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Possible Effects of Water Pollution on the Community Structure of Red Sea Corals

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Abstract

The community structure and species diversity of hermatypic corals was studied during 1969-1973, in two reef flats in the northern Gulf of Eilat, Red Sea: the reef flat of the nature reserve at Eilat, which is chronically polluted by oil and minerals, and a control reef, located 5 km further south, which is free from oil pollution. In 1969, the nature reserve and the control reef had similar coral community structure. In September, 1970, both reefs suffered approximately 90% mortality of corals, as a result of an unexpected and extremely low tide. In 1973 the control reef was "blooming" with a highly diverse coral community, while almost no signs of coral recolonization have been observed at the nature reserve, and it is significantly lower in diversity. It is suggested that phosphate eutrophication and chronic oil pollution are the major man-made disturbances that interfere with coral colonization of the reef flat at the nature reserve. Although no direct evidence is provided that oil damages hermatypic corals, the data strongly suggest that chronic oil spills prevent normal settlement and/or development of coral larvae. It is possible that chronic oil pollution results in either one or a combination of the following: (1) damage to the reproductive system of corals; (2) decreased viability of coral larvae; (3) changes in some physical properties of the reef flat which interfere with normal settlement of coral larvae.

Introduction

The present work deals with the consequences of the synergistic effect of a natural catastrophe, an unexpected and extremely low tide, together with man-made disturbances, mainly chronic oil pollution, on the community structure and species diversity of hermatypic corals at Eilat, Red Sea (Fig. 1). A comparison of the hermatypic coral community structure, in 1969 and 1973, on the reef flat of the nature reserve at Eilat, and at a control reef located 5 km further south (Fig. 2) forms the basis for the conclusions of this work.

Much concern has been expressed in recent publications on the possible damaging effects of oil spills and other industrial pollutants upon coral reefs (Connell, 1970; Johannes, 1970, 1971; Straughan, 1970; Fishelson, 1973b; Eisler *et al.*, 1974). However, most investigations on the effect of oil spills on the fauna of coral reefs provide no conclusive evidence of direct injury or damage to corals (Johannes, 1972).

Spooner (1970) observed healthily growing *Acropora* sp. in Tarut Bay, Saudi Arabia in an area (close to an oil terminal) which suffers from chronic oil pollution. The water depth was 2.5 m at low water, and 4.6 m at high water. Shinn (1972) reported that staghorn corals grow unaffected around tanker loading terminals in the Persian Gulf, and concludes from his observations that crude-oil spills do not pose a significant threat to corals. Rützler and Sterrer (1970) studied the effects of an oil spill, in different habitats along the Atlantic seaboard of Panama, including rocky shores, coral reefs, and mangroves. Close to 20,000 barrels of diesel oil and Bunker C were released during and after this incident. The reefs seemed to be the least affected communities of all. Rützler and Sterrer assume that corals escaped damage because they were submerged, and did not come into direct contact with the oil. Gooding (1971) reported on extensive destruction of associated reef fauna off the harbour entrance at Wake Island (Pacific Ocean). Numerous invertebrates and fishes were killed, yet no mention was made of any damage to corals.

In laboratory experiments, using large aquaria, Grant (1970) found that the coral *Favia speciosa* was not affected by floating crude oil. Lewis (1971) pointed out that Grant did not use sealed vessels, and it may be assumed that some of the volatile portions of the crude oil escaped. Lewis exposed 4 coral species to crude oil and oil-spill detergent. The results indicated that all 4 species were sensitive to oil pollution, and they developed ruptures in the oral discs of the polyps. However, as indicated by Johannes (1972), Lewis' experiments cannot be representative of what might occur during an oil spill, when volatiles would escape to the atmosphere.

The first field evidence that some reef-building corals can be seriously damaged if coated with oil was provided by Johannes *et al.* (1972)

in some preliminary experiments. Twenty-two coral species were partially exposed above the sea water level to Santa Maria crude oil for 1.5 h. Complete breakdown of tissue occurred on those areas to which oil adhered in patches of more than a few mm diameter. No signs of regeneration were observed at the affected areas, while portions to which oil did not adhere appeared healthy.

Man-Made Disturbances and Natural Catastrophes at Eilat

The Gulf of Eilat is the most eastern of the two northern horns of the Red Sea, separated by the Sinai Peninsula (see general map, Fig. 1). The reefs of Eilat are of the fringing type, with scleractinian corals as the most important hermatypic organisms (Loya and Slobodkin, 1971). The nature reserve of the Eilat coral reefs is located 3 km south of the newly-developing port of Eilat, and approximately 1 km south of two major oil terminals (Fig. 2). 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 towards the nature reserve. It does not, however, reach the control reef, which is situated further south.

Signs of oil are constantly visible all along the shore of the nature reserve at Eilat. There is a thin oil coating on stones and pebbles along the beach up to the high-water mark (Fig. 3) in a strip 2 to 3 m wide. No such oil coating is evident along the beach of the control station which may, therefore, be considered as relatively free from oil pollution.

The major method used to clean up an oil spill at Eilat is by laying straw along the low-water mark to absorb the oil. Occasionally, oil dispersants are used, but only in the immediate surroundings of the oil terminals.

Although oil is the major polluting agent in the northern Gulf of Eilat, there are additional disturbances caused by man in this area. Among other facilities, the major port of Eilat (Fig. 2) has large storage houses for fertilizers, especially phosphates. Whilst loading the phosphate on ships for export, large quantities are blown by the northern wind, and sink onto the coral reefs further south. Fishelson (1973b) discussed the possible effects of this phosphate eutrophication in the shallow lagoon waters of the nature reserve, coupled with the chronic oil spills in this area. He emphasized the expansion of the algal community at the cost of corals, and the prevention of normal development of food chains in the reef surroundings.

The heated effluents released by a power and desalination plant located approximately 5 km north of the nature reserve (Fig. 2) comprise another man-made environmental disturbance. The temperature of the returned water at the Eilat desalination plant often reaches 39°C. The shallow-water area immediately neighboring the plant's water outlet is very low in diversity of animals and plants.

Dafni (personal communication), in a series of experiments and observations, found a significantly lower diversity of fauna accompanying dead coral colonies of *Stylophora pistillata* around the desalination plant, as compared to the nature reserve.

Another point that should be mentioned is the direct damage, mainly coral breakage, caused by numerous tourists who visit the reefs of Eilat

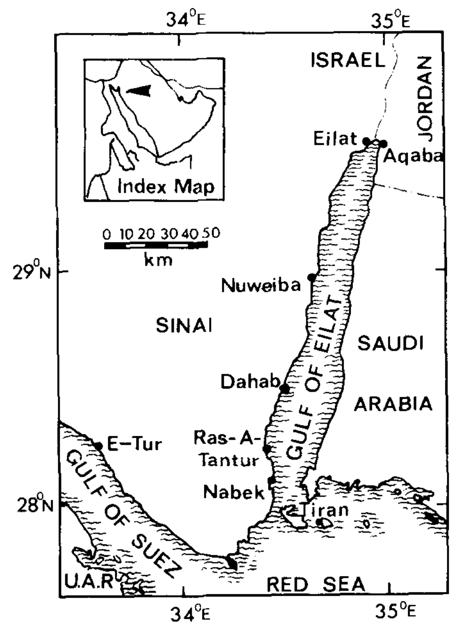

Fig. 1. General map of Gulf of Eilat

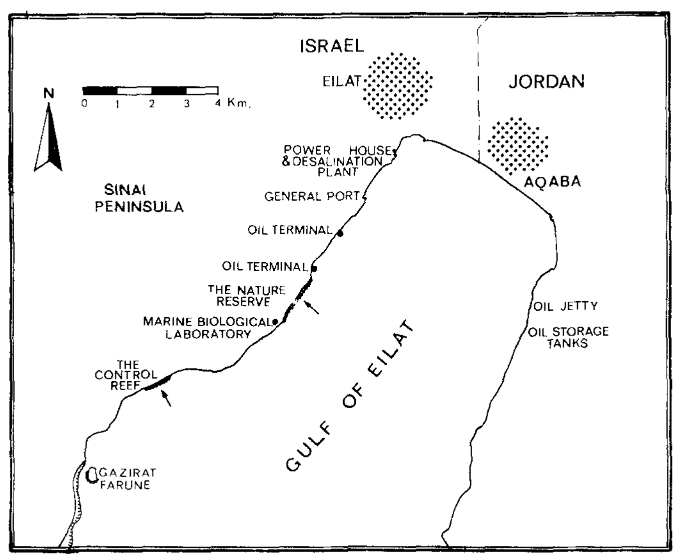

Fig. 2. Index map of northern Gulf of Eilat, showing study locations — nature reserve and control reef

Fig. 3. Oil pollution at coral nature-reserve of Eilat. Oil strip, approximately 3 m wide, can be seen along shore up to high-water mark

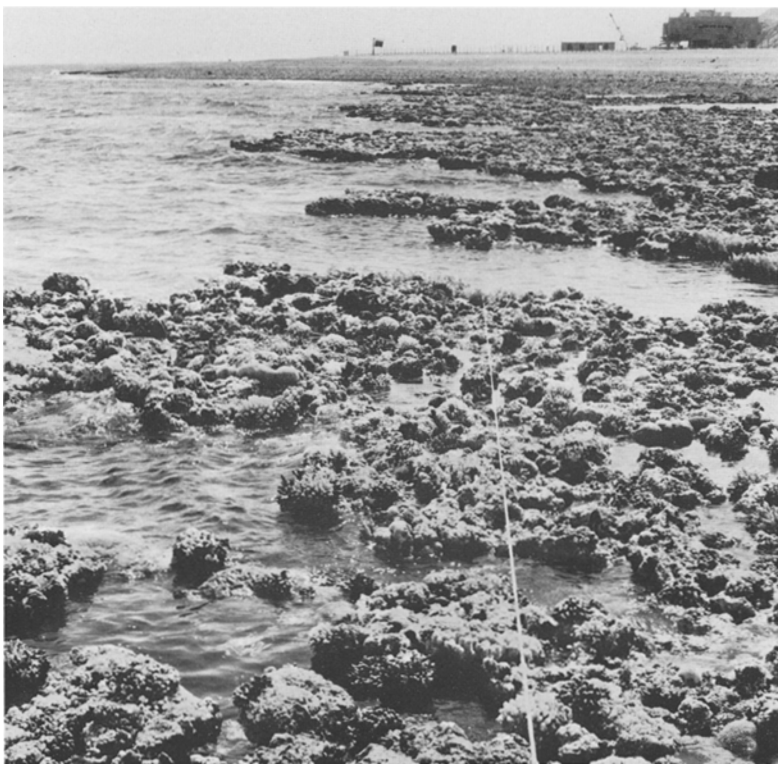

Fig. 4. Unexpected, catastrophic, low tide at coral reefs of Eilat (September, 1970)

and in particular the nature reserve. This is further discussed below.

An unexpected and extremely low tide occurred at the northern part of the Gulf of Eilat from 15-20 September, 1970 (Loya, 1972). The water level fell approximately 20 to 25 cm below the reef flat, the lowest level observed at Eilat during the last 10 years at least (Fig. 4). It may be assumed that a combination of astronomical and meteorological features caused the low tide, but this is still under discussion.

As a result of the low tide, the reef flats of the northern part of the Gulf of Eilat were completely exposed to the air and sun during the hottest portion of the day. The air temperature at 14.00 hrs ranged from a minimum of 33.8°C on 16 September to a maximum of 38.4°C on 18 September. The immediate consequences of the low tide were a mass killing of approximately 90% of the scleractinian corals on the reef flats along the northern part of the Gulf (Fig. 4). The high lethal temperatures and desiccation were probably the direct cause of the sudden mortality of the corals.

After the killing low tide, the reef flats of the nature reserve and the control station could be considered as "islands" in the sense of MacArthur and Wilson (1967), denuded from their organisms, and almost "ecologically virgin". Both reefs were open for new settlement of coral propagules, as well as regeneration of those colonies not entirely desiccated.

Methods

The community structure of the coral reefs at Eilat was studied in detail in 1969 by means of line transects, as described by Loya and Slobodkin (1971) and Loya (1972). The transects were run parallel to each other and parallel to the shore-line, with a fixed interval of 1 m between adjacent transects. Each transect was 10 m long; this had previously proved to be an adequate sample size for the reefs of the Gulf of Eilat (Loya, 1972). For the purpose of this work, an individual colony was defined as any colony growing independent of its neighbors (i.e., whenever an empty space was recorded between two adjacent colonies). In cases where an individual colony was clearly separated by the death of the intervening parts, the separate parts were considered as one individual. Any coral species which overlapped the line was recorded and its projected length on the line was measured to the nearest centimeter. The hydrozoans *Millepora dichotoma* and *M. platyphylla* were also included in this study, since they are important frame-builders of the reef flat.

Twenty-one transects 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. This enabled the same transects to be re-surveyed during the spring of 1973.

The data provide estimates of the number of coral species, number of colonies, percent of total living coverage, and diversity of corals, at both sites. For the diversity analysis, I chose to use Shannon and Weaver's (1948) index of diversity, $H'_N = -\sum_{i=1}^{s} pi\ ln\ pi$, where pi is the proportion of individuals of species i (i = 1, 2, ...s).

Results

Table 1 provides some data on the frequency of oil spills around the nature reserve between 1971-1973, although data concerning amounts of oil spilled is unavailable. In the beginning of October, 1973, the Yom-Kippur war broke out and, thus, no data is available for October-December, 1973. It should be emphasized that the data presented in this table represent only major oil spills (i.e., when the nature reserve is completely blackened by oil) reported to the Israeli Ministry of Transportation. Minor oil spills occurring around the terminals are not included.

Table 2 presents data concerning coral living-coverage and number of colonies of the 10 commonest coral species on the reef flat of the nature reserve in 1969 and 1973.

The community structure of hermatypic corals at the nature reserve changed drastically between 1969 and 1973. Some dominant coral species on the reef flat in 1969 almost disappeared after the catastrophic low tide of September 1970. Today, the reef flat at Eilat looks very grey and unattractive (Fig. 5), and is dominated by algae, in contrast to the rich coral growth and great diversity of this reef in 1969 (Loya, 1972). *Stylophora pistillata*, for example, the most abundant coral species on the reef flat of the nature reserve in 1969, has drastically decreased and has almost disappeared from the reef flat (Table 2).

In 1969, 181 colonies of *Stylophora pistillata* were counted in 21 transects on the reef flat of the nature reserve. Only 4 living colonies were counted in 1973, in the same transects. In 1969, *S. pistillata* ranked No. 1 in its relative contribution to the total abundance and living coverage of the reef flat. In 1973, this species ranked No. 7 in its relative contribution to the living coverage and No. 6 in its relative abundance.

Being an opportunistic species (see Loya, 1972), *Stylophora pistillata* could have been expected to invade the reef flat of the nature reserve quickly. The fact that 3 years after the catastrophic low tide not a single young colony of *S. pistillata* has been observed among the nature-reserve transects suggests that some critical factor is interfering with the recolonization or normal development of this species.

Table 1. Number of oil spills in vicinity of coral nature-reserve at Eilat

Month	Year 1971	1972	1973
January	2	1	4
February	1	1	3
March	1	2	6
April	3	3	3
May	2	3	1
June	2	1	4
July	4	2	7
August	4	5	1
September	2	1	5
October	3	6	nd[a]
November	2	4	nd
December	2	4	nd
Total	28	33	34

[a]nd: No data available.

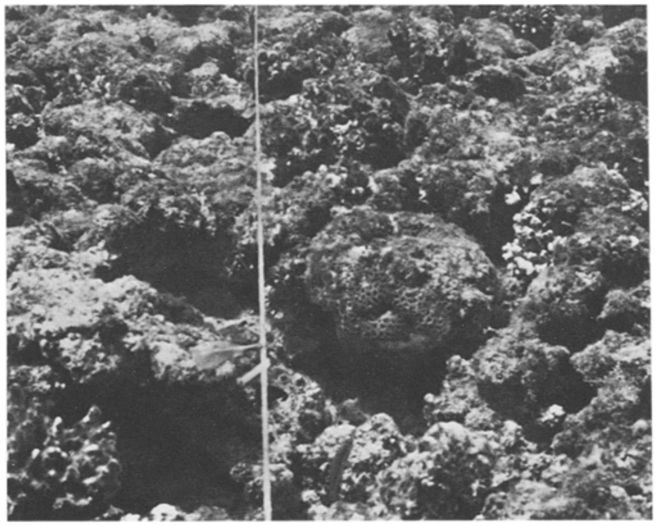

Fig. 5. General view of reef flat of nature reserve in 1973. Almost no recolonization of young coral colonies has been observed since catastrophic low tide of September, 1970

Table 2. Community structure of hermatypic corals on reef flat of nature reserve at Eilat. Data present total living coverage and number of colonies per 21 transects of 10 commonest species in 1969 compared to 1973

Species	Cover (cm) 1969	Cover (cm) 1973	% decrease in cover	No. of colonies 1969	No. of colonies 1973	% decrease in colonies
Stylophora pistillata	1320	28	97.8	181	4	97.8
Millepora dichotoma	1214	146	87.9	84	26	69.0
Cyphastrea microphthalma	882	320	63.7	94	42	55.3
Favia favus	603	123	79.6	90	23	74.4
Porites lutea	429	194	54.7	27	23	14.8
Echinopora gemmacea	389	30	92.3	23	3	86.9
Acropora variabilis	325	15	95.3	29	2	93.1
Platygyra lamellina	304	30	90.1	44	5	88.6
Acropora scandens	249	5	97.9	27	1	96.3
Fungia fungites	171	14	91.8	39	3	92.3

Table 3. Community structure of hermatypic corals at control reef. See legend to Table 2 for further details

Species	Cover (cm) 1969	Cover (cm) 1973	% decrease in cover	No. of colonies 1969	No. of colonies 1973	% increase in colonies
Cyphastrea microphthalma	1044	717	31.3	83	124	49.4
Millepora dichotoma	536	447	16.6	59	87	47.4
Favia favus	458	377	17.6	40	64	60.0
Favites abdita	300	183	39.0	28	33	17.8
Echinopora gemmacea	288	241	16.3	18	25	38.8
Pavona decussata	245	147	40.0	23	15	-34.7
Goniastrea pectinata	213	199	6.5	16	30	87.5
Platygyra lamellina	181	191	+5.5	13	29	123.0
Porites lutea	161	140	13.0	13	27	107.6
Favia speciosa	126	93	26.2	12	13	8.3

The percent decrease in the number of colonies at the reef flat of the nature reserve ranged from 15% (*Porites lutea*) to 98% (*Stylophora pistillata*). The percent decrease in the living coverage of the same two species ranged from 55% to 98% (Table 2). It should be noted that, while most of the species at the nature reserve showed a similar trend in pattern of decrease of living coverage and number of colonies (i.e., percent decrease in number of colonies and living coverage did not differ significantly), *P. lutea* showed an interesting deviation from this pattern. The decrease in living coverage of *P. lutea* was approximately 55%, whereas the decrease in the number of colonies of this species was only 15%. In other words, a relatively large number of small-sized colonies (i.e., young colonies) of *P. lutea* were recorded in 1973 as compared to 1969. Thus, *P. lutea* is the only species that has showed some limited success in reinvading the reef flat of the nature reserve.

Most of the coral colonies recorded in 1973 at the nature reserve were only partially exposed to the air during the killing low tide. Parts of the living tissue of these colonies started regenerating, while other parts were dead and, in many cases, covered by fouling algae such as *Dichotrix* sp., *Hydroclathrus clathratus*, *Sphacelaria tribuloides*, *Turbinaria elatensis* and *Pocockiella variegata* (see Fishelson, 1973a, b).

Analysis of the community structure of the control reef in 1973 (Table 3) reveals a completely different picture than that of the reef flat of the nature reserve in the same year. There is a general trend of increased numbers of colonies in most of the species recorded in 1973 as compared to 1969 (Fig. 6). Thus, in 1973, a total of 124 colonies of *Cyphastrea microphthalma* were counted out of 12 transects, while only 83 colonies had been counted in the same transects in 1969. In two cases, the number of colonies recorded in the 1973 transects were more than twice the number recorded in 1969. The percent increase in the number of colonies of *Platygyra lamellina* and *Porites lutea*, for example, was more then 100. *Pavona decussata* was the only species among the 10 commonest species at the control reef that showed a considerable decrease (approximately 35%) in relative abundance in 1973 as compared to 1969. However, excluding *Platygyra lamellina*, which showed an increase of 5.5% in its total living coverage, all the other corals showed a decrease in living coverage (Table 3).

Fig. 7 compares the average values of various statistics (per transect) measured at the nature reserve and the control reef in 1969 and 1973. After testing for equality of variance, *t*-tests were run on the different averages obtained. No significant differences were found in 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 compared to the nature reserve.

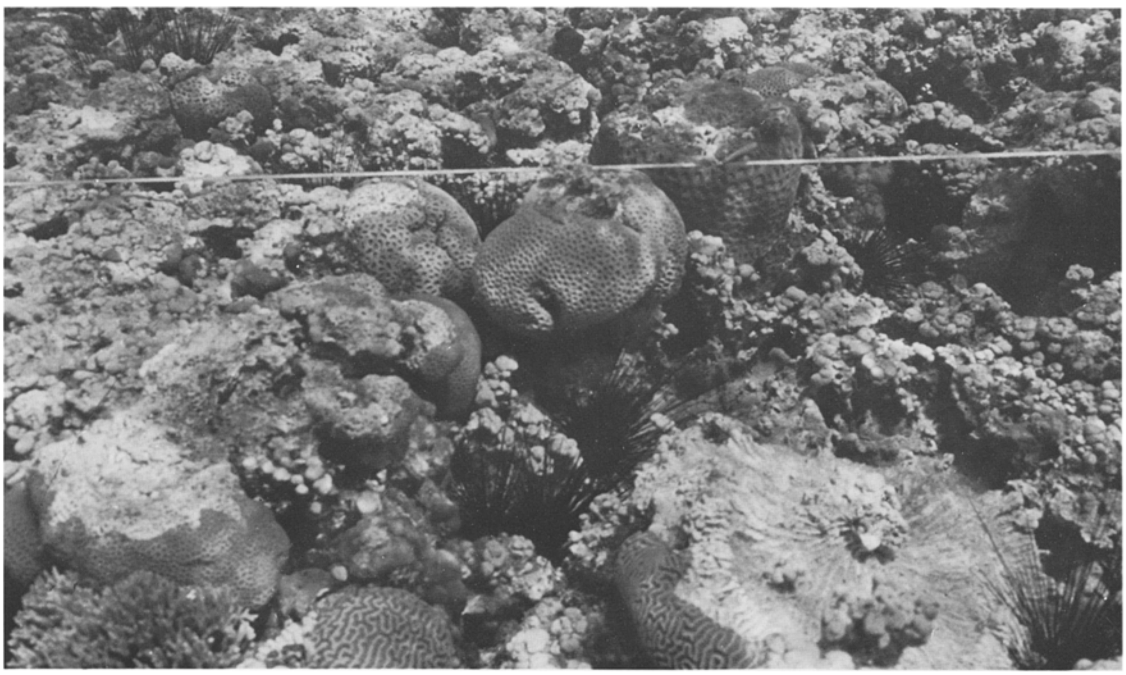

Fig. 6. General view of reef flat of control reef. Since catastrophic low tide of September, 1970, reef flat of control reef has been successfully recolonized by numerous young colonies of various coral species

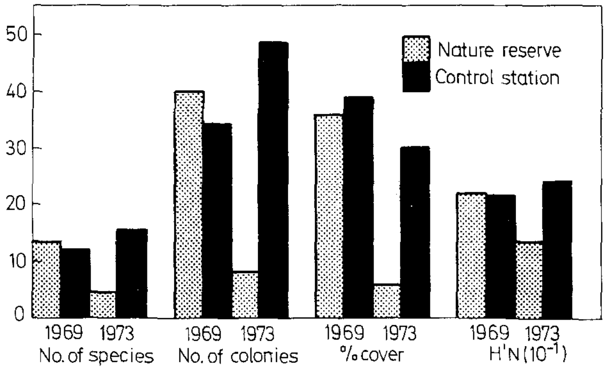

Fig. 7. Comparison between average values of various statistics (per transect) measured at nature reserve and control reef in 1969 and 1973. H'N: Shannon and Weaver's (1948) index of diversity

In the nature reserve, the average number of species per transect, as well as the number of colonies, living coverage, and diversity were significantly lower in 1973 than in 1969 (*t*-tests, $P<0.05$). It is interesting that, at the control reef, all these parameters (except living coverage) were significantly higher in 1973 compared to 1969. The average living coverage per transect at the control reef in 1973 was significantly lower in 1973 than in 1969 ($P<0.05$). It follows that, if the average number of colonies per transect increased in 1973 while the average living coverage decreased, then a large number of colonies should be young and newly established at the control reef.

Discussion

After the catastrophic low tide of 1970, the reef flats of the nature-reserve and the control reef were open for recolonization of young coral colonies. No harm has been done to corals at a depth below the water level of the low tide (i.e., approximately 20 to 25 cm below the reef flat). It is reasonable to assume that potentially the same coral propagules existed in both localities and, thus, a theoretically similar rate of recolonization of young coral colonies could have been expected. However, analysis of the 1973 data clearly demonstrates that, while the control reef has been invaded and recolonized by numerous young corals, almost no signs of such settlements were found at the reef flat of the nature reserve.

An important question in the analysis of the community structure of the nature reserve and the control reef is to what extent the coral community in 1973 represents a community of recolonizing colonies rather than colonies that regenerated. Unless one assumes that the rate of regeneration in both localities is the same, there is no direct way to distinguish, from the results of this work, between the relative contribution to the living coverage made by recolonization and that contributed by regeneration. Since the effect of water pollution, and particularly oil pollution, on the rate of regeneration in corals is not known, I shall avoid this line of assumption.

At the reef flat of the nature reserve, very few young colonies were recorded (mainly *Porites lutea*) and, thus, the major contribution to the 1973 living coverage was due to regeneration of old colonies. Fishelson (1973a) points out that, in some instances, it took only 6 months for full regeneration of some coral colonies. Although regeneration has also been occurring at the control reef, the major contribution to the 1973 living coverage and abundance of colonies there was due to recolonization of young colonies.

The obvious explanation for the deteriorating situation of the coral nature-reserve at Eilat is disturbances caused by man to this environment. Among the possible disturbances mentioned earlier, thermal pollution seems the least likely. The relatively large distance of the desalination plant from the reefs further south (Fig. 2) prevents any detrimental effects on the reef communities around the nature reserve. Nevertheless, more research should be done along these lines, especially concerning long-term effects of thermal pollution on coral-reef communities.

Although breakage of corals by man is much more frequent at the nature reserve, it does also occur at the control reef. This factor alone cannot explain the fact that 3 years after the catastrophic low tide, almost no recolonization of corals took place at the nature reserve.

Phosphate eutrophication of the shallow lagoon at the nature reserve (see Fishelson, 1973b) may be a significant factor in creating better conditions for algal growth and, thus, increasing competition for space between algae and corals. However, one can find many large areas on the reef flat of the nature reserve which are completely clear of algae or other organisms that may compete with corals for space; yet, no young hermatypic corals can be found in these areas. It seems, therefore, that some extreme environmental disturbance prevents colonization of corals at the reef flat of the nature reserve. As previously discussed, the most pronounced disturbances at the nature reserve are chronic oil spills.

It is suggested that synergistic effect of algae on the one hand, and some soluble oil fractions on the other hand, are the major factors in preventing coral colonization of the reef flat at the nature reserve of Eilat. Since the consequences of phosphate pollution at the nature reserve were discussed by Fishelson (1973b), I shall concentrate on the possible consequences of chronic oil pollution, and hypothesize on its possible harmful effects on the reproduction of corals.

Although no mention has been made in the literature concerning damaging effects of oil pollution on the reproductive system of corals, there are several reports dealing with this problem in relation to other marine organisms. In his book "Oil pollution and marine ecology", Nelson-Smith (1972) mentions several investigations concerned with the effects of oil pollution on different early stages in the life cycle of marine animals. Thus, a 50 to 90% mortality was reported for eggs of *Sardinus pilchardus* as a result of oil pollution in Cornish waters after the "Torrey Canyon" incident.

Künhold (1969) kept herring eggs (*Clupea harengus*) and fry in sea water, under various crude oils, in concentration of 10 ml/1, and observed mortalities between 70 and 100%, within the first 3 or 4 days. Eggs which hatched, even if placed in the oily water at a late stage, gave rise to a high proportion of deformed larvae. Mironov (1972) found that crude and fuel oils at 0.1 µl/1 killed half his batch of *Rhombus maeoticus* eggs within 2 days and, at higher concentrations, they all died. Most of the larvae hatching at lower concentrations were deformed, inactive, and died after 1 day. Blumer *et al.* (1971) report that mussels which appeared to be unharmed after the West Falmouth oil spill (Sanders *et al.*, 1972) failed to reproduce, while mussels from nearby areas unaffected by the spill were reproducing normally. Wells (1972) has demonstrated the acute toxicity of the emulsions of crude oil on lobster larvae at very low concentrations. Fu-Shiang Chia (1973) exposed 14 species (5 phyla) of pelagic larvae to 0.5% of No. 2 diesel oil in sea water, and found that most of them survived from 3 to 72 h. Cohen (1973) exposed colonies of the alcyonarian *Heteroxenia fuscescens* to high concentrations of Iranian crude oil, under conditions of continuous water flow, in large tanks. Numerous larvae were seen expelled in the tank containing the oil, while no larvae were seen in the control tank.

Eisler *et al.* (1974) conducted a series of laboratory studies at Eilat on different Red Sea animals, using a commercial chemical oil dispersant and various crude oils. These authors derive some tentative conclusions concerning the indirect harmful effect of oil and oil dispersants on egg-capsule deposition by the mollusc *Drupa granulata*. They demonstrate that fecundity of *D. granulata* seems to be a direct function of *Mytilus variabilis* consumption and that predation rate on *M. variabilis* by *D. granulata* significantly decreases when both are exposed to crude oil. When *M. variabilis* and *D. granulata* were exposed to initial immersion in 10 ml/1 Iranian crude oil for 168 h, the average number of egg capsules deposited by individual *D. granulata* over 28 days of post-treatment period was only 4.2, while 14.2 eggs were deposited on the average in the control experiments.

Although the present results do not provide evidence that corals are d i r e c t l y damaged by oil, the data strongly suggest that chronic oil pollution prevents, in some way, colonization of young coral colonies. This interference may be due to some chemical changes in the physical properties of the reef flat, or to some biological interference connected with the corals themselves. It is possible that oil damages the reproductive system of corals, which may interfere with coral larvae production, or there might be adverse effects on the viability of the larvae themselves, inhibiting them from successful settlement and normal development. Although oil dispersants are only occasionally used and at a relatively large distance from the nature reserve, they may only enhance the harmful effects of oil spills, as demonstrated by Lewis (1971), Eisler *et al.* (1974) and others. In the control station, where no signs of oil are evident, there has not been any interference with recolonization and the reef flat has been successfully invaded by numerous young colonies.

Thus, one of the basic differences between the consequences of chronic man-made disturbances and natural catastrophes on coral reefs is the possibility of non-reversibility of this environment to its normal community structure as a result of continuous interference by man. Further experiments are being carried out seeking more direct evidence for the possibility that oil has harmful effects on the reproductive system, or larval viability of scleractinian corals.

The effects of oil pollution may be regarded on a short-term basis with an immediate effect, or on a long-term basis of chronic character. Nevertheless, little attention has been given to what happens with oil once it is out of sight (Murphy, 1971). Sanders and his group at the Woods Hole Oceanographic Institute (Sanders *et al.*, 1972), found that long after visible traces of oil disappeared from the sea, various oil fractions were present in sizeable quantities in the bottom sediments, up to 13 m depth. Where oil has been found, very high mortalities of bottom organisms have been recorded. Bacterial degradation of the oil is slow, with the less-toxic straight-chain hydrocarbons being the first to decline in quantity.

In view of Sanders' findings, we badly need research on the long-term effects of oil on coral-reef communities. On a long-term basis, the frequent oil spills occurring in the vicinity of the nature reserve at Eilat might have catastrophic consequences on a wide variety of coral-reef communities. Moreover, we do not know the possible long-term effects of various soluble oil fractions (especially the low boiling, aromatic hydrocarbons) on corals, nor on a variety of other coral-reef organisms. In addition, it is quite possible, especially in the surroundings of the coral reefs of Eilat, that an oil spill coincides with a spring low-tide, where many corals are exposed above water. The consequences of such an event would be catastrophic to the corals, as shown by Johannes *et al.* (1972).

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