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The Occurrence and Cause of Midsummer Zooplankton Declines: Cyanobacteria and the Implications for Freshwater Ecology

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To the Graduate Council:

I am submitting herewith a dissertation written by Nicholas K. Brown entitled "The Occurrence and Cause of Midsummer Zooplankton Declines: Cyanobacteria and the Implications for Freshwater Ecology." I have examined the final electronic copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Ecology.

Dewey L. Bunting, Major Professor

We have read this dissertation and recommend its acceptance:

Accepted for the Council:

Carolyn R. Hodges

Vice Provost and Dean of the Graduate School

(Original signatures are on file with official student records.)

To the Graduate Council:

I am submitting herewith a dissertation written by Nicholas Kirkpatrick Brown entitled "The Occurrence and Cause of Midsummer Zooplankton Declines: Cyanobacteria and the Implications for Freshwater Ecology." I have examined the final copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Ecology.

Dewey L. Bunting, Major Professor

We have read this dissertation
and recommend its acceptance:

Edward E.C. Clebsch

Accepted for the Council:

CW Minkel
The Graduate School

THE OCCURRENCE AND CAUSE OF MIDSUMMER ZOOPLANKTON DECLINES: CYANOBACTERIA AND THE IMPLICATIONS FOR FRESHWATER ECOLOGY

A Dissertation
Presented for the
Doctor of Philosophy
Degree
The University of Tennessee, Knoxville

Nicholas Kirkpatrick Brown

December 1984

To Annie

May your inborn love of nature be
permitted and encouraged by our
generation and yours.

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ABSTRACT

The current paradigm of lacustrine ecology is that zooplankton communities are structured by the nature and intensity of predation upon them. One corollary to this paradigm is that the observed phenomenon of midsummer zooplankton decline is caused by predation. A second is the hypothesis of "biomanipulation." One aspect of "biomanipulation" proposes that in certain circumstances the removal of predators of zooplankton might result in reduced algal biomass. The assumption of both these corollaries is that aquatic food webs are manipulable from the top.

The data supporting predation-caused midsummer declines and biomanipulation are examined analytically and theoretically by considering biomass, foraging cost and evolution. It is concluded that the present data suggest it is more likely that algal biomass and composition determine zooplankton community structure at a given time than does predation.

Two comparative studies were first conducted:

1. The zooplankton communities in a variety of lakes, half of which contained dense, stratified populations of the blue-green alga (cyanobacterium) *Oscillatoria* spp. and half of which did not, were surveyed. Lakes containing *Oscillatoria* were found to have limnetic zooplankton populations skewed toward the small end of the size spectrum of the zooplankton from all the lakes.

2. A variety of small aquatic ecosystems were monitored through the summer to see if midsummer declines occurred and, if so, in which

lakes. No midsummer declines were found associated with predation while two declines were associated with cyanobacteria and/or food limitation.

A series of experiments was then performed to ascertain the mechanism by which Oscillatoria might cause a midsummer decline and ultimately structure zooplankton communities and to determine the relative effect of predation on zooplankton. These experiments indicated that introducing or greatly increasing predator density did not restructure zooplankton communities:

1. Ceriodaphnia lacustris and Diaptomus oregonensis were introduced to whole lakewater taken from a cyanobacteria stratum (primarily Oscillatoria sp. filaments) in Arco Lake, Minnesota during a midsummer zooplankton decline. While C. lacustris and D. oregonensis suffered 100% mortality after 18 hours in the filaments, the same two species experienced 75% survivorship in the same water which had first been filtered.

2. Glass plates were suspended in an Oscillatoria stratum in Lake Josephine, Minnesota and in Oscillatoria which had been removed to various depths. By counting filaments adhering to the glass plates it was determined that Oscillatoria's tendency to adhere increased both as the summer progressed and as it was removed from its preferred depth of stratification.

3. Predation experiments were performed by both excluding the zooplankton predator Pimpales promelas ("fathead minnow") from a large area of littoral zone and similarly enclosing a range of densities of Pimpales in Lake Josephine, Minnesota. While increased

densities of *Pimpales* were found to cause temporary zooplankton declines (analogous to midsummer declines), zooplankton populations did not rise in the absence of *Pimpales* and were not ultimately effected in the enclosures because *Pimpales* soon switched to ingesting sediments and epiphytic algae and zooplankton populations returned to their original levels.

4. Finally, a larger complex body of water (Lake Itasca, Minnesota) with both a predator capable of exerting heavy predation on zooplankton (young of the year yellow perch) and a perennial midsummer shift from a diatom - green algal community to blue-greens was monitored throughout a summer and experiments were performed to ascertain whether its midsummer decline were more closely correlated with larval fish migration (predation) or blue-green succession. *In situ* exclosure experiments, laboratory observation of algal-zooplankter interaction and sediment traps all indicated that the declines were associated with blue-green succession rather than predation. These experiments and observations also indicated that the mechanism of this particular decline was the difficulty certain zooplankton experience in clearing filamentous blue-greens (*Oscillatoria* spp.) with their postabdomen when the filaments are secreting mucopolysaccharides and thus tend to adhere to the plankter's filtering apparatus.

Observations indicated that the secretion of mucopolysaccharides by *Oscillatoria* is a response to its being driven from a preferred stratification in the water column (by stormed caused mixing or secchi) and encountering a different nutrient and light regime.

Further observations indicated that, while a large limnetic cladoceran (*Daphnia galeata*) actually succumbed to the filaments, most littoral species appear adapted to surviving the period during which filaments adhere by reducing carapace gape and movement.

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Predation, Size Efficiency, and "Biomanipulation"

In 1965 Brooks and Dodson suggested that predation and competition were the primary forces shaping freshwater zooplankton communities. This concept has since become widely accepted among zooplankton ecologists.

Brooks and Dodson sampled a series of Connecticut lakes, half of which contained landlocked populations of the normally marine clupeoid planktivore Alosa psuedoharengus ("alewife") and half of which did not. Lakes with alewives had zooplankton populations skewed toward the small end of a size spectrum (represented by the smaller Ceriodaphnia lacustris and Bosmina longirostris). Lakes without alewives had populations skewed toward the large end of the spectrum (represented by the larger Daphnia galeata and D. catawba). They also found significantly different populations in pre- and post- alewife data for a lake into which alewives had been introduced.

In a conclusion which has since been greatly extended (see below) Brooks and Dodson hypothesized:

> The difference in populations was due to alewife predation which was selective of larger zooplanktonic herbivores (the "predation" hypothesis).

> That in the absence of planktivore predation, large herbivores

(being more efficient at collecting small particles and being able to collect large particles as well) competitively exclude smaller herbivores. Conversely, in the presence of predation, there is competitive release of small herbivores which then predominate (the "size efficiency" hypothesis).

From the beginning "structure" has been used in the sense that fish are not only capable of eliminating zooplankton species by predation but that this predation can indirectly shape the whole food web. The Brooks and Dodson "predation and size efficiency hypothesis" has been the impetus for further elaboration of the role of predation in shaping aquatic food webs:

> Paine and Zaret's study (1973) of Gatun Lake in Panama ascribes not only the restructuring of a fish community to introduction of a piscivore but in turn restructuring of at least two more trophic levels and even the possible increase in malaria due to decreased predation (two trophic levels down) upon mosquito larvae.

> Shapiro et al. (1975) have proposed the notion of "biomanipulation" of freshwater communities. The theory of biomanipulation proposes not only that herbivorous zooplankton might reduce blooms of algae and that zooplankton communities are manipulatable in the Brooks-Dodson sense but that the introduction of predators of predators of zooplankton thus might affect algal biomass. "Biomanipulation" has held a great deal of appeal because of the proposal by its proponents that it might obviate the use of algacides and the expense of

waste water treatment.

> Zaret's (1980) recent book "Predation and Freshwater Communities" postulates seven states of increasing predation (both vertebrate and invertebrate) and predicts zooplankton commmunity structure solely upon the "state" of predation. While the importance of the "physical environment" is acknowledged, the assumption of the book is clearly that predation is the primary force shaping zooplankton communities. The importance of algae, either as a food source for or as an encumbrance to zooplankton, is not acknowledged or mentioned.

This, indeed, is a pervasive role ascribed to predation in structuring freshwater communities, especially when experimental evidence for it is quite sparse. Most of the experiments which have been performed have been within the confines of the laboratory or have consisted of placing a relatively large number of mature fish in a small enclosure (usually less than $1\ m^2$) and monitoring zooplankton numbers. In these experiments, the confined biomass of fish exceeds by several magnitudes what one would normally find in a natural setting, and their confinement is a pervasive treatment effect not only upon the fish but upon the zooplankton. In short the experimental evidence shows nothing more than that fish will eat what is available when confined in close quarters and when not allowed to forage. It is a very long inference from these experiments to "biomanipulation" by predation.

As an alternative explanation of forces structuring freshwater communities, roles at the base of food webs should be examined. Many, if not most, species of larval fish are crucially dependent upon the zooplankton community as a food source (i.e. there is a period during which they are gape-limited and zooplankton constitute the major, if not sole, food source within the size range of the gape limitation) (Zaret 1980). There is also a growing body of evidence that certain zooplankters may not be able to tolerate certain algal populations and concentrations. A summary of the evidence from the literature follows:

> There is a continuing question as to the effect of blue-green toxins on zooplankters (Lefevre 1950; Gentile and Maloney 1969; Schindler 1971; Arnold 1971; Crowley 1973).

> Porter and Orcutt (1980) have shown certain algae to be nutritionally inadequate and/or unmanageable for certain zooplankters.

> Filamentous forms of certain algae have been shown to clog the filtering apparatus of certain filter feeding zooplankton.
The energy cost is more acute in the larger cladocerans (Porter and McDonough 1984).

> The disappearance of larger cladocerans has been temporally correlated with an increase in blue-green filaments (Gliwicz 1977; Pace and Orcutt 1981; Edmondson and Litt 1982; Richman and Dodson 1983), but there has been some doubt as to the existence and/or nature of the causal mechanism (Webster and Peters 1978; Porter and Orcutt 1980; Lampert 1981; Starkweather 1981; Holm et al. 1983; Porter and McDonough 1984; Infante and Abella in prep.).

It should be increasingly clear that there is an alternative hypothesis to structuring by predation and "size efficiency." Perhaps it is much more predictive of what one will find in a given lacustrine system to start with the realization that morphometry (and thus mixing in the water column) and nutrient regime are quite predictive of algal succession (Reynolds 1982). Perhaps algae are determinative of zooplankton populations which, in view of the importance of zooplankton to larval fish, are in turn determinative of the fish populations which are self sustaining in equilibrium conditions.

Brooks and Dodson did not attempt to negate the alternative hypothesis. They realized that the Connecticut lakes varied considerably in their physical aspects, but algal succession was not considered. This in spite of the fact that many of the alewife lakes were known to experience midsummer algal blooms (Anon 1959).

The extrapolations from their work and hypothesis (the pervasiveness of the predation paradigm in freshwater ecology) are particularly puzzling because, simultaneously, the notion of control of prey populations by predators was being severely tested in terrestrial ecology. Two classic examples are the Lynx-Hare cycles (Meslow and Keith 1968; Keith and Windberg 1978) and the Kaibab deer (Caughley 1970).

This is merely to indicate the alternative hypothesis ought to be tested. It is not to say that distinctions between terrestrial and lacustrine ecosystems might not support the predation hypothesis and, indeed, the tenets of "biomanipulation." As Hairston et al. (1960)

have pointed out, algal populations, unlike terrestrial plant communities, tend to "crash" whether grazed or not. Thus, periodic reduction of algae by grazing, as well as the depletion of lacustrine herbivores by predation, might be in accord with the general observation that the rate of carbon deposition, when compared to photosynthesis over geologic time, is negligible in the biosphere as a whole (Hutchinson, 1948).

However, it must also be pointed out that a typical organic carbon profile of north-temperate lake sediments indicates increased carbon deposition contemporaneous with the activities of modern man. This increase in most cases is a departure from a longer period of stable carbon deposition --what has been refered to as "trophic equilibrium" (Hutchinson 1969). Increased carbon content in sediments is subject to varying interpretations which might be dependent upon ecological interactions between algae and herbivorous zooplankton (Whiteside 1983). Thus the question whether (or in what circumstances) lacustrine ecosystems are structured by predation or by algal composition is not only relevant to attempts to deal with cultural eutrophication (biomanipulation) but also to paleolimnology.

In addition to the role of predation, the need to experimentally and rigorously examine the notion of competition (i.e. "size efficiency" in freshwater ecology) has been recognized and is now being ardently debated by ecology in general (summarized by Lewin 1983). Brooks and Dodson recognized the analogy of this aspect of their hypothesis to the "common and well-known phenomenon among congeneric birds (co-existing species of which may differ principally in body size, beak size and size of food taken)." What was then viewed as a "common and well-known phenomenon" is now key in a most interesting debate (see, e.g., Simberloff and Boecklen 1981).

Theoretical and Analytical Questions Posed by the Alternative Hypothesis

Because lacustrine ecology has generally not tended to view predation and algal determination as alternative hypotheses there is a host of ecological questions which should at least be outlined at this point.

> It has been fairly well demonstrated that fish in the confines of a laboratory, being visual predators, select larger opaque particles over smaller or transparent ones. This comports with the Brooks-Dodson hypothesis. But, at some point, well before large cladocerans could be driven to extinction (by predation) in a lake, the animals would be rare enough that search costs might be quite high relative to available biomass. Can foraging theory indicate at what point its marginal cost would exceed its benefit to the planktivore? Might not the fact that Brooks and Dodson found large zooplankters not rare but non-existent in the "alewife" lakes in itself indicate an explanation other than predation?

> What does evolutionary theory have to say about the likelihood of a predator driving its primary or preferred prey to extinction? Is it more likely to occur with an introduced predator (which did not co-evolve with its prey)?

> Some accounting of biomass would be useful in all of these situations in which control of prey by predator is hypothesized to see if control is physically possible or probable in simple terms of biomass. This is especially true of the aspect of "biomanipulation" which posits that algal populations may be controlled by grazing. A rigorous look at algal biomass and growth rate versus zooplankton biomass and generation time is needed.

The examination of the alternative hypothesis is not simply of importance to ecological theory removed from immediate practical significance in the management of water resources. It would be fair to say that the fisheries profession as a whole has accepted the notion from limnology and freshwater ecology that food webs are largely controlled from the top --at least in lacustrine systems. The euphemism of "reclaiming" a lake belies this. For an introduced species (or community for that matter) of fish to be self sustaining in an equilibrium sense, there must be the proper support below it in the food web. Some proportion of the species' larval young must survive and mature, and the true importance of zooplankton as a food source for gape limited larval fish is just now being made clear (Mills 1983; Whiteside et al. 1984). If algal populations do in fact structure zooplankton populations, how they do so is of utmost importance to the fisheries profession. Furthermore, the known sensitivity of most blue-greens to pH (Shapiro et al. 1975) makes the question doubly relevant in the context of "acid rain."

The Pivotal Importance of Midsummer Declines

A number of workers have realized the importance of and have investigated midsummer declines of zooplankton in North American and Scandinavian lakes (Goulden 1971; Keen 1973;1976; Whiteside 1974; Daggett and Davis 1974; Whiteside et al. 1978; Williams 1978; Williams and Whiteside 1978; Doolittle 1982). Coincident with a precipitous population decline, all obvious environmental factors (temperature, availability of food, etc.), as well as birth rates, are apparently at their optima. Moreover, the phenomenon has been documented in a variety of lake types over a geographic range from Minnesota to Pennsylvania, Newfoundland, and Scandinavia (Figure 1). Without exception, studies of midsummer declines have concluded that predation, either vertebrate of invertebrate, was the sole or primary cause. Several of these studies provide compelling evidence of the coincidence of predator movement or activity and the decline of zooplankton. However, none of the studies has monitored algal assemblages during a midsummer decline.

In contrast to the sea (Sverdrup 1953), primary production in lakes generally takes place in non-homogeneous layers and there are considerable gradients of temperature and concentrations within the photic zone which lead to unstable conditions for primary production when there is mixing or seiche in the water column (Findenegg 1965). It is becoming increasingly clear that mixing (or the lack thereof) in lacustrine systems is intimately related to summer succession of algal species (Reynolds 1982).

Sampling of algae in a lacustrine ecosystem at one point in time

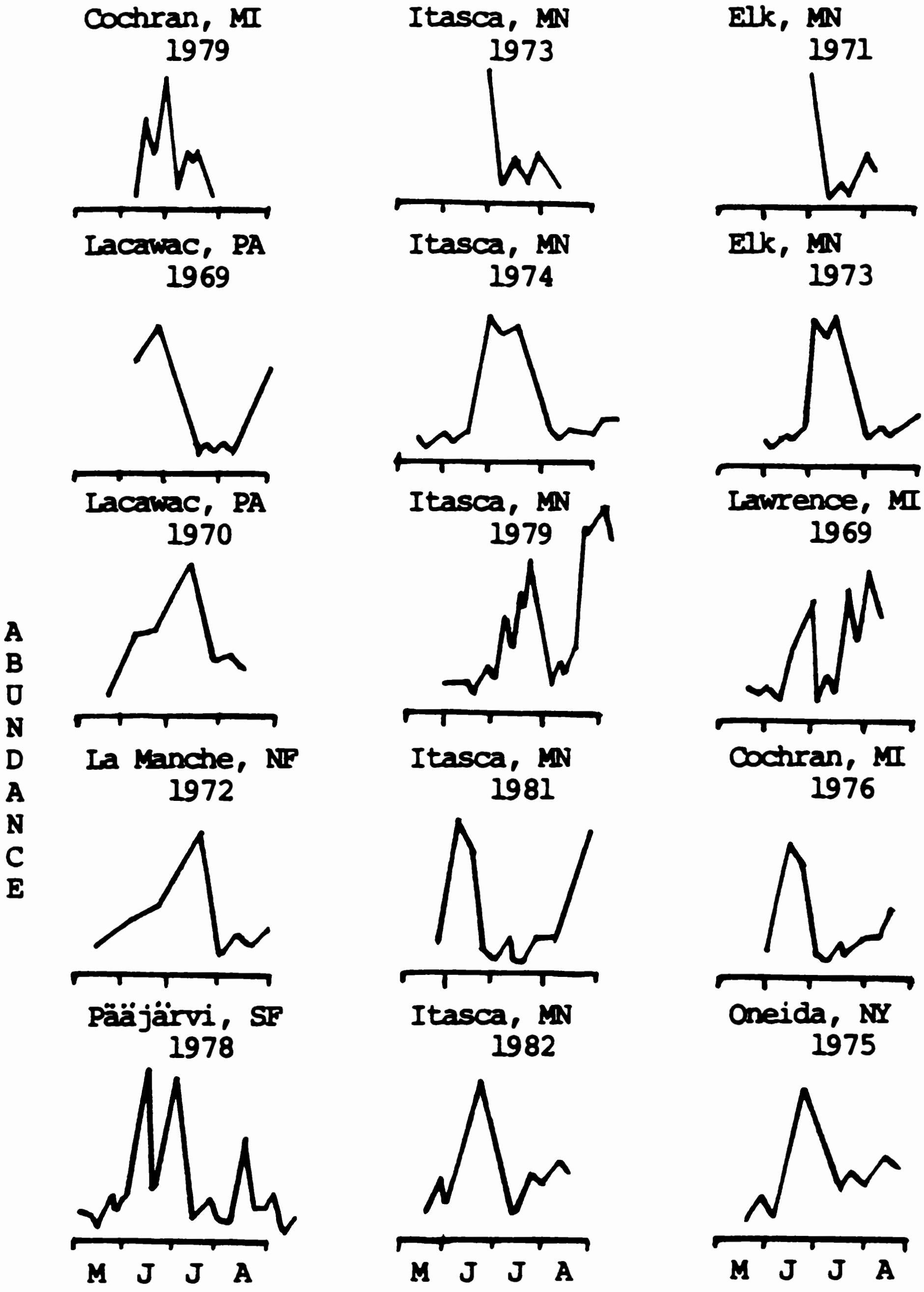


Figure 1. Documented midsummer declines in North American and Scandinavian lakes (after Whiteside 1984).

indicates very little about the summer dynamics of that system. Likewise, if one is to test the alternative hypothesis that zooplankton populations are determined by algal composition rather than structured by predation, a static sampling (such as in the Brooks and Dodson survey) indicates very little. A given species may be perennially present before, but not after, a decline (thus biasing a sample at either point). Both predation (hatching and movement of larval fish) and algal composition vary widely through midsummer. An understanding of midsummer declines is therefore a prerequisite to any definitive statement of the forces shaping lacustrine ecosystems.

Summary

The need for an examination of the alternative hypothesis to predation and size efficiency in the context of midsummer declines is indicated by:

(1) The two decades of extension of the hypothesis (both to other trophic levels and situations not involving alewives) without a direct test of its alternative.

(2) The static nature of the original Brooks and Dodson survey.

(3) The imperative of firmly understanding structure in lacustrine systems both in efforts to combat cultural eutrophication and acid rain and in routine management of fish resources.

(4) The importance of trophic relationships to deposition of lacustrine sediment in view of attempts by paleolimnoligists and quarternary geologists to interpret past climate and to predict the

impact of future climatic change on lacustrine ecosystems.

(5) Its importance to general ecological theory.

II. ANALYTICAL AND THEORETICAL CONSIDERATIONS OF BIOMASS, FORAGING COST, AND EVOLUTION

The two most studied lacustrine ecosystems (with reference to midsummer declines) are Lake Itasca, Minnesota and Lake Oneida, New York. Both lakes have large yearly hatches of yellow perch (Perca flavescens) to which their midsummer zooplankton declines have been attributed. Both lakes also experience midsummer blooms of blue-greens. To provide a later background for analysis of field experiments, the following analytical and theoretical considerations were made with particular reference to those two systems:

Biomass

The 1979 littoral zooplankton decline in Lake Itasca was of the order of 450,000 organisms per square meter of substrate (Doolittle 1982). In the two to three days of the zooplankton decline a conservative estimate of zooplankton biomass drop is between 16.4 and 40.8 g per m^2 of littoral zone. (The wet weight of one adult Chydorus sphaericus is ca. 0.041 mg. C. sphaericus is among the smallest and most numerous zooplankters in the littoral.)

Young of the year (YOY) perch (to whom the decline was attributed) weigh approximately 140 mg (length 20 mm) when they migrate from mid-lake to the littoral at an age of approximately 40 days. In the ten days following movement inshore they gain approximately 20 mg or 2 mg per day (Swindoll 1981). Assuming an conservative (for larval fish) 10% (Humphrey 1979) conversion rate this works out to about 300-540 YOY perch for every m^2 of littoral zone. This, quite simply, seems to be more fish or predation than could physically be there.

Mills and Forney (1983) attribute several declines of Daphnia pulex biomass (ca. 400 mg/m^3) in Lake Onieda, N.Y. to predation by perch (biomass ca. 17 kg/ha). They conclude that in some years perch biomass of less than 10 kg/ha does not control D. pulex biomass of 200 mg/ha.

If one converts both biomass estimates to the same scale, it does appear that the perch could easily consume the D. pulex biomass. In fact, this calculation suggests that the perch must have substantial alternative food sources in Lake Oneida. What remains, however, after considering the data, is substantial doubt as to whether the perch cause the D. pulex decline or whether a decline in D. pulex is at least partially causative of the yearly decline in YOY perch documented in Lake Oneida.

A rough accounting of zooplankton and algal biomass is also illustrative. If dimensions of a typical planktonic filamentous blue-green (e.g. Oscillatoria rubescens) are used to compute its volume, and the same thing is done for a large zooplankter (such as D. pulex), it may be shown that D. pulex has one hundred times the volume of a filament of O. rubescens. Two D. pulex per ml (2,000 D. pulex per liter) is an extemely high density. 10^6 filaments of O. rubescens per ml is quite possible and a frequent occurence when it stratifies in situ (i.e. the biomass differential in bloom conditions is minimally of the order of five magnitudes). Under optimal conditions, D. pulex has a biomass doubling time of 72 hours (Munro 1974) and O. rubescens of 10 (Fogg 1965). There is at least some doubt that D. pulex could control O. rubescens by grazing under bloom conditions.

The notion of biomanipulation (in the sense of the top of the food web being able to control cultural eutrophication once bloom conditions are reached) therefore seems unlikely just from the standpoint of the relative trophic biomasses involved. When the physical and chemical characteristics encountered in Oscillatoria spp. are considered (see below) the hypothesis that it structures zooplankton and not vice versa gains plausibility.

Considerations of the Increasing Cost of Foraging

The mathematics of encounter probabilities (Gerritsen and Strickler, 1976) and cost of foraging (Royana, 1971) are not the type of considerations which are immediately useful to those with the responsibility of fisheries management. However, most would agree that predator speed, prey speed, and prey density are among the crucial variables. Due to the suddenness of the decline in Lake Itasca, the parameter of major importance is probably change in prey density. Within the crucial one meter of water column (above the Chara-water interface in the littoral), the change in prey density (a decrease from 450,000 to 10,000 organisms per m^2 of substrate) may be stated as a decrease in density from approximately an animal for every two milliliters of water to one animal for every liter of water.

This in turn would be equivalent to a YOY perch encountering a dozen animals within the radius of body length prior to the decline and having to travel at least a body length in the proper direction to encounter a single animal at post-decline density. A YOY perch would thus have to orient itself and move at least its body length (20 mm) in a time such that the prey is unable to dodge 2.4 mm (the mouth-gape of a 20 mm YOY perch).

Therefore, if predation were the cause of the zooplankton population decline in the littoral zone of Lake Itasca, foraging cost might become prohibitively high well before the low point densities are reached. In addition it would seem that predation would fall much more heavily on slow moving species (such as the D. pulex in Lake Oneida) than on the faster more maneuverable copepods. Doolittle's (1982) data on Lake Itasca, however, shows proportional losses in all groups.

Gerritsen and Strickler's (1977) analysis is apparently the only rigorous abstract mathematical model of predator - prey encounters with specific application to aquatic ecosystems. They borrow a two dimensional analysis by Kohlas (1967) of encounter probabilities for aircraft of the Swiss Air Force, combine it with Koopmans (1956) analysis for naval operations research and extrapolate into three dimensions. The geometry of the model is depicted in Figure 2. It considers a predator with an encounter radius R (an encounter radius reflecting such things as the predator's speed and ability to detect movements in the water) swimming with velocity v and a prey animal

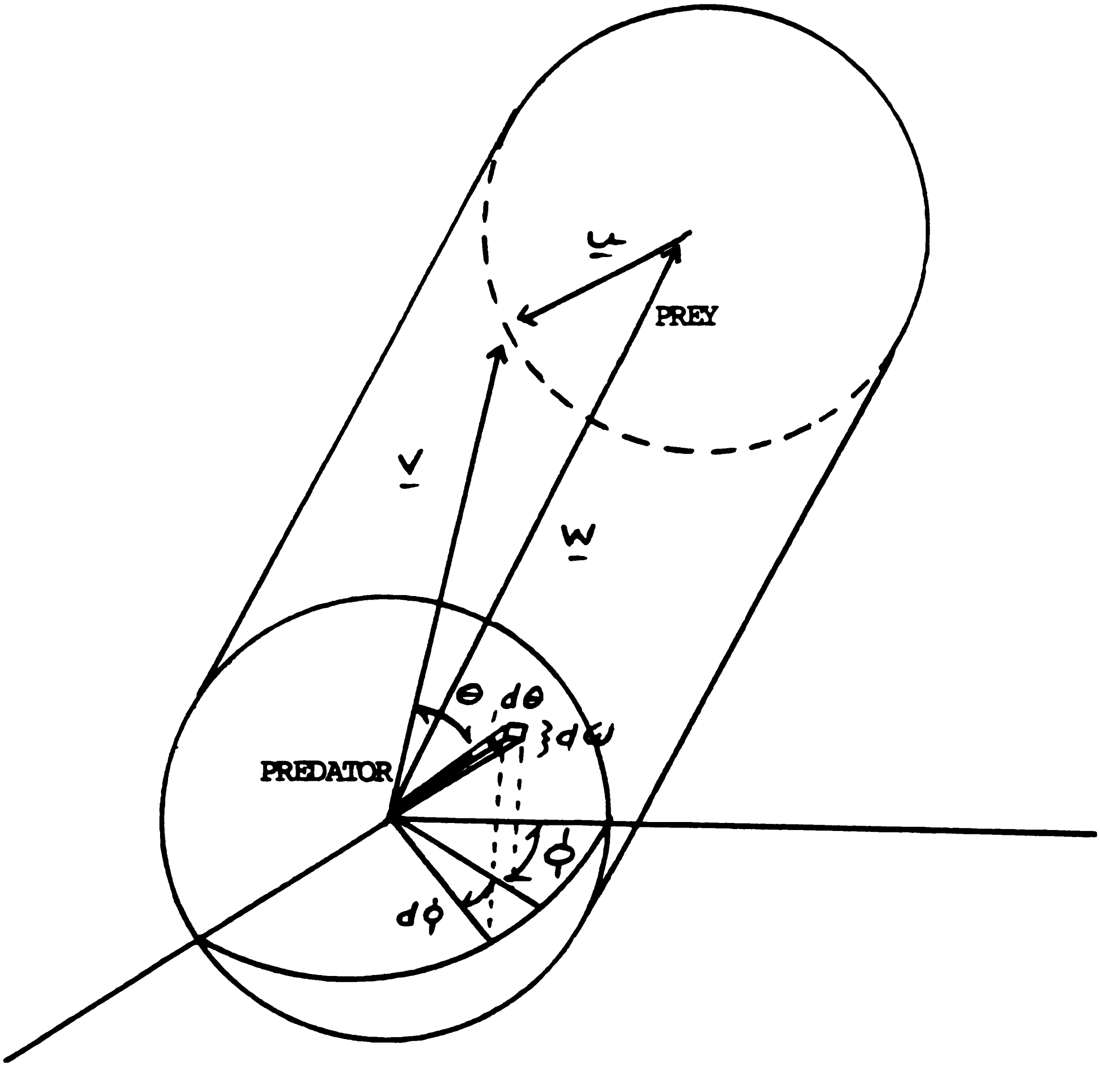


Figure 2. The encounter sphere of a predator and the volume it sweeps as the predator searches for prey (after Gerritsen and Strickler 1977). See text for explanation.

swimming with velocity u. The essence of the model is contained in the equation:

$$Z_p = \frac{\pi R^2 N_H}{3}\left(\frac{u^2 + 3v^2}{v}\right)$$

where Z_p is the encounter rate of a predator with its prey (or the total number of prey entering the sphere per unit time) and N_H is the density of prey. The Greek parameters in Figure 2 are the polar co-ordinates and track angles defined by Gerritsen and Strickler in their derivation of the above formula. As the derivation is completely stated in their work, and in view of the desire to apply the model rather than criticize it and the simplifications addressed below, it would serve no purpose to restate the derivation here.

The model's application to midsummer declines is quite simplified because initially the only independent variable undergoing drastic change within the short duration of the decline is prey density. There is, at least initially, no reason to presume that prey get slower or that predators get faster or more perceptive. It can be seen that encounter rate is directly proportional to prey density (i.e. search time = foraging cost is inversely proportional to prey density).

Prey density in the 1979 Lake Itasca littoral decline decreased by a factor of approximately 25. The Lake Oneida limnetic decline in 1975, however, is a four hundred-fold decrease in prey density. This may be insignificant or simply ambiguous in terms of stating whether either decline was due to predation. It could be that in both cases prey were so numerous at the outset that foraging cost became significant only at the end. It cannot be said that either decline continued after the cost to a potential predator was so great that *a fortiori* there must have been a cause other than predation. Nor, for the same reason, can a comparison be made on this alone between Lake Itasca and Lake Oneida or littoral and limnetic declines, as interesting as those speculations might be.

What can be speculated are the effects (based on the Gerritsen - Strickler model) of varying factors other than prey density. It is generally accepted that YOY perch are visual predators. Thus, their encounter radius (R) would undoubtedly be affected by water clarity. In Lake Itasca (and also Lake Oneida, apparently) secchi disk readings (a measure of water clarity) often vary quite rapidly (due to algal blooms and/or turbulence). In Itasca a change in secchi reading from 3 m to 1 m in less than 24 hours is frequent near the annual green to blue-green shift and littoral zooplankton decline (personal observation). Assuming that reducing visibility by a factor of 3 would have a comparable effect on predator encounter radius R, how is encounter probability (Z_P) affected? It can be easily seen from the general equation that Z_P varies with the square of R. Thus for every 2 m decrease in visibility encounters would be reduced by 75%.

The speed of prey (zooplankton) might also be considered. A concentration of filaments has been observed (see discusion in later section) to negatively affect zooplankton movement. The model predicts that encounters are also *directly* related to the square of *prey* velocity. (This may initially seem counterintuitive, but if one considers that the derivation of the model predicts and then assumes ambush, it is not). If filament concentration simultaneously reduces predator visibility and prey speed as the square of both and those factors compound one another, we can see that a doubling of filament concentration might reduce the encounter rate by a factor of 16 or 94%. Thus, Gerritsen and Strickler's model would predict filament concentration to be a much more crucial factor in the water column than prey density.

Evolutionary Considerations

Even without the considerations of cost-benefit above, it would seem intuitively anomolous that a predator would evolve the means to drive its preferred prey to extinction within its own ecosystem (in the Brooks-Dodson sense of "structuring"). If prey and predator co-evolved, it would seem more likely, other factors being equal, that prey would evolve methods of escape over evolutionary time. Predation exerts selection for fitness (the ability to escape) upon the prey. The converse would not seem to hold under the conditions of declining prey populations. In fact, even if one assumes for purposes of argument that midsummer declines are caused by predation, this is what happens. There is a tremendous reduction in numbers but not beyond the point of no return. The base of the food web returns for another year.

The important consideration is that the alewives did not co-evolve with their prey. Regardless of whether that has significance in evolutionary terms, it would not seem valid to extend the predation hypothesis to the great majority of freshwater ecosystems which do not contain a normally marine but landlocked planktivore without a rigorous test.

Summary

Examination of the data in view of biomass, foraging cost and evolution, at a minimum, leaves open the question whether midsummer declines may be algally caused. Some aspects of the Lake Itasca and Lake Oneida declines indicate likelihood of algal cause. In no respect do they negate an algal cause.

III. CHOICE OF STUDY SITE AND GENERAL RESEARCH PLAN

The potentially fruitful setting in which to test the predation hypothesis against its alternative (algal determinance of zooplankton communities) seemed to be one in which the following could be carried out:

1.

A survey of the zooplankton communities of varied lakes, half containing perennial blue-green populations and half not, on the chance that a correlation between that factor and size distribution might be revealed.

2.

Monitoring of a number of small bodies of water, some of which contained blue-greens (but not predation) and some of which contained predation (but not blue-greens), throughout the summer to see if certain ecosystems experienced midsummer declines and others did not. Unlike a static survey (#1 above), this documenting of community dynamics over time would also indicate whether the point in time at which one samples a given lake highly biases the perception of its zooplankton community.

3.

The greatest potential, but also the greatest difficulty of execution, lies in the use of *in situ* exclosures and enclosures in an ecosystem which contains both factors (predation and blue-greens), during a midsummer decline, to observe their independent effects on zooplankton communities.

This general research plan was pursued at the University of Minnesota's Biological Research Station within Lake Itasca State Park located in northern Minnesota approximately 100 miles south of the Canadian border and 100 miles east of Duluth. Due to the recent geological history of the area, the environs of the station contain hundreds of lakes (Figure 3). The lakes possess a wide diversity of morphometries and algal, macrophytic, zooplankton, and fish populations. In addition, there are lakes which, because of the presence of the park, have remained relatively undisturbed since European settlement of the area, as well as nearby lakes which have experienced a range of logging and agriculture in their watersheds.

The area is generally of glacial till laid down in apparently several advances of the ice 12 - 20,000 years b.p. (Wright 1972). The undisturbed watersheds are of northern coniferous and hardwood forest: *Pinus resinosa* (red or Norway pine), *Picea glauca* (white spruce), *Larix laricina* (tamarac), *Betula papyrifera* (white birch), *Populas tremuloides* (popple), *Quircus rubra* (gray oak) etc. Numerous kettle holes or ice block depressions are the present ponds and lakes. The morainic material which surrounds them is calcareous sandy loam which bears evidence of being washed and reworked by melting ice fronts (Figure 4).

Figure 3. High altitude photograph of study area. The scale is 1:119,380 and Lake Itasca, Lower Lasalle, and Heart Lake Quadrangles comprise the area photographed.

Figure 4. Low altitude photograph of Lake Itasca.

IV. COMPARATIVE STUDIES

The 1981 Lake Survey of Zooplankton Communities with Reference to the Cyanobacterium Oscillatoria

a. Methods

The survey was similar to that of Brooks and Dodson (1965) in that there was no attempt to document seasonal dynamics of communities. Zooplankton in a series of lakes were sampled during a two week period in midsummer (15 July - 1 August). Samples of limnetic species were taken with vertical tow nettings (0.5 m, 64 micron mesh net) and subsamples counted until totals of 1000-1500 specimens were reached for each lake. Also, as in the Brooks-Dodson survey, a particular factor separated the Minnesota lakes into two categories. Instead of presence or absence of a planktivore (alewives), the lakes (otherwise varying widely in morphometry and size) either contained or did not contain a dense, planktonic, stratified layer of the blue-green cyanobacterium Oscillatoria spp. The presence or absence of these strata was generally known to be perennial from previous research (Baker and Brooks 1971, A.J. Klemmer personal communication) but was confirmed during the survey with a transmissometer (Montedoro-Whitney model TMU3) and a depth specific sampler (Goulterman and Clymo 1969). A 1 m light path was used for all lakes. The sampler was used in conjunction with $^5/_8$" Tygon plastic tubing and an ITT Jabco self-priming "water puppy" pump.

Optical density profiles, temperature profiles, identification of *Oscillatoria* to species and estimates of filament densities for the *Oscillatoria* lakes are contained in Figure 5. Filament density estimates were made by filtering known volumes of water through a gridded membrane filter (millipore, 47 mm, 0.45 micron) and counting grids by the changing average method (Lind 1979). Profiles of the lakes not containing stratified *Oscillatoria* are shown in Figure 6. No attempt was made to determine the effect of stratified *Oscillatoria* on diurnal migration of various zooplankters, whether *Oscillatoria* undergoes lysis in midsummer or at ice-on with a consequent effect on zooplankters, etc.

b. Results

The zooplankton communities of the two categories of Minnesota lakes fell into significantly different size distributions which were similar to the Connecticut data (Figure 7 and Table 1). The mean size in the *Oscillatoria* lakes was 0.771 mm and in the non-*Oscillatoria* lakes was 1.494 mm (Table 2). In addition, the survey uncovered a possible analogy to Brooks and Dodson's findings in Crystal Lake (Crystal Lake in Connecticut was sampled prior to and then following alewife introduction with the finding that prior and post populations were significantly different in size distribution). Arco Lake in Minnesota is a small meromictic kettle lake which had been studied extensively prior to 1981 by several workers. Zooplankton populations prior to 1981 in Arco were quite different from those found in 1981. *D. pulex* had been present as a large population in Arco for at

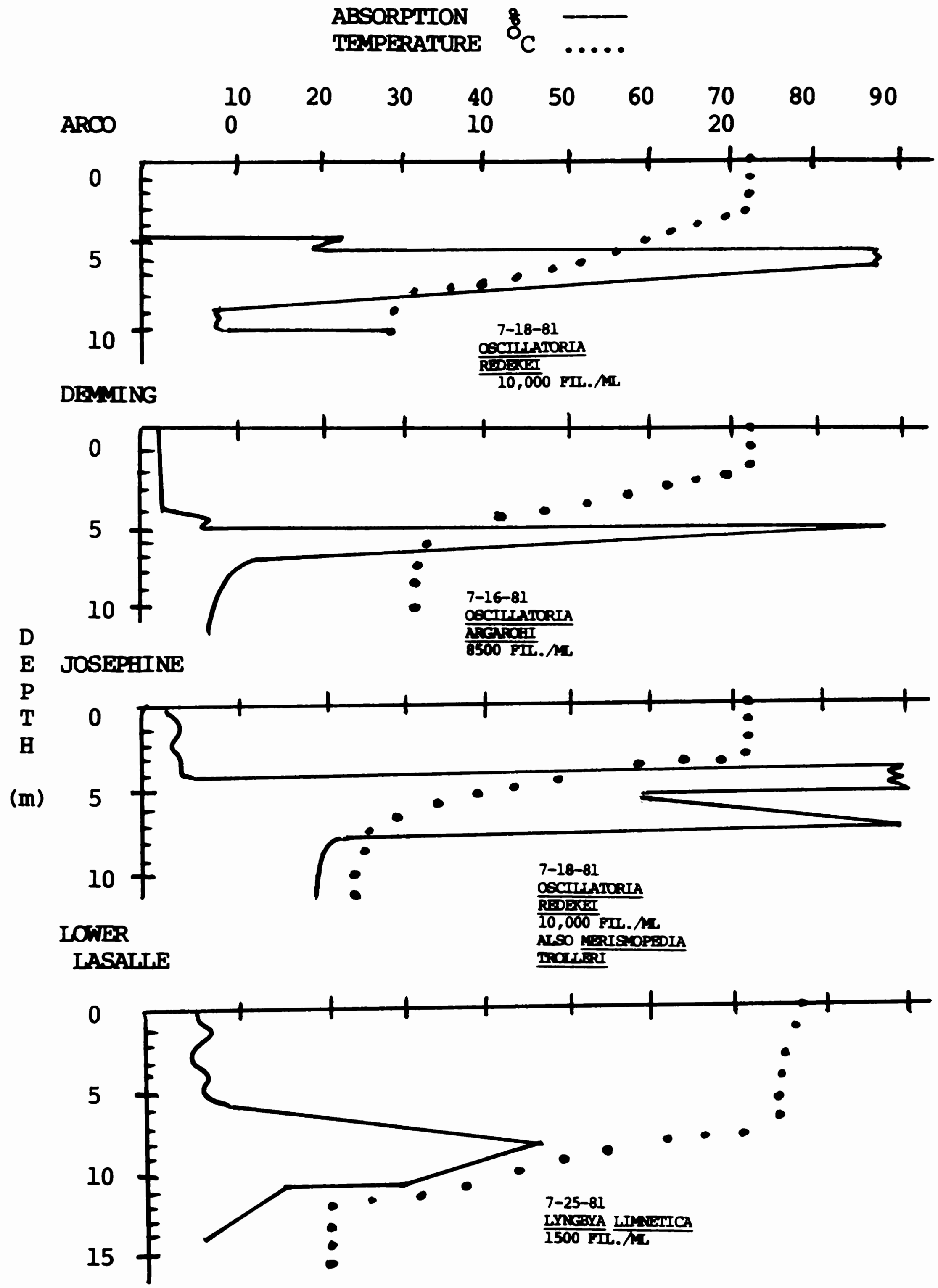


Figure 5. Optical density profiles, identification of Oscillatoria to species, and estimates of filament densities for the stratified Oscillatoria lakes.

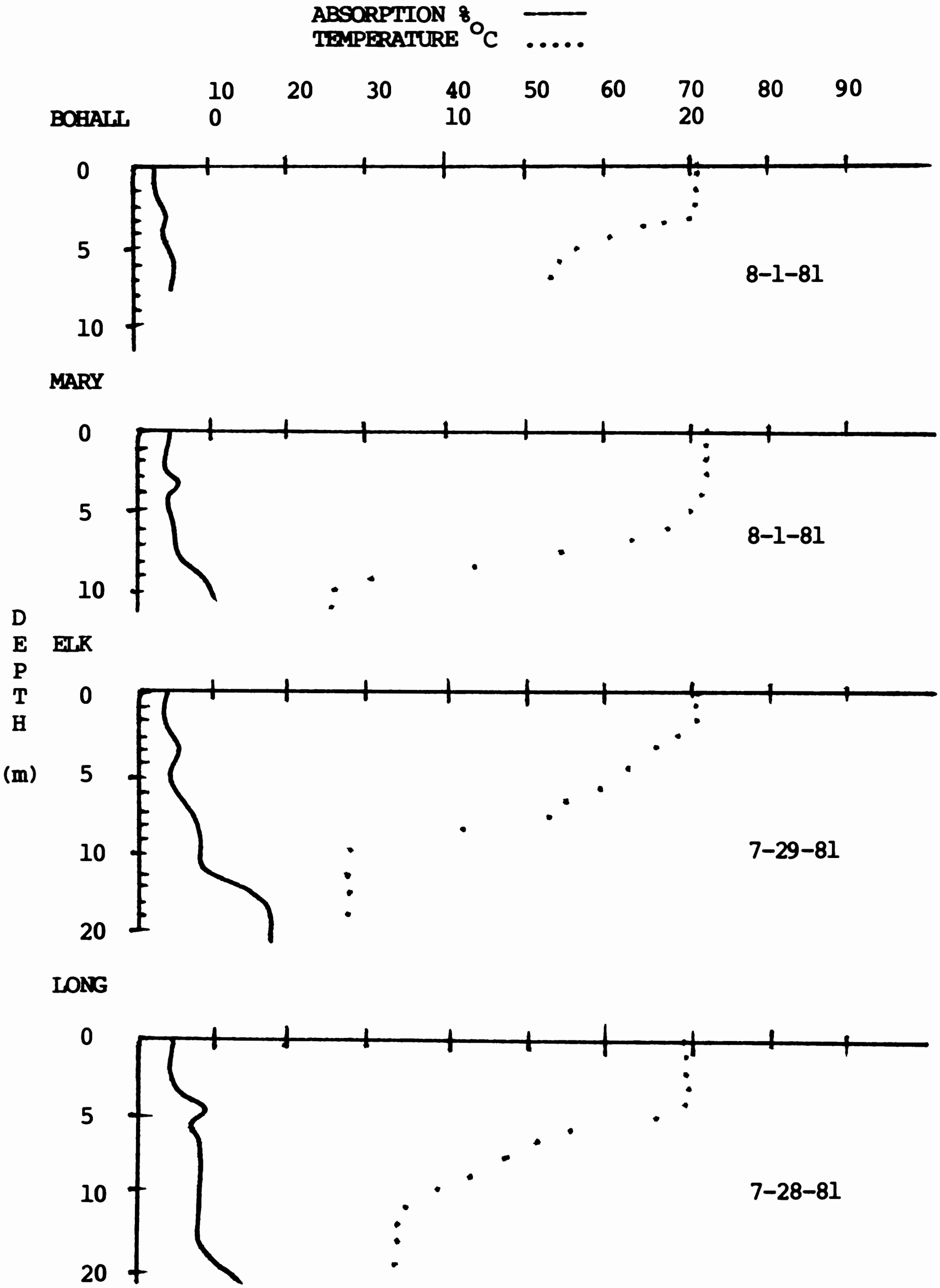


Figure 6. Optical density and temperature profiles of the non-*Oscillatoria* lakes.

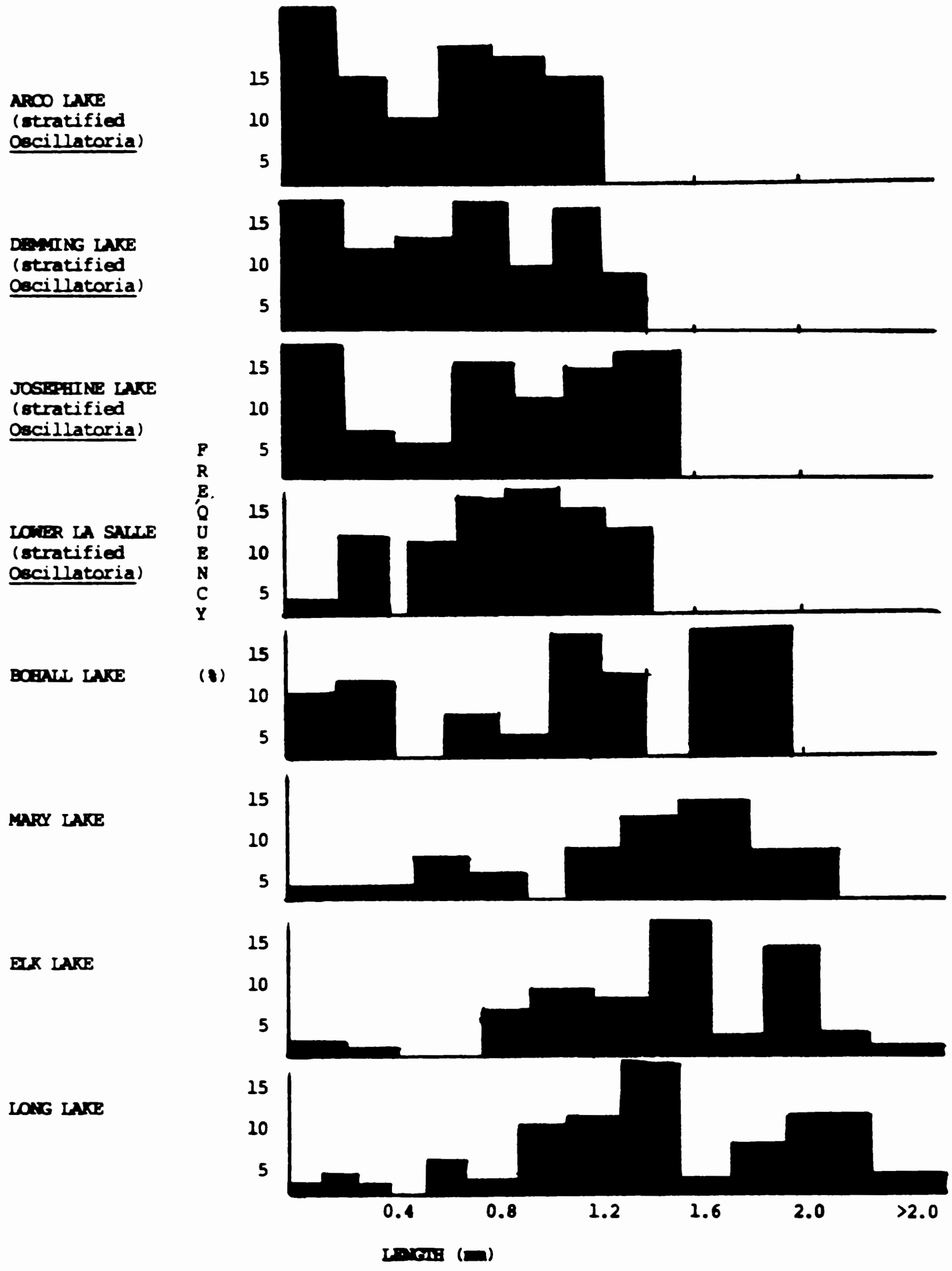


Figure 7. Histograms of the size distribution of the zooplankton communities for *Oscillatoria* lakes and lakes not containing (at least in dense planktonic strata) *Oscillatoria*.

Table 1. Relative frequency of limnetic zooplankton in lakes with and without stratified *Oscillatoria*.

	Lakes without *Oscillatoria*				"K" Pond 1982 (no osc.)	"K" Pond 1983 (osc.)	Lakes with *Oscillatoria*			
Organism	B	M	E	Lo			A	D	J	LLa
Cladocera										
Leptodora kindtii (5mm)		*	*	*						
Daphnia pulex (2.1mm)	41			9	48					
Daphnia galeata (2mm)		35	20	11						
Holopedium spp. (1.5mm)		10								
Moina sp. (0.9mm)			*	*					*	
Diaphanosoma brachium (0.8mm)	5		9				11	12		
Ceriodaphnia lacustris (0.8mm)		*	7	*		10	15	11	23	43
Bosmina spp. (0.33mm)	8	*	*	6					*	11
Copepoda										
Macrocyclops albidus (2.1mm)		*	6	10						6
Diaptomus clavipes					26	13				
Diaptomus oregonensis (1.3mm)	29	27	20	18			28	23	35	17
Mesocyclops edax (0.9mm)		6	6	20				*	11	19
Tropocyclops prasinus (0.5mm)		*	*	*				12	*	*
Nauplii	*	10	*		*		6	17		8
Rotifera										
Asplanchna spp. (0.4mm)	10			*	*	6	15	12	6	*
Keratella spp. (0.2mm)	6	*	*	*	6	35	25	20	15	*
Protozoans					<10	>30				
Dimensions										
Area (ha)		23.0	109	65.0	1.51		1.39	3.62	3.0	98
Maximum depth (m)		12.3	29.0	24.0	3.0		10.2	17.0	10.3	60
Relative depth	N.A.	2.27	2.46	2.64	N.A.		7.67	7.92	5.27	5.73

* Present but less than 5%.

Table 2. Comparison of mode and mean zooplankton size for *Oscillatoria* and non-*Oscillatoria* lakes.

Lake	mode (mm)	mean (mm)
(*Oscillatoria*)		
Arco	0.2	0.726
Demming	0.8	0.701
Josephine	1.2	0.882
Lower La Salle	0.8	0.775
(Non-*Oscillatoria*)		
Bohall	2.0	1.370
Mary	1.9	1.762
Elk	1.8	1.424
Long	1.5	1.423

least six years prior to 1980 (J. Underhill pers. comm.). Neither *D. pulex*, any other large cladocerans, nor any other potential vertebrate predators of *D. pulex* could be found despite a thorough search in 1981. The stratified algae in Arco in 1981 were dense (>9,000 filaments per ml) and *Oscillatoria redekei* (Figure 5). Previous researchers (Baker and Brooks 1971) found a dense stratum in Arco but list it as *Anabaena* sp. and *Merismopedia trolleri*. Doolittle (1977) found *Oscillatoria* in Arco but only in minor concentration and did not mention stratification.

c. Discussion

The history of stratified *Oscillatoria* in the Arco, Demming (previously Danger), Josephine chain of lakes is an interesting but unclear story. Klemmer (1982) has studied buoyancy response of Demming's layer to nutrients since 1972 and states the layer to have been quite stable in depth and presence since that time. Hooper (1942) inventoried the entire algal, zooplankton, and fish communities and did not find *Oscillatoria*. However, while he did depth specific samples, they were at 1m intervals which may not have overlapped *Oscillatoria*'s stratum in Demming. Therefore it is unclear when *Oscillatoria* became established in Demming. Likewise, it is not known whether 1981 was the first appearance of *Oscillatoria* in Arco, although two studies previous to the 1980 dissappearance of *D. pulex* did not indicate its presence in a dense stratum (Baker and Brooks 1971; Doolittle 1977). In addition to Arco, later research disclosed another association of the appearance of *Oscillatoria* and the disapppearance of a large cladoceran (again *D. pulex*). "K" Pond is a small (1.51 ha) shallow (maximum depth 3 m) pond which had for at least six years prior to 1983 contained a dense population of *D. pulex* (>500 *D. pulex* / 1). In 1982 algae in "K" Pond were monitored closely in connection with research concerning the pond's increasing eutrophication due to agricultural runoff. The 1982 the summer succession in "K" Pond was certainly eutrophic with *Anabaena* spp. appearing in early June and *Aphanizomenon* spp. (twice appearing suddenly in the grass blade form) representing the culmunation of the summer succession (personal observation). *Oscillatoria* was not seen despite frequent and extensive sampling. In 1983 *Oscillatoria redekei* was noticed in substantial numbers shortly after ice-off and *Oscillatoria* (var. Lyngbya) *limnetica* appeared later in the summer. For the first summer in at least six years *D. pulex* did not appear and the size distribution of "K" Pond's zooplankton community shifted toward the smaller end of a size spectrum (Table 1 and Figure 8).

In spite of the lack of experimentation and its "phenomenological" (Lynch 1979) nature, the 1981 survey and the Arco and "K" Pond events at least created an inference both for algal determination of zooplankton community structure and the involvement of *Oscillatoria*. Although a mechanism was not known at this point, these inferences played a large part in shaping subsequent research.

Most workers who have investigated the effect of various concentrations of filamentous blue-greens on zooplankters have used *Anabaena* filaments in laboratory conditions. Within the Minnesota

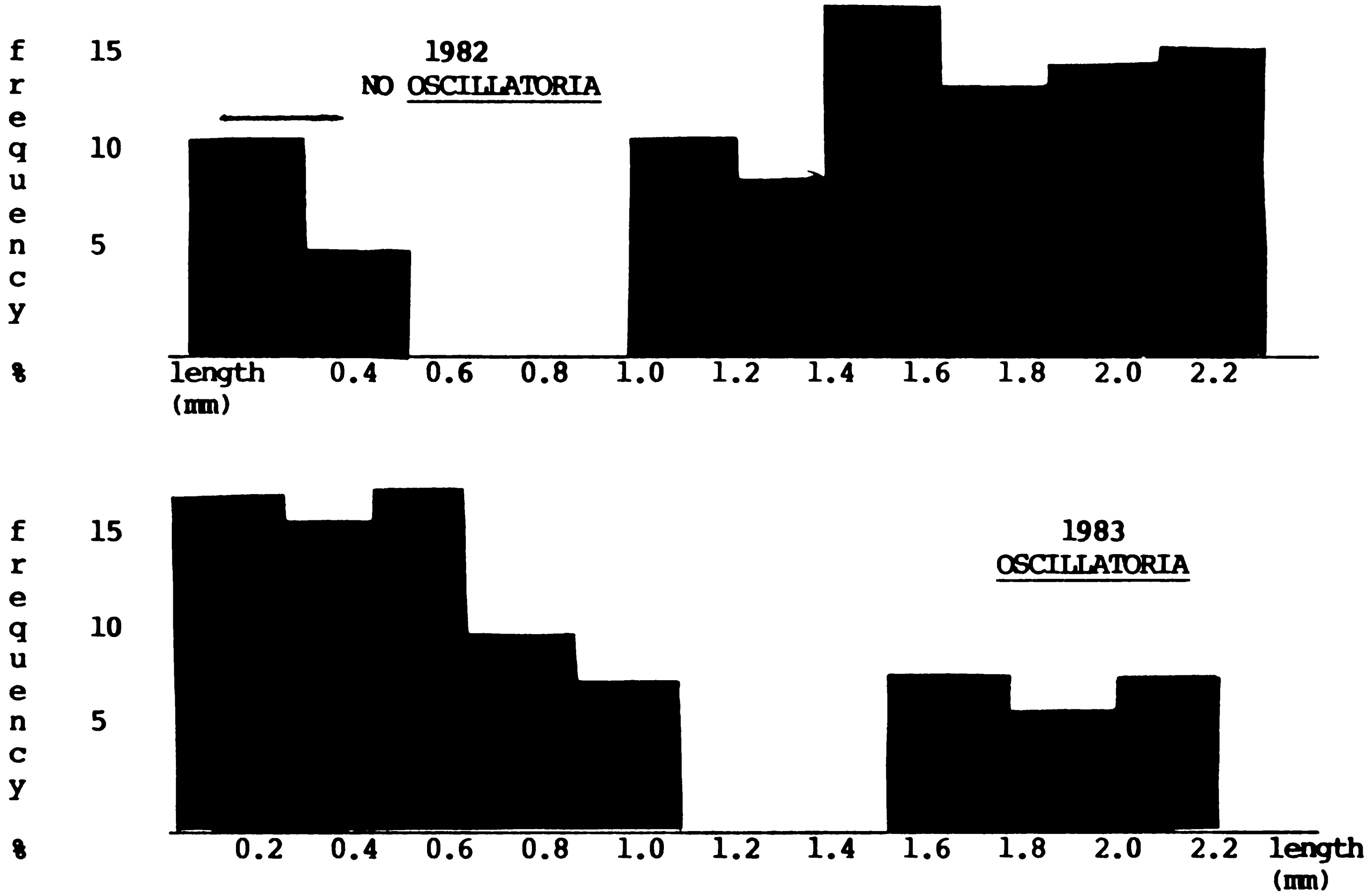


Figure 8. Size distributions of "K" Pond zooplankton communities before (1982) and after (1983) appearance of Oscillatoria.

lakes which are the subject of the instant study, several forms of *Anabaena* frequently occur. However, the occurrence of *Oscillatoria* is not only more ubiquitious (when in stratified form), but after *Anabaena* in successional sequence and more temporally correlated with zooplankton declines in those lakes in which declines have been documented (personal observation).

In spite of current uncertainties in blue-green taxonomy the distinction between *Anabaena* and *Oscillatoria* would certainly seem intact. More importantly the traditional taxonomic distinctions are central to ecological considerations *in situ*. *Oscillatoria*'s more pervasive tendency to form and collapse gas vesicles to regulate buoyancy, rise, sink and stratify in the water column is quite central to many of the aquatic ecosystems with which the instant studies are concerned. On the other hand *Anabaena*'s ability to form heterocysts, fix nitrogen, and sometimes produce toxins distinguishes it ecologically.

Within the genus *Oscillatoria*, however, the traditional taxonomy would seem in disarray. Virtually every morphological feature (trichome length, trichome width, shape of apical cell, etc.), upon which numerous species have been defined (see, e.g. Desikachary 1959, for a traditional treatment), has been suggested by those whose training has been in microbiology as a factor subject to environmental variance (Rippka et al. 1978). More importantly, there would seem little doubt that the traditional distinction between *Oscillatoria* and *Lyngbya* (presence or absence of a mucilaginous sheath) is often environmental variance (Carr and Whitton 1982). Later research indicated that Oscillatoria can exude mucopolysaccharides which can have a pervasive effect on certain zooplankton.

A Comparative Study of Potential Causes of Midsummer Declines - 1982

a. Methods

Selected small bodies of water were sampled throughout the summer to determine if midsummer declines occurred and, if so, in which bodies of water. These ponds and small lakes were chosen with two objectives in mind. The first was that each pond or lake have a different potential cause of midsummer decline. The second was that each of these potential causes be as isolated as possible. Specifically, ecosystems with a complex of potential predators, systems with complex morphometries (and the difficulty of sorting out littoral - limnetic interaction) and systems which contained both blue-greens and predators were avoided. A listing and summary of the predominant characteristics of each of the selected bodies of water follows:

Arco Lake is a small (1.39 ha) meromictic kettle (ice block depression) lake of high relative (7.67) depth (10.2 m) with no appreciable littoral zone and containing no vertebrate predators. One of the lakes in the 1981 survey, it contains a dense perennial stratified layer of blue-greens (Figure 5). It was chosen in an attempt to isolate stratified blue-greens as a potential cause of midsummer decline.

Josephine Lake (Z=10.3 m) is of similar origin and surface area (3.0 ha) to Arco and the only lake in the group with an appreciable littoral zone. Josephine is apparently meromictic or dimictic in some years and meromictic in others (personal observation). It was fishless with the possible exception of yellow suckers (Catostomers commersoni --a bottom feeding non-planktivore) during 1981. Like Arco, Josephine was surveyed in 1981 and is a stratified Oscillatoria lake (Figure 5). It was chosen due to its lack of vertebrate predators, the presence of Oscillatoria and the opportunity to sample both littoral and limnetic zooplankton. In addition, Josephine is distinguished from Arco by a long axis which sometimes aligns with the wind, a lower relative depth, and less shelter from surrounding hills and trees. As a result, Josephine's water column is more volatile than Arco's.

"K" Pond is of similar area (1.9 ha) to Arco and Josephine but of shallow depth (3.0 m) and highly eutrophic due to agricultural runoff. It was fishless during 1981 and 1982. "K" Pond was chosen because of its lack of vertebrate predators, hypertrophy and perennial series of blue-green blooms.

"L" Pond is about 2 ha in area, has a maximum depth of 2 m, and perennially contains a small population of adult Pimpales promelas (fathead minnows) at the beginning of the summer. In prior years juvenile Pimpales appeared in late June and appeared to reach a maximum at the beginning of July. It was chosen in an attempt to isolate a midsummer increase in a planktivore population in the absence of blue-greens. ("L" Pond is slightly acidic (PH 6-7) and has never contained blue-greens in appreciable numbers.)

For each of the two lakes (Arco and Josephine), vertical hauls of the entire water column were made at center lake every 48 hours at least two hours after sunset with a 0.5 m 64 micron mesh net. Five 5 ml Hensen "Stempel" pipette subsamples (with replacement) were counted (minimum 150 zooplankton per count) from each haul on each date to arrive at population density and relative abundance estimates. The procedure was identical for the two (shallower) ponds except that undulating instead of vertical hauls (length = 15 m) were made. For the one body of water with an extensive littoral zone (Lake Josephine), the littoral zone was sampled with funnel traps so that for Josephine there are estimates for both littoral and limnetic populations. Three sets of funnel traps (three funnels and bottles each) were deployed (6 m apart) on each sampling date over uniform Potamogeton sp. in Josephine's littoral zone. All animals in all nine bottles were counted to arrive at density and relative abundance estimates. The samplers were a modification of, and worked on the same principal as, the littoral patern sampler designed by Whiteside and Williams (1975). The modification was also designed by Whiteside and consists of three funnels (diameter 12 cm) supported in a triangular pattern (12 cm to a side measured from center funnel to center funnel) attached to a 0.5 m x 0.5 m x $^1/_2$" plexiglass sheet. Bottles atop the funnels were 250 ml clear plastic.

b. Results

Arco Lake. The Arco zooplankton community experienced a significant decline in the absence of vertebrate predators. Numbers of the only potential invertebrate predator (Chaoborus) were low at the time of the decline and disappeared during it (Figure 9, Table 3).

Lake Josephine. experienced a littoral decline but limnetic populations remained high well into mid August when sampling stopped. (Figure 9, Tables 4 and 5) The littoral decline occurred two days after the most severe storm of the summer with winds gusting to 60 mph. Transects of transmisometer profiles as well as depth specific samples both before and after the storm indicated disturbance of the Oscillatoria stratum and its presence in the littoral subsequent to the storm (Figure 10).

"L" Pond. After the usual spring buildup after ice-off, "L" Pond's zooplankton community remained remarkably stable through the summer and experienced no decline in total zooplankton despite a fairly dense swarm of young fatheads which first appeared on 1 July (Figure 9, Table 6). There was one significant decline in rotifers alone which may have been due to fathead predation.

"K" Pond. There was no decline in "K" Pond in the absence of predation and the presence of sufficient food (Figure 9, Table 7). Its zooplankton community in general (and a dense population of Daphnia pulex in particular) remained high without interruption into late August when sampling stopped. In addition, an early bloom of Anabaena and later bloom of Aphanizomenon flos-aquae were not associated with a zooplankton decline. What is interesting in this look at "K" Pond is that while those two blue-greens appeared and had no effect, Oscillatoria did not appear. (In a subsequent year Oscillatoria did appear with results discussed in the prior section: See Figure 8).

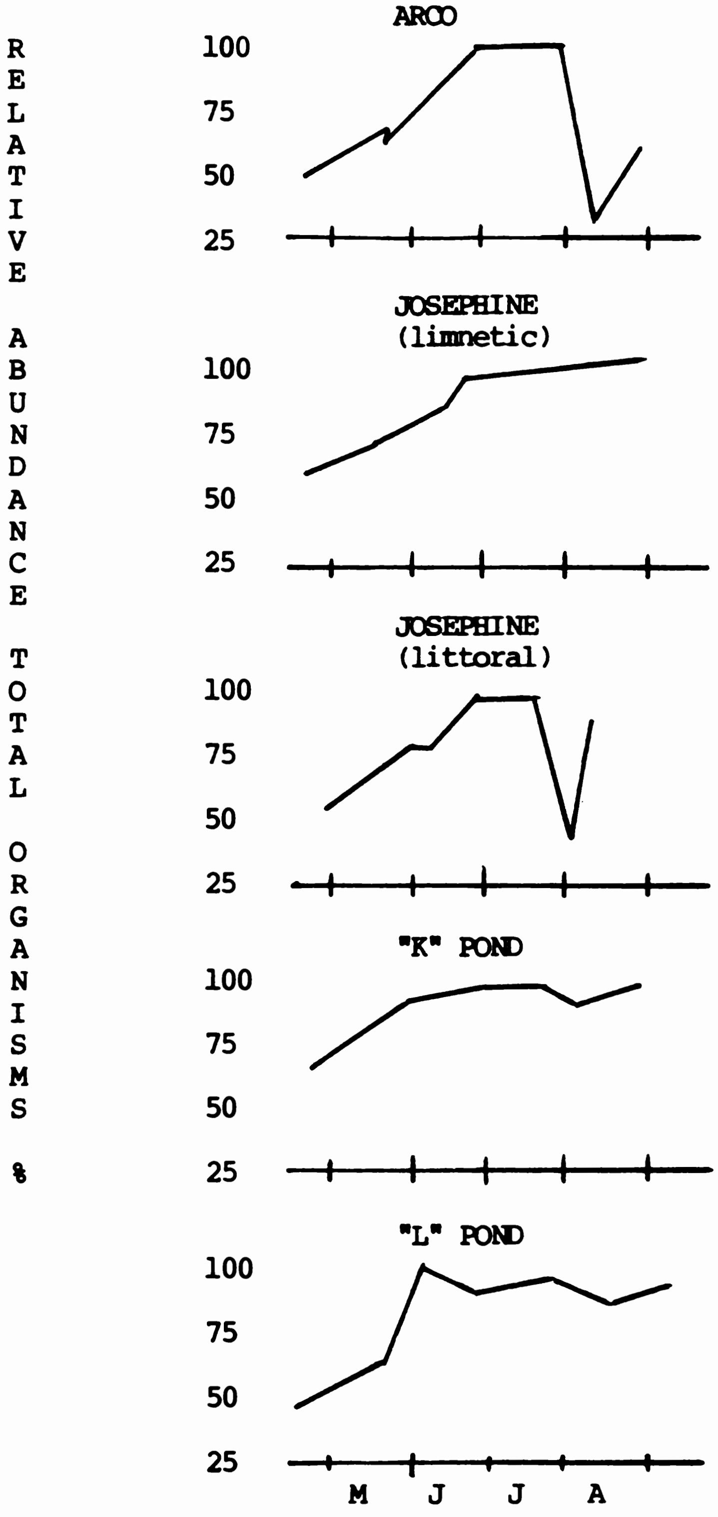


Figure 9. Comparison of summer population dynamics in the selected small bodies of water - 1982.

Table 3. Arco Lake zooplankton densites (organisms/m^3, with standard error of the mean based on ten counts) on selected representative dates (1982) by taxonomic grouping with principal representatives listed.

DATE	CLADOCERA (Ceriodaphnia lacustris)	COPEPODA (Diaptomus oregonensis)	ROTIFERA (Keratella, Asplanchna)	INSECTA (Chaoborus)	MISC. (Mites)	TOTAL
14 June	1,628	4,128	5,136	928	95	11,915
	571	1,027	1,578	92	43	3,528
1 July	1,752	4,638	5,328	865	83	12,608
	502	982	2,451	101	28	2,506
1 August	2,149	5,361	6,569	962	128	15,169
(p)	807	1,281	2,701	146	62	3,129
12 August	329	928	1,563	104	92	3,016
(1)	98	109	329	59	38	1,025
DIFFERENCE BETWEEN PEAK AND LOW						
Numerical	-1,299	-4,443	-5,006	-856	-36	-12,153
Percentage	-60	-83	-73	-90	-4	-80
t statistic	7.079***	10.903***	5.818***	17.230***	1.565ns	11.627***

* = Significant at .05 level ** = Significant at .01 level *** = Significant at .001 level ns = Not Significant p = Peak 1 = Low

Table 4. Lake Josephine limnetic zooplankton densities (organisms/m^3, with standard error of the mean based on ten counts) on selected representative dates (1982) by taxonomic grouping with principal representatives listed.

DATE	CLADOCERA (*Ceriodaphnia*, *Sida crystallina*)	COPEPODA (*Dioptomus oregonensis*)	ROTIFERA (*Keratella*)	INSECTA (*Chaoborus*)	MISC.	TOTAL
20 June	909	3,176	2,917	567	104	7,673
	211	1,238	603	59	36	2,109
1 July	1,575	2,904	4,327	925	125	9,856
	489	728	1,456	147	56	1,254
15 July	1,437	3,272	4,601	876	238	10,424
(p)	604	1,256	1,013	256	109	1,567
15 August	1,128	2,875	4,269	925	265	9,462
(l)	329	979	966	304	108	1,238
20 August	1,328	3,069	4,484	1,021	302	10,204
	511	1,156	875	404	156	9,256
DIFFERENCE						
Numerical	-309	-397	-332	+49	+27	-962
Percentage	-21	-12	-7	+6	+11	-9
t statistic	1.421ns	0.788ns	0.750ns	0.390ns	0.556ns	1.523ns

* = Significant at .05 level ** = Significant at .01 level *** = Significant at .001 level ns = Not Significant p = Peak l = Low

Table 5. Lake Josephine littoral zooplankton densities (organisms/m^2, with standard error of the mean based on nine counts) on selected representative dates (1982) by taxonomic grouping with principal representatives listed.

DATE	SEMIPLANKTONIC CLADOCERA (*Sida crystallina*)	CHYDORUS	COPEPODA (*Mesocyclops edax*)	AMPHIPODA (*Hyalella azteca*)	INSECTA (*Chironomus*)	OSTRACODA	TOTAL
14 June	3,049	6,277	1,865	649	528	967	13,335
	1,287	2,094	925	221	249	276	1,692
1 July	4,251	8,211	2,065	782	649	1,089	17,047
	1,349	3,265	1,062	165	301	512	1,785
15 July	4,563	9,120	3,457	989	947	1,245	20,371
(p)	1,621	3,928	1,237	305	565	629	3,401
28 July	301	122	229	331	990	145	2,116
(l)	116	109	115	227	519	100	638
15 August	3,782	7,540	2,963	829	928	836	16,878
	943	4,271	1,231	365	210	414	1,654
DIFFERENCE							
Numerical	-4,262	-8,998	-3,228	-658	-17	-1,100	-14,931
Percentage	-93	-98	-93	-67	-2	-88	-73
t statistic	8.293***	7.241***	8.217***	5.473***	2.641*	5.461***	17.011***

* = Significant at .05 level   ** = Significant at .01 level   *** = Significant at .001 level   ns = Not Significant   p = Peak   l = Low

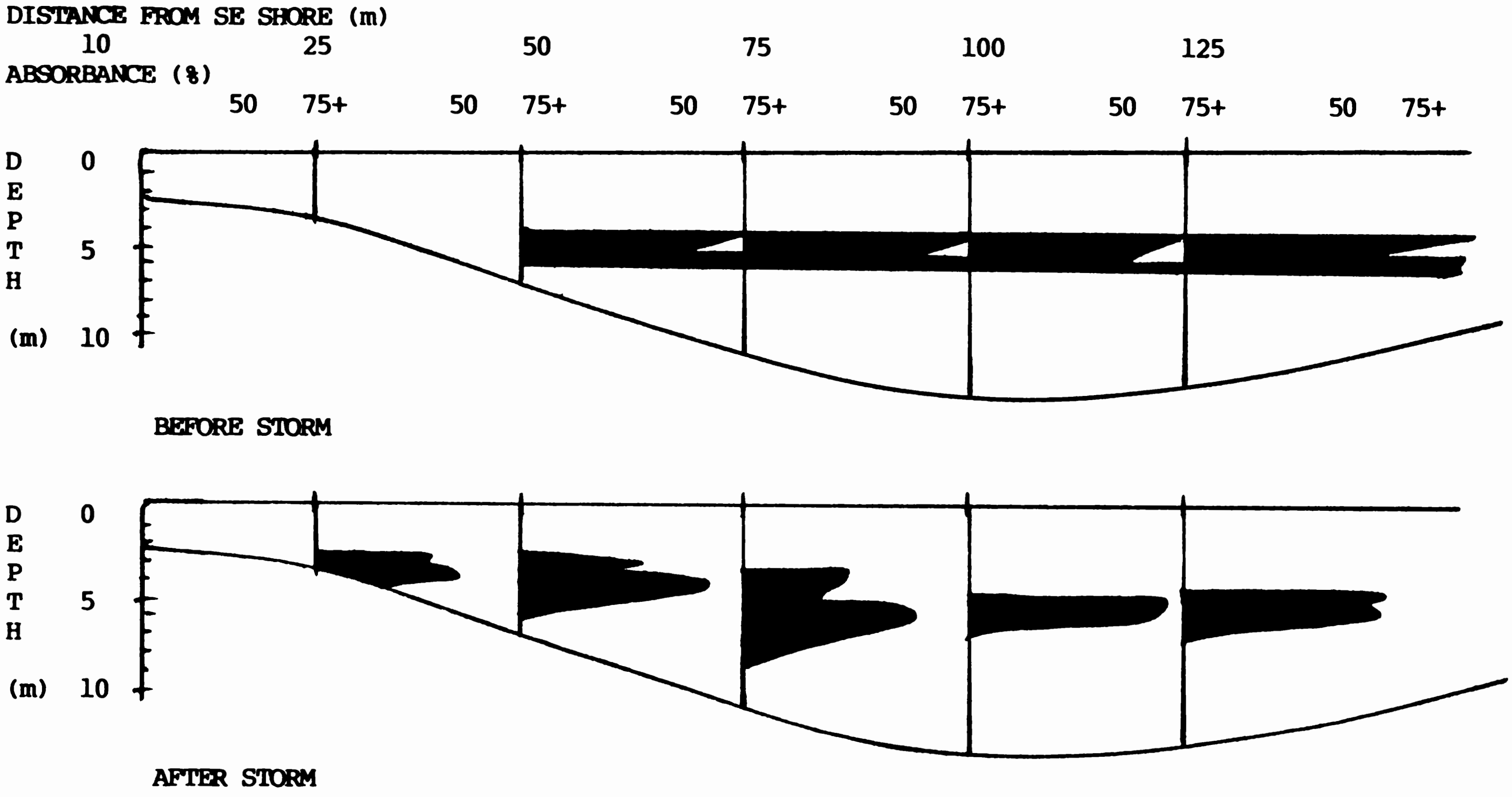


Figure 10. Comparison of optical density profiles and filament density in Lake Josephine before and after storm with severe winds.

Table 6. "K" pond zooplankton densities (organisms/m^3, with standard error of the mean based on ten counts) on selected representative dates (1982) by taxonomic grouping with principal representatives listed.

DATE	CLADOCERA (Daphnia pulex)	COPEPODA (Dioptomus clavipes)	ROTIFERA (Brachionus, Keratella)	INSECTA (Chaoborus)	TOTAL
14 June	50,272	17,678	35,229	8,042(p)	111,221
	12,084	6,081(p)	10,294	1,965	20,780
1 July (p)	51,102	15,845(1)	43,812(p)	6,543	117,302
	8,649	4,828	11,489	986	17,496
28 July (1)	48,987	16,489	33,067(1)	4,437	102,980
	10,482	5,750	8,648	1,238	23,622
1 August	50,078	16,254	36,019	4,525	106,876
	12,121	3,281	10,845	1,554	15,481
14 August	49,324	17,067	37,015	3,621(1)	107,027
	8,824	2,561	9,789	1,280	12,031
DIFFERENCE					
Numerical	-2,205	-1,833	-10,745	-4,422	14,322
Percentage	-4	-1	-25	-55	-12
t statistic	.492ns	.746ns	2.363*	5.963***	1.541ns

* = Significant at .05 level ** = Significant at .01 level *** = Significant at .001 level ns = Not Significant at .05 level p = Peak 1 = Low

Table 7. "L" pond zooplankton densities (organisms/m^3, with standard error of the mean based on ten counts) on selected representative dates (1982) by taxonomic grouping with principal representatives listed.

DATE	CLADOCERA (Daphnia pulex)	COPEPODA (Diaptomus clavipes)	AMPHIPODA (Hyallela azteca)	INSECTA (Chaoborus)	ROTIFERA (Keratella azplanchna	TOTAL
14 June	696	538	130	56	4,565	5,985
	225	316	25	22	555	1,289
1 July	729	638	165	120	5,218	6,870
	268	278	36	63	610	1,565
15 July	695	679	225	690	1,257	3,546
	129	228	41	225	229	1,041
1 August	710	692	229	120	4,029	5,788
	301	196	38	61	345	1,655
DIFFERENCE						
Numerical	-34	nd	nd	nd	-3,961	-2,242
Percentage	-4					-32
t statistic	.361ns				19.224***	5.441***

* = Significant at .05 level ** = Significant at .01 level *** = Significant at .001 level ns = Not Significant nd = No Decline

c. Discussion

The 1982 summer analysis of these four small and relatively simple bodies of water shaped later research in several respects. First, that there were indications of at least three potential causes of midsummer declines: food limitation (Arco Lake), predation ("L" Pond), and interaction with blue-green algae (Lake Josephine). Second, in addition to the cause of midsummer declines not being monolithic, it was apparent that one of the causes in itself was quite complex. "K" Pond experienced blue-greens in concentrations greatly exceeding those in Lake Josephine but in this case there was not a correlative zooplankton population decline.

Summary and Synthesis of the Comparative Studies

The survey of *Oscillatoria* and non-*Oscillatoria* lakes indicated that lakes with stratified *Oscillatoria* had zooplankton communities skewed toward the small end of the size spectrum. This skewedness was analogous to that Brooks and Dodson associated with alewives. The comparative study of midsummer declines further indicated a connection between stratified *Oscillatoria* and declines. Declines occurred in the two stratified *Oscillatoria* lakes (Arco and Josephine) but not in either "K" Pond (in spite of hypertrophy and successive blooms of cyanobacteria but not *Oscillatoria*) or in "L" Pond (absence of blue-greens). Neither of these comparative studies, however, delineated a causal mechanism by which *Oscillatoria* might eliminate larger species of zooplankton or affect a midsummer decline.

The studies did indicate that, if a mechanism exists: (1) it affects cladocerans and copepods alike, and (2) it affects both littoral (Lake Josephine) and limnetic (Arco) populations although not necessarily simultaneously in the same lake. The experimental studies which follow were intended to delineate both a mechanism by which *Oscillatoria* might affect zooplankton communities and further to discern the relative roles of predation and algae in structuring zooplankton communities within the context of midsummer declines.

V. EXPERIMENTAL STUDIES

Experimental Analysis of the Arco Lake Decline

In an attempt to eliminate or substantiate either food limitation or *Oscillatoria* (or both) as a cause of the midsummer decline which was observed in the absence of predation in Arco Lake in 1982, laboratory and in situ experiments were performed.

a. Methods

Filament counts (gridded membrane filter, changing average method described in section IVa) were made of water in Arco's upper 2 m and water from its 5 m stratified *Oscillatoria* layer during the midsummer decline of 1982. While the density at 5 m was in excess of 9,000 filaments per ml, *Oscillatoria* was not effectively present in the upper 2 m (an average of approximately 2 liters of water had to be filtered to encounter a filament).

Representative zooplankters (groups of 15 *Ceriodaphnia lacustris* and 15 *Diaptomis oregonensis*) were taken from Arco during the decline and introduced to each of the following treatments in gently aerated aquaria:

(1) Whole lakewater from the upper 2 m of Arco's water column.

(2) Whole lakewater from the upper 2 m of Arco's water column supplemented with a motile green alga (*Chlamydomonas* sp.).

(3) Whole lakewater from the 4 m *Oscillatoria* stratum in Arco.

(4) Filtered (0.45 micron millipore) lakewater from the 4 m stratum in Arco.

(5) Chlamydomonas supplemented filtered (0.45 micron millipore) lakewater from the 4 m stratum in Arco.

C. lacustris and D. oregonensis were chosen not only because they were representative cladocera and copepoda from Arco (Table 3), but because both species were visible to the naked eye and mortalities could be observed and removed with a pipette for microscopic examination without disturbing the surviving zooplankton. In addition to the laboratory aquaria treatments, two biomonitors (Schitling et al. 1974) were suspended in Arco at a depth of 4 m. One biomonitor contained 10 each of the representative species in distilled water. The other treatment was identical except that the distilled water was Chlamydomonas supplemented.

b. Results

While survival was almost 100% in the Chlamydomonas supplemented water from Arco's upper water column, there were no living cladocerans and copepods suffered 50% mortality after 72 hours in the unsupplemented water (Figure 11). There was 100% mortality in the 4 m whole lakewater whether it was supplemented or not (Figure 12) and yet 70% of the animals survived in the filtered and supplemented 5 m water (Figure 13). Eight of the original ten D. oregonensis and three of the original ten C. lacustris were alive and apparently unaffected after a week in the unsupplemented biomonitor. All ten of the original D. oregonensis and six of the original C. lacustris were alive and apparently unaffected in the supplemented biomonitor. Microscopic examination revealed Oscillatoria filaments

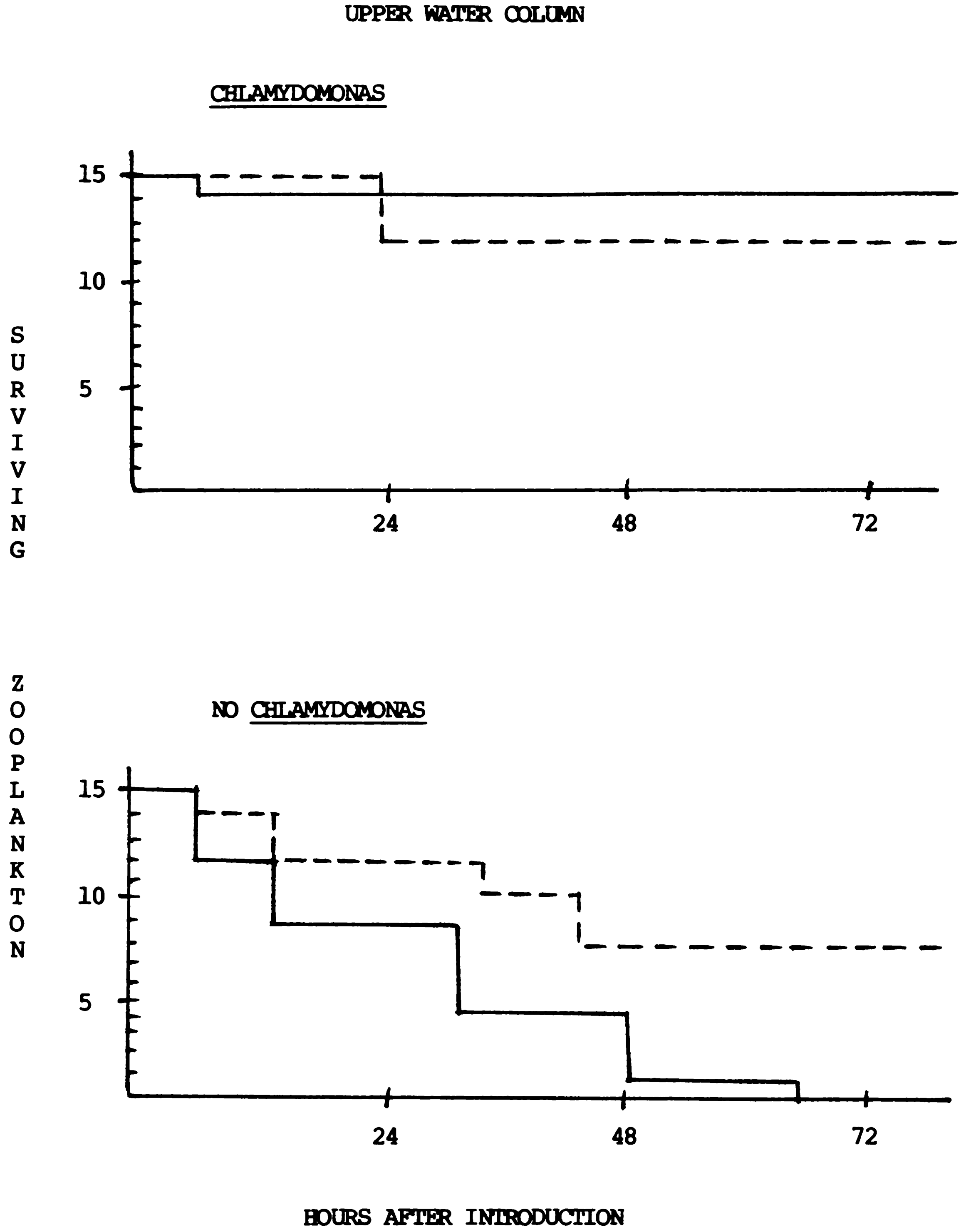


Figure 11. Survival of C. lacustris (——) and D. oregonensis (- -) in supplemented and unsupplemented whole lakewater from Arco's upper 2 m.

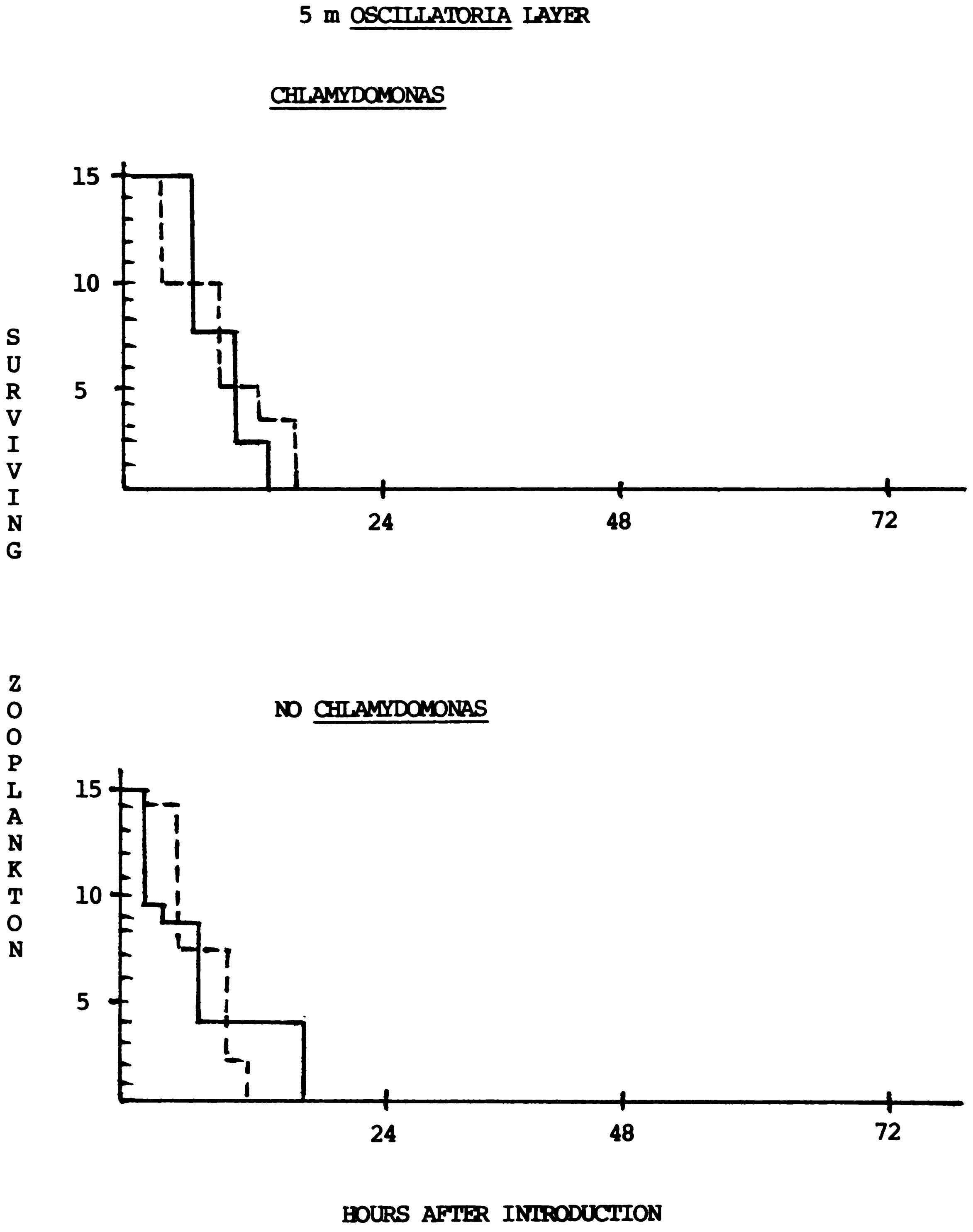


Figure 12. Survival of *C. lacustris* (——) and *D. oregonensis* (- -) in supplemented and unsupplemented whole lakewater from Arco's 5 m *Oscillatoria* layer.

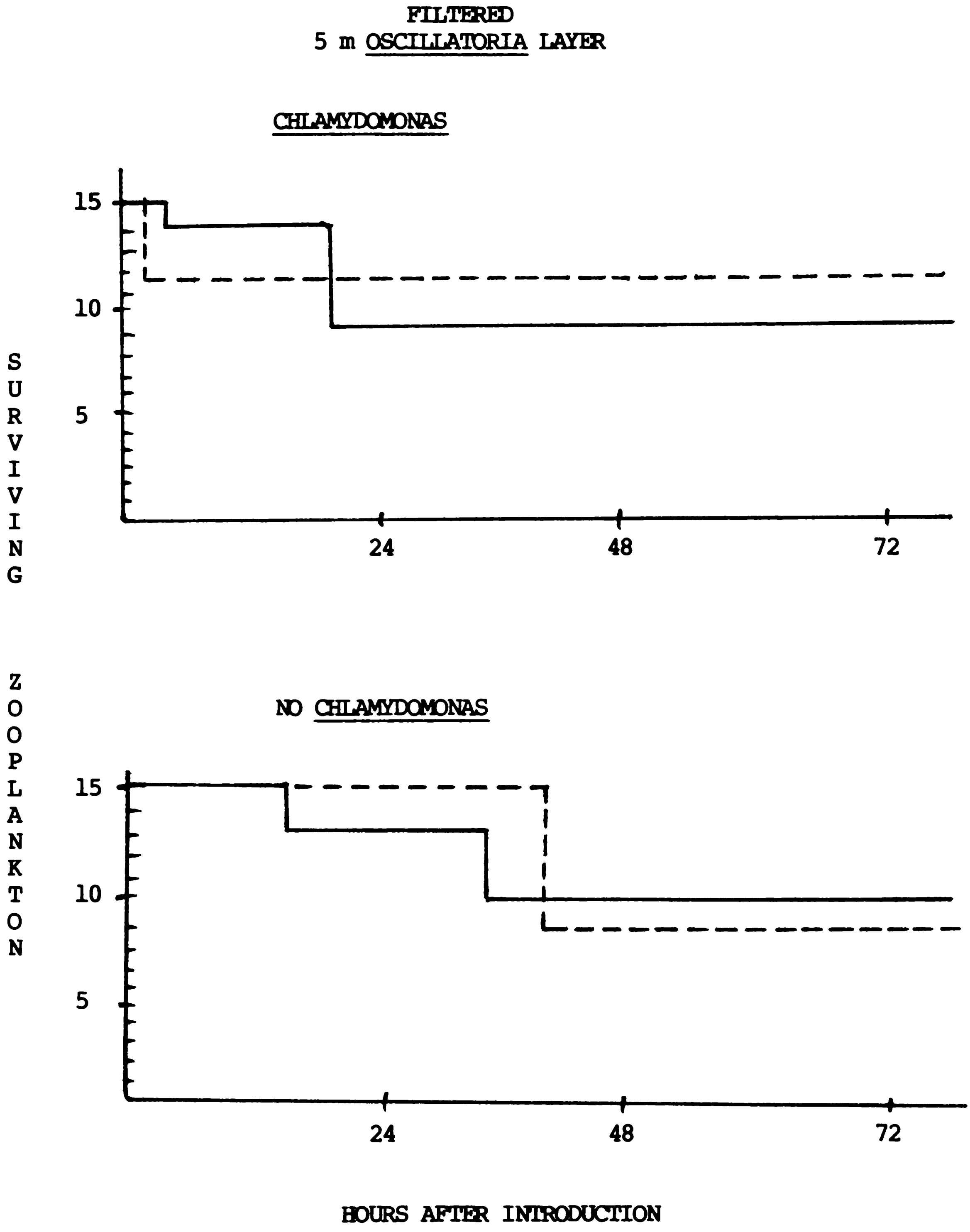


Figure 13. Survival of C. lacustris (——) and D. oregonensis (- -) in supplemented and unsupplemented filtered lakewater from Arco's 5 m Oscillatoria layer.

adhering to the filtering setulae of both *C. lacustris* and *D. oregonensis*.

c. Discussion

It is difficult to evaluate the significance of these initial experiments. The natural environmental conditions of planktonic stratifying blue-greens are notoriously difficult, if not impossible, to duplicate in the laboratory. *In situ* stratification by the device of gas vacuolization is a complex response to nutrients low in the water column and available light in the upper water column (Klemmer et al. 1983).

When placed in aquaria in the lab *Oscillatoria* is undoubtedly subject to drastic environmental change in spite of attempts to duplicate temperature and light conditions. Natural nutrient flux is virtually impossible to duplicate because of the complex interaction of meromictic Arco's anoxic sediments, a bacterial layer and the algal layer. However, there would seem little doubt that under some conditions, the filaments are capable of causing significant mortality to both *C. lacustris* and *D. oregonensis* (Table 12 and 13). The mechanism is apparently filamentous *Oscillatoria*'s interference with filtering setulae. In view of later experiments (see below), the mortality experienced by those two species in the laboratory was at least partially due to physiological changes in *Oscillatoria* upon removal from the lake. The biomonitor experiments would also indicate that the mechanism is not a toxin but more probably a compounded effect of *Oscillatoria*'s clogging of filtering apparata and food limitation (Figure 11). Not only is there the increased energy expended in trying to reject the filaments but less food is able to enter. In addition there is less algae of a palatable variety present when Oscillatoria predominates in situ.

Why a midsummer decline? Oscillatoria stratifies shortly after ice-off and declines rarely occur before 1 July. The most immediate explanation would be a combination of food limitation usually occuring late in summer (due to less frequent rain and therefore reduced allochthonous nutrient influx) and zooplankton as a result migrating or sinking (either diurnally or otherwise) deeper in the water column to obtain food and encountering Oscillatoria. A simpler and more plausible explanation would be physiological changes in Oscillatoria itself which increase its tendency to adhere. Procaryotic cells in general are known to adhere in circumstances of nutrient limitation although the mechanism is not well understood (Lewin 1984). It is this possibility which the following experiment was designed to examine.

In Situ Evaluation of Oscillatoria's Tendency to Adhere

The Lake Josephine littoral decline, the Arco limnetic decline, and laboratory experience with Oscillatoria raised an inference that the cyanobacterium increased its tendency to adhere to surfaces: (1) as middle or late summer approached, and (2) as it was moved out of its preferred stratification. A biochemical explanation of exocellular mucopolysaccharides was beyond the scope of a study aimed at algal - zooplankton interactions. However, a simple field test of the two pronged inference was performed:

a. Methods

(1) At the beginning of each of seven successive weeks, gridded glass plates were suspended at 5 m depth in Lake Josephine's stratum of Oscillatoria for one week. At the end of each week the plates were removed and filaments adhering to the plates per cm^2 were microscopically estimated by changing average counts. Each of the successive weeks was begun with fresh glass plates so that the estimates were of filaments adhering per cm^2 per week.

(2) In addition, at the beginning of each of the seven weeks whole lakewater from the 5 m layer was pumped into biomonitors (in which gridded glass plates were suspended) and the biomonitors suspended at depths of 4 m, 3 m, 2 m, 1 m, and 0 m (top surface of biomonitor in contact with surface of the lake). At the end of each of the weeks, the plates were removed, filaments counted, and biomonitors cleaned of all filaments and the process repeated.

b. Results

There was a tendency for filament adherence to increase both as the summer progressed and with distance removed from preferred depths of stratification (Figure 14).

c. Discussion

In spite of the primitive state of our understanding of the

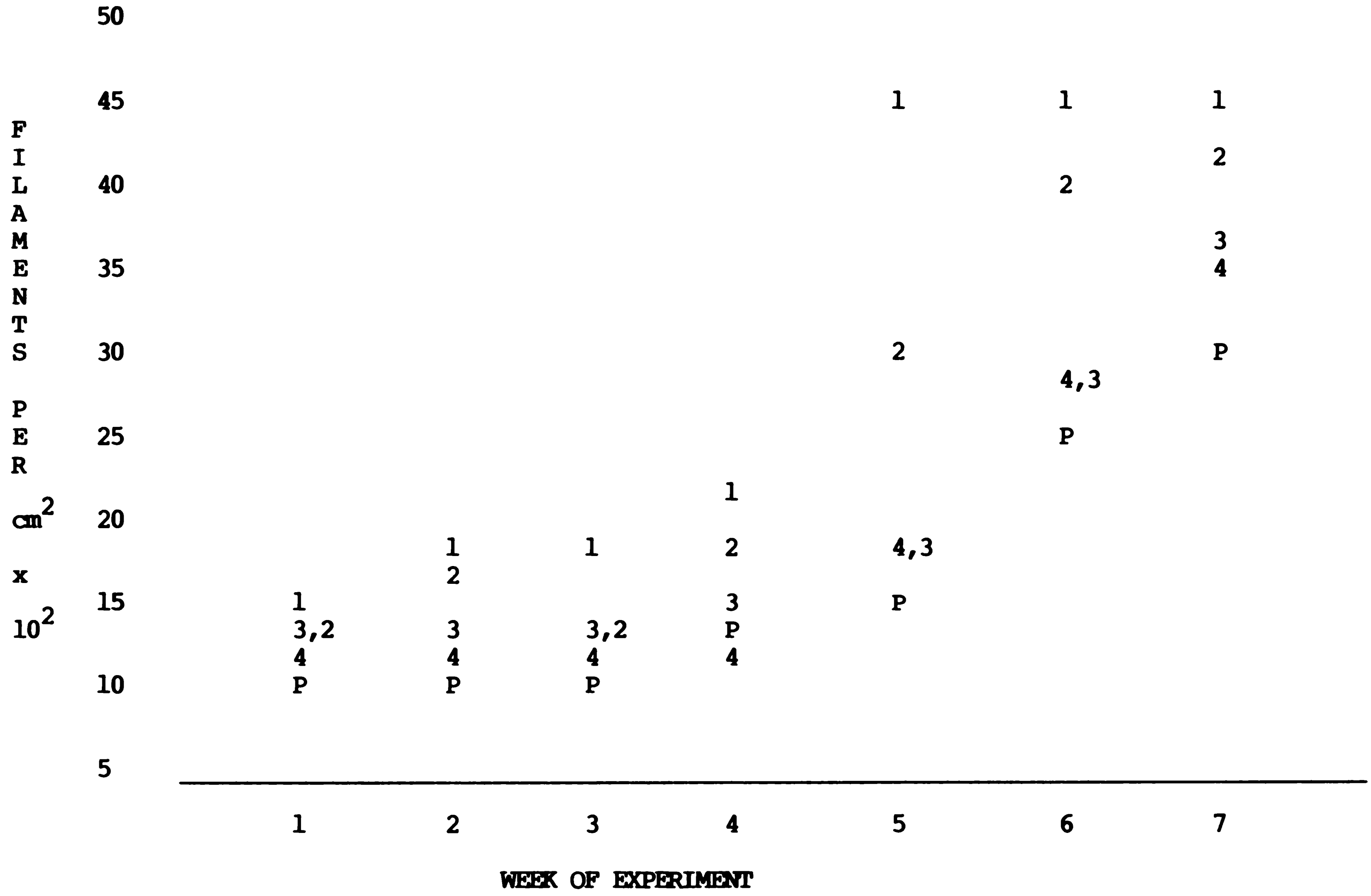


Figure 14. Adherence of <u>Oscillatoria</u> (filaments per cm^2 per week) at its preferred depth of stratification (p) and upon removal to depths of 4, 3, 2, 1, and 0 m in seven successive weeks in midsummer.

biochemistry and ecological role of the production of exocellular mucopolysaccharides, the results of this experiment are striking and may hold the key to understanding the mechanism of Oscillatoria's role in midsummer declines. Future research aimed at separating the effects of increased light and altered nutrient flux when Oscillatoria is removed from its preferred stratum should be quite useful to attempts at biomanipulation. For example, such knowledge would allow prediction as to whether early summer (or even winter) artificial mixing of a lake (Shapiro 1975) might lead to increased water clarity as well as a preferred alteration of the trophic state of a given body of water in mid or late summer. However, this experiment would indicate that it is very unlikely that filter feeding zooplankton could affect that result once a significant biomass of Oscillatoria is established in midsummer.

The Lake Josephine Predation Experiments

Lake Josephine was fishless when it was sampled in 1981 (Table 1, Figure 3). A dense population of fathead minnows (Pimpales promelas) appeared in the lake in the spring of 1982.

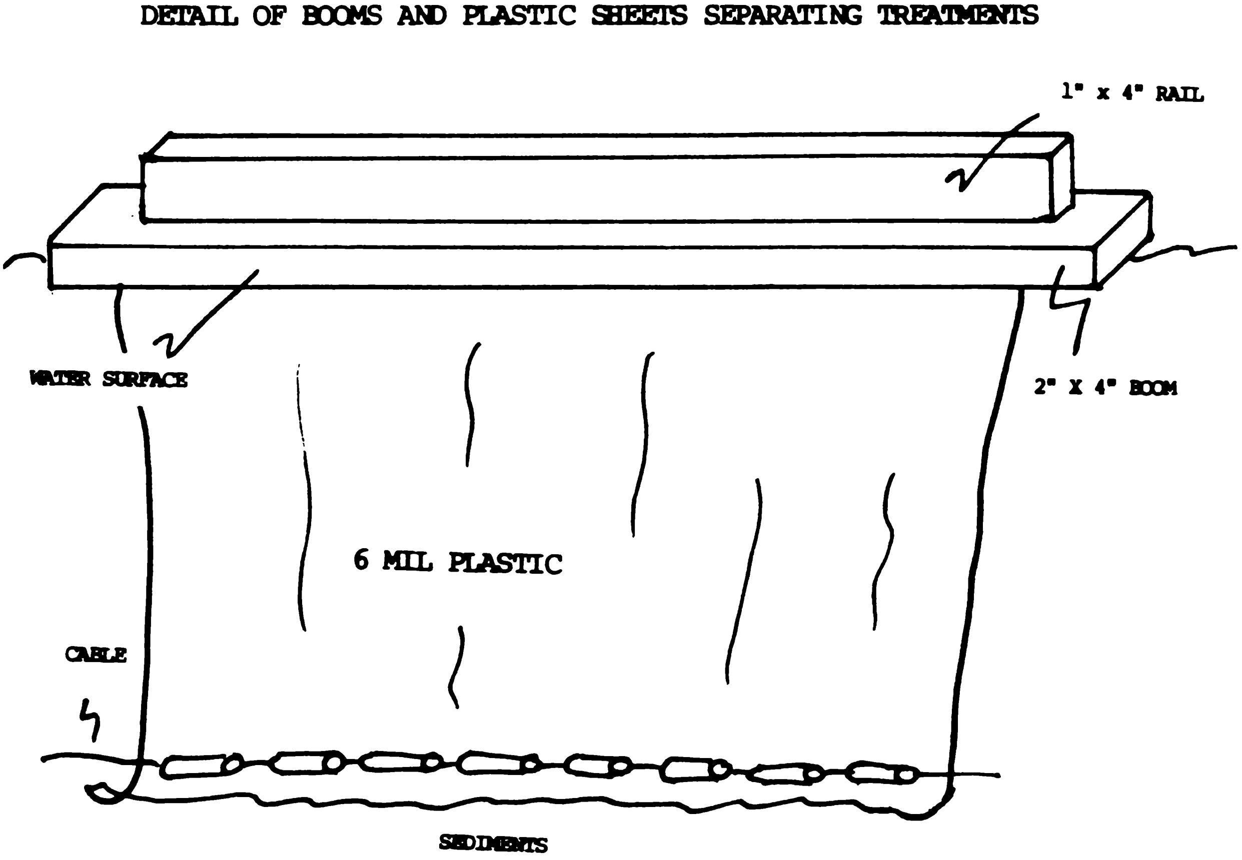
Pimpales is known for its hardiness and ability to withstand low O_2 concentrations and for being extremely prolific. The minnow was widely introduced at one point by the Minnesota Department of Natural Resources as a substitute for DDT in mosquito control. The appearance or introduction of Pimpales has been reported by several workers as restructuring zooplankton communities (see discussion in Zaret, 1980).

Pimpales' appearance in Lake Josephine not only provided us with the opportunity to compare 1981 and 1982 zooplankton communities in Josephine, but the incipient population of Pimpales was so dense (initial seining of one small inlet netted in excess of 4,000 minnows) that there were more than enough readily available potential predators to run large scale enclosure - exclosure experiments to evaluate the effect of predation upon the Lake Jpsephine's littoral zooplankton community.

a. Methods

Four treatments and a control were placed in the lake over uniform Potamogeton sp. by enclosing sections of littoral zone with 6 mil clear plastic floated on wooden booms at the surface and anchored in the sediment with cable strung through cylindrical concrete weights. Each of these five compartments contained approximately 1,250 m^2 of littoral zone. The structure of the compartments as well as their general location in Lake Josephine is depicted in Figure 15.

Each compartment was seined after partitioning. The compartments were then treated as follows: No fish were returned to compartment one. What was perceived from the initial seining as the average density for the lake littoral zone was returned to the "control" (1,250 minnows, or approximately one minnow per m^2 of littoral zone). Twice that (2,500 minnows, or two minnows per m^2 of littoral zone) were placed in compartment two, 3,750 minnows were placed in compartment three, and 5,000 minnows in compartment four. Zooplankton in the four treatments, in the control, and the lake littoral itself



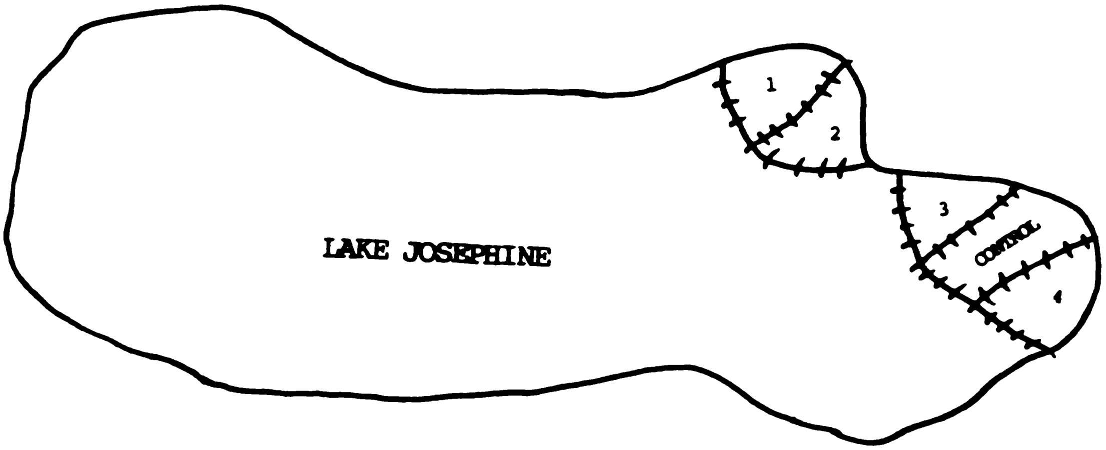


Figure 15. Sketches depicting construction and arrangement of treatments in Lake Josephine.

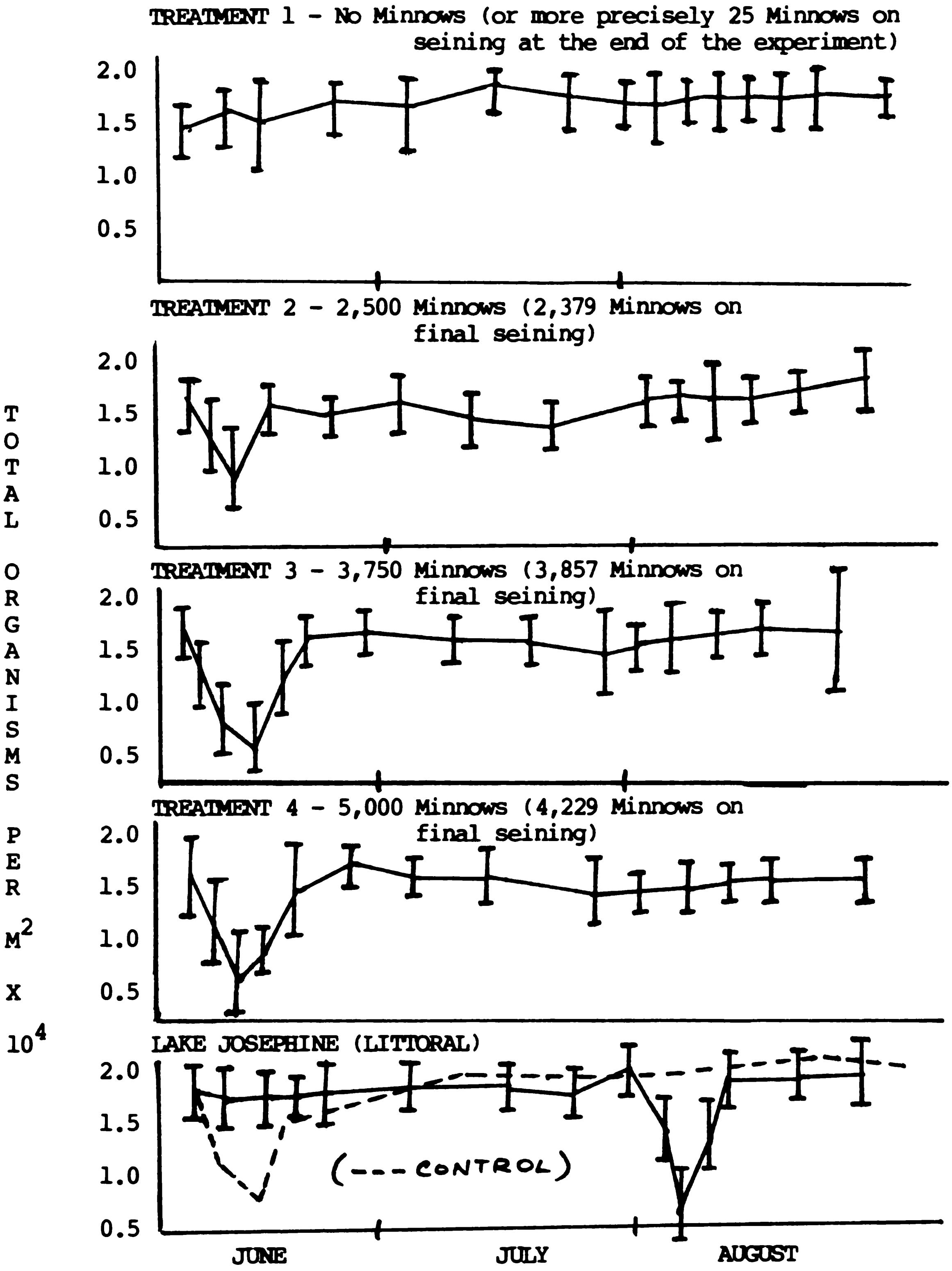
were sampled every 48 hours. Four littoral funnel traps (described in section IV above) were used for each treatment on each sampling, and animals were counted as the experiment progressed. Gut analyses of minnows from all treatments, the control and the lake were done at two times described below.

b. Results

Initially, as expected, populations fell in all but the fishless treatment. Unexpectedly the control fell as well and the fishless treatment did not rise. By two and one-half weeks into the experiment, however, all treatments had populations within + or - 4% of the lake itself (Figure 16).

Gut analysis of fifty minnows from the lake at the outset of the experiment indicated *Pimpales* was consuming both plankton and epiphytic algae in roughly equal proportions by volume. *Pimpales* did not appear to be ingesting sediments at this point. Gut analyses of twenty-five *Pimpales* from the control and each of the treatments after populations had fallen and then returned to their original level revealed the minnows' diet to be almost entirely epiphytic algae and ingested sediment. Identifiable zooplankton carcasses constituted far less than one percent of the wet weight of all contents examined. However, minnows in the lake itself (not enclosed) were still consuming equal proportions of zooplankton and epiphytic algae.

Seining at the end of the experiment indicated that *Pimpales* populations in all treatments and the lake were within 15% of their initial levels although some minnows had sloshed or jumped over the



TREATMENT 1 - No Minnows (or more precisely 25 Minnows on seining at the end of the experiment)

TREATMENT 2 - 2,500 Minnows (2,379 Minnows on final seining)

TREATMENT 3 - 3,750 Minnows (3,857 Minnows on final seining)

TREATMENT 4 - 5,000 Minnows (4,229 Minnows on final seining)

LAKE JOSEPHINE (LITTORAL)

Figure 16. Littoral zooplankton density estimates (total organisms/m^2 x 10^4) with standard error of the mean from twelve counts in Lake Josephine, the control and four treatments - 1982.

booms and the herons (personal observation) obviously could recognize treatment #4 as containing the densest population of minnows.

By far the most striking aspect of the Lake Josephine experiments, however, was that the littoral population in the lake experienced a midsummer "crash" while those in the enclosures did not (see Figure 16). Again the blue-green *Oscillatoria* was implicated. Not only did the decline follow a storm and suspected seiche as in 1981, but *Oscillatoria* was found in Josephine's littoral zone and not within the plastic treatments. In addition, the plastic enclosures, taken out several weeks after the crash, had *Oscillatoria* adhering to the outside (lakeside) but not the treatment side.

c. Discussion

The Lake Josephine experiments indicated that greatly increased (or decreased) predator density did not "restructure" or more than temporarily affect littoral zooplankton at the level one finds in that lake. The fact that zooplankton in the littoral zone of Josephine did not rise when a heavy density of potential predation was removed indicates that predation was not initially "structuring" that community. And when the density of potential predators was quadrupled without ultimate effect one has to begin to at least question the whole notion of structure by predation. A comparison of pre and post *Pimpales* introduction to limnetic zooplankton populations merely adds emphasis to that question (Figure 17).

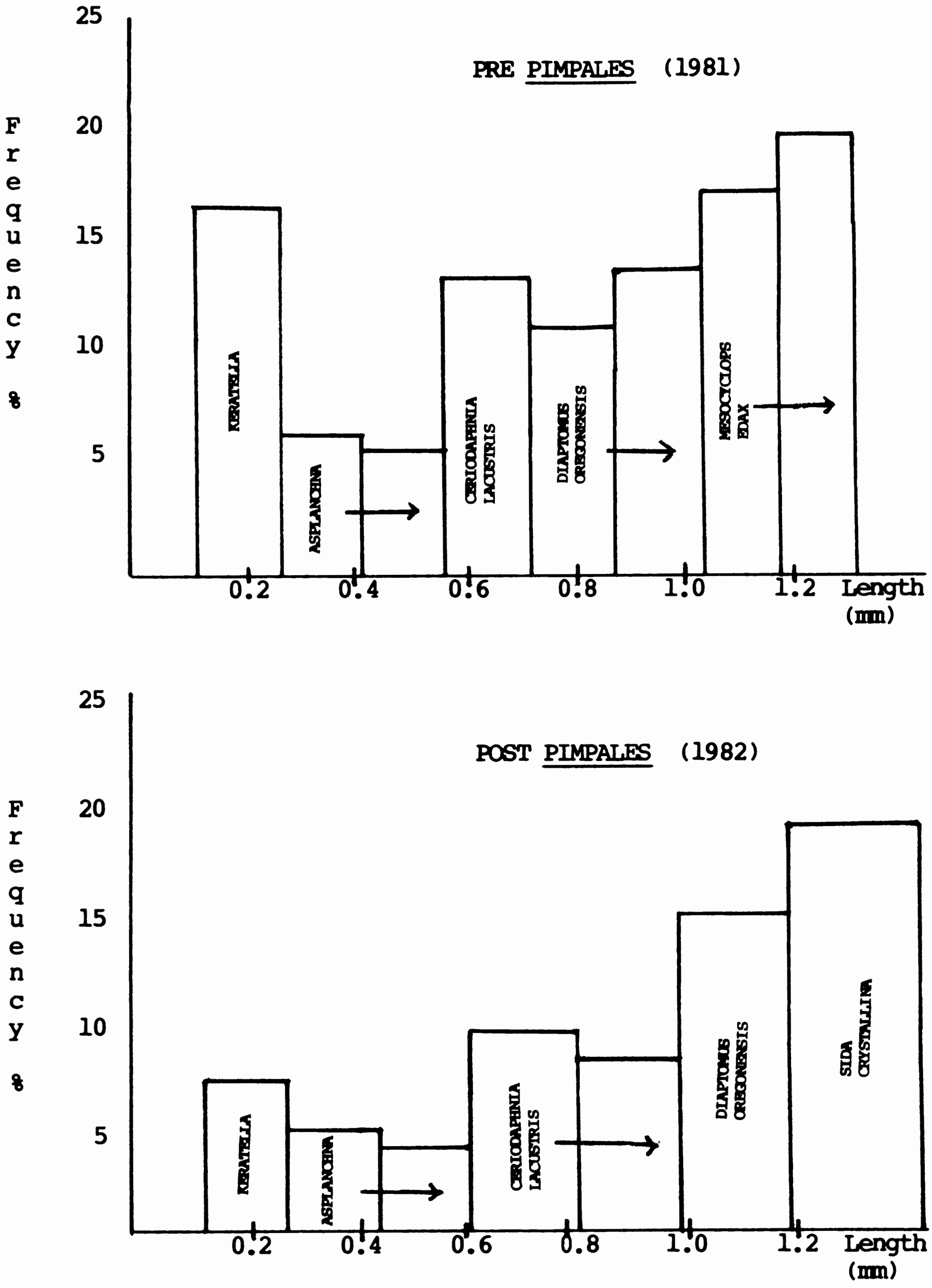


Figure 17. Comparison of pre (1981) and post (1982) Pimpales introduction zooplankton communities in Lake Josephine.

While increasing predator density did not have an ultimate effect, it did cause an initial drop until the treatments returned to their original levels. This is, in general, the pattern of a midsummer decline. In-shore migration of larval perch (which, unlike Pimpales, are gape limited to zooplankton) is a heavy increase in predator density and it has at times coincided with a temporary population decline. The Lake Josephine enclosure drops should be kept in perspective, however. They differ from Lake Itasca declines in at least three respects. The declines were slower (almost two weeks compared with the two or three day "crash" in Itasca). Secondly, the biomass drop in Itasca is fully a minimum of ten times that which occurred in the Josephine exclosures. Thirdly, although the density of larval fish in Itasca is not known, it is unlikely that it approaches, either in biomass or numbers, that of Pimpales in the Josephine enclosures.

In addition to the initial declines in the enclosures in which Pimpales density was increased, a decline of almost the same magnitude was observed in the control (Figure 16). This may indicate a treatment effect even in enclosures as large (1,250 m^2) as those in Lake Josephine. It should be recalled that most of the experimental studies upon which the predation hypothesis is based have utilized enclosures of only a few m^2 in area and have relied upon a single sampling of zooplankton.

Lastly, it needs to be reemphasized that, while they were otherwise fruitful, the most significant effect of the Lake Josephine treatments was the unintended one of excluding Oscillatoria from a portion of the littoral zone and thereby ostensibly preventing a midsummer decline. It was this discovery which shaped the subsequent Lake Itasca experiments.

The Lake Itasca Experiments

Lake Itasca, Minnesota (Figures 3 and 4) is naturally eutrophic with fully 55% of its area estimated as littoral zone (Cole and Underhill 1965). Described as a "hard carbonate" lake (Moyle 1945), it has an estimated gross productivity of 1.24 g $C/m^2/d$ and net productivity of 0.44 g $C/m^2/d$ (Megard 1968). Cole and Underhill have also estimated its average benthic standing crop as the third richest in North American freshwater lakes (4.5 g dry weight/m^2 across the sublittoral and profoundal zones).

An analysis of algal, zooplankton, and planktivore roles in Lake Itasca is more difficult in several respects than in any of the smaller, less complex bodies of water so far addressed. In addition to its higher productivity and greatly increased diversity at all trophic levels, its extended littoral zone and relatively unprotected two mile length make for a much more volatile water column even after summer stratification. In contrast to stability (Arco and Demming Lakes) in the face of a storm with severe winds or even a seiche which brings limnetic algae into the littoral zone (Lake Josephine), Lake Itasca has been observed to completely overturn even in midsummer (Baker and Brooks, 1971). Lake Itasca experiences midsummer declines of zooplankton both in the littoral and limnetic although limnetic declines may not occur every year (M.C. Whiteside pers. comm.).

Maximum littoral declines of the order of 500,000 animals per square meter have been documented (Doolittle, 1982) (Lake Josephine experiences maximum declines of the order of 30,000 animals per m^2).

The regularity and magnitude of Itasca's midsummer littoral decline (as well as the great diversity of zooplankton involved) has led to its being the most studied decline in North America. Itasca's littoral decline has invariably been ascribed to predation:

1.

Williams's (1978) study attempted to eliminate the possibility of any "chemical" cause of the crash by use of biomonitors. By Williams's description: "Biomonitors are clear plexiglass, 500 ml chambers which utilize membrane filters to cage organisms within the natural environment. The selectivity of the membranes permits the transfer of some ions and some molecules but not bacteria. The physical - chemical conditions inside the Biomonitor equilibrate with the surrounding lake waters within 12 hours (Schliting et al., 1974)." The biomonitors, due to their membrane enclosed ends, would have excluded not only bacteria but also algae. The fact that populations rose in the biomonitors at the same time lake populations fell, supports rather than negates, an hypothesis of algal cause.

2.

Williams (1978) and Doolittle (1982) both offer the observations that birth rates determined by egg ratios do not decline, and that no ephipial eggs are present during midsummer crash, as support for a predation hypothesis. Laboratory experiments show blue-green toxins may act very quickly and the Lake Josephine experiments show that a considerable increase in density in filament concentration can occur in several hours of high winds. An algal caused decline would not necessarily affect egg ratios or cause ephipial eggs.

3.

Doolittle's conclusion (that the cause of the littoral decline is YOY perch predation which migrate from mid-lake to the littoral zone in midsummer) is based upon the use of submerged exclosures constructed of 1 m^3 frames covered with 6 ml clear plastic on four sides and screened on the top. Their small size allowed only one sampling. Because the plastic would have greatly reduced water circulation and therefore infusion of phytoplankton as well as provided a surface for nutrient starved cells to adhere to, the timing of sampling would have been extremely critical and perhaps the treatment effect was to prevent the crash. The key to a definitive answer as to the cause (or causes) of the midsummer decline lies in the use of larger enclosure - exclosures.

In general the problems with small enclosures are sampling and treatment effects. The problems with large exclosures are the physical ones of putting them in place, of clearing out fish initially, and of designing the equipment so that its integrity be maintained for the duration of the experiment. No large exclosure has yet confirmed the hypothesis that predation causes the decline. The two years a large exclosure was attempted in Itasca the supposedly protected population (from fish, not blue-greens) crashed almost contemporaneously with that in the lake (Doolittle, pers. comm.).

4.

The quickness with which most midsummer declines rebound might be evidence that blue-green interactions are involved. The chemical dissipation or loss of buoyancy of the population could occur quite quickly, whereas YOY yellow perch are known to remain in the littoral for the rest of the summer. The fish have no ostensible reason to relax predation pressure until they grow to a size at which the taking of larger prey becomes possible.

5.

The shoreward migration of YOY perch, even without its causal or even temporal correlation with the decline of littoral zooplankton, is a striking and interesting phenomenon. Like the littoral crash, the migration is rapid with the bulk of the population making the shift from open water to the littoral in a matter of days. As potential causes of the migration, it would seem that an increase in predation or a dwindling of food resources would likely be a more gradual phenomenon. In contrast algal blooms are by definition rapid. An algal phenomenon is not inconsistent with either of the known phenomena but, in fact, may be explanative of both.

6.

An intriguing part of Doolittle's data is his finding that the size structure of the zooplankton community was significantly different before and after the midsummer crashes of 1979 and 1980. The 1981 differences were not significant.

Based on Werner's (1974) finding that "the optimum prey is 0.59 times the mouth size of the fish" (perch coming inshore at approximately 20 mm length), Doolittle concluded that heavier losses in the smaller categories suggested predation by perch. He could not explain a greater loss in the smaller categories of ostracods (not eaten by perch). In addition, the losses were proportional in all categories (the smaller categories were simply originally more numerous). These results might just as easily be explained by an algal event, especially in view of Porter's (1984) showing that blue-green filaments have a greater respiratory and rejection cost to larger cladocerans.

a. Experimental Design

The Lake Itasca work had two aspects:

(1) Our first objective was simply to monitor zooplankton and the two potential causes of midsummer decline to see if, on the basis of temporal coincidence, one of the causes could be eliminated and the other confirmed. If littoral zooplankton declined before, or considerably after, inshore migration of perch, that would be a strong inference they were not the cause of the decline. On the other hand, if the decline coincided with an algal bloom, that would be a strong inference that the bloom was the cause.

(2) The second objective was to attempt to place two treatments

in the lake, one shielding a representative littoral zooplankton population from fish and the other from algal blooms. If one, and only one, of the protected populations remained at high level while populations in the lake as a whole fell that would be a strong indication that either predation or algae was the primary cause of the decline.

b. Methods and Materials

Two treatments were placed over a large uniform bed of Chara in Lake Itasca. The treatments were constructed of commercial $^3/_4$" polyvinyl chloride (PVC) frames (using altered commercial plumbing fittings) which were 3 meters to a side (covering 9 m^2 of the substrate Chara) and of sufficient height to clear the lake surface in approximately 2 m of water. In treatment #1 (the "net treatment") the PVC frame was covered with $^1/_{16}$" nylon mesh anchored in the sediment with cable and cylindrical concrete weights. Treatment #2 (the "plastic treatment") was identical except 6 mil clear plastic was substituted for netting.

Both treatments were initially cleared of fish. Previous experimenters had experienced difficulty in seining due to fish escaping either under the seine into the Chara substrate or around the seine between its ends and the exclosure. This problem was solved by mounting the seine on a specially constructed PVC frame. The frame was outlined with $^1/_{32}$" diameter holes (facing outward) on its bottom three sides and was pressurized (100 lbs./in^2) via an on board air compressor. The jets of air were quite effective in clearing fish out of the Chara and keeping them in front of the seine and away from its sides.

Zooplankton were then sampled every 48 hours in the two treatments and the lake using funnel traps (described in section IV). A variety of methods were used to simultaneously sample algae in the two treatments and the lake. While, with hindsight, the most expeditious method was to count filaments of Oscillatoria adhering (per unit time) to glass plates suspended at the Chara-water interface other equipment was used to monitor algae and track the initiation and senescence of blooms in the vicinity of the treatments: A Van Dorn sampler, a depth specific sampler, and the device of sending a diver to open sampling bottles at specific areas or depths.

Crude sediment traps were monitored daily in the two treatments, the limnetic, and the littoral zone to determine if animals were falling out of the water column. Traps consisted of 6cm diameter glass funnels stoppered at the narrow end and covered at the wide end with a special plastic fitting (a coffee can lid) until put in place by a diver. The funnels were then uncapped when in position and capped before removal for inspection and analysis.

In addition to the work being done in the lake, zooplankton populations representative of the limnetic and littoral populations were set up in aquaria in the University of Minnesota lakeside laboratory. Lake water (both filtered and unfiltered) from various depths in the limnetic and littoral was introduced on several dates to these populations and zooplankter movement, respiration, carapace gape and survivorship observed.

c. Results

Young of the year (YOY) yellow perch (to whom the decline had previously been attributed) migrated inshore on 2 June. Littoral zooplankton experienced two sharp declines (or "crashes"): one on 8 - 10 July and one on 20 - 22 July. Limnetic cladocerans (mainly Daphnia galeata) experienced a sharp decline on 24 July. All three of these declines were more closely associated with the presence of Oscillatoria than larval perch. Transmisometer profiles and sampling indicated the existence of a dense (maximum density > 6000 filaments per ml) stratum of Oscillatoria spp. in the limnetic of the north arm of Itasca for at least the week preceeding 1 July. Sampling with a depth specific sampler indicated this stratum as approximately 0.5 - 1.0 m in thickness at 4 m depth (Figure 18). The layer was visible (before mixing by a storm with severe winds on 2 July) on several occassions to a diver swimming at night with a spotlight. Despite repeated sampling, Oscillatoria was not found in the littoral in any concentration (> 25 filaments per ml), nor was any Oscillatoria adhering to glass plates placed in the littoral zone before 2 July (Figure 19).

The storm of 2 July was the most severe of the summer (4.68 inches of rain in less than five hours and damaging winds), and caused mixing through the thermocline. The mid-lake stratum of Oscillatoria lost its integrity (Figure 18) and high numbers of Oscillatoria filaments were first found in the littoral on 3 July (Figure 19). (Secchi readings on 2 July before the storm were 3 m+ and just less than 1 m on 5 July). Oscillatoria filaments were

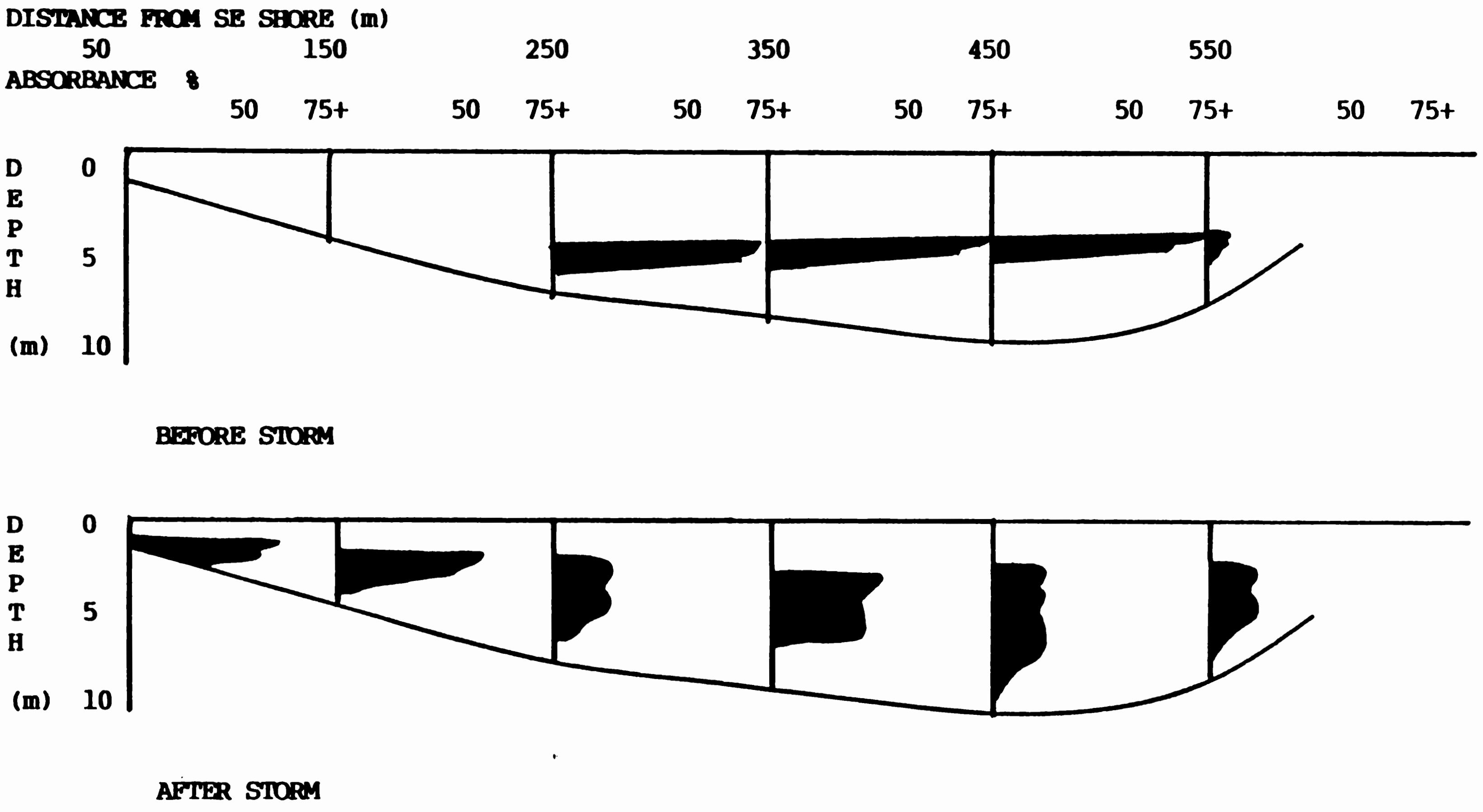


Figure 18. Comparison of optical density profiles and filament density in Lake Itasca before and after storm with severe winds on 2 July.

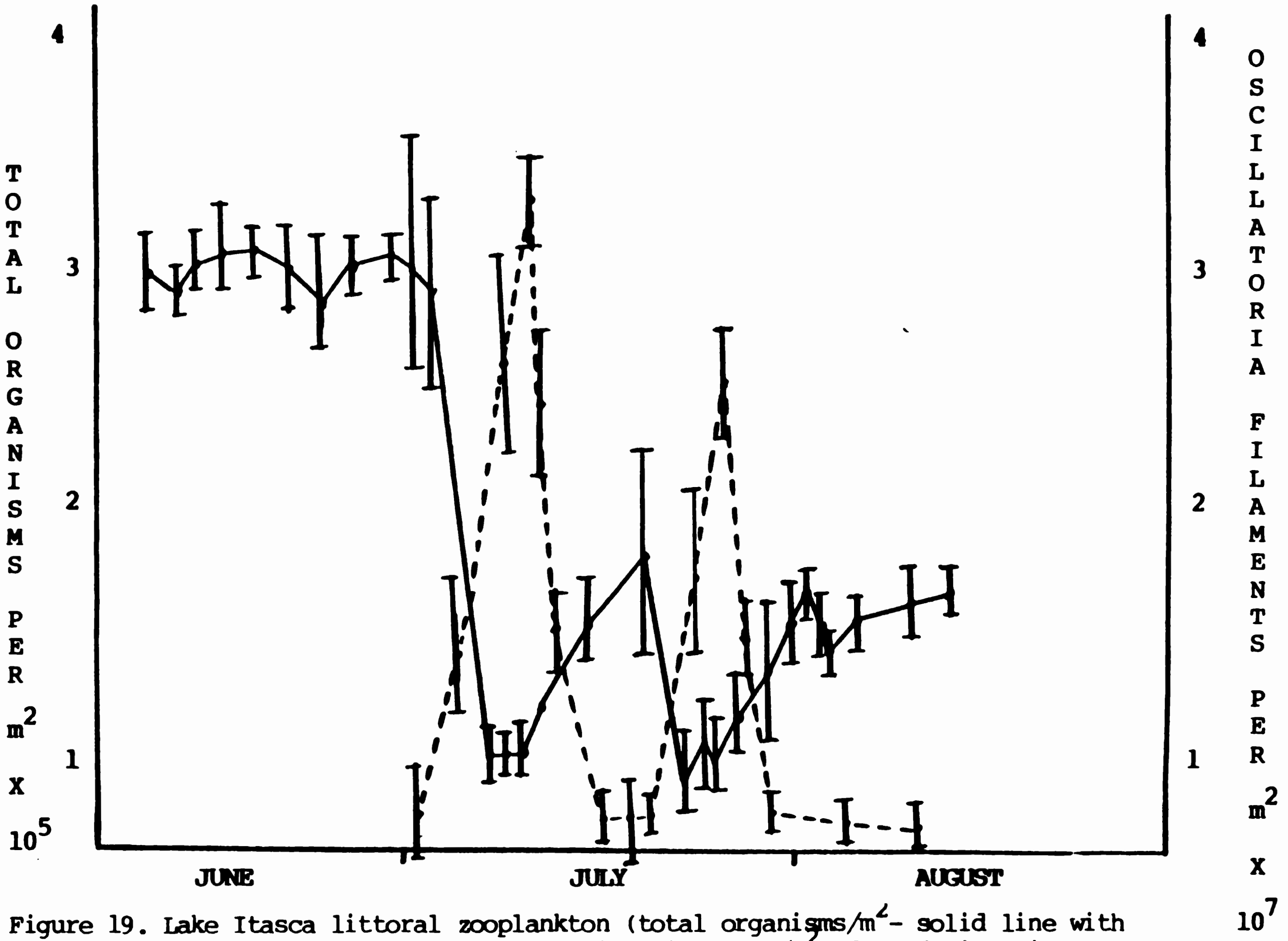


Figure 19. Lake Itasca littoral zooplankton (total organisms/m^2- solid line with standard error of the mean) and Oscillatoria (filaments/m^2- dashed line with standard error of the mean) at the Chara-water interface. Oscillatoria numbers were determined by counting filaments adhering (per 24 hour period) to glass plates suspended at Chara-water interface.

first noticed in the net treatment on 4 July but never appeared in the plastic treatment until its removal on 25 July (Figure 20).

While there was some rain on 3 July there were four days of intense sunshine beginning on 4 July. During this period Oscillatoria filaments at the Chara-water interface in the littoral and the net treatment began to exude mucopolysaccharides and to adhere to the glass plates. Lysis and production of hormogonia were also observed. On 8 July sampling indicated the first precipitous decline of zooplankton in the littoral zone and the net treatment but not the plastic treatment (Figures 19 and 20).

The adherence of filaments at the Chara-water interface was short lived (Figure 19), although Oscillatoria remained in the upper water column of both the littoral and limnetic in abundance (> 500 filaments per ml, integrated sample of top 4 m) until 19 July when these filaments began to loose buoyancy, lyse and settle out of the water column. This occurred initially in the littoral zone and then followed in the limnetic. These events were temporally correlated with the second littoral decline and the limnetic decline (Figure 19).

Introduction of filaments of varying concentrations both before and after the storm of 2 July to the laboratory populations of zooplankton led to the following observations:

1. Adhering filaments at lake concentration were 100% fatal to the limnetic D. galeata within six hours (Figure 21). While the possibility of toxins was not completely ruled out, the mechanism appears to be not toxins but mucopolysaccharides exuded by the filaments (often in the form of a sheath) which adhere to the

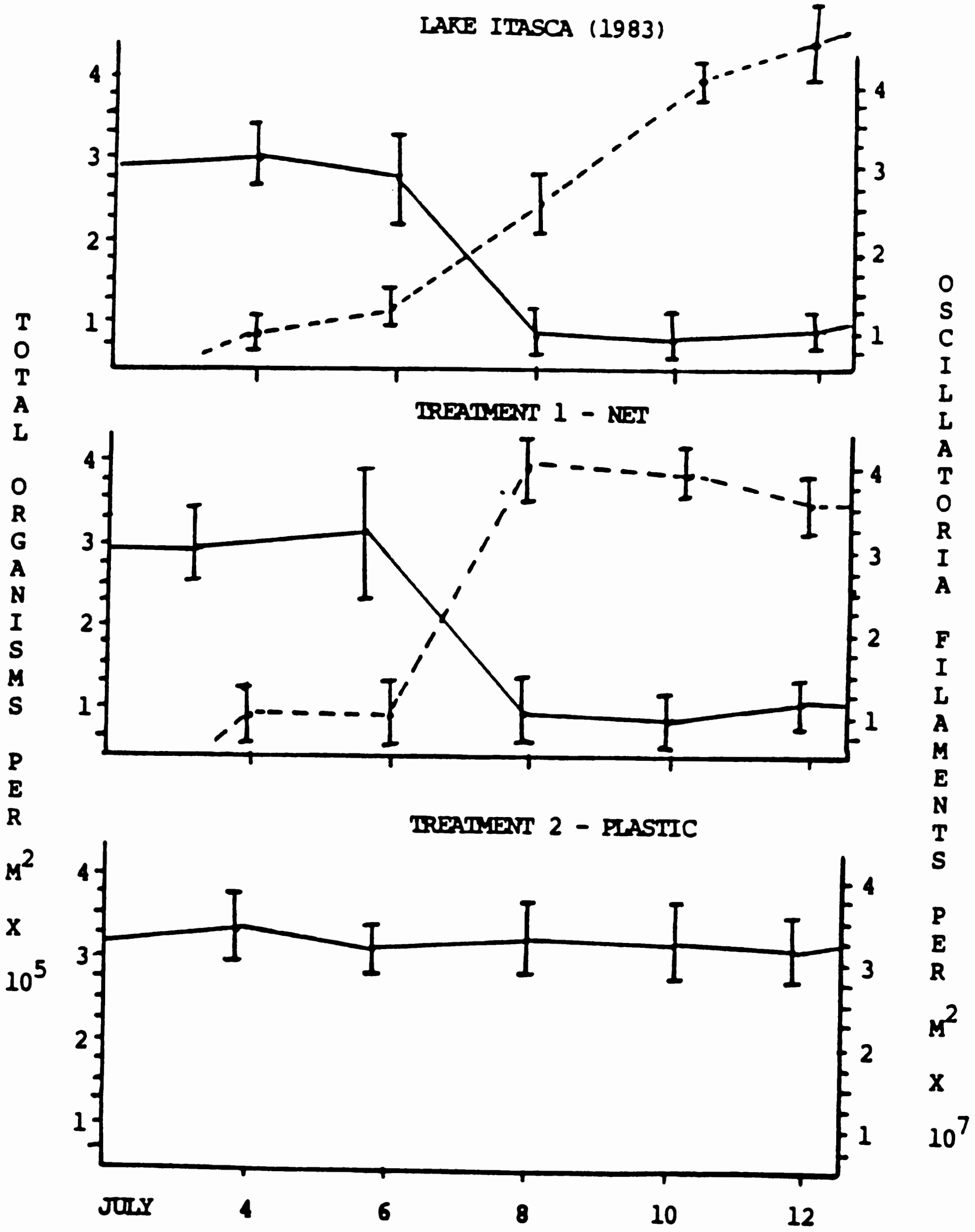
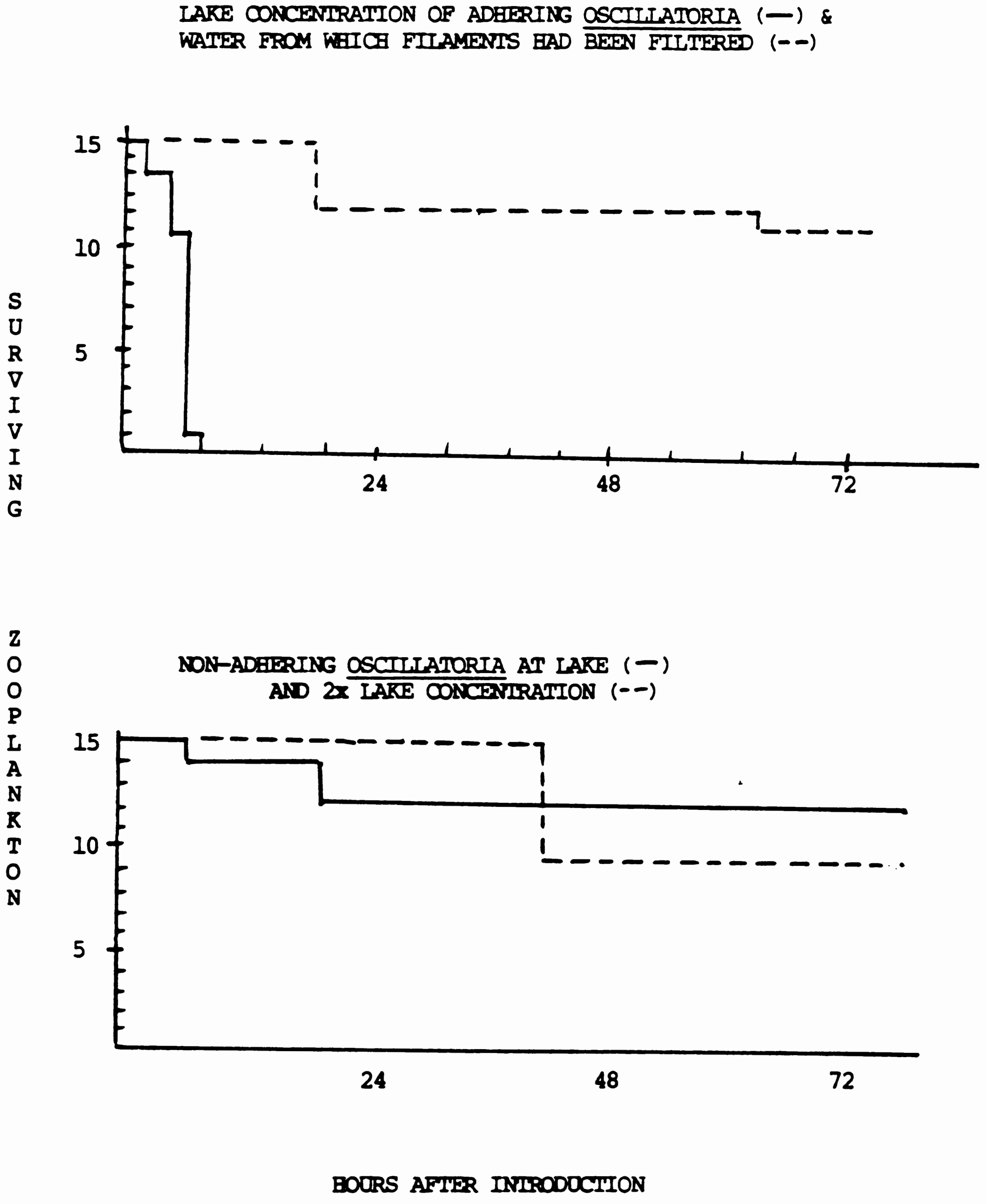


Figure 20. Littoral zooplankton (organisms/m^2 x 10^5- solid line) and Oscillatoria (filaments/m^2 x 10^7- dashed line) both with standard error of the mean in Lake Itasca and two treatments during first decline of summer of 1983. Oscillatoria numbers were determined by counting filaments adhering to glass plates suspended at Chara-water interface (per 24 hour period).



LAKE CONCENTRATION OF ADHERING *OSCILLATORIA* (—) &
WATER FROM WHICH FILAMENTS HAD BEEN FILTERED (--)

NON-ADHERING *OSCILLATORIA* AT LAKE (—)
AND 2x LAKE CONCENTRATION (--)

Figure 21. Survival of limnetic *D. galeata* in adhering and non-adhering filaments at mid-lake concentrations.

filtering setulae such that the plankters filtering apparatus cannot be cleared by use of its postabdomen. Filtered (.45 micron millipore) lake water containing lysing filaments did not similarly cause increased mortality in *D. galeata* (Figure 21). However, increased respiration and decreased carapace gap were noted.

2. Non adhering filaments (taken from the lake before the storm) did not have this effect (Figure 22) even at twice lake concentration.

3. Adhering filaments at lake concentration caused all littoral animals examined except chironomids to greatly reduce movement and generally remain at the bottom of aquaria or petri dishes in which they were examined under the microscope. Animals examined included *Chydorus sphaericus*, *Pleuroxus* spp., *Graptolebris testudenaria*, *Acroperus harpae*, *Camptocercus rectorostris*, *Alonella excisa*, *Alona affinis*, *Eurycercus lamellatus* and *Sida crystallina*, *Tropocyclops prasinus*, *Mesocyclops edax*, *Macrocyclops albidus*, and *Chironomus* spp. However, the great majority of these species (with the notable exceptions of *Sida*, *Macrocyclops* and *C. sphaericus*) resumed movement and suffered less than 10% mortality when removed to whole lake water (without filaments) after as long as 120 hours exposure to lysing filaments. *Sida* and all three copepods suffered greater than 75% mortality and *C. sphaericus* slightly less than 50%.

4. Non-lysing filaments at 2 times lake concentration did not cause mortality in any littoral species examined (including *Sida crystalina*).

5. Adhering filaments at concentrations found at the

Chara-water interface were 100% fatal to larval yellow perch within 24 hours whereas filtered whole lake water from the same interface resulted in no mortality or other visible effect within 72 hours (Figure 22). Furthermore, larval perch appeared to be able to sense lysing filament concentration and attempted to avoid it. When filaments were slowly siphoned into one side a 30 x 30 x 60 cm aquarium partitioned in the middle except for a 2 cm x 2 cm opening they moved from the filament side through the opening within an average time of twenty minutes. The average for filtered lake water exceeded two hours.

6. Monitoring of the sediment traps indicated that at no time during the summer were significant numbers of littoral zooplankton (with the notable exception of ostracods) going to the sediments. A precipitous increase in live ostracod numbers in the sediment traps coincided with their decline in the funnel traps. Limnetic traps clearly indicated that *D. galeata* was dying and falling out of the limnetic during the decline of 24 July.

d. Discussion

There are aspects of the Lake Itasca work, which because of time limitations of one field season, are crude approximations or indications (the sediment traps, the laboratory experiments, etc.). The sum total of the 1983 work, however, leaves no doubt that, during that summer, in a major unpolluted body of water, algae were a much more significant determination of zooplankton populations than predation.

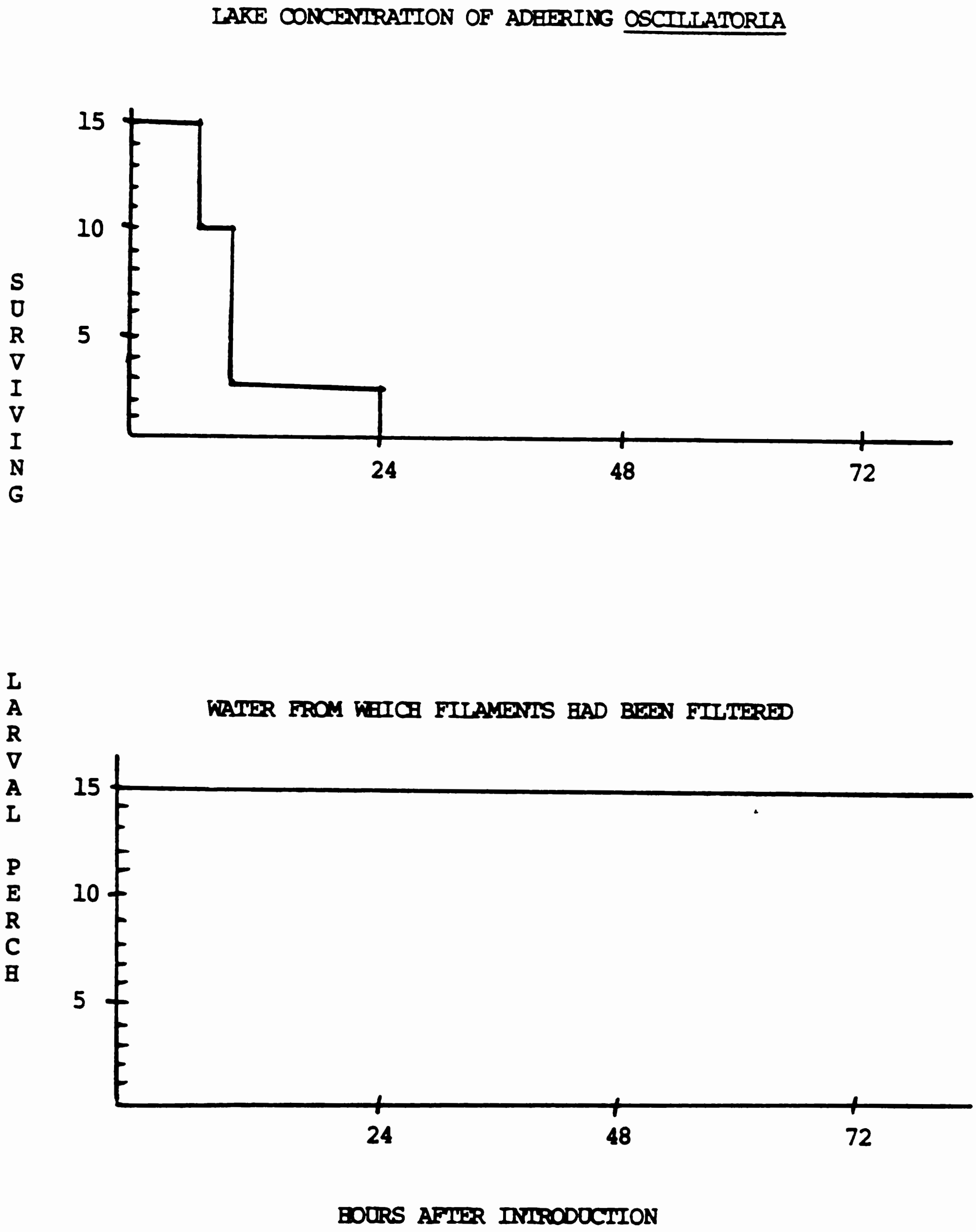


Figure 22. Survival of larval *Perca flavescens* in adhering filaments and filtered lakewater.

It would no longer appear valid, in any body of water which experiences blooms of cyanobacteria populations, to ignore those populations in a conclusion which posits structuring of the community by predation, predation as a cause of midsummer decline, or that the algae community may be "biomanipulated" by removing predators of filter feeding zooplankton.

The Itasca work also indicates that what has been viewed previously as a monolithic littoral decline may in fact be a very complex event in which different organisms react quite differently to an influx of blue-green filaments. Ostracods apparently go to the sediments, the larger chydorids seem to take refuge in _Chara_ or macrophytes, and _C_. _sphaericus_ and the copepods seem to move up in the water column (perhaps in the process experiencing increased predation).

Summary and Synthesis of the Experimental Studies

In the course of these studies, the cyanobacterium _Oscillatoria_ was again associated with limnetic and littoral midsummer declines in three bodies of water which varied widely in size, morphometry, and nutrient regime. The Arco experiments implicated _Oscillatoria_ in a decline even though the alga remained stratified and there was no vertical mixing or seiche. In the other two lakes, seiche (Lake Josephine) and mixing through the thermocline (Lake Itasca) were proximate causes of the declines. In those two lakes we were able to prevent declines by shielding a zooplankton population from _Oscillatoria_.

The Lake Josephine experiment indicates: (1) Oscillatoria's tendency to adhere increases as the summer progresses. (2) The tendency to adhere is accellerated when Oscillatoria is moved upward from its preferred stratification by mixing or seiche.

Both the Arco and Itasca experiments indicate that when Oscillatoria is exuding mucopolysaccharides it may be fatal to some filter feeding limnetic species and affect the movement of many littoral species of zooplankton.

In those experiments (Lake Josephine and Lake Itasca) in which predators were either removed or greatly increased in density, neither an increase in prey, an ultimate decrease in prey, nor a restructuring of the size distribution of the zooplankton community was observed. In addition, in the experiments in which we observed a temporary zooplankton decline with an increase in predator density, there was some doubt as to whether this was in fact due to increased density or a treatment effect (confining of the minnows) because the control (with no increase in predator density) also experienced an initial decline.

VI. CONCLUSION AND SPECULATION

What is <u>not</u> shown here is disproof of the predation and size efficiency hypothesis nor an indication that predation never contributes to, or in some circumstances may cause a midsummer decline. What is shown are strong indications that the picture is far more complicated than the mainstream (and many of the eddys) of the literature have tended to treat it. Those most interested in fish or zooplankton have tended to ignore algae and the theoretical considera- tions which indicate algae cannot be ignored. Phycologists have tended to such things as taxonomy, nutrient uptake or ultrastructure. The bacteriologists have recently become interested in the biochemistry of the cyanobacteria (both intra- and extracellular) but have not examined algal interaction with the zooplankton.

It may well be that alewives are capable of reshaping the zooplankton community in a lake. But, after twenty years of the predation and size efficiency hypotheses, and numerous extrapolations, the original qualifications pointed out by its authors remain and should be recalled and reemphasized:

1. The alewives did not co-evolve with the prey they were hypothesized as "structuring." That fact alone makes a generalization to lakes not containing alewives dangerous. It makes the extrapolations either one trophic level removed ("biomanipulation") or to specific events (midsummer declines) without a rigorous test of alternative hypotheses even more dangerous.

2. Although Brooks and Dodson found some support for the hypothesis (although not as clear cut) in some of the larger Finger Lakes containing alewives, they noted the persistence of large zooplankters in spite of Alosa's presence in the Laurentian Great Lakes. Some of the Great Lakes are remarkably oligotrophic (notably Superior, less so Huron) with correlative algal communities. Others have undergone dramatic cultural eutrophication. The Great Lakes would therefore be fertile ground (figuratively speaking) to examine the question: Are zooplankton communities more closely correlated to algal communities or to the predation they experience?

What the Minnesota surveys and experiments show is that there is not only a strong theoretical basis but ample field evidence for an alternative (and more generalized) hypothesis which is suggested by laboratory work of Porter and Gliwicz among others.

The 1981 lake survey revealed an association of zooplankton community size structure in a variety of aquatic ecosystems with the presence or absence of stratified cyanobacteria. The 1982 comparative study of midsummer declines shows not only that those declines cannot be simply explained, but that in the majority of instances in which they occurred, predation could be excluded as a cause.

The Lake Josephine experiments show that the increased density of Pimpales only temporarily affected zooplankton density in that lake's littoral zone. This finding contrasts with the general notion of structure by predation (Zaret 1980), but is bolstered by the study of Pleasant Pond, Minnesota (Lynch 1979) which concluded that the disappearance of a much heavier density of the slower, larger D. pulex was not due to predation.

The Lake Itasca experiments clearly showed that algal phenomena are highly relevant to midsummer dynamics in both the littoral and limnetic zooplankton communities. The sediment traps indicate a definite limnetic decline but indicate that the littoral decline may be a sampling phenomenon by which decreased movement results in fewer animals in traps.

While the examination of factors causing Oscillatoria to exude mucopolysaccharides and/or to lyse was beyond the scope of the instant study, the following observations and speculations may be offered. The production of extracellular polysaccharide by blue-greens has been reported in quantities up to 7 mg per litre of filtrate (Fogg 1952). It has been hypothesized that cyanobacteria may exude sheaths or mucilage as a light shielding mechanism (Walsby, 1974). It is also generally recognized that many procaryotic organisms, including cyanobacteria, tend to exude carbohydrate complexes (which play a part in enabling them to adhere to surfaces) when they are nutrient starved. Either or both of these possibilities might be suggested when Oscillatoria is driven from its stratification in deeper nutrient rich water to the shallower littoral zone (with less nutrients and more available light) by mixing or seiche. The lysing of cells would seem to indicate photooxidative conditions (high O_2, low CO_2 and high irradiance) which are quite likely as photosynthesis peaks at the Chara-water interface in midsummer.

Future research cannot ignore and must examine in detail the chemistry and ecology of exocellular products of the cyanobacteria. Predation is certainly a consideration in freshwater ecosystems but, in view of the results shown here, it may be a minor consideration compared to the larger (and presently less understood) biomasses at the base of the food web both for ecological theory and water resource management. A more complete understanding of the apparent ability of at least some of the cyanobacteria to turn on and turn off the production of mucilage holds much more potential for "biomanipulation" than the sum total of the twenty years of research which has been invested in the predation and size efficiency hypothesis. In addition to the potential an understanding of the allelopathic influence of extracellular products might hold for understanding and perhaps manipulating algal sequence (Keating 1977), future knowledge of extracellular mucopolysaccharides might allow the prevention of midsummer zooplankton decline to the benefit of young of the year fish stock.

The mechanism of the observed effect Oscillatoria has on zooplankton requires not only the secretion of a polysaccharide complex but that the polysaccharide complex be viscous. Viscosity or "stickiness" is apparently related to the proportion of oxidized monosaccharides (uronic acids) in the polymer strands (V. Puvanesarajah pers. comm.). A simple and quick test for uronic acids exists (Blumenkrantz and Asboe-Hansen 1973). This test holds the potential for not only predicting midsummer zooplankton declines but for determining to what extent mucopolysaccharide production is controlled by the organism's internal biorythm and/or the nutrient and light regimes to which it is subjected.

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