



Spread of helminth parasites of water frogs of the *Pelophylax esculentus* complex (Amphibia: Anura) on the Black Sea shore, Odesa region, Ukraine, after the destruction of the Kakhovka dam in June 2023

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Abstract. The destruction of the dam of the Kakhovka Hydroelectric Power Plant in June 2023 during the Russian full-scale invasion of Ukraine caused large-scale changes in the ecosystems of southern Ukraine, including the sudden influx of massive flooding of freshwater, chemicals, and living organisms into the brackish coastal zones of the northwestern Black Sea region. This event led not only to industrial pollution but also to the unpredictable displacement of numerous species, including endangered frogs from destroyed freshwater habitats into new ecosystems. One of the potential consequences of this displacement is the appearance of new helminth infections downstream, which may affect the structure of parasite communities and the health of native fauna. The present study aimed to identify the species composition and features of the helminth fauna of the *Pelophylax esculentus* complex (*P. ridibundus* and *P. esculentus*) collected on the coast of the Odesa region after the flooding. Between 6–26 June 2023, a total of 28 individuals of *Pelophylax esculentus* complex (17 *P. ridibundus* and 11 *P. esculentus*) found on the seashore after the flood were collected for parasitological analysis. A total of 22 helminth species were identified, including 15 trematodes, five nematodes, one cestode, and one acanthocephalan. Fourteen (63%) species were adult forms, while the remainder were larval stages. A total of 15582 parasite specimens were recorded, dominated by the metacercariae of *Codonocephalus urniger* and *Tylodelphys excavata*, which accounted for over 70% of all the parasite specimens. Species richness and abundance were higher in *P. ridibundus* (20 species) compared to *P. esculentus* (14 species). Infracommunities were more heterogeneous in *P. esculentus*, reflecting potential multiple origins of frog individuals from different populations upstream. The observed differences between the two host species may be related to their specific body size, ecological origin, and routes of displacement. The relatively high number of larval stages highlights the role of amphibians as intermediate and paratenic hosts for a wide range of internal parasites whose definitive hosts include birds, snakes, turtles, and mammals. These findings suggest a potential risk of parasite introduction into new ecosystems and emphasize the need for epizootiological monitoring under post-disaster conditions. Catastrophic hydrological events can serve as a mechanism for the transfer of both host species and their parasites, disrupting ecosystem stability and threatening local fauna. Helminthological monitoring in areas of ecological disasters is essential for detecting hidden consequences and for developing measures to conserve biodiversity.

Key words. Landscape transformation, animal health, amphibians, helminths, ecocide, warfare ecology.

Introduction

In recent years, the number of natural disasters caused by climate change and accelerating anthropogenic pressures

has increased significantly, raising serious concerns within the scientific community (IPCC 2023, WMO, 2024). These processes are most evident in zones affected by military conflicts, such as the Russian full-scale invasion of

Ukraine, where habitat degradation and destruction have reached unprecedented scales since World War II in Europe (VASYLIUK et al. 2015, MARUSHCHAK et al. 2024, NEKRASOVA et al. 2024). In the eastern and southern regions of Ukraine, this has led to massive and large-scale disruptions of human populations but also of ecosystem integrity, structure and functioning, threatening regional biodiversity (VASYLIUK et al. 2015, ZINENKO et al. 2023, NEKRASOVA et al. 2025).

In international discourse, such actions are increasingly referred to as ecocide (NEKRASOVA et al. 2024), meaning the voluntary large-scale destruction of natural environments that causes irreparable harm to ecosystems, undermines their recovery capacity, and often leads to species extinction (HIGGINS et al. 2013). Ecocide is considered a grave environmental crime, and in recent years, its recognition under international law, including the Rome Statute of the International Criminal Court, has been widely debated (Article 441, Criminal Code of Ukraine).

The most striking example of such environmental disaster during the Russian full-scale invasion of Ukraine, so far, occurred on 6 June 2023, with the destruction of the Kakhovka dam, the largest hydraulic infrastructure of Ukraine, on the Dnipro River in Kherson Oblast, eastern Ukraine. The dam provided water from the Kakhovka Reservoir (18 km³ of freshwater, equivalent to the Great Salt Lake in the United States) that supplied water for cooling the Zaporizhzhia Nuclear Power Plant, and for irrigating areas of southern Ukraine and northern Crimea. The destruction of this major infrastructure resulted in massive flooding throughout the entire Lower Dnipro River Plain, where numerous cities and villages but also natural reserves lie. This flooding triggered the release of unknown quantities of industrial, potentially toxic chemicals, but also the displacement of biological materials, including herpetofauna species and associated parasites as well as novel pathogens up to the brackish and coastal habitats of the northwestern Black Sea region previously uninhabited by them (VASYLIUK et al. 2025, TYTAR et al. 2024). Among these species were the European pond turtle (*Emys orbicularis* LINNAEUS, 1758), snakes (*Elaphe sauromates* PALLAS, 1811, *Dolichophis caspius* GMELIN, 1789), and relict populations from the Dnipro estuary of Danube crested newts (*Triturus dobrogicus* KIRITZESCU, 1903), and frog species of the *Pelophylax esculentus* complex (MARUSHCHAK et al. 2024, 2025, VASYLIUK et al. 2025).

The large-scale landscape changes caused by the destruction of hydraulic structures represent one of the most destructive forms of human impact on nature, especially when combined with pollution and the displacement of biota. However, the ecological consequences of warfare remain insufficiently studied, particularly regarding secondary effects such as the spread of parasitic organisms and infections into new ecosystems (TYTAR et al. 2023, 2024). The mortality or dispersal of herpetofauna, accompanied by the potential spread of their parasites and their introduction in new areas, presents a hidden yet potentially serious threat to both biodiversity and epizootic safety. Hel-

minths, especially macroparasites with complex (heteroxenous) life cycles, are sensitive bioindicators of environmental change and trophic network structure (KOPRIVNIKAR et al. 2012, MARCOGLIESE 2005, ČEIRĀNS et al. 2021, 2023). Their occurrence, diversity, and community structure are closely tied to local ecology, the presence of intermediate and definitive hosts, and habitat conditions (JOHNSON et al. 2004). Therefore, studying the helminth fauna of amphibians can provide important insights into ecosystem disruption due to both technogenic and military factors.

In Ukraine, the helminth fauna of water frogs (*Pelophylax esculentus* complex: Marsh frog *Pelophylax ridibundus* and water frogs *Pelophylax esculentus*) has been studied only sporadically and very unevenly across regions. Most research has been conducted in the northern and western parts of the country (MAZURMOVYCH 1951, MAGUZA 1973, MARUSHCHAK et al. 2017, KUZMIN et al. 2020). Thus, the lower Dnipro region, especially areas below the destroyed Kakhovka hydraulic power plant, remains poorly described by parasitological research. Most importantly, the absence of data on helminths potentially introduced by displaced amphibians following the disaster prevents a full assessment of risks to the northwestern Black Sea ecosystems and highlights the need for long-term monitoring.

This study aims to determine the species composition and structure of the helminth communities of amphibians from the *Pelophylax esculentus* complex found on the coast of the Odesa region, lower Dnipro, after the destruction of the Kakhovka dam. The objectives of the study include: (1) the inventory of amphibians and helminths collected in the coastal territories; (2) the determination of the potential origin and transmission pathways of the helminths; (3) the assessment of the likelihood of parasite fauna introduction into new habitats; and (4) a discussion in the context of postwar transformations of natural communities and threats to biodiversity.

Material and methods

As part of a long-term herpetological monitoring conducted in the Odesa region (Ukraine) along the coastal zone of the Black Sea, field surveys were carried out in areas adjacent to the Sukhyi Estuary (near the village of Burlakova Balka), drainage canals and temporary water bodies, as well as coastal sites from 6 June 2023 (the date of the destruction of the Kakhovka dam) to 26 June 2023. The survey consisted of collecting the specimens found in accumulations of organic and anthropogenic debris (Figs 1, 2). Every specimen was identified at the species level based on morphological characteristics (NEKRASOVA & MOROZOV-LEONOV 2001). A fraction of collected specimens (see Results) was collected for further helminthological studies in the laboratory. There, frogs were euthanized by lidocaine injection into the spinal cord, autopsied and examined for helminths. Collected trematodes, cestodes and nematodes were washed in saline and fixed with heated 70% alcohol. Acanthocephalans were placed in distilled water and kept

there for 2–24 hours, until complete evagination of the proboscis and relaxation of the trunk. Thereafter, they were fixed in 70% alcohol. Encysted juvenile stages of trematodes and nematodes were extracted from the cysts with thin needles and fixed with heated alcohol. Before examination and identification, helminths were cleared in lactophenol (a mixture of equal volume parts of glycerin, phenol, water, and lactic acid) for 0.5–4 hours.

For each helminth species in each host sample, the infection prevalence, intensity, total and mean abundance were calculated as defined by BUSH et al. (1997). Additionally, the relative abundance of each species was calculated as the percentage of its specimens in the whole samples of helminths. Confidence intervals of infection prevalence and mean abundance were calculated with Quantitative Parasitology 3.0 software (RÓZSA et al. 2000) using the

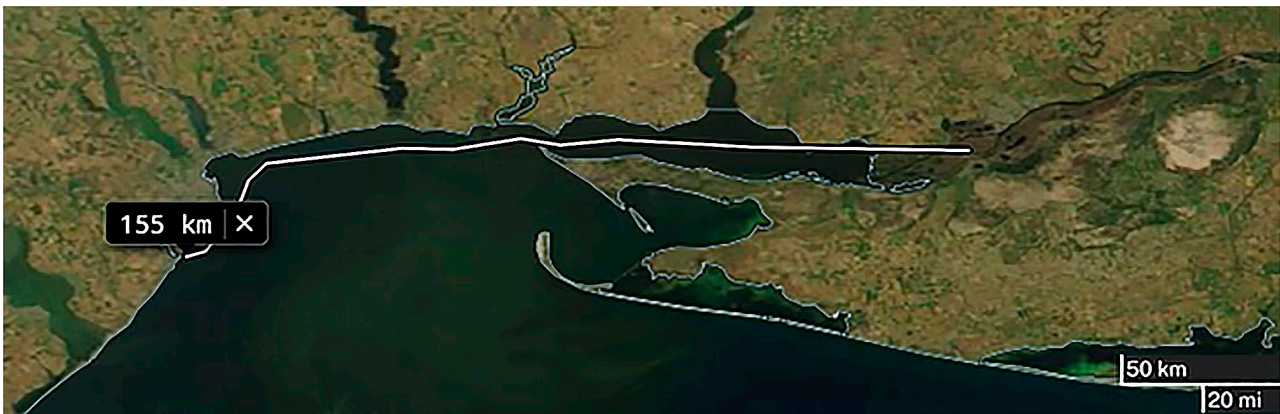


Figure 1. Map of the condition of the Kherson floodplains and the Black Sea coast in June 2023 following the destruction of the Kakhovka Hydroelectric Power Plant: animal migration route during the flooding towards the Odesa region (worldview.earthdata.nasa.gov).



Figure 2. Representatives of the *Pelophylax esculentus* complex: *P. ridibundus* and *P. esculentus* near a pile of plant debris on the shore of the Black Sea (Odesa region). Photo: O. NEKRASOVA.

Stern and bootstrap methods. Accordingly, helminth species were distinguished and identified as statistically uncertain if the lower limit of confidence interval of its infection prevalence was lower than the minimum possible infection prevalence in the sample (i.e., the infection prevalence of one host individual infected by the particular helminth species), or if the lower limit of confidence interval of its mean abundance was 0. The Quantitative Parasitology 3.0 program was also used to estimate the significance of differences in the infection prevalence and mean abundance by the unconditional exact test (UET) and the bootstrap-t test (BTT), correspondingly, for each helminth species in the two host species samples. The similarity between helminth infracommunities was estimated using the Bray-Curtis index, visualized by nMDS 2-dimensional plot and analyzed using the SIMPER routine in PRIMER 6 software (CLARKE & GORLEY 2006). Values are given as mean \pm SD and statistical significance was set with the threshold of 5% using ABC Software.

Results

During the study conducted on the desalinated coastal zone of the Black Sea in the Odesa region, a total of 145 individuals of water frogs *Pelophylax esculentus* complex were found both near saline waters and among storm-washed debris piles including: construction materials, metal pieces, fragments of tree roots and wetland plants (e.g., rhizomes of yellow water lilies *Nuphar* sp., white water lilies *Nymphaea* spp., common reed *Phragmites australis* Cav. Trin. ex Steud., bulrush, and others) that were most likely used as floating platforms (Fig. 2). Out of these specimens, ten males and seven females of *P. ridibundus* (snout-vent length 77.9 ± 11.1 mm, range 59–97 mm) and nine males and two females of *P. esculentus* (64.7 ± 7.7 mm, range 51–79 mm) were collected for further helminthological studies.

In the pooled 28 frogs, 15582 helminth specimens were found (13195 [85%], and 2387 [15%] specimens in 17 *P. ridibundus* and eleven *P. esculentus*, respectively). Helminths were assigned to 22 species: one species of acanthocephalans, one species of cestodes, 15 species of trematodes, and five species of nematodes (Table 1). Out of the 22 helminth species, 20 were found in *P. ridibundus*, 14 in *P. esculentus*, and twelve species were shared by the two frog species (Table 1). Marsh frog *P. ridibundus* was found to host adult forms of trematodes (*P. loossi*, *H. asper*, and *H. variegatus*), nematodes (*I. neglecta* and *C. ornata*), metacercariae of *E. colubrimurorum* and *P. cloacicola*, and plerocercoid of *S. erinaceieuropei*. The three latter species were recorded each in only one host specimen. Finally, *I. neglecta* and *C. ornata* were found each in 2 host specimens. These last five species were considered statistically uncertain in the sample based on confidence intervals of the infection prevalence and abundance (see Table 1). Only one specimen of the water frog *P. esculentus* was found to host the nematodes *O. bialata* and *S. contortus*, each of these parasites being represented by one single specimen. Therefore, only *P. loossi*, *H. asper*,

and *H. variegatus* significantly contributed to the faunistic differences between the two helminth samples. Furthermore, three species (namely the acanthocephalan *A. ranae* and the trematodes *P. medians* and *P. confusus*) had the infection prevalence significantly higher in *P. ridibundus* than in *P. esculentus* (UET $p < 0.01$). Mean abundance of *T. excavata* in *P. ridibundus* was also significantly higher than in *P. esculentus* (BTT $p = 0.01$) due to the much larger infection intensity in the former host (Table 1).

Fourteen helminth species were found in adult stages. The majority of them (11 species, 79%) were found in the digestive tract of the frogs: the trematode *H. ovocaudatus* was found in the stomach; the acanthocephalan *A. ranae*, the nematode *O. bialata*, and the trematodes *C. loossi*, *O. ranae*, *P. claviger*, *P. medians*, and *P. confusus* were in the small intestine. The trematode *D. subclavatus* and the nematodes *C. ornata* and *Strongyloides* sp. dwelled in the rectum. The trematodes *H. asper* and *H. variegatus* were found in the lungs. The nematode *I. neglecta* was found in the throat and leg muscles.

Eight helminth species were represented by juvenile stages: plerocercoid of the cestode *S. erinaceieuropei* found in the thigh muscles, third-stage larva of the nematode *S. contortus* found encysted in the intestine wall, and metacercariae of the trematodes *A. monticelli*, *E. colubrimurorum*, *P. cloacicola*, *S. sphaerula* (encysted on the surface of internal organs), *C. urniger* (encysted in the body cavity, muscles, spinal canal, testes and ovaries), and *T. excavata* (free in the spinal canal). In female frogs heavily infected with *C. urniger*, the majority of metacercariae were observed in the reproductive tractus: for instance, 1515 (69%) of 2196 cysts of *C. urniger* collected from a female *P. ridibundus* were found in the ovaries (Fig. 3).

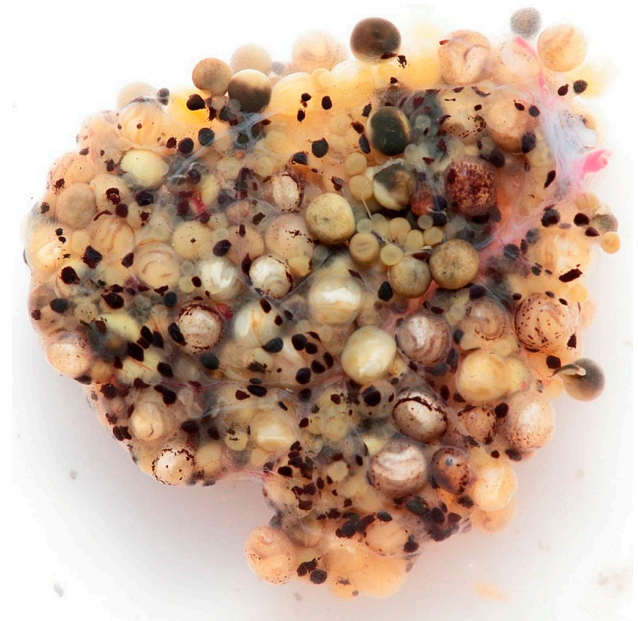


Figure 3. Fragment of the ovary of *Pelophylax ridibundus* infected with numerous cysts of *Codonocephalus urniger*.

Spread of helminth parasites of water frogs on the Black Sea shore

Table 1. Infection parameters of helminth species parasitizing *Pelophylax ridibundus* (n = 17; upper value) and *P. esculentus* (n = 11; lower value). P% – infection prevalence, % (95% confidence intervals in parentheses); MA – mean abundance (95% confidence intervals in parentheses); I – infection intensity (mean, median in brackets and range in parentheses); A – number of specimens in sample; RA% – relative abundance, %; significant differences in P and MA are marked in bold. plc – plerocercoid; mtc – metacercaria; L3 – third-stage larva; * – only 1 host infected.

Species	P%	MA	I	A (RA%)
Acanthocephala: Palaeacanthocephala				
1. <i>Acanthocephalus ranae</i> (SCHRANK, 1788)	88.2 (65–97.9) 36.4 (13.5–66.7)	3.24 (2.06–4.47) 1.45 (0.27–3.27)	3.7 [3] (1–8) 4 [4] (1–7)	55 (0.42) 16 (0.67)
Platyhelminthes: Cestoda				
2. <i>Spirometra erinaceieuropaei</i> (RUDOLPHI, 1819) (plc)	5.9 (0.3–28.7) 0	0.06 (0–0.18) 0	1* 0	1 (0.01) 0
Platyhelminthes: Trematoda				
3. <i>Astiotrema monticelli</i> STROSSICH, 1904 (mtc)	5.9 (0.3–28.7) 18.2 (3.3–50)	0.18 (0–0.53) 0.18 (0–0.36)	3* 1 [1] (1–1)	3 (0.02) 2 (0.08)
4. <i>Codonocephalus urniger</i> (RUDOLPHI, 1819) (mtc)	94.1 (71.3–99.7) 90.9 (59.6–99.5)	377.7 (208.1–737.2) 126.8 (52.3–307.8)	401.3 [252] (9– 2,196) 139.5 [69] (1–701)	6,421 (48.7) 1,395 (58.4)
5. <i>Diplodiscus subclavatus</i> (PALLAS, 1760)	94.1 (71.3–99.7) 90.9 (59.6–99.5)	9.47 (4.47–19.12) 5.18 (2.82–9.18)	10.1 [3.5] (1–51) 5.7 [4] (1–17)	161 (1.2) 57 (2.4)
6. <i>Encyclometra colubrimurorum</i> (RUDOLPHI, 1819) (mtc)	5.9 (0.3–28.7) 0	0.06 (0–0.18) 0	1* 0	1 (0.01) 0
7. <i>Haematoloechus asper</i> LOOSS, 1899	47.1 (25.3–71.3) 0	1.65 (0.59–4.94) 0	3.5 [1.5] (1–15) 0	28 (0.21) 0
8. <i>H. variegatus</i> (RUDOLPHI, 1819)	41.2 (19.6–65) 0	1.18 (0.47–2.65) 0	2.9 [2] (1–8) 0	20 (0.15) 0
9. <i>Halipegus ovocaudatus</i> VULPIAN, 1859	23.5 (8.5–48.9) 18.2 (3.3–50)	0.59 (0.12–1.41) 0.45 (0–1.18)	2.5 [2.5] (1–4) 2.5 [2.5] (2–3)	10 (0.08) 5 (0.21)
10. <i>Opisthioglyphe ranae</i> (FROELICH, 1791)	82.4 (58.3–95) 72.7 (40.4–92.1)	36.59 (17.88–62.12) 11.55 (4.09–36.09)	44.4 [26] (1–133) 15.9 [7.5] (1–75)	622 (4.7) 127 (5.3)
11. <i>Paralepoderma cloacicola</i> (LUHE, 1909) (mtc)	5.9 (0.3–28.7) 0	0.06 (0–0.18) 0	1* 0	1 (0.01) 0
12. <i>Pleurogenes claviger</i> (RUDOLPHI, 1819)	52.9 (28.7–74.7) 27.3 (7.9–59.6)	0.94 (0.47–1.53) 0.82 (0.18–1.82)	1.8 [1] (1–4) 3 [3] (2–4)	16 (0.12) 9 (0.38)
13. <i>P. loossi</i> AFRICA, 1930	52.9 (28.7–74.7) 0	9.82 (1.06–43.82) 0	18.6 [3] (1–146) 0	167 (1.3) 0
14. <i>Pleurogenoides medians</i> (OLSSON, 1876)	100 (80.4–100) 63.6 (33.3–86.5)	78.71 (46.06–126.2) 27.45 (7.91–81.09)	78.7 [44] (4–306) 43.1 [14] (4–190)	1,338 (10.1) 302 (12.6)
15. <i>Prosotocus confusus</i> (LOOSS, 1894)	88.2 (65–97.9) 9.1 (0.5–40.4)	14.94 (7.65–27.82) 5.18 (0–15.55)	16.9 [9] (1–59) 57*	254 (1.9) 57 (2.4)
16. <i>Strigea sphaerula</i> (RUDOLPHI, 1803)	17.6 (5–41.6) 36.4 (13.5–66.7)	1.53 (0.29–4.41) 4.91 (0.82–15.27)	8.7 [6] (5–15) 13.5 [7] (3–37)	26 (0.2) 54 (2.3)
17. <i>Tylodelphys excavata</i> (RUDOLPHI, 1803) (mtc)	100 (80.4–100) 90.9 (59.6–99.5)	238.9 (141.8–361.4) 32.18 (12.36–65.91)	238.9 [123] (4–710) 35.4 [15] (2–125)	4,062 (30.8) 354 (14.8)
Nematoda: Chromadorea				
18. <i>Cosmocerca ornata</i> (DUJARDIN, 1845)	11.8 (2.1–35) 0	0.12 (0–0.29) 0	1 [1] (1–1) 0	2 (0.02) 0
19. <i>Icosiella neglecta</i> (DIESING, 1851)	11.8 (2.1–35) 0	0.29 (0–1.06) 0	2.5 [2.5] (1–4) 0	5 (0.04) 0
20. <i>Oswaldocruzia bialata</i> MOLIN, 1860	0 9.1 (0.5–40.4)	0 0.09 (0–0.27)	0 1*	0 1 (0.04)
21. <i>Spiroxys contortus</i> (RUDOLPHI, 1819) (L3)	0 9.1 (0.5–40.4)	0 0.09 (0–0.27)	0 1*	0 1 (0.04)
22. <i>Strongyloides</i> sp.	5.9 (0.3–28.7) 9.1 (0.5–40.4)	0.12 (0–0.35) 0.64 (0–1.91)	2* 7*	2 (0.02) 7 (0.29)

In the helminth sample from *P. ridibundus*, seven species predominated by their infection prevalence of 80–100%: the acanthocephalan *A. ranae* and the trematodes *P. medians*, *D. subclavatus*, *P. confusus*, *O. ranae*, *C. urniger*, and *T. excavata*. Other helminth species had an infection prevalence of 53% (*P. loossi* and *P. claviger*) or lower (Table 1). Five trematode species predominated in the sample from *P. esculentus*: *P. medians*, *D. subclavatus*, *O. ranae*, *C. urniger*, and *T. excavata*. Their infection prevalence was from 63.6% (*P. medians*) to 90.9% (*D. subclavatus*, *C. urniger*, *T. excavata*). Other helminth species were found in less than half of the examined *P. esculentus* (Table 1).

In both species, metacercariae of trematodes *C. urniger* and *T. excavata* predominated by their abundance. They comprised 79.4% of all helminths collected from *P. ridibundus* and 73.3% of all helminths from *P. esculentus* (Table 1, Fig. 4). As a consequence, other helminth species had much lower relative abundance in each species. In *P. ridibundus*, five more helminth species had their relative abundance higher than 1%: *P. medians* (10.1%), *O. ranae* (4.7%), *P. confusus* (1.9%), *P. loossi* (1.3%), and *D. subclavatus* (1.2%). Total relative abundance of other 13 species was $\leq 1.3\%$ (Fig. 2). In the sample from *P. esculentus*, five species, in addition to *C. urniger* and *T. excavata*, had their relative abundance higher than 1%: *P. medians* (12.6%), *O. ranae* (5.3%), *P. confusus* (2.4%), *D. subclavatus* (2.4%), and *S. sphaerula* (2.3%). The total relative abundance of the other 7 species was 1.7%.

In the samples from *P. ridibundus*, helminth infracommunities consisted of 7–12 species (mean 9.4, median 9) and 66–2576 specimens (mean 776.2, median 703). Species richness and helminth abundance in the infracommunities from *P. esculentus* was lower: 4–9 (mean 5.8, median 6) species and 25–893 (mean 217, median 131) specimens. SIMPER analysis demonstrated that the differences between infracommunities in the two frog species (average dissimilarity 76.1%) were mostly due to the higher abundance of *C. urniger*, *T. excavata*, *P. medians*, and *O. ranae* in *P. ridibundus* compared to *P. esculentus*. Besides this, the average similar-

ity between helminth infracommunities from *P. ridibundus* was higher than that between the infracommunities from *P. esculentus*: 36.7% vs. 24.4%. Higher heterogeneity of the helminth sample from *P. esculentus* is evident also in the nMDS visualization of the similarity between the infracommunities based on the Bray-Curtis index (Fig. 5).

Discussion

Our study shows evidence of massive long-distance displacements of marsh frogs *P. ridibundus* and water frogs *P. esculentus* originated from areas that were affected by the destruction of the Kakhovka dam downstream Kakhovka Reservoir up to the brackish and coastal waters of the Black Sea, in the Odesa region. This indicates a passive transport of animals from the lower Dnipro River over a distance of more than 155 km (Figs 1–2). This is supported by our discovery of hybrid forms of *P. esculentus* (Fig. 6) that have already been recently described as characteristic of the Kherston floodplains (MEZHHERIN et al. 2023), confirming that individuals were swept away with the 18 km³ of water that were flushed way due to the destruction of the dam. Most amphibians perished due to the high speed of the flood and unfavorable conditions, including ongoing military actions and secondary effects such as intense eutrophication and mass algal blooms (MOYSIYENKO et al. 2023, VASYLIUK et al. 2025). However, some surviving animals, such as frogs, began migrating into nearby freshwater bodies (including the Sukhyi Estuary, Dniester Estuary, and private ponds) where native amphibians were also present (Fig. 6, Nekrasova 2015). Frog individuals found on the coasts of the Black Sea were observed on artificial and vegetal floating debris. In normal contexts, frogs are almost exclusively observed partly or totally submerged. Our unusual observations in Odesa region can be explained by the fact that either the animals were recovering from a state of extreme tiredness resulting from being swept away by the heavy flush and/or the animals were experiencing inappropriate environmen-

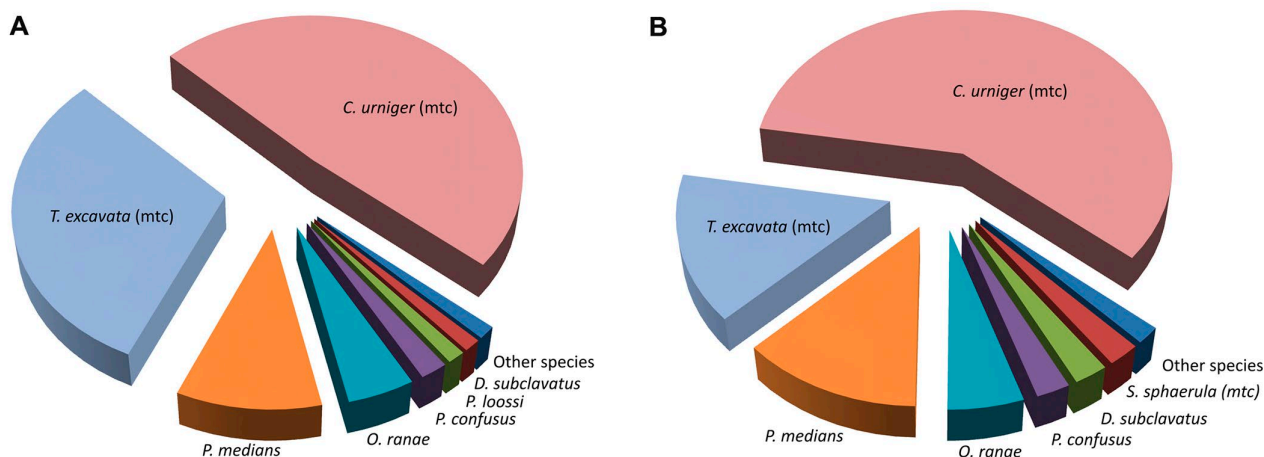


Figure 4. Relative abundance of helminth species in *P. ridibundus* (A) and *P. esculentus* (B).

tal conditions (i.e., salty waters) they attempted to escape by avoiding being in water.

Our study demonstrates that abrupt changes in hydrological conditions – such as that provoked by the destruction of the Kakhovka dam – result in massive displacements of animal species, as also recently reported in larger species such as the Mediterranean turtle during natural extreme flood events (PRIOL et al. 2024). Importantly, our study additionally shows that such displacement of frogs also in-

duces the transfer of their parasites into sensitive ecosystems inhabited by native fauna. In this context, the study of helminth fauna becomes particularly significant, as it makes it possible to identify the current state of parasite communities and the potential mechanisms of their spread and establishment in new biotopes. The number of 22 helminth species we found in the 28 specimens of the *Pelophylax* complex from the present study was similar to the helminth species richness previously reported in Ukraine. For instance, in Kharkiv region, Rezvantseva et al. (2010) identified 18 different species of helminths in a similar quantity of *P. ridibundus* (n = 23) and *P. esculentus* (n = 24), each frog hosting 15 helminth species. A historical study performed on larger frog sample sizes throughout the larger area of the Danube Delta in the Odesa region with 206 examined *P. ridibundus* resulted in a more diversified community of 31 helminth species (VOLGAR-PASTUKHOVA 1959). More recently, KUZMIN et al. (2020) found a total of 27 helminth species in 86 *P. ridibundus* and 57 *P. esculentus* from 13 localities in northern Ukraine. These three studies, including ours, show that the more the sampling, and the larger the study area, the more helminth species are identified. Interestingly, the number of helminth species recorded in the latter study was higher in *P. esculentus* than in *P. ridibundus* (24 vs. 20 helminth species, respectively), as opposed to our findings (14 vs. 20 helminth species, respectively), presumably because of the larger sample size for marsh frogs.

Out of the 22 helminth species identified in the present study, eight (36%) were found as larval stages. Former studies reported similar results, with proportions of larval helminths ranging from 22% (REZVANTSEVA et al. 2010) to 33%



Figure 5. nMDS visualization of Bray-Curtis similarity between helminth infracommunities in the studied sample of *Pelophylax esculentus* complex.



Figure 6. Hybrid *P. esculentus* in the Sukhyi Estuary (Odesa region, photo by O. NEKRASOVA).

(KUZMIN et al. 2020). Consistent with their most exhaustive monitoring of the rich ecosystem of the Danube Delta, VOLGAR-PASTUKHOVA (1959) reported as many as 14 (45%) helminth species at larval stages in *P. ridibundus*. Importantly, among the larval forms we found in our study, three trematode species (*A. monticelli*, *E. colubrimurorum* and *P. cloacicola*) were previously reported as accomplishing their development in snakes, especially in *Natrix* spp. (SHARPILO & ISKOVA 1989). Similarly, we also found adult forms of nematodes (*S. contortus*) known to parasitize the European pond turtle *Emys orbicularis* (SHARPILO 1976), adult trematodes *T. excavata* in the white stork *Ciconia* spp., *C. urniger* in ardeid birds, and *S. sphaerula* parasitizing corvids (ISKOVA et al. 1995). The cestode *S. erinaceieuropei*, widely distributed in Europe (KUCHTA et al. 2021), reaches maturity in carnivorous mammals and its definitive hosts in Ukraine are mostly Canidae (KORNYUSHIN et al. 2011).

Metacercariae of *T. excavata* and *C. urniger* were found in almost all examined frogs and reached an extremely high abundance, with on average from 158 to 276 specimens per frog, respectively (Table 1). Previously, both species were recorded in the Odesa region (VOLGAR-PASTUKHOVA 1959), yet with an infection prevalence in *P. ridibundus* significantly lower for *C. urniger* (6.2%) and for *T. excavata* (48.3%). Our results suggest that the introduction of *Pelophylax* complex from the lower part of the Dnipro into habitats along the north-western coasts of the Black Sea is a potential risk of increased infection of local frogs, as well as birds (storks, bitterns and herons) with these parasites.

Based on abundance and infection prevalence, the trematodes *P. loossi*, *H. asper* and *H. variegatus* were considered statistically certain species in *P. ridibundus*, whereas they were absent from *P. esculentus*. None of these three helminth species is specific to *P. ridibundus*, since each of them have been previously recorded in various *Pelophylax* complex (SHARPILO & ISKOVA 1989, SHIMALOV 2009, REZVANTSEVA et al. 2010, POPIOLEK et al. 2011, HERCZEG et al. 2016, KUZMIN et al. 2020). We presume that the specimens of *P. esculentus* examined in the present study originated from habitats poorly favorable for the transmission of *C. loossi*, *H. asper* and *H. variegatus* compared to the predilected habitat of *P. ridibundus*. Interestingly, we found significant differences in the infection prevalence for *A. ranae*, *P. medians* and *P. confusus* between the two host species. Our results contrast with the two other former studies, where *O. ranae* was found to occur more frequently in *P. ridibundus* than in *P. esculentus*, whereas the infection prevalence of *A. ranae*, *P. medians* and *P. confusus* was similar between the two hosts (REZVANTSEVA et al. 2010, KUZMIN et al. 2020). The higher infection prevalence of these three species in *P. ridibundus* found in our study may be due to the different habitats of *P. ridibundus* and *P. esculentus*. Besides this, the examined individuals of *P. ridibundus* were larger than those of *P. esculentus* and might, therefore, harbor larger numbers of helminth species and specimens. Species richness in helminth infracommunities was shown to be positively correlated with the host size in some amphibian hosts (HAMANN et al. 2010, KUZMIN et al. 2020).

An additional threat is posed by mass algal blooms triggered by the influx of organic matter, which may have led to the death of aquatic organisms and disruption of food chains (KUYBIDA et al. 2019). Such events are capable of increasing parasitic pressure on both introduced and native species. It is especially important to note that as water quality changed due to blooming, followed by increasing salinity, frogs moved as far as possible from the sea, and were found along roads, in canals, and in private ponds.

Conclusions

Our study demonstrates the massive ecological impacts of the destruction of the Kakhovka dam during the Russian full-scale invasion in summer 2023, with the large-scale displacement of endangered frog species into unsuitable habitats, up to the marshlands and blackish waters of the coasts of the Black Sea. Most importantly, this displacement leads to the spread of highly diversified helminth parasites in these new habitats, with potential infection of a large range of species, including other amphibians, but also snakes, turtles, waterfowl, predatory birds and mammals, including protected species. Despite the limited sample sizes used in our study, our results suggest that the study *Pelophylax* frogs originated from rather healthy ecosystems, as supported by both the diversity of helminth species and the presence of various larval helminths using frogs as intermediate or paratenic hosts. Further, the observed values of helminth infection suggest that the water frogs *P. esculentus* specimens collected in our study after the destruction of the Kakhovka dam originated from at least two different populations, as supported by the heterogeneity of helminth infracommunities among individuals of this frog species. As a conclusion, our study provides ecological evidence, and supports the discourse of the Presidency of Ukraine, of the ecocidal nature of the destruction of the Kakhovka dam by the Russians. This also underscores the importance of comprehensive monitoring and impact assessment of such events to safeguard biodiversity.

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