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THE IMPORTANCE OF VARIOUS SPECIES OF MOLLUSCS – SECOND INTERMEDIATE HOSTS – IN MAINTAINING THE CIRCULATION OF POLYCHOSTAL SPECIES OF TREMATODES IN THE WATER BODIES OF THE UKRAINIAN POLISSYA

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Background. The paper considers the importance of various species of molluscs as second intermediate hosts in the circulation of polyhostal species of trematodes in the Ukrainian Polissya. It was found that the metacercariae of trematodes are concentrated mainly in the most abundant individuals both in a particular water body and in the region as a whole. The specificity of trematodes for a particular intermediate host is determined by the influence of a number of environmental factors. Due to a significant decline in populations of many mollusc species as a result of anthropogenic alteration of the environment, there is a need to determine the species composition of trematode metacercariae in freshwater molluscs in the region, with emphasis on their importance in maintaining local and regional populations of these helminths.

Materials and Methods. The study of trematode metacercariae in gastropods from water bodies of the region was carried out in 2002–2012 and 2022. The molluscs were collected manually or with a net, using conventional methods in malacology. During the study period, more than 50,000 specimens of molluscs from 5 families were examined: Lymnaeidae, Bulinidae, Planorbidae, Bithyniidae and Viviparidae. The morphology of metacercariae was studied on live specimens using vital stains. The extent of invasion was determined during the helminthological dissection of the molluscs. Statistical analysis of the data was performed using Statastica 8.0. The Yates corrected Chi-square test with Bonferroni correction was applied.

Results. Nineteen species of trematode metacercariae, including three species of cercariae, were found in 22 species of molluscs from water bodies in the region. For

9 trematode species, new mollusc species were found to act as a second intermediate host. In 8 out of 16 identified trematode species, the same mollusc species play the role of first and second intermediate host. The findings of the present study indicate that the majority (56.25 %) of the identified trematodes were found in two or more molluscs of different families, acting as second intermediate hosts.

Conclusions. Metacercariae, whose host specificity is usually much broader, are concentrated in the most common mollusc species in the region or even in a particular water body, which are potential second intermediate hosts of these helminths. In the distribution of trematodes at the metacercariae stage, the species composition of mollusc communities and the number of their individual species mainly determine the possibility of a parasite-host encounter.

Keywords: trematode fauna, second intermediate host, molluscs, extensive infection, metacercariae

INTRODUCTION

Over the course of evolution, life cycles of many trematode species have become more complex due to the addition of a second intermediate host to the already established mollusc-vertebrate cycle. The emergence of a second intermediate host not only contributed to expanding the possible range of definitive hosts, but also to reducing the element of chance in the parasite's developmental cycle. In a significant number of polyhostal trematode species, the function of the second intermediate host is often performed by molluscs of different classes, regardless of which hosts serve as the definitive host. Mollusc hosts, in which cercariae and metacercariae are formed, are an important link in the spread of trematodes in vertebrate populations, including livestock and humans (Żbikowska & Nowak, 2009).

In the life cycle of trematodes, after encystation in the external environment or penetration into the body of the intermediate host, cercariae undergo metamorphosis or certain stages of morphogenesis and transform into metacercariae (Stadnichenko, 2014). This stage of maritae development is characterised by a broader host specificity than parthenites of the same species, which is due to a rather late formation of the biological system "metacercaria – second intermediate host" in the process of phylogenesis (Stadnichenko, 2014).

To date, the most detailed data on trematode metacercariae from molluscs of Ukraine are presented in the works of V. I. Zdun (1961), G. I. Vergun (1962), M. I. Chernogorenko (1983), O. S. Kudlay (2009), A. P. Stadnychenko (2014) and O. P. Zhytova (2023). However, there is still a lack of information on the species composition of trematode metacercariae in molluscs of the Ukrainian Polissya, in particular the specificity of metacercariae of different trematode species in relation to different host categories (Zhytova & Korniushyn, 2017).

The specificity of a parasite to a particular host is a dynamic phenomenon determined by a number of environmental factors. The specificity of the parasite to the host also changes under the influence of environmental factors.

Considering the dramatic transformations of the natural environment caused by global climate warming and various anthropogenic factors, specifically, pollution of most aquatic ecosystems by radionuclides and other pollutants, leading to structural changes in aquatic communities (Zhytova & Korol, 2021; Sheluk *et al.*, 2023), it becomes important to determine the role of various species of molluscs – second intermediate hosts of Ukrainian Polissya water bodies in maintaining the circulation of polyhostal species of trematodes. The study of the role of freshwater molluscs in the biological cycles of trematodes is of great interest for understanding the evolutionary pathways of parasites and patterns of their distribution (Akramova *et al.*, 2024). Therefore, the aim of this study was to determine the species composition of trematode metacercariae and the role of their intermediate molluscan hosts in the distribution of these parasites in the water bodies of Polissya, Ukraine.

MATERIALS AND METHODS

The material for the research was based on gastropod collections of more than 50,000 specimens from 5 families, namely Lymnaeidae (15 species), Bulinidae (3 species), Planorbidae (4 species), Bithyniidae (2 species) and Viviparidae (3 species), collected in 2002–2012 and 2022.

The basis of this work was the collection of trematode metacercariae obtained by opening the molluscs. Molluscs were collected manually or with a net according to conventional methods (Stadnychenko, 1990, 2006). Molluscs were identified by conchological data, taking into account their anatomical data (Stadnychenko, 1990, 2004). The material was processed according to the recommendations of V. I. Zdun (1961). Parasitological studies were carried out according to generally accepted methods (Zdun, 1961; Zhytova, 2023). The morphology of metacercariae was studied on live specimens using vital stains (Zdun, 1961; Zhytova, 2023). The monograph of V. I. Zdun (Zdun, 1961), M. I. Chernogorenko (Chernogorenko, 1983) and some articles in domestic and foreign journals describing the life cycle of trematodes were used to determine the species of metacercariae. In order to confirm the species identity and to obtain trematode marites, we performed infection experiments (Zhytova, 2023).

The identification of the species of trematode larvae was carried out in accordance with the monographs of V. I. Zdun (1961) and M. I. Chornogorenko (1983); materials from individual articles on the life cycle of trematodes published in Ukrainian and foreign journals in the period from 1962 to 2024 was also used.

In order to study the infection of molluscs by metacercariae of a certain trematode species and to analyse the distribution of polyxenous species among molluscan hosts, we used the index of extensive infection (EI), calculated the general occurrence index (OI_g) and the partial occurrence index (OI_p) using the following formulas.

The statistical evaluation of the mollusc infestation (infection rate) was carried out as proposed for the characterisation of the level of fish infection: $Q\% \pm m\%$ – where Q is the mean infestation rate, m is the deviation from the mean.

The error to the mean was determined by the following formula:

$$m = \frac{\delta}{\sqrt{n}},$$

where δ is the range of variability; n – number of dissections.

The range of variability was determined using the following formula:

$$\delta = \pm\sqrt{Q\% \cdot (100\% - Q\%)}.$$

$$OI_g = \frac{Nb_i}{Nb_t} \cdot 100\%; \ OI_p = \frac{Nb_i}{Nb_p} \cdot 100\%,$$

Nb_i – number of water bodies where molluscs infected with this trematode species were found; Nb_t – number of water bodies where molluscs were collected; Nb_p – number of water bodies where this mollusc species was found.

They represent the proportion (in %) of water bodies in which a certain species of molluscs was infected with this species of trematodes in the total number of water bodies surveyed or the number of water bodies in which this species of molluscs was found (Zhytova & Kornyushyn, 2017).

As an additional criterion for evaluating a particular mollusk species in the distribution of a particular trematode species in the region, a scoring system was also used, which was calculated by multiplying the indicators of the extent of invasion and the total invasion index.

$$UP = EI \cdot OI_g,$$

where UP is the value of a particular mollusc species in the distribution of a particular trematode species in points (Zhytova & Kornyushyn, 2017).

The infection rates were analyzed using the Statistica 8.0 software. The Yates corrected Chi-square test with Bonferroni correction was applied.

RESULTS AND DISCUSSION

During the study period, metacercariae of 19 trematode species, including three cercariae species, were found in 22 species of freshwater molluscs of the Ukrainian Polissya (see **Table**).

Qualitative composition of trematodes at the metacercariae stage of freshwater gastropods in the Ukrainian Polissya water bodies

Mollusc species	Family, species of trematode	Infestation rate, %.
1	2	3
Lymnaea (*Lymnaea*) *stagnalis* (Linné, 1758)	Family Strigeidae Railliet, 1919	
	Cotylurus cornutus (Rudolphi, 1808)	2.81±1.39
	Tetracotyle sp.	0.71±0.32
	Family Echinostomatidae Looss, 1899	
	Echinoparyphium aconiatum Dietz, 1909	0.98±0.11
	Echinoparyphium recurvatum (Linstow, 1873)	1.06±0.16
	Echinostoma revolutum (Fröhlich, 1802)	1.04±0.11
	Echinoparyphium cinctum (Rudolphi, 1802)	2.0±1.04
	**Echinostoma miyagawai* Ishii, 1923	4.37±0.48
	Hypoderaeum conoideum (Bloch, 1782)	2.81±1.39
	Family Plagiorchiidae Lühe, 1901	
	Plagiorchis laricola Skrjabin, 1924	2.52±1.44
	Family Telorchiidae Looss, 1899	
	Opisthioglyphe ranae (Fröhlich, 1791)	1.03±0.19
Lymnaea corvus Gmelin, 1791	Family Strigeidae Railliet, 1919	
	Cotylurus cornutus (Rudolphi, 1808)	0.90±0.27
	Family Echinostomatidae Looss, 1899	
	Echinoparyphium aconiatum Dietz, 1909	2.28±0.76
	Echinoparyphium recurvatum (Linstow, 1873)	0.27±0.19
	Echinostoma revolutum (Fröhlich, 1802)	1.41±0.70
	Hypoderaeum conoideum (Bloch, 1782)	0.44±0.25

Continued Table

1	2	3
Lymnaea (*Stagnicola*) *palustris palustris* (O. F. Müller, 1774)	Family Strigeidae Railliett, 1919 *Cotylurus cornutus* (Rudolphi, 1808) Family Echinostomatidae (Fröhlich, 1802) *Echinoparyphium aconiatum* Dietz, 1909 *Echinoparyphium recurvatum* (Linstow, 1873) *Echinostoma revolutum* (Frohlich, 1802) *Hypoderaeum conoideum* (Bloch, 1782)	 0.22±0.08 1.52±0.87 0,42±0,18 0.44±0.01 0.27±0.09
Lymnaea balthica (Linné, 1758)	Family Echinostomatidae Looss, 1899 *Echinoparyphium aconiatum* Dietz, 1909	 7.40±5.04
Lymnaea atra atra (Schranck 1803)	Family Echinostomatidae Looss, 1899 *Echinoparyphium aconiatum* Dietz, 1909 *Echinostoma revolutum* (Fröhlich, 1802)	 2.31±0.93 0.77±0.54
Lymnaea danubialis (Schranck 1803)	Family *Echinostomatidae* Looss, 1899 **Echinostoma stantchinskii* Semenov, 1927	 12.50±11.69
Lymnaea ovata (Draparnaud, 1805)	Family Echinostomatidae Looss, 1899 *Echinoparyphium aconiatum* Dietz, 1909 **Echinoparyphium recurvatum* (Linstow, 1873) *Echinostoma revolutum* (Fröhlich, 1802) *Echinoparyphium cinctum* (Rudolphi, 1802) *Hypoderaeum conoideum* (Bloch, 1782)	 0.75±0.25 4.20±4.08 3.79±2.15 3.44±2.39 5.0±3.44
Lymnaea fontinalis (Studer, 1820)	Family Echinostomatidae Looss, 1899 *Echinoparyphium aconiatum* Dietz, 1909 *Moliniella anceps* (Molin, 1859)	 4.34±3.01 5.0±4.88
Lymnaea tumida Held, 1836	Family Echinostomatidae Looss, 1899 *Echinoparyphium aconiatum* Dietz, 1909 **Echinostoma revolutum* (Fröhlich, 1802)	 4.35±0.93 3.45±1.02
Lymnaea auricularia (Linné, 1758)	Family Strigeidae Railliet, 1919 *Cotylurus cornutus* (Rudolphi, 1808) Family Echinostomatidae Looss, 1899 *Echinoparyphium aconiatum* Dietz, 1909 *Echinostoma revolutum* (Fröhlich, 1802)	 3.57±3.50 1.45±0.72 2.16±1.07
Lymnaea lagotis (Schranck, 1803)	Family Echinostomatidae Looss, 1899 *Echinostoma revolutum* (Fröhlich, 1802)	 3.61±2.05
Lymnaea patula (Da Costa, 1778)	Family Echinostomatidae Looss, 1899 *Echinoparyphium aconiatum* Dietz, 1909 **Echinostoma revolutum* (Fröhlich, 1802)	 2.70±1.88 1.18±0.83
Lymnaea psilia psilia Bourguignat, 1862	Family Echinostomatidae Looss, 1899 **Echinoparyphium aconiatum* Dietz, 1909	 3.57±2.48
Planorbarius corneus (Linné, 1758)	Family *Strigeidae* Railliet, 1919 *Cotylurus cornutus* (Rudolphi, 1808) Family Echinostomatidae Looss, 1899 *Echinoparyphium aconiatum* Dietz, 1909 *Echinoparyphium recurvatum* (Linstow, 1873) **Echinostoma mijagawai* Ischii, 1932 *Echinostoma revolutum* (Fröhlich, 1802) **Echinostoma robustum* Yamaguti, 1935 *Hypoderaeum conoideum* (Bloch, 1782) Family Telorchiidae Looss, 1899 *Opisthioglyphe ranae* (Fröhlich, 1791)	 5.51±0.34 0.79±0.14 0,98±0.21 0.38±0,27 1.9±0.39 0.47±0.23 0.49±0.14 0.87±0.36

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1	2	3
Planorbarius banaticus (Lang, 1856)	Family Strigeidae Railliet, 1919 **Cotylurus cornutus* (Rudolphi, 1808)	 6.67±4.55
Planorbarius purpura (O. F. Müller, 1774)	Family Strigeidae Railliett, 1919 **Cotylurus cornutus* (Rudolphi, 1808)	 11.11±6.04
Planorbis planorbis (Linné, 1758)	Family Echinostomatidae Looss, 1899 *Echinostoma revolutum* (Fröhlich, 1802) *Echinostoma mijagawai* Ischii, 1932 *Hypoderaeum conoideum* (Bloch, 1782)	 2.13±0.67 0.45±0.15 0.67±0.67
Anisus (*Anisus*) *spirorbis* (Linné, 1758)	Family Echinostomatidae Looss, 1899 *Echinoparyphium aconiatum* Dietz, 1909	 1.38±0.97
Bithynia (*Bithynia*) *tentaculata* (Linné, 1758)	Family Cyathocotylidae Mühling, 1898 **Cyathocotyle bithyniae* Sudarikov, 1974 Family Echinostomatidae Looss, 1899 *Echinoparyphium aconiatum* Dietz, 1909 *Echinoparyphium recurvatum* (Linstow, 1873) *Echinostoma chloropodis* (Zeder, 1800) *Hypoderaeum conoideum* (Bloch, 1782) Family Lissorchiidae Magath, 1917 *Palaeorchis* sp. **Parasymphylodora parasquamosa* Kulakova, 1972 Family Stomylotrematidae Poche, 1926 **Lateotrema arenula* (Creplin, 1825)	 0.36±0.26 0.50±0.22 10.52±3.52 4.37±1.75 0.20±0.14 6.80±2.48 4.55±2.57 2.09±1.20
Contectiana (*Contectiana*) *contecta* (Millet, 1813)	Family Echinostomatidae Looss, 1899 *Echinoparyphium aconiatum* Dietz, 1909 *Echinoparyphium recurvatum* (Linstow, 1873) *Hypoderaeum conoideum* (Bloch, 1782) *Neocanthoparyphium echinatoides* (Filippi, 1854) Family Lissorchiidae Magath, 1917 **Asymphylodora imitans* Mühling, 1898	 4.0±0.75 8.7±2.4 4.76±2.32 2.73±1.91 14.80±6.82
Viviparus (*Viviparus*) *viviparus* (Linnaeus, 1758)	Family Echinostomatidae Looss, 1899 *Echinoparyphium aconiatum* Dietz, 1909 *Echinoparyphium recurvatum* (Linstow, 1873) *Echinostoma revolutum* (Fröhlich, 1802) *Hypoderaeum conoideum* (Bloch, 1782) *Neocanthoparyphium echinatoides* (Filippi, 1854)	 1.21±0.36 0.73±0.42 1.01±0.41 6.29±2.15 2.56±0.37
Contectiana (*Contectiana*) *listeri* (Forbes et Hanley, 1853)	Family Echinostomatidae Looss, 1899 **Echinoparyphium recurvatum* (Linstow, 1873) **Neocanthoparyphium echinatoides* (Filippi, 1854)	 8.57±6.97 0.97±0.96

Note: * – Species for which intermediate hosts are listed for the first time

Analyses of the data obtained revealed that the four most common species of trematodes from the family Echinostomatidae, parasites of birds, had the widest range of molluscs. *E. aconiatum* was found in 16 species of molluscs belonging to the families Lymnaeidae, Bulinidae, Planorbidae, Bithyniidae and Viviparidae. Accordingly, trematodes of *E. revolutum* were found in 12 species of molluscs, *H. conoideum*, *E. recurvatum* – in 10 species, *H. conoideum* – in 9 species. At the same time, parthenites and cercariae of these species were found only in two to four species of molluscs.

For the trematode of *E. aconiatum*, *L. stagnalis* ranked first among molluscs – second intermediate host – the OI_p of metacercariae of these trematodes was 49.06 % (26 out of 53 reservoirs), respectively OI_g (out of 63 reservoirs) – 41.26 % (**Fig. 1**). The second most important was *P. corneus* – the index of occurrence of metacercariae was 26.08 % (12 out of 14 water bodies) and 19.04 % (out of 63 water bodies). *L. palustris, L. corvus, L. ovata, C. contecta,* and *V. viviparus* accounted for a significant proportion, the index of occurrence of *E. aconiatum* (out of 63 water bodies) in these hosts was 6.34 % for the first, 4.76 % for the other three and 3.17 % for the last mollusc species. In all other mollusc species, including a rather common *B. tentaculata* (10 water bodies), metacercariae of these trematodes were found only in one water body. Regarding *A. spirorbis*, the occurrence index is 100 % (2 out of 2) and 3.17 (out of 63 water bodies), EI – 0.57 %, UP – 1.81 points.

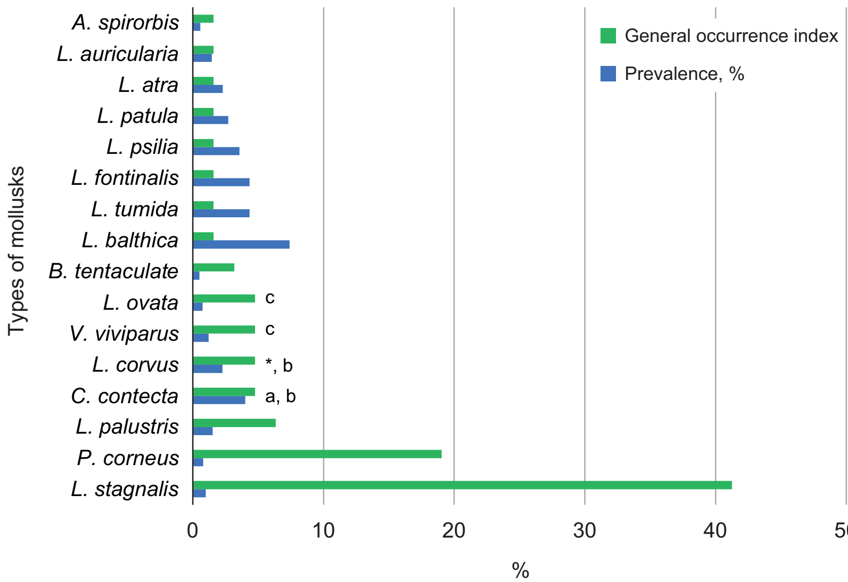

Fig. 1. Infection rates of different mollusc species with the *E. aconiatum* trematode
Notes: the difference in infection rates is significant (determined using Yates corrected Chi-square with Bonferroni correction): a – p <0.00313, * p = 0.0034 vs *L. stagnalis*; b – p <0.00313 vs *P. corneus*; c – p <0.00313 vs *C. contecta*

Accordingly, the distribution index (UP) for *L. stagnalis* was 40.43 points and for *P. corneus* – 20.6 points. Thus, the most abundant species in the water bodies of the region, *L. stagnalis* and *P. corneus,* play the main role in the distribution of *E. aconiatum* trematodes.

The *E. revolutum* trematode was also characterised by a rich list of second intermediate hosts – 12 species from the families Lymnaeidae, Planorbidae and Viviparidae. However, similar to the previous trematode species, the main role was played by *L. stagnalis* with an occurrence index of 44.23 % (23 out of 53 water bodies) and 36.51 % (out of 63 water bodies). The rate of invasion was 1.04 %, the UP – 37.97 points (**Fig. 2**).

In *P. corneus* and *P. planorbis*, the incidence rates were somewhat lower, 20.83 % (7.94 %) and 21.05% (6.35 %), despite a relatively high level of infection of these molluscs with *E. revolutum* metacercariae, 1.9 % and 2.13 %, UP – only 15.09 and

13.53 points. Infection of six other mollusc species (*L. auricularia, L. palustris, L. ovata, L corvus, L. tumida, V. viviparus*) was detected in two to three water bodies (total occurrence index – 3.17–4.76 %, infection rate – 1.01–3.79 %) and three (*L. patula, L. atra, L. lagotis*) – only in one water body, with an ITz of 1.59 %, the infestation rate of 1.18–3.61 % and a relatively high UP of 1.88, 2.15 and 5.74 respectively. The involvement of these species in the spread of *E. revolutum* was rather low.

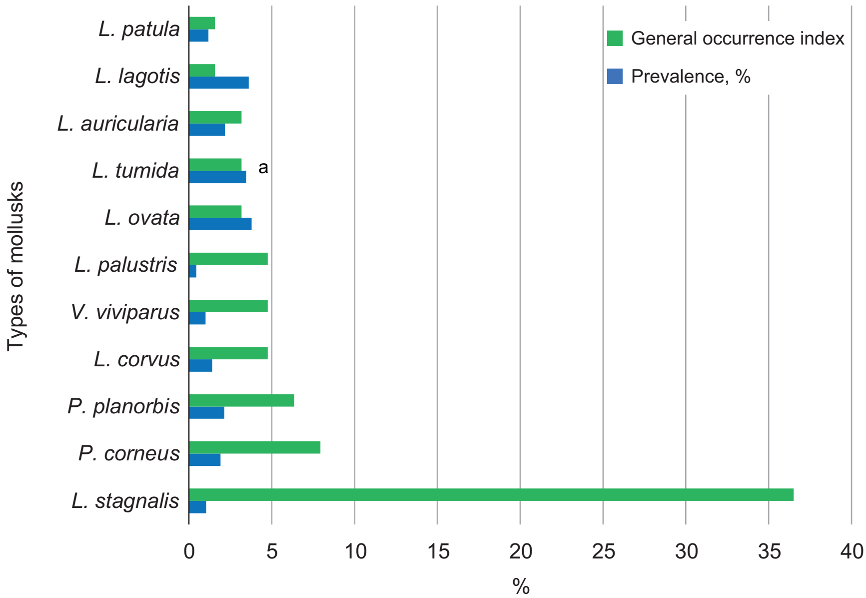

Fig. 2. Infection rates of different mollusc species with the *E. revolutum* trematode
Notes*:* the difference in infection rates is significant (determined using Yates corrected Chi-square with Bonferroni correction): a – p <0.00455 vs *L. stagnalis*

For the *E. revolutum* trematode, which was somewhat less common in the region than the previous species, the common host for the metacercariae of this trematode species was *L. stagnalis*. The infection rates of these molluscs with *E. recurvatum* were close to those of the previous trematode species. The index of occurrence of *E. recurvatum* metacercariae in *L. stagnalis* was only 9.52 % and 7.93 % respectively, the infestation rate was 1.06 %, the UP reached 8.41 points (**Fig. 3**). *L. ovata* and *P. corneus*, whose infection with *E. recurvatum* metacercariae was detected in three water bodies, also played a significant role. Accordingly, the OI_p for the first mollusc species was 27.27 %, for the second – 6.52 %, the OI_g index of occurrence to the total number of water bodies for both species was 4.7 6%, and the UP reached 20 and 4.66 points.

A much lower value of OI_g was found for *P. planorbis*, *B. tentaculate* and *V. viviparus* (3.17 % for all three), while OI_p was almost the same as for the previous species, being 10.52 %, 20% and 11.11 % respectively. Among these hosts, *B. tentaculate* stood out with a relatively high infection rate (10.52 %) and a corresponding UP – 33.35 points. Slightly lower values were recorded for *P. planorbis* and *V. viviparus*, EI – 0.29–0.73 %, with UP of 0.92 and 2.31 points, respectively. For the remaining molluscs (*L. corvus, L. palustris, C. listeri, C. contecta*), the occurrence index in relation to the total number of water bodies was 1.58 %. Among these four molluscs, *C. contecta* clearly stood out with an OI_p of 14.28, an EI of 8.7 % and a relatively high UP of 13.54 points. The other three molluscs, *L. corvus*, *L. palustris* and *C. listeri*, had lower levels of infection, with EI of 0.27 %, 0.42 % and 4.76 % respectively, which also determined the level of UP that reached 0.38, 0.66 and 7.52 points respectively.

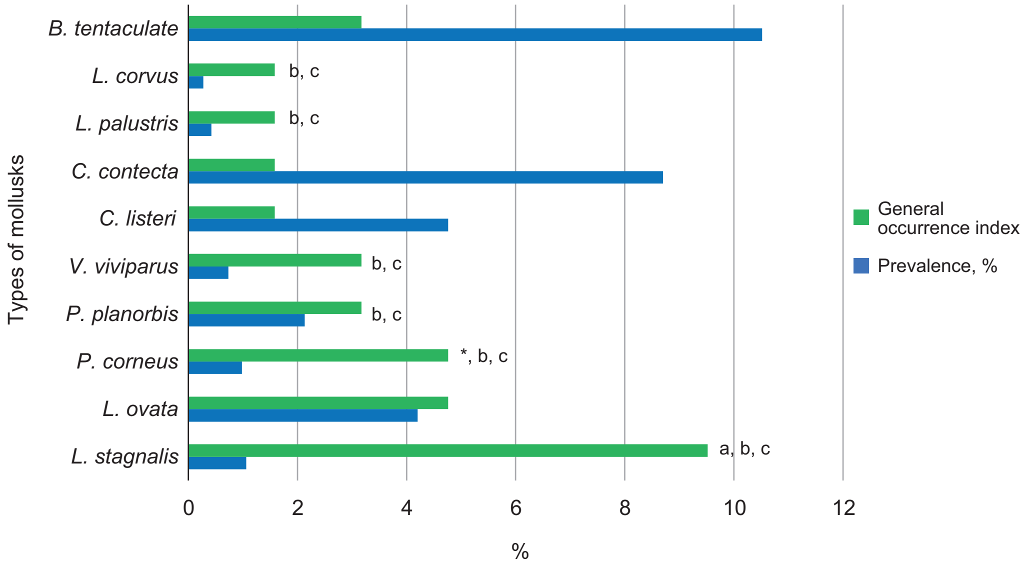

Fig. 3. Infection rates of different mollusc species with the *E. recurvatum* trematode
Notes: the difference in infection rates is significant (determined using Yates corrected Chi-square with Bonferroni correction): a – p <0.005, * p = 0.0087 vs *P. planorbis*; b – p <0.005 vs *B. tentaculata*; c – p <0.005 vs *C. contecta*

A comparative analysis shows that among the molluscs – the second intermediate hosts of *E. recurvatum* – *L. stagnalis* plays the leading role in the circulation of this trematode due to its wide distribution and a slightly higher occurrence of the trematode metacercariae in this mollusc species in various types of water bodies in the region. The role of other mollusc species in the circulation of trematodes is somewhat less pronounced despite the relatively high infection rates and occurrence of *E. recurvatum* in molluscs because the distribution of individuals in the water bodies studied in the region is somewhat lower compared to *L. stagnalis*.

For *H. conoideum*, nine mollusc species from four families were recorded as second intermediate hosts (see **Table**). Among the hosts of metacercariae of the first species, *L. stagnalis* occupies a leading position with an occurrence index of 15.38 % (8 out of 52 water bodies) and 12.7 % (out of 63 water bodies), EI – 2.81 %, UP – 35.68 points (**Fig. 4**). Almost the same infection rate was detected for *P. corneus*, whose occurrence index is 17.39 % and 12.69 % (out of 63 water bodies), EI is much lower – 0.49 %, UP – 6.21 points. Some other species of lymneids also exhibit high occurrence indices, in particular *L. ovata* – 36.36 % (4 out of 11 water bodies) and *L. palustris* – 33.35% (3 out of 6 water bodies), but the occurrence index (in relation to the total number of water bodies) is much lower – 6.34 % and 4.76 %, respectively, UP – 31.70 and 1.29 points. The role of *V. viviparus* can be considered as secondary, since the occurrence index is 16,67% (3 з 18 water bodies) and 4.76 % (out of 63 reservoirs), respectively, UP – 9.37 %.

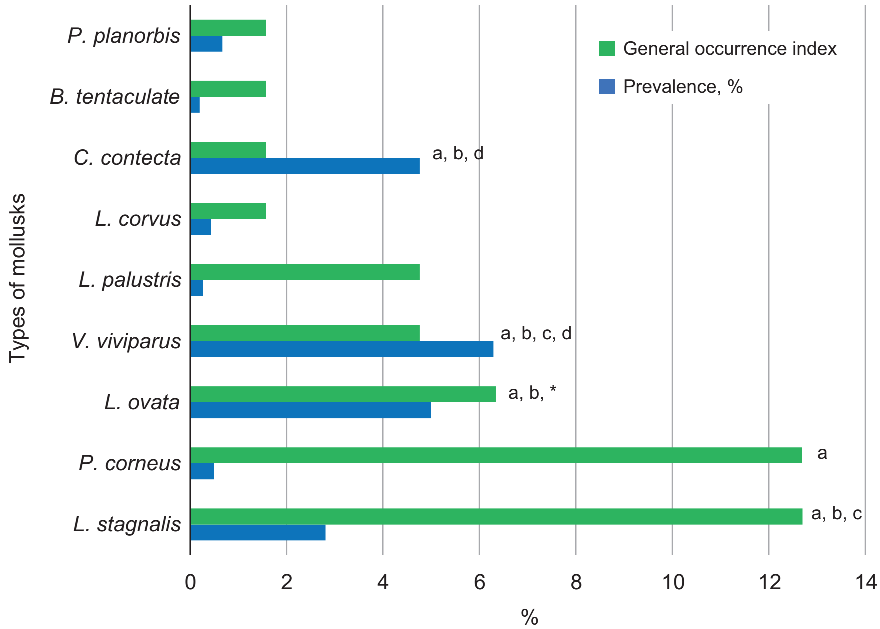

Fig. 4. Infection rates of different mollusc species with the *H. conoideum* trematode
Notes: the difference in infection rates is significant (determined using Yates corrected Chi-square with Bonferroni correction): a – p <0.0056 vs *L. palustris*; b – p <0.0056 vs *B. tentaculata*; c – p <0.0056, * p = 0.0072 vs *P. corneus*; d – p <0.0056 vs *L. corvus*

The remaining species, *L. corvus, P. planorbis, B. tentaculata* and *C. contactta* were infected with *H. conoideum* metacercariae in only one of the water bodies studied (1.58 %), OI_p – 14.28 %, 5.26, 10 and 14.29 % respectively. The highest infection rates among the mentioned molluscs were registered for *C. contactta*, 4.76 %, UP – 7.52 points, for *B. tentaculata* these rates are somewhat lower, 0.22 % and 2.33 points, respectively. Even lower rates were recorded for *L. corvus* and *P. planorbis*, 0.44 % and 0.67 %, and UP – 0.69 and 1.06 points. Therefore, the molluscs *L. corvus* and *P. planorbis* can be considered as rare second intermediate hosts for the metacercariae of the *H. conoideum* trematode in the region.

Three species of molluscs were recorded as the second intermediate hosts of *N. echinatoides* trematode in the region (see **Table**). High incidence rates were recorded for *V. viviparus*, OI_g is 3.17 %, OI_p is 11.11 %, with EI – 2.56 %, UP is 8.12 points. In *C. contecta*, metacercariae of *N. echinatoides* were found in two of the studied water bodies, OI_p – 28.57 %, OI_g – 3.17 %, EI – 2.73 %, UP – 8.65 points. Molluscs of *C. listeri* were rarely found, infected - only in one reservoir, OI_g is minimal, 1.58 %, OI_p – 16.67 %, infection rate – 0.97 %, and UP – 1.53 points. Thus, the leading role in the circulation of *N. echinatoides* belongs to *V. viviparus* and *C. contecta*. Considering that *C. listeri* was less common in the water bodies of the region, its role in the spread of this trematode is insignificant.

Metacercariae of *O. ranae* were found in two species of molluscs. Among them, the most infected was *L. stagnalis*, the incidence rates were quite high, 55.77 % and 46.03 %. Accordingly, the high UP – 47.41 points with a relatively low infection, EI – 1.03 %. As for *P. corneus*, it was infected with metacercariae of *O. ranae* in only two out of 46 water bodies where it was detected, OI_p – 4.34 % and OI_g – 3.17 %. The infection rate was much lower than that of *L. stagnalis*, 0.87 %, UP – 2.76 points. Therefore, the role of *P. corneus* in the circulation of the *O. ranae* trematode is insignificant.

The *E. cinctum, E. mijagavai, E. stantchinskii, E. robustum, E. chloropodis, M. anceps, P. laricola* and *C. bithyniae* trematodes, whose metacercariae are found in one to three mollusc species, are extremely rare in the region. It is therefore difficult to assess the role of a particular host species in their spread.

The data obtained indicate that most of the identified trematodes are characterised by a wide range of second intermediate hosts, which is due to their low specificity for the second intermediate host compared to the first, which is confirmed by studies of other scientists (Wojdak *et al*., 2013). According to L. Roberts *et al*. (2009), most digenetic trematodes infect only one mollusc species as a first intermediate host, but can also infect other species as a second intermediate host.

Analysis of the data showed that the predominant category of trematodes identified (56.25 %) was found in two or more molluscs, which serve as secondary intermediate hosts. According to the existing hypothesis (Wojdak *et al*. 2013), when trematodes are present in the body of the first obligatory intermediate host, in order to reduce its mortality, they prefer other species different from the previous one, using them as a second intermediate host. As evidenced by data from literary sources (Fredensborg *et al.*, 2005; Zhytova *et al*., 2021), as the intensity of infection of the first and second intermediate hosts increases, the survival and physiological state of the hosts may deteriorate, although the weak pathogenesis allowes to avoid the negative consequences of rapid death of the intermediate host. It was found that among the second intermediate hosts there are freshwater molluscs that also play the role of the first obligate intermediate host of trematodes, which characterises the emergence of certain feedback loops between the parasite and the intermediate host. Of the trematodes detected in this study, in 8 species (50 %) the same mollusc species play the role of the first and the second intermediate host. This means that potential intermediate hosts may differ in terms of availability, suitability, probability of transmission of the parasite to the next host or survival, considering that universality in host choice should be preferred (Sapp & Loker, 2000; Basàñez *et al*., 2007).

CONCLUSIONS

Unlike the parthenogenetic stages of trematodes (Zhytova & Kornyushyn, 2017), metacercariae, whose host specificity is usually much broader, are mainly concentrated in individuals of the most common mollusc species in the region or even in a specific water body – potential second intermediate hosts of these helminths. The degree of specificity in this case is caused by a significant advantage of the action of environmental factors, in particular the species composition of freshwater mollusc communities, their population density, which is indirectly related to hydrological conditions, and the nature of the biocenosis. All these factors determine a greater or lesser probability of meeting individuals of parasites and hosts. The same factors determine the species composition of intermediate hosts at the regional level, and thus the characteristics of the region studied in comparison with others.

At the local level, there is always a clear association of polyhostal parasite species at all stages of their life cycle with other mollusc host species. In almost all cases, a certain parasite-host system is formed, in which host specificity and environmental factors play a key role.

COMPLIANCE WITH ETHICAL STANDARDS

Conflict of Interest: the author declares that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Human Rights: this article does not contain any studies with human subjects performed by the author.

Animal studies: all international, national and institutional guidelines for the care and use of laboratory animals were followed.

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ЗНАЧЕННЯ РІЗНИХ ВИДІВ МОЛЮСКІВ – ДРУГИХ ПРОМІЖНИХ ХАЗЯЇВ ВОДОЙМ УКРАЇНСЬКОГО ПОЛІССЯ У ПІДТРИМАННІ ЦИРКУЛЯЦІЇ ПОЛІГОСТАЛЬНЫХ ВИДІВ ТРЕМАТОД

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Обґрунтування. Розглянуто значення різних видів молюсків як других проміжних хазяїв у циркуляції полігостальних видів трематод на території Українського Полісся. Встановлено, що метацеркарії трематод зосереджуються переважно в особинах, котрі є найбільш поширеними як у конкретній водоймі, так і у регіоні загалом. Специфічність трематод до певного проміжного хазяїна залежить від впливу низки екологічних чинників. У зв'язку зі значним скороченням популяцій багатьох видів молюсків унаслідок антропогенної трансформації природного середовища постає необхідність визначати видовий склад метацеркарій трематод у прісноводних молюсків регіону з акцентом на їхнє значення у підтримці локальних і регіональних популяцій цих гельмінтів.

Матеріали і методи. Дослідження метацеркарій трематод у черевоногих молюсків з водойм регіону виконували протягом 2002–2012 рр. та 2022 р. Молюски збирали вручну або за допомогою сачка, застосовуючи загальноприйняті в малакології методи. За період дослідження обстежено понад 50 тис. екземплярів молюсків із 5 родин: Lymnaeidae, Bulinidae, Planorbidae, Bithyniidae та Viviparidae. Морфологію метацеркарій вивчали на живих екземплярах з використанням вітальних барвників. Визначення екстенсивності інвазії здійснювали під час гельмінтологічного розтину молюсків. Статистичний аналіз даних проводили за допомогою програм Statistica 8.0 та Excel.

Результати. У 22 видів молюсків водойм регіону виявлено 19 видів метацеркарій трематод, з них 3 види – церкарієумів. Для 9 видів трематод знайдено нові види молюсків, які виконують роль другого проміжного хазяїна. У 8 видів трематод із 16 виявлених роль першого та другого проміжних хазяїв виконують ті ж самі види молюсків. За результатами досліджень встановлено, що більшість (56,25%) виявлених нами трематод наявні у двох і більше молюсків різних родин, які виступають як другий проміжний хазяїн.

Висновки. Метацеркарії, гостальна специфічність яких зазвичай набагато ширша, зосереджуються в найбільш поширених у регіоні чи навіть у конкретній водоймі видах молюсків – потенційних других проміжних хазяях цих гельмінтів. У поширенні трематод на стадії метацеркарія видовий склад поселень молюсків, чисельність їхніх окремих видів зумовлюють, головно, ймовірність контакту паразита з хазяїном.

Ключові слова: трематодофауна, другий проміжний хазяїн, молюски, екстенсивність ураження, метацеркарії

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