THE RISE AND FALL OF A DOMINANT PLANKTIVORE: DIRECT AND INDIRECT EFFECTS ON ZOOPLANKTON

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Abstract. We analyzed a 14-yr time series (1976–1989) of planktivorous fish and zooplankton from Lake Mendota, Wisconsin. Planktivory increased between 1977 and 1978 due to an increase in biomass of that year class and decreased in August 1987 after a summer kill of cisco in the lake. Yellow perch (Perca flavescens) and other cisco year classes contributed <25% of the total planktivory during 1978 to 1987. Time series analysis revealed that this 10-yr pulse in planktivory rates was associated with changes in the Daphnia species and biomass. In years with low planktivory, higher biomass of daphnids dominated by Daphnia pulicaria developed earlier in the spring and lasted longer into the summer. This was also associated with an earlier and longer spring clear-water phase. In years with high planktivory rates, daphnid biomass was generally lower and dominated by the smaller Daphnia galeata mendotae. However, there was no significant effect of planktivory on the early summer peak in Daphnia biomass that is associated with a clear-water phase. The dynamics of this Daphnia peak are apparently regulated by Daphnia-algae interactions and not by planktivory rates. The seasonal and interyear changes in Daphnia species composition can be explained by the combined effects of planktivory, dynamics of food resources, and the physiological ecology of the two Daphnia species. There was no significant effect of increased planktivory on total zooplankton biomass due to a compensatory increase in cyclopoid copepods and no response by calanoid copepods.

The recent history of Lake Mendota illustrates a 10-yr period of predation imposed by a single year class of a large, long-lived, obligate planktivore. It is an example of variability in a lake ecosystem scaled to the life-span of a dominant fish species.

Key words: cisco; Daphnia; fish; Lake Mendota; planktivory; time series; zooplankton.

INTRODUCTION

The link between fish and zooplankton is a cornerstone in current attempts to integrate predator and nutrient control pathways in aquatic ecosystems (Oksanen et al. 1981, Shapiro and Wright 1984, Carpenter et al. 1985, McQueen et al. 1986, Persson et al. 1988). A causal relationship between fish planktivory and zooplankton species composition and abundance has been firmly established since the early work of Hrbacek et al. (1961) and Brooks and Dodson (1965), although the mechanisms involved can be complex and include release of invertebrate predation (Dodson 1974) and varying levels of competitive interactions among zooplankton species (DeMott 1989). Recent reviews include Lazarro (1987), Northcote (1988), Mills and Forney (1988), and Glowiwicz and Pijanowska (1989). Abundance of planktivorous fish is highly variable between years because of the notoriously variable year class strength of many important planktivores (Sissenwine 1984). There may therefore be a temporal scale of variability in lake ecosystems related to the life-span of a dominant fish species (Carpenter 1988). Analysis of long time series is necessary for testing this hypothesis. Unfortunately, few long-term (over 10 yr) zooplankton data series exist that also include data on planktivorous fish and the few that do often rely on indirect measures of fish abundance such as indices from limited trawl surveys, etc. (Emmons and Litt 1982, Scavia et al. 1986, Jasby et al. 1990; but see Lamens 1988, Mills and Forney 1988, Benndorf 1990, and Lyche et al. 1990).

Whole-lake manipulations are necessary for testing
hypotheses of food web interactions in natural systems, and these manipulations need to be strong enough to allow us to observe a response above the natural inter- and intrayear variability (Walters 1986, Carpenter and Kitchell 1988, Carpenter 1990). Strong manipulations can be difficult to implement in large lakes, especially when the lake is heavily used by the public (Kitchell 1992). It is therefore important to also take advantage of natural perturbations as an opportunity for learning and as a complement to experimental manipulations (Carpenter 1990). Scientific "exploitation" of natural events often yields important insights into food web dynamics (e.g., de Bernardi and Guissani 1978, Kohler and Nye 1981, Scavia et al. 1986, Siegfried 1987, McQueen et al. 1989, Hall and Ehlinger 1990, Wurtsbaugh and Berry 1990).

In this paper, we analyze a 14-yr time series (1976–1989) of planktivorous fish and zooplankton in Lake Mendota, Wisconsin, a large (40 km², mean depth 12.7 m, maximum depth 25.3 m) eutrophic lake adjacent to the University of Wisconsin–Madison campus. Cisco (Coregonus artedi) was the dominant planktivorous fish in 1987 before a major summer kill that removed 90% of the population (Vanni et al. 1990, Luecke et al. 1992, Rudstam et al. 1992b). Here, we document that one cisco year class hatched in 1977 was the major planktivore in the lake through 1987, a period of 10 yr. We use intervention analysis, a time series method (Wei 1990), to show that increased planktivory during this "cisco decade" was associated with lower Daphnia biomass and a shift to a smaller Daphnia species. The smaller Daphnia was, in turn, associated with a later and shorter spring clear-water phase. This study is one of the first direct observations of a temporal scale of variance in a lake ecosystem that is related to the life-span of a dominant fish species.

Shorter term, seasonal changes in zooplankton abundances and species composition have also been attributed to changes in predation rates, particularly to increased predation from young-of-year (YOY) fish in summer and autumn (Sommier et al. 1986, Mills and Forney 1988, Hewett and Stewart 1989, Rudstam et al. 1992b). However, planktivorous fishes have long life-spans relative to their zooplankton prey. In a closed system like Lake Mendota, planktivorous fish cannot respond numerically to seasonal changes in zooplankton abundances. The response of planktivorous fish to seasonally varying resources is limited to behavioral or functional responses, modulated by the temperature dependence of fish consumption rates (Northcote 1988, Gliwicz and Pijanowska 1989). Luecke et al. (1990, 1992) argued that the Daphnia population in Lake Mendota is regulated by fish planktivory in the spring and in late summer, but not during the early summer peak in Daphnia associated with the clear-water phase (typically occurring in late May and June). Here, we use seasonal intervention analysis to test this hypothesis with the 14-yr time series.

**Materials and Methods**

**Zooplankton**

Integrated zooplankton samples were collected with vertical net tows (15 cm diameter conical net, Nitex number 20 screening, 75–80 µm mesh) from 0.5 m above the lake bottom to the surface in water depths 21–24 m near the deepest point in the lake as part of a long-term limnological research study of Lake Mendota conducted by the Wisconsin Department of Natural Resources' Bureau of Research (Lathrop and Carpenter 1992b). Sampling was generally conducted every 2 wk during the open-water period until late November or early December and once or twice during the winter months. In 1977 and 1978, samples were taken at approximately monthly intervals in the open-water period. Net efficiency was estimated as 50% based on comparisons on three separate dates of abundances of major zooplankton groups sampled with the net and with a 10 cm diameter flexible tube sampler (range between dates 0.42–0.58; Lathrop and Carpenter 1992b). Zooplankton samples were preserved with 4% formalin (sugared formalin and seltzer water were used after 1985). Three to five separate 1-mL subsamples were counted, representing ~2–3% of the total sample. All Daphnia and the first 5–10 specimens of other species were measured in each subsample (total length excluding the tail spine, up to 400 Daphnia measured during peak abundances). Zooplankton densities were standardized to numbers per square metre over a 20-m water column (see Lathrop and Carpenter 1992b). Biomass was computed using length–mass regressions from Lynch et al. (1986) for Daphnia spp. and from Downing and Rigler (1984) for all other species. Species composition, biomass, and seasonal dynamics obtained from these samples were similar to results obtained from independent samples collected during the ice-free season, 1987 to 1989, with a metered Clark-Bumpus net (Lathrop and Carpenter 1992b). Comparison of all samples taken < 4 d apart in 1987–1989 (38 comparisons) resulted in an average difference between our vertical net and the Clark-Bumpus tows of 0.3 ± 0.6 g/m² (mean ± 1 SE) for Daphnia and 2.3 ± 1.6 g/m² for total zooplankton biomass.

**Fish**

The open-water fish populations of Lake Mendota have been surveyed during the end of August or first half of September using vertical gill nets and acoustics since 1981 as part of the Long-Term Ecological Research–Northern Temperate Lakes project. Vertical gill nets (4 m wide, 18–23 m deep, 19-, 25-, 32-, 38-, 51-, 64-, 89-, and 127-mm stretch, multifilament mesh) were suspended from the surface to the bottom in 18–23 m deep water (1981–1982, 1984–1989) or in 13–15 m deep water (1983). The nets were set for 48 h and checked every 6 h in 1981 and every 24 h in 1982–1989. Additional samples were collected from April
through October in 1986–1989 with monofilament mesh nets of the same mesh sizes and construction (Luecke et al. 1990, 1992).

Mesh sizes were chosen to minimize the size selectivity of the combined gang of gill nets. The calculated relative retention probability varied between 0.65 and 1 for 80–450 mm long cisco and perch (Berst 1961, Rudstam et al. 1984). This size range included the lengths of cisco and perch present in the lake during autumn sampling. Uncorrected catch data should therefore reasonably well represent the size structure of cisco and perch in the lake and we did not correct catches for the size selectivity of the nets. From 1981 to 1985, length was measured on all fish caught and mass was measured on the first five fish in each 10-mm size class. Scale samples were taken from the side of the body close to the pectoral fin and above the lateral line on the weighed fish. From 1986 to 1989, length, mass, and scale samples were taken on all fish caught. Additional scales for aging were available through a survey of ice anglers conducted by the University of Wisconsin–Madison Ecology of Fishes class in February of 1977, 1979, 1980, and 1981.

Cisco scales showed both winter and summer growth checks. Cisco ages determined from scales were validated by following the development of the strong 1977, 1982, and 1983 year classes, by comparison with otoliths (Rudstam 1983), and by comparisons with length frequencies (Fig. 1). Ciscos could be aged at least up to age 12. Perch were difficult to age after age 4 due to crowded annuli. Older age groups were lumped in the age class 4 and over. The perch scales collected in the winters of 1977–1981 were also aged by Woolsey (1986) with similar results.

Acoustic data were collected both day and night with a 70 kHz portable single-beam echosounder (Simrad EV/M, half power to half power beam width 11.2°, pulse length 0.6 ms, TVG [Time Varied Gain] of 40 log R). Calibrations with standard targets in 1989 and 1990 showed only small (1 decibel [dB]) difference between this unit and the specifications given by Simrad when purchased in 1981. In 1987, the data were computer processed in the field. In other years the signals were recorded on cassette tapes. Unfortunately, some tapes were recorded at too high a gain and could not be used (including all tapes from 1984). Since large cisco (300–400 mm, target strength of ~36 dB; Lindem and Sandlund 1984, Rudstam et al. 1987) were common from 1981 through the summer of 1987, we used the targets from this fish group as an in situ check of tape recorder gain and system performance.

The acoustic signals were converted to fish abundances using analysis of single fish echoes (deconvolution for 1987 data, Clay 1983, HADAS program for other years, Lindem 1990). These two methods give the same fish abundances for fish densities <8000 fish/ha (Rudstam et al. 1988). The analyses yield abundances of different fish size classes when these are sufficiently distinct (Lindem and Sandlund 1984, Rudstam et al. 1987). The two abundant open-water fish species in Lake Mendota, cisco and perch, differed substantially in length. Yearling cisco were larger than 250 mm in the summer whereas yearling to 5-yr-old perch ranged from 120 to 250 mm (Fig. 1). The acoustic abundances were divided in two groups, targets above ~40 dB and targets between ~46 and ~40 dB. With the target strength to length relationship given by Lindem and Sandlund (1984), these groups correspond to fish sizes larger than 250 mm (considered cisco in 1981–1987 when cisco dominated this size class) and fish between 120 and 250 mm (considered perch). In 1988 and 1989, we used the proportion of cisco in the larger size class from gill net catches to estimate the proportion of "cisco-size" targets attributable to cisco. Abundances in the top metres of water cannot be measured with acoustics, and abundances in these water layers were estimated from gill net catches. Net catches close to the surface rarely exceeded 5% of total catch as both cisco and perch are concentrated in the lower epilimnion in the autumn (Rudstam and Magnuson 1985, Luecke et al. 1990, McCarty 1990).

In all years, one south-north transect and one east-west transect across the whole lake were surveyed. These transects were repeated some years. In 1988–1989, we surveyed additional transects following a zigzag pattern across the lake. A survey consisted of between 2 and 4 h of recordings, corresponding to a survey length of 15–30 km. Water depths shallower than 5 m were not sampled. Estimates of variance were obtained by analyzing 6–8 km long subsets of the total survey, yielding
estimates of fish abundances in the lake for most sampling occasions. Survey maps and additional details on the acoustic sampling are in Rudstam and Johnson (1992).

Total planktivity rates by cisco and perch were estimated using bioenergetic models developed for perch (Kitchell et al. 1977) and for bloater (Coregonus hoyi) (based on several Coregonus species; Luecke et al. 1992; L. G. Rudstam et al., unpublished manuscript) and the computer program by Hewett and Johnson (1987). Consumption necessary to account for observed growth was calculated using an annual simulation period. These models require input of occupied temperatures, diet, and energy density (energy content per unit mass) of fish and prey. Fish are often distributed in water temperatures close to that preferred, but low oxygen levels in the hypolimnion of Lake Mendota force cisco into higher water temperatures during the summer and early autumn (Rudstam and Magnuson 1985). Here we assumed that the fish reside in water temperatures closest to the preferred temperature (16°C for cisco, L. G. Rudstam et al., unpublished manuscript, and 23°C for perch, Kitchell et al. 1977) that also contained oxygen concentrations above 4 mg/L. This assumption provides a good approximation to the seasonal changes in depth distribution of cisco and perch observed in Lake Mendota (Luecke et al. 1990; L. G. Rudstam, personal observation). Temperature and oxygen profiles were available from R. C. Lathrop (unpublished data) and Brock (1985). The diets of cisco and perch were dominated by Daphnia, Leptodora, and copepods from 1987 through 1989 (Luecke et al. 1992). We used an energy density of 2930 J/g wet mass for the prey and an energy density of 4600 J/g wet mass for perch (Luecke et al. 1992). Energy density of coregonid in general increase with fish size from approximately 2400 J/g wet mass for a 1-g fish to 9200 J/g wet mass for a 100-g fish (Gunckel 1981; L. G. Rudstam et al., unpublished manuscript). Energy density of cisco in Lake Mendota also varies with season and decreases from approximately 9200 J/g wet mass to 7530 J/g wet mass over the summer (data from 1987, Luecke et al. 1992). These changes in energy density with cisco size and season were incorporated in the bioenergetics calculations. Consumption in wet mass was transformed to dry mass using a dry to wet mass ratio of 0.2 (Downing and Rigler 1984).

Statistical analysis

Intervention analysis is a time series technique used to test for nonrandom change in a response variable following a change in an input variable. Ecological applications are discussed by Carpenter (1990, in press) and Jassby and Powell (1990); thorough and rigorous explanations are given by Box and Tiao (1975) and Wei (1990). Intervention analysis tests the null hypothesis that no change occurred in the response time series, in a manner that accounts for autocorrelation and seasonality (if any) in the data. A significant result means that the response series changed nonrandomly following the change in the input variable; it does not prove that the input variable caused the change (Carpenter et al. 1989; Carpenter, in press). Any causal interpretation hinges on ecological evidence; the statistical result merely indicates that there is something nonrandom to explain.

Intervention analysis involves first fitting an autoregressive moving average model to the response series to account for autocorrelation and/or seasonality (Wei 1990). Then an additional model term is added for the effects of the input series on the response series. The change in the input is represented by a dummy time series, for example, with values of zero before the change and one afterward. The model for effects of the input series can take a variety of forms to represent delayed, ramped, asymptotic, or step changes in the response series (Box and Tiao 1975). We used the simplest and most conservative model, a step change with no lag. If the model for effects of the input series has parameters that are significantly different from zero, then we infer that a nonrandom change has occurred in the response series. This procedure may underestimate the effect of the input variable, because some of the variance removed by the autoregressive moving average model may in fact be due to the input series (Carpenter, in press). This point is moot if the input model is significant.

Intervention analyses were performed using zooplankton time series as responses and cisco as inputs. Response series were total zooplankton biomass, total Daphnia biomass, cyclopoid biomass excluding nauplii, calanoid biomass excluding nauplii, and proportion of total daphnid biomass attributable to Daphnia pulcaria. All biomass values were in grams dry mass per square metre. Each year was divided into 13 4-wk periods (tetraweeks), and the average biomass was computed from all measurements made in each tetraweek. Winter is a period of very slow biological activity, and samples were less frequent during winter months. To reduce the number of missing values in the series, we merged the first two tetraweeks (1 January–25 February) and the last two tetraweeks (4 November–31 December) to yield 11 time periods in each annual cycle. This procedure left 17 remaining missing data points in the series of 154 observations, of which 10 occurred during a 1st, 2nd, or 11th time period. Each of these remaining missing points was assigned the mean value for the appropriate time period over all other years. This procedure is conservative in the sense that it makes it more difficult to detect interyear differences such as input effects. Since missing data occurred mainly in the winter, we may fail to detect effects of cisco during that season.

Two types of intervention analysis were performed, one to test for overall effects of changes in planktivity, and the other to test for season-specific effects. All time
series analyses were performed using the ARIMA procedure of the Statistical Analysis System (SAS 1988).

To test for overall effects, we fit seasonal autoregressive models of the form

\[(1 - \phi_1 B - \phi_2 B_2)(1 - \phi_1 B_1 - \phi_2 B_2)(Z(t) - C) = \alpha(t) + \alpha S,
\]

where \(Z(t)\) is the time series of the response variable, \(C\) is a constant, the \(\phi\) are autoregressive parameters, \(B_2\) is the backshift operator \((B_2 Z(t) = Z(t - 2))\), \(\alpha(t)\) is the time series of residuals, \(\alpha\) is the intervention effect, and \(S\) is the dummy variable that represents the intervention. A significant \(\alpha\) term indicates that the change in the cisco was followed by a nonrandom change in the zooplankton. \(S\) is zero when cisco are rare (1976–1977 and 1988–1989) and one when they are abundant (1978–1987). The models were identified using autocorrelation and partial autocorrelation functions. These diagnostics never indicated the need for moving average terms. Residual series from all models had no significant autocorrelations. The \(\phi_2\) terms were needed for only certain time series (proportion of \(D.\) pulex, biomass of calanoid copepods). Calanoid copepods did not have a significant seasonal pattern and the \(\phi_1\) term was omitted from that analysis.

To test for seasonal effects, we fit models of the form

\[(1 - \phi_1 B - \phi_2 B_2)(1 - \phi_1 B_1 - \phi_2 B_2)(Z(t) - C) = \alpha(t) + \alpha_1 S_1 + \alpha_2 S_2 + \alpha_3 S_3 + \alpha_4 S_4 + \alpha_5 S_5,
\]

where the dummy variables \(S_i\) represent planktivory effects in each of five time blocks or seasons (winter, spring, early summer, late summer, and autumn). All other terms in the seasonal models have the same definitions as in the overall intervention analyses. If an intervention term \(\alpha_1\) is significantly different from zero, then zooplankton during season \(i\) changed nonrandomly following a change in cisco. Each \(S_i\) is zero except for certain time periods during years with high cisco densities (1978–1987), when values of one are assigned. \(S_1\) represents winter planktivory (time periods 1–2, days of the year 1–84). \(S_2\) represents spring planktivory (time periods 3–4, days of the year 85–140). \(S_3\) represents early summer planktivory (time periods 5–6, days of the year 141–197). \(S_4\) represents late summer planktivory (time periods 7–8, days of the year 198–254). \(S_5\) represents autumn planktivory (time periods 9–11, days of the year 255–365).

**RESULTS**

**Zooplankton**

In 1976 to 1989, a peak of *Diacyclops thomasi* in the winter and early spring was followed by a peak in *Daphnia (D. galeata mendotae* or *D. pulex*) in May and June (Fig. 2). Later in the summer, *Daphnia* decreased and copepods (the calanoid *Skistodiaptomus oregonensis*, *Leptodiaptomus sicoloides*, and *Agalodiaptomus clavipes* and the cyclopoids *Mesocyclops edax* and *Acanthocyclops vernalis*) generally increased in abundance. In some years, there was a second peak of *Daphnia* in the autumn. Other cladocerans (*Chydorus sphaericus*, *Diaphanosoma birgei*, *Bosmina longirostris*, and *Eubosmina coregoni*) were only occasionally common. Retifers were rare (see also Lathrop and Carpenter 1992b).

There were differences in *Daphnia* species composition among years (Fig. 2). In 1976, 1977, 1988, and 1989, the larger *D. pulex* dominated in the spring and summer while *D. galeata* was relatively rare. In these years, *Daphnia* contributed the largest fraction of total zooplankton biomass. With the exception of 1986, *D. galeata* was the dominant daphnid in the spring and summer of 1978–1987. *D. pulex* was rare from 1978 through 1983, increased from 1984 to 1986, and was rare again in 1987. In the spring of 1986, both daphnids occurred in similar numerical abundances (Lathrop and Carpenter, 1992b), but *D. pulex* had a much larger biomass because of its greater body size (Fig. 2). *Daphnia* biomass during the
autumn months were low in 1971-1983 compared to the other years (Fig. 3). *D. galeata* was generally the dominant autumn daphnid, although *D. pulicaria* was present in 1976 and 1988-1989 and *D. reticulata* occurred in similar numerical abundances but lower biomass than *D. galeata* in 1978-1987. The average daphnid length decreased from 1977 to 1978, stayed below the long-term average from 1979-1983, and started to increase again in 1984. Lengths in 1989 were similar to lengths in 1976 (Fig. 3). Associated with the change in *Daphnia* species was a change in copepod abundances. *Diacyclops* was more abundant when *D. galeata* was the dominant daphnid (1978-1987) than when *D. pulicaria* dominated (1976-1977, 1988-1989). There was no comparable change in calanoid copepod biomass or in total zooplankton biomass (Fig. 2).

The spring peak in *Daphnia* (defined as a biomass >3 g/m²) was longer and started earlier during *D. pulicaria* years than during *D. galeata* years ($P < .001$, Mann–Whitney test, Fig. 4), although peak biomass was not consistently smaller in 1978–1987 compared to 1976–1977, and 1988–1989 (Fig. 2). The spring clear-water phase also started earlier and lasted longer during *D. pulicaria* years than during *D. galeata* years ($P < .001$, Mann–Whitney test, Fig. 4).

**Fish: vertical gill nets**

A total of 10 fish species were caught in autumn vertical gill nets from 1981 through 1989 but perch and cisco accounted for 85–98% (average 93%) of the total number of fish caught. Cisco and perch also dominated samples collected in spring and summer of 1986 to 1989 and for nets set at an intermediate station (14 m depth) in 1987–1989 (Luecke et al. 1990; L. G. Radstrom, unpublished data). Fish <120 mm were only present in the autumn of 1988 (YOY black crappie). YOY perch were not present in the open-water gill nets.
even in years with strong recruitment. YOY perch are 70–90 mm long in the middle of September in Lake Mendota and should have been caught by these gill nets if present. This size group of perch is abundant in catches in the same nets from other lakes (Rudstam and Magnuson 1985). Perch represented 86–98% of fish <250 mm with the exception of 1985 when a total of only 35 fish were caught in this size range (Fig. 5).

Cisco dominated the >250 mm fish size group (88–98%) before the die-off in 1987. The only cisco age class <250 mm in the autumn was the YOY (Fig. 1).

Both the cisco and perch populations were dominated by a few strong year classes. This was most pronounced for cisco. The 1977 year class made up 55% of the cisco caught in 1981, the first year of gill netting, and continued to dominate the cisco population throughout the 1980s despite some recruitment in 1982 and 1985 (Fig. 6). Perch also had a strong year class in 1977 that dominated the catch in 1981. Subsequent good year classes occurred in 1981, 1982, 1983, and 1985. There has been no strong perch year class since 1985 (Fig. 6; Rudstam et al. 1992a). Increasing number of perch in the >250 mm size group in 1988 and 1989 is due to the increasing size of the 1985 year class (Fig. 5). Length at age did not vary greatly between different years, although the 1977 year class of both perch and cisco grew more slowly than the year classes formed in 1981–1985.

**Fig. 6.** Age class composition of perch and cisco in Lake Mendota from 1976 to 1989. The number of aged fish each year is noted above each bar. Fish from 1976 to 1980 were caught with hook and line through the ice during the following winter. Fish from 1981 to 1989 were caught in gill nets in August–September. Perch are separated into four age groups because of difficulty in aging older fish and because of the large number of cohorts in the perch population. No scales were available for cisco in 1976–1978 and 1980, and no perch scales were available for 1977. The age structure depicted for 1977 perch is from Woodley (1986).


**Fish: acoustics**

Acoustic abundance estimates are available for cisco and perch for 1981–1989 except for 1984 (both species) and 1987 (perch). Cisco abundance was over 600 fish/ha (300 kg/ha) in 1941 (Figs. 7 and 8). There was a 30% reduction in cisco between September 1982 and September 1983 despite some recruitment in 1982. This decrease represents a cisco summer kill that occurred in August 1983 (Magnussen and Lathrop 1992, Rudstam et al. 1992a). After 1983, the population declined by ~15% per year to 200 fish/ha (165 kg/ha) in July 1987. The large die-off of cisco in August 1987 removed >90% of the remaining population. Another die-off in August 1988 further reduced the popula-
perch in May 1988 (Rudstam and Johnson 1992). The mark-recapture estimate of the perch population in the spring of 1988 was 218 perch/ha (95% CI: 180–268), which should be compared to an average acoustic estimate for 1988 of 319 perch/ha (95% CI: 177–461). Estimates of the perch population in the end of 1989 based on the 1988 mark-recapture study and harvest calculated from annual lake-wide creel surveys (Johnson and Staggs 1992) range between 116 (no natural mortality) and 53 perch/ha (30% natural mortality). This is also consistent with the acoustic estimate from September and October 1989 (99–117 perch/ha).

**Planktivory rates**

We combined acoustic abundance estimates and age structure data to reconstruct the cisco populations in Lake Mendota back to 1976. Since 95% of the cisco population in 1981 was from the 1977 year class, we can back-calculate the population size for the period 1977–1981 using the average mortality rate observed in years with no summer kill (15%, range 8–22%). We further assumed that mortality in excess of the 15% annual natural mortality rate was caused by the summer kills in August of 1983, 1987, and 1988. The development of the cisco population in Lake Mendota is based on these assumptions is depicted together with the acoustic abundances in Fig. 7. All age groups including YOY were assumed to be feeding on zooplankton in the open water throughout the year.

Like the cisco population, the perch population in 1981 was also dominated by a 1977 year class. Mortality rates of perch in Lake Mendota consist of both fishing and natural mortality, and total adult mortality was estimated to be 50% per year by Johnson et al. (1992, based on detailed data for the 1987–1989 time period). This is consistent with the decline in the perch population since 1986 observed with acoustic (Fig. 7). We used this mortality rate to back-calculate perch abundances from the 1981 estimate to the summer of 1978 when age 1 perch of the 1977 year class recruit to the open water. Woolsey (1986) estimated the perch population in February 1977 to be 10% of the population in February 1979 based on an analysis of catch-per-effort data from ice anglers in February 1977–1980. The catch per line per hour was 1.8 perch in February 1977, 0.4 perch in February 1978, and 12.0 perch in February 1979 (Woodsey 1986). Perch abundance in 1976 must have been low compared to 1977–1980 since perch hatched earlier than 1977 were rare in samples from 1977 through 1981 (Fig. 6). Here we assume the perch population in February 1977 to be 10% of the population in February 1979.

Perch in Lake Mendota occur in the open water as fish larvae, move into the littoral zone at a size of ~25 mm TL (Post et al. 1992), and are caught in littoral sampling gear (gill nets, fyke nets, shoreline seines) in late summer and autumn of their 1st yr (Luecke et al. 1990, McCarty 1990, Johnson et al. 1991). Perch prob-
ably do not use the open water again until the autumn of their 2nd yr (age 1). Gill nets set at the deep hole caught no age 1 fish from the strong 1985 year class in May of 1986 (total catch of 15 perch) or in July of 1985 (198 perch), but 45% of the autumn catch were age 1 fish that year (27 perch). Our acoustic abundance estimates of the pelagic perch population corroborate these observations from gill nets. We observed an increase in "perch-size" targets following the strong 1985 year class first in the autumn of 1986 (Fig. 7). Thus, we assumed that perch recruit to the open water pelagic fish populations as age 1 in late summer (August). This assumption causes a sharp rise in our estimates of pelagic perch populations in late summer in years after a strong perch year class (1978, 1982, 1983, 1984, 1985; Fig. 7).

Planktivory is a function of fish biomass, allometric relationships governing respiration and consumption, and species-specific differences in response to temperature. Bioenergetic models account for these differences and can be used to estimate food consumption based on observed growth (Kitchell 1983). Perch were divided into four age groups (age 1, 2, 3, and ≥4) according to catches in gill nets and assumed to grow according to the average perch growth rate observed in 1976-1989. Cisco were represented by the 1976, 1977, 1982, 1985, and 1989 age classes using observed cohort-specific growth rates. The resulting estimates of planktivory show a large increase from 1977 to 1978 (as a result of the large 1977 cisco and perch year classes) and a large decrease in the summer of 1987 (Fig. 8). Planktivory is strongly dominated by cisco, in particular by the 1977 year class. This single year class contributed between 65 and 88% of the total daily planktivory between 1977 and 1987 with the exception of brief periods in the summer with high water temperatures. Perch contributed <25% of daily planktivory from 1977 to 1987 during most of the year (Fig. 8). Planktivory rates decreased from 1979 to 1987 by ≈50%, primarily a result of an aging cisco population, with a somewhat larger decline in August 1983 associated with a minor summer cisco kill.

Effect of planktivory on zooplankton dynamics

The intervention analysis revealed that high cisco planktivory was associated with a significant negative effect on total Daphnia biomass and on the proportion of D. pulicaria, a significant positive effect on cyclopid biomass, but no significant effects on total zooplankton or calanoid biomass (Table 1). The intervention was initiated in the beginning of 1978 and maintained until the cisco summer kill in August 1987. This is the period when peak spring and autumn planktivory rates (dry mass consumption) exceeded 0.1 g m⁻² d⁻¹.

The seasonal intervention analysis (Table 2) showed significant negative effects of planktivory on the proportion of D. pulicaria in all seasons and on the total Daphnia biomass in winter, spring, and late summer, but not in early summer, the time period associated with the peak in abundances of Daphnia and a clear-water phase. Effects on autumn Daphnia biomass were marginally significant ($P < .10$). Cyclooids were positively affected by planktivory during winter, spring, and early summer, but not during late summer and autumn. Thus, the effects on cyclooids were primarily on the winter and spring population of Dicaryochels thomasi. Effects on total zooplankton and calanoid biomass were not significant for any season. There are also indications of a response of Daphnia to the absolute level of planktivory (Fig. 9). The period between 1979 and 1983 had the highest estimated planktivory rates and the lowest proportion of D. pulicaria. The spring, late summer, and autumn Daphnia biomass values were very low during these years. Again, we see less effect of planktivory on Daphnia biomass during the early summer. As planktivory decreased from 1984 through 1987, we observed more variable biomass and also one year with relatively high proportion of D. pulicaria (1986). The year 1978 also had relatively lower planktivory rates than 1979–1983 and higher biomass of Daphnia and proportion of D. pulicaria. The smallest Daphnia, D. retrocurva, was present in late summer and autumn primarily during the

<table>
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* The intervention, an increase in total planktivory in 1978 (from the 1977 year class of cisco and perch), is maintained until August 1987 (cisco summer kill). The shift parameter α tests for nonrandom changes in the time series associated with the intervention. A negative value for α represents a decrease in the response variable and a positive value indicates an increase in the response variable associated with the increased planktivory. df = 150 and all t ratios > 2 are significant at the 5% level.
Table 2. Results of time series intervention analyses for seasonal effects of a shift in planktivory on zooplankton biomass and on proportion of total Daphnia biomass consisting of Daphnia pulicaria (see Table 1).*

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<th>Estimate</th>
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<th>df</th>
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* The intervention is divided into five seasonal components, winter (w), day of year 1–84, spring (s), day of year 85–140, early summer (e), day of year 141–195, late summer (l), day of year 196–245, and autumn (a), day of year 246–365, $t$-tests were significant at the 0.05 level.

Discussion

The seasonal patterns of abundance and species replacements of zooplankton in Lake Mendota between 1976 and 1989 are typical of temperate eutrophic lakes (Summer et al. 1986, DeMott 1989). They were also similar to earlier studies in Lake Mendota (reviewed by Lathrop and Carpenter 1982), to results from paleoecological analysis (Kitchell and Sanford 1992) and to independent data sets collected during the same time period (Pedros-Alio and Brock 1985, Luecke et al. 1992). Our 14-yr data set spans a time period in Lake Mendota with dramatic changes in the planktivorous fish population and concomitant changes in planktivory rates. Planktivore biomass shows both a large increase from 7 to 37 kg/ha from 1977 to 1978 and a large decrease (from 200 to 50 kg/ha in August 1978) during this time period. The estimates of planktivory resulting from these changes depend on assumptions and ob-

![Figure 9. Species composition and dry biomass of Daphnia in the spring (April–mid-May), early summer (mid-May–mid-July), late summer (mid-July–late August), and autumn (September–December) time periods. Our estimates of average total fish planktivory during these time periods are overlaid as a solid line.](image-url)
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...observations on fish abundance, energy density, growth rates, and occupied temperatures as well as on assumptions of fish physiology incorporated in the bioenergetics models. The main sources of error are in the abundance estimates and in the bioenergetics models. Growth rates have been relatively constant over the study period and energy densities of cisco and perch have been measured and are comparable to values for these and similar fish species from other lakes (Kitchell et al. 1977, Gunkel 1981). Allowing 50% of cisco or perch to reside in 4°C colder or warmer water (when possible) changes in planktivory estimates in any one time period with <17% (with the exception of time period 7 for cisco when 4°C warmer water can result in 35% lower consumption rates as temperatures are close to lethal). Errors associated with fish abundance estimates may be as high as ±50% for any one measurement; however, the consistent patterns observed over years indicate higher overall confidence in our estimates (Fig. 7). Assuming a coefficient of variation in abundance estimates of 30% and a similar uncertainty in the bioenergetics models would result in an overall coefficient of variation of ~40% (first-order error propagation of independent variables; Meyer 1975). This uncertainty is smaller than the order of magnitude change in planktivory over the study period. Also, the intervention analysis depends on relative, not absolute changes, and relative changes are subject to less error than the absolute values.

Most of the change in planktivory over the 14-yr time period can be attributed to the rise and fall of the 1977 year class of cisco. Coregonids are often a dominant open-water planktivore in both eutrophic and oligotrophic northern temperate lakes (De Bernardi and Guissani 1975, Svärdson 1976, Hamrin 1983, Lang and Lang 1984, Rudstam et al. 1987, Helminen et al. 1990, Reinhertsen et al. 1990). This change in planktivory was associated with changes in the species composition of *Daphnia*, in total *Daphnia* biomass, in the timing and duration of the spring/early summer *Daphnia* peak and clear-water phase, but not in total zooplankton biomass. Effects on total zooplankton biomass have been observed in several other studies (Andersson et al. 1978, Henrikson et al. 1980, several references in Gliwicz and Pijanowska 1989 and Gulati et al. 1990, but see McQueen et al. 1989). This lack of effect on total zooplankton biomass was due to a compensatory increase in cyclopid biomass with higher planktivory rates and an insignificant response of calanoid biomass. However, large *Daphnia* are the key link transmitting effects of planktivorous fish to lower trophic levels (Pace 1984, McQueen et al. 1986, Leibold 1990, Sarnelle 1992) and *Daphnia* dominated grazing rate estimates from 1987 through 1989 in Lake Mendota (Vanni et al. 1992).

Alternative explanations for the observed changes in zooplankton include responses to (1) predation by other adult and juvenile fish species, (2) predation by invertebrate predators, (3) changes in abiotic factors like nutrient loading and temperature, and (4) changes in algal abundance and composition. None of these alternative explanations is tenable in Lake Mendota.

Perch biomass did increase in 1978 and decrease from 1986 through 1989, but perch contributed <25% of total planktivory during 1977–1987 (except during brief periods of hot summers). In some lakes, larval and early juvenile stages of perch are important planktivores (Post and McQueen 1987, Mills and Forney 1988). However, in Lake Mendota, perch only use the open-water zone when <25 mm (Post et al. 1992) and feed primarily on copepods during that time (Schael et al. 1991). Other planktivorous fish in the lake include white bass (*Morone chrysops*), black crappie (*Pomoxis nigromaculatus*), white crappie (*Pomoxis annularis*), freshwater drum (*Aplodinotus grunniens*), and bluegill (*Lepomis macrochirus*) (Rudstam et al. 1992a). Crappies (both black and white) were common in Lake Mendota in the beginning of the 1980s (crappies constituted 59% and perch 37% of the angler catch in 1981/1982; Lathrop et al. 1992), but planktivory from crappies and other species are partly included in the perch planktivory estimates because we assumed all “perch-size” acoustic targets to be perch.

Invertebrate planktivores may respond to lower planktivory rates and contribute to changes in zooplankton (Dodson 1974, Gliwicz and Pijanowska 1989, Lunte and Luecke 1990). Lunte and Luecke (1990) calculated that the predatory cladoceran *Leptodora* could be a significant source of mortality for *Daphnia* in Lake Mendota in the end of June and July 1987, when *Daphnia* densities were very low and *Leptodora* densities were high. However, *Leptodora* abundance has not changed much over the 14-yr time period, and this predator is never present in the lake until after the middle of June (Lathrop and Carpenter 1992b). *Chaoborus* larvae are rare (Lathrop 1992b). Cyclopoid copepods generally feed on small prey and could possibly suppress *D. galeata* relative to *D. pulex*. But cyclopoids were more common during *D. galeata* years than during *D. pulex* years (Fig. 2, Table 1). Estimates of planktivory rates from both fish and invertebrate predators for the years 1987–1989 indicated that cisco was the dominant planktivore before the die-off in 1987 (Luecke et al. 1992). We therefore conclude that invertebrate predators could not have caused the observed changes in the zooplankton community.

There is no indication that the observed changes occurred as a response to varying spring temperatures, day of ice-out or nutrient loading. The earlier start of both the spring *Daphnia* peak and the spring clear-water phase during *D. pulex* years was not associated with warm temperatures. Average water temperature (at 5 m depth) at the start of the spring peak was 7.3°C (range 5.6°–9.9°C) during *D. pulex* years and 14.4°C (range 10.4°–16.2°C) during *D. galeata* years. There were no significant correlations between ice-out...
day (varying between day-of-year 71 and 126) or between April total phosphorus (TP) concentrations (varying between 0.07 and 0.16 mg/L; Lathrop 1992a) and the start/duration of the spring Daphnia peak and spring clear-water phase \( (P > .10, r \) ranging between \(-0.09 \) and 0.23 for all eight comparisons). In contrast, the start and duration of the spring Daphnia peak was highly correlated with the start and duration of the clear-water phase \( (r = 0.924 \) and 0.886, respectively, \( P < .01 \)). Algal growth is not nutrient limited during the clear-water phase. Dissolved reactive phosphorus, representing a large proportion of the spring TP, remains high until the beginning of the summer blue-green algal blooms when concentrations decline to analytical detection (0.004 mg/L phosphorus) (Lathrop 1992a, Vanni et al. 1992).

Finally, there were no shifts in algal species composition in spring or summer associated with the change in Daphnia. Generally, a spring phytoplankton peak consisting of small edible algae (cryptophytes and diatoms) was followed by a clear-water phase and, later in the summer, by varying intensities of blue-green algal blooms (Aphanizomenon, Microcystis, Anabaena, and Oscillatoria). The dinoflagellate Ceratium hirundinella dominated in the summer of 1983 and 1987. The autumn was again dominated by algae other than blue-greens. See Lathrop and Carpenter (1992a, b) for a more detailed analysis of the interaction between Daphnia, algae, and nutrients in the lake.

Direct and indirect effects on copepods

The lack of response of total zooplankton biomass to increased planktivory was the result of an increase in cyclopoid biomass during the winter and spring in years with high planktivory and low Daphnia biomass. Cyclopoid copepods were only present in cisco diets during early spring (Luecke et al. 1992). A positive relationship between coregonid and cyclopoid biomass was also observed by Hamrin (1983). Positive relationships between a prey and its predator can be the result of indirect effects caused by the reduction of a dominant competitor (Paine 1966). Large Daphnia have been shown to negatively affect cyclopoids in large enclosure experiments (Soto 1985, Vanni 1986). Vanni (1986) suggested the most likely cause for reduced abundance of cyclopoids after the introduction of large Daphnia pulex to be competition for food resources between Daphnia and cyclopoid nauplii. Cyclopoids have much lower clearance rates on algae than daphnids and calanoids (Adrian 1991), and cyclopoid nauplii are more sensitive to starvation mortality than calanoid nauplii (Soto and Hulbert 1991a). This competitive interaction would be stronger with D. pulex than with D. galeata because D. pulex is active at low temperatures and can be quite common during the winter when Diacyclops is most abundant. Calanoid copepods were rarely eaten by adult cisco and perch in the lake (Luecke et al. 1992), and are often not affected by large Daphnia in experiments. (DeMott 1989, but see Soto 1985 and Soto and Hulbert 1991a). In addition, calanoids tended to have peak abundances during summer when Daphnia biomass was relatively low. These observations suggest little direct or indirect effects of planktivory on calanoid copepods in Lake Mendota.

Daphnia species replacement

A decrease or elimination of selected prey species, often larger Daphnia, when planktivory increases is one of the best documented and predictable results in limnology (Hrbacek et al. 1961, Brooks and Dodson 1965, many examples in Gullot et al. 1990 and in Glowiwcz and Pijanowska 1989). This was also observed in the present study. In Lake Mendota, both perch and cisco selected large cladocerans (Daphnia and Leptodora) over copepods (Luecke et al. 1992). Because in Lake Mendota D. pulex mature at a larger size (1.6 mm) than D. galeata (1.2 mm; Y. Allen, Center for Limnology, University of Wisconsin, personal communication) we expect D. galeata to be favored under conditions of high planktivory. A dominance of smaller species and a decrease in size at first reproduction is a common response of zooplankton communities to high fish predation (Threlkeld 1979, Vanni 1987, Northcote 1988, Glowiwcz and Pijanowska 1989). Because D. pulex has been found to be competitively superior to D. galeata (Leibold 1990), we expect D. pulex to be dominant under conditions of low planktivory.

Luecke et al. (1990) analyzed birth and death rates of Daphnia galeata in Lake Mendota during 1987. They concluded that fish planktivory could control the D. galeata population in late summer and autumn but could not cause the precipitous decline in D. galeata observed in the early summer at the end of the Daphnia peak. Mortality from planktivorous fish was insignificant during the early summer Daphnia peak. The peak abundance of Daphnia was associated with a clear-water phase and low birth rates indicating food limitation of the daphnid. Luecke et al. (1990) suggested that D. galeata escape control by planktivorous fish in the early summer as abundant spring phytoplankton and higher temperatures increase birth rates. D. galeata then overgraze their resources, causing a clear-water phase, and subsequently decrease due to mortality from starvation and low birth rates to levels that again can be controlled by planktivorous fish. This hypothesis predicts that Daphnia biomass should be negatively affected by planktivory during the winter and spring and during the late summer and autumn, but not during the early summer peak. This expectation was supported by the seasonal intervention analysis (Table 2).

D. pulex is not only dominated D. galeata in years with low planktivory, it almost completely excluded D. galeata in the spring and summer in Lake Mendota. However, D. galeata tended to replace D. pulex during late summer and autumn even at these low
planktivory rates. These observations suggest complex interactions between predation, food resources, and the physiological characteristics of the two *Daphnia* species. The following differences between the two species are supported by experimental studies in the literature: (1) *D. pulex* have higher filtering rates and population growth rates at cold temperatures than *D. galeata* (Burns 1969, Threlkeld 1979, 1980, Leibold 1990), (2) *D. pulex*, but not *D. galeata*, is negatively affected by temperatures around 22°C-25°C when food is low (Hall 1964, Threlkeld 1980), (3) *D. pulex* has a lower incipient food threshold than *D. galeata* except at high temperatures (Goulden et al. 1982, Tessier et al. 1983, Gliwicz and Lampert 1990) and (4) *D. pulex* has a higher resistance to starvation than *D. galeata* (Threlkeld 1976). Our observations on the two species in Lake Mendota also support these experimental studies. *D. pulex* had larger clutch sizes than *D. galeata* early in the spring of 1990 when both species were initially present (Y. Allen and L. G. Rudstam, unpublished data). Also, *D. pulex*, but not *D. galeata*, continued to produce some eggs during the clear-water phase (Luecke et al. 1992).

The following complex hypothesis would explain both the inter- and intrayear *Daphnia* species replacement patterns observed in Lake Mendota and also be consistent with the differences in physiological ecology of the two species stated above. When planktivory by cisco is low, *D. pulex* increase at low temperatures in early spring, overgraze their resources and cause a clear-water phase (Fig. 4). *D. galeata* require warmer temperatures to start increasing in numbers in the spring but cannot increase at that time because the food resources have been depleted by *D. pulex* below the incipient food threshold of *D. galeata*. *D. pulex* continue to dominate the early summer partly because of high resistance to starvation, but decrease in late summer as high water temperatures and low concentrations of edible algae or interference from large blue-green filaments (Gliwicz and Lampert 1990) result in negative population growth. Later in the year, higher temperatures favor *D. galeata* and this species may dominate in late summer and early autumn.

When planktivory by cisco is high, *D. pulex* cannot increase in early spring partly because coregonids have high feeding rates at low temperatures (L. G. Rudstam et al., unpublished manuscript). High planktivory rates of cisco at low temperatures eliminate the low temperature refuge from summer fish predation for *D. pulex* (Shapiro 1990). This refuge has been implicated in the coexistence of several daphnid species in other lakes (Threlkeld 1979, Stich and Lampert 1984, Tessier and Welser 1991). As water temperature increases and a spring bloom of edible algae develops, the reproductive rate of the daphnids increases faster than the relatively slow increase in cisco planktivory rates. Maximum feeding rates of the related bloater (*Coregonus hoyi*) are reached at only 16°C (L. G. Rudstam et al., unpublished manuscript). *D. galeata* can therefore escape control by planktivory and overgraze their resources causing a clear-water phase. Because *D. galeata* is less starvation resistant than *D. pulex*, the early summer *Daphnia* peak is shorter and the population decline faster than when *D. pulex* dominates in the spring and early summer (Fig. 4). When cisco predation was moderate (1984–1987), a second peak of *Daphnia* was observed in early autumn when edible algae increase. This autumn peak was less pronounced when cisco predation was higher (1979–1982; see Fig. 9). *D. galeata* and not *D. pulex* will dominate because of its lower susceptibility to size-selective planktivory.

This scenario suggests that predation, structure of the habitat, and the physiological ecology of the dominant planktivore interact with the competitive abilities of the two species at different food levels and temperature conditions to cause the observed patterns of seasonal and interyear species replacement. Single-factor explanations for observed patterns in zooplankton communities are seldom sufficient (Bengtsson 1987, DeMott 1989).

**Time scales of variability and long-lived planktivores**

Our analysis indicates that *Daphnia* species composition and biomass in Lake Mendota was affected for a period of 10 yr (1978–1987) by the success of one year class of a dominant long-lived planktivore. Carpenter (1988) hypothesized that there should be a peak in temporal variability of lower trophic levels related to the life-span of the dominant fish species, in his example the piscivore. Carpenter and Leavitt (1990) found evidence of such scaling of variability in the fossil pigments from a small northern lake. Our study is perhaps the first to directly document variability in the zooplankton community scaled to the life-span of a long-lived fish species (cisco). But, in contrast to the prediction by Carpenter (1988), this fish is a planktivore. Piscivorous fish are gape-limited predators, and there is therefore a potential refuge in size for large planktivorous fish (Hambright et al. 1991). Cisco outgrow their predators in Lake Mendota during their first 2 yr of life. Walleye (*Stizostedion vitreum*), currently the most common piscivore in Lake Mendota, tend to select cisco-shaped prey <30% of their own length (Nielsen 1980). By the end of their 1st yr (and a length of 150 mm), cisco would only be vulnerable to predation by age 5 and older walleyes (Johnson et al. 1992). By the end of their 2nd yr (and a length of 250–300 mm), cisco are in principle invulnerable to predation. Thus, once a large population of cisco is established, piscivory cannot reduce population densities. Effects of an exceptional planktivore year class can therefore last for time periods of a decade or longer. Dominance of a single year class for >10 yr has also been observed for vendace (*Coregonus albula*) (Sandlund et al. 1991).
This situation could be common in many lakes with large-bodied, primarily planktivorous, fishes and needs to be considered in studies of time lags and transmission of variance associated with food web interactions and the trophic cascade (Gophen 1990, Hambright et al. 1991). Other investigators reporting effects of variable year class strength of planktivorous fishes on zooplankton generally discuss the immediate effects of planktivory from the YOY fishes. For example, 2-yr cycles in zooplankton species composition and abundance are associated with 2-yr cycles in roach Rutilus rutilus (Cryer et al. 1986) and vendace Coregonus albula recruitment (Hamrin and Persson 1986). In Oneida Lake, YOY yellow perch are the main planktivores, and effects on Daphnia are evident primarily during the first summer after a strong recruitment event (Mills and Forney 1988).

In closed systems, fish cannot respond numerically to fast increases in their zooplankton prey (Northcote 1988, Glowiak and Pijanowska 1989). A behavioral or functional response by the predator is limited in scope and allows the prey to escape control by predation when conditions are favorable for population growth, such as during the spring bloom of edible algae. These differences in response ability of a prey and its predator will contribute to population outbreaks and to the instability of lake ecosystems. During the clear-water phase, the interactions between Daphnia and algae in Lake Mendota revert to a classic two-level predator-prey cycle (Murdock and McCauley 1985, Lampert et al. 1986, Sommer et al. 1986, Lucecke et al. 1992), a dynamic that may set the stage for later blooms of blue-green algae (Carpenter 1992, Lathrop and Carpenter 1992b).

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