

Temperature sensitivity of gamogenesis in littoral cladocerans and its ecological implications

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ABSTRACT

Temperature sensitivity of chydorid (*Cladocera*, *Chydoridae*) gamogenesis in southern Finland was examined. Chydorid sweep net samples and littoral surface water temperature measurements of seven lakes were taken weekly. Percentage abundances of gamogenetic females were used to estimate the temperature optima and tolerances for gamogenesis of individual chydorid species. The estimations were carried out using a weighted averaging (WA) technique. The results indicated that the optimum temperature of gamogenesis ranged between 7.0 and 9.7 °C and the total tolerances were between 2.0 and 4.7 °C suggesting a species-specific response for gamogenesis. *Alonella nana* and *Chydorus sphaericus* s.l. had the lowest optima, which was possibly due to their ubiquitous ecological preference and wide geographical distribution. *Camptocercus rectirostris*, *Alonella excisa* and *Grabtoleberis testudinaria* had high optima for their gamogenesis. These estimations provide first numerical autecological data on gamogenesis of natural and contemporary chydorid populations. Furthermore, the results provide species-specific estimations of the effect of the present climate warming on chydorid reproduction patterns. This information can be useful background data in global change assessments regarding freshwater lakes.

Key words: Chydoridae, sexual reproduction, temperature, freshwater lakes, weighted averaging

1. INTRODUCTION

Environmental sensitivity of species determines their geographical distribution and abundance in particular ecosystems and habitats. According to their environmental sensitivities species may be characterized as eurytopic (wide) or stenotopic (narrow), and a wide tolerance of a specific environmental factor provides an advantage in competition. The significance of environmental sensitivity in a species, usually measured as optima and tolerances for a specific environmental factor such as temperature, is emphasized due to environmental changes. Such changes are driven, accelerated and intensified by human activities. For example, global warming is already having pronounced effects on terrestrial and aquatic ecosystems and is dramatically changing physical and chemical environments (IPCC 2007), causing re-distribution and extinction of species with narrow environmental sensitivities (Korkeamäki & Suhonen 2002; Thomas *et al.* 2004). Thus, the role of temperature in determining species' distribution and abundance is becoming accentuated.

In aquatic ecosystems, such as freshwater lakes a variety of environmental characters including: pH, oxygen, color, littoral vegetation, bottom substrata, and temperature differ substantially even within a small geographical region. Thus, the distribution and abundance of aquatic fauna, for instance littoral cladocerans of the family Chydoridae (chydorids) are forced by many environmental factors, such as nutrient availability (Whiteside 1970), pH (Deneke 2000), aquatic vege-

tation (Quade 1969), and predation (Williams 1983). Chydorids appear to be ecologically rather tolerant, since the same species inhabit a wide range of different environments, as shown in studies on chydorid distribution patterns (Korhola 1999; Sweetman & Smol 2006). The ecological plasticity of chydorids may be enhanced by their reproduction strategy: cyclical parthenogenesis. This strategy consists of parthenogenetic (asexual) reproduction under favorable conditions, and gamogenetic (sexual) reproduction that leads to diapausing resting eggs under unfavorable conditions (Frey 1982). The role of gamogenesis and resting eggs in the wide ecological plasticity of chydorids is clear, as resting eggs are viable for a long time and subsequently result in the emergence of new populations upon the return of favorable environmental conditions.

Temperature has been described to be an important environmental factor that affects the distribution and abundance of aquatic organisms (Weckström *et al.* 1997; Luoto 2009). In cladocerans, temperature has a direct effect on metabolism and growth rate (Bottrell 1975; de Eyto & Irvine 2001), and also an indirect effect on their habitat quality (Williams 1982; Rautio 1998). In general, temperature is also known to work as an important inducer for the hatching of resting eggs (Vandekerkhove *et al.* 2005) and also for sexual reproduction aimed at diapausing resting eggs (Stross 1969a, b).

Even though the role of temperature in gamogenesis in cladocerans including chydorids is recognized, the temperature sensitivity of gamogenesis in individual cladoceran species has not been previously reported.

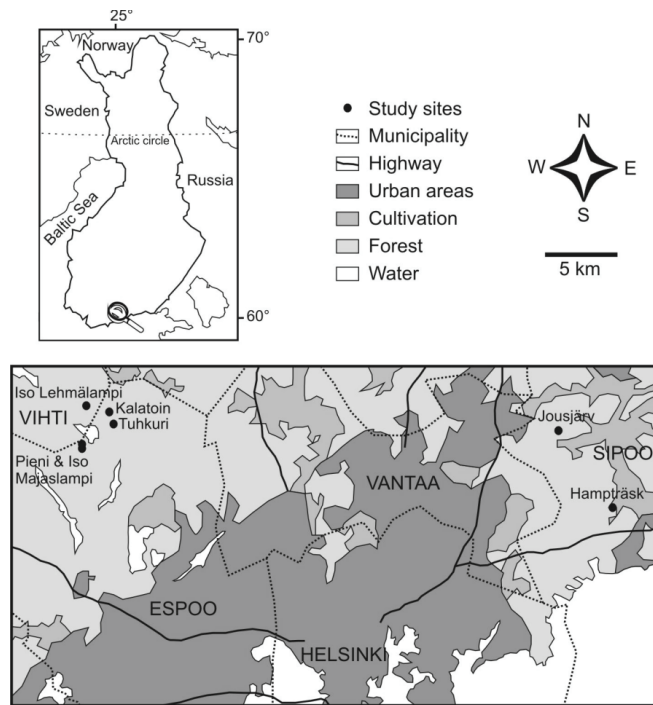


Fig. 1. Locations and geographical settings of the study lakes.

Tab. 1. Measured water temperatures ($^{\circ}\text{C}$) from the study lakes during the autumn (September 11–November 14, 2005).

	Sep 11	Sep 19	Sep 26	Oct 3	Oct 9	Oct 17	Oct 24	Oct 30	Nov 7	Nov 14
Kalatoin	14.6	11.4	13.2	12.1	10.8	8.0	6.4	4.5	6.3	5.6
Tuhkuri	15.3	12.0	14.0	12.4	11.6	8.1	6.7	5.5	7.7	6.2
Iso Lehmälampi	15.2	12.4	12.7	12.6	11.6	8.8	7.0	4.7	6.3	6.1
Hampträsk	13.1	11.5	12.4	12.1	11.5	7.3	6.4	4.3	7.3	7.0
Pieni Majaslampi	17.1	13.9	13.8	13.5	12.2	10.0	8.2	5.0	6.5	6.0
Iso Majaslampi	16.3	12.5	13.8	13.2	11.9	9.2	7.6	4.3	4.9	6.0
Jousjärvi	12.0	10.4	11.1	11.1	10.2	6.9	7.5	4.0	6.8	6.4

Recently, Nevalainen and Sarmaja-Korjonen (2008a) suggested that some chydorid species may have individual demands for specific water temperatures and the development of gamogenesis and that this variability may further enhance the ecological performance of the species as a whole. We based the current paper on this suggestion, and present results of temperature sensitivity of chydorid gamogenesis obtained by field observations from southern Finland. Our main objectives are to describe species-specific water temperature sensitivity data of chydorid gamogenesis in natural communities and argue their significance in relation to ecological plasticity and species distribution under changing environments.

2. METHODS

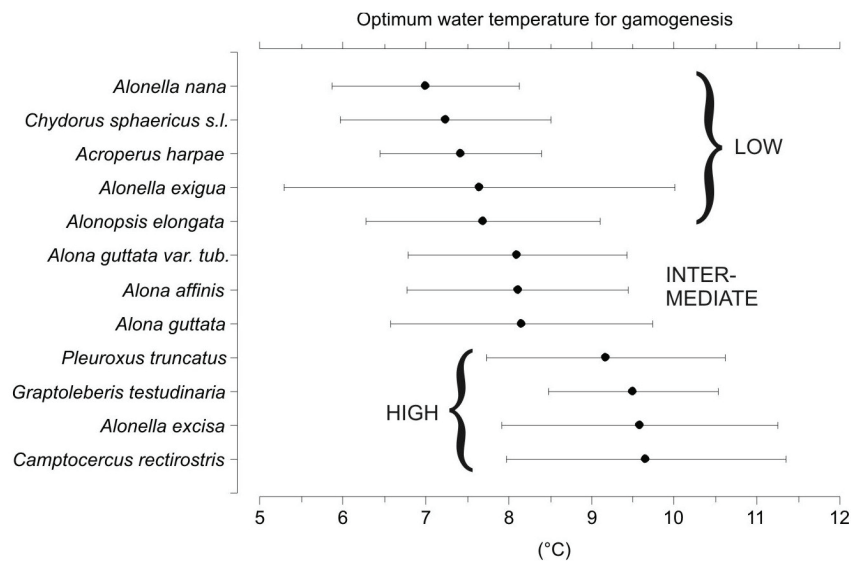
Seven freshwater lakes situated in southern Finland in the Helsinki district were sampled for littoral cladocerans weekly during the fall of 2005 (Fig. 1). The lakes were small (0.5–13.7 ha) and their limnological characteristics ranged from oligo- to eutrophy (spring TP <10-

$30 \mu\text{g L}^{-1}$), from clear to brown water (spring color 5–125 Pt $\mu\text{g L}^{-1}$), and from acidic to circumneutral (spring pH 4.4–7.0). The environmental characteristics of the study lakes are described in detail by Nevalainen and Sarmaja-Korjonen (2008b). Water temperature during the sampling period varied between 4.0 and 17.1 $^{\circ}\text{C}$ (Tab. 1). The sampling period lasted from early September to mid November, constituting 10 sampling occasions per lake, totaling 70 samples.

The cladocerans were sampled using a standard 100- μm sweep net from the shore of the lakes and from three sampling spots in every lake and stored in small jars with alcohol. In the laboratory the samples were mounted on preparation slides and analyzed by a light microscope. Cladocerans were identified to species level and according to reproduction mode (parthenogenetic female, gamogenetic female, male) and counted until 100 individuals were encountered. In some lakes the oncoming winter precluded this minimum count, because chydorids had become scarcer. The nomenclature is based on Røen (1995) and the author names are tabulated in table 2.

Tab. 2. Number of occurrences, mean percentage abundances and gamogenetic statistics of the most common chydorids in the seven study lakes.

	Occurrence	Mean abundance	Gamogenesis		
			Counts	Max	N2
<i>Alonella nana</i> (Baird)	7	50.1	36	30.8	21.1
<i>Chydorus sphaericus</i> s.l.	7	6.0	17	6.4	12.7
<i>Acroperus harpae</i> (Baird)	6	11.6	24	14.4	11.6
<i>Alonella exigua</i> (Lilljeborg)	2	0.2	4	2.7	3.1
<i>Alonopsis elongata</i> (Sars)	4	6.3	21	16.7	13.5
<i>Alona guttata</i> var. <i>tub.</i> Kurz	7	6.6	23	20.6	10.7
<i>Alona affinis</i> (Leydig)	5	2.5	14	4.8	8.7
<i>Alona guttata</i> Sars	7	4.5	25	8.7	15.7
<i>Pleuroxus truncatus</i> (Müller)	4	1.2	9	3.7	7.4
<i>Graptoleberis testudinaria</i> (Fischer)	7	0.6	5	1.9	4.5
<i>Alonella excisa</i> (Fischer)	7	6.9	32	10.9	18.1
<i>Camptocercus rectirostris</i> Schoedler	4	0.2	3	1.9	2.7

**Fig. 2.** Estimated weighted averaging (WA) water temperature optima and tolerances for gamogenesis of the 12 most common chydorid species.

Temperature optima and tolerances for gamogenetic females of individual species in the lakes were estimated by weighted averaging (WA) regression using the program C2, ver. 1.5.0 (Juggins 2007). In the estimation the species importance values (abundances) are used as weights in calculating the average. The method of the weighted averaging is reasonably good when the whole range of species' distribution is covered by the samples. However, if only a part of the range is covered, the estimate will be biased and shifted in the direction of the tail that is not truncated. The relative abundances of only gamogenetic females were used in these estimations, because males can occur without gamogenetic females and thus do not necessarily indicate sexual reproduction with resting egg production (Shan 1969; Nevalainen 2008).

3. RESULTS

Of the chydorid fauna *Alonella nana*, *Chydorus sphaericus* s.l., *Alona guttata*, *Alona guttata* var. *tuber-*

culata, *Graptoleberis testudinaria*, and *Alonella excisa* occurred in all the lakes during the fall sampling period (Tab. 2). The most abundant species in fall chydorid communities was *A. nana* and other common taxa included *Acroperus harpae*, *A. excisa*, *A. guttata* var. *tuberculata*, *Alonopsis elongata*, and *C. sphaericus* s.l. Gamogenesis occurred frequently with *A. nana*, *A. excisa*, *A. guttata*, and *Alonopsis elongata* as indicated by the effective number of gamogenetic occurrences (N2) (Tab. 2).

The estimated WA optima and tolerances for fall gamogenesis in the 12 most common chydorid species found are illustrated in figure 2. The results show that the optimum temperature for gamogenesis of all observed species was below 10 °C, ranging within 7.1–7.9 °C for low, 8.0–8.9 °C for intermediate, and 9.0–9.7 °C for high temperature optima. *Alonella nana* had the lowest (7.1 °C) and *Camptocercus rectirostris* the highest (9.7 °C) optima. In addition to *A. nana* the chydorid species with low (<8.0 °C) optima for gamogenesis

were *Chydorus sphaericus* s.l., *Acroperus harpae*, *Alonella exigua* and *Alonopsis elongata*. Apart from *Camptocercus rectirostris* the species with the high optima (>9.0 °C) included *Pleuroxus truncatus*, *Graptoleberis testudinaria*, and *Alonella excisa*. The temperature tolerances varied between 2.0 and 4.7 °C, being narrowest in *Acroperus harpae* and widest in *Alonella exigua*.

4. DISCUSSION

Unfortunately, there is very little previous numerical data available on species and abiotic environmental linkages in natural and contemporary chydorid communities. Most of the preceding work associated with these species-environment links were obtained by using paleolimnological methods and perspectives (e.g., Bigler *et al.* 2006; Kattel *et al.* 2008) utilizing subfossil cladoceran assemblages in surface sediments. As stated by Lotter *et al.* (1997) and Bigler *et al.* (2006), knowledge about distribution and optima and tolerances of freshwater biota is still very fragmentary. Chydorid species-specific ecological optima and tolerances have been described and published so far for total phosphorous by Brodersen *et al.* (1998) and for surface-water temperatures by Kattel *et al.* (2008). These studies encompassed lakes from geographically restricted areas therefore providing estimations for local ecologies. Weckstöm & Korhola (2001) stated that one should be cautious in referring to such estimations of ecological data obtained from studies in other regions. However, such data can be used as basic autecological guidelines and are very useful as comparative data.

Kattel *et al.* (2008) emphasized that in addition to temperature a wide variety of environmental factors affect cladocerans and therefore estimating cladocerans' response solely by their temperature sensitivity is challenging. Furthermore, temperature has both direct (Bottrell 1975; de Eyto & Irvine 2001) and indirect (Rautio 1998) roles in affecting cladocerans. For example, a relationship between cladocerans and: mean summer temperature has been shown by Lotter *et al.* (1997), mean July surface water temperature and mean July temperature by Bigler *et al.* (2006), and mean summer surface water temperature by Kattel *et al.* (2008). According to the WA estimations for temperature sensitivity of chydorid gamogenesis in the present study, the water temperature optima for the most commonly occurring chydorid species in southern Finland varied between 7.0 and 9.7 °C thus having a total range of 3.7 °C (Fig. 2). In respect to the previously published distributional data, *A. harpae* and *A. elongata* appear to have some preference for colder lakes (Rautio 1998; Korhola 1999; Kattel *et al.* 2008). Their findings possibly coincide with the present study's results of low temperature optima for gamogenesis in those species. Gamogenesis occurs in low water temperatures giving these species the opportunity to reproduce as late as

possible via more efficient parthenogenesis. *Graptoleberis testudinaria* had high temperature optima for gamogenesis: a finding which is consistent with the results of Kattel *et al.* (2008) who reported a high mean summer surface water optimum for its occurrence.

The lowest water temperature optima were recorded for the two ubiquitous species *Alonella nana* and *Chydorus sphaericus* s.l. This finding may clarify their success in many types of environments (Duigan 1992; de Eyto *et al.* 2003; Belyaeva & Deneke 2007). The results suggest that they consistently rely on parthenogenetic reproduction during most of the fall period and have optimum conditions for gamogenesis later during the fall as water temperatures decrease towards those of winter levels. *Alonella nana* and *Chydorus sphaericus* s.l. had rather similar and narrow tolerances for the gamogenesis (2.3 and 2.5 °C, respectively), which also suggests that their reproduction strategy is optimized. In cyclical parthenogens, such as the chydorids, the contribution to the population growth is expressed mainly via parthenogenetic individuals, and the ecological cost of gamogenesis is high (Doncaster *et al.* 2000). Therefore, the two chydorid species probably benefit from parthenogenetic reproduction occurring late during the open-water season. Consequently, their low optima for gamogenesis may enhance their ecological plasticity allowing them to inhabit a wide range of freshwater conditions.

Cyclical parthenogenesis as a reproduction strategy provides a high potential for adaptations that increase the plasticity of the chydorids, but comprehensive investigations are lacking. The current preliminary results suggest that chydorid species may respond individually to water temperature changes with gamogenesis and this behavior may increase their ecological plasticity. The current study's data from southern Finland showed a clear water temperature range in the temperature optima (3.7 °C) and total tolerances (2.7 °C) for gamogenesis, which suggests that the species may have different temperature requirements for successful gamogenesis. For example, it is possible that high temperature requirements for successful gamogenesis may restrict the distribution of certain chydorid species in the high latitude regions. Thus, the geographical distribution of chydorid species may partly be controlled by the temperature sensitivity of their gamogenesis.

It is expected that the annual mean temperature in Finland will rise between: 1-3 °C by the 2020s, 2-5 °C by the 2050s, and 2-7 °C, by the 2080s, relative to the baseline period 1961-1990 (Jylhä *et al.* 2003). The present results suggest that the chydorid species having low water temperature optima for gamogenesis (*Alonella nana*, *Chydorus sphaericus* s.l., *Acroperus harpae*, *Alonopsis elongata*, and the *Alona* species) may have to alter their reproduction patterns to survive in the study lakes when the water temperatures increase. This is because these species have low temperature optima and narrow tolerances for gamogenesis (Fig. 2), and thus

they may have to rely more on parthenogenetic reproduction than hitherto. Although by having a low optimum for gamogenesis, *Alonella exigua* has a wide tolerance, which possibly enables its success in increased water temperatures.

The current data was obtained from a restricted area and should be widened to cover lakes from different regions in Finland to give a more comprehensive picture on temperature sensitivity of chydorid gamogenesis. Furthermore, not only distribution but also reproduction patterns of chydorids should be examined in other European regions from the Mediterranean to the Arctic Ocean for more comprehensive ecological environmental assessments.

5. CONCLUSIONS

Chydorid species exhibit individual temperature requirements for successful gamogenesis. Low temperature optima for gamogenesis may enhance plasticity of some species, giving them a competitive advantage during the fall and a potential for wider geographical distribution. Under the present climatic warming conditions the temperature-mediated species-specific reproduction strategies may be altered and have prolonged effects on the population dynamics of chydorids and thus intensive research on this area of ecology is considered necessary.

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