

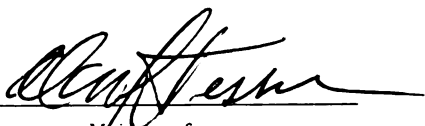
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Performance trade-offs across a natural resource gradient

By

Kristen H. Desmarais

A THESIS

**Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of**

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ABSTRACT

Performance Trade-offs Across a Natural Resource Gradient

By

Kristen H. Desmarais

Smaller-bodied zooplankters are commonly found in the surface waters of lakes inhabited by warm-water planktivorous fish. The typical explanation for this pattern is that small-bodied species are more resistant to predation risk. Though vertebrate planktivory is undoubtedly an important factor explaining this pattern, resources (competition) may also be important.

I compared Daphniidae species inhabiting lakes with expected differences in resource availability in two reciprocal transplant experiments. Laboratory life tables were used in order to measure fitness while still accessing changes in the components of fitness. Natural resources were utilized to achieve a more representative response than high quality laboratory food. The primary result of these experiments was that species inhabiting lakes that differ in resource availability exhibited a performance trade-off across a natural resource gradient. This trade-off can be generally expressed as differential sensitivity to resource change, possibly due to differential adaptation to resource quality.

To Mom and Dad

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PREFACE

Smaller bodied zooplankton species are typically found in the surface waters of lakes inhabited by warm-water fish planktivores. The general explanation for the dominance of small-bodied zooplankton involves an inverse relationship (trade-off) between vulnerability to fish predation and competitive ability (i.e. size selective predation and the size-efficiency hypothesis (SEH); Hrbáček et al. 1961, Brooks and Dodson 1965, Hall et al. 1976). Small adult body size and lack of pigmentation allow small zooplankton taxa to withstand size-selective vertebrate planktivory better than larger species which, according to the SEH, are better competitors and would dominate in the absence of vertebrate predation.

The restriction of size-selective fish planktivores to the warm water mixing zone allows zooplankton to reduce mortality by diel vertical migration (DVM) into the deep-water refuge during the day (Wright and Shapiro 1990, Tessier and Welser 1991). Thus, lake depth (refuge availability) and zooplankton community body-size are correlated (Tessier and Welser 1991) which could be interpreted as the product of a gradient in warm-water fish planktivory. The largest, most visible species are found in low fish planktivory environments such as the deeper waters of lakes (e.g. *D. pulicaria*, Leibold and Tessier 1991). Smaller species of *Daphnia* (e.g. *D. rosea*, *D. retrocurva*) are found in the surface waters of deep lakes and migrate into the deep-water refuge during the

day. The smallest, least visible zooplankton species (e.g. small *Daphnia*, *Bosmina*, *Ceriodaphnia*) are found in shallow lakes with no refuge.

Though vertebrate planktivory is undoubtedly an important factor in this observed distribution pattern, other factors (e.g. resources-competition, abiotic factors, parasitism) may influence this pattern. Resources were of particular interest to me for two reasons. First, differences in predation risk should also be related to resource differences. That is, in low predation risk environments, low mortality of zooplankton should result in intense competition for few resources while the opposite should be true under high predation environments (high mortality, low competition, high resources). Resources also differently affect the outcome of competition between species of zooplankton, implying that some species are adapted to compete well in a low resource environment and do not perform as well in a higher resource environment (Romanovsky and Feniova 1985, Tessier and Goulden 1987, Bengtsson 1987). Extensive laboratory research documents the effects of resource richness on zooplankton (especially *Daphnia*) life histories (e.g. Richman 1958, Arnold 1971, Schwartz and Ballinger 1980, Lynch 1989, Vanni and Lampert 1993), and there is evidence that the response can vary significantly among species (Hrbáčková and Hrbáček 1976, Infante and Litt 1992). Given that variation in resource richness can affect species differently, it is likely that resources could have an effect on the distribution of the dominant Daphniidae species. Thus, I was interested in how the life history of Daphniidae species typically inhabiting environments of different predation risk and hence likely different resource environments would compare. Specifically, would species display performance trade-offs in adaptation to their resource condition in parallel to body-size adaptations to the predation risk condition?

The thesis contains two major chapters, a final synthesis, and two appendices.

Chapter 1 is a preliminary examination of how natural resources in lakes that differ in the presence or absence of a major fish planktivore, the blue-gill (*Lepomis macrochirus*), affect the life-history performance of *Daphnia*. The size-selectivity and size-efficiency hypotheses utilized to explain the distribution of *Daphnia* species makes a simple prediction. In the absence of vertebrate predation, the larger bodied *Daphnia* species (better competitor) should be capable of invading (e.g. instantaneous growth rate (r) > 0) the epilimnion of lakes. However, if resources are an important factor influencing zooplankton distributions, then the larger bodied species may not perform well (e.g. $r < 0$) in the epilimnion resource.

Life tables were conducted in the laboratory using the natural resources from Lawrence Lake (planktivore present; *D. rosea*, small-bodies species; low resources) and Wintergreen Lake (planktivore absent; *D. pulex*, large-bodied species; high resources) to compare the performance of the respective *Daphnia* inhabitants in a reciprocal transplant design. The use of life tables allowed me to quantify fitness (as measured by r) while accessing changes in the components of fitness (survivorship, fecundity, time to maturity, and growth). Thus, I used r as a summary measure of performance and could mechanistically explain between lake differences using the life history components. The results of this experiment suggested the presence of a performance trade-off between species (smaller-bodied species performed better in lower resources compared to the larger bodied species, while the opposite was true at higher resources).

Chapter 2 contains a more general examination of how low and high fish planktivory can affect resource richness and the adaptation of species to this resource

richness gradient. This chapter was done in collaboration with my advisor, Alan Tessier. We explore four lakes that represent two classes of lake depth (and thus the presence or absence of a refuge) and quantify phytoplankton resource availability and compare life history performance of the dominant daphniids from these lakes. Laboratory life tables and natural resources were utilized in a reciprocal transplant design to mechanistically explain across-resource life history differences. A performance trade-off was again observed but its relation to body-size was opposite of that suggested by Chapter 1. A final synthesis attempts to combine chapters 1 and 2 into a general perspective for comparison with the SEH.

Appendix A contains the research I did to validate a previously untested methodology needed to conduct my life table research. The species of *Daphnia* I chose to use as a representative deep lake migratory form is difficult to examine in the laboratory due to a tendency to become trapped in the surface film. Though the exact cause of this entrapment is unclear, it seems to be related to both behavior (migratory) and morphometry (laterally flattened and helmeted, Wesenberg-Lund 1926). The surface film culturing problem I encountered seems to be a general problem which could greatly affect our perception of zooplankton life history. This appendix examines how different levels of cetyl alcohol affect the performance of two *Daphnia* species, one typically susceptible (*D. rosea*) and a species not susceptible (*D. pulicaria*) to surface film entrapment.

Appendix B contains the bootstrapping program used to generate the 95% confidence intervals for the instantaneous growth and net reproductive rates. This appendix also contains a detailed description of how to use the program, how to set up the necessary data file (with an example), and a line-by-line description of the program.

CHAPTER 1

Performance trade-offs between *Daphnia* from low and high productivity habitats

INTRODUCTION

Species of the genus *Daphnia* are typically the most important herbivores in the limnetic zones of temperate lakes during the summer. Populations of *Daphnia rosea*, their close relatives, and other small zooplankton, typically dominate the epilimnion of lakes throughout the summer in the northern U.S. and southern Canada (Tessier and Welser 1991, Gliwicz and Pijanowska 1989). The general explanation for this pattern is that small adult body size and lack of pigmentation allow these taxa to withstand vertebrate planktivory in the epilimnion better than larger and more visible species (Hrbáček 1961, Brooks and Dodson 1965, Hall et al. 1976). Larger bodied species of *Daphnia* are also common in this region, but are typically found in small ponds (e.g. *D. pulex*, Brooks 1957) or the deeper waters of lakes (e.g. *D. pulicaria*, Leibold and Tessier 1991), these habitats are both lower planktivory habitats compared to the epilimnion of lakes (Wright and Shapiro 1990).

Though vertebrate planktivory is the common explanation for this observed distribution pattern, other factors (e.g. competition for resources, abiotic factors, parasitism) may contribute to this pattern. Resource are of particular interest because resource levels have been shown to differently affect the outcome of competition between

species of zooplankton (Goulden et al. 1982, Romanovsky and Feniova 1985, Tessier and Goulden 1987, Bengtsson 1987). Generally, in these competition experiments, the larger species outcompeted the smaller species under high resources but the opposite occurred in low resources. Thus, resource levels could have an effect on the distribution of the dominant *Daphnia* species in lakes.

The predator hypothesis explaining the distribution of *Daphnia* species makes a simple prediction. In the absence of vertebrate predation, the larger bodied *Daphnia* species should be capable of invading the epilimnion of lakes because they are believed to be better competitors. However, if resources are an important factor influencing zooplankton distributions, then the larger bodied species may not be able to invade (e.g. negative r) the epilimnion. In addition, if a species is adapted to the resource assemblage from which it was collected, then another species from a very different resource habitat should do poorly in comparison.

To test the predictions of this resource hypothesis, I compared the performance of an unusual population of *D. pulex* from Wintergreen Lake in southwestern Michigan which behaved similarly (e.g. dominated the epilimnion) as the typical population of *D. rosea*, represented by the Lawrence Lake population. Life tables were conducted in the laboratory using the natural resources from each lake in a reciprocal transplant design. The use of life tables allowed me to quantify fitness as measured by the instantaneous growth rate (r) while still accessing changes in the components of fitness (survivorship, fecundity, time to maturity, and growth). Thus, I used r as a composite measure of performance and could mechanistically explain across-resource changes using the life history components.

BACKGROUND

Lawrence Lake and Wintergreen Lake are small, dimictic, hardwater, glacial lakes located within 5 km of the W. K. Kellogg Biological Station in southwest Michigan. Lawrence Lake is oligotrophic (total phosphorus at turnover = $9 \mu\text{g L}^{-1}$), having a phytoplankton assemblage dominated by diatoms and flagellates (Taylor and Wetzel 1988). In contrast, Wintergreen Lake is hypereutrophic (total phosphorus at turnover $>300 \mu\text{g L}^{-1}$) due to high nutrient loading from migratory Canada Geese (Manny et al. 1975) with a phytoplankton assemblage rich in filamentous blue-green algae (personal observation). The summer mixing zone in both lakes is three to four meters. Additional limnological details about these lakes can be found in Wetzel (1983) and Threlkeld (1977).

The summer zooplankton in both lakes is dominated by the genus *Daphnia* (Leibold 1988, 1991; Mittelbach et al. 1995). Two *Daphnia* species vertically partition the available depth habitats in each lake. In Lawrence Lake, *Daphnia rosea* is found in the metalimnion during the day and migrates up to the epilimnion at night. I refer to this population as *D. rosea*, but its actual taxonomic affinity in the *D. galeata* complex is unclear (Taylor and Hebert 1993). In contrast, *D. pulicaria* largely remains in the hypolimnion both day and night (Leibold 1988). In Wintergreen Lake, a population of hybrid *D. pulex* x *D. pulicaria* coexist with *D. pulicaria*. These two forms are phenotypically similar but are distinguishable by electrophoresis at the Ldh locus (Hebert et al. 1989). I refer to this hybrid as *D. pulex* (Loaring and Hebert 1981). In Wintergreen Lake, *D. pulex* occupies a niche similar to that of *D. rosea*; it is largely restricted to the shallow mixing zone. The *D. pulicaria* in Wintergreen Lake are more abundant in the deeper water as in Lawrence Lake (Tessier, unpublished data).

Although the major limnological difference in these lakes is their trophic status, they also differ in their planktivory levels. The major fish planktivore in Lawrence Lake is the bluegill sunfish (*Lepomis macrochirus*) which forages actively on *D. rosea* (Mittelbach 1981). In contrast, Wintergreen Lake has no effective vertebrate planktivore due to winterkill and subsequent manipulations of the fish fauna (Mittelbach et al. 1995, Hall and Ehlinger 1989). However, Wintergreen Lake does have abundant populations of invertebrate predators, particularly *Chaoborus punctipennis* and *C. albiens*.

The most common explanation for why *D. pulex* is not in Lawrence Lake would be that it is excluded by size-selective fish predation, being larger and more pigmented than *D. rosea* (Zaret 1980). An alternative explanation is that *D. pulex* is outcompeted by *D. rosea*. Additionally, there is the reciprocal question of why *D. rosea* is not common in Wintergreen Lake. Hence, by studying zooplankton performance in these lake resources: Lawrence (oligotrophic, moderate planktivory) and Wintergreen (eutrophic, negligible planktivory), I was able to examine the potential importance of resource based mechanisms in structuring the species composition in the epilimnetic habitat.

METHODS

I conducted a reciprocal transplant experiment using epilimnetic water from the two lakes and isolates of the two species, *D. rosea* and *D. pulex*, collected from each lake. Four life tables, representing each species raised in each lake water, were started simultaneously on 14 July, 1994 with forty individuals each, and monitored until the death of all individuals. Most *D. rosea* individuals became trapped in the surface film of the Lawrence Lake water and 50% died within three days. The *D. pulex* displayed no surface

film problems. I repeated the life table for both species in the Lawrence Lake water resource starting on 1 August 1994 and continued until 20 August 1994. I added a small amount of cetyl alcohol to both of these August life tables, which prevented all surface film problems. In low concentrations, cetyl alcohol, a surfactant, does not inhibit fecundity or survivorship of *Daphnia* (Appendix A).

The *D. pulex* were gathered on 27 June at 2200 hours from the epilimnion (0-2m) of Wintergreen Lake using a Schindler-Patalas trap. Forty-five adult *Daphnia* were haphazardly chosen, to prevent a size bias in the clones selected, and placed into beakers containing high concentrations of the green algae *Ankistrodesmus falcatus*. I did acetate gel electrophoresis on all animals that reproduced to distinguish *D. pulex* from *D. pulicaria*; nine isolates of *D. pulex* were identified. The *D. rosea* were gathered on 11 July at 2200 hours from the epilimnion (0-4m) of Lawrence Lake with a conical net. Approximately 100 *D. rosea* adults were haphazardly chosen and placed into 250 ml flasks. These *D. pulex* and *D. rosea* were cultured under standard laboratory conditions (Tessier and Consolatti 1989). Food levels were kept high (50,000 cells *A. falcatus* ml⁻¹ day⁻¹) and the algal water was a filtered 1:1 mixture of two other lakes.

Both the July and August life tables were started by placing neonates of both species (<1 day old) individually into 150 ml beakers containing 100 ml of either the Lawrence or Wintergreen epilimnion water resource. Animals were incubated at 24°C with a light cycle of 16:8 L:D to reflect the summer epilimnetic conditions in these lakes. I collected epilimnetic water every morning from approximately 0.5 m below the waters' surface at a central location in each lake with a 20 L polyethylene carboy. Lake water was then screened through an 80 µm mesh to remove zooplankton and dispensed to beakers.

Individuals were transferred using a wide bore pipette. The 100 ml of water resource was gradually increased to a maximum of 150 ml as the animals grew. Glassware was rinsed every day and washed every third day.

Animals were examined daily for individual survival, number of offspring produced, and molts. Molted carapaces were measured from the base of the tail spine across the longest length of the carapace using a Wild Stereoscope at 25x or 50x magnification.

The statistical analyses were run using the August Lawrence Lake life table data for both species, unless otherwise noted, and the July Wintergreen Lake life table data for both species. The product-limit method of SAS (SAS 1989) procedure Lifetest was used to test for age-specific survivorship (l_x) and time to maturity differences using the Log-rank and Wilcoxon tests, because failure-time data are non-normally distributed (Fox 1993). Analyses of variance (ANOVA) were run on carapace growth rate, length on days 12 and 13, and number of molts produced by day 10, using SYSTAT (Wilkinson 1992) with treatments lake and species as fixed effects. ANOVA assumptions were met. If a significant two-way interaction occurred, specific contrasts were run using the overall ANOVA error term. To quantify carapace growth rate, for each animal I calculated the model I regression slope for carapace length as a function of age (in days) after first transforming both variables to natural logarithms to achieve linearity.

The instantaneous rate of increase, r (d^{-1}), was iterated for each life table using a variation of Newton's approximation and the stable age equation (Lotka 1956):

$$1 = \sum l_x m_x e^{-rx}.$$

The net reproductive rate (R_0) was also calculated:

$$R_0 = \sum (l_x m_x).$$

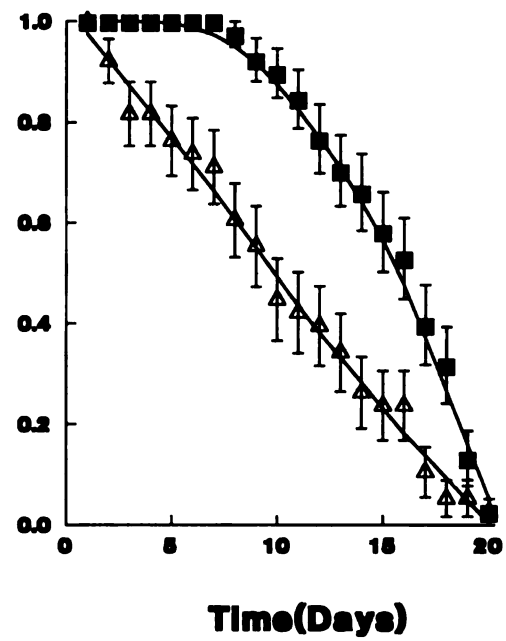
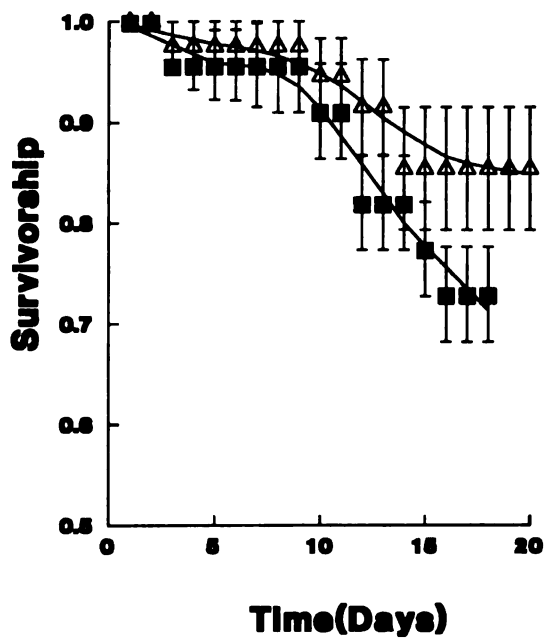
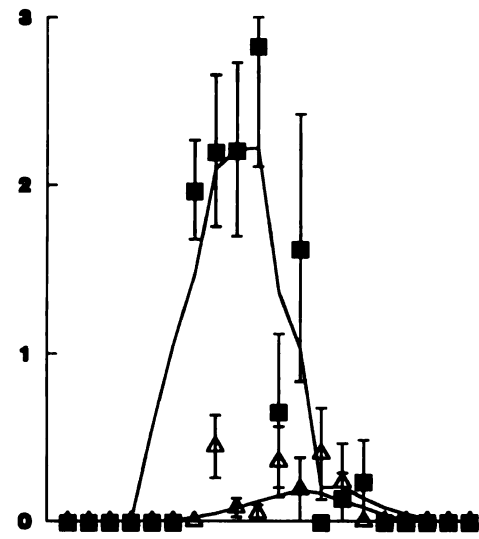
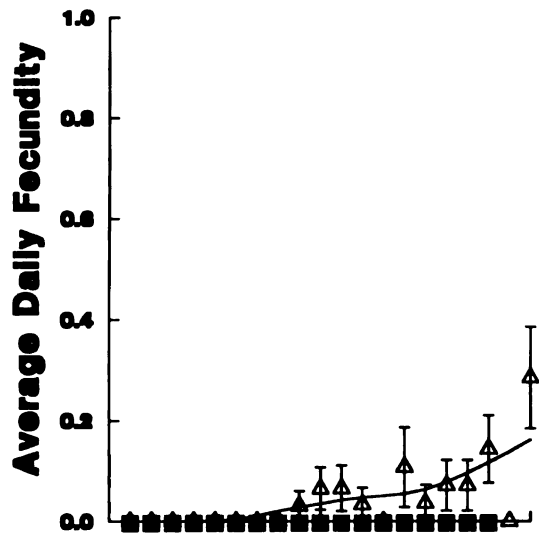
I wrote a SAS macro program to bootstrap the 95% confidence intervals around both r and R_0 with 1,000 re-samples of 40 randomly chosen individuals with replacement (Appendix B). A copy of the SAS program is available from me or via the internet at <http://kbs.msu.edu/~desmarais/bootstrap.html>.

RESULTS

There was no significant difference between the survivorship of *D. rosea* and *D. pulex* in Lawrence Lake through day 18 (df=1, Log rank chi-square=1.36, P=0.24) when survivorships exceeded 70% (Figure 1). In addition, survivorship in the two Lawrence Lake *D. pulex* life tables (July vs. August) was not significantly different (df=1, Log rank $\chi^2=1.22$, P=0.27). In contrast, the two Wintergreen Lake life table populations had almost 0% survivorship by day 18 (Figure 1). *Daphnia pulex* exhibited a higher survivorship than *D. rosea* throughout the Wintergreen life table (Log rank $\chi^2=13.69$, df=1, P<0.00, Figure 1) primarily due to higher juvenile survivorship (Table 1).

In Lawrence Lake, daily fecundity was low and time to maturity was long compared to Wintergreen Lake (Figure 1). In Lawrence Lake, *D. rosea* produced up to four clutches of 1-2 individuals during the three weeks of the experiment, while *D. pulex* never reproduced (Figure 1). Note that in the July Lawrence life table, three *D. pulex* produced a clutch of one neonate with an average ($\pm$ SE) time to maturity of 17.66 ± 1.73 ,

Figure 1 Average daily fecundity (neonates female⁻¹, upper) and survivorship (lower) of both species in Lawrence (left) and Wintergreen (right) lakes. All error bars indicate ± 1 standard error unless otherwise noted. Symbols: open triangle=*D. rosea* and closed square=*D. pulex*.



still significantly less than the time to maturity of the August *D. rosea* life tables ($df=1$, Chi-square=21.65, $P=0.001$). In Wintergreen Lake water, *D. pulex* produced up to 5 clutches of 3-14 neonates and over 95% of the individuals reproduced. In comparison, *D. rosea* in Wintergreen Lake water produced up to two clutches of 1-3 neonates and only 25% of the individuals reproduced. In addition, *D. pulex* matured significantly earlier than *D. rosea* in Wintergreen Lake water (Table 3; $df=1$, $\chi^2=50.56$, $P=0.0001$).

The instantaneous rate of increase (r) of both *Daphnia* species in Lawrence Lake indicated that it was the poorer of the two water resources (Figure 2). Both species had their best relative performance when raised in the lake water from which it was collected (Figure 2). While *D. rosea* had an r that was not different from zero in both lakes; *D. pulex* did not reproduce in Lawrence Lake ($r = -\infty$), but had an $r = 0.265$ in Wintergreen Lake. Because the Lawrence Lake life tables were ended on day 18 without *D. pulex* reproducing, a realistic maximum possible r after this date (e.g.: if one *D. pulex* reproduced the next day) would be -0.157day^{-1} , still less than that of *D. rosea*. In addition, note that the July Lawrence *D. pulex* had an $r = -0.140$, again less than that of the Lawrence *D. rosea*. Hence, *D. pulex* was very sensitive to the resource change while *D. rosea* was quite insensitive in overall performance. Examination of an alternate summary measure of performance, net reproductive rate (R_0), qualitatively revealed the same pattern (Figure 2).

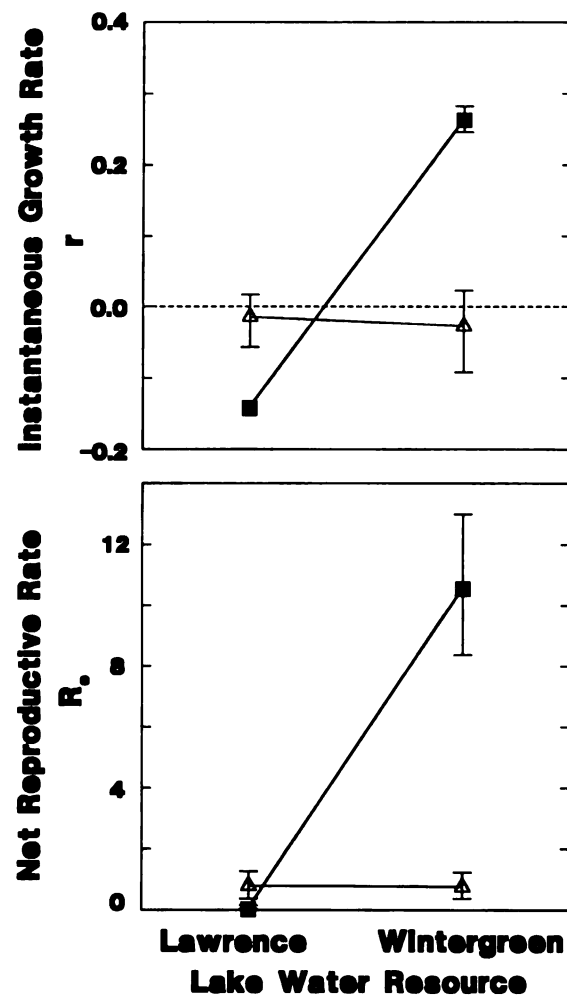


Figure 2 Adjusted bootstrapped estimates of r (upper) or R_0 (lower) values (day^{-1}) for both species in Lawrence and Wintergreen lakes, except for the *D. pulex* r in Lawrence Lake (see text). Error bars are bootstrapped 95% confidence intervals. Symbols as in Figure 1.

Table 1 Summary statistics for the reciprocal transplant experiment using Wintergreen and Lawrence lake water. Values are means $\pm$ standard errors, with sample size in parenthesis.

	Lawrence <i>Daphnia rosea</i>	Lawrence <i>Daphnia pulex</i>	Wintergreen <i>Daphnia rosea</i>	Wintergreen <i>Daphnia pulex</i>
Time to maturity (days)	15.00 $\pm$ 1.16(14)	-----	8.27 $\pm$ 0.52(11)	6.55 $\pm$ 0.12(39)
Percent Matured	35%	0.0%	27.5%	97.5%
Length of Molt at maturity (mm)	1.03 $\pm$ 0.01(5)	1.28 $\pm$ 0.03(16)	1.04 $\pm$ 0.06(6)	1.40 $\pm$ 0.01(18)
Molt length on days 12&13 (mm)	1.06 $\pm$ 0.02(17)	1.10 $\pm$ 0.05(10)	1.23 $\pm$ 0.02(14)	1.81 $\pm$ 0.02(20)
Number of molts produced by day 10	5.00 $\pm$ 0.15(31)	5.24 $\pm$ 0.14(21)	5.24 $\pm$ 0.18(17)	5.80 $\pm$ 0.10(35)
Juvenile Survivorship	93.9%	89.8%	57.5%	100%

Table 2 Results from the reciprocal transplant experiment in Lawrence and Wintergreen lake water of two-way analysis of variance with factors lake and species and specific contrasts.

	Length on Day 12&13 $r^2 = 0.923$			Number of molts by Day 10 $r^2 = 0.190$			Growth Rate (summarized as slope) $r^2 = 0.560$		
2-way Anova	df	F	P	df	F	P	df	F	P
Lake	1	294	0.00	1	7.84	0.01	1	113	0.00
Species	1	142	0.00	1	7.95	0.01	1	0.43	0.51
Lake*Species	1	106	0.00	1	1.32	0.25	1	11.7	0.00
Specific Contrasts									
1 -1 0 0	1	1.15	0.29	-----			1	7.84	0.01
0 0 1 -1	1	285	0.00	-----			1	4.08	0.05
1 0 -1 0	1	25.2	0.00	-----			1	27.0	0.01
0 1 0 -1	1	352	0.00	-----			1	96.9	0.00

There was a significant interaction between species and lake in growth rate (Figure 3; $df=1$, $F=11.72$ $P<0.00$, Table 2). In the Lawrence Lake water, *D. rosea* grew faster than *D. pulex* such that the smaller species, *D. rosea*, had the same molt size as *D. pulex* by days 12 and 13 ($df=1$, $F=1.15$, $P=0.29$, Table 1 & 2). In Wintergreen Lake, *D. pulex* grew faster and remained significantly larger than *D. rosea* as shown by its larger size on days 12 and 13 ($df=1$ $F=294$ $P<0.00$, Table 1 & 2). *Daphnia rosea* showed no difference in the number of molts produced by day 10 compared between lakes ($df=1$, $F=0.94$, $P=0.33$, Table 2) while *D. pulex* showed an increase in the number of molts produced in Wintergreen Lake by day 10 compared to Lawrence Lake ($df=1$, $F=22.8$, $P<0.00$, Table 1 and 2).

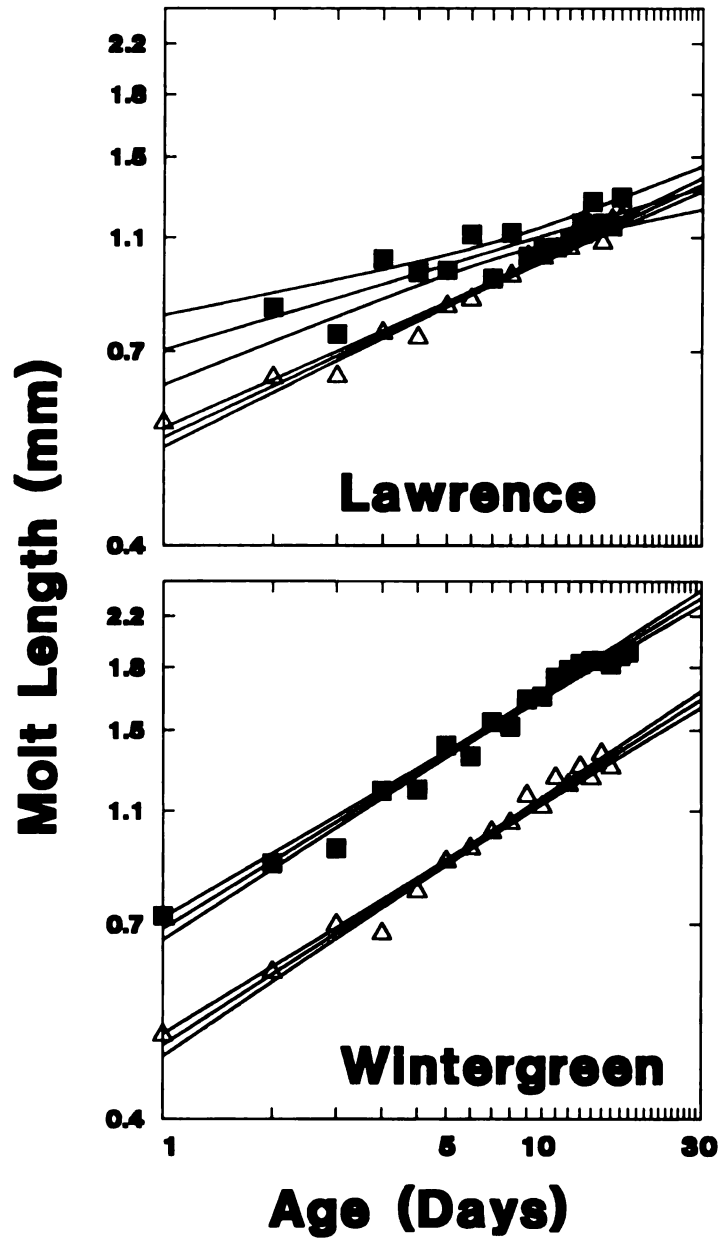


Figure 3 Growth rates based on average molt sizes on a log-log scale for both species in Lawrence (upper) and Wintergreen (lower) lakes including the 95% confidence intervals. Symbols as in Figure 1.

DISCUSSION

The performance measures, r and R_0 , indicated that each species was the superior performer when raised in the water from which they were collected. *Daphnia pulex* was more sensitive to the resource change than was *D. rosea*, resulting in an interaction between resource level and species. In addition, the observation of a negative population growth rate for *D. pulex* in both the July and August Lawrence Lake life tables suggested that exploitative competition was an explanation for why *D. pulex* is not present in Lawrence Lake. In the Wintergreen Lake water, however, *D. pulex* performed much better than did *D. rosea* whose r was not different from zero.

When raised in the Lawrence Lake water both species had low mortality, but growth and fecundity patterns differed between the species. *Daphnia rosea* grew faster than *D. pulex*, and *D. rosea* matured during the study when *D. pulex* did not. The fast growth, early maturation time and small size at maturation of *D. rosea* may be an important adaptation in an environment with low resources and size selective predation, as occurs in Lawrence Lake.

In comparison, growth in Wintergreen Lake water was better than in Lawrence Lake and more similar between the species. However, both survivorship and fecundity differed between the species. *Daphnia pulex* had such a higher fecundity than *D. rosea*, that differences in time to maturity and survival become immaterial to r and R_0 . However, the earlier time to maturity and higher juvenile survivorship indicated that *D. pulex* could better utilize the higher Wintergreen Lake resource.

Daphnia pulex performance was more sensitive to differences between lakes than was that of *D. rosea*. The most apparent difference was in fecundity. Survivorship was

high for both species in Lawrence Lake, while in Wintergreen Lake both species had a high mortality rate and *D. rosea* had lower juvenile survivorship than *D. pulex*. In addition, *D. pulex* showed a larger increase across resources than *D. rosea* in percent matured, growth rate, molt length on day 12 & 13, and number of molts produced.

The differences in sensitivity to the resource change might be a result of adaptation, if these lake habitats consistently differ in mean resource level or seasonal variation. Lawrence Lake has a low resource availability throughout the summer (Tessier, unpublished data). The results of the July and August *D. pulex* life tables further support this idea as there were only small decreases in fecundity and growth and no differences in survivorship. Hence, adaptation to chronic, low resources would be more beneficial for *D. rosea* than sensitivity to varying resources. In comparison, Wintergreen Lake has a high mean resource, but that resource undergoes substantial seasonal fluctuations (Threlkeld 1979). Epilimnion resources decrease throughout the summer (Standish, unpublished data) and poor quality blue-green algae become dominant. In addition, storm events can potentially mix the lake due to its shallow mean depth, returning a large amount of nutrients to the epilimnion from the anoxic hypolimnion (Reynolds 1990). Thus, it would be advantageous for *D. pulex* to be highly responsive to increasing resources.

A performance (r) trade-off was evident as the species' rank order switched from Lawrence Lake to Wintergreen Lake. Other studies have suggested that smaller species compete best in low resources and larger species can outcompete smaller species under high resources (Romansvsky and Feniova 1985, Bengtsson 1987). Possibly, performing well in a high resource results in mediocre performance in low resources for *D. pulex* but

relatively good performance in the low resources restricts *D. rosea* from doing well in higher resources.

The negative instantaneous rate of increase (r) observed for *D. pulex* raised in both July and August Lawrence Lake waters would prohibit the invasion of *D. pulex* into Lawrence Lake. *Daphnia rosea* had a significantly higher r and would therefore be able to competitively exclude *D. pulex* because of density dependent resource regulation (Leibold 1988). Similarly, Neill (1978) found that *D. pulex* were competitively excluded by *D. rosea* from low food montane lakes, although he found that juvenile survivorship was affected. Thus, without invoking size selective vertebrate predation, the resource environment seems to be a sufficient explanation for the absence of *D. pulex* in Lawrence Lake. Size selective predation by bluegill could only further decrease the r of the larger and more pigmented *D. pulex*.

In contrast to the Lawrence life table, the *D. rosea* Wintergreen life table indicates that in early August, *D. rosea* would not be able to invade Wintergreen Lake as it would not be able to increase its population size. In comparison to *D. rosea*, *Daphnia pulex* population growth in Wintergreen Lake agrees with the high r laboratory life tables as the population size greatly increased during the summer to eventually displace *D. pulicaria* from the hypolimnion.

The small fecundity increase of *D. rosea* with an apparently large increase in food appears to be unusual. Contrary to the present study, Goulden et al. (1982) and Vanni and Lampert (1992) found for *D. rosea*, with increases in a high quality algal food concentration, an increase in survivorship, a substantial increase in fecundity and a decrease in time to maturity. In addition, with several concentrations of a natural

resource, Hall (1964) found a large increase in fecundity with little change in survivorship. It seems possible that the Lawrence Lake *D. rosea* are adapted to low food conditions where most other *D. rosea* reported in the literature were adapted to higher resources, however this is difficult to determine as the lake resource condition from which the clones were collected is not usually published. Alternatively, the small fecundity increases could be due to the effect of other stresses in Wintergreen Lake differentially affecting the smaller *D. rosea*, such as blue-green algae (Gliwicz and Lampert 1990).

There appears to be a trade-off between fecundity and survivorship in this experiment; increased fecundity and growth was associated with decreased survivorship. The literature contains some qualitatively similar trends for changing food quantity and quality. Arnold (1971) found an increased fecundity associated with decreased survivorship when the quantity of algae was increased. Swartz and Ballinger (1980) looked at three different algal species and found similar results. When fed *Pediastrum duplex*, *D. pulex* had a shorter life span and a larger brood size; when fed the poorer quality *Melosira ambigua*, *D. pulex* had a longer lifespan and a smaller brood size. However, other studies have found an increase in survivorship with increased food concentration. For example, Paloheimo and Taylor (1987), Goulden et al. (1982), and Vanni and Lampert (1992) found an increase in fecundity and survivorship with an increase in the concentration of a high quality algal food. In addition, with several concentrations of a natural resource, Hall (1964) found a large increase in fecundity with little change in survivorship.

An inconsistent observation of a trade-off between fecundity and survival may be explained by a unimodal relationship between mean survivorship and food concentration

(Frank et al. 1957, Lynch and Ennis 1983, Lynch 1989, McCauley et al. 1990a). In a study examining a gradient of high quality algal food concentrations, Lynch (1989), found a critical food concentration below which *D. pulex* survivorship increased with increasing food concentrations and above which survivorship decreased. The argument has been made that the decreased survivorship associated with increases in fecundity past the critical food concentration are unrealistic as field conditions would never approach this level (McCauley et al. 1990a); but the results of this study possibly suggest otherwise.

Though survivorship was measured in only two resource habitats in this experiment, a large decrease in survival was observed in both species and associated with higher fecundity, suggesting that there could be a cost to reproduction. However, the decreased survivorship in Wintergreen Lake could be due to other factors, such as the high concentration of blue green algae, the high incidence of *Chaoborus*, and/or high levels of parasitism. There is little agreement concerning the expected lifespan under high food conditions, but survivorship is generally >60% by day 20 (Hall 1964, Neill 1978, Goulden et al. 1982, Vanni and Lampert 1988, Lynch 1989, McCauley et. al. 1990a). In comparison, both *D. pulex* and *D. rosea* in the Wintergreen Lake resource had around 0% survivorship by day 20.

High densities of *Chaoborus sp.* (>1/L) occur in Wintergreen Lake (Mittelbach, unpublished data). The kairmones produced by this predator have been shown to produce a demographic and morphological change in *Daphnia* (Black and Dodson 1990 and references therein). During the Wintergreen life table experiment, some *D. pulex* neonates were observed with neck teeth, a response to *Chaoborus* kairmones which has been shown to affect the life history of *D. pulex* by increasing time to maturity and decreasing

survivorship (Black and Dodson 1990). It is possible that the Wintergreen Lake water resource produced a similar effect on *D. rosea* survivorship.

Another possible cause of the high mortality seen in Wintergreen Lake could be due to interference effects of blue-green algae (Gliwicz and Lampert 1990). The blue-green alga, *Aphanizomenon*, is known to be present in Wintergreen and becomes very prevalent by the end of the summer (Desmarais, personal observation). A third possible cause of the rapid mortality could be the presence of the parasitic yeast *Metschnikowia*. The incidence of fungal parasites has been shown in other lakes to increase over the summer and is correlated with increasing anoxia; a measure of increased population densities as available habitat is compressed (Tessier and Geedey, unpublished data). *Metschnikowia* was observed on both *D. rosea* and *D. pulex* raised in Wintergreen Lake and could have a large effect on survivorship.

In summary, I present evidence that the life history response of a particular *Daphnia* species varied depending upon the resource environment. *D. rosea* from Lawrence Lake were adapted to this low resource environment while the Wintergreen *D. pulex* seem to be adapted to do well in an apparently higher resource environment. A performance trade-off indicates that these *Daphnia* do not perform equally across the two resource habitats. This suggests that resource based mechanisms could contribute to the determination of species composition in the epilimnetic habitat.

Chapter 2

Performance trade-offs across a natural resource gradient

INTRODUCTION

Hairston et al. (1960) proposed that because the terrestrial landscape is green, herbivores must be limited by predators. This rather simplistic, yet intriguing hypothesis generated extensive research, debate, and model development (e.g., Fretwell 1977, Oksanen et al. 1981, Mittelbach et al. 1988, Leibold 1989). Simply stated, Hairston et al. (1960) envisioned three trophic levels in terrestrial systems where each exploit the level directly below creating alternating trophic densities along the food chain. Their underlying thesis, that a trophic level is regulated by density-dependent competition for food if resources are rare or primarily regulated by predation if resources are abundant, is still hotly debated in the form of bottom-up and/or top-down (trophic cascade) arguments (e.g. McQueen et al. 1989, Power 1992a, Abrams 1993, Strong 1992). Despite this ongoing debate, there is general agreement concerning the existence of alternating trophic densities in some systems.

Extensive research has shown that systems which exhibit a strong trophic cascade have particular characteristics because they are all fairly homogenous systems containing a "keystone" herbivore and predator, and the primary producers tend to be lower plants (Strong 1992). For example, the presence of a top predator in a river food chain (fish)

resulted in a strong cascade creating low densities of damselfly nymphs (and other predators), high densities of algivorous chironomids, and a low standing crop of algae (Power 1990). However, the trophic cascade was dependent upon the absence of a physical refuge for the damselfly nymphs. In the presence of a refuge (gravel), the impacts of fish predation were decoupled from their damselfly nymph prey resulting in no further density changes along the food chain (Power 1992b). Thus, alternating densities along the food chain depend on each trophic level being tightly coupled with the next.

Lake plankton communities can also contain alternating densities along the food chain and they exhibit the characteristics typical of systems which are vulnerable to a trophic cascade. They are fairly homogeneous systems with a "keystone" predator (planktivorous fish) and herbivore (zooplankton, esp. *Daphnia*), and the autotrophs are lower plants (phytoplankton). However, lakes differ in depth (presence or absence of thermal stratification), which provides a contrast in herbivore refuge availability (Tessier and Welser 1991) and thus the impact of a trophic cascade. In shallow lakes, the water remains unstratified during the summer allowing the planktivorous fish (e.g. *Lepomis macrochirus*) to forage throughout the water column. These predators are size-selective and thus reduce the average zooplankton body-size and allow small-bodied species to dominate (Brooks and Dodson 1965, Mittelbach et al. 1995). However, in deeper lakes which stratify during the summer, these warm water planktivores are restricted to the upper mixing zone above the thermocline (Werner et al. 1977). This creates a deep-water refuge which larger zooplankton can use during the day (diel vertical migration) to remain abundant in the lake (Wright and Shapiro 1990, Tessier and Welser 1991).

We are interested in how lake depth might relate to phytoplankton resource

availability. Tessier and Welser (1991) predict very different zooplankton communities dependent upon the depth of the lake and thus the presence or absence of a refuge. In the shallow lakes with no refuge, the zooplankton communities are dominated by smaller species of *Daphnia*, *Ceriodaphnia* and *Bosmina* which are able to withstand high fish predation levels. In deeper lakes with a refuge, the zooplankton community should be dominated by larger *Daphnia* such as *D. pulicaria* and *D. rosea*. In shallow lakes with tightly coupled trophic levels, high fish predation and low densities of small zooplankton, there should be high phytoplankton resource availability. In deeper lakes, a refuge allows larger body-sized species of zooplankton to remain abundant, which should result in low phytoplankton resource availability.

Differences in resource availability in shallow versus deep lakes could be caused by a change in the quantity and/or quality of the phytoplankton community. An abundance of large-bodied zooplankton can have a significant selective effect on the phytoplankton community, favoring grazer-resistant algal species (Porter 1977; Lynch and Shapiro 1981; Vanni 1986, 1987). A reduction in density of high quality algae has also been shown to increase the density of more resistant, lower quality algae (Leibold 1989, Vanni 1987). Thus, in deep lakes containing a larger-bodied zooplankton community, both algal quality and quantity should be low. However, in shallow lakes with a small-bodied zooplankton community, both the quality and quantity of algae should be high. Although the effect of lake depth-refuge availability on the phytoplankton availability (via trophic cascade) seems general, we know of no explicit test of these predictions.

Extensive laboratory research documents the effects of resource density and quality on zooplankton (esp. *Daphnia*) life histories (e.g. Richman 1958, Arnold 1971,

Schwartz and Ballinger 1980, Lynch 1989, Vanni and Lampert 1992, Boersma and Vijverberg 1995). In general, higher resource richness typically results in faster maturation times and larger clutch sizes, although response can vary significantly among species (Hrbáčková and Hrbáček 1976, Infante and Litt 1985). Given that changes in resource richness can affect species differently, it is likely that a species commonly found in a particular resource environment may be adapted to perform well in that resource. Hrbáčková and Hrbáček (1976) suggest that *D. pulex* is adapted to the periodical nature of their pool habitat by being able to quickly take advantage of resource increases. Other studies have shown that relative performance can change across a resource gradient; some species are adapted to compete well in a low resource environment but do not do as well in a high resource environment (Romanovsky and Feniova 1985, Bengtsson 1987).

Three hypotheses emerge from our focus on lake depth as an important plankton-structuring agent. First, because we expect the planktivore-herbivore trophic levels to be more tightly coupled in shallow versus deep lakes, the former should maintain a higher resource availability for zooplankton. Secondly, we hypothesize that the dominant zooplankton species inhabiting shallow, high resource lakes should be adapted to perform well at high resource levels, while the dominant species inhabiting deep, low resource lakes should be adapted to perform well at low resource levels. Thus, we anticipate a performance trade-off across the natural resource gradient of shallow to deep lakes. Finally, differential grazing pressure on the phytoplankton of shallow versus deep lakes should create a contrast of resource quality, in addition to resource quantity. We expect that such qualitative differences in the resource base would influence any performance trade-off expressed by the grazing species.

BACKGROUND

To examine the above hypotheses, four study lakes (Lawrence, Warner, Three Lakes III, and Lower Crooked) were chosen for their differences in lake depth, but were as close as possible in other physical, chemical, and biological parameters. The four study lakes are located within 15 km of the W.K. Kellogg Biological Station of Michigan State University in southwest Michigan. The inorganic water chemistry is slightly alkaline, extremely well buffered, calcium-rich and oligotrophic with a mean total phosphorus at turnover of 10.5 ± 1.44 (mean $\pm$ SE). Each lake has a similar fish community that is dominated by Centrarchids, as is typical of most lakes in the northcentral United States (Osenberg et al. 1988). Bluegill sunfish (*Lepomis macrochirus*) is the primary planktivore, and actively forages on the zooplankton community at dawn and dusk (Werner et al. 1977, Mittelbach 1981).

These four lakes differ primarily in their mean depth, creating two replicates for the two lake depth categories. Lawrence and Warner lakes are both deep (13 m and 16 m, respectively) and stratify during the summer. Three Lakes III and Lower Crooked are both shallow (<4 m) and do not stratify during the summer. The difference in mean depth between the shallow and deep lakes is correlated to predictable differences in the zooplankton community composition (Tessier and Welser 1991). The summer zooplankton communities in the two deep lakes are dominated in the surface waters by *Daphnia rosea*. *Daphnia rosea* refuges in the metalimnion and hypolimnion during the day to decrease the impact of fish predation and migrates up to the epilimnion at night (Leibold and Tessier 1991, Leibold 1988). I refer to this population as *D. rosea*, but its

actual taxonomic affinity in the *D. galeata* complex is unclear (Taylor and Hebert 1993). *D. pulicaria* is also present in these lakes but largely remains in the hypolimnion both day and night (Leibold 1988). In comparison, the shallow lakes are composed of much smaller-bodied species dominated by *Ceriodaphnia reticulata*, but including *D. retrocurva*, *D. dubia*, *D. ambigua*, *Bosmina*, and *Chydorus* spp. (unpublished data).

METHODS

Quantifying the resource gradient

A simple, quantitative comparison of food resources available for herbivorous zooplankton in different lakes is difficult to obtain because of variation in the resource composition, (phytoplankton species, detritus, size distribution) and biochemistry. To assess the resource conditions in each of our four study lakes from the perspective of a daphniid, we chose a single clone of *Daphnia* (an obligate asexual clone of *D. pulex*) to use in a bioassay. This clone was isolated from a small pond at KBS and is a suspected hybrid between *D. pulex* and *D. pulicaria* (electrophoresis indicates it is heterozygote at lactate dehydrogenase; Hebert et al. 1989). In trials involving a range of natural lake resources, this clone was both extremely sensitive (in growth rate response) and mirrored the responses of other *Daphnia* species and clones to a wide range of resource conditions (Tessier and Tsao submitted manuscript). We used specific growth rate of juveniles raised on each lake water resource, but under laboratory controlled temperature and light conditions, as our measure of resource conditions for comparison among the four lakes.

D. pulex was maintained in laboratory culture at 20°C, fed high food concentrations (>1 mg carbon L^{-1} day $^{-1}$ of *Ankistrodesmus falcatus*) and raised in filtered lake water (1:1 mixture of Gull and Pleasant lakes, Barry Co. MI., Tessier and Consolatti 1989, 1991). Neonates (< 24 h old) were collected from adults of age 15-30 days (3rd-8th clutch) to start all growth rate assays. Approximately 22 neonates were randomly assigned to each lake water treatment and a group were harvested to measure initial dry mass. We collected epilimnetic water every morning from approximately 0.5 m below the waters' surface at a central location in each lake with a 4 L polyethylene container. The lake water was screened through 80 μ m mesh to remove other zooplankton and brought to 20°C. Animals were changed daily to the freshly collected lake water and new glassware, and cultured in an incubator at 20°C with 16:8 h light cycle. After 4 days of growth, all animals were harvested to measure final dry mass. Dry mass was measured using a Cahn electrobalance sensitive to 0.1 μ g, after animals were dried for 24 h at 55-60°C. We estimated the specific growth rate (μ g μ g $^{-1}$ day $^{-1}$) of each cohort of animals as the $[\ln(\text{final dry mass}) - \ln(\text{initial dry mass})]/4$ days (Tessier and Goulden 1987). As a replicate measure for each lake, we ran a second cohort growth experiment identical in procedure to the first cohort but initiated one day later, for each lake. Hence, the two cohorts of neonates, i.e. each 4 day growth assay, produced two estimates of resource conditions for each lake. This procedure was repeated every 3 weeks for all lakes throughout June, July and August 1995.

Comparison of species performance across the resource gradient

Because *Ceriodaphnia reticulata* is the most abundant daphniid in the shallow lakes and *Daphnia rosea* the most abundant daphniid in the epilimnion of the deep lakes in summer, we chose these two taxa for comparison in each of the resources from the four study lakes. In all, we conducted eight life tables consisting of each species raised in the epilimnetic lake water resource from each lake, but under laboratory controlled temperature and light conditions. Life tables using Lawrence (deep) and Lower Crooked (shallow) lake waters were started on 9-10 and 10-11 July, respectively (or days 38-39 and 39-40 from June 1). The Warner (deep) and Three Lakes III (shallow) life tables were started on 5 and 7 August, respectively (or days 65 and 67 from June 1). Despite the different starting dates between lakes, life tables for the two species were always started at the same time for each lake resource because the experimental focus was a comparison of the relative performance of the two species. The Lawrence Lake life tables contained 40 individuals of each species, while the other life tables each contained 30 individuals. The Lawrence, Warner, and Three Lakes III life tables were continued until obvious survivorship differences were apparent, 26, 18, and 16 days, respectively. The Lower Crooked life tables were continued for 33 days with no apparent survivorship differences. To all eight of these life tables we added a small amount of cetyl alcohol which prevented surface film problems without inhibiting performance (Appendix A).

The two species were collected from the field twice, approximately three weeks before the start of a life table, to minimize laboratory culture time. *Daphnia rosea* was collected from the epilimnion of Lawrence Lake and *C. reticulata* was collected from the

epilimnion of Lower Crooked Lake using a conical net. More than 30 adults of each species were isolated to collect a representative sample of the population variation. All animals were haphazardly chosen to prevent a size bias in the clones selected, and placed into flasks containing high concentrations of the green algae *Ankistrodesmus falcatus*. All *D. rosea* and *C. reticulata* were cultured under standard laboratory conditions for several generations (Tessier and Consolatti 1989). Food levels were kept high (50,000 cells *A. falcatus* ml⁻¹ day⁻¹) and the algal water was a filtered 1:1 mixture of two lakes, not connected to the four study lakes.

To begin all life tables, neonates of both species (<1 day old) were individually placed into 50 ml flasks containing the appropriate water resource. We collected epilimnetic water every morning from approximately 0.5 m below the waters' surface at a central location in each lake with a 4 L polyethylene container. Lake water was then screened through an 80 μ m mesh to remove zooplankton, aerated, and dispensed to flasks. The 50 ml flask size for *C. reticulata* was not changed throughout the experiment while *D. rosea* flask size was increased to 125 ml before animals achieved maturation size due to the greater growth of *D. rosea*. Animals were transferred daily to freshly collected water using a wide bore pipette and were incubated at 24°C with a 16:8 h L:D photoperiod which was similar to the summer epilimnetic conditions in these lakes. Glassware was rinsed every day and washed at least once a week.

Animals were monitored daily for individual survival, number of offspring produced and molt size at maturity. Molted carapaces were measured at maturity from the base of the tail spine across the longest length of the carapace using a Wild

Stereoscope at 50x magnification.

Comparison of species performance across a resource quantity gradient

In late August, we conducted an experiment to compare the life history response of *D. rosea* and *C. reticulata* across a food quantity gradient created by the dilution of a single natural algal assemblage. This experiment consisted of eight life tables, i.e. each of the two species (collected in late July), raised in the Lower Crooked Lake water resource and three serial dilutions of this resource (0.5, 0.25, 0.125). Water for the dilution series was collected daily using a 20 L polyethylene carboy plunged below the surface from a central location of the lake. The water was diluted by using the appropriate amount of glass-fiber (A/E Gelman) filtered Lower Crooked Lake water. After dilution, the water was aerated to thoroughly mix the resource and then dispensed into Erlenmeyer flasks. Each life table contained 15 individuals. All life tables were carried out at least through the first four clutches (except for the *D. rosea* 0.125 dilution life table which only produced 1 clutch in the time *C. reticulata* produced 5-8), 14 days for undiluted and 0.5 dilution life tables and 22 days for the 0.25 and 0.125 dilution life tables. All other culture and life table methods were identical to those previously described.

Analyses

We contrasted the resource availability (*D. pulex* specific growth rate; SGR) of deep and shallow lakes with a repeated measures analysis of variance (ANOVAR) using Systat (Wilkinson 1992). The four lake experiment and the dilution

experiment were analyzed using SAS (1989) Lifetest procedure to test for age-specific survivorship differences and time to maturity differences between species using the Log-rank test (Fox 1993). Length at maturity was examined using ANOVA with lake and species factors considered fixed effects. ANOVA assumptions were met. Instantaneous rate of increase (r), was iterated for each life table using a variation of Newton's approximation and the stable age equation (Lotka 1956):

$$1 = \sum l_x m_x e^{-rx}.$$

The net reproductive rate (R_o), was also calculated:

$$R_o = \sum (l_x m_x).$$

We used a SAS macro program to bootstrap the 95% confidence intervals around both r and R_o with 1,000 re-samples of 30 (40 in the Lawrence Lake life tables, 15 in the dilution life tables) randomly chosen individuals. The SAS program is available via the World Wide Web at <http://kbs.msu.edu/~desmarais/bootstrap.html> or Appendix B.

Model I regression was used to relate the instantaneous rate of increase and net reproductive rate with the independent measure of the lake resource (*D. pulex* SGR). Because the four life table experiments were started at slightly different times relative to when the SGR was measured in each lake, we estimated a SGR for the start of each life table by linear interpolation of available values. The dilution experiment was similarly analyzed except that these values were log transformed to linearize the data.

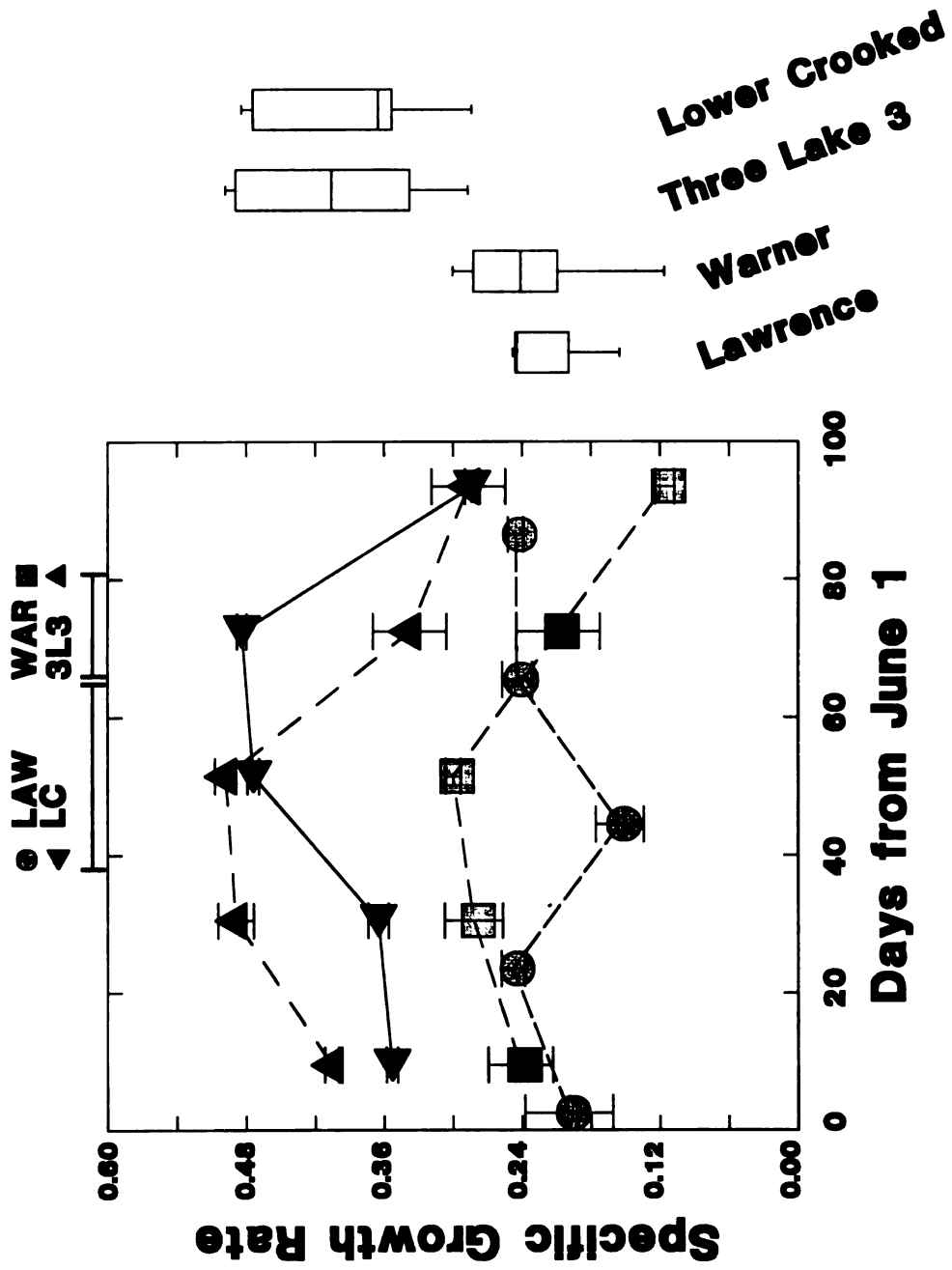
RESULTS

Quantifying the resource gradient

Throughout the summer, the *D. pulex* raised in resources from shallow, unstratified lakes (i.e. Three Lakes III and Lower Crooked lakes) had consistently higher specific growth rates (SGR) than when raised in resources from deep, stratified lakes (i.e. Warner and Lawrence lakes, Figure 4). Thus, the resource conditions from the perspective of the daphniid were clearly associated with the two categories of lake morphometry (df=1, F=456, P=0.002). The shallow, unstratified lakes supported almost two times the growth that the deep, stratified lakes supported (mean SGR $\pm$ SE, 0.40 ± 0.03 and 0.22 ± 0.02 , respectively). The four lakes also exhibited temporal variation in resources but this did not result in a consistent overall trend (time effect not significant, df=4, F=1.90, P=0.20) nor in a significant time by lake interaction between shallow and deep lake categories (df=4, F=0.62, P=0.66).

An unplanned result, due to the temporal resource variation, was that the four lakes resolved into a resource gradient during the times that the life table experiments were conducted. Thus, the ranking of the lake resources from the perspective of *D. pulex* measured during these life table experiments (day 1 SGR, $\mu\text{g } \mu\text{g}^{-1} \text{ day}^{-1}$) was: Lawrence Lake (0.18), Warner Lake (0.24), Three Lakes III (0.38), and the highest resource was from Lower Crooked Lake (0.41). These differences in specific growth rate translate into substantial differences in life table performance.

Figure 4 Temporal change in specific growth rates ($\mu\text{g } \mu\text{g}^{-1} \text{ day}^{-1}$; including box plots, at right) of *Daphnia pulex* in the four study lakes during the summer. The starting date and duration of the species comparison life tables are indicated above the figure. Symbols: light symbols=deep lakes (circle=Lawrence, square=Warner) and dark symbols=shallow lakes (upright triangle=Three Lakes III, left triangle=Lower Crooked).

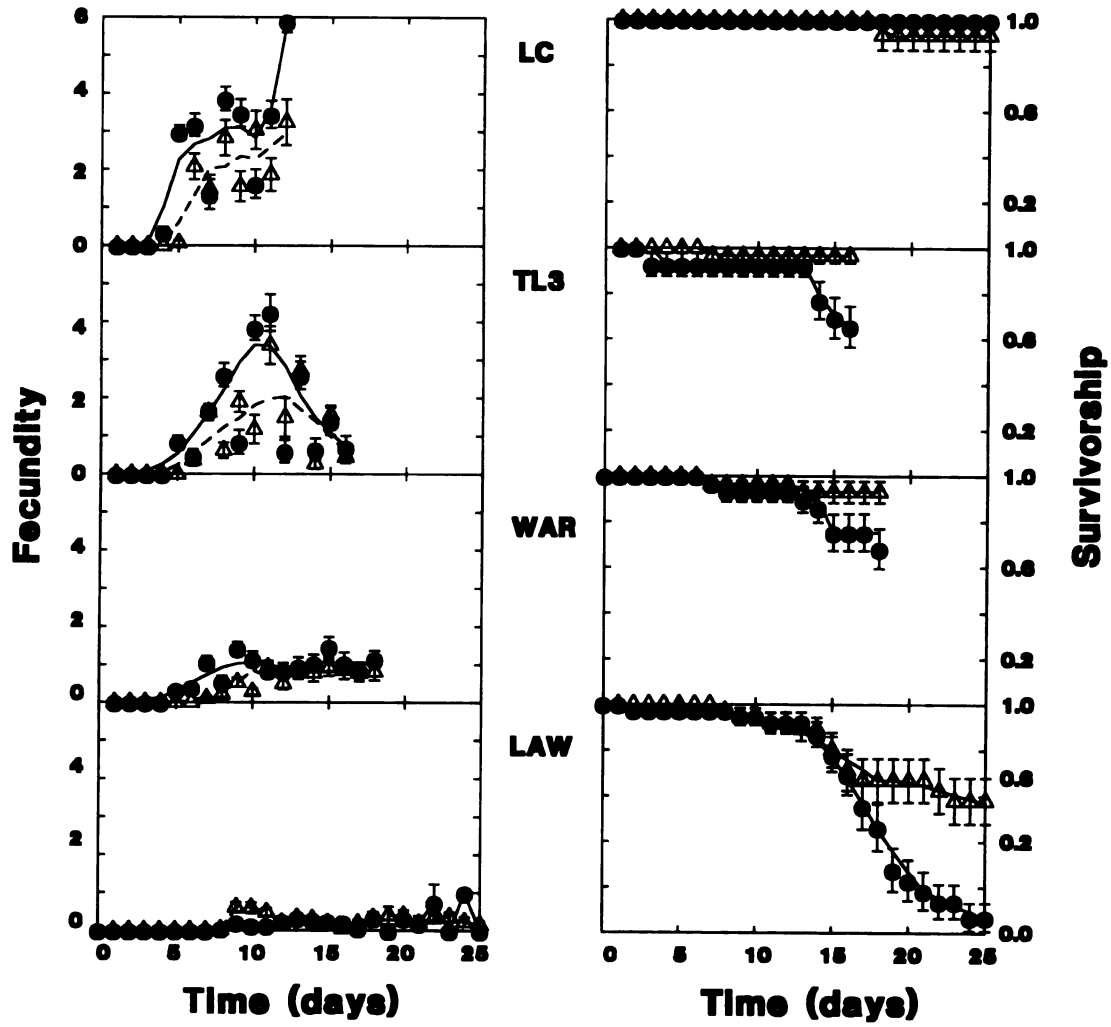


Comparison of species performance across the resource gradient

As expected, the average daily fecundity for both *Ceriodaphnia reticulata* and *Daphnia rosea* increased across the resource gradient as defined by the specific growth rate of *D. pulex* (Figure 5). Therefore, each species had the same rank preference; although the response of the two species in each lake was distinct. *Daphnia rosea* had a higher average daily fecundity ($0.30 \text{ neonates female}^{-1} \text{ day}^{-1}$) in the lowest resource (Lawrence Lake) compared to *C. reticulata* (0.25). However, the average daily fecundity of *C. reticulata* was higher in the richer resource lakes (i.e. Warner, Three Lakes III, Lower Crooked) compared to *D. rosea*. In the higher resource lakes, *C. reticulata* typically also produced a clutch every 1.5 days while *D. rosea* never produced a clutch faster than every 2 days. Finally, *C. reticulata* produced the first clutch an average of 1-3 days faster than did *D. rosea* in the high resource conditions while *D. rosea* produced the first clutch an average of one day faster than *C. reticulata* only in the lowest resource condition (Figure 6). The average length at maturity was similar among lakes for each species. As expected, *C. reticulata* had a small average molt size ($0.47 \pm 0.003 \text{ mm}$, $n=4$) compared to *D. rosea* ($1.09 \pm 0.011 \text{ mm}$, $n=4$).

Overall, survivorship for both species was better in the high resource lakes compared to the low resource lakes, but juvenile survivorship was high ($>90\%$) for both species in all lake resources (Figure 5). In the highest lake resource (Lower Crooked) there were no survivorship differences between species because of high adult survivorship ($>95\%$) during most of the life table. However in the lower resource lakes, the adult survivorship of *D. rosea* was significantly better than that of *C. reticulata*. In Three Lakes III and Warner lakes, *D. rosea* survivorship remained $>90\%$ while *C. reticulata*

Figure 5 Average daily fecundity (left) and survivorship (right) for both species in each lake resource from highest to lowest: LC=Lower Crooked, TL3=Three Lakes III, WAR=Warner, and LAW=Lawrence lakes. Symbols: open triangle=*D. rosea* and closed circle=*C. reticulata*. (Survivorship Log-rank tests, df=1: LC $\chi^2=0.66$, P=0.42; TL3 $\chi^2=8.84$ P=0.003; WAR $\chi^2=5.23$, P=0.02; LAW $\chi^2=8.32$, P=0.004)



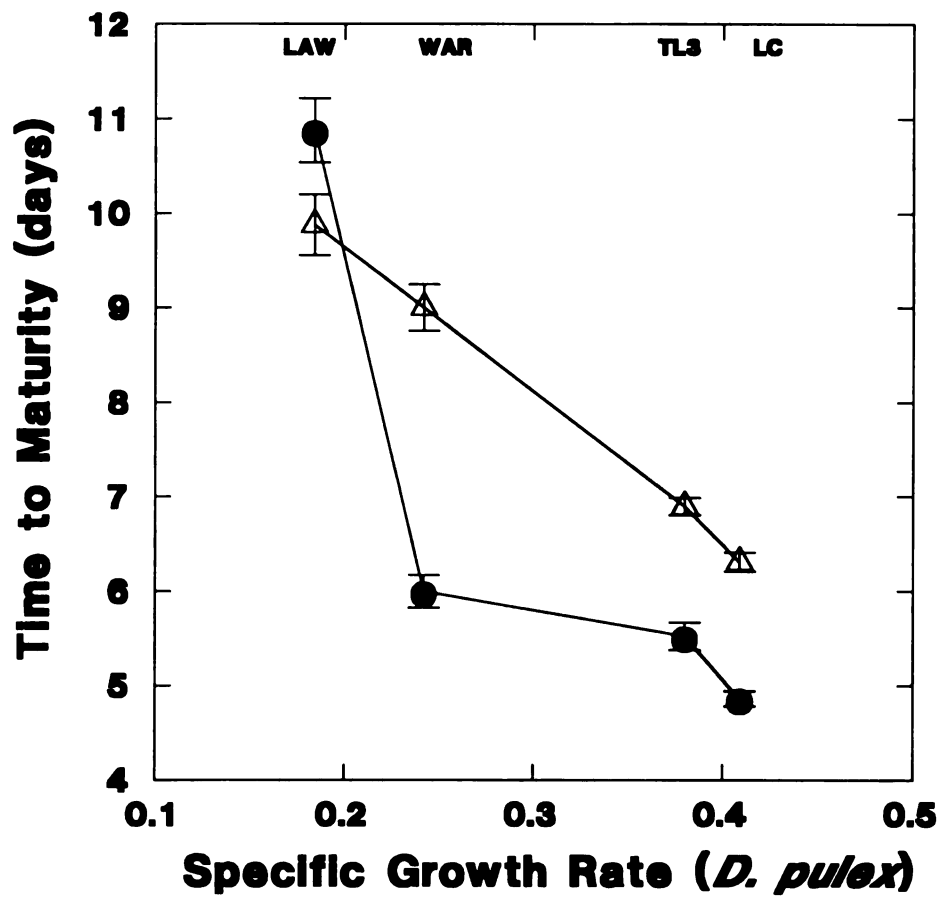


Figure 6 Time to maturity for both species in each lake resource (SGR). Symbols as in Figure 5. (Log-rank tests, df=1: LC $\chi^2=47.68$, $P=0.0001$; TL3 $\chi^2=33.72$, $P=0.0001$; WAR $\chi^2=48.11$, $P=0.0001$; LAW $\chi^2=7.36$, $P=0.007$)

survivorship began to decline around day 15 and fell below 60% by the end of the experiment (day 16 for Three Lakes III and day 18 for Warner). In the lowest resource lake (Lawrence), survivorship declined over the first two weeks to 80% for both species. After this time, *D. rosea* survived much better than did *C. reticulata*, falling to only 60% compared to the poor *C. reticulata* survivorship of <10% by the end of the experiment (day 26).

The two summary measures of performance, instantaneous growth rate (r) and net reproductive rate (R_0), produced a similar pattern across the lake resource gradient (Figure 7). Each species had the same rank preference of resources. In the lake resource producing the poorest overall performance for both species (i.e. Lawrence Lake), *D. rosea* had a higher r and R_0 than did *C. reticulata*. However, in the lakes containing higher resources (i.e. Warner, Three Lakes III, Lower Crooked), *C. reticulata* performed better than did *D. rosea*. The bootstrapped confidence intervals clearly indicate that there was a performance tradeoff for these two species across the measured resource gradient because the better performer in the high resource condition (i.e. *C. reticulata*) was the poorer performer in the low resource condition. There was a highly significant fit for r and R_0 in both *D. rosea* and *C. reticulata* as function of the resource gradient across the four lakes quantified by the SGR of *D. pulex* (*D. rosea* linear regressions, r : $r^2=0.982$, $F=108$, $P=0.009$ and R_0 : $r^2=0.997$, $F=770$, $P=0.001$; *C. reticulata* linear regressions, r : $r^2=0.886$, $F=15.5$, $P=0.059$ and R_0 : $r^2=0.929$, $F=26.0$, $P=0.036$). Thus, the species can be characterized as primarily differing in their response sensitivity (i.e. slope) to the resource gradient (Figure 7).

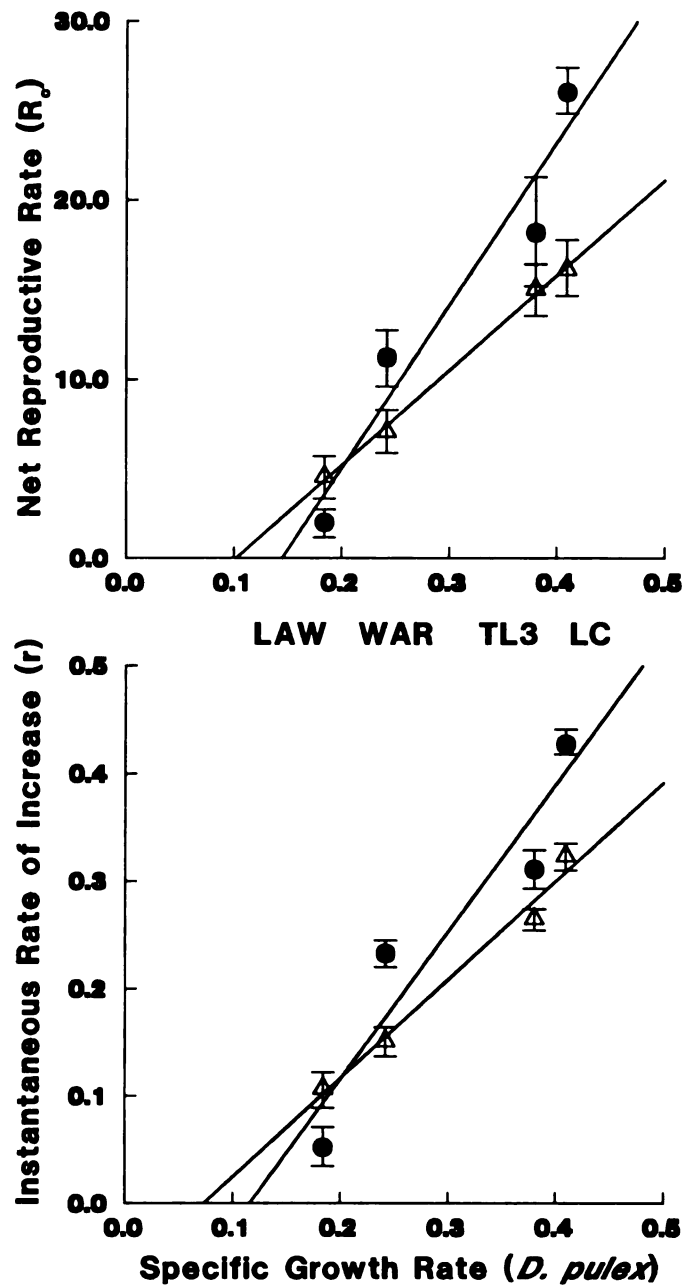


Figure 7 R_0 (upper) and r (lower) for *D. rosea* and *C. reticulata* in each lake resource (SGR). Error bars are bootstrapped 95% confidence intervals. Symbols as in Figure 5.

Comparison of species performance across a resource quantity gradient

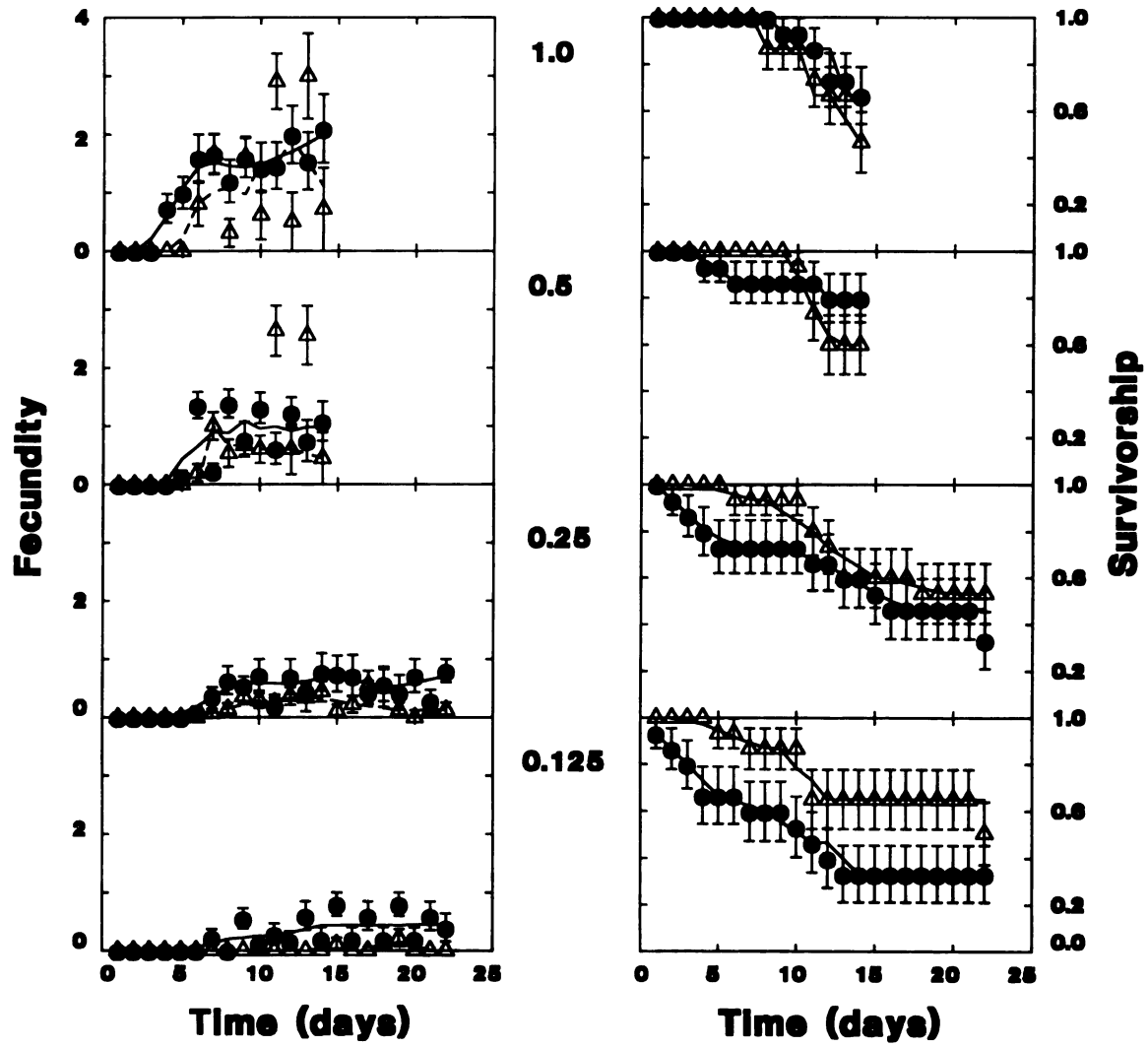
As expected, the dilution of Lower Crooked Lake water decreased the average daily fecundity (neonates female⁻¹day⁻¹) for both species (Figure 8). Fecundity was higher in the 1.0, 0.25 and 0.125 dilutions for *C. reticulata* (1.485, 0.540, and 0.372) compared to *D. rosea* (1.347, 0.251 and 0.056). However, in the 0.5 dilution, *D. rosea* had a larger average daily fecundity than did *C. reticulata* (1.026 and 0.887, respectively). In addition, *C. reticulata* produced clutches much faster than did *D. rosea*, especially in the undiluted resources. Finally, *C. reticulata* produced the first clutch an average of 1-5 days faster than did *D. rosea* in all four dilutions (Figure 9).

The survivorship of *D. rosea* in the two most dilute resources (0.25 and 0.125 dilutions) was consistently higher throughout the life tables than that of *C. reticulata*. In comparison, survivorship in the two highest resources (undiluted and 0.5 dilution) was similar between species (Figure 8). This result is similar to the pattern seen in the four lake comparison because both species had a similar survivorship in the high resource lakes while *D. rosea* had a higher survivorship than *C. reticulata* in the lower resource lakes. However, this apparent difference in survival in the dilution experiment was not significant, most likely because of the large error bars and the small sample size, especially near the end of the life tables. An unexpected result of the dilution experiment was that the juvenile survivorship of each species was very poor in the highly diluted treatment compared to any of the lakes in the previous experiment.

There was no evidence of a performance tradeoff between species across the resource quantity gradient created with the dilution of a natural algal assemblage (Figure 10). *Ceriodaphnia reticulata* had a larger r and R_0 than did *D. rosea* in each dilution.

Both species had a significantly linear (after log-transformation) decrease in r across the dilution series (*C. reticulata* linear regression r : $r^2=0.995$, $F=423$, $P=0.002$ and R_0 : $r^2=0.979$, $F=92.2$, $P=0.011$ and *D. rosea* linear regression r : $r^2=0.938$, $F=30.5$, $P=0.031$ and R_0 : $r^2=0.880$, $F=14.6$, $P=0.062$). The bootstrapped 95% confidence intervals indicate a significantly higher r for *C. reticulata* in both the lowest and highest resource, while the r for the 0.25 and 0.50 dilutions are more similar between species. The higher r and R_0 of *C. reticulata* across all dilutions was the result of a faster maturation time, larger daily average fecundities, and faster production of clutches across the dilution series compared to *D. rosea*.

Figure 8 Average daily fecundity (left) and survivorship (right) for each species in each of four dilutions of Lower Crooked Lake resource. Resource concentration is indicated between the graphs from highest (upper) to lowest (lower). Symbols as in Figure 5. (Survivorship Log-rank tests df=1: undiluted $\chi^2=1.11$, $P=0.29$; 0.5 dilution $\chi^2=1.08$, $P=0.30$; 0.25 dilution $\chi^2=1.13$, $P=0.29$; 0.125 dilution $\chi^2=2.11$, $P=0.15$)



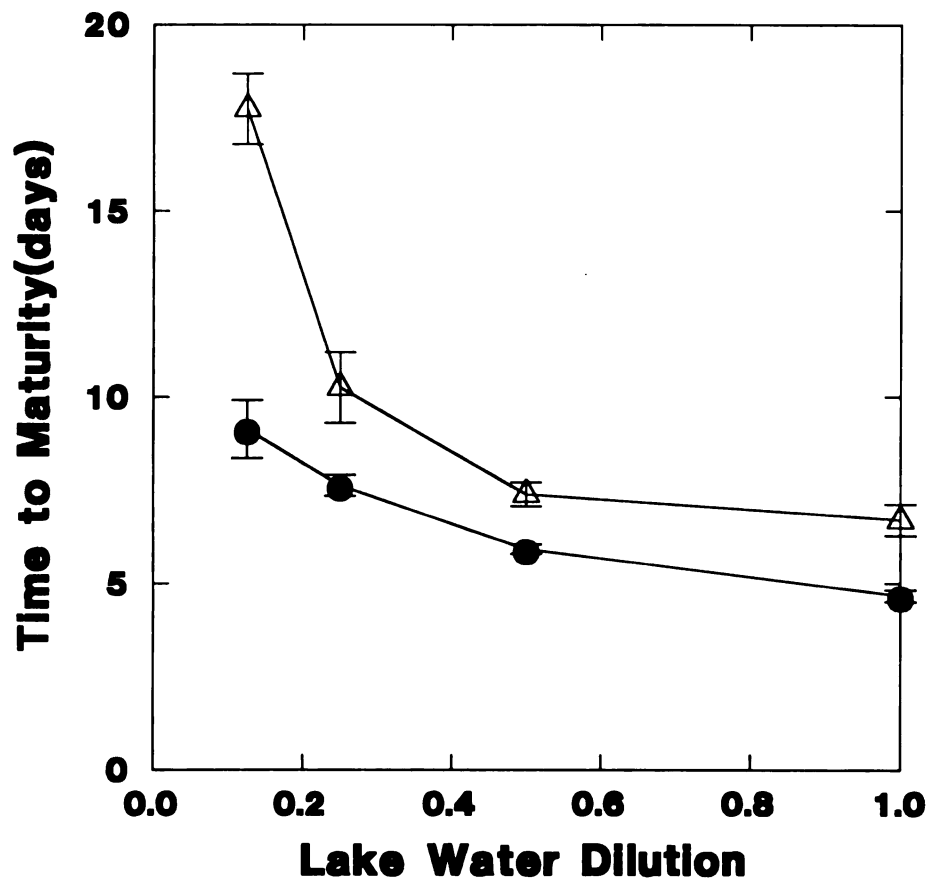


Figure 9 Time to maturity for both species in the four dilutions of Lower Crooked Lake resource. Symbols as in Figure 5. (Log-rank tests, $df=1$: undiluted LC $\chi^2=25.84$, $P=0.0001$; 0.05 dilution $\chi^2=17.73$, $P=0.0001$; 0.25 dilution $\chi^2=12.95$, $P=0.0003$; 0.125 dilution $\chi^2=9.19$, $P=0.002$)

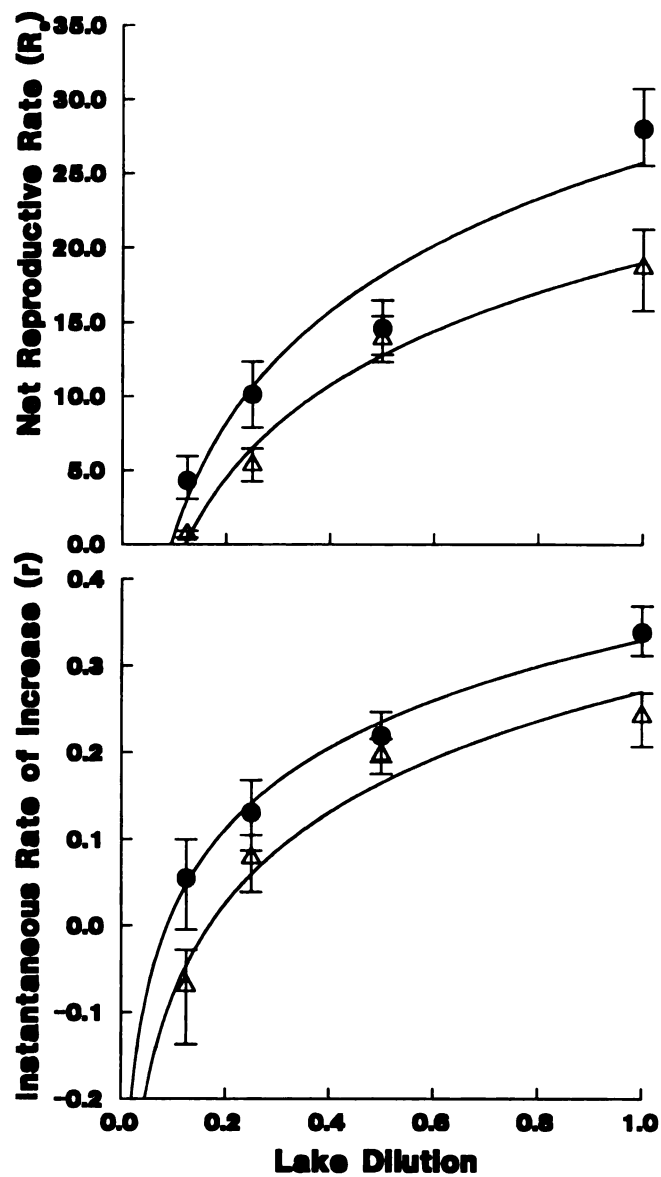


Figure 10 R_0 (upper) and r (lower) values for both species plotted in each of the four dilutions of Lower Crooked Lake resource. Curves were fit with a log function because of the serial dilution. Error bars are bootstrapped 95% confidence intervals. Symbols as in Figure 5.

DISCUSSION

Lakes differing primarily in their mean depth, and hence refuge availability, contained predictably different resources throughout the summer, as perceived by a representative daphniid. The presence of a deep-water refuge for zooplankton (Wright and Shapiro 1990, Tessier and Welser 1991) apparently reduces the strength of interaction between epilimnetic predators (warm-water fish) and migratory zooplankton. That is, the refuge provides large-bodied grazers a behavioral opportunity (diel vertical migration) which allows them to co-exist with an efficient fish planktivore. Although fish effectively exclude these grazers from the shallow epilimnion waters during the day, at night they migrate into this habitat and forage actively (Haney and Hall 1975). In lakes lacking a deep-water refuge, this same fish planktivore eliminates large-bodied grazers and as predicted, these lakes contained consistently higher resources.

The difference in SGR between the shallow and deep lakes is substantial and reflects large differences in r and R_0 for both species between lake types. This presumably indicates that the population dynamics of grazers in these two lake types also greatly differ. Specifically, zooplankton in shallow lakes must have larger specific growth, reproduction, and death rates compared to zooplankton in deep lakes. This suggests the possibility of large differences in secondary productivity in the two lake types, which could have an important effect on the planktivore populations. For example, the dominant fish planktivores in these lakes (bluegill sunfish) undergo an ontogenetic niche shift (Mittelbach 1981, Mittelbach and Osenberg 1993). Most work in this area concerns two life stages; the juveniles which forage in the littoral zone on benthic prey, and the adults which forage in the pelagic zone on zooplankton (Werner and Hall 1988). In addition, a

younger, larval stage also forages in the pelagic zone on the plankton (Rettig, personal communication). In contrast with adults, larval fish have difficulty securing large *Daphnia* prey (Hansen and Wahl 1981, Tessier 1986) and instead depend on smaller-sized zooplankton. Hence, lake basin geometry can impact planktivore populations by determining both the proportion of littoral zone (juvenile habitat) to open water (adult habitat), and by the presence or absence of a deep-water zooplankton refuge (quality of prey for larval fish versus adults). Our results further suggest that a contrast in secondary production of both large and small prey also exists for lakes which vary in basin shape. Standing crop and productivity of small zooplankton, both greater in shallow lakes, suggests a general improvement in conditions for larval growth and reproduction in this lake type compared to deeper lakes.

An alternative, bottom-up mechanism could also contribute to the differences in algal resource availability as related to lake depth. Mean depth can greatly affect the extent to which turbulent mixing (from wind) will resuspend nutrients from sediments into the water column for use by phytoplankton. Relatively shallow lakes will experience greater resuspension of phosphorus-rich sediments by mixing, which is effectively an increased nutrient loading (internal recycling) for the phytoplankton (Fee 1979). It is likely that this higher nutrient recycling could improve resource richness as perceived by daphniids. For example, Sterner (1993) has demonstrated that a higher growth rate of algae results in higher algal quality for *Daphnia*. A shift in competitive interaction among the algal species and/or changes in biochemical composition of the algae may contribute to the effect. In contrast, nutrient loss by sinking from the epilimnion of deep, stratified lakes (Reynolds 1984, Levine et al. 1986) should not only reduce algal productivity but may

decrease the quality of the algal resource for grazers. Whatever the balance between top-down and bottom-up mechanisms, our results illustrate that resource richness for grazers was consistently better in the shallow lakes, and suggests a general dependence of trophic structure on basin shape.

The differences in resource richness across lakes resulted in very different life histories for the two dominant epilimnetic zooplankters in these lakes. *Ceriodaphnia reticulata* and *Daphnia rosea* exhibited a performance trade-off across this natural resource richness gradient. The species from the richest resource performed best (in terms of r and R_0) in the richer resources compared to the species from the poorest resource. Conversely, the species from the poorest resource performed better in the poorest resource compared to the species from the richest resource. This performance trade-off was due to differences in the life history strategies of these two species. In the richer resources, *C. reticulata* matured faster than *D. rosea* and produced more clutches (of a similar or slightly smaller size) in a shorter period of time. In the poorest resource, *D. rosea* matured faster than *C. reticulata* and produced initially larger clutch sizes.

The cause of this observed performance trade-off across the resource richness gradient may involve changes in both resource quality and quantity. An increase in the specific growth rate of *Daphnia* can be caused by either an increase in the quantity (Tessier and Goulden 1987; Lynch 1989, 1992) or quality (Groeger et al. 1991, Sterner et al. 1993) of resources. To distinguish between these causes, the dilution experiment manipulated only the quantity of the richest resource (i.e. Lower Crooked Lake). The result was that *C. reticulata* performed better than *D. rosea* across all dilutions because *C. reticulata* consistently matured faster and produced more clutches than *D. rosea*. Thus,

the performance trade-off between species was not primarily due to a change in resource quantity, but due to unknown changes in resource quality among lakes. Although the dilution experiment indicates that resource quality underlies the contrast in resource richness between the two lake types, it sheds no light on the nature of that qualitative change. The results also do not exclude the likely possibility that quality and quantity of algal resource are positively correlated across lakes.

A shift in the algal species composition probably contributed to the gradient in resource richness. The richest resource lake (Lower Crooked) contained an extensive array of small algal species, especially dominated by Chlorococcales (personal observation), which are considered highly edible (Porter 1973, 1977; Vanni 1987), and thus a high quality food for Cladocerans. In comparison, the poorest resource lake (Lawrence) was dominated by gelatinous algae and large dinoflagellates (Taylor and Wetzel 1988) which are resistant to consumption and digestion, and benefit from high grazing pressure on more vulnerable algae (Porter 1973, 1977; Vanni 1986; Leibold 1989).

Differences in algal composition among the lakes may also differentially affect species performance through a change in the size-distribution of resources. There is some evidence that the small-bodied *Ceriodaphnia* can capture and utilize small-sized particles more effectively than larger species (Porter et al. 1983, Bogdan and Gilbert 1987, DeMott 1995). Lynch (1978) noted that competition in a natural pond varied seasonally between *C. reticulata* and *D. pulex* and that the algal size-class distribution data before and after this competitive switch indicated a suppression of bacteria and smaller algae when *Ceriodaphnia* was dominant compared to a suppression of larger size classes when *Daphnia* was dominant. If the high resource lakes contain a greater proportion of their

algae in small size classes, then *C. reticulata* would experience quantitatively more resource than *D. rosea*, which could explain why *C. reticulata* did best in high resource lakes. In the low-richness lakes, a larger size distribution of algae would benefit *Daphnia* over *Ceriodaphnia* and could explain why *D. rosea* performed better in the lowest resource compared to *C. reticulata*.

The fact that the resources of the deep and shallow lakes are consistently different throughout the summer suggests the possibility that the zooplankton inhabitants could be adapted to the particular algal assemblage. It is evident that *Daphnia* species differentially utilize (growth and reproduction) algal species in a way that can not be predicted by changes in algae quality, shape or chemistry. For example, Infante and Litt (1985) found that the *Daphnia* species which was present in Lake Washington throughout the year grew and reproduced much better on a larger fraction of the algal species tested than the species which was found only seasonally in the same lake. This would indicate that resource adaptation is possible, even though the mechanism is unclear.

The different life history strategies displayed by the two species across the natural resource gradient reflects adaptation to both their respective predation and resource condition. Body-size differences suggest adaptation to the differences in predation intensity between the two habitats as would be predicted by the size-selectivity and size-efficiency hypotheses (Hrbáček et al. 1961, Brooks and Dodson 1965, Hall et al. 1976). That is, the small body-sized *C. reticulata* are more resistant to fish predation while the larger body-sized *D. rosea* dominate under lower predation intensity because they are better competitors. However, this study also indicates that *C. reticulata* are superior, in terms of r and R_0 , at high resources. Hence, even if the predation regime were not size-

selective, our results suggest that *C. reticulata* would dominate over *D. rosea* in the shallow lakes because of a better ability to exploit high resources and balance a high death rate with a high birth rate. A more general explanation for the dominance of the two species in the two lake types must consider both body-size and a trade-off in exploitative ability at high versus low resource richness.

This adaptation to resource level for these species can be generally expressed as differences in their sensitivity to resource change. Specifically, we define sensitivity as the change in performance (r and R_0) across a gradient of resource richness. The species from the lowest resource had a lower sensitivity to resource change than the species adapted to the highest resource richness. Thus, a cost of adapting to a low resource richness could be a low sensitivity to resource change. This lower sensitivity of *D. rosea* was observed for its performance in both the natural resource gradient and the gradient created by the dilution of the highest resource richness. The performance trade-off across resource richness was pervasive, similarly affecting various aspects of the life history, including clutch size (and average daily fecundity), and time to maturity. Other studies have shown a similar performance trade-off such that species which perform relatively well in a low resource environment do not perform relatively well in a higher resource environment (Goulden et al. 1982, Romanovsky and Feniova 1985, Stemberger and Gilbert 1985, Tessier and Goulden 1987, Bengtsson 1987).

The independent measure of resource richness, SGR, was an excellent predictor of performance, explaining over 90% of the variance in r and R_0 for both species across resource level. It is likely that this bioassay method of measuring resources is robust to phylogenetic distance because the performance of the two zooplankton species

representing two separate genera was well predicted by a *Daphnia* species from a different subgenera (Colbourne and Herbert 1996). Despite these phylogenetic differences, SGR measured during the juvenile period (a four day assessment) was an excellent predictor of overall survival and reproduction. This tight relationship suggests not only that juveniles and adults daphniids perceive the resource environment in much the same way, but that large differences in resource composition among lakes can be explained as a simple gradient in resource richness. The phylogenetic independence of this conclusion and its generality across resource lake types deserves more attention.

Despite the large body of literature which explores the effect of resource quality and quantity on zooplankton life history, there have been no general comparisons of species collected from consistently different resource habitats. Our results suggest that the previously documented effects of lake depth on zooplankton species composition and body-size (i.e. refuge effect) also affects resource richness (including algal quality). We further show that species typically found at opposite ends of this predation/resource gradient are locally adapted to the resource conditions of their typical habitats resulting in a performance trade-off across lake types. We suggest that this resource adaptation can be generally defined as a trade-off in sensitivity to resource richness. The likelihood that resource richness varies in a predictable way with lake basin shape and evidence for species adaptation to a particular natural resource assemblage suggests directions for further research.

SYNTHESIS

It is a well known fact that vertebrate predation has a direct effect on the average body-size of the zooplankton community (Hrbáček et al. 1961, Brooks and Dodson 1965, Hall et al. 1976). Vertebrate predators feed more efficiently on larger, more visible size classes resulting in a community dominated by small-bodied zooplankton (Werner and Hall 1974). Resources also differentially affect zooplankters and could reinforce this pattern if performance changed in a manner similar to predation risk. The three species of Daphniidae examined in this study were from habitats representing a range of predation risk and resource availability.

Though not directly measured in this study, vertebrate predation risk was inferred by the absence (high vertebrate predation risk) or presence (medium) of a deep-water refuge, or the functional absence of a vertebrate predator (low). This gradient in predation risk, as expected, was directly related to changes in body-size. That is, higher fish predation risk was associated with a smaller body-size of the dominant zooplankter. Resource availability (as inferred by individual growth rates), on the other hand, was non-linearly related to fish predation risk and thus body-size (Figure 11).

Chapter 1 explored two lakes (Lawrence, Wintergreen) which demonstrated an inverse relationship between vertebrate predation risk and resource availability. That is, a change in vertebrate predation risk from moderate (Lawrence) to low (Wintergreen)

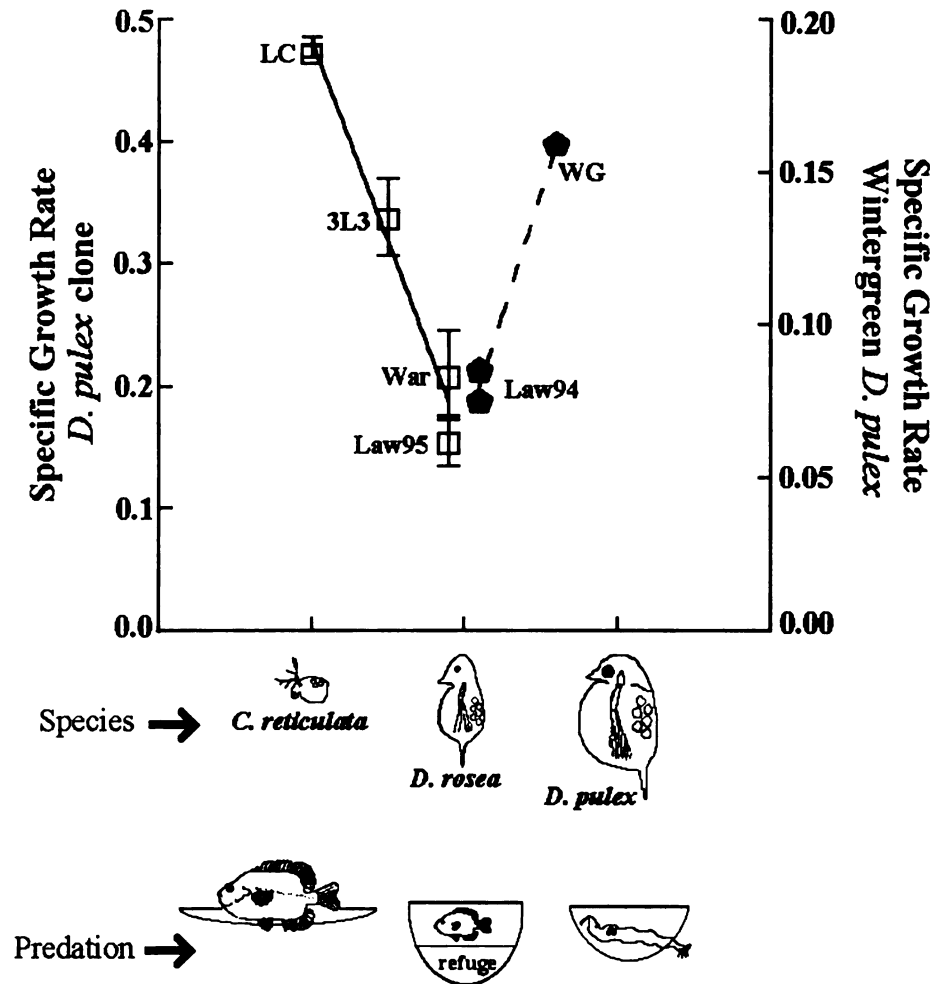


Figure 11 The change in resource availability across a gradient in species body-size and predation risk (see text) measured by either the SGR of a clonal *D. pulex* (solid line, open squares) or by the SGR of the Wintergreen *D. pulex* estimated from length using the length-weight regression for *D. pulex* of McCauley et al. 1990b (broken line, filled pentagons).

was correlated with an increase in resource availability. Though lacking an effective vertebrate predator, Wintergreen Lake does contain a high density of an invertebrate predator (*Chaoborus*, a phantom midge larva) which preferentially forage on the smaller size-classes of zooplankton (gape limited) and select for a larger body-sized community. Resources were not measured independently from the life tables, but higher resource availability was inferred in Wintergreen Lake compared to Lawrence Lake due to a higher SGR of the Wintergreen *D. pulex* (including larger clutch sizes and an earlier time to maturity) in Wintergreen Lake compared to Lawrence Lake. The two species examined demonstrated different sensitivities to low and high resources resulting in a performance trade-off where the species from the lowest resource (*D. rosea*) performed relatively better in that resource while the species from the highest resource (*D. pulex*) performed relatively better in that resource.

Chapter 2 explored four lakes (Lawrence, Warner, Three Lakes III and Lower Crooked) and demonstrated that resource availability was directly related to lake depth and thus refuge availability, which modifies vertebrate predation risk. That is, in lakes of higher predation risk, resources were high while in lakes of moderate predation risk, resources were lower. Resources were independently measured in these experiments by the specific growth rate of a clone of *D. pulex*. Again, I saw that the species pair demonstrated different sensitivities to a resource gradient resulting in a performance trade-off. The species from the lowest resource lake (*D. rosea*) performed relatively better on that poor resource compared to the species from the high resource lake (*C. reticulata*) which performed relatively better on that high resource.

Thus, resource availability decreased from the high vertebrate predation risk

environments (i.e. Lower Crooked, Three Lakes III) to the moderate vertebrate predation risk environments (i.e. Warner, Lawrence) but increased from the moderate predation risk environment (i.e. Lawrence) to the low vertebrate predation risk environment (i.e. Wintergreen, Figure 11). A possible mechanistic explanation for the observed non-linear resource distribution across a gradient of vertebrate predation risk is an overall non-linear mortality regime imposed by a combination of vertebrate and invertebrate predators on the zooplankton. That is, I would speculate that in the low vertebrate predation risk environment, the zooplankton again experience a high mortality risk, especially in the juvenile size-classes, due to the abundance of the invertebrate predator (*Chaoborus*). This high mortality risk could again create high resource availability for the remaining zooplankters via the same trophic cascade effects discussed in Chapter 2.

The species I examined were adapted to their respective resources in the sense that each species always performed better compared to the others in the resource from which they were collected. Whether this reflects a general trade-off in adaptation to a resource richness gradient or a specific local adaption to a particular resource assemblage is untested. However, the simple prediction of the size-efficiency hypothesis which suggests that larger species should always perform best in the absence of fish predation seems insufficient as an explanation for species distribution in the lakes I studied.

APPENDICES

APPENDIX A

KEEPING *DAPHNIA* OUT OF THE SURFACE FILM

Appendix A

Keeping *Daphnia* out of the surface film

Species of the genus *Daphnia* are an important component of planktonic systems. Although all are generalized filter feeders; the different species encompass a broad range of body sizes, behaviors, and seasonal phenologies and they dominate lentic environments worldwide (Fernando et al. 1987, Hrbáček 1987). *Daphnia* bridge the gap between laboratory and field studies because of their ecological importance and convenient life histories (cyclic parthenogens with a short generation time). As such, *Daphnia* are model organisms for addressing both ecological and evolutionary questions (Edmondson 1987).

However, some *Daphnia* species are difficult to culture due to a tendency to become trapped in the surface film. Though the exact cause of this entrapment is unclear, these more vulnerable *Daphnia* typically have some or all of the following characteristics: they occupy epilimnetic habitats, behaviorally remain near the surface, are laterally compressed (Wesenberg-Lund 1926) or possess taller helmets (e.g. *D. cucullata*, *D. rosea*) compared with more rounded species (e.g. *D. magna*, *D. pulex*).

In a survey of *Daphnia* literature from the last nine years, I found a significantly unequal representation of species studied in the field versus the laboratory (Table 3). Despite a rich diversity of forms within this genus, only a few, mostly 'pond-like' species,

Table 3 Results of a literature search (Cambridge Life Sciences, abstracts from 5,000 serial publications) of papers published between 1986-1995. This search included all papers with *Daphnia* in the abstract (excluding toxicology studies) and separated the *Daphnia* species, where possible, into categories of study location: laboratory or field.

The field category includes genetic work as indicative of species distribution.

Phylogenetically similar species were lumped as noted if sample sizes were small and the species had a similar lab/field partition. Pearson $\chi^2=138.0$, Monte Carlo estimated $P<0.000$ with a 99% CI of 0.000-0.0005 after 10,000 table resamplings.

	field	laboratory
<i>D. ambigua</i>	0	13
<i>D. carinata</i>	8	5
<i>D. cucullata</i>	16	10
<i>D. galeata</i>	25	19
<i>D. galeata mendotae</i>	31	7
<i>D. hyalina</i>	36	16
<i>D. longispina</i>	36	9
<i>D. magna</i>	20	104
<i>D. obtusa</i>	8	8
<i>D. pulex</i>	50	79
<i>D. pulicaria</i> + <i>D. catawba</i>	34	14
<i>D. retrocurva</i> + <i>D. parvula</i>	13	2
<i>D. rosea</i>	14	6

are routinely used in laboratory studies. For example, *D. magna* was well studied in the laboratory (104 studies) but poorly represented in field studies (20 studies). On the other hand, *D. galeata mendotae* was frequently studied in the field (31 studies) but much less well studied in the laboratory (7 studies). The poorly studied forms may possess morphologies, phylogenies, or behaviors quite different from the frequently studied species and thus this unbalanced representation may bias our understanding of *Daphnia*.

An easy solution for surface film entrapment is to decrease surface water tension by adding a surfactant. The technique of using cetyl alcohol to reduce surface tension has been used widely in Europe (e.g., at the Max-Planck-Institut für Limnologie at Plön), but the idea's originator is unknown (W. Lampert, personal communication). Cetyl Alcohol [$\text{CH}_3(\text{CH}_2)_{14}\text{CH}_2\text{OH}$], a white waxy solid, is not water soluble. Clinical studies have shown that this surfactant, which is commonly used in cosmetics, is nontoxic, practically nonirritating when applied to the skin and eyes of rabbits, and not mutagenic (Johnson 1988). Thus, use of cetyl alcohol to culture forms susceptible to surface film entrapment should be greatly beneficial with no expected negative effects. However, I could find no published paper that cites the use of cetyl alcohol to decrease *Daphnia* (or other zooplankton) surface film entrapment.

In this study I examine the effect cetyl alcohol has on *Daphnia* life histories. A species that suffers from surface film problems, *Daphnia rosea*, was studied with the expectation that cetyl alcohol should improve growth and reproduction by decreasing the time spent trapped in the surface film. In addition, *Daphnia pulicaria* was studied with the expectation that cetyl alcohol should not affect growth and reproduction because this species is rarely trapped by the surface film.

The clonal cultures of *D. pulicaria* and *D. rosea* used in this experiment were both isolated from Gull Lake (Kalamazoo Co., MI) in 1991 and cultured under standard laboratory conditions (Tessier and Consolatti 1989). Food levels were kept high (30,000-40,000 cells ml⁻¹ of *Ankistrodesmus falcatus*) and the animal culture was a filtered 1:1 mixture of water from Gull and Pleasant (Barry Co., MI) lakes.

The effect of cetyl alcohol on *D. rosea* and *D. pulicaria* was examined using cohort life tables. The two experiments each contained three treatments of 25 neonates (<24 hours old) placed in an equal volume of water (100ml) in individual Erlenmeyer flasks (*D. rosea*) or beakers (*D. pulicaria*) having a surface area of 2.28 cm² and 24.88 cm², respectively. The three treatments were a control (no cetyl alcohol), a low (1.26 ± 0.12 mg), and a high (10.6 ± 1.00 mg) amount of cetyl alcohol, which was gently dropped onto the surface water where it floated. However, in the high treatments, I commonly found cetyl alcohol flakes near the bottom of the glassware within 24 hours.

I started the *D. pulicaria* life tables on 22 January 1995 and the *D. rosea* life tables on 6 March 1995. I changed the water and food daily and fed the animals 30,000 *A. falcatus* cells ml⁻¹ day⁻¹. The glassware was rinsed daily with distilled water and changed every third day. The animals were incubated at 24°C with a 16:8 L:D photoperiod.

The data recorded for each individual included frequency of entrapment in the surface film, survivorship, and fecundity. Every day, I removed trapped animals from the surface film by dropping water from a pipette onto the animal. Survivorship was measured daily throughout the experiment until there were obvious differences among treatments; day 24 for *D. rosea* and day 39 for *D. pulicaria*. Only clutch sizes of adult molts one through four were recorded because later reproduction contributes little to the

cohort growth rate (Jacobs 1978). In each treatment, I measured the length of five neonates from the fifth clutch of at least four haphazardly chosen mothers. Length was the distance from the base of the tail spine to the most anterior part of the head. I then dried these neonates at 60°C overnight and weighed them using a Cahn electrobalance (0.1 μ g). In addition, I measured adult length at the end of each experiment.

The same statistical analysis was done for the two experiments using SAS (1989). The Lifetest procedure tested for age-specific survivorship and time to maturity differences between the control and the two cetyl alcohol treatments using the Log-rank test (Fox 1993). A repeated measures analysis of variance (ANOVA) examined the effect of cetyl alcohol on the size of clutches one through four. One-way ANOVA contrasted treatment effects of surface film entrapment, size and weight of fifth clutch neonates, and adult length at end of experiment. ANOVA assumptions were supported. The instantaneous rate of increase (r) was iterated using a variation of Newton's approximation for each life table from the stable age equation (Lotka 1956):

$$1 = \sum l_x m_x e^{-rx}.$$

As an alternate estimate of fitness, the net reproductive rate (R_0) was calculated:

$$R_0 = \sum (l_x m_x).$$

Where l_x is age-specific survivorship, m_x is age-specific fecundity, and x is the time interval in days. I wrote a SAS macro program to bootstrap the 95% confidence intervals around r and R_0 with 1,000 re-samples of 25 randomly chosen individuals with replacement. A copy of the SAS bootstrapping program is available from me or via the World Wide Web at <http://kbs.msu.edu/~Desmarais/bootstrap.html>.

The most vulnerable period for surface film entrapment in the *D. rosea* control treatment was during the juvenile stage, because surface film entrapment decreased markedly after the first week. The addition of cetyl alcohol dramatically reduced *D. rosea* surface film entrapment from 1.91 trappings individual⁻¹first week⁻¹ to almost no entrapment (Table 4, df=2, F=34.50, P<0.000). Adult *D. rosea* survivorship was similar in the control and low cetyl alcohol treatment with >80% of the animals alive after three weeks. In the high cetyl alcohol treatment, adult survivorship was much lower with <10% of the animals alive after three weeks (Figure 12, df=1, $\chi^2=30.75$, P=0.0001). *Daphnia rosea* matured a day earlier when cetyl alcohol was added at low or high levels compared to the control (Table 4, low: df=1, $\chi^2=5.08$, P=0.024; high: df=1, $\chi^2=3.05$, P=0.081). Clutch sizes were similar in the control and high treatment but smaller than the clutch sizes of the low treatment (Figure 13, df=2, F=6.53, P=0.003).

Overall, the *D. rosea* from the low cetyl alcohol treatment outperformed those from both the control and high treatment (Table 4). The larger r and R_0 in the low treatment was due to a larger average clutch size and faster maturation time. The performance measure, r , was similar for the control and high treatment even though the high treatment had a lower survivorship and a faster rate of clutch production while the control treatment had a higher survivorship and a slower clutch production. However, the cumulative measure of performance, R_0 , was smaller in the high treatment compared to the control because of increased adult mortality.

The neonates produced during the experiment in the three treatments had a similar length and weight (Table 4, length: df=2, F=1.82, P=0.20 and weight: df=2, F=1.95,

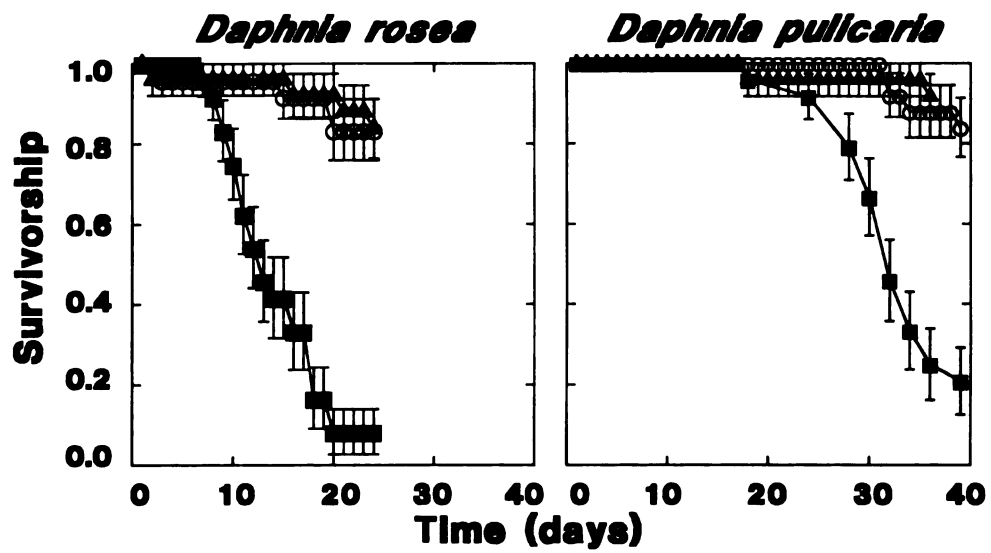


Figure 12 The age-specific survivorship of *D. rosea* (left) and *D. pulicaria* (right). All error bars indicate ± 1 standard error unless otherwise noted. Symbols: open circle=control, shaded triangle=low treatment, closed square=high treatment.

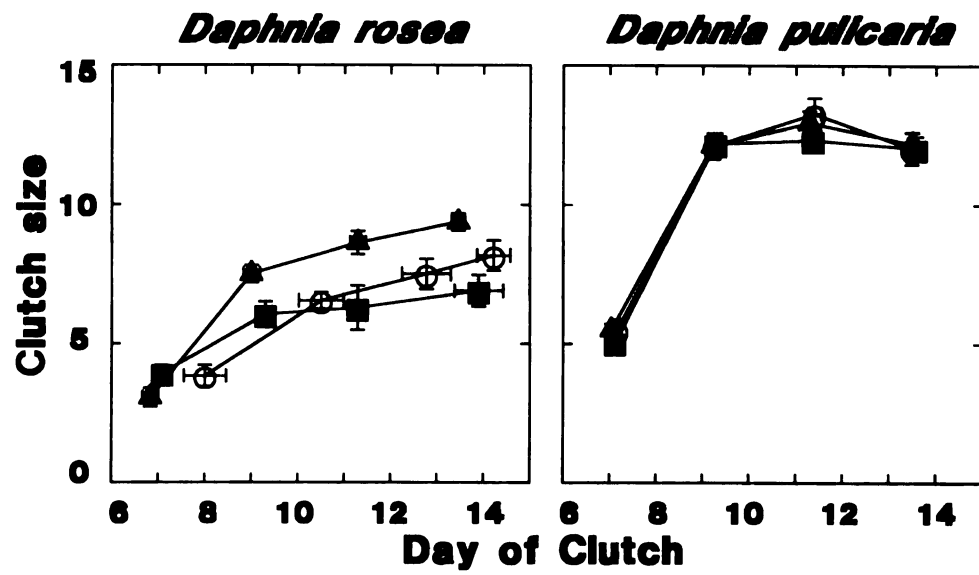


Figure 13 Clutch size, through clutch 4, plotted against the average day of the clutch for *D. rosea* (left) and *D. pulicaria* (right). Symbols as in Figure 12.

Table 4 Life history parameters (means $\pm$ 1 S.E., with sample size in parenthesis) of *Daphnia* to the three cetyl alcohol treatments (see text).

	control	low	high
<i>D. rosea</i>			
surface film entrapment (trappings ind. ⁻¹ first week ⁻¹)	1.91 $\pm$ 0.32 (23)	0.04 $\pm$ 0.04 (24)	0.00 $\pm$ 0.00 (24)
time to maturity (days)	8.0 $\pm$ 0.45 (23)	6.83 $\pm$ 0.16 (24)	7.08 $\pm$ 0.16 (24)
r [95% CI] (day ⁻¹)	0.29 [0.26-0.31]	0.33 [0.31-0.34]	0.29 [0.26-0.31]
R ₀ [95% CI] (day ⁻¹)	18.6 [14.6-22.1]	26.3 [23.4-28.7]	14.5 [10.6-18.1]
adult length (mm)	2.34 $\pm$ 0.029 (20)	2.41 $\pm$ 0.002 (19)	2.35 $\pm$ 0.00 (1)
neonate length (mm)	0.75 $\pm$ 0.01 (5)	0.73 $\pm$ 0.009 (5)	0.72 $\pm$ 0.008 (5)
neonate weight (mg)	2.58 $\pm$ 0.06 (5)	2.35 $\pm$ 0.14 (5)	2.27 $\pm$ 0.12 (5)
<i>D. pulicaria</i>			
surface film entrapment (trappings ind. ⁻¹ first week ⁻¹)	0.36 $\pm$ 0.16 (25)	0.00 $\pm$ 0.00 (24)	0.00 $\pm$ 0.00 (25)
time to maturity (days)	7.16 $\pm$ 0.09 (25)	7.04 $\pm$ 0.04 (24)	7.12 $\pm$ 0.07 (25)
r [95% CI] (day ⁻¹)	0.38 [0.37-0.39]	0.38 [0.37-0.39]	0.37 [0.37-0.38]
R ₀ [95% CI] (day ⁻¹)	42.0 [39.3-44.6]	43.4 [41.8-45.1]	41.6 [39.5-43.7]
adult length (mm)	2.93 $\pm$ 0.03 (21)	2.94 $\pm$ 0.022 (22)	2.74 $\pm$ 0.06 (5)
neonate length (mm)	0.68 $\pm$ 0.01 (5)	0.69 $\pm$ 0.01 (4)	0.68 $\pm$ 0.01 (4)
neonate weight (mg)	2.67 $\pm$ 0.07 (5)	2.68 $\pm$ 0.18 (4)	2.59 $\pm$ 0.09 (4)

P=0.18). Adult length at the end of the experiment was the same between the control and low treatment (Table 4, $df=1$, $F=1.51$, $P=0.24$). The high treatment was not included in the length analysis because of the small sample size ($n=1$) at the end of the experiment.

As expected, *D. pulicaria* individuals experienced little surface film entrapment (Table 4). Survivorship in the low concentration of cetyl alcohol was similar to the control (Figure 12, $df=1$, $\chi^2=0.62$, $P=0.43$), but adult survivorship in the high treatment decreased dramatically after three weeks (Figure 12, $df=1$, $\chi^2=22.15$, $P=0.0001$). By day 34, survivorship in the high treatment was <20% while the control and low treatments were both >80%. *Daphnia pulicaria* matured at the same time as all three treatments (Table 4, low: $df=1$, $\chi^2=1.30$, $P=0.25$; high: $df=1$, $\chi^2=0.15$, $P=0.69$). Overall, cetyl alcohol had no effect on the first four clutch sizes (Figure 13, $df=2$, $F=2.68$, $P=0.72$). Performance, as measured by r was also similar across treatments (Table 4). However, the cumulative measure of performance, R_o , was slightly lower in the high treatment due to decreased survivorship (Table 4). The fifth clutch neonate length and weight were similar across treatments (length: $df=2$, $F=0.23$, $P=0.80$ and weight: $df=2$, $F=0.16$, $P=0.86$). In addition, cetyl alcohol did not affect adult length (Table 4, $df=2$, $F=0.79$, $P=0.46$).

In conclusion, a low level of cetyl alcohol is highly effective in reducing the surface film entrapment of a *Daphnia* species typically susceptible to such a problem (e.g., *D. rosea*). The decreased time spent in the surface film shortened maturation time and increased clutch size, most likely due to reduced stress and increased food intake. In a species that does not exhibit surface film problems (e.g. *D. pulicaria*), a low level of cetyl

alcohol had no effect on the measured parameters (Table 4), indicating that this substance is not toxic to *Daphnia* in low quantities.

An unexpected result of this study was that the high cetyl alcohol treatments decreased survivorship in both species. This strong response to high levels of cetyl alcohol is most likely some type of interference effect because cetyl alcohol was commonly seen on the bottom of the container after 24 hours. Perhaps, because cetyl alcohol is not water soluble, the crystals in the water were ingested and caused damage to the gut or the filtering appendages. The increased mortality due to the high cetyl alcohol treatment occurred faster for *D. rosea* compared to *D. pulicaria*, 50% mortality was reached on day 13 and 32, respectively. This could be the result of glassware surface area differences creating a higher surface area concentration of cetyl alcohol in the flasks used with *D. rosea* compared to the beakers used with *D. pulicaria*. If surface area concentration is the relevant measure, then the concentration of the low *D. rosea* treatment (0.55 mg cm^{-2}) is similar to the concentration of the high *D. pulicaria* treatment (0.43 mg cm^{-2}). However, the increased mortality seen in the high *D. pulicaria* treatment was not seen in the low *D. rosea* treatment, but this could have been because the *D. rosea* experiment was ended earlier than the *D. pulicaria* experiment.

The high cetyl alcohol treatments also reduced clutch size in both species. This effect is clear in the *D. rosea* experiment because the clutch sizes of the high treatment were equal to or lower than the control, which apparently was strongly affected by the stress of surface film entrapment. Thus, a high level of cetyl alcohol negates the benefit of eliminating surface film entrapment, with the added cost of increased mortality.

I recommend the use of a low level ($\sim 10 \mu\text{g ml}^{-1}$, or $50 \mu\text{g cm}^{-2}$) of cetyl alcohol

when working with *Daphnia* species susceptible to surface film problems. In addition, I also recommend the use of a culturing container which minimizes surface film area (e.g. Erlenmeyer flask). Cetyl alcohol was effective in preventing *Daphnia* entrapment in the surface film and resulted in improved performance in terms of clutch size and time to maturity, with no negative effect on survivorship. Although cetyl alcohol did not inhibit performance at low concentrations, investigators should be cautious with the concentration applied. At high concentrations, cetyl alcohol can decrease individual reproduction and survival. Because the mechanism of this inhibition is unknown; it is prudent to assume that threshold concentrations may vary with species and other environmental conditions.

APPENDIX B

BOOTSTRAPPING PROGRAM

APPENDIX B

BOOTSTRAPPING PROGRAM

BOOTSTRAPPING PROGRAM INTRODUCTION

The program, designated RRO.SAS, to bootstrap instantaneous growth rates (r) and net reproductive rates (R_0) was modified by K. H. Desmarais from a general bootstrapping routine written by S. J. Tonsor on 12-Oct-1993 for SAS version 6.07 running in the VMS operating system. To obtain this program and supporting files via the world wide web, see the internet address: <http://kbs.msu.edu/~desmarais/bootstrap.html>.

The supporting files needed to run this SAS job are:

- 1.)FILEIN.IPT: specifies the raw data file from which rro.sas will bootstrap.
- 2.)PARAMS.IPT: defines important macro-variables used throughout rro.sas.
- 3.)RROPROC.IPT: the procedure which calculates a r and R_0 values from each bootstrapped data set.
- 4.)RROVMSOP.IPT: VMS command file which limits version numbers of files created during the bootstrapping program.
- 5.)a raw data file, you create by doing the following (see example: RAWDATA.DAT):
 - A.) Enter your raw life table data in the following format (the data must be contained in a file format accessible to the sas version specific to your operating system). Enter the data with each row representing an individual in the life table. Reading across each row from left to right, the columns are: the number designation of that individual(indiv), the daily individual fecundities(&varstri, see params.ipt for specifics), the day of death(dod), and whether or not that individual was censored(censored).

Daily fecundity is the number of young born per individual per time interval. The number of daily fecundity columns for all individuals will be the same and equal to the maximum age(maxage) of individuals in the life table (or the maximum age of fecundity). Note that the time intervals must be uniform across the life table.

When an individual dies, enter a period for each daily fecundity until the end of the data set(maxage), so that average fecundities will be calculated as number of young born per individual alive.

The censored data (1 or 2) tells SAS, if '2', that individual died normally. If '1', then that individual was not terminated by natural death (say accidentally lost or

the life table was ended before all individuals died). Using proc lifetest, the product-limit method was chosen to calculate survivorship.

B) Modify FILEIN.IPT and PARAMS.IPT according to the directions contained in each file.

C) Check RROVMSOP.IPT for necessary changes depending upon your operating system.

NOTE, the files RRO.SAS and RROPROC.IPT should not need any modifications.

RRO.SAS - Main Bootstrapping Program

```

/*Note: all comments not part of the main program and supporting files are designated
between star-slashes. */

%include 'rrovmsop.ipt';      /*This bit of code is needed with the VMS operating */
                             /*system to limit the existing versions of work files. */

%include 'params.ipt';       /*Params tells sas how many bootstrapped data sets */
                             /*of what size you want. It also defines other */
                             /*macro-variables used in the program. */

Data sasuser.boot0 (replace=yes); /*The raw data set is read into the library */
                                /*sasuser with the name of boot0. */

%include 'filein.ipt';       /*Reads in the raw data, using infile and input */
run;                          /*statements. */

%macro bootie;               /*This macro directs the bulk of the program. The
                             output is in the rro.lis file, and will contain:
                             1.)the mean of the bootstrapped r-values
                             2.)average survivorship and fecundity of the raw
                                data with standard error or confidence intervals
                             3.)the r and  $R_0$  values calculated from the raw data set
                             4.)the PROC UNIVARIATE output on the adjusted r and
                                 $R_0$  values
                             5.) the 95% confidence intervals for both r and  $R_0$  */

options nodate linesize=80;  /*For a more detailed log file during troubleshooting,
add mprint mlogic and symbolgen to the options list. */

%local EYE;
```

```

%do eye = 1001 %to 1000+&NSAMPLES; /*This loop repeatedly, randomly */
data boot&eye (drop = choice); /*subsamples with replacement from the raw data*/
  retain seed &lastseed; /*set &nobserva of times to create a bootstrapped*/
  call ranuni(seed,rand0); /*data set that rroproc.ipt uses to iterate r and R0.*/
  CHOICE = int(rand0 * n) + 1; /*This loop continues until it has created */
  set sasuser.boot0 point=choice nob=n; /*&nsamples of bootstrapped data sets */
  BOOT = &eye;
  i + 1; /*Note: the reason the eye loop starts at */
  if i > &nobserva then stop; /*1000 is due to the way that SAS stores and */
  output; /*retrieves temporary work files. */

/*Defines the seed for starting each new */
/*bootstrapped data set by using the last */
data _null_; set boot&eye; /*seed chosen in the previous bootstrapped */
/*data set. */

  if _n_=&nobserva then call symput('lastseed',seed);
run;

/*After each bootstrapped data set is */
%include 'rroproc.ipt'; /*created, rroproc is called on to calculate the */
%end; /*r and R0 of each bootstrapped data set. */

data zllboots; set curr1001; /*All bootstrapped estimates of r and R0 are */
%local el; /*concatenated (appended) in this loop to */
%do el = 1002 %to 1000+&nsamples; /*create the file work.zllboots which will */
  data zllboots; /*contain all of the bootstrapped r and R0 values */
  set zllboots curr&el; /*when the loop is finished. */
run;
%end;

data zbmean; set zllboots;
proc means noprint mean; /*The means of the bootstrapped r and R0's are */
var mltr4 rosum; /*calculated from zllboots and called 'mltr' or */
output out = zbmean /*'rosum' and output to the data set work.zbmean.*/
  mean = mltr mrosum;
run;
proc print; title 'Mean of the Bootstrapped r & Ro-values';

/*Defines 'mltr' as a macro-variable called */
data _null_; set zbmean; /*'bootmean.'(mean of the bootstrapped r's) */
if _n_=1 then call symput('bootmean',mltr); /*and defines 'rosum' as the macro- */
if _n_=1 then call symput('robmean',mrosum); /*variable 'robmean'. */
run;

data boot&eye;set sasuser.boot0; /*This statement defines the raw data set to */

```

```

/*be used by rroproc.ipt. This final run of */
%include 'rroproc.ipt'; /*rroproc.ipt calculates the r and R0 value */
/*from the raw data set. Then symput defines */
data _null_; set curr&eye; /* them as the macro-variables 'realr' and 'realro' */
if _n_=1 then call symput('realr',litr4);
if _n_=1 then call symput('realro',rosum);
proc print; title 'The r & Ro-value Calculated from the Raw Data Set';
run;

data fecund;set boot&eye; /*These statements print the fecundity and */
proc means n mean stderr; /*standard error of the raw data to the lis file. */
var &varstri;
title 'Fecundity Summary Statistics from the Raw Data Set';
run;

data survdat;set curv2; /*These statements print the survivorship and */
if _censor_=1 then delete; /*upper and lower confidence intervals, */
proc print; /*calculated from the raw data, to the lis */
/*file. */

title 'Survival Summary Statistics from the Raw Data set';
run;

data zcalc; set zllboots; /*This adjusts each bootstrapped r and R0 value */
adjustr=litr4-&bootmean+&realr; /*by subtracting the mean of the bootstrapped */
adjustro=rosum-&robmean+&realro;
run; /*r or R0's and adding the r or R0 value from */
/*the raw data. */
/*This adjusts the bias in the bootstrapped */
/*estimates. REF: Noreen, E.W. 1989. */
/*Intensive methods for testing hypotheses: */
/*an Introduction. Wiley & Sons, New York. */

data distrib; set zcalc; /*This produces the output describing the */
options linesize=80; /*adjusted bootstrapped r and R0 value */
proc univariate plot normal; /*distribution. See the rro.lis file for output. */
title "&mytitle"; /*Modify &mytitle in the file PARAMS.IPT. */
title2 "Output from bootstrap shift of &nsamples bootstrapped data sets";
title3 "and &nobserva observations per data set";
var adjustr adjustro; /*Note: the double quotes allow sas to */
/*resolve macro-variables. */

output out=percent pctlpts=2.5 97.5 pctlpre=p_r p_ro;
run; /*This calculates the 95 percentiles.

data last; set percent;
proc print; /*Prints and labels the 95 percentiles. */

```

```

title2 'Note: output for r = p_r; output for Ro = p_ro';
title3 '    with percentiles 2.5 (2_5) and 97.5 (95_5)';
run;

```

```

data reallast;set zllboots;                                /*These statements are optional, and */
proc print;                                                /*print the full file of r and R_o's */
title "&mytitle";                                          /*created from each bootstrapping */
run;                                                        /*routine.                          */

```

```

%mend bootie;
%bootie;

```

FILEIN.IPT - Supporting File 1

/*This file defines the raw data set from which rro.sas will bootstrap.

The INFILE statement specifies the name of the raw data file. The INPUT statement specifies the variables sas will read from the data file. Indiv is the designation number of the individual, &varstring resolves to a list of the daily fecundities (see params.ipt for details), dod is the day the animal died, and censored indicates whether or not that animal died a natural death.

MODIFY:

- 1.)the infile statement by entering the name of your data file in single quotes.
- 2.)firstobs=4 accordingly, this statement specifies the line location at which SAS will begin reading the data. (This is convenient if you want to make comments or label each column in the data set so that the data doesn't start on the first line. This statement is optional otherwise. See file rawdata.dat for an example)

*/

```

INFILE 'rawdata.dat' firstobs=4;
INPUT indiv &varstri dod censored;

```

PARAMS.IPT - Supporting File 2

/*This file defines some important macro-variables used throughout rro.sas.

NSAMPLES = the number of bootstrapped data sets to be drawn

NOBSERVA = the number of randomly drawn observations per data set

MAXAGE = the last day on which fecundity occurred(or this can also be the last day of the life table)

LASTSEED = any positive integer of less than 10 digits.

In each of the eye loops in rro.sas, the retain statement needs an initial seed to start the random number generator. In eye=1, 'lastseed' is the number specified below. In the remainder of the eye loops, 'lastseed' will be equal to the last 'seed' number from the previous execution of the eye loop.

MYTITLE = the first label for the output univariate data (this is optional, if you don't want to specify this line, just put a blank in the parenthesis)

Varstri is a string of variables which will be used throughout the program to reference the fecundity input variables from the raw or bootstrapped data sets. The %let addelims and varstri statements initialize these variables. Addelims adds a delimiter(space) between the variables. The rest of varstri is defined in the macro %stri program at the end of this file.

You must modify these five macro-variables accordingly:

*/

%let NSAMPLES = 1000;

%let NOBSERVA = 40;

%let MAXAGE = 14;

%let LASTSEED = 356893;

%let MYTITLE = %str(Data file = RAWDATA.DAT, example data, 9-March-1995);

%let addelims=%str(); /*These two statements initialize these variables and */
 %let varstri= ; /*are used in macro stri which requires no modification.*/

%macro stri; /*Creates a string of variables used throughout */
 /*the program to reference daily fecundity variables. */

%do age=1 %to &maxage;

 %let varstri=&varstri &addelims m&age;

%end;

%mend stri; /*Varstri resolves to the following (if maxage=5): */

%stri; /* m1 m2 m3 m4 m5 */

RROPROC.IPT - Supporting File 3

%macro calcr; /*Goal: iterate r, output as 'litr4' in data set r4 and calculate R_0 , output as 'dayro' in data set R, merge the two and output in data files curr&eye.

Each time the random number generator has created a bootstrapped file from the raw data file, this macro uses that bootstrapped data set boot&eye, in the column format of indiv, m1...m(&maxage), day of death(dod) and censored, to:

- 1.)calculate mean fecundity and survivorship schedules.
- 2.)iterate the instantaneous growth rate (r).
- 3.)iterate the net reproductive rate (R_0).

This file is also called on later in rro.sas to calculate r & R_0 from the raw data set.

```

proc means noprint mean;          /*Fecundity means are calculated and output */
  var &varstri;                   /*as a row of average fecundities. Note that */
  output out=curv mean=&varstri;   /*correct data entry is important, see filein */
  title;                          /*for instructions. */

proc transpose data=curv out=curv1 name=mx;
  var &varstri;                   /*Changes the row of average fecundities to a */
                                   /*column designated col1. */

proc lifetest width=1 method=pl ninterval=&maxage
  data=boot&eye outs=curv2 noprint;
  time dod*censored(1);          /*Calculates average survivorship using the */
run;                             /*product-limit(pl) method. See pg. 1044 in */
                                   /*the SAS/STAT User's Guide for details. */

data curv3; set curv1;           /*Designates a variable 'totcol' which */
  totcol+1;                      /*starts at one and adds one for each line. */
run;                             /*This is needed to merge the fecundity and */
                                   /*survivorship data sets. */

data curv4;                      /*The output from Proc Lifetest defines the */
set curv2(keep=dod survival _censor_); /*first interval as zero and the next */
                                   /*interval two, the if/then statement changes */
if dod=0 then dod=1;             /*the zero interval to one. Also, the output */
day=dod;                        /*contains lines of the censored data, these */
if _censor_=1 then delete;       /*are not needed and are deleted here. */
run;

data _null_; set curv4;          /*Proc Lifetest only calculates and outputs */
call symput ('surv'||left(_n_),survival);/*survival data when the survival has */
run;                             /*changed from the previous day. However, the */
                                   /*data used to iterate r must have daily */

```

```

proc datasets;
modify curv3;
rename totcol=day;
rename col1=fec;
quit;

data work.curv5;
merge work.curv3 work.curv4;
by day;
run;

data curves; set curv5;
if survival ne . then
do;
newsurv=survival;
x+1;
end;
else
newsurv=symget('surv' || left(x));
run;

data curves; set curves(keep=day fec newsurv);
run;

data R; set curves;
dayro = fec * newsurv;
proc means noprint sum;
var dayro;
output out=drosum
sum=rosum;
run;

data drosum; set drosum(keep=rosum);
run;

data curves; set curves;
proc means noprint sum;
var fec;
output out = dfecsum

```

/* survivorship, so each unique survivorship */
 /* output from proc lifetest is designated as */
 /* a sequential macro variable surv1,surv2,etc. */
 /* Totcol is renamed 'day' so the fecundity and */
 /* survivorship datasets can be merged. Also, */
 /* 'col1' is renamed 'fec', this column was */
 /* created from transposing the fecundity data. */
 /* Finally, this merges the fecundity and */
 /* survival datasets. NOTE: the days */
 /* on which the survival did not change will be */
 /* filled with a period as merging by day. */
 /* The pl method only calculates and outputs */
 /* changes in survival, the days with no change */
 /* contain a period in the survival column. */
 /* The if/then commands here reference the */
 /* macro-variable 'survx' to fill in the days */
 /* where survivorship was not altered with the */
 /* last value of survivorship. This is done by */
 /* incrementing x when there is a change in */
 /* survival. Thus, 'newsurv' contains the */
 /* old survivorship values with the periods */
 /* replaced by the last previous survival value */
 /* The keep statement puts the day, fecundity, */
 /* and survivorship variables into the file */
 /* work.curves. */
 /* R_o is calculated here and output as the variable */
 /* 'rosum' in the file drosum. */
 /* This line eliminates all variables except */
 /* in the file drosum. */
 /* This calculates the sum of fecundity and */
 /* outputs it as a variable 'fecsum'. This is */
 /* important if your data set has low fecundity */
 /* and it is possible that some bootstrapped */

```

sum = fecsum; /*datasets contain no reproduction. This */
run;title; /*sets up a way to circumvent the r-iteration. */

data _null_; set dfecsum; /*This creates macro-variable 'sumfec' from */
if _n_=1 then call symput('sumfec',fecsum); /*the variable 'fecsum'. */
run;

%if &sumfec>0 %then /*If there is fecundity, then the if/then statement is*/
%do; /*true and the following do/end statement will */
/*iterate r. The data set 'curr&eye' will contain */
/*the final r-value as the variable 'litr4' */

data iter1;
set curvs; /*The procedure used to iterate r was adapted */
d=fec*newsurv; /*from a method based on Newton's */
e=day*d; /*approximation suggested by Chuck Bell, */
/*former Michigan State University, */
/*Zoology 892 student. */

proc means noprint sum;
var d e;
output out=sum1 sum=sumd sume;
run;

data r1; set sum1;
lnd=log(sumd); /*Note here that 'log', according to SAS, is the */
litr1=(sumd*lnd)/sume; /*natural log. */
call symput ('r',litr1);
run;

%do jay=2 %to 4; /*Four iterations where chosen here as sumg */
data sum&jay;set iter1; /*typically converges to one by that iteration. */
g=2.7182818**(-&r*day)*d;
h=g*day;

proc means noprint sum;
var g h;
output out=sum&jay sum=sumg sumh;
run;

data r&jay;set sum&jay;
lng=log(sumg);
litr&jay=&r+((sumg*lng)/sumh);
call symput ('r',litr&jay);
run;
%end;

```

```

data r4; set r4(keep=litr4);
run;

data curr&eye;                                /*This procedure merges each r and R0 dataset */
merge work.r4 work.drosum;                    /*and are the output data sets referenced in the */
run;                                           /*concatenation procedure. */
%end;

%else
%do;                                           /*If sumfec > 0 is false, this else statement */
data curr&eye;                                /*creates an empty data set, indicating that r */
run;                                           /*was negative infinity (i.e. fecundity was zero), */
%end;                                         /*which will be read as '.' when concatenated. */
                                           /*If used, the .lis file will contain a variable */
%mend calcr;                                /*count which tallys the # of missing values. */

%calcr;

```

RROVMSOP.IPT - Supporting File 4

/*This file does the following:

- 1.)the data statements create empty data sets which are needed in the following VMS commands. RROPROC.IPT creates a version of these data files during each execution of the eye loop in RRO.SAS.
- 2.)The x 'set file...' statements limit the number of existing versions of each of the files listed in the data statements to one (or two). This decreases the amount of storage space used during the execution of rro.sas (e.g.: if &nsamples=1000, then ~21,000 work files would be created during rro.sas' execution without rrovmsop.ipt, compared to ~2,000 files with rrovmsop.ipt). However, note that even if rrovmsop.ipt is not included, the sas work directory IS deleted after a successful execution of the program, though run-time is slower.

```

data curv; data curv1; data curv2; data curv3; data curv4; data curv5; data curves;
data curvs; data dfecsum; data iter1; data r; data r1; data r2; data r3; data r4;
data sum1; data sum2; data sum3; data sum4; data zllboots; run;

```

```

x 'set file sas$worklib:curv*.saseb$data/version=1';
x 'set file sas$worklib:dfecsum.saseb$data/version=1';
x 'set file sas$worklib:iter1.saseb$data/version=1';
x 'set file sas$worklib:r*.saseb$data/version=1';
x 'set file sas$worklib:sum*.saseb$data/version=1';
x 'set file sas$worklib:zllboots.saseb$data/version=2';
x 'set file sas$worklib:r.saseb$data/version=2';

```

RAWDATA.DAT - Supporting File 5, example data file

in	1	2	3	4	5	6	7	8	9	10	11	12	13	14	dod	cens
1	0	0	0	0	0	0	0	0	0	.	.	.	.	.	10	2
2	0	0	0	0	0	0	1	.	.	.	.	.	.	.	8	2
3	0	0	0	0	0	0	0	0	0	.	.	.	.	.	10	2
4	0	0	0	0	0	0	0	0	.	.	.	.	.	.	9	2
5	0	0	0	0	0	0	4	0	1	0	0	.	.	.	12	2
6	0	0	0	0	0	0	4	0	6	.	.	.	.	.	10	2
7	0	0	0	0	0	0	3	0	0	.	.	.	.	.	10	2
8	0	0	0	0	0	0	0	0	0	.	.	.	.	.	10	2
9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	14	1
10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	14	1
11	0	0	0	0	0	0	.	.	.	.	.	.	.	.	7	2
12	0	0	0	0	0	0	0	0	0	0	0	0	0	.	14	2
13	0	0	0	0	0	.	.	.	.	.	.	.	.	.	6	2
14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	14	1
15	0	0	0	0	0	0	0	4	.	.	.	.	.	.	9	2
16	0	0	0	0	.	.	.	.	.	.	.	.	.	.	5	2
17	0	0	0	0	0	0	4	0	0	0	0	0	0	0	14	1
18	0	0	0	0	.	.	.	.	.	.	.	.	.	.	5	2
19	0	0	0	0	0	0	5	0	0	0	.	.	.	.	11	2
20	0	0	0	0	0	0	4	0	.	.	.	.	.	.	9	2
21	0	0	0	0	0	0	0	0	0	0	.	.	.	.	11	2
22	0	0	0	0	0	0	0	0	.	.	.	.	.	.	9	2
23	0	0	0	0	0	0	0	0	0	0	.	.	.	.	11	2
24	0	0	0	0	0	0	2	0	0	0	0	.	.	.	12	2
25	0	0	0	0	0	0	4	0	0	.	.	.	.	.	10	2

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