Ultimate reasons for summer diapause of *Daphnia* in a permanent lake

Mirek Ślusarczyk, Bernadette Pinel-Alloul and Malorie Gelinas

Production of resting stages is a common strategy of genome protection against strong selective forces used by many organisms inhabiting environments that suffer cyclic deterioration (Williams 1996). In freshwater habitats of the temperate zone, production of resting stages is commonly associated with drastic changes in abiotic (e.g. over-freezing) or biotic (e.g. shortage of resources) conditions of the environment during winter. In some habitats however, diapause is also observed in summer. While “summer diapause” of freshwater organisms inhabiting ephemeral habitats may have a clear-cut explanation of survival during temporal deterioration of the physical conditions of the environment (Williams 1996), the ultimate reasons for this seasonal phenomenon in permanent lakes appear more ambiguous. The few studies reporting summer diapause of pelagic cladocerans indicate its possible association with the clear water phase (Threlkeld 1979, Jankowski 2003, Cáceres & Tessier 2004 a, b), a seasonal phenomenon occurring in late spring or early summer in many eutrophic lakes (Sommer et al. 1986).

The clear water phase is a relatively short period (days to weeks) of high water transparency and low phytoplankton biomass resulting from high grazing rate of fast growing populations of large-body cladoceran filterers (most commonly of the genus *Daphnia*). High grazing pressure of zooplankton may reduce standing crop of edible algae and promote development of inedible phytoplankton (Sommer et al. 1986), which in turn may limit reproduction of herbivorous zooplankton (Hulsmann 2003). On the other hand, strong pressure of invertebrate predators (De Bernardi 1974, Hovenkamp 1989) or of young of the year (YOY) planktivorous fish (Mills & Forney 1983) that hatch synchronously in spring, when planktonic cladocerans have their peak of density, may greatly impact planktonic grazers. Fry of most freshwater fish feed readily on zooplankton in their early ontogenetic stages before they switch to some other food sources at older stages of development. In turn, dominant populations of large-bodied cladocerans may be decimated or exterminated and further replaced by smaller, less vulnerable planktonic herbivores (Sommer et al. 1986).

Regardless of which, if any, of the mentioned reasons (lack of edible phytoplankton or high predation pressure) plays the key role in shaping this seasonal event, consequences for large bodied cladocerans are repetitively terminal. Consequently, large bodied cladocerans either disappear completely from the water column or remain there in low densities throughout summer. From an individual perspective, it should be more profitable to produce resting eggs in advance or during the terminal season than count on unlikely survival in an active stage. Surprisingly, records of the “clear water phase diapause” of planktonic cladocerans in permanent lakes are much less common than evidence of their seasonal decline in abundance. Existing reports of summer diapause of *Daphnia* in permanent lakes of the temperate zone concern *D. pulicaria* in North America (Threlkeld 1979, Cáceres & Tessier 2004 a, b), *D. magna* (Lampert 1991) and *D. galeata* (Jankowski 2003) in Europe. However, ultimate reasons for this summer diapause were not the focus of these studies.

Hereby, we report main results of a study for which the primary objective was to reveal the ultimate causes of the clear water phase diapause of *Daphnia pulicaria* observed in Lake Brome located in southwest Quebec, Canada.
Lake Brome is a middle-size (area: 14.4 km²), shallow (max. depth: 12.2 m), eutrophic, dimictic freshwater ecosystem inhabited by both planktivorous invertebrates and fish. This study reports seasonal changes in the demography of the large bodied *D. pulicaria* and in the abiotic and biotic factors that could possibly influence its chances for survival and reproduction. Samples were collected at weekly or biweekly intervals from late April until early August of 2002.

Of two species of *Daphnia* (*D. pulicaria* and *D. mendotae*) recorded throughout the research period in the inspected lake, the larger *D. pulicaria* produced resting eggs during our study. Production of resting eggs was observed from early June until early July and was most intense in the mid-June when over 30% of all females carried dormant eggs. The incidence of ephippial production coincided with three potential ultimate reasons for diapause in the pelagic zone: low concentration of edible algae, high density of predacious larvae of water midge *Chaoborus* sp., and high density of YOY yellow perch (*Perca flavescens*). Neither the seasonal analysis of weight/length relationship nor of lipid content of *D. pulicaria* revealed substantial resource limitation of *Daphnia* during the studied period. Predacious impact of *Chaoborus* on *D. pulicaria*, though not measured directly, did not seem to be decisive either. Density of *Chaoborus* was relatively low in mid-July when the density of *D. pulicaria* declined abruptly.

Several lines of arguments indicate fish predation as the main reason for the spring/summer diapause and further decline of *D. pulicaria*.

Visually hunting fish predators prey selectively on large bodied zooplankton. Seasonal analysis of the demography of *D. pulicaria* revealed strong size-selective mortality of large bodied individuals beginning the end of June. This coincided with an increase in predation pressure on *D. pulicaria* by YOY perch, as indicated by gut content analysis combined with fish density assessment. Moreover, the starting date of resting egg production in the population of *D. pulicaria* preceded the intensification of the predacious pressure of YOY fish by a period equal to theoretically estimated “optimal time of diapause induction” *sensu Taylor* (1980) and *Hairston & Munns* (1984). Finally, the small-bodied *D. mendotae* did not produce resting eggs in concert with larger *D. pulicaria* during the study period. This would diminish the role of food depletion or predation by *Chaoborus* in shaping this seasonal phenomenon (since both factors should affect smaller-bodied *D. mendotae* more severely) and would support the idea of fish predation as the most likely reason for the clear water phase diapause of *D. pulicaria* in the lake Brome.

**Key words:** 🐠, 🐠, 🐠, 🐠, 🐠

**Acknowledgements**

The research was supported by GRIL (Groupe de Recherche Interuniversitaire en Limnologie, Université de Montreal) and KBN (Polish Committee for Scientific Research 6PO4C 03718). We thank **Alexandra Rutherford**, **Ginette Méthot** and **Beata Binek** for technical assistance in field and analytical studies.

**References**


Authors’ address:
M. ŚLUSARCZYK, Department of Hydrobiology, University of Warsaw, Banacha 2, 02–097 Warszawa, Poland. E-mail: m.s.slusarczyk@uw.edu.pl
B. PINEL-ALLOUL & M. GÉLINAS, Département de sciences biologiques, Université de Montréal, C.P. 6128, Succ. Centre-ville, Montréal, Québec, H3C 3J7.