

SEASONAL SUCCESSION AND THE STRENGTH OF INTRA- AND INTERSPECIFIC COMPETITION IN A *DAPHNIA* ASSEMBLAGE¹

SHIXI S. HU AND ALAN J. TESSIER

Department of Zoology and W. K. Kellogg Biological Station, Michigan State University,
East Lansing, Michigan 48824-1115 USA

Abstract. Species of the genus *Daphnia* are generalized filter-feeders and potentially strong competitors, yet several species often coexist in the open waters of lakes. We investigated the population dynamics and competitive interactions of two *Daphnia* species in Gull Lake, Michigan. In each of 3 yr *D. pulicaria* was always common, while *D. galeata mendotae* became abundant only in late summer. The summer invasion of *D. galeata mendotae* was associated with a decline in abundance of *D. pulicaria* in some, but not all years. Decline of *D. pulicaria* was strongly predicted by the loss of oxygen from deep water during summer, which resulted in greater spatial overlap between the species, and by changes in the quality of the phytoplankton resources.

We employed in situ enclosures to manipulate the density of each species and quantify the intensity of intra- and interspecific competition. Repeated competition experiments demonstrated that the relative exploitative ability of the species reversed from early to late summer. Strong interspecific competition was often observed, but its strength varied with juvenile or adult stage, and with season. *Daphnia pulicaria* juveniles were always affected strongly by interspecific effects, while *D. galeata mendotae* juveniles were impacted largely by intraspecific effects. The relative strength of intra- and interspecific competition on adults reversed from early to late summer for each species. The magnitude of intra- and interspecific effects on *D. pulicaria* adults was similar during early summer, but by late summer interspecific effects were much stronger than intraspecific effects. The reverse was true for *D. galeata mendotae* adults; interspecific effects greatly decreased in late summer. This seasonal shift in the nature of competitive interactions provides an explanation for seasonal succession in this *Daphnia* assemblage.

Key words: *Daphnia*; interspecific competition; intraspecific competition; population dynamics; resource partitioning; seasonal succession; stage-structure; vertical migration; zooplankton.

INTRODUCTION

Competition for limiting resources forms the basis of much ecological and evolutionary theory. Although a consensus of empirical work concludes that competition occurs commonly in nature (Gurevitch et al. 1992), this alone is not particularly informative. As emphasized by Goldberg and Barton (1992), the link between empirical and theoretical studies of competition remains weak, because few experimental studies address patterns of occurrence, population and community consequences, or the nature of intra- and interspecific competitive ability. In truth, we have a poor understanding of how competitive mechanisms translate (i.e., scale in time and space) into species patterns of abundance and distribution.

One of the best documented patterns in community ecology is the cyclical succession of zooplankton species that occur in temperate zone lakes (Hutchinson 1967, Sommer 1989). Taxonomically similar species often display markedly different population dynamics in the same lake. The resulting, seasonal patterns of

species turnover are often quite consistent from year to year in a given lake (Kratz et al. 1987). Numerous descriptive studies have shown that a combination of resource limitation and predation typically regulates zooplankton populations and drives seasonal successions (Threlkeld 1987). However, experimental manipulations of zooplankton communities have focused mainly on predation, especially fish planktivory (Gliwicz and Pijanowska 1989). Relatively few field studies have explored nonpredatory mechanisms of zooplankton coexistence and succession despite evidence that exploitative competition does occur in zooplankton assemblages (DeMott 1989, Rothhaupt 1990).

Zooplankton seasonal successions provide an ideal framework for exploring a central issue in community ecology: the role of temporal variation in competitive interactions. If species differ in environmental optima, shifts in competitive abilities can occur whenever environmental conditions change. The concept of temporal change in competitive interactions was first formulated by Hutchinson (1961) as a solution to the “paradox” of plankton species coexistence, and is the basis of much current theory in species coexistence (Abrams 1984, Chesson 1986, Ellner 1987, Ebenhöh 1992).

¹ Manuscript received 31 May 1994; revised and accepted 7 February 1995.

Rarely have experiments examined temporal variation in rank performance or competitive ability (e.g., Pake and Venable 1995), but the few experimental studies of zooplankton succession all conclude that competitive hierarchies are not static through time (Lynch 1978, Smith and Cooper 1982, DeMott 1983).

A lack of separation of intra- from interspecific effects characterizes many studies (including Goldberg and Barton 1992) including plankton communities (Smith and Cooper 1982 is an exception). This distinction is particularly relevant for crustacean zooplankton species, which undergo developmental changes in habitat use and diet. For these taxa, age structure can substantially alter competitive interactions (Neill 1975, Lynch 1978). Hence, while there is evidence that exploitative competition contributes to seasonal succession, the nature of these competitive interactions (intraspecific vs. interspecific, and ontogenetic change) is largely unexplored.

To better understand the role of competition in zooplankton succession, we combined 3 yr of population dynamic studies with seasonal, in situ manipulations of two, closely related species. We address four general questions. (1) Are there temporal changes in rank performance of the two species that are consistent with the seasonal pattern of species succession? (2) How does the relative intensity of competition differ for each species through time? (3) Does the relative strength of intra- and interspecific competitive effects differ with species or time? (4) Do juveniles and adults of each species experience competitive interactions in the same way? Clearly, these questions are not independent and it is the intersection of temporal variation, intra- and interspecific effects, and ontogenetic stage that defines our interest in this study.

BACKGROUND

In freshwater, calcium-rich lakes of the midwest United States, and Michigan in particular, 3–4 species of the crustacean genus *Daphnia* often coexist or replace one another seasonally (Woltereck 1932, Lane 1975, Threlkeld 1979, Cipolla 1980, Dorazio et al. 1986, Leibold 1991, Tessier and Welser 1991): *D. pulicaria*, *D. galeata mendotae*, *D. rosea* (and hybrids; Taylor and Hebert 1993), and *D. retrocurva*. These species generally differ in adult body size, however all undergo substantial growth throughout life, resulting in broad size overlap at the population level. Furthermore, diets are believed to be very similar for all species, suggesting the potential for strong competition (Kerfoot and DeMott 1984).

A widely invoked hypothesis to explain assemblage composition and succession of daphniids emphasizes a predation–competition trade-off. Large-bodied species are considered superior competitors, but more vulnerable to visual predators than small-bodied species (Brooks and Dodson 1965, Hall et al. 1976, Vanni 1986). When intensity of fish predation increases in

summer due to recruitment and temperature, large daphniid species are sequentially replaced by smaller species (Jacobs 1977, Seitz 1980). Fish predation decreases in fall and the species replacement reverses, supposedly due to exploitative competition. This hypothesis has been modified to include effects of interfering particles (e.g., Kirk and Gilbert 1990, Gliwicz and Lampert 1991), but retains an emphasis on body size, as do hypotheses involving invertebrate predators (Dodson 1974). While controversial, most literature on *Daphnia* shares the assumption that large body size confers superior competitive ability in the absence of interfering particles, or abiotic stress.

Although a strong interaction of predation and resource competition likely influences daphniid community structure in most lakes, it is also likely that the nature of competition is more complex than a static competitive hierarchy (Bengtsson 1987). Furthermore, a large overlap among *Daphnia* species in population body size structure, due to genetic (Leibold and Tessier 1991, Tessier et al. 1992) and ontogenetic variation, suggests that factors other than size-selective predation contribute to species successions. There has, however, been little exploration of other hypotheses. In particular, although diets are similar among *Daphnia* species (DeMott 1983, Infante and Edmondson 1985, Kerfoot et al. 1985), the resource base is very heterogeneous and species might differ in their abilities to utilize (e.g., assimilate) the different components (e.g., algal species). Furthermore, exploitative efficiencies of different species may interact with abiotic variables (e.g., temperature or oxygen), which change both seasonally and with water depth. Although coexisting species of zooplankton typically differ in vertical habitat use or diel vertical migration behavior (Makarewicz and Likens 1975), experimental studies of competition in zooplankton have rarely employed enclosures deep enough to mimic the full range of depth habitats available in a natural, dimictic lake.

In this study we investigate seasonal replacement and competitive interactions between two species of *Daphnia* in Gull Lake, a large (822 ha surface area, 33 m maximum depth) mesotrophic, hardwater, dimictic lake in southwest Michigan. Limnological details are presented in Moss (1972a,b), Tague (1977), and Moss et al. (1980). Three species of *Daphnia* are observed in the zooplankton of Gull Lake, (*D. pulicaria*, *D. galeata mendotae*, and *D. retrocurva*), but only the first two are common and the focus of our study. *Daphnia pulicaria* is the most abundant daphniid in the lake and is present at all times of the year. *Daphnia galeata mendotae* appear during July as juveniles (hatching from resting eggs), and increase greatly in density during August into September. The population typically produces resting eggs in late fall and disappears from the open water during winter. *Daphnia galeata mendotae* is often confused with *D. rosea*, the problem being apparent hybridization (Taylor and Hebert 1993). We

refer to the Gull Lake population as *D. galeata mendotae* because individuals expressed tall helmets. However, a study of genetic structure in this and other local populations of this species complex awaits further work.

Several aspects of Gull Lake make it an ideal setting in which to examine competitive interactions between *Daphnia* species. Compared with other local lakes planktivory in Gull Lake is low and *Daphnia* populations are typically food limited (Leibold and Tessier 1991). Two species of fish planktivores occur in Gull Lake, yellow perch fry (*Perca flavescens*) and bluegill (*Lepomis macrochirus*). However, an abundance of piscivores, including bass (*Micropterus salmoides*, *M. dolomieu*), pike (*Esox lucius*), and stocked trout (*Salvelinus namaycush*) and salmon (*Salmo salar*), apparently keep densities of these planktivores low (Dexter 1991). Interestingly, under these conditions of low planktivory in Gull Lake, body sizes of *D. pulicaria* and *D. galeata mendotae* are quite similar (Leibold and Tessier 1991). Despite these contrasts with other lakes, the seasonal pattern of *Daphnia* succession in Gull Lake is generally representative of most other local, deep lakes (Tessier and Welser 1991). Hence, an understanding of competitive interactions in Gull lake is relevant to *Daphnia* interactions in lakes throughout the Great Lakes basin.

METHODS

Field sampling and analysis

We sampled Gull Lake near its deepest location in the central basin of the lake. Water temperature and oxygen were measured at 1-m intervals throughout the water column using a YSI model 57 meter, every 2–3 wk during June through September in 1989, 1990, and 1991. Temperature stratification in the water column of a lake provides protection for zooplankton from warmwater fish planktivores. *Daphnia* can avoid fish predation by remaining in the cold hypolimnetic water during daylight hours (a refuge sensu Wright and Shapiro 1990, Tessier and Welser 1991). However, during summer the bottom waters typically experience a progressive loss of oxygen, which begins in the deepest water and gradually extends upward, decreasing the available refuge for *Daphnia*. We defined oxygen concentrations below 0.5 mg/L as anoxic and considered such water depths as unavailable habitat for *Daphnia*.

Algal samples were taken at 2–3 wk intervals from the top 9 m of the center of the lake using a plastic tube, which produced an integrated sample for the entire epilimnion. The water samples were fixed with acid-Lugol's solution and concentrated by settling. Concentrated samples were examined at 750 \times and taxa were identified to genus. We counted the number of cells of each genus observed in a minimum of 50 microscope fields per sample at 375 \times using a Mahoney-Palmer cell.

Daphnia population density was sampled once to twice a week during the summers of 1989, 1990 and 1991, using a 32-cm diameter conical tow net. In reporting density in the lake we assumed a 100% net filtration efficiency from a standard depth of 30 m. We collected three, replicate vertical hauls from the lake's central basin on each sampling date, and preserved them with cold sugar-formalin. We examined animals at 25 \times with a stereomicroscope, and measured body length, lipid-ovary index, clutch size, and egg stage on at least 50–120 haphazardly chosen individuals. Five egg development stages were recognized according to criteria in Threlkeld (1979). Animals were usually examined within 8 h of collection so that lipid-ovary indices (1–3 scale) would be unbiased (Tessier and Goulden 1982). We counted total number of *Daphnia* in each sample according to species and the three general categories of juvenile, adult, and gravid adult. The difference between juvenile and adult was based on a minimum body length at maturity typical of these populations (1.5 and 1.4 mm for *D. pulicaria* and *D. galeata mendotae*, respectively). The average coefficient of variation among the replicated vertical tow net samples for numbers of total *Daphnia* was 17.4%.

The egg-ratio method of Rigler and Downing (1984) was used to calculate per capita birth rates. This technique combines information on water temperature, the distribution of eggs among developmental stages, and the number of eggs per individual to estimate an instantaneous, per capita rate (b) of egg hatching in the population. We used a weighted (by adult abundance summed over day and night sampling) average of water temperatures at each depth inhabited by each species separately, to calculate the average temperature for egg development on each date (Prepas and Rigler 1978). Estimation of egg development time from temperature was based on equations given in Bottrell et al. (1976). We determined the vertical depth distribution of adults of each species during midday and midnight by a monthly sampling with a Birge closing net. These diel samples were collected as integrated 5-m strata from 0 to 30 m (i.e., six samples representing 0–5, 5–10, . . . 25–30 m).

Population growth rates (r) were calculated from the density values N_1 and N_2 from two successive sampling dates t_1 and t_2 . As with birth rate, r is measured in units of day⁻¹.

$$r = \frac{\ln(N_2) - \ln(N_1)}{t_2 - t_1}.$$

The death rate (d) for a given period of days $t_2 - t_1$ was calculated as the difference between b (averaged from b of t_1 and b of t_2) and r :

$$d = b - r.$$

Differences in population birth, growth and death rates between the two *Daphnia* species were compared by paired t tests, with the number of replicates equal

to one less than the number of dates sampled each year. We examined relationships among algal abundance and composition, the extent of hypolimnetic anoxia, and the density and birth rates of the two *Daphnia* species using Pearson correlation, based upon a single replicate for each date.

In situ competition experiments

In order to examine the seasonal variation in competitive ability of the two *Daphnia* species, one set of experimental treatments was established each month of June, July, and August 1991. In each set of experiments, we employed 16–20 large polyethylene bags as field enclosures. Each enclosure was 10 m long, 0.03 m² surface area, and held 300 L of water. Four enclosures were attached to a plexiglass collar on top and a metal anchor on bottom. To fill the enclosures with lake water and natural phytoplankton but exclude all daphniids, we placed a net of 130- μ m mesh over the top of each enclosure. We then lowered the collar and four enclosures to a depth of 15 m in the lake. While being pulled to the lake surface, each enclosure filled with water passing through the net, and was then fully inflated using additional surface water. After removing the nets, we added experimental animals to each enclosure, which was then covered with water-tight polyethylene attached to the collar, submerged to 5 m below the water surface, and suspended from a buoy. Therefore, each enclosure was positioned from 5 to 15 m in the water column, and hence, crossed the thermocline in the lake.

This experimental enclosure system is efficient for short-term field manipulations (Tessier et al. 1992); each set of treatments lasted only 6 d, which is equivalent to nearly one generation for daphniids in our experiments. We consider each enclosure to be one replicate of a treatment. We created five treatments that were different density combinations of the two species. Animal density in the monospecific G (*D. galeata mendotae*) and P (*D. pulicaria*) treatments were 3.3 individuals/L, which was similar to the estimated density of total *Daphnia* in the lake. Pilot experiments in the previous summer had demonstrated that at this density animals in the enclosures maintained similar performance (body lipid and reproductive rates) as the lake populations (S. S. Hu, *unpublished data*). Hence, these monospecific treatments served as controls. The GG and PP treatments also represented monospecific treatments, but at twice lake densities; the contrast of these treatments with each control allowed estimation of intraspecific competition of *D. galeata mendotae* and *D. pulicaria*, respectively. The GP (or PG) treatment represented an equal mixture of the two species each at control density, and the contrast of this treatment with its respective control allowed for estimation of interspecific competition.

Sixteen enclosures were utilized for the experiment conducted from June 21 to 27, whereas in the exper-

iment of 25–31 July, and 16–22 August, 20 enclosures were used. Hence, there were at least three replicates for each treatment in the June experiment, and four replicates for each treatment in the July and August experiments.

All *D. galeata mendotae* used in the experiments were imported from nearby Lawrence Lake (see Wetzel 1983 for limnological details). This was done for four reasons: (1) *D. galeata mendotae* abundance varies seasonally in Gull Lake and none would be available for the June experiment, (2) Lawrence Lake is very similar in water chemistry and trophic status to Gull Lake (hardwater, alkaline, oligotrophic), (3) the *D. galeata mendotae* in Lawrence Lake are similar in morphology and behavior to those in Gull Lake, and (4) population density and resource limitation are relatively constant in Lawrence Lake throughout summer (A. J. Tessier and M. Leibold, *unpublished data*). All *D. pulicaria* used in the experiments were collected from Gull Lake.

The two species were collected separately by sampling only certain water depths at particular times of the day. Relatively pure cultures of *D. galeata mendotae* were collected in all 3 mo by sampling in only the top 5 m of Lawrence Lake during night or early morning hours. Similarly, *D. pulicaria* were isolated from Gull Lake, even after *D. galeata mendotae* invasion in late summer, by sampling with a closing net at night or in early morning waters deeper than 10 m. Subsamples were quickly counted to estimate the density of each collection (species). We then mixed animals of a given species and density in a bucket and dispensed aliquots to bottles for random allocation to treatment enclosures. We completed collection and allocation of animals to enclosures within 4 h to reduce stress on the animals.

After 6 d of incubation in the lake, all animals from each replicate enclosure were harvested and preserved in cold sugar-formalin. Samples were processed within a couple of days under the dissection scope. From each enclosure population, we haphazardly selected 60 individuals and measured body length, lipid-ovary index (1–3 scale), clutch size, and egg developmental stage. We also examined another 10–20 adults to better estimate mean clutch size. Subsamples were counted to estimate the total population size in each enclosure.

We summarized experimental data into four variables for each species: mean juvenile lipid index, mean adult fecundity, change in population density expressed as a percentage of the initial density, and age structure expressed as the percentage of the population composed of juveniles. Means of these variables from each enclosure were analyzed to detect treatment effects (SAS 1990). Control G and P treatments were compared to evaluate relative performances of the two species in each month (experiment). We used a *t* test to contrast adult fecundity between these two controls, and a non-parametric Kruskal-Wallis test to contrast juvenile lipid index. Other treatment effects were analyzed separately

for each species and each month. We analyzed adult fecundity by ANOVA and planned contrasts representing intraspecific effects (G vs. GG, and P vs. PP), and interspecific effects (G vs. GP, and P vs. PG). Population density change was also analyzed by ANOVA with the same planned contrasts. We employed a non-parametric Kruskal-Wallis test to analyze juvenile lipid index. Type I error was set at $P = 0.05$, but since power was generally low we interpret effects with a $P < 0.10$ as marginally significant.

We combined experimental results from the 3 mo to test for treatment by month (June, July, and August) interactions for *D. galeata mendotae* (GP and GG) and *D. pulicaria* (PG and PP) using ANOVA on adult fecundity and population age structure. A significant interaction in the analysis of adult fecundity would indicate temporal variation in strength of inter- vs. intraspecific competition. Finally, enclosure mean values across all treatments and experiments were examined using Pearson correlation to test for relationships among age structure, adult fecundity, and juvenile lipid index.

In the June experiment, one enclosure from G treatment was removed from analysis due to leakage, which resulted in extremely low survival. In the July experiment, one block came free from the suspension buoy and sank. Results of all treatments in this block were markedly deviant from the other replicate blocks, and it was removed from analysis. In August, one enclosure from both P and PP treatment each was lost due to vandalism.

Since statistical analysis revealed significant treatment effects, we defined two metrics of competition intensity in order to describe variation among months, species, and age classes (competition index: Wilson and Tilman 1991, and effect size: Gurevitch et al. 1992). Both measures gave qualitatively and statistically the same results (Hu 1994), so we present here only the single metric of competition index (CI). We estimated the CI for two performance variables (juvenile lipid index and adult fecundity) in the following way:

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

where \bar{Y}_c is the mean of a performance variable from G or P treatments (controls), depending on species. \bar{Y}_e is the mean of that same performance variable from GG or GP treatments for *D. galeata mendotae*, and PP or PG treatments for *D. pulicaria*. In this way we estimate standardized indices for both intra- and interspecific competition intensity, which range from a low of 0 (no competition) to a high of 1.

The relative strength of interspecific competition to intraspecific competition was estimated by examining the ratio of calculated competition intensities:

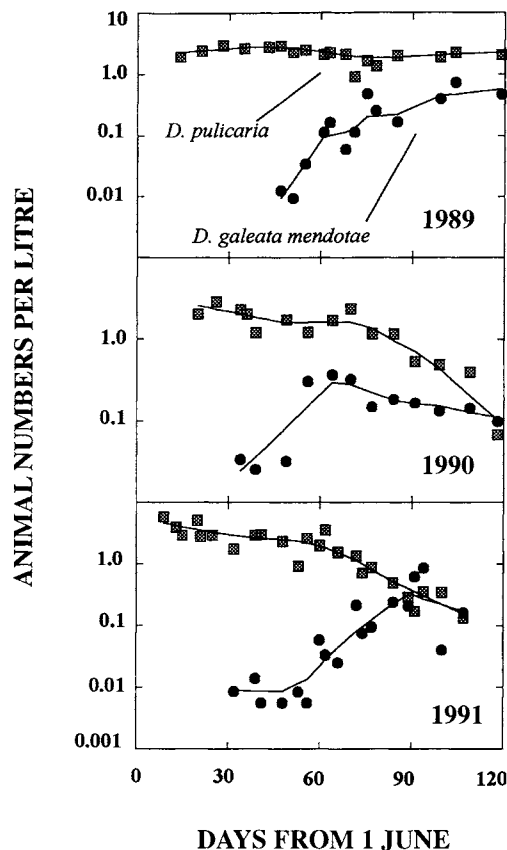


FIG. 1. Annual and seasonal variation in *D. pulicaria* (squares) and *D. galeata mendotae* (circles) density expressed as number per litre on a log scale. Each data point represents the mean of 2–3 field samples. Lines represent smoothed values using a locally weighted smoothing function, LOWESS (Cleveland 1981).

$$\frac{CI_{\text{INTERspecific}}}{CI_{\text{INTRAspecific}}}$$

A ratio of 1 indicates that the two species were equivalent (per individual) in competition impact. Ratios greater than 1 indicate that interspecific competition is stronger than intraspecific competition; ratios smaller than 1 indicate the reverse.

RESULTS

Daphnia population dynamics

Daphnia pulicaria population density typically peaked in June (3–6 individuals/L), declined in August and September, increased again in fall, and remained abundant throughout each winter (S. S. Hu, unpublished data; Fig. 1). Midsummer *D. pulicaria* densities were very similar in all 3 yr (2–3 individuals/L in June–July). A substantial August decline in this population occurred in 1990 and 1991, and densities were < 0.5 individuals/L by September. In contrast, the population density never fell below 1 individual/L during summer 1989.

TABLE 1. Average *Daphnia* population birth rate (b), growth rate (r), and death rate (d). Data summarized as mean (± 1 SE) for each summer, or across all three summers.

	<i>D. galeata mendotae</i>			<i>D. pulicaria</i>		
	Mean	N	SE	Mean	N	SE
All 3 yr						
b	0.404	23	0.090	0.061	56	0.006
r	0.026	40	0.036	-0.044	53	0.021
d	0.360	23	0.092	0.107	52	0.023
1989						
b	0.341	7	0.148	0.037	17	0.004
r	0.076	12	0.055	-0.009	16	0.021
d	0.272	7	0.142	0.049	15	0.023
1990						
b	0.341	9	0.091	0.084	15	0.014
r	0.012	11	0.034	-0.040	14	0.022
d	0.322	9	0.107	0.122	14	0.033
1991						
b	0.549	7	0.238	0.063	24	0.009
r	0.000	17	0.072	-0.071	23	0.043
d	0.496	7	0.240	0.135	23	0.045

Daphnia galeata mendotae usually first appeared in July, peaked in August–September (up to 0.8 individuals/L), and after sexual (resting egg) reproduction in fall disappeared from the plankton each winter (S. S. Hu, unpublished data; Fig. 1). Among years, there was no obvious relationship between population densities of *D. galeata mendotae* and population densities of *D. pulicaria*. During 1991 densities of the two species were negatively correlated ($r = -0.537$, $P < 0.022$, $N = 18$), while in 1990 ($r = 0.178$, $P < 0.562$, $N = 13$) and 1989 ($r = -0.185$, $P < 0.545$, $N = 13$) they were basically independent.

In all three summers, *D. pulicaria* population birth, growth and death rates were typically low ($\bar{b} = 0.06$, $\bar{r} = -0.04$, $\bar{d} = 0.11$; Table 1). This was especially evident during 1989, when population rates remained near zero ($\bar{b} = 0.04$, $\bar{r} = -0.01$; Fig. 2). In the later two summers, however, population growth rate showed greater variation and overall was negative (for 1990, $\bar{r} = -0.04$; for 1991, $\bar{r} = -0.07$). Seasonal variation in birth rate was minor in all years, and bore no relationship to population density or population growth rate. Death rates did vary among years and seasons; they were substantially higher in 1990 and 1991 than in 1989. In all 3 yr, there was a tendency for death rates to increase during late June to early July, and in 1990 and 1991 death rates increased again in mid to late August (Fig. 2). These two periods were times when *D. pulicaria* densities declined.

Daphnia galeata mendotae birth rates ($\bar{b} = 0.40$) and death rates ($\bar{d} = 0.36$) were generally much higher than that of *D. pulicaria* ($t = 3.89$, $df = 21$, $P < 0.001$ and $t = 3.00$, $df = 21$, $P < 0.007$, respectively; Table 1, Fig. 3). The population growth rate was also higher ($\bar{r} = 0.026$) than that of *D. pulicaria*, indicating the invasive nature of *D. galeata mendotae* dynamics. The

higher birth rates in *D. galeata mendotae* were partially due to its higher adult fecundities, and partially due to the fact that this species occupied shallower (and hence warmer) water compared with *D. pulicaria*. Higher temperatures affect birth rates by decreasing egg development time. *Daphnia galeata mendotae* birth rates were highest at the time when this species was increasing in population density, but declined by the end of summer to values only slightly higher than those of *D. pulicaria*.

There was no overall relationship between the population birth rates of the species ($r = 0.185$, $P < 0.409$, $N = 22$). However, when examined as two time blocks a different pattern emerged. During the period of *D. galeata mendotae* rapid population growth (prior to mid-August), there was a nonsignificant, negative trend between the birth rates ($r = -0.67$, $P < 0.223$, $N = 5$). After *D. galeata mendotae* was established (August–September), the birth rates were positively associated ($r = 0.422$, $P < 0.104$, $N = 16$).

Juvenile lipid and adult fecundity

As a measure of resource availability, we assessed body lipid content of juveniles and fecundity of adults.

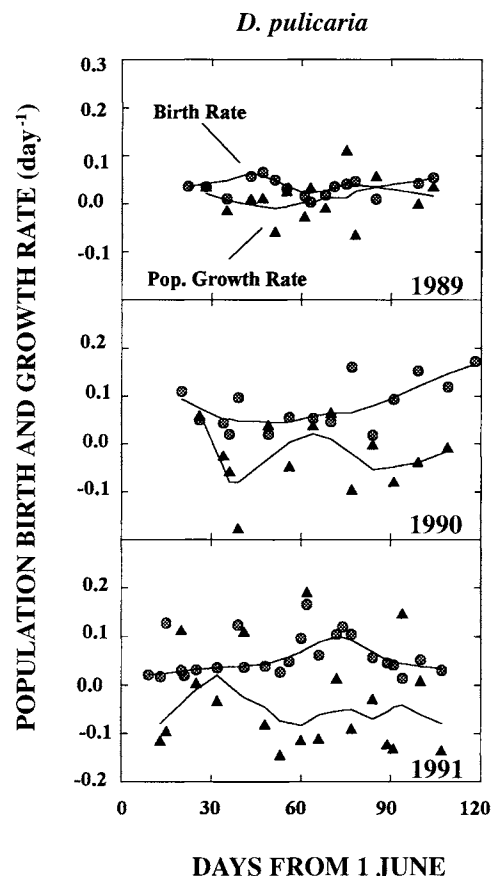


FIG. 2. Population growth rates (triangles) and birth rates (circles) for *D. pulicaria* during each of the three study summers. Lines represent smoothed values as in Fig. 1. Vertical spacing between smoothed lines for birth and growth rates is interpreted as an estimate of death rate.

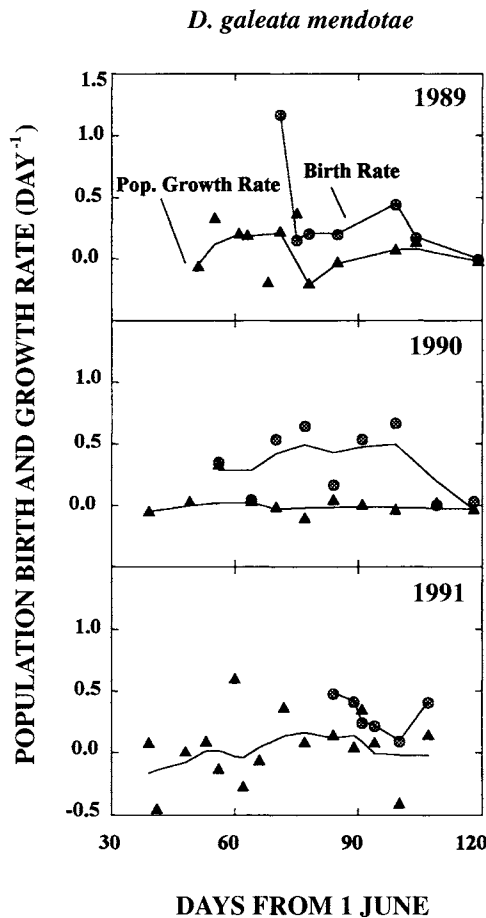


FIG. 3. Population growth rates (triangles) and birth rates (circles) for *D. galeata mendotae* during each of the three study summers. Lines represent smoothed values as in Fig. 1, but note different scale. Vertical spacing between smoothed lines for birth and growth rates is interpreted as an estimate of death rate. In July and sometimes in early August, animal density was too low to estimate birth rates.

Body lipid of juveniles was low in *D. pulicaria* in all summers (Fig. 4), but especially in 1991 ($\bar{X} = 0.019$; Table 2). In 1989 and 1990 the early summer was characterized by higher values of juvenile lipid that declined in late summer. This summer variation was especially evident in 1989, when juvenile body lipid was relatively high in June, declined in July, and then increased again at the end of summer.

Adult fecundity in *D. pulicaria* declined from June to July and then increased near the end of each summer (Table 2, Fig. 5). In general, however, values varied little around one egg per adult. There was a positive relationship between juvenile lipid content and adult fecundity in 1989 ($r = 0.64$, $P < 0.013$, $N = 14$), a weak association in 1990 ($r = 0.49$, $P < 0.07$, $N = 15$), but no relationship between these two indices was evident in 1991 ($r = -0.176$, $P < 0.38$, $N = 27$). This suggests that resource availability for adults was not

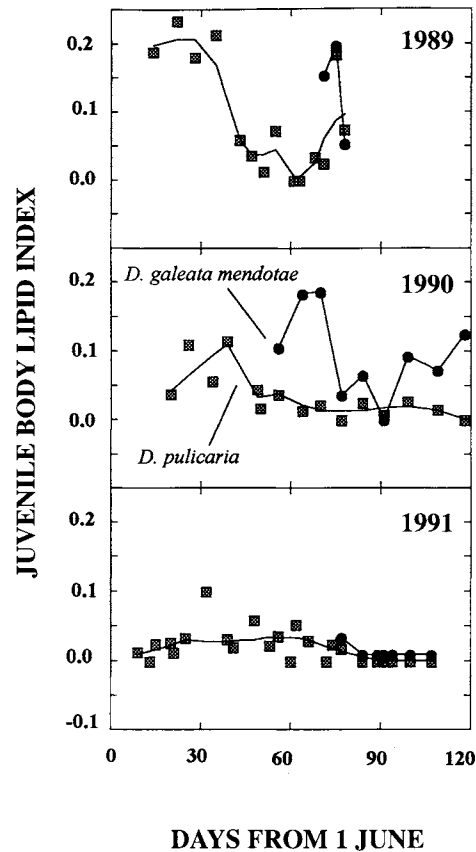


FIG. 4. Mean body lipid index for juvenile *D. pulicaria* (squares) and *D. galeata mendotae* (circles) during each of the three study summers. Lines represent smoothed values as in Fig. 1.

always equivalent to that for juveniles, especially at times of decline in *D. pulicaria* density (1991).

In all three summers, *D. pulicaria* was characterized by low levels of juvenile body lipid, adult fecundity, and population birth rates (Figs. 2, 4, 5), suggesting

TABLE 2. Average *Daphnia* juvenile lipid index and adult fecundity (eggs per adult). Data summarized as mean (± 1 SE) for each summer, or across all three summers.

	<i>D. galeata mendotae</i>			<i>D. pulicaria</i>		
	Mean	N	SE	Mean	N	SE
All 3 yr						
Lipid index	0.075	20	0.017	0.050	57	0.012
Fecundity	1.679	24	0.234	0.989	62	0.071
1989						
Lipid index	0.135	3	0.042	0.094	14	0.023
Fecundity	1.548	7	0.249	0.709	18	0.088
1990						
Lipid index	0.107	10	0.021	0.065	16	0.034
Fecundity	2.130	10	0.404	1.147	17	0.120
1991						
Lipid index	0.005	7	0.005	0.019	27	0.005
Fecundity	1.167	7	0.463	1.078	27	0.124

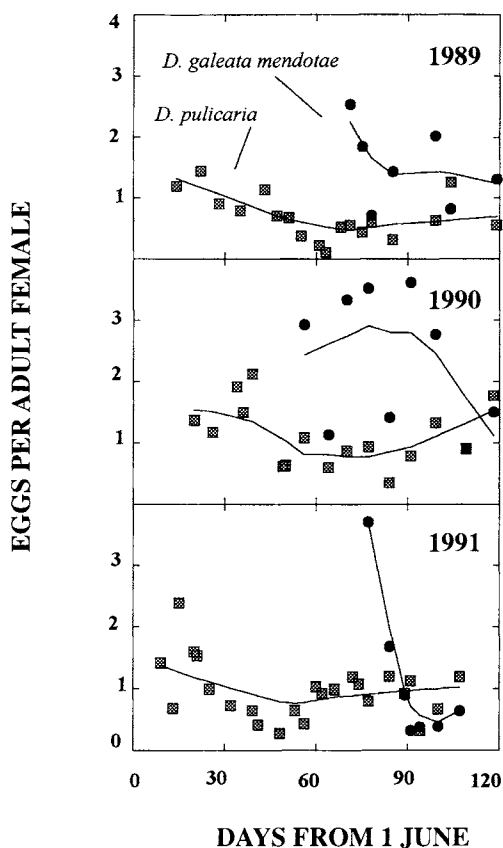


FIG. 5. Mean clutch size of adult *D. pulicaria* (squares) and *D. galeata mendotae* (circles) during each of the three study summers. Lines represent smoothed values as in Fig. 1.

low resource availability. However, there was no correlation between adult fecundity and population growth rates, or between birth rates and population growth rates, suggesting that population growth rate was not simply recruitment limited. Across the 3 yr there was an association between annual, mean juvenile lipid and annual, mean population growth rate ($r = 0.99$, $P < 0.08$, $N = 3$), whereas there was no relationship with adult fecundity.

Daphnia galeata mendotae had higher adult fecundity ($P < 0.003$) and juvenile body lipid ($P < 0.003$) than *D. pulicaria* (Table 2). Unlike birth rates, adult fecundity is not directly affected by temperature or population age structure. Therefore, this contrast in individual condition suggests a difference in resource use between the two species. Both juvenile lipid and adult fecundity of *D. galeata mendotae* were highest when the population first invaded the plankton (lipid mean = 0.119, fecundity mean = 2.487 before 19 August) and declined later on (lipid mean = 0.046, fecundity mean = 1.276 after 19 August).

Habitat availability

The rate of oxygen loss in the hypolimnion of Gull Lake varied substantially during the 3 yr of study (Fig.

6). In 1989, hypolimnetic anoxia did not occur until September. In 1990, hypolimnetic anoxia occurred ≈ 2 wk earlier and developed to a larger scale. The worst year was 1991; anoxia in the hypolimnion occurred in middle July, and extended to a shallower depth than in the previous two summers.

The rate of oxygen depletion in the hypolimnion was associated with decreases in abundance of *D. pulicaria*. Across all years, there was a negative correlation between anoxia extent (measured in metres from lake bottom) and *D. pulicaria* density ($r = -0.59$, $P < 0.016$, $N = 60$). There was no correlation, however, between anoxia extent and *D. galeata mendotae* density ($r = 0.33$, $P < 0.219$, $N = 43$).

The loss of a deep water habitat during summer 1991 was associated with movement of the *D. pulicaria* population into shallower depths, and thereby, greater spatial overlap at night with the *D. galeata mendotae* (12% in 1989 vs. 35% in 1991, Fig. 7). In addition, during both day and night, the difference in average depths between the two species was much less in 1991 than in 1989.

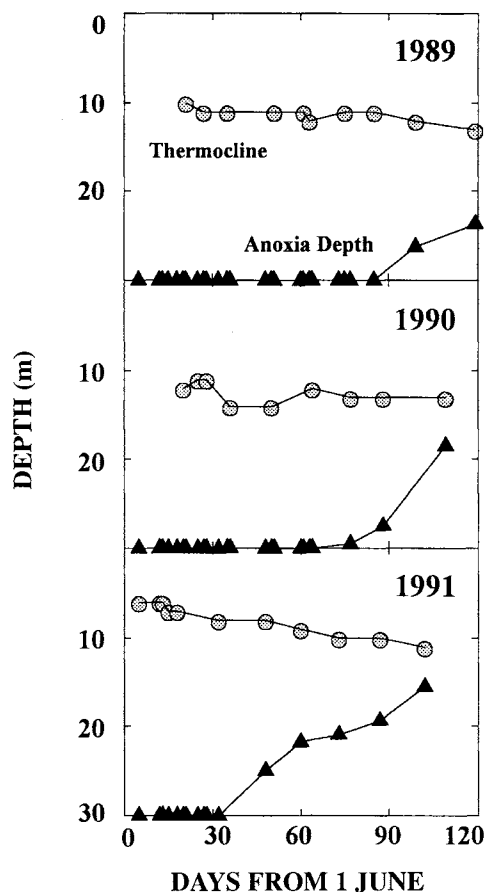


FIG. 6. Seasonal changes in the thermocline depth (maximum rate of temperature change with depth [circles]) and depth of 0.5 mg/L oxygen isopleth (triangles). Water column between these two depths is considered a refuge from fish predation.

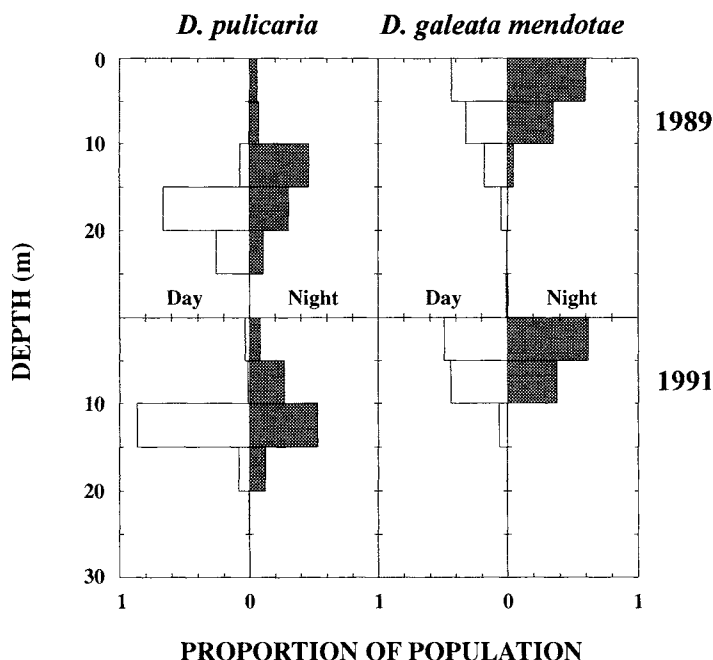


FIG. 7. Comparison of diel vertical position (population depth distribution) of *D. pulicaria* and *D. galeata mendotae* in Gull Lake during early September 1991 and 1989. Daytime overlap of species is low in both years, but nighttime overlap increases from 12% in 1989 to over 35% in 1991.

The negative correlation between hypolimnetic anoxia and the density of *D. pulicaria* is potentially explained by the fact that anoxia reduces available habitat space. Since the extent of hypolimnetic anoxia increases as summer progresses, the physical space available for *D. pulicaria* is reduced. To correct for this space restriction, we recalculated *Daphnia* density for each date using only the depth space utilized by the middle 80% of the population (rather than the full 30 m assumed in Fig. 1). This "actual experienced" density still shows a strong seasonal decline in 1990 and 1991 (Fig. 8). This suggests that the average quality of the inhabited environment and not just the amount of habitat was reduced in late summer of 1990 and 1991. Two likely explanations for this are: (1) restriction of *D. pulicaria* to a poorer quality habitat, or (2) an overall seasonal change in resources.

Resources

The phytoplankton assemblage observed in Gull Lake during the three study summers was quite diverse and included diatoms (especially *Cyclotella*), Chrysophytes (especially *Dinobryon*), Chlorophytes (especially *Sphaerocystis* and *Oocystis*), Cryptophytes (especially *Cryptomonas*), Cyanobacteria (especially *Anacystis*, *Chroococcus*), Euglenophytes (especially *Trachelomonas*), Pyrrophyta (especially *Peridinium*), and numerous unidentified microflagellates. The general pattern of algal taxa succession was typical of temperate zone, oligo-mesotrophic lakes. Diatoms, flagellates, and other highly edible algae were dominant in early summer and were replaced in later summer by taxa having larger cell size, and/or colonial structure (e.g., Cyanophyta, gelatinous Chlorophyta).

To provide a general summary of this heterogeneous resource base, we lumped all algal taxa into two ecological categories, high vs. low quality (Fig. 9), based on edibility (cell/colony size), digestibility (presence of gelatinous sheaths or tough cell walls), and suspected nutritional value (Lefèvre 1942, Porter 1973, Infante and Litt 1985). There was overall greater availability of high quality phytoplankton taxa in 1989 than in the later 2 yr. The peak of low quality algae in 1989 was not only of lesser magnitude, but also occurred later in summer than in the other 2 yr. Flagellates and other high quality resources were least abundant in the summer of 1991.

There is a positive correlation between the extent of hypolimnetic anoxia (metres from lake bottom) and the density of low quality algae ($r = 0.55$, $P < 0.027$, $N = 13$), and a negative correlation between anoxia extent and density of high quality algae ($r = -0.66$, $P < 0.014$, $N = 13$). Not surprisingly there is a striking, positive association between the extent of hypolimnetic anoxia and the ratio of low to high quality algal abundance ($r = 0.72$, $P < 0.002$, $N = 13$). Changes in the phytoplankton assemblage are also associated with changes in *D. pulicaria* density, which is negatively correlated with low quality algae ($r = -0.74$, $P < 0.001$, $N = 13$) and with the ratio of low to high quality algae ($r = -0.76$, $P < 0.001$, $N = 13$). *Daphnia galeata mendotae* density, in contrast, is only weakly associated with density of low quality algae ($r = 0.38$, $P < 0.148$, $N = 10$), but positively correlated with the ratio of low to high quality algae ($r = 0.49$, $P < 0.055$, $N = 10$).

Competition experiments—June

In the June experiment, densities in the enclosures declined by 20–40%, but no differences in population

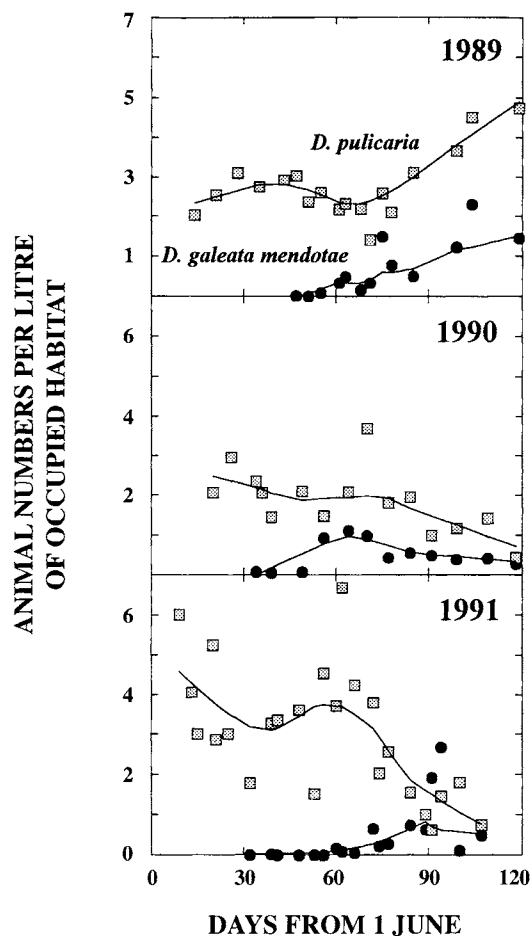


FIG. 8. Annual and seasonal variation in *D. pulicaria* (squares) and *D. galeata mendotae* (circles) density expressed as numbers per litre of occupied habitat (defined as the thickness of water column that contained $\geq 80\%$ of the population). Each data point represents the mean of 2–3 samples. Lines represent smoothed values as in Fig. 1.

growth were detected among treatments or species. *Daphnia pulicaria* controls (P) tended to have higher juvenile lipid index ($\chi^2 = 2.33$, $df = 1$, $P < 0.127$) and adult fecundity ($T = 2.60$, $df = 3$, $P < 0.080$; Fig. 10) than that of *D. galeata mendotae* controls (G).

Among *D. pulicaria* treatments there was no strong evidence of intraspecific competition in juveniles but the effect was clear in adults (juvenile lipid, $\chi^2 = 1.19$, $df = 1$, $P < 0.275$; adult fecundity $F = 12.76$, $df = 1, 7$, $P < 0.009$). Interspecific competition was, however, apparent in both juveniles and adults (juvenile lipid, $\chi^2 = 3.13$, $df = 1$, $P < 0.077$; adult fecundity $F = 9.18$, $df = 1, 7$, $P < 0.019$).

Among *D. galeata mendotae* treatments there was evidence of intraspecific competition in juveniles (juvenile lipid, $\chi^2 = 3.00$, $df = 1$, $P < 0.083$), but no significant difference in adult fecundity ($F = 1.48$, $df = 1, 3$, $P < 0.311$). In contrast, interspecific competition was not apparent in juveniles ($\chi^2 = 2.21$, $df = 1$,

$P < 0.643$), and only weak effects were seen in adults ($F = 3.96$, $df = 1, 3$, $P < 0.141$).

Competition experiments—July

Enclosure densities in the July experiment declined by no more than 20%, and population growth did not differ among treatments or species. As in June, *D. pulicaria* performed better than *D. galeata mendotae*. The P treatment displayed higher juvenile lipid ($\chi^2 = 5.40$, $df = 1$, $P < 0.020$) and higher adult fecundity than the G treatment ($T = 2.93$, $df = 4$, $P < 0.043$; Fig. 10).

Among *D. pulicaria* treatments there was higher juvenile lipid ($\chi^2 = 3.13$, $df = 1$, $P < 0.077$) and adult fecundity in P vs. PP treatments ($F = 18.23$, $df = 1, 7$, $P < 0.004$). The P treatment also had higher juvenile

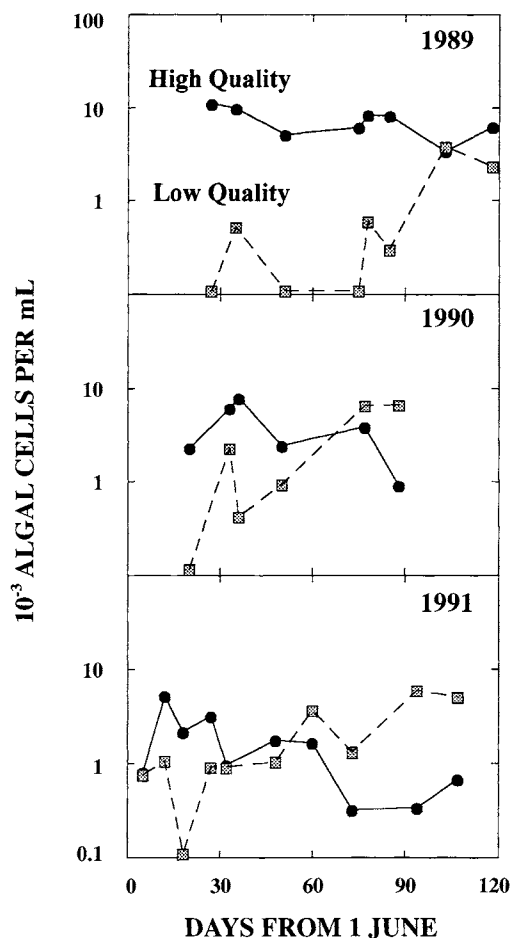


FIG. 9. Seasonal changes in abundance of two ecological groupings of phytoplankton in Gull Lake during each of the three study summers. Low quality algae includes all blue-greens (composed mostly of colonial *Anacystis* and *Anabaena*) and other gelatinous, or large cell/colony algae. High quality algae includes all single-cell flagellated taxa, and other small taxa also believed to be readily assimilated. Abundance expressed as numbers of cells per millilitre on a log scale. Blue-green density was expressed at 1/20th of actual cell density in order to make more comparable to the larger cell sizes of other taxa.

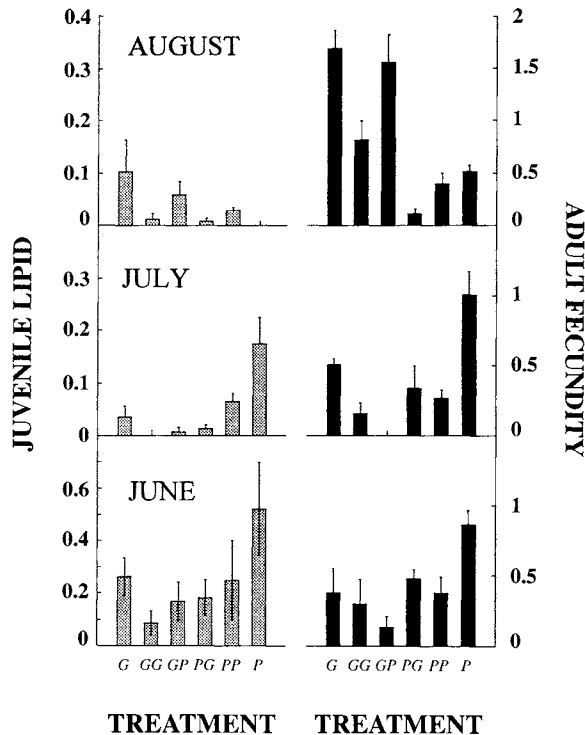


FIG. 10. Responses of *Daphnia* adults (clutch size of adults; right panels, black bars) and juveniles (body lipid index; left panels, shaded bars) to the three experimental treatments imposed upon each of the two species in each of the 3 mo during 1991. G, GG, and GP represent responses of *D. galeata mendotae* and P, PP, and PG represent responses of *D. pulicaria*. Height of bars indicate treatment means ± 1 SE based upon 2–4 replicate water column enclosures.

lipid ($\chi^2 = 3.86$, $df = 1$, $P < 0.050$) and adult fecundity ($F = 13.13$, $df = 1, 7$, $P < 0.009$) than the PG treatment. Hence, both intra- and interspecific competition effects were evident for *D. pulicaria* in July (Fig. 10).

Among *D. galeata mendotae* treatments there was higher juvenile lipid ($\chi^2 = 3.11$, $df = 1$, $P < 0.078$) and adult fecundity ($F = 20.11$, $df = 1, 8$, $P < 0.002$) in G vs. GG (Fig. 10). The G treatment also had a significantly higher fecundity ($F = 41.26$, $df = 1, 8$, $P < 0.002$), but no difference in juvenile lipid than the GP treatment ($\chi^2 = 1.86$, $df = 1$, $P < 0.172$). Both inter- and intraspecific competition were, therefore, apparent in adults, whereas in juveniles, interspecific competition was not as evident as intraspecific effects.

Competition experiments—August

In the August experiment, enclosure densities declined by no more than 20%, and population growth did not differ among *D. pulicaria* treatments. However, for *D. galeata mendotae*, the GG and GP treatments had greater population declines than the G (control) treatment. The relative performance of the two species in the control treatments was reversed from the earlier 2 mo; *D. pulicaria* performed more poorly than *D.*

galeata mendotae (juvenile lipid, $\chi^2 = 3.94$, $df = 1$, $P < 0.047$; fecundity $T = 5.93$, $df = 6$, $P < 0.001$; Fig. 10).

Daphnia pulicaria juveniles performed poorly (low body lipid) in all treatments, and there were no significant differences. However, adults showed higher fecundity in P vs. PG ($F = 18.38$, $df = 1, 7$, $P < 0.004$), but no difference from PP ($F = 1.39$, $df = 1, 7$, $P < 0.276$). Therefore, only interspecific competition was detected.

In contrast, *D. galeata mendotae* experienced intraspecific competition as stronger than interspecific competition. The G treatment showed a slightly greater juvenile lipid index ($\chi^2 = 1.92$, $df = 1$, $P < 0.166$), higher adult fecundity ($F = 8.62$, $df = 1, 9$, $P < 0.017$), and better population growth ($F = 7.76$, $df = 1, 9$, $P < 0.021$) than the GG treatment. However, there were no apparent differences between G and GP treatments in adult fecundity ($F = 0.19$, $df = 1, 9$, $P < 0.67$) or juvenile lipid ($\chi^2 = 0.021$, $df = 1$, $P < 0.884$). The G treatment did, however, have a significantly higher population growth than the GP treatment ($F = 7.68$, $df = 1, 9$, $P < 0.022$). For *D. galeata mendotae*, therefore, intraspecific competition effects were evident in juvenile and adult performances and overall population growth; interspecific competition effects were evident only in overall population growth.

Seasonal patterns of performance

No significant differences in *D. pulicaria* age (size) structure were seen among the three experiments ($F = 1.05$, $df = 2, 6$, $P < 0.405$); adults constituted $35 \pm 11\%$ (SE) of the population on each experimental date. *Daphnia pulicaria* exhibited a seasonal decline in juvenile and adult performance; they performed best during June, and worst in August ($\chi^2 = 8.72$, $df = 2$, $P < 0.008$ for juvenile lipid; $F = 4.57$, $df = 2, 6$, $P < 0.062$ for adult fecundity).

Daphnia galeata mendotae populations exhibited some seasonal change in age (size) structure ($F = 14.57$, $df = 2, 6$, $P < 0.005$). July and August were similar in having 60% adults, but in June only 30% of the population were adults. However, no significant effects of age structure were found on the performance of juveniles ($r = -0.34$, $P < 0.31$) or adults ($r = 0.43$, $P < 0.24$). *Daphnia galeata mendotae* juveniles performed best in June, and slightly poorer in the July and August experiments ($\chi^2 = 4.98$, $df = 2$, $P < 0.07$). Adult fecundity, however, improved from June to August ($F = 23.92$, $df = 2, 6$, $P < 0.001$).

Intraspecific competition experienced by *D. pulicaria* adults was greatest in June and July, and very low in August (Fig. 11). The intensity of interspecific competition, however, was highest in August, and lower in June and July. For juveniles, however, both intra- and interspecific competition increased from June to July, but the performance of *D. pulicaria* juveniles was so

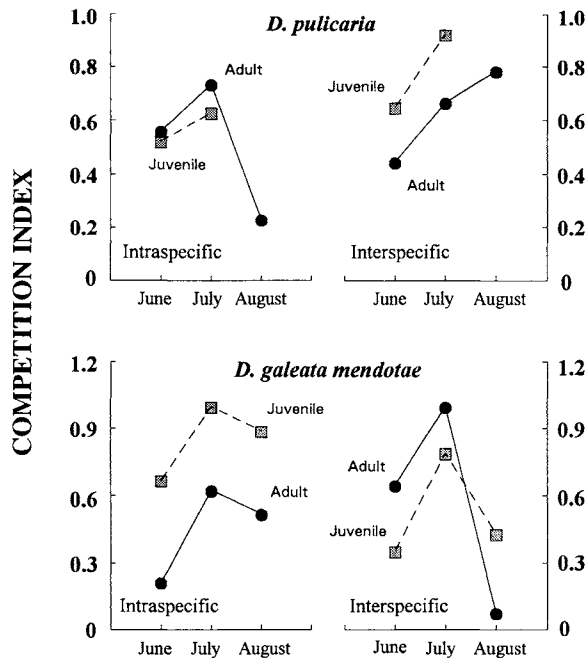
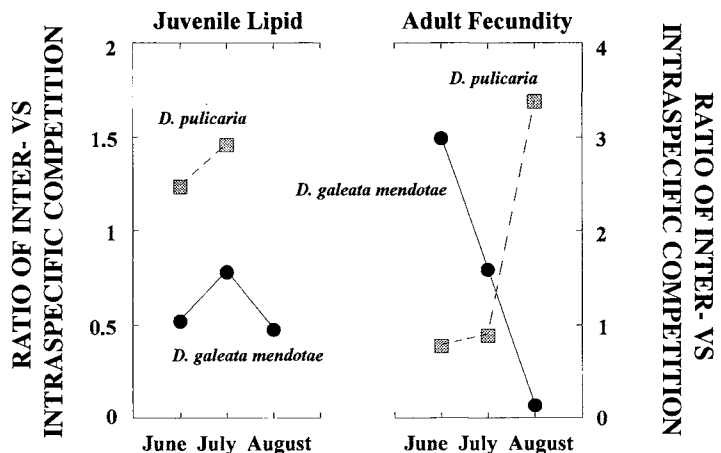


FIG. 11. Strength of interspecific (right panels) and intraspecific (left panels) competition expressed as a competition index that ranges from 0 to 1 (low to high, respectively). Top panels indicate competition intensity experienced by *D. pulicaria* juveniles (squares) and adults (circles); bottom panels indicate competition intensity experienced by *D. galeata mendotae* juveniles and adults. No values could be calculated for *D. pulicaria* juveniles during August since control responses were zero.

poor in August, neither intra- nor interspecific competition could be measured (Fig. 11).

Intraspecific competition experienced by *D. galeata mendotae* was lowest in June, strongest in July, and remained strong in August (Fig. 11). Interspecific competition intensity was strongest in July, but dropped to its lowest level in August. In fact, there was no measurable interspecific effect on adult fecundity during August.

FIG. 12. Relative strength of interspecific and intraspecific competition experienced by *D. pulicaria* (squares) and *D. galeata mendotae* (circles) juveniles (left panel) and adults (right panel). Relative strength expressed as the ratio of interspecific over intraspecific competition indices presented in Fig. 11. No value could be calculated for *D. pulicaria* juveniles during August as in Fig. 11.



Daphnia pulicaria juveniles always experienced interspecific competition as stronger than intraspecific competition, i.e., ratios of inter- to intraspecific effects were always greater than 1 (Fig. 12). Further, analysis of variance revealed no interaction between type of competition and season in juvenile performance ($F = 0.07$, $df = 2, 15$, $P < 0.932$). In adults, however, the ratios of inter- to intraspecific competition effects increased from close to 1 in June and July to ≈ 4 in August (Fig. 12). This indicates that interspecific competition was similar to intraspecific competition during the early summer, but much stronger during August. Analysis of variance revealed a marginally significant interaction between type of competition and season in adult performance ($F = 2.90$, $df = 2, 15$, $P < 0.086$).

In contrast to *D. pulicaria*, interspecific competition was always less intense than intraspecific competition for *D. galeata mendotae* juveniles (the ratio of inter- and intraspecific competition was always less than 1; Fig. 12). Seasonal change in these ratios was not great, and no interaction between type of competition and season was detected in juvenile responses ($F = 0.50$, $df = 2, 17$, $P < 0.61$). For adult performance, however, the ratio of inter- to intraspecific competition decreased with season, from > 3 in June to < 0.2 in August (Fig. 12). Analysis of variance revealed a significant interaction between type of competition and season ($F = 5.72$, $df = 2, 17$, $P < 0.013$).

Seasonal variation in the relative intensity of inter- to intraspecific competition on juvenile performance was not concordant with variation in the relative intensity of competition types on adult performance; this was true for both species.

DISCUSSION

This study revealed that competitive interactions between two congeners were often strong and asymmetric, depended upon ontogenetic stage, and most importantly, were temporally variable. Furthermore, temporal change in competitive superiority was concordant

with shifts in relative abundance of the species, suggesting that competition was an important force determining species succession. The notion that species interactions can be strongly asymmetric yet unstable over relatively short time scales is not generally appreciated, especially when the species are similar in taxonomy, body size, and feeding biology as are the two *Daphnia* we studied.

These results contribute to what is a general debate concerning the nature of competition in zooplankton assemblages. Many investigators have suggested that interspecific competition among similar forms is a strong force, and have emphasized spatial and temporal niche partitioning (Tappa 1965, Makarewicz and Likens 1975, Hoenicke and Goldman 1987) or predator-mediated coexistence (Jacobs 1977, Tessier 1986, Leibold 1991) to explain coexistence. More recently, others have argued that coexistence of similar species (and clonal genotypes) represents a balance of inter- and intraspecific competition. Despite periods of intense competition, species exclusion is slow compared to environmental changes that continuously alter the rank superiority of species and maintain diversity (Hebert and Crease 1980, Bengtsson 1986, 1993, Weider 1992).

Both processes were evident in Gull Lake. During some periods, we detected strong competition, but inter- and intraspecific effects were similar in strength (e.g., adults in July). At other times, competition was both strong and asymmetric, and associated with dominance of one species or a change in species relative abundance in the lake. These results suggest that taxonomic/morphological similarity alone does not always indicate similarity in the strength of inter- and intraspecific effects. However, they also illustrate that temporal shifts in relative competitive ability do play an important role in the maintenance of diversity.

Temporal change in species performance

The succession of these two *Daphnia* species in Gull Lake is consistent with a hypothesis that their rank exploitative ability reverses seasonally. Results from single-species control enclosures revealed that *D. pulicaria* juvenile and adult performance declined, while *D. galeata mendotae* adult and juvenile performance increased or was sustained from June to August. These results provide support for the general hypothesis that seasonal successions within zooplankton assemblages involve temporal reversals in exploitative ability of species (Lynch 1978, Smith and Cooper 1982, DeMott 1983, 1989).

An alternative hypothesis to explain the decline of *D. pulicaria* in late summer of some years in Gull Lake is selective predation by young-of-the-year yellow perch, the most common planktivore in the lake. The timing of appearance of young perch in the plankton of Gull Lake is typical of most temperate lakes in that fish are commonly seen during June and July, but during August and September switch to a more demersal

habit (Mills and Forney 1983, Tessier 1986). This pattern does not easily explain decreases in *D. pulicaria* density, which typically do not occur until August and September. Fish predation also does not explain the reduced performance of juvenile and adult *D. pulicaria* in the lake and enclosures during late summer, nor explain why the similar-sized adult *D. galeata mendotae*, which carried much higher clutch sizes (and hence were highly visible), could increase so rapidly at the same time *D. pulicaria* were declining.

Temperature is also unlikely a direct cause of the performance reversal for these two *Daphnia* species in Gull Lake. Although there is evidence that *D. pulicaria* prefer cooler temperatures than *D. galeata mendotae* (Threlkeld 1980, 1987, Hu 1994), water temperature in Gull Lake did not vary much during June through August, and was quite similar among summers (Hu 1994). In contrast, density of the two *Daphnia* species changed markedly from June to September and varied among years. Furthermore, *D. galeata mendotae* never appeared in Gull Lake before July, while the same species in other local lakes appears and increases anywhere from May to August (Cipolla, 1980; C. K. Geedey, *personal communication*). Such variation in timing of rapid population increase cannot be explained by a species characteristic preference or threshold temperature. This is not to imply that temperature plays no role in the coexistence of these two species. The more extreme temperatures associated with spring, fall, and winter seasons, and the hypolimnion habitat may restrict *D. galeata mendotae* to summer, surface waters.

Others have reached similar conclusions regarding temperature change and rank performance of different species. DeMott (1983), in a study of *Daphnia* succession quite similar to ours, found no correlation between temperature and the relative performance of two competing species. He documented a seasonal shift in competitive superiority that was strong enough to result in complete replacement of one species by the other within 1–2 mo. DeMott concludes that changes in resource quality rather than physical-chemical changes underlay this competitive shift, which repeated in each of two summers. Similarly, Smith and Cooper (1982) observed strong interspecific competition and a rapid reversal of cladoceran species dominance in a pond that exhibited little variation in temperature. In contrast, others have suggested that differential response to high (Lynch 1978, Moore and Folt 1993) or low (Allan 1977) temperatures can contribute to zooplankton species succession. The hypothesis that temperature plays an important direct role in shaping zooplankton assemblages is reasonable, but largely untested.

The impact of habitat loss from deep water anoxia on the abundance of *D. pulicaria* was evidenced by a negative correlation across all 3 yr of data. When we standardized the density of *D. pulicaria* by the actual space inhabited by the animals, however, we still found substantial population declines in late summer 1990

and 1991. This suggests that some aspects of habitat (or resource) quality is also degrading. Since *D. galeata mendotae* live primarily in the shallow water epilimnion, anoxia in the deep hypolimnion does not directly affect them.

Variation in the composition of phytoplankton resources was also correlated with changes in population density of *D. pulicaria*. When diatoms and flagellates were abundant, *D. pulicaria* juveniles had higher body lipid and population density was higher than when colonial blue-green and gelatinous green algae became common. It is reasonable to presume that a seasonal decline and among-year variation in quality of the resources affected the carrying capacity for *D. pulicaria*. In the lake population, however, reductions in resource quality had no negative effects on adult fecundity or population birth rates. Rather, it was increased death rates in late summer 1990, and 1991, which caused the seasonal and among-year differences in *D. pulicaria* density.

We suggest that a major effect of reduced resource quality was slowed development and decreased survivorship of juveniles. The negative effects of low quality food on daphniids are expected to be most dramatic on juveniles compared to adults (e.g., Threlkeld 1979, Vanni and Lampert 1992). Among-year variation in *D. pulicaria* population growth rates was associated with variation in juvenile body lipid. Hence, while adult fecundity and birth rates were largely maintained in late summer, we hypothesize that poor growth and survival of juveniles reduced recruitment into adult stages and caused population growth rate to decline. Similar conclusions have been reached by others investigating resource limitation of cladoceran populations (e.g., Romanovsky 1984, Ghilarov 1985, Threlkeld 1985). Evidence to support this hypothesis was seen in life table studies conducted during the summer of 1991 (Hu 1994) and will be presented elsewhere. When raised in epilimnetic water from Gull Lake, survival of juvenile *D. pulicaria* was very poor and resulted in a negative population growth rate.

In contrast to *D. pulicaria*, the density of *D. galeata mendotae* increased during late summer each year. Initially, this population increase was associated with far higher adult fecundity and population birth rate than for *D. pulicaria* at the same time. Interestingly, juvenile performance did not change greatly among months. Somehow, adult *D. galeata mendotae* were able to exploit the "low quality" summer resources differently or more effectively than *D. pulicaria*. This contrast was also evident in laboratory life table studies, which compared each species raised on the same resources (Hu 1994). *Daphnia galeata mendotae* displayed markedly higher survivorship and fecundity than *D. pulicaria* when raised in water and resources from the late July and August epilimnion of Gull Lake.

Competitive interactions

Our approach to measuring competition utilized an experimental design similar to that employed by plant and vertebrate ecologists (Keddy 1989), but rarely employed by plankton ecologists. Most prior experiments in plankton community ecology have studied population level responses, and hence, employed long-term manipulations (Hairston 1989). Our design allowed us to separate inter- from intraspecific effects by measuring short-term response of individuals to manipulations of species density. Further, by repeating the manipulations in time we address temporal change in these competitive effects. Finally, our use of 10 m long enclosures represents a uniquely realistic approach to studying zooplankton competition in thermally stratified lakes. Considering the abundant literature documenting habitat selection and species segregation in zooplankton (e.g., Leibold 1990, 1991), it is essential that field manipulations employ an appropriate scale of enclosure.

The in situ competition experiments demonstrate that regardless of any habitat or resource partitioning that might exist, strong exploitative competition commonly occurred between these two *Daphnia* species. Furthermore, the strength and nature of competition depended upon month and age class. Although we cannot rule out interference competition in interpreting our experimental results, its effect is unlikely to be important given the low densities (3 individuals/L) and similar size of the animals involved.

Juveniles experienced competition as a largely asymmetric interaction; *D. pulicaria* juveniles were most strongly affected by interspecific competition, while *D. galeata mendotae* juveniles experienced intraspecific effects as strongest. This asymmetry did not change throughout summer.

Asymmetric competition was also experienced by adults, but the relative strength of intra- and interspecific effects reversed from early to late summer for each species. In early summer, *D. pulicaria* adults experienced inter- and intraspecific effects as roughly similar in strength, while *D. galeata mendotae* adults experienced interspecific effects as much stronger than intraspecific competition. By August, however, the situation was both reversed and more asymmetric. From *D. pulicaria*'s perspective, interspecific effects became much stronger than intraspecific effects, while the opposite was true for *D. galeata mendotae*.

This temporal change in strength of interspecific competition suggests that *D. galeata mendotae* should displace *D. pulicaria* in late summer, which was precisely the pattern of succession observed in the lake during 1990 and 1991. In 1989, however, *D. galeata mendotae* were able to increase to similar peak densities in late summer, with no apparent decrease in density of *D. pulicaria*. The implication is that in 1989,

the actual intensity of interspecific competition remained low for *D. pulicaria*.

The difference in hypolimnetic anoxia among years resulted in changes in the vertical habitat use by *D. pulicaria*, causing greater spatial overlap with the *D. galeata mendotae* in 1991 compared with 1989. Annual variation in habitat compression may explain the persistence of *D. pulicaria* density in some summers, but does not explain the seasonal shift in strength of interspecific effects measured in the enclosures during 1991. The enclosures did not extend deeper than 15 m and so were always within the oxygenated part of the vertical habitat space. Hence, we suggest that the emergence of *D. galeata mendotae* as the superior competitor in late summer is related to a seasonal change in resource composition. This change appears to strongly influence adult *D. galeata mendotae* fecundity and birth rates, allowing the species to "invade" the lake plankton each summer.

The interaction of stage (age or size) and species differences in habitat or resource use is recognized to structure population dynamics and species interactions in several taxa (e.g., Ebenman and Persson 1988, Ösenberg et al. 1992). In *Daphnia*, stage structure is clearly important to dynamics of even single species in simple, predator-free environments (Goulden and Hornig 1980, McCauley et al. 1990). Furthermore, several studies have emphasized that competitive interactions among zooplankton species are strongly influenced by stage structure (e.g., Neill 1975, Matveev 1985, 1987). However, nearly all previous studies of zooplankton competition have been conducted in laboratory vessels (e.g., Goulden et al. 1982, Romanovsky and Feniova 1985, Milbrink and Bengtsson 1991), or shallow field enclosures (e.g., Lynch 1978, Smith and Cooper 1982, DeMott 1983, Vanni 1986), both of which provide little habitat heterogeneity. In many lakes, however, not only do different species vary in their preferred habitat depths, but juveniles often segregate from adults. In Gull Lake, *D. pulicaria* inhabited deeper waters than *D. galeata mendotae*, and juveniles of both species preferred shallower depths than adults (Hu 1994, Leibold et al. 1994).

These stage and species differences in habitat use behavior provide an explanation for the static difference in the strength of interspecific and intraspecific competition experienced by juveniles of the two species. *Daphnia galeata mendotae* juveniles stayed in the top few metres in the water column and were, therefore, widely separated from the average adult *D. pulicaria*. In contrast, *D. pulicaria* juveniles lived deeper and overlapped in habitat use with adult *D. galeata mendotae*. Considering the far greater individual feeding rate of adults compared with juveniles (Lampert 1987), it is understandable that *D. pulicaria* juveniles always experienced interspecific competition as stronger than intraspecific competition, while for *D. galeata mendotae* the situation was always reversed. Despite strong

evidence of both vertical and horizontal patchiness in zooplankton assemblages (Folt et al. 1993), its general significance in mediating stage-structured population interactions is poorly studied.

Although we purposely chose a lake with low planktivory for our study, it is likely that the temporal and stage-structured effects we illustrate in Gull Lake will be of general importance in most lakes. Most planktivores forage in a manner that is both size selective and habitat specific, and as a consequence, modify not only density, but also size (stage) structure and habitat use of their zooplankton prey (Zaret 1980, Gliwicz and Pijanowska 1989, Leibold 1991). Such predators, therefore, have the potential to fundamentally alter the nature of competitive interactions among their zooplankton prey. While it is recognized that predation does not preclude strong competition among zooplankton species (e.g., Vanni 1987) our understanding of the richness of these interactions is still in its infancy.

ACKNOWLEDGMENTS

Work presented here is in partial fulfillment of Ph.D. requirements for S. S. Hu at Michigan State University. Hu acknowledges support from the Department of Zoology, W. K. Kellogg Biological Station, and the Ecology and Evolutionary Biology Program at Michigan State University. Tessier acknowledges support from NSF grant BSR 90-07597, and NSF-RTG grant DIR 91-13598 and the Gull Lake Quality Organization. We thank D. Hall, M. Leibold, and G. Mittelbach for advice on general approach and experimental design. D. Straney, D. King, W. DeMott and two anonymous reviewers provided valuable feedback on early drafts. C. Geedey, C. Huckins, M. Leibold, A. Turner, and A. Young helped with field work. This is KBS contribution number 772.

LITERATURE CITED

- Abrams, P. 1984. Variability in resource consumption rates and the coexistence of competing species. *Theoretical Population Biology* 25:106–124.
- Allan, J. D. 1977. An analysis of seasonal dynamics of a mixed population of *Daphnia*, and the associated cladoceran community. *Freshwater Biology* 7:505–512.
- Bengtsson, J. 1986. Life histories and interspecific competition between three *Daphnia* species in rockpools. *Journal of Animal Ecology* 55:641–655.
- . 1987. Competitive dominance among Cladocera: are single-factor explanations enough? *Hydrobiologia* 145:19–28.
- . 1993. Interspecific competition and determinants of extinction in experimental populations of 3 rockpool *Daphnia* species. *Oikos* 67:451–464.
- Bottrell, H. H., A. Duncan, Z. M. Gliwicz, E. Grygierek, A. Herzig, A. Hillbricht-Ilkowska, H. Kurasawa, P. Larsson, and T. Weglenska. 1976. A review of some problems in zooplankton production studies. *Norwegian Journal of Zoology* 24:419–456.
- Brooks, J. L., and S. I. Dodson. 1965. Predation, body size and composition of plankton. *Science* 150:28–35.
- Chesson, P. L. 1986. Environmental variation and the coexistence of species. Pages 240–256 in J. Diamond and T. J. Case, editors. *Community ecology*. Harper & Row, New York, New York, USA.
- Cipolla, M. J. 1980. Sexual dynamics of *Daphnia* populations in six Michigan lakes. Dissertation. Northwestern University, Evanston, Illinois, USA.
- Cleveland, W. S. 1981. LOWESS: a program for smoothing

- scatterplots by robust locally weighted regression. *American Statistician* **35**:54.
- DeMott, W. R. 1989. The role of competition in zooplankton succession. Pages 195–252 in U. Sommer, editor. *Plankton ecology*. Springer-Verlag, Berlin, Germany.
- . 1983. Seasonal succession in a natural *Daphnia* assemblage. *Ecological Monographs* **53**:321–340.
- Dexter, J. L., Jr. 1991. Gull Lake. Michigan Department of Natural Resources, Status of Fishery Resource Report **91-4**.
- Dodson, S. I. 1974. Zooplankton competition and predation: an experimental test of the size-efficiency hypothesis. *Ecology* **55**:605–613.
- Dorazio, R. M., J. Bowers, and J. Lehman. 1986. Food web manipulations influence grazer control of phytoplankton growth rates in Lake Michigan. *Journal of Plankton Research* **9**:891–899.
- Ebenhöh, W. 1992. Temporal organization in a multi-species model. *Theoretical Population Biology* **42**:152–171.
- Ebenman, B., and L. Persson, editors. 1988. *Size-structured populations: ecology and evolution*. Springer-Verlag, Berlin, Germany.
- Ellner, S. 1987. Alternate plant life history strategies and coexistence in randomly varying environments. *Vegetatio* **69**:199–208.
- Folt, C., P. C. Schulze, and K. Baumgartner. 1993. Characterizing a zooplankton neighbourhood: small-scale patterns of association and abundance. *Freshwater Biology* **30**:289–300.
- Ghilarov, A. M. 1985. Dynamics and structure of cladoceran populations under conditions of food limitation. *Archiv für Hydrobiologie* **21**:323–332.
- Gliwicz, Z. M. 1985. Predation or food limitation: an ultimate reason for extinction of planktonic cladoceran species. *Archiv für Hydrobiologie* **21**:419–430.
- Gliwicz, Z. M., and W. Lampert. 1990. Food thresholds in *Daphnia* species in the absence and presence of blue-green filaments. *Ecology* **71**:691–702.
- Gliwicz, Z. M., and J. Pijanowska. 1989. The role of predation in zooplankton succession. Pages 253–298 in U. Sommer, editor. *Plankton ecology*. Springer-Verlag, Berlin, Germany.
- Goldberg, D. E., and A. M. Barton. 1992. Patterns and consequences of interspecific competition in natural communities: a review of field experiments with plants. *American Naturalist* **139**:771–801.
- Goulden, C. E., and L. L. Hornig. 1980. Population oscillations and energy reserves in planktonic Cladocera and their consequences to competition. *Proceedings of the National Academy of Sciences (USA)* **77**:1716–1720.
- Gurvitch, J., L. L. Morrow, A. Wallace, and J. S. Walsh. 1992. A meta-analysis of competition in field experiments. *American Naturalist* **140**:539–572.
- Hall, D. J., S. T. Threlkeld, C. W. Burns, and P. H. Crowley. 1976. The size-efficiency hypothesis and the size structure of zooplankton communities. *Annual Review of Ecology and Systematics* **7**:177–208.
- Hairston, N. G., Sr. 1989. *Ecological experiments*. Cambridge University Press, Cambridge, England.
- Hebert, P. D. N., and T. J. Crease. 1980. Clonal existence in *Daphnia pulex* (Leydig): another plankton paradox. *Science* **207**:1363–1365.
- Hoenicke, R., and C. R. Goldman. 1987. Resource dynamics and seasonal changes in competitive interactions among three cladoceran species. *Journal of Plankton Research* **9**:397–417.
- Hrbáčková, M., and J. Hrbáček. 1978. The growth rate of *Daphnia pulex* and *Daphnia pulicaria* (Crustacea: Cladocera) at different food levels. *Věstník Československé Společnosti Zoologické* **2**:115–127.
- Hu, S. S. 1994. Competition in a seasonal environment: *Daphnia* population dynamics and coexistence. Dissertation. Michigan State University, East Lansing, Michigan, USA.
- Hutchinson, G. E. 1961. The paradox of the plankton. *American Naturalist* **95**:137–146.
- . 1967. *A treatise on limnology*. Volume 2. Wiley, New York, New York, USA.
- Infante, A., and W. T. Edmondson. 1985. Edible phytoplankton and herbivorous zooplankton in Lake Washington. *Archiv für Hydrobiologie* **21**:161–172.
- Infante, A., and A. H. Litt. 1985. Differences between two species of *Daphnia* in the use of 10 species of algae in Lake Washington. *Limnology and Oceanography* **30**:1053–1059.
- Jacobs, J. 1977. Coexistence of similar zooplankton species by differential adaptation to reproduction and escape in an environment with fluctuating food and enemy densities. II. Field analysis of *Daphnia*. *Oecologia* **30**:313–329.
- Keddy, P. A. 1989. *Competition*. Chapman and Hall, London, England.
- Kerfoot, W. C., and W. R. DeMott. 1984. Food web dynamics: dependent chains and vaulting. Pages 347–381 in D. G. Meyers and J. R. Strickler, editors. *Trophic interactions within aquatic ecosystems*. American Association for the Advancement of Science Selected Symposium Number 85. Westview Press, Boulder, Colorado, USA.
- Kerfoot, W. C., W. R. DeMott, and D. L. DeAngelis. 1985. Interactions among cladocerans: food limitation and exploitative competition. *Archiv für Hydrobiologie* **21**:431–452.
- Kirk, K. L., and J. J. Gilbert. 1990. Suspended clay and the population dynamics of planktonic rotifers and cladocerans. *Ecology* **71**:1741–1755.
- Kratz, T. K., T. M. Frost, and J. J. Magnuson. 1987. Inferences from spatial and temporal variability in ecosystems: long-term zooplankton data from lakes. *American Naturalist* **129**:830–846.
- Lampert, W. 1987. Feeding and nutrition in *Daphnia*. *Memorie dell'Istituto Italiano di Idrobiologia* **45**:143–192.
- Lane, P. A. 1975. The dynamics of aquatic systems: a comparative study of the structure of the four zooplankton communities. *Ecological Monographs* **45**:307–336.
- Leibold, M. 1991. Trophic interactions and habitat segregation between competing *Daphnia* species. *Oecologia* **86**:510–520.
- Leibold, M., and A. J. Tessier. 1991. Contrasting patterns of body size for *Daphnia* species that segregate by habitat. *Oecologia* **86**:342–348.
- Leibold, M., A. J. Tessier, and C. T. West. 1994. Genetic, acclimatization and ontogenetic effects on habitat selection behavior in *Daphnia pulicaria*. *Evolution* **48**:1324–1332.
- Lefèvre, M. 1942. L'utilisation des algues d'eau douce par les Cladocères. *Bulletin Biologique de la France et de la Belgique* **76**:250–276.
- Lynch, M. 1978. Complex interactions between natural coexploiters *Daphnia* and *Ceriodaphnia*. *Ecology* **59**:552–564.
- Makarewicz, J. C., and G. E. Likens. 1975. Niche analysis of a zooplankton community. *Science* **190**:1000–1003.
- Matveev, V. F. 1985. Competition and population time lags in *Bosmina* (Cladocera, Crustacea). *Internationale Revue der Gesamten Hydrobiologie* **70**:491–508.
- . 1987. Effect of competition on the demography of planktonic cladocerans—*Daphnia* and *Diaphanosoma*. *Oecologia* **74**:468–477.
- Milbrink, G., and J. Bengtsson. 1991. The impact of size-selective predation on competition between 2 *Daphnia* species—a laboratory study. *Journal of Animal Ecology* **60**:1009–1028.
- Mills, E. L., and J. L. Forney. 1983. Impact on *Daphnia*

- pulex* of predation by young yellow perch in Oneida Lake, New York. Transactions of the American Fisheries Society **112**:154–161.
- Moore, M., and C. Folt. 1993. Zooplankton body size and community structure: effects of thermal and toxicant stress. Trends in Ecology and Evolution **8**:178–182.
- Moss, B. 1972a. Studies on Gull Lake, Michigan. I. Seasonal and depth distribution of phytoplankton. Freshwater Biology **2**:289–307.
- . 1972b. Studies on Gull Lake, Michigan. II. Eutrophication-evidence and prognosis. Freshwater Biology **2**:309–320.
- Moss, B., R. Wetzel, and G. H. Lauff. 1980. Annual productivity and phytoplankton changes between 1969 and 1974 in Gull Lake, Michigan. Freshwater Biology **10**:113–121.
- Neill, W. E. 1988. Community responses to experimental nutrient perturbations in oligotrophic lakes: the importance of bottlenecks in size-structured populations. Pages 236–258 in B. Ebenman and L. Persson, editors. Size-structured populations. Springer-Verlag, Berlin, Germany.
- . 1975. Experimental studies of microcrustacean composition and efficiency of resource utilization. Ecology **56**:809–826.
- Osenberg, C. W., G. G. Mittelbach, and P. C. Wainwright. 1992. Two-stage life histories in fish: the interaction between juvenile competition and adult performance. Ecology **73**:255–267.
- Pake, C. E., and D. L. Venable. 1995. Is coexistence of Sonoran desert annuals mediated by temporal variability in reproductive success. Ecology **76**:246–261.
- Porter, K. G. 1973. Selective grazing and differential digestion of algae by zooplankton. Nature **244**:179–180.
- Prepas, E., and F. H. Rigler. 1978. The enigma of *Daphnia* death rates. Limnology and Oceanography **23**:970–988.
- Reynolds, C. S. 1992. Dynamics, selection and composition of phytoplankton in relation to vertical structure in lakes. Archiv für Hydrobiologie **35**:13–31.
- Rigler, F. H., and J. A. Downing. 1984. The calculation of secondary productivity. Pages 19–58 in J. A. Downing and F. H. Rigler, editors. A manual on methods for the assessment of secondary productivity in freshwater. International Biological Program Handbook 17. Blackwell Scientific, Boston, Massachusetts, USA.
- Romanovsky, Y. E. 1984. Prolongation of postembryonic development in experimental and natural cladoceran populations. Internationale Revue der Gesamten Hydrobiologie **69**:613–632.
- Romanovsky, Y. E., and I. Y. Feniova. 1985. Competition among Cladocera: effects of different levels of food supply. Oikos **44**:243–252.
- Rothhaupt, K. O. 1990. Resource competition of herbivorous zooplankton: a review of approaches and perspectives. Archiv für Hydrobiologie **118**:1–29.
- SAS. 1990. SAS procedures version 6.0. SAS Institute, Cary, North Carolina, USA.
- Seitz, A. 1980. The coexistence of three species of *Daphnia* in the Klostersee. I. Field studies on the dynamics of reproduction. Oecologia **45**:117–130.
- Smith, D. W., and S. D. Cooper. 1982. Competition among Cladocera. Ecology **63**:1004–1015.
- Sommer, U., editor. 1989. Plankton ecology: succession in plankton communities. Springer-Verlag, Berlin, Germany.
- Stemberger, R. S., and J. J. Gilbert. 1985. Body size, food concentration and population growth in planktonic rotifers. Ecology **66**:1151–1159.
- Tague, D. F. 1977. The hydrologic and total phosphorus budgets of Gull Lake, Michigan. Master's thesis, Michigan State University, Michigan, USA.
- Tappa, D. W. 1965. The dynamics of the association of six limnetic species of *Daphnia* in Aziscoos Lake, Maine. Ecological Monographs **35**:395–423.
- Taylor, D. J., and P. D. N. Hebert. 1993. A reappraisal of phenotypic variation in *Daphnia galeata mendotae*: the role of interspecific hybridization. Canadian Journal of Fisheries and Aquatic Sciences **50**:2137–2146.
- Tessier, A. J. 1986. Comparative population regulation of two planktonic cladocera (*Holopedium gibberum* and *Daphnia catawba*). Ecology **67**:285–302.
- Tessier, A. J., and C. E. Goulden. 1982. Estimating food limitation in cladoceran populations. Limnology and Oceanography **27**:707–717.
- Tessier, A. J., and J. Welser. 1991. Cladoceran assemblages, seasonal succession and the importance of a hypolimnetic refuge. Freshwater Biology **25**:85–93.
- Tessier, A. J., A. Young, and M. Leibold. 1992. Population dynamics and body-size selection in *Daphnia*. Limnology and Oceanography **37**:1–13.
- Threlkeld, S. T. 1979. The midsummer dynamics of two *Daphnia* species in Wintergreen Lake, Michigan. Ecology **60**:165–179.
- . 1980. Habitat selection and population growth of two cladocerans in seasonal environments. Pages 346–357 in W. C. Kerfoot, editor. Evolution and ecology of zooplankton communities. University Press of New England, Hanover, New Hampshire, USA.
- . 1985. Resource variation and the initiation of midsummer declines of cladoceran populations. Archiv für Hydrobiologie **21**:333–340.
- . 1987. *Daphnia* population fluctuations: patterns and mechanisms. Memorie dell Istituto Italiano Idrobiologia **45**:353–366.
- Vanni, M. J. 1986. Competition in zooplankton communities: suppression of small species by *Daphnia pulex*. Limnology and Oceanography **31**:1039–1056.
- . 1987. Food availability, fish predation, and the dynamics of a zooplankton community coexisting with planktivorous fish. Ecological Monographs **57**:61–88.
- Vanni, M. J., and W. Lampert. 1992. Food quality effects on life history traits and fitness in the generalist herbivore *Daphnia*. Oecologia **92**:48–57.
- Weider, L. J. 1992. Disturbance, competition and the maintenance of clonal diversity in *Daphnia pulex*. Journal of Evolutionary Biology **5**:505–522.
- Wetzel, R. G. 1983. Limnology. Second edition. Saunders, Philadelphia, Pennsylvania, USA.
- Wilson, S. D., and D. Tilman. 1991. Components of plant competition along an experimental gradient of nitrogen availability. Ecology **72**:1050–1065.
- Woltereck, R. 1932. Races, associations and stratification of pelagic Daphnids in some lakes of Wisconsin and other regions of the United States and Canada. Transactions of the Wisconsin Academy of Sciences, Arts, and Letters **27**:487–522.
- Wright, D., and J. Shapiro. 1990. Refuge availability: a key to understanding the summer disappearance of *Daphnia*. Freshwater Biology **24**:43–62.
- Zaret, T. M. 1980. Predation in freshwater communities. Yale University Press, New Haven, Connecticut, USA.