EXPERIMENTAL EVALUATION OF FOOD CHAIN MANIPULATION AS A MEANS FOR PREVENTING ALGAL BLOOMS IN LAKES

by

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ABSTRACT

This study investigated means of manipulating lake food chains to enhance grazing by zooplankton and thereby to decrease algal biomass and to improve water clarity. Experiments were conducted at two levels. We monitored a relatively deep, stratified lake for two years prior and one year following the removal of fish by treatment with rotenone and we manipulated zooplankton, fish, and nutrients in two series of experiments in 7,000 liter mesocosms. Fish removal resulted in a shift in the zooplankton community to larger species, a substantial improvement in water clarity, and a decline in algal biomass. Mesocosm experiments showed that zooplankton communities dominated by moderate-sized native zooplankton or by introduced *Daphnia pulex* were equally effective in preventing algal blooms under both ambient and highly enriched nutrient levels when fish were absent. Introduced *D. pulex* out competed native zooplankton, suggesting that the association of large *Daphnia* with low algal biomass is due to competition, rather than an inability of smaller grazers to prevent algal blooms. The tendency for zooplankton to remain in deep water, especially when fish are present, probably accounts for the observation that zooplankton are more effective in preventing algal blooms in shallow lakes than in deep lakes.
JUSTIFICATION OF WORK PERFORMED

Virtually all water quality problems in lakes in the midwest, including Indiana, are caused by cultural eutrophication. In this process, artificially elevated nutrient inputs accelerate primary production which, in turn, leads to major changes in biological communities and water quality. Blooms of planktonic algae are usually the most obvious and serious problem. Excessive accumulation of algae reduces water clarity, increases the rate of oxygen depletion in deeper waters, and may cause surface scums and odor problems. The focus of practical water quality management programs has centered on reducing nutrient loading, seeking to control eutrophication directly at its source. Since achieving sufficient reduction in nutrient loading is expensive and often technically difficult, new complementary approaches to lake restoration are needed.

This study investigated means of manipulating food chains to enhance grazing and thereby to increase the consumption of algae. Algae are at the base of lake food chains; they are eaten by filter-feeding zooplankton which, in turn, are preyed upon by small fish. The common water flea *Daphnia pulicaria* is a especially efficient grazer of algae and yet, because of its relatively large size, is highly vulnerable to predation from visually-feeding fish. Decreases in the abundance of small planktivorous fish, caused by natural winterkills, rotenone treatment or stocking predatory fish can lead to increases in the size and abundance of filter-feeding zooplankton and subsequent, often dramatic declines in algal biomass without changes in nutrient loading. In addition to fish predation, the large size and poor nutritional quality of some algae, especially blue-greens, are hypothesized to limit the success of large *Daphnia* in eutrophic lakes. Thus, phytoplankton densities in lakes can be strongly influenced by higher trophic levels ("top down effects") and phytoplankton species composition, as well as levels of nutrient loading ("bottom up effects").

The most convincing evidence that small fish can initiate algal blooms by preferentially consuming large *Daphnia* has come from controlled field experiments in large-scale enclosures. For example, my colleagues and I at Dartmouth College used enclosures to test the ability of *Daphnia* to prevent algal blooms in a Vermont trout lake (Levitan et al. 1985). In each experiment we placed a series of 12,000 liter enclosures in the lake and fertilized them with the same levels of nitrogen and phosphorus. Small planktivorous fish were introduced into some enclosures (2-12 fish per enclosure) whereas other enclosures were kept free of fish. In enclosures with fish *Daphnia* declined to very low levels (<1 individual/liter) and dense algal blooms developed (chlorophyll a about 50 μg/liter; Secchi depth about 0.3 meters). In enclosures without fish *Daphnia* increased to about 50-100/liter and the water was virtually crystal clear (chlorophyll a 1-4 μg/liter; Secchi disk clearly visible at the bottom at 3 meters). Edible green algae
dominated the phytoplankton in enclosures both with and without fish.

There is nothing mysterious about these results; at a density of 50/liter, we estimated that the Daphnia population was able to filter a volume equivalent to 100% of the water column per day. On the other hand, the total numbers of zooplankton actually increased in the fish enclosures. However, as in the classical study by Brooks and Dodson (1965), the species which coexisted with fish were small-bodied forms with low feeding rates and narrow diets (mainly Bosmina, Daphnia, and rotifers). We also observed that stocking another Vermont trout lake with highly piscivorous brown trout led to a decline in the abundance of golden shiners, an increase in the abundance of Daphnia and an improvement in water clarity.

The ability of large Daphnia to prevent algal blooms has been documented in other enclosure studies (e.g. Andersson et al. 1978; Lynch and Shapiro 1981; Schoenberg and Carlson 1984), and when planktivore populations in small lakes and ponds have been reduced by natural causes, such as winter-kill (Schindler and Comita 1972) or by artificial means, such as fish toxins (Henrikson et al. 1980) or stocking regimes (Fott et al. 1979). Recently Carpenter et al. (1985) have used a computer model to show that most of the between-year variability in primary productivity and algal biomass observed in lakes can be accounted for by natural variation in the recruitment of planktivorous and piscivorous fish.

Intentional reductions in the abundance of planktivorous fish have recently been used to improve water quality in a several small lakes. Successful approaches have included poisoning all fish with rotenone (Stenson et al. 1978), poisoning followed by stocking a balanced population of planktivores and piscivores (Shapiro and Wright 1984) and stocking with piscivorous fish such as pike or brown trout (Benndorf et al. 1984). Based on a review of the literature, Benndorf (1987) concluded that there may be a threshold level of nutrient loading above which biomanipulation is much less effective. This hypothetical threshold level is probably sensitive to factors such as high pH and low free CO₂, which favor inedible blue-green algae over more readily grazed taxa (Shapiro 1973). Thus, the best approach to preventing or curing eutrophication will often be a combination of food chain manipulation and a reduction in nutrient inputs. Another recent review article pointed out that "top down effects" on phytoplankton abundance appear to be strong in shallow lakes and ponds and much weaker or more ephemeral in deep, stratified lakes (McQueen 1990).

The particular effectiveness of large species of Daphnia in preventing algal blooms appears to result from a combination of four characteristics: 1) high maximal feeding rates, 2) ability to ingest a broad size range of particles, 3) a relatively nonselective feeding mode, and 4) high maximal reproductive rates. The filtering
rates of zooplankton tend to increase with cube of body length (e.g. DeMott 1982) and daphnids exhibit maximal ingestion rates much higher those of copepods of comparable size (Muck and Lampert 1984). Because the maximum size of ingested particles increases linearly with zooplankton body size (Burns 1969), larger daphnids can feed on a broader size range of algae than smaller species. Moreover, unlike copepods, daphnids do not use taste or chemical cues to select between food particles (DeMott 1986, 1989). Daphnia’s nonselective feeding mode and ability to ingest bacteria-sized particles (e.g. DeMott 1985), allows it to improve water clarity by removing not only algae but also bacteria, clay particles and other fine suspended matter (Gliwicz 1986). Finally, Daphnia populations can double in size every 2-3 days with abundant food, at summer temperatures and in the absence of significant predatory mortality (Allan and Goulden 1980; exponential rate of increase 0.3-0.4/day).

Daphnia’s relatively nonselective feeding mode may, however, be a serious disadvantage under some circumstances. Filamentous blue-greens and other algae which are too large to be readily ingested may clog the feeding apparatus, disrupting feeding and requiring energetically expensive rejection movements (Webster and Peters; Gliwicz and Siedlar 1980; Porter and McDonough 1984). Moreover, many of the algae which predominate during summer in eutrophic waters are low in nutritional value and some are even toxic (Porter 1977; Porter and Orcutt 1980; Lampert 1981). Thus, interference from poor quality algae provides an alternative hypothesis to fish predation for the scarcity of large Daphnia in nutrient enriched lakes (Gliwicz 1985; Richman and Dodson 1983). For example, in the case of Lake Washington, the continued presence of the toxic blue-green alga Oscillatoria agardhii was hypothesized to be the reason for the delayed colonization of the lake by Daphnia (Edmondson and Litt 1982; Infante and Abella 1985). In addition to fish and poor quality algae, Daphnia and other crustacean zooplankton are sensitive to pesticides in agricultural runoff (Shapiro 1980a).

The role of algal quality in zooplankton-algae interactions is currently an area of intensive research because of its implications for a basic understanding of pelagic ecosystems as well as its importance for water quality control. The abundance of blue-green algae is usually highest during midsummer to early fall, the time when fish predation is also most intense. Since sharp declines in Daphnia abundance are often observed during this critical period, separating the effects of algal quality and fish predation requires an experimental approach. Much of the evidence for adverse effects of blue-green algae on Daphnia is from laboratory feeding studies and field correlations (e.g. Gliwicz 1977; 1980). Despite this evidence, a number of field enclosure experiments (e.g. Lynch and Shapiro 1981; Schoenberg and Carleson) and whole lake manipulations (e.g. Hendrikson et al. 1980; Fott et al. 1980; Shapiro and Wright 1984) have demonstrated successful control of total algal abundance in lakes with formerly abundant populations of blue-green algae.
In other cases, grazing by Daphnia has been found to improve water clarity but large, difficult to ingest algae have remained abundant (Lynch 1980). One goal of our research was to examine the influence of algal species composition and quality on the nature of zooplankton-algae interactions in enclosures which exclude fish. Thus, these experiments should provide important insights into the nature of interactions between zooplankton and phytoplankton.

"Biomanipulation" is often used as part of fisheries management programs. For example, Galbraith (1967, 1975) found that poisoning planktivorous fish led to colonization of small Michigan lakes by large Daphnia and marked improvement in the growth and survivorship of stocked rainbow trout. Unfortunately, fisheries managers rarely monitor zooplankton, algae and water quality (but see Mills and Shiovone 1982). The effects of Daphnia on water quality are not limited to small lakes and ponds. One beneficial and largely unanticipated result of salmon stocking in Lake Michigan has been the appearance of a large species of Daphnia (D. pulicaria) in offshore waters and a marked increase in water clarity due to Daphnia grazing (Scavia et al. 1986). The recent success of large Daphnia in Lake Michigan is thought to be a consequence of a sharp decline in the planktivorous alewife, the major forage fish in the diet of salmon.

This study was carried out at Wyland Lake, a small (6 acre), moderately deep (maximum depth 13 m) natural lake located on state-owned land in the Tri-County Fish and Wildlife Area near North Webster, Indiana. The planned removal of all fish from a small lake by fisheries biologists from the Indiana Department of Natural Resources provided an unusual opportunity to study interactions between fish, zooplankton, and phytoplankton in a relatively deep, strongly stratified natural lake. The specific objectives of the project were:

1. To test the ability of native zooplankton and introduced large Daphnia (D. pulicaria) to prevent algal blooms in Wyland Lake when fish are removed.

2. To test experimentally possible limitations on the abilities of grazers to control algae in a stratified, moderately deep lake. This included tests of competition between zooplankton species, an examination of the effects of algal composition on zooplankton populations, testing the effects of nutrient loading, and a preliminary analysis of the effects of zooplankton depth distributions and migratory behavior.
REVIEW OF METHODOLOGY USED

Experiments were conducted at two levels: whole-lake removal of fish via rotenone treatment and manipulations of fish, zooplankton and nutrients in large-scale (about 7,000 liter) mesocosms.

1. Whole-lake Fish Manipulation---The actual rotenone treatment of Wyland Lake was carried out during September, 1989 and was conducted and financed by the Indiana Department of Natural Resources. In order to interpret the effects of fish removal on the zooplankton and phytoplankton communities we monitored a number of parameters during two field seasons prior to the treatment (April-September 1988 and 1989) and one field season following the treatment (April-August 1990; data collection is continuing, supported, in part, by a grant from the National Science Foundation). The following physical, chemical, and biological parameters were monitored weekly or biweekly during the "growing seasons" of all three years:

1. Measurements of temperature and dissolved oxygen throughout water column using a Yellow Springs Instruments temperature-oxygen probe.


3. Phytoplankton and water chemistry were sampled with a 3 meter PVC pipe in order to obtain an integrated sample of epilimnetic waters. Analysis of soluble reactive phosphorus and chlorophyll a followed Strickland and Parsons (1972), and analysis of particulate organic carbon (POC), total phosphorous and nitrogen follow the methods of Wetzel and Likens (1979). Phytoplankton were preserved with Lugol's fixative and their density and species composition determined using the Utermohl inverted microscope technique. Samples for the analysis of phytoplankton, chlorophyll, and POC were collected at 4m on each sampling date using a Van Dorn sampler and less frequently at greater depths.

4. Zooplankton were sampled using vertical tows of a Wisconsin plankton net. Additional day and night samples were occasionally collected at 1 m depth intervals with a 25 liter Schindler trap to determine the depth distributions of various species and to calibrate the filtration efficiency of the plankton net. Abundance, species composition, and egg production of zooplankton were determined by counts under a dissecting microscope. The reproductive state, including the number of eggs carried by females was determined to examine the effects
of fish, food, and competitors on zooplankton birth and death rates (Edmondson 1968; DeMott 1980).

2. Large-scale Mesocosm Experiments—Large-scale enclosures suspended within lakes have proved to be very effective in experimental studies of interactions between fish, zooplankton, phytoplankton, and nutrients (e.g. Anderson et al. 1978; Lynch and Shapiro 1981; Neill 1978; DeMott and Kerfoot 1982). Typically, enclosures are large (5,000–30,000 liter) polyethylene bags filled with lake water, sealed at the bottom, open at the top, and suspended from a floating raft. Enclosures provide opportunities for relatively long-term, replicated experiments under near-natural conditions. For example, in lakes where fish predation is not important, population densities of zooplankton and algae in untreated enclosures and values of oxygen and temperature show very close agreement with lake values for two to three months (DeMott and Kerfoot 1982; Neill 1984).

Most enclosure studies have been conducted in shallow (2–4 m) lakes. Neill (1978, 1984), however, has successfully used enclosures extending from the surface to 15 m depth. In most previous studies with zooplankton, enclosures have been filled with surface water or water pumped from various depth. In contrast, the approach used here was designed to enclose a relatively undisturbed water column. Polyethylene cylinders were be supported by circular hoops of plastic tubing and covered at the bottom by coarse screening. The purpose of the screening was to prevent the entry or escape of fish. During deployment, weights were attached to the bottom of each to pull it down through the water column. The enclosures were then suspended from wooden rafts which were anchored to the bottom of the lake.

A. 1989 Experiment—Two sets of large-scale enclosure experiments, each about two months in duration, were conducted: one during the summer of 1989 and one during late spring-early summer, 1990. Each series of experiments used polyethylene bags 1.0 m in diameter and extending well into the oxygen-free hypolimnion (9 m). The 1989 experiment involved three replicates of each of three treatments: 1) fishless enclosures with natural zooplankton, 2) fishless enclosures with natural zooplankton and introduced Daphnia pulicaria from Little Crooked Lake, and 3) fish enclosures with two bluegills per bag, natural zooplankton, and added Daphnia pulicaria. Assuming that small fish are responsible for the decline in water quality in Wyland Lake, we predicted that water quality would remain poor in enclosures with bluegills, improve somewhat in fishless enclosures with native zooplankton, and further improve in fishless enclosures with introduced Daphnia pulicaria. These experiments were also designed to provide data on competition between D. pulicaria and native zooplankton.

B. 1990 Experiment—The 1990 experiments were similar in design except that phosphorous and nitrogen were be added to some
enclosures at a rate of 20 µg/liter P as phosphate and 160 µg/liter N as nitrate per week for the upper 3 m of each enclosure. This experiment was designed, in part, to simulate conditions in lakes receiving high nutrient inputs from agricultural runoff or sewage treatment plants. Thus, this experiment tested the ability of native and introduced zooplankton to prevent algal blooms under conditions of heavy nutrient loading. There were two replicates for each of five treatments: 1) native zooplankton, 2) native zooplankton with weekly additions of N and P, 3) native zooplankton with introduced D. pulicaria, 4) native zooplankton with introduced D. pulicaria and weekly nutrient additions, and 5) native zooplankton, introduced D. pulicaria, weekly nutrient additions and 2 small bluegills. This experimental design also provided a test of whether nutrients levels influence the outcome of competition between introduced Daphnia pulicaria and native zooplankton.

Each series of large enclosure experiments was run for approximately 8 weeks. As described above for the lake sampling, we monitored a variety of physical, chemical, and biological parameters in each enclosure on a weekly schedule during both years. These data were needed to document treatment effects and to provide insights into details of grazer-algae interactions which may accentuate or detract from the ability of zooplankton to control algal biomass. Laboratory analysis was done at the Crooked Lake Biological Station, a well-equipped facility managed by the PI (W.R. DeMott) and located near Columbia City, Indiana.
DISCUSSION OF RESULTS AND THEIR SIGNIFICANCE

1. Historical Data and the Fish Communities—Unlike the situation in most lakes in the midwest, there is no farming or residential development in Wyland Lake's watershed. Since the entire watershed is forested, nutrient loading should moderate. Between-year differences should be associated with differences in rainfall, with no long-term trends expected. The fish community at Wyland Lake, however, has been drastically manipulated by fisheries biologists from the Indiana Department of Natural Resources (DNR). The combination of stable nutrient loading and fisheries management makes Wyland Lake a good place to look for "top down effects" on phytoplankton abundance and water clarity.

A DNR survey conducted in June 1970 revealed a fish community dominated by stunted bluegills. Only 12% of the bluegills caught in a gill net were considered "catchable" (>5.5 inches, >14 cm) and only a single small bass was found in a total catch of 95 fish. The following year, because of the poor quality of the fish community, Wyland Lake was treated with rotenone to kill all fish and restocked with bluegills and largemouth bass. Water clarity and dissolved oxygen levels showed a marked improvement and, for this reason, the lake has been stocked with rainbow trout since 1975. A perceived decline water quality during the 1980's led to the decision to retreat the lake with rotenone during September, 1989. Collection and measurement of fish which came to the surface following the 1989 rotenone treatment confirmed that Wyland Lake was populated by small-bodied planktivores. No bass or rainbow trout were found and stunted bluegills, golden shiners and pumpkinseeds were most abundant (Fig. 1). Unfortunately a small number of bluegills and golden shiners survived the rotenone treatment and successfully reproduced during late spring, 1990. Although the fish biomass was drastically reduced by the rotenone treatment, we cannot assume that fish predation was negligible during summer 1990.

Figure 2 compares Secchi disk transparency during our intensive pretreatment monitoring with data collected by occasional DNR surveys. The observation that all of the DNR data (open squares) fall below our estimates (circles) offers good support for the notion that water clarity declined during the 1980's. The extremely clear water observed in 1973 (Secchi depth > 7m) is interesting, since this is the first data following the rotenone treatment in 1971, and it occurred when the fish community exhibited a good balance between largemouth bass (12% of total catch) and bluegills (23%).

Not surprisingly, a decline in oxygen in deeper water is associated with the decline in water clarity. Late summer measurements revealed that O₂ levels > 1 ppm were found at 6 m during 1975 and 1979 but that O₂ declined to < 1 ppm at 3-4 m during 1988 and 1989 (Fig. 3). Assuming that rainbow trout require >4 ppm O₂ and temperatures <20°C, rainbow trout would have found a
suitable late-summer habitat during 1975 and 1979 but no suitable habitat during 1984, 1988, and 1989. Fisheries data support the hypothesis the "carry over" potential for rainbow trout has declined in recent years. For example, during July 1979, rainbow trout comprised 33 of 53 fish captured in gill nets, whereas not a single trout was recovered following the treatment with rotenone in September, 1989.

2. Response of Wyland Lake to Fish Removal--As mentioned above, we have monitored Wyland Lake for two field seasons prior and one field season following fish removal via rotenone treatment.
Fig. 2. Comparison of Secchi depth data collected during pretreatment monitoring in 1988 and 1989 (circles) with historical data from the Indiana DNR (squares).

Differences between the three years could be due to both the "top down effects" of fish removal and differences in weather. A severe drought occurred during summer 1988 whereas rainfall was much above normal during spring-summer 1990. Other lakes that we monitored (i.e. Crooked Lake and Little Crooked Lake) exhibited good water clarity and reduced algal biomass during 1988, the drought year, and reduced water clarity and increased algal biomass during 1990, the wet year. This is consistent with the expectation that increased rainfall should lead to increased nutrient loading. In contrast, water clarity in Wyland Lake exhibited a notable improvement during 1990 (Fig. 4). Since chlorophyll a and fine (<100 µm) POC are indicators of algal biomass, similar trends in these parameters confirm that the between-year trends in water clarity are due to changes in algal biomass (Fig. 4; Table 1).

Table 1. Mean values for Secchi depth (m), chlorophyll a (µg/liter), and POC (µg/liter) from May through late July of 1988, 1989, and 1990. Data are expressed as mean ±SE for 8 dates in 1988, and 10 dates in 1989 and 1990. POC data for 1989 were unavailable at the time this report was written.

<table>
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<tbody>
<tr>
<td>Secchi depth</td>
<td>2.4±0.17</td>
<td>2.5±0.16</td>
<td>3.4±0.31</td>
</tr>
<tr>
<td>Chlorophyll a</td>
<td>6.4±1.09</td>
<td>9.3±1.24</td>
<td>3.8±0.59</td>
</tr>
<tr>
<td>POC</td>
<td>952±90</td>
<td></td>
<td>263±31</td>
</tr>
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Fig. 3. Late-summer depth profiles for dissolved \textit{O}_2 in Wyland Lake.

As mentioned earlier, fish feed visually and tend to remove preferentially large-bodied zooplankton. Figure 5 compares the size distributions of crustacean zooplankton from Wyland and Little Crooked Lakes during May, 1988. At this time, Wyland Lake was dominated by very small species, especially the cladocerans \textit{Bosmina longirostris}, \textit{Ceriodaphnia reticulata}, and the copepod \textit{Tropocyclops prasinus}. Brooks and Dodson (1965) reported that these same species dominate in New England lakes subject to intensive fish predation and since that time the same pattern has been observed in lakes throughout the world (reviewed by Gliwicz and Pijanowska 1989). We predicted that fish removal would result in a shift to a zooplankton community dominated by larger-bodied species as in Little Crooked Lake (i.e. the cladocerans \textit{Daphnia pulicaria} and
Fig. 4. A comparison of Secchi depth, chlorophyll a (0-3 m depth), and fine (<100 μm) POC (0-3 m depth) during two years prior (1988-89) and one year following (1990) treatment with rotenone.
Daphnia hyalina and the copepod Diaptomus birgei). The dominance of large-bodied zooplankters in the absence of fish predation is due to either their competitive superiority over smaller species (reviewed by DeMott 1989) or their reduced vulnerability to invertebrate predators (reviewed by Gliwicz and Pijanowska 1989).

Fish removal resulted in major changes in the zooplankton community in the predicted direction (Figs 6 and 7). The three species typical of zooplankton communities undergoing intensive fish predation all exhibited marked declines or complete extinction. The small cladocerans Bosmina and Ceriodaphnia were abundant during 1988 and 1989 but declined drastically during 1990. Ceriodaphnia was uncommon by late June and Bosmina exhibited a similar decline in July (microscope counts for July are not yet complete). The small copepod Tropocyclops exhibited a different pattern. It was very abundant during 1988, scarce during summer 1989 and completely absent during 1990. Three Daphnia species occurred in the lake all three years (D. catawba, D. ambiguа, and D. parvula). Typical of populations undergoing intensive predation, the largest adult size was < 1 mm during 1988 and 1989, but somewhat larger during 1990.

![Figure 5](image-url)

Fig. 5. Comparison of the size distributions of zooplankton collected in May, 1988 from Wyland Lake (open bars) and Little Crooked Lake (solid bars).
(1.3 mm). Population densities were relatively high during 1988 and 1990 but exhibited a sharp midsummer decline during 1989. The moderately large copepod Diaptomus birgei (adult females 1.5 mm) was scarce during 1988 and 1989 but became abundant during 1990 (Fig. 7). Large Daphnia pulicaria were not observed in the lake, even though several plankton tows of zooplankton from Little Crooked Lake were stocked in the lake.

2. Lake Enclosure Experiments—Large enclosure experiments were run to help clarify the mechanisms underlying the changes in the lake and to allow more controlled manipulations of fish, zooplankton, and nutrients. The 1989 enclosure experiment tested the effects of excluding fish (control treatment), introducing Daphnia pulicaria from Little Crooked Lake, and adding bluegill sunfish. As expected, enclosures with fish exhibited reduced Secchi clarity, increased chlorophyll biomass and increased poc (Fig. 8; ANOVA, each p<0.01). There were no consistent differences between the Daphnia and control treatments (p>0.05). Secchi depth values for the lake were intermediate between the fish enclosures and the enclosures without fish.

Both fish and Daphnia treatments had significant effects on the native zooplankton community (Fig. 9). The smallest cladoceran, Bosmina, increased in response to fish predation whereas all other species declined in response to fish predation. The two smallest cladocerans, Bosmina and Ceriodaphnia, both declined in the Daphnia treatment, relative to the control enclosures (Fig. 9). This can be attributed to competition for food with the introduced Daphnia pulicaria. In contrast, Diaphanosoma appeared to be slightly enhanced by the presence of D. pulicaria.

Unexpectedly, native Daphnia exhibited sharp declines in all enclosures, even those without fish (Fig. 9). This suggests that the sharp decline in Daphnia which occurred in the lake at the same time (Fig. 6) cannot be attributed solely to fish predation. Water clarity in the lake was poor at this time and algae were moderately abundant (Fig. 4). Two factors may have been involved in the midsummer demise of native Daphnia. First, the food quality of the dominant algae may have been poor. Since we have considerable data on the abundance and composition of algae, further analysis of these data may provide insights into food quality effects. Second, reduced water clarity led to reduced O₂ in deeper water. As will be shown later, Daphnia remain in relatively deep water during the daylight hours. Thus, reduced water clarity may lead to a deterioration of Daphnia’s deep-water habitat.

The 1990 enclosure experiment tested the effects increased nutrient loading as well as fish predation and additions of Daphnia pulicaria. The results provide a strong demonstration of the ability of zooplankton to prevent algal blooms under conditions of high nutrient loading (Fig. 10). Near the end of the experiment, Secchi values ranged from 5-6 m in enclosures without nutrients or
Fig. 6. Seasonal and between-year changes in the abundance of cladocerans. Data are means ± SE for two replicate vertical tows per date (note log-scale).
Fig. 7. Seasonal and between-year changes in the abundance of copepods. Data are means ± SE for two replicate vertical tows per date (note log-scale).

fish, 4-5 m in enclosures with nutrients and without fish, but decline to < 1 m in enclosures with nutrients and with fish.
Chlorophyll a, a measure of algal biomass, ranged from 1-3 μg/liter in the enclosures without nutrients or fish, from 2-10 μg/liter in enclosures with nutrients and without fish, and from 20-60 μg/liter in enclosures with both nutrients and fish. Enclosures with and without large Daphnia pulex exhibited similar patterns of water clarity and algal biomass (Fig. 10). This suggests that the presence or absence of fish is more important than the size and species composition of the zooplankton in determining water clarity. The association often noted between clear water and large Daphnia may be due to the tendency for large Daphnia to be competitively dominant under conditions of low fish abundance, rather than an inability of moderate-sized zooplankton to increase water clarity.

The effects of fish predation on zooplankton in the 1990 experiment were qualitatively similar to the results of the previous year. It appears, however, that the effects of fish predation were less severe in the nutrient-enriched enclosures in 1990 in comparison to the unenriched enclosures in 1989. In contrast to results from the previous year, all species, including Daphnia
Fig. 8. Results of the 1989 mesocosm experiments; effects of fish enclosure (control), introduction of Daphnia and additions of bluegills on water quality parameters. Each data point is the mean for 3 replicate enclosures.

*pulicaria*, survived in enclosures with fish (Fig. 11). All species of Daphnia were strongly depressed by fish, Ceriodaphnia was initially depressed but recovered towards the end of the experiment, and Bosmina and Diaphanosoma exhibited little or no net change. Presumably, the direct effects of predation were offset by increased food for zooplankton, and predation efficiency declined near the end of the experiment as water clarity was drastically reduced.

Comparisons between enclosures with and without added D. pulicaria reveal strong competitive suppression of native zooplankton in enclosures both with and without added nutrients.
Fig. 9. Results of the 1989 mesocosm experiment; effects of fish exclosure (control), additions of Daphnia and additions of fish on the population dynamics of zooplankton. Data are means for 3 replicate enclosures (note log-scale).
Fig 10. Results of the 1990 mesocosm experiment; effects of fish exclosure (control), and additions of nutrients, Daphnia, and fish on water quality parameters. Data are means for pairs of replicate enclosures (note log-scales).
(Fig. 12). As in the previous year's experiments, Diaphanosoma appeared to suffer the least from competition with introduced D. pulicaria, whereas Ceriodaphnia was most strongly depressed in abundance. A study of the depth distributions of zooplankton within enclosures helps to explain these species differences (Fig. 13). During day, Daphnia pulicaria was strongly concentrated between 5-7 m depth.

The tendency of Diaphanosoma to be most abundant between 1-3 m may explain its reduced sensitivity to competition from D. pulicaria. Overall, however, we conclude that despite a very restricted daytime depth distribution, D. pulicaria has a surprising ability to depress the abundance of other zooplankton and to prevent algal blooms. A night time vertical series showed that D. pulicaria does migrate toward the surface during darkness. The recent discover that the presence of fish can lead to reduced vertical migration (e.g. Tessier and Welser in press) suggests that the effects of fish on zooplankton behavior could be quite important in deep lakes (Lampert 1988). In deep lakes, phytoplankton blooms in surface waters could occur if fish restrict the vertical migration of zooplankton, even if predation is not a major cause of zooplankton mortality. Zooplankton in deep water might then decline to due declines in food conditions and oxygen concentrations. Thus, deep water refuges with sufficient O₂ and food are necessary for the coexistence of larger zooplankton (especially Daphnia) and fish (Wright and Shapiro 1990).

As part of this study we have collected considerable additional data, including counts of about 150 phytoplankton samples, observations on zooplankton reproductive rates, and additional information on water temperature, dissolved O₂, and nutrients. We have begun analyzing these data and will include them in later publications. We will also continue monitoring Wyland Lake at least through September 1990.
Fig. 11. Results of the 1990 mesocosm experiment; effects of fish predation on zooplankton dynamics. Each data point is a mean ± SE for a pair of replicate 7,000 liter enclosures.
Fig. 12. Results of the 1990 mesocosm experiments; effects of the addition of Daphnia pulicaria and Daphnia hyalina from Little Crooked Lake on native zooplankton from Wyland Lake. Open circles are enclosures without added Daphnia whereas solid circles are enclosures with added Daphnia. The left column of figures are represent enclosures without added nutrients whereas the right column represent nutrient-enriched enclosures. Each data point represents the mean ± SE for a pair of replicate enclosures (note log-scales). Microscope counts are not yet complete for the second replicate for July 5 and for all samples from the last sampling date, July 12, 1990.
Fig. 13. Results of the 1990 mesocosm experiment; effects of Daphnia additions on the depth distributions of native Wyland Lake zooplankton. Samples were collected with a 25-liter Schindler trap at 1 m depth intervals. Open circles represent enclosures without added Daphnia; solid circles represent enclosures with added Daphnia. For each species, the figure on the left represents an enclosure without added nutrients, whereas the figure on the right represents a nutrient-enriched enclosure. Each data point represents a single enclosure; samples from replicate enclosures still being counted.
PRINCIPLE FINDINGS, CONCLUSIONS, AND RECOMMENDATIONS

Our results demonstrate that removing small planktivorous fish from a lake can result in substantial improvements in water quality. This occurred under the ambient, moderate nutrients levels found in Wyland and under heavy nutrient loading in the 1990 enclosure experiments. Unexpectedly, the enclosure experiments showed that the native zooplankton community dominated by small to moderate-sized species was just as effective in preventing algal blooms as was a community with introduced large *Daphnia pulicaria*. The enclosure experiments also showed that large *D. pulicaria* strongly suppressed native zooplankton through competition for food. Thus these experiments suggest that the association between large daphnids and clear water is due to the tendency for large species to dominate when fish are scarce, and does not reflect an inability of small grazers to prevent algal blooms. Since native *Daphnia* and *Ceriodaphnia* were both depressed by fish, it appears that these member of the *Daphnia* family are effective in strongly depressing algal abundance. Lynch and Shapiro (1981) also found that communities dominated by *Ceriodaphnia* were effective in preventing algal blooms.

Since the primary reason for removing fish from Wyland Lake was to improve conditions for rainbow trout, it is clear that reducing the abundance of small planktivorous fish in lakes is quite compatible with good fisheries management practices. A correlation between good trout lakes in Michigan and the presence of large *Daphnia* (Galbraith 1975) is probably due to three factors. First, large *Daphnia* are used by trout as food. Since trout only eat the largest *Daphnia*, however, trout have very little impact on *Daphnia* abundance and size (Galbraith 1967). Second, the presence of large *Daphnia* in a lake is indicative of a low abundance of small warm-water fish which compete with trout for other food resources, such as insect larvae. Finally, large zooplankton, and especially, large *Daphnia* help to improve water clarity and this helps to maintain oxygen in the deeper cooler waters required by trout during the summer.

Rotenone treatment is only practical in small lakes and its effects only last as long as small planktivorous fish are significantly reduced in abundance. Rotenone treatment should probably be followed by stocking with piscivorous fish, such as largemouth bass, muskies, or brown trout. Even a few surviving planktivores such as bluegills and golden shiners will rapidly increase in abundance following rotenone treatment. In the complete absence of predators and with abundant food, they might quickly surpass pretreatment levels. Thus, by the end of next, Wyland Lake may suffer from higher levels of planktivory and poorer water quality than pre-treatment levels. The results of the 1971 treatment, suggest, however, that stocking with bass might allow at least several years of improved water quality.
Large predators such as salmon, bass, and muskies might be stocked in larger lakes to improve both fishing and water quality. The effects of stocking are likely to be less dramatic than the effects of removing all or nearly all fish by rotenone treatment. A review of effects of stocking predators suggests that this approach is most likely to be effective when nutrient loading is also reduced (Benndorf 1987). Thus, the best approach is one which attempts to increase the abundance of large piscivorous fish while simultaneously reducing nutrient loading.

As show by our results, many zooplankton, especially Daphnia tend to remain in deep water during the day. Such populations often migrate to the surface at night but may avoid surface waters even during the night when fish are abundant (Lampert 1987). These behaviors probably help account for the reduced impact of zooplankton on water clarity in deep lakes relative to shallow lakes (McQueen 1990). Furthermore, our enclosure experiments suggest that reduced water clarity results in a deterioration of Daphnia’s deep-water habitat. Thus, fish may adversely affect Daphnia directly by predation, and by indirectly causing a deterioration of the deep-water habitat. Behavioral and ecological interactions at the herbivore and predator trophic levels clearly have important consequences for water quality in lakes.
NUMBER AND DISCIPLINE OF STUDENT ASSISTANTS

A total of seven undergraduate biology majors were supported by the project, including four students from Indiana-Purdue University at Fort Wayne, one student from Purdue University, West Lafayette, one student from the University of California at Berkeley, and one student from Iowa College. These students completed three special research projects for credit.
EMPLOYMENT STATUS OF SUPPORTED WITH WRRC FUNDS

Of the seven students supported by WRRC funds, five are still undergraduates, one is beginning graduate school at the University of Michigan, and one plans to work as a high school science teacher.
SOURCES CONSULTED


Queens's Printer, Ottawa.

