

# The vertical distribution of zooplankton in brackish meromictic lake with deep-water chlorophyll maximum

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**Abstract** We examined the dynamics of the vertical stratification of physical, chemical and biological factors in a brackish meromictic lake with a deep-water chlorophyll maximum (Shira Lake, Russia, Khakasia) during the growing season and estimated how the vertical distribution of these factors influences the vertical distribution of the zooplankton community. The vertical distribution of zooplankton was restricted by the anoxic hypolimnion. Nauplii and younger copepodites (C1–C3) of the copepod, *Arctodiaptomus salinus*, and the rotifer, *Brachionus plicatilis*, were found in the upper warm waters. During summer stratification the maximum of *A. salinus* biomass, which consisted mainly of older copepodites (C4–C5) and females, was associated with the deep-water maximum of biomass of green algae, which are the preferred diet for this species. The vertical distribution of the rotifer *Hexarthra oxiiuris* was bimodal with numerical peaks in the epi- and hypolimnion. Reproduction peaks of dominant species were separated in time. The reproduction peak of *A. salinus* was at the beginning of summer when *A. salinus* constituted

up to 99% of total zooplankton biomass. The development of rotifers was detected after the reproduction peak of *A. salinus* when the biomass of rotifers reached 50% of total zooplankton biomass.

**Keywords** Meromictic lake · Stratification · Zooplankton · Vertical distribution · Deep water chlorophyll maximum · Anoxic hypolimnion

## Introduction

The vertical distribution of zooplankton is one of the factors determining the functioning of aquatic ecosystems. The vertical distribution of zooplankton reflects habitat preferences, which are specific for species and animals of different age and sex (Lampert et al., 2003; Primicerio, 2003). The vertical distribution of zooplankton changes over time. Diel vertical migration (DVM) is responsible for short-term changes in the vertical distribution of zooplankton, while seasonal and ontogenetic migrations determine long-term changes in the vertical distribution. Considerable research has been conducted to understand the mechanisms determining the vertical distribution of zooplankton (Heptner, 1996; Zakardjian et al., 1999; Han & Straskraba, 2001). However, mechanisms that are responsi-

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ble for the specific vertical distribution of zooplankton in a lake are not always clear (Bayly, 1986; Ohman, 1990).

Meromictic lakes are a promising environment to investigate factors affecting the vertical distribution of zooplankton. These lakes are characterized by pronounced vertical gradients in various physical, chemical and biological factors (Del Don et al., 2001). The vertical stratification of these factors creates various microhabitats for zooplankton. Thus, meromictic lakes provide an excellent opportunity to investigate in situ the effect of various factors on the vertical distribution of zooplankton. However, detailed comparative data on the vertical distribution of zooplankton and physical, chemical and biological parameters in meromictic lakes are scarce.

Brackish meromictic Shira Lake (Russia, Republic of Khakasia) is a suitable water body to investigate the effect of environmental factors on the vertical distribution of zooplankton. The lake is permanently divided into oxic and anoxic zones by the chemocline. There are pronounced vertical gradients in light, temperature, salinity and dissolved oxygen concentration in the pelagic zone of the lake in summer (Degermendzhy & Gulati, 2002). The lake is also characterized by a deep-water algal maximum below the thermocline in summer (Gaevsky et al., 2002) and by a dense population of chemocline bacteria (Pimenov et al., 2003). Thus, the main microhabitats for zooplankton include the warm and food-poor epilimnion; the colder but algae-rich metalimnion; and the cold, bacteria-rich but low oxygen hypolimnion. The pelagic zooplankton community of Shira Lake consists of only three zooplankton species, including one Copepoda species (*Arctodiaptomus salinus*) and two species of Rotifera (*Brachionus plicatilis* and *Hexarthra oxiiura*) (Platonova, 1956; Zotina et al., 1999).

An important characteristic of Shira Lake, which is important for the investigation of the vertical distribution of zooplankton, is the absence of ichthyofauna and carnivorous zooplankton. Consequently, predation is not an important factor shaping the vertical distribution of zooplankton in the lake. In this case the vertical distribution of zooplankton is mainly determined by the vertical stratification of physical,

chemical and biological parameters. As the stratification of the oxic water layer occurs in summer, the effect of gradients in different factors on the vertical distribution of zooplankton can be estimated by comparing the differences in the vertical distribution of zooplankton between seasons. Thus, the purpose of this work was to investigate the dynamics of the vertical stratification of the major physical, chemical and biological factors in meromictic Shira Lake during growing season and to infer how the vertical distribution of these factors influences the vertical distribution of the zooplankton community.

### Materials and methods

Shira Lake is a stratified meromictic water body situated in the Republic of Khakasia (Russia) (54°30' N, 90°14' E). A general description of the lake ecosystem was presented by Zotina et al. (1999); more detailed data are in Gulati and Degermendzhy (2002). Data on the vertical distribution of the major physicochemical and biological parameters of the lake ecosystem were collected at the deep pelagic station (23 m deep). Sampling and measurements were performed at midnight (0000–0200 h) and noon (1200–1400 h) at 13 June, 14 July, 12 August and 18 October 2001, at 1 m intervals starting from surface down to the depth of 15 m. Sampling was performed with a 4-l discrete point water sampler (Molchanov bathometer). Three litres of each sample were taken to count the zooplankton densities at each depth. The zooplankton were concentrated, preserved in 70% ethanol and later counted under a light microscope (×32). Rotifers, *Brachionus plicatilis* and *Hexarthra oxiiuris*, and nauplii, copepodite of young stages C1–C3 (0.50–0.75 mm), copepodite of later stages C4–C5 (0.80–1.00 mm), males and females of *Arctodiaptomus salinus* were recorded during counting of zooplankton samples. The average depths of different species and instars were calculated as:

$$\bar{d} = \sum_{i=0}^{15} \frac{i \cdot n_i}{n},$$

where:  $i$  – sampling depth,  $n_i$  – the number of animals present in the sample from the  $i$ th depth,  $n$  – the total number of animals.

The remaining 1 l was used to determine hydrogen sulphide and chlorophyll  $a$  concentrations. Hydrogen sulphide was determined according to Standard Methods (1989) and the chlorophyll  $a$  content was determined on double beam UV/VIS spectrophotometer UVICOM 943 (Kontron Inst., Italy) after pigments extraction in ethanol according to Nusch (1980).

Vertical profiles of temperature, dissolved oxygen and redox-potential were measured with Data Sonde 4 (Hydrolab Corp., USA) (except for June measurements when dissolved oxygen was determined by standard Winkler method (Abakumov, 1983) and temperature with submerged thermometer). Wet zooplankton biomass was calculated by converting zooplankton population density into biomass (Vinberg, 1979).

The Brunt Vaisala frequency (buoyancy frequency  $N$ ) was calculated as (Doronin, 1978):

$$N^2 = \frac{-g}{\bar{\rho}} \cdot \frac{\partial \rho}{\partial z}$$

where:  $g$  – free fall acceleration (m per s<sup>2</sup>),  $\bar{\rho}$  – the average water density for the entire depth measured (kg per m<sup>3</sup>),  $\rho$  – water density at specific depth (kg per m<sup>3</sup>),  $z$  – depth (m). The density of water was calculated from the temperature, salinity and water pressure by equations presented in Gill (1986).

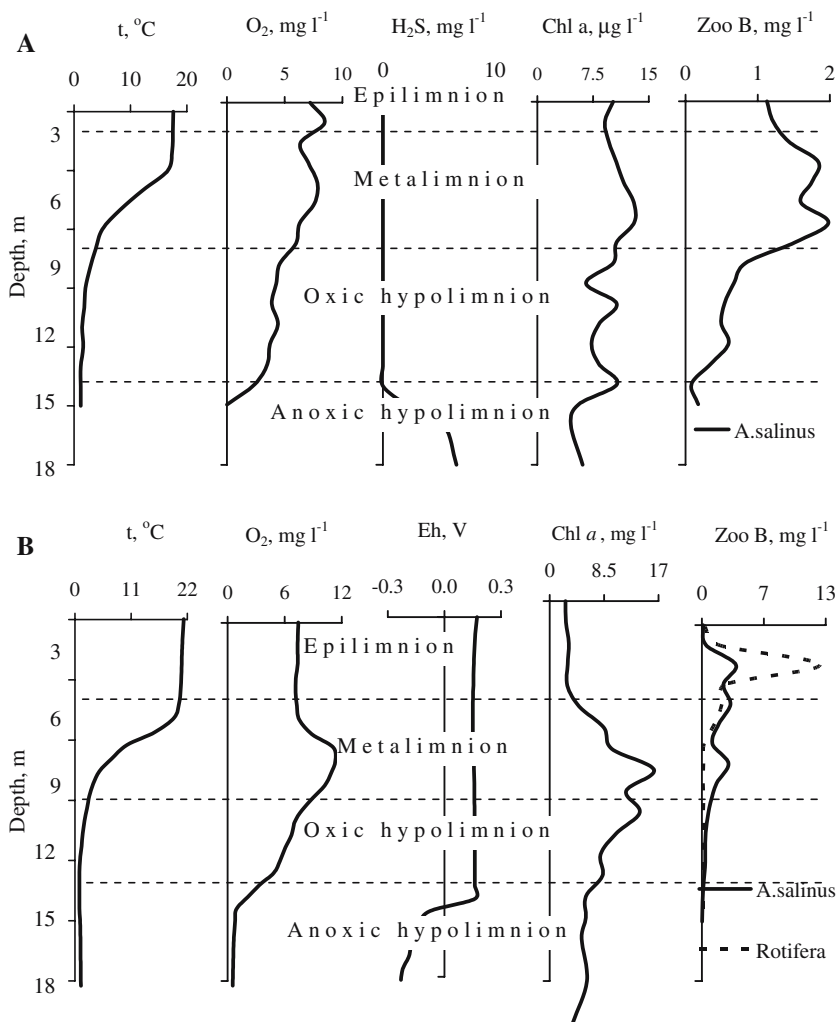
General patterns of the vertical distribution of zooplankton during summer stratification were analyzed with repeated measures ANOVA, where the proportions of animals in the epi-, meta- and hypolimnion were selected as dependent variables, sampling time (day or night) and species and their instars were selected as categorical predictors (factors) and months (June, July and August) as repeated measures. To detect difference in the general pattern of the vertical distribution between different species and instars, we performed paired comparisons between all tested species and instars (*A. salinus* males, females, younger and

older copepodites and nauplii, *B. plicatilis*, *H. oxiiuris*), which resulted in 21 paired comparison. To analyze the difference in the vertical distribution of each tested species and instar, we performed post hoc Tukey HSD test. The difference in the vertical distribution of all species and instars in the upper waters between day and night samples was analyzed with  $T$  test for dependent samples. All calculations were performed with the STATISTICA 6.0 package.

## Results

### The dynamics and patterns of lake stratification

On the basis of vertical profiles of temperature, dissolved oxygen and redox-potential, the water column can be divided into distinct habitats (Fig. 1). The depth of the epilimnion (temperature decrease  $<1^\circ\text{C m}^{-1}$ ) increased as a result of warming of the surface waters during summer. The lower boundary of epilimnion shifted from the depth 3 m in June to the depth 6 m in August (Fig. 1). Anoxic hypolimnion ( $E_h < 0$ ) was below the depth 13–14 m during summer. Even though the lake was already stratified in June, the chlorophyll  $a$  was distributed uniformly. Deep-water chlorophyll maximum located at the boundary of the metalimnion (temperature decrease  $>1^\circ\text{C m}^{-1}$ ) and the hypolimnion (temperature decrease  $<1^\circ\text{C m}^{-1}$ ) was observed in July and August. The location of the deep-water chlorophyll maximum corresponded to previous data (Gaevsky et al., 2002). Maximum concentration of dissolved oxygen was observed just above the chlorophyll maximum. In October, the thermocline was situated between 10 and 12 m and coincided with the chemocline. The vertical profiles of water density and Brunt Vaisala frequency (Fig. 2) demonstrated that in summer the water column was divided into two compartments. In summer, the pycnocline was created by the temperature dependent density stratification. During fall, destratification moved the pycnocline down to the depth of 11 m (Fig. 2, October).



**Fig. 1** Vertical profiles of physicochemical and biological parameters in Shira Lake (June **(A)**, July **(B)**, August **(C)**, October **(D)** 2001). X-axis: t—temperature, O<sub>2</sub>—dissolved

oxygen concentration, H<sub>2</sub>S—hydrogen sulphide concentration, Eh—redox-potential, Chl *a* chlorophyll *a* concentration, Zoo B—the wet zooplankton biomass

The dynamics of zooplankton total numbers and biomass (Fig. 3)

Pelagic zooplankton in Shira Lake was represented by two species of Rotifera (*B. plicatilis* and *H. oxiiuris*) and one Copepoda species (*A. salinus*). The total numbers of *A. salinus* population were stable ( $500\text{--}600 \times 10^3$  animals per m<sup>2</sup>) during the whole observation period; the maximum biomass was recorded in June (20 g per m<sup>2</sup>) and then gradually declined to October (14 g per m<sup>2</sup>). In June, rotifers were represented only by *H. oxiiuris* ( $90 \times 10^3$  animals per m<sup>2</sup>). At that time

the total biomass of rotifers (0.2 g per m<sup>2</sup>) was less than 1% of the total zooplankton biomass. The reproduction peak of both *B. plicatilis* ( $1000 \times 10^3$  animals per m<sup>2</sup>) and *H. oxiiuris* ( $360 \times 10^3$  animals per m<sup>2</sup>) was recorded in July. As a result, the biomass of rotifers (16.5 g per m<sup>2</sup>) amounted to 50% of the total zooplankton biomass. In August, the biomass of rotifers decreased to 8 g per m<sup>2</sup> mainly due to decreased numbers of *B. plicatilis* ( $500 \times 10^3$  animals per m<sup>2</sup>). Further in October, the zooplankton contained rather few individuals of *B. plicatilis* ( $40 \times 10^3$  animals per m<sup>2</sup>), the numbers of *H. oxiiuris* were still relatively

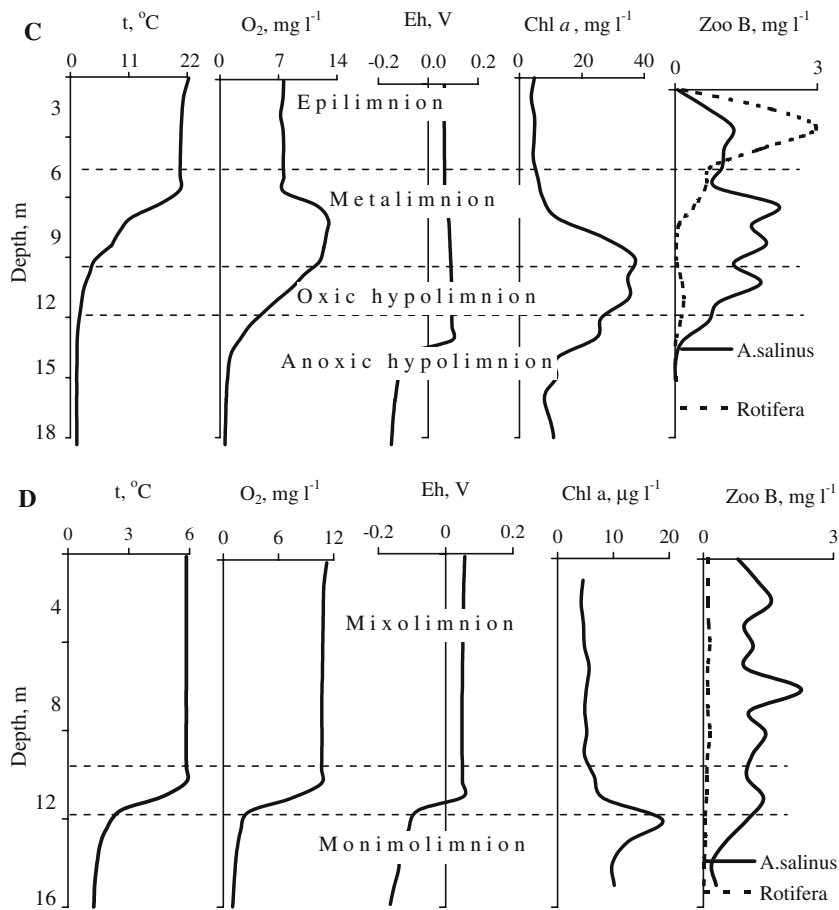


Fig. 1 continued

high ( $220 \times 10^3$  animals per  $\text{m}^2$ ), and the biomass of rotifers ( $1.2 \text{ g per m}^2$ ) decreased to 8% of total zooplankton biomass.

#### The vertical distribution and age and sex structures of zooplankton

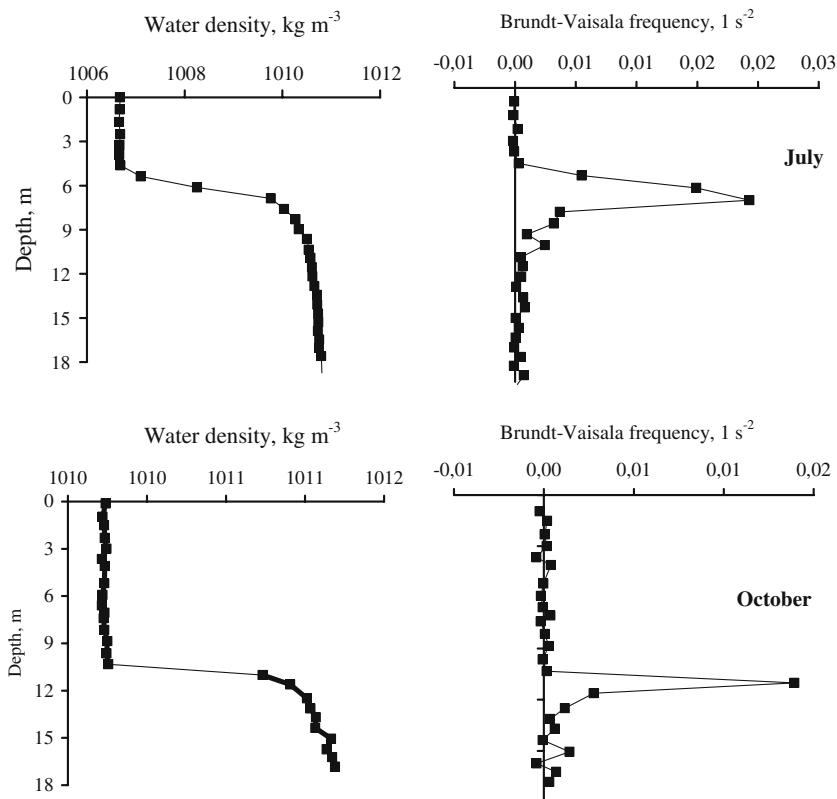
Detailed dynamics of the vertical distribution of the *A. salinus* population are shown in Fig. 4. Proportions of animals in different habitats and results of their comparison with post hoc Tukey HSD test are presented in Table 1.

The proportion of males in the population varied from 8 to 17%. The vertical distribution of males during summer stratification was heterogeneous with the maximum in the epilimnion. The proportion of males in the epilimnion was

significantly higher than in the meta- and hypolimnion. In October, males were distributed uniformly down to the depth 10 m.

The proportion of females in the population was maximal in June (13%) and later decreased, to 5% in October. Females were distributed uniformly in the epi- and metalimnion in October. During summer stratification, a deep-water maximum in the vertical distribution of females was detected in the metalimnion (at a depth of 4–8 m in July and 6–10 m in August).

The proportion of females in the metalimnion was significantly higher than in the hypolimnion. In summer, the proportion of egg-bearing females was  $20 \pm 2\%$ , the fecundity  $1.72 \pm 0.15$  eggs per female. These parameters were neither depth- nor date-dependent. In October, egg-bearing females were not detected.



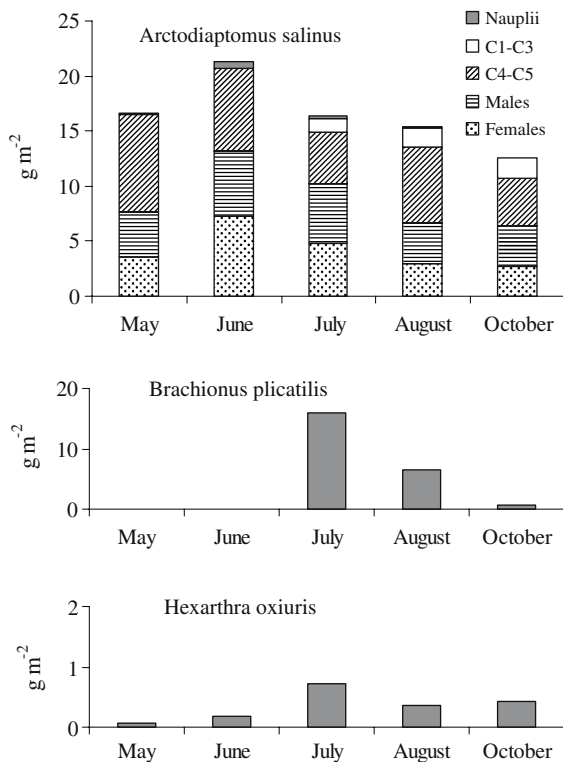
**Fig. 2** The vertical distribution of water density and Brunt Vaisala frequency in Shira Lake (July, October 2001)

In June, the density of the overwintered later copepodites C4–C5 (body length  $>0.75$  mm) was relatively high ( $16\text{--}20 \times 10^3$  animals per  $\text{m}^3$ ) and their proportion in the population of *A. salinus* was equal to 46%. The proportion of copepodites C4–C5 decreased during summer (33% in July and 17% in August) and increased back to 36% in October. During summer stratification high densities of copepodites C4–C5 were recorded in the meta- and hypolimnion. The proportion of copepodites C4–C5 in the metalimnion was significantly higher than in the epi- and hypolimnion. The average depth of later copepodites increased during summer (more than half of later copepodites were observed in the oxic hypolimnion in August). In October, they were distributed uniformly over the mixolimnion.

Younger copepodites (C1–C3 copepodites with the body length  $<0.75$  mm) were not detected in the population of *A. salinus* in June. They increased in numbers from July (22% of

the *A. salinus* population) to August (53% of the *A. salinus* population). In July, younger copepodites were observed only in the epilimnion (density 20 animals per l). In August they were observed not only in the epilimnion (30 animals per l) but also in the meta- (16 animals per l) and hypolimnion (4 animals per l). The proportion of younger copepodites in the epilimnion was significantly higher than in two other habitats. In October, the proportion of copepodites C1–C3 in the population of *A. salinus* was equal to 45%, and they were distributed uniformly in the mixolimnion.

The proportion of nauplii in the population of *A. salinus* was maximal in June (27%). It decreased during the summer season to 13% in August. There were almost no nauplii in *A. salinus* population in October (their proportion in *A. salinus* population was less than 1%). In all samples (except for the night data in June), most of the nauplii were observed in the epilimnion.



**Fig. 3** The dynamics of the biomass of dominant zooplankton species in Shira Lake in the growing season of 2001

The population of *B. plicatilis* inhabited solely the epilimnion. The difference between the proportions of *B. plicatilis* in the epilimnion and the meta- and hypolimnion was significant. The vertical distribution of *H. oxiiuris* was bimodal with two maximum densities (up to  $50\text{--}60 \times 10^3$  animals per  $\text{m}^3$ ) in the epilimnion (at a depth of 1–4 m) and the hypolimnion (at a depth of 9–12 m). The proportion of *H. oxiiuris* in the metalimnion during summer stratification was significantly lower than in two other habitats.

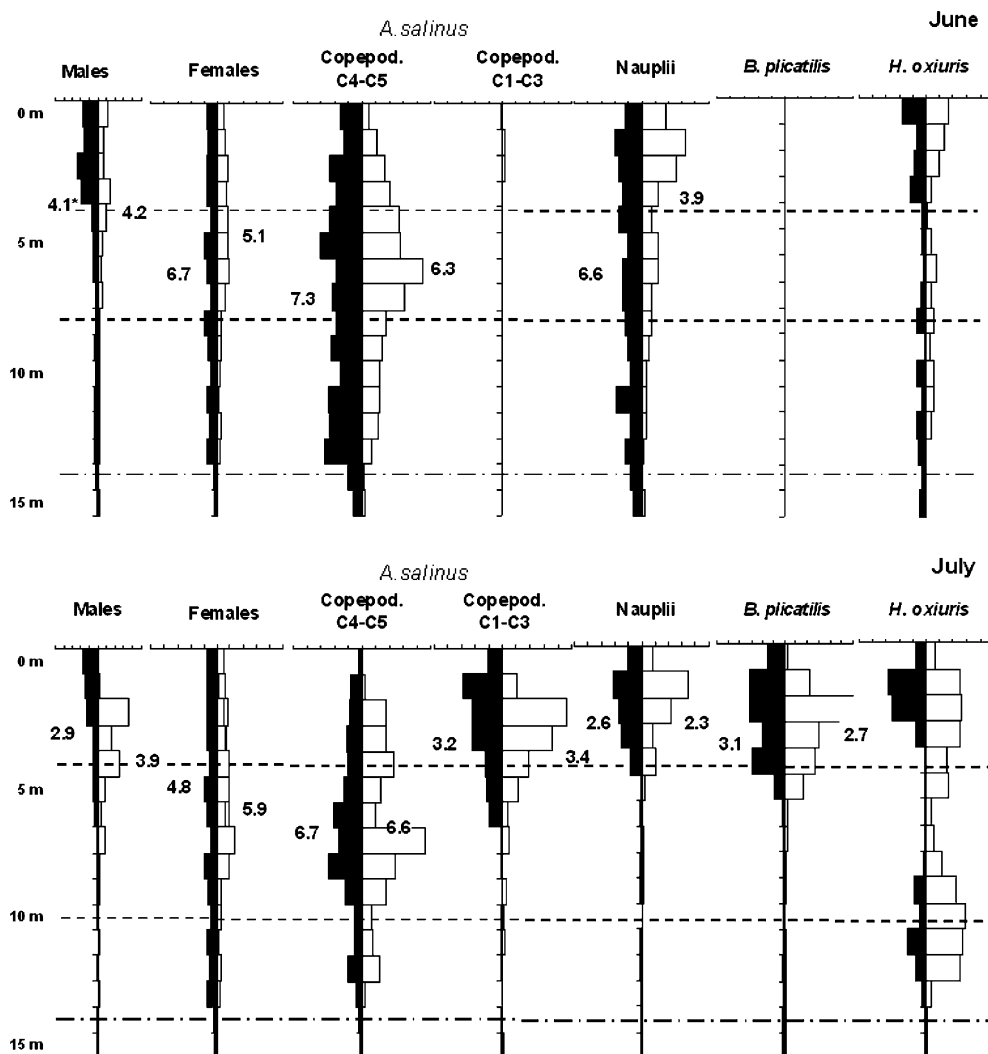
The difference between the day and night vertical distributions of zooplankton was observed in the epilimnion. All sampled species and instars in the period of high solar radiation and stable stratification of the lake (July and August) avoided the surface waters in the daytime (Fig. 4). The difference between the proportions of animals in surface waters (the sampling depth zero) during the day and the night was significant both in July and August (*T* test for dependent samples,  $P = 0.03$  and  $P = 0.0001$ ).

Paired comparisons between all tested species and instars (*A. salinus* males, females, younger and older copepodites and nauplii, *B. plicatilis*, *H. oxiiuris*) demonstrated that there is a difference in the general pattern of the vertical distribution between different species and instars (Table 2). *B. plicatilis*, nauplii and C1–C3 copepodites of *A. salinus* (the fraction of zooplankton of the smaller size) preferred surface waters and in general had the same pattern of vertical distribution (the difference between these groups was insignificant according to multivariate test). The vertical distribution of females and C4–C5 copepodites of *A. salinus* (the fraction of zooplankton of the larger size) had deep water density maximum and their pattern of vertical distribution was significantly different from those of Rotifera species and other instars of *A. salinus*. The pattern of the vertical distribution of *A. salinus* males can be classified as intermediate—they tend to occupy the epilimnion; however, the pattern was significantly different from those of all groups except for C1–C3 copepodites. The bimodal vertical distribution of *H. oxiiuris* with maxima in the epi- and hypolimnion was significantly different from those of other Rotifera species and all instars of *A. salinus*.

## Discussion

The analysis of the dynamics of the development of zooplankton community should be accompanied by the information on the vertical distribution of zooplankton. Our data demonstrate that the reproduction peaks of different zooplankton species were separated in time whereas different species and ontogenetic stages of the same species were separated in space.

The reproduction peak of *A. salinus* was observed at the beginning of summer. At that time, *A. salinus* dominated the zooplankton. We detected only one reproduction peak of *A. salinus* during the growing season. Copepodites, which dominated the population at the beginning of the season, developed into adult males and females and produced nauplii. The cohort of nauplii produced at the beginning of the season developed into young



**Fig. 4** Day (open bars) and night (black bars) vertical distributions of zooplankton in the pelagic zone of Shira Lake. The total length of X-axis is equal to 50 animals per l except for July and August for *B. plicatilis* (200 animals per l) and July and August for *H. oxiiuris* (100 animals per l). The dash lines divide the water column on epi-, meta-

ger copepodites C1–C3 (the proportion of this ontogenetic stage in the population was maximal in August) and further, in October, into C4–C5 copepodites. Although the proportion of egg-bearing females and their fecundity were constant throughout the season, no second reproduction peak in the middle to end of the summer was detected. The vertical distribution of *A. salinus* accounts for this fact. Females resided in the warm epilimnion during the first reproduction peak (June). Later (in July and August), most of the

and hypolimnion, the dash line with dots denotes the depth of the chemocline. \*Numbers on the graphs denote the average depth of specific zooplankton group. Sampling in the daytime in October was only to the depth of 10 m due to weather conditions

larger copepodites C4–C5 and females resided in meta- and hypolimnion, where, under the effect of cold temperature, their development slowed down. The general pattern observed in the vertical distribution of *A. salinus* is the increase in the average depth of copepodites and females during the season (Fig. 4).

It has been hypothesized that the ontogenetic migration, at least in marine Copepoda, can be described as the descent of animals from a specific depth accompanied by the diffusion of animals



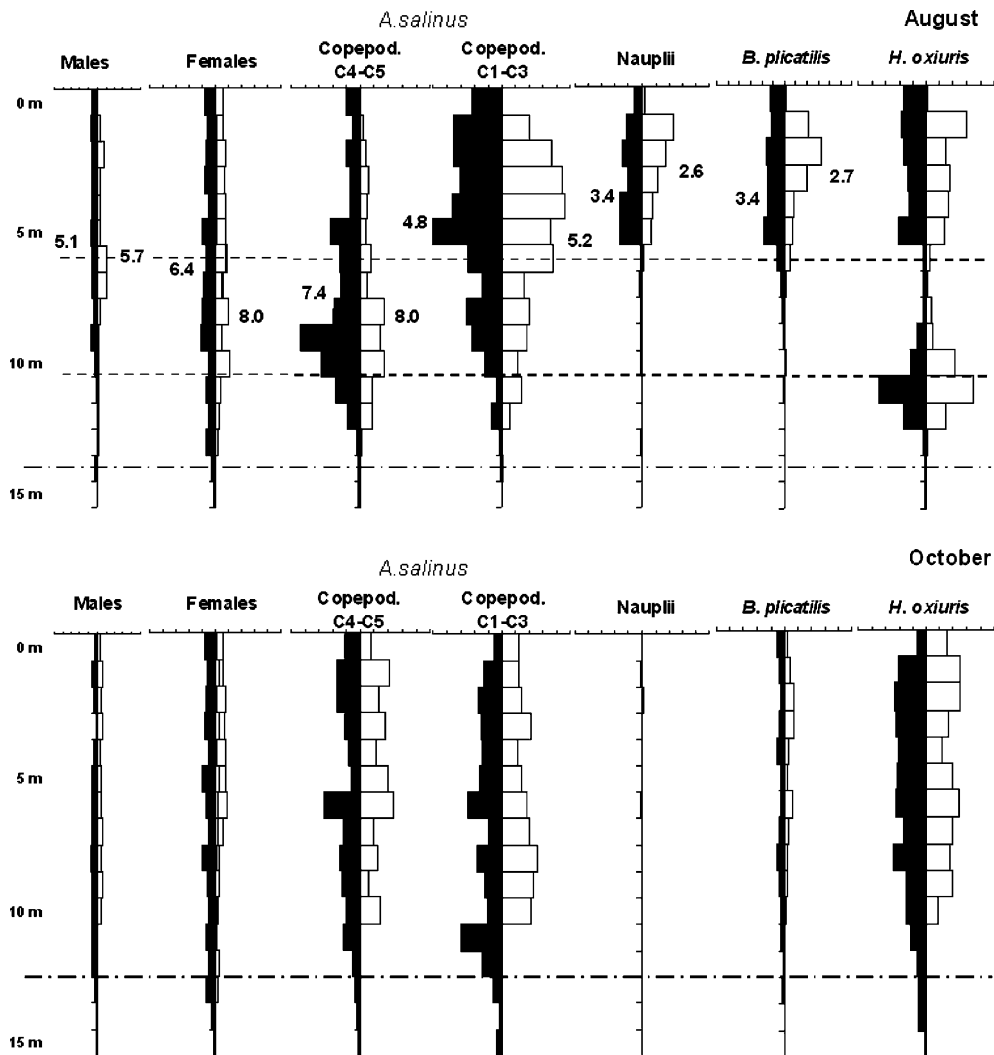


Fig. 4 continued

(Rudyakov, 1986). Also, it was proposed by Pasternak & Arashkevich (1999) that the seasonal descent of copepods at a specific ontogenetic stage into deep waters is specific both for marine and freshwater Calanoida. Our data confirm this hypothesis. Thus, the population of *A. salinus* was vertically separated in space. While nauplii and copepodites C1–C3 resided in the epilimnion, females and copepodites C4–C5 were at deeper depths (Tables 1 and 2). It can be proposed that the divergence of these age groups reduces food competition in the warm epilimnion and allows the younger age groups of *A. salinus* to develop and other species to reproduce.

The development of rotifers was detected after the reproduction peak of *A. salinus*. The population of *B. plicatilis* was observed only in the epilimnion, whereas the population of *H. oxiiuris* had a bimodal vertical distribution with numerical peaks in the epi- and hypolimnion. According to Rudyakov (1986), the bimodal vertical distribution of a population is indirect evidence for either clonal- or age-related differences in the vertical distribution of animals. At present, we cannot explain this phenomenon, as it was impossible to separate *H. oxiiuris* population into different age groups during microscope counting.

**Table 1** Proportions of animals aggregated over three summer months in different water habitats (epi—epilimnion, meta—metalimnion, hypo—hypolimnion)

The water habitat	The proportion of animals $\pm$ S.E.							
	<i>A. salinus</i>		<i>B. plicatilis</i>		<i>H. oxiiuris</i>			
	Males	Females	C4–C5 copepodites	C1–C3 copepodites	Nauplii			
Epi	0.60 $\pm$ 0.06	0.33 $\pm$ 0.05	0.25 $\pm$ 0.02	0.79 $\pm$ 0.07	0.76 $\pm$ 0.11	0.88 $\pm$ 0.01	0.51 $\pm$ 0.03	
Meta	0.30 $\pm$ 0.05	0.45 $\pm$ 0.03	0.45 $\pm$ 0.02	0.15 $\pm$ 0.06	0.14 $\pm$ 0.06	0.09 $\pm$ 0.01	0.14 $\pm$ 0.04	
Hypo	0.10 $\pm$ 0.02	0.22 $\pm$ 0.05	0.30 $\pm$ 0.03	0.06 $\pm$ 0.02	0.10 $\pm$ 0.05	0.03 $\pm$ 0.01	0.35 $\pm$ 0.03	
Probabilities for post hoc	$P_{\text{epi-meta}} = 0.015$	$P_{\text{meta-hypo}} = 0.04$	$P_{\text{epi-meta}} = 0.004$	$P_{\text{epi-meta}} < 0.001$	$P_{\text{epi-meta}} = 0.006$	$P_{\text{epi-meta}} < 0.001$	$P_{\text{epi-meta}} < 0.001$	$P_{\text{epi-meta}} < 0.001$
Tukey HSD test		$P_{\text{meta-hypo}} = 0.02$	$P_{\text{epi-hypo}} < 0.001$	$P_{\text{epi-hypo}} = 0.005$	$P_{\text{epi-hypo}} < 0.001$	$P_{\text{meta-hypo}} = 0.01$		
$P_{\text{epi-hypo}} = 0.001$								

The vertical distribution of zooplankton was restricted by the anoxic hypolimnion. The oxic-anoxic interface (the boundary between the oxic and anoxic hypolimnion) was located at a depth of 14–15 m in summer months and at a depth of 11 m in October (Fig. 1). This restriction was most pronounced in summer when the oxic-anoxic interface practically “cut” the vertical profiles of zooplankton distribution (Fig. 4, June, July, August). In October, copepodites and males of *A. salinus* and *H. oxiiuris* were detected several meters below the chemocline. Anoxic conditions do not always induce the avoidance of the anoxic waters in zooplankton. For example, in a coastal meromictic lake during the day the calanoid copepod *Acartia tonsa* migrated several meters below the oxycline and remained in the anoxic water (DeMeester & Vyverman, 1997). The authors suggested that crustaceans used the anoxic environment as a refuge from planktivorous fish. Predator avoidance is not the sole stimulus inducing migration of zooplankton to low oxygen conditions. For example, in meromictic Mahoney Lake, the copepod *Diaptomus connexus* was concentrated directly above the chemocline just above the phototrophic bacterial layer (Overmann et al., 1999). Phototrophic bacteria represented at least 75–85% of the diet of *D. connexus* (Overmann et al., 1999). In this case, the main stimulus, which induced the migration of copepods down to the low-oxygen waters was the dense population of phototrophic bacteria concentrated at the oxic-anoxic interface.

During summer stratification (August), the population density of purple sulphur bacteria in the chemocline of Shira Lake reaches up to 500 mg dry weight per  $\text{m}^3$  (Kopylov et al., 2002). Probably, with the autumn decrease of phytoplankton biomass in the oxic waters, the zooplankton begin feeding on the bacterial community of the chemocline, which results in the change of the shape of the vertical distribution. However, this hypothesis remains to be experimentally verified.

We start our analysis of the effect of various physicochemical and biological factors on the vertical distribution of zooplankton from the October data. When the mixolimnion was not stratified (Fig. 1, October) the vertical distribu-

**Table 2** The probability of a significant difference in the general pattern of the vertical distribution between different species, age and sex instars according to multivariate test of significance for paired comparisons

		<i>A. salinus</i>				<i>B. plicatilis</i>	<i>H. oxiiuris</i>
		Males	Females	C4–C5 copepodites	C1–C3 copepodites	Nauplii	
<i>A. salinus</i>	Males		$P = 0.02$	$P < 0.001$	n.s.	$P = 0.04$	$P < 0.0001$
	Females	$P = 0.02$		n.s.	$P < 0.0001$	$P < 0.0001$	$P < 0.0001$
	C4–C5 copepodites	$P < 0.001$	n.s.		$P < 0.0001$	$P < 0.0001$	$P < 0.0001$
	C1–C3 copepodites	n.s.	$P < 0.0001$	$P < 0.0001$		n.s.	$P < 0.0001$
	Nauplii	$P = 0.04$	$P < 0.001$	$P < 0.0001$	n.s.	n.s.	$P < 0.001$
<i>B. plicatilis</i>		$P < 0.0001$	$P < 0.00001$	n.s.	n.s.	$P < 0.0001$	
<i>H. oxiiuris</i>		$P < 0.0001$	$P < 0.0001$	$P < 0.0001$	$P < 0.001$	$P < 0.0001$	

tion of zooplankton was uniform. There were no different habitats in the oxic water column as the vertical profiles of temperature, dissolved oxygen and chlorophyll *a* concentrations were uniform. However, as demonstrated by data obtained in June, the thermal stratification of the mixolimnion is not a sufficient condition to induce the inhomogeneous vertical distribution of zooplankton. In the early to mid June, the main physicochemical and biological parameters in Shira Lake become stably stratified (Gaevsky et al., 2002). Comparing day and night vertical distributions of zooplankton suggests that their vertical distribution is not stable. The vertical distribution of zooplankton over the mixolimnion at night was practically uniform (except for the distribution of males) (Fig. 4). The vertical distribution of zooplankton observed twelve hours later (daytime) demonstrated stratification in the distribution of nauplii and older copepodites. This difference between vertical distributions observed within a short period of time may be explained by the weather conditions and, probably, by the attendant homogeneous distribution of chlorophyll *a*. There was a strong wind during night sampling in June, which may have mixed the epilimnion. When the wind dropped and water masses stabilized, zooplankton redistributed in accordance with its habitat and physiological preferences.

The uniform pattern of vertical distribution of nauplii can be explained by the uniform distribution of females (Fig. 4, June). In this case, the reproduction of the population over the entire

water column may have led to the uniform distribution of nauplii. However, this hypothesis has not been supported by the other data. Both in July and August, most of females were found in the metalimnion, the proportion of egg-bearing females was independent of the sampling depth, but nauplii were still located in the epilimnion. It is not clear from our data whether females reproduced only in the upper warm waters and came to the surface for the reproduction, or they reproduced over the entire water column and hatched nauplii ascended to the epilimnion.

A stable stratification of physical, chemical and biological parameters was observed in July and August. At that time, the population of *A. salinus* was characterized by a deep water maximum of older copepodites and females. As mentioned before, for all instars of *A. salinus* (except for nauplii and males) the average depth increased with time. At the same time, a deep water chlorophyll maximum was observed in the lake. According to previous data (Gaevsky et al., 2002), the deep-water chlorophyll maximum (located at a depth of 8–12 m) has a complex structure, in which different algal species occupy different depths (the maximum of the biomass of green algae is above the maximum of the biomass of blue-greens). The maximum of the biomass of the *A. salinus* population was located just above the deep-water chlorophyll maximum and coincided with the maximum of the biomass of green algae (Fig. 1). Laboratory investigation of the phytoplankton diet of *A. salinus* from Shira Lake demonstrated that animals consumed practically

all dominant phytoplankton species but preferred the green algae *Dictyosphaerium tetrachotomum* and *Oocystis submarina* (Tolomeev, 2002). *Dictyosphaerium tetrachotomum* is one of the dominant phytoplankton species in Shira Lake (its biomass constitutes up to 30% of the total phytoplankton biomass) with the maximum of biomass located at a depth of 8 m (Gaevsky et al., 2002). Thus, the maximum of *A. salinus* biomass was associated with the maximum of the biomass of green algae, which are the preferred diet for this species.

The effect of the deep-water chlorophyll maximum on the vertical distribution of zooplankton has recently become the subject of several investigations (Lampert et al., 2003; Lampert & Grey, 2003; Winder et al., 2003). It has been hypothesized that in the systems with deep-water chlorophyll maximum the vertical distribution of zooplankton should follow the ideal free distribution (IFD) with costs (Lampert et al., 2003). In this case, in the absence of predation, zooplankton chooses between different habitats in order to optimize their fitness. The pattern of the vertical distribution will depend on the temperature and food vertical profiles. Indeed, it was demonstrated both in large indoor columns with the deep-water chlorophyll maximum below the thermocline (Lampert et al., 2003) and in a lake with the deep-water chlorophyll maximum (Winder et al., 2003) that a large proportion of zooplankton stayed in the deep cold waters. In our case, older copepodites and females also stayed below the thermocline and just above the deep-water chlorophyll maximum. The pattern of the vertical distribution of these instars in Shira Lake coincided with the conceptual model of the fitness distribution of zooplankton in vertical gradients of temperature and food and with the vertical distribution of *Daphnia* in the mesocosm with the established thermocline and hypolimnetic algal maximum (Lampert et al., 2003). However, it should be emphasized that the vertical distribution of other instars (nauplii, younger copepodites and males) did not follow this conceptual model.

The growth rate of zooplankton depends on temperature (Lee et al., 2003). Trying to explain the nocturnal upward vertical migrations of

*Daphnia* species in a lake with the deep-water algal maximum, Winder et al. (2003) proposed that warm water conditions may be important for developing eggs. Our data suggest that warm water conditions are important for the young instars of *A. salinus*. Both nauplii and C1–C3 copepodites resided in the epilimnion at the time when the maximum of chlorophyll *a* was located below the thermocline. We did not measure the growth rate of different instars of *A. salinus* in Shira Lake, but we can propose that nauplii and younger copepodites select the location that maximizes their fitness and ensures highest growth rate.

Another possible reason for the observed vertical distribution of *A. salinus* is different life strategies of different instars. The main aim of the younger part of the population (nauplii and younger copepodites) is to mature during a short season (Shira Lake is covered by ice in November and opens by the end of May), while females and older copepodites have to transform a significant portion of food consumed into lipid reserves for overwintering. In this case, cold, low-oxygen hypolimnion is an appropriate place as the transformation of food into lipid reserves is more effective at low temperature and deficiency of oxygen (Svetlichny et al., 2000).

The main difference between day and night vertical distributions of zooplankton was observed in the epilimnion. All species and instars avoided surface waters during daytime (Fig. 4, July, August). We assume that the observed vertical distribution of zooplankton in the epilimnion was induced by the effect of intense solar radiation as there are no active, visually-guided zooplankton predators (either fish or carnivorous zooplankton) in Shira Lake. This pattern of the vertical migrations of zooplankton in the surface waters is most probably related to the negative phototaxis of zooplankton to the ultraviolet radiation (Storz & Paul, 1998; Leech & Williamson, 2001). The observed avoidance of the surface waters can be the induced reaction to the effect of UV radiation, which is known to damage the DNA resulting in developmental defects (Rubin, 1987) or cause lethal outcome to zooplankton exposed to natural levels of solar ultraviolet radiation (Williamson et al., 1994).

There were no large-scale diel vertical migrations observed in Shira Lake. This could be an expected conclusion, because large-scale vertical migrations are likely to occur when the lake is inhabited by planktivorous fish. It is widely accepted that predator avoidance behavior is the reason of diel vertical migration for many zooplankton species (Lampert, 1993; Loose, 1993). However, the role of the amphipod *Gammarus lacustris* in the dynamics of the ecosystem of Shira Lake is not clear. This species occupies an intermediate benthic-planktonic ecological niche, inhabiting the pelagic zone of the lake (Yemelianova, 2002). It was shown in laboratory experiments that *G. lacustris* could suppress the numbers of *A. salinus* and rotifers in experimental vessels (Yemelianova et al., 2002). In addition, the effect of crowded water produced by dense population of *G. lacustris* induced changes in the vertical distribution of *Arctodiaptomus* in laboratory conditions (Zadereev & Gubanov, 2002). However, this is insufficient evidence of predator–prey relationships between these species. It is not clear whether *G. lacustris* acts as a predator or as a phytoplankton and detritus feeder in Shira Lake.

In conclusion, the vertical distribution of zooplankton in meromictic Shira Lake depends both on the stratification of physicochemical and biological parameters of the ecosystem and on the biological peculiarities of different species and instars of zooplankton. The ecosystem with the various microhabitats separated in space give zooplankton an opportunity to select habitats optimal for their fitness. We can propose that observed in Shira Lake the separation in space of dominant species and different age instars is aimed to reduce intra- and interspecific food competition. To reduce food competition further, reproduction peaks of dominant species are separated in time. The dynamics of zooplankton community and its vertical distribution in Shira Lake can be described as successive occupation of available microhabitats by different species and instars. However, it is not clear yet whether this strategy is an optimal habitat choice to maximize fitness or also a strategy to ensure the development of the population and community. Future research should estimate food competition between and within different zooplankton species in

a stratified meromictic lake during growing season to understand mechanisms responsible for the vertical distribution and dynamics of zooplankton community.

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