BIOMANIPULATION: AN ECOSYSTEM APPROACH TO LAKE RESTORATION[1]

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Despite rapidly rising interest in lake restoration and increasing support for various technologies and approaches for rehabilitation of lakes, little attention has been devoted to the possibility of restructuring the biological communities of lakes as a direct approach to combating eutrophication. Instead, the vast majority of effort has been channeled into projects aimed at eliminating nutrient influx to lakes. To illustrate, in the recent *Survey of Lake Rehabilitation Techniques and Experiences* by Dunst *et al.* (1974) there are catalogued, in addition to such procedures as chemical treatment for weed and algae eradication, about 320 applications, ranging from wastewater treatment to lake bottom sealing, aimed at restricting nutrient loadings. Only 58 applications of so-called biological controls are listed and of these 32 are for control of macrophytes—mostly by herbivorous fish. Twenty-one are fish-management schemes for the sake of the fish population, and only five are aimed directly at reducing the abundance of algae. Of these five, one is a microstraining experiment done at Clear Lake, California, and four involve use of such fish as silver carp, Mississippi silversides, and other planktivores. Thus, leaving aside the macrophyte and fish-management studies and omitting the Clear Lake study, limnologists have devoted about 99 percent of their effort in resolving the algal problems of lakes to the nutrient level, and only 1 percent of their efforts have involved bona fide attempts at what we would call biomanipulation.

This emphasis on reducing nutrients and particularly phosphorus inputs is understandable. After all, eutrophication implies enrichment with nutrients, and many of the lakes arousing most interest because of their eutrophic condition are in that condition because man has made them so. His activities in disposing of wastes, fertilizing fields, feeding cattle, and paving streets have resulted in vastly increased inputs of nutrients to aquatic systems. Therefore, what better way to reverse eutrophication than to reverse these activities, or at least their effects. And it works. At least it works if one has the money and the will as in Lake Washington (Edmondson 1972) and Shagawa Lake (Malueg *et al.* 1973) and others, and if nothing else has happened to the lake, i.e., if the sediments have not become so enriched with phosphorus that they act as a source rather than a sink, as happened in Lake Trummen (Bjork 1972) and perhaps in Lake Sammanish (Rock *et al.* 1974). It is, in short, a logical approach. But should it be virtually the only approach? Considering the costs involved ($130 million for Lake Washington) and the large numbers of eutrophic lakes that cannot be restored by these means because their nutrient inputs are not controllable, or because their sediments are too heavily loaded with nutrients, or because the rate at which they receive nutrients from diffuse sources prohibits in-lake treatments, we feel that alternative approaches are necessary. In particular, we feel that limnologists and engineers must realize that lake basins are containers for ecosystems and not just containers for primary production. This is important because, as Patten (1973) has pointed out, ecosystem components are mutually dependent so that the system has the property of complete controllability and control points for attacking eutrophication exist everywhere in the ecosystem, not just at the nutrient and producer levels. Not only do the reciprocal relationships between ecosystem components allow control of these components in predictable fashion but the control capability is considerably amplified by the fact that each higher trophic level contains at least an order of magnitude less energy and matter than the one preceding it. Thus, rather than consider consumers, particularly top ones, as being unimportant because of the small percentage of the total energy and matter of the ecosystem in them, it is more likely that higher trophic levels are capable of exerting profound controlling influences because of their position in the interactive structure of ecosystems. To quote Patten directly, "Thus, ecosystems in fact seem to be constructed to take advantage of the reciprocal relation..., endowing upper trophic level organisms with significant inherent control capabilities." He continues, "Theoretically, remote control may be more important in ecosystems than direct control. That is, parameters far removed from a state variable in the interconnection network may be more significant in controlling that state than other, more closely associated parameters." In the context of this paper Patten states, "In eutrophication research, the distinct possibility exists that small (inexpensive), well chosen and correctly timed...manipulations of ecosystem parameters which are remote from the nutrient-primary production subsystem may be able to produce dramatic improvements in water quality for the amount of control effort expended."

The purpose of this paper is to present the preliminary results of our efforts to control ecosystem parameters to combat eutrophication. Although Patten does consider that modeling of the eutrophication process must be well advanced before the principles he enumerates can be applied with assurance, we have chosen to work

intuitively and empirically in the hope of making progress sooner. In our approach we attempt to manipulate various levels of the food chain, assuming that nutrient input is fixed and cannot be reduced to the extent where significant reduction of primary production occurs.

As our goal is to reduce the abundance of phytoplankton, clearly it is desirable to increase the numbers of zooplankters—particularly filter feeders. However, there seems at this time no real possibility of accomplishing this directly, although Fritsch (1953) was able to demonstrate that adding pantothenic acid to cultures of Daphnia pulex did increase the fecundity of the Daphnia significantly, apparently by increasing egg production and lengthening the lifespan. Murphy (1970) was unable to repeat fully the work, finding no effect on the lifespan. He did find that pantothenic acid caused a very striking increase in the number of viable young of D. pulex. However, the economic aspects are likely to be discouraging. Murphy found that a concentration of 20 ppb of pantothenic acid was enough to cause a significant effect. Assuming that this concentration would have to be established in the top 3 m of a lake, this would require about 0.6 kg/ha which at the current small lot price for pantothenic acid amounts to about $38/ha. Even assuming a cost half as great for bulk quantities, $20/ha is a significantly high cost for a treatment that would in all probability have to be repeated annually, assuming that it worked at all. However, despite the potential cost and despite our rather inconclusive preliminary experiments in the laboratory we intend to test this approach further in the field.

A surer method for increasing zooplankton abundance would be to ensure their survival and longevity by decreasing predation on them. There are several possible ways to do this. One way would be to kill off all the fish in the lake. This procedure is regularly done as a means of restructuring fish populations, and frequently results in increased Secchi disk transparencies (D. Shodeen, personal communication 1973). This may be the result of increased numbers of zooplankton organisms grazing on the phytoplankton, but it also may have a completely different explanation, as described later. However, as killing off all fish is likely to be considered impractical as a general approach to lake restoration, attention could be turned on the fish most directly involved—the zooplanktivores.

Evidence that zooplanktivore abundance has a controlling effect on zooplankton abundance comes from two directions. The first is where zooplanktivores have been added to systems by stocking them. For example, Rozmajzlova-Rehackova (1966) studied a reservoir heavily overstocked with perch (Perca fluviatilis) to 95 percent of the entire fish stock. This resulted in a scarcity of cladocerans which were replaced by nanno-zooplankton and a consequent increase in phytoplankton. In another instance, Galbraith (1967) showed that stocking lakes with rainbow trout (Salmo gairdneri), and perch completely eliminated Daphnia pulex within four years. The same result followed when Anderson (1972) introduced trout to three formerly fish-free alpine lakes and eliminated the dominant zooplankters, a Diaptomus and two Daphnia, within two to six years; and when Grygierek et al. (1966) added 1-gram carp fry to ponds and eliminated Daphnia magna. Finally, Hurlbert et al. (1972), using artificial ponds, eliminated Daphnia and Chydorus by adding Mosquitofish (Gambusia).

The other type of evidence that manipulation of fish can affect zooplankton abundance comes from cases where zooplanktivores have been removed not by poisoning out all fish but by adding piscivores that prey on them. A large experiment of this type was inadvertently performed in Gatun Lake in Panama. Here Zaret and Paine (1973) found that the accidental introduction of the piscivore Cichla drastically reduced the abundance of almost all secondary carnivores in that part of the 90,000 acre lake through which it spread. In particular it almost eliminated Melaniris, a zooplanktivore, with the result that changes have occurred in the composition of the zooplankton. Already the standing crop of phytoplankton is lower in those areas characterized by Cichla predation, and greater changes are expected.

These examples suggest very strongly that control of zooplankton abundance via higher trophic-level manipulation is feasible and often leads to the expected reciprocal change in algal abundance.

These changes in algal abundance are not necessarily brought about by increased numbers of zooplankters, at least not solely by increased numbers. Frequently, as suggested by Brooks and Dodson (1965), because zooplanktivores appear to select larger forms, changes in predation pressure bring about changes in zooplankton community structure. These changes, which may occur on a vast scale, as in Lake Michigan due to introduction of the alewife (Wells 1970), lead to changes in the intensity of grazing on the phytoplankton. For example, Burns (1968) has shown that the maximum size of food particles ingested by Bosmina and six species of Daphnia increased with mean body size of the animals. Furthermore, Burns (1969) has found that filtration rates of four species of Daphnia are approximately proportional to the squares or even the cubes of their respective body lengths. Thus, changes in size of zooplankters may be even more important than changes in their numbers. This is especially true in eutrophic lakes that have a higher ratio of net phytoplankton to nannophytoplankton than do oligotrophic lakes. In the
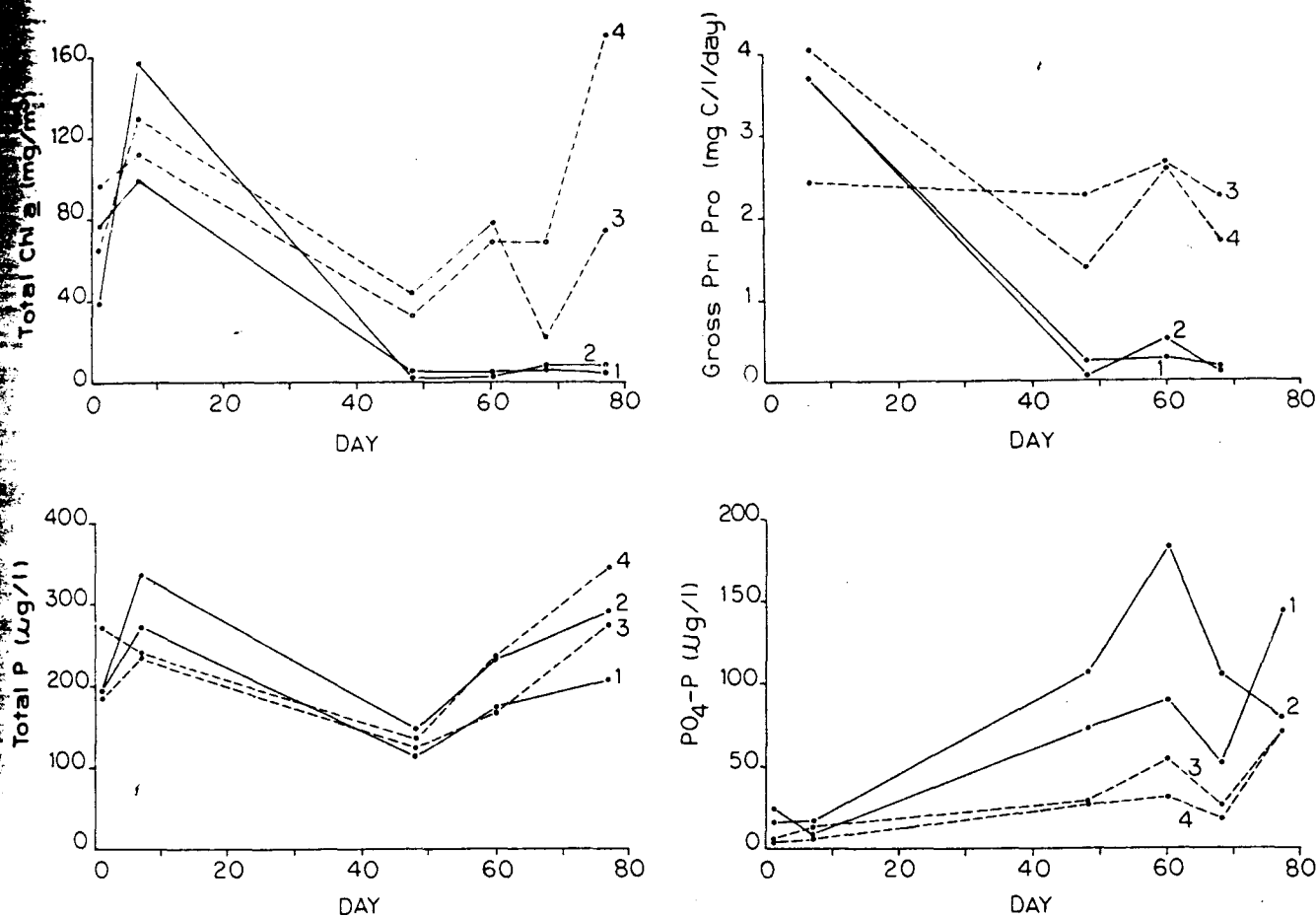
Fig. 1. Chemical and biological responses in 4 enclosures placed in a small pond containing *Daphnia pulex*
1. Control, no fish
2. Control, nutrients added
3. 20 perch fingerlings added
4. 40 perch fingerlings added

study by Hrbacek *et al.* (1961), on the Poltruba backwater of the Elbe River, fish poisoning resulted in an increase in transparency and a decrease in algal abundance despite a diminution in numbers of zooplankters. However, whereas *Daphnia hyalina* in the year preceding poisoning was absent, it represented 80 percent of the zooplankton in the year following poisoning. Contrariwise, in Rozmajlova-Rehackova's (1966) study, the phytoplankton increased despite the abundance of rotifers and copepods after the cladocerans had been removed by the stocked perch. This same effect was noted by White (1972), who added fish (perch, roach, and chub) to tertiary sewage lagoons.

Our own preliminary studies in this field have been most encouraging. During the summer of 1973 we carried out two experiments. The first was conducted in Lake Emily, a small shallow lake in St. Paul, Minnesota. Two sets of four polyethylene bags 1 m in diameter and 3 m deep,

and sealed at their bottoms, were suspended from rafts and filled with the lake water containing its native population of algae and zooplankters, including *Daphnia*. In each set, the first two bags served as controls, and the third and fourth bags had young perch added. The results showed that the presence of the added perch had a significant effect in increasing the algal abundance and consequently decreasing the transparency. In a second experiment polyethylene enclosures 3 m in diameter and 1.3 m deep were set up in Williams Pond. This 1 hectare pond normally has abundant populations of *Daphnia pulex*. Four enclosures were established. The first served as a control. The third and fourth had 20 and 40 fingerling perch introduced respectively. The second was fertilized periodically to add the nutrients equivalent to those excreted by the 40 perch (Lamarra 1975).

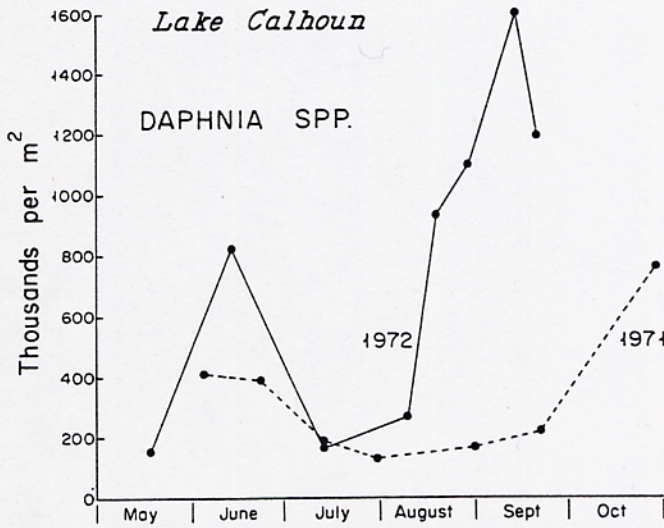The data in Figure 1 show that merely adding the

Fig. 2. Response of *Daphnia* to artificial circulation in Lake Calhoun during 1972. Circulation was begun Aug. 4.

zooplanktivores (enclosures 3 and 4) resulted in a significant increase in rates of photosynthesis and chlorophyll concentrations over the two control systems (enclosures 1 and 2). Note too that although the total phosphorus concentrations in all four enclosures remained similar, orthophosphate concentrations were considerably higher in enclosures 1 and 2—those in which the zooplankters were actively grazing. Thus, elimination of zooplanktivores, or at least their absence, resulted in low algal concentrations in the face of high nutrient concentrations, while intensified predation on the herbivores resulted in much higher concentrations of algae.

Can these manipulations be carried out on a large enough scale and in such a manner as to restore lakes? As noted before, fish poisoning would act toward this end, at least in lakes where predation on zooplankton is already high, and it can be done on a relatively large scale. However, it suffers from several deficiencies. It is fairly expensive, it cannot be applied to very large lakes, it removes desirable fish as well as zooplanktivores, and it is only temporary, as zooplanktivores are likely to be carried into the lake again—probably via the fisherman's bait bucket. On the other hand, elimination of zooplanktivores by stocking lakes with piscivores is a measure that can be applied to lakes of almost any size (witness Gatun Lake, and the introduction of Coho salmon to Lake Michigan) at relatively modest cost. Other game species do not necessarily disappear and the effects are likely to be long-lasting. While not all zooplanktivores appear to be capable of being controlled in this fashion, e.g. northern pike *(Esox lucius)* has been reported to have little effect on blue-gill sunfish *(Lepomis macrochirus)* (Beyerle 1970), one of the more important zooplanktivores in the United States, the yellow perch *(Perca flavescens)*, seems to be controllable by stocking lakes with muskellunge *(Esox masquinongy)*. In 1956 (Gammon and Hasler 1965; Schmitz and Hetfeld 1965), two lakes in Wisconsin were stocked with large yearling muskellunge at a rate of about 25 fish/ha, and within three years populations of mature perch had declined to the point where their numbers could not be estimated. During subsequent years the populations of perch less than 150 mm in length recovered somewhat, possibly due to the increasing size and mortality of the muskellunge, which apparently did not reproduce in the two lakes stocked.

One possible way to reduce the numbers of planktivores not readily controlled by carnivores might be to spread disease among them. Fish diseases are usually
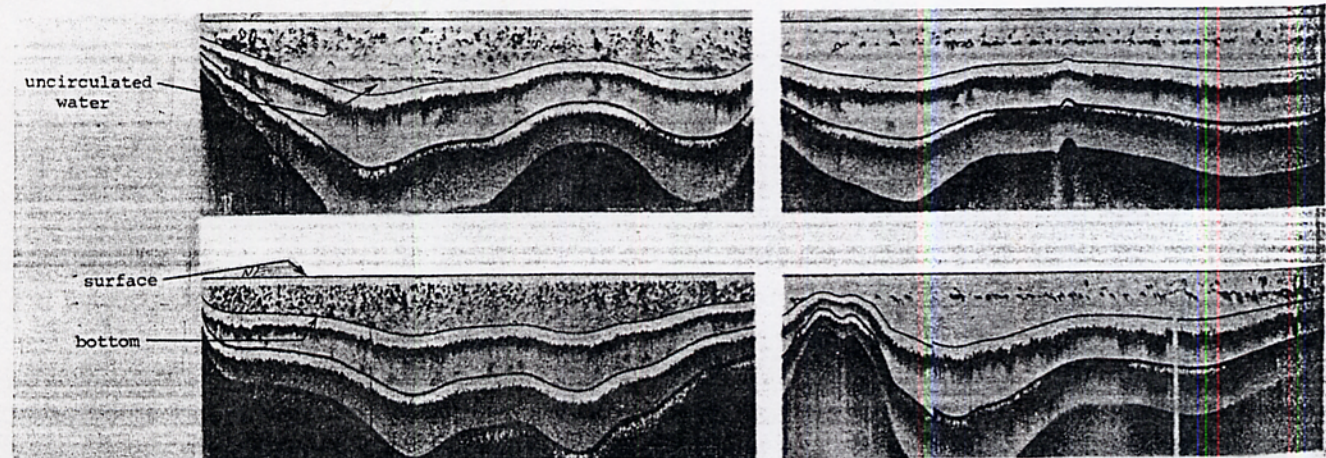

Fig3. Echograms from Lake Calhoun. Right, before artificial circulation; left, after artificial circulation. (The portion below the line labeled "bottom" represents multiple echoes).

species specific and frequently take a large toll. White (1972), has described a case where mass mortality of perch in certain reservoirs in England led to an abundance of *Daphnia* and reductions in phytoplankton blooms.

An alternative to this approach is to manipulate the physical environment in such a manner as to reduce predation on the zooplankton. During the summer of 1972 an experiment was done in which Lake Calhoun, a 172 ha, 27 m deep lake in Minneapolis, was artificially circulated with compressed air (Shapiro and Pfannkuch 1973). The purpose of the experiment was to reduce the abundance of blue-green algae. Unfortunately, because of a combination of circumstances discussed later, blue-green algal abundance increased. But analysis of the zooplankton data by Robert

Carlson revealed an interesting thing—*Daphnia* abundance rapidly increased more than eightfold and remained high for the next two months of observation (Figure 2). It is possible that part of the increase was caused by the increased food supply, but of all the zooplankters that showed increases in abundance—Cyclopoids, *Diaptomus*, *Bosmina*, *Diaphanosoma*, and *Daphnia*—the biggest one, *Daphnia*, showed the greatest increase. Furthermore, *Daphnia pulex*, absent from Lake Calhoun the year before, became reasonably common following circulation. Our interpretation of these data is that the circulation, by bringing oxygen to the depths of Lake Calhoun, lessened predation pressure on the zooplankton by diluting them throughout a greater volume of water, thereby reducing contacts between the zooplankters and fish. Evidence for this comes from Figure 3, which is an echogram showing how before circulation fish were restricted to shallow depths while following circulation they descended much deeper. Test nettings confirmed these distributions and showed that a large proportion of the fish were indeed yellow perch (J.F. Walsh, personal communication 1972).

Two other factors may contribute to zooplankton changes caused by lake circulation. O'Brien and de Noyelles (1972) have suggested that high pH is lethal to some zooplankters. Circulation generally reduces pH. Second, circulation also generally reduces epilimnetic temperatures. It has recently been demonstrated (Lynch, unpublished manuscript, 1975), that *Daphnia pulex* in particular has its optimal size near 20°C, i.e. above this temperature a relatively greater proportion of food intake is required for maintenance. Therefore, it would appear that lake circulation, in addition to any other benefits that might accrue, should increase zooplankton abundance and size and be useful as a method to control algae.

Finally, modification of the zooplankton population of a lake may be brought about by deliberate stocking of desirable forms. There is no reason why, once zooplanktivore activity has been reduced by carnivores, large herbivores such as *Daphnia magna* could not be introduced to aid in controlling larger, perhaps colonial algae.

Earlier it was noted that poisoning fish out of lakes frequently led to increased transparency, and that in addition to lessened zooplanktivore activity there was yet another possible explanation. This other explanation had long been suspected to be the demise of bottom-feeding fish such as carp, which stir up sediments and possibly release nutrients by this disturbance. However, the work of Fitzgerald (1970), showing that sediments may actually sorb phosphate in aerobic systems suggested that this explanation was too simple, and that if the bottom fish were releasing nutrients some other mechanism must be
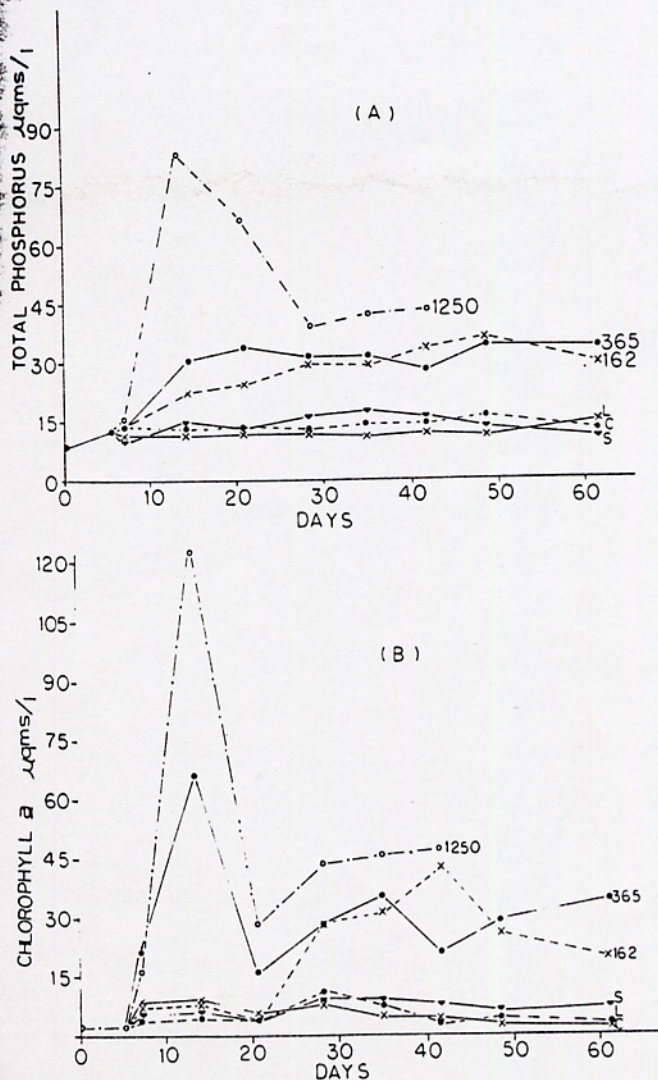

Fig. 4. Effects of adding carp to enclosures open to the sediments. The numbers refer to fish density as Kg/ha. The fish were added on day 7. L = lake, C = control, S = stirred.

involved. A study of this mechanism has been completed and is in press (Lamarra 1975). It may be summarized as follows: A series of experiments was performed in which carp *(Cyprinus carpio)* were added to polyethylene enclosures 3 m in diameter placed in a variety of lakes and ponds. When the carp had access to the sediments, phosphorus levels and, more importantly, chlorophyll levels in the enclosures increased (Figure 4). These data were verified in a 1 ha pond divided into four with plastic sheeting. Proof that the phenomenon was not caused by the simple stirring of the sediments by the fish was obtained by periodic mechanical stirring of the sediments in the small enclosures—no phosphorus was released and no algae grew. Furthermore, when carp were captured from various lakes and imprisoned in plastic bags they released significant quantities of phosphorus. In the enclosure experiments the phosphorus concentrations (Figure 4a), and subsequently the chlorophyll concentrations (Figure 4b), rose to a peak rapidly, then diminished somewhat and remained constant. To determine whether this meant that the food supply became limiting or that the loss rate (due to sedimentation by algae) increased, some of the enclosures were wrapped in black plastic to exclude light and therefore prevent photosynthesis. In these enclosures the levels of phosphorus increased continally, this time as PO_4-P, and interestingly it was discovered that large amounts of ammonia were liberated simultaneously. Thus, carp apparently are not simply phosphorus pumps but nutrient pumps. Figure 5 and 6 illustrate the type of excretion data obtained with individual fish and the relationships of excretion to fish size
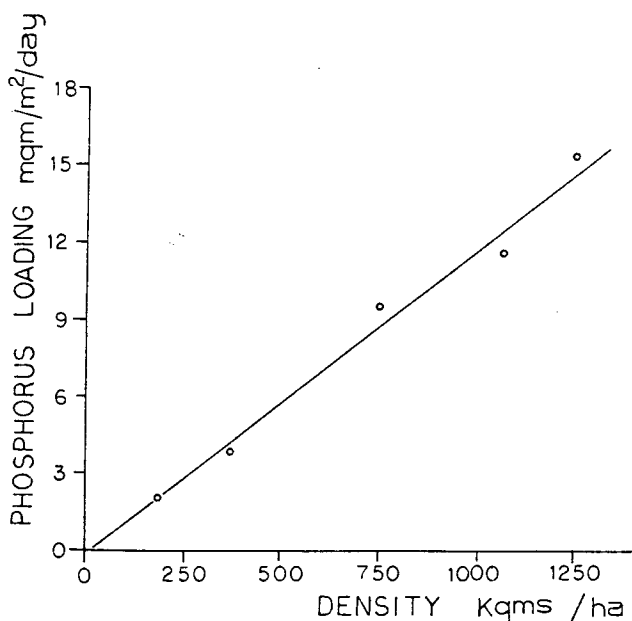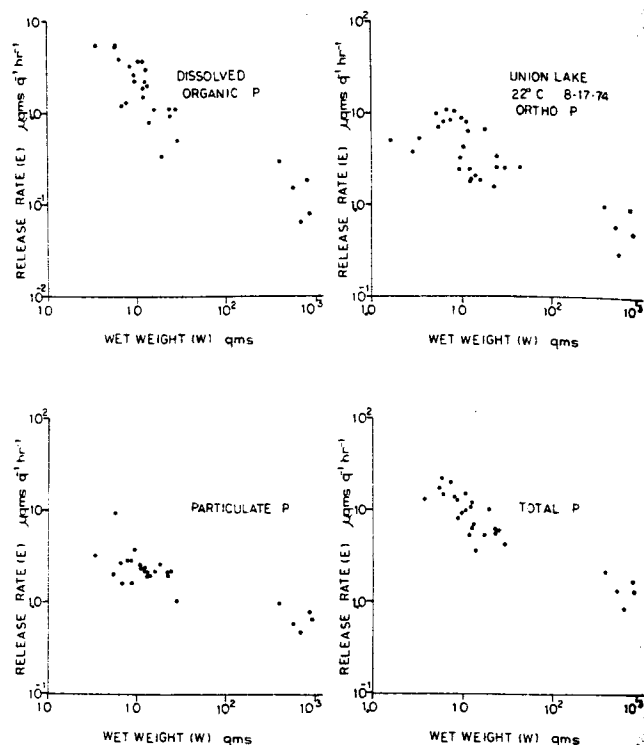

Fig. 6. Release of various forms of phosphorus by different sized carp.

and density. With these data it is possible to calculate the rate of phosphorus return from sediments by a given number of carp of a given size distribution. It is a significant figure. This, then, is a case where fish manipulation has effected a change at the primary producer level, not through effects on predation but through effects on nutrient regeneration. However, in this case the fish are not high on the trophic scale—they are low. It would appear, then, that fish manipulation in lakes may be a very powerful tool to control algal populations.

The scheme outlined above for controlling algae via higher trophic-level manipulation is predicated on the ability of zooplankton to graze algae down to low concentrations. While this is not the place for a detailed review of the trophic relations between algae and zooplankton, several facts are pertinent. Zooplankters, particularly filter feeders, do eat algae and are capable of effecting large changes in standing crops (Porter 1972). Certain algae, particularly large filamentous forms, are relatively unaffected by grazers (Porter 1973). Some blue-green algae such as *Aphanizomenon flos-aquae* are apparently utilizable by filter feeders, while others such as *Microcystis* and *Anabaena* are not (Sorokin 1968). Grazing by zooplankters may shift algal populations toward undesirable forms, either by selectively increasing their relative proportion in the population or by providing

Fig. 5. Relation between fish density and phosphorus release. Data from days 7 to 14, Fig. 4A.

nutrients to them via nutrient release or nutrient absorption during passage through the guts of the zooplankters (Porter 1975). Therefore, under some circumstances increasing zooplankton abundance may decrease algal populations but under other conditions, where inedible species are present, increased grazing, could have little beneficial effect.

To ensure against such an eventuality it would be valuable to be able to manipulate algal populations themselves so as to favor the growth of small, nonfilamentous, nongelatinous forms (mostly greens), that could be eaten by most grazing zooplankters. This is now
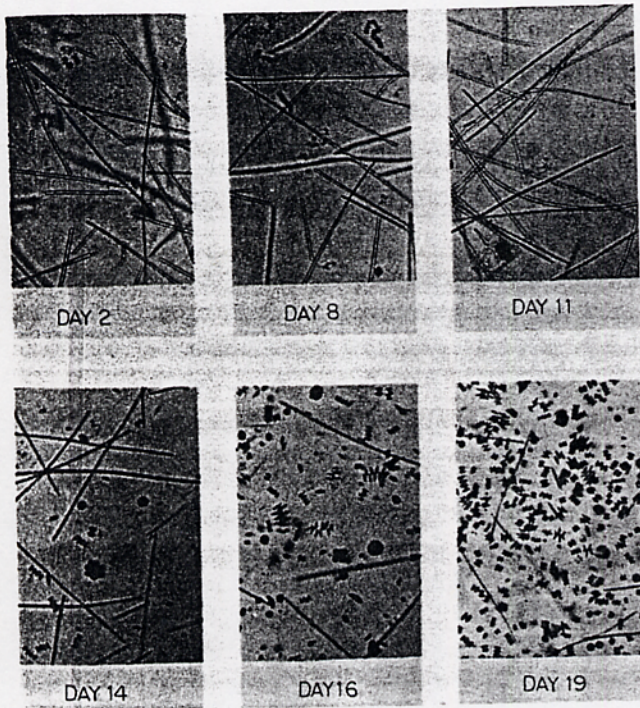

Fig. 7. Changes in an algal population maintained at pH 5.5 by addition of CO_2.

possible, at least on a small scale. King (1970) suggested that one of the reasons that blue-green algae became predominant over greens in highly enriched lakes is because of their relatively great efficiency at taking up CO_2 at the low levels found under the high pH conditions in these lakes, i.e. at low CO_2 levels blue-greens can outcompete greens. This suggested that, given a mixed population of greens and blue-greens, adding nutrients should increase the predominance of blue-greens, but adding nutrients plus CO_2 or even lowering the pH with acid should increase the percentage of greens. Experiments were performed in 2 m^3 plastic bags suspended in a small lake and the predictions proved true (Shapiro 1973). The results were dramatic. In ten days or less, addition of nutrients plus carbon dioxide, or acid, allowed a population of filamentous, gelatinous,

blue-green algae to become a population of uni-algal and small colonial greens, while nutrient addition without CO_2 or acid increased the abundance of the presumably inedible forms.

Although the experiments seem to substantiate King's hypothesis, Goldman et al. (1974) proposed several alternative interpretations of the reason for the results. According to them, algal growth is proportional to the concentration not of free CO_2 but of total inorganic carbon. Thus, adding CO_2 increased the total carbon available (although adding HCl could not have done this), and allowed the greens to become abundant. Second, they feel that the pH changes resulting from added CO_2 may have caused changes in the availability of phosphate, etc.

In order to study the phenomena further to elucidate its mechanism and to determine its feasibility as a full-scale lake manipulation technique, other studies were done in 1974. The preliminary results are of significance here.
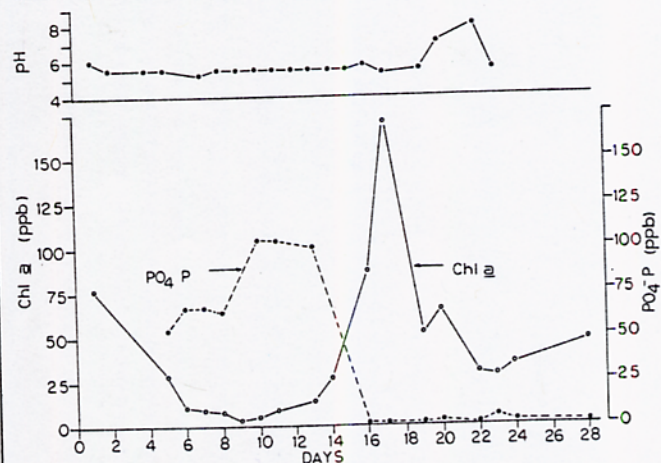

Fig. 8. Changes in PO_4—P and chlorophyll a in an algal population maintained at pH 5.5 by addition of CO_2. The CO_2 was turned off on day 18.

One of the first aspects studied was how much change must be brought about to cause the algal shift. Two series of polyethylene bag enclosures (1 m in diameter and 2 m deep) sealed at the bottom were set up in Lake Emily. pH electrodes were inserted, and the water in each bag was stirred periodically with compressed air. Phosphorus and nitrogen were added at concentrations of 100 ppb PO_4—P and 700 ppb NO_3/NH_3—N respectively. A series of pH stats controlled the input of CO_2 gas for one series and dilute HCl for the other series. The pH values were maintained at 5.5, 6.5, 7.5, 8.5, and approximately 9.5, this last without adjustment. The algae in the CO_2—controlled bags with pH values of 5.5, 6.5, and 8.5 showed the shift to greens. The algae in the HCl—controlled bags at pH 5.5, 6.5, 7.5, and 8.5 also changed to greens. The results are shown for a pH

5.5 CO_2 bag in Figure 7. In some experiments the change began relatively soon after the manipulation was begun. This may mean that continual manipulation may not be necessary but that the population need only be started on its course.

A second consideration investigated was whether the effect was specific to Lake Emily, on which all the work has been done. Experiments with four other lake waters showed that it was not. The algal shift occurred in 3 of the 4.

A third consideration was the possibility of specific circumstances or interferences that might prevent the algal shift. Two such contingencies were found. The first arises from the absence or near absence of green algae in the phytoplankton. During one series of experiments we found it necessary to seed the systems with a small inoculum of green algae—less than 0.5 percent of the biomass. Investigation showed that the greater the inoculum the more rapid the shift. The possibility of inoculating a small lake is not out of the question but a more reasonable approach would be to consider beginning manipulation while green algae were still present to some extent.

Possible interference with the phenomenon was discovered through consideration of the mechanism of the algal shift. Although the mechanism is still under study and has not been resolved, we had observed that in most cases where the shift took place it was preceded as shown in Figure 8 by a decrease in chlorophyll and an increase in dissolved orthophosphate in the water. Presumably this phosphate was released by the blue-greens and would provide for the subsequent growth of the greens. It was also known from previous work by the senior author on kinetics of phosphate uptake by algae that whereas various blue-green algae tested were able to distinguish phosphate from arsenate, the several green algae tested were not capable of making this distinction and accordingly were much less effective at phosphate uptake in the presence of arsenate than were the blue-greens. As many Minnesota lakes have large concentrations of arsenate in them (Chamberlain and Shapiro 1969), as a result of the use of sodium arsenate as an agent to eliminate macrophytes, it seemed wise to determine whether the presence of arsenate would outweigh the inherent advantages to the greens brought about by low pH or CO_2 additions. Two experiments were done during the summer. In both cases arsenate was added as sodium arsenate to a concentration of 100 ppb before nutrients were added, and CO_2 was bubbled into the bags. In one case the algal shift occurred, but it was delayed over the control by 4 to 5 days. In the second case the shift did not occur after 26 days, although the arsenate-free control changed within 14 days.

Although this does show that arsenate can prevent the algal shift phenomenon, the danger of this actually being a problem is becoming less. Use of arsenate in lakes in Minnesota was banned in 1967, and it is rapidly becoming depleted. For example, in 1968 Lake Calhoun had a surface water concentration of arsenic of 132 ppb, and in 1974 it was 19 ppb. However, the arsenate interference does tend to corroborate the fact that a transfer of phosphate from the blue-greens to the greens occurs as an essential part of the algal shift.

The success of the arsenate experiment suggested that another finding from the earlier phosphate kinetics studies might also be utilized. The presence of small concentrations of chlorine depresses the velocity of phosphate uptake by blue-green algae more than it depresses phosphate uptake by green algae. This suggested that instead of attempting to shift blue-green populations to greens by adding CO_2 or lowering the pH, it might be possible to achieve the same effect by adding chlorine and allowing the greens to outcompete the blue-greens for phosphate. Several such experiments were carried out in bags in Lake Emily. Chlorine was added as sodium hypochlorite over a period of five days to a final concentration of 750 ppb, during which the nutrients were gradually increased to 100 ppb PO_4-P and 1000 ppb NO_3/NH_3-N. As anticipated, the percentage of greens increased, but the blue-greens did not disappear so completely as with CO_2 additions. Further experiments were done in the laboratory using water from Lake Emily and four other lakes in much the same fashion, and these were more successful. The blue-green algae disappeared in 3 of the 5 systems and were replaced by green algae. In every case the pH remained above 9.

Following laboratory experiments with HCl and chlorine, feeding studies using Daphnia magna (after adjustment of pH to 9.0) showed that the algae produced were edible by this zooplankter. This was particularly true in the case of the greens grown in the presence of chlorine, which apparently had no effect on the Daphnia.

The three agents described that cause the shift from blue-greens to greens, namely HCl, CO_2, and Cl_2, may not be the only ones capable of doing this. Although the results have been explained above on the basis of competition for CO_2 or phosphate, another possible explanation lies in the presence, in natural waters, of cyanophages capable of lysing blue-green algae (Shilo 1971). The initial decline in chlorophyll and the release of soluble phosphate shown in Figure 8 suggest, in fact, that lysis is occurring. Thus it may be that high CO_2 or low pH or the presence of chlorine stresses the blue-greens and make them susceptible to the viruses. The often sudden demise of the blue-greens adds support to this idea. If this hypothesis proves correct, many agents may be found to achieve the same effect.

Nonetheless, it is worth asking whether any of the

described methods could be applied in large-scale treatments. In fact, chlorine has already been used on a large scale. Accordingly to Windle Taylor (1953), the Metropolitan Water Board of London, England, has used controlled chlorination in two North London water supply reservoirs since 1945 to eliminate the large populations of *Stephanodiscus hantzschii* that used to interfere with the use of the reservoirs. The two reservoirs, each 8 ha in area and 2–4 m deep, are chlorinated intermittently with chlorine gas at their inlets, according to the abundance of the diatoms. Windle Taylor reports that if too much chlorine is applied, a growth of minute Chlorophyceae develops consisting mainly of *Chlamydomonas* or *Mallomonas*. In our own experiments with chlorine the alga that developed was also a small green, as yet unidentified. Another large-scale application of chlorine was discussed by Derby (1956), in which chlorine was injected into the hypolimnia of two water-supply reservoirs in California to eliminate reducing conditions and the changes in water chemistry accompanying these conditions. These reservoirs were 25 and 43 ha in area and 30 and 40 m deep, respectively. Finally, chlorination has been applied on a large scale in Green Lake in Seattle, where it was necessitated by hygienic conditions at the beaches (Sylvester and Anderson 1964).

Thus, the technology to use chlorine is available, the cost low, and the effectiveness significant. Unfortunately, chlorine is detrimental to many organisms, such as certain fish (Brungs 1973), so its use must be tempered. The only large-scale uses of CO_2 in water appear to be in such procedures as the recarbonation of municipal waters that have been softened by the lime-soda method. Such a direct procedure of injecting CO_2 into a large lake or burning natural gas under its surface to release CO_2 might be expensive, but the cost could be lessened considerably. Early work by Robinson *et al.* (1969), showed that artificial circulation of lakes by mechanical means or by compressed air had as one of its effects lowering of the pH. This lowering probably resulted from three factors— dilution of the algal population, exposure of the circulating waters to the atmosphere, and distribution of CO_2 accumulated in the hypolimnion. Accordingly, direct injection of CO_2 could be used as an adjunct to artificial circulation. There is a possibility that the decrease in algal populations and the shift from blue-greens to greens that Robinson *et al.* (1969), and others (Malueg *et al.* 1971; Weiss and Breedlove 1973), have found following circulation is a result of the lowered pH and increased CO_2 brought about by the circulation. Although other theories have been proposed to explain the phenomenon, e.g. effects on sinking rates of different forms (Bella 1970), or alteration of the light regime of the algae (Lorenzen and Mitchell 1973), none appear to be totally satisfactory. For example, in some cases circulation has led to increased abundance of blue-green algae (Lackey 1971), and this would be unlikely if the mechanism that caused the shift to greens were based on light. Our feeling is that the blue-green/green shift is primarily related to pH change, and the reason some circulation ventures do result in the shift while others do not rests on whether or not the pH declines as a result of circulation. A study of six cases where algal data and pH data are both supplied supports this contention. In four of these cases, Malueg *et al.* (1971), in an Oregon Pond, Robinson *et al.* (1969), in a lake in Kentucky, Weiss and Breedlove (1973), in a lake in North Carolina, and the New Hampshire Pollution Control Commission (1971), in a lake in New Hampshire, the reports describe blue-green to green shifts, and in all four cases the circulation had resulted in lowered pH in the surface waters. In the other two cases, Lackey (1971), in Colorado and Lake Calhoun in Minneapolis (Shapiro and Pfannkuch 1973), where circulation did not result in the algal shift but rather in more abundant blue-green algae, the pH was not significantly affected by the circulation. Presumably in the latter two cases circulation increased the nutrient availability in the euphotic zone by circulating stored nutrients from the hypolimnion to the extent that the inputs of CO_2 were overbalanced by the increased use of CO_2 due to photosynthesis, and pH stayed high.

It would appear, then, that circulation must be done in such a manner as to bring the waters into contact with the atmosphere but not to circulate hypolimnetic nutrients. One way to do this might be to circulate only the epilimnion either with or without the addition of CO_2. The mode and timing of circulation should also be selected in the light of the possibility of other advantages to be gained, e.g. dilution of fish populations and subsequent lessening of predation on zooplankton.

CONCLUSIONS

The purpose of this paper is to emphasize the necessity of treating lakes as ecosystems. Too long have limnologist looked to engineers to resolve the problems of eutrophication, and too often the only method considered has been the elimination of nutrient input. This method will work in some cases but it cannot be called upon to completely restore lakes that have been made eutrophic for a long time. The reason is that increased nutrient flux to lakes sets in motion processes that work together to stabilize the eutrophic condition. Consider an oligotrophic lake. As the input of nutrients to the lake increases, algal productivity begins to increase as more diatoms and green algae are produced. This increase in production leads to

diminished concentrations of dissolved oxygen in the hypolimnion and ultimately, if productivity is high enough or the hypolimnion small enough, to anoxic conditions. In addition to accumulations of nutrients in the hypolimnion, nutrients are released from the sediment, and hydrogen sulfide may accumulate. The phosphorus content of the surface sediments increases. At the same time as these changes occur in the hypolimnion, chemical changes occur in the epilimnion—increases in pH due to photosynthetic use of CO_2, depletion of PO_4-P in the water, etc. These chemical changes lead to changes in the communities of organisms living in the lake. The varied bottom fauna of the oligotrophic lake becomes replaced with chironomids. Cold-water fish including carnivores are replaced by fish such as carp and bullheads that can tolerate low concentrations of dissolved oxygen. These fish then recycle nutrients that ordinarily would remain in the sediments. In the epilimnion the elevated pH leads to an increase in the proportion of blue-green algae as a result of their ability to out-compete greens and diatoms for CO_2 and PO_4 at higher pH. The ability to get CO_2 and PO_4 allows certain blue-greens to use fixation to ensure that their nitrogen needs are fulfilled. The low phosphate concentrations act to shift the equilibrium between water and macrophytes, so that macrophytes act as phosphorus pumps and release phosphate into the lake. As the blue-greens become abundant they shade out greens and diatoms. Furthermore, they tend to remain abundant, as many are not eaten by zooplankton and in fact may even be toxic to zooplankton. The zooplankton are suppressed by the lack of food, the presence of possibly toxic food, high pH, and predation—the latter resulting from an abundance of fish such as perch. In addition to becoming fewer, zooplankters become smaller. The perch become abundant because of the disappearance of some of the predators, and the increase, at least for a while, in their food supply.

Obviously, not all of these changes can be reversed simply by lessening the nutrient flux, as the effects of a fire cannot be reversed simply by withdrawing the match that causes the fire. The greater the extent to which the changes have occurred, the more certain it is that nutrient removal alone will not suffice. Other measures must be taken to reverse actively the biological consequences of over-fertilization. It may even be possible, as we have suggested, to reverse the biological consequences even if the nutrient flux cannot be reduced. Our own work has shown that chlorophyll concentrations and primary productivity can be kept low in the face of high nutrient concentrations simply by the grazing activities of zooplankters. Considering that a 1 kg increase in the weight of one carnivore added to control zooplanktivores implies consumption of 1 metric ton of algae, we feel that biomanipulation, i.e. utilization of

the interrelationships inherent among ecosystem parameters, is worth trying.

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