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# The effect of trematode infection on the content of certain lipid groups in the organism of *Planorbarius purpura*

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**Abstract.** Investigating the effect of trematode infection on the physiological and biochemical status of freshwater molluscs is an important area of hydrobiological research, as trematodes are widespread parasitic organisms capable of significantly affecting the metabolic homeostasis and adaptive capabilities of their host organisms. The aim of this study was to determine the nature of changes in the content and tissue-organ distribution of total lipids and their individual groups (triacylglycerols, phospholipids and cholesterol) in the haemolymph, hepatopancreas, mantle and foot of *Planorbarius purpura* under the influence of trematode infection. The content of total lipids was determined by the gravimetric method following extraction using the Folch method, whilst that of individual lipid groups was determined by one-dimensional thin-layer chromatography. Statistical analysis of the results was carried out using one-way analysis of variance. It was established that trematode infection causes pronounced tissue-specific changes in the content and ratio of individual lipid groups in the bodies of the studied molluscs. In the hepatopancreas of infected animals, a statistically significant increase in total lipid content of 87.6% was recorded ($p < 0.001$), whilst in the foot and haemolymph this figure decreased by 21.1% and 41.18%, respectively ($p < 0.05$). This increase in total lipid content in the hepatopancreas may be associated with the accumulation of triacylglycerols and the development of compensatory and adaptive responses in the molluscs' bodies.

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The content of phospholipids and cholesterol decreased in most of the tissues and organs studied under trematode infection, which may indicate a disruption in the structural organisation of biological membranes. The exception was the mantle of *P. purpura*, in which the cholesterol content increased by 44.4% ($p < 0.01$). Analysis of the tissue- and organ-specific distribution of individual lipid groups showed that phospholipids were quantitatively predominant in the hepatopancreas, mantle, foot and haemolymph of intact molluscs. Under conditions of trematode infection, the most pronounced changes were observed in the hepatopancreas, mantle and foot of *P. purpura*, where the proportion of triacylglycerols increased, whilst in the haemolymph, phospholipids remained the dominant lipid group. Thus, trematode infection is accompanied by marked tissue-specific changes in the content and distribution of individual lipid groups within the body of *P. purpura*. The parameters determined can be used as biochemical markers of the physiological and biochemical status of freshwater molluscs during the biomonitoring of aquatic ecosystems

**Keywords:** freshwater molluscs; total lipids; triacylglycerols; phospholipids; cholesterol; biochemical indicators

## Introduction

Freshwater molluscs, which are one of the most numerous and widespread groups of aquatic invertebrates, play an important role in the functioning of aquatic ecosystems, as they form part of most aquatic communities. Owing to their high abundance and significant biomass, they participate in material cycles and energy conversion, the formation of trophic links, and also serve as an important food source for fish, waterfowl, shorebirds and other members of the aquatic fauna. At the same time, many species of freshwater molluscs act as the first intermediate hosts for digenean trematodes, whose parthenogenetic generations develop within their bodies.

The relationship within the "parasite-host" system is antagonistic in nature, as the parasite utilises the host's body as a habitat and a source of nutrients. The development of parthenogenetic generations of trematodes is accompanied by changes in the physiological and biochemical state of the host mollusc, which may manifest as histopathological lesions of organs, disturbances in growth and development, suppression of reproductive function, and alterations in metabolic processes. The complex nature of the effects of trematode infection is highlighted by the work of H.-A.A. Dokmak *et al.* (2024), who identified changes in biological, trophic, physiological, biochemical and histological parameters in the bodies of *Biomphalaria alexandrina* and *Bulinus truncatus*, infected with *Schistosoma mansoni* and *S. haematobium* respectively.

The study of interaction mechanisms in the "trematode-mollusc" system remains an important area of modern parasitology and the physiology of aquatic organisms, as the host mollusc's response to trematode infection occurs at various levels of its physiological and biochemical organisation. A number of studies point to the complexity of the interaction mechanisms between *B. glabrata* and *S. mansoni*. In particular, L. Lu *et al.* (2022) demonstrated that the nature of the response depends on the molluscs' susceptibility to the parasite and the characteristics of the course of the infection, whilst I.F. Abou-El-Naga & N.M.F.H. Mogahed (2024) summarised data on the immunomolecular characteristics of the interaction between the mollusc and the parasite.

Alongside changes in defence mechanisms, the development of trematodes is accompanied by a reorganisation of the host mollusc's metabolic processes. To meet their own metabolic needs, growth and the development of larval stages, the parasites utilise the host's resources,

amongst which lipids play a significant role. In the body, lipids perform energetic, structural and regulatory functions, ensuring the storage and mobilisation of energy resources, the formation of cell membranes and the maintenance of their structural and functional organisation. According to Y.G. Jeon *et al.* (2023), one form of metabolic energy storage is neutral lipids, in particular triacylglycerols (TAG), whilst phospholipids (PL) and cholesterol (CH), as noted by D. Huster *et al.* (2024), are important components of biological membranes and determine their structural and functional properties.

Given the functional role of these compounds, changes in the content of individual lipid groups may reflect a redistribution of energy resources and a reorganisation of metabolic processes in molluscs. The involvement of lipid metabolism in the physiological and biochemical response of molluscs to trematode infection is supported by recent literature data. A.H. Hassan *et al.* (2021) identified changes in the levels of TAGs, PL and cholesterol in the digestive gland-gonad complex and haemolymph of infected *Nerita polita*, whilst E. Simphor *et al.* (2024) documented differences in metabolic profiles, particularly lipid components, in *B. glabrata* during *S. mansoni* infection. The involvement of fatty acid metabolites in the parasite-host interaction is also indicated by the study by O.C. Friesen *et al.* (2022), who identified changes in the profile of oxylipids secreted by *Planorbella pilsbryi* into the environment during *Echinostoma trivolvis* infection. Thus, the results obtained for various "trematode-mollusc" systems indicate the important role of lipid metabolism reorganisation in the physiological and biochemical response of molluscs to infection.

Furthermore, the results of previous studies indicate species- and tissue-organ-specific differences in lipid metabolism in freshwater molluscs. A comparative analysis of *Lymnaea stagnalis* and *Unio pictorum*, conducted by G.Ye. Kyrychuk *et al.* (2023), revealed species-specific differences in the content and distribution of individual lipid groups, whilst a recent lipidomic study by D. Ilyaskina *et al.* (2025) demonstrated that the nature of changes in individual lipid components in *L. stagnalis* depended on the characteristics of the biological material under investigation. Taken together, the results obtained indicate the species- and tissue-organ-specific nature of lipid metabolism in molluscs and the variability of its reorganisation under the influence of external factors. At the same time, biological and physiological-biochemical differences between representatives of various taxonomic groups of molluscs may determine the specificity of their metabolic reactions, which highlights the need to verify the established patterns in other members of the malacofauna.

Alongside members of the family *Lymnaeidae*, the family *Planorbidae* comprises lung-breathing molluscs that are widely distributed in freshwater bodies; they play an important role in the functioning of aquatic ecosystems and, at the same time, serve as intermediate hosts for many species of digenean trematodes. One of the common species of this family is *Planorbarius purpura* (Müller, 1774), for which changes in a number of physiological and biochemical parameters have been observed during trematode infection, although the specific features of the reorganisation of lipid metabolism in these animals during the development of parthenogenetic generations of trematodes remain insufficiently understood.

The aim of this study was to determine the nature of changes in the content and tissue- and organ-specific distribution of total lipids and their individual groups (triacylglycerols, phospholipids and cholesterol) in the haemolymph, hepatopancreas, mantle and foot of *Planorbarius purpura* under the influence of trematode infection.

## Materials and Methods

The study material consisted of freshwater pulmonate molluscs *Planorbarius purpura* (Müller, 1774) with similar size and mass characteristics (shell diameter: 26.3-32.5 mm; mass: 3.72-5.51 g). The molluscs were collected in May 2025 from the Kodnianka River (Berdychiv District, Zhytomyr

Region). Mass was determined using electronic scales accurate to 0.01 g, while morphometric parameters were measured using callipers. After collection, the molluscs were acclimatised to laboratory conditions over a period of 14 days. All specimens were kept under identical conditions of lighting, water temperature (18-20°C) and pH (7.3-7.7), and were fed macerated cabbage leaves. To prevent the accumulation of mollusc exometabolites in the water, the water in the aquariums was replaced daily with settled water having the same physico-chemical characteristics.

The presence of trematode infection was determined based on the results of microscopic examination of temporary histological sections prepared from the hepatopancreas of each *P. purpura* specimen. A total of 45 molluscs were examined, and the prevalence of trematode infection was 26.7%. For biochemical analysis, 10 infected individuals (experimental group) and 10 uninfected individuals (control group) with the closest possible mass and size characteristics were selected ($n = 10$ in each group). *Haemolymph* was obtained by direct bleeding, after which the molluscs were dissected and the hepatopancreas, mantle and foot were collected. The biological material obtained was analysed individually for each specimen immediately after dissection. An individual mollusc was considered one biological replicate. A total of 320 biochemical determinations were performed, each in triplicate; the mean of the three parallel determinations was used for subsequent statistical analysis.

Total lipids were extracted using a mixture of chloroform and methanol (2:1) according to the Folch method (Folch *et al.*, 1957), after which non-lipid impurities were removed with a 1% potassium chloride solution. The total lipid (TL) content was determined by the gravimetric method. Lipids were separated into individual groups by ascending one-dimensional thin-layer chromatography on "Silufol" plates (Czech Republic) using a solvent system of hexane : diethyl ether : glacial acetic acid (70:30:1). The chromatograms were developed using vapours of crystalline iodine. Lipid fractions were identified on the basis of their retention factors (*Rf*) by comparison with purified standards of the corresponding lipid classes and using specific reagents. After development of the chromatograms, the corresponding lipid zones were scraped from the plates and used for subsequent quantitative analysis. The amount of non-polar lipids was determined using the bichromate method, whilst the phospholipid content was assessed based on the inorganic phosphorus content following mineralisation and reaction with ammonium molybdate (Kates, 1972). The content of total lipids and their individual groups was expressed in mg/g of raw tissue (organ).

Statistical analysis of the results was carried out using the Statistica 10.0 software package (StatSoft Inc., Tulsa, OK, USA). To assess the effect of trematode infection on the content of individual lipid groups, one-way analysis of variance (One-way ANOVA) was applied. Statistically significant differences between groups were determined using Tukey's post-hoc test (Tukey HSD). To assess the similarity of the lipid profiles of the tissues under investigation, hierarchical cluster analysis was performed using Ward's method with standardised Euclidean distance. Differences were considered statistically significant at $p < 0.05$.

During the studies, the principles of humane treatment of experimental organisms and the requirements for the conservation of biodiversity and the rational use of biological resources were adhered to, in accordance with Order No. 249 of the Ministry of Education and Science, Youth and Sports of Ukraine (2012) and the Convention on Biological Diversity (1992).

## Results and Discussion

The response of lipid metabolism in aquatic organisms to adverse environmental factors, including those of biotic and anthropogenic origin, is complex, and changes in the qualitative composition of lipids may reflect both damage to cellular structures and the development of adaptive responses aimed at maintaining organismal functioning. Analysis of the content of individual

lipid groups makes it possible to assess the direction of lipid metabolism, the extent to which energy and biosynthetic resources are involved in the adaptive reorganisation of metabolism, as well as the patterns of the organism's metabolic response to adverse environmental factors (Tunholi-Alves *et al.*, 2011).

In the presence of trematode infection, the adaptive capacity of molluscs may be substantially limited, as the development of parthenogenetic generations of the parasite is accompanied by a complex reorganisation of the host organism's defence and physiological and biochemical responses, as well as histopathological changes in tissues, disruption of the functional activity of internal organs and destabilisation of metabolic processes. Collectively, these effects may lead to depletion of the host organism and reduce its ability to maintain physiological homeostasis under changing environmental conditions (Dokmak *et al.*, 2024; Loker, 2025). Therefore, particular attention in this study was given to the analysis of total lipids, as well as the most functionally significant lipid groups – TAG, PL and CH, changes in the content of which characterise different aspects of lipid metabolism and reflect the specific features of energy and biosynthetic metabolism.

Analysis of total lipid content in the tissues and organs of *P. purpura* demonstrated pronounced tissue specificity in their distribution under normal conditions and substantial reorganisation under trematode infection. In uninfected molluscs, the highest TL content was found in the foot, where it exceeded the corresponding values in the hepatopancreas and mantle by 32.4% and 55.5%, respectively. At the same time, the lowest level of the parameter examined was recorded in the haemolymph (Fig. 1).

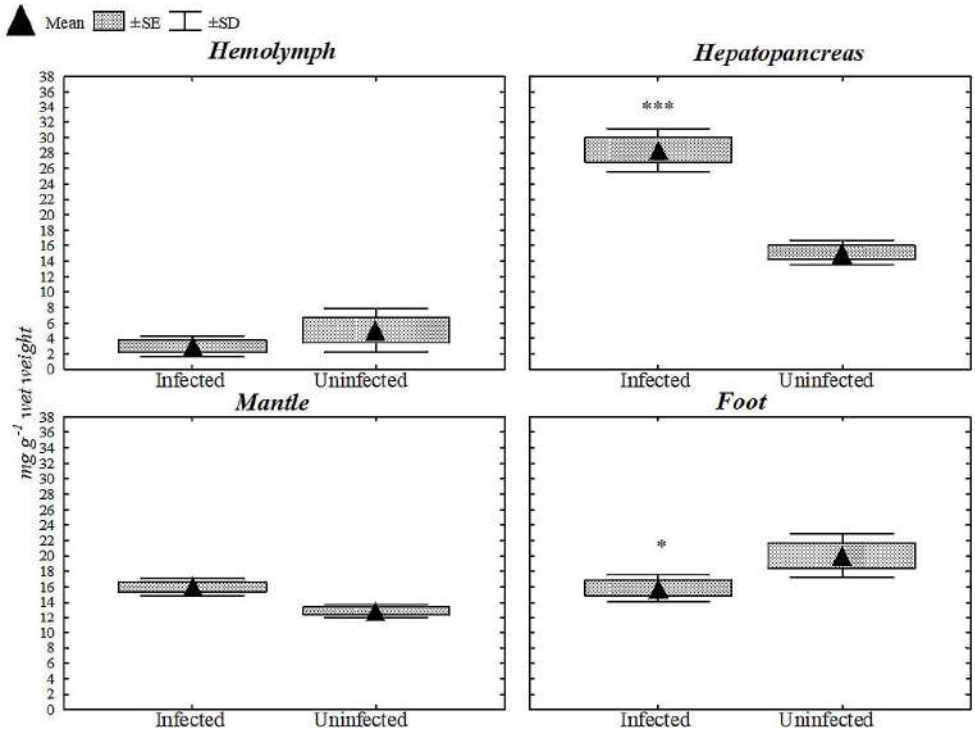



***Figure 1.*** *Total lipid content in the tissues and organs of Planorbarius purpura under trematode infection*

**Note:** * – $p < 0.05$; *** – $p < 0.001$ compared with uninfected molluscs
**Source:** authors' own work

In order of increasing total lipid content, the tissues and organs formed the following metabolic sequence: haemolymph → mantle → hepatopancreas → foot. This pattern of tissue distribution of total lipids reflects the functional specialisation of individual organs. The high lipid content in the foot is likely linked to its leading role in enabling locomotion and the significant energy expenditure required for the mollusc's movement. At the same time, the high content of total lipids in the hepatopancreas is consistent with its role as the primary organ for the storage and metabolism of nutrients.

Under trematode infection, the pattern of tissue distribution of total lipids changed. The highest content was observed in the hepatopancreas, where it exceeded the corresponding values in the mantle and foot by 78.1% and 79.7%, respectively, and that in the haemolymph by 9.55-fold. The lowest content, as in the control group, was recorded in the haemolymph. Under these conditions, the metabolic sequence was as follows: haemolymph → foot → mantle → hepatopancreas. The reorganisation of the metabolic sequence reflects substantial changes in lipid metabolism in the host mollusc under trematode infection. The changes in the positions of the hepatopancreas and foot within the sequence may indicate a shift in the balance between metabolic demands and lipid reserves in these organs, while the consistently lowest total lipid content in the haemolymph is probably attributable to its predominantly transport function and the absence of a major role as a depot for lipid compounds.

The results of one-way analysis of variance (One-way ANOVA) showed that trematode infection caused statistically significant changes in the content of TL, TAG, PL and CH in the tissues and organs of *P. purpura* ($p < 0.05$-$0.001$), with the magnitude and direction of these changes depending on both the tissue and the lipid group.

The most pronounced changes in TL content were recorded in the hepatopancreas, where its level in infected molluscs increased by 87.6% ($p < 0.001$) compared with the control. Given that the hepatopancreas is the main site of development of the parthenogenetic generations of trematodes and simultaneously plays a key role in the storage and metabolism of nutrients, this pattern may reflect reorganisation of lipid metabolism in the organ under parasitic burden. Under these conditions, the increase in TL content is probably associated with changes in the relative proportions of individual lipid components and redistribution of metabolic resources between storage, structural maintenance and energy metabolism. Similar changes in metabolic processes in the hepatopancreas under trematode infection were described by T.M.F. Mendes *et a*l. (2019) in *B. glabrata*, in which infection with *S. mansoni* was accompanied by a complex reorganisation of metabolism. The results obtained for *P. purpura* are consistent with the general direction of these changes and provide grounds for considering the increase in TL content in the hepatopancreas as one of the possible manifestations of the organ's metabolic response to infection.

In the mantle of *P. purpura*, an increase in the parameter under consideration of 23.8% was also recorded; however, these changes were considerably less pronounced than those observed in the hepatopancreas. This pattern is probably associated with the physiological role of the mantle, which participates in secretory processes and is responsible for shell formation (Alesci *et al*., 2024). In this context, the moderate accumulation of lipids in this organ may reflect a reorganisation of lipid metabolism associated with the structural and secretory functions of the mantle under parasitic load.

In contrast to the hepatopancreas and mantle, a reduction in total lipid content of 21.1% and 41.18%, respectively ($p < 0.05$), was observed in the foot and haemolymph of *P. purpura* following trematode infection, suggesting a redistribution of lipid reserves within the mollusc's body. Particularly telling is the reduction in these parameters in the haemolymph, which performs a transport function and facilitates the transfer of metabolites between organs. This trend may be linked to

increased transport of lipid components to organs with heightened metabolic demands, primarily to the hepatopancreas, where parthenogenetic generations of trematodes develop. At the same time, the decrease in TL content in the foot is probably attributable to more intensive utilisation of lipid reserves to meet the energy requirements of locomotion. It is known that locomotion in gastropod molluscs is achieved through the contractile activity of the foot muscles and is accompanied by considerable metabolic expenditure, the magnitude of which depends on the characteristics of the animal's locomotor behaviour (Calow, 1974). Thus, under trematode infection, which is accompanied by a complex reorganisation of host mollusc metabolism, increased energy requirements may promote the mobilisation of lipid reserves in the foot. A similar direction of changes was reported by L.V. Muzyka & G.Ye. Kyrychuk (2020) in *Lymnaea* stagnalis, in which a decrease in total lipid content in the foot was also recorded during the development of parthenogenetic generations of trematodes.

In addition, the decrease in total lipid content in the haemolymph and foot of the molluscs may be associated not only with the redistribution of lipid components between tissues and organs, but also with the activation of lipolytic processes. Under increased energy requirements, the hydrolysis of storage lipids is accompanied by the release of fatty acids, which may be utilised as energy substrates in β-oxidation reactions in animal tissues (Nelson *et al.,* 2021). At the same time, the decrease in lipid content may be associated with insufficient replenishment of the lipid pool owing to reduced rates of lipogenesis or decreased availability of lipid substrates. Similar alterations in lipid metabolism under trematode infection were reported by V.M. Tunholi-Alves *et al*. (2011) in *B. glabrata* infected with *E. paraensei*, in which changes in TAG and CH content were detected in the haemolymph, while alterations in the neutral lipid profile were observed in the digestive gland-gonad complex. The pattern identified in the present study is partly consistent with these findings, as the decrease in TL content in the haemolymph of *P. purpura* was accompanied by an increase in TL content in the hepatopancreas, indicating a divergent reorganisation of lipid metabolism between the tissues and organs of the host mollusc. Variability in the content of individual lipid components under trematode infection was also reported by A.H. Hassan *et al*. (2021) in *Nerita polita*, where the nature of the changes depended on the lipid fraction and biological material examined. This heterogeneous metabolic response may be associated with the specificity of individual host-parasite systems, which are characterised by differences in parasite interactions with host tissues and in the molecular mechanisms underlying these interactions (Langleib *et al.*, 2026). Thus, differences in the direction and magnitude of changes in lipid metabolism among different mollusc species may reflect the species-specific nature of their metabolic response to trematode infection.

Alongside changes in total lipid content, the dynamics of individual lipid groups – TAG, PL and CH – in the organism of *P. purpura* were analysed, enabling a more detailed characterisation of the reorganisation of the lipid profile under trematode infection. One-way analysis of variance revealed a statistically significant effect of trematode infection on the content of triacylglycerols in the tissues and organs of *P. purpura* ($F = 10.90$; $p < 0.001$) (Fig. 2). It was found that the effect of the factor led to a 1.44-2.51-fold increase in the quantitative indicators of TAG content in the body of *P. purpura* compared with the control. The most pronounced accumulation of this lipid group (2.51-fold; $p < 0.05$) was recorded in the hepatopancreas of the studied animals. As noted by R.W. Klemm & P. Carvalho (2024), triacylglycerols are one of the primary forms of energy storage, and the relationship between their synthesis, accumulation and mobilisation determines the characteristics of lipid and energy metabolism. In this context, the observed accumulation of TAGs most likely reflects a reorganisation of the mollusc's energy metabolism during trematode

infection. It is also possible that the increase in TAG content is associated with the temporary storage of fatty acids in a form accessible for their subsequent use in energy and biosynthetic processes. At the same time, the smallest increase in TAG content compared with the control group was recorded in the foot of the infected molluscs (by 44.1%), which likely reflects the specific features of its energy metabolism associated with sustaining the locomotor activity of these animals.

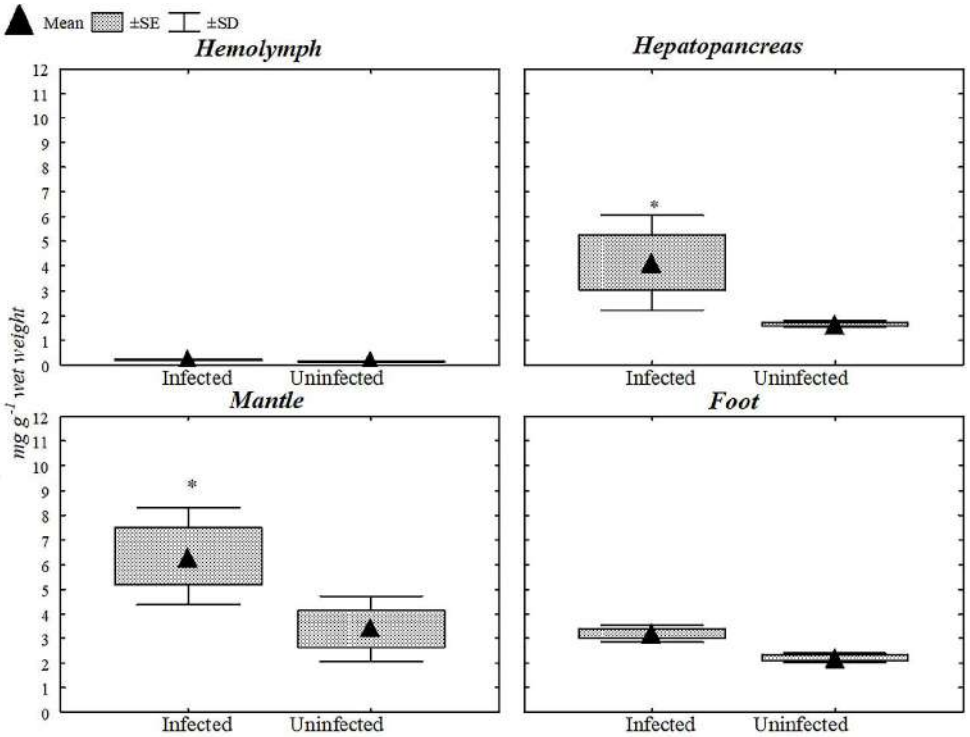



***Figure 2.*** *Triacylglycerol content in the tissues and organs of Planorbarius purpura under trematode infection*

**Note:** * – $p < 0.05$ compared with uninfected molluscs
**Source:** authors' own work

The results obtained indicate a reorganisation of the storage lipid pool of *P. purpura* under trematode infection, manifested by TAG accumulation in the tissues and organs examined. However, this direction of change is not universal across different "mollusc-trematode" systems. In contrast to the TAG accumulation established in *P. purpura*, H. Alves *et al.* (2014) reported a decrease in TAG content in the haemolymph and digestive gland-gonad complex of Bradybaena similaris during the development of *Eurytrema coelomaticum*. S.R. Bandstra *et al.* (2006) also demonstrated a decrease in TAG content in the digestive gland-gonad complex of *B. glabrata* infected with *E. caproni*, whereas no statistically significant changes in this parameter were detected at the whole-organism level. Such differences in the direction of TAG changes may be associated with species-specific characteristics of both molluscs and trematodes, the intensity and developmental stage of infection, parasite localisation, as well as the functional specificity of the tissues and organs examined.

The physiological and biochemical characteristics of host species may also be of considerable importance. In particular, *P. purpura* belongs to

the planorbids, a group of freshwater pulmonate molluscs characterised by a haemoglobin-based oxygen transport system in the haemolymph, in contrast to the haemocyanin-based system found in many other molluscs. This species-specific characteristic may be one of the factors determining differences in the metabolic response of molluscs to trematode infection. Evidence of a complex reorganisation of the energy metabolism of the host mollusc under parasitic infection is also provided by the findings of T.M.F. Mendes *et al.* (2019), obtained for *B. glabrata* infected with *S. mansoni*.

At the same time, when interpreting the changes observed, it is necessary to distinguish between the metabolic response of the host organism and the metabolic requirements of the parasite. M.L. Bexkens *et al.* (2019) demonstrated that *Schistosoma mansoni* does not utilise fatty acids through β-oxidation for its energy requirements; instead, it takes up and modifies host fatty acids, incorporating them into biosynthetic processes and into the composition of phospholipids and neutral lipids. This provides grounds for considering the dependence of trematodes on host lipid substrates as one of the potential factors contributing to the reorganisation of lipid metabolism in the "host-parasite" system. However, the results obtained do not allow the contribution of this mechanism to the observed TAG accumulation to be established unequivocally, since the changes in lipid metabolism may have resulted from the combined effects of the parasite and the physiological response of the host mollusc. With regard to phospholipids, in contrast to triacylglycerols, trematode infection was accompanied by a decrease in their content in the tissues and organs of *P. purpura* by 20.6-64.2% compared with the control (Fig. 3).

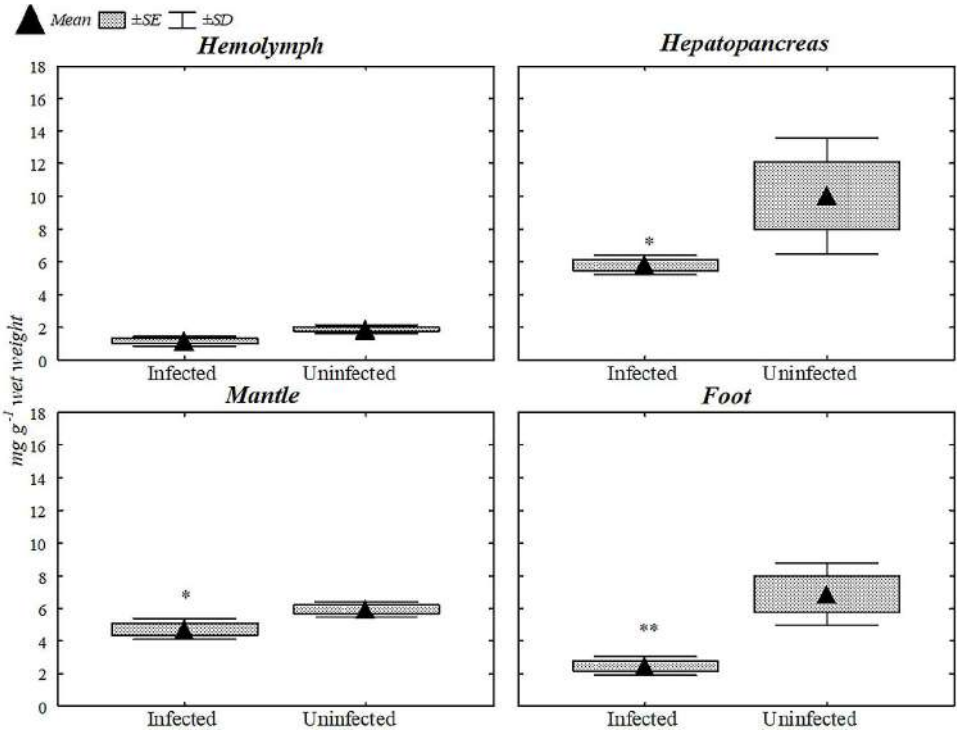



***Figure 3.*** *Phospholipid content in the tissues and organs of Planorbarius purpura under trematode infection*

**Note:** * – $p < 0.05$; ** – $p < 0.01$ compared with uninfected molluscs
**Source:** authors' own work

Whereas TAGs perform primarily an energy-storage function in living organisms, phospholipids are the principal structural components of biological membranes and largely determine their integrity, permeability and functional activity (Pamplona, 2008). Thus, this decrease in their content probably reflects structural reorganisation of cellular membranes. The most pronounced changes were recorded in the foot of infected molluscs, where phospholipid content was 64.2% lower than in the control ($p < 0.01$), which may indicate changes in the structural organisation of cells and, consequently, potentially affect the functional properties of the organ as a whole. Trematode infection is also known to be accompanied by physiological and behavioural changes in intermediate hosts, which in some cases may increase the likelihood of parasite transmission to the subsequent host (Dokmak *et al.*, 2024). A tendency towards a decrease in phospholipid content was also observed in the haemolymph of the molluscs (by 38.8%); however, the difference from the control group was not statistically significant ($p > 0.05$).

Of particular interest is the decrease in PL content in the hepatopancreas of the animals examined, by 42.2% compared with the control ($p < 0.05$). Given the structural role of PL in the formation and functioning of biological membranes, this pattern may be associated with a reorganisation of the balance between their synthesis, utilisation and degradation under trematode infection. The involvement of the phospholipid pool in biochemical reorganisation within the "mollusc-trematode" system is consistent with the results of D.A. Azimov *et al.* (2026), who identified changes in the phospholipid and fatty acid composition of the hepatopancreas of *Lymnaea auricularia* infected with the parthenogenetic generations of *Schistosoma turkestanicum*. At the same time, the direction of the mollusc's metabolic response may depend on the characteristics of the particular host-parasite system, as demonstrated by the results of E. Simphor *et al.* (2024) obtained for *B. glabrata* with different compatibility phenotypes towards *S. mansoni*. Thus, the decrease in PL content established in *P. purpura* may be regarded as one of the manifestations of the complex reorganisation of the structural lipid pool under trematode infection. The more pronounced response of the hepatopancreas may be associated with its key role in lipid metabolism and, given the localisation of the parthenogenetic generations of trematodes in this organ, with the reorganisation of metabolic processes and redistribution of biosynthetic resources within the organ.

Another possible factor contributing to the decrease in PL content under trematode infection may be the intensification of free-radical oxidation processes, since polyunsaturated fatty acids incorporated into membrane PLs are highly susceptible to peroxidation. The products of this process may cause oxidative damage to cellular components and disrupt their structural and functional organisation (Pamplona, 2008). Thus, it cannot be excluded that enhanced oxidative processes during trematode infection may also contribute to the reduction of the phospholipid pool in the hepatopancreas of *P. purpura*. At the same time, determination of the total PL content does not allow the contribution of individual phospholipid fractions to the observed changes to be established. Thus, to elucidate the mechanisms underlying reorganisation of the phospholipid pool in *P. purpura* under trematode infection, further investigation of the qualitative composition, content and relative proportions of individual phospholipid fractions would be valuable. The importance of analysing individual molecular species of phospholipids is supported by recent studies of host-parasite systems, which have demonstrated the functional role of individual lipid components in inter-organism interactions (Kidner *et al.*, 2024). Analysis of CH content in the organism of *P. purpura* revealed different responses of the tissues and organs examined to trematode infection. In the haemolymph, hepatopancreas and foot of infected molluscs, the content of this lipid decreased by 13.5-27.8% compared with the control. In contrast, an opposite pattern was recorded in the mantle, where CH content increased significantly by 44.4% ($p < 0.01$) (Fig. 4).

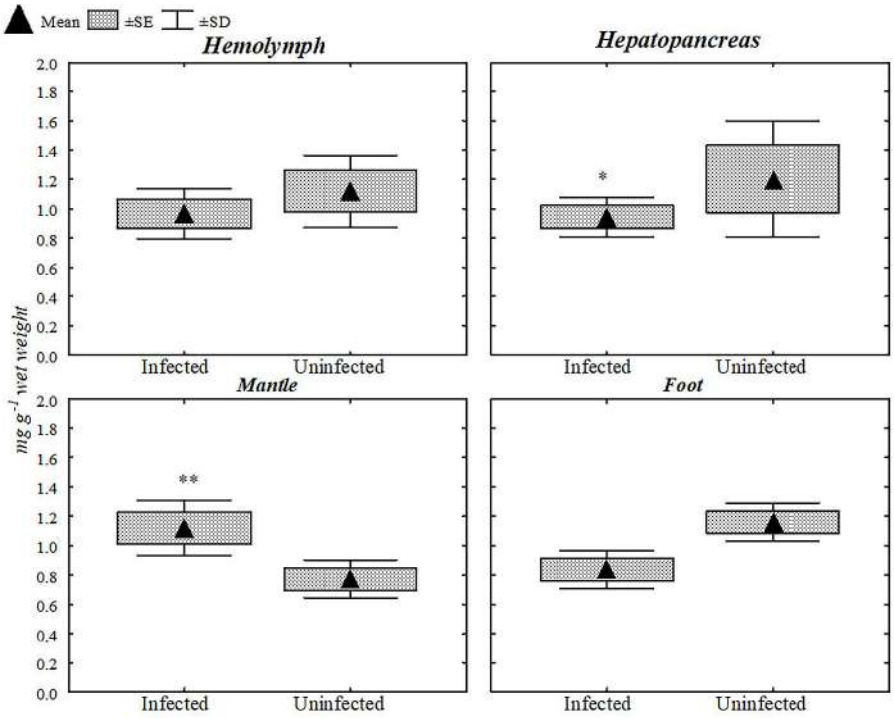



***Figure 4.*** *Cholesterol content in the tissues and organs of Planorbarius purpura under trematode infection*

**Note:** * – $p < 0.05$; ** – $p < 0.01$ compared with uninfected molluscs
**Source:** developed by the authors

The observed decrease in CH content in the haemolymph, hepatopancreas and foot of *P. purpura* is generally consistent with the changes in the cholesterol pool reported under parasitic infection; however, the differing direction of changes between tissues and organs indicates tissue- and organ-specific metabolic responses. Thus, A.H. Hassan *et al.* (2021) identified changes in cholesterol content in the haemolymph and digestive gland-gonad complex of *Nerita polita* infected with larval stages of trematodes, with the direction of changes in the digestive gland-gonad complex depending on the type of infection. A decrease in CH content under trematode infection was also reported by V.M. Tunholi-Alves *et al.* (2011) in *B. glabrata* infected with *E. paraensei*. Such variability in the observed changes may reflect differences in the functional demands placed on individual tissues and their involvement in the metabolic response to parasitic infection.

As demonstrated by I. Mardešić *et al.* (2023), CH is an important structural component of biological membranes and contributes to the regulation of their physicochemical and functional properties; therefore, changes in its content may be associated with reorganisation of the structural lipid pool and alterations in the functional state of cells. In this context, the CH dynamics observed in *P. purpura* may also reflect changes in the intensity of its utilisation in structural and metabolic processes, as well as differences in the uptake, transport and redistribution of cholesterol between individual tissues and organs of the host mollusc. According to E. Ikonen & V.M. Olkkonen (2023), maintenance of cholesterol homeostasis involves coordinated regulation of its uptake, synthesis and intracellular

transport between membrane compartments. Under trematode infection, changes in the balance between these processes may result in redistribution of the cholesterol pool between individual tissues and produce tissue-specific changes in its content. At the same time, quantitative measurements of CH content alone do not allow the contribution of individual metabolic processes to the observed changes to be established unequivocally. Thus, the observed dynamics should be regarded as a complex metabolic response to trematode infection.

The accumulation of cholesterol in the mantle of infected molluscs deserves particular attention, as, unlike the other tissues and organs examined, it was not characterised by depletion of the sterol pool. On the contrary, the increase in CH content in this organ probably indicates its redistribution between tissues and represents one of the manifestations of compensatory reorganisation of lipid metabolism, aimed at maintaining the structural stability and functional properties of cellular membrane.

Analysis of the proportions of individual lipid classes within the total lipid pool provides additional insight into the nature of metabolic reorganisation in the organisms examined. In uninfected *P. purpura*, phospholipids accounted for the largest proportion of the total lipid pool in all tissues and organs examined, particularly in the hepatopancreas (66.4%) and mantle (48.3%). Under trematode infection, the proportions of individual lipid classes changed in all tissues and organs examined. The most pronounced reorganisation was observed in the hepatopancreas, where the proportion of phospholipids decreased 3.24-fold (to 20.5%), whereas the contribution of triacylglycerols increased to 14.6%. A similar trend was observed in the foot and mantle, where a decrease in the proportion of phospholipids was accompanied by a corresponding increase in the contribution of triacylglycerols. The greatest increase in the proportion of TAGs was recorded in the mantle (to 40.4%), whereas in the foot it increased to 20.2%. In contrast to the tissues and organs examined, the structure of the total lipid pool in the haemolymph remained relatively stable. These results indicate that trematode infection affects not only the absolute content of individual lipid classes but also their relative proportions within the total lipid pool, with the nature of these changes depending on the functional characteristics of the tissues and organs examined. The results of cluster analysis complemented the data obtained from one-way analysis of variance and made it possible to assess the similarity of lipid profiles among different tissues and organs of *P. purpura* under trematode infection (Fig. 5). The most pronounced separation on the dendrogram was observed for the hepatopancreas of *P. purpura*, whose lipid profile in uninfected molluscs was most similar to that of the foot, whereas under trematode infection, the hepatopancreas was observed to form a separate cluster, reflecting a marked difference in the ratio of the lipid groups studied within the organ where parthenogenetic generations of trematodes are localised and develop. The lipid profiles of the mantle and foot in the control and experimental groups remained relatively similar, whilst the haemolymph, regardless of the presence of trematode infection, occupied the most distant position amongst the tissues studied, which is likely due to its transport function.

Thus, the comparative dynamics of the content of the lipids under investigation suggest that, under the influence of trematode infection, there is not only a redistribution of lipid resources between the tissues and organs of *P. purpura*, but also a change in the balance between the various pathways of intracellular lipid metabolism. The observed increase in TAG content against a background of a reduction in the PL pool may reflect the predominant diversion of fatty acids towards the synthesis of reserve lipids, whilst their utilisation for the formation of structural components of cell membranes is simultaneously restricted. Such a reorganisation is biochemically feasible, as the metabolic pathways for the synthesis of triacylglycerols and phospholipids

share common intermediate products, notably phosphatidic acid and diacylglycerols. Depending on the functional state of the cell, these compounds can be utilised both for the synthesis of membrane phospholipids and for the formation of TAGs (Nelson *et al.*, 2021).

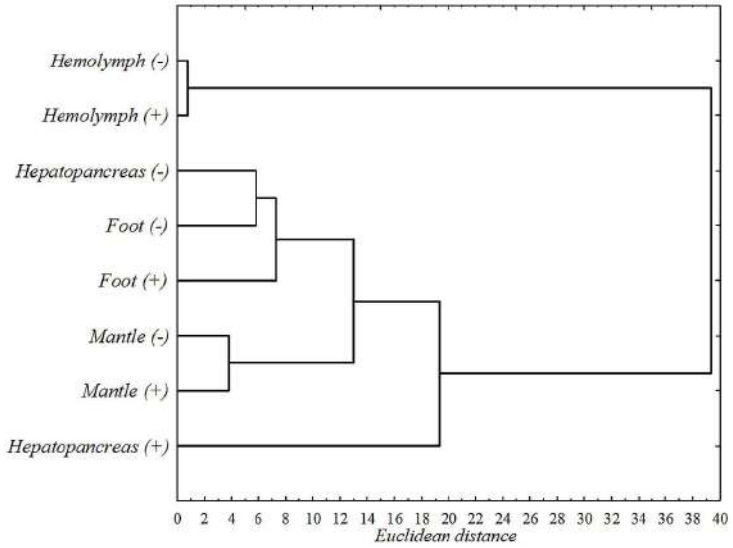



***Figure 5.*** *Dendrogram of hierarchical cluster analysis of the lipid profiles of the tissues and organs of Planorbarius purpura under trematode infection*
**Note:** (+) – infected molluscs; (–) – uninfected molluscs
**Source:** authors' own work

It is also possible that the reduction in phospholipid content is partly due to their hydrolytic degradation, as a result of which the fatty acids released through the deacylation of membrane phospholipids may either be re-esterified to form triacylglycerols or utilised as energy substrates in β-oxidation reactions in mollusc tissues. In this case, the accumulation of TAGs may reflect the temporary storage of excess fatty acids, thereby providing a reserve of substrates for subsequent energy utilisation (Nelson *et al.*, 2021).

Thus, trematode infection is likely to alter the proportions of storage and structural lipid groups, resulting in an increased proportion of TAGs among the lipid groups examined. This reorganisation may serve to maintain the short-term energy supply of the host organism, while simultaneously limiting the resources available for cellular membrane renewal and maintenance of their structural and functional integrity.

## Conclusions

It has been established that, during trematode infection, statistically significant changes occur in the levels of total lipids, triacylglycerols, phospholipids and cholesterol ($p < 0.05$-$0.001$) in the tissues and organs examined for *P. purpura*; the nature of these changes was tissue-specific. The observed trends indicate a complex reorganisation of lipid metabolism in *P. purpura* under trematode infection, in which the accumulation of total lipids in the hepatopancreas and mantle was accompanied by a decrease in their content in the haemolymph and foot; this likely indicates a redistribution of lipid resources and a shift in the orientation of the host's energy and anabolic metabolism.

The hepatopancreas of the molluscs proved to be the most sensitive to trematode infection, with the content of total lipids and triacylglycerols increasing by 1.88 and 2.51 times, respectively

($p < 0.001$), whilst the levels of phospholipids and cholesterol in the organ, conversely, decreased. A similar accumulation of triacylglycerols following trematode infection was also characteristic of the other tissues and organs studied, where their content increased by 44.1-86.4%. At the same time, the content of phospholipids and cholesterol decreased in the vast majority of the *P. purpura* organs studied. An exception to the general trend was the mantle of the infected molluscs, in which a 44.4% increase in cholesterol content was recorded ($p < 0.01$). This indicates a shift in the ratio of reserve to structural lipids and a disruption in their tissue- and organ-specific distribution during trematode infection.

The results of the cluster analysis complemented the data from the one-way analysis of variance and demonstrated differences in the ratios of the lipid groups studied between the tissues of intact and infected molluscs. Based on an analysis of the relative content of individual groups within the total lipid pool, it was found that phospholipids dominated in all tissues and organs of the control molluscs, whereas during trematode infection the pattern of their distribution shifted towards an increase in the proportion of triacylglycerols.

The results obtained provide the first comprehensive characterisation of the tissue- and organ-specific distribution of total lipids and their individual groups in the body of *P. purpura* under trematode infection and expand current understanding of the biochemical mechanisms of interaction within the "host-parasite" system. The patterns identified are of great importance for assessing the physiological and biochemical status of freshwater molluscs as key components of aquatic ecosystems and intermediate hosts of trematodes, and may also serve as a basis for further research into the impact of parasitic infections on the functioning of aquatic populations, which is important for the conservation of aquatic biological resources and the maintenance of the ecological stability of freshwater ecosystems. A promising area for further research is to elucidate the characteristics of changes in lipid metabolism depending on the species of trematode, the intensity of the infection, and the developmental stage of the parasite.

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## Conflict of Interest

None.

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# Вплив трематодної інвазії на вміст деяких груп ліпідів в організмі *Planorbarius purpura*

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**Анотація.** Дослідження впливу трематодної інвазії на фізіолого-біохімічний стан прісноводних молюсків є важливим напрямом гідробіологічних досліджень, оскільки трематоди є поширеними паразитичними організмами, здатними суттєво впливати на метаболічний гомеостаз та адаптаційні можливості організмів-хазяїв. Метою роботи було встановити характер змін вмісту та тканинно-органного розподілу загальних ліпідів та їхніх окремих груп (триацилгліцеролів, фосфоліпідів і холестеролу) у гемолімфі, гепатопанкреасі, мантії та нозі *Planorbarius purpura* за дії трематодної інвазії. Вміст загальних ліпідів визначали ваговим методом після екстракції за методом Фолча, окремих груп ліпідів – методом одновимірної тонкошарової хроматографії. Статистичну обробку результатів здійснювали із застосуванням однофакторного дисперсійного аналізу. Встановлено, що трематодна інвазія спричиняє виражені тканинно-специфічні зміни вмісту та співвідношення окремих груп ліпідів в організмі досліджених молюсків. У гепатопанкреасі інвазованих тварин зафіксовано статистично достовірне збільшення вмісту загальних ліпідів на 87,6 % ($p < 0,001$), тоді як у нозі та гемолімфі цей показник знижувався відповідно на 21,1 і 41,18 % ($p < 0,05$). Таке збільшення вмісту загальних ліпідів у гепатопанкреасі може бути пов'язане з накопиченням триацилгліцеролів і розвитком компенсаторно-пристосувальних реакцій організму молюсків. Вміст фосфоліпідів і холестеролу за дії трематодної інвазії знижувався у більшості досліджених тканин і органів, що може вказувати на порушення структурної організації біологічних мембран. Винятком була мантія *P. purpura*, у якій вміст холестеролу зростав на 44,4 % ($p < 0,01$). Аналіз тканинно-органного розподілу окремих груп ліпідів показав, що у гепатопанкреасі, мантії, нозі та гемолімфі інтактних молюсків кількісно переважали фосфоліпіди. За умов трематодної інвазії найбільш виражені зміни відзначено у гепатопанкреасі, мантії та нозі *P. purpura*, де зросла частка триацилгліцеролів, тоді як у гемолімфі домінуючою групою ліпідів залишалися фосфоліпіди. Отже, трематодна інвазія супроводжується вираженими тканинно-специфічними змінами вмісту та розподілу окремих груп ліпідів в організмі *P. purpura*. Визначені показники можуть бути використані як біохімічні маркери фізіолого-біохімічного стану прісноводних молюсків під час біомоніторингу водних екосистем

**Ключові слова:** прісноводні молюски; загальні ліпіди; триацилгліцероли; фосфоліпіди; холестерол; біохімічна індикація