



## Species composition and structural organization of the littoral zooplankton communities in the Oleksandrivka Reservoir (Ukraine)

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Today, the issue of researching reservoirs, which are an important source of human water supply and are significantly affected by anthropogenic factors, is gaining more and more relevance. Research on the Oleksandrivka Reservoir is highly important since the safety of operation of the South-Ukrainian NPP depends on the functioning of this reservoir. The research material was samples of littoral zooplankton, which is a bioindicator of changes in the aquatic environment. During the research, both classical methods and the original method of standardizing the number and localization of zooplankton sampling stations within different types of reservoir were used. As a result of original research, the species composition and structural organization of littoral zooplankton communities in different parts of the Oleksandrivka Reservoir were analyzed for the first time. A total of 126 species of zooplankton were registered, of which 96 were observed in this reservoir for the first time. The rotifer *Euchlanis dapiidula* was discovered for the first time in the fauna of Ukraine. The peculiarities of the formation of the faunal spectrum, trophic groups, complex of dominant species, distribution of biotopes, distribution in different parts of the reservoir, density, biomass, as well as seasonal and daily dynamics of littoral zooplankton groups were also clarified. It was established that the biomass of phytoplankton has a statistically significant effect on the density and biomass of zooplankton.

**Keywords:** plankton; rotifers; cladocerans; copepods; littoral zone; freshwater ecosystem; Ukraine.

### Introduction

At the present stage of hydrobiology and ecology development, much attention is being paid to biodiversity research and conservation (Dudgeon et al., 2006), the impact of anthropogenic load on aquatic ecosystems (Aris et al., 2015) and their irreversible succession changes (Sommer, 1989; Olmo et al., 2016; Li et al., 2023). Human economic activity causes the restructuring of both the individual constituents of aquatic ecosystems (in particular, animal communities) and their structural and functional organization as a whole (Bucola et al., 2015). An example of such processes is the conversion of rivers to reservoirs with another hydrological regime. Today reservoirs are Ukraine's main type of water bodies (Khilchevsky et al., 2020). Therefore, there is no doubt that it is necessary to elucidate the ways and directions of the anthropogenic transformation of their ecosystems, characterized by significant intensity and a short flow period. The canyon reservoirs of the South Ukrainian Energy Complex deserve special attention. Thus, the Oleksandrivka Reservoir, which is bounded on both sides by high granite shores, was filled by the lowest levels in the South-Bug Cascade on the Southern Bug River in 1927.

The least studied are the littoral ecosystems of reservoirs that occupy shallows up to 2 m deep (Pashkova, 2008). They are characterized by high levels of biodiversity (Cronin et al., 2006) and complex structural and functional organization (Sampaio et al., 2002). At the same time, zooplankton is an important component of aquatic ecosystems, which plays an important role in their substance turnover and energy transformation (Hébert et al., 2017). Most zooplankton representatives belong to 1st and 2nd levels of consumers (Kiorboe, 2011), and zooplankton is the basis of the feed base for young fish and fish-planktophages at higher trophic levels (Swierzowski et al., 2000; Jack & Thorp, 2002). Most zooplankton representatives have a longer life cycle than bacterioplankton and phytoplankton (Rodrigues et al., 2018; Znachor et al., 2020; Pinto et al., 2021), and

less complex individual behavior than fish (Prhalová et al., 2003; Castanheira et al., 2016). Therefore, the transformation of zooplankton groups can likely be regarded as an indicator of changes in littoral ecosystems and as a biological element in the assessment of reservoir water quality (Almeida et al., 2020). This work aimed to investigate the species composition and structural organization of littoral zooplankton communities of the Oleksandrivka Reservoir.

### Materials and methods

The objective of the study was representatives of the main groups of zooplankton: rotifers (Eurotatoria), cladocerans (Branchiopoda, Cladocera), and copepods (Copepoda). Rotifers from subclass Monogononta, cladocerans, and copepods were determined to species. Rotifers from subclass Bdelloidea were determined to taxon of superspecies rank.

208 samples of littoral zooplankton were collected from the mesotrophic Oleksandrivka Reservoir in different seasons of 2006, 2008–2010, and 2013–2015. The material was collected by filtering 50 liters of water through a conical plankton net with a mesh size of 100 µm within four standardized sampling stations (Trokhymets, 2011; Fig. 1): base station I – left bank of the upper part of the reservoir (lotic zone), 47°47.129' N 31°10.811' E; base station II – right bank of the middle part of the reservoir (transitional zone), 47°42.802' N 31°11.267' E; base station III – left bank of the middle part of the reservoir (transitional zone), 47°44.110' N 31°11.681' E; base station IV – right bank of the lower part of the reservoir (lentic zone), 47°42.042' N 31°13.704' E. Each station of the reservoir is a section for taking samples that are tied to a specific geographical point. Samples were taken at different points in the water area of each station: in the thickets of different formations of higher aquatic vegetation (overgrown biotope) and the areas free from macrophytes (not overgrown biotope).

Formations of the common reed (*Phragmites australis* (Cav.) Trin. ex Steud.) and lesser bulrush (*Typha angustifolia* L.) were dominant in the upper part of the Oleksandrivka Reservoir. The arrowhead (*Sagittaria sagittifolia* L., 1753), common duckweed (*Lemna minor* L.), common duckmeat (*Spirodela polyrrhiza* (L.) Schleid.), yellow water-lily (*Nuphar lutea* (L.) Smith), rigid hornwort (*Ceratophyllum demersum* L.), clasping leaf pondweed (*Potamogeton perfoliatus* L.), sago pondweed (*Potamogeton pectinatus* (L.) Böerner) and other species of macrophytes formed an association with these formations. The projective cover of higher aquatic plants varied from 30% to 70%. The formations of clasping leaf pondweed formed in the middle and lower parts of the reservoir, and formed associations with the rigid hornwort, soft hornwort (*Ceratophyllum submersum* L.), spiny water nymph (*Najas marina* L.), and common duckmeat. A large number of filamentous algae with a predominance of representatives of the genus *Spirogyra* was also observed within the experimental sections of the reservoir. The projective cover of higher aquatic plants ranged from 10% to 90%.

Samples were collected for the overall analysis: one sample at a time in the different formations of higher aquatic plants and not overgrown biotopes of the four experimental stations. Seasonal studies were conducted to identify trends in the formation of the modern structure of littoral zooplankton communities: spring, summer, and autumn. Samples of littoral zooplankton were collected in the summer four times a day to find out the features of their daily migrations: in the daytime – from 12 noon to 2 p.m., in the evening – from 6 to 8 p.m., at night – from 12 midnight to 2 a.m., and in the morning – from 6 to 8 a.m.

Subsequent sample processing, zooplankton identification, and analysis of the obtained data were performed according to the conventional hydrological methods (Witty, 2004; Segers, 2007; Bledzki & Rybak, 2016). We used the analysis of the following indicators of the structural organization of littoral zooplankton communities and their seasonal-daily dynamics (Romanenko, 2006): species richness; faunistic spectrum – the percentage of the species number of the main taxonomic groups (rotifers, cladocerans, copepods); frequency of species occurrence – the ratio of presence of a species within the water area of different experimental stations to the total number of experimental stations (in %); the trophic spectrum is the percentage of the number of species of major trophic groups (peaceful, predators, polyphages); the spatial structure is an analysis of zooplankton communities of different parts of the reservoir and their biotopes; density and biomass; complexes of dominant species. Zooplankton density and biomass indices were described using the following categories (Romanenko, 2006): “very low” is <5 thousand ind./m<sup>3</sup> and <0.3 g/m<sup>3</sup>; “low” – 5–50 thousand ind./m<sup>3</sup> and 0.3–1.0 g/m<sup>3</sup>; “below average” – 51–250 thousand ind./m<sup>3</sup> and 1.1–5.0 g/m<sup>3</sup>; “average” – 251–500 thousand ind./m<sup>3</sup> and 5.1–10.0 g/m<sup>3</sup>; “above average” – 501–1000 thousand ind./m<sup>3</sup> and 10.1–20.0 g/m<sup>3</sup>; “high” – 1001–2500 thousand ind./m<sup>3</sup> and 20.1–30.0 g/m<sup>3</sup>; “very high” – >2500 thousand ind./m<sup>3</sup> and >30.0 g/m<sup>3</sup>.

All statistical analyses were performed using R 3.2.3 (R Development Core Team, 2015). The multifactorial analysis for 18 factors was conducted: seasons, reservoir parts, biotopes, the flow velocity of water (V), water temperature (t), water acidity (pH), oxygen content in water (O<sub>2</sub>), young fish density as a major predator (Nf), phytoplankton biomass as a feed base (Ph), the concentration in water of cations (Na<sup>+</sup>, K<sup>+</sup>, Ca<sup>+2</sup>, Mg<sup>+2</sup>, NH<sub>4</sub><sup>+</sup>) and anions (Cl<sup>-</sup>, SO<sub>4</sub><sup>-2</sup>, NO<sub>3</sub><sup>-</sup>, NO<sub>2</sub><sup>-</sup>, HCO<sub>3</sub><sup>-</sup>). Indicators of zooplankton (on which the influence of the above factors was tested) were: the species richness of zooplankton (S), rotifers (Sr), cladocerans (Scl), copepods (Sc); the density of zooplankton (N), rotifers (Nr), cladocerans (Ncl), copepods (Nc), ostracods and larvae of bivalve mollusks (Nov); the biomass of zooplankton (B), rotifers (Br), cladocerans (Bcl), copepods (Bc), ostracods and larvae of bivalve mollusks (Bov).

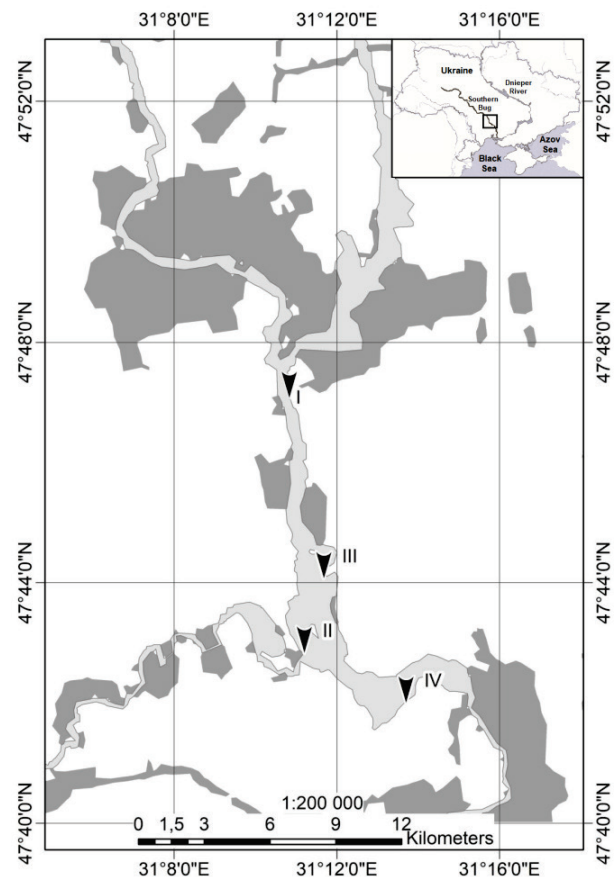
In addition, the Jacquard (J) and Jacquard dom. (J<sub>dom</sub>) indexes were used during the data analysis (Romanenko, 2006).

All authors declare that the study was conducted following the ethical standards of their national research committee.

## Results

Zooplankton of the littoral zone of the Oleksandrivka Reservoir was characterized by high species richness – 126 species, 96 of which were re-

gistered in this reservoir for the first time (marked in Table 1 as \*). Rotifers were represented by 60 species of subclass Monogononta (two of them were identified to genera level) and subclass Bdelloidea spp. Cladoceran crustaceans comprised 45 species. Copepod crustaceans were represented by 21 species and order Harpacticoida spp.



**Fig. 1.** Mapping scheme of the Oleksandrivka Reservoir with the standardized stations of hydrobiological research (the map was developed with the free and open geographic information system QGIS): I–IV – basestations

The faunistic spectrum of the species composition of littoral zooplankton was the following: rotifers – 47.6%, cladocerans – 35.7%, copepods – 16.7%. Monogononta rotifers from the order Ploima were represented by 56 species from 13 families. They dominated both among rotifers and zooplankton as a whole. Representatives of this order made up 44.4% of the total number of species of all zooplankton groups. Monogononta rotifers of order Flosculariacea included 4 species (3.2%) of four families. Cladocerans from 28 species (22.2% of the zooplankton species richness) belonged to the family Chydoridae. Representatives of another 17 species (13.5%) of crustaceans were a part of the other five families. Copepods included representatives of three orders. They were dominated by individuals of the order Cyclopoida, which was represented by one family Cyclopidae. Its species richness was 18 species or 14.3% of the total species richness of zooplankton. Copepods from order Calanoida included two families – Diaptomidae and Temoridae, with two species (1.6%), and order Poecilostomatoida was represented by only one species – *P. rylowi* (0.8%). Thus, 91 species (72.2% of the species richness of zooplankton) represented rotifers of the family Brachionidae, cladocerans of the family Chydoridae, and copepods of the family Cyclopidae.

The frequency of species occurrence varied widely in different parts of the reservoir. Thus, 42 out of 126 species (33.3%) of zooplankton were registered in the littoral zone of all four stations of the Oleksandrivka Reservoir during the seven-year study. There was a tendency of growth of the frequency of species occurrence from rotifers to crustaceans if we consider it in the context of the faunistic spectrum of zooplankton groups: the proportion of rotifers with 100% occurrence is 18.3% (11 of 60 species), cladocerans – 42.2% (19 of 45 species), copepods – 57.1% (12 of 21 spe-

cies). The frequency of zooplankton species occurrence with registration within one station of the lotic zone showed the opposite tendencies (dominance of rotifers): the proportion of rotifer species with 25% frequency of occurrence was 36.7% (22 of 60 species), cladocerans – 26.7% (12 of 45 species), copepods – 4.8% (1 of 21 species).

In general, the following species complex has the highest species occurrence with different years: rotifers are *B. quadridentatus* and *E. dilatata*; cladocerans – *A. rectangularis*, *D. brachyurum*, and *G. testudinaria*; copepods – *A. americanus*, *E. serrulatus*, *E. velox*, and *T. crassus*. The fresh-

water group was most important in the zooplankton community – 124 species (98.4%). A single species represented invasive saltwater and marine groups – copepod *Eurytemora velox* (0.8%). *Paraergasilus rylovi* (0.8 %) lives in freshwater and brackish water bodies, so assigning it to any group is difficult. The last species is a parasite of freshwater and brackish water fish, in search of which it keeps in the water column in the form of plankton. Therefore, it can sometimes be registered in littoral zooplankton samples.

**Table 1**  
Taxonomic diversity of the littoral zooplankton of the Oleksandrivka Reservoir

Classes, orders	Families	Genera (species)	
Eurotatoria	Trichocercidae	<i>Trichocerca</i> ( <i>T. bidens</i> (Lucks)*, <i>T. elongata</i> (Gosse)*, <i>T. pusilla</i> (Jennings)*, <i>T. rattus</i> (O.F. Müller)*, <i>T. stylata</i> (Gosse)*)	
	Synchaetidae	<i>Synchaeta</i> ( <i>S. longipes</i> Gosse*, <i>S. pectinata</i> Ehrenberg*, <i>S. stylata</i> Wierzejski), <i>Polyarthra</i> ( <i>P. dolicoptera</i> Idelson, <i>P. major</i> Burckhardt*, <i>P. vulgaris</i> Carlin*), <i>Ploesoma</i> ( <i>P. hudsoni</i> (Imhof)*)	
	Scaridae	<i>Scaridium</i> ( <i>S. longicaudum</i> (O. F. Müller)*)	
	Asplanchnidae	<i>Asplanchna</i> ( <i>A. priodonta</i> Gosse, <i>A. sieboldii</i> (Leydig)*)	
	Lecanidae	<i>Lecane</i> ( <i>L. bulla</i> (Gosse)*, <i>L. closterocerca</i> (Schmarda)*, <i>L. luna</i> (O. F. Müller)*, <i>L. lunaris</i> (Ehrenberg)*, <i>L. quadridentata</i> (Ehrenberg)*)	
	Epiphanidae	<i>Epiphaneis</i> ( <i>E. senta</i> (O. F. Müller)*, <i>Epiphaneis</i> sp. Ehrenberg*)	
	Lepadellidae	<i>Cohurella</i> ( <i>C. colurus</i> (Ehrenberg)*, <i>C. obtusa</i> (Gosse)*, <i>C. uncinata</i> (O. F. Müller)*), <i>Lepadella</i> ( <i>L. patella</i> (O. F. Müller)*, <i>L. quadricarinata</i> (Stenroos), <i>L. rhomboides</i> (Gosse)*)	
	Euchlanidae	<i>Dipleuchlanis</i> ( <i>D. elegans</i> (Wierzejski)*), <i>Tripleuchlanis</i> ( <i>T. plicata</i> (Levander)*, <i>Euchlanis</i> ( <i>E. calpidia</i> Myers*, <i>E. dapidula</i> Parise*, <i>E. deflexa</i> (Gosse)*, <i>E. dilatata</i> Ehrenberg, <i>E. incisa</i> Carlin*, <i>E. lyra</i> Hudson*, <i>E. pyriformis</i> Gosse*)	
	Brachionidae	<i>Brachionus</i> ( <i>B. angularis</i> Gosse, <i>B. bennini</i> Leissling*, <i>B. calyciflorus</i> Pallas, <i>B. leydigii</i> Cohn*, <i>B. nilsoni</i> Ahlstrom*, <i>B. plicatilis</i> O. F. Müller*, <i>B. quadridentatus</i> Hermann, <i>B. urceolaris</i> O. F. Müller*, <i>B. variabilis</i> Hempel*), <i>Keratella</i> ( <i>K. cochlearis</i> (Gosse), <i>K. quadrata</i> (O. F. Müller), <i>K. tropica</i> (Apstein)*), <i>Notcholca</i> ( <i>N. acuminata</i> (Ehrenberg)*, <i>N. squamula</i> (O. F. Müller)*), <i>Platylabus</i> ( <i>P. quadricornis</i> (Ehrenberg)*)	
	Flosculariidae	<i>Conochilus</i> ( <i>C. unicomis</i> Rousselet*), <i>Lacimularia</i> ( <i>L. flosculosa</i> (O. F. Müller)*)	
	Testudinellidae	<i>Testudinella</i> ( <i>T. patina</i> (Hermann)*)	
	Filiniidae	<i>Filinia</i> ( <i>F. longiseta</i> (Ehrenberg)*)	
	Mytilinidae	<i>Mytilina</i> ( <i>M. ventralis</i> (Ehrenberg)*)	
	Notommatidae	<i>Cephalodella</i> ( <i>C. Gibba</i> (Ehrenberg)*, <i>Cephalodella</i> sp. Bory de St. Vincent*)	
	Trichotriidae	<i>Trichotria</i> ( <i>Trichotria pocillum</i> (O. F. Müller)*)	
Cladocera	Sididae	<i>Sida</i> ( <i>S. crystallina</i> (O. F. Müller)*), <i>Diaphanosoma</i> ( <i>D. brachyurum</i> (Lievins))	
	Daphniidae	<i>Daphnia</i> ( <i>D. cucullata</i> Sars, <i>D. longispina</i> (O. F. Müller)), <i>Simocephalus</i> ( <i>S. serrulatus</i> (Koch)*, <i>S. vetulus</i> (O. F. Müller)*), <i>Moina</i> ( <i>M. macrocopa</i> (Straus)*, <i>M. rectirostris</i> (Leydig)*), <i>Ceriodaphnia</i> ( <i>C. affinis</i> Lilljeborg*, <i>C. quadrangula</i> (O. F. Müller)*), <i>Scapholeberis</i> ( <i>S. mucronata</i> (O. F. Müller)*)	
	Macrothricidae	<i>Macrothrix</i> ( <i>M. hirsuticornis</i> Norman & Brady*, <i>M. laticornis</i> (Jurine)), <i>Ilyocryptus</i> ( <i>I. agilis</i> Kurz*, <i>I. sordidus</i> (Lievins)*)	
	Bosminidae	<i>Bosmina</i> ( <i>B. longirostris</i> (O. F. Müller))	
	Leptodoridae	<i>Leptodora</i> ( <i>L. kindtii</i> (Focke))	
	Chydoridae	<i>Camptocercus</i> ( <i>C. rectirostris</i> Schoedler*), <i>Acroperus</i> ( <i>A. harpae</i> (Baird)*), <i>Anchistropus</i> ( <i>A. emarginatus</i> Sars*), <i>Graptoleberis</i> ( <i>G. testudinaria</i> (Fischer)), <i>Chydorus</i> ( <i>C. latus</i> Sars*, <i>C. ovalis</i> Kurz*, <i>C. piger</i> Sars*, <i>C. sphaericus</i> (O. F. Müller)), <i>Disparalona</i> ( <i>D. rostrata</i> (Koch)*), <i>Picripleuroxus</i> ( <i>P. laevis</i> Sars*, <i>P. striatus</i> Schödler*), <i>Pleuroxus</i> ( <i>P. aduncus</i> (Jurine), <i>P. trigonellus</i> (O. F. Müller), <i>P. truncata</i> (O. F. Müller)*, <i>P. uncinatus</i> Baird*), <i>Alona</i> ( <i>A. affinis</i> (Leydig)*, <i>A. costata</i> Sars*, <i>A. guttata</i> Sars, <i>A. intermedia</i> Sars*, <i>A. quadrangularis</i> (O. F. Müller), <i>A. rectangularis</i> Sars*), <i>Alonella</i> ( <i>A. excisa</i> (Fischer)*, <i>A. exiqua</i> (Lilljeborg)*, <i>A. nana</i> (Baird)*), <i>Leydigia</i> ( <i>L. acanthocercoides</i> (Fischer)*, <i>L. leydigii</i> (Leydig)*), <i>Oxyurella</i> ( <i>O. tenuicaudis</i> (Sars)*), <i>Pseudochydorus</i> ( <i>P. globosus</i> (Baird))	
	Copepoda	Diaptomidae	<i>Eudiaptomus</i> ( <i>E. gracilis</i> (Sars))
		Temoridae	<i>Eurytemora</i> ( <i>E. velox</i> (Lilljeborg)*)
		Cyclopidae	<i>Macrocyclus</i> ( <i>M. albidus</i> (Jurine)*), <i>Eucyclus</i> ( <i>E. denticulatus</i> (Graeter)*, <i>E. macrurus</i> (Sars)*, <i>E. serrulatus</i> (Fischer)), <i>Colpocyclus</i> ( <i>C. dulcis</i> Monchenko*), <i>Cryptocyclus</i> ( <i>C. bicolor</i> (Sars)*), <i>Paracyclus</i> ( <i>P. affinis</i> (Sars)*, <i>P. poppei</i> (Rehberg)*), <i>Ectocyclus</i> ( <i>E. phaleratus</i> (Koch)*), <i>Cyclops</i> ( <i>C. strenuus</i> Fischer*, <i>C. vicinus</i> Ulianine), <i>Acanthocyclus</i> ( <i>A. americanus</i> (Marsh)), <i>Megacyclus</i> ( <i>M. viridis</i> (Jurine)), <i>Diacyclops</i> ( <i>D. bicuspidatus</i> (Claus)*), <i>Mesocyclus</i> ( <i>M. leuckarti</i> (Claus)), <i>Microcyclus</i> ( <i>M. varicans</i> (Sars)*), <i>Thermocyclus</i> ( <i>T. crassus</i> (Fischer), <i>T. oithonoides</i> (Sars)*)
		Ergasilidae	<i>Paraergasilus</i> ( <i>P. rylovi</i> Markewitsch*)

Note: \* – first registration.

Three groups of zooplankton were revealed in the trophic spectrum. The former include non-predators who feed on small organisms by filtration and gathering. The species composition of these first-order consumers reached 101 species or 80.2% of the total species composition of zooplankton. The basis of this trophic group was rotifers with 57 species, below them cladocerans with 47 species, and copepods were represented by only one non-predator species. The second group unites 12 species (9.5%) of euryphagous with predominant among them copepods – 10 species, and rotifers with two species. Cladocerans were absent in this trophic group. The third group included second-order consumers (predators and the parasite *P. rylovi*), represented by 13 species (10.3%). They included one species of rotifer, two species of cladoceran, and nine species of copepod. The ratio of non-predatory and predatory zooplankton was 10/1.

The littoral zone of the Oleksandrivka Reservoir did not contain higher aquatic vegetation immediately after raising the water level in the reservoir to 14.7 m in the summer of 2006. The projective cover of macrophytes gradually increased in the following years. The overgrown biotope

was poorly expressed in the spring and autumn. In general, the rotifer-cladocerans complex of zooplankton dominated in reeds and the biotopes without macrophytes (Table 2). Rotifers slightly dominated in the open areas of the littoral zone of the reservoir, which can be explained by the introduction of the pelagic component in the littoral zooplankton communities. The formations of different species of higher aquatic plants saw a gradual decrease in the species composition of rotifers and an increase in the presence of cladocerans in the direction: of reed → bulrush → pondweed.

An analysis of the species composition of the littoral zooplankton of different parts of the Oleksandrivka Reservoir showed that species richness was highest within the middle part. Thus, 72 zooplankton species were found in the upper part of the reservoir, 94 were registered from the water area near the right bank of the middle reservoir part, 90 – from the water area near the left bank of the middle part of the reservoir, and 73 zooplankton species were found in the lower part. A low and medium degree of similarity marked the comparison of species lists of the littoral

zooplankton of the upper reservoir part and its other parts (Table 3). A high degree of similarity was registered for species lists of zooplankton of middle and lower reservoir parts. The differences between the species lists of the zooplankton of the four experimental stations were mainly found for rotifers ( $J = 43.8 \pm 3.23$ ;  $\text{lim} - 33.3\text{--}54.5$ ), which were characterized by high species richness and, to a lesser extent, for cladocerans ( $J = 63.0 \pm 9.26$ ;  $\text{lim} - 51.2\text{--}86.1$ ) and copepod crustaceans ( $J = 74.9 \pm 8.58$ ;  $\text{lim} - 63.5\text{--}95.0$ ). Thus, the differences in the littoral zooplankton communities of the headwaters from other parts of the reservoir can be explained by the presence of lotic conditions in the upper part of the reservoir, which cause the formation of a specific complex of rotifers.

**Table 2**

Species representation of the littoral zooplankton in different formations of macrophytes and places without plants in the Oleksandrivka Reservoir (%)

Biotopes	Rotifers	Cladocerans	Copepods
Reed formations	40.1	35.6	24.3
Bulrush formations	38.8	40.1	21.1
Pondweed formations	33.7	41.9	24.4
Without macrophytes	45.3	37.3	17.4

**Table 3**

Species similarity of the littoral zooplankton communities (J, %) of different parts of the Oleksandrivka Reservoir

Parts of reservoir	The upper part	The middle part, the right bank	The middle part, the left bank
The middle part, the right bank	48.2	–	–
The middle part, the left bank	50.0	72.2	–
The lower part	48.3	59.0	63.1

The dominant complexes of littoral zooplankton in different years included: rotifers – *B. calyciflorus*, *B. quadridentatus*, *E. dilatata*, *K. quadrata*, and *T. bidens*; cladocerans – *B. longirostris*, *Ch. piger*, *Ch. sphaericus*, *D. cucullata*, *D. brachyurum*, *D. rostrata*, and *S. crystallina*; copepods – *A. americanus*, *E. serrulatus*, *E. velox*, *M. leuckarti*, and *Th. crassus*.

Spatio-temporal dynamics of the structural organization of the littoral zooplankton communities in the Oleksandrivka Reservoir. Spatial-temporal dynamics of the littoral zooplankton communities were investigated in 2009–2010.

**Seasonal dynamics.** Peculiarities of seasonal dynamics of species composition and structure of littoral zooplankton communities of Oleksandrivka Reservoir were published in the previous article (Trokhymets & Lukashov, 2016). However, questions remain unanswered as to what factors influence the formation of seasonal dynamics of the species composition, density, and biomass of zooplankton communities and their taxonomic groups. Several methods of statistical analysis were used for this purpose (Table 4, Fig. 2). The concentration of oxygen, most cations, and anions depends on the seasons since the temperature is a catalyst for many chemical processes and their activity. In turn, it was shown that the biomass of phytoplankton had a significant impact on the density and biomass of both zooplankton as a whole and most of its groups.

**Daily dynamics.** In the summer, to study the dynamics of the changes in the spatial structure of littoral zooplankton communities in different periods of the day and the features of zooplankton migrations, daily investigations were conducted within the lower part of the Oleksandrivka Reservoir. 28 species of littoral zooplankton were detected in the formations of macrophytes in the afternoon and 17 species were found in the biotopes without macrophytes. 26 and 21 species were recorded within different biotopes in the evening, at night – 28 and 22 species, in the morning – 30 and 35 species. In this case, the species composition of littoral zooplankton in macrophyte thickets had mainly a high degree of similarity during the day, but a degree of similarity was low in the biotopes without macrophytes (Table 5).

Quantitative indicators of littoral zooplankton varied during the day, and their changes in different biotopes were specific. A stable density with a gradual increase at night hours was typical for littoral zooplankton in the biotopes without macrophytes. Instead, the peak of the increase in the den-

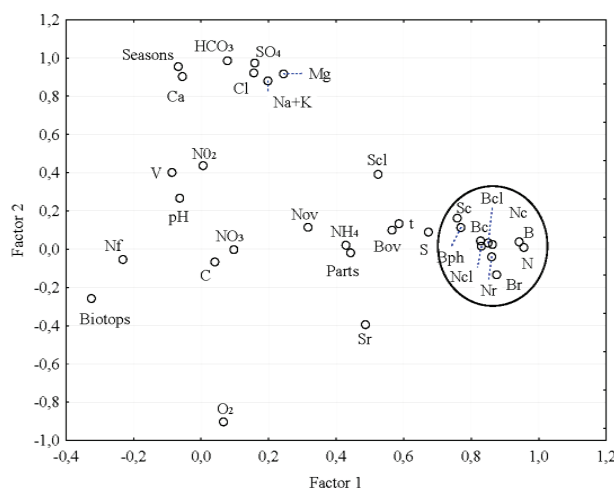
sity of littoral zooplankton was reached at night, when its concentration increased by almost 1.5 times compared to the evening hours (Fig. 3).

**Table 4**

Multifactor analysis of the influence of significant environmental factors on the seasonal dynamics of the littoral zooplankton communities of the Oleksandrivka Reservoir

Variable	Factor 1	Factor 2	Factor 3
Seasons	-0.067	0.953	0.090
O <sub>2</sub>	0.066	-0.903	-0.250
NO <sub>3</sub>	0.097	-0.002	0.712
HCO <sub>3</sub>	0.078	0.985	-0.036
SO <sub>4</sub>	0.159	0.973	0.045
Cl	0.156	0.921	0.007
Ca	-0.055	0.902	0.159
Mg	0.244	0.916	-0.156
Na+K	0.198	0.879	0.032
Bph	0.769	0.113	-0.137
Sc	0.758	0.161	-0.063
N	0.956	0.009	0.130
Nr	0.860	-0.039	0.030
Ncl	0.829	0.015	0.113
Nc	0.863	0.024	0.183
B	0.942	0.038	0.159
Br	0.875	-0.133	0.036
Bcl	0.850	0.032	0.143
Bc	0.828	0.042	0.176

Notes: the table shows only those factors that were significant; factor loadings (varimax normalized); extraction: principal components (marked loadings are >0.70).



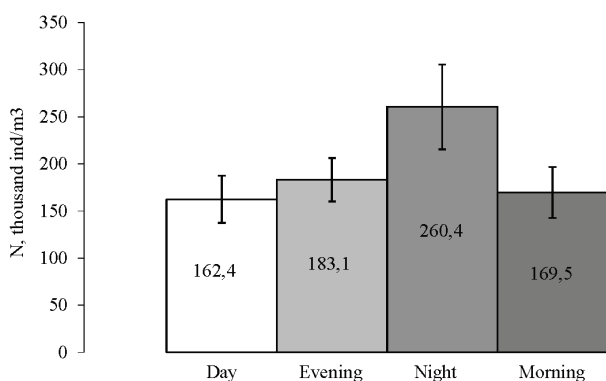
**Fig. 2.** Influence of environmental factors on the formation of the littoral zooplankton communities of the Oleksandrivka Reservoir: factor loadings (factor 1 vs. factor 2); rotation (varimax normalized); extraction (principal components)

**Table 5**

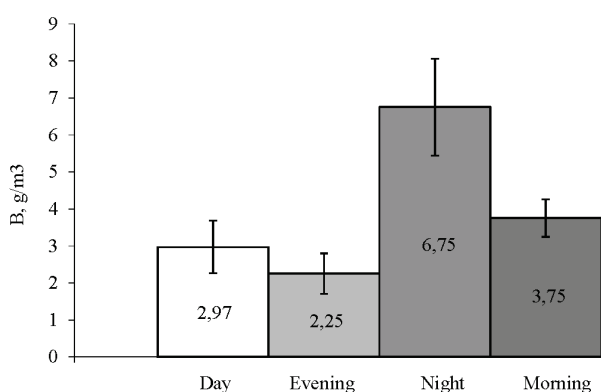
Comparison of the daily dynamics of species composition (J) of the littoral zooplankton of the Oleksandrivka Reservoir

Periods of the day	Day	Evening	Night	Morning
Macrophyte biotopes				
Day	–	58.2	51.3	45.6
Evening	48.4	–	54.6	51.6
Night	43.9	46.3	–	46.7
Morning	36.3	51.4	42.6	–
Biotopes without macrophytes				

The dynamics of daily changes in biomass showed similar trends as those for density. In general, littoral zooplankton had higher biomass among macrophytes (Fig. 4), where it grew 3 times at night (from 2.25 g/m<sup>3</sup> in the evening to 6.75 g/m<sup>3</sup> at night). Outbreaks of the growth of cladoceran *D. brachyurum* account for the dramatic growth of zooplankton biomass in macrophytes at night. This species of cladoceran had a large individual mass, which provides high rates of the total biomass of littoral zooplankton.



**Fig. 3.** Daily dynamics of the density of littoral zooplankton communities in formations of aquatic plants of the Oleksandrivka Reservoir: mean  $\pm$  standard deviation;  $P < 0.05$ ;  $n = 16$



**Fig. 4.** Daily dynamics of the biomass of littoral zooplankton communities in formations of aquatic plants of the Oleksandrivka Reservoir: mean  $\pm$  standard deviation;  $P < 0.05$ ;  $n = 16$

The dominant complex of littoral zooplankton included five species in different biotopes during the day: rotifers *B. quadridentatus* and *E. dilatata*, cladocerans *D. brachyurum*, and *S. crystallina*, and copepods *M. leuckarti*. The dominant zooplankton were represented by four species in the evening: rotifers *B. quadridentatus* and *E. dilatata*, cladoceran *D. brachyurum*, and copepod *A. americanus*. The dominant complex of zooplankton combined three species of cladocerans (*B. longirostris*, *Ch. sphaericus*, and *D. brachyurum*) at night. Five species of zooplankton dominated in the littoral zone in the morning: rotifer *E. dilatata*, cladocerans *D. brachyurum*, and *L. kindtii*, copepods *E. velox* and *M. leuckarti*. A comparison of daily changes of dominant complexes of zooplankton species is presented in Table 6.

**Table 6**

Comparison of the daily dynamics of dominant species complexes ( $J_{dom}$ ) of the littoral zooplankton of the Oleksandrivka Reservoir

Periods of the day	Day	Evening	Night
Evening	50.0	–	–
Night	14.3	16.7	–
Morning	42.9	28.6	14.3

## Discussion

The total species diversity of littoral zooplankton was 126 species in the mesotrophic Oleksandrivka Reservoir in the original studies. This number is high for mountain (canyon) reservoirs. So, researchers found 45 species of zooplankton in the average size canyon Roman Reservoir in the Czech Republic (Seda & Devetter, 2000). The similar species richness of zooplankton is characteristic of other mountain (canyon) reservoirs located in the different regions of the Earth: researchers found 29 species in 49 small Côte d'Ivoire reservoirs in Africa (Aka et al., 2000); 21 species of zooplankton were registered for the Prado Reservoir that is located in the Colombian Andes of South America (Guevara et al., 2009). This can be

explained by the fact that the water level in the Oleksandrivka Reservoir was raised twice during the study period from 8 to 14.7 m in 2006 and from 14.7 to 16.0 m in 2010. As a result, a more pronounced littoral zone of the reservoir with different macrophyte associations was formed, and the usual zooplankton groups included floodplain species. Therefore, many years of research made it possible to better investigate the reservoir and register the different littoral zooplankton communities that formed during successional processes in littoral ecosystems. This can explain also the large number of new species in the Oleksandrivka Reservoir (76% of the total number of zooplankton). The rotifer *E. dapidula* was first discovered for the first time in the fauna of Ukraine. However, this species was also recorded during parallel studies of zooplankton in the littoral zone of the Kyiv and Kaniv Reservoirs (Trokhymets, 2014; Trokhymets, 2016).

The faunistic spectrum of littoral zooplankton was characterized by the predominance of rotifers (47.6%), which can be explained by the canyon structure of the Oleksandrivka Reservoir and the preservation of rheophilic conditions within its water area. At the same time, rotifers, sensitive to changes in the habitat, had a much lower frequency of species occurrence (18.3% of species). The predominance of the rotifer complex is also characteristic of zooplankton communities of many other canyons and mountain reservoirs. Thus, rotifers are represented by 27 species in the Roman Reservoir, and crustaceans – by 18 (Seda & Devetter, 2000). Rotifers numbered 20 species in 49 small Côte d'Ivoire reservoirs in Africa, cladocerans – 6, and copepods – 3 (Aka et al., 2000). Rotifers represented 6 species in the Prado Reservoir, cladocerans – 5, and copepods – 1 (Guevara et al., 2009). This can be explained by the fact that lotic conditions are preserved in canyon reservoirs, which are more favorable for rotifers than crustaceans.

On the other hand, a significant proportion of the zooplankton community is composed of cladocerans (35.7%). This is due to the successive raising of the reservoir's water level to the levels of 14.7 and 16.0 m. As a result, large areas of the shoreline were flooded, which contributed to the formation of the littoral zone and its overgrowth by macrophytes. Thus, the littoral zooplankton communities of the Oleksandrivka Reservoir were formed by both pelagic forms and coastal phytophilous groups that were brought from the actual biofund of this reservoir and other reservoirs. This was confirmed by the highest frequency of copepod species occurrence (57.1% of species) as the most stable part of the zooplankton community during all the years of study.

Most species of littoral zooplankton belong to the freshwater group and non-predators, which is typical for other studies in reservoirs of different regions of the planet (Aka et al., 2000; Seda & Devetter, 2000; Guevara et al., 2009). However, representatives of one species of the brackish water group were found in our samples. It was a copepod crustacean *E. velox*. The fact is that this species is euryhaline. Euryhaline species began to settle in the reservoirs after the formation of reservoirs with slow water flow, gradually moving upstream. For example, this species is common in the upper part of the Dnieper River – Kyiv and Kaniv Reservoirs (Trokhymets, 2014; Trokhymets, 2016). The question of how representatives of this species cross river sections between different reservoirs remains unanswered. Visual observations of waterfowl allow us to hypothesize that eggs of many species of zooplankton can be transferred from one reservoir to another by birds in their feathers and feet. For example, similar hypotheses have already been expressed regarding Antarctic copepods (Trokhymets et al., 2024).

The species composition of littoral zooplankton varied considerably within different parts of the Oleksandrivka Reservoir. Thus, a low and medium degree of similarity of littoral zooplankton communities was revealed in the upper part and other parts of the reservoir, and a high degree of similarity was revealed between the middle and lower reservoir parts. This can be explained by the average size of the reservoir and the formation of a pronounced littoral zone after a consistent rise in water level. Therefore, species change even under rheophilic conditions in thickets of different macrophyte formations within different parts of the reservoir. These data indicate the formation of persistent species of cladocerans and copepods in the littoral zooplankton communities within different parts of the reservoir. The species nuclei of rotifers are less stable in the littoral communities of zooplankton, and their composition varies in different parts of the reservoir. The higher species representation of zooplankton is associated with a mo-

re pronounced littoral zone in the middle part of the reservoir and more complex associations of macrophytes based on the formations of clasping leaf pondweed. The difference between the zooplankton of the upper reservoir and its other parts can be explained by the conservation of the flow conditions within its boundaries, the formation of zooplankton communities from the rheophilic river components, and the specificity of the macrophyte formations. This is evidenced by data from other researchers collected within other reservoirs of Ukraine (Pashkova, 2004; Pashkova, 2008). Instead, the hydrological conditions and macrophytes formations of the middle and lower parts of the reservoir differ little, which provided a high degree of similarity in the species lists of these parts of the reservoir.

Temperature has a serious effect on the abundance of zooplankton species as a factor in enhancing the development of macrophytes (Yin et al., 2018). Multivariate analysis of our data showed that the density and biomass of different taxonomic groups of littoral zooplankton and their communities are triggered by phytoplankton biomass as the main feed object. Therefore, it can be generalized that the formation of the species richness of littoral zooplankton in reservoirs is significantly influenced by temperature, and the density and biomass of zooplankton are influenced by the biomass of phytoplankton as the main forage object.

Daily dynamics of littoral zooplankton groups are associated with the migration of representatives of this group of aquatic organisms, which results in the restructuring of the species structure of littoral zooplankton groups. It should be noted that stable groups of zooplankton do not form in the biotopes without macrophytes of the medium-sized reservoir with strong current water in different periods of the day. Instead, the water flow plays a smaller role in the redistribution of zooplankton in overgrown biotopes and their migration activity comes first. This is due to the nocturnal migration of zooplankton to the shore and the water surface. However, data from other researchers suggest that the migration characteristics of littoral zooplankton may vary depending on the abiotic conditions of reservoirs and features of biotic interactions inside ecosystems (Wojtal et al., 2003).

## Conclusions

The structural and functional organization of the littoral zooplankton communities in the Oleksandrivka Reservoir was investigated for the first time. A total of 96 species was observed in the reservoir for the first time, and the rotifer *E. dapidula* was first described for the fauna of Ukraine. Rotifers predominated in the faunistic spectrum and non-predator representatives predominated in the trophic spectrum of the littoral zooplankton. Representatives of the rotifer-cladoceran complex of zooplankton dominated in thickets of reeds and biotopes without macrophytes. The zooplankton composition of different parts of the reservoir was characterized by a high degree of similarity. The complex of dominant species includes five species of rotifers, seven species of cladoceran crustaceans, and five species of copepod crustaceans. Phytoplankton biomass affects zooplankton density and biomass. Zooplankton was characterized by an increase in the density and biomass at night and a decrease of these quantities in other periods of the day in daily dynamics, which is related to its daily migrations.

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