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Life cycle of *Tonnacypris glacialis* (Crustacea: Ostracoda)

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Abstract: *Tonnacypris glacialis* (G.O. Sars, 1890) is a meiobenthic species widely distributed in Arctic freshwater lakes. Field study of its life cycle as well as the laboratory experiments showed clearly that only one generation of this ostracod species occurs during the vegetation season, and that the condition necessary for the next generation to appear is eggs freezing.

Key words: Arctic, Spitsbergen, Ostracoda, reproductive strategies, temperature, palaeoecological indicator.

Introduction

Tonnacypris glacialis (G.O. Sars, 1890) was reported first from the Arctic in the first half of the 20th century (Alm 1915; Olofsson 1918; Bronstein 1947). The life cycle of this species was described as limited to one season, however, according to Olofsson (1918), two generations may occur during one summer and then usually the overwintering stage are eggs. This opinion is still common (Griffiths *et al*. 1998). *Tonnacypris glacialis* is a parthenogenetic organism (Little and Hebert 1997). Juveniles appear at the end of June or July and gravid females approximately 2 weeks later (Olofsson 1918; Griffiths *et al*. 1998). According to Griffiths *et al.* (1918) *T. glacialis* occurs in the reservoirs with temperature range of 5.9+/-3.2°C. For this reason and for the occurrence of this species in the freshwaters of north-central and north-eastern Europe in the Pleistocene, *T. glacialis* was considered to be a palaeoecological indicator (Griffiths *et al.* 1998) and the indicator in the palaeolimnological research (Wetterich *et al.* 2005).

Investigated area, material and methods

Study sites. — The material was collected from shallow freshwater lakes located in Fuglebergsletta, Kvartistsletta, Pálffjodden, Gnálodden areas and in the

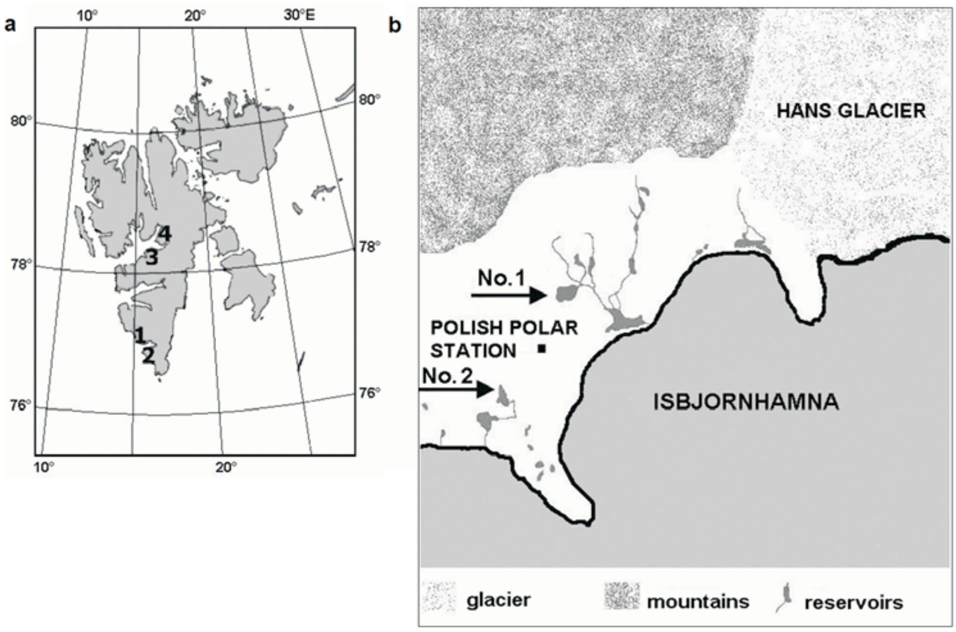

Fig. 1. Study area: (a) Spitsbergen 1 – Fuglebergsletta, Kvartistsletta, the moraines of Werenskiold and Hans glaciers, Gnálodden, 2 – Pálffjodden, 3 – Longyearbyen, 4 – Ebbadalen. (b) The freshwater lakes No. 1 and No. 2 located in the neighbourhood of the Polish Polar Station in Hornsund.

moraines of Werenskiold and Hans glaciers in Ebbadalen, as well as in the neighbourhood of Longyearbyen (Fig. 1a). Most samples were collected in freshwater reservoir No. 1 located in the vicinity of the Polish Polar Station in Hornsund (Fig. 1b).

The analyses of hydrological conditions of the studied freshwater bodies indicated a very good oxygenation, and pH ranging from 6.54 to 10.39. The maximal water temperature depended on the lake type and on the air temperature in a particular hydrological period. Active hydrological period begun in June with a spring flood due to snow cover melting in the coastal plains and ended at the beginning of October, when glacier ablation and permafrost thawing terminated and rivers were frost-bound to the bottom (Bartoszewski 1998). Maximal temperature observed in moraine reservoirs during hydrological period was 14.5°C. Conductivity had different characteristics and seasonal variability in the examined lakes (58.5–1153 μS/cm). Some shallow lakes located in the coastal area demonstrated low salinity (0.1–0.7 psu) resulting from the influence of marine aerosols (Nowiński and Wiśniewska-Wojtasik 2006).

Observations made by the Polish Polar Station in Hornsund suggest that the vegetation seasons are not of the same length throughout years. Long-standing observations revealed occurrence of warmer and colder periods (Rodzik and Stepko 1985; Ustrnul 1987; Węsławski and Adamski 1987). In case of tundra reservoirs the thawing process is slow because the plant cover forms an isolation layer (Wójcik and Marciniak 1987). So, tundra reservoirs thaw late – usually at the end of June and at the beginning of July (Krzyszowska 1985; Kuziemski 1959; Pulina *et al*. 1999). The thawing of young moraine reservoirs is different: it starts about two or three weeks earlier in comparison to tundra reservoirs because of the lack of the above isolation layer (Pirożnikow and Górniak 1992) and light absorbing suspended patrticles (Bartoszewski 1988, Pękala 1980, Wojciechowski 1989).

Field sampling. — Samples were collected in 1995, 1996, 1998, 1999, 2000 and in 2001. Most of the samples were collected in the lake No. 1, always from the same place in the SW part of this reservoir. The 1995 sampling period was the longest – it began on 8th of June, when the reservoir was still covered with ice, and ended on 19th of October, since later the lake started to freeze. Samples were collected with a net dipper (0.05 mm mesh) – the volume of each sample was about 200 ml. The material was sorted out in the laboratory of the Polish Polar Station in Hornsund. Ostracods were identified to the species and developmental stages were determined. Most of the material was preserved in 70% ethanol. Some samples were preserved in 4% formaldehyde and taken to the laboratory for further analysis. In subsequent years sample collection started when the lake was completely frozen (1996, 1998, 1999, 2000, 2001 – the lake No. 1, 1998, 2000 – the lake No. 2 and 1999, 2000 – the moraine of Werenskiold glacier reservoir). In summer sample collection was done less systematically than in 1995 but during the whole summer, what enabled verification and filling gaps in earlier data. To complete the temperature data in natural waterbodies, where *T. glacialis* occurs in Spitsbergen, two stations of different hydrological regimes were chosen and analysis of the twenty- four hours' temperature variation was carried out. The measurements were made above the bottom sediment every 15 minutes for 24h (automatically readings of a conductometer: LF 330 / set WTW). As a result of the analyses of twenty-four hours temperature changes of water above the sediment in selected reservoirs No. 1 and No. 2 (Table 1).

Material analysis. — The analyses of relative abundance (D) and life span of all developmental stages were based upon the data collected in 1995 from reservoir No. 1. The life spans of particular stages (t) were calculated in four possible ways.

1. t_F – difference between the day [$N_F(x_{i+1})$] when the first individuals of the stage x_{i+1} were observed in samples and the day [$N_F(x_i)$] when the first individuals of stages x_i were observed

$$t_F(x_i) = N_F(x_{i+1}) - N_F(x_i) \qquad i = 1, 2,\ldots, 9$$

2. t_L – difference between the last day [$N_L(x_i)$] when stages x_i were observed and the last day [$N_L(x_{i-1})$] for stages x_{i-1}; calculations only for stages II-Ad

$$t_L(x_i) = N_L(x_i) - N_L(x_{i-1}) \qquad i = 2, 3,\ldots, 9$$

Table 1

Water temperature range measured above the sediment in lakes No. 1 and No. 2

Lake No. 1			Lake No. 2		
Date	Temperature [°C]		Date	Temperature [°C]	
	min	max		min	max
13/14.06.2000	0.4	2.0	24/25.06.2000	5.5	8.7
17/18.06.2000	0.1	2.7	28/29.06.2000	2.7	6.8
25/26.06.2000	1.1	5.4	06/07.07.2000	7.2	8.6
05/06.07.2000	2.6	6.2	12/13.07.2000	8.6	10.2
11/12.07.2000	3.6	7.9			
11.06.2001	0 (frozen sediment)	0.3	15.06.2001	0.3	1.2
26.06.2001	4.3	10.8	26.06.2001	6.2	10.0
02.07.2001	7.2	10.6	17.07.2001	8.7	10.3
16.07.2001	7.8	11.3	12.08.2001	6.6	8.5
24.07.2001		14.0	25/26.08.2001	6.2	8.0
02.08.2001		12.5			
11.08.2001	5.8	9.7			
21.08.2001		11.0			
24.08.2001	4.4	9.3			
27.08.2001		9.5			

Table 2

Results of *Tonnacypris glacialis* cultures

Temperature	Time of culture	Result
11 ± 2°C	2 months	One life cycle, adult and eggs after 1.5–2 month
18 ± 2°C	1.5 month	One life cycle, adult and eggs after 1.0–1.5 month
18 ± 2°C	12 months	One life cycle, adult and eggs after 1.0–1.5 month. Rest of time eggs only
20 ± 0.5°C	1.5 month	One life cycle, adult and eggs after about 1.0 month
20 ± 2°C	15 months	One life cycle, adult and eggs after about 1.0 month. Rest of time eggs only
23 ± 0.5°C	1.5 month	One life cycle, adult and eggs after 3 weeks–1.0 month
25 ± 0.5°C	17 days	Low activity after two weeks, dead before 17 days
28 ± 0.5°C	48 hours	Low activity after 24 hours, dead before 48 hours
32 ± 0.5°C	24 hours	Dead before 24 hours

3. t_M – difference between the number of the middle day $[N_M(x_{i+1})]$ of the time of when the developmental stage x_{i+1} was observed and the number of the medium day $[N_M(x_i)]$ of the observed time when the developmental stage x_i was observed: calculations only for stages I–VIII

$$t_M(x_i) = N_M(x_{i+1}) - N_M(x_i) \qquad i = 1, 2, \dots, 8$$

where $N_M(x_j) = N_F(x_j) + 1/2[N_L(x_j) - N_F(x_j)] \qquad j = 1, 2, \dots, 9$

4. t_D – difference between the number of day when the maximum value of relative abundance of stage x_{i+1} was observed and stage x_i; calculations only for stages II–VIII

$$t_D(x_i) = N_D(x_{i+1}) - N_D(x_i) \qquad i = 2, 3, \ldots, 8$$

Cultures

Cultures of *T. glacialis* were grown to verify the data collected in the field and to describe the brooding process. Table 2 shows the comparison of the conditions in these cultures.

Furthermore, cultures were grown to reveal the tolerance level of *T. glacialis* towards the increase of water temperature. Then it was compared to the values typical for freshwater lakes in Arctic regions, both mentioned in the literature and observed in the field during the present study.

Some cultures started in early spring on the sediment taken from the frozen and snow covered lake No. 1. Sediment samples from this lake were kept in the freezer at -30°C during 2 days to examine the effect of freezing to hatching.

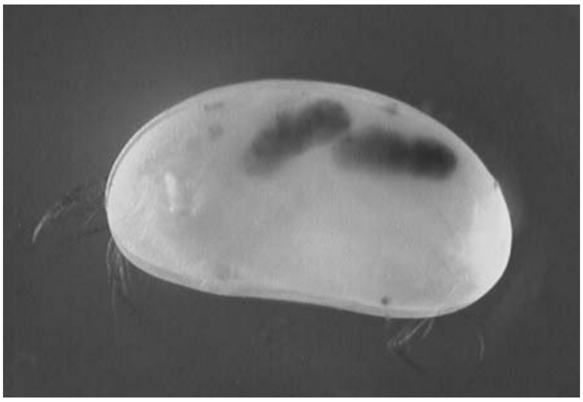

Fig. 2. *Tonnacypris glacialis*, adult female.

Results

More then 5000 individuals of *T. glacialis* (Fig. 2) from 25 reservoirs were examined. Two months were enough for representatives of this species to go through all developmental stages, to mature and lay eggs. Occurrence of particular stages in the samples taken in the 1995 active hydrological period is shown in Table 3. Occurrence of developmental stages in the following seasons (1996, 1998 and 2001) is shown in Fig. 3a–c. Relative abundances of developmental stages in the samples taken in the Arctic summer 1995 are shown in Fig. 4. The life span of subsequent stages is shown in Table 3.

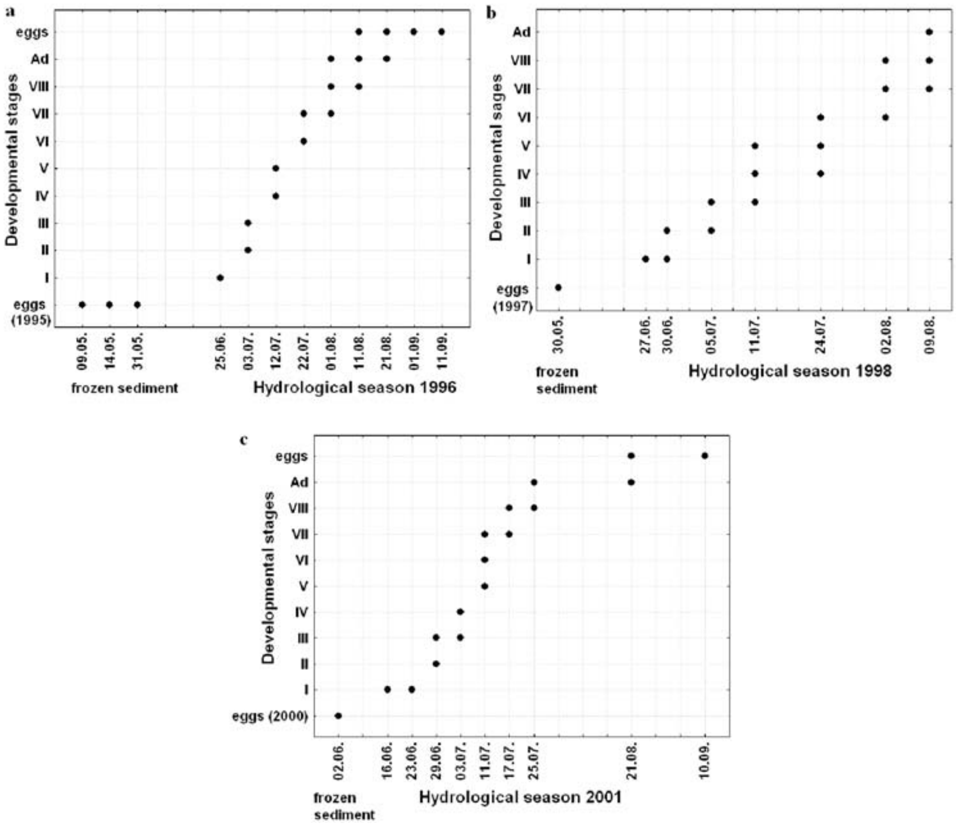

Fig. 3. *Tonnacypris glacialis* – the time of development of particular stages; occurrence of the particular stage in a sample has been marked with dots. (a) On the basis of the data from 1996; eggs (1995) – eggs from 1995 hydrological season. (b) On the basis of the data from 1998; eggs (1997) – eggs from 1997 hydrological season. (c) On the basis of the data from 2001; eggs (2000) – eggs from 2000 hydrological season.

The second generation of *T. glacialis* was never observed in any of the studied lakes in the same active hydrological period, regardless of its duration. Furthermore, none of the developmental stages, except eggs, was ever found in the samples taken from frozen sediment. This suggests that *T. glacialis* needs phase change ice/water to start the next generation.

Eggs of *T. glacialis* in frozen sediment wintered in relatively high temperature. The lowest temperature of frozen sediment in the lake No. 1 during Arctic winter 1999 was – 4.0°C (unpublished data, Polish Polar Station, Hornsund). In an experiment, frozen sediment from the lake No. 1 was kept in freezer in the temperature of -30°C during 2 days. After thawing none individuals of *T. glacialis* were hatched. During winter eggs of *T. glacialis* rest in the sediment in a comparatively high temperature.

Table 3

Time of the development of particular stages of *Tonnacypris glacialis* (on the basis of the data from 1995 and samples from the lake No. 1)

Date (1995)	The following days of observations	The developmental stages										Number of individuals in the sample
		I	II	III	IV	V	VI	VII	VIII	Ad	eggs	
08.06	1	+										20
11.06	4	+	+									24
14.06	7	+	+									17
16.06	9	+	+									33
18.06	11	+	+									15
20.06	13		+									15
22.06	15		+	+								11
24.06	17		+	+								11
26.06	19		+	+								16
28.06	21		+	+	+							31
30.06	23		+	+	+							30
02.07	25			+	+	+						23
04.07	27			+	+	+	+					40
06.07	29			+	+	+	+					43
08.07	31				+	+	+					42
10.07	33				+	+	+	+				46
12.07	35					+	+	+				34
14.07	37						+	+	+			45
16.07	39						+	+	+			38
18.07	41						+	+	+			44
20.07	43							+	+			18
22.07	45							+	+			16
24.07	47								+	+		19
02.08	56									+		12
07.08	61									+		15
13.08	67									+	+	23
17.08	71									+	+	25
22.08	76										+	0
29.08	83										+	0
07.09	91										+	0
12.09	96										+	0
17.09	101										+	0
22.09	106										+	0
27.09	111										+	0
02.10	116										+	0
07.10	121										+	0
12.09	126										+	0
19.09	133										+	Frozen sediment
29.09	143										+	

Time of life for developmental stages	I	II	III	IV	V	VI	VII	VIII	Ad
t_F	3	11	6	4	2	6	4	10	20
t_L	–	12	4	4	2	6	4	2	24
t_M	7.5	8.5	5	3	4	5	3	17	–
t_D	–	6	8	2	6	6	6	9	–

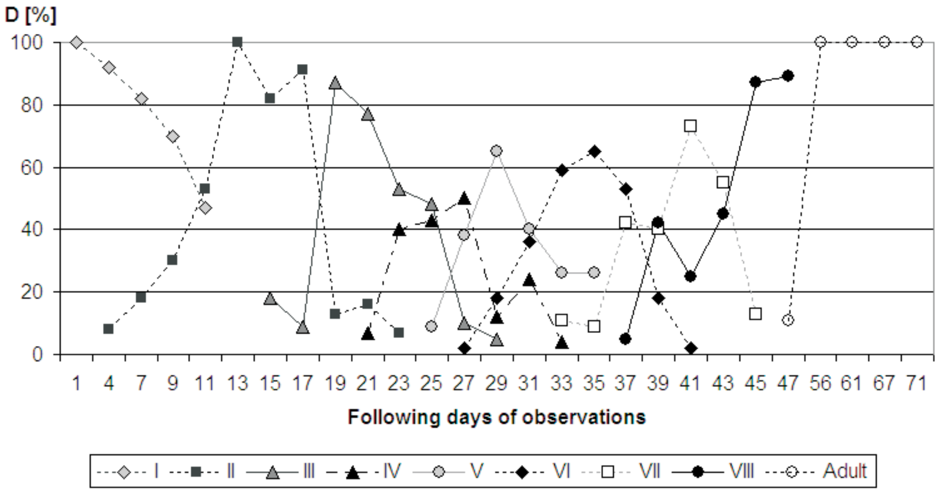

Fig. 4. Relative abundance of *T. glacialis* developmental stages on following days of observations (on the basis of the data from 1995 and samples from the lake No. 1).

Such reproductive strategy is based upon radical shortening of the developmental stage. To be well prepared to live actively as soon as the lake thaws, the animal is already in the first larval stage remaining in egg shell. Observations made in the season 1999 enabled a thorough analysis of the hatching process. In the course of 10 hours after thawing of the sediment, shell of the wintering egg of *T. glacialis* is remodelled. The first signal is a restructuring of a part of the shell in front of the nauplial eye, then the next stages of the shell opening are visible. After hatching, an individual in the first developmental stage immediately starts active life and preying. The colour of the individuals in the first developmental stage is intensely orange, in the second stage – light orange and in the third developmental stage olive-green, typical for all other developmental stages of *T. glacialis.* As the observations suggest, the freezing period is essential for young individuals to hatch. Young individuals were not observed in the cultures even after a long growing period (12–15 months). Although adults occurred and completed ontogenesis after 1–2 months, the next generation did not appear at all. It is worth mentioning that in the cultures, the species coexisting widely with *T. glacialis* in the lakes of Spitsbergen, such as *Diacyclops crassicaudis* (G.O. Sars, 1863) and *Candona rectangulata* Alm, 1914*,* survived and reproduced successfully in the course of the culture growth.

The temperature affects the time of individual developmental stages of *T. glacialis*. Summer air average temperatures (June, July and August) were different during the years of study: 3.2°C in 1995, 3.0°C in 1996, 4.1°C in 1998, 3.8°C in 2001 (Marsz and Styszyńska 2007). The time of development was shorter in summer of 1998 and 2001 when the average temperature in July was higher comparing to 1995 and 1996. The length of development of IV–VII developmental stages is the shortest. It may be an effect of higher water temperature in July than in June (Table 1). Moreover, the variable duration of bottom sediments' melting cause that the individuals of the first developmental stage appear during a rather long period.

Disturbances in the developmental cycle of *T. glacialis* were not observed in temperatures up to of 23°C. Constant temperature rise to higher values (25–32°C) resulted in the death of animals. However, short every day temperature rise up to 32°C did not disturb the development of *T. glacialis*.

In natural conditions, depending on the lake type, temperature in midsummer may change from a few degrees in deeper tundra lakes fed by rivulets or streams with snow thawing water, up to 14.5°C in the moraine, fully exposed shallow lakes with dark bottom sediment (Nowiński and Wiśniewska-Wojtasik 2006). Because of these large differences, which exist even in close stations, the developmental cycle of *T. glacialis* may start at a different time and may have somewhat different duration. Moraine lakes thaw about two weeks earlier than the majority of little tundra lakes. However, the differences between the thaw times of small tundra lakes may also reach three weeks. The eggs from the previous season are laid in the sediment. In the tundra lakes, the eggs were laid at the end of July and the beginning of August. In the shallow moraine lakes they were laid earlier, often as early as the second half of July. Such a short time to go through the whole developmental cycle enables *T. glacialis* to complete its development not only before the lakes freeze but also before they dry out, which happens quite often in case of shallow, small moraine lakes, and some tundra lakes. The lakes dry out most often in the second half of summer depending on the thickness of the snow cover in spring, precipitation in active hydrological period and sunshine. In deep moraine reservoir (depth of 3.5 m) with water colder than in other moraine ponds, adults were observed in first part of September.

Some cultures were also grown to show the relationship between the duration of the developmental period and temperature (Table 2). In laboratory conditions, when temperature was about 20°C, developmental cycle was shortened to about 1 month.

Precise calculation of the length of life of subsequent developmental stages in natural environment is rather difficult, because temperature in lakes fluctuates during summer and during the day. Tables 1 and 3 show that the length of life stages is inversely proportional to the temperature. This relation was observed also in cultures (Table 2). If we calculate the life span for one generation using the shortest time for one stage, which is 3.25 days (average value for IV stage) we obtain that this span for one generation is 29.25 days (at the average temperature of about 10–12°C, Table 1). This result is compatible with laboratory observations (Table 2, 11°C), because time of life for adult is longer then 3.25 days (about 20 days). If we calculate the life span of one generation using the minimum time for following stages (Table 3) we will obtain as a result 47 days. It is also compatible with laboratory observations.

Discussion

The life cycle of *T. glacialis*, with reference to the developmental larval and adult stages as well as to the egg laying period is to some extent consistent with earlier observations (Olofsson 1918). However the occurrence of two generations within one season is described in the literature (Olofsson 1918; Bronstein 1947; Griffiths *et al.* 1998). This conclusion might have been drawn due to the false assignment of the first developmental stages of *T. glacialis* and *C. rectangulata*; the latter species, co-occuring with *T. glacialis*, has a developmental cycle lasting for several seasons (Wojtasik, own results). The orange colour of eggs and the 1st developmental stage of *T. glacialis* (appearing at the beginning of the vegetation season) is the same as the colour of older developmental stages of *C. rectangulata*. Dark olive-green shells of *T. glacialis* camouflage the presence of orange eggs. In addition, the eggs and the 1st developmental stages of *C. rectangulata,* appear at the end of July, when the life cycle of *T. glacialis* is coming to an end, and are milky white. Having fragmentary data from the whole vegetation season it is easy to assign the 1st orange developmental stage of *T. glacialis* to *C. rectangulata,* and the milky white 1st stages of the latter to *T. glacialis.* This might have been the reason of the erroneous conclusions drawn by Olofsson (1918) that two generations of *T. glacialis* may develop in one season. Thus, the examination of the samples taken in the subsequent seasons from the frozen sediments was extremely valuable and allowed an unambiguous interpretation. It enabled me to watch closely the hatching process of young individuals and to find out that other developmental stages of *T. glacialis* never occurred in that time of hatching.

Developmental strategy observed, based on radical shortening of the developmental stage was not so short as reported by Olofsson (1918) and Griffiths *et al*. (1998) (2 weeks). In natural environment the life time of one generation was variable and lasted about 59–66 days in 1995, about 47 days in 1996, about 43 days or longer in 1998, longer then 35 days in 2001 (Table 3 and Fig. 3). In laboratory conditions the shortest time observed was about three weeks (23°C) or, in the temperature 20°C – one month (the first adult females but without eggs were observed in cultures after 25 days).

Considerable shortening of the life cycle caused by the rise of water temperature, was already observed in ostracods (Szczechura 1971; Geiger 1990). The water in moraine reservoirs thaw earlier then in tundra ponds and may warm up quite substantially, up 10°–14°C (Nowiński and Wiśniewska-Wojtasik 2006), which in the case of *T. glacialis* speeds up its developmental cycle. The studies in numerous Arctic localities showed that this species occurs in reservoirs of the temperature of 5.9+/-3.2°C (Griffiths *et al.* 1998). Because of this temperature range and the occurrence of the species in the Pleistocene in freshwaters of north-central and north-eastern Europe, authors of that article have suggested to consider *T. glacialis* as a paleoecological indicator. Some doubt appears, however, taking into account my observations made in the natural environment and laboratory cultures. They suggest that the factor limiting the distribution of *T. glacialis* is not the narrow temperature range proposed by the authors, but severe winter conditions, which causes freezing of the bottom sediments. The latter is an essential factor for young individuals to hatch. The tolerated temperature range is, however, considerably wider; in cultures the temperature of 32°C is lethal before 24 hours, at 28°C reduced activity was observed after 24 hours, while at 23°C and lower – *T. glacialis* were alive and preyed throughout the culture growth. In Spitsbergen the natural conditions such as high tolerance to high temperatures allows this species to settle in the reservoirs with short thermal inflows. In this case continental climate characterized by severe winter and warm summer would be also appropriate for this species, which would change the range of temperature in the Pleistocene, for which *T. glacialis* would be an indicator. The present range of *T. glacialis* occurrence, cited in the literature does not give an unambiguous answer because it includes the Canadian Arctic, Greenland, Iceland, Spitsbergen, Scandinavia and Novaya Zemlya. We have no information about its possible occurrence in freshwaters of Siberia. Such an information would be necessary to draw more substantiated conclusions concerning life of *T. glacialis* in its natural environment. There may be, nevertheless, other unnoticed causes limiting the occurrence of *T. glacialis* to the Arctic, besides the necessity of eggs freezing.

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