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Seasonal dynamics and interspecific competition in Oneida Lake *Daphnia*

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Abstract I investigated the population dynamics and competitive interactions of two species of the suspension-feeding crustacean *Daphnia* in Oneida Lake, N.Y. Both species have persisted in the lake for decades, but their water-column densities are negatively correlated. The larger *Daphnia pulicaria* dominates in some years, the smaller *D. galeata mendotae* in others, and in some years one species replaces the other seasonally. Although this pattern results in part from annual variation in vertebrate predation pressure, predation alone cannot explain the irregular daphnid dynamics. In 1992–1995, I examined the water-column abundances, birth and death rates of both species. *D. pulicaria* dominated in two years, *D. galeata mendotae* was replaced by *D. pulicaria* in one year and in 1994, both species persisted in low numbers. To test the effect of temporal changes on the strength of intra- and interspecific competition on both juvenile and adult daphnids, I manipulated a series of field enclosures in 1994 and 1995. The outcome of competition varied within and between years, and its effects were most evident at the highest densities and lowest resource levels. For adults of both species, the effects of interspecific competition were detected more often than those of intraspecific competition. Lipid reserves (a metric of fitness) among juveniles were generally low, with those of *D. galeata mendotae* often being less than those of *D. pulicaria*. Contrary to the results of other studies examining competition in daphnids, spatial segregation and predictable within-year reversals in competitive dominance most likely do not play a large role in fostering coexistence of the Oneida Lake daphnids. Instead, coexistence of these

competitors is promoted by interannual variation and long-lived diapausing eggs.

Key words Competition · Population dynamics · Zooplankton · Coexistence

Introduction

The importance of interspecific competition in natural systems has been a source of debate since the development of the Lotka-Volterra models (Lotka 1925; Volterra 1926). As recently as the early 1980s, field experiments designed to test for interspecific competition were still relatively rare, and there remained a great deal of speculation about the frequency of competition in nature (Connell 1983; Schoener 1983). Even though Schoener (1983) and Connell (1983) both concluded that competition in nature was common, controversy still exists about its role in structuring communities (Grace and Tilman 1990; Wilson and Tilman 1991; Nudds and Wickett 1994). As pointed out by Goldberg and Barton (1992), simply demonstrating that competition occurs does not necessarily suggest that it has influential ecological or evolutionary consequences in a particular system.

The annual succession of plankton species found in many lakes has made these systems popular for exploring competitive interactions (see reviews by Bengtsson 1987; DeMott 1989; Rothhaupt 1990). Zooplankton species shifts also often seem to result from the interaction of predation and competition (Gliwicz and Pijanowska 1989) and various studies have clearly demonstrated the ability of vertebrate predation to structure planktonic communities (e.g., Hrbáček 1962; Brooks and Dodson 1965; Post and McQueen 1987; Black and Hairston 1988; Leibold 1989; Gliwicz 1994). However, whether or not competition is a dominant force in pelagic communities remains controversial, despite numerous examples of interspecific competition among plankton species (Bengtsson 1987).

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This controversy persists in part because competition experiments conducted under different environmental conditions often have different outcomes. Plankton ecologists have long searched for a reliable predictor for the outcome of competition (e.g., body size; Brooks and Dodson 1965; Hall et al. 1976), but this search may be futile. In a review of competition among cladoceran zooplankton, Bengtsson (1987) found that when the same species combinations were examined under different conditions, the outcome varied between experiments in 16 of 21 cases. Environmental conditions in natural systems are constantly changing and many factors (e.g., resource quantity and quality, temperature, abundance of competitors) interact in complex ways. Consequently, to understand fully the role of competition in natural communities, experiments must be conducted not only across systems, but multiple times within a system as well. As a result, the contribution of competition to community interactions is still poorly understood in most aquatic systems.

For these reasons, predicting the role of competition in the daphnid assemblage of Oneida Lake, N.Y. is not straightforward. Oneida Lake is a large (206.7 km²), shallow (maximum depth 16.8 m, mean depth 6.8 m), eutrophic lake located on the Ontario Lake Plain in central New York. Two closely related species of the suspension-feeding crustacean *Daphnia*, the smaller *D. galeata mendotae* and the larger *D. pulicaria*, have coexisted in the lake for at least 30 years, but their densities are negatively correlated. Cohort strength of the primary planktivore, young-of-the-year yellow perch (*Perca flavescens*), varies markedly from year to year, and the negative correlation in daphnid water-column densities has been hypothesized to result from variable predation and competition (Mills and Forney 1987; Mills et al. 1987). In the years 1964–1986, Mills and Forney (1987) found that *D. galeata mendotae* typically dominated when biomass of young-of-the-year yellow perch was high, whereas years with low perch biomass were often dominated by *D. pulicaria*. As a result, they concluded that predation was the primary regulating factor in the daphnid assemblage, and in years with low planktivory, *D. pulicaria* competitively excluded its smaller congener.

However, effects of competition were not addressed experimentally and there are reasons to expect that *D. pulicaria* may not always be the superior competitor in Oneida Lake. First, dense Cyanobacteria blooms of *Microcystis*, *Anabaena* and *Aphanizomenon* can last from July through September (Greeson 1971). Because smaller species are often more efficient at excluding interfering particles, mechanical interference by filamentous or colonial Cyanobacteria often leads to a greater reduction in feeding rate in larger species (Gliwicz and Siedlar 1980; Hawkins and Lampert 1989; Gliwicz and Lampert 1990). Second, although the lake is naturally productive, Wagner (1983) has documented evidence for food limitation within the daphnid assemblage. Tillmann and Lampert (1984) found that smaller species can

become the dominant competitor under severely limiting resource levels because they are able to reproduce at much lower food concentrations than larger species. Third, the orientation of the lake in the direction of the prevailing winds prevents permanent summer stratification, and maximum mean water temperatures typically reach 25°C (Mills et al. 1978). Even the deepest waters can exceed 20°C. Because there is evidence that *D. pulicaria* can suffer reduced reproduction at high temperatures (Threlkeld 1979; Hu 1994), this lack of a cool-water refuge might lead to poor performance of the Oneida Lake *D. pulicaria*. Lastly, Hu and Tessier (1995) recently found a seasonal reversal in the rank order of competitive abilities between *D. pulicaria* (larger) and *D. galeata mendotae* (smaller) in Gull Lake, Mich. Consequently, there is no reason to expect that *D. pulicaria* will always outperform *D. galeata mendotae*.

To understand better the role of competition in the population and community dynamics of the two *Daphnia* species in Oneida Lake, N.Y., I combine four years of observational data with results from five *in situ* competition experiments to address the following questions. (1) Are individuals of these two populations affected by intra- and/or interspecific competition? (2) Do these effects vary within and between years or is one species always the superior competitor? (3) How do the interactions of these species in Oneida Lake compare to their interactions in other lakes? (4) If competition does occur, what mechanism best explains species coexistence in this lake?

Unlike seasonal dynamics in other systems (e.g., DeMott 1983; Hu and Tessier 1995), in Oneida Lake these species do not follow a predictable succession every year, making within-year reversals in competitive dominance an unlikely candidate for the maintenance of species diversity. Moreover, in many lakes examined thus far, daphnid coexistence is promoted by spatial segregation of species across the thermocline (Tappa 1965; Leibold 1991; Tessier and Welser 1991; Hu and Tessier 1995), but this type of segregation is prevented in Oneida Lake by its homothermal conditions. Consequently, this study provides information on the interactions of daphnids in a fundamentally different type of system than those previously investigated, one lacking both significant vertical structure and constant seasonal dynamics. In addition, rather than focusing solely on those processes affecting the water-column population, I discuss the role of long-lived dormant eggs in the coexistence of these two species.

Materials and methods

Annual patterns

I collected two replicate zooplankton samples from the main sampling station of the Cornell Biological Field Station on Oneida Lake (12 m depth) at weekly intervals during the ice-free seasons of 1992–1995. Samples were taken every 3–4 weeks during periods of ice cover. In 1992 and 1993, zooplankton were collected with a

Clarke-Bumpus plankton sampler, with built-in flow meter and a 75- μm mesh net, by oblique tow from approximately 1 m above the bottom to the surface. During ice cover and in the 1994 and 1995 ice-free seasons, samples were collected with a 0.5-m-diameter conical net (75 or 150 μm) towed vertically from 1 m above the bottom to the surface. Samples were preserved in 70% ethanol and subsamples were counted under a Wild M8 stereo-dissecting microscope at $\times 25$ until a minimum of 100 individuals from each species had been identified (when possible). Large volumes of each sample (10–100%) were searched for rare individuals.

In summer 1993–1995, 30 or more live animals of each species (when possible) were collected every 3–7 days. Body length (mid-point of the eye to base of the tail spine) and clutch size were measured immediately to calculate *Daphnia* birth rates. When live animals could not be assayed, clutch sizes were estimated from preserved samples. Juvenile condition was assessed on dates associated with the competition experiments in 1994 and 1995. Individual daphnids were assigned a rank score (0–3) based on the size and abundance of stored lipid droplets (Goulden and Hornig 1980).

Population growth rates (day^{-1}) were calculated from water-column abundance (N) on two successive sampling dates (t_1 and t_2):

$$r = \frac{\ln(N_{t_2}) - \ln(N_{t_1})}{t_2 - t_1}$$

I used the egg ratio method to calculate birth rates (day^{-1}) for each species (Edmondson 1960; Paloheimo 1974):

$$b = \frac{\ln[(E/N) + 1]}{D}$$

based on the number of eggs per individual (E/N) and the temperature-dependent development time, D . For *D. pulicaria*, development times were calculated using an equation derived from the data of Eslová (1959) and Gulbrandsen and Johnsen (1990). Hall's (1964a) data were used to calculate development time of *D. galeata mendotae*. Death rates, d , in each population were then estimated by taking the difference between birth and realized growth rates.

Competition experiments

I performed two field experiments in 1994 and three field experiments in 1995 to examine the effects of competition in these species. The experimental design follows that of Tessier et al. (1982) and Hu and Tessier (1995). In each experiment, between 16 and 20 cylindrical polyethylene bags were filled with the natural phytoplankton assemblage. Each bag was attached to a 0.03-m² opening in a Plexiglas frame at the top (four per frame) and an anchor at the bottom. To fill the bags, I placed a 150- μm mesh net over the top of each enclosure and lowered the frame 9 m in the water-column. As the frame was pulled to the surface, the tubes filled with the natural phytoplankton assemblage while most zooplankton species were

excluded. Each enclosure was fully inflated by pouring buckets of surface water through the mesh. Once filled, the *Daphnia* were added and the bags were completely sealed with an additional piece of polyethylene. The bags were then completely submerged by suspending each frame from a line approximately 2 m beneath the lake surface.

Each experiment consisted of five treatments: two contained only *D. galeata mendotae*, two contained *D. pulicaria* alone, and one contained both species. Bags assigned to half-ambient treatments (0.5 \times) contained one species at half the total ambient daphnid density in Oneida Lake. Ambient-density treatments (1 \times) also contained only one species but at twice the density of the 0.5 \times treatments, and thus served as a test for intraspecific competition under natural conditions. The final treatment (Mix) consisted of a 50:50 mixture (by numbers of individuals) of the two species, each at half-ambient density. By comparing results from the Mix treatment to the 0.5 \times and 1 \times treatments, the effects of interspecific competition could be measured against the effects of intraspecific competition for each species. Because the mixture treatment contains information on both species, the five experimental treatments produced six categories for analysis (*D. galeata mendotae* 0.5 \times , 1 \times , Mix; *D. pulicaria* 0.5 \times , 1 \times , Mix). On each date, the number of animals added to the ambient-density bags reflected the total ambient daphnid density in Oneida Lake. Initial densities, enclosure volumes, and replicates/treatment are presented in Table 1.

Due to the changing daphnid assemblage, the procedure for collecting the animals differed between years. In 1994, both species were present in Oneida Lake at low densities for much of the summer. On the morning of each experiment, *Daphnia* were collected from Oneida Lake by towing a 500- μm mesh net through the water column for several minutes. This large mesh size primarily collected adult *Daphnia* and other large species (e.g., *Leptodora*, *Epischura*). Before being transferred into the appropriate treatment, the animals were sorted to species under a dissecting microscope. In 1995, only *D. pulicaria* was present in Oneida Lake, which eliminated the need to hand-sort each species. The day of each experiment, I collected *D. galeata mendotae* from Crystal Lake, N.Y., located approximately 60 km northeast of Oneida Lake, and *D. pulicaria* from Oneida Lake. Aliquots of the appropriate amount were then transferred directly into the bags. Each aliquot was scanned visually and large predators (e.g., *Leptodora*, *Epischura*) that had been collected were removed by pipette.

To establish food conditions at the start of each experiment, depth-integrated phytoplankton samples were collected with a 12-m length of Nalgene tubing. Samples were preserved immediately in acid-Lugol's solution. After concentration, transects in a settling chamber were counted and cells were identified to family or genus. Additionally, to estimate initial phytoplankton biomass, I collected duplicate samples by filtering water onto Whatman glass-fiber filters, which were subsequently frozen until analysis for chlorophyll *a*. Pigments were extracted in 90% acetone and absorbences were determined spectrophotometrically both before and after acidification (Strickland and Parsons 1972).

Table 1 Initial conditions for the in situ competition experiments. All daphnid densities are reported as animals l^{-1} . Ambient-density bags contain animals at approximately the same density as the water-column, and thus test for intra- and interspecific competition at ambient densities. In 1994, enclosures were 1 m long in July and 1.67 m long in August. All tubes were 5 m long in 1995. Oneida

Lake surface and bottom water temperatures varied by less than 4°C. Ambient phytoplankton concentrations are expressed as cells $\times 10^3 \text{ ml}^{-1}$. Lower-quality cells are Cyanobacteria (*Anabaena*, *Gloeotrichia*, *Microcystis*, and *Aphanizomenon*) whereas Higher-quality cells are cryptophytes, green algae and diatoms

| | Total daphnid water-column density | Half-ambient treatment (0.5 \times) | Ambient-density treatments (1 \times , Mix) | Enclosure volume (l) | Number of replicates per treatment | Average water temperature (°C) | Higher-quality cells | Lower-quality cells | Total cells |
|-------------|------------------------------------|--|---|----------------------|------------------------------------|--------------------------------|----------------------|---------------------|-------------|
| July 1994 | 6.4 | 3 | 6 | 30 | 3 | 24 | 1.7 | 6.8 | 8.5 |
| August 1994 | 3.8 | 2 | 4 | 50 | 3 | 22 | 2.6 | 35.5 | 38.1 |
| June 1995 | 20.4 | 10 | 20 | 150 | 4 | 19 | 1.4 | 0 | 1.4 |
| July 1995 | 1.6 | 1 | 2 | 150 | 4 | 23 | 3.1 | 77.3 | 80.4 |
| August 1995 | 11.9 | 6 | 12 | 150 | 4 | 24 | 4.1 | 72.8 | 76.9 |

Each experiment lasted 4(1994) or 5(1995) days which nearly represents the time from the hatching of an egg until first reproduction for these species at summer temperatures (Table 1). At the end of each experiment, all animals were collected and preserved in cold sugar-formalin. In 1994, I counted the entire contents of each bag to determine final population densities, whereas I used four replicate subsamples in 1995. From each enclosure, 40–60 individuals were examined within 3 days at $\times 25$ under a dissecting scope, and body length, clutch size, and juvenile lipid index (0–3) were recorded using an ocular micrometer in 1994 and a digitizing pad and Sigma Scan 3.4 in 1995. To obtain a better estimate of clutch size, additional *Daphnia* were examined until at least 60 adults had been censused, or the entire sample had been searched. All *D. galeata mendotae* over 1.3 mm and all *D. pulicaria* over 1.6 mm were considered to be adults, based on the typical size of first reproduction in these populations (C.E. Cáceres, unpublished data).

The effects of competition were assayed by three measures: fecundity (eggs per adult), juvenile lipid index, and population growth (calculated as a percentage of initial population density). The fecundity data were log transformed to reduce heteroscedasticity. Data for each variable were analyzed by ANOVA with planned contrasts for intraspecific competition (0.5 \times vs. 1 \times) as well as contrasts for interspecific competition (0.5 \times vs. Mix). When significant interspecific competition was detected, the contrast of mixture vs. ambient density (Mix vs. 1 \times) was also included to separate statistically the impacts of inter- vs. intraspecific competition. Type I error was set at $\alpha = 0.05$ in all analyses.

In addition, I calculated an index of competitive effects (IC) as a summary statistic for both inter- and intraspecific competition effects on adult fecundity:

$$IC = \frac{(\bar{Y}_c - \bar{Y}_e)}{\bar{Y}_c}$$

where \bar{Y}_c is the mean of the variable from the half-ambient treatments (0.5 \times) and \bar{Y}_e is the mean from the experimental treatment (1 \times for intraspecific competition, Mix for interspecific competition). This index, developed by Hu and Tessier (1995), ranges from a low of 0 (no detectable competition) to a high of 1. By taking the difference of the IC for inter- and intraspecific competition, the relative strengths of the two processes can be estimated. A difference of zero indicates equal effects of individuals of the same or other species. Positive values for the difference suggest that the effects of interspecific competition are stronger than intraspecific competition whereas negative values indicate the reverse.

In the July 1994 experiment, one group of bags was lost during collection. Consequently, data were only available for two replicates in all treatments except for ambient-density *D. galeata mendotae* that contained three replicates. In the July 1995 experiment, one replicate of the half-ambient density *D. pulicaria* treatment was excluded because a larval fish was inadvertently added to the enclosure, which resulted in very low survivorship of the *Daphnia*. Lastly, the ambient-density *D. galeata mendotae* treatments in the August 1995 experiment had three replicates instead of four because too few animals were initially added to one of the bags.

Statistical analyses were performed in Data Desk 5.0 and Systat 5.2.1, both for the Macintosh.

Results

Annual patterns

Unlike the *Daphnia* assemblage in many other lakes, the water-column densities of *D. galeata mendotae* and *D. pulicaria* in Oneida Lake did not show a repeatable seasonal pattern between years (Fig. 1). In 1992, *D. galeata mendotae* dominated the water-column for most of the season until being completely replaced by

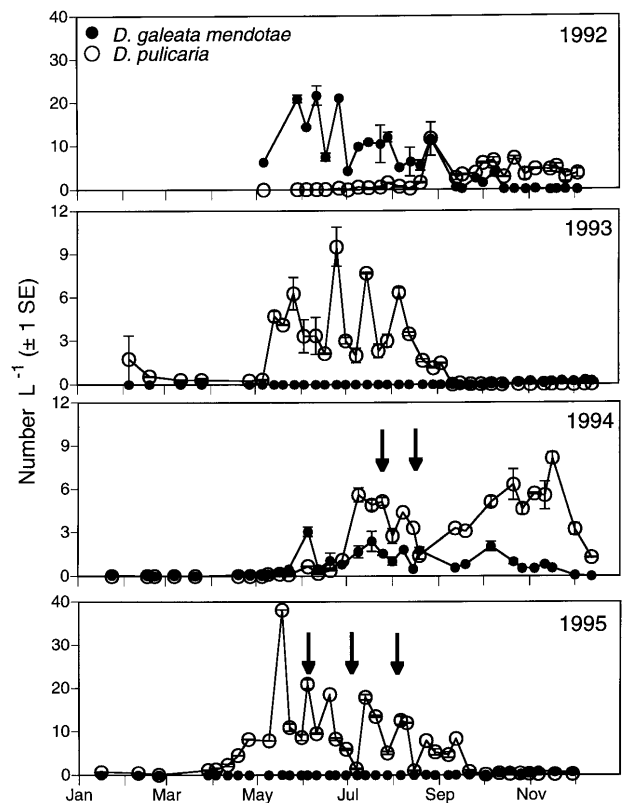


Fig. 1 Average water-column abundances (animals $L^{-1} \pm 1$ SE) for *Daphnia galeata mendotae* and *D. pulicaria* in Oneida Lake, N.Y. Arrows indicate the dates of the five competition experiments (see text). Note the reduced y-axis in 1993 and 1994

D. pulicaria in the fall. Maximum *D. pulicaria* densities in 1993 only reached about $10 L^{-1}$, which is four times less than spring peaks in previous years (Mills and Forney 1987; E.L. Mills, unpublished data). The following spring (1994), both species emerged from diapausing eggs (Cáceres, in press) and remained at low densities ($< 4 L^{-1}$) until midsummer at which point *D. pulicaria* began to increase with the eventual disappearance of *D. galeata mendotae* from the water column. Only *D. pulicaria* emerged from the sediment in the spring of 1995 (Cáceres, in press). This 1995 daphnid population reached the high densities found in 1992 and previous years (Mills and Forney 1987). This trade-off in dominance of the water-column seen in 1992–1995 is representative of the long-term dynamics of the two populations. Over the years 1964–1995, mean monthly water-column densities of the two species showed a strong negative correlation (Spearman rank $r_s = -0.259$, $t = -4.27$, $n = 256$, $P < 0.005$, Fig. 2; Braner 1988), a result that holds even when only the non-zero values are considered (Spearman rank $r_s = -0.195$, $t = -2.23$, $n = 128$, $P < 0.025$).

In the years 1992–1995, birth rates in the *D. pulicaria* population were lowest in 1992, the year that its congener dominated the water column (Fig. 3). However, as 1992 was also the year in which *D. pulicaria* was least

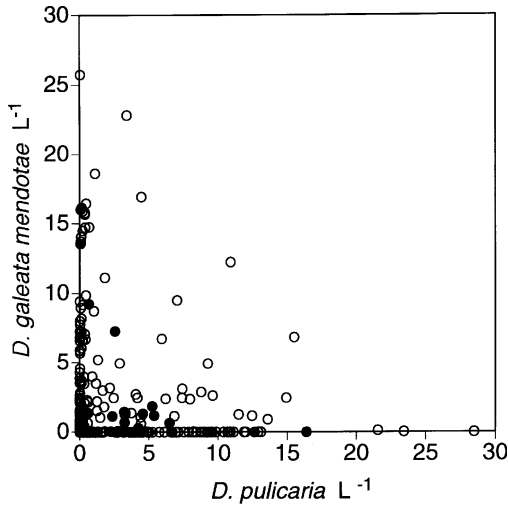


Fig. 2 Mean monthly water-column abundances of *D. galeata mendotae* and *D. pulicaria* in Oneida Lake, N.Y., 1964–1995. Open circles are the monthly averages found in 1964–1991 (Mills and Forney 1987; E.L. Mills, unpublished data). Closed circles are the monthly averages 1992–1995

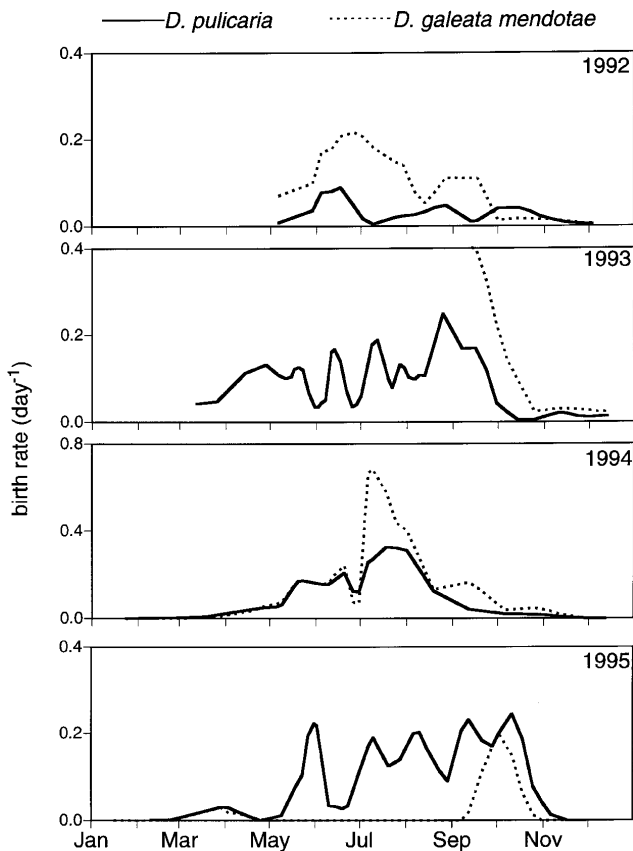


Fig. 3 Annual estimates of birth rates for *D. pulicaria* and *D. galeata mendotae* in Oneida Lake, N.Y. At least 27 separate estimates for *D. pulicaria* were smoothed with Trewess (trimmed resistant weighted scatterplot smooth) with a smoothing span of 2% and a trimmed mean of 10%. For *D. galeata mendotae*, only 14 and 11 points were available in 1993 and 1995, respectively. Solid lines indicate the birth rate in the *D. pulicaria* population whereas the stippled line represents the *D. galeata mendotae* population. Note the difference in scale in 1994

abundant, this result may be an artifact of sampling error resulting from small sample sizes. In 1992 when *D. galeata mendotae* dominated the water column, its birth rates exceeded those for *D. pulicaria* from May until October, at which time *D. pulicaria* began to replace it in the water-column (Fig. 1). Obtaining accurate estimates of the *D. galeata mendotae* birth and death rates in 1993 and 1995 was difficult due to the sampling error associated with small sample sizes. In 1994, *D. galeata mendotae* experienced peak birth rates of almost 0.8 day^{-1} , nearly twice the maximum birth rate observed in 1992. Death rates in the two populations were also variable within and between years with those of *D. galeata mendotae* often being higher than those of *D. pulicaria* (Fig. 4).

Competition experiments: resources

The annual succession of Oneida Lake phytoplankton has been documented in several studies (Greenson 1971; Wagner 1983; Mills et al. 1987). Following ice-out, the

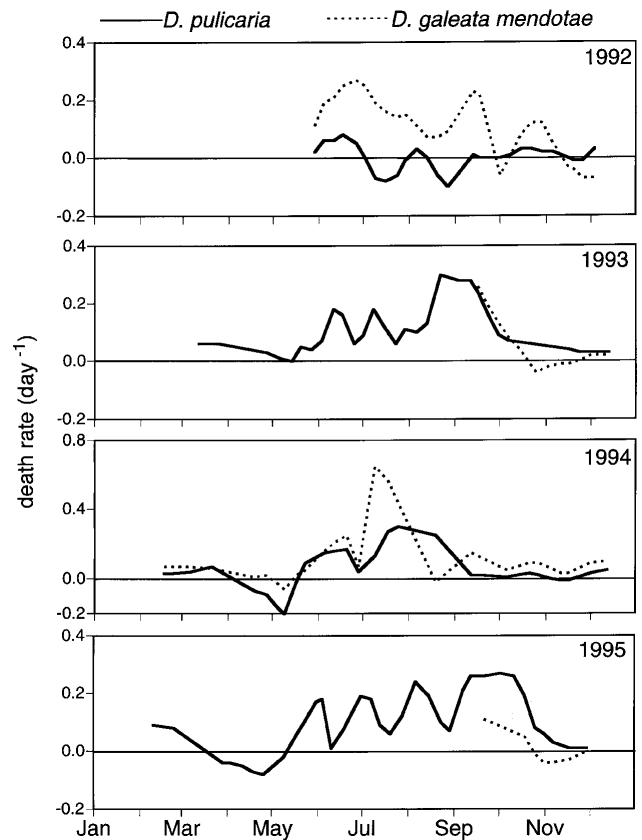


Fig. 4 Death rates, calculated as the difference between the birth rate and the realized population growth rate. Solid lines indicate the death rate in the *D. pulicaria* population whereas the stippled line represents the *D. galeata mendotae* population. Negative death rates can result from sampling error associated with small sample sizes, migration from other parts of the lake, or the hatching of diapausing eggs. Note the difference in scale in 1994

algal assemblage is dominated by chain-forming diatoms, primarily *Aulacoseira* spp. (= *Melosira*). A period of low phytoplankton biomass exists from late May through late June or July, when green microalgae and several species of cryptophytes dominate the community. As the summer progresses, Cyanobacteria begin to replace the smaller green algae. From late July through September or October various species of Cyanobacteria including *Gloeotrichia*, *Aphanizomenon*, *Anabaena*, and *Microcystis* are the most abundant phytoplankton. In some years, the cyanobacterial bloom is followed by another diatom bloom in late fall.

The phytoplankton assemblages on the dates corresponding to the competition experiments in 1994 and 1995 followed the expected successional pattern. To summarize the wide variety of species found in Oneida Lake, I categorized the phytoplankton counts into two groups, higher and lower quality (Table 1) based on size, edibility, and suspected nutritional value (reviewed by Lampert 1987). Chlorophytes, cryptophytes, and diatoms were classified as higher-quality food whereas filamentous and colonial Cyanobacteria were assigned to the lower-quality group.

The June 1995 competition experiment was run during the clear-water phase, hence resource levels were the lowest of the five experiments (Table 1). In general, cell densities were higher in 1995, but chlorophyll a values did not increase in concert (Table 2). This result can be explained by the interannual variation in the dominate Cyanobacteria species. The 1994 cyanobacterial bloom was dominated by filamentous *Aphanizomenon* and *Anabaena*, whereas colonial *Microcystis* was more common the following year. Large colonies of small-celled *Microcystis* can greatly increase cell counts without a concurrent increase in chlorophyll a levels (Table 1).

Analysis of competitive effects

Population growth

Population growth (calculated as a percentage of initial values) of both species was not significantly affected by intra- or interspecific competition in any of the five experiments (ANOVA, all planned contrasts, $P > 0.05$). With one exception, population sizes in the enclosures increased over initial densities by approximately $2 \pm 5\%$ (SE). The single exception was in August 1994 when the final population sizes in all three *D. galeata mendotae* treatments were approximately equal to the starting conditions whereas *D. pulicaria* populations increased by approximately 60% ($F_{1,17} = 7.844$, $P = 0.016$). As the mean fecundity (eggs adult⁻¹) and the percent of adults in the final population did not differ between the species, the lack of population growth in the *D. galeata mendotae* enclosures in August 1994 probably represents poor juvenile survivorship across all of its enclosures.

Adult fecundity

In the July 1994 experiment, mean adult fecundity in both species decreased from the half-ambient to ambient-density treatments (ANOVA, *D. galeata mendotae*, 0.5× vs. 1×, $F_{1,7} = 6.14$, $P = 0.042$, 0.5× vs. Mix, $F_{1,7} = 7.86$, $P = 0.026$; *D. pulicaria*, 0.5× vs. 1×, $F_{1,7} = 9.92$, $P = 0.016$, 0.5× vs. Mix, $F_{1,7} = 11.24$, $P = 0.012$, Fig. 5). However, there was no significant difference between the one- and two-species ambient-density treatments (1× vs. Mix) in either species (*D. galeata mendotae*, $F_{1,7} = 0.35$, $P = 0.572$; *D. pulicaria*, $F_{1,7} = 0.04$, $P = 0.845$). Hence, both intra- and interspecific competition were detected but a direct impact of one species on the other, versus merely a density effect, did not exist.

There was no significant difference among fecundities in the August 1994 experiment (ANOVA, $F_{5,12} = 1.53$, $P = 0.250$). Resource levels had increased since July 1994 and daphnid densities had declined by a third. Despite the appearance of more favorable conditions, fecundity in the 0.5× treatment of both species was lower than in the previous experiment (one-tailed *t*-test, $t_8 = 2.69$, $P = 0.013$). Whereas in July 1994, adult females in the 0.5× treatment carried 2.44 eggs (95% CI

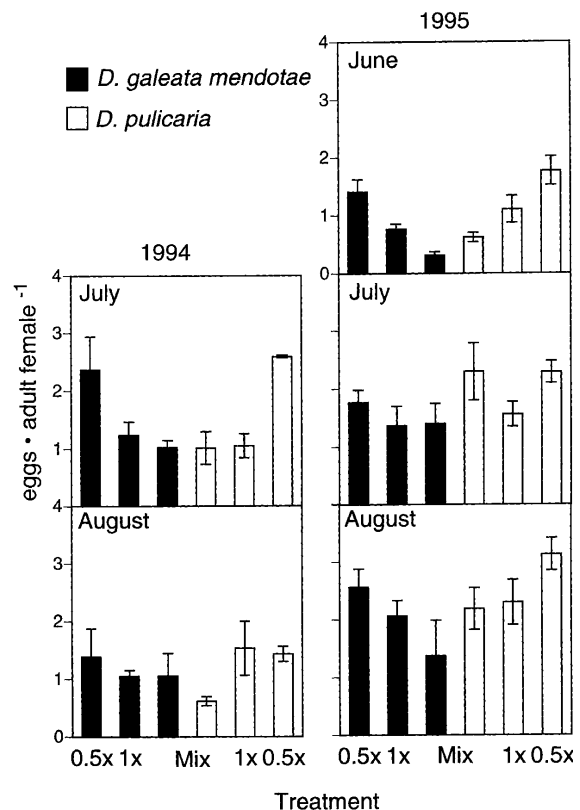


Fig. 5 The average adult fecundity (calculated from untransformed data) from in situ competition experiments. The *D. galeata mendotae* mixture treatment in August 1995 includes the extreme outlier (see text for details). Error bars are 1 SE of the mean

1.74–3.42 from log-transformed data), adults in August were producing only 1.41 eggs (95% CI 0.85–2.04).

During the clear-water phase the following year (June 1995), the effects of competition on fecundity were highly significant (ANOVA, $F_{5,18} = 15.25$, $P < 0.0001$, Fig. 5). All planned contrasts were significant for both species (*D. galeata mendotae*, 0.5× vs. 1×, $F_{1,18} = 6.89$, $P = 0.017$, 0.5× vs. Mix, $F_{1,18} = 44.38$, $P < 0.0001$, 1× vs. Mix, $F_{1,18} = 16.29$, $P < 0.001$; *D. pulicaria*, 0.5× vs. 1×, $F_{1,18} = 5.16$, $P = 0.036$, 0.5× vs. Mix, $F_{1,18} = 20.79$, $P < 0.001$, 1× vs. Mix, $F_{1,18} = 5.23$, $P = 0.034$). Therefore in each species, both intra- and interspecific competition affected reproduction. Moreover, in both *D. galeata mendotae* and *D. pulicaria*, reproduction was affected more by members of the other species than by conspecific individuals.

By July 1995, when ambient daphnid densities had dropped to fewer than 2 l^{-1} , neither intra- nor interspecific competition was evident among adults of either species. There were no significant fecundity differences among treatments (ANOVA, fecundity $F_{5,17} = 1.81$, $P = 0.165$). The lack of significant competitive effects is not surprising given that daphnids were added in the lowest densities of all five experiments; half-ambient treatments only contained *Daphnia* densities of 1 l^{-1} .

Once daphnid densities had increased to nearly 12 l^{-1} in August 1995, competitive effects on reproduction were again detected (ANOVA, $F_{5,17} = 2.42$, $P = 0.034$). Differences between the *D. galeata mendotae* 0.5× and 1× treatments were not significant, but fecundity in the Mix treatment was much less than in the 0.5× treatment ($F_{1,17} = 8.69$, $P = 0.009$). Fecundity in the Mix treatment [1.14 eggs adult⁻¹ (95% CI from log-transformed data 0.41–3.17)] was not significantly less than fecundity in the 1× treatment [2.02 eggs adult⁻¹ (95% CI 1.09–3.73)] when all four replicates were included ($F_{1,17} = 3.96$, $P = 0.063$). However, the variation among the four *D. galeata mendotae* Mix populations was primarily due to one outlier that was 3.5 times higher than the other three replicates, and the most extreme outlier found in all five experiments (largest Studentized residual value). Removing this outlier led to a significant difference between the 1× and Mix populations

[0.83 eggs adult⁻¹ (95% CI 0.64–1.07), $F_{1,15} = 18.67$, $P < 0.001$].

The effects of competition on fecundity, as summarized by the index of competition, are presented in Table 2. *D. galeata mendotae* experienced significant interspecific effects on three occasions whereas significant intraspecific effects, as shown by ANOVA, were only detected twice. The same result was found for *D. pulicaria* as well, although the dates when significant interactions were found differed between the species. In 1994, *D. pulicaria* exposed to the interspecific competition treatment experienced a reduction in fecundity that was greater than or equal to the reduction in fecundity seen in *D. galeata mendotae*. In contrast, in 1995, *D. galeata mendotae* suffered a greater reduction in fecundity while in the mixture treatment than that observed for *D. pulicaria*. Only for *D. pulicaria* in July 1995 did the effects of intraspecific competition exceed the effects of interspecific competition; however, this result was not significant.

Finally, in all five experiments, the half-ambient treatments of *D. pulicaria* and *D. galeata mendotae* did not differ in fecundity (All $P > 0.245$) indicating that both performed equally in the absence of the other species. That this result held for both the *D. galeata mendotae* collected from Oneida Lake (1994) and the *D. galeata mendotae* collected from Crystal Lake (1995) suggests that the two populations perform similarly on the Oneida Lake phytoplankton.

Juvenile lipids

In 1994, the degree of food limitation in both juvenile and adult *Daphnia*, as assayed by lipid stores, was quite severe. Of all the animals examined from both 1994 experiments, only three individuals had any visible lipids, indicating a poor nutritional status for the daphnids of both species. Lipid stores were also extremely rare in individuals taken from the water-column. Although this result does not provide any direct evidence about the role of intra- and interspecific competition in this assemblage, it does suggest strong food limitation (Tessier and Goulden 1982).

Table 2 Index of competition (IC) summarizing competitive effects on adult fecundity in *D. galeata mendotae* and *D. pulicaria*. Values were calculated as the difference between the mean fecundity in the 0.5× treatment and the 1× (Intra) or Mix (Inter) treatment, relative to the mean in the 0.5× treatment (see text for details). An asterisk

in the IC values indicates comparisons where significant effects were found in adult reproduction. The reported *D. galeata mendotae* interspecific IC in August 1995 does not include the extreme outlier (see text). When all four replicates are included, the interspecific IC for *D. galeata mendotae* is 0.5

| | Ambient daphnid density | Chlorophyll a ($\mu\text{g l}^{-1}$) \pm 1SE | <i>D. galeata mendotae</i> | | | <i>D. pulicaria</i> | | |
|-------------|-------------------------|--|----------------------------|----------|----------------------------|---------------------|----------|----------------------------|
| | | | IC Intra | IC Inter | Difference (Inter – Intra) | IC Intra | IC Inter | Difference (Inter – Intra) |
| July 1994 | 6 | 4.3 \pm 0.2 | 0.5* | 0.6* | 0.1 | 0.6* | 0.6* | 0.0 |
| August 1994 | 4 | 6.2 \pm 0.3 | 0.2 | 0.2 | 0.0 | 0.0 | 0.6* | 0.6 |
| June 1995 | 20 | 2.6 \pm 0.0 | 0.5* | 0.8* | 0.3 | 0.4* | 0.7* | 0.3 |
| July 1995 | 2 | 4.1 \pm 0.4 | 0.2 | 0.2 | 0.0 | 0.3 | 0.0 | -0.3 |
| August 1995 | 12 | 3.3 \pm 0.5 | 0.2 | 0.7* | 0.5 | 0.3 | 0.3 | 0.0 |

The degree of food limitation was potentially less severe in 1995; lipids were detected in all treatments in all three experiments. The rank score of juvenile lipid storage varied between treatments in the June (ANOVA, $F_{5,18} = 6.06$, $P = 0.002$) and July ($F_{5,17} = 4.12$, $P = 0.012$) competition experiments, but not in the August experiment ($F_{5,17} = 1.48$, $P = 0.248$, Fig. 6). In June 1995, the average rank score of lipid reserves in juveniles of the *D. galeata mendotae* 0.5× treatment was approximately half that of the average rank score of juvenile *D. pulicaria* 0.5× animals ($F_{1,18} = 14.2$, $P = 0.002$). Results from the three *D. galeata mendotae* treatments did not differ from one another; all *D. galeata mendotae* juveniles were storing fewer lipids than the *D. pulicaria* 0.5× treatment. Moreover, although the *D. pulicaria* 1× treatments did not differ from the 0.5× or the Mix (0.5× vs. 1×, $F_{1,18} = 1.61$, $P = 0.221$, 1× vs. Mix, $F_{1,18} = 0.789$, $P = 0.386$), there was a significant drop in lipid storage in the *D. pulicaria* juveniles in the Mix treatment relative to the 0.5× treatment ($F_{1,18} = 4.6$, $P = 0.045$). Therefore, the significant competitive effect seen in juvenile *D. pulicaria* lipid storage cannot be definitively assigned to intra- or interspecific competition.

Juvenile daphnids in July 1995 appeared to be more food limited than juveniles in the June 1995 experiment

(Fig. 6). Moreover, although ambient conditions in July 1995 seemingly did not affect adult fecundity (Fig. 5), juveniles of both species showed indications of food limitation. Under plentiful food conditions, the lipid index should approach a value of 3, whereas in July 1995, the maximum value observed in any treatment was less than 0.5. Furthermore, the 1× and Mix treatments of *D. galeata mendotae*, although not significantly different from the score in the 0.5× treatment, both have values near zero. These results provide no direct evidence of competition; however, they are useful indicators of limiting conditions.

Discussion

Temporal dynamics

It is evident from both field and experimental data that the outcome of interactions between *D. galeata mendotae* and *D. pulicaria* in Oneida Lake are not static over time. As a result, assigning a definitive role for competition in the observed water-column dynamics (e.g., consistent competitive dominance by one species) is not possible. Moreover, even though predation and competition are often viewed as alternative structuring mechanisms, there does not seem to be a single force driving daphnid species composition in Oneida Lake. Instead, it is likely that temporal variability in predation, resources, and abiotic factors interact to produce the observed dynamics.

First, fluctuating planktivore abundance undoubtedly influences daphnid water-column dynamics (Mills and Forney 1987; Mills et al. 1987). In 1961–1986, densities of young-of-the-year yellow perch on 1 August ranged from less than 1000 fish ha⁻¹ to over 35,000 fish ha⁻¹ (Mills and Forney 1987). Years with high fish densities were often associated with dominance by *D. galeata mendotae*, whereas the larger species dominated in low-fish years. Consequently, Mills and Forney (1987) concluded that predation regulated daphnid species structure.

However in the years 1992–1995, the daphnids continued to trade dominance despite the fact that maximum midsummer young-of-the-year perch densities only reached 6,200 fish ha⁻¹ (VanDe Valk and Rudstam 1996). In the years since 1986, other planktivores such as white perch (*Morone americana*) and gizzard shad (*Dorosoma cepedianum*) have increased in abundance in Oneida Lake, adding to the intensity of predation on the *Daphnia* (Roseman et al. 1996; VanDe Valk and Rudstam 1996). However, including the dynamics of these two additional planktivores does not explain fully the observed daphnid assemblage. For example, in 1994, total daphnid densities were less than 5 l⁻¹ for much of the year despite the fact that yellow perch densities remained low and both the white perch and gizzard shad populations were two orders of magnitude less than their

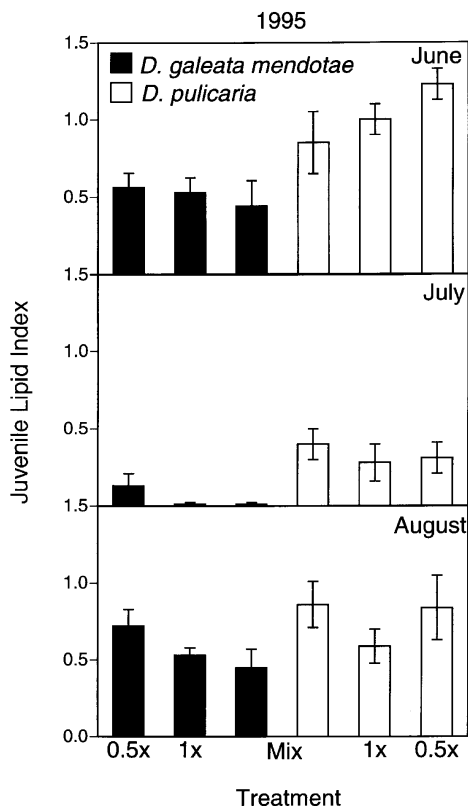


Fig. 6 Juvenile lipid index (0–3) for *D. galeata mendotae* and *D. pulicaria* in 1995 competition experiments. Data for the 1994 experiments are not shown because the index for both *Daphnia* species in all treatments was effectively zero. Error bars are 1 SE of the mean

average seasonal abundance (VanDe Valk and Rudstam 1996). Although planktivores serve as a significant source of mortality for *Daphnia* in Oneida Lake (Mills and Forney 1983; Prout et al. 1990), vertebrate predation alone cannot explain the irregular daphnid dynamics.

Alternatively, the zooplankton assemblage can be affected by predatory invertebrates. Predation by other invertebrates often results in higher mortality rates in smaller species compared with their larger congeners (e.g., Dodson 1974; Zaret 1980; Janicki and DeCosta 1990). In Oneida Lake, the large death rates observed for *D. galeata mendotae* relative to *D. pulicaria* in 1992 and 1994 (Fig. 4) may have resulted from predatory invertebrates. In 1994, the predacious cladoceran *Leptodora kindtii* was present in the water-column from July to October at densities ranging between 0.02–0.06 animals l^{-1} (C.E. Cáceres, unpublished data). In other systems, *Leptodora* has been implicated in exerting considerable predation pressure on populations of *D. galeata mendotae* (e.g., Hall 1964b; Cummins et al. 1969; Lunte and Luecke 1990). Lunte and Luecke (1990) found that *Leptodora* could account for all mortality in the *D. galeata mendotae* population in Lake Mendota, but the *Leptodora* densities they documented were an order of magnitude higher than those found in Oneida Lake whereas summer daphnid densities in the two lakes were comparable. Although predation by *Leptodora* was not strong enough to completely eliminate the *D. galeata mendotae* population from the Oneida Lake water-column, the increase in this predatory invertebrate during late summer and fall may be responsible in part for the often high death rate in the *D. galeata mendotae* population (Fig. 4).

Additionally, because *D. galeata mendotae* and *D. pulicaria* have different predicted thermal optima (Lynch 1978; Threlkeld 1980; Hu 1994), annual fluctuation in mean water-column temperature may contribute to their seasonal dynamics. There has been a great deal of speculation, but little experimental evidence, concerning the role of temperature in zooplankton succession (e.g., Allan 1977; Moore and Folt 1993; Moore et al. 1996). It has been suggested that larger species such as *D. pulicaria* prefer cooler temperatures and smaller species may dominate at higher temperatures (Lynch 1978; Threlkeld 1980). Because there is no cool hypolimnetic refuge in Oneida Lake, the recurring fluctuations between the species' abundances might be explained by a thermal effect (i.e., warmer years are dominated by *D. galeata mendotae* and cooler years by *D. pulicaria*). This was not the case for the four years studied. Mean water column temperatures were highest in 1995 (26°C) and lowest in 1992 (21°C) (C.E. Cáceres unpublished data; E.L. Mills unpublished data), exactly the opposite result expected from the predicted thermal preferences. Even though temperature surely must play a role in the season dynamics of these populations (e.g., birth rates are temperature dependent), it does not seem to be a principle structuring factor.

Competitive effects

Because predation and abiotic factors (i.e., temperature) cannot fully explain the daphnid water-column dynamics, competition is a likely alternative. Since competition experiments were not conducted in 1992 and 1993, information regarding the competitive ability of each species in those seasons is unavailable. However, the relative performance of each species can be assessed by field birth rate estimates (DeMott 1983). In 1992, when *D. galeata mendotae* dominated the system from May to September, its birth rate exceeded that of *D. pulicaria*. Although this is not direct evidence of competitive superiority, it does suggest that *D. galeata mendotae* used the resource base more effectively than did *D. pulicaria*. The following year, when *D. pulicaria* dominated the water-column, a comparison of birth rates is not as informative because *D. galeata mendotae* was not present until September. Birth rates are not synonymous with competitive ability. Nevertheless, because results from the competition experiments suggest that fecundity is often affected by the presence of a congener, field-collected birth rate data are useful indicators of each species' performance on the ambient resource, and suggest the potential for interannual fluctuations in competitive ability.

In the two years the competition experiments were conducted, the outcome of competitive interactions between *D. galeata mendotae* and *D. pulicaria* varied temporally. These results were in part density dependent, as illustrated by the absence of competitive effects when daphnid densities were less than 2 l^{-1} , and large interspecific effects (among adults) when densities were 20 l^{-1} . Because resources varied between experiments as well, a ranking of competitive effects based on density alone is not possible. However, it is clear that the larger *D. pulicaria* is not always a clearly superior competitor as predicted by the size-efficiency hypothesis (Brooks and Dodson 1965).

The results of the competition experiments provide some insight into the observed water-column dynamics. For example in July 1994, the year both species remained in low numbers in the water-column, the effects of intraspecific competition could not be separated from interspecific effects on fecundity in either species. This suggests that competitive effects were merely the result of daphnid density and neither species disproportionately influenced its congener. However, in the mixture treatments of the August 1994 experiment, reproduction of *D. pulicaria* declined more than that of *D. galeata mendotae* (relative to each species' 0.5× treatment, Table 2). This was the sole instance where the smaller species affected its larger congener more than it was affected by the presence of the larger species. Nevertheless, this effect was not enough to suppress completely the *D. pulicaria* population, which eventually dominated the water column that year at a time when the abundance of *D. galeata mendotae* was declining (Fig. 1). Because the water-column densities of

D. galeata mendotae never exceeded those of *D. pulicaria* despite equal or higher population birth rates, *D. galeata mendotae* suffered a higher mortality rate for much of 1994 (Fig. 4).

As predation levels were not exceptionally high in 1994, starvation may have been a significant source of mortality in the daphnid populations that year. Tessier et al. (1983) found that individuals with a greater lipid storage were able to persist much longer under starvation conditions. Given the lack of lipids in both the experimental and water-column juveniles, it is reasonable to propose that juveniles of both species experienced a high mortality rate in 1994 (Fig. 4). However, results from *in situ* life table experiments (C.E. Cáceres, unpublished data) conducted in 1992 indicate that this starvation mortality may be greater for *D. galeata mendotae* juveniles. Under ambient low-food conditions in Oneida Lake, juvenile *D. galeata mendotae* had reduced survival (50%) compared with either juvenile *D. pulicaria* (67%) or with individuals of both species given adequate food (80% and 78%, respectively). Finally, the results of the 1995 competition experiments are consistent with the water-column patterns: *D. pulicaria* decreased the fecundity of *D. galeata mendotae* females more strongly than *D. galeata mendotae* suppressed *D. pulicaria*.

Coexistence of competitors

The work presented here is the third *in situ* experimental exploration of competitive interactions between *D. pulicaria* and *D. galeata mendotae*. However, each study obtained different results for the outcome of competition, and each suggests different mechanisms for the coexistence of competitors. Leibold (1991) found that in Lawrence Lake, Mich., *D. pulicaria* was restricted to the hypolimnion whereas *D. galeata mendotae* migrated between the hypolimnion and the epilimnion. He therefore concluded that spatial segregation across the thermocline and selective predation by fish on *D. pulicaria* were the most likely explanations for daphnid coexistence in that system. Hu and Tessier (1995) examined the daphnids of nearby Gull Lake, Mich., and suggested that not only spatial segregation but also changes in the rank order of competitive abilities within a season were important in maintaining diversity. Low planktivore levels in Gull Lake led Hu and Tessier (1995) to discount size-selective predation as an important driving force in their system.

Oneida Lake lacks the vertical habitat heterogeneity that promotes daphnid coexistence in the two Michigan lakes. Thus, even though the same daphnid species occur in all three lakes, neither Leibold's (1991) nor Hu and Tessier's (1995) conclusions can explain daphnid coexistence in Oneida Lake. Because spatial habitat segregation seems to be an unlikely explanation for the coexistence of competitors in Oneida Lake, invoking a non-equilibrium explanation for the maintenance of

species diversity seems to be more appropriate. However, the competitive reversals within a season observed by Hu and Tessier (1995) were not seen in Oneida Lake. If competitive reversals are occurring at all, they must be occurring between years. Because both species experienced periods of complete absence from the water column over the four-year study period, it seems unlikely that any type of temporal variation (e.g., competitive reversals or fluctuating predation intensity) would, by itself, provide a sufficient explanation for the coexistence of the two species.

An alternative mechanism for the coexistence of these competitors is that many zooplankton species produce long-lived diapausing eggs which can remain viable for decades or even centuries (Hairston et al. 1995; Hairston and Cáceres 1996; Cáceres, in press). By extending life spans, these dormant propagules create overlapping generations in a stage immune to the effects of competition. Even when competition drives all active individuals of one daphnid species from the water column, long-lived eggs provide a reliable colonization source for future years.

A growing body of theory has shown that overlapping generations, in combination with temporally fluctuating competition, can promote the coexistence of competing species (e.g., Chesson and Warner 1981; Ellner 1987; Pake and Venable 1995). However the role of dormant eggs is rarely considered in the interpretation of zooplankton population dynamics. I have shown elsewhere that both *Daphnia* species store tens of thousands of diapausing eggs in the sediment of Oneida Lake, that these eggs are capable of remaining viable for over a century, and that they provide a reliable colonization source for the water-column populations (Cáceres, in press). As a result, even though species periodically disappear from the water-column, long-term coexistence of these daphnids in Oneida Lake is promoted by the long-lived eggs and interannual environmental variation (Cáceres 1997). Moreover, because large numbers of diapausing eggs are produced by a variety of pelagic organisms (reviewed by Hairston 1996) it is likely that this sediment refuge is important in maintaining daphnid species diversity in other lakes as well. For example, dormancy is clearly an important factor in promoting daphnid coexistence in Gull Lake, since the *D. galeata mendotae* population is refounded each year from diapausing eggs (Hu and Tessier 1995). Consequently, a full understanding of water-column dynamics requires consideration of the contribution of recruitment of individuals from the sediment. Exploring community dynamics with this added dimension of diapause in mind may provide a common explanation for coexistence of competing species and a mechanism for the maintenance of species diversity in zooplankton assemblages.

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