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Stability and instability of marine ecosystems, illustrated by examples from the Red Sea*

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ABSTRACT: With all the limitations of novelty, ecology today is able to discern certain practices that may be destructive to the existing ecosystems, and to predict what the damages in the systems will be if preventive measures are not taken. The aim of this paper is to present some ideas about the importance of predictable evolution of all the compounds of ecosystems leading toward the development of climax communities, with high homeostatic power. Recent perturbations, caused mostly by human activity, have disturbed the predictability of events, and as a result also the stability of ecosystem development. Such disturbances produce situations de novo in ecosystems, cause reselection of the biological partners, and eliminate the more sensitive ones. These ideas are illustrated in several investigations performed in the coral reef region of the Gulf of Aqaba, Red Sea. The results of these studies showed that the perturbations caused by man's activity increase the instability of coral reef ecosystems. This is illustrated by a decrease in the affinity of samples taken at the same spot and a decrease in the evenness of distribution. These changes produce new forms of ecosystems, unpredictable as to their final stages of development.

INTRODUCTION

The biological world, terrestrial or aquatic, is composed of a persistent web of interactions among the organisms involved, as related to their environmental resources. Such webs of interactions are called ecosystems. According to my definition, an ecosystem is the sum of organic and inorganic factors observed in a defined place, convenient to be analysed together. In such a way in various habitats, various ecosystems are formed by different setups of organic and inorganic phenomena, regulated by a very large number of feedback loops of considerable homeostatic power. This means that in most cases the ecosystems identified by us are integral parts of larger biological entities, and the limits drawn by us for ecosystems are in fact the limits of our ability to analyse. Within all such systems sensory-response activities integrate all the parts and in most cases form some kind of equilibrium, a buffer system acting against changes. Such interactions on a global scale exist between oceans and atmosphere,

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feeders and food, biological and physical nature, and in man – between social structure and technology.

MODELS OF ECOSYSTEM DEVELOPMENT

It seems that during the evolutionary process in some cases of ecosystem development, almost total conformity was achieved between organisms and their environments. In the tropical regions the coral-reef ecosystems are the product of such conformity, and as shown by various investigations, they are also most sensitive to changes in environmental parameters. Any perturbation in such a well-adjusted system causes

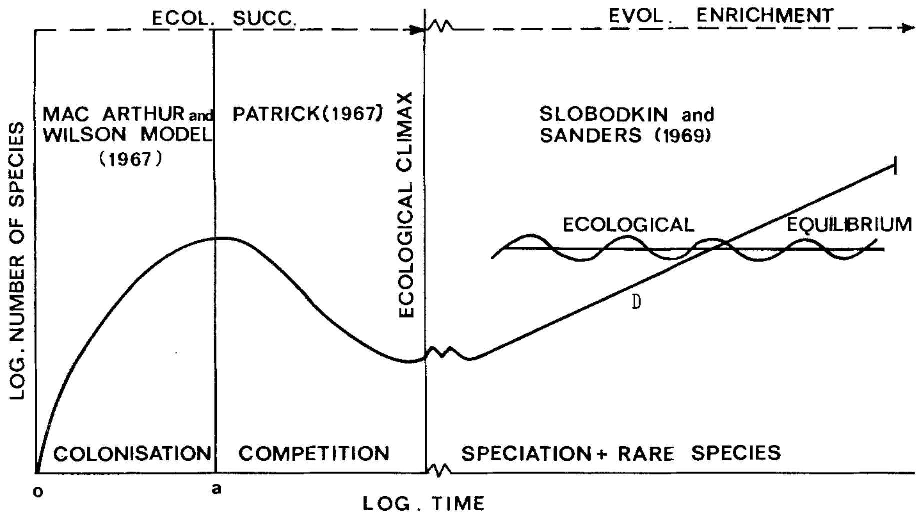

Fig. 1: Model of ecosystem development in an evolutionary stable environment. D = diversity

a deviation from the natural equilibrium and changes in the ecosystem. Ecology only recently has made substantial advances in system analysis, especially in regard to ecosystem stability. This has facilitated the formulation of equations and theoretical postulations that help to analyse health and survival of ecosystems. Figure 1 incorporates the information available, including results of theoretical models as well as results of various experiments. The main goal of the curve* shown is to use the ideas of MacArthur & Wilson (1966) as well as the work of Patric (1967), Slobodkin & Sanders (1969), Wilson (1969) and my own observations, thus presenting a scheme of evolutionary development of an ecosystem – a population of species. The basic postulation in this development is the importance of predictability for ecosystem development. The higher the predictability, the higher the ecosystem's stability.

* This curve, based on Wilson (1969), was developed in discussions with Prof. L. B. Slobodkin of S.U.N.Y., USA.

In our model, two stages of ecosystem development are prominent. The first one, the successive stage, during which colonisation and competition with time produces an ecologically stable climax situation. In this case, climax means that the probability for a new species to enter the system is much lower than that for additional specimens

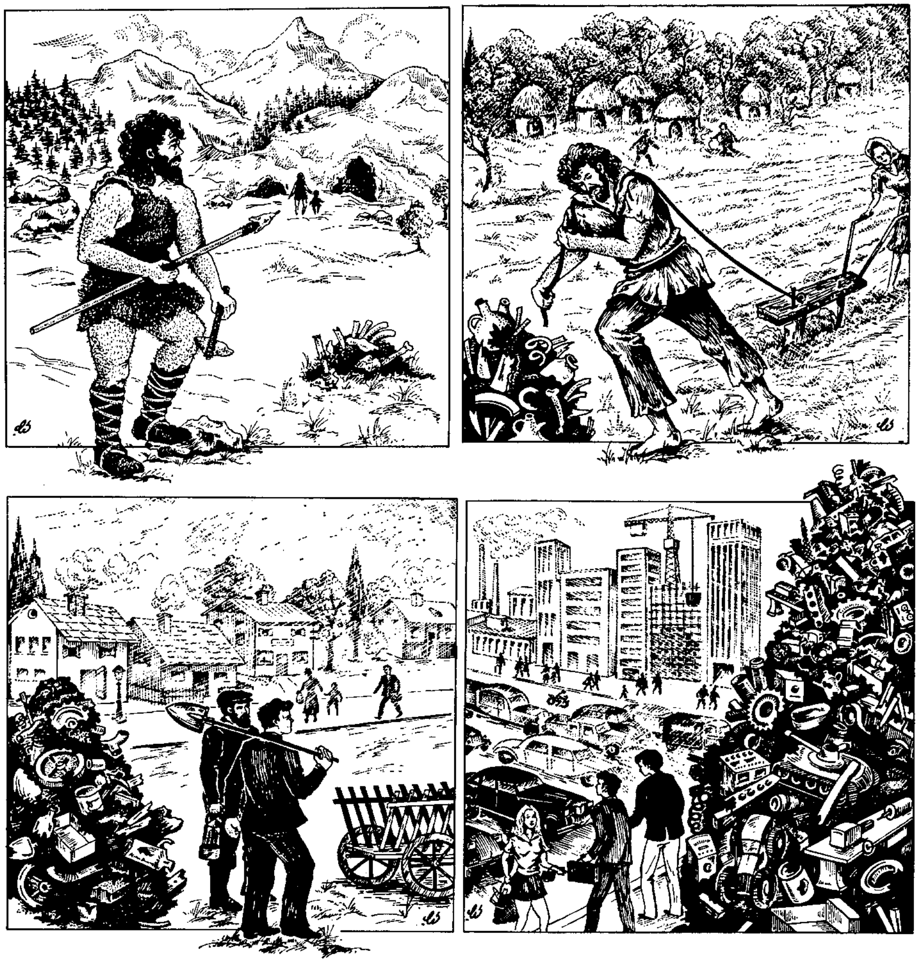

Fig. 2: Characteristic steps in the evolution of mankind regarding the impact on the ambient ecosystem. Upper left: Primigenius; right: Agrarius; lower left: Urbanicus; right: Technocratus (Drawn by Mr. Z. Schäffer)

of existing species. The second stage of evolutionary enrichment occurs in the climax ecosystem by means of genetic speciation, as well as by invasion of rare species, usually extreme specialists utilising specific microhabitats. All this occurs under predicted environmental conditions and leads toward diversification and an ecological equilibrium. The composition of species will remain more or less constant, regulated by an intrinsic feedback mechanism – illustrated on the graph by the lower oscillatory line. This stability is based on the central assumption that the changes occurring within the framework of important environmental parameters, are predictable, and that the sensory mechanisms represented in the ecosystem are capable of dealing with them.

Proceeding from this point of view, the following postulations are formulated:

The ability of the eco-buffer system to control is based on: (1) regular physico-chemical parameters; (2) stable biological interactions; (3) predictable energy flow.

Species diversity in a controlled system is a function of (1) time of development; (2) carrying capacity of the habitat; (3) environmental complexity; (4) immigration-extinction rates.

Within and along with natural ecosystems, human populations developed, and finally went through some stages that in short could be described as transition from limited consumption to unlimited utilization (Fig. 2). In the beginning, the Primigenius man was part of the ecosystem, being a predator himself as well as prey for other predators. The agricultural man (Agrarius) started the green invasion, modifying habitats, and thus reducing their stability and inducing numerous pests. With time the city man (Urbanicus) and, more recently, the technical man (Technocratus) developed. Their activities caused a rapid increase in the perturbation of natural systems, especially through pollution – the overloading of ecosystems with biologically significant substances. In most cases, for most of the substances, the natural buffer-system of the "Umwelt" is insufficient. Consequently, changes occur. An example of this is given in our work concerning the influence of rising ambient P-contamination on survival of corals. Increased phosphorus levels do not kill coral tissue directly, but cause changes in mucus production, which in turn affect changes in microbial populations on the coral mucus leading to diseases of the coral and death. In nature such killing of coral tissue will bring about drastic changes in the whole system (Fishelson, 1973).

Influenced by natural and unnatural catastrophies, ecosystems lose their stability and as a consequence, it becomes more difficult to predict system dynamics. Phenomena of this kind occurred, for example, on the coral reef close to Eilat (Red Sea) where the reef platform was frequently influenced by perturbations (Fishelson, 1973a, b; Loya, 1975). If a perturbation occurs only once, the system is able to regenerate after a certain period of recovery (Fig. 3). But if the perturbations are frequent and unpredictable, then recovery is often impossible and the components of the ecosystem undergo a reselection, during which those sensitive to the perturbation disappear and those less sensitive take over (Fig. 3). Such developments were observed on the coral reef close to Eilat harbor, where frequent disturbances by oil and phosphates gradually killed the coral cover, making room for algae and other less sensitive organisms.

This not only changed the animal cover on the coral platforms but also produced more extreme changes in the fish populations found here. This is exemplified by the investigation performed by Slobodkin & Fishelson (1974) on the importance of the cleaner fish *Labroides dimidiatus* and its cleaning stations as focal points for fish species composition analysis. As Figure 4 shows, a drastic change occurred in the fish population observed at single stations if we compare the years 1969 and 1974. Additional observations performed in 1976 showed that, together with additional destruction of the local coral habitat, some of the cleaners disappeared altogether, and this of course was marked by an additional reduction in the fish population.

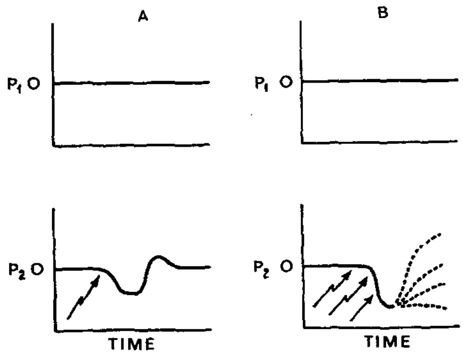

Fig. 3: Reactions to perturbations of an 0-stage population (P, 0). A: Recovery after a single perturbation; B: Selective developments after frequent perturbations

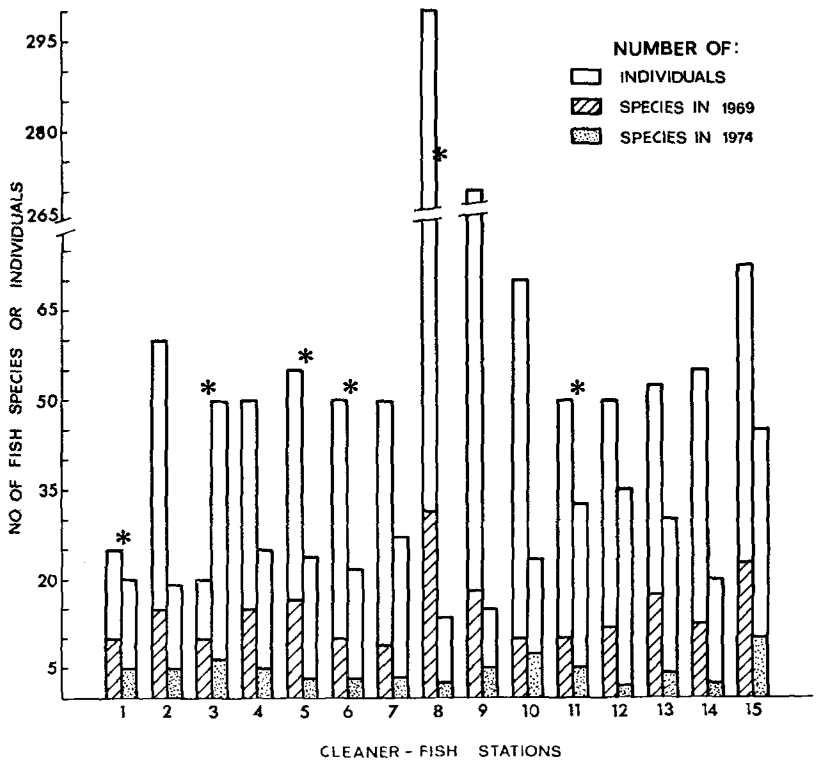

Fig. 4: Changes observed in fish populations visiting cleaner-fish stations of *Labroides dimidiatus* (*: stations that disappeared in 1976)

Thus, the rate of change within the ecosystem depends on the frequency of perturbations and their impact on the system. This can be postulated as follows:

In any ecosystem: (1) short time interferences will cause deviations from the evolutionary stability; (2) this will decrease the energy flow stability and biological regularities.

The outcome of this will depend on: (1) the frequency of environmental perturbation; (2) the power with which these influence the biological world.

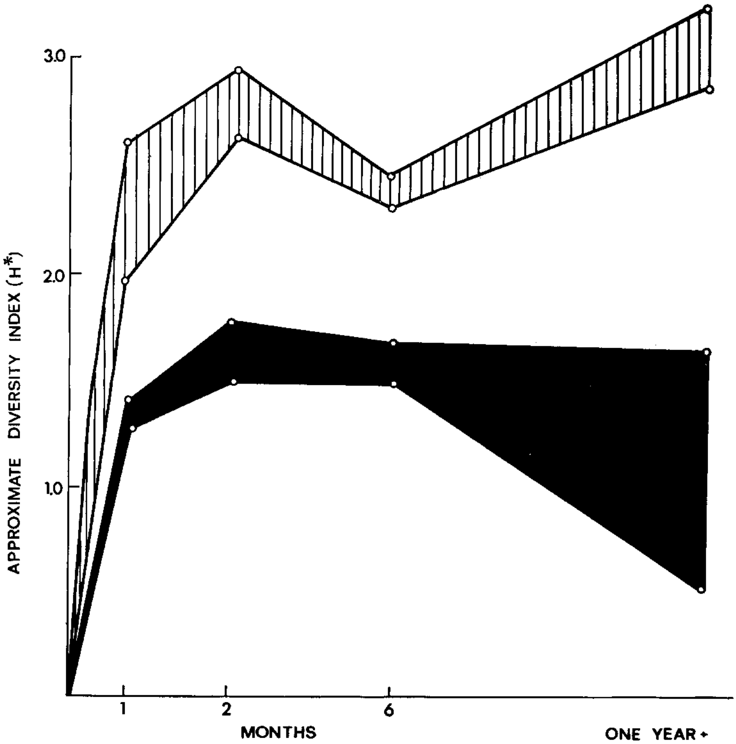

Fig. 5: Development and succession of an animal-plant community on coral skeletons implanted in a clean (upper part) and in a polluted (lower part) area in Eilat shallow-water littoral. (Redrawn, with changes, according to a figure in the M. Sc. thesis of our student, Mr. Y. Dafni)

The usefulness of these postulations, as well as of the ecosystem model (Fig. 1) was proved in several experiments. One experiment involved the implantation of cleaned coral skeletons into shallow waters of the coral habitats close to Eilat. Of the places chosen some are clean, others are influenced by human activities and highly overloaded with organic material. The implanted "bare" surfaces of coral skeletons served as terra nova for the invasion of various organisms. After some time, the coral colonies were collected and the total population found on them analysed. An approximate diversity index based on identification of higher taxonomic units, showed a high correlation with the species diversity index (H) and was used for the calcula-

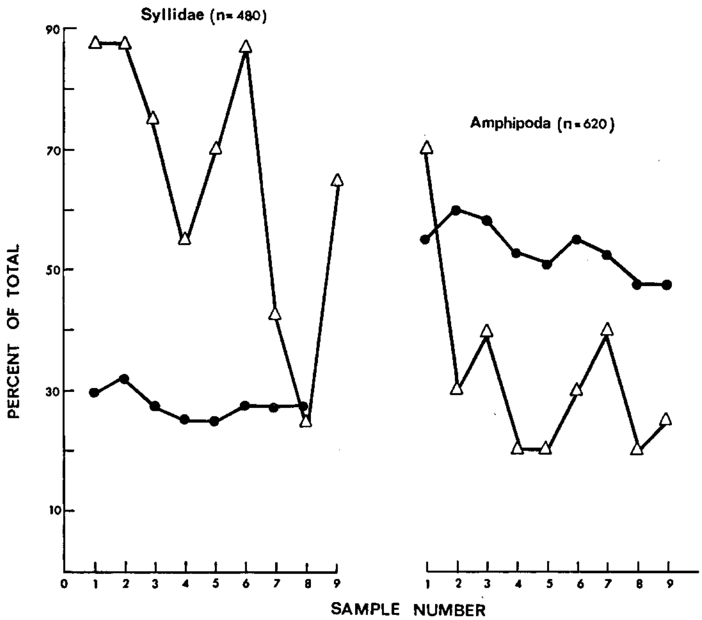

Fig. 6: Stability and instability of syllid Polychaeta and Amphipoda, in 9 samples collected from the algae *Ulva lactuca* from disturbed (triangles) and stable (filled circles) localities

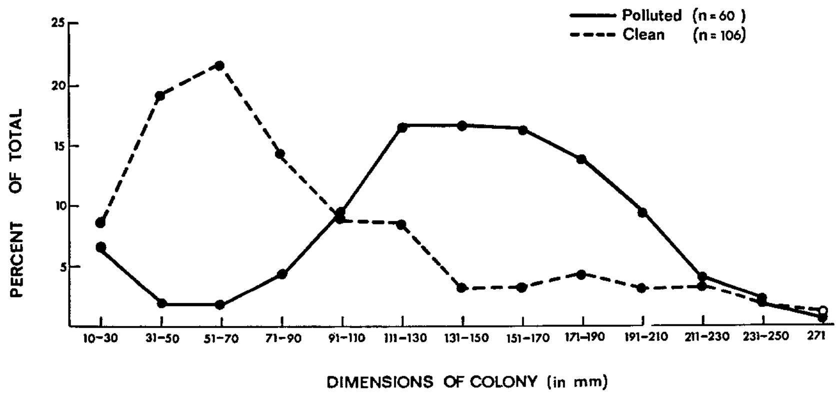

Fig. 7: Age-groups of faviid-corals from a polluted region (entire line, n = 60) and a clean region (broken line, n = 106) of a coral habitat at Eilat

tions. As demonstrated in Figure 5, population developments on the coral skeletons implanted in the clean habitats are much like the developmental line presented in Figure 1. This indicates that under certain conditions, in stable environments, some micro-ecosystems may alter their equilibrium even after a short successive development. On the other hand, the animal population that developed on the coral skeletons implanted in the disturbed habitats, not only did not reach stability, but showed a wide dispersal of sample contents and lack of affinity among them. This is marked by the wide shape of the curve. Hence, if the perturbations within an ecosystem are frequent and strong, they will eliminate the more sensitive compounds of the system and leave the more euryecous, opportunistic organisms. Such selection will push back the ecosystems to some stages of successive development (Fig. 1), opening space for additional species to invade the system. Such types of interactions will be especially dangerous in tropical ecosystems, particularly in coral reefs, complex systems of plant-animal-environment interactions, characterised by high stability and predictability.

Investigating such shallow-water coral reef ecosystems, one becomes impressed by the high mutual affinity of its various parts. It seems that the coral reefs are maximally adapted to their environment and because of this, exhibit a minimum tolerance to environmental changes. If such a system is disturbed, the first change that becomes evident is the decrease of affinity between its various parts. This situation is illustrated in Figure 6, which compares samples of epiphytic animals collected on the algae *Ulva lactuca*, in two different habitats – one clean and stable, the other disturbed by waste

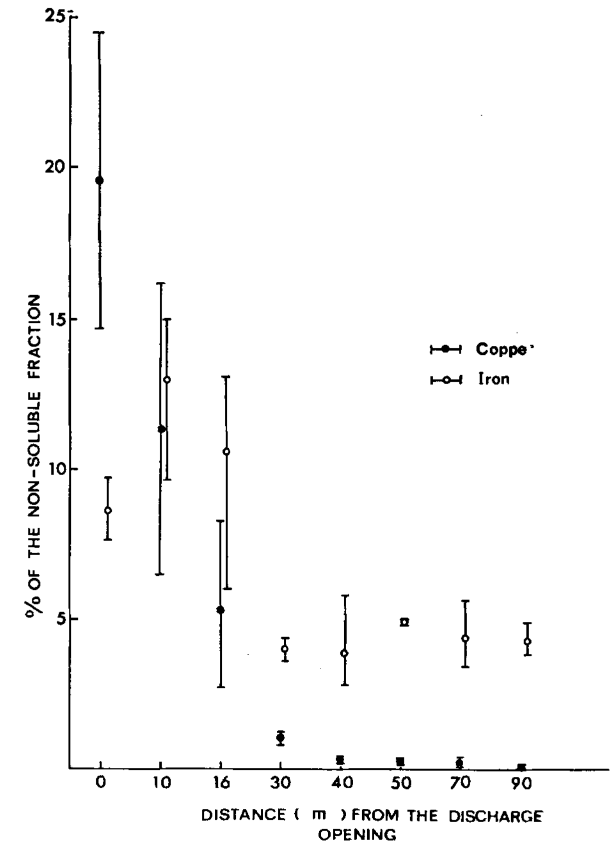

Fig. 8: Distribution of inoculated ions (copper and iron) in soft bottom sediments opposite the water-discharge opening of a power plant at Eilat

Table 1

Variation in bottom-community structure in a 380 cm² sample on a polluted site at Eilat
(A, B, C = 3 samples every other month)

Taxa	1			10			20			30			40			50		
	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C
Ostracoda	0	0	0	0	0	0	0	0	2	0	0	6	0	0	2	2	4	2
Amphipoda	0	0	2	0	2	4	0	3	2	0	2	6	0	12	8	6	8	4
Tanaidacea	0	0	1	0	6	0	0	2	4	0	8	12	0	14	10	0	8	2
Copepoda	0	1	4	0	8	1	4	0	6	9	9	4	17	16	5	26	10	30
Foraminifera	0	0	10	0	0	8	6	2	10	25	7	32	15	22	48	80	42	60
Polychaeta	0	0	1	0	4	10	36	12	24	80	35	58	60	48	72	82	70	75
Nematoda	12	10	45	130	20	160	180	300	120	< 300	220	180	140	200	100	95	40	60
Bivalvia	0	0	20	102	40	0	80	82	0	45	20	40	16	20	0	8	4	4
Gastropoda	0	0	12	2	0	10	0	6	18	2	21	20	8	18	4	12	20	2

heat from a power plant. Both the syllid Polychaeta and Amphipoda reveal stable populations in the undisturbed habitat, contrary to low stability demonstrated in the perturbed habitat.

Change toward instability of a coral community due to perturbations is illustrated also in Figure 7, which provides measurements of age-class distribution of faviid corals from both a polluted and non-polluted region. From these data it is evident that the polluted region is poor in juvenile corals, as compared to the unpolluted one. The absence of a sufficient number of small colonies, killed by algae overgrowth, will gradually denude this region of faviid corals. Finally, a new ecosystem may be formed. Almost total denuding of coral reefs in the Gulf of Aqaba

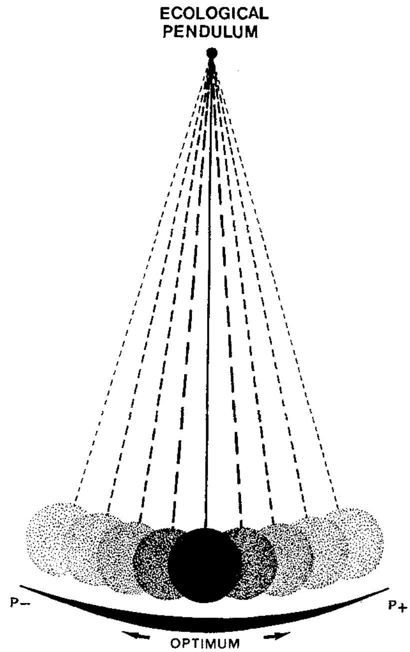

Fig. 9: For ecosystems to act in predictable ways, the ecological pendulum must attain maximum distance from the pessima (plus or minus)

(Red Sea) was described by Fishelson (1973) and Loya (1975). If denuded areas are disturbed continuously, they become dominated by algae: the algal species depend on season and type of perturbation. But, as shown by Loya, if the perturbation disappears, the habitat shifts back toward stability, and may show, at least for a certain time, an increase in the number of species, even if compared to the pre-perturbation stage of the ecosystem. Thus, reduction in stability may in one instance produce a monotonic population, whereas in other cases a rise in species diversity may occur.

Reduction in stability of an ecosystem is also illustrated by our investigations on benthic communities in shallow, soft bottoms at Eilat. The sampling area was located opposite a small power and desalination plant discharging waste heat, enriched with metal ions from the tubing, into the sea. The polluting ions could be recorded as far as 50 to 60 m from the discharge point (Fig. 8). For control, a topographically similar region was chosen within a non-disturbed area some 15 km from the first one. Samplings showed that great differences existed between the animal communities of the two areas. The main difference was the total absence of higher Crustacea from the polluted region. As these are the main consumers of other meiobenthic organisms, their absence facilitates the domination of Nematoda, Copepoda and other small animals. Repeated sampling of these two areas over short intervals revealed reduced stability and sample resemblance in the disturbed region (Table 1). By contrast, the communities in the undisturbed area remained almost unchanged, and samples had a very high degree of resemblance. The instability of sample composition in the disturbed region seems to be due to the unpredictability with which various physical parameters of the water outflow influence the system.

In all such cases, the usual models of ecosystem structure, assuming relatively high stability, must be replaced by other models and analyses, taking into consideration short time intervals and reduced stability. The models published by Levin & Paine (1974) dealing with disturbed ecosystems, are pioneering progress in this direction.

CONCLUSIONS

Summarising the ideas and experiments presented, we may postulate that perturbations caused by man's activities in shallow waters: (1) lead to selective types of ecosystems, dominated by opportunistic species; (2) produce physically controlled ecosystems, instead of biologically controlled ones.

The degree of stability of an ecosystem can be measured (1) by the fluctuation (pendulum) regularity of physical factors; (2) by numerical regularities of the animal community, especially species turnover; (3) by the percentage of species represented with opportunistic life cycles.

As demonstrated, tropical marine ecosystems subject to stress due to variations in environmental factors, change from well-balanced to unbalanced. Such ecosystems lose their climax situation, are always in some stage of successive development and are very unpredictable as to their final structure. In each major perturbation, the biological spectrum of an ecosystem will be a compromise between temporary invaders and resident opportunists able to withstand the perturbation.

It seems that the rate of change of temporary invaders, and not the opportunists, will characterise the degree of instability of the system. The organisms permanently found in newly-disturbed ecosystems are a measure of environmental stress, whereas the turnover of species expressed as dissimilarity of samples, characterises the degree of the ecosystem's stability. Consequently, today two types of extreme ecosystems are observable: one type – evolutionary extreme ecosystems, like salt lakes and dead seas are monotonous in population composition and highly stable. The second type – man-made extreme ecosystems are mostly polyspecific in their population, with changing types of conformity between themselves and their environmental parameters. This causes a very pronounced instability. Such types of ecosystems are produced in shallow water marine habitats, and they are characterised by a high degree of instability.

These changes, from the evolutionary stable to environmentally unstable ecosystems, impose a new responsibility on the scientific community, because the existing feedback mechanisms and buffer systems of the ecosystem are unable to deal with them. With all the limitations of novelty, ecology today is able to discern certain practices that may be destructive, and predict what the damages in man's eco-world will be, if measures against such practices are not taken. So, it seems that even with limited information available, ecologists and scientists, in general, must take part in the production of "boundary conditions" like game rules, inside of which, and only inside of which, rational action is possible. It seems to me that the ecosystem pendulum (Fig. 9) must be kept moving in the sphere of optimal control, till we know more about how to handle nature. Moving toward the unknown future, we should not forget the well-known present.

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