

# Is competition important to arctic zooplankton community structure?

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## SUMMARY

1. *Daphnia pulex* and *Daphnia middendorffiana* are commonly found in the Toolik Lake region of arctic Alaska. These two species are very similar morphologically, although their natural distributions differ markedly: *D. pulex* is restricted to shallow ponds, while *D. middendorffiana* is widely distributed and found in a variety of ponds and lakes. We compared the reproductive capabilities of *D. pulex* and *D. middendorffiana* grown under similar resource conditions and in the absence of the invertebrate predator *Heterocope septentrionalis*. *In situ* life table and mesocosm experiments were conducted in Toolik Lake and Dam Pond, habitats that have historically contained natural populations of *D. middendorffiana*, but never *D. pulex*.

2. *Daphnia pulex* exhibited a significantly higher net growth rate than *D. middendorffiana* in both life table and mesocosm experiments although *D. pulex* has never been found in either Toolik Lake or Dam Pond. *Daphnia middendorffiana* exhibited a negative net growth rate in Dam Pond, which had lower resource levels than Toolik Lake. Therefore, the smaller *D. pulex* appears to have a lower food threshold concentration than the larger *D. middendorffiana*.

3. Our results indicate that *D. pulex* is a superior resource competitor in the Toolik Lake region. These results combined with distributional patterns suggest that the restricted distribution of *D. pulex* in these arctic lakes and ponds cannot be explained by resource competition alone. We suggest that in the presence of *H. septentrionalis*, predation is an important factor structuring arctic zooplankton communities in the Toolik Lake region.

*Keywords:* Arctic, competition, *Daphnia middendorffiana*, *Daphnia pulex*, Toolik Lake

## Introduction

Understanding which factors determine the distribution of species is of central importance to ecologists. It has long been known that predation plays a major role in structuring freshwater zooplankton communities (Brooks & Dodson, 1965; Dodson, 1974; O'Brien, 1987). Both invertebrate and vertebrate predators utilise zooplankton, although they exhibit differences

in selectivity based on prey size. As a result, the type of predators present in a system can determine both the size structure and species composition of the resulting zooplankton communities (Dodson, 1974; Gliwicz & Pijanowska, 1989).

Much less is understood about the effects of resource competition on zooplankton community structure. Competition does occur in nature (e.g. Hu & Tessier, 1995; Caceras, 1998), but its overall relative importance in comparison to predation remains unclear. Historically, body size has been used as a measure of zooplankton competitive ability. Brooks & Dodson (1965) first suggested that larger-bodied

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individuals were competitively superior to smaller-bodied individuals because they were dominant in the absence of planktivorous fish. They attributed this dominance to a perceived competitive advantage associated with large body size because of increased filtering efficiency and lower metabolic requirements of large-bodied species (Size Efficiency Hypothesis, SEH; Brooks & Dodson, 1965). However, it has since been shown that the presence of, or dominance by, larger zooplankton species in the absence of planktivorous fish is often not because of competition, but reflects the presence of invertebrate predators that differentially prey on smaller-bodied individuals (Dodson, 1974; Luecke & O'Brien, 1983; Arnot & Vanni, 1993; O'Brien, 2001).

We have studied the impact of competition in arctic zooplankton communities. Specifically, we were interested in the relative competitive abilities of two *Daphnia* species: *D. pulex* and *D. middendorffiana*. These two species are morphologically very similar (Dodson, 1984), but do not co-occur and their natural distributions in arctic Alaska differ markedly. For example, *D. middendorffiana* is widely distributed and occurs in a variety of ponds and in lakes (O'Brien & Luecke, 1988). In contrast, *D. pulex* is found only in shallow ice-wedge ponds (O'Brien & Luecke, 1988).

The observed distributional differences between *D. pulex* and *D. middendorffiana* likely result, at least in part, from varying susceptibilities to predation by the invertebrate calanoid copepod predator *H. septentrionalis* (Luecke & O'Brien, 1983; Dodson, 1984; O'Brien & Luecke, 1988). *Heterocope septentrionalis* feeds much more effectively on *D. pulex* than it does on *D. middendorffiana*, and adult *D. middendorffiana* are virtually invulnerable to *H. septentrionalis* predation (Luecke & O'Brien, 1983; O'Brien & Luecke, 1988). While these effects of *H. septentrionalis* predation on *D. pulex* and *D. middendorffiana* have been well documented, no studies have thoroughly examined the competitive abilities of these two morphologically similar species.

The distributional dominance of *D. middendorffiana* in the Toolik Lake region suggests that it has an advantage over *D. pulex* in most arctic systems. However, initial evidence suggested that *D. pulex* actually exhibits a higher growth rate than *D. middendorffiana* (Dzialowski & O'Brien, unpublished data). In order to test this hypothesis, we conducted *in situ* life table and mesocosm experiments in habitats

that have historically contained populations of *D. middendorffiana*, but never *D. pulex*, to compare the competitive abilities of these two species when grown under similar resource conditions and in the absence of predation.

## Methods

The research presented in this study was conducted at the Toolik Lake Research Station the site of the Arctic Long Term Ecological Research (LTER) program, located on the foothills of the Brooks Mountain Range (68°38'00"N, 148°36'15"W) in Arctic Alaska (O'Brien, 1992). The *Daphnia* used in these experiments were collected from sites located in the vicinity of Toolik Lake. *Daphnia middendorffiana* were collected from Dam Pond, a small impoundment constructed by ALYESKA Pipeline Corporation (1.5 m maximum depth; 1500 m<sup>2</sup>) located on the shore of Toolik Lake, and *D. pulex* were collected from Berm Pond 1, a small (0.5 m maximum depth; 750 m<sup>2</sup>) ice wedge pond located 2 km south of the Toolik Lake Field Station.

### Life table experiments

*In situ* life table experiments were conducted in Toolik Lake, a large (1.5 km<sup>2</sup>, 25 m maximum depth) multiple kettle basin lake (O'Brien, 1992) and in Dam Pond. The crustacean zooplankton community of Toolik Lake consists of *D. middendorffiana*, *Daphnia longiremis*, *Bosmina longirostris*, *Diaptomus pribilofensis*, and *Cyclops scutifer*, and the lake contains both planktivorous arctic grayling and *H. septentrionalis* (O'Brien, Buchanan & Haney, 1979). In contrast, Dam Pond contains *D. middendorffiana*, *D. pribilofensis*, and *C. scutifer*, and *H. septentrionalis* is the only predator. Both Toolik Lake and Dam Pond have been sampled routinely for many years as part of the LTER monitoring program and have supported populations of *D. middendorffiana* for this time, while the presence of *D. pulex* has never been reported in either habitat (W.J. O'Brien, personal observation).

Preceding the start of the life table experiments, 15 each of gravid *D. middendorffiana* and *D. pulex* were collected from the field and isolated in individual 70 mL tissue culture flasks with filtered (105 µm) Toolik Lake water. These organisms were monitored until they released their young (within 24 h), at which

time the neonates were pooled and used to start the life table experiments. Twenty neonates of each species were randomly selected, and placed into individual 70 mL tissue culture flasks containing filtered lake water. The tissue culture flasks used in this experiment had two circular holes (1.5 cm diameter) that were covered with 225 µm Nitex netting. This netting allowed water within the flasks to exchange with the surrounding environment and thus provided the *Daphnia* with the natural algal community available in these habitats. Ten flasks for each species were suspended in both Toolik Lake and Dam Pond at a depth of 0.5 m. An additional subset of 20 neonates from each species was also measured in order to determine the average body length (top of head to base of tail) of the individuals at the start of the experiment.

The tissue culture flasks were monitored daily, at which time we recorded survivorship and fecundity values. During this time, all neonates were counted, removed and discarded from the flasks, which were then re-supplied with filtered (250 µm) lake water from their respective habitats. Every third or fourth day the flasks were transferred to the laboratory and the total body lengths of the experimental individuals were measured. Length measurements and life table experiments were conducted until day 27.

Weekly measurements of chlorophyll *a*, used as a measure of available algal resources (Lampert & Sommer, 1998), were taken from both Toolik Lake and Dam Pond in the water surrounding the submerged tissue culture flasks. A grab sample was collected from just below the surface and returned to the laboratory where chlorophyll *a* concentrations were determined using methanol extractions.

The rate of increase,  $r$  (day<sup>-1</sup>), was calculated for both *D. middendorffiana* and *D. pulex* populations using Euler's equation:

$$1 = \sum e^{-rx} l(x) b(x)$$

where  $x$  is the age (days),  $l(x)$  is age-specific survivorship, and  $b(x)$  is age-specific fecundity (Gotelli, 2002). As only a single  $r$ -value was calculated for each species grown in each habitat in the life table experiments, no statistical comparisons were made.

### Mesocosm experiments

Experiments were conducted in mesocosms filled with 26 L of Dam Pond water that was first filtered (105 µm) to remove all crustacean zooplankton. Replicated populations of each species were then established in monoculture by adding 100 gravid *D. middendorffiana* (3.85 L<sup>-1</sup>) to three mesocosms and 100 gravid *D. pulex* (3.85 L<sup>-1</sup>) to three mesocosms. In addition, a third treatment consisting of both 50 gravid *D. pulex* and 50 gravid *D. middendorffiana* was also established in triplicate. After the addition of *Daphnia* to the mesocosms, they were covered with a coarse mesh netting to prevent invasions by unwanted organisms and were then partially suspended in Dam Pond for thermal consistency. Phosphorus was added to the mesocosms at weekly interval in order to maintain resource levels similar to ambient levels assuming a 5% loss rate per day (O'Brien, personal communication).

The mesocosms were maintained for 21 days, during which time weekly zooplankton samples were collected with 3 randomly placed stabs of a 0.848 L PVC sampler (total sample volume = 2.54 L). These samples were filtered through a 225 µm mesh screen and taken to the laboratory where all of the collected *Daphnia* were enumerated under a dissecting microscope. Growth rates ( $r$ , day<sup>-1</sup>) were then estimated for each *Daphnia* species grown in monoculture and together in each mesocosm using:

$$r = (\ln N_t - \ln N_0) t^{-1}$$

where  $N_t$  is the population density at time  $t$  (days) and  $N_0$  is the population density at time zero (Gotelli, 2002). Using this formula we calculated total net growth rates based on data from the entire 21 day experiment, as well as growth rates at weekly intervals.

All statistical analyses were completed using MINITAB version 12.0, SAS version 9, and Sokal & Rohlf (1995). Data are presented as the mean ± standard error unless otherwise stated.

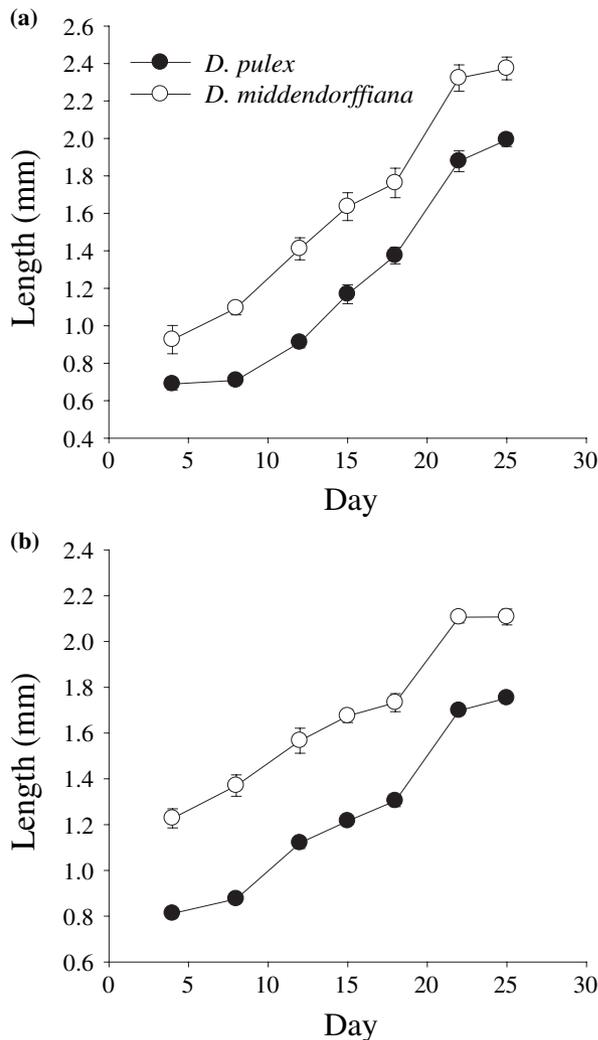
## Results

### Life table experiments

Chlorophyll *a* concentrations were significantly higher in Toolik Lake than in Dam Pond ( $t$ -test;  $P = 0.007$ ).

The average chlorophyll *a* concentrations in Toolik Lake were  $1.86 \pm 0.19 \mu\text{g L}^{-1}$  compared with  $0.83 \pm 0.083 \mu\text{g L}^{-1}$  in Dam Pond.

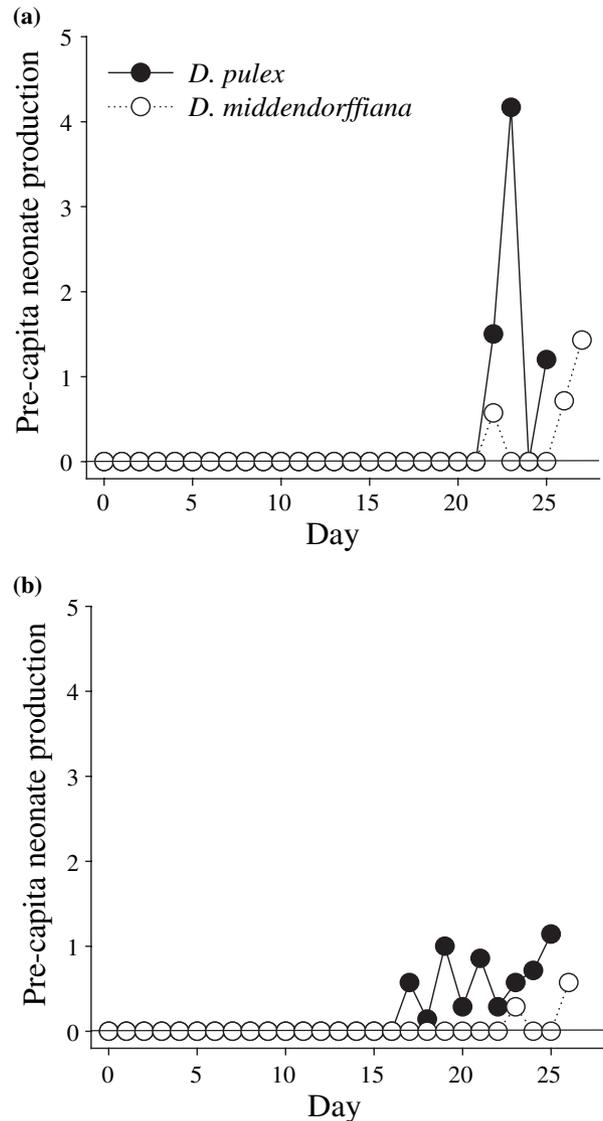
The average total body length of the *D. pulex* neonates ( $0.68 \pm 0.0069 \text{ mm}$ ) used to start the experiment was significantly smaller (*t*-test;  $P < 0.001$ ) than the average total body length of the *D. middendorffiana* neonates ( $1.09 \pm 0.0095 \text{ mm}$ ) used to start the experiment (Fig. 1). *Daphnia pulex* body lengths remained significantly smaller than *D. middendorffiana* body lengths in both Toolik Lake (RM-ANOVA;  $P < 0.001$ ,  $F_{1,88} = 213.4$ ) and Dam Pond (RM-ANOVA;  $P < 0.001$ ,



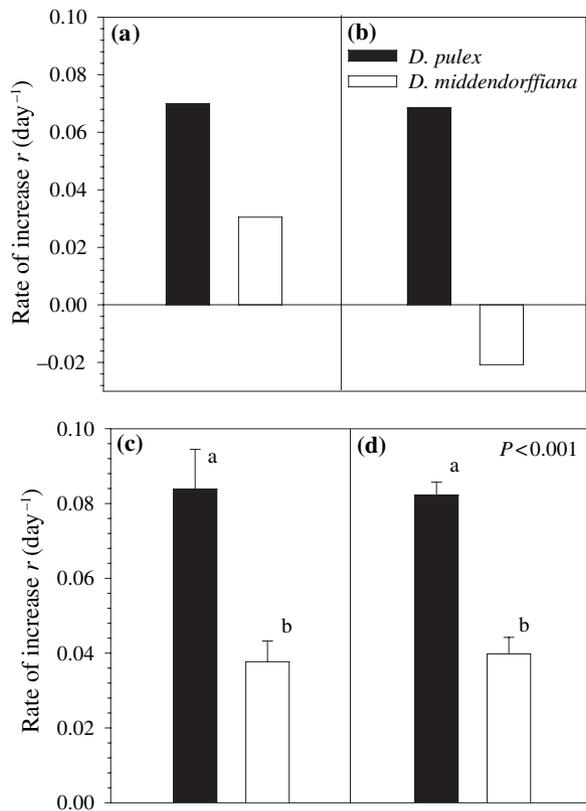
**Fig. 1** Average body length measurements of individual *Daphnia* grown in Toolik Lake (a) and Dam Pond (b) in *in situ* life table experiments.

$F_{1,88} = 234.2$ ) throughout the course of the experiment (Fig. 1).

Total reproductive output was low in each habitat, and the first reproductive event did not occur for either species before day 21 in Toolik Lake and day 17 in Dam Pond (Fig. 2). However, *D. pulex* did exhibit a higher net rate of increase (*r*) than *D. middendorffiana* in both habitats (Fig. 3). In addition, there was no intraspecific difference in the *r*-values calculated for *D. pulex* grown in Toolik Lake and Dam Pond. In contrast, there appeared to be a difference in the *r*-values calculated for *D. middendorffiana* grown in the two habitats. For



**Fig. 2** Per-capita neonate production for *Daphnia* grown in Toolik Lake (a) and Dam Pond (b) in *in situ* life table experiments.



**Fig. 3** Intrinsic rate of increase ( $r$ ,  $\text{day}^{-1}$ ) for individuals grown in Toolik Lake (a) and Dam Pond (b) in *in situ* life table experiments and from mesocosm experiments where *D. pulex* and *D. middendorffiana* were grown in monoculture (c) and together (d). Note that only one intrinsic rate of increase was calculated for each species grown in each habitat during the *in situ* life table experiments, and therefore no statistical analysis was completed for A and B. Different letters represent significant differences between treatments in C and D.

example, the  $r$ -value for *D. middendorffiana* grown in Toolik Lake was  $0.033 \text{ day}^{-1}$  compared with  $-0.021 \text{ day}^{-1}$  for individuals grown in Dam Pond (Fig. 3).

#### Mesocosms

Similar to the *in situ* life table experiments, *D. pulex* exhibited a significantly higher (ANOVA;  $P < 0.001$ ) rate of increase than *D. middendorffiana* in the Dam Pond mesocosms (Fig. 3). For example, the average growth rate of *D. pulex* grown alone in the mesocosms was  $0.084 \pm 0.01 \text{ day}^{-1}$  over the entire 21-day experiment. In contrast, the average growth rate of *D. middendorffiana* grown alone in the mesocosms was  $0.038 \pm 0.006 \text{ day}^{-1}$ .

When each species was grown in monoculture they appeared to reach stable population densities by day 14, although this density was higher for *D. pulex* ( $28.04 \pm 1.05 \text{ L}^{-1}$ ) than *D. middendorffiana* ( $12.86 \pm 1.05 \text{ L}^{-1}$ ) (Fig. 4a). Similarly, the growth rates calculated for each species in monoculture over the course of the experiment suggested that each species was near carrying capacity (i.e.  $r \sim 0$ ) (Fig. 4c). The presence of one species did not result in a significant overall reduction in the growth rate of the other species when they were grown together in mesocosms (Fig. 3). However, analyses of densities over the course of the experiment suggest that *D. middendorffiana* densities were declining in the presence of *D. pulex* by the end of the experiment (Fig. 4b). In addition, analysis of growth rates calculated at weekly intervals shows that in the presence of *D. pulex*, the growth rate of *D. middendorffiana* was negative by the second week of the experiment (Fig. 4d).

#### Discussion

Despite years of research, the role that competition plays in structuring zooplankton communities is still uncertain. Using life table and mesocosm experiments we compared the reproductive capabilities of two species of *Daphnia* that are commonly found in the Toolik Lake region. Under similar resource conditions and in the absence of predation, we found that *D. pulex* consistently exhibited a significantly higher net growth rate than *D. middendorffiana*. This was true when these two species were grown in both Toolik Lake and Dam Pond, habitats that have contained populations of *D. middendorffiana* for at least 25 years, but never *D. pulex*.

While *D. pulex* exhibited a higher growth rate in both habitats, it also consistently had a smaller body size than *D. middendorffiana* (Fig. 1). In addition, *D. middendorffiana* was unable to maintain a positive growth rate during *in situ* life table experiments in Dam Pond, which had lower resource levels than Toolik Lake. As *D. middendorffiana* is able to maintain a population in this habitat naturally, food concentrations were likely lower in our culture flasks than in the surrounding habitats. This provided an opportunity to test for relationships between body size and food threshold concentrations, the resource level where assimilation is equal to respiration (Gliwicz, 1990).

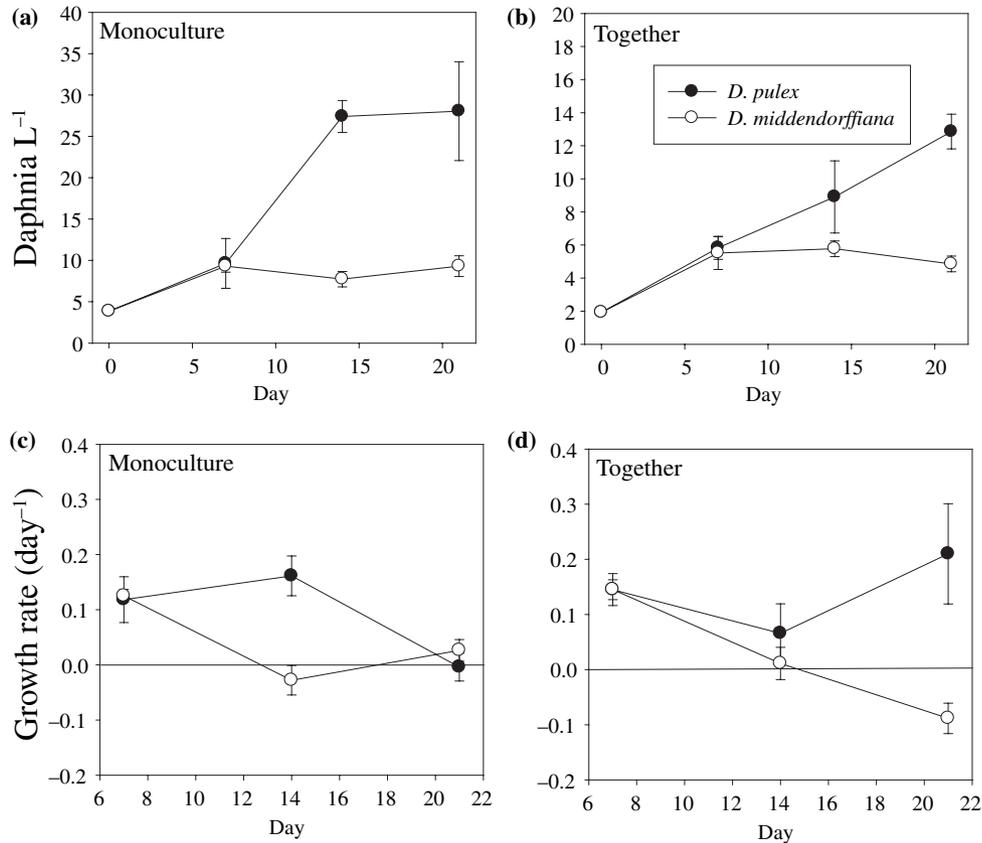


Fig. 4 Time trends for the densities of *Daphnia* in the mesocosm experiments for individuals grown in monoculture (a) and together (b) and the corresponding growth rates ( $r$ , day<sup>-1</sup>) calculated at weekly intervals (c and d).

The use of body size as a measure of zooplankton competitive ability remains controversial. Gliwicz (1990) found that larger species exhibited lower food threshold concentrations. However, contradictory experimental evidence suggests that food threshold concentrations vary with food quantity, quality, temperature, and life stage (see DeMott, 1989 for review and references within Steiner & Roy, 2003). Clearly, when resources were low in our Dam Pond tissue culture flasks, *D. middendorffiana* experienced a higher FTC than the smaller *D. pulex*. Therefore, we believe that our results directly contradict the predictions of the SEH (Brooks & Dodson, 1965) and further question the use of zooplankton body size as a measure of competitive advantage at low resource levels.

Despite the observed difference in net growth rates between the two species, the presence of *D. pulex* did not appear to have a negative impact on the overall initial growth rate of *D. middendorffiana* when these

two species were grown together in mesocosms (Fig. 4d). However, when we looked at the growth rates of these two species at weekly intervals, we found that *D. middendorffiana* exhibited an increasingly negative growth rate in the presence of *D. pulex* (Fig. 4d). In contrast, when grown in monoculture populations *D. middendorffiana* reached densities and growth rates near carrying capacity (i.e.  $r \sim 0$ ; Fig. 4). We believe that if these experiments had been allowed to continue, the smaller *D. pulex* would have been able to out-compete the larger *D. middendorffiana*, ultimately leading to its extinction from these mesocosms in the absence of predation.

The lack of strong competitive interactions in the experimental mesocosms may have resulted from the experimental design that we used in this study. For example, it would have been more appropriate to use an equal number of individuals of each species in both the monoculture and in the two species treatments. It is likely that under this scenario, intraspecific

competition between the two species would have been more pronounced. However, we believe that the results that were obtained from the mesocosm experiments, in combination with the results from the life table experiments strongly suggest that *D. pulex* is competitively superior to *D. middendorffiana* in Toolik Lake and Dam Pond.

If *D. pulex* is a superior resource competitor in Toolik Lake and Dam Pond, as our results demonstrate, why is it not found in these habitats and why is its distribution restricted in the Toolik Lake region in general? Moreover, why does it not out-compete *D. middendorffiana* in nature? Below we discuss several hypotheses that help to explain the restricted distribution of *D. pulex* in arctic lakes and ponds and the inability of *D. pulex* to displace *D. middendorffiana*.

Most attempts to understand zooplankton community structure have focused on size-selective predation (Brooks & Dodson, 1965; Hall *et al.*, 1976). Invertebrate predators are only slightly larger than their prey and as a result slight differences in body shape and size can significantly affect prey vulnerability (e.g. Tollrian, 1995). In our study, *D. middendorffiana* was consistently larger than *D. pulex* when grown in both habitats (Fig. 1). *Daphnia pulex* is 50 times more vulnerable to *H. septentrionalis* predation than *D. middendorffiana* (Luecke & O'Brien, 1983). Based on these differences in susceptibility, several authors have suggested that *H. septentrionalis* is responsible for excluding *D. pulex* from arctic ponds. In addition, there is a strong relationship between *D. middendorffiana* and *H. septentrionalis* in nature (O'Brien & Luecke, 1988; O'Brien, 2001). For example, Hebert & Loaring (1980) found an association between *D. middendorffiana* and *H. septentrionalis* in 99 of 100 arctic ponds sampled near Manitoba, Churchill; similarly, O'Brien & Luecke (1988) found that these two species co-occurred in 14 of 29 arctic ponds sampled in the Toolik Lake region. Evidence also suggests that *H. septentrionalis* can eliminate the more vulnerable *D. pulex* from ponds. In a 5-year study, O'Brien (2001) found that when *H. septentrionalis* was added to a small arctic pond, it was able to vastly reduce the *D. pulex* population within 3 years. Therefore, in habitats where invertebrate predators are present such as Toolik Lake and Dam Pond, *D. middendorffiana* is able to dominate despite the observed differences in growth rate because of its reduced susceptibility to an

invertebrate predator that can effectively eliminate *D. pulex* from these habitats.

While theory predicts that the larger *D. middendorffiana* should dominate in the presence of invertebrate predation, smaller-bodied individuals such as *D. pulex* should have an advantage in the presence of planktivorous fish (O'Brien, 1987). Reaction distance of planktivorous fish is highly correlated with zooplankton body size (Conifer & Blades, 1975), and several studies have found that planktivorous fish can effectively eliminate large bodied zooplankton species from lakes and ponds (Brooks & Dodson, 1965; Hall *et al.*, 1976). Therefore in arctic lakes that contain planktivorous fish, *D. pulex* should have an advantage over the larger *D. middendorffiana*. However, this pattern is not observed in nature; *D. pulex* does not co-exist with fish in arctic lakes (O'Brien *et al.*, 2004). While this pattern initially contradicts predator-prey theory, evidence suggests that vertebrate planktivory in arctic lakes is low. Using stable isotope data, Luecke (unpublished data) found that in several arctic lakes, fish apparently rarely fed on zooplankton and instead fed on emerging insects. Grayling had a carbon-13 signature more like emerging insects than zooplankton. Furthermore, in an analysis of 104 arctic lakes in the Toolik Lake region O'Brien *et al.* (in press), found that planktivory by fish had a rather weak impact of zooplankton community structure. Hence, in arctic lakes such as Toolik Lake, where planktivorous fish and *H. septentrionalis* co-exist, invertebrate predation may be a more important force structuring zooplankton communities and may keep *D. pulex* from directly competing with *D. middendorffiana*. Similarly, Winder, Burgi & Spaak (2003) found that in high elevation mountain lakes, where predation by planktivorous fish was also low, larger zooplankton species were able to exist because of the presence of invertebrate predation.

Of course, the restricted distribution of *D. pulex* in the Toolik Lake region might simply reflect its inability to disperse to new habitats. However, recent experimental research suggests that zooplankton communities are saturated with species, and that they are more likely limited by biotic interactions (Shurin, 2000). Shurin (2000) found that when a diverse species assemblage representing a regional species pool was introduced into several small ponds, invading species were highly unsuccessful and accounted for less than 4% of the total zooplankton biomass in the invaded

communities. In addition, Cohen & Shurin (2003) found that zooplankton were effective dispersers at least over short distances (up to 60 m). Combined, these results suggest that zooplankton communities are not dispersal-limited, but instead limited by biotic interactions such as competition and predation. Therefore, we believe that *D. pulex* is not dispersal limited in arctic lakes and ponds, and that its restricted distribution reflects biotic interactions with *H. septentrionalis*.

Why does *D. pulex* dominate only small, relatively shallow ponds in the Toolik Lake region? A complete understanding of the arctic distributions of *D. pulex* and *D. middendorffiana* requires knowledge of why *D. middendorffiana* and *H. septentrionalis* are excluded from these small ponds. The results from the life table and mesocosm experiments suggest that the dominance of *D. pulex* likely reflects competitive superiority over *D. middendorffiana*. With respect to *H. septentrionalis*, O'Brien & Luecke (1988) suggested that this predator was unable to persist in these small ponds because of abiotic constraints. In their survey of several arctic ponds, they found that *H. septentrionalis* was never present in ponds shallower than 0.3 m (O'Brien & Luecke, 1988). In addition, a recent 6-year study suggests that *Heterocope* cannot successfully invade small, shallow ponds (O'Brien, unpublished data). O'Brien (unpublished data) found that after multiple introductions, *H. septentrionalis* was unable to invade small ponds that are similar in size to those typically inhabited by *D. pulex*. However, *H. septentrionalis* quickly invaded the large ponds included in this experiment. We suggest that if *H. septentrionalis* was able to persist in these ponds, it could eliminate the competitively superior *D. pulex* and allow the more predation resistant *D. middendorffiana* to successfully invade and reproduce. Consistent with this hypothesis, O'Brien (unpublished data) found in his invasion study, that *D. middendorffiana* was only able to invade several large ponds after the successful invasion of *H. septentrionalis* and reduction or elimination of *D. pulex* (O'Brien, unpublished data).

Under similar resource conditions and in the absence of predation, *D. pulex* is a superior resource competitor to *D. middendorffiana*. We believe these results in conjunction with the distributional patterns observed in the Toolik Lake region (O'Brien & Luecke, 1988) suggest that competition may be important in

structuring these arctic zooplankton communities in the absence of the invertebrate predator *H. septentrionalis*. When *H. septentrionalis* is present however, predation is a dominant factor structuring zooplankton communities in the Toolik Lake region of arctic Alaska.

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