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Different life-history trade-offs of two *Daphnia* species (Cladocera, Crustacea) under natural conditions as the response to predation and competition

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Abstract – *Daphnia longispina* (O. F. Müller 1785) and *Daphnia cucullata* (G. O. Sars 1862), despite co-existing in similar densities in the lake, showed different demographic cycles. To search the causes of such variances between the two *Daphnia*, selected population parameters (density, body proportions, reproductive output) were correlated with the density of five dominant and potentially competitive species of Cladocera. The same parameters were estimated in relation to predation pressure of vertebrates (planktivorous fish) and invertebrates (*Leptodora kindtii* (Focke 1844)). The obtained results show that competition had no apparent impact on life-histories of *Daphnia*. Different strategies of the two *Daphnia* resulted from the uneven effect of invertebrate and vertebrate predators. *D. longispina* that was affected by planktivorous fish and *Leptodora kindtii* invested in reproduction and carried big egg-clutches. *D. cucullata,* which was insignificantly influenced by fish, displayed low reproductive output but changed their body proportions in the process of cyclomorphosis when occurring with *L. kindtii*. Other life-history trade-offs altered during the year, in accordance with the intensity of predation pressure.

Key words: Biological interactions / *Daphnia* / life-history / predatory pressure / competition

Introduction

Specific combinations of physiological and genotypic trade-offs are favoured as a result of natural selection in every population. A set of these specific traits as the only combination of variables comprising temporal course of density pattern, reproductive output and growth rate is defined as life history (Stearns, 1992). For some animals life-history is very plastic and it can change along with changes in the type and exertion of stressors (Boeing *et al.*, 2006). Among many types of stressors altering life-history of the species under impact the most important ones are predation and competition.

Predators of freshwater zooplankton are composed of vertebrate (mainly planktivorous fish) and invertebrate animals. Both groups have size-specific impact on *Daphnia*: planktivorous fish positively select large specimens and well visible females carrying eggs (Brooks and Dodson, 1965; Zaret and Kerfoot, 1975), invertebrates predate on small, young individuals (Pastorok, 1980; Pijanowska, 1990). The role of vertebrate predators in determining zooplankton communities in lakes and in altering the structure from dominance by large-sized species to dominance by small-sized ones has been well reported (Kerfoot, 1980; Lazzaro, 1987; Gliwicz and Pijanowska, 1989). Some studies suggest that invertebrate predators may substantially regulate zooplankton communities (Dodson, 1972; Lane, 1979; Brabrand *et al.*, 1986). *Leptodora kindtii* used in the study as an invertebrate predator is a common pelagic cladoceran which prefers to feed on other species of Cladocera, especially *Daphnia* (Karabin, 1974; Hovenkamp, 1990; Lunte and Luecke, 1990; Wojtal *et al.*, 1999, 2008). Despite its low abundance in lakes, *L. kindtii* is an effectively grazing predator able to remove up to 35% of *Daphnia* (Hall, 1964; Wright, 1965).

Competition among cladocerans results from food limitation. *Daphnia* are able to compete with other cladoceran species due to their specific feeding behaviour attributable to their ability to filter particles in a wide range of sizes: from bacterioplankton to relatively large phytoplankton (DeMott and Kerfoot, 1982; Kerfoot *et al.*, 1985; Vanni, 1986; Matveev, 1987). The consequences of competition in populations of Cladocera are shifts in peak densities of competitors, slowdown growth, reduced juvenile survival and changes in their clutch-size (Goulden *et al.*, 1982; Smith and Cooper, 1982; Boersma, 1995).

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D. longispina and *D. cucullata*, taken as the subject of the study, are a very common and widely distributed component of the zooplankton community in the pelagic zone of temperate lakes (Patalas, 1954; Korovchinsky, 2000). The aim of this work was to compare life-history trade-offs of the two *Daphnia* and to determine whether and how vertebrate and invertebrate predation pressure and interspecific competition affect their life histories.

Materials and methods

The research was carried out in deep (38.8 m) Lake Piaseczno (51°23'03"N, 23°01'46"E) situated in Łęczna – Włodawa Lakeland (eastern Poland). The lake is dimictic, so in summer and winter the temperature and oxygen stratification typical for the temperate zone occurs here. The lake represents the mesotrophic status. During the study period the average primary production achieved 11.13 µg Chl a.dm^{-3} (Czernaś and Serafin, 2007) and total organic carbon oscillated between 2.7 and 3.7 mg C.dm^{-3} (Adamczuk, unpublished data).

In order to obtain the most representative results, the material was collected in the pelagial and the littoral. In the pelagial, the sampling site was located in the deepest part of the lake, and samples were taken every 1–2 m intervals in epilimnion and 3–5 m intervals in meta- and hypolimnion. In the littoral five sites of sampling were determined and samples were taken vertically with 1–2 m intervals. From April to November, 23 samples were collected once a month, for a total of 184 samples. In further procedures every sample was investigated separately and the obtained results were averaged for every term of research.

The samples were sieved through in a 70 µm mesh net and preserved in formalin and glycerine solutions. Cladocerans were classified and counted to calculate their abundance, which was expressed as the number of individuals per m^3. The head height (the distance between the highest point of the head and the middle of the eye), the carapace length (the distance between the middle of the eye and the origin of tail spine) and the tail spine length (the distance between the origin and the tip of tail spine) of at least 50 adult specimens of every *Daphnia* species were measured for every term of research. Ovigerous females were counted to obtain the proportion of those egg-bearing to the total number of individuals. Eggs were enumerated and the number of eggs per ovigerous female was defined as brood-size. The size at maturity (SAM) of *Daphnia* was estimated with the method proposed by Stibor and Lampert (1993). On the basis of abundance, the structure of dominance of Cladocera was estimated to nominate the species that were dominant and potentially competitive to *Daphnia*. The pressure of *L. kindtii* on *Daphnia* was estimated from consumption rates of *Leptodora* presented in the literature (Herzig and Auer, 1990; Herzig, 1995; Wojtal *et al*., 1999).

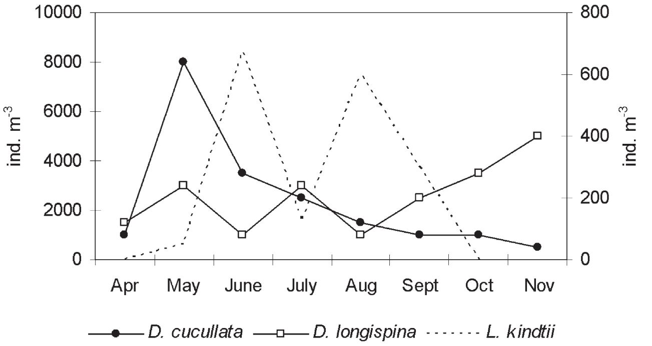

Fig. 1. Seasonal changes in density of *Daphnia* (left axis) and *L. kindtii* (right axis) in Lake Piaseczno.

Fish for food analysis were collected by fyke-nets in the littoral and gillnetts in the pelagial. Netting was carried out in May, July and October. In the laboratory the fish were analyzed for their stomach content. In total, 49 American catfish (*Ictalurus nebulosus*), 42 bleak (*Alburnus alburnus*), 59 roach (*Rutilus rutilus*), 45 perch (*Perca fluviatilis*) and 43 European whitefish (*Coregonus albula*) were analyzed. The feeding selectivity of the fish towards *Daphnia* was evaluated according to Jacobs' formula: $D = (r - p)/(r + p - 2rp)$, where r = proportion of the prey in the gut content, p = proportion of the same item in the environment (Jacobs, 1974). The values of the formula range between -1 and 1, whereas 0 means lack of selectivity.

For statistical analyses all data were log-transformed to approximate the normal distribution. One-way ANOVA with *post-hoc* Bonferroni tests was run to determine the abundance, body-size and reproductive characters in order to assess their seasonal variability. Spearman correlation coefficients were used to estimate the influence of planktivorous fish, *L. kindtii* and dominant Cladocera on life-history trade-offs of *Daphnia*.

Results

Seasonal density

The analysis of *Daphnia* density revealed that both species showed a similar average number of individuals (2400 ± 2500 ind.m^{-3} for *D. cucullata* and 2600 ± 1400 ind.m^{-3} for *D. longispina*). Although the two *Daphnia* started with similar abundance in April (1000 ind.m^{-3} for *D. cucullata* and 1500 ind.m^{-3} for *D. longispina*), just in May *D. cucullata* reached the peak density (8000 ind.m^{-3}) to steadily drop in the following months. *D. longispina*, in turn, displayed regular monthly density fluctuations until September and grew steadily during October and November (Fig. 1).

Body proportions

The average size of adult individuals of the two *Daphnia* was very similar: 1343 µm (range: 1113–2030 µm) for *D. longispina* and 1331 µm (range: 941–1828 µm)

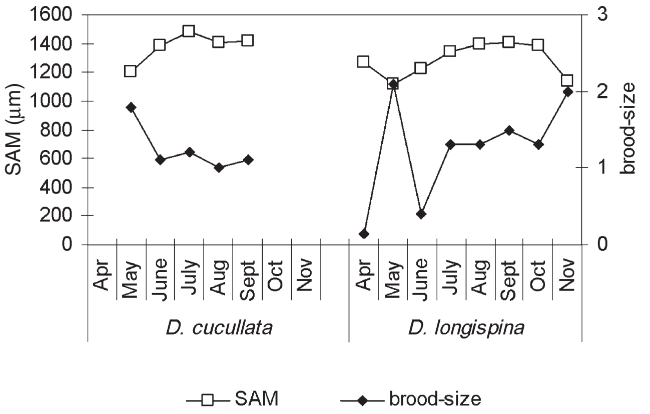

Fig. 2. Size at maturity and brood-sizes of *Daphnia*.

for *D. cucullata*, but only *D. cucullata* showed significant seasonal changes in size ($F = 35.08$, $p = 0.002$, ANOVA). During the research almost all *D. longispina* were comprised in 1000–2000 µm of length (with the superiority of individuals with the size to 1500 µm), only in November 2% of the population were bigger than 2000 µm. Body proportions of *D. longispina* showed statistically insignificant differences: the head constituted 54–107 µm (4.8–9.1% of the total body length), the carapace measured 600–685 µm (58–61%), and the tail spine ranged in length from 374 µm to 408 µm (26.6–35.9%). The smallest *D. cucullata*, below 1000 µm of length, occurred only in April and May, and in the rest of the studied period individuals of the size between 1000–1500 µm and 1500–2000 µm (in minor number) were found. *D. cucullata* were characterized by the elongation of their head. In May the head was more than twice longer than in April, and during the year its size ranged from 60 µm to 316 µm (5.1–27.3% of the total body size) ($F = 26.36$, $p = 0.07$, ANOVA). The length of the carapace was between 514 µm and 695 µm (50–54.3%), and the length of the tail spine measured 289–380 µm (21.9–3.4%) ($F = 39.07$, $p = 0.02$, ANOVA).

Reproductive output

Of the two species, *D. longispina* seemed to invest more into reproduction. It was clearly seen in the number of females carrying eggs: their proportion constituted 0.8–11.8% of the population, while in population of *D. cucullata* only 0–4.7% individuals were ovigerous. The highest number of ovigerous *D. longispina* was found in May and in October–November, and the lowest in June and August. Most *D. cucullata* carried eggs in May, and then their share gradually declined, so in October and November no females with eggs were found in samples. A comparison of their size at maturity (SAM) and the average size of broods showed that the smallest *D. longispina* carrying eggs were found in May and November, *i.e.* in the months when the biggest broods were observed ($r = -0.32$, $p = 0.011$) (Fig. 2). *D. cucullata* revealed the lowest values of SAM in May and August and did not show any correlations between SAM and the size of broods.

Table 1. Spearman correlation coefficients between body-size and brood-size at *Daphnia*.

	Brood size	
	D. cucullata	*D. longispina*
Total body size	$r = -0.15$ $p = 0.47$	$r = 0.29$ $p = 0.021$
Head height	$r = -0.55$ $p = 0.004$	$r = 0.02$ $p = 0.87$
Carapace length	$r = 0.13$ $p = 0.53$	$r = 0.34$ $p = 0.006$
Tail spine length	$r = -0.07$ $p = 0.72$	$r = 0.32$ $p = 0.11$

Ovigerous *D. cucullata* carried from 1 to 3 eggs, but most of them (57.7%) had only 1 egg, whereas *D. longispina* carried 1–5 eggs, and the biggest proportion of females (42%) had 2 eggs. One-way ANOVA test proved significant temporal differences in the brood size only for *D. longispina* ($F = 8.67$, $p = 0.035$). The brood size of *D. longispina* correlated with their total body length ($r = 0.29$, $p = 0.021$) and the carapace length ($r = 0.34$, $p = 0.006$). The brood size of *D. cucullata* showed a significant negative correlation with the height of the head ($r = -0.55$, $p = 0.004$) (Table 1).

Predation risk of planktivorous fish

An analysis of the stomach content of five dominant fish species revealed that *D. cucullata* and *D. longispina* were the preferred food only for the European whitefish. *D. cucullata* were found in 57.4%, and *D. longispina* in 38.1% of the guts, while their amount ranged between 8.3% (*D. longispina*) and 30% (*D. cucullata*) of all cladocerans that were found in the guts of the whitefish. The occurrence of *Daphnia* in intensities of the remaining fish species (American catfish, bleak, roach and perch) ranged between 1.7–25.6% (*D. cucullata*) and 0–23.5% (*D. longispina*) and their proportion in the guts was 0.02–4.75% in case of *D. cucullata* and 0–2.95% for *D. longispina*. The value of Jacobs' coefficient indicates that *D. longispina*, despite its lower proportion in the diet of the fish, was the preferred food item ($D = 0.4$), contrary to *D. cucullata* ($D = -0.35$). Correlation coefficients between the abundances of *D. longispina* and *D. cucullata* in the lake *versus* the guts of the fish suggest that the foraged fish influenced negatively the density of *D. longispina* ($r = -0.93$, $p = 0.024$ for the European whitefish, $r = -0.69$, $p = 0.009$ for all the fish) (Table 2).

Predation risk of *Leptodora kindtii*

A successful development of *L. kindtii* in Lake Piaseczno started in June and lasted to September, with two density peaks occurring in June and August (Fig. 1). Of the two *Daphnia*, *D. longispina* seemed to be more sensitive to *Leptodora*'s predation, as their collapses in density corresponded with the occurrence of *L. kindtii* in densities higher than 500 ind.m^{-3} ($r = -0.72$, $p = 0.044$).

Table 2. Spearman correlation coefficients between number of *Daphnia* in guts of fish and density of *Daphnia* in the lake.

	D. cucullata	*D. longispina*
American catfish	$r = 0.37$ $p = 0.4$	–
Roach	$r = 0.13$ $p = 0.99$	$r = -0.74$ $p = 0.47$
Perch	–	$r = 0.91$ $p = 0.26$
European whitefish	$r = 0.54$ $p = 0.63$	$r = -0.93$ $p = 0.024$
Bleak	$r = 0.29$ $p = 0.6$	–
Total fish	$r = 0.15$ $p = 0.62$	$r = -0.69$ $p = 0.009$

Table 3. Spearman correlation coefficients between density of *L. kindtii* and selected parameters of *Daphnia*.

	D. cucullata	*D. longispina*
Density	$r = -0.03$ $p = 0.93$	$r = -0.72$ $p = 0.044$
Number of ovigerous females	$r = -0.16$ $p = 0.069$	$r = -0.57$ $p = 0.013$
Brood-size	$r = -0.27$ $p = 0.502$	$r = -0.46$ $p = 0.052$
Size at maturity	$\mathrm{r} = 0.30$ $p = 0.09$	$r = 0.63$ $p = 0.047$
Head height	$r = 0.48$ $p = 0.023$	$r = -0.54$ $p = 0.16$
Carapace length	$r = 0.03$ $p = 0.93$	$r = -0.08$ $p = 0.84$
Tail spine length	$r = -0.31$ $p = 0.45$	$r = 0.53$ $p = 0.017$
Total body length	$r = 0.24$ $p = 0.55$	$r = -0.02$ $p = 0.95$

The number of *L. kindtii* also correlated significantly with the length of the tail spine ($r = 0.53$, $p = 0.017$), as well as with the number of ovigerous females ($r = -0.57$, $p = 0.013$), the size at maturity ($r = 0.63$, $p = 0.047$) and the brood size ($r = -0.46$, $p = 0.052$) of *D. longispina*. In case of *D. cucullata*, only the length of the head showed a significant positive relation ($r = 0.48$, $p = 0.023$) to the density of *Leptodora* (Table 3).

Interspecific competition

Cladocera in the studied lake were represented by 39 taxa. The most common and abundant species were *Diaphanosoma brachyurum* (Liévin 1848), *Ceriodaphnia quadrangula* (O. F. Müller 1785), *Bosmina coregoni* Baird 1857, *Bosmina longirostris* (O. F. Müller 1785) and *Chydorus sphaericus* (O. F. Müller 1785). The two *Daphnia* displayed a high stability regarding their occurrence, as *D. cucullata* was found in 46.1% and *D. longispina* in 55.7% of the samples. However, they did not contribute considerably to the total density of cladocerans, as *D. cucullata* constituted 5% and *D. longispina* only 3.7% of all cladocerans. Spearman correlations between the number of the prevailing species of Cladocera and some parameters of *Daphnia* showed that the developmental pattern of both *Daphnia* did not result directly from either mutual competitive exclusion or competition of dominant cladocerans (Table 4).

Discussion

Although both species were characterised by similar densities, they displayed different life strategies. *D. cucullata* showed quite a stable demographic cycle. Ovigerous females constituted maximally 5% of the population, and the smallest individuals with broods were found in May. Three eggs at maximum were found in the broods, but over 50% of females carried 1 egg. The reduction of brood sizes coincided with cyclomorphosis, when *D. cucullata* formed a helmet and changed their body proportions. The demographic cycle of *D. longispina* had a dual course. In spring (April, May) and autumn (October, November) a high contribution of ovigerous females to the population coincided with the smallest size of individuals embracing reproduction. Five eggs at maximum were found in the broods, but most females had 2 or 3 eggs in a brood. In summer months (June, July, August, September), ovigerous females constituted an inappreciable part of population, and reproducing individuals showed higher sizes than in the former cycle. At maximum 2 eggs were found in their broods.

Predation of planktivorous fish is the major force shaping zooplankton communities, and *Daphnia*, due to their large and conspicuous bodies, are more vulnerable to being captured by visually hunting planktivorous fish than other cladocerans (Brooks and Dodson, 1965; Hall *et al.*, 1976; Lazarro, 1987). According to Brooks and Dodson (1965) and many later papers, the biggest species and the biggest specimens within the cladoceran population are preferred food items for planktivorous fish. Of the two species, *D. longispina* (as the bigger *Daphnia*), should be the first to be eliminated by fish. Indeed, high correlations between the density of *Daphnia* in the lake and their amounts in the intestines of fish, as well as values of Jacobs' coefficient, suggest that predation of fish had stronger effect on the population of *D. longispina* than on *D. cucullata*. Avoiding *D. cucullata* by foraging fish in Lake Piaseczno is consistent with the results obtained in Mazurian lakes, where *D. cucullata*, as the smallest *Daphnia* in northern Europe (Hawkins and Lampert, 1989), was ignored by fish as a food item (Pijanowska, 1990). A conspicuous impact of *Leptodora kindtii* on both *Daphnia*, in particular *D. longispina,* was also observed. In June and August, when the density of *L. kindtii* amounted to 675 $\mathrm{ind.m^{-3}}$ and 600 $\mathrm{ind.m^{-3}}$, the density of *D. longispina* considerably declined. Moreover, at the time of the increasing density of *L. kindtii* cyclomorphosis at *D. cucullata* was observed, which is a measure of protection against invertebrate predators (Pijanowska, 1990). The size structure of *Daphnia* in Lake Piaseczno could be

Table 4. Spearman correlation coefficients between density of dominant Cladocera and some trade-offs of *Daphnia*.

	D. cucullata			*D. longispina*		
	Total density	Density of ovigerous females	Brood-size	Total density	Density of ovigerous females	Brood-size
Diaphanosoma brachyurum	$r = 0.10$ $p = 0.16$	$r = -0.002$ $p = 0.97$	$r = 0.05$ $p = 0.48$	$r = 0.01$ $p = 0.88$	$r = -0.004$ $p = 0.93$	$r = -0.02$ $p = 0.75$
Ceriodaphnia quadrangula	$r = -0.03$ $p = 0.66$	$r = -0.03$ $p = 0.64$	$r = -0.02$ $p = 0.73$	$r = -0.06$ $p = 0.44$	$r = -0.09$ $p = 0.22$	$r = -0.09$ $p = 0.21$
Bosmina longirostris	$r = 0.26$ $p = 0.01$	$r = 0.16$ $p = 0.32$	$r = 0.12$ $p = 0.09$	$r = 0.23$ $p = 0.002$	$r = 0.17$ $p = 0.02$	$r = 0.18$ $p = 0.01$
Bosmina coregoni	$r = -0.09$ $p = 0.22$	$r = -0.05$ $p = 0.49$	$r = -0.03$ $p = 0.66$	$r = 0.20$ $p = 0.0007$	$r = 0.21$ $p = 0.004$	$r = 0.17$ $p = 0.02$
Chydorus sphaericus	$r = -0.03$ $p = 0.65$	$r = -0.08$ $p = 0.26$	$r = -0.08$ $p = 0.23$	$r = -0.03$ $p = 0.65$	$r = -0.04$ $p = 0.63$	$r = -0.05$ $p = 0.5$
Daphnia cucullata	–	–	–	$r = 0.29$ $p = 0.0001$	$r = 0.34$ $p = 0.01$	$r = 0.22$ $p = 0.02$
Daphnia longispina	$r = 0.33$ $p = 0.002$	$r = 0.29$ $p = 0.001$	$r = 0.35$ $p = 0.0001$	–	–	–

the result of vertebrate and invertebrate predation impact. Vertebrates eat selectively large-sized zooplankters whilst invertebrates typically select small or medium-sized prey. Hanazato and Yasumo (1989) found that in ponds where vertebrate (topmouth gudgeon) and invertebrate predators (phantom midge larva) occurred, small and large-sized cladocerans were scarcely found. A similar phenomenon was observed in Lake Piaseczno. It has been reported that adult females of *D. cucullata* achieve 1–2 mm of length, and *D. longispina* measuring 1.3–3 mm (Šramek-Hušek *et al.*, 1962), whereas in Lake Piaseczno the size of most individuals of the two *Daphnia* ranged between 1 and 1.5 mm. Wojtal *et al.* (1999) found that the size of *D. cucullata* caught by *L. kindtii* in Sulejów Reservoir (Poland) was between 400–700 µm. In Lake Piaseczno the specimens of *D. cucullata* smaller than 1000 µm occurred in April and in May when *L. kindtii* did not exist in the lake, and *D. longispina* bigger than 2000 µm were found in November only, when the feeding pressure of planktivorous fish is generally weaker. Egg-bearing females are subjected to size selective feeding of fish far more than non-bearing individuals because of their greater visibility (Gliwicz and Boavida, 1996). However, in Lake Piaseczno the number of egg-bearing *D. longispina* was also probably controlled by *L. kindtii*. In May ovigerous females that carried big broods participated considerably in the population. In July, when *L. kindtii* peaked, their number collapsed. Moreover, in summer when *L. kindtii* appeared, reproducing *D. longispina* showed larger sizes than in spring and autumn. Such an alteration in the number and size of ovigerous females could be a direct consequence of *Leptodora* predation on small specimens and/or indirect impact of *Leptodora* which forced *Daphnia* to reproduce at bigger sizes. In the first case, the mortality of juveniles resulted in a shortage of potentially reproducing adults, and in the second case the time interval to first reproduction lagged due to a longer growth time and could result in a lower number of egg-carrying females.

Some studies on *Daphnia* species showed evidence of strong competitive interactions with coexisting Cladocera (DeMott and Kerfoot, 1982; Kerfoot *et al.*, 1985; Vanni, 1986; Matveev, 1987). A high level of competition for relevant food resources may cause possible starvation of young individuals or their slower growth making them vulnerable to starving for a longer period, so a boost in brood sizes is a symptom of mortality of instars as a result of a starvation set from competitive influence of other cladocerans. Although research on vertical distribution of Cladocera in Lake Piaseczno showed that diel occurrence of *Daphnia* results from competitive equilibrium between species (Adamczuk, 2009), the presented results displayed that in the seasonal aspect there were no strong negative interactions between either both species of *Daphnia* or between *Daphnia* and the dominant cladocerans, and the populations of the two *Daphnia* proceeded independently on the development of the dominant Cladocera.

Survival and fecundity are the central traits in life-history evolution because they both contribute directly to fitness. *D. longispina* and *D. cucullata* existing in Lake Piaseczno allocated energy differently: the former to breed and the latter to survive. When *D. longispina* managed with predation pressure by carrying big broods, *D. cucullata* restricted their egg production to cyclomorphose. Both strategies are energy expensive. Cladocerans, when maturing, allocate about 80% of their energy to reproduction that results in a growth slowdown (Gabriel, 1982). Riessen (1984) found that *Daphnia* with an elongated helmet produces 40–45% fewer eggs compared to round-headed individuals. To answer how these strategies contribute to the seasonal maintenance of density by *Daphnia*, experiments under controlled conditions need to be conducted. However, it is plain that in autumn, when *L. kindtii* vanished and predation pressure of fish weakened, fecund *D. longispina* managed to restore their population, while the density of shape-changing *D. cucullata* decreased to almost nonentity.

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