

Swim or rest during the winter – what is best for an alpine daphnid?

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With 6 figures

Abstract: Surviving the winter is a special challenge for herbivorous aquatic invertebrates in the alpine region due to the long period of ice cover and cessation of primary production. Since there can still be open water under the ice in lakes and ponds, aquatic invertebrates can be active if they have enough stored resources. Daphnids usually survive the difficult winter period by producing and depositing resting eggs (ephippia) at the end of the summer. Some daphnids in alpine lakes and ponds, however, have a mixed strategy by both producing ephippia and living active in the water during the winter. We ask why these two strategies coexist stably: Do individuals both produce ephippia and stay active during the winter or do they only have resources for one of the strategies? We studied this phenomenon by sampling of *Daphnia umbra* twice per month from June to September and monthly the rest of the year in an alpine pond at Finse, Norway, 1207 m a. s. l. The species reproduced parthenogenetically in August and early September, with sexual reproduction of ephippia starting in late August. Highest ephippia densities were found in October, with about 10 % females carrying such eggs. The remaining females did not carry eggs but stored large reserves of lipids. During the winter, population size decreased, as did accumulated lipids. In spring, very few winter-active daphnids had survived until the ice melted and active winter survival seemed not to be a successful strategy during the year of study. Accumulating lipid reserves is assumed to be a special adaptation to postpone reproduction until spring which is unusual in daphnids. It is in contrast to their food dependent reproduction taking place during the summer, and it appears paradoxical that those specially adapted active winter survivors almost disappeared just before ice break-up. Most likely due to year to year variation in the conditions under the ice, the relative success of the two strategies varies. Parasitism, predators and available volume of open water under the ice might be the main factors. Ephippia producing females seem to have less lipids than those without ephippia, indicating that the two strategies compete for the animals resources and that the former might have problems with surviving the winter as active animals.

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Key words: *Daphnia umbra*, winter survival, reproduction strategy, lipid droplets, fishless alpine pond.

Introduction

Zooplankters vary in life history traits such as age at maturity, adult size and age specific fecundity (ROFF 2002). They divide their resources between metabolism, growth, energy storage, protection and reproduction, and their challenge is how to allocate the resources in such a way to maximize fitness. The problem of winter survival has led to evolution of two different reproduction modes (GILBERT & WILLIAMSON 1983). The first is a **food dependent reproduction**, which is an immediate reproduction when food is available, and **food independent reproduction** which is based on earlier stored resources. In the latter mode, reproductively mature females delay egg production until conditions are favourable for their progeny (VENTURA & CATALAN 2005). Copepods in alpine and arctic regions, both marine and freshwater, tend to have a food independent reproduction mode as an adaptation to life cycles of one year or more. In contrast, the rotifers, cladocerans and some calanoid copepods with a shorter life cycle normally have food dependent reproduction. When the food resources decrease in the autumn, many of those organisms that show a food dependent mode of reproduction form resting stages. Most commonly, they have some sort of dormancy throughout winter, ranging from slightly reduced metabolism to a complete diapause (ALEKSEEV & STAROBOGATOV 1996).

There are, however, some species of *Daphnia* (Cladocera, Crustacea) that exhibit a mixed strategy (GLIWICZ et al. 2001, VENTURA & CATALAN 2005). They have food dependent reproduction in summer, but in autumn both make resting eggs (diapause eggs) and build up large reserves of lipids for an active winter survival, most likely a preparation for a food independent reproduction in the spring. It is unclear, however, whether the same individuals produce both the resting stages and thereafter stay active in the water, or if individuals pursue only one of the two strategies. The question we ask is how the two different winter survival modes can occur simultaneously without out-competing each other.

We studied a *Daphnia* population that has this mixed strategy for surviving winter in alpine regions. *Daphnia pulicaria* populations with a mixed strategy have earlier been found in the Tatra mountains in Poland (GLIWICZ et al. 2001) and in the Pyrenees in Spain (VENTURA & CATALAN 2005) while in this study we investigated a population of *Daphnia umbra* (TAYLOR et al. 1996). Earlier authors dealing with the population in our alpine pond referred to this species as *D. longispina* (BORGERAAS & HESSEN 2002, HOBÆK & WOLF 1991). How-

ever, recent molecular studies revealed that it is a separate species and so far called *D. umbra* although there still is a dispute about the name (HOBÆK & SKAGE submitted). *D. umbra* has been studied by various authors because of its dark pigmentation which on the one hand is supposed to protect them against UV light, but on the other hand makes the animals particularly vulnerable to fish predation (SAEGROV et al. 1996). It is well known that daphnids can survive the winter both in an active phase and as resting eggs (CÁCERES & TESSIER 2004), but it is only in alpine systems that the tendency of storing lipids during the autumn was observed. The amount of lipid droplets in daphnids is normally considered as an indicator of good food conditions (TESSIER & GOULDEN 1982) and not something appearing when food availability is diminishing. This should indicate that lipid storage is a special adaptation for survival in this type of alpine environment.

We followed the development of a population of *Daphnia umbra* qualitatively through the autumn 2004 and spring 2005 and quantitatively since May 2005 to April 2006, to see how they allocated resources for survival and reproduction through out the year. Although it might be that the same individual both producing resting eggs and trying to survive the winter in an active phase, there might be a conflict in allocating resources. The questions we asked were whether the two modes can occur simultaneously, and what conditions favour dormancy over winter survival in an active phase. We also ask whether choosing the one strategy might exclude or reduce the success of the other.

Study site

Our study site is a small shallow pond, called Stasjonsdammen or F0 by HOBÆK & WOLF (1991), close by the Alpine Research Center at Finse, Norway (60° 36' N, 7° 30' E) 1207 m a. s. l. in the north-western part of Hardangervidda in Southern Norway (Fig. 1). Finse lies in the low alpine zone, about 250 meters above the current climatic tree line. The climate is slightly oceanic, with moderately cold winters (for the altitude and latitude) and cool summers. The annual mean temperature is about -2.0 °C and the mean precipitation ca. 1030 mm, much of which falls as snow (<http://www.bio.uio.no/fellesavdelinger/finse/location.html>).

The pond is oligotrophic and is normally covered with ice eight months a year, from late October to the end of June. The maximum depth is 3.3 m. The pond is fishless, but with some invertebrate predators, such as *Chaoborus flavicans*, *Megacyclops gigas*, *Polyphemus pediculus* and various Dytiscidae. The abundant herbivorous cladocerans in the pond besides *Daphnia umbra* are

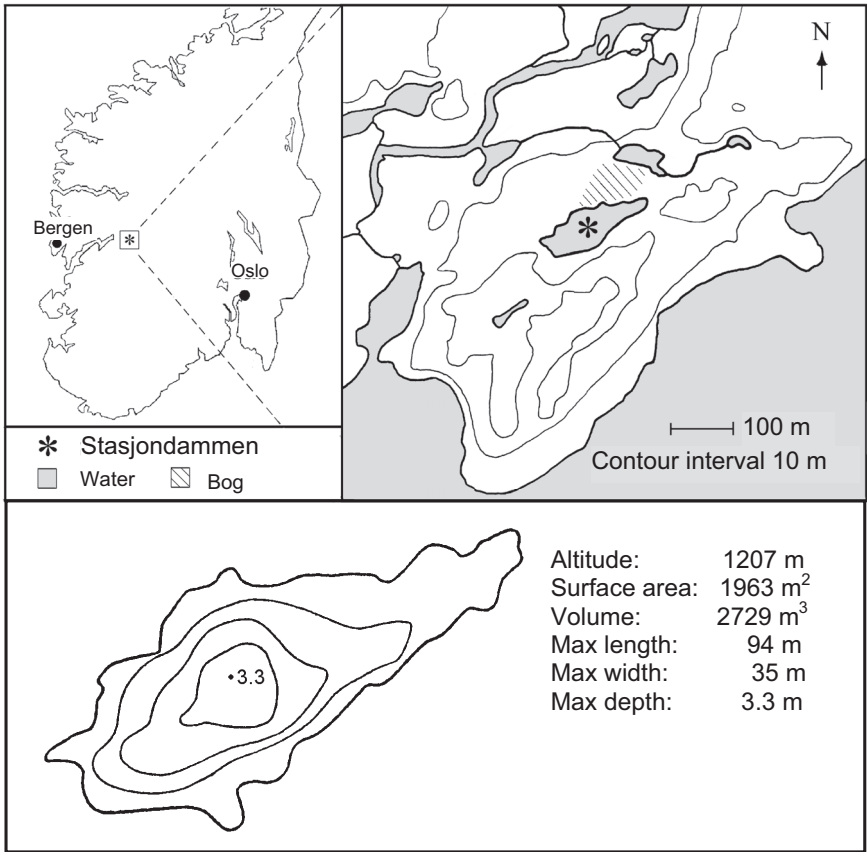


Fig. 1. Maps of the study area and bathymetric map of the Stasjonsdammen (F0).

Bosmina longispina, *Holopedium gibberum*, and *Chydorus* sp. The Copepod *Cyclops scutifer* is abundant.

Methods

In autumn 2004 and spring 2005, animals were collected monthly with a 90 µm plankton net to get material for size distributions, reproduction and changes in lipid droplets through the winter (qualitative sampling). Monthly quantitative samples were added starting in April 2005, using a 4.21 volume sampler, normally through the ice. Samples were taken at 1 and 2 m depth with 5 replicates of each. In the first quantitative sampling 12 May 2005 we had problems with coming through the 1.8 m ice and made only 2 holes, took two samples and filtered 8.41 of water. We use a motorized drill for making the holes. Zooplankton samples were preserved in sugar formaldehyde and counted. Size (measured as the distance between top of the head and the base of the

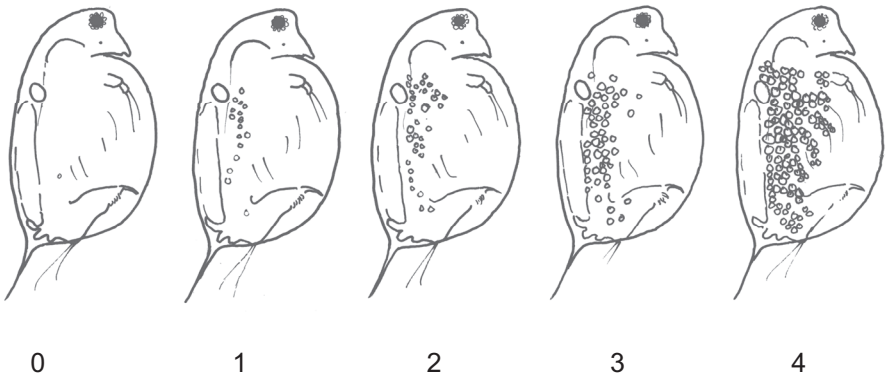


Fig. 2. Lipid index from 0 to 4 extended from TESSIER & GOULDEN (1982). The small roundings visualize lipid droplets. Score is determined on the amount of droplets on the body. In score 4 the droplets are also attached to the appendices.

caudal spine), sex, and egg type and number were established. Algal (food) biomass was estimated by chlorophyll-*a* analysed with standard methods (extraction with acetone). A temperature sensor at the deepest point in the pond recorded the bottom temperature hourly since 1996. In addition the temperature, oxygen concentrations were measured with a YSI oxymeter at each sampling occasion from May 2005 to April 2006.

To score the animals for the content of lipid droplets, microscope digital photos were taken of 25 live animals each sampling time. From August 2005 about 100–200 individuals were examined at every sampling occasion to get a better documentation of the size, sex and egg distribution. We used the lipid index introduced by TESSIER & GOULDEN (1982). However, in late autumn, the content of lipid droplets in the daphnids from Finse was much higher than the maximum 3 in their index, and we had to add one more unit, 4, for the animals maximally filled with lipid droplets (Fig. 2). In stage 4, droplets accumulate not only around the main body, but extend also out to the filtering appendices. GLIWICZ *et al.* (2001) who had a similar problem with animals containing many lipid droplets, expanded the index scale to 5. However, they did not characterize categories 4 and 5, and we found it sufficient to expand the index only to 4. The scoring process is subjective, and for reducing eventual bias, the two authors scored the animals in the pictures independently and without knowing when the picture was taken. We used the mean score for our analyses.

On 12 May and 6 June 2005, 10 sediment cores were taken (diameter 6.4 cm giving a surface area of 0.0032 m²). The upper 2 cm of the core was examined under stereo microscope, but also kept 14 days in pond water at room temperature to estimate hatching rates of remaining ephippia.

Results

Temperature, oxygen and chlorophyll-*a*

The bottom temperature in the pond is shown in Fig. 3, showing the variance over the last five years. The highest temperature was found in July–August while the water was coldest in October just before the pond is covered with ice and in May at the end of the winter season. During the ice free period, surface and bottom temperatures were approximately equal and did not differ by more than about 0.5 °C. During the period of ice cover there was a gradient from about 0 °C immediately under the ice to the recorded bottom temperature. In extremely cold winters, the spring minimum temperature on the bottom goes down to almost zero, but not below. This indicates that in some years the pond might be very close to bottom freezing with very small areas with open water under the ice. Other years, the minimum bottom temperature in spring is about 4 °C, allowing a larger volume of water under the ice. The two years from which we have collected animals are fairly different with regard to temperature. The bottom temperature in the end of the winter was almost 4 °C in 2004, while in 2005 the temperature went down to 2.4 °C. On 12 May 2005, the temperature at 2.5 m was as low as 1.0 °C while the bottom temperature was 2.5 °C. In 2004, the ice disappeared about 8 June, in 2005, on 24 June. We did not have the maximum ice thickness for 2004, but in 2005 it was found to be 1.80 m at the end of the winter.

During the period of open water, oxygen concentrations were found to be only slightly below equilibrium with air, but under the ice oxygen concentra-

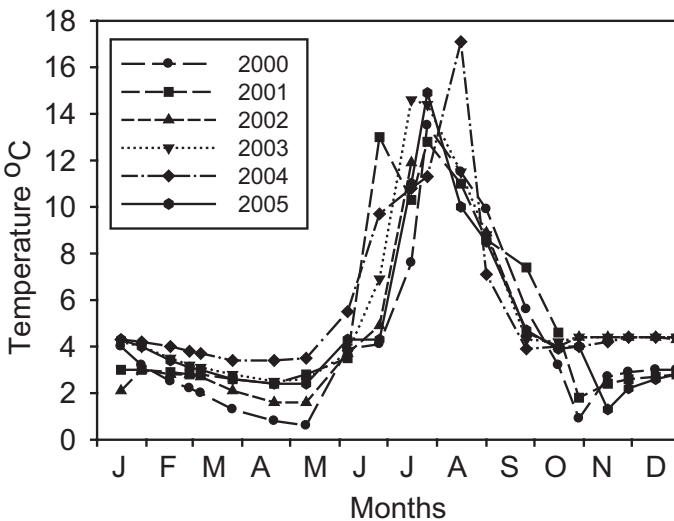


Fig. 3. Bottom temperature in the pond recorded through the last six years.

tions decreased. In May 2005, the oxygen at 2.5 m depth was $6.8 \text{ mg O}_2 \text{ l}^{-1}$ indicating only moderate oxygen depletion, but in January 2006, the reduction of oxygen under the ice had already started and only $3.4 \text{ mg O}_2 \text{ l}^{-1}$ was measured at 3 m depth. Although the values are much lower than saturation values, these concentrations are most likely not critical for the daphnids under the ice.

The pond had very clear water all through the summer, and even in the end of June one could see the plankton net on the bottom at 3.3 m depth. The chlorophyll data showed a small amount of phytoplankton all through the

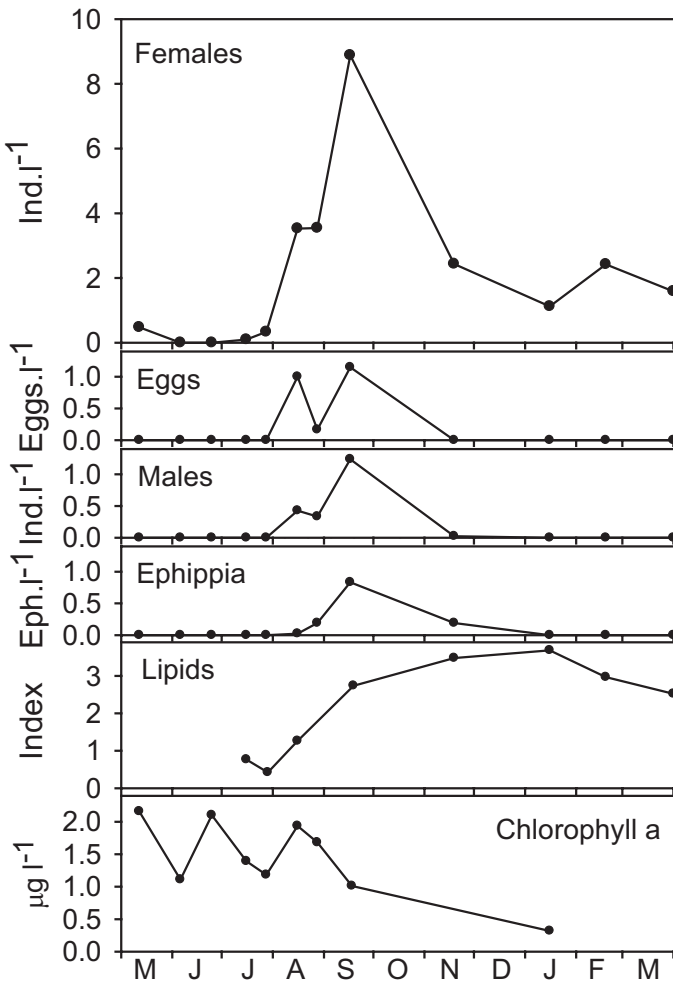


Fig. 4. Density of females, males, ephippia and eggs, average lipid index and chlorophyll-*a* concentrations from May 2005 to April 2006 in the pond from May 2005 to January 2006.

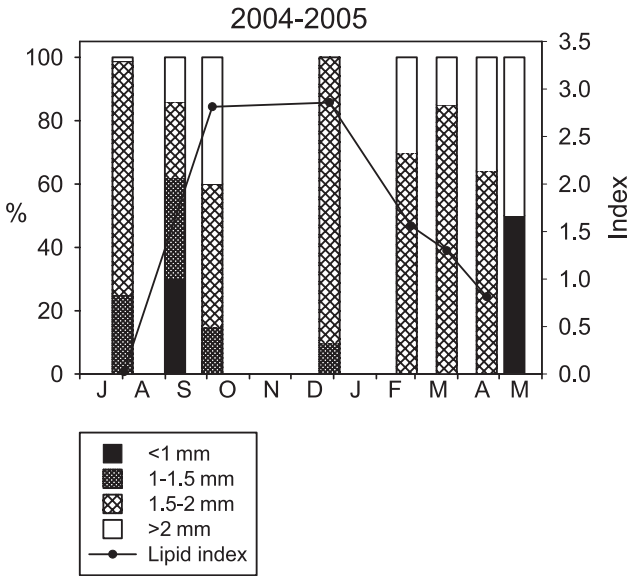


Fig. 5. Size distribution and average lipid index in the *Daphnia umbra* population in 2004–2005.

summer (Fig. 4), varying between 1 and $2.2 \mu\text{g l}^{-1}$. It decreased during autumn to about $0.3 \mu\text{g l}^{-1}$ in January 2006.

Size distribution

The size distribution of daphnids for the two years of investigation is shown in Figs 5 and 6. The number of first generation hatchlings from resting eggs was so small that we were not able to recognize it with ordinary sampling. Their progeny, however, appeared in the middle of July and they reached maturity in the end of July or early August. The two years under study differed: in 2004 no neonates were found early in the year, in contrast to 2005 where the neonates from what we expected as the second generation could be found already by the end of July. However, the main recruitment period came in August and September in both years resulting in a size distribution containing all size classes. The population contained only animals larger than 1.5 mm after reproduction stopped in the end of the year.

Reproduction

At the time of the first qualitative sampling on 1 August in 2004, 80 daphnids were examined and neither of them had eggs nor ephippia, 5 % were males. About 75 % were larger than 1.5 mm indicating that a large proportion of the

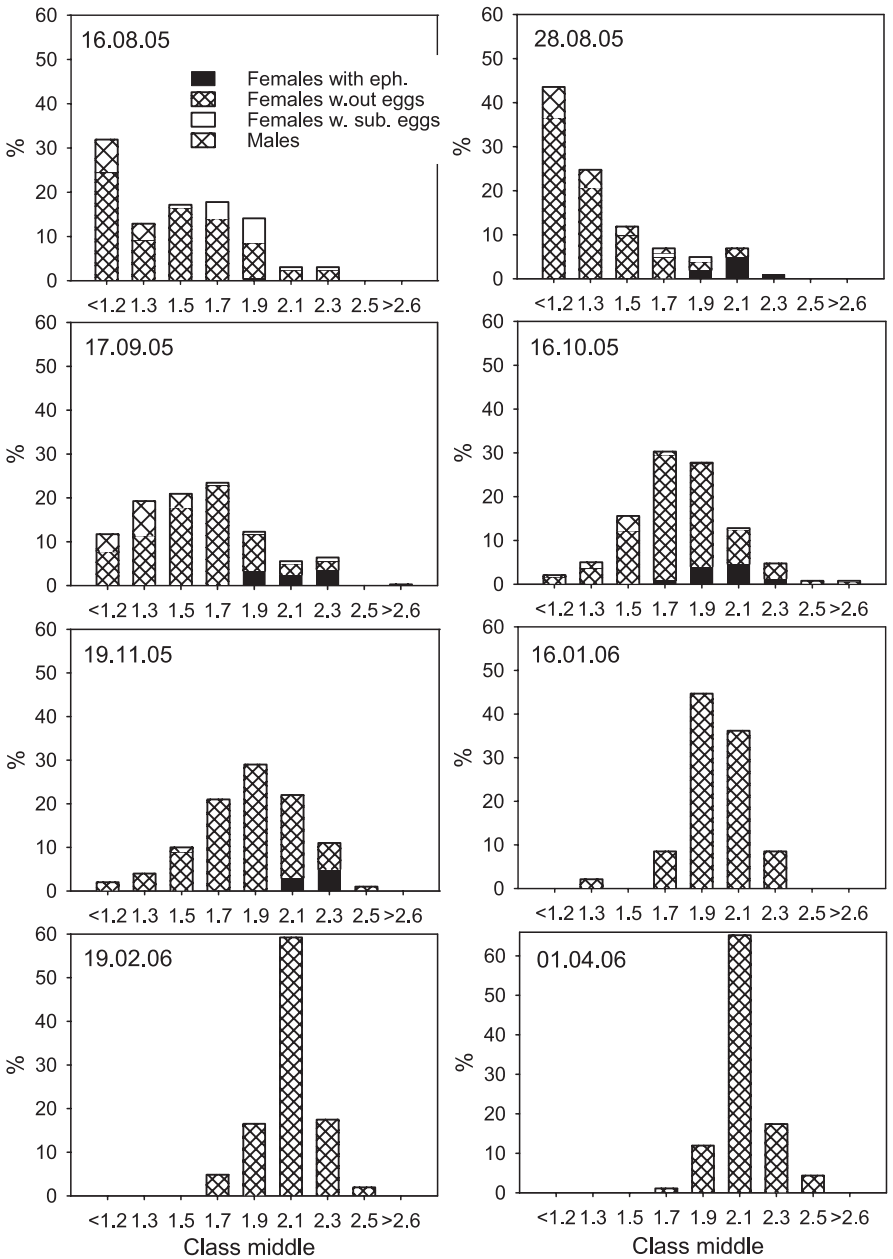


Fig. 6. Size distribution of *Daphnia umbra* males and females without eggs, with eggs and with ephippia at 8 occasions in 2005–2006.

individuals should be large enough to have eggs, as the smallest egg carrying females found during the investigation was 1.6 mm. None of the animals caught on 1 August 2004 was smaller than 1 mm, indicating almost no reproduction in the end of July. Based on this, we assume that the main bulk of the population in August of 2004 was the second generation animals, the progeny of those animals that were juveniles at the time of ice break. On 8 September about 30 % of the females were smaller than 1 mm and 30 % larger than 1.5 mm (Fig. 5), with 19.4 % males. 8 % of the females carried ephippia, and these were all small females between 1.6–1.9 mm. Only a few females carried subitaneous eggs averaging 0.38 eggs per female, indicating that some asexual reproduction still took place. During the rest of the autumn 2004 and until summer 2005, none of the animals examined had subitaneous eggs.

In spring 2005, when the quantitative sampling started, we found a couple of neonates in the samples from 12 May. This indicated that some hatching had taken place. Since none of the adult females carried subitaneous eggs, the neonates most likely had hatched from resting eggs. In the 5 core samples from 12 May, we found two *Daphnia* ephippia with and one without eggs, and in the five from 06 June two with one egg and two without eggs. This would correspond to 2176 eggs per m² or about 1.51 l⁻¹ if the whole pond were covered with ephippia. However, the numbers of ephippia in the sediment were very low, and the few ephippia we found were from the middle of the pond and we do not know whether this was representative for the distribution pattern of the ephippia in the pond. If, for example, only the sediment at a water depth of 2 m was covered with *Daphnia* ephippia, it would give a hatching equal to 0.46 ind. l⁻¹, if all eggs were to hatch. However, even with this most conservative estimate the resting eggs might still be contributing significantly to the initiation of the summer population. None of the *Daphnia* ephippia with eggs found in the sediment samples hatched after 14 days in pond water, but a small amount of *Bosmina* and *Holopedium* hatched. This could indicate that the main hatching from ephippia had already taken place in May.

No animals were found in the quantitative samples from June neither before nor after the ice break. This could indicate that the numbers of survivors both from ephippia and over wintering females were extremely low. A few juveniles appeared on 16 July, but the first egg carrying females were found only on 28 July more than a month after the ice break. Then 16 out of the total of 17 mature females from a net haul had subitaneous eggs, with an average of 8.3 eggs per female. The population was still so small that in the quantitative samples there were only neonates. The population continued to produce subitaneous eggs until November, although with decreasing clutch size (Fig. 4). The first males appeared in the middle of August and reached highest relative densities by the end of that month (13.6 % of the population on 28 August), decreasing again until the end of November when less than 1 % of the animals

caught were males. The first females with ephippia appeared simultaneously with the males, but the highest density was found later in the autumn. The highest proportion of ephippial females was found in the qualitative sample in October (11.3 % at 16 October) (Fig. 6) (thin ice prevented quantitative sampling). On 19 November there were still 8 % females with ephippia but no males, and on 16 January 2006 all ephippia carrying females had disappeared.

Population size

The development of the population is shown in Fig. 4. Net samples from 22 April 2005 indicated that there were still many animals left in the water, but when we started the quantitative sampling about a month later (12 May) (by filtering 8.4l), we got only two adults without eggs and two neonates. Samples taken on 6 May about 18 days before ice break yielded no individuals, and daphnids were also absent in the samples just after the ice break at 25 June. On 16 July a few medium sized juveniles were found and a couple of weeks later (28 July) the first newborn were registered. The density increased during August and September and peaked in the middle of September with almost 9 ind. l^{-1} . From then on it decreased and from 16 January the estimates varied between 1 and 2 ind. l^{-1} .

Lipid index

The development of the lipid index is shown in Figs 4 and 5. Lipids were scarcely recognized in the animals taken at the end of July or beginning of August both years. The juveniles found on 16 July, however, had more lipids than the egg carrying sisters found about two weeks later. However, during the autumn the animals built up their storage of lipid droplets and reached a maximum close to the end of the year. The two years were slightly different and the daphnids seemed to have accumulated more lipids in 2005 than in 2004. In spring 2005 the lipid index declined from January and reached a mean score of about 1 by the end of April. A similar trend was found in 2006. The lipid index of animals with ephippia seems to be less than of those without ephippial eggs. In the quantitative samples from 10 October the mean score was 3.18 and 3.80 respectively giving a significant difference with a Mann-Whitney test ($p < 0.01$).

Discussion

It has been reported from many lowland lakes in the temperate zone that daphnids might spend the winter in an active phase (CÁCERES & TESSIER 2004), but

fewer instances have been reported from alpine lakes. LARSSON (1978) found a few individuals of adult *Daphnia longispina* (sen. str.) under the ice in Øvre Heimdalsvatn in the central mountain area of southern Norway and GLIWICZ et al. (2001) and VENTURA & CATALAN (2005) studied *Daphnia pulex* surviving the winter in an active phase in the Tatra mountains in Southern Poland and the Pyrenees in Spain respectively. In both *D. pulex* studies they found that winter survivors initiated the coming summer population by asexual reproduction. We could not document that the summer population was initiated by asexual reproduction by overwintering animals. However, the small number of survivors in May 2005 still had lipid droplets and could theoretically have contributed to the start of the summer population, but for some reason they seemed not to do so. Most likely the main inoculation in summer 2005 this year came from the resting eggs.

One might ask whether this was a typical situation or just something that appears from year to year depending on the environmental variation. Since the winter and spring conditions are generally highly variable, most likely the number of survivors varies. In 2005 the spring was very cold with very thick ice cover and the conditions for the active survivors could have been particularly difficult in that year. We observed a difference in lipid content between our two years of study and it could be that food competition in the autumn might vary giving different possibilities for accumulating lipid droplets. Also the invertebrate predators might be present in different abundance from year to year and similarly eventual parasites might be more common under certain conditions. On some of the digital pictures of the animals it looks as if the filtering appendices are covered with some mucus looking "gloves" possibly preventing the animals from filtering algae out of the water (LARSSON & WATHNE, unpubl.).

The main period for asexual reproduction was August and September in both years. It was slightly earlier in 2005 than 2004, but in both years the delay between ice break and increase of the populations was substantial. A similar situation was registered by GLIWICZ et al. (2001). We interpret this as a combination of a very small start population after the ice break combined with low temperature. If one uses the development time for daphnids at different temperatures given by GELLER (1987), the adult animals we found in the end of July should be the second generation, or more precisely, the offspring from the few juveniles present at ice break. Since we found neonates already in the middle of May, this may be the start of the first cohort, but with temperatures below 4 °C degrees more than 50 days are needed to reach maturity, and the first adults should then theoretically appear in the beginning of July.

The abundance of daphnids in the end of July is a result of the initial population at ice break. If the initial population is large, the density in early August should be higher than if it is small. In 2005 the density of daphnids was

about 0.3 ind l⁻¹ in transition between July and August, indicating that the daphnids at that time were not density limited and we could assume the initial density to be very low. We did not have any density data for 2004, but the high proportion of adult sized animals without eggs at 1 August could have been a result of an already established density limitation. However, both in 2004 and 2005 there was a marked reproduction period in August and September increasing the population density and mixing the size groups. Both sexual and asexual reproduction took place at the same time although asexual reproduction dominated in the beginning and sexual in the end of the autumn.

Males reached almost 20% of the population in 2004 and also in September 2005 they were more frequent than females with ephippia. This indicates that the population was ready for massive sexual reproduction. However, females with ephippia did not exceed 12% of the population. It might be that we did not recognize all the females carrying ephippia, and that females after producing their only ephippium, continued barren only increasing their lipid storage. However, the samples were taken with about one month intervals and the intermoult time in September, with a temperature below 5 °C, should be almost 20 days (BOTIRELL et al. 1976). Thus, if they all were to produce resting eggs, we would have expected that the majority in our samples would have carried ephippia. Instead, it looks as if the majority of the females did not engage in sexual reproduction. They were large enough to carry eggs but they do not in spite of high abundance of males. The majority seemed to opt for the accumulation of lipids. The lower lipid content in ephippia females compared with females without ephippia indicates that there is high cost to both produce ephippia and being active during the winter, and therefore they mainly chose one of the strategies.

Surprisingly, however, was that the accumulation of lipids could continue until December and January although the measured chlorophyll became much less than 1 µg chl-*a* l⁻¹.

The accumulation of lipids in the winter-active animals was much more than what has been found in lowland lakes and it is typical that we had to add an extra category to the lipid index made by TESSIER & GOULDEN (1982). We think this is a special adaptation for life under the ice. Even *D. umbra* kept in laboratory cultures over a longer time, showed higher contents of lipids, than other species (LARSSON & WATHNE, unpubl. obs.). Interesting is that a completely different species like *D. pulicaria* showed very similar tendencies in the Tatra mountains and the Pyrenees. The copepod *Cyclops scutifer* that has a one year or longer life cycle in the Norwegian mountains (ELGMORK & EIE 1989, LARSSON 1978) also stores lipids, and storage of large amounts of lipids are well known from marine plankton like *Calanus* spp. in the Arctic and Euphausiacea (krill) in the Antarctic (HAGEN & AUDEL 2001). It seems obvious that lipid accumulation is an adaptation for energy storage for a long period of

almost no food for zooplankton. The observed reduction in lipid content in *D. umbra* during the winter seems to fit into this picture. Interesting is that this accumulation of lipids appears both in arctic and alpine regions and that phylogenetically very different species have developed the same ability.

The remaining question is, however, why the daphnids accumulate lipids instead of investing more in resting eggs? The death rate is very high during the winter (Fig. 4) and in the beginning of April 2006 the population size was only about 10% of the population maximum in September. What we found in spring 2005 also underlines that the winter active strategy is very dangerous. So why are the accumulated lipids not being used only for resting eggs?

There are various possible causes. On the one side the active winter survival strategy is successful in other habitats, and it could well be that the circumstances in 2005 caused a failure of this strategy. The low temperature might have been a reason both directly and indirectly. The large insect larvae might have taken a larger toll of the population in this year than in others because the volume under the ice was particularly small this year, which could also have increased the transmission rates in parasites in the reduced volume of water. On the other side, there are probably limitations for the resting egg strategy also. Since our pond is fishless, there are various invertebrate predators present that may overtax the hatchlings from resting eggs. It is supposed that ephippia itself is resistant to predation to some extent, but that might not be the case if beetles, chironomids and other insect larvae are trying to eat them. When we found empty ephippia in the sediment it could be due to hatching, but it could also be due to egg predation. Also when the resting eggs hatch, the neonates are very vulnerable to invertebrate predation. Possibly this reduces the amount of ephippial offspring that contributes to the summer inoculation. To uncover the real reasons it is necessary to do particular predation experiments simulating winter conditions.

Since *D. umbra* has two different strategies, one might expect that they both have to be successful at times, otherwise one of the two should have disappeared. The investment in a food independent reproduction strategy is so fundamental that it is unlikely that it will be unsuccessful every year. Our conclusion so far is that in some years the winter active animals are very successful, in other years the ephippia strategy might win. Our next task is to identify the factors that are responsible for the different success. It is shown that years can vary dramatically with respect to temperature and the 2005 spring was colder than normal. Since the daphnids are not alone in the pond, competitors, predators and parasites may vary in abundance and success. If some predators are fewer one year than another, the survival in spring could be very much altered.

Acknowledgements

We thank RONALD P. SEMYALO, ANNA SANDVEN, LISE JOHANSEN and HELENE HYS-TAD for helping us in the field work, and HARALD STEEN and ERICA LESLIE for the support on the Alpine Research Center – Finse. We thank LAWRENCE KIRKENDALL, an anonymous referee for comments to our manuscript and GAUTE VELLE for allowing us to use his figure with map of the sampling site. We are also thankful to the University of Oslo and the University of Bergen allowing us to use the facilities at the research station. We are very thankful to the Norwegian Meteorological Institute for providing us with the temperature data in the pond.

References

- ALEKSEEV, V. R. & STAROBOGATOV, Y. I. (1996): Types of diapause in Crustacea: Definitions, distribution, evolution. – *Hydrobiologia* **320**: 15–26.
- BORGERAAS, J. & HESSEN, D. O. (2002): Diurnal patterns of antioxidant activity in alpine and arctic *Daphnia* under in situ UV-radiation. – *Arch. Hydrobiol.* **156**: 83–95.
- BOTTRELL, H. H., DUNCAN, A., GLIWICZ, Z. M., GRYGIEREK, E., HERZIG, A., HILLBRICHT-ILKOWSKA, A., KURASAWA, H., LARSSON, P. & WEGLENSKA, T. (1976): A review of some problems in zooplankton production studies. – *Norw. J. Zool.* **24**: 319–456.
- CÁCERES, C. E. & TESSIER, A. J. (2004): Incidence of diapause varies among populations of *Daphnia pulicaria*. – *Oecologia* **141**: 425–431.
- – (2004): To sink or swim: Variable diapause strategies among *Daphnia* species. – *Limnol. Oceanogr.* **49**: 1333–1340.
- ELGMORK, K. & EIE, J. A. (1989): 2-Year and 3-Year life-cycles in the planktonic copepod *Cyclops scutifer* in 2 high Mountain lakes. – *Holarct. Ecol.* **12**: 60–69.
- GELLER, W. (1987): On estimating the age and the development time of *Daphnia* as a function of body size and temperature. – *J. Plankton Res.* **9**: 1225–1230.
- GILBERT, J. J. & WILLIAMSON, C. E. (1983): Sexual dimorphism in zooplankton (Copepoda, Cladocera, and Rotifera). – *Annu. Rev. Ecol. Syst.* **14**: 1–33.
- GLIWICZ, Z. M., ŚLUSARCZYK, A. & ŚLUSARCZYK, M. (2001): Life history synchronization in a long-lifespan single-cohort *Daphnia* population in a fishless alpine lake. – *Oecologia* **128**: 368–378.
- HAGEN, W. & AUDEL, H. (2001): Seasonal adaptations and the role of lipids in oceanic zooplankton. – *Zool.-Analysis Complex Syst.* **104**: 313–326.
- HOBÆK, A. & SKAGE, M. (submitted): Distribution and genetic variation of *Daphnia umbra* in Northern Europe. – *Freshwat. Biol.*
- HOBÆK, A. & WOLF, H. G. (1991): Ecological genetics of Norwegian *Daphnia*. II Distribution of *Daphnia longispina* genotypes in relation to short-wave radiation and water colour. – *Hydrobiologia* **225**: 229–243.
- LARSSON, P. (1978): The life cycle dynamics and production of zooplankton in Øvre Heimdalsvatn. – *Holarct. Ecol.* **1**: 162–218.
- ROFF, D. A. (2002): Life history evolution – Sinauer Associates, Inc., Sunderland, U.S.A.

- SÆGROV, H., HOBÆK, A. & L'ABÉE-LUND, J. H. (1996): Vulnerability of melanic *Daphnia* to brown trout predation. – J. Plankton Res. **18**: 2113–2118.
- TAYLOR, D. J., HEBERT, P. D. N. & COLBOURNE, J. K. (1996): Phylogenetics and evolution of the *Daphnia longispina* group (Crustacea) based on 12S rDNA sequence and allozyme variation. – Mol. Phyl. Evol. **5**: 495–510.
- TESSIER, A. J. & GOULDEN, C. E. (1982): Estimating food limitation in cladoceran populations. – Limnol. Oceanogr. **27**: 707–717.
- VENTURA, M. & CATALAN, J. (2005): Reproduction as one of the main causes of temporal variability in the elemental composition of zooplankton. – Limnol. Oceanogr. **50**: 2043–2056.

Submitted: 7 February 2006; accepted: 20 April 2006.