POLISH POLAR RESEARCH
vol. 24, no. 2, pp. 167–172, 2003

The long-lasting resistence of diapausing eggs from Arctic Cladocera frozen at –18°C

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ABSTRACT: Mud samples from two lakes in West Greenland were kept frozen at –18°C for 18 years. When they were thawed, 4 Cladocera species hatched from diapausing eggs: *Daphnia pulex* (De Geer, 1778), *Macrothrix hirsuticornis* (Norman et Brady, 1867) and *Chydorus arcticus* (Røen, 1987), which are by far the most abundant Cladocera species in the high Arctic north of 74°N. Another species was *Alona quadrangularis* (O. F. Müller, 1785), which occurs up to 72°N. All these species gave rise to parthenogenetic offspring and produced ephippia within a time frame comparable to an Arctic summer season. Up to 9 other Cladocera species were likely to be present in the original populations, but did not hatch anymore after 12 years.

Key words: Arctic, Cladocera, diapausing eggs.

Introduction

The important role of long-lasting diapause in the evolution of freshwater crustaceans has been outlined by several authors, for instance Fryer (1996) and Cáseres (1997). In Cladocera diapause is always linked to diapausing eggs, which preserve their populations in waterbodies during periods of difficult or even lacking living conditions, often caused by droughts or low temperatures. We are speaking about temporary waters in these cases, since the waterbody itself is then replaced either by air or, as in Arctic regions, by ice (Jacobi and Meijering 1978). On the other hand interruptions of suitable living conditions can also be caused by factors changing the water quality. An example is the fluctuation of salt contents in ponds which are subject to episodical intrusions of seawater during marine stormfloods (Meijering 1970, Jacobi and Meijering 1979). This means that unsuitable living conditions can be prolonged for several seasons, making it unclear when living conditions for zooplankton will reappear. One response of Cladocera to these challenges is their capability to remain in diapause for years. Species from such a type are ready to settle in ecological borderlands, for example in high Arctic

Fig.1. Sampling of Cladocera in the lake of Kangârssuk, West Greenland, in August 1977.

regions, where low temperatures and short summer seasons have a formative influence. It would be interesting to know, whether Cladocera species from high Arctic regions have special adaptations to resist extremely low temperatures and lack of time during short summers.

Material and methods

In August 1977 mud samples were taken from two locations in West Greenland. One was a small lake on Kangârssuk, a peninsula at Fortune Bay on the south coast of Disko-Island (69°16' N, 53°50' W) (Fig.1), and the other a small lake on the hills near Søndre Størmfjord airport (67°02' N, 50°37' W) (Fig. 2). The mud was kept dripping wet and so brought to Europe, and after arrival the samples were kept frozen at –18°C in a deepfreeze. This was done in order to be able to hatch the diapausing eggs and determine the zooplankton species composition of these sites.

After 12 years, in February 1990, half of each mud sample, some 300 ml each, were thawed up in 5-l-aquaria at 2°C in the course of 2 days and than warmed to about 10°C within some 10 days. Initially the water in the cultures was not aerated until it became cloudy from rotting processes in the mud. It was then replaced by new tapwater and aerated successively. The cloudy water was kept separately and was used to feed the Cladocera that were hatched. The cultures were kept in a partly subterranean room at a window, where they were exposed to night- and day-

Fig.2. Lake above Søndre-Strømfjord-Airport, West Greenland, where Cladocera were sampled in 1977 and 1995. On the horizon the inland icecap is visible.

light and slightly fluctuating temperatures around 10°C. Pelagic Cladocera were always visible in the relatively clear water of the cultures, but the benthic species were hidden in the mud on the bottom. Therefore the mud was examined once a week to determine the Cladocera alive; only a few species were fixed in alcohol to confirm the determinations, while all the others were released in the cultures. At these occasions data on the state of development and the production of subitan and diapausing eggs were gathered.

After 18 years, in October 1995, the other half of the mud samples were thawed and treated in the same way as described before.

In July 1995 Cladocera were sampled at the same sites near Fortune Bay and Søndre Strømfjord in West Greenland by U. Ozols. These samples were instantly fixed in alkohol for species determination.

Results

After more than 12 years of dormancy in –18°C, 4 Cladocera species hatched from diapausing eggs collected in both lakes on Kangârssuk and near Søndre Strømfjord in Greenland. These were the pelagic *Daphnia pulex* (De Geer, 1778) and the benthic *Macrothrix hirsuticornis* Norman et Brady, 1867, *Alona quadrangularis* (O. F. Müller, 1785) and *Chydorus arcticus* Røen, 1987. After another

6 years of dormancy the same species hatched. So 4 Cladocera species were able to withstand –18˚C as diapausing eggs in frozen mud for at least 18 years.

Up to 9 other species are likely to have been present in the mud samples of 1977, since they were found in the same sites, sampled by U. Ozols in 1995. These were *Simocephalus vetulus* (O.F. Müller, 1776), *Scapholeberis mucronata* (O.F. Müller, 1785), *Ceriodaphnia quadrangula* (O.F. Müller, 1785), *Bosmina coregoni* Baird, 1857, *Eurycercus glacialis* Lilljeborg, 1887, *Acroperus harpae* (Baird, 1835), *Alona affinis* (Leydig, 1860), *Graptoleberis testudinaria* (Fischer, 1848) and *Polyphemus pediculus* (Linne, 1761).

Dapnia pulex hatched quickly and started to produce subitan eggs already in the 5th week after thawing and ephippia in the 7th, at a mean temperature of 7.7˚C up to then. It should be mentioned that *Daphnia pulex* is able to produce ephippia already in a second adult instar of ex-ephippio females. In *Macrothrix hirsuticornis* ephippia are produced only by F_1-females. This species laid subitan eggs in the 8th week after thawing and ephippia in the 15th. The mean temperature during this period was 10.7˚C. The same mean temperature applies to *Chydorus arcticus*, which took 6 and 15 weeks to produce subitan and resting eggs respectively. *Alona quadrangularis* needed 6 weeks for subitan eggs and 12 weeks for ephippia at a mean temperature of 9.7˚C.

Discussion

In recent years considerable progress has been made in the investigation of egg banks and depositions of diapausing stages of zooplankton in stagnant inland waters. They form a reservoir from which populations can arise whenever suitable living conditions occur. In these egg banks diapausing dormant stages can survive for many years. So the biocenotic potential of a site can be preserved for long periods of time. The literature on this subject was reviewed by Brendock and De Meester (2003). Dormant stages can remain in diapause even for decades (Hairston *et al*. 1995).

During sampling in 1977 and 1995 *Daphnia pulex*, *Simocephalus vetulus*, *Macrothrix hirsuticornis*, *Eurycercus glacialis*, *Acroperus harpae*, *Alona quadrangularis* and *Chydorus arcticus* were found in the lake on Kangârssuk at 69˚16'N. With the exception of *Simocephalus vetulus* and *Macrothrix hirsuticornis*, these Cladocera species were already known from that site (Røen 1962, Bennike 1995). The lake near Søndre Størmfjord, situated on 67˚02'N, was only sampled in 1977 and 1995, and here all species of Kangârssuk were found as well as 6 additional Cladocera such as *Scapholeberis mucronata*, *Ceriodaphnia quadrangula*, *Bosmina coregoni*, *Alona affinis*, *Graptoleberis testudinaria* and *Polyphemus pediculus*. So 4 out of 13 species, which were likely to be present in the mentioned sites, hatched from resting eggs after an exposure to –18˚C for 12 and even 18 years. One of them,

Alona quadrangularis, occurs in Greenland up to 72°n, but *Daphnia pulex*, *Macrothrix hirsuticornis* and *Chydorus arcticus* are known even in Peary Land in North Greenland at 82°n (Røen 1962, 1968).

In the high Arctic north of 74° 9 Cladocera species were found on Ellesmere Island (Røen 1981), Greenland (Røen 1962) and Svalbard (Spitsbergen including Bear Island) (Husmann *et al*. 1978). In 60 sites on Ellesmere Island 82% were settled by *Daphnia pulex* and 55% by *Chydorus arcticus*. In Greenland a frequency of 38% of *Daphnia pulex* was found in 252 inland waters, 42% of which contained *Chydorus arcticus* and 17% *Macrothrix hirsuticornis*. All the other 6 Cladocera species occur only sporadically or are extremely rare north of 74°N. From an ecological point of view it is remarkable that the only really widespread and abundant Cladocera species of the high Arctic all belong to those able to survive a low temperature regime of –18°C for so many years. Of all other species likely to have been involved in this study only *Alona quadrangularis* had the same resistence; they all are limited to regions south of 74°N. So a long lasting resistence of the diapausing eggs to low temperatures can be considered as one adaptation of Cladocera in high Arctic inland waters.

With respect to the time needed from the beginning of suitable living conditions to hatching and the production of subitan and diapausing eggs, the females of *Daphnia pulex* and *Macrothrix hirsuticornis* in this study extensively followed the time frame as under natural conditions (Meijering 1979, Meijering and Jacobi 1978) and would have fitted well within the frame of short and cool summer seasons in Arctic waters (Rakusa-Suszczewski 1963).

Acknowledgements. — I would like to thank Mr. U. Ozols for his readiness to resample the 2 sites in Greenland. I am also grateful to Dr. Piet Spaak for his critical remarks and useful suggestions.

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Received 12 September 2002
Accepted 5 May 2003