The Effect of Heterocope Predation on Zooplankton Communities in Arctic Ponds

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The effect of *Heterocope* predation on zooplankton communities in arctic ponds[1]

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Abstract

The influence of *Heterocope septentrionalis,* a predacious calanoid copepod, on five species of arctic pond zooplankton is investigated. Prey species coexisting with *Heterocope* are relatively invulnerable to predation, but prey species found in *Heterocope*-free ponds are very susceptible to predation. Increasing hunger level of the predator resulted in higher *Heterocope* feeding rates on *Daphnia pulex.* In experiments at 5°, 10°, and 15°C *Heterocope* fed at a greater rate on cladoceran prey at higher temperatures, but there was no effect of temperature for copepod prey. Visual observations showed that *D. pulex* is more vulnerable to *Heterocope* predation than *Daphnia middendorffiana* because of its smaller adult size and its inability to escape the grasp of *Heterocope.* A field experiment suggested that *D. pulex* would probably be excluded from ponds containing *Heterocope,* but *D. middendorffiana* could increase its population density even in the presence of the predator.

The importance of predation to community structure has been intensively studied in freshwater ecosystems. In large bodies of water where vertebrate predators such as planktivorous fish are common, zooplankton communities are comprised mainly of small species (Hrbáček 1962; Brooks and Dodson 1965; Nilsson and Pejler 1973; O'Brien et al. 1979*b*). Dodson (1974) first suggested that invertebrate predation, which focuses heavily on smaller zooplankton, may be regulating community structure in shallow ponds where fish are absent; the few studies done to date confirm Dodson's prediction (Neill and Peacock 1980; Hebert and Loaring 1980). With both vertebrate and invertebrate predators in the same lake, the outcome of these two opposing predation pressures leads to a more complex zooplankton species assemblage (Kerfoot 1978; Kerfoot and Peterson 1980; O'Brien et al. 1979*b*). Arctic ponds and lakes offer ideal situations in which to study these events since all possible combinations of vertebrate-invertebrate predation occur.

Our study focuses on zooplankton communities in shallow ponds where the ponds freeze solid during winter, excluding any fish which might have invaded the pond. It was conducted at the Toolik Lake Limnological Research Camp along the Alyeska Pipeline haul road about 200 km south of Prudhoe Bay. The area surrounding Toolik Lake is morainal and has ponds from very shallow to 4–5 m deep and lakes from 5–25 m deep. The distribution of zooplankton in the lakes has been discussed by O'Brien et al. (1979*a,b*) and O'Brien and Schmidt (1979) and other aspects of zooplankton distribution by Luecke and O'Brien (1981). Here we consider the zooplankton community structure in shallow ponds and some possible mechanisms causing the observed community composition. In many of the shallow ponds of the region, *Heterocope septentrionalis,* a large, predacious calanoid copepod, occurs in great abundance and actively preys on the other zooplankton present. Several ponds, however, lack *Heterocope* and have quite different zooplankton species compositions. Because we have observed no chemical or physical differences among these ponds, we ascribe the difference in zooplankton communities to the absence or presence of *Heterocope* predation. We used laboratory feeding trials and visual observations of *Heterocope* predation on all pertinent zooplankton species to investigate differential vulnerability to *Heterocope.*

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A long term in situ feeding experiment with *Heterocope* and two prey species was used to clarify further the effect of *Heterocope* predation in structuring these zooplankton communities.

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Materials and methods

Zooplankton pond distribution—All samples were collected with a 155-μm-mesh plankton net during June and July 1978, 1979, and 1980. Two vertical tows were taken from the center of each pond and all species identified according to Edmondson (1959). Depth of the ponds was established by dropping a weighted line. Of the 50 ponds and lakes sampled, 21 did not contain fish; only these were considered in the analysis. Ten were quite far from camp and were sampled only twice, but no incongruities were found in samples for these ponds. The remaining 11 ponds, close to Toolik, were sampled several times each year. During midsummer their species composition rarely changed. During early spring and again in fall cyclopoid copepods became more abundant in all ponds.

Determination of feeding rate coefficient—*Heterocope* predation experiments for the five most common prey species (*Daphnia pulex, Daphnia middendorffiana, Bosmina longirostris, Cyclops scutifer,* and *Diaptomus pribilofensis*) were done under a variety of conditions. Twenty adults of a single species were placed in a 1.6-liter Plexiglas bioassay chamber (O'Brien and Kettle 1981) with 2–5 *Heterocope* and the chamber was submerged in a constant temperature bath; control chambers were without the predator. After 12 h the number of live prey individuals was counted under a Wild dissecting microscope. A

feeding rate coefficient was calculated for each experiment according to Dodson (1975).

$$\text{FR} = (\ln R_0 - \ln R_t)/Pt$$

where FR is feeding rate coefficient (liters·*Heterocope*$^{-1}$·d^{-1}), R_0 is initial prey density (individuals·liter^{-1}), R_t is prey density at time (t), P is predator density (*Heterocope*·liter^{-1}), and t is time (days). We used five *Heterocope* per chamber with the less vulnerable prey to assure a measurable feeding rate; two per chamber were used with vulnerable prey to keep all prey individuals from being consumed in a given trial. We starved all *Heterocope* used in the feeding experiments for 12 h before testing. Prey were freshly collected and allowed to acclimate to the experimental temperatures before being tested.

The bioassay chambers inside the water bath were subjected to low intensity, diffuse natural light which proved best to avoid clumping of either predator or prey during a feeding experiment. Identical experiments were run with different-sized *D. middendorffiana* to test for the effects of prey size on the feeding rate of *Heterocope*.

Effects of hunger—To investigate the effects of hunger and satiation, we extended the basic 12-h feeding rate experiments to 48 h. Each 1.6-liter chamber contained 20 *D. pulex* and one *Heterocope*. The mortality of prey in the chambers was determined every 4 h, dead prey were replaced with live *D. pulex*, and the chambers returned to the bath. Since each chamber contained only one *Heterocope*, the feeding history of each predator could be followed.

Observations of Heterocope *feeding*—To better understand the mechanisms behind different feeding rates, we observed *Heterocope* feeding on *D. middendorffiana* and *D. pulex* with one predator and 20 adult individuals of either prey contained in the 1.6-liter chambers placed inside a 20-liter aquarium. A digital stopwatch ran continuously during the observation period and three events were scored and timed: encounter of predator

Table 1. Distribution of zooplankton in shallow ponds near Toolik Lake, Alaska. D—Dominant; A—abundant; R—rare (<5% of sample).

Pond	Depth (m)	Heterocope	D. midd.	D. pulex	Bosmina	Diaptomus	Cyclops	Other
S-1	0.3				D			
S-2	0.3				D		R	Polyphemus
S-3	3.5				D	A	R	
S-4	1.0		A	A	D	A	R	
S-14	3.5		D			A		Chaoborus
Poly	0.3			D				
Walden	0.5			D				Branchinecta
Slough	0.3			D				
Road I	0.5			D				
Pipe	0.3			D				
NE-15	1.8				D			
Camp	1.5	A	D			A	R	Branchinecta
S-10	1.0	A	D			A		
S-13	0.3	A	D			A		
NE-7	2.0	R	A			D		
NE-8	2.0	A	D			A		
NE-9	2.0	R	A			D		
NE-10	3.0	R	A			D		
NE-10c	1.5	A	D			R	R	
NE-16	3.0	R				D	R	
Runway	1.5	A	A			D		Branchinecta

and prey, attack of predator on prey, and capture of prey by predator. Encounters are defined as any time the *Heterocope* and prey item came close enough to react to one another. An attack is defined as any time the *Heterocope* lunged toward a prey item. A successful capture was scored whenever a prey item was killed. Handling times for each successful prey capture were also recorded. From a 1-cm grid etched on the back of the aquarium the relative velocities of predator and prey were measured by recording the number of grid lines crossed in a given period. Each observational period lasted 2 h, yielding a total of 8 h of observations for *D. pulex* and 10 h of observations for *D. middendorffiana*.

Field predation experiments—To test the expected impact of *Heterocope* predation on the two *Daphnia* species, we did a field experiment in a pond near the lab. Four plastic cylinders (40 × 85 cm) were filled with pond water filtered through a 50-μm plankton net, a styrofoam collar was fitted around the top of each, and the floating containers were towed out and anchored in place. We placed 150 *D. middendorffiana* and 150

D. pulex of adult size in each container and added 50 *Heterocope* to two of them; the other two served as controls. After 21 days the containers were drained and the remaining animals of each species counted. Fifty prey individuals from each treatment were measured to determine the mean size and variance of the population.

Results and discussion

Various arctic limnologists have noted a striking distribution of pond zooplankton (Dodson 1979; O'Brien et al. 1979*a*; Hebert and Loaring 1980). *Heterocope* and *D. middendorffiana* almost always co-occur and dominate ponds in which they are present, but when *Heterocope* is absent from a pond, other zooplankton species are often abundant, with *D. pulex* or *Bosmina* generally dominating. (*Diaptomus* spp. are common in most ponds and not highly correlated with *Heterocope*.) This distribution is frequent in the Toolik area. Ten of the 21 shallow, fishless ponds are dominated by *Heterocope* and *D. middendorffiana* (Table 1). In those ponds *Diaptomus* is common throughout the summer and *C. scutifer*
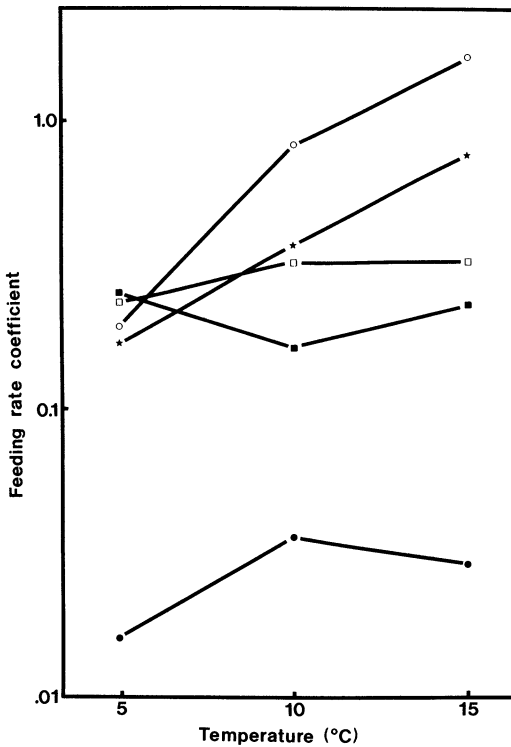
Fig. 1. Feeding rate coefficient for *Heterocope* feeding on five prey species at 5°, 10°, and 15°C. *Daphnia middendorffiana* (2.4 mm)—●; *Cyclops* (1.0 mm)—□; *Diaptomus* (1.0 mm)—■; *Bosmina* (0.8 mm)—★; *Daphnia pulex* (1.8 mm)—○.

occurs predominantly in the early spring and fall. *Branchinecta paludosa* is present in small numbers in some of the ponds. Neither *Bosmina* nor *D. pulex* was found present with *Heterocope*. In the 11 ponds from which *Heterocope* was absent, *D. pulex* dominated in five, *Bosmina* in three, and in one both occurred.

The two remaining ponds do not fit into the common species distribution patterns. One pond (S-14) is dominated by *D. middendorffiana* even though *Heterocope* is absent; however *Chaoborus*, another large invertebrate predator, is present and may be exerting a predatory pressure similar to that of *Heterocope*. In the other pond (NE-16) *Heterocope* is common but *D. middendorffiana* is absent, and *Diaptomus* and *Cyclops* are the only other zooplankton recorded. There

is no apparent reason why *D. middendorffiana* is absent from this pond.

Feeding rate coefficients—Considering the above distribution, we became interested in the effects of *Heterocope* on zooplankton community structure. We began our investigation with laboratory experiments designed to allow a comparison of the feeding rate of *Heterocope* on five zooplankton prey: *D. middendorffiana*, *D. pulex*, *D. pribilofensis*, *Cyclops* spp., and *B. longirostris*.

Assumptions of the feeding rate coefficient are that the predator and prey encounter each other randomly within the bioassay chamber, that there is no interference among predators, and that the predator exhibits a type 1 functional response (Holling 1959) over the range of prey densities during an experiment.

Since low levels of diffuse light kept the predators and prey from clumping within the chambers the first assumption appears justified. In preliminary experiments the feeding rate coefficient of individual *Heterocope* on *D. pulex* remained constant when 2–8 *Heterocope* per container were used but declined when >8 predators were added. We used a maximum of 5 *Heterocope* to avoid the problems of predator-predator interference.

Most invertebrates investigated show a type 2 or type 3 functional response (Hassell et al. 1977), but we varied both predator and prey densities to avoid drastic changes in prey densities during an experiment. Thus even if *Heterocope* does show a type 2 or type 3 functional response, over the narrow range of prey densities tested, a type 1 functional response will closely approximate reality.

The feeding rate coefficients for *Heterocope* on the five prey species at 5°, 10°, and 15°C are plotted in Fig. 1. A two-way ANOVA (Sokal and Rohlf 1969) showed significant feeding rate differences for different species ($F = 3.197, P > 0.05$) but no overall effect of temperature on feeding rate (Table 2). The interaction term was also significant ($F = 9.966, P > 0.001$), indicating that temperature af-

Table 2. Mean *Heterocope* feeding rate coefficient ± SE on the five prey species tested at three temperatures.

Prey species	5°C	10°C	15°C
D. pulex	0.190±0.037	0.835±0.245	1.640±0.200
D. middendorffiana	0.016±0.010	0.036±0.007	0.029±0.019
Cyclops	0.283±0.041	0.327±0.055	0.335±0.018
Diaptomus	0.254±0.048	0.166±0.032	0.238±0.048
Bosmina	0.178±0.021	0.346±0.084	0.744±0.161

fected the species differently. The feeding rate of *Heterocope* on *D. pulex* and *Bosmina* increased at increased temperatures. An increased metabolic rate of the predator may result in higher hunger levels and an increased feeding rate. The encounter rate may also increase if either predator or prey increases swimming speed as a result of increased metabolic rate. Since *D. pulex* and *Bosmina* have minimal abilities to evade *Heterocope* attack, a higher encounter rate would lead to a higher predation rate. There is little change in predation rate on either *Diaptomus* or *Cyclops* with changing temperature, but both have considerable abilities to evade *Heterocope* attack by swimming out of the way (pers. obs.). In this case, as temperature increases predator encounter rate may increase, but so also may evasion ability. In a study on grayling planktivory (Schmidt and O'Brien 1982) the predator's capture efficiency of a copepod prey decreases at higher temperature. The feeding rate of *Heterocope* on *D. middendorffiana* increased only slightly over the temperature range tested, presumably due to its difficulties in handling this prey.

Heterocope fed on the five prey species to extremely different degrees. *Bosmina* and *D. pulex* were heavily preyed on at all temperatures tested, while *D. middendorffiana* is practically invulnerable to predation by *Heterocope* once it has attained adult size. The two copepods, *Diaptomus* and *Cyclops*, exhibited intermediate vulnerability to *Heterocope* predation. These patterns conform with the distribution of the prey species in the ponds. *Daphnia pulex* and *Bosmina* do

not occur with *Heterocope* in any of the ponds sampled. *Daphnia middendorffiana* occurs only with *Heterocope*; and *Diaptomus* and *Cyclops* appear both with and without the predator. Although *Cyclops* is most abundant in ponds when *Heterocope* is absent (early spring and late fall), no direct effect can be assumed because *Cyclops* population density goes through a similar cycle in ponds without the predator.

There are comparable patterns in ponds around Churchill, Manitoba (Hebert and Loaring 1980), and near Barrow, Alaska (Dodson 1979). Ponds containing *Heterocope* are dominated by *D. middendorffiana*, but when *Heterocope* is absent either *D. pulex* is abundant or, in the Churchill area, a vulnerable morph of *D. middendorffiana* is dominant. In the ponds around Toolik Lake *D. pulex* and *Bosmina* are dominant when *Heterocope* is absent.

It seems very likely that the combination of *D. pulex* or *Bosmina* with *Heterocope* is unstable. If these species should come into contact, as must surely occur with so many arctic ponds nearly confluent, *Heterocope* will quickly eliminate the cladocerans. If no alternative prey is present, the *Heterocope* would likely starve. The cladocerans could then become abundant again through reintroduction or the hatching of resting eggs. A very shallow extension of Camp pond (Polypond) showed this phenomenon quite well. Camp pond is nearly 1.5 m deep and contains large numbers of *Heterocope*, which invade the shallow Polypond during high water. In the drier years of 1977 and 1978 the connection between
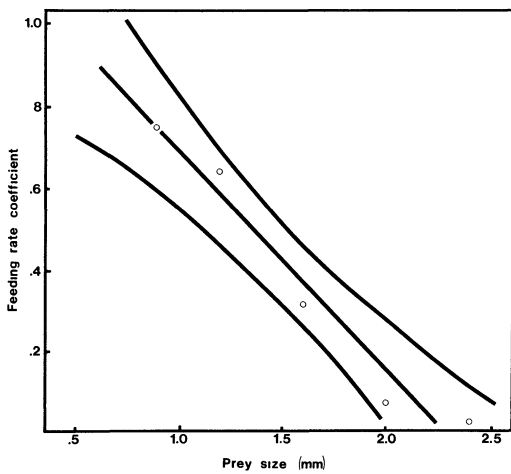
Fig. 2. Feeding rate coefficient for *Heterocope* feeding on *D. middendorffiana* of various size. Means of five size classes are plotted along with 95% C.L. of the least-squares regression line.

Camp pond and Polypond dried up. *Heterocope* became scarce in Polypond and *D. pulex* became extremely abundant (>100·liter⁻¹). In the wetter years of 1979 and 1980 the two ponds never separated. *Heterocope* remained abundant and *D. pulex* was always only marginally present.

We investigated the possible effect of chemical or physical factors in the distribution of *D. pulex*, *D. middendorffiana*, and *Heterocope*. Luecke and O'Brien (1981) showed that a green morph of *Heterocope*, restricted to deeper lakes with fish, is more susceptible to light toxicity than the pond-dwelling red *Heterocope*. Phototoxicity does not seem to keep the red morph *Heterocope*, *D. pulex*, or *D. middendorffiana* from shallow ponds. When *D. pulex*, *D. middendorffiana*, and *Heterocope* were exposed to natural light intensities, *D. pulex* was most susceptible to the damaging effects of sunlight. Since *D. pulex* dominates the plankton of many of the very shallow ponds (Table 1), the effects of phototoxicity are probably not important in the distribution of these species. That other chemical or physical factors influence zooplankton distribution is unlikely because *Heterocope* survived and the two *Daphnia*

species even reproduced while held in flow-through Plexiglas cylinders in ponds in which they never or rarely occurred.

The mechanisms behind the dominance of either *D. pulex* or *Bosmina* in the *Heterocope*-free ponds are not clear. In ponds near Barrow, *D. middendorffiana* produces a single parthenogenetic brood followed by serial production of ephippial eggs (Stross 1969). However, in our study ponds *D. middendorffiana* produces at least three parthenogenetic broods before entering ephippial production. From a life table study of the two *Daphnia* species and *Bosmina*, *D. middendorffiana* appears to be the better competitor (O'Brien unpubl.). Ponds dominated by *D. pulex* tend to dry up in some years; perhaps its resting stage is more tolerant of these conditions than the other local zooplankters. Alternatively, *D. pulex* may be dispersed more easily and thus can quickly recolonize ponds after temporary dry periods.

Daphnia middendorffiana co-occurs with *Heterocope* except in one instance (Table 1). We found large *D. middendorffiana* with *Heterocope*, while small *D. middendorffiana* was very rare. We investigated the feeding rate of *Heterocope* on different-sized *D. middendorffiana* at 10°C (Fig. 2). Small *D. middendorffiana* is moderately vulnerable to *Heterocope* predation. As an individual nears egg-carrying size (2.0 mm), vulnerability decreases markedly. O'Brien et al. (1979*b*) reported similar size-dependent predation on *D. pulex* by *Heterocope*. Although the size range of a prey species may not be a particularly good indicator of its vulnerability (Li and Li 1979), *Heterocope* is intensely selective on smaller individuals of the two daphnids tested here.

The timing of life history events of zooplankton predators and their prey may be crucial to the survival of these species (Strickler and Twombly 1975). *Daphnia middendorffiana* appears in Toolik area ponds earlier (26 May 1980) than *Heterocope* (June 1980), so that the first generation of the year is quite large by the time *Heterocope* matures and is protect-
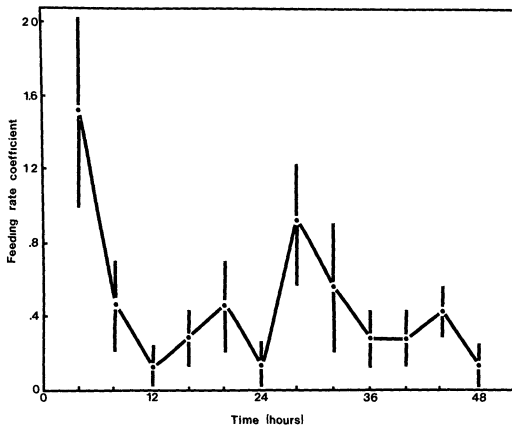
Fig. 3. Feeding rate coefficient for individual *Heterocope* feeding on *D. pulex* for 48 h. Containers were scored and replenished with prey every 4 h ($X \pm$ SE; number of replicates, 4).

Fig. 4. Change in feeding rate coefficient calculated as a function of hunger level from data in Fig. 3 ($X \pm$ SE).

ed from predation. Ensuing generations are probably heavily preyed on by *Heterocope* and probably very few of these individuals attain adulthood. Thus size-selective predation by *Heterocope* on *D. middendorffiana* may allow the stable co-existence of these two zooplankters in arctic ponds.

Effects of hunger—Hunger is important in the feeding rate and selectivity of many invertebrate predators (Holling 1965; Fedorenko 1975; Pastorok 1980). We followed single, individual *Heterocope* through a 48-h period, recording how many *D. pulex* were eaten at 4-h intervals (Fig. 3). Feeding rate was greatest during the first 4 h after the predator's 12-h starvation period; after this the feeding rate dropped to a low level and remained relatively constant for the rest of the experiment. A small increase in feeding rate between 24 and 28 h may be due to a diel periodicity or to random fluctuation.

Feeding rate coefficients were calculated for each *Heterocope* every 4 h and then grouped according to the individual's previous 4-h feeding rate, which was used as a hunger index; the ensuing increase or decrease in feeding rate was plotted as a function of this hunger index (Fig. 4). Kendall's coefficient of rank correlation (Sokal and Rohlf 1969) was significant ($N = 56$, $n = 8$, $P < 0.01$) when
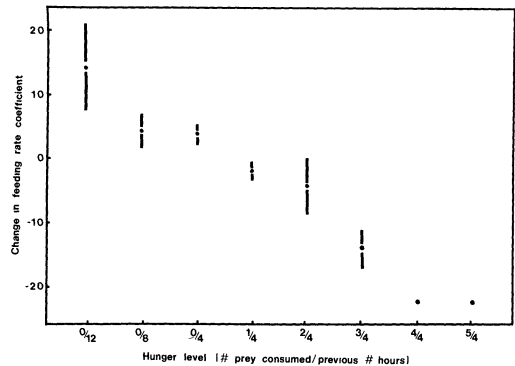
hunger level was compared to increase in feeding rate. Feeding rate declined as more prey items were consumed in the previous 4 h. The linearity of this relationship is artificial due to the arbitrary scaling of the hunger level variable; however, it is clear that the feeding history of an individual *Heterocope* will determine the feeding activity measured in any given feeding bout. In the feeding rate experiments with all five prey species (Fig. 1), the copepods were also starved for 12 h to standardize hunger levels. The feeding rates in these experiments are higher (0.835 to 0.462) than the composite *Heterocope* feeding rate measured over the 48-h period. The initial hunger level of the predator is responsible for this overestimate.

Direct observation of Heterocope *predation*—Despite anatomical similarities, there are tremendous physiological and ecological differences between *D. pulex* and *D. middendorffiana*. *Daphnia pulex* is much more susceptible to oil toxicity (Skvorc 1980) as well as to the photooxidizing aspects of sunlight (Luecke and O'Brien 1981). *Daphnia pulex* is the species most vulnerable to predation by *Heterocope* and *D. middendorffiana* the least. We watched *Heterocope* feeding on these two species to determine the causes of this difference. *Heterocope* predation can be thought of in terms of three independent events: encounter, attack, and capture. We recorded the occurrence

Table 3. Summary of the predation sequence for observations involving one *Heterocope* and 20 *Daphnia* in 1.6-liter containers.

	D. pulex	*D. middendorffiana*
Encounter probability (E), encounters/search time (min)	0.168	0.597
Attack probability (A), attacks/encounters	0.301	0.505
Capture probability (C), captures/attack	0.889	0.020
Handling time, minutes/prey item	44.9	28.8
E × A × C = captures/minute (search time)	0.0449	0.0060

of each event and the handling time of each prey ingested. Once a prey is grasped, the *Heterocope* must manipulate it by rotating it with the first and second maxillae while scraping out the carapace with the first pair of swimming legs. Occasionally *Heterocope* would lose the prey during this rotation. Often the *Heterocope* was able to relocate a falling prey item by swimming in concentric loops as does *Epischura* (Kerfoot 1977). Once dead prey fall to the bottom of the chamber, it seems very difficult for the *Heterocope* to find them. In a separate experiment *Heterocope* could not locate freshly killed *D. pulex* placed on the bottom of a chamber. Thus it seems that *Heterocope* does not use chemoreception when searching for prey or that the bottom of the container interferes with its ability to capture prey.

The encounter probability of *Heterocope* with *D. middendorffiana* is a bit higher than that with *D. pulex* (Table 3). *Daphnia middendorffiana* adults (2.4 mm) are larger than *D. pulex* adults (1.8 mm), and larger prey generally have a larger encounter radius (Gerritsen and Strickler 1977). *Daphnia middendorffiana* also has a greater cruise velocity (0.356 cm·s^{-1}, SE = 0.187) than *D. pulex* (0.161 cm·s^{-1}, SE = 0.110), which increases encounter probability. *Daphnia middendorffiana* was attacked more frequently by *Heterocope*, and this again may be due to its larger size (Kerfoot 1977). However, since *D. middendorffiana* frequently escapes attacks by *Heterocope*, increased attack probability is probably the result of multiple attacks on one individual. We often saw the same *D. middendorffiana* individual subjected to several successive attacks by *Hetero-*

cope; attacks on *D. pulex* were almost always successful, so multiple attacks were rare.

The biggest difference between *D. pulex* and *D. middendorffiana* with respect to *Heterocope* predation is in capture success. The capture probability of *Heterocope* on *D. pulex* is 40 times greater than that on *D. middendorffiana*. Part of this may result from the size differences between the adults; however, experiments with equal-sized *Daphnia* reveal a tremendous difference in prey vulnerabilities (O'Brien pers. obs.). The carapace of *D. middendorffiana* is much stronger than that of *D. pulex*. Dodson (pers. comm.), using a pressure gauge, found that the carapace of *D. middendorffiana* could withstand significantly more force before breaking than that of *D. pulex*. The tough carapace of *D. middendorffiana* is probably an adaptation to invertebrate predation, particularly from those predators which, like *Heterocope*, do not engulf prey whole. Prey vulnerability to *Acanthocyclops* predation is also primarily due to carapace characteristics (Li and Li 1979).

The handling time for the two *Daphnia* species also differed. Even though *D. pulex* is smaller, *Heterocope* handled it for an average of 16 min per animal longer than *D. middendorffiana* (Table 3). We could observe that *Heterocope* could ingest nearly all of a *D. pulex*, while only the head and inner body parts of a *D. middendorffiana* were consumable. The softer carapace of *D. pulex* is again probably the reason for this difference. Smyly (1970) and Williamson (1980) reported similar handling times for copepods preying on cladocerans.
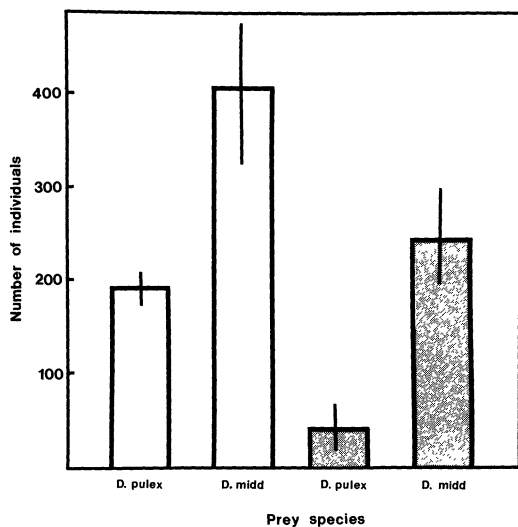
Fig. 5. Numbers of *D. pulex* and *D. midden-dorffiana* in the absence (open) and presence (stippled) of *Heterocope* at the end of the field experiment. Means and ranges calculated from two replicate containers are shown.

Fig. 6. Size frequency distribution for *Daphnia* in the absence (above) and presence (below) of *Heterocope* in the field experiment.

The probability of a successful ingestion is then the product of the probabilities of encounter, attack, and capture of the prey by the predator. *Daphnia pulex* was 8 times more vulnerable than *D. middendorffiana* to *Heterocope* predation in the 2-h observed feeding bouts. When handling times are subtracted from the feeding rate coefficient experiments (Fig. 1), *D. pulex* was calculated to be 16 times more vulnerable than *D. middendorffiana*. The discrepancy between these two methods for calculating prey vulnerability is probably due to differences in experimental design. The feeding rate coefficient experiments were run for 12 h, the observations for 2 h. There was a strong indication that handling times decreased with increasing satiation of the predator, as also reported by Williamson (1980) for *Mesocyclops*. Handling times calculated from 2-h feeding bouts with starved *Heterocope* are probably overestimates. When handling times are not subtracted from the 12-h feeding experiments, *D. pulex* was only 10 times more vulnerable than *D. middendorffiana* to predation by *Heterocope*.
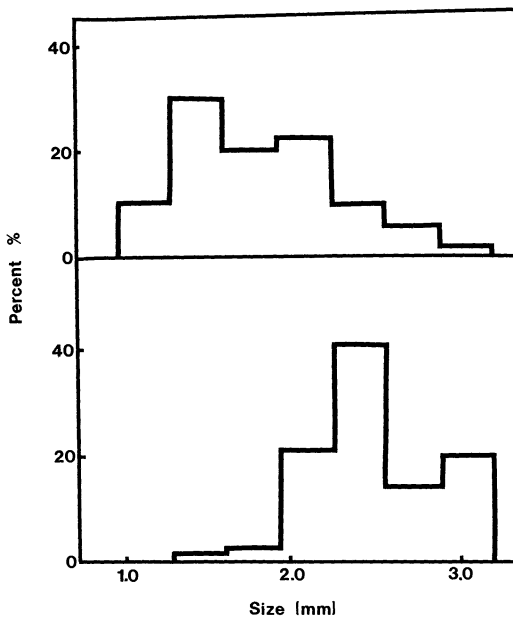
Field experiments—In laboratory ex-periments *Heterocope* showed an extremely high feeding rate on *D. pulex* and a barely measurable one on large *D. middendorffiana*. *Heterocope* and *D. pulex* almost never coexist in the ponds, nor do *D. pulex* and *D. middendorffiana*. We designed a field experiment to determine if *Heterocope* would drive *D. pulex* to extinction and if either *D. pulex* or *D. middendorffiana* would competitively exclude the other; both hypotheses could explain the noncoexistence of the two daphnids.

We added 150 adults of each species of *Daphnia* to four 100-liter containers and placed them in a nearby pond. We added 50 *Heterocope* to two of the containers. After 21 days we recorded the number of each species remaining (Fig. 5). In the absence of *Heterocope*, the populations of both daphnids increased, but *D. middendorffiana* became twice as numerous as *D. pulex*. Life table data from the previous summer indicated that *D. middendorffiana* ($r = 0.103$) could out-reproduce *D. pulex* ($r = 0.094$). In the presence of *Heterocope*, *D. middendorffiana* was

able to increase slightly, but numbers of *D. pulex* declined drastically so that the former became six times as plentiful as the latter.

Heterocope is apparently quite capable of over-exploiting *D. pulex*. In one of the containers with *Heterocope*, *D. pulex* became dangerously close to extinction in just 21 days; if the experiment had been extended for another week, it probably would have disappeared from both *Heterocope* containers. From the results of the non-*Heterocope* containers, it is unclear if either species of *Daphnia* could competitively exclude the other. Although both increased in abundance, *D. middendorffiana* reproduced faster. A longer term experiment where densities were allowed to reach saturation would be needed to reach a firm conclusion.

Although the presence of *Heterocope* reduced the density of *D. middendorffiana*, it was still able to increase from the initial density. This would be expected from the laboratory experiments. The initial adult *D. middendorffiana* is not very susceptible to *Heterocope* predation. The offspring of initial individuals, however, are much more susceptible (Fig. 2). A few make it through this vulnerable period and become part of the reproducing population. Examination of the sizes of 50 *Daphnia* from each container again demonstrates that small individuals are most heavily preyed upon (Fig. 6). A relatively safe adult population assures the output of a constant supply of small individuals, most of which are consumed by *Heterocope*.

In conclusion, *H. septentrionalis*, the top predator in many shallow arctic ponds, has a dramatic influence on the zooplankton species composition. Due to its high feeding rate on *D. pulex* and *Bosmina*, *Heterocope* can exclude these species from shallow ponds. *Heterocope* can feed effectively on *D. pribilofensis*, particularly at low temperatures, but *Diaptomus* is found in most ponds with or without *Heterocope*. *Cyclops scutifer* also appears in ponds both with and without the predator. *Daphnia middendorffiana* is vulnerable only in its early instars; once

adult, it is virtually free from predation by *Heterocope*.

The differences in *Heterocope* predation on *D. middendorffiana* and *D. pulex* are caused by differences in the predator's capture success on the two. *Daphnia middendorffiana* can avoid capture due to its hard carapace and larger adult size. The difference in carapace strength causes *D. pulex* to be so vulnerable to *Heterocope* predation that the two species do not coexist. The varying degrees of prey vulnerability throughout the life cycle of *D. middendorffiana* allow the stable coexistence of *Heterocope* and this prey.

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