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## Demography of a natural population of *Daphnia retrocurva* in a lake with low food quality

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**Abstract.** The hypothesis was tested that *Daphnia* exhibit low population recruitment in a lake with phosphorus (P)-deficient food, where *Daphnia* populations failed to increase in response to greatly lowered minnow density. Egg ratio analysis was performed on *Daphnia retrocurva* from L110 of the Experimental Lakes Area, Ontario, in 1994. L110 has high food abundance (siston carbon (C) ~ 100  $\mu\text{M}$  C), but the seston is P deficient (C:P atomic ~ 600). Chrysophytes dominated the algal community. The fish community in this lake was manipulated in 1993 and 1994 by the addition of northern pike, *Esox lucius*. Zooplanktivorous minnows were greatly reduced after the piscivore addition, but the expected increase in abundance of the *Daphnia* to this altered predation regime was not observed. If food quality constrains the response of the *Daphnia* to changed predation, there should be low recruitment in the relatively sparse *Daphnia* population in this lake. Birth rates estimated by standard egg ratio analysis were  $<0.1 \text{ day}^{-1}$  for most of the sample period. In comparison to annual averages from the literature, recruitment in L110 was moderately, but not dramatically, low. *Daphnia* exhibited pronounced 'normal' vertical migration (up at night, down during the day) all year, and a strongly declining size at first reproduction through the season. Population density and birth rates seemed to show much less short-term change than previously observed in other lakes. Although the demographic predictions for food quality constraints seemed clear, *in situ* demography unfortunately neither supported nor strongly rejected the overall hypothesis of food quality limitation in this lake with very high C:P ratios. Possibly, direct demographic effects of low food quality will be difficult to observe in nature.

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### Introduction

Dynamics of herbivorous zooplankton populations in nature are determined by factors influencing both their mortality and their reproduction (Luecke *et al.*, 1990; Boersma, 1994). Size-selective predation is recognized as one of the key factors in zooplankton ecology (Gliwicz and Pijanowska, 1989). However, there is also considerable evidence for a strong influence of resources in controlling zooplankton growth rates (DeMott, 1989; Müller-Navarre and Lampert, 1996). For example, the total quantity of available food can be tightly related to the production of eggs (Lampert, 1978).

In recent years, it has been suggested that food quality is also an important factor determining zooplankton fitness. Thus, large quantities of poor quality food might yield low zooplankton growth, even if that food is readily ingested. Cyanobacteria tend to be nutritionally poor quality food for crustacean growth (Lampert, 1981; Repka, 1996). Studies associating zooplankton growth with the biochemical content of algae suggest that individual unsaturated fatty acids might also be important (Ahlgren *et al.*, 1990; Müller-Navarra, 1995). Other studies indicate that individual elements, particularly phosphorus, may be important dimensions in food quality (Sterner *et al.*, 1993). Based on laboratory growth studies (Sterner *et al.*, 1993) and on mass-balance models (Hessen and Andersen, 1992; Urabe and Watanabe, 1992), algal foods with a molar carbon:phosphorus (C:P) ratio  $> \sim 300$  have been considered poor foods for *Daphnia*. This threshold ratio

is given only as an approximate benchmark, and in fact is expected to vary under conditions such as different food quantities (Sterner, 1997). Experiments with P supplements found improved growth of *Daphnia* feeding on foods of high C:P, unambiguously demonstrating a direct dietary P deficiency (Urabe *et al.*, 1997). *Daphnia* have perhaps among the highest P demands of all zooplankton due to their high body P content (Andersen and Hessen, 1991). Based on these mechanistic studies, we can predict that lakes of high seston C:P ratio should be poor environments for the growth of *Daphnia*, but not necessarily other zooplankton herbivores.

To date, most studies of food quality related to element ratios have been based on laboratory measurements of animal growth on individual species of algae of tightly controlled composition. In particular, we lack information on the relative success of *Daphnia* in natural environments of comparable chemical composition to the laboratory studies. Natural features, such as vertical and horizontal gradients in food quality, fluctuating chemical and physical parameters, predation and multi-species algal communities, could potentially limit the importance of the results from simplified unialgal laboratory systems. Experiments by MacKay and Elser (1998) showed lower juvenile growth and lower reproduction for *Daphnia* feeding on high C:P L110 seston than on a similar quantity of low C:P seston of the nearby L979. Their study clearly indicates a potential for food quality limitation on natural seston. However, detailed demography of the animals in the lake itself, exposed to all the spatial and temporal variability of the natural lake, and incorporating the entire life table (as summary demographic parameters such as per capita reproductive rate or mortality rate do) is needed as a further test for the importance of nutritional limitation of zooplankton growth.

Here, egg ratio analysis (Edmondson, 1960; Paloheimo *et al.*, 1982) was used to try to determine rates of reproduction and mortality through one growing season in a natural population of *Daphnia retrocurva* in a lake with seston of high C:P ratio. The study was conducted in L110 of the Experimental Lakes Area, Ontario. Prior to 1992, this small, dimictic, oligotrophic lake had not been experimentally manipulated, nor had it been systematically sampled, but the lake was known to lack piscivorous fish. In 1992, the lake was sampled intensively and in the following 2 years the piscivorous northern pike, *Esox lucius*, was introduced (for more details, see Elser *et al.*, 1998). The year of this study was 1994. In spite of the near elimination of the minnows following the pike introduction (Elser *et al.*, 1998; George, 1994), *Daphnia* failed to become dominant (Figure 1). Minnow catch per unit effort (CPUE) estimates in 1994 were <10% of 1992 values, and by 1995 became essentially zero. Nevertheless, *Daphnia* remained <10% of the total zooplankton community. Such a lack of a *Daphnia* response to greatly relaxed predation could conceivably be due to several things: (i) physical or chemical conditions incompatible for *Daphnia*; (ii) continued mortality from small numbers of remaining minnows or from invertebrate predators; or (iii) low recruitment due to food quantity or quality. *Daphnia* survive for many days when cultured on L110 water (R.W.Sterner, personal observation) so hypothesis (i) does not seem likely. The remaining two hypotheses can presumably be tested by detailed demographic information. According to hypothesis (ii), high mortality

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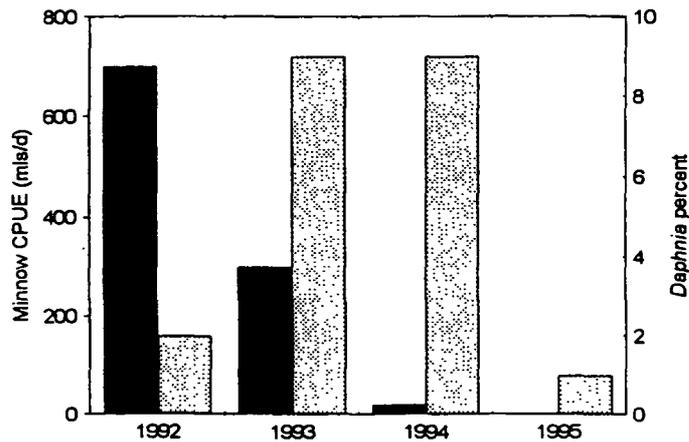


Fig. 1. Interannual variation in cyprinid minnow (dark bars) and *Daphnia* (gray bars) in L110. Piscivores were introduced early in 1993 and again stocked in 1994. Minnows are given as catch per unit effort (CPUE) and *Daphnia* are given as a percent of the total zooplankton biomass.

can be expected, but according to hypothesis (iii) low reproduction can be expected. Thus, by determining *in situ* reproductive and mortality rates, I hoped to be able to distinguish between these alternatives.

To date, most studies on food quality have examined rates of biomass gain in pre-reproductive animals. Population dynamics in nature though are determined by the entire life table schedule of mortality and reproduction. Full life tables of zooplankton on differing food qualities are not yet available. Nevertheless, it is logical to presume that diminished juvenile growth rate should have a substantial depressing effect on population recruitment due to increased age at first reproduction, which is one of the life history parameters most influential in population growth rates. Thus, although we do not yet know the full effect of differing qualities of food on different life table components, we might still expect poor quality food to translate into low population recruitment.

### Method

#### *Study site*

L110 (94°49'W, 49°44'N) is a naturally oligotrophic, stratified lake in the Experimental Lakes Area (ELA), Ontario. The lake has a surface area of 5 ha and a maximum depth of 13 m. Mean summertime chlorophyll *a* for 1994 was 3.2  $\mu\text{g l}^{-1}$ . Minnow species composition and size structure are given elsewhere (George, 1994). Phytoplankton were enumerated according to standard procedures at the ELA and on a different sample schedule from the rest of the parameters in this paper. The most abundant algae were chrysophytes (Table I). Half or more of the biovolume of the algae was in cells <30  $\mu\text{m}$  and thus of a size normally considered easily grazed (Figure 2). Algae in the epilimnion were very much dominated by small cells, while larger cells were more prevalent in the metalimnion.

**Table I.** Dominant phytoplankton species by volume in L110, 1994. For size structure, see Figure 2. Data were provided by Dr D.Findlay, Freshwater Institute, Manitoba

May	<i>Synura sphagnicola</i> <i>Uroglena botrys</i> <i>Uroglena volvox</i> <i>Dinobryon bavaricum</i>
June	<i>Merismopedia tenuissima</i> <i>Synura sphagnicola</i> <i>Chrysochromulina laurentiana</i>
July	<i>Synura sphagnicola</i> <i>Uroglena volvox</i> <i>Chrysochromulina laurentiana</i>
August	<i>Chrysochromulina laurentiana</i> <i>Rhizosolenia erienne</i> <i>Chrysochromulina parva</i> <i>Peridinium inconspicuum</i>
September	<i>Synura sphagnicola</i> <i>Chrysochromulina laurentiana</i> <i>Gymnodinium</i> sp.

Filamentous algae were always a very small percentage of the total algal community. The *Daphnia* in the lake in this year were assigned to the taxon *D.retrocurva*, though unlike the characteristic form of this species, the *Daphnia* in L110 did not possess a helmet.

#### *Chemical/elemental*

Sampling began on 5 June and ended on 26 August, 1994. All samples were taken at a single station at the point of maximum depth. Measurements of seston came from triplicate pooled mixed layer (PML) samplings of three epilimnetic depths. Seston PMLs were filtered through 80 µm Nitex to remove zooplankton. Vertical profiles of seston chemistry were performed on six dates through the season. Particulate C and P were measured on seston collected on GF/F filters (Whatman, Inc., nominal pore size = 0.7 µm). Direct enumeration of filtrates indicated that >85% of L110 bacteria were captured on these filters (Sterner *et al.*, 1996). Means and standard deviations of these three observations of C and the C:P ratio were calculated for each date. Based on the minimal selectivity of *Daphnia* feeding (DeMott, 1982) and on the predominance of algae in the easily grazed range (Figure 2), it was assumed that these measurements of seston are a sufficient approximation of the actual resource base of these animals.

#### *Zooplankton*

At approximately twice-weekly intervals, the lake was visited twice within a single 24 h period (once at night and once during daylight). Vertical profiles of the *Daphnia* were obtained by collections with a 15 l Plexiglas Schindler–Patalas trap with 80 µm mesh at meter intervals from 0 to 10 m (referred to as ‘Schindler samples’ below). Although the lake has a maximum depth of 13 m, attempts to sample below 10 m frequently drew sediment in the Schindler trap. Between one

Demography of *D.retrocurva* in a lake with low food quality

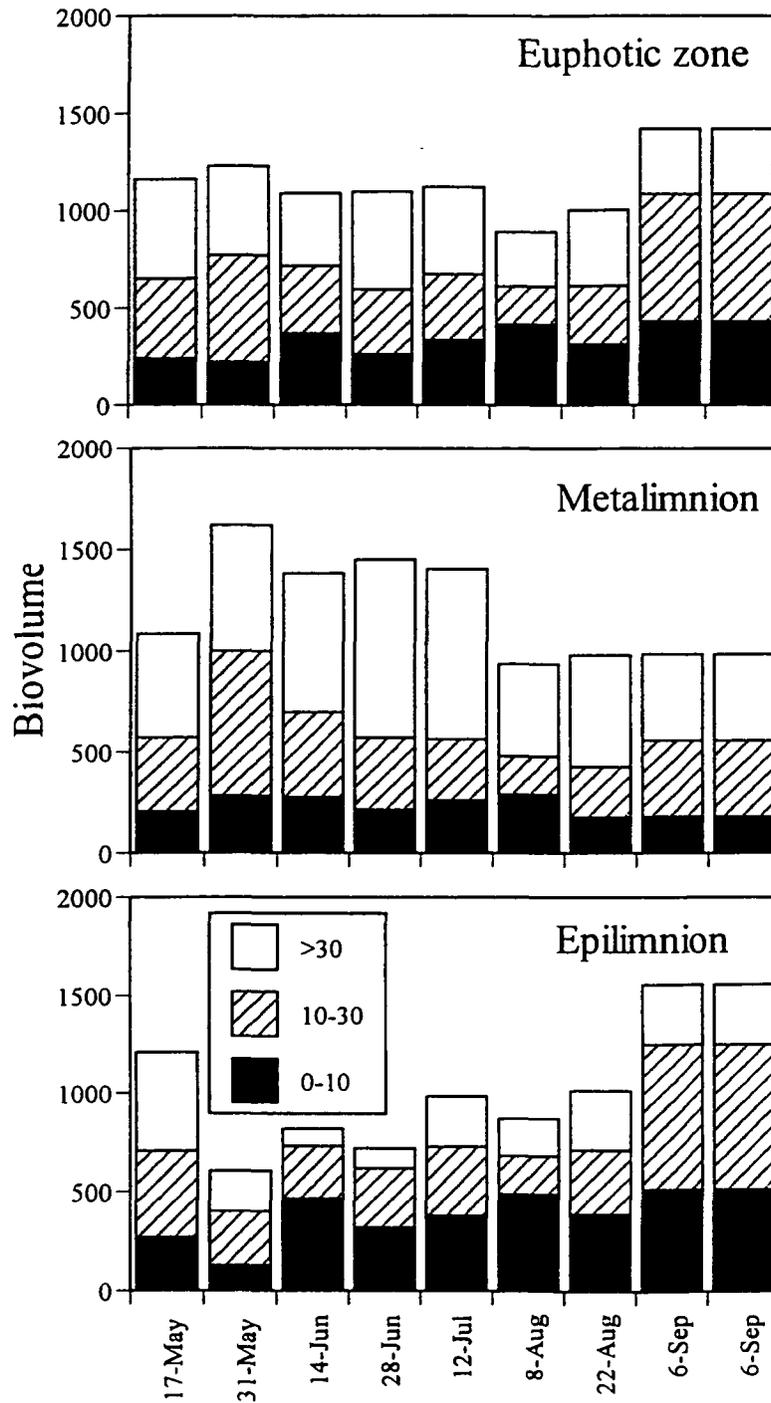


Fig. 2. Algal biomass (mg m<sup>-3</sup>, fresh weight) within size categories. Data courtesy of Dr D.Findlay, Freshwater Institute, Manitoba. For species list, see Table I.

and three samples were taken at each depth interval, depending on animal density. Temperature was recorded at meter intervals. During daylight sampling, vertical tows from the lake bottom to the water surface were taken with a Wisconsin-style plankton net (80  $\mu\text{m}$ ). Animals were preserved in Lugol's and refrigerated until they were counted and measured. For community analysis, the epilimnetic zooplankton were sampled once per week (day and night) at three depths within the mixed layer using the Schindler trap. These zooplankton PMLs were split into thirds using a plankton splitter (ARI, Inc., Seattle, WA), and one of the fractions was preserved for enumeration. The other fractions were used to determine the nutrient content of the total zooplankton community; nutrient data will be presented elsewhere. Zooplankton were counted and sized to determine the composition of the community. All crustacean zooplankton were identified and enumerated in each PML sample, except for rotifers and copepod nauplii which were subsampled. Individual lengths were measured until the SD was <10% of the mean length for each taxon. Lengths were converted to biomass using the length-weight regressions in Malley *et al.* (1989).

Schindler samples of individual depths were combined and the total number of *Daphnia* at each depth was determined using a plankton counting wheel. Samples from vertical net tows were examined under higher magnification using a Hensen-Stemple pipet for subsampling and a Sedgwick-Rafter cell. *Daphnia retrocurva* were measured for length (tip of head to base of body excluding head and tail spine) and clutch sizes were recorded. The total number of animals sized varied with population density and was generally 50–150, but was less on some dates early and late in the season.

Sufficient sample sizes were present to permit statistical analysis of egg stages during the period 30 June–1 August. All animals in these samples were examined, and the stage of the eggs was recorded as 1–5 according to published criteria (Threlkeld, 1979). About 10% of animals had distended brood carapaces, and loose eggs were observed in the samples. Stages of these loose eggs were not quantified. For statistical analysis,  $\chi^2$  tests were performed comparing the numbers of eggs observed in three egg stage categories (stage 1, 2, and 3–5, d.f. = 2) to an expected distribution based on the reported duration of each of these egg stages (Threlkeld, 1979).

#### *Demographic calculations*

To determine the temperatures to use for calculation of egg development time (below), the mean temperature experienced over a 24 h period was determined by multiplying the fraction of animals at a given depth by the temperature at that depth, and summing the results. Day and night means were thus obtained, and then averaged for an overall mean temperature. In the absence of information on exact timing of migration, day and night temperatures were weighted equally. On nearly all dates, the integral number of animals within the water column was greater at night than during the day. I was concerned about this difference in the total number of animals enumerated between daytime and night-time samples. Accordingly, a second mean temperature was calculated assuming that 100% of

the individuals not encountered during daytime experienced the lowest temperature (occurring at 10 m). This assumption is valid if all of the 'missing' individuals migrated to depths below those which could be effectively sampled and thus were not captured by the Schindler trap. For similar reasons, the number of animals in the night-time samples was used to determine population densities. Egg development time ( $D$ , days) was calculated from temperature ( $T$ , °C) using the formula:

$$\ln(D) = 3.3956 + \ln(T) - 0.3414(\ln(T))^2$$

(Bottrell *et al.*, 1976). Recruitment ( $b$ , day<sup>-1</sup>) was then calculated by:

$$b = \ln\left(\frac{E}{D} + 1\right)$$

where the egg ratio,  $E = (\text{total eggs})/(\text{total individuals})$ , is calculated from the vertical tow samples. The net growth rate ( $r$ , day<sup>-1</sup>) in the interval  $t = i$  to  $t = j$  (days) was calculated as:

$$r = \frac{\ln(N_j/N_i)}{j - i}$$

and the mortality rate ( $d$ , day<sup>-1</sup>) was calculated by:

$$d = b - r$$

## Results

The zooplankton community in L110 in 1994 was dominated primarily by calanoid copepods, particularly *Leptodiatomus minutus* and *Epischura lacustris* (Figure 3). Cyclopoids were *Tropocyclops* and *Mesocyclops*. Non-daphnid cladocerans were *Bosmina*, *Diaphanosoma* and *Holopedium*. Rotifers were *Keratella*, *Polyarthra*, *Tricocerca*, *Asplanchna* and *Conochilus*. *Chaoborus* were observed in the samples, especially at night, but the samples lacked enough individual *Chaoborus* to provide reliable estimates of their density. *Daphnia* were a moderate contributor to biomass in mid-season when they made up ~30% of the night-time zooplankton biomass, but only a few percent of the daytime biomass, so that the maximal percentage of day-night averages was 16% on July 26. The *Daphnia* were monospecific.

Both seston carbon and the ratio of C:P were relatively constant during the study period (Figure 4). Mean seston C was 83.6 μM. Epilimnetic seston C:P in L110 averaged 605 and always exceeded 400, meaning that the epilimnetic seston in L110 was always above empirically determined estimates of the food quality threshold (i.e. was presumably poor quality food). Seston C:P ratios generally declined with increasing depth, but were still high in the majority of the water column. Values <300 were observed almost exclusively at 10 m or below; thus, I

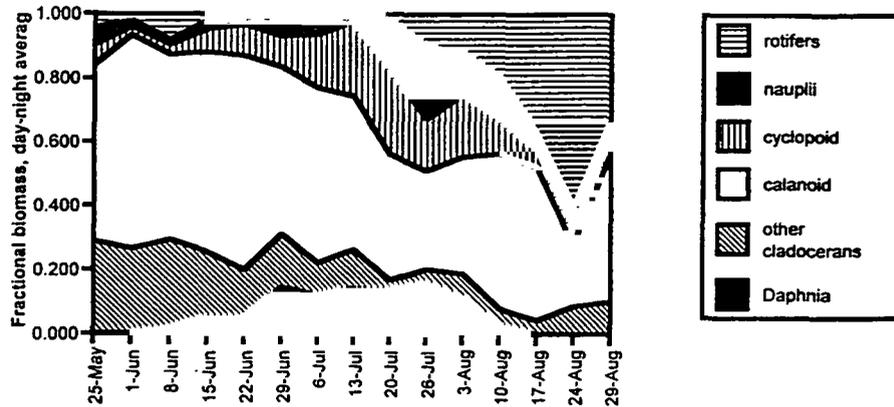


Fig. 3. Proportional abundance of major zooplankton groups. Samples from averages of six PMLs (three day and three night). Copepodid stages are included in either the 'calanoid' or 'cyclopoid' categories.

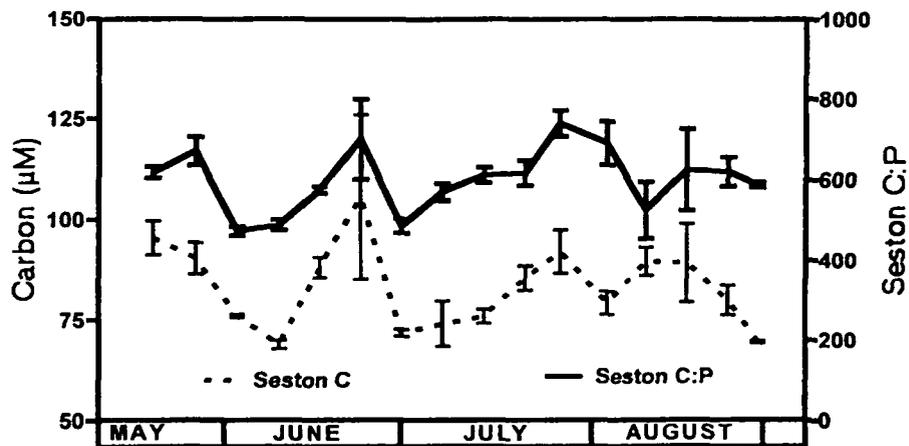


Fig. 4. Food quantity (seston C,  $\mu\text{mol l}^{-1}$ , solid line) and food quality (seston C:P, molar, dashed line) in L110. Error bars are  $\pm 1$  SE ( $n = 3$  PMLs).

conclude that almost the entire water column consisted of a poor resource for *Daphnia* growth, though not uniformly so.

*Daphnia retrocurva* density showed a distinct monophasic growth pattern with a single peak of density occurring on July 24 when the night density reached  $13 \text{ l}^{-1}$  (Figure 5A). Mean night density over the study period was  $3.1 \text{ l}^{-1}$ . During the day, individuals were always concentrated in depths below the thermocline, while during the night, observed peak densities were generally at or just above the thermocline (Figure 6). *Daphnia retrocurva* showed a pronounced 'normal' migration (up at night, down during the day) throughout the entire sampling season.

Demography of *D. retrocurva* in a lake with low food quality

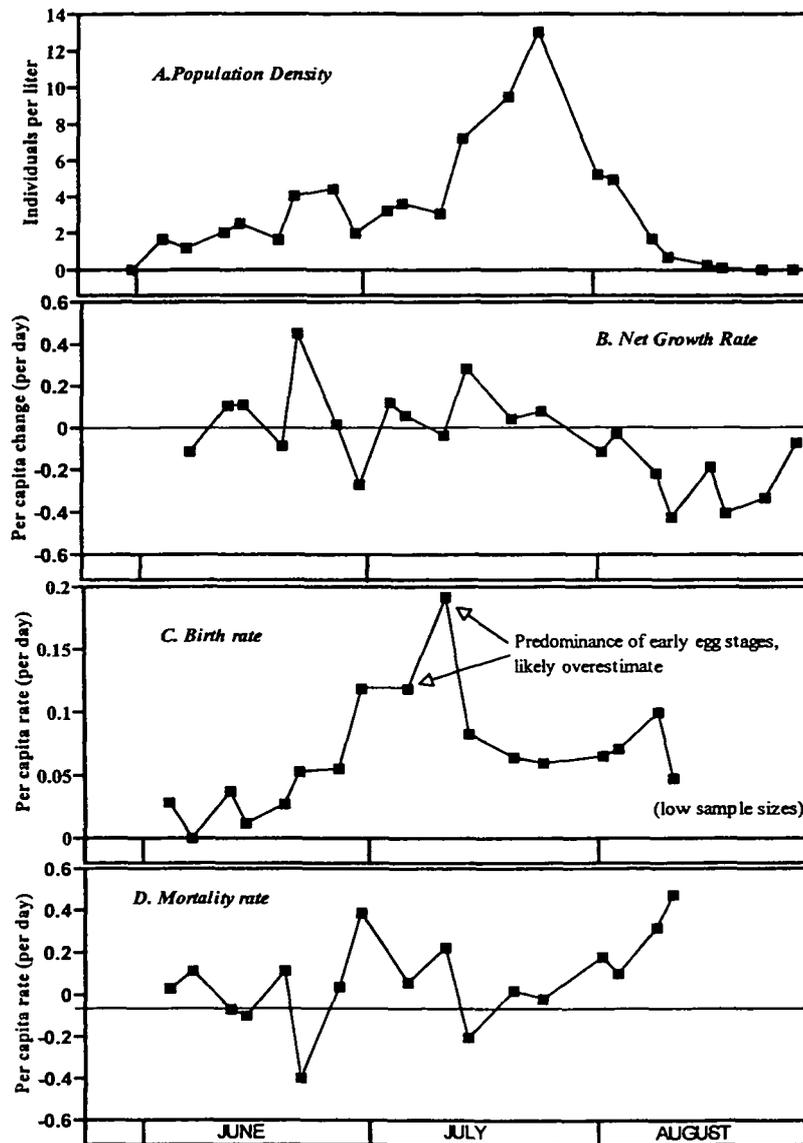


Fig. 5. *In situ* demography of *D. retrocurva* in L110, ELA. (A) *Daphnia retrocurva* density. (B) Instantaneous rate of change ( $r$ ,  $\text{day}^{-1}$ ). (C) Birth rate ( $b$ ,  $\text{day}^{-1}$ ). The two dates indicated had unexpectedly high numbers of early stage eggs, possibly indicating overestimation of reproduction. (D) Death rate ( $d$ ,  $\text{day}^{-1}$ ).

Surprisingly, the large number of ‘missing’ animals in the daytime samples had almost no effect on the calculated demographics. Daytime temperatures were already very low since most animals were found in the cold hypolimnion during those hours. Thus, the mean daytime temperature was little changed by factoring in the contribution from the ‘missing’ animals at the lowest depth. Development

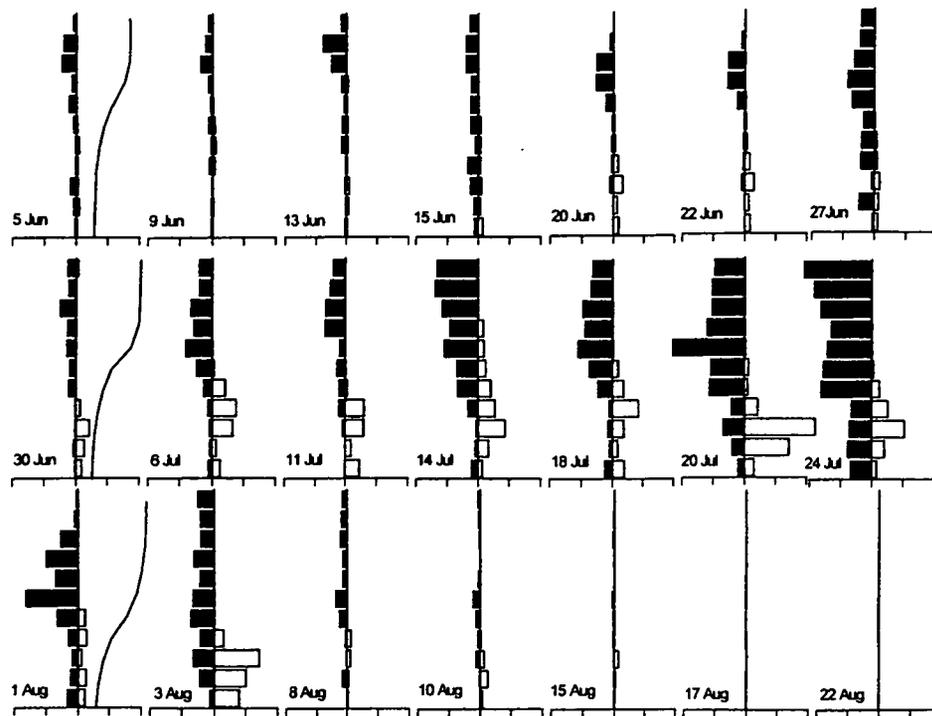


Fig. 6. Vertical distribution of *D. retrocurva* during the night (dark bars) and day (open bars) along with representative temperature profiles for three dates (lines). The figure does not include the earliest and latest sample dates in Figure 4, where sample sizes were close to zero. For graphical clarity, the axes are not numbered. Vertical: depth (m) from 0 (top) to 10 m (bottom). Horizontal: individuals per liter or temperature ( $^{\circ}\text{C}$ ), with space between tick marks equal to 10 (ind.  $\text{l}^{-1}$  or  $^{\circ}\text{C}$ ).

times averaged 7.2 days (range 5.1–10.0) when missing animals were unaccounted for and averaged 7.7 days (range 6.4–10.4) when missing animals were accounted for. Birth rates presented here are based on the assumption that missing daytime animals were at the lowest depth.

The net growth rate ( $r$ ) showed no clear seasonal trends, except perhaps for the end of the season when rates were always negative (Figure 5B). In contrast, per capita birth rates ( $b$ ) were distinctly seasonal, and rather smoothly increasing then decreasing. The birth rate was very low early in the season, and demonstrated a single mid-season peak of  $\sim 0.2 \text{ day}^{-1}$  several weeks before the population density peak (Figure 5C). A likely overestimation of  $b$  at this peak is discussed below. The mean birth rate over the study period was  $0.071 \text{ day}^{-1}$ . Mean brood size (total eggs divided by total adults) was 1.35, and showed no clear seasonal trend. Reproduction calculated per adult was  $0.171 \text{ day}^{-1}$  averaged over the season; again, there was no clear seasonal trend in this parameter. Death rates, which are calculated from  $b$  and  $r$ , and thus include the variability inherent in both calculations, fluctuated until the very end of the season when they appeared to show a tendency to increase, although it is difficult to separate signal

from noise (Figure 5D). Several dates had negative mortality rates which are either due to variability inherent in population sampling or to hatching of resting eggs, or both.

Size structure showed pronounced changes through the sampling season. For each date, the minimum size (millimeters) of gravid individuals was first determined to give an estimate of the size at first reproduction. Size at first reproduction clearly declined through the season from ~1 mm to ~0.7 mm (Figure 7A). Since this is an estimate of a minimum value, one can expect a bias due to sample size. However, sample sizes peaked in the middle of the growing season when density peaked, and no relationship between sample size and the minimum size of gravid individuals was observed (not shown). Thus, the observed reduction in size at first reproduction does not appear to be an artifact of differential sampling. Using the estimated size at first reproduction for each date, a ratio of juveniles to adults was then calculated (Figure 7B). One of these values (June 20) was considerably higher than all other values; this date had the highest estimated size at first reproduction (Figure 7A) and had a juvenile to adult ratio >13. The ratio was recalculated based on the size at first reproduction from the preceding sampling date, which brought the juvenile to adult ratio closer to the seasonal trend, although it was still the maximum value for the year (Figure 7B).

The size structure showed a great preponderance of juveniles in the population early in the season, with a sharply reduced share of juveniles up until mid-July when the ratio increased again. Such a pattern is essentially the inverse of the observed per capita birth rates (Figure 5C), with the date of the greatest number of adults compared to juveniles (minimum of the juvenile to adult ratio) also showing the maximum per capita birth rate.

Egg stages on some sample dates were highly significantly skewed toward representation by early stages (Table II). No sample dates had egg stages skewed toward later stages. Two dates in the middle of the season had very strong skewing (July 6 and 11). Interestingly, these two dates correspond to the peak in reproductive rate (Figure 5C), although not to the peak in population size (Figure 5A).

## Discussion

The reigning paradigm for zooplankton populations in seasonal environments is for a rapid response to quickly shifting changes in physical (e.g. temperature) and

**Table II.** Observed numbers of eggs within each egg stage as defined by Threlkeld (1979). Chi-square analysis is based on the number of eggs expected from egg stage durations in the same reference

Date	Stage 1	Stage 2	Stages 3-5	$\chi^2$	<i>P</i>
June 30	10	9	11	0.14	0.93
July 6	48	25	12	32.1	<0.001
July 11	51	15	11	48.1	<0.001
July 18	41	41	35	3.13	0.21
July 26	79	76	69	5.00	0.08
August 1	24	12	15	6.87	0.03
Total	253	178	153	54.2	<0.001

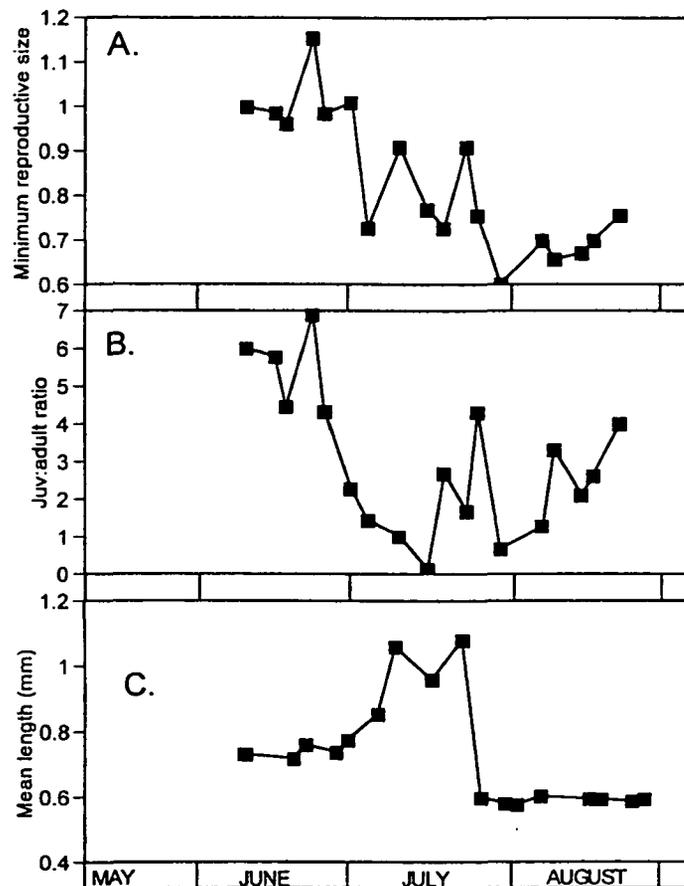


Fig. 7. Changes in the minimum size of observed gravid females (A), in the ratio of juveniles to adults in the population (B) and in mean length in the population (C).

biological (food abundance, predation) parameters (Lampert *et al.*, 1986). One such example is the 'clear water phase' (Lampert, 1993) when overgrazing of algae results in severe food depletion and subsequent starvation. Egg ratio studies often indicate such large and rapid shifts both in reproduction and mortality rates over time scales of several days. In this small, oligotrophic lake on the Precambrian Shield, the zooplankton community as a whole did indeed show changes as the season progressed (Figure 3). The target species of this study, *D.retrocurva*, varied in abundance many fold during the course of the growing season (Figure 5A). However, the demographics of this population were not indicative of a population reacting quickly to fast-changing physical and biological influences. There were in fact only gradual changes in per capita birth rate (Figure 5C). Thus, this particular population does not appear to have fine-scale seasonal dynamics controlled by physical factors such as temperature, or by food abundance and composition which are very constant during the year, or even by large changes in

predation pressure which would affect mortality rate. One obviously important aspect to the lack of change in the *Daphnia* demographics was in the relative constancy of mean temperature. The mean temperature experienced by the *D. retrocurva* through the sample period only varied from a minimum of 8.2°C to a maximum of 11.8°C. The very small range in mean temperature experienced by the *D. retrocurva* meant that egg development time was also nearly constant during the study. Epilimnetic temperature ranged only slightly more widely from 17 to 22°C. Algal biomass, species composition and P content were also remarkably constant in L110 (Figures 2 and 4).

Calculated mortality rates showed no clear seasonal trend, although individual days showed some high values. Mortality is calculated from both  $b$  and  $r$ . There was little short-term variability in  $b$ , so most of the short-term variability in  $d$  came from  $r$ . It is entirely plausible that most of this short-term variation in  $r$  is derived from sampling variability; thus, I am reluctant to over-interpret the changes from day to day in mortality. However, there is no evidence that the pattern of increase and then decrease of *D. retrocurva* density during the year resulted from higher mortality at the end of the year when the population was declining. *Daphnia retrocurva* had a clear seasonal pattern of increase and decrease in reproductive rate and in density, with a short lag between the seasonal maximum in reproduction and the seasonal maximum in density. *Daphnia retrocurva* abundance more closely resembled changes in reproduction than changes in mortality.

More than anything else to which I could attribute these seasonal changes in recruitment, size structure seemed to be paramount. The beginning of the season showed a 30 day period of consistently increasing share of adults in the population. Per capita birth rates (recruits divided by total population size) also increased consistently during the same period. Such a shift in size structure may reflect a single large juvenile cohort which matures very slowly, such that when a large enough fraction of this cohort attains reproductive maturity, per capita reproduction is then high, due primarily to the shift in size structure toward reproductive individuals. Lynch (1980) characterized *D. retrocurva* as a species which continues to grow, and whose clutch size continues to increase, after it achieves reproductive maturity. Continued growth thus should continuously increase per capita reproduction of a single large cohort, all else being equal. Mean animal size fell dramatically after the peak in reproduction, signaling perhaps the contribution of the large number of juveniles produced during the reproduction peak.

The observed decrease in age at first reproduction (Figure 7A) is consistent with other studies indicating a great plasticity to this phenotypic character. Variation in size at first reproduction has been attributed to clonal succession (Boersma and Vijverberg, 1994), or fish predation (Dini *et al.*, 1987; Dini and Carpenter, 1988, 1991, 1992; Weider and Pijanowska, 1993), as well as to changed predation on different sizes of adults (Lampert, 1993). Food conditions have also been implicated (references in Lampert, 1993).

A major hypothesis motivating this study was that *Daphnia* are recruitment limited in lakes such as L110 that have poor quality food. Inhibited recruitment

could account for the lack of response of *Daphnia* to the reduction of minnows in this lake (Elser *et al.*, 1998) and could help resolve some of the reasons for the variability in the intensity of the trophic cascade in lakes. *In situ* demography is an independent means to examine the hypothesis that food quality limits *Daphnia* in L110 (MacKay and Elser, 1998). So, the major question is: 'Are the observed recruitment rates consistent with poor food quality?'

The mean reproduction of *D. retrocurva* in L110 in 1994 was 0.071 day<sup>-1</sup>, corresponding to a population doubling time of 10 days. Recruitment appeared highest in mid-season. This same period was where there was a strong skewing toward early stage eggs (Table II). Virtually all egg ratio studies assume that egg mortality is identical to adult mortality. However, one study (Boersma and Vijverberg, 1995) observed high levels of non-developing eggs with a possible overestimate of *in situ* reproduction of 50–100% during times of low reproductive rate when the incidence of non-developing eggs is high. This recent study suggested that non-developing eggs should be most common during times of nutritional stress. Non-developing eggs have been observed in laboratory populations of *Daphnia* growing on foods of high C:P ratio, similar to the ratio observed in L110 (R.W.Sterner, unpublished; J.Urabe, unpublished). Removing the values of high reproduction during the two samples with strong skewing to early stage eggs lowers mean annual reproduction slightly to 0.066 day<sup>-1</sup>. The question remains, though, is this a sign of inhibited recruitment?

To construct a comparison population of values, a literature survey of egg ratio-determined *Daphnia* recruitment rates was undertaken. A total of 44 lake-years in 14 different studies were found (Table III). Methods were not entirely consistent in this set of studies. One major difference was in the means of calculating 'per capita' recruitment. Some studies base this figure on the reproductive rate per adult animal, while others base it on the rate per total individuals. The rate was calculated both ways in this study for comparison. For most entries in Table III, figures from published studies were digitized, and a mean for the entire sampling sequence in a single year for a given *Daphnia* taxon was calculated (unweighted for population size). As such, these values are very crude. They do not indicate, for instance, brief periods of either very high or very low recruitment, except in how those periods contribute to the mean. These data are perhaps sufficient only to ask the question of whether or not *Daphnia* recruitment in L110 is strongly and consistently depressed relative to the measurements in the literature. Inspection of Table III reveals that although the recruitment rates observed in this study are considerably less than the maximum *Daphnia* annual mean recruitment rates, they are near the median and thus are not dramatically low compared to the literature sample.

Certain specific comparisons are also notable in Table III. For one, the *Daphnia* in L110 did not have a dramatically different seasonally averaged recruitment rate than the *Daphnia* spp. from Peter Lake and Paul Lake, where *Daphnia* did respond to fish manipulations (Soranno *et al.*, 1993). *Daphnia* recruitment rates in L110 were also not dramatically different from nearby L979 where *Daphnia* became very numerous in response to an increase in the water level (Paterson *et al.*, 1997). Thus, the recruitment rates observed here do not look extremely low

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**Table III.** Birth rate estimates from the literature. Studies were divided into two major groups: those which reported birth rates per adult ('*b/adult*') and those which reported birth rates per total individuals ('*b/total*'). Some studies did not state explicitly which methods were used, and the best guess was then made based on the wording of the methods in those papers. Temperatures came either from the same source as the birth rate estimates or from other sources when sufficient information could be found to permit the effective temperature to be calculated. Months are reported with Jan = 1, Feb = 2, etc. Within the two groups '*b/adult*' or '*b/total*', studies are sorted from high to low birth rates. The present study is listed in both groups. References: (1) Antonsson, 1992; (2) Boersma and Vijverberg, 1995; (3) George and Edwards, 1974; (4) Hall, 1964; (5) Hoenicke and Goldman, 1987; (6) Hovenkamp, 1990; (7) Mason and Abdul-Hussein, 1991; (8) Paterson *et al.*, 1997; (9) Ringelberg *et al.*, 1991; (10) Shahady, 1993; (11) Soranno *et al.*, 1993; (12) Stich and Lampert, 1981; (13) Taylor and Slatkin, 1981; (14) Urabe, 1990

Species	Lake	Year	Months	Temp.	<i>b/adult</i>	<i>b/total</i>	Ref.
<i>Daphnia</i> spp.	Peter L.	1989	5-9	10	0.087		11
<i>Daphnia</i> spp.	Peter L.	1987	5-9	10	0.111		11
<i>Daphnia</i> spp.	Paul L.	1984	5-9	10	0.116		11
<i>Daphnia</i> spp.	Peter L.	1984	5-9	10	0.127		11
<i>Daphnia</i> spp.	Peter L.	1990	5-9	10	0.136		11
<i>D. cucullata</i>	L. Vechten	1988	5-9	NA	0.138		6
<i>Daphnia</i> spp.	Paul L.	1985	5-9	10	0.145		11
<i>D. retrocurva</i>	L110	1994	5-9	11	0.171		This study
<i>Daphnia</i> spp.	Paul L.	1987	5-9	10	0.188		11
<i>D. hyalina</i>	L. Vechten	1988	5-9	NA	0.194		6
<i>Daphnia</i> spp.	Peter L.	1988	5-9	10	0.194		11
<i>Daphnia</i> spp.	Paul L.	1989	5-9	10	0.199		11
<i>Daphnia</i> spp.	Paul L.	1990	5-9	10	0.200		11
<i>Daphnia</i> spp.	Peter L.	1985	5-9	10	0.202		11
<i>Daphnia</i> spp.	Paul L.	1986	5-9	10	0.213		11
<i>Daphnia</i> spp.	Peter L.	1986	5-9	10	0.231		11
<i>Daphnia</i> spp.	Paul L.	1988	5-9	10	0.235		11
<i>D. parvula</i>	Jordon Res.	1990	4-7	NA	0.268		10
<i>D. parvula</i>	Jordon Res.	1989	4-7	NA	0.290		10
<i>D. hyalina</i>	Ardleigh Res.	1981	1-12	12		0.033	7
<i>D. hyalina</i>	L. Constance	1977	5-11	8		0.041	12
<i>D. hyalina</i>	Ardleigh Res.	1982	1-12	11		0.043	7
<i>D. hyalina</i>	Eglwys Nynydd	1970	1-12	10		0.052	3
<i>D. hyalina</i>	L. Maarsseveen	1989	4-9	13		0.058	9
<i>D. hyalina</i>	Eglwys Nynydd	1971	1-12	10		0.061	3
<i>D. longispina</i>	Thingvallavatn	1977	7-12	7		0.063	1
<i>D. rosea</i>	Castle L.	1982	6-9	NA		0.064	5
<i>D. rosea</i>	L979	1994	6-9	NA		0.071	8
<i>D. retrocurva</i>	L110	1994	5-9	11		0.071	This study
<i>D. galeata</i>	L. Constance	1977	5-11	11		0.084	12
<i>D. galeata</i>	Ogochi Res.	1982	5-7	NA		0.096	14
<i>D. rosea</i>	L979	1992	6-9	NA		0.100	8
<i>D. longispina</i>	Thingvallavatn	1976	7-12	7		0.113	1
<i>D. rosea</i>	L979	1993	6-9	NA		0.117	8
<i>D. middendorffiana</i>	Castle L.	1982	6-9	NA		0.136	5
<i>D. galeata</i> × <i>cucullata</i>	L. Vechten	1991	3-12	NA		0.145	2
<i>D. galeata</i> × <i>cucullata</i>	L. Vechten	1990	1-12	NA		0.151	2

either in comparison to the whole literature population, or in comparison to sites where *Daphnia* have been observed to dominate the zooplankton community.

Thus, although Table III is perhaps the best (or only) comparison data set to ask whether the *Daphnia* in L110 are recruitment limited, interpretation of this table is highly problematic. The importance of distinguishing among the species

is made clear by noting that *D.hyalina* is obviously a relatively slow-recruiting species compared to other taxa. Unfortunately, the present study seems to be the first to report on the *in situ* demography of *D.retrocurva*. Temperature is an obviously important factor in plankton production in general (Shuter and Ing, 1997). Fortunately, the majority of studies that provided temperature data (or references to papers with relevant temperature data) had mean effective temperatures very close to the 11°C temperature of the present study. Inspection of the birth rate data from the literature used to construct this table suggests that maximum birth rates generally were much higher in other studies than in the present one. However, I judged that this parameter was highly unstable statistically, and I therefore did not attempt to compile and analyze the values formally. Finally, it should be noted that many of the *Daphnia* populations in the literature survey may be subjected to various challenges to their recruitment rate, such as poor quality food, toxic blue-greens, inedible algae, and the like, and we cannot assume that they represent a population of animals growing under nutritionally adequate conditions. From the above considerations, it is clear that the utility of the comparison in Table III is regrettably limited.

If the failure of *Daphnia* to increase when minnow predation in L110 was lowered was not due to a strong, consistent inhibition of reproduction, what then can it be? Two other explanations are: (i) the *Daphnia* in L110 are not, in fact, recruiting at low rates, and their failure to dominate the plankton is instead a product of predation by remaining minnows or other predators (including, perhaps, egg predation; Gliwicz and Boavida, 1996); (ii) recruitment is moderately and chronically limited by the poor food quality in the lake, but is not dramatically lowered.

Food quantity, as indicated by seston C, was relatively constant at ~80  $\mu\text{mol l}^{-1}$  throughout the season (Figure 4). Most of this seston is in a size range which is grazeable by *Daphnia* (Figure 2). The total quantity of particulate food in this lake always well exceeded starvation thresholds, which are ~1  $\mu\text{mol C l}^{-1}$  (Gliwicz, 1990). It was also high compared to estimates of saturation levels of food from field studies. For example, Müller-Navarre and Lampert (1996) recently showed saturation of *D.galeata* growth in the Schösee, Germany, at seston C of ~40  $\mu\text{mol C l}^{-1}$ . Lately, several studies have pointed to individual unsaturated fatty acids as likely causes of the quality of algae as food for freshwater zooplankton. Fatty acids were not measured in the L110 seston in the present study, but the lake was chrysophyte dominated (Table I). Chrysophytes are generally rich in unsaturated fatty acids (Ahlgren *et al.*, 1990).

A curious feature of the *D.retrocurva* in L110 was their continued normal migration in spite of the greatly lowered abundance of minnows in the lake. Vertical migration has been shown to be rapidly induced by alterations in fish abundance (Dini and Carpenter, 1991). Thus, either the L110 *D.retrocurva* are genetically incapable of adopting a non-migrating strategy, or the proximate causes for the migration were present in the lake during the study period. In spite of reduced minnow abundance, minnow influence may have still been sufficient during 1994 to effect a vertical migration in the *Daphnia*. However, continued sampling in 1995 (not shown) indicated a further reduction in minnow abundance

compared to 1994, but an even lower total abundance of *Daphnia* (see Elser *et al.*, 1998) that continued to migrate. A second potential advantage to migration, in addition to possible escape from a sparse minnow population, is the vertical gradient in seston quality. Williamson *et al.* (1996) recently argued that vertical gradients in resources may be considerably more important in vertical migration than has previously been recognized. As stated earlier, seston had a generally higher P content lower in the water in L110 than in the epilimnion. Resources alone, though, are incapable of explaining why the population spends daytime hours in the dark rather than some other pattern.

In conclusion, the *in situ* demographics of this potentially food quality-limited *Daphnia* population were consistent with recruitment limitation due to poor food quality—recruitment rates were slightly below the median of a literature sample. However, even in this lake with a very high seston C:P ratio and thus presumably very low food quality, the *Daphnia* were still recruiting at moderate rates. If poor food quality exerts its influence by a moderate penalty in recruitment rather than a severe one, detecting it in the field will be quite difficult.

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