Contrasting migration behaviour of *Daphnia pulicaria* and *D. galeata* × *hyalina*, in avoidance of predation by 0+perch (*Perca fluviatilis*) *

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Abstract

In spring and early summer, a small population of the large-bodied *Daphnia pulicaria* coexists with a much larger population of the medium-sized hybrid *Daphnia galeata* × *hyalina* in the epilimnion of Lake Maarsseveen (The Netherlands). When large shoals of juvenile perch (*Perca fluviatilis*) appear in the open water, both species start to migrate vertically. Since *D. pulicaria* has a larger body-size than *D. galeata* × *hyalina*, and is therefore competitive dominant over the hybrid, it is unlikely that both species interact via their common food resource, but they react both to fish predation. However, since they differ in size, and therefore in vulnerability for fish predation, both species adopt different strategies. The smaller bodied, and less vulnerable *D. galeata* × *hyalina* exhibits diel vertical migration ascending to the surface at dusk, and staying there during the night. In this way, benefiting from the higher temperatures of the surface layers. In contrast, the large-bodied, and more vulnerable *D. pulicaria* selects the deep cold hypolimnion water layers as refuge against fish predation. In this way it benefits from a safe habitat, free from fish predators, but on the other hand suffers from low water temperatures, which decrease its fitness. It is likely that the relatively higher temperature in the upper water layers serves as a proximate factor for the downward migration of *D. pulicaria*.

Introduction

It is now generally accepted that diel vertical migration is a behavioural strategy of the pelagic zooplankton to avoid predation (see reviews by de Meester et al., 1999; Ringelberg, 1999). The normal upward migration – to the waters surface at night, and a down ward migration to the deeper layers during the day – are avoidance responses to visually predating fish. Generally, larger daphnids migrate to deeper layers, and thus maintain a deeper day-depth, than smaller daphnids (Stich & Lampert, 1981; Pijanowska & Dawidowicz, 1987). Low temperatures and poor food conditions in the deeper layers impose fitness costs that are traded off against the escape from mortality. Hence, an ascent at night to the warmer food-rich near surface layers is a prerequisite. The strong trade-off prevents that zooplankton stay continuously at the day depth, out of the predation zone. Migration will stop as soon as the predation pressure by the fish decreases sufficiently. Predation pressure and, therefore also the diel vertical migration, is mainly a function of predator biomass, but is also influenced by the size of the predator. 0+ fish are generally the most important planktivores in freshwater lake ecosystems. Since these juvenile fish show generally a high mortality during the course of the year, predation pressure also correspondingly changes seasonally, with the highest predation pressure during the summer months.

Predation avoidance is the ultimate reason for diel vertical migration, but there is also a proximate aspect to it. Without a daily trigger, diel migration behaviour would not be possible. Loose (1993a) has demonstrated experimentally that the diel vertical migration behaviour of *Daphnia* does not occur in the absence of changes in light intensity at dawn and dusk even if the fish cues are present. It is clear that the phototactic reaction to the rate of relative change in light intensity, at sunrise and sunset, are the proximate factor causing diel vertical migration (Ringelberg, 1964; Ringelberg et al., 1991). The swimming in response to light intensity change is the primary physiological mechanism underlying diel vertical migration, but other factors as food (satiation level) and fish released infochemicals, may modify this response. Whereas low food levels may inhibit the diel migration, high levels of infochemicals in water, released by fish, may induce it (de Meester et al., 1999). Depending on environmental conditions most medium- and large-sized *Daphnia* spp. in lakes exhibit diurnal vertical migration for a longer or shorter time during the year (but see Pijanowska & Dawidowicz, 1987).

Many zooplankton populations do not migrate vertically in a diel pattern, but have nevertheless a very distinct vertical distribution (Pijanowska & Dawidowicz 1987). We agree with de Meester et al. (1999) that diel vertical migration can be best considered as a special case of depth selection behaviour. However, to avoid confusion in terminology, we will use the term 'diel vertical migration' only for behaviour in which depth preference changes over a diel cycle and we will use the term 'depth selection' for all other (non-diel) types of depth selection. For depth selection behaviour, as for the diurnal migration behaviour, the larger *Daphnia* spp. generally select during daytime a greater depth than that by the smaller species. Depth selection during both the day and the night is, in addition to the presence of predator, also influenced by factors such as temperature, oxygen concentration, light intensity, UV radiation and food concentration (George, 1983, Winder & Spaak, in press). So far, however, these factors have been much less well studied from a physiological point of view (de Meester et al., 1999).

Within the *Daphnia* population different clones may differ in their diel migratory or depth selection behaviour. Müller & Seitz (1993) showed that different clonal groups within *D. galeata* and *D. galeata × cucullata* populations in a south-western German lake differed distinctly in their diel vertical migration behaviour in the course of the year. Furthermore, the closely related *D. hyalina × galeata* clones differed significantly in day- and night-time vertical distribution under experimental conditions in large plankton towers (de Meester et al., 1995). Whereas different clones of *D. pulicaria* showed different depth selection behaviour, causing differences in vertical distributions within and between the lakes (Tessier & Leibold, 1997).

In our study lake, Lake Maarsseveen, generally two *Daphnia* spp. coexist: the medium body-sized *D. galeata × hyalina* and the larger *D. pulicaria*. This body size contrast results in different vulnerabilities to fish predators. The positive size selectivity of zooplanktivorous fish is well documented (Zaret, 1980). Hence, during periods of intensive planktonic feeding *D. pulicaria* will be more vulnerable to predation by fish than *D. galeata × hyalina*. On the other hand, the larger body size of *D. pulicaria* provides it with a higher competitive ability in resource exploitation. At low food concentrations *D. pulicaria* might be able to replace the smaller *D. galeata* (Gliwicz & Lampert, 1990; Kreutzer & Lampert, 1999). The open water of Lake Maarsseveen is dominated by 0+ perch only (Flik et al., 1997), this results in a strong seasonal variation in the intensity of zooplanktivory. In this study we attempt to unravel how food conditions, temperature conditions and predation by fish affect the depth distribution of *Daphnia*. Temperature was taken into account as a potential steering factor because preliminary analysis of field data on *D. pulicaria* in Lake Maarsseveen suggested that a relationship existed between increasing (surface) temperatures during end of May and early June and the induction of a downward migration, which resulted in selection for greater depths strata. Since already much is known about the diel vertical migration behaviour of *D. galeata × hyalina* in Lake Maarsseveen (e.g., Ringelberg, 1991; Ringelberg et al., 1991; Flik & Ringelberg, 1993; Ringelberg & Flik, 1994), we focus in this study on the vertical migration and depth selection behaviour of *D. pulicaria*. Our three main objectives are: (1) to describe in detail the vertical migration and depth selection behaviour of *D. pulicaria* in Lake Maarsseveen, (2) to compare the seasonal variation in depth selection behaviour of *D. pulicaria* with the diel vertical migration behaviour of the coexisting *D. galeata × hyalina*, and (3) to identify the potential proximate causes and ultimate reasons for the observed behaviour of *D. pulicaria*.

Materials and methods

Study area

Lake Maarsseveen is a mesotrophic lake situated at 40 km from Amsterdam. It has a surface area of 70 ha, an average depth of about 10 m and a maximum depth of 30 m. The lake is rectangular in shape and has a small littoral zone. Temperature stratification builds up in May and lasts till early November. The epilimnion extends to about 7 m depth. For extensive descriptions of the physical, chemical and biological characteristics, see Ringelberg (1981) and Swain et al. (1987).

Sampling zooplankton

Sampling was carried out from 1992 to 1998, generally starting at the end of April, just before the start of vertical migration. Routine sampling was carried out with nine plankton torpedoes which were equipped with a 150-μm mesh gauze to sample zooplankton (Swain & Royackers, 1986; Ringelberg et al., 1991). The torpedoes were simultaneously towed along the longitudinal axis of the lake at depth intervals of 2.5 m from 1.25 (surface) to 21.25 m (near the bottom). The torpedoes were towed for about 500 m, which corresponded to a sample volume of ca. 70 l per torpedo. The corrections for the distance towed were made with propeller readings. For the description of the depth distribution of D. pulicaria during the sampling period, 1992–1998, we pooled the information from all seven years. But, to relate the depth distribution of this species with temperature we compared the observations only for the four years (1992, 1993, 1994, 1998) for which at least five day and night observations were available.

The vertical distribution of Daphnia was monitored for two to six sampling dates per year. On each sampling occasion, the animals were sampled around noon and mid-night. In 1998 a more detailed sampling programme was carried out using a different sampling method. Two closing nets (diameter mouth 12 cm, length 3 m, mesh size 95 μm) in one frame were operated from a crane system (Bürgi, 1983). The sampling depth interval and range (0–20 m) were essentially the same as for the torpedo sampling. The capture efficiency of the closing net for daphnids (D. pulicaria) was 3–30 times higher than with the torpedo sampler (B.J.G. Flik, personal observation).

Fish stock assessments and gut content analysis

Acoustic surveys with two types of echosounders (Eagle Mach I, Simrad EY 500 split-beam echo sounder) showed that juvenile 0+ fish dominated the open water (>99% by numbers) and that their vertical distribution was limited to 2–6 m depth. Bongo and trawl net catches showed that all fish caught in the open water belonged to one species: perch. Although the juvenile perch showed an extreme shoaling behaviour during the day, these shoals broke up during the night and their distribution became much more homogenous (Flik et al., 1997, Duncan et al., 1999). Therefore, fishing was always carried out during the night. During 1992–1994 and in 1998 the juvenile perch were caught usually at weekly intervals during May–July, using horizontal tows with two Bongo-nets (Hydrobios) towed behind a catamaran at a speed of ca. 2.5 m s^{-1}. Hauls of ca. 1500 m in length were made at 3 m depth from 23.00 to 01.30 h (local time). Catches of both nets were pooled and preserved in 4% formalin.

From each sample in 1998, nine to fourteen fishes were taken at random to count in their stomachs the number of total daphnids, D. pulicaria, and the total number of microcrustaceans. A comparison during the second week of June 1998 of the net fish catch using Bongo net and the catch estimates from the acoustic survey (Simrad EY 500 split-beam echosounder) showed that the density estimates based on Bongo net catches were only 6.5% lower than those using the acoustics. Thus, the former method allows reasonably accurate estimation of juvenile perch abundance, not only because of the night fishing, but probably also because of the rectangular morphometry of the lake, in addition to the poorly developed littoral zone (Ringelberg et al., 1997).

The increasing size of the fish, resulted in decreasing catching efficiencies of the Bongo nets for the 0+ fish from approximately early July onwards. To correct for this bias we calculated the relative biomass based on the exponential decrease in numbers (catch per unit effort) during the period May–June (days 130–181). For each relative abundance time series, exponential decrease constants were calculated (Ringelberg et al., 1997). These constants were used to calculate relative 0+ perch abundance, starting arbitrarily with a population size of 100 on day 130 (May 10) being the day around which the eggs hatch each year. Average length per sampling date was calculated for the first six years (1992–1997), and mean biomass

was calculated using the length weight relationship for perch given by Jachner (1989). For 1998 measured weights were used. The relative biomass was calculated by multiplying the date dependent weight by the date dependant relative abundance. To facilitate comparison among years, for each year the maximum biomass was taken as 100%.

Laboratory experiments

Since we expected fish released infochemicals or elevated temperature to be the trigger for the downward migration of *D. pulicaria*, we investigated in the laboratory the influence of 'fish water' and temperature on the depth distribution of one clone of this species. Infochemical-free water was obtained by aerating the lake water by circulation over a sand filter for at least two days. 'Fish water' was obtained from a 30-l aquarium filled with filtered lake water with five juvenile perch (fork length 5–6 cm). During the acclimatisation period, every day half of the water was replaced by fresh filtered lake water, whereas during the experiment no water was replaced. Water temperature was kept constant at 15 °C. Twenty-five daphnids were introduced into a Perspex tube (60 cm high, 10 cm in diameter) with filtered lake water. The tube was illuminated from above with an incandescent lamp, with a light intensity of 1 μmol m^{-2} s^{-1} at the water surface using a the light: dark regime was 12:12 h. We used only one tube at the time, there were no controls. Before the start of the experiment daphnids were acclimatized for at least 24 h to the conditions in the tubes. The vertical distribution of the individual daphnids was monitored every 24 h. Every morning several readings were made of the vertical position of individual daphnids in the water column by counting the number of daphnids per 6-cm strata.

We first tested in an experiment the effects of infochemicals released by fish at a high concentration. The duration of this experiment was 72 h; we used one tube (no replicates). After 24 h, 50% of 'fish water' was added to the tube with the daphnids. Thirty-six hours thereafter, when the effects of these infochemicals is supposed to have ceased (Loose, 1993b), we also tested the effects of water temperature increase from 15 to 25 °C. In the second experiment we tested the effect of temperature in replicate by repeating the experiment three times. The whole experiment took 18 days. Initially the animals were acclimatized for 72 h in the tubes at 10 °C; subsequently the temperature was gradually raised over 48 h from 10 to 20 °C.
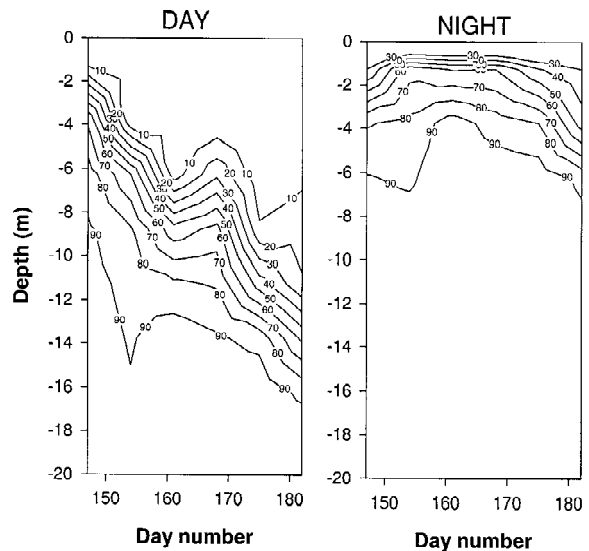

Figure 1. The seasonal variation in day- and night-time vertical distribution of *D. galeata* × *hyalina* in Lake Maarsseveen based on vertical hauls with a closing net (1998), expressed in percentiles (80% of the population is located between the 10th and the 90th percentile line). Time is given in day numbers.

For the first experiment, generally, four observations were carried out around 24, 29, 48, and 70 h after the start of the experiment. Each observation was based on the vertical position of 25 individual daphnids, this resulted in ca. four mean values per observation day. The confidence limits were calculated on basis of these mean values. In the second experiment, the same number of observations were carried out around 72, 96, 120, and 144 h after the start of the experiment. In this experiment three replicates were carried out, and confidence limits were calculated on basis of the mean values of each replicate.

Results

Field observations

The vertical distribution during the day and night time in 1998 of *D. galeata* × *hyalina* and *D. pulicaria* in Lake Maarsseven are described in Figures 1 and 2. *D. galeata* × *hyalina* showed a clear diel vertical migration pattern, starting in the second half of May (around day 140) and ending in mid July (day 196). *D. pulicaria* started its migration around the day 140 (ca. 20 May). The downward movement continued until the population had reached deepest part, close to the lake bottom by mid June (day 170). The daphnid pop-
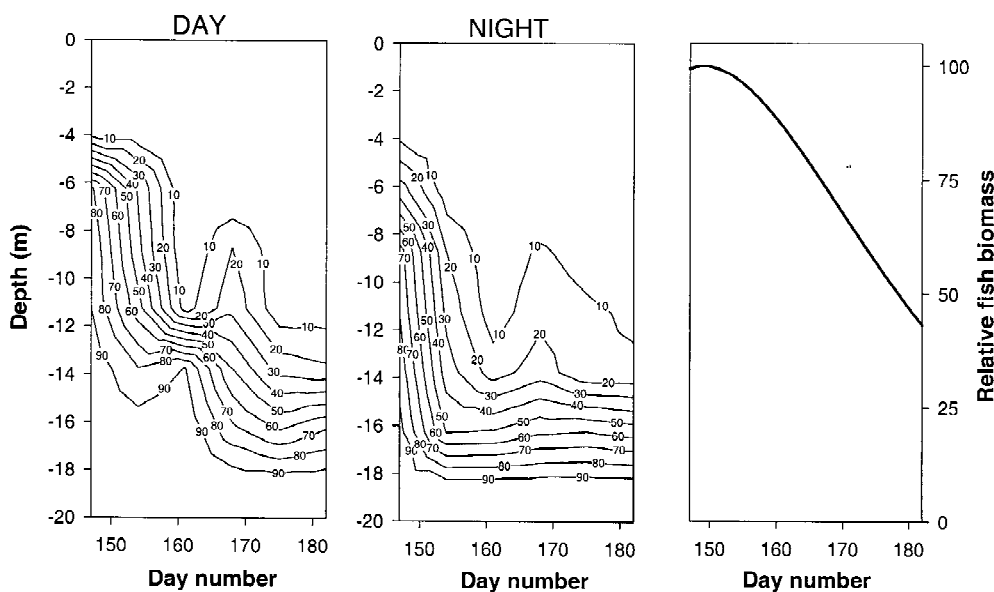
Figure 2. Left hand and middle panels: the seasonal variation in day- and night-time vertical distribution of *D. pulicaria* in Lake Maarsseveen based on vertical hauls with a closing net (1998), expressed in percentiles (80% of the population is located between the 10th and the 90th percentile line). Right hand panel: seasonal variation in relative fish biomass (%) in 1998 (data from Van Gool & Ringelberg, 2002). Time is given in day numbers.
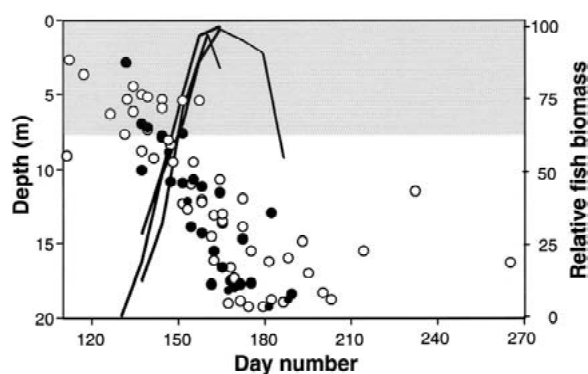

Figure 3. Seasonal variation in mean population depth at noon (open circles) and at midnight (black dots) of *D. pulicaria* during seven successive years (1992–1998) in Lake Maarsseveen related to the relative biomass (%) of 0+ perch (1992, 1993, 1994; solid lines). All *Daphnia* observations based on torpedo-catches. Fish biomass was only quantified in 1992, 1993, 1994 and 1998. For the fish biomass in 1998 see Figure 2. Time is given in day numbers; indicated is the water layer inhabited by the 0+perch (grey area), based on measurements with an echo sounder (Eagle, Mach 1).

ulation remained in the deeper layers both during day and night even after the fish-biomass has decreased towards much lower levels (Fig. 3).

The detailed observations in 1998 based on vertical hauls with a closing net were corroborated by the extensive study during 1992–1998 using torpedo

sampling (Fig. 3). The same pattern was repeated from year to year. As soon as the relative fish biomass approached its maximum at the end of May or by the first week of June, *D. pulicaria* started to migrate downwards. The daphnids did not come up during the night, but gradually migrated downwards and remained there for the rest of the year.

Since *D. pulicaria* did not exhibit diel vertical migration it is unlikely that the changes in light intensity at dawn and dusk triggered migration. Concomitant with the start of migration by the daphnids the epilimnion started warming up. Therefore, we considered temperature to be a likely candidate for the proximate factor for triggering migratory behaviour. To examine this we compared the vertical migration and depth selection behaviour of *D. pulicaria* with the concurrent temperature changes in the lake during 1992, 1993, 1994 and 1998. In all these years *D. pulicaria* started to migrate when the temperature in the epilimnion increased above approximately 16 °C (Fig. 4). This is apparently attributable to avoidance of the higher temperature in the surface waters. At the onset of descent, the mean population density showed a maximum and ca. 35% of the adult females were carrying epihippia, which is relatively high (Table 1). The clutch size of the parthenogenetic females was low (i.e., ca. 2.0 eggs per female), but almost constant during the

Table 1. Seasonal variation in densities (n m^{-3}), mean clutch size, and percentage of females with ephippia of *D. pulicaria* in Lake Maarsseveen in 1998 (closing net catches). Also given are the seasonal variation in the mean length (fork length) of 0+ perch, with the standard deviation of the mean (SD) and the percentages of total *Daphnia* and *D. pulicaria* in the stomach contents. Clutch size is expressed as mean number of eggs per ovigerous partenogenetic female, females with ephippia as the percentage of females with ephippia relative to the total number of females with eggs, percentage of *Daphnia* in the stomach contents relative to the total number of microcrustacean zooplankton

Date	Day No.	*D. pulicaria*			0+ perch	0+ perch	0+ perch
		Mean density (n m^{-3})	Mean clutch size (N_i)	Females with ephippia (%)	Mean length (SD) (mm)	Stomach content % *Daphnia* (N_s)	Stomach content % *D. pulicaria* (N_s)
May 27	147	415	2.1 (31)	36.3	16.8 (2.33)	11.7 (12)	0.0 (12)
June 3	154	1275	1.9 (94)	29.8	20.4 (4.40)	39.9 (11)	0.0 (11)
June 10	161	706	1.9 (121)	5.5	24.2 (6.57)	39.6 (14)	0.0 (14)
June 17	168	494	2.2 (99)	4.8	25.1 (6.16)	54.4 (10)	0.0 (10)
June 24	175	316	2.0 (52)	1.4	31.4 (4.46)	24.2 (11)	0.6 (11)
July 1	182	53	1.9 (20)	0	30.8 (4.71)	31.9 (9)	0.0 (9)

N_i = number of individuals observed; N_s = number of perch stomachs analysed.

whole period, meaning that food conditions in the deep hypolimnion near the bottom substrates were approximately as good as in the epilimnion (Table 1).

Gut contents of fish

The feeding preference of the 0+ perch was studied by analysing the fish stomach contents. At the end of May the fish were still small (ca. 1.7 cm) and were mainly feeding on smaller crustaceans (i.e., *Bosmina* spp. and juvenile copepod instars), as a result the numerical proportion of daphnids in its diet was low (Table 1). From early June onwards daphnids were eaten in substantial proportions and generally 30-50% of the stomach contents (numbers) were daphnids (Table 1). Most of the daphnids found in the guts were *D. galeata* × *hyalina*, and those of *D. pulicaria* were extremely low.

Laboratory observations

In our first experiment, before any treatment was applied, the daphnids appeared to be extremely positively phototactic; the mean population depth was ca. 5 cm below the surface (Fig. 5). Their depth distribution did not change after the addition of a large volume of 'fish water'. However, only after the temperature was raised from 15 to 25 °C, did the mean population depth increase from 5 cm to ca. 13 cm. In our second experiment, in which temperature was the only variable, temperature was gradually raised from 10 to approximately 20 °C. The mean population depth of the daphnids started to decrease from ca. 6 cm towards 12 cm below the surface after the temperature increased above ca. 14 °C. A further increase of temperature to ca. 20 °C resulted in an even lower population depth of 15 cm below the surface (Fig. 6). The maximum mean depth selected by the daphnids in both experiment is 13–15 cm. In absolute terms, this is only a short distance realised in a 60-cm long tube during a period of 72 h (first experiment) or 144 h (second experiment). Hence, the question remains why they are not migrating to a larger depth in the course of the experiment, whereas under field conditions they migrate till a depth of ca. 20 m? Two environmental conditions may limit the depth selected by the daphnids. Firstly, in the lake there is a gradient from warm water at the surface towards cold water in the hypolimnion, whereas this temperature gradient is lacking in the tube. Furthermore, light conditions in the tube are completely different from the light conditions in the field. Hence, it is not possible to translate directly results from the laboratory to the field.

Discussion

Our results clearly show that *D. pulicaria* does not exhibit any diel vertical migration behaviour in Lake Maarsseveen (Figs 2 and 3). During the 7-year study we observed the seasonal behaviour pattern repeated
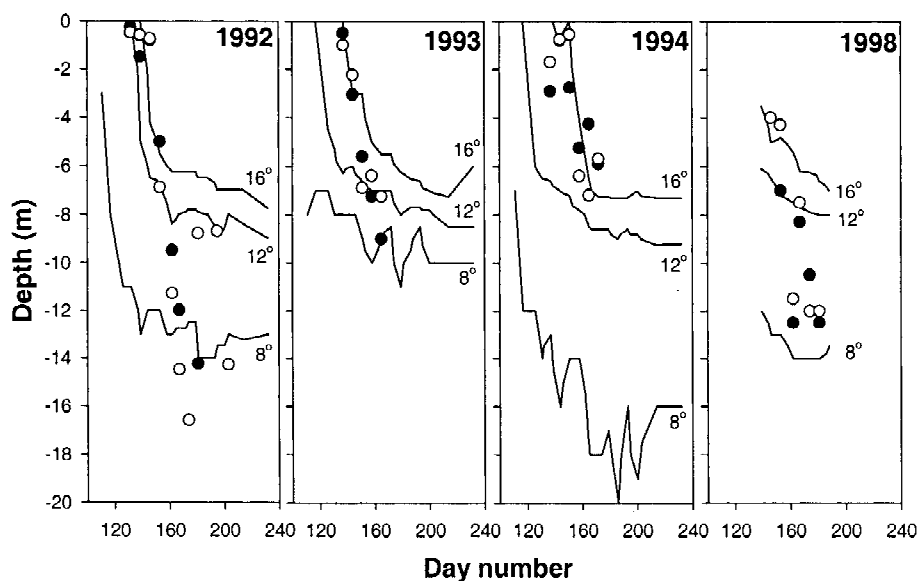
Figure 4. The depth distribution of the *D. pulicaria* population in Lake Maarsseveen in relation to water temperature during four years (1992, 1993, 1994 and 1998). Open circles represent day-time, and black dots night-time observations Population depths is given as the 10th percentiles, below this point 90% of the total population is present. The 8, 12 and 16 °C isotherms are indicated. Results of 1992–94 are based on torpedo-catches, 1998 is based on closing net catches.
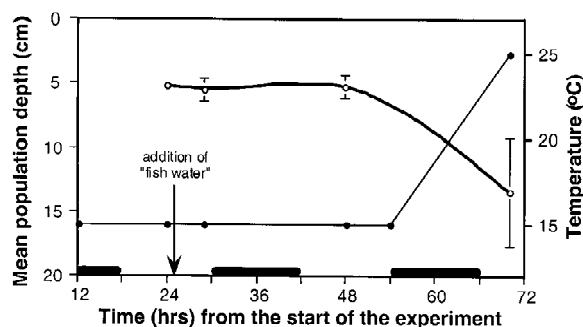

Figure 5. Mean population depth of *Daphnia pulicaria* (open circles) after a high concentration of 'fish water' is added after 24 h and an increase of the temperature (black dots) after 50 h. Error bars represent 95% confidence limits; horizontal thick black bars represent dark periods.
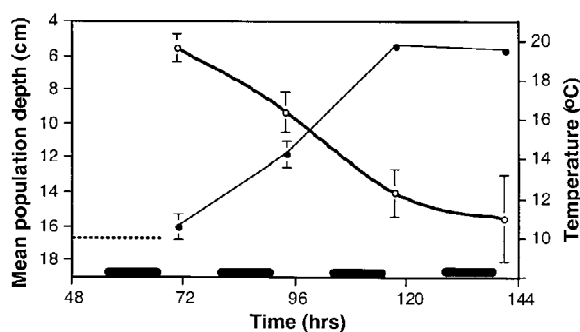
Figure 6. Mean population depth of *Daphnia pulicaria* (open circles) after an increase of the temperature (black dots). Before that increase the animals were acclimatized for about 3 days at 10 °C (dotted line). Error bars represent 95% confidence limits; horizontal thick black bars represent dark periods.

annually. In spring, the *D. pulicaria* population started occupying the surface layers during day and night until the end of May or the first week of June, followed by a downward migration and settling down in the water layers near the bottom by mid June. Thereafter, the population does not come up again during the same year. In contrast, the coexisting *D. galeata* × *hyalina* starts its diel vertical migration around the same time as *D. pulicaria* starts its downward migration. *D. galeata* × *hyalina* stops its diel migration around the end of July after which it again occupies

the warm surface waters during the day (Ringelberg et al., 1991). Judging from the numbers of the two *Daphnia* spp. observed in the stomach contents of the 0+ perch, the strategy of *D. pulicaria* is very successful, much more successful than the diel migration strategy of *D. galeata* × *hyalina*. However, there are also costs involved for *D. pulicaria*. Staying in the cold water in the hypolimnion day and night, instead of returning to the warm surface layers at night, decreases the egg development rate and the individual growth rate, as well as markedly lowers the birth rates. The re-

duced birth rate in concert with a moderate mortality is probably responsible for the decreasing population density of *D. pulicaria* in late June and early July. Since the presence of fish is ruled out in these deeper layers, it would probably be an invertebrate predator. Most likely *Leptodora* reduced the numbers of small juvenile *D. pulicaria*. During the second half of June and early July this predator showed relatively high densities of 15–30 ind m^{-3} and during the day it occupied the same deep-water layers as the daphnid (J. Vijverberg, own obs.).

A comparison of our observations on *D. pulicaria* with those reported in the literature is hampered by taxonomic problems. We identified *D. pulicaria*, both on basis of morphology (Dr E. Stuchlik, pers. comm.), and on basis of enzyme electrophoresis (Michaela Brehm, pers. comm.). Until ca. 20 years ago, however, *D. pulicaria*, because of its very similar morphology, was often wrongly identified as *D. pulex*. Recently, it has now become increasingly clear that the two species distinctly differ in their habitats, *D. pulex* occupying eutrophic shallow ponds and ditches, and *D. pulicaria* the larger and deeper water bodies (Flössner, 2000). In the following discussion we have, therefore, assumed that *D. pulex* reported from larger and deeper water bodies were actually *D. pulicaria*. For all such cases we have placed the specific name in quotes (= *D. 'pulicaria'*).

Most of the few detailed studies that exist on the depth selection of *D. pulicaria* report both diel migration behaviour and a depth selection for the cold hypolimnion. Bell & Ward (1970) reported the diel depth distribution of *D. pulicaria* (for species identification, see Ward, 1981) in West Blue Lake (Manitoba, Canada) to vary seasonally. There was no diel migration in May, with most daphnids occupying the intermediate depth (3–10 m) in warm water. There was, however, a weak diel migration in August: most of the population stayed the whole night in deeper (20–25 m) and colder water below the thermocline, but ascended to intermediate depths during day-time. In September, the animals exhibited the classical diel vertical migration behaviour, ascending into the surface at night and moving downwards into the deeper water layers (10–15 m) at day.

Lane (1975) found that in Gull Lake (Michigan, USA) in October 1965 and in September 1966 *D. 'pulicaria'* stayed day and night in deep cold water. About a month later in 1966, however, the daphnids exhibited a clear diel migratory behaviour, staying near the surface during the night. Threlkeld (1979)

observed in Wintergreen Lake (Michigan, USA) *D. pulicaria* from April until July, when the daphnid population became extinct. During spring, the population inhabited day and night the epilimnion, the downward migration started around mid June. The diel variation was weak and was limited to the metalimnion. A further downward migration into the hypolimnetic water was probably prevented by the ca. 4-m anaerobic layers up to the bottom (Threlkeld, 1979). Leibold & Tessier (1991) made an excellent study of the diel vertical distribution of *D. galeata mendotae* and *D. pulicaria* in six Michigan Lakes in relation to the risk of predation by fish. They demonstrated a distinct relationship between predation risk and the depth distribution of *D. pulicaria*. The animals clearly preferred to stay in the upper water layers when fish predation was low. In the extreme case of Gull Lake, with a very low predation risk, *D. pulicaria* shared day and night their habitat, the epilimnetic waters, with *D. galeata mendotae*. In the, Lawrence Lake, with a medium fish predation risk, *D. pulicaria* showed a weak diel vertical migration during May and June but started a downward descent in the second half of June. Concurrently, *D. galeata mendotae* also started its diel vertical migration, which it continued until the last observation in September.

Thus, although information on the vertical migration and depth selection behaviour of *D. pulicaria* in literature is limited, it does suggest that the downward migration behaviour of *D. pulicaria* is a direct response to its increasing vulnerability to fish predation in summer. In most lakes, in spring and early summer, when fish predation pressure is still low, this species exhibits diel vertical migration, but as soon as the predation pressure increases the downward migration starts. The situation in autumn seems to be more variable: in most cases the daphnids stay down, but diel vertical migration with occupying the warm surface layers at night, or even staying permanently at the surface layers, may also occur. It is cleat that this varied behaviour is directly related to the intensity of fish predation. When predation pressure is very weak (Gull Lake: Leibold & Tessier, 1991) *D. pulicaria* is day and night at the surface, showing no vertical migration at all. But, when predation pressure becomes somewhat higher, this species starts diel vertical migration (Bell & Ward, 1970; Lane, 1975), when the predation pressure increases even more, it starts with its downward migration towards deeper and colder water layers (Bell & Ward, 1970; Lane, 1975; Leibold & Tessier, 1991). In Lake Maarsseveen this species shows no diel

vertical migration before they start its downward migration. This can be explained by the very low fish biomass in the open water zone during spring (i.e., first 3 weeks of May). This is because the 0+ fish, which comprise all the population, are still very small at that time and mainly inhabit the littoral zone. However, during late May and early June because of the migration of the fish larvae from the littoral zone and the fast growth of the fish larvae in the open water of the epilimnion, fish biomass is increasing steeply. Therefore, before *D. pulicaria* has the time to develop diel migration behaviour it starts to migrate down because of the heavy fish predation.

That the migration behaviour of *D. pulicaria* can be very variable is supported by literature. Most probably the *D. pulicaria* populations comprise different clones that differ in migration behaviour as is already known for *D. pulicaria* (Tessier & Leibold, 1997) and for *Daphnia* spp. from the '*galeata*' group (Müller & Seitz, 1993; de Meester et al., 1995). Depending on selective forces, of which predation will be the most important one, one clone type with its specific migration behaviour will dominate the population at a certain time in the year. Since the extent of predation often changes seasonally, it is not surprising that migration behaviour varies in the course of a year. In view of this, it may seem surprising at first sight that *D. pulicaria* in Lake Maarsseveen shows such a consistent and stable behaviour, not only during 1 year but even during several successive years. This can probably be explained by two factors, specific for the Lake Maarsseveen ecosystem. Firstly, the very simple predator population (one fish species, one year class), which causes a very seasonal and very predictable predation pressure, including the variations herein. Secondly, the low genetic diversity of the *D. pulicaria* population in Lake Maarsseveen, i.e. only three multi-locus-genotypes of which one is predominant, comprising more than 90% of the density (Michaela Brehm, pers. comm.).

In Lake Maarsseveen the biomass of pelagic fish is at its maximum during the end of May and early June. It is therefore tempting to consider the infochemicals from fish act as a trigger for the migration behaviour of the *D. pulicaria*. However, this seems unlikely since in our experiment the daphnids did not change their depth distribution on adding the infochemicals. Temperature seems to be a more likely trigger for the migration for these zooplankters. During May 1998, when the surface water in the lake is warmed up very rapidly to 16 °C and higher, we observed a downward

movement of the animals. A similar pattern was observed for three other years for which we have data on day- and night-time depth distribution of the animals and water temperature. Our experimental data corroborate the potential importance of temperature as proximate factor for the migration behaviour of *D. pulicaria.* From an evolutionary point of view it makes sense that a water temperature above ca. 16 °C triggers the daphnids to move to deeper water layers. Because in most years this increase in temperature coincides with a sharp increase in the fish biomass and the start of 0+ fish feeding on daphnids. Before that time, the 0+ perch is gape limited and feeds mainly negatively size selective and avoids daphnids (Wong & Ward, 1972). After the descent to the deeper water layers, the mean clutch size remains almost constant, suggesting that food conditions in the deeper water layers are relatively good for *D. pulicaria* as compared with the warm surface layers. Algal densities in the hypolimnion were only ca. 25% of the densities in the epilimnion (Vos et al., in press), but we expect that *D. pulicaria* is also utilising heterotrophic flagellates and detrital particles with attached bacteria as food, which will be readily available in the hypolimnion. Experimental work showed that both food types when used to supplement algal foods may contribute to the production of young (Sanders et al., 1996; Repka et al., 1998). Therefore, we conclude that although the temperatures higher than ca. 16 °C probably act as trigger for the downward migration of *D. pulicaria* in Lake Maarsseveen, the relatively good food conditions very near the bottom may prevent an ascending behaviour later in the season.

Two species co-exist in Lake Maarsseveen: *D. pulicaria* and *D. galeata × hyalina.* Since *D. pulicaria* has a larger body-size than *D. galeata × hyalina*, and is therefore competitive dominant over the hybrid, it is unlikely that both species interact via their common food resource, but that they react both to fish predation. However, since they differ in size, and therefore in vulnerability for fish predation, both species adopt different strategies. The smaller bodied, and less vulnerable *D. galeata × hyalina* exhibits diel vertical migration ascending to the surface at dusk, and staying there during the night. In this way, benefiting from the higher temperatures of the surface layers. In contrast, the large-bodied, and more vulnerable *D. pulicaria* selects the deep cold hypolimnion water layers as refuge against fish predation. In this way benefiting from a safe habitat, free from fish predators, but on the

other hand suffering from low water temperatures that decrease its fitness.

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