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Source: *Ecology*, Vol. 64, No. 5 (Oct., 1983), pp. 1145-1156
Published by: Ecological Society of America
Stable URL: http://www.jstor.org/stable/1937825
Accessed: 15/06/2009 13:56

Ecology, 64(5), 1983, pp. 1145–1156

SPECIES- AND AGE-SPECIFIC DIFFERENCES IN BACTERIAL RESOURCE UTILIZATION BY TWO CO-OCCURRING CLADOCERANS[1]

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Abstract. The trophic interaction between zooplankton and bacteria was examined to determine how this food web linkage varied with resource abundance and consumer species and age. Life table experiments and feeding-rate measurements were conducted with two species of co-occurring cladocerans, *Daphnia parvula* and *Ceriodaphnia lacustris*. Cohorts of these cladocerans were followed from birth to death and fed either no food (particle-free lake water), natural bacteria only (1-μm filtrate of lake water), whole lake water, or lake water enriched with 10^4 cells/mL of the green algae *Chlamydomonas reinhardi*. By comparing cohorts grown in lake water to those grown in enriched lake water, we also determined the extent of food limitation in the natural populations of these two potentially competitive species. As bacterial densities increased from winter through summer, the ability of the larger species, *Daphnia parvula*, to grow and reproduce on the bacterial fraction also increased. Bacteria, however, were never a primary resource for *Daphnia*. The rate of population increase (r) was always negative even at the highest in situ concentrations of bacteria ($1–2 \times 10^7$ cells/mL). The smaller species, *Ceriodaphnia lacustris*, was able to increase ($r = 0.070$) on bacteria alone at lower bacterial concentrations (5×10^6 cells/mL). *Ceriodaphnia* juveniles had the highest age-specific survival rates (l_x) on bacteria. The improved survivorship was not due to higher feeding rates on bacteria by *Ceriodaphnia*. Neither age nor species when adjusted for the effect of body mass accounted for a significant portion of the variance in filtering rates on bacteria. Natural field food concentrations were always suboptimal, based on comparisons of growth rates, reproduction, and r values for the cohorts grown in lake water vs. enriched lake water. Rates of increase (r), however, were always substantially greater than zero in the lake water treatment for both species, indicating that food is not the primary factor that causes seasonal declines of the cladoceran populations in this lake.

These results demonstrate a differential utilization efficiency of the smallest resource size-classes by these two zooplankton species. The experiments also indicate the dynamic nature of the trophic interaction between zooplankton and bacteria. The strength of this food web pathway varies with both the seasonal abundance of bacteria and the age, size, and type of zooplankton consumer.

Key words: age structure; bacteria; body size; Cladocera; fecundity; food limitation; food webs; growth; resources; zooplankton.

INTRODUCTION

Although food webs are generally analyzed as static structures (May 1973, Cohen 1978, Pimm 1980), natural trophic interactions are dynamic. Food web linkages and interaction strengths (sensu Paine 1980) may vary with seasonal changes in the environment and with shifts in the population structure of key species. Evidence for this view comes from experimental studies of freshwater planktonic food webs. Seasonal changes in phytoplankton prey types and shifts in the age structure, distribution, and activity of vertebrate and invertebrate predators are known to affect food web linkages involving zooplankton (Brooks and Dodson 1965, Hall et al. 1976, Porter 1973, Dodson 1974, Porter 1977, Lynch 1979, Hurlbert and Mulla 1981, Lynch and Shapiro 1981, Neill 1981). An aspect of planktonic food webs which remains poorly understood is how detrital and bacterial production affect zooplankton dynamics (Porter et al. 1979).

Based on studies of Lake Erken, Nauwerck (1963) proposed that primary production in some lakes is insufficient to support zooplankton production. Analyses of lake and pond carbon budgets suggest that zooplankton obtain a substantial proportion of their carbon from detritus pathways via bacteria (Wetzel 1975:611–613). Recent advances in methodology have confirmed that bacteria are both numerically abundant (Hobbie et al. 1977, Watson et al. 1977, Hobbie 1979, Porter and Feig 1980) and significant producers of biomass (Fuhrman and Azam 1980) in the plankton.

Many studies demonstrate that zooplankton can ingest and assimilate radioactively labeled bacteria (Monakov and Sorokin 1961, McMahon and Rigler 1965, Sorokin 1966, Haney 1973, Gophen et al. 1974, Lampert 1974, Gophen 1977, Starkweather et al. 1979, and marine references cited in Hollibaugh et al. 1980). In some cases, zooplankton species have also been cultured on bacteria through early life history stages (Tezuka 1971, Gophen et al. 1974) and even for numerous generations (Rodina 1950 as cited in Hrbáček

[1] Manuscript received 1 March 1982; revised 1 October 1982; accepted 22 October 1982.

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1977, Starkweather et al. 1979). The applicability, however, of these findings to natural systems has been criticized (Peterson et al. 1978, Porter et al. 1979, Hollibaugh et al. 1980) because laboratory-cultured bacteria were used. These are considerably larger (1–2 μm) than most planktonic forms, which are <1 μm in maximum dimension and 0.1 μm^3 in maximum volume and occur primarily as free-living cells rather than as colonies or attached to detrital particles (Daley and Hobbie 1975, Ferguson and Rublee 1976, Bowden 1977, Hobbie et al. 1977, Watson et al. 1977, Zimmerman 1977, Hobbie 1979, Porter and Feig 1980).

To overcome these limitations, ingestion of natural bacteria by zooplankton has been investigated. *Daphnia* spp. and *Polyartemiella hazeni* ingested the bacteria found in lake water, but at lower rates than obtained for larger yeast cells (Peterson et al. 1978). The marine larvacean *Oikopleura dioica* also ingested radioactively labeled planktonic bacteria at rates up to 100% of its body mass per day (King et al. 1980). Neither study demonstrates whether bacteria are an important food resource, but both do suggest that bacteria alone will not supply sufficient energy to maintain these consumers.

The purpose of our study was to examine directly whether natural bacteria serve as a resource for two co-occurring cladocerans, *Daphnia parvula* and *Ceriodaphnia lacustris*, and to test how this trophic interaction varies with resource abundance and consumer size. Life table experiments were conducted with cohorts of each species grown in lake water, lake water fractioned to isolate bacteria, lake water enriched with a high-quality food (*Chlamydomonas reinhardi* [Porter and Orcutt 1980]), and lake water filtered to remove all food. Feeding rates on bacteria were also measured to identify any differences between the two species and between juveniles and adults within the species.

Three explicit hypotheses were tested. The first was a test of an assumption of the size-efficiency hypothesis that there is no difference in feeding among zooplankton at the low end of the food particle size spectrum (Brooks and Dodson 1965, Hall et al. 1976). Two species which exhibit a differential ability to feed, grow, and reproduce on the fine-particle fraction would falsify this aspect of the size-efficiency hypothesis. The life table approach also allowed an examination of age and, therefore, size-specific differences within a species. Our second hypothesis was that younger cladocerans due to their smaller size and presumably finer-filtering apparatus, would feed at higher rates and grow and survive better than older animals on the bacterial size fraction. A third hypothesis was that seasonal variation in bacterial abundance would be reflected in the consumer's ability to utilize this resource. Three experiments were run with *Daphnia parvula* at times of minimum, maximum, and intermediate bacterial densities to test if growth and reproduction increased across the range of in situ concentrations found at the study site. Together these hypotheses provide a test of the strength and dynamics of the food web link between cladoceran zooplankton and bacteria in a system where bacteria are abundant and bacterial production is considered important (Porter and Feig 1980, Pace 1982).

The experimental design also allowed observations on the extent of food limitation in natural populations. By comparing cohorts grown in lake water to those grown in lake water enriched with *Chlamydomonas*, it was possible to assess whether, and to what extent, the field populations of these two potentially competitive species (Lynch 1978) were food limited at three seasons of the year.

Methods

Experimental design and life table procedure

All animals and water used in the experiments were obtained from Lake Oglethorpe, a 30-ha monomictic lake (z_{max} = 8.5 m) located 20 km southeast of Athens, Georgia. Detailed descriptions of the lake as well as bacteria and zooplankton sampling methods and data can be found in Porter and Feig (1980), Pace and Orcutt (1981), and Pace (1982).

Experiments with *Daphnia parvula* were run during the winter, spring, and summer, which represented periods of minimum, increasing, and maximum bacteria densities, respectively. *D. parvula* is abundant in the lake for most of the year (5–60 individuals/L) except in late summer and early fall, when it becomes rare (<0.1 individuals/L). A single experiment was also conducted with *Ceriodaphnia lacustris* during the spring, when it was abundant (90 individuals/L) in the lake. Each experiment consisted of four treatments: (1) no food: lake water filtered free of food particles, (2) 1-μm filtrate: food (principally bacteria) passing through a 1-μm filter, (3) lake water: sieved to remove larger particles, and (4) enriched lake water: *Chlamydomonas reinhardi* added. Water was collected from the field and processed into the treatment groups daily (see *Water fractionation procedure*).

Before each experiment, *Daphnia parvula* and *Ceriodaphnia lacustris* were isolated from Lake Oglethorpe and maintained in the laboratory on filtered lake water and *Chlamydomonas* for 2–4 wk to obtain a large number of egg-bearing females. Egg-bearing females were isolated into the various treatment media, and their newborn young (<24 h old) were removed and used to initiate the experiment. Experimental animals were grown individually in glass vials (volume = 22 mL) and transferred to a clean vial with fresh feeding suspensions made from lake water collected each day of the experiment. Shed carapaces, number of young produced, and deaths were recorded at each daily transfer. Cohort sizes in each treatment ranged from 18 to 24 animals.

Animals were moved to fresh feeding suspensions

daily in order to maintain food concentrations as close to in situ levels as possible. Dissolved oxygen, pH, bacterial, and algal cell concentrations did not change significantly over a 24-h period in vials (volume = 30 mL) containing the large cladoceran *Daphnia magna* (size-range 0.8–4.9 mm), except at the lowest algal concentration (*Chlamydomonas reinhardi* at 10^3 cells/mL), where concentrations were significantly reduced by feeding (Porter and Orcutt 1980). Aside from the no-food controls, food concentrations in the present experiments were lowest in the 1-μm filtrate. We measured the change in bacterial concentrations over 24 h in vials ($n = 3$) containing the 1-μm filtrate and single *Daphnia parvula* adults (size-range 0.9–1.3 mm) at 20°C. Mean bacterial concentrations actually increased 21%, reflecting the balance between losses due to grazing and growth over the 24-h period. These results emphasize the necessity of changing the experimental medium frequently in studies where controlling food concentrations is of interest.

Life table experiments were run in environmental chambers at constant temperatures (±1.0°) of 25° in summer (started 14 August 1979), 8° in winter (started 26 January 1980), and 20° in spring (started 6 May 1980) under "cool-white" fluorescent lighting (3 $\mu E \cdot m^{-2} \cdot s^{-1}$, 16:8 h L:D cycle). These temperatures approximated the average temperatures that the field population experienced except in the winter, when 8° represented the highest temperature encountered.

To determine the concentrations of bacteria available during the experiments, cell counts were made periodically on the collected lake water. The acridine orange direct count method was used, as described by Porter and Feig (1980).

By following individuals throughout their lifespan, it was possible to calculate the mean body size at death (measured from the top of the carapace to the base of the tail spine, to the nearest 0.013 mm), life span, and number of young per female for each treatment group. These data were analyzed with a nonparametric Kruskal-Wallis ANOVA, followed by a Dunn multiple comparison test for pairwise comparisons between treatments when appropriate (Hollander and Wolfe 1973). Significant differences noted in the results are always at the .05 level. For each treatment cohort, a life table of age-specific survivorship and fecundity was established, and the realized rate of increase r was calculated by solving the Characteristic Equation of Lotka as described in Poole (1974). Because replicate cohorts were not run within each treatment, this parameter could not be tested statistically.

Water fractionation procedure

To establish the treatment media, a pooled series of water samples was collected daily from the upper half of the Lake Oglethorpe water column. Collections were made at a deep central station, using a 1-L PVC Kemmerer water bottle. Previous work had shown that these are the depths over which cladocerans vertically migrate during stratification and to which they tend to congregate during winter mixis, especially when surface waters are warming (J. Orcutt, *personal communication*).

The pooled water sample was returned to the lab and filtered through a 26-μm sieve to remove crustaceans and most of the rotifers. The sieved water constituted the "lake water" treatment. A portion of this was then centrifuged to remove large particles and filtered through a 0.22-μm Millipore filter. Filters were rinsed carefully in distilled water prior to filtration to remove any adhering detergents which might be toxic to cladocerans. Microscopic examination of the 0.22-μm filtrate indicated that all the algae were removed and that bacterial densities were similar to blank counts obtained with the acridine orange direct count method. The 0.22-μm filtrate constituted the "no-food" treatment.

To isolate bacteria from the rest of the plankton, lake water was filtered through a 1-μm Unipore filter. The quantity of bacteria passing through such a filter is a function both of the size of the bacteria and the volume of water filtered. Over the annual cycle of 1979, >90% of the bacteria were small cocci and rods <1 μm in maximum dimension as determined by quantitative direct counts (M. L. Pace, K. G. Porter, and Y. S. Feig, *personal observation*). Prior to each experiment, different volumes of lake water were filtered to determine what amounts could be size-fractioned before the filter began to clog and the efficiency of bacterial passage through the filter was reduced. Table 1 compares counts of unattached bacteria in the 1-μm filtrate to those of whole lake water for different filtration volumes. In winter the lake water was highly turbid (Secchi depths 0.5–1.0 m) due to the suspension of fine clay particles from watershed runoff and benthic mixing. The filters clogged rapidly under these circumstances. A 50-mL filtration volume was used for the experiment, which represented a compromise between drastically reduced bacterial densities in the filtrate and the constraints in obtaining enough filtered water (400 mL) each day for an experimental cohort. Similar results were obtained in the spring (data not shown). In summer the epilimnion of the lake clears (Secchi depths of 2–4 m), and at this time 100 mL passed through the filter with no detectable loss of bacteria (Table 1).

All algae were removed by a 1-μm filter, and microscopic examination of the filtrate indicated bacteria were the primary food resource in the 0.2–1.0 μm size-range. Fine inorganic and organic particles were also present but at relatively low concentrations.

For the enriched treatment, the green alga *Chlamydomonas reinhardi* (5.7 × 6.8 μm) was harvested from axenic log-phase cultures by centrifugation and then resuspended in lake water at 10^4 cells/mL. Concentrations were quantified by Sedgewick-Rafter counts.

TABLE 1. A comparison of counts of unattached bacteria in lake water and after passage through a 1-μm (Unipore) filter for different filtration volumes. Values ($\bar{x} \pm$ SE) are based upon acridine orange direct counts of bacteria in 10 fields of a single slide in the winter experiment and 10 fields of two slides ($n = 20$) in the summer experiment.

	Number of bacteria per field			
	Winter experiment			
		Volume filtered		
	Lake water	25 mL	50 mL	100 mL
$\bar{x} \pm 1$ SE	84.2 ± 7.4	76.6 ± 5.0	62.2 ± 3.8	29.1 ± 2.0
% in filtrate	...	91	74	35
	Summer experiment			
		Volume filtered		
	Lake water	100 mL	200 mL	
$\bar{x} + 1$ SE	102.9 ± 5.0	104.0 ± 5.1	clogging observed	
% in filtrate	...	100	no count	

Previous work in our laboratory has shown that *C. reinhardi* alone at 10^4 cells/mL will support cladoceran growth and reproduction (Porter and Orcutt 1980).

Feeding rates on bacteria

Feeding rates of *Daphnia* and *Ceriodaphnia* on bacteria were measured using the direct count method of Peterson et al. (1978). Four replicate groups of adults and juveniles of each species were sorted from cultures and placed in filtered lake water (0.22-μm filter) to remove any adhering bacteria. After 1 h the medium was replaced by drawing off the 0.22-μm filtrate and replacing it with freshly collected 1-μm lake water filtrate. Animals were allowed to feed for 2 h and then narcotized with carbonated water and preserved in a sucrose Formalin solution. A 1-mL subsample for bacterial counts was withdrawn from each feeding suspension at the beginning and end of the experiment. Samples were preserved in formalin and counted by the acridine orange direct count method. Experiments were run at room temperature (21–23°C) in glass vials (volume = 22 mL) containing 17–36 animals. Filtered lake water (1-μm filter) controls containing no animals were also sampled at 0 and 2 h to correct for any changes in bacterial concentrations not due to grazing. In a preliminary time course experiment (samples taken at 0.5, 1, 2, and 4 h) with *Daphnia parvula*, filtering rates were constant for 2 h and declined thereafter. A similar result was obtained by Peterson et al. (1978). Our preliminary work also indicated that animals placed in 0.22-μm filtrate of lake water did not increase bacterial concentrations above background levels.

Filtering rates were determined by the equation:

$$\text{mL}\cdot\text{animal}^{-1}\cdot\text{h}^{-1} = 1/t \times \ln(C_o/C_t) \times V/N,$$

where C_o and C_t are the initial and final bacterial concentrations, t is the time of the experiment, V is the volume of the feeding suspension, and N is the number of animals in the experimental container. Both C_o and C_t were corrected for blank counts of 0.22-μm-filtered lake water. Because bacteria increased 21% in the 1-μm lake-water filtrate containing no animals, C_o was adjusted in each experimental vial by the method of Frost (1972). Specific rates (microlitres filtered per microgram dry mass per hour) were also determined by replacing N in the above equation with M, the total mass of animals in the container. Masses were determined from length measurements of the preserved experimental animals, using the methods and length-mass regressions described in Pace and Orcutt (1981).

RESULTS

Lowest bacterial densities were observed during the winter experiment, with intermediate densities in the spring, and highest concentrations in the summer (Table 2). The winter and summer densities represent the extremes of bacterial concentration for the upper half of the Lake Oglethorpe water column (M. L. Pace, K. G. Porter, and Y. S. Feig, *personal observation*). Free bacteria (unattached to particles) accounted for 88% of the total bacteria in the winter and 94% in the spring and summer. These forms passed through a 1-μm filter and were the principal food for the cladocerans in the 1-μm-filtrate treatment. The average volume of planktonic bacterial cells is generally 0.05–0.10 μm^3 (Ferguson and Rublee 1976, Bowden 1977, Hobbie et al. 1977, Watson et al. 1977, Zimmerman 1977). The biomass of free bacteria available to zooplankton for the different experiments can be calculated by assuming a cell density of 1.07 g/mL, a dry- to wet-mass ratio of 0.23, and a carbon to dry-mass ratio of 0.5 (Bowden 1977, Watson et al. 1977). Calculated bacterial C biomasses were 8.6–17.2, 30.2–60.3, and 92.3–184.6 μg/L for the winter, spring, and summer experiments, given the above conversion factors and the range of mean cell volumes generally found. Threshold C concentrations of ≈50 μg/L of a suitable food resource

TABLE 2. Densities of attached, free, and total bacteria found in the upper half (0–3.5 m) of Lake Oglethorpe water column during the course of the life table experiments. $\bar{x} \pm 1$ SE; n = no. of sampling dates.

Experiment	Bacteria (cells/mL)			n
	Attached	Free	Total	
Winter	$1.8 \pm 0.23 \times 10^5$	$1.4 \pm 0.24 \times 10^6$	$1.6 \pm 0.25 \times 10^6$	4
Spring	$3.7 \pm 0.58 \times 10^5$	$4.9 \pm 0.36 \times 10^6$	$5.2 \pm 0.33 \times 10^6$	4
Summer	$6.0 \pm 0.12 \times 10^5$	$1.5 \pm 0.05 \times 10^7$	$1.6 \pm 0.04 \times 10^7$	10

are required by *Daphnia pulex* for growth (Lampert and Schober 1980). If bacteria were a suitable food resource for *Daphnia parvula*, the biomass available in the different experiments suggested that little or no growth would be expected in winter, threshold levels of growth would occur in spring, and substantial growth would be expected in summer.

Growth of Daphnia

It was not possible to measure growth in terms of change in body length from birth to death because neonates of these small cladocerans frequently became trapped in the surface film when measured. The body size of siblings of the neonates used in the experiments was measured (Table 3), and significant differences (ANOVA, $F = 13.5$, $P < .0001$) were observed among experiments, but within an experiment the coefficient of variation for the body size of sibling neonates was <12%. Because of this relatively low variation, we assumed that neonate size had little influence on final body size in an experiment, so that body size at death served as a measure of total growth.

For all three experiments, body size at death and hence growth rates in the enriched lake water (ELW) were significantly greater than in the lake water (LW) treatment, which was in turn greater than the 1-μm filtrate (OMF) treatment (Table 4). There was no difference in final body size between the no-food (NF) and OMF treatments for the winter experiments. The low concentrations of bacteria found at this time of year (Table 2) were insufficient for growth, unlike the spring and summer experiments where body size at death in the OMF treatment was significantly greater than NF (Table 4). Summer animals grown in the OMF treatment had a final body size 67% of that in the ELW. For the spring experiment, animals in the OMF grew to only 45% of the body size of ELW animals (Table 4).

Longevity and age-specific survivorship of Daphnia

Across experiments, the mean life spans of *Daphnia* reflected differences in the experimental temperatures, with summer animals having the shortest life spans and winter animals the longest (Table 5). Within an experiment, life spans were affected by food concentrations. A pattern similar to the growth results was observed for the mean life span of *Daphnia* in the OMF treatment. In the winter, mean life span in the OMF treatment was not significantly greater than in the NF treatment, while in the spring and summer, life spans in the OMF treatment were longer (Table 5).

Survivorship curves reflected the age-specific effects of the different treatments. In winter 20% of the LW cohort died during the first 22 d and after this point the LW and ELW curves were similar (Fig. 1a). The NF and OMF curves showed little difference except that 25% of the OMF cohort survived beyond the 9th d when the last animals in the NF treatment died (Fig. 1b).

In spring and summer, survivorship curves for the OMF treatment were intermediate between NF and the LW and ELW treatments (Fig. 1c, d). In the spring OMF treatment, there was a decline in mortality after an initially high rate, when over 30% of the cohort died in the first 6 d (Fig. 1c). In the summer experiment a similar pattern was observed. Over 30% of the cohort died in the first 4 d, and subsequently, mortality was more gradual, resembling the rate in the LW treatment (Fig. 1d).

Reproduction of Daphnia

In each experiment for the number of young produced per female, treatments were ranked by the Dunn multiple comparison test ($P < .05$) as follows: ELW > LW > OMF (Table 6). Reproduction was never observed in the NF treatment, and no reproduction occurred in the OMF treatment in the winter experiment. Reproduction in the OMF was generally poor, with two females producing a total of 7 young in the spring, and eight females producing a total of 21 young in the summer. Those females which survived to reproduce in the OMF treatment generally had two broods ($\bar{x} = 2.1$, $n = 10$ females).

TABLE 3. Body size (mm) of siblings of the neonates used in the experiments.

Experiment	n	$\bar{x} \pm 1$ SE
Winter	25	0.52 ± 0.006
Spring	22	0.49 ± 0.005
Summer	15	0.47 ± 0.005

TABLE 4. Body size at death (mm) for *Daphnia parvula* cohorts.

Treatment	Winter*		Spring†		Summer†	
	$\bar{x} \pm$ SE	n	$\bar{x} \pm$ SE	n	$\bar{x} \pm$ SE	n
No food (NF)	0.52 ± 0.009	21	0.49 ± 0.009	20	0.49 ± 0.013	24
1-μm lake-water filtrate (OMF)	0.53 ± 0.011	20	0.67 ± 0.039	18	0.73 ± 0.039	23
Lake water (LW)	1.22 ± 0.064	20	1.14 ± 0.042	19	0.99 ± 0.024	23
Enriched lake water (ELW)	1.50 ± 0.031	22	1.48 ± 0.059	20	1.09 ± 0.020	23

* ELW > LW > OMF = NF.
† ELW > LW > OMF > NF.

Population growth rates of Daphnia

The low rates of increase (r) observed in the winter experiment were due to slow development caused by the lower experimental temperature (8°C), as even in the ELW treatment rates of increase were low relative to the other experiments. In the spring and summer, high positive growth rates were observed in both the LW and ELW treatments (Table 7). The realized rates of increase in the OMF treatment were always less than zero, indicating that bacteria alone will not support population growth.

Utilization of bacteria by Ceriodaphnia

Ceriodaphnia utilized bacteria more effectively than did *Daphnia*. The OMF cohort had a positive rate of increase (r) (Table 8) at spring bacterial concentrations of 5×10^6 cells/mL (Table 2), indicating that *Ceriodaphnia* can survive and grow on bacteria alone. In the NF control all animals died within 3 d, without molting. Growth in OMF as measured by body size at death was 81 and 79% of the final size attained in the LW and ELW treatments, respectively. Relative growth by *Ceriodaphnia* in the OMF was substantially greater than that observed for *Daphnia* in the spring experiment where final body size in the OMF treatment was 59 and 45% of that observed in LW and ELW, respectively (Table 4). While bacteria are a sufficient resource to support growth in this species, food particles >1 μm are also important. In the LW treatment body size at death was larger, the life span longer, and the number of young per female greater than in the OMF treatment (Table 8).

Ceriodaphnia survivorship in the OMF treatment was initially high, unlike the case for *Daphnia* (Fig. 2). Eighty percent of the cohort survived through the first 11 d of the experiment. Subsequently, mortality was high, and there was a steep and nearly linear decline in cohort survival (Fig. 2).

Food limitation

In all three experiments, growth (Table 4) and reproduction (Table 6) of *Daphnia* were substantially greater in the ELW treatment relative to the LW treatment. Food concentrations then were always limiting in the field (defined as the difference between r values in LW and ELW treatments); however, in each experiment r for the LW cohort was greater than zero (Table 7). Field food concentrations were, therefore, sufficient to support population increase at all times of the year. Other factors must ultimately control the population dynamics of *Daphnia* in this lake.

The single experiment with *Ceriodaphnia* was started at a time when this population generally increases (J. Orcutt, *personal communication*), and food concentrations in the LW treatment were as expected sufficient to support high rates of population growth (Table 8). An unexpected result was the similar levels of growth and reproduction in the LW and ELW treatments (Table 8). The *Chlamydomonas* algae in the ELW treatment did have an enriching effect on the food supply, since earlier (Table 8) and higher initial rates of reproduction were observed in this treatment. However, life spans were shorter, and fewer broods were produced by animals in the ELW treatment (Table 8). The higher mortality of *Ceriodaphnia* in the ELW was not due to an anomaly in the algae culture, because algae from the same cultures were used to prepare the enriched treatment for both *Ceriodaphnia*

TABLE 5. Individual life span in days for *Daphnia parvula* cohorts.

Treatment	Winter*		Spring†		Summer‡	
	$\bar{x} \pm$ SE	n	$\bar{x} \pm$ SE	n	$\bar{x} \pm$ SE	n
No food (NF)	5.8 ± 0.34	21	3.6 ± 0.18	20	3.1 ± 0.29	24
1-μm lake-water filtrate (OMF)	7.1 ± 0.54	20	12.1 ± 2.07	18	8.6 ± 1.19	24
Lake water (LW)	62.1 ± 5.93	20	26.2 ± 2.70	19	12.4 ± 0.77	24
Enriched lake water (ELW)	89.9 ± 4.57	22	25.7 ± 2.32	20	15.8 ± 0.66	24

* ELW > LW > OMF = NF.
† ELW = LW > OMF = NF.
‡ ELW > LW > OMF > NF.

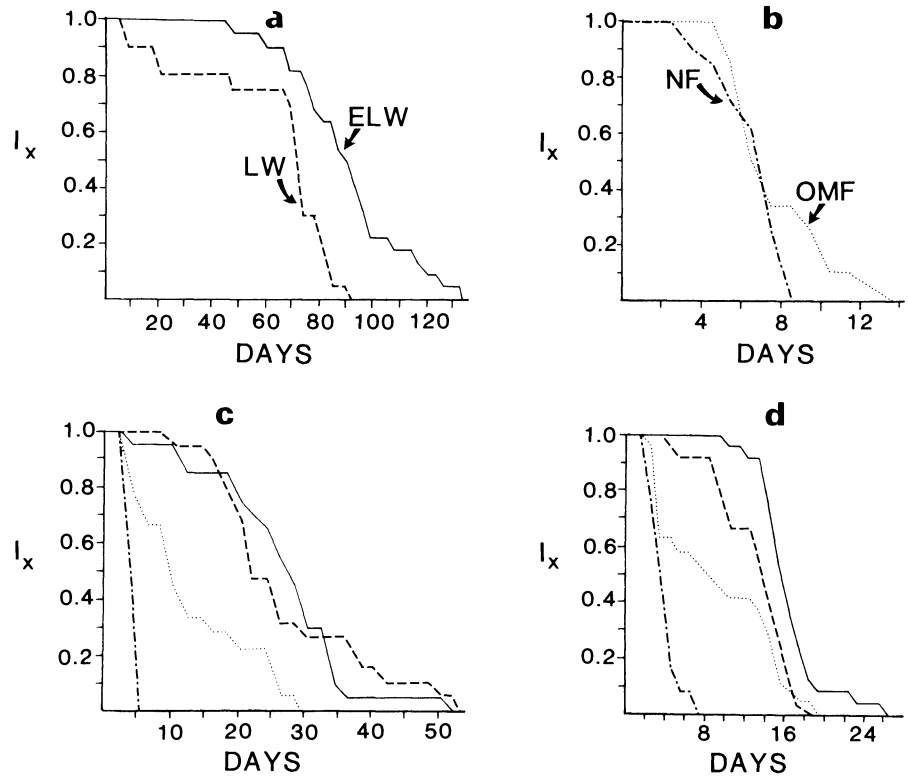

FIG. 1. Survivorship curves of *Daphnia parvula* cohorts for the (a and b) winter, (c) spring, and (d) summer experiments, where l_x is the proportion of the cohort surviving to age x (in days after birth). ELW equals the enriched lake water treatment, LW = lake water, OMF = 1-μm filtrate of lake water, and NF = no food.

and *Daphnia*. *Daphnia* in the spring experiment had similar life spans (Table 5) in the LW and ELW treatments and significantly more growth (Table 4) and reproduction (Table 6) in the ELW. Possible explanations of the reduced life span of *Ceriodaphnia* in the enriched treatment are that food size was too large or concentrations were too high, causing clogging of the feeding apparatus, high rates of rejection of collected food, higher energetic costs in feeding, and earlier mortality. The latter phenomenom has been documented for *Daphnia magna* at very high food concentrations in controlled laboratory experiments (Porter et al. 1982).

Feeding rates on bacteria

Results of the life table experiments suggested that *Ceriodaphnia* and particularly *Ceriodaphnia* juveniles might have higher feeding rates on bacteria than *Daphnia*. To test this hypothesis, we measured feeding rates on bacteria for four groups of animals sorted into juveniles (smaller than egg-bearing females) and adults (egg carrying females or individuals that are the same size as egg-bearing females). The sorting procedure resulted in a range of individual masses in each category, with a slight overlap between juveniles and adults (Table 9). Mass-specific filtering rates were highest for juvenile *Ceriodaphnia*; however, these animals were also smaller than the *Daphnia* juveniles (Table 9). *Daphnia* and *Ceriodaphnia* adults had similar masses and similar mass-specific filtering rates (Table 9). A regression of $\log_{10}$ dry mass vs. $\log_{10}$ filtering rate explained much of the variance ($r^2 = .85$). Analysis of covariance on the data adjusted for mass indicated that neither species ($F = 0.01$, $P > .9$), age ($F = 0.00$, $P > .9$), nor the interaction of species and age ($F = 0.13$, $P > .7$) was a significant factor in explaining the residual variance.

DISCUSSION

The results of the life table experiments falsify one aspect of the size-efficiency hypothesis (Brooks and Dodson 1965, Hall et al. 1976) by demonstrating differential utilization of resources <1 μm. Although differences in ingestion rates could not be detected, the smaller species *Ceriodaphnia* increased when it utilized only the bacterial size fraction, while *Daphnia* did not. These experimental results suggest an alternative mechanism for shifts in the size structure of zooplankton communities. If the size distribution and turnover rates of the resource base shift to an increased importance of smaller size fractions, then the ability of smaller species to exploit the predominate

TABLE 6. Total number of young produced per female for *Daphnia parvula* cohorts. n = number of females.

Treatment	Winter*		Spring*		Summer*	
	$\bar{x} \pm$ SE	n	$\bar{x} \pm$ SE	n	$\bar{x} \pm$ SE	n
1-μm filtrate (OMF)	0		0.4 ± 0.27	18	0.9 ± 0.30	24
Lake water (LW)	24.0 ± 3.46	20	23.5 ± 3.35	20	8.8 ± 0.99	24
Enriched lake water (ELW)	67.9 ± 7.41	22	66.3 ± 7.85	20	14.3 ± 0.81	24

* ELW > LW > OMF.

food could facilitate a shift in zooplankton community structure from larger to smaller forms. Selective predation by fish could also produce this pattern. One way to differentiate between these two mechanisms would be to examine the fecundity of individual species. If differential resource utilization explains the shift, decreased fecundity would be expected for larger species during succession. Fecundity should not decrease for larger species if predation is causing the shift.

Differences in feeding ability did not account for the differences observed between the two cladocerans in the life table experiments. Both species ingested bacteria at rates similar to those expected based on body mass alone. Many studies infer similarities and differences between consumers, from measures of niche overlap based on prey size utilization and relative ingestion rates (Gliwicz 1969, Pianka 1976, Poulet 1978, Richman et al. 1980). However, the best evidence of resource utilization abilities comes from studies that demonstrate whether species can actually grow and reproduce on a given set of resources. If we had simply measured bacteria concentrations and feeding rates of *Ceriodaphnia* and *Daphnia*, we would have concluded that bacteria concentrations and filtering rates were sufficient to support both species for roughly half of the year (May to October).

The differential ability of *Ceriodaphnia* to use bacteria also allows an alternative explanation for the mechanism of competitive dominance described in a previous study. Lynch (1978) found that *Ceriodaphnia reticulata* replaced *Daphnia pulex* during the summer in a small Minnesota pond. *Ceriodaphnia* appeared to survive better at low food concentrations, and *Daphnia* juveniles were sensitive to the food concentration depression caused by *Ceriodaphnia*. Results of an enclosure experiment at the time of the replacement supported this explanation. Lynch, however, did not consider small bacteria (<1 μm), because they were not resolved by the light microscopy technique he used to count bacteria and algae. A sufficient biomass was probably available in the bacterial size fraction of this productive pond (Lynch and Shapiro 1981) to favor *Ceriodaphnia*, thereby allowing it to out-survive rather than to exclude competitively *Daphnia* at what appeared to be low food concentrations.

Within a species our hypothesis was that age and, therefore, size would also be related to the ability to use smaller food particles. The shape of the survivorship curves for the OMF cohorts was used as a test of this hypothesis. *Ceriodaphnia* conformed to the prediction, while *Daphnia* did not. In all three experiments juvenile *Daphnia* had high mortality rates, while mortality rates were lower for the portion of the cohort which survived beyond this initial critical phase. Other studies have demonstrated that juvenile *Daphnia* are particularly susceptible to food-limiting conditions (Neill 1975, Lynch 1978, Goulden and Hornig 1980). For *Ceriodaphnia* juveniles survivorship was high. All but one animal in the experimental cohort survived to the third instar. Mortality rates increased for older and larger animals (Fig. 2), suggesting a shift in the size of food particles required for further growth. Differences in feeding rates between juveniles and adults did not account for these results, as age was not a significant factor in determining bacterial filtering rates. This result implies that *Ceriodaphnia* juveniles had a higher efficiency of resource utilization at the same rate of ingestion relative to the other age-classes.

Age-specific differences such as the one for *Ceriodaphnia* should be considered in evaluating patterns of resource utilization. Theoretical models of biotic interactions (competition, mutualism, predation) do not normally include age (see summaries in Maynard-Smith 1974, Roughgarden 1979). Experimental studies of zooplankton indicate that age structure is important in determining the course of species interactions (Neill 1975, Lynch 1978).

Natural food concentrations were always less than optimal for *Daphnia parvula* based on the comparisons of the LW and ELW treatments. Food levels, however, were well above threshold concentrations required for growth and reproduction. Similar results were obtained by Hrbáčkova-Esslova (1963) for two species of *Daphnia* grown in natural and enriched lake water. Weglenska (1971) did not observe any increase

TABLE 7. Realized rate of increase r (d^{-1}) for *Daphnia parvula* cohorts.

Treatment	Winter r	Spring r	Summer r
1-μm filtrate (OMF)	···	−0.046	−0.013
Lake water (LW)	0.086	0.235	0.335
Enriched lake water (ELW)	0.122	0.365	0.377

in cladoceran growth rates when she compared animals raised in natural food to animals grown in concentrated natural food. Apparently, the animals in this eutrophic lake were not food limited at the time of her experiments. Natural food concentrations also supported substantial growth and reproduction throughout the summer for two species of *Daphnia* incubated in situ in Wintergreen Lake (Threlkeld 1979).

In the experiments of Hrbáčkova-Esslova (1963), Weglenska (1971), Threlkeld (1979), and the present study, animals were transferred to fresh feeding suspensions daily to maintain concentrations and compositions as close to in situ levels as possible. However, some settling occurred, and consequently, increased concentrations of particles were available at the bottom of the vessels during the 24-h period. While planktonic bacteria (0.5–0.8 μm) settle at a rate of only $\approx$1 mm/d (Jassby 1975), average in situ settling rates of 7–32 cm/d have been measured for phytoplankton, and detritus settles at even faster rates (Burns and Rosa 1980). In addition, some cladocerans, when confined in containers, spend more time in the bottom, especially at lower food concentrations (Burns 1969, Horton et al. 1979). Animals in the LW treatment probably experienced food concentrations that were higher than in situ, and this treatment would then underestimate the degree of food limitation. Despite this underestimation, the results of our study and those cited above provide evidence that food concentrations do not cause the population declines of cladocerans in these lakes; however, all the experiments were conducted in lakes which range from meso-eutrophic (Oglethorpe) to hypereutrophic (Wintergreen). In more oligotrophic systems, food limitation is probably an important factor for cladoceran populations.

The ability of *Daphnia* to survive, grow, and reproduce on bacteria increased with an increase in the in situ concentrations of bacteria. The result supported our third hypothesis that the trophic link between bacteria and zooplankton is a dynamic one depending partly on the abundance of bacteria. However, the direct linkage between *Daphnia* and bacteria is weak.

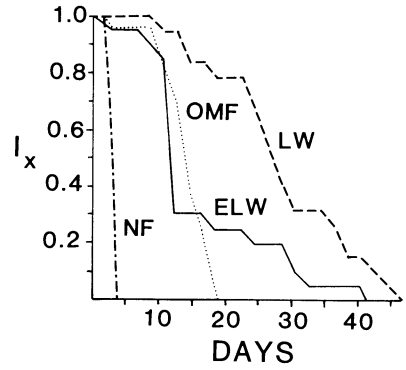

FIG. 2. Survivorship curves of *Ceriodaphnia reticulata* cohorts for the spring experiment, where l_x is the proportion of the cohort surviving to age x (in days after birth). ELW equals the enriched lake water treatment, LW = lake water, OMF = 1-μm filtrate of lake water, and NF = no food.

Biomass estimates made from direct counts indicated that sufficient carbon (92–185 μg/L) was present in the bacterial fraction during summer to support population growth. The negative rate of increase (r) for the *Daphnia* cohort indicated that even at a high biomass this resource is not sufficient for the population. For a species like *Daphnia* alternative trophic pathways mediated by planktonic protozoa may link bacterial production to zooplankton production (Porter et al. 1979, Pace and Orcutt 1981).

The significance of bacterial resources increases during the course of seasonal succession (this study) and from oligotrophic to eutrophic lakes (Gliwicz 1969). It has been hypothesized that the principle food web pathways change accordingly, with detritus and bacteria forming the resource base of the system (Nauwerck 1963, Gliwicz 1969, Hillbrict-Ilkowska and Weglenska 1970, Saunders 1972, Sprules 1980). However, across lakes, variations in phytoplankton biomass and especially nannoplankton biomass explain a substantial amount of the variation observed in crustacean zooplankton biomass (McCauley and Kalff 1981), suggesting to these workers the alternative hy-

TABLE 8. Life table results for the spring experiment with *Ceriodaphnia lacustris*. Data are means ± SE.

Treatment	n	Body size at* death (mm)	Life span† (d)	No. of young* per female	Age at first‡ reproduction (d)	No. of broods§	r (d^{-1})
No food (NF)	20	0.30 ± 0.004	2.2 ± 0.11	0	...	...	...
1-μm filtrate (OMF)	20	0.60 ± 0.012	13.9 ± 0.91	2.2 ± 0.49	9.1 ± 0.48‖	1.5 ± 0.32	0.070
Lake water (LW)	19	0.74 ± 0.018	28.7 ± 2.37	19.8 ± 1.68	6.9 ± 0.12	6.6 ± 0.57	0.242
Enriched lake water (ELW)	20	0.76 ± 0.022	16.5 ± 2.20	16.6 ± 1.95	6.3 ± 0.16¶	3.7 ± 0.50	0.312

* ELW = LW > OMF > NF.
† LW > ELW = OMF > NF.
‡ ELW < LW < OMF.
§ LW > ELW > OMF.
‖ n = 15.
¶ n = 19.

TABLE 9. Filtering rates of *Daphnia parvula* and *Ceriodaphnia lacustris* fed bacteria ($\bar{x} \pm 1$ SE, $n = 4$).

Species	Age	Mean and range of individual masses (μg dry mass)	Filtering rate (mL·animal·h^{-1})	Specific filtering rates (μL·μg^{-1}·h^{-1})
Ceriodaphnia	Juvenile	0.85 (0.27–2.96)	0.13 ± 0.02	152 ± 20.3
Daphnia	Juvenile	1.76 (0.75–3.81)	0.19 ± 0.01	110 ± 4.7
Ceriodaphnia	Adult	4.34 (2.04–9.88)	0.28 ± 0.01	65 ± 4.9
Daphnia	Adult	4.46 (3.36–8.69)	0.31 ± 0.03	68 ± 5.0

pothesis that bacteria and detritus may not be particularly important food resources. A similar dicotomy of viewpoints is found among marine ecologists (Pomeroy 1974, 1977). Clarification will come from further experiments that manipulate natural bacteria, detritus, and their micro- (ciliates and rotifers) and macro- (crustacean) consumers.

While this study has emphasized the differences between the two species of zooplankton, some degree of species aggregation into functional groups is frequently the only way to examine communities and food webs. Body size was closely related to differences in resource utilization for the two species considered here. Community and food web theory may benefit from models that are organized on the basis of body size rather than species (see, for example, Hall et al. 1976, Peters 1978, Cousins 1980). The dynamic aspects of web structure also require consideration. For zooplankton the strength of the trophic linkage with bacteria will vary both with the abundance of bacteria and the size structure of the zooplankton community.

ACKNOWLEDGMENTS

This research was supported by grant DEB-8005582 from the National Science Foundation to K. G. Porter and a graduate fellowship to M. L. Pace from the University of Georgia. We would like to thank Judy Meyer and Gene Helfman for their many cups of coffee, early-morning discussions, and on-site support. A. Hooten and G. Rogers provided technical assistance, and S. Stewart aided in numerical analysis and programming. This paper benefitted from discussions with J. Orcutt and E. McCauley. It is contribution 11 to the Lake Oglethrope Limnological Association (LOLA).

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