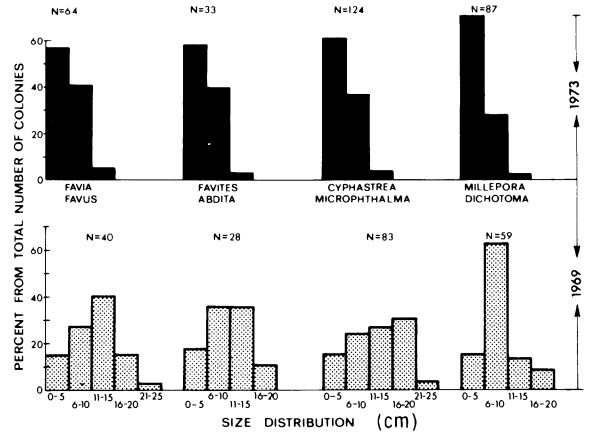


FIG. 7. Size distribution of the four most abundant coral species on the control reef in 1969 and 1973.

as compared to 1969, was due to the large number of young (small), and newly established colonies.

Figure 7 compares the size distribution of the four most abundant coral species on the control reef in 1969 and 1973. It is apparent that in 1973 most of the colonies fell into the smallest size categories, while in 1969 the majority of corals were distributed in much larger size categories. It may be argued that, since some of the colonies were only partially killed during the low tide, they potentially increase the number of colonies recorded in the smallest size categories. However, this is not the case because in most of the colonies having parts of their tissue intact during the low tide, complete regeneration occurred within 6–12 months and they regained their initial size (Fishelson 1973a). In the few cases where corals were not fully regenerated and were separated by the deaths of intervening parts, the separate parts were still considered as one individual colony. Hence, the higher proportion in the smallest size categories of the 1973 coral community (Fig. 7) suggests that recovery of the control reef has been mainly due to recolonization by coral planulae rather

TABLE 1. Percent recovery of the most abundant coral species on the control reef in 1973 due to recolonization vs. regeneration

Species	No. colonies 1969	Mortality		No. colonies 1973	Recolonization (%)	Regeneration (%)
		No. colonies 1970	(%)			
<i>Cyphastrea microphthalma</i>	83	63	30	124	75.8	24.2
<i>Millepora dichotoma</i>	59	78	13	87	85.1	14.9
<i>Favia fava</i>	40	80	8	64	87.5	12.5
<i>Favites abdita</i>	28	93	2	33	94.0	6.0
<i>Echinopora gemmacea</i>	18	87	2	25	92.0	8.0
<i>Pavona decussata</i>	23	83	4	15	73.3	26.6
<i>Goniastrea pectinata</i>	16	72	4	30	86.6	13.3
<i>Platygyra lamellina</i>	13	88	2	29	93.1	6.9
<i>Porites lutea</i>	13	70	4	27	85.2	14.8

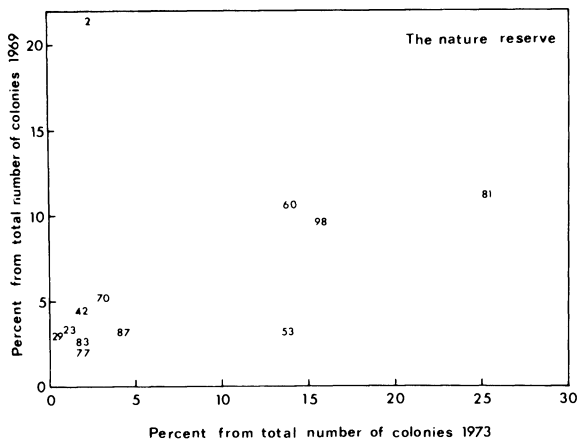


FIG. 8. The relative contribution to the total number of colonies of the 12 commonest coral species on the nature reserve reef flats in 1969 and 1973.

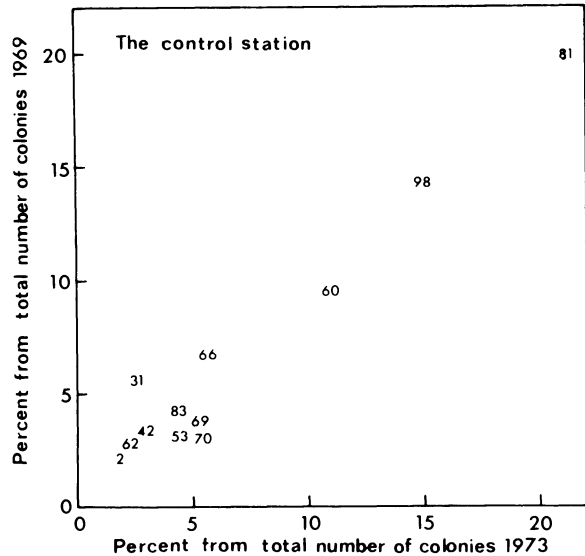


FIG. 9. The relative contribution to the total number of colonies of the 12 commonest coral species on the control reef flat in 1969 and 1973.

than regeneration of survivors. Yet, it is important to consider what proportion of the coral colonies regenerated from survivors vs. originated from larval settlement in the 1973 coral community of the control reef. Since the reef flats were only 5 km apart and the extreme environmental conditions during the low tide were virtually identical in both places, it was reasonable to assume that, within a species, similar degrees of mortality occurred in both localities.

Table 1 compares the percent recovery due to recolonization vs. regeneration in the 1973 most abundant coral species on the control reef. Expected values of mortality rates were assigned to the coral species at the control reef on the basis of observed mortality rates of the same species at the nature reserve. Series of photographs taken at both places during the low tide confirmed the estimates of the degree of mortality of different coral species. I conclude that recolonization of the control reef by coral larvae after the catastrophic low tide is the major reason for its fast recovery. Figures 4-7 and Table 1 show that the commonest species on the control reef flat in 1969 had the highest rates of recruitment after the catastrophic low tide. A similar

recruitment pattern was reported by Grigg and Maragos (1974) who observed that coral species with the highest rates of recruitment on submerged lava flows at Hawaii were among the most common species in surrounding areas. Connell (1974) marked permanent quadrats on the reef at Heron Island, Australia, and found that in all areas the commoner species all had high rates of recruitment and mortality, and maintained their abundance.

A comparison between the nature reserve and the control reef

If we accept as a measure of community stability the likelihood of return to a former configuration after external perturbation (a definition derived from thermodynamics, see Margalef 1969), it is interesting to determine the specific configuration of the reef flat coral communities 3 years after the catastrophic low tide.

Table 2 presents a comparison between average values of various statistics (per transect) measured

TABLE 2. A comparison between average values of various statistics (per transect) measured at the nature reserve and the control reef in 1969 and 1973. All *t*-tests performed on the 1969 average values were nonsignificant ($p > 0.05$); all the 1973 pairs differed significantly ($p < 0.05$)

Locality	Year	Species (n)	Colonies (n)	Cover (%)	H'_S index
Nature reserve	1969	13.48	40.10	36.06	2.231
Control reef	1969	12.00	34.66	39.30	2.206
Nature reserve	1973	4.85	8.35	6.18	1.375
Control reef	1973	15.75	48.75	30.32	2.403

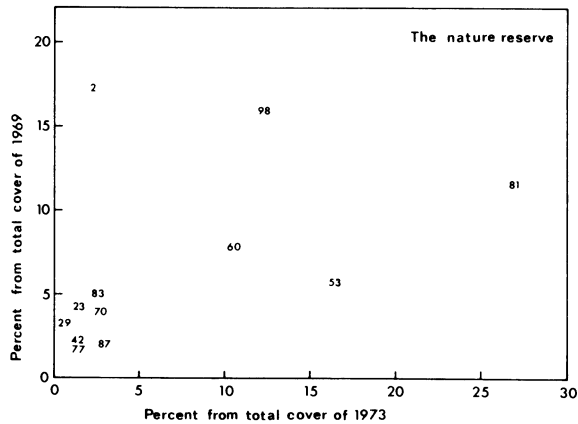


FIG. 10. The relative contribution to the total living coverage of the 12 commonest coral species on the nature reserve reef flat in 1969 and 1973.

at the nature reserve and the control reef in 1969 and 1973. After testing for equality of variances, *t*-tests were run on the different averages obtained. No significant differences were found between the coral community structure of the nature reserve and the control reef in 1969 ($p > 0.05$), when the average number of species, number of colonies, living coverage, and diversity per transect were taken into account. However, in 1973 all these factors were significantly higher ($p < 0.05$) at the control reef, as compared to the nature reserve.

Figures 8 and 9 present the correlations between the percent contribution of each of the 12 commonest coral species to the total number of colonies at the nature reserve and the control reef in 1969 and 1973. The correlations between the percent contribution of each species to the total living coverage in both localities before and after the catastrophic low tide is presented in Figs. 10 and 11. The data were subjected to the arcsine transformation (Sokal and Rohlf 1969). The species code numbers are plotted on the graphs, in place of the corresponding points, describing the relative percent contribution of each species.

While a significantly high correlation was obtained at the control reef (Fig. 9) for the contribution of each species to the total number of colonies before and after the low tide ($r = 0.947$, $p < 0.05$), a nonsignificant correlation was obtained at the nature reserve (Fig. 8) for the same parameters ($r = 0.404$, $p > 0.05$). Similarly, the correlations between the contribution of each species to the total living coverage in both localities in 1969 and 1973 have indicated different patterns. A significant correlation ($r = 0.971$, $p < 0.05$) was obtained for the control reef (Fig. 11), while a nonsignificant correlation ($r = 0.529$, $p > 0.05$) was found for the nature

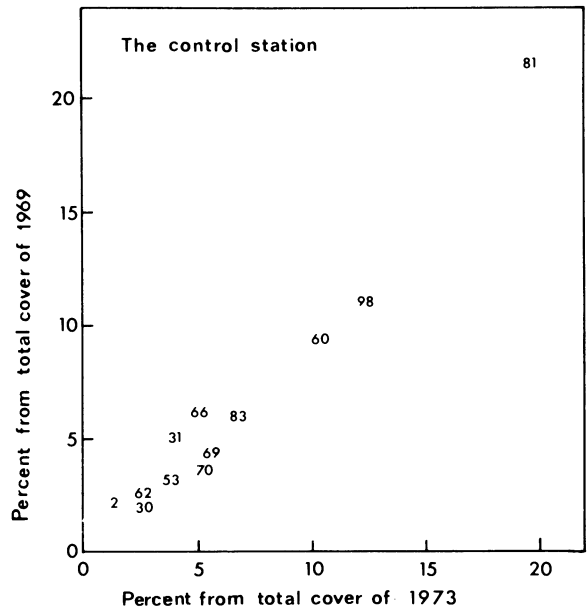


FIG. 11. The relative contribution to the total living coverage of the 12 commonest coral species on the control reef flat, in 1969 and 1973.

reserve (Fig. 10). That is, 3 years after the catastrophic low tide the hermatypic coral community structure of the commonest species at the control reef has returned to a composition similar to that before the catastrophe, while a drastic change has occurred at the nature reserve. However, the community structure has changed in both localities with respect to rarer species. At the nature reserve many of the rarer species were extinct as a result of the low tide (Fig. 1, Table 3), while 10 new species colonized the control reef by 1973.

Table 3 summarizes the relative changes in the total number of coral species and colonies recorded at the nature reserve and the control reef during 1969–1973. Some of the comparisons in Table 3 were tested for equality of two percentages (Sokal and Rohlf 1969). Note the slightly higher but insignificant ($p > 0.05$) mortality at the nature reserve (85%) compared to the control reef (81%), which reflects the relatively larger proportion of branching species at the nature reserve (Figs. 1 and 4). Fishelson (1973a) thus showed that during the low tide, brain corals were more resistant to desiccation than branching growth forms. Nevertheless, there was no significant difference ($p > 0.05$) in the overall extent of community regeneration between the nature reserve (15%) and the control reef (19.2%), while the extent of recolonization (expressed as average number of colonies per transect originated from larval settlement) was 23× greater on the control reef.

TABLE 3. The relative changes in the total number of coral species and colonies recorded at the nature reserve (21 transects) and the control reef (12 transects) during 1969-1973

	Nature reserve	Control reef
Total number of species in 1969	42	33
Total number of species in 1973	23	39
Number of new species recorded in 1973	0	10
Number of missing (= extinct) species in 1973	19	4
Decrease or increase in number of species in 1973 vs. 1969 (%)	-45.2	18.2
Total number of colonies in 1969	842	416
Total number of colonies in 1970 (= survivors after low tide)	128	80
Total number of colonies in 1973	166	585
Mortality after low tide, 1970 vs. 1969 (%)	85.0	81.0
Decrease or increase in number of colonies in 1973 vs. 1969 (%)	-80.0	40.0
Survivors (regeneration) from the 1969 population, 1970 vs. 1969 (%)	15.0	19.2
Percent of the 1973 population originated from regeneration of survivors	77.0	13.6
Percent of the 1973 population originated from recolonization	23.0	86.3
Extent of recolonization (= average number of colonies per transect originated from larval settlement)	1.8	42.1
Extent of regeneration (= average number of colonies per transect originated from survivors)	6.4	6.6

If we accept as a measure of environmental predictability the variation among successive periods in the pattern of periodic phenomenon (Colwell 1974), then the control reef flat is more predictable than the nature reserve. Yet, when a comparison is made between the predictability and stability of non-polluted reef flats vs. deep reefs at Eilat, a distinction should be made between long-term predictability and short-term stability (*sensu* Slobodkin and Sanders 1969, Colwell 1974). It is suggested that the control reef flat represents an environment of short-term stability and lower predictability when compared to the immediate deep-water reef.

DISCUSSION

In this study clear differences have been indicated between the chronically polluted nature reserve and the control reef in the pattern and extent of recovery of coral communities. 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,

or (c) changing some physical properties of the reef flat, thus interfering with normal settlement of coral larvae. Naturally, any combination of these effects is also possible resulting in the inhibition of coral recolonization at the nature reserve. However, the control reef represents a situation where a system returns to its former configuration after a severe perturbation (Figs. 9 and 11). Therefore, I conclude that one of the differences between man-made polluting activities and natural catastrophes on coral reefs is the possibility that the human-perturbed environment will not return to its former configuration, while reconstitution of reef areas denuded by natural disturbances is mainly a function of time. I shall not discuss the nature reserve further, but rather will try to explain the surprisingly fast rate of recolonization and the high species diversity of corals reattained at the control reef.

Three years after the catastrophic low tide more colonies and more species per transect were recorded at the control reef than before the catastrophe. Although the total living coverage has not yet reached its former situation, it is estimated that within 5-6 yr from the low tide full recovery will take place. Repeated census of the control reef in 1975 confirmed this expectation (Y. Loya and Y. Benayahu, *personal observation*).

The death of corals due to catastrophic low tides has occurred in the past on the reef flats of Eilat, according to L. B. Slobodkin (*personal communication*), since large specimens of the brain coral *P. lamellina* on the reef flat often have a dead top with several ring-shaped living-circles around an eroded center. Large *Platygyra* specimens show as many as three concentric rings and there is a significant correlation between the diameter of the coral and the number of such rings. Nevertheless, since the growth rate of *Platygyra* is not known, no estimates could be made as to the frequency of the low-water events at the northern Gulf of Eilat.

The control reef flat represents a habitat that is periodically but irregularly disturbed by extremely low tides. It seems that the best strategy for a coral to succeed in invading such an unpredictable environment would be high reproduction rate, high growth rate (to use up the resources before other competing species could exploit the habitat), and high dispersal rate. Such species have often been called fugitive (Hutchinson 1951), opportunistic (MacArthur 1960, Hutchinson 1967), or *r*-strategists (MacArthur and Wilson 1967). Grassle and Grassle (1974) expand the definition of opportunistic life history from the more narrowly defined processes of *r*-selection and *K*-selection. Opportunistic species have opted for high reproductive rates, short life spans, large population sizes, wide physiological

tolerances, broad dispersal abilities, density independent mortalities, and poor competitive abilities (Grassle and Grassle 1974). Most of these characteristics are exhibited by the most common coral species on the reef flat.

Since space is one of the most pronounced limiting factors on coral reefs, rapid growth and encrusting growth form seem to be advantageous traits in reef areas that are open for recolonization after a catastrophe. Hence, *Cyphastrea microphthalmia* and *M. dichotoma* which together contribute $\approx 37\%$ (Fig. 11) of the total living coverage of the control reef dominate it in their encrusting growth form. The usual growth form of *M. dichotoma* is vertical plates laterally united in honeycomb-like masses. This growth form is typical of the outer edges of the reef flat at Eilat, forming the fire coral belt or *Millepora* zone (Loya and Slobodkin 1971). However, on the reef flat, *M. dichotoma* usually commences growth in its encrusting growth form occupying as much space as possible with a rapid growth rate. The same principle holds for *C. microphthalmia*, which usually has hemispherical growth form. Only at a later stage (when space becomes limiting on the reef flat) and at a much slower rate, do these species start to develop their usual growth form.

It is probably safe to suggest that the most opportunistic species among the shallow water corals of Eilat would breed throughout the year, and are thus most likely to be the first to recolonize occasional denuded areas on the reef. Maximal species diversity can be expected just before interspecific competition first becomes significant (Wilson 1969) since from that point on we can expect the most opportunistic corals to be competitively excluded by more specialized species. Grassle's (1974) description of the mosaic of coral distributions at Heron Island closely parallels this speculation. However, the unpredictable and extremely low tides at the Gulf of Eilat seem to interfere with this scheme and prevent resource monopolization of the reef flat.

Resource monopolization by corals may take place through competitive interactions such as predation (Lang 1971, 1973), rapid growth (Connell 1974), overtopping morphology (Porter 1974), or possibly in areas where low environmental predictability favors a single opportunist. The effect of biological and physical disturbances on a local succession of coral communities (Porter 1972a, 1974; Grigg and Maragos 1974) appears to be similar to the effect of such disturbances on intertidal communities (Paine 1966) or benthic communities (Dayton et al. 1974), where they prevent resource monopolization and promote diversity. Porter (1972a, 1974) studied the effects of physical and biological processes,

especially predation and competition in eastern tropical Pacific and western Caribbean coral communities. He found coral coverage to be positively correlated with species diversity (H'_c) on Caribbean reefs. Conversely, a significantly negative correlation was found between coral coverage and diversity in eastern Pacific coral communities. Where cover was high, diversity was low, and vice versa. Porter (1974) speculated that the high degree of coexistence on Caribbean reefs is due to a "balance of abilities" divided among the Caribbean corals, such that no one species is competitively superior in acquiring and holding space. However, at undisturbed eastern Pacific reefs, *Pocillopora damicornis*, which has rapid growth and high digestive dominance (*sensu* Lang 1973), competitively excludes other corals, except in areas where disturbances such as *Acanthaster* predation (Porter 1972a) offset space monopolization. Grigg and Maragos (1974) reported such negative relationships between coral coverage and diversity (H'_c) on submerged lava flows at Hawaii. They found that the oldest and undisturbed flows have the highest coral cover but lowest diversity and speculated that this may be due to interspecific competition for space which leads to resource monopolization. However, in areas exposed to heavy swell and periodic storm damage, they found that coral living cover was low and diversity high, regardless of the age of the colonizing surface, possibly a consequence of less competition for space.

It is suggested that the unpredictable catastrophic low tides at Eilat, may act as diversifying force in a way similar to *Acanthaster* predation in the eastern Pacific (Porter 1972a) or storm and swell damage in Hawaii (Grigg and Maragos 1974, Porter 1974). The frequency of extremely low tides at the Gulf of Eilat seems to be such that the "species equilibrium" in the sense of Wilson (1969) is never reached on the reef flats, and interspecific competition does not have an opportunity to carry on to completion.

Figure 12 presents hypothetical curves suggested to reflect the patterns of succession following disturbance on the reef flat and at the *Millepora* zone, which supports similar patterns previously described for coral communities by Porter (1974) and Grigg and Maragos (1974). The higher diversity recorded on the control reef in 1973 as compared to 1969, may reflect a situation where diversity continues to increase in time after a catastrophe (AB and A'B' in Fig. 12), until a point is reached when space becomes limiting and competitive interactions between species may cause a decline in diversity (BC and B'C'). As previously shown, the time interval between A and B ($= T_1$) and A' and B' ($= T_3$) are in the order of 5–7 yr. The time interval T_2 and T_4 are expected to be much longer and more

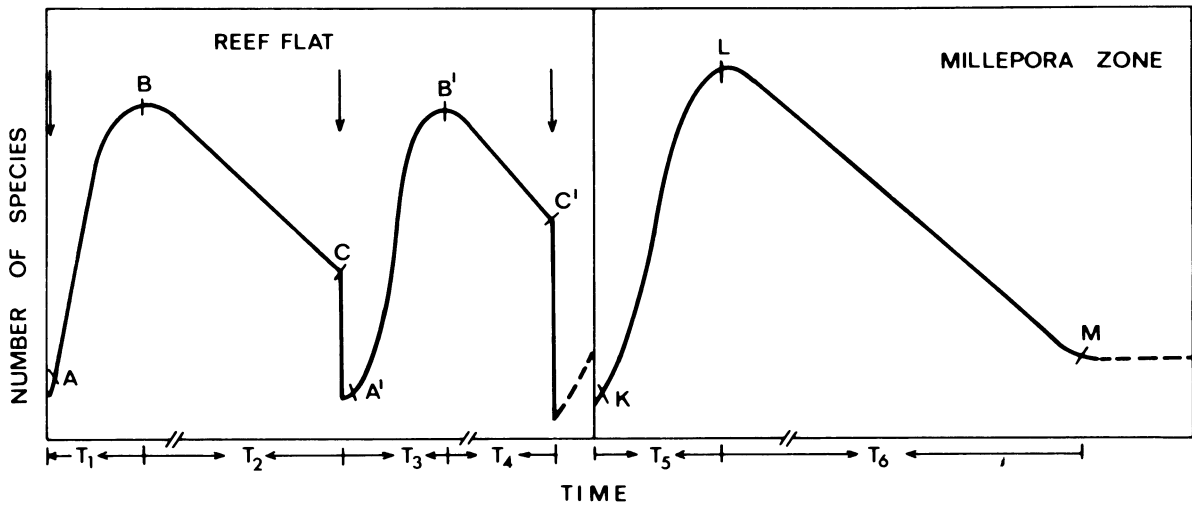


FIG. 12. The effect of catastrophic low tides (indicated by arrows) on coral succession, at the reef flat and *Millepora* zone of the Eilat reefs.

variable, maybe 15–30 years or more. In contrast to the reef flat community, the *Millepora* zone, situated 0.5–2.0 m below the reef flat, is not exposed to the air during the lowest water levels, although physical conditions are still rigorous in this zone (wave action, fluctuations in temperature, and salinity). Here, interspecific competition is not interrupted by catastrophic low tides, and has a chance to become complete (Fig. 12). Due to space monopolization by *M. dichotoma*, this zone has high living coverage but low diversity. Six transects performed at the *Millepora* zone (data derived from Loya 1972) showed a significant negative correlation ($r = 0.828$, $p < 0.05$) between living coverage and diversity (H') similarly to undisturbed areas in the eastern Pacific (Porter 1974) or Hawaii (Grigg and Maragos 1974). It is possible to speculate that domination by a single species occurs only in areas where low environmental predictability favors a single opportunist. In support of this, one can mention the reef flats in San Blas, off the Atlantic coast of Panama, which are almost exclusively composed of *Porites furcata* (Porter 1974). This opportunistic species is at the bottom of the digestive dominance hierarchy (Lang 1973), but its physiological tolerance to desiccation and surface salinity fluctuations allows it to escape in shallow water from competitive exclusion (Porter 1974).

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APPENDIX I

SPECIES CODE NUMBER

Code Number	Species
2	<i>Stylophora pistillata</i>
6	<i>Seriatopora caliendrum</i>
7	<i>Seriatopora spinosa</i>
8	<i>Seriatopora angulata</i>
9	<i>Pocillopora danae</i>
11	<i>Astreopora myriophthalma</i>
12	<i>Montipora lobulata</i>
14	<i>Montipora venosa</i>
15	<i>Montipora verrucosa</i>
16	<i>Montipora tuberculosa</i>
19	<i>Montipora monasteriata</i>
20	<i>Montipora erythraea</i>
22	<i>Acropora nasuta</i>
23	<i>Acropora variabilis</i>
24	<i>Acropora hemprichi</i>
29	<i>Acropora scandens</i>
30	<i>Pavona varians</i>
31	<i>Pavona decussata</i>
33	<i>Pavona clavus</i>
34	<i>Pavona explanulata</i>
41	<i>Coscinarea monili</i>
42	<i>Fungia fungites</i>
45	<i>Fungia scutaria</i>
50	<i>Goniopora lichen</i>
53	<i>Porites lutea</i>
54	<i>Porites studeri</i>
55	<i>Porites alveolata</i>
57	<i>Alveopora daedalea</i>
60	<i>Favia favius</i>
61	<i>Favia stelligera</i>
62	<i>Favia speciosa</i>
63	<i>Favia doreyensis</i>
64	<i>Favites pentagona</i>
65	<i>Favites virens</i>
66	<i>Favites abdita</i>
67	<i>Favites halicora</i>
68	<i>Goniastrea retiformis</i>
69	<i>Goniastrea pectinata</i>
70	<i>Platygyra lamellina</i>
72	<i>Platygyra subdentata</i>
73	<i>Platygyra rustica</i>
75	<i>Hydnophora microconus</i>
76	<i>Hydnophora contignatio</i>
77	<i>Leptastrea purpurea</i>
78	<i>Leptastrea bottae</i>
79	<i>Leptastrea transversa</i>
80	<i>Cyphastrea serailia</i>
81	<i>Cyphastrea microphthalma</i>
82	<i>Cyphastrea chalcidicum</i>
83	<i>Echinopora gemmacea</i>
86	<i>Galaxea fascicularis</i>
87	<i>Acanthastrea echinata</i>
89	<i>Lobophyllia hemprichi</i>
93	<i>Gyrosmillia interrupta</i>
98	<i>Millepora dichotoma</i>
99	<i>Millepora platyphylla</i>