

Life Cycle, Ecology, and Timing of *Macrothrix hirsuticornis* Norman & Brady (Cladocera, Crustacea) in Svalbard

By M. P. D. Meijering *

Summary: In arctic populations of *Macrothrix hirsuticornis* life cycles are mainly governed by temperature. This was found by using laboratory cultures in combination with the analysis of population samples from waters in Svalbard. In arctic waters ex-ephippionid ♀♀ usually produce gamogenetic F₁-♀♀ together with a high percentage of ♂♂, which have to fertilize the resting eggs. Temperatures around 14°C, which are very rare in waters of Svalbard, will induce parthenogenetic ♀♀ in the F₁- and even the F₂-generation, a mode of reproduction normally found in *Macrothrix*-populations of Central Europe. This was found in laboratory cultures of *M. hirsuticornis* from Bear Island, and there was evidence, that a similar cycle occurs in warm wells in Spitsbergen. The arctic distribution of *M. hirsuticornis* mainly depends on temperature, which regulates the speed of individual development. But this can only be understood together with the length of time, during which suitable life conditions are given. Physiological adaptations to life in waters in high latitudes could not be found, in spite of the extreme northern occurrence of *M. hirsuticornis*.

Zusammenfassung: In arktischen Populationen von *Macrothrix hirsuticornis* werden die Zyklen vorwiegend von der Temperatur bestimmt. Dies ergab sich aus Untersuchungen im Labor, die in Kombination mit der Analyse von Populationsproben aus Binnengewässern Svalbards durchgeführt wurden. In arktischen Gewässern produzieren ex-ephippionid ♀♀ gamogenetische F₁-♀♀ sowie einen hohen Prozentsatz ♂♂, welche die Dauereier befruchten müssen. Temperaturen um 14°C, die jedoch in den Gewässern Svalbards nur sehr selten erreicht werden, induzieren parthenogenetische ♀♀ in der F₁-Generation, ggf. sogar auch noch in der F₂-Generation, eine Fortpflanzungsweise, wie sie in Zentral-Europa regelmäßig auftritt. Dies wurde in Laborzuchten von *M. hirsuticornis* der Bären-Insel gefunden, und es gibt Anhaltspunkte, daß ähnliche Reproduktionszyklen in temperierten Quellen auf Spitzbergen vorkommen. Die arktische Verbreitung von *M. hirsuticornis* hängt vorwiegend von der Temperatur ab, welche die Geschwindigkeit der Individualentwicklung steuert. Das wird jedoch erst verständlich bei gleichzeitiger Betrachtung der verfügbaren Zeitspanne, in der günstige Lebensbedingungen gegeben sind. Physiologische Adaptationen an ein Leben in Gewässern hoher Breitengrade konnten nicht gefunden werden, trotz des extrem nördlichen Auftretens von *M. hirsuticornis*.

INTRODUCTION

During the expedition to Svalbard of the Max-Planck-Institute of Limnology in 1975 work was carried out on the distribution and ecology of Cladocera in arctic inland waters. Results on the distribution of the 6 Cladocera species in the entire archipelago and with consideration to the different types of biotopes were given earlier (HUSMANN, JACOBI, MEIJERING & REISE 1978). More detailed results from Bear Island on the same subject, together with items on the general limnology of 35 waters, investigated on the island, have already been published (JACOBI & MEIJERING 1978). It was pointed out, that the 3 main species, *Daphnia pulex*, *Macrothrix hirsuticornis* and *Chydorus sphaericus*, were found in several stable populations. In other sites, the occurrence was just sporadic, and finally there were waters without one species or the other. Chemical differences between the sites were too small, as that they could be regarded to be responsible for the patterns of distribution. So a closer look at the biology, life cycles and timing of the Cladocera was desirable. In the present paper *Macrothrix hirsuticornis* will be dealt with from an ecophysiological point of view. Laboratory experiments on this species were carried out in order to get a lead for an analysis of population development of *M. hirsuticornis* in Spitsbergen and on Bear Island.

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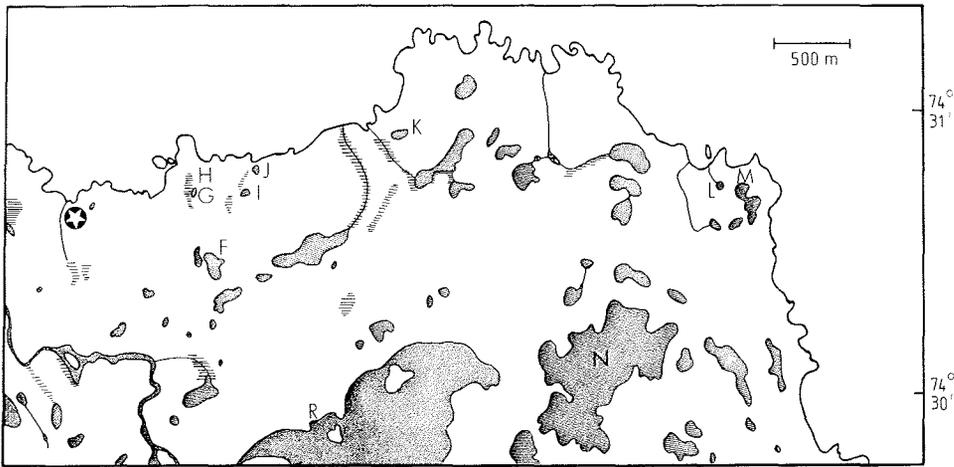


Fig. 1: Waters investigated along the NE-coast of Bear Island, especially sites G, K and M. ☆ = Björnøy Radio.

Abb. 1: Untersuchte Gewässer an der NE-Küste der Bären-Insel, insbesondere die Probenstellen G, K und M. ☆ = Björnøy Radio.

General features

Tab. 1 gives temperature and chemical features of selected sites on Bear Island and Spitsbergen. These were chosen since they showed the whole range of differences in the state of development of *Macrothrix* populations. The results on the other sites visited (see JACOBI & MEIJERING 1978) ranged within the same framework; they were archived. The ponds and shallow lakes presented from Bear Island are given in Figs. 1 and 2.

The 2 sites from Spitsbergen are easily to be identified. The lagoon on Brandalspynten lies little more than 2 km NW of Ny Ålesund in NW-Spitsbergen on 78°57' N, 11°53' E.

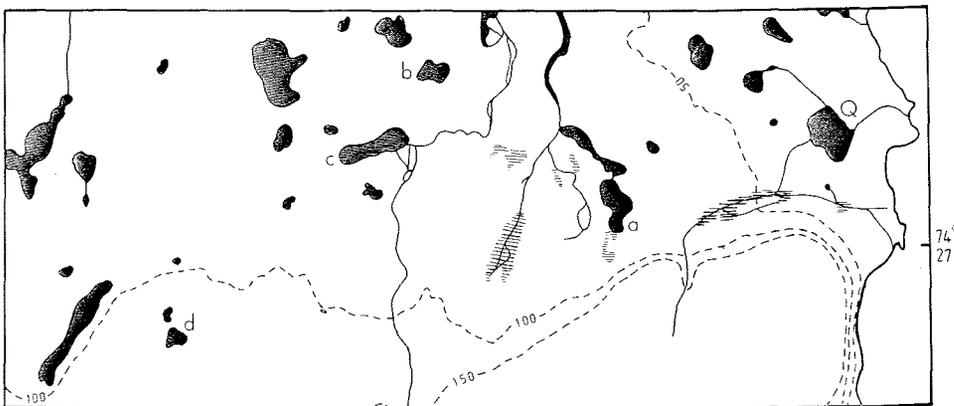


Fig. 2: Waters investigated NW of Mount Misery on Bear Island, especially sites a and b. Both maps are based on "Björnøya", 1 : 25 000 (Norsk Polarinstitut, Oslo 1944).

Abb. 2: Untersuchte Gewässer NW des Elendsberges auf der Bären-Insel, insbesondere die Probenstellen a und b. Beide Karten basieren auf „Björnøya“ 1 : 25 000 (Norsk Polarinstitut, Oslo 1944).

This shallow, triangle-shaped lake is separated from the Kongsfjord by a low barrier of sand and gravel. Towards the land, the shore of the lake is covered by vegetation, and it was on this SW-shore, that population samples were taken. The electric conductivity of the lagoon is rather high, caused by chlorides from marine origin.

The thermal Jotunwells at the head of the Bockfjord lie on 79°28' N, 13°17' E. In the upper sinterbasins *Macrothrix* was found, and from here the values of Tab. 1 were obtained. The water of the wells has a very high electric conductivity, but here the alkalinity is high as well. *Macrothrix* specimens were collected within a range of temperature of between 11.5 and 14.5°C, differences which were due to the waters exposure to the air temperature of 5.0°C.

Site	Temp. °C	pH	Electr. cond. µmho	Chloride meqv/l	Alkalinity meqv/l
G: Temporary pond south of Kapp Posadowsky, B.I.	4.0—9.5	5.4	93	0.86	0.90
K: Pond near Lundenaeringen, B.I.	5.0—10.5	6.0	133	0.79	1.24
M: Mosavatnet, northern bay, B.I.	4.0—8.0	5.8	214	1.81	0.84
a: Southern pond of Thetingtjørnene, B.I.	3.0—6.5	5.2	120	0.54	1.44
b: South-eastern pond of Svellieltjørnene, B.I.	4.5	5.4	69	0.63	0.52
Br. p.: Lagoon on Brandalspynten, NW-Spitsbergen	8.0—8.5	5.8	680	6.85	1.54
Jot. w.: Jotunwells, Bockfjord, NW-Spitsbergen	11.5—14.5	7.0	1736	12.28	10.43

Tab. 1: Geographical, temperature and chemical features of sites on Bear Island (B.I.) and Spitsbergen.

Tab. 1: Geographische, Temperatur- und chemische Daten von Probenstellen auf der Bären-Insel (B.I.) und Spitzbergen.

METHODS

Details about chemico-physical measurements and sampling techniques were given earlier (HUSMANN et al. 1978, JACOBI & MEIJERING 1978). Population samples were taken with a casting net, whose mesh width was 150 µ. The animals were preserved in 70% alcohol.

In order to get resting eggs to breed cultures, detritus was taken from ponds G, K and M (Fig. 1) on Bear Island. However, ex-ephippion-♀♀ were obtained only from pond K, which could be understood from the state of population development in that site. The detritus was dried on filter paper, and after the return of the expedition it was kept in the refrigerator at -18°C. From this material cultures were bred.

Measurements of body length were carried out with an ocular micrometer. Living *Macrothrix* are difficult to handle, since they are restless on slides. As very little water can be left around them during measurements, it is necessary to do all the work in a room with constant temperature, in order to avoid warming up. Heart frequency was measured with a stop watch (for further details see MEIJERING 1958, 1972).

Mass cultures were bred in 21 x 20 x 7 cm aquaria containing detritus and moss from pond K and tap water. There was constant light (500 lux), and temperatures were kept constant within the working room. Within the cultures temperatures were 3.0—4.5°C (mean value 3.8°C), 7.5—9.2°C (mean value 8.3°C), 13.5—15.2°C (mean value 14.3°C), and 17.4—21.1°C (mean value 19.4°C) respectively. The electric conductivity was between 272 and 313 µS, the pH 7.0—7.4, the mean values of O₂ were 12.6 mg/l in 3.8°C, 11.5 mg/l in 8.3°C, 9.5 mg/l in 14.3°C, and 8.9 mg/l in 19.4°C, so near the point of saturation, where it was kept constant by continuous aeration of the aquaria together with oxygen from growing moss of pond K.

From these cultures hatching ex-ephippio-♀♀ were isolated in glass tubes with a diameter of 2 cm, containing some detritus from the mass cultures and 15 ml of the culture water. Every day, half of this water was exchanged while the animals were checked. The water was brought back into the mass cultures, and fresh water was taken from there. In every tube there was 1 animal. Only F₁-♀♀ in the adolescent instar were kept together with a ♂. For each series, 25–30 ♀♀ were taken and observed during the entire lifespan of up to nearly 9 months.

During the daily check-ups the state of each animal was noted, exuvia were removed, moulted ♀♀ were measured, newly hatched young from parthenogenetic ♀♀ were counted and separated. As far as these young were not kept for constant observation, they were left in separate tubes for at least one week, after which sex could be determined; after that they were released in the mass cultures. So the cycle of *Macrothrix* went on in the cultures, and at its end most of the water was removed and the detritus was brought back into the refrigerator. This material could be used 4 times. Now, 4 years later, it is still available. All the experiments were spread throughout the year, regardless of the arctic seasons.

RESULTS

Growth

Growth curves of ex-ephippio-♀♀ are given in Fig. 3 for 3 different temperatures. From the 1. juvenile instar just a few values could be obtained, since the moult at its end takes place very shortly after hatching. In 8.3°C ex-ephippio-♀♀ grow steadily from the 2. juvenile to the 1. adult instar, after which the growthrate declines. In the 1. adult instar these ♀♀ reach more than 700 μ, and after that more than 900 μ so far as they have a

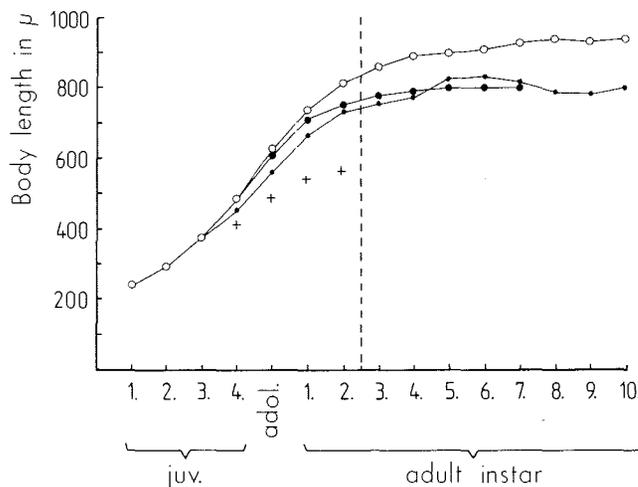


Fig. 3: Growth curves of ex-ephippio-♀♀ of *M. hirsuticornis* under laboratory conditions of 8.3° C (○), 3.8° C (●), and 19.4° C (●); + = gamogenetic F₁-♀♀. Dotted line: Maximum age under natural conditions.

Abb. 3: Wachstumskurven von ex-ephippio-♀♀ von *M. hirsuticornis* unter Laborbedingungen von 8.3° C (○), 3.8 C (●) und 19.4° C (●); + = gamogenetische F₁-♀♀. Punktierte Linie: Maximalalter unter Freilandbedingungen.

long lifespan. Growth in colder and warmer cultures was the same as far as the juvenile phase was concerned, but towards its end growthrates in 3.8 as well as in 19.4°C fell behind those in the 8.3°C-group. The mean size values of old ♀♀ did not exceed 800 μ. For maximum figures see Tab. 2. In the F₁-generation growth was nearly identical in all

groups of temperature conditions. In Fig. 3 the animals in 8.3°C were given as an example. While young juveniles of both the ex-ephippio- and the F₁-generation cannot be distinguished, growth rates in the late juvenile, adolescent and 1. adult instars are markedly smaller in F₁-♀♀ than in ex-ephippio-♀♀.

Reproduction

At first the animals in the series of 14.3°C has to be mentioned, which proved to be very different from the 3 others. Here the ex-ephippio-♀♀ produced parthenogenetic ♀♀ and ♂♂, and it was not earlier than in the F₂-generation, that gamogenetic ♀♀ appeared together with ♂♂ and still a certain amount of parthenogenetic ♀♀.

The ex-ephippio-♀♀ in 14.3°C showed the same growth curve as those in 8.3°C, and they had their first young 33 days after thawing. The parthenogenetic F₁-♀♀ were smaller than those of the ex-ephippio-generation. In the 1. adult instar values between 560 and 670 μ were found, and the average was 613 μ. So this group cannot be compared with the others. All the other groups either in higher as well as in lower temperatures produced ♂♂ and gamogenetic ♀♀ as a F₁-generation. However, in old gamogenetic ♀♀ of the 8.3°C group some very few subitan eggs were produced, but this not earlier than in the 4. adult instar.

Ex-ephippio-♀♀ in 8.3°C produced on the average 9.86 young in the 1. adult instar, but after that the number of young per clutch increased to 13.88 in the 3. adult instar, after which it decreased slightly to 12.06 in the 5. and then steadily down to 1.33 in the 10. adult instar. Tab. 2 shows, that in 8.3°C the average number of young per 1. brood was higher than in ex-ephippio-♀♀ of both other temperature-groups. In 8.3°C the maximum number of young was found to be 22 in a 4. adult instar. In 3.8°C the maximum was 13 young in a 2. adult instar, and in 19.4°C the maximum was 14 young in a 5. adult instar.

The number of young was positively correlated with the size of the ex-ephippio-♀♀, which was shown for the 1. adult instar. The correlation was particularly clear in the group of 8.3°C. In both other groups, most ♀♀ were smaller and the numbers of their young showed more variation (Fig. 4).

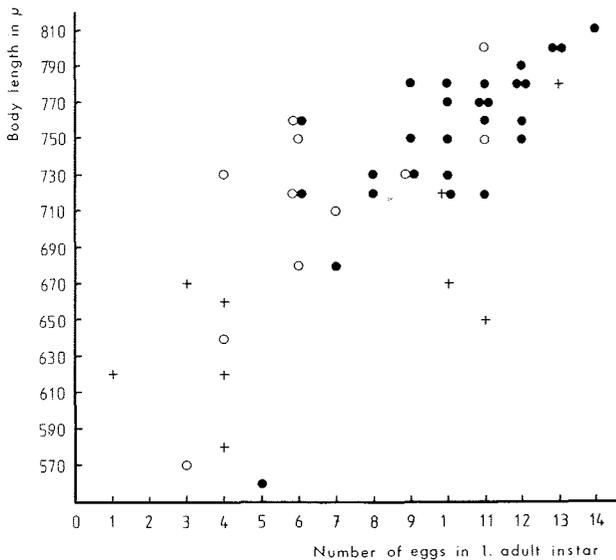


Fig. 4: Relation between body length and number of eggs in the 1. adult instar of ex-ephippio-♀♀ under laboratory conditions of 8.3° C (●), 3.8° C (○), and 19.4° C (+).

Abb. 4: Verhältnis zwischen Körperlänge und Anzahl der Eier im 1. adulten Stadium von ex-ephippio-♀♀ unter Laborbedingungen von 8.3° C (●), 3.8° C (○) und 19.4° C (+).

Resting eggs were never produced by ex-ephippio-♀♀, not even when very old. A continuous production of subitan eggs was observed in all temperature conditions. Resting eggs were laid exclusively by ♀♀ of the F₁- or subsequent generations. In 8.3°C the oldest F₁-♀ reached the 11. adult instar with permanent production of resting eggs. In the majority only 1 resting egg will be laid per instar. In 22.2% of the broods 2 resting eggs were laid. Double broods occur from time to time in most gamogenetic ♀♀.

Within the broods of the ex-ephippio-♀♀ there is a high percentage of ♂♂, which increased with temperature (Tab. 2). Special reference should be given to the animals in 8.3°C, the most common temperature in Svalbard waters settled by *Macrothrix*. Here the relation of male to female offspring was 1:2. The presence of ♂♂ is absolutely necessary to

Temperature in °C	maximum body length in μ	mean number of young in 1. ad. instar	maximum number of young per brood	% of ♂♂ in offspring	time in days from thawing to end of 1. adult instar	time in days from thawing to death of last ex-E.-♀
3.8	870	6.58	13	17.1	92	269
8.3	980	9.86	22	33.6	41	156
19.4	910	6.66	14	51.3	19	63

Tab. 2: Data on growth, reproduction, and time of development of *M. hirsuticornis* under laboratory conditions in different temperatures.

Tab. 2: Daten zu Wachstum, Fortpflanzung und Entwicklungszeit von *M. hirsuticornis* unter Laborbedingungen und verschiedenen Temperaturen.

make resting eggs fertile. ♀♀ in isolation from ♂♂ actually do lay resting eggs, but without any exception these will disintegrate in the brood pouch within less than 2 days. This never happened, when a ♀ and a ♂ were kept together in a tube. After fertilization the resting eggs will become red and spherical; without fertilization they will stay brownish and elleipsoid until they disintegrate.

Time of development

In Fig. 5 a semi-schematic presentation is given showing the time of individual development of ex-ephippio- and F₁-♀♀, based on average values from the cultured animals under two different temperatures. In 8.3°C juvenile instars each take 3—4 days, an adolescent instar 5—6, and adult instars about 8 days. These figures are valid for ex-ephippio-♀♀. Gamogenetic F₁-♀♀ have juvenile and adolescent instars of the same type, while adult instars are a little shorter, lasting about 7 days under these conditions. In 3.8°C instars

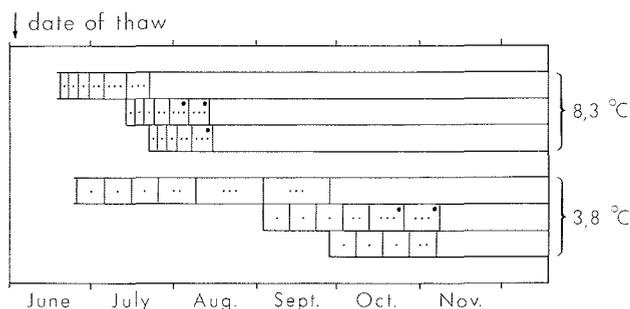


Fig. 5: Semi-schematic time tables of *M. hirsuticornis* under laboratory conditions with different temperatures. Juvenile instars are marked by 1, adolescent instars by 2, and adult instars by 3 points. ● = resting eggs. Further explanation see text.

Abb. 5: Halb-schematische Zeitpläne von *M. hirsuticornis* unter Laborbedingungen bei verschiedenen Temperaturen. Juvenile Häutungsstadien sind mit 1, adoleszente mit 2 und adulte mit 3 Punkten markiert. ● = Dauereier.

of ex-ephippio-♀♀ took 10 days in the juvenile phase, 14 when the ♀♀ were adolescent and 25 in the adult phase of life. Adult instars of gamogenetic ♀♀ lasted about 13 days in 3.8°C.

Hatching from resting-eggs occurred 16—17 days after the date, when the frozen cultures were brought into 8.3°C. The corresponding time in 3.8°C was 22 days. The first clutch of young, however, was released after 41 days in 8.3°C, but not earlier than after 92 in 3.8°C (Tab. 2). From Fig. 5 the time can be taken, after which F₁-♀♀ will lay resting eggs; 65 days in 8.3 and 145 in 3.8°C. It is obvious, that this delay of 80 days in the cooler medium is to some extent caused by later hatching from resting eggs, but over all and predominantly by the retardation within the instars of active animals.

In Fig. 5 the results from 8.3°C were plotted against a scale of the calendar. The position within this scale was chosen according to the state of development of the pond G population (Fig. 8) on Bear Island on July 3rd, 1975, when some 60% of the ex-ephippio-♀♀ were adolescent and some 30% in the 1. adult instar. From this point the date of thaw was determined, which gave the position of the lifetables in 3.8°C. So we get an idea of what could happen (or not) in free-living populations. Under conditions of the 8.3°C-group, new resting eggs would be available after the 1. week of August, in the 3.8°C-group not earlier than in the last week of October.

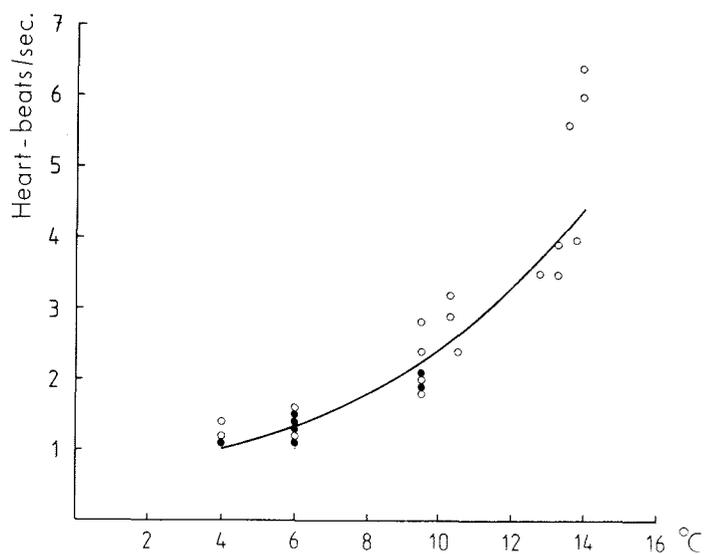


Fig. 6: Heart rate of adult ex-ephippio-♀♀ of *M. hirsuticornis* in pond G on Bear Island and in a pond in Adventdalen in Spitsbergen (see MEIJERING 1972). ○ = single measurement. ● = 2—4 measurements.

Abb. 6: Herzfrequenz adulter ex-ephippio-♀♀ von *M. hirsuticornis* in Tümpel G auf der Bären-Insel und in einem Tümpel im Adventstäl auf Spitzbergen (siehe MEIJERING 1972). ○ = Einzelmessung, ● = 2—4 Messungen.

Survival in laboratory cultures was very good. The maximum longevity in each temperature-group was given in Tab. 2. And it should be stressed, that during the great number of adult instars performed by ex-ephippio- as well as by gamogenetic ♀♀ reproduction was continued until the end of life. In Fig. 5, however, only that part of the lifespan is shown which has a chance to be realized under natural conditions.

Results from measurements of the heartrate of adult ex-ephippio-♀♀ in ponds of Svalbard are given in Fig. 6. From this curve it can be calculated, that the heartbeat frequency at 8.3°C is double as high as in 3.8°C.

Populations in natural biotopes

Adolescent ♀♀ are easily recognized from their small and empty broodpouches in connection with more or less developed ovaries. In early stages of population development, i.e. as long as it is possible to exclude 2. adult instars, 1. adult instars are recognizable as well. In Figs. 7 and 8 the average values of body length in these 2 instars are given together with the respective maximum and minimum figures. Results from the population samples are plotted against those from the laboratory in 8.3°C.

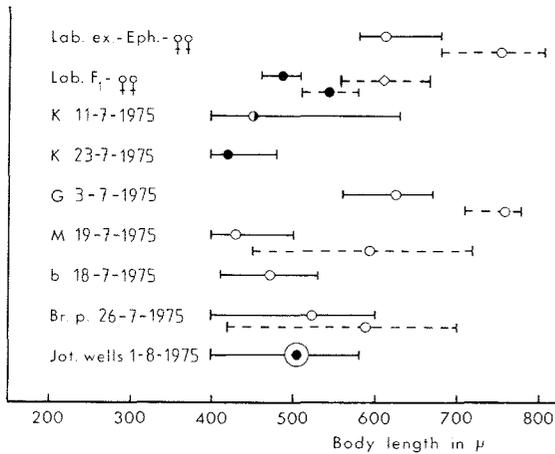


Fig. 7: Adolescent (continuous line) and 1. adult (dotted line) instars of *M. hirsuticornis* in the laboratory as well as in several sites in Svalbard as plotted against body length. Maximum and minimum figures are given together with the average, in which ○ means ex-ephippio-♀♀, ● gamogenetic F₁-♀♀, ⬤ both generations present, and ◇ parthenogenetic F₁-♀♀. ⊙ = both gamogenetic and parthenogenetic F₁-♀♀.

Abb. 7: Adoleszentes (ausgezogene Linie) und 1. adultes (gestrichelte Linie) Stadium von *M. hirsuticornis* im Labor und an verschiedenen Probenstellen in Svalbard in Relation zur Körperlänge. Maximal- und Minimalwerte begrenzen die Linien, auf der zudem der jeweilige Mittelwert erscheint, bei dem sich ○ auf ex-ephippio-♀♀, ● auf gamogenetische F₁-♀♀ bezieht. ⬤ = beide Generationen vorhanden, ◇ = parthenogenetische F₁-♀♀, ⊙ = sowohl gamogenetische als parthenogenetische F₁-♀♀.

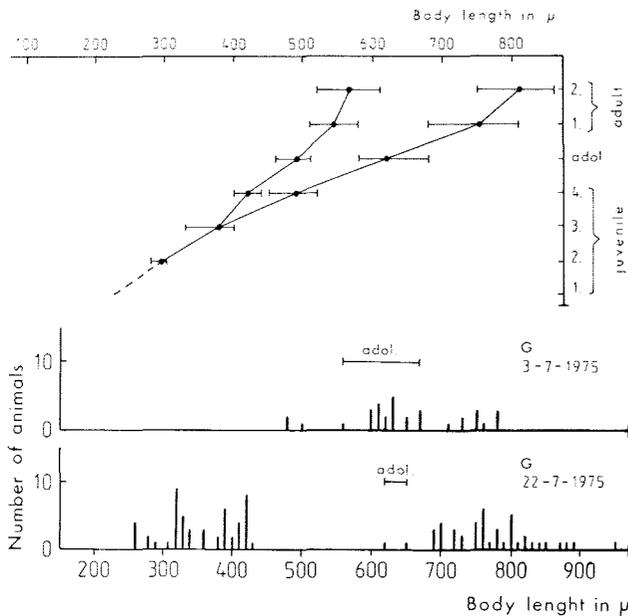


Fig. 8: Growth curves and range of sizes in different instars of *M. hirsuticornis* in the laboratory at 8.3° C. Right curve represents ex-ephippio-♀♀, left curve gamogenetic F₁-♀♀. Below: Population of *Macrothrix* in pond G.

Abb. 8: Wachstumskurven und Größenvariation in verschiedenen Häutungsstadien von *M. hirsuticornis* im Labor bei 8.3° C. Rechte Kurve repräsentiert ex-ephippio-♀♀, linke Kurve gamogenetische F₁-♀♀. Unten: Population von *Macrothrix* in Tümpel G.

In pond G on Bear Island the size of the ex-ephippιο-♀♀ in all instars corresponds closely with those of the animals kept in the laboratory (Fig. 8). On July 3rd, 1975, there were only a few juveniles in the 4. instar, another group was adolescent and the rest in the 1. adult instar. On July 22nd, 1975, F₁-juveniles were present, from which some had reached the 3. juvenile instar. Ex-ephippιο-♀♀ now were in the 1., 2. and a few in the 3. adult instar.

The population of pond K on Bear Island was more advanced (Fig. 9). On July 11th, 1975, the F₁-generation was already present in all juvenile instars, the adolescent and 1. adult instar. But there were still ex-ephippιο-♀♀, a few in the adolescent, others in the 1. adult instar. The animals in pond K were a little smaller than in pond G and the laboratory (Fig. 7). On July 23rd, 1975, only a few juveniles were still present in pond K, the adolescent ♀♀ exclusively belonged to the F₁-generation, and the rest were adults from both generations, bearing resting or subitan eggs respectively. There was, however, no indication of ♀♀ in the 2. adult instar of the ex-ephippιο-generation.

In Mosevatnet (M, Fig. 10) on Bear Island the animals were markedly smaller than those in the laboratory (Fig. 7). On July 19th, 1975, the population predominantly consisted of ex-ephippιο-♀♀ in the 1. adult instar, others were still adolescent, and there were some ♀♀ of the F₁-generation, mainly from the 2. juvenile instar. Most adults had subitan eggs or half developed embryos, and a few already young in their brood pouches.

In pond b on Bear Island (Fig. 10) *Macrothrix* was also smaller than in the laboratory (Fig. 7). On July 18th, 1975, there were only ex-ephippιο-♀♀ of the 4. juvenile and the adolescent instar. Similarly, the population of pond a on Bear Island (Fig. 10, was in a very early state of development on the same date, containing juveniles from the 3. and 4. instars.

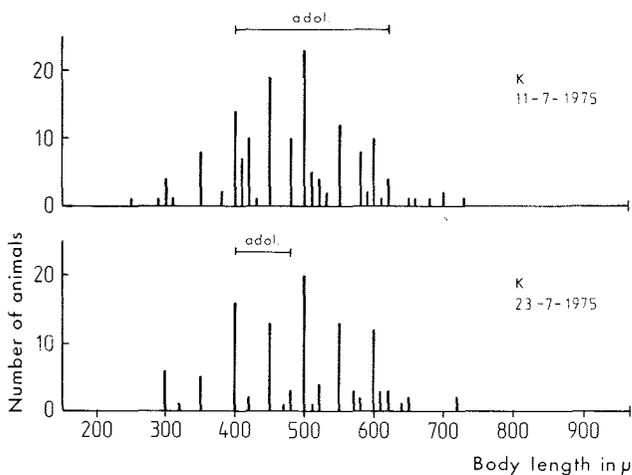


Fig. 9: Population of *M. hirsuti-cornis* in pond K on Bear Island.

Abb. 9: Population von *M. hirsuti-cornis* in Tümpel K auf der Bären-Insel.

The animals in the lagoon of Brandalspynten in Spitsbergen were also smaller than the laboratory specimens (Fig. 7). On July 26th, 1975, there were only ex-ephippιο-♀♀ from the adolescent and 1. adult instar (Fig. 11). On August 8th, 1975, no more adolescent ♀♀ were found, since all had entered the 1. adult instar. Some adults already reached the 2. adult instar, and their young were mainly in the 3. and some as far as the 4. juvenile instar.

The most complicated population was found in the Jotunwells on the coast of the Bockfjord, Spitsbergen (Fig. 11). These animals were of the same size as those in the laboratory, as was indicated by adolescent F_1 -♀♀ (Fig. 7). The following instars were recognizable: Juveniles in all 4 instars, adolescent instars covering sizes of gamogenetic ♀♀ as well as larger ones, small adults in the size class of parthenogenetic F_1 -♀♀ bearing subitan eggs, and larger adult ♀♀, which may be subsequent instars of the F_1 - or still surviving ex-ephippio-♀♀.

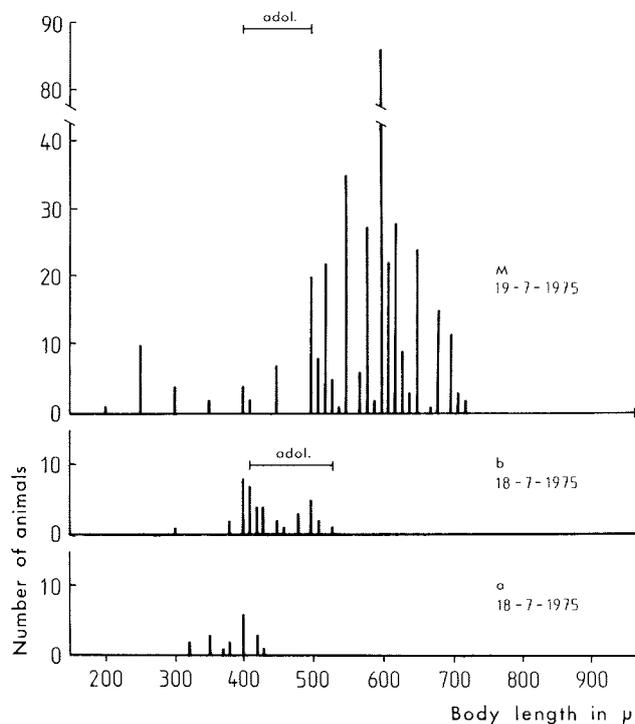


Fig. 10: Populations of *M. hirsuticornis* of ponds a and b, as well as of the shallow lake M on Bear Island.

Abb. 10: Populationen von *M. hirsuticornis* von Tümpeln a und b, sowie des Flachsees M auf der Bären-Insel.

DISCUSSION

Widely varying figures about the size of *Macrothrix hirsuticornis* can be found in literature. WESENBERG-LUND (1894) gave 2 mm for adult ♀♀ from Greenland. From the same region, specimens were collected by NYSTRÖM, which proved to be 0.75 mm (FOX 1962). RØEN (1968) found them in Peary-Land up to 1 mm long. In inner fjord areas of West-Spitsbergen OLOFSSON (1918) found ♀♀ being 1—1.2 mm. BERG (1933) found the biggest ex-ephippio-♀ in a Danish pond to be 1.33 mm long, which coincides with material from a Frisian island (MEIJERING 1961), where 1.35 mm was observed. These animals, however, reached 1.65 mm in the laboratory (HUCHZERMAYER 1963). It is obvious, that there is a considerable variability of size within the species. But it is not clear, that these are due to races, which were described by LILLJEBORG (1901). He found *M. hirsuticornis* s. str. from Sweden to be 0.6—0.96 mm long as adult ♀♀, and these figures are very much like those we determined in Svalbard (0.42—0.95 mm). The largest ♀ in the laboratory cultures was 0.98 mm in its 5. adult instar. So the growth of *M. hirsuticornis* in our laboratory cultures can be looked upon to be representative.

Environmental conditions have influence on the growth curves. *Macrothrix* in 3.8°C were smaller than those in 8.3°C. HUCHZERMAYER (1963) bred them in 13°C and found 1.2 mm for the 1. adult instar of ex-ephippio-♀♀. This temperature is of ecological importance in temperate regions, but not in Svalbard. Our animals in room temperature were smaller

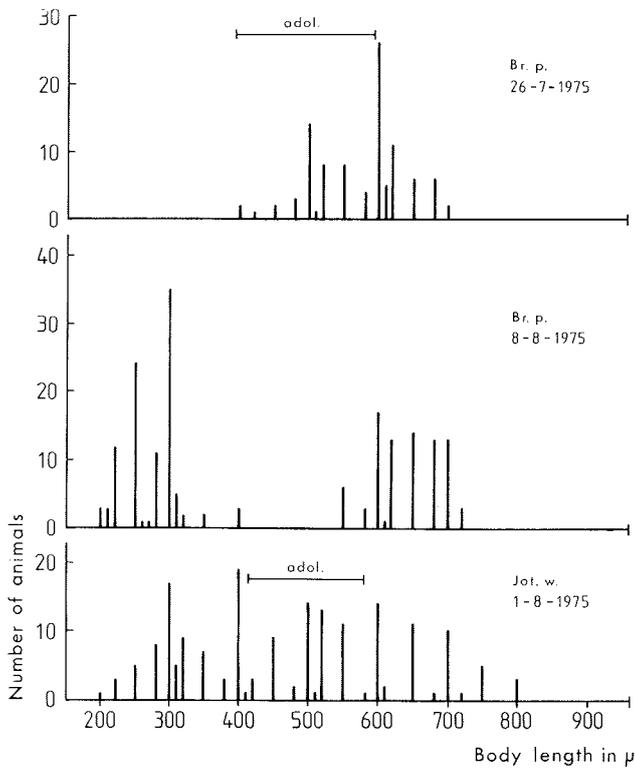


Fig. 11: Populations of *M. hirsuticornis* in lagoon on Brandalspynten and in the Jotunwells in NW-Spitsbergen.

Abb. 11: Populationen von *M. hirsuticornis* in einer Lagune auf Brandalspynten und in den Jotunquellen in NW-Spitsbergen.

again, an indication of suboptimal conditions for this cold-stenotherm species. But also Frisian *Macrothrix* in 18°C reduced the number of young per instar and heart rate (HUCHZERMAYER 1963) and is more or less limited to the cooler months of the year (MEIJERING 1970).

The size of *Macrothrix* varied under different laboratory conditions, but also in natural biotopes. Considerable differences were found between pond G on Bear Island and the nearby Mosevatnet, especially when adolescent instars of ex-ephippio-♀♀ are taken for comparison. In order to make a correct analysis of population samples possible, these differences in growth must be considered. In pond G the growth of the ex-ephippio-♀♀ followed that of the laboratory animals in 8.3°C, while others remained smaller. RØEN (1968) found differences in size of *Macrothrix*-populations in two ponds in Peary-Land in N-Greenland.

Big ex-ephippio-♀♀ are rare in natural biotopes. This is not only a matter of different growth, but very much of survival as well. Only in laboratory cultures can a physiological longevity (BODENHEIMER 1938) be expected, as it was shown for *Daphnia magna* (MEIJERING 1958, FRITSCH 1962, MEIJERING & v. REDEN 1965) as well as for Frisian

M. hirsuticornis (HUCHZERMAYER 1963, MEIJERING & v. REDEN 1965). Longevity of the specimens from Svalbard coincides with those from Frisian islands, reaching 15 instars as a maximum lifespan, and 10 of these were adult instars, during which ex-ephippio-♀♀ continued to reproduce. Under natural conditions, however, the ecological longevity is dramatically shorter. In most sites one will not find ♀♀ older than in the 1. adult instar, which in Svalbard is the only adult instar of importance for population development. This was already supposed by OLOFSSON (1918). Only in pond G on Bear Island there were some ex-ephippio-♀♀ in the 2. and very few in the 3. adult instar.

The size of Cladocera-♀♀ and the number of eggs per brood are positively correlated. This partly has to be explained from increasing rates of reproduction during the adult instars, as far as animals under laboratory conditions are concerned (GREEN 1956, HUCHZERMAYER 1963), but there is also a relation between size and the number of eggs within the 1. adult instar (GREEN 1956), which may depend on the amount of food available (LAMPERT 1978). Regarding these facts, Svalbard *Macrothrix* not only coincides with Swedish specimens described by LILLJEBORG (1901), but it is likely that they are close to Frisian populations as well, and that differences in size are just due to differences in food concentrations. *M. hirsuticornis* on the Frisian island of Spiekeroog live in eutrophicated ponds (MEIJERING 1970), and size figures from there are close to those given by OLOFSSON (1918) from the Isfjord region in Spitsbergen. Additionally, the number of subitan eggs found by HUCHZERMAYER (1963) was close to those in our laboratory cultures in 8.3°C as far as the 1. adult instar was concerned (10.66 and 9.86 respectively); in later instars, however, HUCHZERMAYER found up to 52 young per clutch, while in our material the maximum figure was only 22.

The structure of the population cycle in high arctic regions is different from those in Central Europe, since the ex-ephippio-generation only produces gamogenetic ♀♀ and ♂♂, which quickly brings to an end further population development and guarantees the formation of resting eggs within the shortest possible time. This mode of reproduction was described by OLOFSSON (1918) and RØEN (1968). From the present results it can be confirmed, that ex-ephippio-♀♀ can only produce subitan eggs, even if able to complete physiological lifespans in the laboratory, and regardless what temperature conditions are. The F₁-generation on the other hand may reproduce parthenogenetically if temperatures for longer periods are around about 14°C, which, however, is very rare in Svalbard. In lower temperatures the F₁-generation will produce resting eggs, as we found them doing in most sites investigated. On Bear Island temperatures in 35 waters varied between 2.5 and 12.5°C during July, 1975, and the mean figure was 6.2°C (JACOBI & MEIJERING 1978). The only warmer sites visited in Svalbard were the Jotunwells in N-Spitsbergen, and it was here, that relatively small parthenogenetic ♀♀ with subitan eggs were found aside gamogenetic ♀♀ with resting eggs, which both belonged to the F₁- or probably even a subsequent generation. These are further indications, that physiologically there is little difference between *M. hirsuticornis* of high and medium latitudes. The mode of reproduction in Svalbard is subject to environmental conditions, and although the formation of resting eggs already in the F₁-generation appears as a quick and therefore sure way to reach the goal of the cycle within the short time of an arctic summer, this cannot be regarded as a special arctic adaptation, since short cycles are linked to suboptimal environmental conditions, and they occur in temperate regions in just the same way.

In the present laboratory cultures the percentage of ♂♂ was high. This can be understood in context with the fact, that resting eggs of *M. hirsuticornis* unlike those of high arctic *Daphnia pulex* (EDMONDSON 1955) must be fertilized. This was already supposed by RØEN (1968). On the basis of the laboratory results in 8.3°C it can be calculated, that one out of three F₁-specimens cannot directly share in producing resting eggs. However,

this figure is partly counterbalanced by the fact, that there is a certain amount of double broods of resting eggs within the 1. (and in general last) adult instar of the gamogenetic F_1 -♀♀. The percentage was 22.2% in our cultures, but this may be more, since RØEN (1968) found double-broods in a majority of gamogenetic ♀♀ in Peary Land. But in Svalbard the mode of cycling will have as a consequence, that from 1 hatching ex-ephippio-♀ some 10 young can be produced in the 1. adult instar, 3 of them being ♂♂, which has to fertilize some 8—9 resting eggs produced by 7 gamogenetic ♀♀. This extremely low rate of reproduction has to cover mortality within the juvenile and adolescent phases of the lifespan. In temperate regions much longer cycles make *M. hirsuticornis* far more successful, and from this point of view the species must be considered to be at the periphery of its distribution area, when it is found in Svalbard or N-Greenland.

The speed of individual development depends on temperature, as was indicated by heart rates of *M. hirsuticornis* in Svalbard ponds. In relation to temperature, heart rates in Svalbard are not higher than in Central Europe (see HUCHZERMAYER 1963), so that there is no adaptive acceleration of metabolism to the very short time of suitable conditions in the arctic summers. This was found earlier in *Daphnia pulex* (MEIJERING 1972, 1975) and in *Mysis relicta* (LASENBY & LANGFORD 1972). The present results give an impression of the time scale of individual development in temperatures commonly found in inland waters of Svalbard. This timing in the laboratory seems to be representative for natural conditions as well, since the progress of population development between one sampling date and another (see lagoon of Brandalspynten and pond G) was very similar to what could be expected from the laboratory results. These time scales are very stable in crustaceans (FRITSCH 1962, MEIJERING & TEICHMANN 1978).

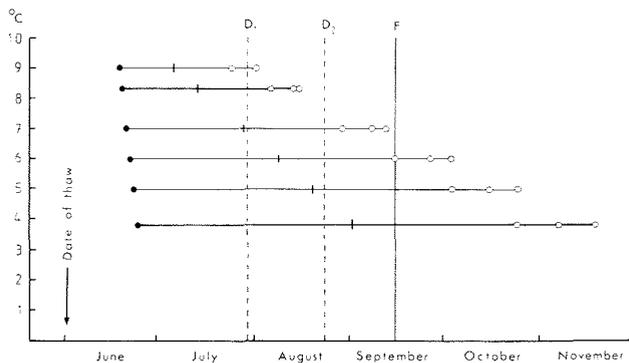


Fig. 12: Schematic representation of *Macrothrix*-cycles under different temperatures. Heavy lines: Results from the laboratory. Thin lines: Extrapolated cycles. ● = hatching from resting eggs, | = first young released, ○ = new resting eggs. D_1 and D_2 are probable dates, when a site becomes dry, F = date of freezing.

Abb. 12: Schematische Darstellung von *Macrothrix*-Zyklen bei verschiedenen Temperaturen. Dicke Linien: Laborresultate. Dünne Linien: Extrapolierte Zyklen. ● = Schlüpfen aus Dauereiern, | = erste Jungen freigelassen, ○ = neue Dauereier. D_1 und D_2 markieren Daten, an denen Tümpel austrocknen könnten, F einen möglichen Termin des Einfrierens.

Fig. 12 shows the time scale of development of *M. hirsuticornis* found in 8.3 and 3.8°C, together with interpolations of 5, 6, 7 and 9°C, which all were plotted against the summer season of Svalbard. Assuming that thawing in shallow waters starts in the beginning of June, hatching of resting eggs can be expected during the 3. week of June, almost regardless of temperature. After hatching temperature becomes very important. A mean temperature of 8°C will bring resting eggs of the F_1 -generation in the 2. week of August, providing such a pond will not dry up before. In such a case, the population will die out. In 4°C, however, resting eggs cannot be expected earlier than in the middle of October, which in shallow waters will be too late. Temperatures in standing waters of Spitsbergen drop down rapidly during the 1. week of September (RAKUSA-SUSZCZEWSKI 1963, PIETRUCIEN 1977), and in the middle of September the water will freeze. *M. hirsuticornis*

is mainly a litoral species, but sometimes they are found in deep water (SKRESLET & FOGED 1970), where the water will stay open on a very low level of temperature. In shallow waters, i. e. in ponds and the litoral of lakes, the common biotope of *M. hirsuticornis* (HUSMANN et al. 1978), one has to calculate that a mean temperature of 6°C in July and August is the lowest in which the species can complete its cycles.

In July, 1975, temperatures on Bear Island were extremely low, and the mean temperature of 6.2°C in 35 waters (JACOBI & MEIJERING 1978) must have been critical. But some waters showed higher, others lower temperatures. In consequence the speed of population development was different. Pond K on Bear Island was 1°C warmer than pond G, since K gets shelter from a hill against northern winds. The first resting eggs were found in the population of K on July 19th, 1975, while in G on July 22nd the population progressed not further than to F₁-specimens in the 4. juvenile instar. On the basis of 8°C another 2 weeks were necessary to get resting eggs. In pond a, which lies under the influence of melt water from Mount Misery, population development was in the state of 3. and 4. instar juveniles from the ex-ephippion-generation. On the basis of 8°C, this is 5—6 weeks behind the population of pond K, but on the basis of 6°C, which is more realistic in pond a, another 9—10 weeks would have been necessary to reach the state of resting eggs. This means, that there was no chance left to come to that point before the beginning of the winter. The populations described by RØEN (1968) from ponds on Flaghøjsletten and near Lersø in Peary Land, were similar to pond G on Bear Island.

Obviously all resting eggs will develop, as soon as there is open water, regardless what the temperatures are. This means, that populations once activated, either will reach the goal of the cycle or will become extinct. This is a typical feature in temporary waters, not only in the arctic, but in other regions as well (PRÓSZYNSKA 1962, MEIJERING 1970, S. JACOBI & MEIJERING 1979).

The distribution of *M. hirsuticornis* on Bear Island, which does not depend on chemical differences between the waters (JACOBI & MEIJERING 1978), can be understood from the temperature regime, but only in connection with considerations on the time, which is available. Most suitable biotopes are temporary ponds, which warm up rapidly, but only those, which will not dry up earlier than the first half of August. In such ponds, stable and well developed populations of *M. hirsuticornis* can be expected. Waters of less than 6°C as an average temperature during July and August cannot be settled, as was found in the mountainous area of Bear Island. Others in between may have sporadic occurrences of the species. These were also found by RØEN (1968) in Peary Land. The most successful populations of *M. hirsuticornis*, however, will be in regions, where for longer periods the average temperature will be around 14°C. But these are rare in Svalbard.

As high arctic waters were settled relatively recently, and since *M. hirsuticornis* develops not more than 2 generations per year, it is not surprising, that no special adaptation to the arctic environment was developed. The species, however, was preadapted to short periods of suitable life conditions. Additionally it must be kept in mind, that the arctic sites of *M. hirsuticornis* are still in contact with populations in regions further south, as far as they are exposed to influences from bird migrations.

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