to 7000 mg/100 ml in human plasma (*3*). The flow of aqueous humor is across the lumen, from inner to outer wall. The inner wall has openings that are 0.1 to 1.0 μm in diameter, the outer wall has large openings up to 80 μm which lead to the veins in the episclera.

With these facts in mind, perhaps what has been seen in both dog artery and human canal of Schlemm is a structure common to many endothelial cells. These projections may take part in the exchange of fluid across the endothelial cell by increasing surface area, rather than having an effect on the longitudinal flow of fluid. Their frequency was much greater in the dog pulmonary artery than in the Schlemm's canal in the human, which might relate to a more rapid rate of flow of fluid across the endothelial wall in the lung than in the eye.

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12 November 1971

Stability of Enriched Aquatic Ecosystems

In a recent report (*1*) Rosenzweig has suggested, on the basis of several mathematical two-species interaction models, that undesirable "instability should often be the result of nutritional enrichment." Although his arguments may confirm this prediction in the case of his two-species model, the extrapolation of his prediction to natural ecosystems appears to us unwarranted, both on experimental and on other grounds.

During the past year we have been engaged in adding 100 tons (90 metric tons) of fertilizer to a 12,000-acre (4,850-hectare) oligotrophic lake (mean depth, 200 m) located on Vancouver Island. Nutrients were added in solution at a rate of 5 tons per week from June to October 1970. Detailed results of the effect of this addition will be reported elsewhere (*2*), but the essential features of our experiment will be given here because they demonstrate a beneficial effect of nutrient enrichment in contrast to Rosenzweig's generalized conclusion.

The rate of nutrient addition to our lake was calculated, from phytoplankton growth rates of the natural flora, to produce an effect equivalent to a doubling of the standing stock of phytoplankton every 7 days. The total annual input of nutrients was further adjusted to double the amount of available inorganic nitrogen in the euphotic zone and to increase the amount of available phosphate by a factor of about 5; with these additions the natural ratio of nitrogen to phosphorus in the lake water was changed from approximately 70 : 1 to 30 : 1. Our purpose was to increase the productivity of the natural flora and fauna in the lake but to avoid a condition of undesirable eutrophication or a change in the diversity of food organisms leading to the production of up to 4×10^6 to 8×10^6 sockeye salmon less than 1 year of age in the lake. These objectives were substantially achieved in that the water clarity throughout the period of enrichment remained little changed (the secchi disk disappeared from view at a depth of water of 11 ± 2 m), the standing stock of primary producers remained unchanged (chlorophyll a, 0.4 ± 0.2 mg/m^3) except for a brief period immediately after the first addition of nutrients in June 1970, and the species composition of the zooplankton was little affected. However, the rate of primary production was at least double that recorded in 1969, the year before fertilization, and the standing stock of zooplankton was increased by a factor of about 8. The mean weight of the fish increased by approximately 40 percent as compared with values for the previous year (*3*). Thus it has been possible to enrich artificially a large body of water without causing either undesirable eutrophication or the elimination of species as suggested by Rosenzweig (*1*). The principal food organisms selected by the young salmon were as follows: *Epischura* (June to August 1970), *Holopedium* (September 1970 to February 1971), and *Bosmina* (March to May 1971). The salmon's ability to feed on each of these species was in itself a negation of Rosenzweig's prediction, since, in spite of increased production, trophic stability was maintained in that the diversity of food organisms was substantially the same before and after nutrient enrichment.

Quite apart from our own experiment, natural enrichments of aquatic systems occur throughout the world and these result in higher productivity. Upwelling along the Peruvian coast and in the Antarctic are two outstanding examples of natural enrichments.

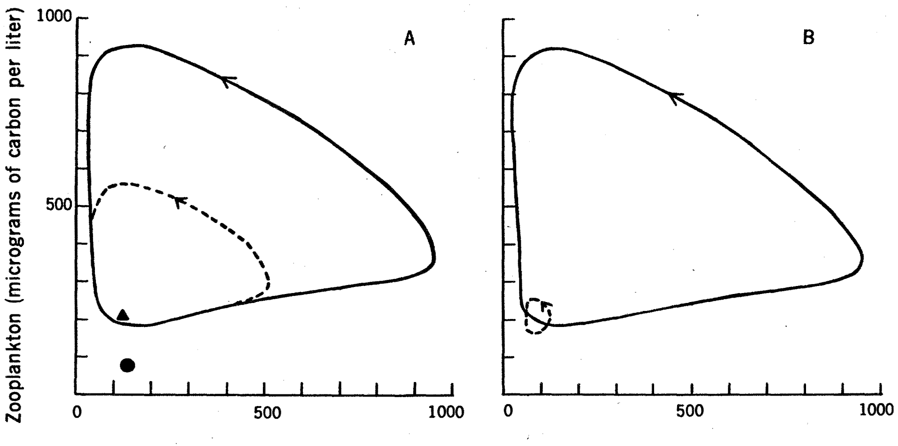

Fig. 1. Zooplankton concentration as a function of phytoplankton concentration through steady-state oscillation. For (A), *k* is equal to 14 percent per day and *r* is equivalent to a doubling time of 3 days. Phosphate concentrations ($\times 10^{-6}$ gram atom of phosphate phosphorus per liter) are as follows: (solid circle) 0.4; (triangle) 0.8; (dashed line) 1.2; (solid line) 1.50. For (B), the phosphate phosphorus concentration is 1.5×10^{-6} gram atom per liter and *r* is equivalent to a doubling time of 3 days. The values of *k* are: (solid line) 14 percent per day; (dashed line) 22 percent per day.

A modified version (*4*) of an existing model (*5*) was used to compute sequences of stocks and production of phytoplankton and zooplankton occurring as a result of interactions between nutrients, plant and animal growth, and grazing by the zooplankton. We specified the rate of feeding by the zooplankton (and the mortality of the phytoplankton) by using a modification (*6*) of the Ivlev (*7*) ration curve. This expression was also used by Rosenzweig (*1*) in his equations 1, 4, and 6. Here, however, a threshold concentration of phytoplankton, below which the animals cease to feed, was incorporated. Nutrient limitation was modeled on the assumption that the assigned plant growth rate becomes linearly proportional to nutrient concentration below a threshold value. Effects of mixing and regeneration in supplying nutrients were also included.

We modeled enrichment here by increasing the concentration of nutrients in the water mixed vertically into the euphotic zone, while holding the mixing rate constant. Other means of modeling enrichment inherent in the model will be dealt with elsewhere (*8*). In addition to variations in the enrichment, the effects of using two different values of the assigned plant growth rate (*r*) and the maximum attainable rate of ingestion (*k*) by the zooplankton were tested.

The effects of a given change of nutrient concentration in water supplied to the euphotic zone depended markedly on the values used for *r* and *k*. With the low value of *k* (equivalent to a ration of 14 percent of the body weight per day in excess food) and the higher value of *r* (giving a doubling time of about 3 days in a 12-hour light, 12-hour dark cycle), enrichment indeed decreases stability in that the amplitude of the steady-state oscillation in stocks in the two trophic levels increases from negligible to pronounced (Fig. 1A), with an increase in the mean concentration of zooplankton and phytoplankton. The system is prevented from collapsing by virtue of the fact that the zooplankton cease feeding below the threshold concentration of phytoplankton. However, in the lower portion of the range of enrichment the nutrient input may be doubled with little effect on stability or plant stock, as found in our lake experiment, in contrast to the impressions conveyed by Rosenzweig (*1*). At a moderate level of enrichment the character of the oscillation was markedly affected by the use of the higher value of *k* (equivalent to a daily ration of 22 percent of body weight in excess food), with which the amplitude of oscillation and mean stocks were decreased (Fig. 1B).

The relation of stability to changes in enrichment was also changed by using the lower value of *r* with the higher value of *k*. As shown in Fig. 2, the amplitude of oscillation was again little changed by enrichment at low nutrient concentrations, then increased rapidly, but remained relatively steady as nutrient supply increased from moderate to high values. Moreover, mean standing stocks of phytoplankton were virtually constant over a sixfold range of enrichment. The mean concentration of zooplankton increased up to moderate rates of nutrient supply, then remained relatively steady with further increases. Thus, with the higher *k* value and the chosen values for other parameters, the system is largely limited by grazing above some threshold of enrichment. This result was obtained when the lower value of the plant growth rate was used, but also occurs with the higher assigned value. It will be shown elsewhere that other parameters also have a marked effect on the results of enrichment predicted by the model presented here and that generalization from a limited number of examples may be risky (*8*).

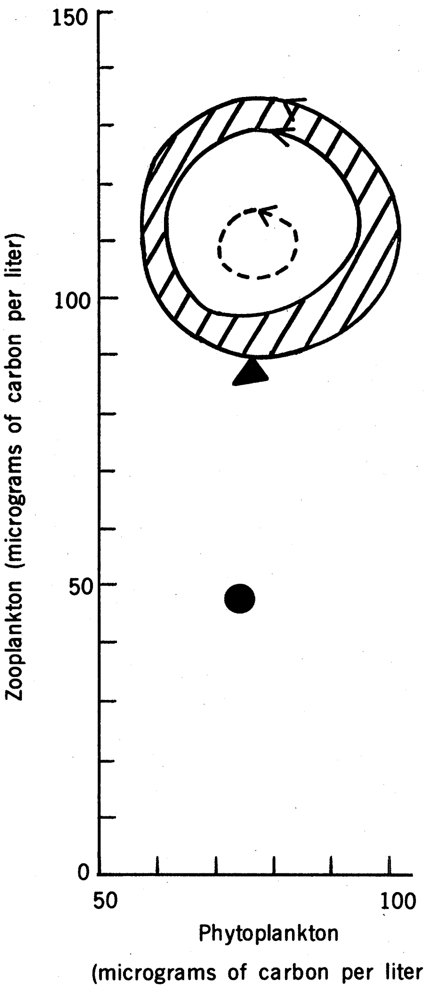

Fig. 2. Zooplankton concentration as a function of phytoplankton concentration through steady-state oscillation, with *k* equal to 22 percent per day and *r* equivalent to a doubling time of 5 days. Phosphate concentrations (× 10^{-6} gram atom of phosphate phosphorus per liter) are as follows: (solid circle) 0.4; (triangle) 0.6; (dashed line) 0.7; (hatched area) 1.2 to 2.0.

Thus, although the form of a model may determine the shape of the isoclines (*1*), the response of a given system to a given degree of enrichment depends, to a large extent, on the values of associated parameters, no matter whether strategies for preventing collapse are incorporated or not.

In nature, systems persist, despite wide ranges of enrichment. Apart from the examples given above, evidence of seasonal, annual, long-term, and geographic (on many scales) changes in enrichment abounds. Evidence of extinction in scales of time (see below) implied by Rosenzweig (*1*) would seem largely restricted to cases of unmanaged unnatural enrichment in which the effects are widely noted only after extensive eutrophication, the early stages of which could actually have been beneficial.

Rosenzweig's results (*1*) might more reasonably have been used to prompt questions such as the following: What are the critical values of enrichment? How does the time to extinction of a system vary with the degree of enrichment? How do critical levels of enrichment and time to extinction vary with other parameters? Why does nature *not* collapse? This last question has been raised by others contemplating extinction in model and experimental systems, for example Huffaker (*9*) and Maly (*10*). Feeding thresholds as used in our experiment form only one of many possible strategies for preventing collapse (*9, 10*). In nursery lakes of the sockeye salmon, such as in the lake we studied, collapse is prevented because most juvenile salmon migrate to sea after 1 year before they become so large and demanding that they could cause extinction of the system upon which the species depends. Feeding migrations (of which those of the juvenile sockeye salmon may exhibit an extreme form), prey refuges, aestivation, resting stages, inhomogeneous distributions, seasonal extremes in environmental conditions, the intricacy of the food web, dependence of prey selectivity on prey abundance, and territoriality are among possible means of preventing collapse.

In a cultured enriched system other options are open to the manager. Man's action in harvesting the excess biomass could protect the system by periodically resetting it to a desired initial value at one extreme, or by keeping it at some productive subcritical steady state at the other. In addition to harvest techniques, such methods as "pasture" and crop rotation, and control of enrichment can be used. In the context of managed systems use of the term "ecological time" by Rosenzweig (*1*) seems unclear. It suggests to us time scales related to those of natural community succession, whereas Rosenzweig (*1*) appears to have dealt with harvested (that is, managed) systems, implying time scales ranging from a few months to a few years.

Rosenzweig's pessimistic conclusions (*1*) may be impeccable within the strict confines of his two-species models, their assumptions, and the choice of values for parameters. However, it is one thing to explore the possibilities inherent in models, but quite another to risk conclusions on a limited range of input values without taking into account discussions already in the literature (*9, 10*) and suggestive evidence from nature.

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Most of the complaint of McAllister *et al.* (*1*) seems to rest on a misunderstanding of my goals. I nowhere intended to imply that all enrichment under all circumstances causes instability. I intended instead to do several other things, among them the following: (i) to point out that enrichment *may* cause destabilization of exploitative interactions; (ii) to warn ecosystem managers (or would-be managers) to be careful; (iii) to offer an alternate explanation for eutrophication in the hope that some of its more mysterious aspects might be understood (two examples: eutrophication without oxygen depletion or the onset of "bloom and bust" oscillations in plankton); and (iv) originally, to understand the experiments of Huffaker *et al.* (*2*). I think that I accomplished all of these goals in my report (*3*).

Two of the conclusions of McAllister *et al.* (*1*) deserve reiteration and explication because they lend support to graphical predation theory and thus to the importance of the warning that I issued in my report (*3*).

1) Their empirical discovery that moderate enrichment can be beneficial. This conclusion is obvious from my model. Moderate enrichment may not produce enough of a shift in the prey isocline to yield instability, a result that can be seen by interpolating a moderately enriched isocline between the "poorest" and "second poorest" isoclines of figure 1 of (*3*). I have illustrated this in Fig. 1.

2) Their conclusion that enrichment yields an increase in the concentration of zooplankton but no change in the steady-state concentration of primary producers. This conclusion is not at all intuitively predictable. However, it is precisely what is predicted by the verticality of the predator isocline (Fig. 1). Enrichment is thus passed on to the predators. Such an empirical verification from a complex and real system was more than I ever dared hope for.

The significance of this result cannot be overemphasized. The destabilization of exploitation by enrichment depends on this verticality. The data of McAllister *et al.* (*1*) therefore constitute powerful evidence that, at least in their case, the dynamics of the ecosystem will definitely be sensitive to too much enrichment. The supporting data of McAllister *et al.* perhaps will convince ecosystem managers of the need to watch carefully for possible exploitational destabilization.

There are many other situations in which an exploitational system will resist the destabilization that enrichment often threatens to bring. In fact, one might well refer to such situations collectively as "Rosenzweig's big nose" and endorse Cyrano's advice: "*Ah! non! C'est un peu court, jeune homme! On pouvait dire. . . . Oh! Dieu! . . bien des choses en somme. . .*" (*4*). Let us now examine two tiny hairs on that nose.

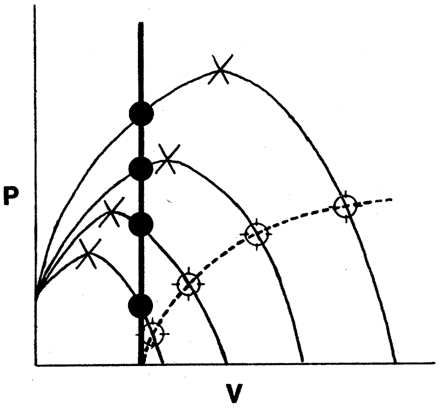
1) Resistance owing to a predator isocline which has a positive slope. A vertical predator isocline depends on the following condition:

$$\partial(d \ln P/dt)/\partial P = 0$$

where P is predator density and t is time. But if predators squabble with each other, this condition is not valid. In that case, if P is large, each predator will require a larger density of victims (V) than it would need if P were small; squabbling takes time and energy. Since the amount of time and energy wasted per predator is likely to increase with increasing P, it is reasonable to model such a predator isocline as a line with positive slope and negative acceleration (see Fig. 1).

2) Resistance owing to the fact that predators do not feed at low victim densities. One of the ways in which MacArthur and I predicted that limit cycles (that is, steady-state oscillations) could be achieved in a natural community is through the existence of a prey haven or equivalently a region of low victim densities at which the predators cease to function as predators (*5*). This has been aptly dubbed a "refugium" (*6*). Salt has recognized the generality of the idea of a refugium by noting that it applies to situations in which predators retreat metabolically when their victims are scarce (*7*). If such a refugium exists, there could be three outcomes: (i) if the equilibrium is a steady state, enrichment could destroy it and produce oscillations where none previously existed. On the other hand, if the equilibrium is unstable, the refugium sends the oscillations into a limit cycle (*5*). Then either: (ii) the limit cycle intersects the V axis, in which case the predators die out; or (iii) the limit cycle does not intersect the V axis, in which case the limit cycle describes the behavior of the real system.

Now McAllister *et al.* (*1*) have built a refugium into their computer model. If, for all tested values of their parameters, their model exhibits a limit cycle, as they say it does, then it never



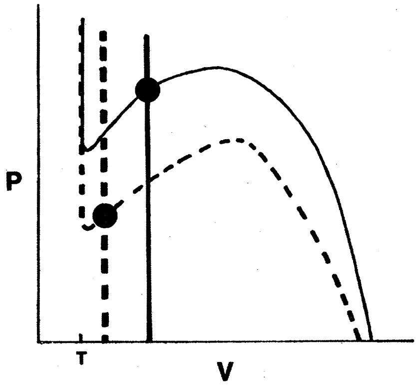


Fig. 1 (left). Enrichment's effect on steady states and stability with two types of predators; *P*, predator density; *V*, victim density. The arched lines are *V* isoclines: the higher the arch, the greater the enrichment of the system. The symbol × indicates the critical point on each arch: equilibria to the right of it are stable; equilibria to the left are unstable. The heavy vertical line is a nonsquabbling predator's isocline. Dots along it indicate the equilibria at various levels of enrichment: the lowest is the original state; the next is a mild enrichment as reported in (*1*), and the equilibrium remains stable; but the two highest equilibria are unstable. The dotted isocline belongs to a squabbling predator. Open circles along it indicate that successively enriched steady states are all stable. Moreover, enrichment here enhances the density of *both* species instead of just the predator. Fig. 2 (right). Increasing the predator's feeding proficiency (k) in a system with a victim refugium. Both *V* isoclines merge into the vertical line segment over *T*, where *T* is the density of victims that the refugium can support. The dashed isoclines depict the system with the more proficient predator. Both systems have an unstable equilibrium and should exhibit a limit cycle oscillation of precisely the shape figured in (*1*), that is, the cycle should be markedly flat on its western edge. In the system with increased k, the equilibrium of both species is reduced. It is also reasonable to expect this system's limit cycle to have a smaller amplitude, because its equilibrium is closer to *T*, the minimum victim density in the limit cycles of both systems. Both Figs. 1 and 2 present only old theories (*3, 5*) plotted at new values of constants.

possesses a stable equilibrium for enrichment to destroy. It is a straw man. Its creators proceed (*1*) to then compound the confusion by equating stability with oscillatory amplitude (*8*). Certainly they are to be commended for raising the issue of amplitude. However, at least one of their results can be predicted from graphical theory (Fig. 2).

McAllister *et al.* (*1*) request clarification of the difference between ecological and evolutionary time. Without attempting to be dogmatic, I was trying in my report (*3*) to suggest that it is possible for an ecosystem to be unstable, to be evolving toward stability, but not ever to reach it because the ecological instability of the ecosystem exterminates it. Such a system would, by definition, be stable in evolutionary time and unstable in ecological time. Evolutionary time is thus merely a long enough period to allow the system to evolve to the point at which its stability will no longer change. Ecological time is a shorter period during which the evolutionary changes in stability are small enough to ignore.

Moreover, it also seems possible for an ecologically perturbed (for example, enriched) system, to be stable in ecological time and yet unstable in evolutionary time. That is to say, the perturbation may create an environment in which ecological instability will be the end result of evolution. The possible consequences of ignoring the evolutionary complications of perturbation cannot, in their turn, be ignored. I think a statement by Schmidt exposes the only reason for ignoring evolution: "The rejection of evolution as an essential basis for the examination of ecological phenomena seems to me to be merely a wilful avoidance of the complexity introduced into ecological concepts by evolution. . ." (*9*).

It is certainly true that upwellings in the ocean have produced highly productive ecosystems. But evolution has had untold eons in which to achieve this result. It is presumptuous and dangerous to assume that human management will be able to produce such systems in the rest of the ocean by pumping up nutrients artificially. Most of the ocean averages less than two trophic levels and might thus be particularly susceptible to exploitational destabilization.

Why do exploitations persist? Why does nature not collapse? Indeed, as McAllister *et al.* (*1*) have noted, in ecological time graphical predation theory is a useful tool to help answer such questions. In fact, most of the supportable items they suggest as predatory stabilizers have already been reported in the literature (*5*). In this reply I have reiterated a few of them: refugia, metabolic retreat, territoriality, and predatory squabbling.

Probably no one has been more awed by the persistence of exploitational systems in evolutionary time than I myself. The relevations of predator-victim coevolution throughout millions of years (*10*) have been simultaneously marvelous and mystifying to me. After all, MacArthur and I had conjectured that natural selection should act on the predators to move them toward extinction (*5*). In a recent paper (*11*), I have proved that natural selection of the victims *will* balance that tendency. The proficiency of the predator and the defenses of its victim reach an evolutionary steady state with respect to each other. If this steady state is also ecologically stable, then predator and victim should coevolve throughout extensive periods of time. Thus graphical predation theory has provided the first Darwinian explanation of why those exploitational ecosystems that have survived generally continue to survive even while undergoing continuous change.

McAllister *et al.* (*1*) worry about my pessimism. However, for the professional ecologist, honest optimism is rooted in the hope that mankind will be realistically pessimistic. I have tried to foster only that pessimism.

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