An in situ test of the effects of food quality on *Daphnia* population growth

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Abstract

In years of low planktivory by fish, midsummer declines and low population abundances of *Daphnia pulicaria* in Lake Mendota, WI, USA have been attributed to poor food quality and low food abundance. This hypothesis has been proposed because of midsummer blooms of blue-green algae in this eutrophic urban lake. We tested the hypothesis by performing in situ food manipulations during the midsummer decline of the *D. pulicaria* population, and during the early autumn low population period. In July, animals held in clear plastic vials containing GF/F filtered lake water exhibited poor survivorship, ceased producing offspring after three days, and had low lipid reserves. Daphnids fed whole-lake water or filtered water enriched with *Chlamydomonas* survived at a significantly higher rate and produced abundant offspring. In September, there were no significant differences in survivorship among treatments, but animals fed water enriched with *Chlamydomonas* produced significantly more offspring than animals in the other treatments. The hypothesis of poor food quality causing the midsummer decline of the *Daphnia* population is not supported by our experiments. Because predation by juvenile fish does not appear to be important in regulating the midsummer *Daphnia* population during these years, alternate hypotheses for the midsummer decline are suggested. These include increased predation by invertebrate predators such as *Leptodora kindtii*, a life history shift by daphnids during midsummer to production of resting eggs, and a combination of low levels of planktivory and deteriorating feeding conditions acting together to cause the population decline.

Introduction

Understanding *Daphnia* population dynamics is a major topic in freshwater ecology because of the important role that daphnids play in lake ecosystems (Peters & de Bernardi, 1987; Lammens *et al.*, 1990). Numerous studies have focused on whether food availability or predation is the dominant mechanism determining the seasonal and interannual patterns of *Daphnia* abundances observed in lakes (Hall, 1964; Gliwicz, 1985; Larsson *et al.*, 1985; Threlkeld, 1979b, 1985; Benndorf & Horn, 1985; Carpenter & Kitchell, 1988; McQueen *et al.*, 1986; Sommer, 1989). Recently it

has become clear that a combination of these factors and the timing of events interact to regulate *Daphnia* dynamics (Cryer *et al.*, 1986; McQueen *et al.*, 1989, Luecke *et al.*, 1990; Leibold, 1989; Rudstam *et al.*, 1993). The testing of multiple hypotheses at different times of the year is therefore required for a more complete understanding of *Daphnia* population dynamics.

The interannual and seasonal dynamics of *D. pulicaria* and *D. galeata mendotae* in Lake Mendota, Wisconsin, USA is strongly affected by the presence of an abundant population of cisco (*Coregonus artedii*) a cold water planktivore (Vanni *et al.*, 1990; Luecke

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et al., 1990, 1992; Rudstam et al., 1993). In years with high cisco abundance (i.e. before a major die off as in the summer of 1987), the large bodied *D. pulicaria* are prevented from increasing in abundance in spring because of predation by cisco. The smaller daphnid *D. galeata* increases in abundance and causes a relatively short clearwater phase. Because very few eggs are produced during the clearwater phase, poor feeding conditions have been assumed to result in the decline of daphnids during midsummer.

Following a dramatic die-off of cisco in 1987, the cisco population has remained at low levels (Fig. 1). Low cisco abundance, and therefore low springtime planktivory, have allowed *D. pulicaria* to increase in early spring and persist into early summer. The spring increase in *D. pulicaria* leads to a prolonged clearwater phase, and apparently allows *D. pulicaria* to prevent *D. galeata* from establishing a substantial population. During these years, *D. galeata* only occurs in very low numbers throughout the spring, summer and fall, but can increase following a late fall diatom bloom. Intensive studies of the behavior and feeding of larval and older planktivorous fishes in Lake Mendota during low cisco years, conducted throughout the ice-free period, indicate that only extremely low predation by fish on daphnids occurs during the summer period (Luecke et al., 1992; Post et al., 1992; T. Johnson, pers. com.) Overall, estimates of daphnid mortality due to the combined predation by fish and invertebrates such as *Leptodora kindtii* and *Mesocyclops edax* are lower than that required to cause the observed midsummer declines of *D. pulicaria* (Luecke et al., 1992).

In contrast to most other eutrophic lakes, the midsummer zooplankton community of Lake Mendota contains very few cladocerans other than daphnids. Potential competitors with daphnids for food, such as *Bosmina* and *Chydorus*, typically occur at densities of less than 0.2 l^{-1} throughout the summer, while *Diaphanosoma* may reach pelagic densities of 1.0 ind. l^{-1} (Luecke et al., 1992). However, during the summer egg ratios of daphnids often decline, while the phytoplankton community shifts to one mostly dominated by cyanobacteria species. Although *D. pulicaria* should be fairly resistant to starvation conditions (Threlkeld, 1976), we have always observed a midsummer decline concurrent with the shifts in phytoplankton composition. This led to the hypothesis that low food availability or poor food quality causes the drastic *Daphnia* population declines in midsummer.

We have tested the hypothesis that food quantity and quality are important factors in the midsummer
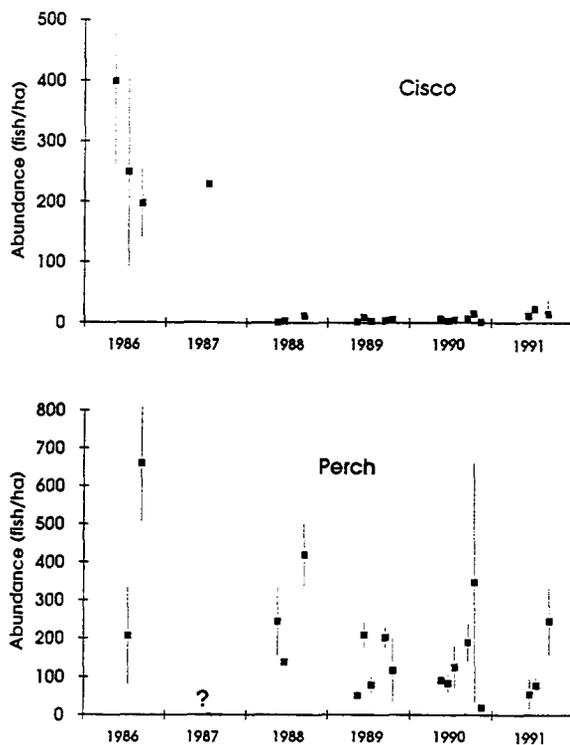

Fig. 1. Abundance (mean±2 s.e.m.) of cisco and yellow perch in Lake Mendota from 1986 through 1991. Abundance of fish was measured with hydroacoustics (single beam, 70 kHz) and divided into two size groups: targets −46 to −40 dB (approximate fish lengths 12 to 25 cm, primarily age-1 and older yellow perch as well as younger cisco, white bass, freshwater drum), and larger than −40 dB (fish larger than 25 cm, primarily age-3 and older cisco, as well as larger perch, white bass and freshwater drum). We used the species composition within these two size groups from gill net catches to estimate the abundance of the two species. These numbers include age-1 and older fish for both perch and cisco and age-0 cisco in the fall. A small number of age-0 cisco were present in the lake in 1989. No age-0 cisco were caught in the lake in 1991. Only cisco abundance was measured in 1987 because surveys were only conducted at night that year and a major proportion of the perch population moves inshore at night. Perch abundance increases in the fall of most years due to increased use of the open water by yearling perch. Perch larger than about 7 cm are vulnerable to these gill nets (age-0 perch in the fall and age-1 perch in the spring and summer should be caught in the net if they used the open water). Details of methods given in Rudstam & Johnson (1992) and also discussed in Rudstam et al. (1993).

decline of *D. pulicaria* and also that poor food conditions maintain low abundances during late summer and fall in Lake Mendota. Survivorship and offspring production by individual *D. pulicaria* were measured during in situ enclosure experiments where food supply was manipulated. Experiments performed during the midsummer decline and during the fall period of

low abundances in 1991 indicate that poor food quality and quantity do not cause the population crash during July, but that the low population size during September may be due to poor feeding conditions.

Methods

Zooplankton and phytoplankton dynamics

Data on population dynamics and seasonal shifts in community composition of zooplankton and phytoplankton were collected at the deepest portion of the lake (deep hole station, maximum depth = 24 m). Comparisons of zooplankton collections made along onshore-offshore transects indicate that the *Daphnia* population dynamics can be assessed accurately using samples from this deep hole station (B. Byom & P. Soranno, pers. com.). Zooplankton samples were collected weekly throughout the ice-free season in 1991. A Wisconsin net (80 μm-mesh, 0.3 m diameter) was hauled from 20 m to the surface on each date to collect zooplankton. Based on calibrations of this net against a tube sampler and a Clarke-Bumpus sampler, a 70% net efficiency was employed in determining the volume of water sampled. Animals were preserved immediately in a 10% buffered sucrose-Formalin solution.

Zooplankton were identified and enumerated at $12 \times$–$50 \times$ magnification. Egg ratios were calculated by dividing the number of eggs observed (including ephippia) by the number of adult daphnid females counted. Seasonal changes in daphnid size were determined by measuring the lengths of individuals on each date using an ocular micrometer at $50 \times$ magnification. Animals were chosen haphazardly from samples, with between 16 and 65 specimens measured per sample.

Integrated phytoplankton samples were obtained by lowering a weighted 8 m length of Tygon tubing through the water column (inner diameter 2.5 cm), capping the upper end, and retrieving & preserving the sample in Lugol's solution. Phytoplankton analyses were performed by Phycotech, Inc. of Indiana. Samples were permanently mounted, identified and enumerated using inverted microscopy. Counts were converted to biovolume estimates following measurement of linear dimensions of each taxa and employing geometric formulae.

Food manipulation experiments

In situ food manipulations were conducted in clear plastic medicine vials (70 ml volume). All vials were incubated during the experiments in a large mesh nylon bag suspended at a depth of 2 m in University Bay, Lake Mendota. *Daphnia pulicaria* were collected from the epilimnion (1–2 m depth) and randomly assigned to vials in each food treatment. Fifty daphnids were tested in each treatment with a single daphnid placed in each vial. We selected animals of the approximate size at first reproduction in Lake Mendota for all experiments (i.e. 1.3 mm).

Animals in the starvation treatment were placed in vials containing epilimnetic water which had been filtered through a Millipore GF/F filter (0.45 μm pore size). The enriched treatment subjected animals to GF/F water which had been enriched by the addition of laboratory cultured *Chlamydomonas vulgaris* (a minimal amount of nutrient medium was also typically included as a result of our procedure). Final concentration of the food in this treatment was 5×10^4 cells ml^{-1}. The third treatment consisted of whole-lake water collected from the epilimnion also and passed through a 153 μm-mesh nylon net to remove zooplankton. Examination of the water used in each treatment indicated that the GF/F water contained no algae and that filtering water through the 153 μm-mesh net did not significantly alter the food quality or quantity compared to that available in the lake. Large species such as *Ceratium hirundinella*, *Closterium spp.*, abundant filaments and bundles of *Aphanizomenon flos-aquae*, as well as colonies of *Microcystis aeruginosa* were present in the whole-lake water.

Vials were filled with fresh treatment water at every monitoring time, and were completely sealed by plastic caps in between these times. Preliminary experiments on changes in dissolved oxygen concentrations in the vials over time indicated that oxygen dropped by less than 10% per day for each treatment. It took more than four days during these preliminary summer trials before oxygen levels dropped enough to cause significant mortality of individuals. We therefore assessed the status of all individuals every 24 hours in our experiments (except for the final two times in September when animals were checked every 48 hours). Temperatures during the July experiment were between 24 °C and 25 °C, and temperatures in September were 21 °C at the start and declined to 17 °C by the end of the study.

On each date, we determined if the daphnid was alive and the number of offspring released during the prior 24 hour period. If alive, the animal was transferred to a vial containing freshly prepared treatment water (offspring were not transferred). On the day an animal was found dead (or on the final day of the experiment) we determined the number of offspring (neonates) produced in the previous 24 hour period, the number of eggs held in the brood chamber, and the lipid content of the adult. We used a lipid index scale similar to that developed by Tessier & Goulden (1982) with zero representing no visible lipids and four indicating high lipid content. Lipid index data are presented only for the July experiment due to loss of data from the September experiment.

Differences in survivorship data among treatments were tested with Peto & Peto's log rank test (Pyke & Thompson, 1986). Wilcoxon's signed rank and the Kruskal-Wallis test were used to determine the significance of differences among the number of offspring produced in treatments. Statistical analyses were performed with the SYSTAT statistical software package (Wilkinson *et al.*, 1992).

Results

Daphnia and phytoplankton development during 1991

Daphnia pulicaria was the dominant daphnid in Lake Mendota during 1991. Following a decline in abundance of overwintering females in early spring, the population increased to a maximum of approximately 25 animals l^{-1} in early May (Fig. 2a). This abundance peak was preceded by a peak in egg production, and coincided with the spring clearwater phase (Fig. 3). A secondary peak in abundance occurred in mid-June, and was followed by a rapid population decline during the first two weeks of July (Fig. 2a). Egg-ratios declined almost one month prior to the population decrease. *Daphnia* abundances remained low during the summer and into the fall, with increases beginning in early October. Egg-ratios remained relatively low throughout the summer and fall, with only minor increases during the population increase in October (Fig. 2a).

The average length of *D. pulicaria* in 1991 fluctuated over the course of the seasons. Just prior to and during the rapid population increase in April animal size also increased (Fig. 2b). Following a decrease in length

during late April, daphnid size remained fairly constant until early July when the average length decreased again. Animal length fluctuated around smaller sizes throughout the late summer and fall until an increase occurred in November when the population again increased in abundance (Fig. 2a). The ratios of adult to immature daphnid densities ranged between 0.35 and 0.75 during the midsummer decline, with no clear relationship to the changes in abundance.

The phytoplankton community underwent seasonal shifts in 1991 similar to those in 1988 and 1989. Following a spring increase in smaller edible algae (cryptophytes and diatoms), a spring clearwater phase occurred with drastic increases in water clarity during May (Fig. 3). After this clearwater phase, cyanobacteria species such as *Aphanizomenon, Microcystis* and the dinoflagellate *Ceratium* increased in importance and dominated the plankton through most of the summer. The shift to dominance by cyanobacteria occurred during the decline phase of the *Daphnia* population in early July (Fig. 2). Large bundles of *Aphanizomenon* and colonies of *Microcystis* were abundant during this period. In October, a bloom of diatom species occurred at the time of fall mixis in the lake.

Experiments during summer decline

There was a significant effect of food manipulation on the survivorship of individual *D. pulicaria* held at ambient temperature and photoperiod (Peto & Peto's log rank test: $X^2 = 12.76$; $P < 0.005$). Animals fed a high concentration of *Chlamydomonas* exhibited the highest survivorship, with more than 60% of the animals still alive at the end of the five day experiment (Fig. 4a top). There was also a significant effect on number of offspring produced (Wilcoxon signed ranks test, $P < 0.05$). Following a one or two day lag, the number of offspring produced by animals in the enriched treatment tripled (Fig. 4a bottom). Additional evidence of the good feeding conditions for these animals is seen in the high lipid content of animals in the enriched treatment (Table 1).

The survivorship of animals fed whole-lake water was not significantly different from that of animals fed the *Chlamydomonas* enriched water ($X^2 = 0.005$; $P > 0.90$). Approximately 60% of the animals remained alive at the end of the experiment (Fig. 4a top). Offspring production increased over the course of the experiment for animals fed whole-lake water. Reproductive output for the whole-lake water fed animals was significantly lower than that observed for the
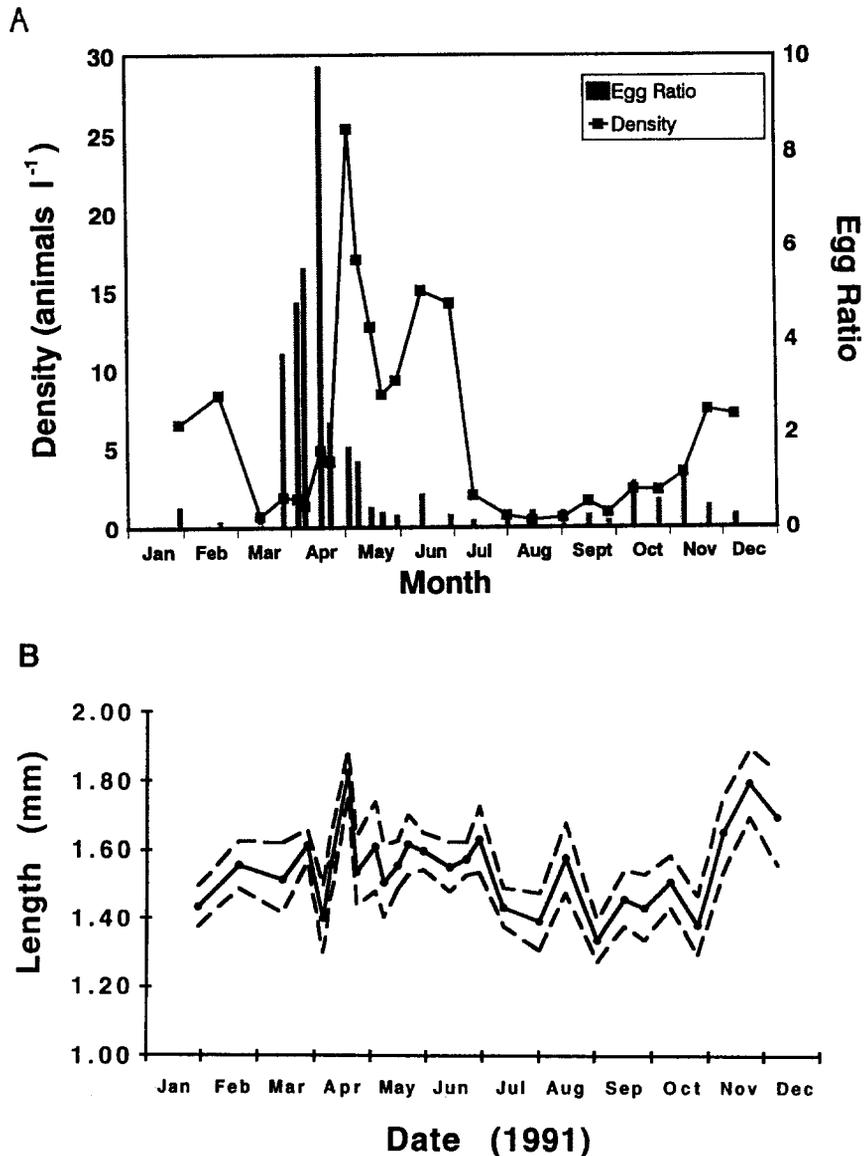
A

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Fig. 2. Daphnia pulicaria population dynamics in Lake Mendota during 1991. (A) Mean abundances (line) and egg ratios calculated as eggs per adult female (bars graph). (B) Mean (solid line) and 1 s.e.m. interval (upper and lower dashed lines) of adult and immature lengths during 1991.

Chlamydomonas fed animals (Wilcoxon test: $P = 0.01$; Fig. 4a bottom) but followed the same general pattern as animals in the enriched treatment. Lipid content was somewhat lower than that of animals in the enriched food treatment (Table 1). Animals placed in GF/F filtered water died at a significantly faster rate than animals in either of the other two treatments (filtered vs. enriched: $X^2 = 8.81$, $P < 0.005$; filtered vs. whole-lake water: $X^2 = 8.79$, $P < 0.005$). Fewer than 30% of the animals survived the starvation conditions for five days

(Fig. 4a top). Following an initial lag similar to that observed in the other treatments, animals held in filtered water failed to produce offspring after only three days (Fig. 4a bottom). These animals also exhibited a lower lipid index than animals in either of the other two treatments (Table 1).
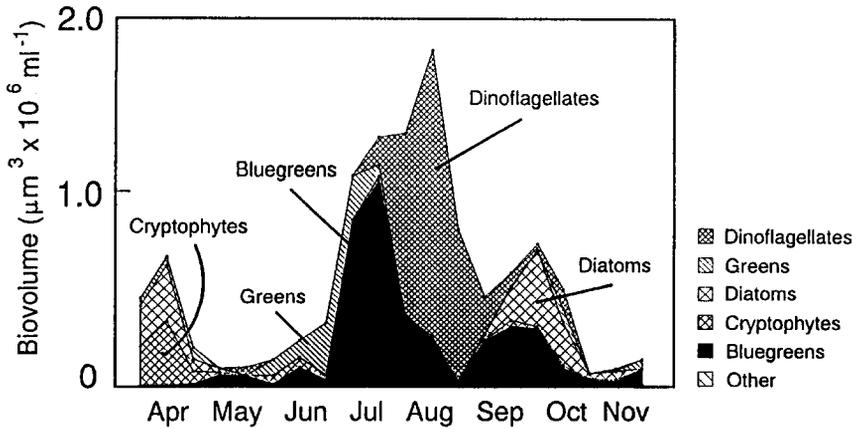
Fig. 3. Abundance and community composition of phytoplankton in Lake Mendota during 1991.

Table 1. Lipid index values for *Daphnia pulicaria* held in enclosures exposed to different food treatments in Lake Mendota, WI during July 1991. The lipid index can range from 0 (no lipids visible) to a maximum of 4. Lipid index values were determined at the end of the experiment. The number of surviving individuals is listed for each treatment.

Treatment	n	Mean lipid index	1 Standard error
Enriched GF/F	28	2.8	0.17
Whole-lake Water	22	1.7	0.37
GF/F Filtered	10	1.0	0.28

Fig. 4 A. Survivorship (top) and neonate production (bottom) of *Daphnia pulicaria* held in enclosures during (a) July experiments and (b) September experiments in Lake Mendota during 1991. Survivorship (I_x) is presented as the proportion of the original number in each treatment alive on each day. Treatments were GF/F filtered lake water (GF/F), GF/F filtered water enriched with *Chlamydomonas* (enriched), and lake water passed through a 153 μm mesh net (whole).

Experiments during fall period

There was no significant effect of the food manipulation on survivorship of *D. pulicaria* held at ambient conditions in mid-September 1991 ($X^2 = 3.59$; $P > 0.10$). Survival of animals in the *Chlamydomonas* fed treatment was again similar to that of animals in whole-lake water (Fig. 4b top). Animals held in filtered water exhibited a lower overall survivorship. However, this difference was not statistically significant.

Production of offspring was highest in the treatment with *Daphnia* fed *Chlamydomonas*, with a maximum of five neonates produced per adult daphnid per day (Fig. 4b bottom). Both the whole-lake water and the GF/F filtered water treatment animals produced relatively low, but non-zero numbers of offspring. Egg-ratios in the whole-lake water treatment did not differ significantly from those estimated from
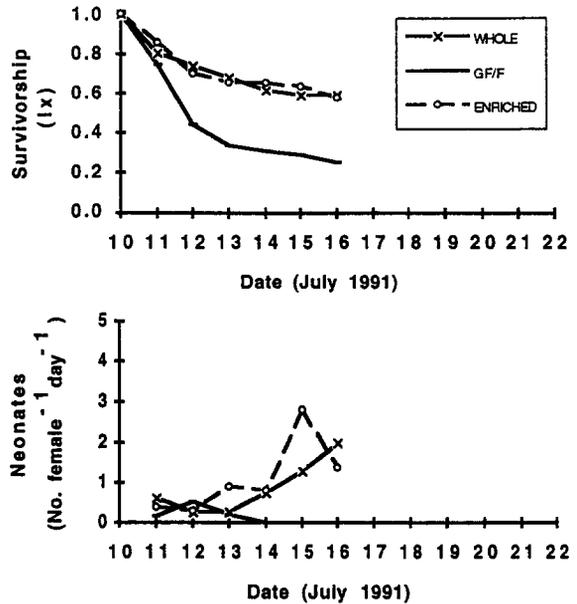
the plankton samples during this experiment (whole-lake water treatment mean = 0.9, plankton mean = 0.4, *t*-test: $P > 0.05$).

There was a seasonal affect on survivorship times in these experiments. Survival was better during the fall
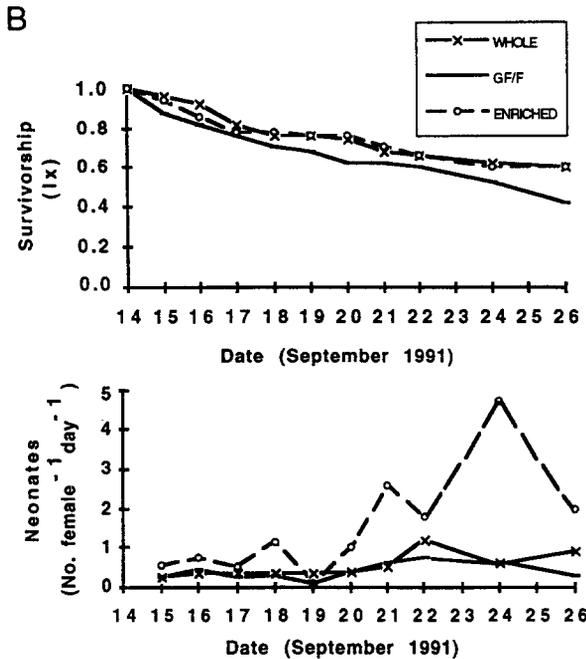
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Fig. 4 B.

experiments (Fig. 4a & 4b – top). Comparisons of survivorship within a treatment among seasons indicate that mortality rates were significantly lower in September than in June (Peto & Peto's log rank tests: $X^2 > 9.0$; $P < 0.005$ for all treatments). In the GF/F filtered water treatment, there was an approximate six-fold increase in starvation times, with 42% of the animals still alive after 12 days (Fig. 4b top).

Discussion

Population dynamics of Daphnia in Lake Mendota

Daphnia population dynamics in Lake Mendota have been shown to be determined by seasonal shifts in intensity of planktivory during years of high fish abundance (Luecke *et al.*, 1992; Vanni *et al.*, 1990; Rudstam *et al.*, 1993). In years with low fish abundance, previous studies indicate that planktivory by fish and invertebrate predators can not explain the midsummer decline of *D. pulicaria* (Luecke *et al.*, 1992; Rudstam *et al.*, 1993). These studies have proposed the hypothesis that the decline of *D. pulicaria* is caused by decreases in available food concentrations following the clearwater phase and perhaps increases of inedible cyanobacteria species during the summer (Vanni *et al.*,

1992, Rudstam *et al.*, 1993). This same explanation is employed in the PEG model of seasonal succession in lakes (Sommer *et al.*, 1986), and is frequently used to explain midsummer declines of daphnids (e.g. Gliwicz, 1985; Sommer, 1989).

Our in situ experimental analysis of this hypothesis for Lake Mendota indicates that individuals fed whole-lake water during the summer period when *D. pulicaria* is drastically declining survive and reproduce as well as animals fed an enriched diet, and do significantly better than starved animals. Daphnids held in enclosures and fed whole-lake water exhibited adequate survivorship and sufficient production of offspring to allow for the maintenance of population abundances in the absence of other mortality factors (Fig. 4a). This finding does not support the contention that low food abundance or poor food quality alone causes the midsummer decline of *D. pulicaria* in Lake Mendota.

During late summer and early fall, low food availability or poor food quality may explain the continued low daphnid abundances (Fig. 2a). *Daphnia* fed whole-lake water in September produced significantly fewer offspring than animals fed *Chlamydomonas* (Fig. 4b). This indicates that food resources in the lake at that time may not have been of sufficient quantity or quality to allow for population growth (Fig. 4b bottom). This conclusion is also supported by the fact that *D. pulicaria* can produce offspring at ambient lake temperatures when well fed, suggesting that low autumn water temperatures probably do not prevent population development during that time period. This explanation also is consistent with the observed increase in *D. pulicaria* abundance following the shift in phytoplankton composition in October from a cyanobacteria and *Ceratium* dominated community to one dominated by diatoms (Fig. 3).

A number of concerns can be raised concerning these types of enclosure experiments. First, overall survivorship in our enclosures was lower than normally expected in these types of experiments. This may have been due to soluble toxins produced by cyanobacteria in the lake, such as *Microcystis*, which are known to produce substances that can affect daphnid survivorship (e.g. DeMott *et al.*, 1991). Our filtering methods would not remove these types of substances from any of the treatments. In addition, although we attempted to select animals of similar sizes for starting the experiments, we did not know the feeding or reproductive history of the animals actually employed. Also, because there is a correlation between female size and number of neonates per brood, our estimate of the

effect of food manipulation on offspring production in enclosures (Fig. 4 bottom) may be biased by growth during the experiment. However, even restricting our analysis to the early part of each experiment (when growth differences among treatments should be minimal) clearly indicates that starved animals cease producing eggs, while those fed either whole-lake water or enriched water continued to produce eggs (Fig. 4). Nevertheless, even considering these potential variables, comparisons against our food enriched and starvation (GF/F filtered) treatments indicate that daphnids fed whole-lake water were surviving, storing lipids, and producing offspring at rates higher than expected during a population decline due to poor feeding conditions.

Midsummer Daphnia population declines

Midsummer declines of daphnids have been studied extensively in other lakes, but no single cause has been found to explain this phenomenon in general. Variation in mortality due to predation by fish and invertebrates has been shown to be important in many studies (e.g. Hall, 1971; Sprules, 1972; DeMott, 1983). In Lake Mendota, however, predation pressure from age 1 and older fish was extremely low in 1991 because cisco did not recover after the 1987 die-off. Also, only weak year classes of other planktivores were produced from 1988 to 1990, possibly as a result of the on-going biomanipulation of piscivore populations (Kitchell, 1992; Luecke *et al.*, 1992; Rudstam *et al.*, 1993).

As a result of the whole-lake biomanipulation in Lake Mendota, there are very extensive data on the role of planktivores in controlling the population of *D. pulicaria*. Estimates of larval fish abundances at nine stations collected on a weekly basis with a purse seine indicate that both yellow perch and white bass had above average year classes in 1991 (T. Johnson, pers. com.). However, predation by these and other young-of-the-year fish is low during June and July. Larval fish are either too small to feed on *Daphnia* (e.g. black crappie, white bass, sunfishes), or have already grown and moved inshore to the littoral zone (e.g. yellow perch; Post *et al.*, 1992; Schael *et al.*, 1991). Previous studies of the movement of yellow perch have shown that these smaller individuals spend both day and night in the nearshore regions (McCarty, 1990). This is supported by the very low catch of fish typically caught in early July in vertical gillnets fished at the deep hole station (Luecke *et al.*, 1992; T. Johnson, pers. com.). Predation by white bass young-of-the-year

could have been significant in September (J. Gala and T. Johnson, in prep.), although white bass biomass was an order of magnitude lower than cisco biomass prior to the 1987 die off (L. Rudstam, unpublished data) and estimates of consumption based on bioenergetics analyses indicate that peak predation by white bass occurred in early June, one month prior to the daphnid population decline in early July (T. Johnson, pers com.).

Although abundances of the invertebrate predator *Leptodora kindtii* typically increase concurrent with the decrease of *D. pulicaria* in early July, previous studies in Lake Mendota have found that estimates of consumption by *L. kindtii*, *Mesocyclops edax*, and fish on *D. pulicaria* are usually lower than the calculated death rates of daphnids during midsummer (Luecke *et al.*, 1992). However, it is difficult to obtain good estimates of *L. kindtii* density because these animals are not captured well using traditional zooplankton collection methods (Lunte & Luecke, 1990; Lathrop & Carpenter, 1992). Other estimates from the literature on feeding rates by *L. kindtii* are 2–5 times greater than those obtained in Lake Mendota, so it is possible that invertebrate predation may be more important than we have thought (e.g. Browman *et al.*, 1989). Observed increases in average daphnid size during the population increase in spring, and the rather large size of animals during the summer when population density was low are consistent with the idea that invertebrate predation on smaller animals may have been occurring (Fig. 2b). In addition, the potential for error in the calculation of death rates using measures of population growth (r) and egg ratios (b) is quite high unless rather restrictive conditions apply in the field population (Taylor, 1988). It would clearly be helpful to have more complete information on population dynamics and feeding rates by invertebrate planktivores such as *L. kindtii*.

A third hypothesis to explain the midsummer decline is that *D. pulicaria* shift to production of resting eggs (ephippia) during June and July each year. Although we do not have quantitative estimates on the number of ephippia produced, we have observed an increase in male *D. pulicaria* and ephippial egg production during June and early July in years of both high (1987) and low planktivore abundances (1988, 1991). This may represent a demographic response to the poor conditions that typically occur in Lake Mendota in late summer (either high planktivory, poor feeding conditions or a combination of both). If the deterioration of environmental conditions for daphnids in late summer is rather predictable (as appears to be the case),

a strategy of shifting to ephippia production would be advantageous. There is a need for further investigation of cues for onset of ephippia production and the role of dormancy in daphnid midsummer dynamics.

Any hypothesis to explain the summer decline of *D. pulicaria* (as observed in most years of low planktivory following the clear-water phase; Vanni *et al.* 1990; Lathrop & Carpenter, 1992; Luecke *et al.*, 1992) must account for the observed changes in egg ratios during the period of decrease, in addition to the actual decrease in daphnid abundance. Food limitation is often the explanation given for the observed change in egg ratios, however predation by visual planktivores on egg-bearing females can also lead to decreases in egg ratios (Threlkeld, 1979a, 1985). There is a slight decrease in size of daphnids during the summer of 1991 which may indicate increased size-selective planktivory (Fig. 2b), but this is based on measurements of only 16 individuals. A number of other lines of evidence do not support the explanation that predation by fish caused the midsummer decline in 1991. As mentioned above, estimates of fish abundances indicate that predation intensity was no greater in 1991 than in the previous years in which predation was too low to explain observed mortality rates (i.e. 1988, 1989; Luecke *et al.*, 1992). Also, we have observed similar midsummer declines in all years of low planktivory regardless of the timing of larval fish populations. Therefore, temporal variation in mortality due to predation by juvenile and larval fish is not a likely explanation. Predation by *L. kindtii* may explain the midsummer dynamics of *D. pulicaria* if our estimates of abundance or feeding rate are extremely low. However, size-selective predation by both larval fish and invertebrate predators would remove smaller individuals, perhaps causing a shift to larger size daphnids.

In summary, it appears most likely that an explanation that includes the combined effects of deteriorating food conditions, low levels of planktivory by both fish and invertebrate predators, and life history responses to the more or less predictably poor conditions in late summer would fit best with the extensive data available from Lake Mendota. Manipulative experiments to test specific hypotheses, like those presented here, are a necessary part of our investigations of field populations, but multiple factors almost certainly determine the dynamics of natural systems. The challenge now is to design new methods of experimentally testing multiple hypotheses concerning the ecology and evolution of these relatively simple, yet dynamic, ecosystems.

Acknowledgments

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