

The variation in the lengths of two co-occurring *Daphnia* species (Crustacea) in the Hubenov Reservoir in years when the chlorophyll-phosphorus ratio was low

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Abstract. During the period 15 May 1975 – 22 June 1977 the mean body length of all the specimens of *Daphnia pulicaria* Forbes, 1893 measured was only slightly longer than that of *D. galeata* Sars, 1863 (1.13 against 1.09 mm). The range in size of individuals in samples collected approximately at three week intervals is 0.85 to 1.46 for *D. p.* and 0.87 to 1.40 for *D. g.* The distribution is far from normal. The standard deviation of the means is smaller than that of the medians and both are larger than that of the smallest and largest individuals. The seasonal patterns in these parameters and the skewness and kurtosis for the two species are not the same. This unexpected asynchrony is partly due to slight differences in when the two species start to actively reproduce each year. The expected increase in length in winter indicating a decrease in predation by fish when temperatures are low did not occur in either species. A clear predominance of young individuals among the specimens measured, which indicates a strong predation pressure, was not recorded except in a few samples. Logarithmic transformation shortens the right tail of the distribution of the lengths of the individuals but does not significantly increase the predominance of young individuals or result in a distribution closer to normal. The linear regressions of the means, medians and the lengths of the smallest and largest specimens, against time, show a decrease in both species. Only the decrease in the length of the largest specimens in samples is statistically significant. The absence of both parallel trends in the seasonal distributions and a predominance of young individuals are discussed in relation to the size-selective effect of fish on zooplankton and expression of congeneric competition.

Key words. *Daphnia*, length distribution, temporal changes, congeneric competition, reservoir.

INTRODUCTION

The importance of body size for understanding interactions in food webs is stressed by Brose et al. 2006. Histograms of length distributions are widely used (e.g. Brooks & Dodson 1965, Hrbáček 1969, Mills & Schiavone 1982, Brett 1992) to demonstrate the differences in size distributions of zooplankton in habitats with low and high fish stocks. One drawback of this method is that it is unsuitable for the quantitative evaluation of moderate differences in the effect of fish on zooplankton, between habitats or between seasons within the same habitat. For this purpose most authors have used mean body length (e.g. Gillooly & Dodson 2000, Havlicek & Carpenter 2001) or mean biomass derived from the length (e.g. Cyr & Pace 1993). From the depicted histograms it is evident that, in most cases, the size distribution of individual species in samples is far from normal and therefore it is not appropriate to use medians or logarithmic transformation for such purposes. The aim of the present contribution is to evaluate in greater detail the distributions in

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the lengths of two co-occurring zooplankters, *Daphnia pulicaria* and *D. galeata*, in Hubenov reservoir during years in which these two species coexisted. Hrbáček et al. (1978, 1994) have shown that in the period 1975–1978 the relation of the concentration of chlorophyll-a to that of total phosphorus in Hubenov reservoir was lower than in other reservoirs (chlorophyll to phosphorus ratio of 0.25 compared to 0.55 in other reservoirs studied). In the chlorophyll-phosphorus regression plot of Dillon & Rigler (1974) these years are clear outliers. In the same period, the average seasonal percentage of cladoceran biomass of large individuals (i.e. those retained on a sieve of 0.7 mm mesh) was exceptionally high (Hrbáček et al. 1994). This is considered to be the result of low predation pressure by fish on the zooplankton compared with the other reservoirs in which *Daphnia pulicaria* is absent.

HABITAT, MATERIAL AND METHODS

Hubenov reservoir is a source of drinking water about 100 km south-east of Praha (Czech Republic), is roughly triangular in shape, with the dam at its base and the inflow at the apex. At the normal operational level, the surface is 522 m a. s. l. and the area 51.6 ha. Maximum and average depths are 17.5 and 5.92 m, respectively. The outflow during the period of the investigation was 8 m deep. The retention period of the reservoir at mean inflow and full capacity is 167 days. The reservoir was completed and filled during 1972. The average concentration of total P during the growing season (April–September used instead of the usual value of the concentration at mixing periods due to short retention time) in 1975–1977 was 21.7 $\mu\text{g.l}^{-1}$ and chlorophyll-a concentration was 5.5 $\mu\text{g.l}^{-1}$.

The reservoir was intensively stocked in the years 1972–1974 with brook and rainbow trout (Albertová et al. 1976). This stock (in total about 500 specimens per ha) decreased in the following years due to disease, angling and poaching. Perch fry started to survive in recordable numbers from 1974 (J. Křížek, pers. comm.). There are no detailed quantitative data on this period of transition of the fish stock from a trout to perch dominated fish community (Vostradovský et al. 1989). Even on the basis of reliable quantitative data on the fishstock it is impossible to quantify the predation pressure of fish on zooplankton because there is little knowledge on the food preferences of the individual size classes of the different species fish during the course of a year as zooplankton are not the only food resource. It is therefore necessary to investigate the predation pressure of fish on zooplankton using another parameter.

Zooplankton, including *Daphnia*, were collected by vertical hauls from the bottom to the surface, in the deepest part close to the dam, using an adapted Apstein plankton net (Straškraba & Hrbáček 1966). The uhelon® netting had a 0.18 mm mesh. Subsamples of the samples used to determine biomass were preserved in formaldehyde. To reduce the influence of cyclomorphosis on body length, the measure used to determine biomass, the distance from the base of the spine to the top of the eye chamber was measured (Jacobs 1962) with an ocular micrometer. Only those samples were evaluated for which one hundred randomly chosen specimens of *D. pulicaria* and *D. galeata* were measured, respectively. We also had one sample from 5 December 1972 (year the reservoir was filled) and 30 samples taken, usually at three week intervals, from 15 May 1975 to 22 June 1977. Thirty seven samples would have been collected if the three week intervals had been strictly maintained. *D. pulicaria* was sufficiently abundant in 22 samples and *D. galeata* in 20 samples.

Statistical parameters were computed and respective graphs were drawn using the Statistica program, version 5 and 6.

RESULTS

Seasonal trend in the means and medians

The mean size of *Daphnia pulicaria* (*D. p.*) in the sample collected on 5 December 1972 is 2.08 mm, median 2.07, largest individual 2.81, smallest 1.01 and standard deviation 0.30 mm. The mean of all individuals (mean of all means) of *D. p.* collected in the period 1975–1977 is 1.13 and mean of medians 1.06 mm. The mean size of all individuals of *Daphnia galeata* (*D. g.*) collected over the same period is 1.09 mm and mean of medians 1.04 mm. These comparisons indicate unexpected small differences in size between these co-occurring species during the period investigated. The standard deviation of the medians is larger than that of the means (0.227 against 0.147 in *D. p.* and 0.192 against 0.123 in *D.g.*) indicating a greater variation in medians from sample to sample.

The coefficients of correlation between mean and median are, in both species, statistically highly significant ($r = 0.94$, $p < 0.001$) but the temporal changes in the means and medians of the

two species (Fig. 1) are not synchronous. Medians are not always smaller than the means and the dates on which this relationship differs are not identical in the species investigated. This is also quantified by the absence of a correlation between the means ($r = 0.25$, $p = 0.32$) and medians ($r = -0.03$, $p = 0.90$) of the two species.

In some samples the numbers of individuals in one, or two adjacent, size classes are more than twice that in any other (Fig. 4, A and B). This very likely indicates a cohort that was initiated over a short period when the birth rates were exceptionally high. The temporal patterns of these samples, indicated by the letters P and G for the respective species in Figs 1 and 3, show that the occurrence of such extreme situations are only partially synchronous and that these dates are not restricted to the beginning of the growing seasons. There is also no clear relationship with the occurrence of extreme values of the means or medians, or their interrelationships.

Regressions of the temporal course of means, and smallest and largest individuals

The small distances between the regression lines (Fig. 2) reflects the small difference in size between both species. The slope indicates there was a decrease in the length of the individual parameters over the period investigated. The slopes of the six regression lines of logarithmically transformed data (not presented here) are nearly identical indicating that the extent of the decrease in the individual parameters is roughly proportionally related to size. Statistically significant is the correlation with time of the largest (*D. p.* $r = -0.65$, $p = 0.001$, *D. g.* $r = -0.61$, $p = 0.005$) and smallest individuals of *D. g.* ($r = -0.46$, $p = 0.04$). The linear regression of largest individuals

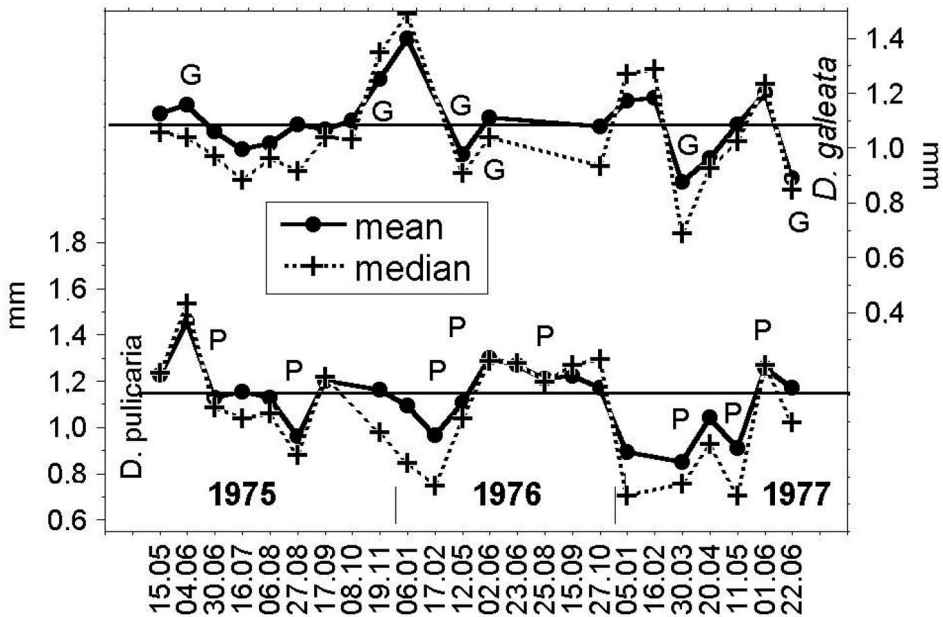


Fig. 1. Mean lengths and medians of *Daphnia pulicaria* (*D. p.*) and *D. galeata* (*D. g.*). Scale on the Y axis: left *D. p.*, right *D. g.* On the X axis the spacing of the dates of the samples does not reflect the time in days proportionally. Horizontal lines represent mean values. P and G indicate samples with a strong dominance of one or two adjacent size classes (the number of individuals in one size class or two adjacent classes is more than twice that in the next most numerous size class).

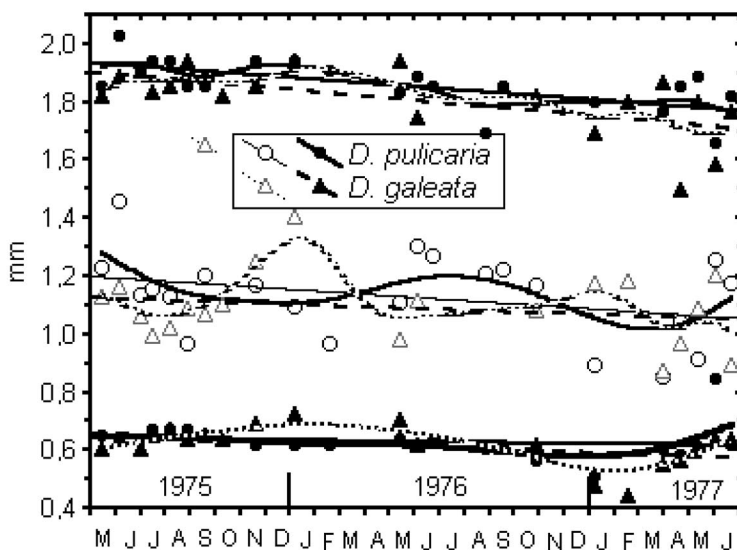


Fig. 2. Maximum, mean and minimum lengths of *Daphnia pulicaria* (circles and full lines) and *D. galeata* (triangles and dotted lines) in samples. Scale on the X axis reflects the periods between samples proportionally. The temporal tendencies are indicated by regression lines and distance weighted least square fit curves (stiffness 0).

suggests that in the period 15 May 1975 – 16 June 1977 there was a decrease of 0.15 in *D. p.* and 0.19 mm in *D. g.* This corresponds to a decrease per year of 0.07 in *D. p.* and 0.09 mm in *D. g.* The decrease between 5 December 1972 and 15 May 1975 in *D. p.* was 0.86 mm, which assuming a linear decrease indicates the decrease was 5.27 times greater per year than in the period 1975–1977. The lowest correlation coefficient is that for smallest specimens of *D. p.* ($r = -0.145$, $p = 0.52$), which is partly a result of the smaller slope. The regressions of means are not statistically significant ($r = -0.33$, $p = 0.13$ for *D. p.* and $r = -0.22$, $p = 0.35$ for *D. g.*). The linear regression suggests a decrease during the period 15 May 1975 – 16 June 1977 of 0.14 in *D. p.* and 0.06 mm in *D. g.* This corresponds to a decrease per year of 0.07 in *D. p.* and 0.03 mm in *D. g.* The decrease between 5 December 1972 and 15 May 1975 in *D. p.* is 0.86 mm. Assuming a linear decrease, the decrease per year in this period is 5.30 times greater than in the period regularly investigated. The regression line of smallest individuals suggests that in the period 15 May 1975 – 16 June 1977 there was a decrease of only 0.005 mm per year in *D. p.* The decrease between 5 December 1972 and 15 May 1975 in *D. p.* was 0.36 mm, which assuming a linear regression, is 12.06 times greater per year than in the investigated period. This decrease, which is considerably greater than that recorded for the mean and maximum values, may be due to the absence of neonates in the sample collected on 5 December 1972. The difference between the mean maximum and mean minimum lengths of *D. p.* is 1.23 mm and of *D. g.* 1.20 mm in the period investigated. The difference between the largest and smallest individuals of *D. p.* on 5 December 1972 was 1.80 mm and that of the sample with the largest difference in the period 1972–1975 was 1.39 mm, and the difference between the largest and smallest individual in the 1975–1977 period was 1.52 mm,

which does not support the suggestion that the difference was due to the absence of neonates in the 1972 sample. The length of the largest individual of *D. g.* is 1.94 mm and that of the smallest 0.44 mm. The difference between the largest and smallest individuals (1.50 mm) is close to that for *D. p.* recorded over the same period.

The low correlation between mean length and time indicates great variation, which is visualized by the distance weighted least square curve fitted to the data (Fig. 2). It has a sinusoidal character but is not related to the expected seasonal minima and maxima influenced by the anticipated seasonal differences in the effects of fish on zooplankton. Moreover it is surprising that the courses of the curves of the two species mirror one another. The distance weighted least square curve fitted to the temporal course of the medians, not presented here, is similar to that of the means, but the corresponding positions of lows and highs of the two species are even more similar and the differences between highs and lows greater. The linear regression of medians indicates an even less significant correlation ($r = -0.27$, $p = 0.21$ for *D. p.* and -0.02 , $p = 0.94$ for *D. g.*) than that of the means, which accords with a larger standard deviation.

The distance weighted least square fit line for the largest specimens is in both species closer to a linear regression than in the case of the means. There is some indication of a seasonal cycle in the sizes of the largest animals in each of the samples (Fig. 2) suggesting, especially in *D. p.*, an increase in the maximum size in colder periods.

The shape of the distance weighted least square curve fitted to the time series of the lengths of the smallest individuals (Fig. 2) in each of the samples of *D. p.* is also close to linear, except in the last but one sample. This may also have been affected by the absence of neonates. In *D. g.* there is an apparently sinusoidal course, which is neither parallel with that of the means nor with that of the largest individuals.

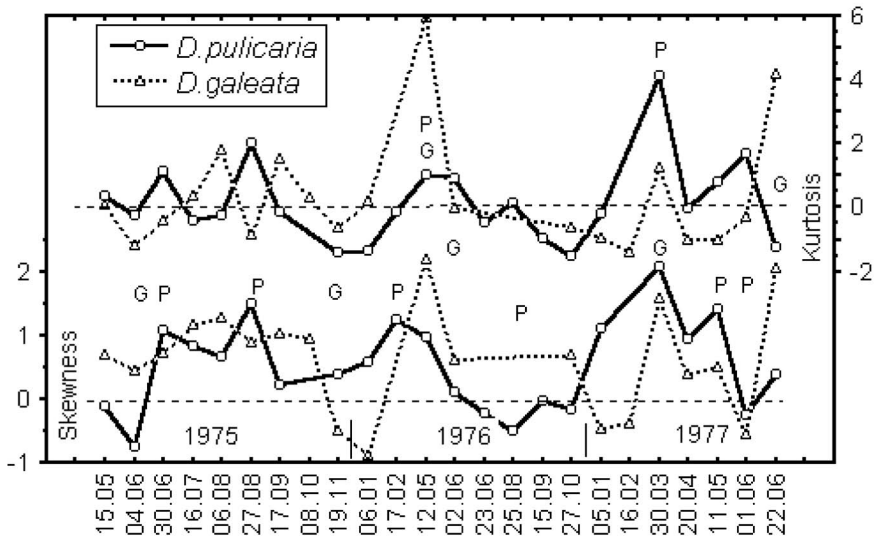


Fig. 3. Skewness (scale left) and kurtosis (scale right) of the size distributions recorded in the samples of *Daphnia pulicaria* (circles and full line) and *D. galeata* (triangles and dashed line). Horizontal dashed lines represent values for a normal distribution. P and G indicate samples with a strong prevalence of one or two adjacent size classes.

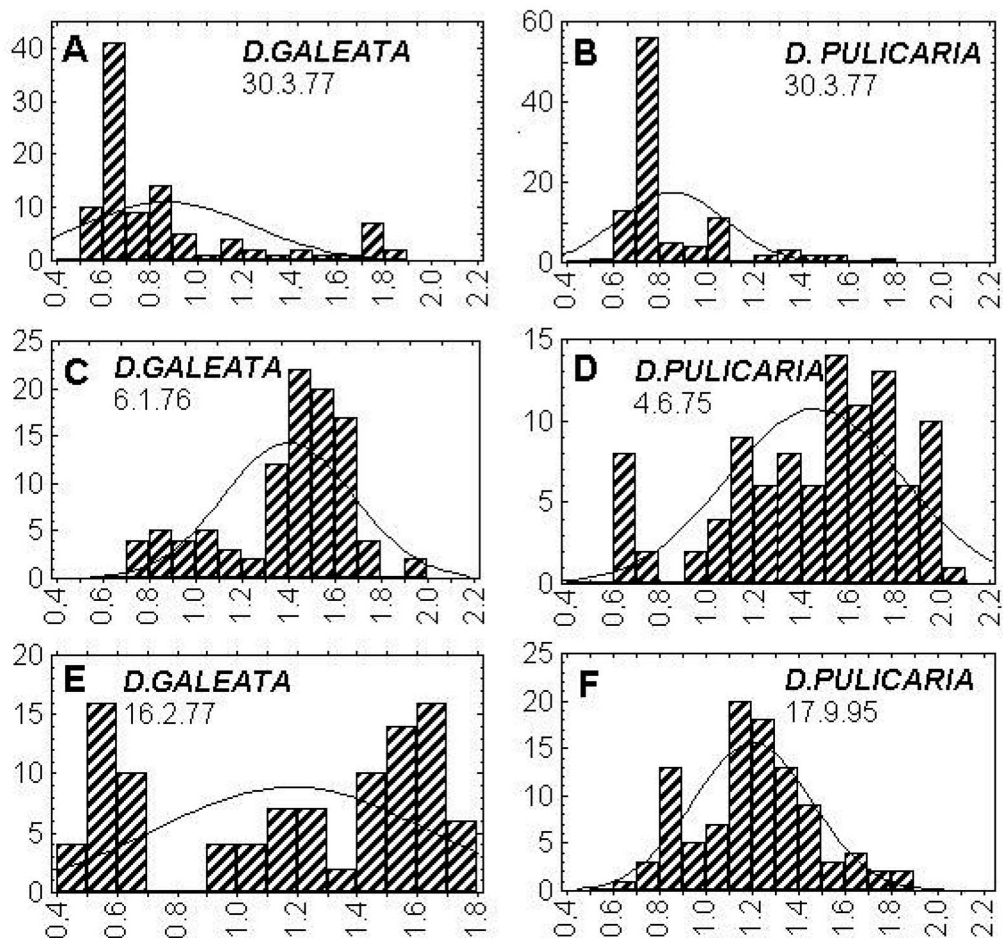


Fig. 4. Histograms of the samples with the smallest (A, B) and largest (C, D) mean values. E illustrates a bimodal distribution and F the sample with the lowest skewness and kurtosis. The scale on the Y axis is frequency and the X axis the upper limits of individual size classes.

Seasonal course of the skewness and kurtosis of the sizes of the individuals in the samples

To obtain an idea of how the size distributions in the samples differ from a normal distribution and how these differences are distributed within the period investigated, skewness and kurtosis of the distributions for individual samples were computed (Fig. 3). Mean values of all individuals of both species are positive for skewness (0.52 in *D. p.* and 0.62 in *D. g.*) and kurtosis (0.16 in *D. p.* and 0.62 in *D. g.*). The skewness and kurtosis of the sample from 17 September 1975 is closest to zero i.e. closest to a normal distribution (Fig. 3 and Fig. 4D) with $p < 0.01$. Fig. 3 also demonstrates that, on individual dates, the deviations from a normal distribution for the two species are not synchronous. Low correlation coefficients between species ($r = 0.29$ for skewness and -0.032 for kurtosis) confirm this, which again suggests that the population development during

the season in these two species is synchronous only during short periods at best. In both species there is some similarity between the seasonal trends in kurtosis on the one hand and skewness on the other, with correlation coefficients of 0.54 ($p = 0.014$) for *D. p.* and 0.34 ($p = 0.30$) for *D. g.* The plausible explanation is that classes with a high number of individuals more or less distant from the average value influence both skewness and kurtosis. The presence of exceptionally numerous cohorts, as indicated in Fig. 3 by P and G for the two species, shows only a restricted relationship to extreme values of skewness and kurtosis or their interactions, which casts doubt on the above explanation.

The skewness of the distribution of the means is -0.364 for *D. p.* and 0.235 for *D. g.*, the kurtosis is -0.967 and -0.223 , respectively. Analogous values for the medians are -0.08 and 0.298 for skewness and -1.357 and -0.624 for kurtosis.

Length distribution in individual samples

Fig. 4 shows histograms of those samples having the smallest (A and B) and largest (C and D) mean sample values for both species. The smallest mean sizes of the two species coincided on 30 March 1977. On this day only *D. p.* had its highest value of skewness and kurtosis (Fig. 3). As mentioned earlier, strong predominance of a single size class seems to be related to increased natality within a relatively short period. Comparison of the histograms for the two species for

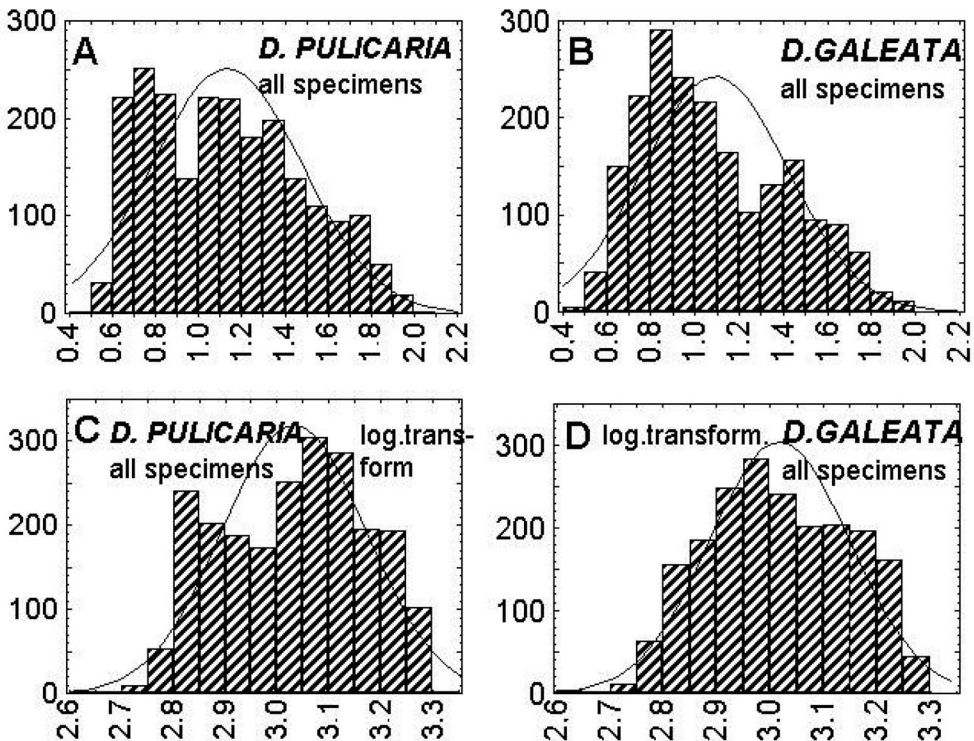


Fig. 5. Histograms of the distribution of the lengths of all individuals measured and their logarithms. Scale on the Y axis the numbers in individual size classes and X axis the upper limit of individual size classes.

the same day suggests that the cohort of maximum natality very probably started earlier in *D. p.* than in *D. g.* Histograms C and D show that in the samples with the maximum mean values the large size classes do not dominate in a way comparable to the dominance of small size classes in samples A and B with minimum mean values. Predominance of old cohorts is most expressed in the bimodal distribution of *D. g.* on 16 February 1977 (Fig. 4E). The relative low frequency of large size classes is also expressed in histograms showing the distributions of all individuals (Figs 5A, 5B). The trend of decreasing length seen in the period investigated, especially of the largest individuals (maximum in Fig. 2), tends, at least partly, to prolong this feature.

Because the lengths of *D. p.* (and other large *Daphnia* species) increase logarithmically between juvenile and adolescent instars when there are favourable feeding conditions (Hrbáček & Hrbáčková-Esslóvá 1960) and the selective reaction of fish to the size of their prey is also related more closely to its logarithmic than linear scale, the distribution of log-transformed lengths was also examined. The logarithmic transformation of all measured lengths (Figs 5C, 5D) decreases the skewness of the *D. p.* distribution from 0.35 to 0.11 and that of *D. g.* from 0.46 to 0.00. These comparisons seem to indicate that logarithmic transformation decreases the skewness, but this is not true generally because the mean skewness of 22 samples of *D. p.* is -0.17 and that of the log-transformed data increases to -0.51 . Analogous values for *D. g.* are 0.46 and 0.15. Transformation increases the kurtosis of the size distributions of all the individuals of *D. p.* measured from -0.853 to -1.024 and for *D. g.* from -0.70 to -0.83 . The mean kurtosis of individual samples is 0.11 for untransformed and -0.34 for transformed data for *D. p.* and 1.04 and 1.02 for *D. g.*

The logarithmic transformation does not change the seasonal course of skewness and kurtosis because the correlation coefficients between the untransformed and transformed values are for *D. p.* 0.97^{***} for skewness and 0.75^{**} for kurtosis and for *D. g.* 0.99^{***} and 0.90^{***} , respectively.

DISCUSSION

As the length distribution of the daphnia is far from normal it is not surprising that there is a difference between means and medians. The former is frequently smaller than the latter (Fig. 1). As there is not an objective advantage in using either of these parameters the preference can be affected by the intention to stress stability or variability.

One outcome of this study is the demonstration that populations of *Daphnia pulicaria* and *D. galeata*, which coexisted for a period of several years and were similarly abundant in the Hubenov reservoir, differ only slightly in body length. The assumption that the upper size limit is due to size-selective predation by fish can be supported by comparison with data in the literature, especially those for habitats where predation by fish is low. In 31 samples from the Queen Elisabeth II Reservoir near London, Chalk (1981) identified and measured three coexisting *Daphnia* species: *D. pulex* (in the opinion of the first author closer to *D. pulicaria* than to *D. pulex*), *D. hyalina* (in the opinion of the first author closer to *D. galeata* than to *D. hyalina*) and *D. magna*. Černý & Bytel (1991) present histograms of the distributions of *D. pulicaria* and *D. galeata* in enclosures without fish and with different numbers of fish. Gillooly & Dodson (2000) present average values for American cladoceran populations based on data from the literature.

The data in Table 1 demonstrate, on the one hand, the methodological difficulties in comparing data from different sources and, on the other hand, that the comparable parameters of size distribution in European habitats are larger for *Daphnia pulicaria* than for *D. galeata* except for the mean minimum length, whereas the American data show the opposite. *D. pulicaria* in the London reservoir, which generally has a low fish stock (Kubečka & Duncan 1994), and in Blatná enclosures without fish is, in all comparable parameters, larger than that of samples from Hubenov in the period 1975 to 1978, but smaller than in Hubenov in 1972.

The *D. pulicaria* in the sample from Hubenov at the end of 1972, when the reservoir was established and stocked with trout, were definitely longer than those in all the other samples from this reservoir. The concentration of total phosphorus in the water of Hubenov reservoir is about one order lower than in the Blatná enclosures or in the London reservoir. The difference in size may therefore, in addition to the effect of different predation levels, be related also to the observation (Hrbáček & Hrbáčková 1967) that, under comparable laboratory conditions, the sizes of neonates of the same or closely related species from habitats of different qualities are indirectly proportional to the concentration of nutrients in the habitat from which the culture was derived. More recently, Macháček (1993) showed that some fish kairomones decrease the size of neonates of *D. pulicaria*. In other words, in habitats low in nutrients and with a low fish stock, not only the largest but also the smallest individuals are larger than in habitats with a larger fish stock and a higher concentration of nutrients.

There is a distinct difference in the size of *D. galeata*, from Hubenov 1975–1977 and those from the other two habitats. The mean size and maximal length of *D. galeata* at Hubenov were 97.4 and 97.1% smaller, respectively, than the *D. pulicaria* in the London Reservoir, and 75.2 and 76%, respectively, than the *D. pulicaria* at Blatná (Table 1). Analogous differences exist in other comparable parameters. This comparison indicates that the difference between the corresponding size parameters of *D. pulicaria* and *D. galeata* are larger in habitats with larger average means and that in Hubenov reservoir in years 1985–1988 *D. pulicaria* was not far from a dramatic decrease in abundance due to predation pressure. This is supported by the conclusion from enclosure experiments (Černý & Bytel 1991) that this species cannot survive in large numbers in habitats where predation decreases the mean size of the largest size class below 1.4 mm.

Table 1. The length of *Daphnia pulicaria* and *D. magna* from different habitats in which *D. pulicaria* and *D. galeata* coexist. Explanations: t.mean – mean length of all individuals from all samples; ma.s.m. – maximum mean; mi.s.m. – minimum mean of a sub-sample from a set of sub-samples; ma.ind. – largest; mi.ind. – smallest specimen in all samples examined. Hubenov – present data from the Hubenov reservoir*; London – Chalk (1981); Blatná – Černý & Bytel (1991); N. America – Gillooly & Dodson (2000). *) For a better comparison the length of the Hubenov *Daphnia* was increased by the distance between the top of the eye chamber and top of the head.

| habitat | t.mean | ma.s.m. | mi.s.m. | ma.ind. | mi.ind. |
|------------------------------------|--------|---------|---------|---------|---------|
| length of <i>Daphnia pulicaria</i> | | | | | |
| Hubenov 1975–1977 | 1.15 | 1.48 | 0.86 | 2.06 | 0.52 |
| Hubenov 1972 | 2.12 | | | 2.87 | 1.02 |
| London | 1.45 | 1.92 | 1.00 | | |
| Blatná | | | | 2.50 | 0.50 |
| North America | 1.75 | | | | |
| length of <i>Daphnia galeata</i> | | | | | |
| Hubenov 1975–1977 | 1.12 | 1.44 | 0.90 | 2.00 | 0.45 |
| % in <i>D. pulicaria</i> 1975 | 97.4 | 97.3 | 104.70 | 97.1 | 86.5 |
| London | 1.09 | 1.58 | 0.75 | | |
| % in <i>D. pulicaria</i> | 75.2 | 82.3 | 75.0 | | |
| Blatná | | | | 1.90 | 0.30 |
| % in <i>D. pulicaria</i> | | | | 76.0 | 60.0 |
| North America | 2.15 | | | | |
| % in <i>D. pulicaria</i> | 186.7 | | | | |
| length of <i>Daphnia magna</i> | | | | | |
| London | 1.66 | 2.92 | 0.75 | | |
| % in <i>D. pulicaria</i> 1975 | 114.5 | 152.1 | 75.0 | | |

D. galeata remained numerous in the enclosures even when fish predation decreased the mean size of the adult individuals below 1.0 mm.

The presence of *Daphnia magna* in the London reservoir is in accordance with the assumed low fish predation pressure and high concentration of food particles. When compared with *D. pulicaria* in all samples it has a greater mean length and, especially, a greater mean maximum length. The smaller size of the mean minimum length is unexpected but is in accordance with the proposed influence of a high concentration of food particles on the size of neonates. The above described interaction of the concentration of edible particles and fish predation evokes the speculation that when extremely low concentrations of particles promote large size in neonates and very high predation by fish, which results in the production of small primiparae (this occurs e.g. in Lake Tanganyika and Lake Baikal) and there is very little space for postembryonic growth. This presumably can lead to the absence of daphnia and perhaps even planktonic cladocerans in such water-bodies.

The predominance of one or two size classes, indicated by the letters P and G for the respective species in Figs 1 and 3, possibly indicate the strong prevalence of one cohort, presumably as a consequence of a short but marked increase in natality. Marked increases in natality can be caused by similar increases in food resources. Data on biovolumes of algae (Fott et al. 1980) and chlorophyll (Hrbáček et al. 1978), respectively, do not reveal a clear discontinuity in the availability of food for cladocerans when particular size classes are predominant. It is possible that the three-week interval between samples is too long for measuring short discontinuities. Alternatively, if the presence of strong cohorts is due to a strong increase in food resources a parallel presence of strong cohorts in coexisting species of the same genus is expected. This expectation is not supported by the present observations. Other plausible explanations, namely occasional formation of swarms of similar sized individuals in open water needs further investigation. Fig. 3 indicates the absence of a similarity in the seasonal pattern of both kurtosis and skewness. This seems to indicate that the competition for food particles between the two species is not as strong as expected from the similarity in the morphology of their filtration apparatus.

Body sizes of American populations (Gillooly & Dodson 2000) present a somewhat different picture from that recorded in Europe: The mean length of *D. galeata* is larger than that of *D. pulicaria* and is larger than the maximum individual recorded in comparable European populations. One possible reason might be the inclusion of the helmet in the total body length. The mean length of American *D. pulicaria* is larger than the mean recorded at Hubenov 1975–1978 and in the London reservoir but smaller than that at Hubenov 1972. The observed changes in length in the Hubenov reservoir and in the Blatná enclosures are more likely to be due to changes in the effect of fish on zooplankton than to changes in temperature. In the opinion of the senior author, the observed geographical differences in mean lengths of cladocerans at different latitudes in America is more closely related to differences in the intensity of the fish predation, induced by the climatic effect on the assemblages of species of fish, than to the direct effect of temperature on cladoceran size.

The largest cladoceran size class in Clear lake, one of the North American Indian River lakes (Mills & Schiavone 1982) with a desirable size structure of fish, was 2.7 mm, which is larger than the maximum length in the period 1975–1977 at Hubenov, but is again smaller than the maximum size recorded in the 1972 sample. The two largest means of cladoceran length recorded in that study are 1.5 and 1.7 mm, which is also larger than recorded at Hubenov in 1975–1977 but smaller than at Hubenov in 1972.

An unexpected result of the present study is the lower sample to sample variation in the length of the longest individual, in samples composed of one hundred individuals, than the sample mean or median. Kožený (2000) has found similar relationships in samples of *D. galeata* from Klíčava

reservoir even when determined for sample sizes of more than five times more individuals. It should be noted that the lengths of the Klíčava population are nearly half that of the Hubenov population and that not a single specimen of *D. pulicaria* was found. Since a lower variation for individuals with extreme values rather than mean values opposes all rules of the statistics of distribution it is necessary to seek a causal explanation. The possibility that the fish quantitatively eliminate all individuals above a certain size is unlikely. It is generally accepted that the intensity of predation by fish is temperature dependent and also other factors may affect the cladoceran size distribution (Hrbáček et al. 2003). Since there is no indication of a regular seasonal change in the size of the largest individuals of *Daphnia*, in either the Hubenov or Klíčava samples, it is assumed that the production of daphnia is influenced in exactly the same way as the predation pressure from fish. This does not seem probable. Dodson (1989) and Macháček (1993) record the effect of fish kairomones on the sizes of primipara and of eggs. It can therefore be assumed that a kairomone influences the physiology of growth of mature daphnia so that when a certain size is reached, somatic growth ceases and all further growth is invested in egg production. An analogous effect of predation on the size of insect nymphs in the last instar just prior to the emergence to adults is recorded in mayflies (Peckarsky et al. 2001).

On the other hand, samples from Drásov reservoir, with a population of *D. galeata* somewhat smaller than that in Klíčava reservoir (data in Kožený 2000), show in one year a clear and, in another year, an unclear seasonal change in the maximum length. Moreover, in this second case the variation in mean size is smaller than that of the largest individuals. From the seasonal course of the histograms of mixed populations of *Daphnia ambigua* and *D. parvula* living in a small eutrophic lake in Michigan (Allan 1977) a noticeable variation from sample to sample in the size of the largest size class is apparent. It is therefore very likely that the small difference in size of two co-occurring *Daphnia* species, and the absence of a seasonal variation in size found in the Hubenov reservoir, occur only in a restricted range of *Daphnia* sizes or, expressed in a different way, only within a restricted range in the intensity of fish predation on *Daphnia*. This range is probably larger than that producing a low chlorophyll to phosphorus ratio (Hrbáček et al. 1994).

The seasonal changes in the size distribution of the biomass of Cladocera, expressed by Hrbáček et al. (2003) as a percentage of cladoceran biomass larger than 0.71 mm in the total cladoceran biomass, clearly indicates that predation by fish has a different effect on cladoceran biomass.

The short right-hand tail of the distribution in Fig. 5A and Fig. 5B seems to support the assumed limitation of the size distribution by predation. Alternatively, the predominance of smaller size classes, both in histograms for individual dates (Fig. 4) and those that summarize the lengths of all individuals measured, is not so pronounced as one would expect in a population limited by predation and as recorded in laboratory experiments simulating size-selective predation (Brett 1992). This is probably due to the fact that, under natural conditions of low food concentration, birth rates are low, the periods between individual instars are relatively shorter in juveniles than in adults (Hrbáčková-Esslová 1962) and the length increments between subadult instars are smaller (Hrbáčková-Esslová 1963). These effects seem to be more pronounced in *D. galeata* than in *D. pulicaria* during the period of observation, which corresponds to the earlier finding of higher growth rates in the latter than in the former species when food is scarce (Hrbáčková-Esslová 1963).

The logarithmic transformation shortens the right tail of the histogram of all specimens measured. This has to be considered when evaluating the size distribution of individual species in size spectra (e.g. Cyr & Pace 1993). The present data cannot, however, be properly used for a detailed study of the size spectra of plankton in Hubenov because the arbitrarily selected constant number of specimens measured from individual samples does not reflect the real frequencies in individual samples on which size spectra are based. The decrease in the right tail of the distribution by logarithmic transformation supports the assumed effect of predation and may indicate one

of the possible causes of deviations from a perfectly smooth continuous curve describing the size distribution of planktonic organisms (Havlicek & Carpenter 2001).

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