Effect of habitat complexity on the distribution of *Ceriodaphnia quadrangula* (O. F. Müller, 1785) (Crustacea: Cladocera) in a deep lake

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Abstract: The aim of the study was to compare the density, body size, and reproduction of the cladoceran, *Ceriodaphnia quadrangula* (O. F. Müller, 1785), in various habitats of Lake Piaseczno (38.8 m deep) in eastern Poland. Samples were taken in the littoral zone (from emergent and submerged vegetation, as well as from open water and the surface layer of water above submerged vegetation) and in the pelagic zone (from the epilimnion, metalimnion, and hypolimnion). The results show that *C. quadrangula* prefers the littoral zone, as it achieves there much higher values of the analysed variables than in the pelagic zone. The number and size of adults (including ovigerous females), as well as brood size achieved equally high values in emergent and submerged vegetation, and much lower values in the other habitats (including pelagic ones). Juveniles also preferred to stay in the littoral zone but displayed clear preferences to none of the habitats.

Keywords: Cladocera, Ceriodaphnia quadrangula, deep lake, distribution, density, body size, reproduction

INTRODUCTION

Ceriodaphnia quadrangula is the most widespread of all *Ceriodaphnia* species, distributed in Europe, Asia, and South America (FORRÓ et al. 2008). Although the species is predominantly found in the littoral zone (HAVENS 1991; KORPONAI et al. 1997; LAURIDSEN et al. 1999), it also occurs in the open water of deep lakes (KOROVCHINSKY 2000; WALSENG et al. 2006). In shallow lakes, *C. quadrangula* usually hides within macrophyte stands (LAURIDSEN et al. 1996; ROMARE & HANSSON 2003), although staying in vegetation patches is disadvantageous for obligatory filter-feeders (JEPPESEN et al. 2002; BURKS et al. 2002), such as *Ceriodaphnia*. However, in deep lakes, *Ceriodaphnia* could display different behavioural patterns, as deep lakes provide a greater diversity of niche types, with different abiotic and biotic conditions important for species distribution (SCHOENER 1974). Differences in biotic conditions in a deep lake are

observed not only between the littoral and the pelagic zones but also within them. In the littoral zone, the type and abundance of plant vegetation changes from nearshore to offshore with increasing depth of the lake (WETZEL 1983). The pelagic zone, in turn, consists vertically of the epilimnion, metalimnion, and hypolimnion, with clear gradients of chemical parameters as well as light, food, and predation pressure.

Because of the common occurrence in the world's freshwaters, *C. quadrangula* has been subject to a number of studies examining its response to abiotic and biotic factors under experimental conditions (e.g. SMYLY et al. 1975; LYNCH 1992; GLADYSHEV et al. 1999; KAPPES & SINSCH 2005; SAVAŞ & ERDOĞAN 2006). However, information on population parameters of *C. quadrangula* under natural conditions is quite scarce. SMYLY (1974) studied the abundance, vertical distribution, and sexual proportions in its populations in small English lakes. LAURIDSEN et al. (1999) studied diel vertical distribution of *Ceriodaphnia* in oligotrophic and mesotrophic lakes. The abundance of *C. quadrangula* as a part of cladoceran communities was also investigated in lakes of various trophic status (i.e. HAVENS 1991; LAURIDSEN & BUENK 1996; LAURIDSEN et al. 1996; JEPPESEN et al. 1997; KORPONAI et al. 1997; KOROVCHINSKY 2000; ROMARE & HANSSON 2003; WALSENG et al. 2006). Due to the scarcity of data about its population dynamics in deep lakes, the aim of the study was to compare the abundance, body size, and reproductive parameters of *C. quadrangula* between biotic zones as well as between different types of habitats within the biotic zones of a deep lake.

MATERIAL AND METHODS

The research was carried out in Lake Piaseczno (51°23`03``N, 23°01`46``E) situated in Łęczna-Włodawa Lakeland (Pojezierze Łęczyńsko-Włodawskie) in eastern Poland. The lake area is 83.2 ha and its maximum depth reaches 38.8 m. The lake is dimictic, so in summer and winter a typical oxygen and temperature stratification occurs.

Seasonal variations in the population of C. quadrangula were monitored monthly from April to November 2003. Samples were taken in the littoral zone among emergent macrophytes (mostly the common reed *Phragmites australis*), among submerged macrophytes (patches dominated by the water milfoil Myriophyllum alterniflorum or by the macroalga Nitella flexilis) as well as from surface water (depth 0-10 cm) and from water above submerged vegetation (depth 1-3 m), and in the pelagic zone in all thermal layers (see below). Zooplankton was collected there around noon, using a 5-litre sampler. In the littoral zone, the material was taken from the surface (4 samples every month), from water above macrophytes (2 samples) and from emergent (2 samples) and submerged vegetation (4 samples). In the pelagic zone, samples were taken every 1–2 m of depth in the epilimnion (3 samples) and the metalimnion (3 samples), and every 3-5 m in the hypolimnion (6 samples), and then pooled into one sample from each thermal layer. Samples were sieved through a 50-um mesh net and next preserved. Individuals classified as C. quadrangula were separated from the samples and counted to calculate their abundance (ind. dm-3). Thirty randomly chosen individuals were measured in each sample. The proportion of juveniles and adults in the population was estimated after determining the size at maturity (STIBOR & LAMPERT 1993) for each of sampling times. Ovigerous females were counted and eggs enumerated. The proportion of egg-bearing females in the population was determined.

The ANOVA Friedman test was used to assess the effect of habitat on the examined parameters. Statistica 5.0 software was used to perform the analyses.

RESULTS

In all sampling sites the first individuals of *C. quadrangula* started to appear in April, and their abundance peaked in May. The population was recorded until September (in the pelagic zone) or October (in the littoral zone), and then declined to almost complete absence.

In the littoral zone, juveniles were abundant and evenly distributed among the studied habitats. Adults preferred to stay in the littoral zone, too, but gathered in great numbers among plants, while their densities above the vegetation were much lower.

In the pelagic zone, densities of both juveniles and adults were low. All individuals found in the epilimnion were immature. The number of juveniles in the meta- and hypolimnion was also higher as compared to adults. Differences in spatial structure of the species were statistically significant ($\chi^2 = 18.66$, P < 0.05 for juveniles, $\chi^2 = 32.37$, P < 0.01 for adults).

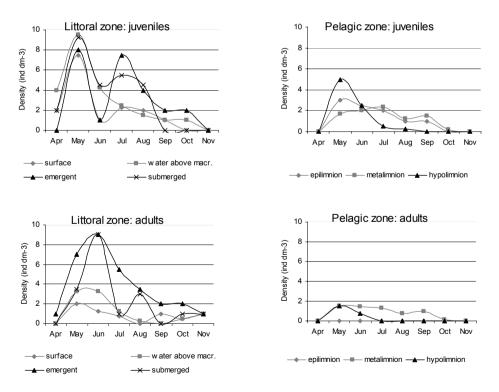


Fig. 1. Seasonal changes in the mean density of juveniles and adults of *C. quadrangula* in various habitats of Lake Piaseczno

In most of the habitats, juveniles peaked in May and July, with a distinct decline in June. Adults reached the highest density in June in emergent and submerged vegetation, and their abundance dropped in the following months. In the other habitats their density was quite low, with only a slight increase in May and June (Fig. 1).

Spatial distribution of *Ceriodaphnia quadrangula* was related to their body size. In the littoral zone, larger juveniles were found at the water surface and in water above the vegetation. Adults showed an inverse trend, as larger individuals were found among emergent and submerged macrophytes. In the pelagic zone, body size of juveniles in the epilimnion was apparently lower than their size in the metalimnion and hypolimnion. Adults, in turn, showed similar body size in all layers of the pelagic zone (Fig. 2). Differences in the spatial structure of differently sized individuals were statistically significant ($\chi^2 = 45.32$, P < 0.01 for juveniles, $\chi^2 = 34.91$, P < 0.011 for adults). Generally, in May and June, the mean size of individuals of this species considerably diminished, probably as a result of increased numbers of juveniles at that time. The only exceptions were the sampling sites located in the littoral zone among submerged vegetation, where the average body size of *C. quadrangula* was always high, irrespective of the season.

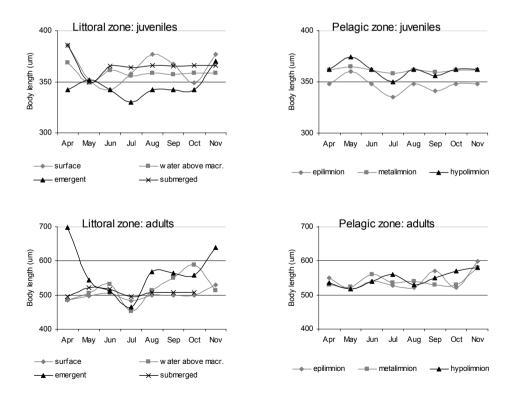


Fig. 2. Body length of juveniles and adults of C. quadrangula in Lake Piaseczno

All the measured individuals of *C. quadrangula* were females. Parthenogenetic females appeared from May to October in the littoral zone, and from May to July in the pelagic zone. Over the year, the bulk of egg-bearing females aggregated mainly among emergent (24%) and submerged vegetation (23.9%). In the pelagic zone, the number of reproducing females was low, as their share did not exceed 7% of their number. Reproducing females carried on average from 1.0 egg in the pelagic hypolimnion to 1.9 eggs in the surface water as well as among emergent vegetation in the littoral zone ($\chi^2 = 15.28$, P < 0.05). On average, individuals displayed highest brood sizes in May (3.5 eggs) and declined to approximately 1 egg in the following months (Fig. 3).

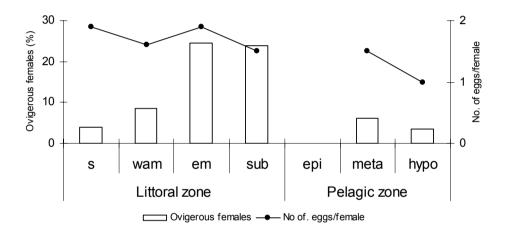


Fig. 3. Proportion of ovigerous females and brood size in the population of *C. quadrangula* in Lake Piaseczno (s = surface; wam = water above mactrophytes; em = emergent vegetation; sub = sub-merged vegetation; epi = epilimnion; meta = metalimnion; hypo = hypolimnion)

DISCUSSION

Results of this study indicate that *C. quadrangula* shows clear preferences in spatial distribution. The species apparently prefers the littoral zone, achieving there much higher values of the studied variables than in the pelagic zone. A clear dominance of juveniles and either low abundance or lack of adults were observed in the pelagic zone. Three explanations of such a distribution pattern are possible: (1) under conditions of no efficient shelters for *Ceriodaphnia* in the pelagic zone, adult big individuals are captured and eaten by planktivorous fish; or (2) adolescent individuals avoid the littoral zone during the day; or (3) juveniles migrate from the littoral to the pelagic zone, but return to the littoral zone after reaching maturity. It is difficult to determine which of these explanations (and maybe all of them) are responsible for the higher abundance of the species in the littoral zone. Anyway, *Ceriodaphnia*

individuals in the littoral zone were larger than the ones found in the pelagic zone in this study.

C. quadrangula was not evenly distributed within the biotic zones, but preferred some of habitats. In the littoral zone, the density and mean size of adults as well as reproductive characters displayed the highest values among macrophytes. Although the average number of eggs was similar in the examined habitats, females with maximum brood sizes were also found among plants. It is controversial if staying among macrophytes is advantageous for C. quadrangula, as food concentration for filterfeeding zooplankton is low in the plant beds, while some macrophyte species may release harmful chemical substances, and the density of invertebrate predators may be high there (SCHRIVER et al. 1995; JEPPESEN et al. 2002). However, it has been reported that zooplankton (especially the larger and thus more vulnerable individuals) move to vegetated habitats under fish predation pressure (CRYER & TOWNSED 1988; LIMA & DILL 1990). Thus the high abundances of egg-bearing females of C. quadrangula in macrophyte patches could be caused by predation avoidance. In parthenogenetic reproduction, Ceriodaphnia produce eggs with a visible yolk sac and yellow pigmentation inside the brood chamber (DODSON & FREY 2001). Hence, because of their greater visibility, egg-bearing females are subjected to size-selective feeding of fish far more than infertile individuals, and the predation vulnerability of ovigerous females increases with brood size (GLIWICZ & BOAVIDA 1996).

In the present research, submerged as well as emergent vegetation was taken into consideration. Based on the previous investigations, each of the vegetation types should affect zooplankton differently. HECK & ORTH (1980) noted that plants with more complex and finely divided leaves provide more protection than robust taxa. Emergent vegetation, in turn, is considered to provide worse shelter for some filterfeeding cladocerans (NURMINEN & HORPPILA 2002) but constitutes an optimal habitat for Ceriodaphnia (CAZZANELLI et al. 2007). In the Finnish Lake Hiidenvesi, Ceriodaphnia had the highest mean body size in emergent vegetation (NURMINEN et al. 2001). The same phenomenon was observed in Lake Piaseczno. Some population parameters, such as the proportion of egg-carrying females and brood size, achieved high values irrespective of vegetation type. Differences in body size of juveniles and adults between macrophyte patches and other habitats in the littoral zone suggest that juveniles, after exceeding some size, migrated from vegetation patches to open water, and then returned to vegetation to give offspring. In cladocerans, juveniles are considered to be more sensitive to starvation than adults (NEIL 1975; LYNCH 1992; TESSIER et al. 1983), so insufficient food supply in vegetation patches could cause juveniles to spread to habitats abounding with accessible food.

In comparison to the littoral zone, the pelagic zone greatly varies vertically in abiotic (physical and chemical) and biotic conditions (including food availability and predator abundance). The epilimnion (i.e. the top thermal layer in the vertical profile) is characterized by the highest water temperature and high food concentration as well as high predation pressure of visually-limited fish. Thus some cladoceran species, despite excellent living conditions, avoid the epilimnion temporarily (conducting diel vertical migrations) or permanently (living in darker water layers).

In this study, *Ceriodaphnia* also avoided the epilimnion, as the highest density of the species was noted in the metalimnion. The *Ceriodaphnia* population in the epilimnion consisted only of juveniles. Due to their smaller body size, juveniles are not as susceptible to fish predation pressure as adults, so their presence in this warm water layer, rich in food, undoubtedly accelerated their maturation. Since the adults avoided the epilimnion, no reproductive processes were observed in that layer. Reproduction of individuals in the metalimnion and hypolimnion showed a similar course, and no apparent differences were found in values of reproductive characters.

Results of this study are only valid for *Ceriodaphnia* distribution during daytime. Some authors, however, observed that *Ceriodaphnia* move between different habitats during day and night (LAURIDSEN & BUENK 1996; JEPPESEN et al. 1997; LAURIDSEN et al. 1999). Up till now, there are no data about diel changes in distribution of juvenile and adult ceriodaphnids, including egg-carrying females. Recognition of day and night distribution of age groups would broaden our knowledge about the behavior of this species, so common in freshwaters of the world.

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