Oecologia (1988) 76:148–154

Oecologia

Predation-driven dynamics of zooplankton and phytoplankton communities in a whole-lake experiment*

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Summary. 1. Species compositions of zooplankton and phytoplankton were followed in Tuesday Lake before and after experimental manipulation of its fish populations (addition of piscivorous largemouth bass, removal of planktivorous minnows). Plankton dynamics were compared to those of adjacent, unmanipulated Paul Lake, where piscivorous fish have been dominant historically. 2. Indices of similarity for the zooplankton communities in the two lakes in 1984 prior to the manipulation were low; however, following the manipulation in spring, 1985, similarity of the zooplankton in the two lakes rose considerably and remained high throughout 1986. This was the result of an increase in Tuesday Lake of previously rare large-bodied cladocerans (*Daphnia pulex, Holopedium gibberum*) which were the dominants in Paul Lake, and the disappearance in Tuesday Lake of the dominant small-bodied copepod *Tropocyclops prasinus*, a minor component of the Paul Lake zooplankton. These observations are consistent with prior observations of the effects of size-selective predation on zooplankton communities. 3. Phytoplankton communities also responded strongly to the manipulation, with similarity indices for the two lakes rising from low levels in 1984 to high levels of similarity in 1985 and 1986, reflecting the decrease of formerly dominant Tuesday Lake taxa which were unimportant in Paul Lake and the appearance or increase in Tuesday Lake of several taxa characteristic of the Paul Lake phytoplankton assemblage. These results clearly show that food web structure can have pronounced effects on community composition at all levels of the food web, and that, just as zooplankton communities are structured by size-selective predation, phytoplankton communities are structured by herbivory. These observations may provide some insight into factors governing the complex distributions of phytoplankton species among various lakes.

Key words: Biomanipulation – Herbivory – Phytoplankton – Predation – Zooplankton

Since the publication of the seminal paper of Hairston et al. (1960), the role of predation pressure in determining and maintaining species abundances and community composition at lower trophic levels has been intensively investigated (Sih et al. 1985). The importance of upper trophic levels in controlling organism densities, intensity of competition, and species composition in lower trophic levels is particularly well-documented in marine benthic systems (Paine 1966, 1971, 1980, Mann and Breen 1972, Estes and Palmisano 1974, Menge and Sutherland 1976, Lubchenco 1986), leading Paine (1966, 1980) to develop the concepts of the "keystone predator" and "strong interactions" to characterize the nature of food web interactions in controlling community composition. Evidence supporting the role of predation in determining the community composition of lower trophic levels is also available from terrestrial habitats (Oksanen et al. 1981, McNaughton 1984). The theory of Menge and Sutherland (1976) predicts that effects of predation will be maximal at low trophic levels in benign environments. We consider the epilimnion of a lake during summer to be benign, and therefore hypothesize that effects of predation will be substantial for herbivorous zooplankton and phytoplankton.

In freshwater systems, predation has long been recognized as a crucial factor governing the community composition of prey organisms in both lakes and streams (Macan 1977, Zaret 1980). The observations and conclusions of Hrbacek et al. (1961) and Brooks and Dodson (1965) about the role of fish in structuring zooplankton communities have subsequently been elaborated and extended into a general frame-work in which phytoplankton productivity, biomass, and species composition are linked ultimately to the magnitude of the predation effects of the top trophic level (Shapiro 1980, Carpenter et al. 1985). Considerable supporting evidence, in the form of mesocosm experiments, observational data, and whole-lake experiments, has accumulated (Hurlbert et al. 1972; Schindler and Comita 1974; Hrbacek et al. 1978; Henrikson et al. 1980; Elliot et al. 1983; Benndorf et al. 1984; Reinertsen and Olsen 1984; Shapiro and Wright 1984; Scavia et al. 1986; Carpenter et al. 1987; Post and McQueen 1987; and others).

Experiments performed in mesocosms cannot encompass the full range of compensatory processes present in natural systems and may tend to exaggerate the impact of the factors that are manipulated (Harris 1986). On the other hand, natural experiments or manipulations of a single lake without a reference (or "control") system cannot evaluate the magnitude of interannual changes that would occur without manipulation (Likens 1985). In the following, we report the changes in zooplankton and phytoplankton community composition resulting from the addition of a top predator (largemouth bass) to an ecosystem previously lacking that predator (Tuesday Lake), and evaluate these

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* A contribution from the University of Notre Dame Environmental Research Center, funded by NSF grants BSR-83-08918 and BSR-86-06271

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changes relative to an adjacent, undisturbed ecosystem in which the predator is abundant (Paul Lake). An earlier paper addressed changes in ecosystem-level variables (trophic-level biomasses, primary production) and summer mean plankton composition following reciprocal fish transfers between Peter and Tuesday lakes, in comparison with undisturbed Paul Lake (Carpenter et al. 1987). Plankton community changes in Tuesday Lake were extensive and complex, while plankton dynamics in Peter Lake could be represented by biomass changes of major functional groups (Carpenter et al. 1987). Therefore, a more fine-grained analysis is needed of plankton dynamics in Tuesday Lake. Here we present plankton community data for Tuesday and Paul lakes at the species level and a monthly time scale. We address the role of predation in the establishment, rather than the maintenance (*sensu* Thorp 1986), of pelagic community composition, and demonstrate that food web structure is a powerful factor in establishing which species of both zooplankton and phytoplankton are present in a lake.

Methods

Study Lakes

Paul and Tuesday lakes are located in the University of Notre Dame Environmental Research Center, Gogebic County, Michigan, USA. Both lakes are small but relatively deep (Paul Lake, area: 1.2 ha, max. depth: 12.2 m; Tuesday Lake, area: 0.79 ha, max. depth: 18.5 m). Fish populations in Paul Lake have been dominated by largemouth bass (*Micropterus salmoides*) since 1975 and planktivorous fish have been absent since 1980; further details regarding the history, fish populations, and basic limnology of Paul Lake are given by M. Elser et al. (1986). Prior to the experimental manipulation in 1985 (see below), piscivorous fish were absent from Tuesday Lake, due to winter anoxia, and soft-bodied planktivores (redbelly and finescale dace, *Phoxinus eos* and *P. neogaeus*; central mudminnows, *Umbra limi*; collectively referred to as "minnows" in the following) flourished, as in other lakes that winterkill (Tonn and Magnuson 1982).

Manipulation

Full details of the 1985 manipulation of the fish populations in Tuesday Lake are given by Carpenter et al. (1987); only the general details will be outlined here. Monitoring of the plankton communities (see below) in both lakes began in 1984 to establish a pre-manipulation baseline. Paul Lake was left undisturbed to serve as a "reference ecosystem" (Likens 1985), to assess interannual changes in the absence of changes in the food web, and as a piscivore-dominated system against which to evaluate plankton changes in Tuesday Lake after piscivore addition. In May, 1985, 375 bass (ca. 45.7 kg) obtained from nearby Peter Lake were introduced to Tuesday Lake, followed by 91 bass (10.1 kg) on 27 July. Additionally, ca. 45000 minnows (56.4 kg) were removed from Tuesday Lake by trapping between 23–31 May, 1985. This represented ca. 90% of the total minnow population in the lake. Little post-release mortality of bass was observed. By mid-July, 1985, the introduced bass had almost completely eliminated the remaining minnow population, and few minnows could be trapped in the lake in 1986 (Carpenter et al. 1987; X. He and J.F. Kitchell, personal communication). Meanwhile, the bass population in Paul Lake was relatively stable during the years of the study (Carpenter et al. 1987; J. Hodgson, personal communication). Large changes in algal community biomass and productivity ensued (Carpenter et al. 1987) and the nature of algal nutrient limitation changed in Tuesday Lake as well, shifting from a predominantly N-limited phytoplankton in the presence of small zooplankton to a P-limited assemblage in the presence of large-bodied cladocerans (Elser et al. 1988).

Routine monitoring

While the lakes were stratified (mid-May to mid-September), monitoring of the lakes took place weekly at a single fixed station located in the deepest portion of each lake. Numerous limnological parameters were measured as detailed in previous publications (J. Elser et al. 1986; M. Elser et al. 1986; Carpenter et al. 1986; Carpenter et al. 1987). Phytoplankton samples were obtained by pooling water taken from three depths in the epilimnion and preserved with Lugol's solution for later examination. Zooplankton were sampled with vertical hauls from just above the lake bottom to the surface, using a 75-μm mesh Nitex net. In 1984, single hauls were made, whereas in 1985 and 1986, duplicate hauls were made and pooled. Filtering efficiencies for the net were determined in each lake for each zooplankton taxon once a year based on vertical profiles made with a Schindler-Patalas trap.

Phytoplankton samples were concentrated by settling, and algal cells identified (after Prescott 1962) and enumerated using an inverted microscope (J. Elser et al. 1986). Biovolume concentration for each species was calculated based on biovolume of individual algal units (exclusive of sheaths, loricae, etc.) and unit concentration in samples, and then converted to fresh weight biomass units ($1\ \mu m^3 = 1 \times 10^{-6}\ \mu g$). Zooplankton were identified, measured, and counted using a dissection microscope and dry weight masses for each taxon calculated from length-weight regressions (Carpenter et al. 1986). Biomass concentration for each species was then calculated from haul contents, average individual dry mass, and net efficiency.

Data analyses

Because of the size of the zooplankton and phytoplankton community composition data sets, only relatively reduced aspects of the relevant data can be presented here. For the zooplankton, the crucial dynamics involve only a few species, so that their responses can be evaluated directly. For the phytoplankton, the changes observed are best described using more highly reduced data. Average abundances and average relative abundances (percentage of total community biomass comprised by each species on a given day) were calculated for each species during the entire sampling season each year, and each year's dominant taxa were then ranked on the basis of these averages (equally weighted). This analysis obscures the short-term phytoplankton dynamics. To compensate for this shortcoming, we present biomass dynamics of selected taxa and similarity indices at a monthly time scale.

Similarity indices

Community composition in the lakes was compared using Sorenson's similarity index (Janson and Vegelius 1981).

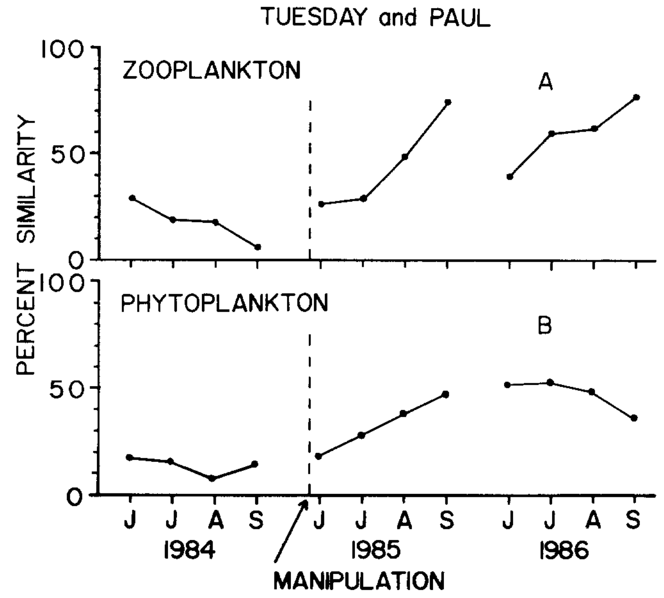

Fig. 1 A, B. Percent similarity between the planktonic communities of Paul and Tuesday lakes for the study period. **A** Zooplankton. **B** Phytoplankton. The dashed line indicates the addition of piscivores to, and removal of planktivores from, Tuesday Lake in May, 1985

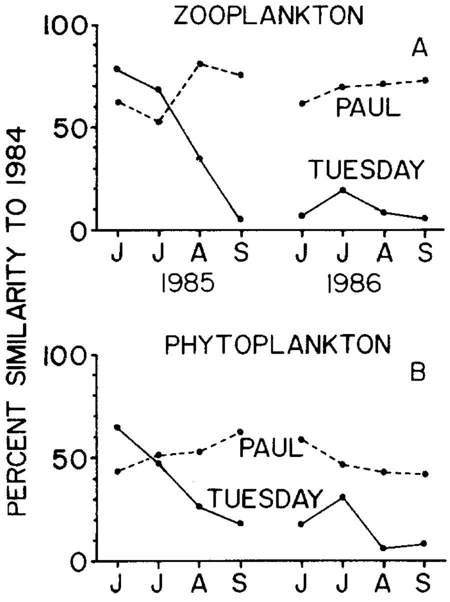

Fig. 2 A, B. Percent similarity of 1985–1986 planktonic communities in each lake to its planktonic community in 1984, for Paul (dashed line) and Tuesday (solid line) lakes. **A** Zooplankton. **B** Phytoplankton

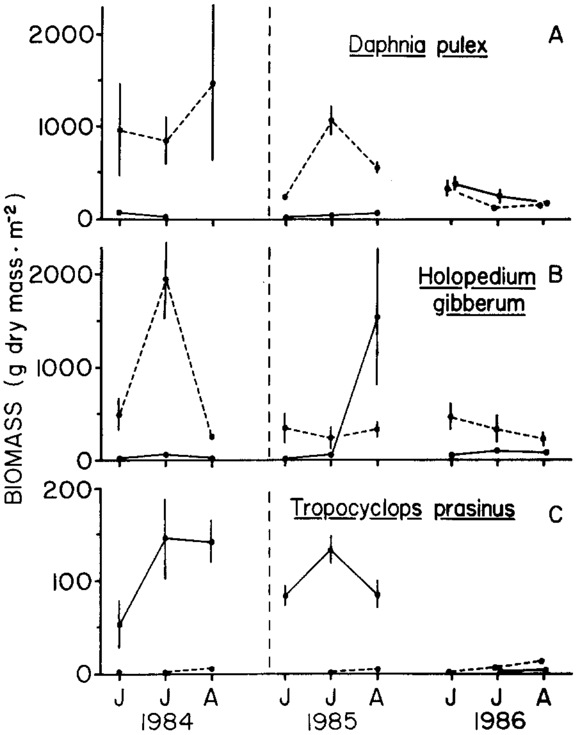

Fig. 3 A–C. Biomass dynamics of dominant zooplankton species in the lakes during the study period. **A** *Daphnia pulex*. **B** *Holopedium gibberum*. **C** *Tropocyclops prasinus*. Paul Lake = *dashed lines*, Tuesday Lake = *solid lines*. The *vertical line* indicates the spring, 1985 manipulation of the Tuesday Lake food web. Error bars are 95% confidence intervals based on 4 or 5 weekly samples per month, and so denote week-to-week variability

Biomasses of zooplankton and of phytoplankton were each first normalized to sum to 100% on each date. Similarities were then calculated for mean relative biomasses for both zooplankton and phytoplankton at monthly intervals in order to smooth weekly fluctuations attributable to phenological variability. Interyear similarities were calculated to compare post-manipulation years (1985 and 1986) with the pre-manipulation year (1984) for both lakes. Interlake similarities were calculated to compare Paul and Tuesday lakes from 1984–1986. A randomization test was used to compare interlake similarities before and after the manipulation (Edgington 1980, p. 268–272). This procedure does not test the null hypothesis that the manipulation had no effect on interlake similarity (Hurlbert 1984). Rather, it establishes whether or not a nonrandom change has occurred which may be attributable to the manipulation (Box and Tiao 1975).

Results

Zooplankton

Major compositional changes in the Tuesday Lake zooplankton community following removal of planktivores and addition of piscivores are indicated by both sets of similarity indices (Figs. 1 A–2 A). In 1984, Tuesday Lake zooplankton were quite different from the zooplankton in Paul Lake. However, following the manipulation Tuesday-Paul similarity increased as the zooplankton community in Tuesday Lake came to resemble that in piscivore-dominated Paul Lake (Fig. 1 A). The seasonal pattern of similarity between the zooplankton of Tuesday and Paul lakes also changed after the manipulation. Differences in pre-manipulation and post-manipulation similarities could not be explained by random permutation of the data ($P = 0.01$). We infer that, as indicated by the year-to-year similarity indices (Fig. 2 A), these responses reflect changes induced in Tuesday Lake by the manipulation, and not interannual changes in unmanipulated Paul Lake. In Paul Lake, similarity between 1985–86 zooplankton and 1984 zooplankton was high and relatively constant, while, in Tuesday Lake, percent similar-

Table 1. Mean daily absolute (Biom, units: µg fresh wt L^{-1}) and relative (Perc) biomass concentration and relative dominance rankings (Rank) of selected phytoplankton species during the study period. Relative dominance ranking of a species represents the mean of its rankings based on mean biomass and on mean relative biomass

Species	1984			1985			1986		
	Rank	Biom	Perc	Rank	Biom	Perc	Rank	Biom	Perc
Paul Lake									
Oocystis lacustris	1	61.0	20.6	6.5	10.7	5.9	5.5	24.1	7.7
Cryptomonas ovata	2	45.3	46.3	1	32.7	20.0	1.5	48.7	14.2
Gloeocystis sp.	3.5	29.3	9.6	3	19.8	10.4	8	17.4	5.0
Synura sp.	3.5	32.5	8.3	20	0.45	0.27	27	0.25	0.07
small flagellated chlorophytes	5	22.0	7.9	4.5	12.2	6.7	5.5	23.1	8.0
Mallomonas caudata	6	20.2	6.9	2	27.5	16.1	1.5	47.6	15.2
Sphaerocystis schroeteri	7	14.1	5.2	14	3.25	1.4	11.5	10.4	2.8
Anabaena circinalis	9	10.1	3.2	6.5	10.9	5.5	7	19.0	6.9
Microcystis sp.	11	7.79	3.0	4.5	11.4	8.5	10	10.9	3.2
Oocystis sp.	·	·	·	·	·	·	3	37.0	9.5
Crucigenia rectangularis	·	·	·	13	4.16	2.4	4	33.1	9.3
	Pre-manipulation			Post-manipulation					
Tuesday Lake									
Peridinium limbatum	1	1185.0	31.8	11	11.3	1.0	13.5	4.15	1.4
Glenodinium quadridens	2	391.0	13.9	4	87.2	8.0	·	·	·
Peridinium pulsillum	3.5	211.8	10.1	3	105.8	10.7	24	0.10	0.08
Chrysochromulina sp.	4.5	198.7	9.2	1	385.0	30.0	22.5	0.28	0.09
Peridinium wisconsinense	4.5	304.3	6.3	15	5.08	0.32	·	·	·
Microcystis sp.	5.5	183.5	7.8	22	1.01	0.19	5	30.5	8.0
small flagellated chlorophytes	7	128.6	3.8	5.5	41.0	5.2	7.5	9.61	3.5
Mallomonas caudata	10.5	39.8	2.0	2	141.4	19.6	1	95.7	28.4
Cryptomonas ovata	13	34.5	1.6	7	20.8	5.9	2	48.9	14.7
Dinobryon cylindricum	29.5	0.19	0.01	28	0.06	0.10	3	47.7	10.3
Oocystis lacustris	·	·	·	18	0.75	1.1	4	31.9	9.1
Glenodinium pulvisculus	·	·	·	·	·	·	6	21.5	7.2

ity to 1984 declined rapidly and substantially following the manipulation in spring 1985.

These changes in similarity index largely reflect the dynamics of the dominant zooplankton species in the two lakes (Fig. 3). Increases in similarity between Paul and Tuesday lakes in 1985 resulted from the modest increase in *Daphnia pulex* biomass (Fig. 3A) and the substantial, but largely transient, increase in abundance of *Holopedium gibberum* (Fig. 3B) in Tuesday Lake. The biomass of *D. pulex* decreased in Paul Lake as it increased in Tuesday Lake. However, total zooplankton biomass declined in Paul Lake throughout the same period, so the relative biomass of *D. pulex* (on which the similarity index in based) changed only slightly. The high degree of similarity between the two lakes in 1986 is clearly the result of increased relative biomass of *D. pulex* and the failure of *Tropocyclops prasinus* to appear in appreciable numbers in Tuesday Lake (Fig. 3C).

Phytoplankton

The phytoplankton community of Tuesday Lake also responded dramatically to the manipulation. In 1984, Tuesday-Paul similarity for the phytoplankton was extremely low, but, in 1985, following the decrease in planktivory and accompanying the changes in the zooplankton community, similarity between the phytoplankton in the two lakes rose steadily (Fig. 1B). High similarity between the two lakes persisted in 1986. Differences in pre-manipulation and post-manipulation similarities could not be explained by random permutation of the data ($P = 0.007$). We infer that these changes reflect the effects of the manipulation on Tuesday Lake phytoplankton, rather than changes in the reference system, as similarity to 1984 was high and constant for Paul Lake during 1985–86 but declined dramatically for Tuesday in post-manipulation years (Fig. 2B).

The species most responsible for the convergence of phytoplankton species composition in the two lakes can be identified by examining the dominant algal taxa in the two lakes throughout the study period. Mean daily relative and absolute biomass for the sampling season, along with rankings, for each species whose mean relative biomass exceeded 1% in any given year are given in Table 1; month-to-month dynamics of absolute biomass of several dominant taxa are presented in Fig. 4.

It is clear from Table 1 that the species composition of Paul Lake was quite stable from 1984–86, with a few relatively minor exceptions: the appearance of two taxa, *Oocystis* sp. and *Crucigenia rectangularis*, as sub-dominants in 1986, and the decreased abundance of *Synura* sp. in 1985–86 relative to 1984. Most of the dominant taxa maintained abundances of similar magnitude throughout the study period, and no dominant species disappeared from the community (Fig. 4 and Table 1).

On the other hand, major changes in the dominant taxa in Tuesday Lake followed the manipulation. Dinoflagellates, a very minor component of the Paul Lake community throughout the study, declined dramatically in Tuesday

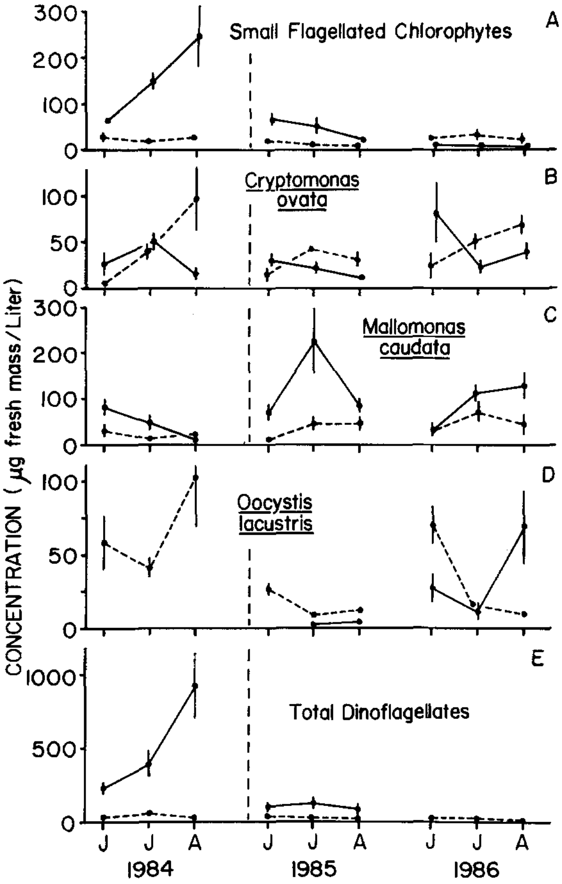

Fig. 4A–E. As in Figure 3, but for phytoplankton. **A** Small flagellated chlorophytes. **B** *Cryptomonas ovata*. **C** *Mallomonas caudata*. **D** *Oocystis lacustris*. **E** Dinoflagellates. Error bars are 95% confidence intervals based on 4 or 5 weekly samples per month, and so denote week-to-week variability

Lake after the manipulation (Fig. 4E), with two previously important species (*Glenodinium quadridens* and *Peridinium wisconsinense*) unobserved in 1986. Small flagellated chlorophytes declined in a similar manner, eventually reaching levels lower than in Paul Lake (Fig. 4A). Some species not observed in Tuesday Lake in 1984, such as *Mallomonas caudata* and *Oocystis lacustris*, increased markedly in post-manipulation years (Fig. 4C, D). Meanwhile, *Cryptomonas ovata* remained relatively unchanged in absolute biomass (Fig. 4B) in the face of increasing grazing pressure which decreased the abundances of most taxa previously dominant in the lake. As a result, the relative biomass of *C. ovata* increased markedly and the taxon was ranked as a dominant in 1986 (Table 1). By 1986, the most dominant taxa in Tuesday Lake were the same as those in Paul Lake: *M. caudata, C. ovata,* and *O. lacustris*. *Dinobryon cylindricum* was also a dominant in Tuesday Lake in 1986 but, while present, was not a major species in Paul Lake.

Discussion

The changes in the zooplankton that occurred in Tuesday Lake following the elimination of planktivorous fish are consistent with the general patterns outlined by Zaret (1980): large-bodied taxa (particularly cladocerans), previously eliminated or held at low levels by efficient size-selective planktivores, replaced previously dominant small-sized species. Two observations in Tuesday Lake suggest processes important in the transition between the two types of zooplankton assemblages. First, *Holopedium gibberum* was first to appear in large numbers following the manipulation, but declined considerably once *Daphnia pulex* had become established (Fig. 3) and algal biomass had declined. This supports previous suggestions that *Holopedium* is a weak competitor and cannot maintain high abundances in the presence of substantial competition from *D. pulex* (Allan 1973). The second observation relevant to processes operating during the transition between community-types is the dramatic decline in the previously dominant *Tropocyclops prasinus* following establishment of the large-bodied cladocerans. Vanni (1986) has demonstrated competitive suppression of *T. prasinus* by *D. pulex*. These observations are consistent with the size-efficiency hypothesis (Brooks and Dodson 1965) which accounts for the absence of small-bodied taxa in the presence of large species in low planktivory lakes. While the mechanisms that exclude such small-bodied zooplankters are debatable (Hall et al. 1976), the dynamics of zooplankton in Tuesday Lake do support general predictions of the size-efficiency hypothesis. Size-selective predation was clearly important in establishing the overall species pool capable of existing in the lake, but competition may have been important in determining the final composition.

Relatively few whole-lake studies have thoroughly evaluated the effects of major changes in zooplankton communities on phytoplankton species composition. Changes in Tuesday Lake are generally consistent with observations from previous work. For example, Benndorf et al. (1984), Reinertsen and Olsen (1984), and Shapiro and Wright (1984) all report increases in the relative abundance of *Cryptomonas* following the appearance of large cladocerans in their manipulated lakes. In addition, Benndorf et al. report increases in *Oocystis* and disappearances of *Peridinium* species, similar to observations made in Tuesday Lake. Mesocosm experiments have also demonstrated the suppression of *Peridinium* and other dinoflagellate taxa by large daphnids in these and other lakes (Bergquist et al. 1986; Vanni 1986; Elser et al. 1987).

Zooplankton species composition (and/or its correlate, size distribution) appears to be the crucial factor leading to changes in algal species composition. For example, despite substantial declines in the biomass of the two zooplankton dominants in Paul Lake in 1985 and 1986 (Fig. 3A, B), the percent similarity of the zooplankton between years was fairly constant (Fig. 2A) and only minor changes in phytoplankton species composition occurred (Fig. 2B). However, when the species composition of the Tuesday zooplankton changed (Fig. 2A), major changes in the phytoplankton ensued (Fig. 2B). Experiments performed in Tuesday Lake in 1983 demonstrated pronounced algal responses to a daphnid assemblage which was very different from the native zooplankton of Tuesday Lake (Bergquist et al. 1985). Further experiments performed before and after the appearance of large cladocerans in Tuesday Lake in 1985 corroborated the importance of zooplankton species composition and size distribution in producing pronounced responses in the phytoplankton (Elser et al. 1987). While the changes in *N* and *P* availability caused by the manipulation (Elser et al. 1988) may have contributed somewhat to the shifts in the phytoplankton community, both the magnitude of compositional changes and evidence from grazing studies during the transitional period (Elser et al. 1987) indicate that differential grazing mortality, rather than resource-based competition, was the dominant factor governing the community changes.

The observation that qualitative changes in the zooplankton community have especially powerful effects on phytoplankton species composition may help explain the disparate conclusions of studies which have evaluated the importance of various loss processes in controlling algal growth *in situ*. In some situations, grazing losses have had only minor effects on daily growth (Jassby and Goldman 1974; Reynolds et al. 1985), whereas in others, grazing losses were important in causing changes in net growth rates of certain species and in altering algal species composition (Crumpton and Wetzel 1982; Tilzer 1984; Lehman and Sandren 1985; Bergquist and Carpenter 1986; Elser et al. 1987). In lakes where the qualitative nature of the zooplankton community is relatively stable intra- and interannually, it is likely that the phytoplankton species present are those already adapted to the ambient grazing conditions, and are either morphologically adapted to resist ingestion (e.g. the extensive spines of *Mallomonas*), are actually *enhanced* by ingestion by zooplankton (e.g. some gelatinous green algae, Porter 1976), or have such high compensatory capacities that elevated grazing loss rates are insignificant. *Cryptomonas* may be an example of the latter mechanism, as indicated by its dynamics in Tuesday Lake in this study. In mesocosm experiments using zooplankton gradients, *Cryptomonas* is ingested but its net growth rates often show neutral or unimodal responses, presumably because of the stimulatory effects of nutrients excreted by zooplankton (Bergquist and Carpenter 1986; Elser et al. 1987). Thus *Cryptomonas* biomass is relatively insensitive to changes in herbivory. In contrast, algal species with slower growth rates which are sensitive to zooplankton composition will be rapidly eliminated from the phytoplankton when the zooplankton change. Consequently, an examination of specific loss processes for the species present in Tuesday Lake in 1986 may well have revealed that zooplankton grazing was not an important process governing the instantaneous net growth rates of most of the species in the community; however, it would have been erroneous to conclude from such information that zooplankton were not a factor determining algal community structure in the lake. This distinction is the same at that made by Thorp (1986) between processes responsible for the establishment and maintenance of zooplankton community structure.

These results have two important implications for biomanipulation, or management of algae by manipulation of the top carnivore in a lake (Shapiro 1980; Shapiro and Wright 1984). First, our data counter recent criticisms of biomanipulation: that data supporting the concept come from either enclosure studies carried out at inappropriate spatial and temporal scales (Harris 1986) or from whole-lake studies that lacked a reference or "control" ecosystem (Post and McQueen 1987). Neither criticism applies to our data. Second, our results show that the history of a food web is a powerful constraint on its current structure. Fish manipulations strong enough to qualitatively alter the zooplankton community are required to evoke appreciable responses from the phytoplankton. Once reconfigured, the communities may show only minor variability until the next major change occurs in the fish assemblage.

Lack of consideration for the temporal variability of lake food webs (Carpenter and Kitchell 1987) and the necessity of strong treatments may lead to disappointment with biomanipulation. For example, Post and McQueen (1987) manipulated fish in large enclosures and thereby altered the relative abundances of small daphnids and bosminids. This relatively small zooplankton response had little effect on the phytoplankton, and prompted Post and McQueen to question the utility of biomanipulation. We agree with Shapiro and Wright (1984) that fish manipulations which alter the densities of large daphnids such as *Daphnia pulex* (or perhaps large calanoid copepods, Henrikson et al. 1980) will have appreciable effects on the phytoplankton. Because of the intrinsic instability of fish populations and consequent temporal variability of the entire limnetic food web (Carpenter and Kitchell 1987), sustained or periodic fish manipulations may be needed to stabilize biomanipulated lakes. Neglect of these issues may cause biomanipulation attempts to fail and lead to premature abandonment of a promising management technique.

G. Evelyn Hutchinson, in the preface to Zaret (1980), credited the classic paper of Brooks and Dodson (1965) with resolving much of the confusion regarding the distributions of zooplankton species between various lakes, and this study certainly corroborates their observations of the effects of size-selective predation on zooplankton communities. However, at present, interlake distributions of phytoplankton species are probably even more of a puzzle than were zooplankton distributions before the work of Brooks and Dodson. The results of this study clearly show that the species composition of phytoplankton in a lake, after environmental constraints are considered, may be a function of the nature of the zooplankton grazers, just as zooplankton species composition reflects the nature of the planktivore community. Thus, in these lakes, the importance of predation at lower trophic levels is consistent with the model of Menge and Sutherland (1976). The extent to which similar processes operate in other systems will undoubtedly reflect the strength of the interactions between the components of the food web (Paine 1980).

Acknowledgements. We thank our collaborators in whole-lake fish manipulations, especially M.M. Elser, J.F. Kitchell, J.R. Hodgson, N.A. MacKay, and P.A. Soranno for their contributions to this work. Helpful comments on an early draft of the manuscript were provided by C. Luecke, R.P. McIntosh, P.J. Richerson, M. Vanni, and an anonymous reviewer. We thank S. Hurlbert for his criticisms of our statistical analyses; we have incorporated some, but not all, of his recommendations. This work, funded by NSF grants BSR-83-08918 and BSR-86-06271, is a contribution from the University of Notre Dame Environmental Research Center. J.J.E. was supported for part of this work by a University of California-Davis Graduate Fellowship.

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Received June 29, 1987