Vestnik zoologii, *51*(4): 295–310, 2017
DOI 10.1515/vzoo-2017-0035

Ecology

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UDC 594:595.122(477.41/42)

THE ROLE OF DIFFERENT MOLLUSK SPECIES IN MAINTAINING THE TRANSMISSION OF POLYHOSTAL TREMATODE SPECIES IN UKRAINIAN POLISSYA WATERS: THE SPECIFICITY OF TREMATODE PARTHENOGENETIC GENERATIONS TO MOLLUSK HOSTS

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The Role of Different Mollusk Species in Maintaining the Transmission of Polyhostal Trematode Species in Ukrainian Polissya Waters: the Specificity of Trematode Parthenogenetic Generations to Mollusk Hosts. Zhytova, E. P., Kornyushyn, V. V. — The significance of different species of freshwater gastropods in transmission of polyxenic trematode species on the territory of Ukrainian Polissya is reviewed, with emphasis on instances of the specificity of trematode parthenogenetic generations to their mollusk hosts. For some hosts of polyhostal trematode parthenitae, the leading part in sustaining the local and regional populations of certain trematode species is confirmed. Groups of the common hosts also play an important role in circulation of these helminthes. In adverse conditions, populations of some trematode species can persist using the secondary and subsidiary hosts. The rare and accidental hosts of certain trematode species do not have a significant effect on their transmission.

Key words: mollusks, trematodes, specificity, Ukrainian Polissya, categories of hosts of trematode parthenitae.

Introduction

The problem of trematode specificity to different categories of hosts is still markedly relevant. Ginetsinskaya (1968) suggests that the mollusks have been the first and only hosts of pro-trematodes. Complex relationship between trematode parthenitae and their mollusk hosts have evolved for a long time. The specificity reflects the historical relationship between the parasite and its host. The earlier such system formed, the narrower is parasite-host specificity.

Shulman (1958) notes that the parasite does not develop the specificity at once but through the lengthy accumulation and stabilization of several adaptive properties. Specificity is always narrower to the hosts in which parasite organogenesis and reproduction occur. Often, the parasite's specificity to a particular host is conditioned by ecological factors. Also, the specificity can change under the influence of environmental factors. Kennedy (1978) too points out that the specificity to hosts is not stable, it is a dynamic phenomenon.

Stadnichenko (2008) emphasizes that recently there is a degradation of the landscapes of Ukrainian Polyssia caused by diversified human activities, particularly the large-scale irrigation, deforestation, etc. Hence the drastically worsened environmental problems which necessitate the detailed studies of the distribution of local trematode populations of certain euryxenic species in different snail hosts in the water bodies of Polyssia. It should be noted that such research is most necessary in assessing and predicting current parasitological situation in view of the significant qualitative and quantitative changes in Ukrainian freshwater malacofauna.

Material and methods

Material used in this research, particularly to analyze trematode specificity, was collected by one of the authors (E. P. Zhytova). Freshwater snails were sampled in various water bodies (rivers, drainage canals, ponds, lakes, reservoirs) and also marshes in the administrative borders of six Ukrainian regions in Polissya. In total, approximately 50 thousand specimens of freshwater gastropod species of the families Lymnaeidae (15), Bulinidae (3), Planorbidae (4), Bithyniidae (2) and Viviparidae (3) were collected (table 1).

The mollusks were sampled using standard hydrobiological methods (Stadnichenko, 1990, 2006). Post-processing of the material was carried out according to V. I. Zdun (1961) and T. A. Ginetsinskaya (1968).

Parasitological examinations of mollusks were carried out according to standard methods (Zdun, 1961; Ginetsinskaya, 1968). Morphology of different trematode generations (sporocysts, rediae, unformed and mature cercariae, metacercariae) which left the mollusks was studied mostly in vivo using vital stains (Ginetsinskaya, 1968; Sudarikov et al., 2002).

Species were identified using monographs by V. I. Zdun (1961); T. A. Ginetsinskaya (1968), M. I. Chernogorenko (1958; 1983). Also, several papers on trematode life cycles published in 1934-2009 were used (Lutta, 1934; Kotova, 1939; Ginetsinskaya, 1957; Grabda, 1959; Styczynska-Jurevicz, 1962; Zdarska, 1964; Dobrovolsky, 1965; Beliakova, 1981; Iskova, 1985; Korol, 2004; Faltynkova, 2008; Kudlay, 2009, and other).

Analysis of distribution of polyxenic trematode species in mollusk hosts and evaluation of rates of snail infection by the trematode species was performed applying such widely used characteristic as prevalence (P). Additionally, if the intensity of the infection was difficult or impossible to calculate (for parthenitae and cercariae of trematodes), such parameters as the occurrence indexes (OI) were determined. All mollusks of one species infected with these parasites collected in a particular body of water were considered as singular occurrence of a certain trematode species. General occurrence index (OI_g) and partial occurrence index (OI_p) were calculated according to formulas given below. They represent the ratio (%) of water bodies inhabited by a certain snail species infected with a certain trematode species to the total number of water bodies or to the number of water bodies in which the mollusk species was found, respectively.

Table 1. The mollusk species composition in the studied water bodies of Ukrainian Polyssia

Family	Mollusk species	OI_m
Lymnaeidae	*Lymnaea stagnalis* (Linné, 1758)	85.25
	Lymnaea corvus Gmelin, 1791	11.48
	Lymnaea palustris (O. F. Műller, 1774)	14.75
	Lymnaea balthica (Linné, 1758)	1.64
	Lymnaea atra (Schranck, 1803)	1.64
	Lymnaea danubialis (Schranck, 1803)	1.64
	Lymnaea truncatula (O. F. Műller, 1774)	11.48
	Lymnaea subangulata Roffiaen, 1868	8.20
	Lymnaea ovata (Draparnaud, 1805)	18.03
	Lymnaea fontinalis (Studer, 1820)	1.64
	Lymnaea tumida Held, 1836	4.92
	Lymnaea auricularia (Linné, 1758)	4.92
	Lymnaea lagotis (Schranck, 1803)	3.28
	Lymnaea patula (Da Costa, 1778)	3.28
	Lymnaea psilia Bourguignat, 1862	1.64
Bulinidae	*Planorbarius corneus* (Linné, 1758)	75.41
	Planorbarius banaticus (Lang, 1856)	1.64
	Planorbarius purpura (O. F. Műller, 1774)	3.28
Planorbidae	*Planorbis planorbis* (Linné, 1758)	31.15
	Anisus septemgyratus (Rossmaessler, 1835)	4.92
	Anisus spirorbis (Linné, 1758)	1.64
	Segmentina nitida (O. F. Műller, 1774)	6.56
Bithyniidae	*Bithynia tentaculata* (Linné, 1758)	16.39
	Opisthorchophorus inflatus (Hansen, 1845)	3.28
Viviparidae	*Contectiana contecta* (Millet, 1813)	11.48
	Contectiana listeri (Forbes et Hanley, 1853)	8.20
	Viviparus viviparus (Linnaeus, 1758)	29.51

$$OI_g = \frac{N_{B_i}}{N_{B_t}} \times 100\%; \quad OI_p = \frac{N_{B_i}}{N_{B_p}} \times 100\%,$$

where NB is the number of water bodies containing the mollusks infected with a particular trematode species; NB_t is the number of water bodies where mollusks were sampled;NB_p is the number of water bodies where the mollusk species was found.

These indexes, to a degree, are analogous to the abundance and the mean intensity of infection indexes.

As an additional criterion of assessment of a gastropod species in the distribution of a certain trematode species in the region, a system of marks was used calculated as multiplying the values of prevalence of infection and general occurrence index (spreading criterion, SC).

$$SC = P \times OI_g.$$

Prevalence of infection was calculated using the cumulative mollusk samples from all water bodies.

SC is the significance of a certain mollusk species for the distribution of a certain trematode species.

In several cases, clarification of the role of a particular mollusk species in the transmission of certain trematode species in the region also involved the mollusk occurrence index which is common in hydrobiological studies. Here it is given as OI_m.

Results and discussion

Altogether 61 trematode species of 21 families were found in gastropod mollusks during the time of research (2004–2012). The families represented by the greatest number of species are Plagiorchiidae (13 species) and Echinostomatidae (12 species). These families also include the most common and widely spread species of the region. Parthenitae and cercariae of 52 trematode species were found, metacercariae of eight species of those were also found in mollusks. Other nine species were only found as metarcercariae.

The widest range of mollusk hosts was characteristic of species of the family Echinostomatidae, most common in Polissya. Particularly, *Echinoparyphium aconiatum* was found in 15 mollusk species, *Echinostoma revolutum* in 12, *Hypoderaeum conoideum* and *Echinoparyphium recurvatum* both parasitized nine mollusk host species. However, the parthenitae of these trematode species were found only in two to four mollusk species.

Of all observed trematode species, 22 (36.10 %) were found in two and more snail host species (table 2). These can be considered poly- or oligoxenic. The degree of specificity of these species to various host species in the studies of the natural infection can be estimated by occurrence indexes, considering also the prevalence (table 2) in different mollusk species.

The results of comparative analysis of infection indexes of polyxenic trematode species for the region are given below.

Trematodes of the family Plagiorchiidae (*Opisthioglyphe ranae*, *Plagiorchis elegans*, *Haplometra cylindracea*) are a significant part of trematode fauna of aquatic mollusks of the region. These are three-host trematodes, with metarcercariae found not only in mollusks but also in other aquatic and amphibiotic invertebrates.

The widest range of hosts in the region is that of *Opisthioglyphe ranae*, perhaps the most common mollusk-infecting trematode species. The infected mollusks were found in 32 water bodies, that is in more than 50 %. Parthenitae and cercariae of this species were found in six snail species (five Lymnaeidae and one Planorbidae species). The highest values of occurrence index were calculated for *L. stagnalis*, OI_p for this trematode species in *L. stagnalis* is 46.15 % (it was found in 24 water bodies of 52 where this snail species was found) and OI_t is 39.34 % (of all studied water bodies). Integrated for the total sample of the certain mollusk species the prevalence of infection (P) is 1.58 % suggesting that *L. stagnalis* provides favorable conditions for the development of *O. ranae* parthenitae (fig. 1, A). Four other Lymnaeidae species (*L. corvus, L. auricularia*, *L. lagotis* and *L. atra*) were infected with *O. ranae* parthenitae. Infected specimens of three of those species (*L. auricularia*, *L. lagotis* and *L. atra*) were found only in one of the studied water bodies each. OI_g of *O. ranae* is minimum for all three species, 1.64. For two of those species, P of *O. ranae* is comparable with that of *L. stagnalis.* The highest values of infection indexes of *O. ranae*

Table 2. *The polyhostal trematode species composition and the prevalence of their parthenitae infection in freshwater gastropods in water bodies of Ukrainian Polyssia*

Family, species of trematode	Mollusk species	Prevalence, %
Diplodiscidae Skrjabin, 1949		
Diplodiscus subclavatus Pall, 1760	*P. planorbis*	0.76 ± 0.19
	S. nitida	1.20 ± 0.18
Paramphistomidae Fischoeder, 1901		
Paramphistomum ichikawai Fukui, 1922	*P. planorbis*	5.65 ± 0.48
	S. nitida	6.33 ± 0.43
Liorchis scotiae Willmott, 1950	*P. planorbis*	14.66 ± 0.79
	S. nitida	3.92 ± 0.52
	A. spirorbis	18.75 ± 3.25
	A. septemgyratus	4.24 ± 0.51
Leucochloridiomorphidae Allison, 1943		
Leucochloridiomorpha constantiae (Mueller, 1935)	*C. contecta*	28.57 ± 1.76
	V. viviparus	7.0 ± 0.62
Fasciolidae Railliet, 1895		
Fasciola hepatica L., 1758	*L. truncatula*	9.20 ± 0.84
	L. subangulata	17.0 ± 0.87
Echinostomatidae (Railliet, 1895)		
Echinostoma revolutum (Froelich, 1802)	*L. stagnalis*	1.24 ± 0.11
	P. planorbis	2.11 ± 0.59
Echinostoma stantschinskii Semenov,1927	*L. stagnalis*	0.89 ± 0.63
	P. corneus	2.63 ± 1.84
Echinoparyphium recurvatum Linstow, 1873	*L. stagnalis*	2.38 ± 0.30
	L. palustris	0.51 ± 0.21
	P. planorbis	0.43 ± 0.14
	P. corneus	0.77 ± 0.34
Echinoparyphium aconiatum Dietz, 1909	*L. stagnalis*	0.81 ± 0.12
	L. palustris	0.27 ± 0.14
Hypoderaeum conoideum (Bloch, 1782)	*L. stagnalis*	0.23 ± 0.07
	L. palustris	0.26 ± 0.12
	L. ovata	1.86 ± 0.31
	P. corneus	2.04 ± 2.01
Monorchiidae Odhner, 1911		
Asymphylodora imitans Mueling, 1898	*P. planorbis*	1.33 ± 1.32
	C. contecta	14.81 ± 6.83
Notocotylidae Luhe, 1909		
Notocotylus attenuaus (Rudolphi, 1809)	*L. stagnalis*	2.86 ± 2.82
	L. ovata	2.59 ± 0.39
	L. auricularia	5.26 ± 5.12
	L. patula	0.99 ± 0.98
	P. corneus	0.75 ± 0.74
Prohemistomatidae (Luts, 1935)		
Paracoenogonimus ovatus Kasturada, 1914	*C. contecta*	2.38 ± 2.35
	V. viviparus	1.0 ± 0.99
Diplostomatidae Poirier, 1886		
Tylodelphys clavata Nordmann, 1832	*L. stagnalis*	7.17 ± 6.89
	L. auricularia	0.67 ± 0.60
Strigeidae Railliet, 1919		
Cotylurus cornutus Rudolphi, 1808	*L. stagnalis*	1.3 ± 0.53
	P. corneus	1.69 ± 1.68
Plagiorchidae Luhe, 1901		
Opisthioglyphe ranae Froelich, 1791	*L. stagnalis*	1.58 ± 0.13
	L. corvus	0.35 ± 0.20
	L. auricularia	1.33 ± 0.94
	L. lagotis	2.41 ± 1.68
	L. atra	0.65 ± 0.60
	P. planorbis	0.46 ± 0.17
Plagiorchis elegans (Rudolphi, 1802)	*L. stagnalis*	1.89 ± 0.17
	L. palustris	2.91 ± 0.77
	L. corvus	0.44 ± 0.25
Haplometra cylindracea Zeder, 1800	*L. stagnalis*	1.33 ± 0.26
	L. palustris	0.43 ± 0.19
Haematoloechidae Freitas et Lent, 1939		
Haematoloechus variegatus (Rudolphi, 1819)	*P. purpura*	4.17 ± 4.08
	P. planorbis	3.07 ± 0.73

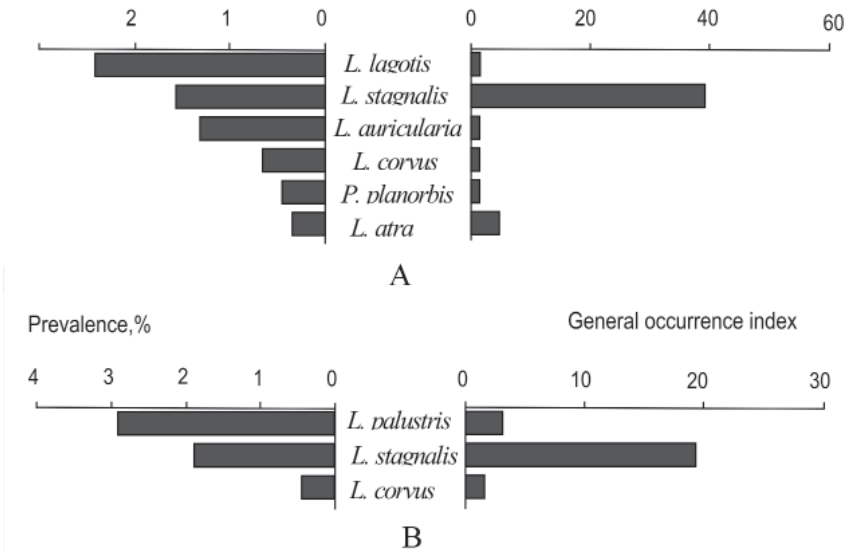

Fig. 1. The distribution of polyxenic trematode species in the parthenitae host species of mollusks: A — *O. ranae*; B — *P. elegans*.

parthenitae are in *L. lagotis* (table 2). This mollusk species seems to be the optimal host for *O. ranae.* However, it is very rare in the region, found in only one water body, and its role in the distribution of the trematode is insignificant. *L. auricularia* is somewhat inferior to *L. stagnalis* in *O. ranae* infection, P is 1.33 %. Therefore, it is an appropriate host for the parthenitae of these trematodes. This species is also rare in the region, it was found in three water bodies (OI_m is 4.92), and it was infected with *O. ranae* only in one of them, hence its role in distribution of this trematode is insignificant. The third Lymnaeidae species, *L. atra*, is much less infected and does not play any appreciable role in the transmission of *O. ranae* in the region. Another Lymnaeidae species, *L. corvus*, seems to be an unsuitable host for the parthenitae of *O. ranae*, and was rarely infected (table 2), though it was observed more often, with OI_m 11.48 (seven water bodies). This ambiguous situation is difficult to appraise regarding the degree of host specificity. In such cases, the spreading criterion index may be of help, including two main characteristics (P and OI_g) and allowing better determination of the role of a host of polyxenic helminth species in the parasite's transmission in the biotopes of a particular region.

Accordingly, the spreading criterion of *L. stagnalis* is 62.16 marks, it is the main host of *O. ranae* parthenitae on the territory of Ukrainian Polissya. For other Lymnaeidae species this criterion is an order of magnitude lower. For *L. lagotis* and *L. auricularia* it is 3.95 and 2.18, respectively. These snail species can be classed as subsidiary hosts of *O. ranae.* Two other Lymnaeidae species, *L. corvus* (with the index value 1.72) and *L. atra* (with the value 1.07) are rare hosts of *O. ranae* parthenitae in the region.

Parthenitae and cercariae of *O. ranae* are also found in one Planorbidae species, *Planorbis planorbis*. This is one of the most common freshwater snail species in the region, its OI_m is rather high (31.15 %). However, specimens of *P. planorbis* infected with this trematode were found in one water body only, OI_g is 1.64, P is very low and SC is only 0.75. Therefore, *P. planorbis* can be considered an accidental host of *O. ranae* parthenitae which is of no importance in the sustenance of local populations of these trematodes in the region.

Plagiorchis elegans is a trematode species widely distributed in the region, and it was found in 10 water bodies. Parthenitae of the trematode were found in three Lymnaeidae species. Its occurrence index values are high in *L. stagnalis* (OI_g 19.23, OI_p 23.08, P 1.89 %) (table 2), SC is 19.23. *L. palustris* is less common in the region. The respective OI_g of

P. elegans parthenitae is lower, 3.28 but the OI_p is not inferior to that of *L. stagnalis*, OI_p 22.22, P is notably higher but SC is lower (9.55). *L. corvus* is rare, found to be infected in one water body only, thus its OI_g is 1.64, P is low, and SC is 0.72.

Hence, the distribution of regional population of *P. elegans* in mollusk hosts is as follows: the leading role in ensuring the successful life cycle of the species at the parthenogenetic stage is played by *L. stagnalis.* At the same time *L. palustris* is better suited for the development of the trematode micropopulations. Howver, these gastropods are rare in the regional water bodies (found in nine water bodies, OI_m 14.75 %). The underlying reason seems to be certain interacting ecological factors resulting in *L. palustris* being a secondary host of *P. elegans* parthenitae in the region. The third species, *L. corvus*, is a rare host of *P. elegans* parthenitae (fig. 1, B).

Only two snail species, *L. stagnalis* and *L. palustris* were registered as hosts of *Haplometra cylindracea* parthenitae (fig. 2, A). The former Lymnaeidae species is characterized by quite a high occurrence and *H. cylindracea* infection indexes. The OI_g reaches 16.39, OI_p is 19.23, though P is low (table 2), and SC is 21.8. All these characteristics are an order of

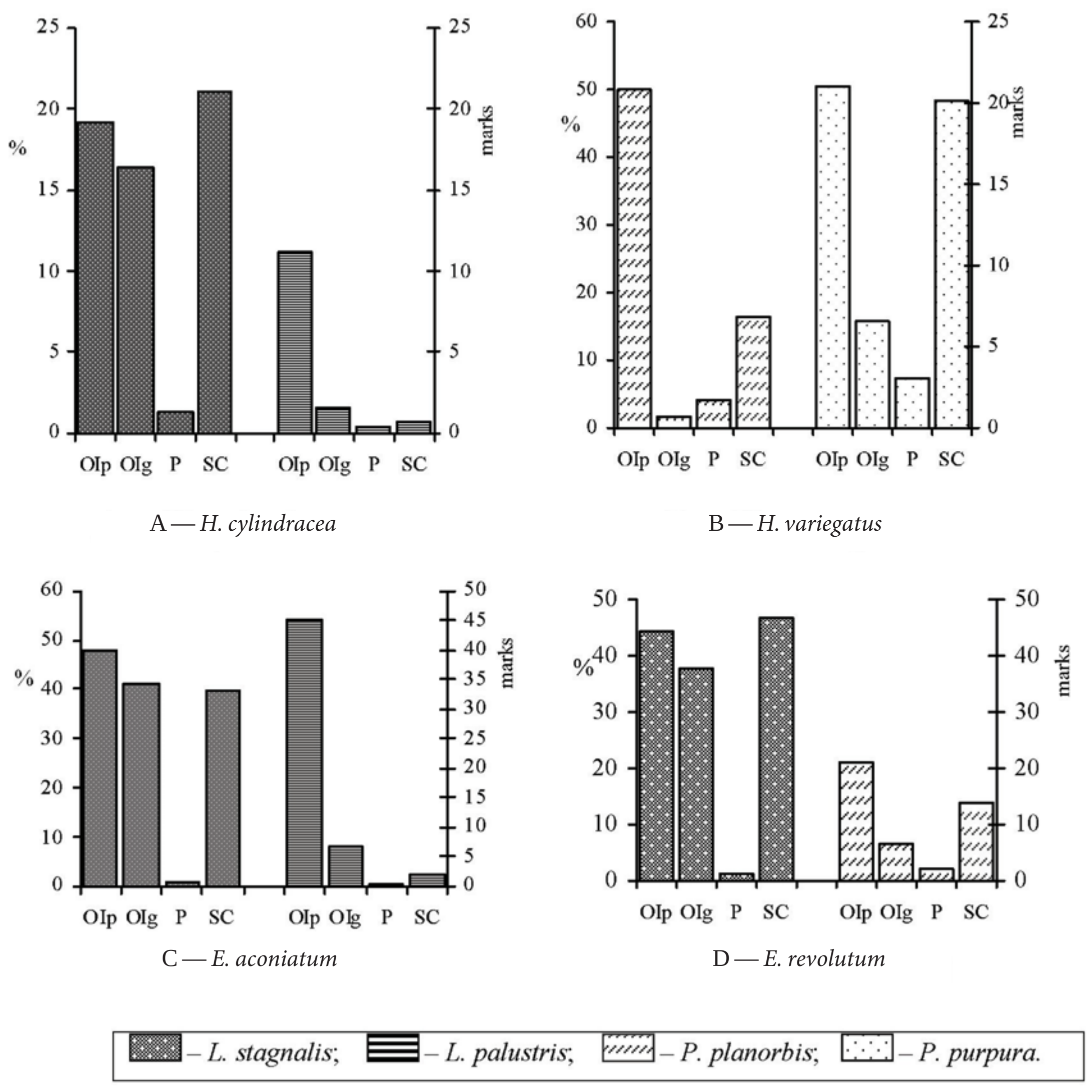

Fig. 2. The distribution of olygoxenic three-host trematode species in the parthenitae host species of mollusks: A — *H. cylindracea*; B — *H. variegatus*; C — *E. aconiatum*; D — *E. revolutum*.

magnitude lower in *L. palustris*: OI_g 1.64, OI_p 0.11, and SC is only 0.71. Correspondingly, *L. stagnalis* is the main host of *H. cylindracea*, and *L. palustris* can be considered as a rare host of this trematode.

One species of the trematode family Haematoloechidae, *Haematoloechus variegates* was found in planorbid species *P. planorbis* and *P. purpura* as cercariae and parthenitae. The infection and occurrence levels of this species parthenitae are somewhat similar (fig. 2, B). The occurrence indexes are slightly higher in the former mollusk species, OI_g 6.56, OI_p 21.05, P is low (table 2) and SC is as high as 20.14. *P. purpura* infected with *H. variegates* were found in only one water body, OI_g 1.64, P is somewhat higher than in the former mollusk species, and SC is accordingly 6.84. Thus, *P. planorbis* is the main host of *H. variegatus* parthenitae, while *P. purpura* due to its rarity is a subsidiary host.

Two out of five trematode species of the family Echinostomatidae, *Hypoderaeum conoideum* and *Echinoparyphium recurvatum*, possessed quite a wide range of hosts), they were found to infect four mollusk species each.

The parthenitae of *Hypoderaeum conoideum*, widely spread in the region, were found in three lymnaeid species (*L. stagnalis*, *L. palustris,* and *L. ovata*) and one planorbid species (*P. corneus*) (fig. 3, A). The parthenitae of *H. conoideum* are not common in the region. For *L. stagnalis*, OI_g is 11.48, OI_p is 13.46. However, despite their very low P rates (table 2), and SC is 2.64. The occurrence of *H. conoideum* parthenitae in *L. ovata* is relatively high, OI_g 6.58, OI_p 36.33. The infection rates are higher than in *L. stagnalis*, but SC is much lower (1.2). This snail species is not very common regionally, OI_m is 18.03 %. The infection rates of *H. conoideum* parthenitae in *L. palustris* are inferior to those for two abovementioned species, OI_g 4.92, OI_p 33.33, and SC 1.28. The species *P. corneus* was infected with *H. conoideum* parthenitae only in one water body. Thus its OI_g is minimal, 1.64. However, the prevalence of infection was much higher than in other freshwater gastropods in the region, and SC is 3.34.

Therefore, *L. ovata* is considered as the most suitable host for *H. conoideum* and can be the main host of parthenitae of this trematode species in Ukrainian Polissya, while *L. stagnalis* and *L. palustris* can be classed as subsidiary hosts. At the same time, *P. corneus* according to the relatively high prevalence of infection is the optimal host of *H. conoideum* parthenitae. Certain factors, possibly the environmental, hydrological and hydrochemical

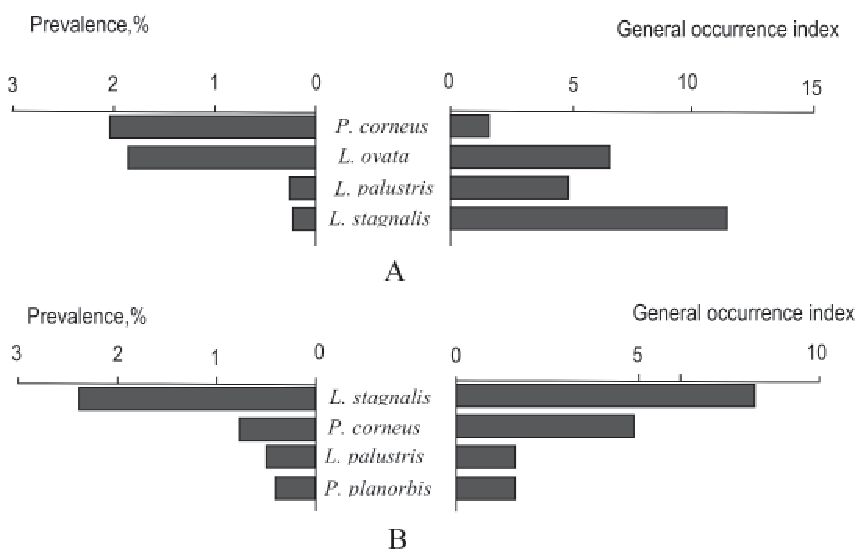

Fig. 3. The distribution of polyxenic trematode species in the parthenitae host species of mollusks: A — *H. conoideum*; B — *E. recurvatum.*

parameters, limit the infection of this snails with *H. conoideum*. Thus infection of *P. corneus* is mostly accidental.

Trematode *Echinoparyphium recurvatum* at the stages of parthenitae and cercariae was found in *L. stagnalis*, *L. palustris*, *P. corneus* and *P. planorbis* (metarcercariae were found in 9 species) (fig. 3, B). Occurrence index of this trematode species in *L. stagnalis* is higher than in other snail species, OI_g 8.2, OI_p 9.62. Infection rates of these hosts are also relatively high (table 2), with SC of 22.9. The infection rates of *P. corneus* are much lower, OI_g 4.92, OI_p 6.52, and SC 3.79. In other mollusk species, *L. palustris* and *P. planorbis*, P is very low. Infected specimens of each of those species were found only in one biotope, OI_g is 1.64, and SC is 0.84 and 0.71 respectively.

Therefore, *L. palustris* and *P. planorbis* can be considered rare hosts of *E. recurvatum* parthenitae in the region. Possibly, these mollusks are not quite suitable hosts for this trematode. The first place in this trematode's transmission is held by *L. stagnalis.*

Echinoparyphium aconiatum is the most common trematode species in the region. It was found in 38 of 61 studied water bodies (62.3 %). This species was registered in 15 mollusk host species, but the parthenitae were found only in two of them. Those are *L. stagnalis* and *L. palustris* (fig. 2, C). The former species is characterized by very high values of occurrence indexes, OI_g 40.98, OI_p 48.07. Parthenitae of *E. aconiatum* were found in these gastropods in 25 water bodies, P was also relatively high (table 2), and SC is 33.19. This gastropod species is the main host of this trematode species in the region. In *L. palustris* all index values of *E. aconiatum* parthenitae infection are much lower. Infected specimens were found only in four biotopes, OI_g 6.56, OI_p 44.4, SC is only 1.77. This is a rare host of *E. aconiatum.*

Echinostoma revolutum is also one of the most common echinostomatid species in the region with very wide range of parthenitae and metarcercariae hosts (12 species). Parthenitae of *E. revolutum* were found in two gastropod species only, *L. stagnalis* and *P. planorbis*; both are widely distributed in Ukrainian Polissya. *L. stagnalis* is characterized by very high values of occurrence indexes of *E. revolutum* parthenitae, OI_g 37.71, OI_p 44.23 (fig. 2, D). Hence the high value of SC, 46.7, while P is low (table 2). This mollusk species is the main host of parthenitae and cercariae of *E. revolutum* in the region.

In *P. planorbis*, the occurrence indexes of *E. revolutum* are lower, OI_g only 6.56 and OI_p 21.05. Despite the higher level of *E. revolutum* parthenitae and cercariae infection, SC is only 13.84. *P. planorbis* seems to provide better conditions for development of *E. revolutum* parthenitae. However, ecological factors particularly the human impact restrict the planorbids' infection and reduce their part in *E. revolutum* transmission to a subsidiary host. Its role in the distribution of this trematode is significantly lesser.

Parthenitae and cercariae of another echinostomatid species, *Echinostoma stantchinskii*, were found in snails belonging to different families, namely, in *L. stagnalis* and *P. corneus* (fig. 4, A). For this regionally rare trematode, *P. corneus* is of utmost importance. All rates of *E. stantschinskii* parthenitae infection are much higher in these mollusks, OI_g 3.28, OI_p 4.35, SC 8.62. At the same time, the occurrence of *E. stantschinskii* parthenitae are significantly lower in *L. stagnalis*, OI_g 1.64, OI_p 1.92, P is much lower and SC is only 1.46. The latter mollusk is a subsidiary host of *E. stantschinskii* in the region.

Several other trematodes of various families: *Paracoenogonimus ovatus* (Prohemistomatidae), *Cotylurus cornutus* (Strigeidae); *Tylodelphys clavata* (Diplostomidae), all known to have three hosts in their life-cycles, were found each in two mollusk hosts in the region.

The next species *Paracoenogonimus ovatus* (Prohemistomatidae) was found in two viviparid species, *V. viviparus* and *C. contecta* once (fig. 4, B). Infection rates of those mollusk species with *P. ovatus* are not high (table 2), and OI_g is 1.64 for both host species. SC is 1.6 in *V. viviparous* and 3.9 in *C. contecta,* while OI_p is 5.56 and 14.29, respectively. Possibly, *C. contecta* is more suitable host for *P. ovatus* parthenitae.

Cotylurus cornutus is one of the most widely distributed species of trematodes observed in mollusks in the region, however, parthenitae and cercariae of this species

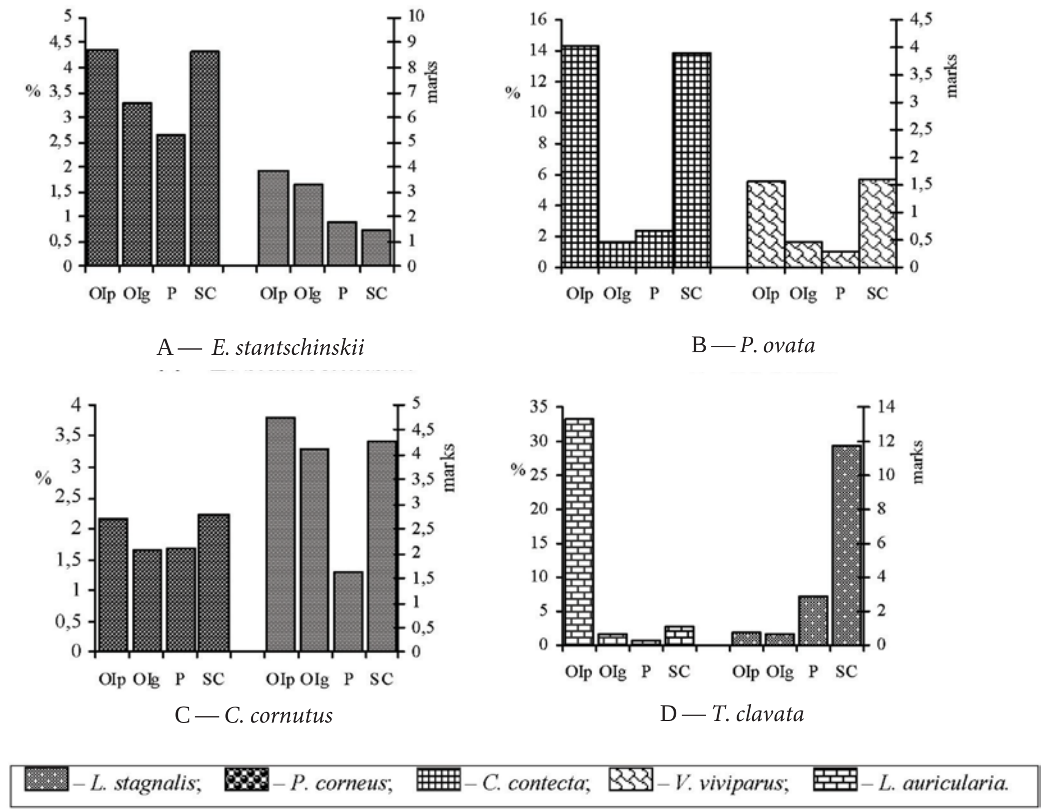

Fig. 4. The distribution of olygoxenic three-host trematode species in the parthenitae host species of mollusks: A — *E. stantschinskii*; B — *P. ovata*; C — *C. cornutus*; D — *T. clavata*.

were only found in *L. stagnalis* and *P. corneus*. The OI_g of *L. stagnalis* is 3.3, OI_p 3.8, P is low, and SC 4.29 (fig. 4, C). The parthenitae of *C. cornutus* were found in *P. corneus* only once, hence OI_g 1.64, OI_p 2.17, P is higher than that for *L. stagnalis*, and SC is 2.8. *C. cornutus* seems not to have high specificity to hosts of parthenogenetic generations. Due to the relatively wider range of *L. stagnalis* in the region and somewhat higher occurrence of parthenitae in this gastropod species, it should be considered the main host of *C. cornutus*. The role of *P. corneus* in the distribution of *C. cornutus* can be described as a common host.

Tylodelphys clavata was found in *L. stagnalis* and *L. auricularia* (fig. 4, D). Infected representatives of both freshwater gastropod species were in one water body, thus OI_g is minimum, 1.64. At the same time, P of *L. stagnalis* is quite high (table 2) and SC is 11.76. P of *L. auricularia* is very low, and SC is 1.1. Thus the main role in *T. clavata* distribution is played by *L. stagnalis*, whereas *L. auricularia* apparently does not provide favorable conditions for the development of this trematode species' parthenitae and is its rare host.

Among poly- and olygoxenic trematodes parasitizing snails of Ukrainian Polissya, there are seven dixenic species (*N. attenuatus*, *L. scotiae*, *P. ichikawai*, *D. subclavatus*, *F. hepatica*, *L. constantinae* and *A. imitans*) which do not have the "second" intermediate host and thus have no metacercaria stage. Their cercariae encyst in the environment into adolescariae or transforms into cercarieum without leaving a mollusk that can infect the definitive host.

One of these species, *Notocotylus attenuatus* occured in five mollusk species, four of which are lymnaeids (fig. 5, A). *L. ovata* infected with this trematode in two water bodies, is characterized by high occurrence indexes — OI_g 3.28, OI_p 18.18, and SC 8.5. This gastropod species is possibly of the major importance in *N. attenuatus* distribution and can be regarded as one of its main hosts. OI_g of three other lymnaeid species (*L. stagnalis*, *L. auricularia*, and *L. patula*) is only 1.64. The highest rates of prevalence are in *L. auricularia* (table 2), also determining the quite high OI_p (33.33) and SC (8.6). According to the infection rates, *L. auricularia* is the best host for the parthenitae of these trematodes though it is somewhat rare in Polyssya (OI_m 4.92 %) and thus can also be considered as one of main hosts. Prevalence rates of *L. stagnalis* are comparable to those of *L. ovata* (table 2), OI_p 1.92, SC 4.69. It is a common host of *N. attenuatus* in the region. As for *L. patula*, its rates of prevalence are much lower compared to those observed in other lymnaeids, with OI_p 50 and SC 1.62. It seems to be poorly suited for the development of *N. attenuatus* parthenitae. It is a rare host of this species. *P. corneus* was also infected only in one water body. Its P is lower than that of lymnaeids, OI_p 2.17, OI_g 1.64 and SC 1.23.Apparently, this species of planorbids can be regarded as rare or accidental host for *N. attenuatus.* Therefore, the main hosts of *N. attenuatus* in the region are *L. ovata* and *L. auricularia.*

Liorchis scotiae is found in four mollusk species: *P. planorbis, S. nitida, A. septemgyratus*, and *A. spirorbis*. *P. planorbis* stands out of those four (fig. 5, B). OI_p of *L. scotiae* in this host is 10.52, OI_g 3.28, and high SC of 48.08. Three other planorbid species were infected with parthenitae of *L. scotiae* in one water body each, and for each of them OI_g is 1.64. But the infection rates of *A. spirorbis* with the trematode *L. scotiae* are quite high (table 2), and its SC is only slightly lower than that of *P. planorbis* (30.75). Other species of mollusks, *S. nitida* and *A. septemguratus,* are now regionally rare. P of both species are similar, 3.92 and 4.24 % respectively, hence the slight difference in SC values (6.43 and 6.95).

Therefore the main host of *L. scotiae* parthenitae in the region is *P. planorbis. A. spirorbis* seems to provide the best environment for *L. scotiae* parthenitae development. However, the limited distribution and low abundance of that gastropod lessens its importance in *L. scotiae* distribution to that one of main hosts. *S. nitida* and *A. septemguratus* are subsidiary hosts of *L. scotiae* in Ukrainian Polissya.

The trematode *Paramphistomum ichikawai* occurs in the region in two mollusk species, *P. planorbis* and *S. nitida*. Parthenitae of *P. ichikawai* occured more often in *P. planorbis*, OI_g is 9.84, OI_p 31.58 (fig. 6, A), and infection rates are quite high (table 2) with SC 55.6. OI_g of *P. ichikawai* parthenitae in *S. nitida* is lower (4.95) but the OI_p is higher (75), and

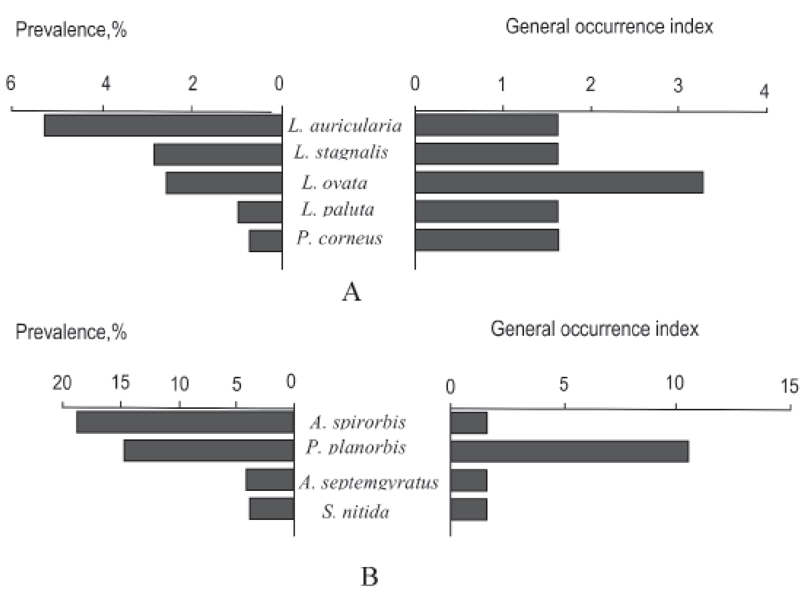

Fig. 5. The distribution of polyxenic trematode species in the parthenitae host species of mollusks: A — *N. attentuatus*; B — *L. scotiae*.

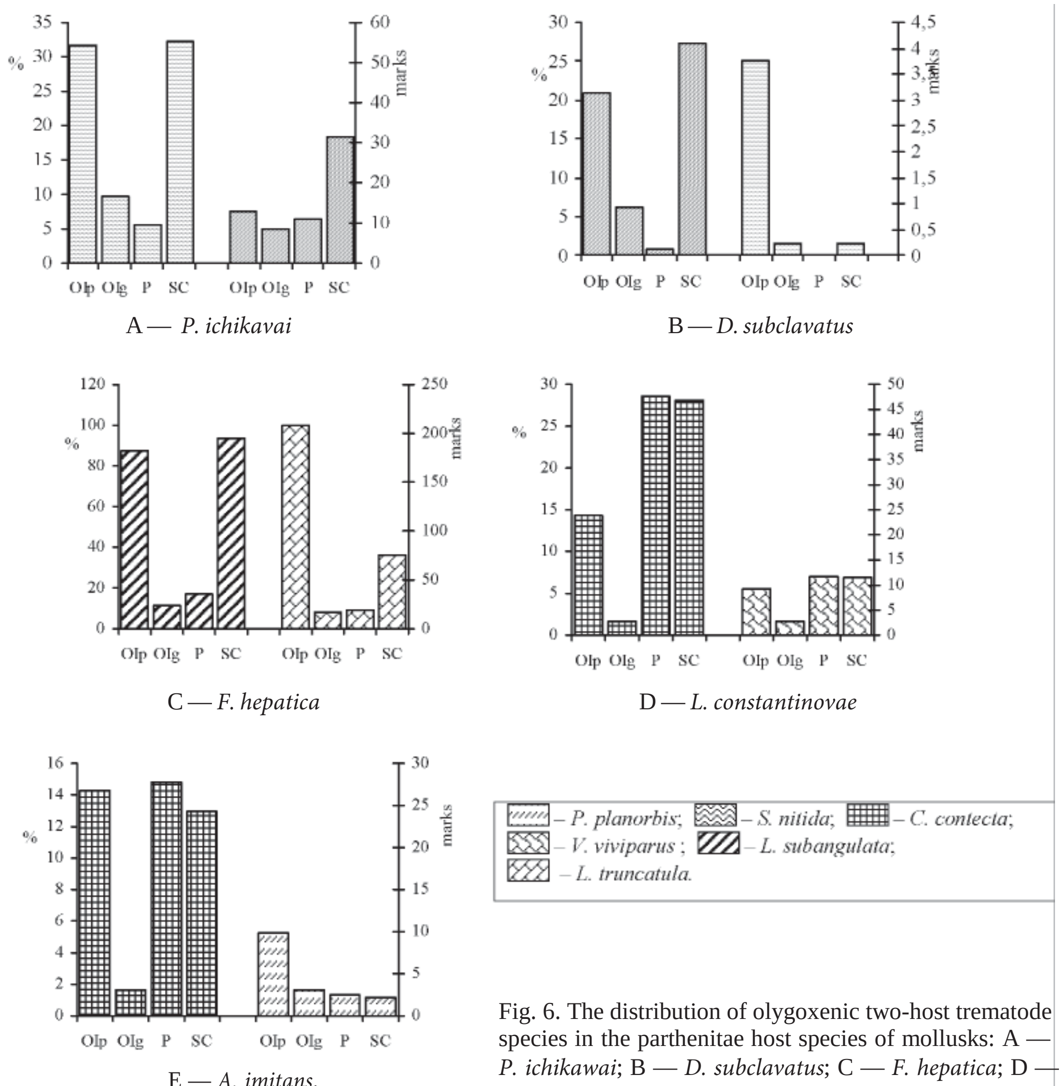

Fig. 6. The distribution of olygoxenic two-host trematode species in the parthenitae host species of mollusks: A — *P. ichikawai*; B — *D. subclavatus*; C — *F. hepatica*; D — *L. constantinovae*; E — *A. imitans*.

infection rates are somewhat higher (SC 31.33). Therefore, *P. planorbis* is more important in sustaining local populations of the trematode in the region and is the main host of parthenogenetic generations. Although *S. nitida* is currently regionally rare (OI_m 6.56 %) it can be considered as a common host of *P. ichikavai*.

Diplodiscus subclavatus is also observed in those mollusk species in the region. As in the case of *P. ichikawai*, high occurrence of *D. subclavtus* was seen in *P. planorbis*, infected specimens were found in all four water bodies, OI_g 6.56, OI_p 21.05, P is low and SC is 5.0 (fig. 6, B). *S. nitida* infected with parthenitae of *D. subclavtus* were observed together with *P. planorbis* infected with this trematode in the same habitat. In the case of *S. nitida* the occurrence is minimum (OI_g 1.64) and the prevalence is lower than in the co-habiting *P. planorbis* (table 2), OI_p 33.33 and SC 0.25. *P. planorbis* is the main host of *D. subclavtus* in the region. *S. nitida* is better suited for the development of the parasite's parthenitae, but it is rarer in the regional water bodies, and thus plays a secondary role in the distribution of *D. subclavatus.*

The trematode *Fasciola hepatica* which parasitizes domestic and wild ruminants is comparatively widely distributed in the region. Parthenitae of the trematode were found in two lymnaeid species: *L. subangulata* and *L. truncatula*. This trematode species is highly specific to the lymnaeids of the group *L. truncatula*. Parthenitae of *F. hepatica* occurred more often in *L. subangulata*, OI_g 11.46, OI_p 87.5 (fig. 6, C). Prevalence rates are also higher (table 2), and SC is 195, which is the highest value for all snail trematodes recorded in the region. In *L. truncatula,* parthenitae of *F. hepatica* occur somewhat rarer: OI_g 8.2, OI_p 100. Infection rates are significantly lower, and SC is 75.44.

Both species are important in the distribution of *F. hepatica* in Ukrainian Polissya. *L. subangulata* is the leading host of this trematode parthenitae in the region, while *L. truncatula* is its main host. This is supported by our previous studies (Zhytova, 2003), according to which the leading role in the distribution of *Fasciola* belongs to *L. subangulata* (OI_m 87.5 %), while *L. truncatula* is among the subsidiary hosts with OI_m of 12.5 %.

The trematode *Leucochloridiomorpha constantinae* was found in two viviparid species, *V. viviparus* and *C. contecta* (fig. 6, D). The infected specimens of each were recorded in only one studied water body. Hence, OI_g is minimum, 1.64. But the infection rates are much higher in *C. contecta*, P is quite high (table 2), OI_p is 14.29 and SC is 46.85. This species can be considered a main host of *L. constantinae*, while *V. viviparus* (OI_p 5.56, SC 11.48) is its common host in the region.

*Asymphylodora imitans (*Monorchidae) was found once in each mollusk host, the snails belonging to different families. In *C. contecta* which is not regionally common (OI_m 11.48 %), OI_g of *A. imitans* is minimum (1.64) but OI_p is quite high, 14.29 (fig. 6, E). P is also relatively high (table 2). Correspondingly, SC is high, 24.29. The indexes of another host species, *P. planorbis*, are significantly lower (OI_g 1.64, OI_p 5.26, and SC is 2.18). Thus, *C. contecta* is the main host of *A. imitans* in the region while *P. planorbis* is an accidental host.

Infections of two mollusk species by one trematode in the same water body were very rare in the region. The exceptions are parthenitae of *F. hepatica* which were found in *L. subangulata* and *L. truncatula* in three water bodies. In all cases, the prevalence was higher in *L. subangulata* than in *L. truncatula.* Very high rates of parthenitae and cercariae of *F. hepatica* infection were registered in the drainage canal No. 5 (Rivne Region). In *L. subangulata* they reached 83.87 %, in *L. truncatula* 80 %. The density of the former mollusk species in the canal is 12.4 specimens per m^2, and the density of the latter is only 2 specimens per m^2. In the drainage canal No. 7 (Zhytomyr Region), P values were much lower, 21.95 % and 13.16 %, respectively. The snail density is also lower, altogether 4.44 specimens per m^2 in *L. subangulata* and 2.33 specimens per m^2 in *L. truncatula.* In the pond No. 8 (Zhytomyr Region), the infection prevalence was low, 4.47 % in *L. subangulata* and 3.8 % in *L. truncatula.* Likewise, the gastropod densities are low, 2.78 and 1.56 specimens per m^2 respectively. These observations support the assumption that *L. subangulata* is the leading host of *F. hepatica* parthenitae in the region. A positive correlation between prevalence and mollusk population density ($R_s = 0.98$, $P = 0.000085$) exists there.

Trematode *D. subclavtus* was found once in both *P. planorbis* and *S. nitida* in the drainage canal No. 7 (Zhytomyr region). P was 1.38 % in the former snail and 0.15 % in the latter one. These data also support the conclusion that in the region, the main host of *D. subclavtus* is *P. planorbis.* However, for *P. ichikavai* which was also found in *P. planorbis* and *S. nitida* together (in the drainage canal No. 9, Zhytomyr Region), the situation is different. The infection rates were higher in *S. nitida*. Prevalence of infection in these mollusks was 14.8 % at the density of 5.46 specimens per m^2, while infection rates of *P. planorbis* were much lower (12.63 %) at a significant mollusk density of 8.55 specimens per m^2. This supports the conclusion that the *S. nitida* is a better host for parthenitae of *P. ichikawai* than *P. planorbis.*

In Ukrainian Polyssya water bodies, 61 trematode species are hereby recorded in freshwater gastropods. Most of them (52 species) are found at the parthenitae (sporocysts, rediae) and cercariae stages. All of them are potentially polyxenic and are found at parthenogenetic stages in various gastropod species outside of the studied region. At the same time in the studied region only 42.31 % of them are found in more than one mollusk species. Only six trematode species (11.54 %) are found in three to six mollusk species, and can be considered polyxenic, 16 species (30.76 %) are found as parthenitae in two mollusk species and therefore are characterized as oligoxenic. Other 30 trematode species (57.69 %) are found currently in Ukrainian Polyssya only in a single mollusk species of 26 studied. Hydro-parasitologists who studied freshwater gastropod infections with trematode parthenitae and larvae in Polissya reservoirs before the large-scale land reclamation efforts, noted a wider diversity of hosts for many polyxenic trematode species (Zdun, 1961; Chernogorenko, 1983).

Our data on the distribution and abundance of freshwater gastropods in the regional water bodies support the malacologists' conclusions (Stadnichenko, 2008; Yanovych, 2008, 2013) about the significantly reduced species diversity and decreased abundance of aquatic gastropods in the water bodies in the last decades. This, subsequently, causes the decreased species diversity of trematodes in mollusks in the majority of studied water bodies. The malacofauna depletion and decreasing mollusk abundance are linked to the fact that the incidence of certain trematode species parasitizing two snail species in one water body is observed very rarely. Also, the structure of the distribution of polyxenic species parthenitae in different species of mollusks usually includes no more than three of the five major categories of host specificity (leading, common, subsidiary, rare and accidental). This also points to the decreased species diversity of malacofauna of Polissya water bodies. Now, the trematode fauna of many water bodies, especially the isolated and with weak water flow is random, following the founder effect.

Summary

The distribution of parthenogenetic trematode generations in the mollusk host species is determined by their specificity both on the level of local populations and regionally. The specificity is a measure of conformity of the host's (in this case, mollusk's) internal environment to the needs of certain parasite species (in this case, trematodes). The specificity of parthenogenetic generations of polyxenic trematode species to different mollusk hosts varies. Its level can be higher or lower depending on the conditions provided by one or another mollusk species for the development and reproduction of parthenitae. High specificity level supports the successful penetration of miracidia to the mollusk specimen, high larval viability and their capacity for development, for undergoing the succeeding stages and changes of parthenogenetic generations. It supports the maximum production of cercariae which leave the mollusk searching for the intermediate or definitive host. The hosts that cannot provide the optimum conditions for the development and reproduction of the parthenitae are the less specific for them and play the subsidiary role in sustaining the local trematode populations.

A sufficiently reliable criterion of the host suitability for the parthenitae of a certain trematode species, given the reasonably large representative sample of the studied mollusks, is the prevalence of infection. The differences in the prevalence are singularly characteristic in case of natural infection of two or more mollusk species in the same water body.

In different water bodies of the same region the ecological parameters (hydrological, hydro-chemical, biotic, anthropic, etc.) can vary a lot, influencing (positively or negatively) their mollusk populations. This affects the species composition of gastropods, population densities of various species, and their distribution in the water body. Correspondingly, the infection indexes of various mollusk species with certain trematode species differ. Averaged data on a large number of various types of water bodies allow evaluating the tightness of the links between the parthenitae of certain polyxenic trematode species to different mollusk species.

The role of definitive vertebrate hosts in sustaining the local populations of trematode species is highly important. The presence of the vertebrate hosts of trematode maritae at the water bodies or at least rare short visits of the hosts to the banks is the obligate condition of mollusk infestation with the trematode parthenitae. However, most trematode species are not highly specific to the vertebrate hosts in which their maritae develop and reproduce. To the contrary, many of the 19 trematode species whose parthenitae are recorded in the regional water bodies are found in two to six mollusk species, have very wide ranges of vertebrate hosts of maritae. The specificity is often not restricted to one vertebrate class. For example, *P. elegans* is found in Ukraine in 39 bird species, seven mammal and four reptilian species; *E. revolutum* in 31 bird and 2 mammal species; *N. attenuatus* in 23 bird and 2 mammal species; *O. ranae* in 9 amphibian and 3 reptilian species, and *C. cornutus* in 19 bird species, *E. recurvatum* in 17 bird species, and *H. conoideum* in 10 bird species. Hence the absence of this or that species of possible definitive host of a certain trematode species in the water body, in the nearby area or even the whole region does not limit the viability of local parthenitae populations in the convenient mollusk hosts.

The ecological factors as a whole, such as climatic peculiarities, seasonal climate conditions, hydrobiological characteristics of the water bodies, biotic composition, and first of all the presence or absence and abundance of intermediate hosts of metarcercariae (if the stage is present in the life cycle) are of the secondary importance to the persistence of local populations of certain trematode species. The ecological conditions of the water body only affect the free-living trematode generations, miracidia and cercariae, which do not spend much time in the environment. The ecological factors only indirectly influence the distribution of local populations of certain trematode species in the more or less suitable for parthenitae development mollusk species.

Conclusion

The data on species composition of mollusk hosts of the parthenitae of polyxenic trematode species in current conditions of Ukrainian Polyssya are summarized. The levels of specificity of parthenogenetic generations of 19 trematode species to various mollusk species are determined. This analysis involved the prevalence level and the original, general and partial, occurrence indexes, and the regional spreading criterion.

It is shown that the major role in sustaining the local and regional populations of certain trematode species is played by the mollusk species, whose internal environment provides the best conditions for the development and reproduction of the parthenitae. These mollusk species can be referred to as leading or main hosts of the parthenogenetic generations of a particular trematode species.

As a rule, among the mollusk hosts of a particular trematode species in the region there are several species which are widely distributed in various types of water bodies and often are infected with parthenitae of this or that trematode species. The moderately high prevalence of infection of such mollusks implies that they provide suitable conditions for the parthenitae and can support the trematode populations on a stable level. Such mollusk species can be considered common hosts of a particular trematode species.

The role of a certain main or common mollusk host species in the distribution of a certain trematode species depends also on the occurrence frequency and abundance of their regional populations. The prosperity of local mollusk populations is defined by a complex of ecological factors, abiotic, biotic and anthropic, influencing the aquatic conditions in which the mollusks live.

In the unsuitable environmental conditions that cause the lack of optimal host species for the exact tramatode species, they can persist for awhile in other mollusk species, the subsidiary or secondary parthenitae hosts which can provide their development and reproduction on a minimum level. The rare and accidental hosts of the trematode parthenitae cannot support their local populations. Infected specimens of such mollusk species are found only in the presence of main or common mollusk hosts of these trematodes in the water bodies.

The environmental factors external to the mollusk-parthenitae system, both abiotic (climatic, weather, hydrological, anthropic) and biotic (mostly hydro-biological) play a secondary part in the distribution of trematodes in the mollusk hosts. They have an indirect impact, affecting the species composition of the mollusks, their populations' abundances and densities, and the persistence of intermediate and definitive hosts of certain trematode species.

We are grateful for the reviewers of our work for their detailed review and helpful comments which allowed to improve significantly this manuscript.

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Received 9 February 2017
Accepted 23 May 2017