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The "Minor Water Bodies" and Their Malacofauna: Are Freshwater Gastropod Communities Usable for Habitat Classification?

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Abstract: The typology of inland water bodies remains a topical issue in limnology. Numerous classifications of freshwater habitats have been proposed, but none of them has gained the universal acceptance. Current global changes and the increasing human impact on freshwater ecosystems make it important to understand the ecological relationships between freshwater animals and their environment. In this study, we tested a typology of the so-called "minor water bodies" proposed in the 1960s by the Polish ecologist Klimowicz. The term "minor water bodies" refers to a group of semi- or impermanent habitats that are prone to periodical or occasional desiccation. The division of habitat categories within this typology was based on qualitative features, and the validity of this classification has never been tested statistically. Here, we used the data on occurrences of 18 species of freshwater and semiaquatic gastropods observed in 86 minor water bodies of the Bolshoy Yugan River basin (Western Siberia, Russia) to test the hypothesis that each type of minor water body, in accordance with the aforementioned classification, maintains its own unique set of species. The statistical analysis confirmed the significant differences between the three habitat types on the basis of their gastropod communities, whereas one type (groundwater springs) appeared to be indistinguishable from the others. Our results show that freshwater gastropod communities are a suitable tool for habitat classification, and, at the same time, they highlight the need to apply statistical methods to *a priori* classifications based on the qualitative approach to the division of habitat types.

Keywords: typology of water bodies; molluscan communities; Western Siberia; freshwater Gastropoda; habitat classification

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1. Introduction

Historically, biological limnology has been a subfield of ecology that studies freshwater environments in a broad sense, and it had been developing as a result of the explorations of large permanent water bodies, such as great rivers and lakes. François-Alphonse Forel, "the founder of modern limnology" [1] (p. 7), studied very large and deep alpine lakes in Switzerland. The first freshwater limnological stations, founded in Europe and North America in the last third of the nineteenth century, were, as well, situated at large lakes, such as that in Plön, North Germany [1–3]. The majority of theoretical advancements in limnology were also based on the study of large freshwater ecosystems [4]. The less extensive freshwater habitats, including small ponds, wetlands, temporary pools, and the like, have attracted much less attention from limnologists, despite the significance of such biotopes in maintaining freshwater biodiversity and for other ecosystem services [5–7]. One of the main problems concerning the small freshwater habitats is their proper classification. We believe that this issue is of more than strictly academic interest. The data on the typology of small water bodies can be useful for conservationists, sustainable development specialists, and decision makers in the fields related to nature management. These ecosystems, as well as the communities of organisms inhabiting them, can be used as potential indicators of environmental changes, especially for those that occur on a local and/or regional scale.

Some approaches to the classification of small water bodies were based on an assumed correspondence between benthic communities and the environmental parameters of their habitats. There are not many examples of the studies exploring this correspondence (e.g., [8–11]). Amongst the earliest attempts to construct a typology on this basis, the works of the Polish hydrobiologist Henryk Klimowicz [12,13] are of special interest to malacologists. This author was convinced that freshwater Mollusca could "provide a basis for a fairly adequate classification of minor water bodies" [12] (p. 90). He used several terms for the designation of this class of habitats, namely, "small water bodies", "seasonal water bodies", and "minor water bodies". For the sake of consistency, we will use the latter variant in our paper. Though Klimowicz's approach cannot be praised as being absolutely pioneering in this field (the author himself quotes several publications of his predecessors e.g., [14–16]), his attempt was one of the first that was based on a thorough survey of a relatively large series of minor habitats, which included a comprehensive exploration of their malacofauna. Klimowicz [13] proposed to restrict the usage of the term "minor water bodies" to a group of impermanent habitats, i.e., those natural water bodies that dry up completely at times. He developed a relatively simple classification scheme of these habitats (Table 1).

Table 1. A tentative classification of minor water bodies developed by Klimowicz [12].

Types		
Oligotrophic	**Eutrophic**	**Dystrophic**
In every type, one may distinguish the following hydrological series:		
1. Through-flow 2. Drained 3. Closed semipermanent 4. Closed intermittent 5. Ephemeral		

It appears that Klimowicz's typology has not gained a wide popularity among the researchers in this field. Biggs et al. [6] do not mention it in their survey of existing classifications of small freshwater habitats. In the current literature, only sporadic citations of Klimowicz's works can be found (e.g., [17–19]). Perhaps his ideas had the most pronounced impact in the former USSR, where some influential malacologists followed Klimowicz in their attempts to classify freshwater habitats.

In 1988, Galina V. Beriozkina and Yaroslav I. Starobogatov published a monograph devoted to the "reproductive ecology" of freshwater pulmonate snails [20]. Despite the title, this book discussed a lot of other topics, including the problem of defining the typology of habitats of aquatic pulmonates. The authors followed Klimowicz's approach and, using it as the starting point, developed their own classification of minor water bodies (Table 2). They argued that each habitat type harbours some specific set of mollusc species. On the other hand, Beriozkina and Starobogatov [20] (p. 24) noted that the boundaries between the habitat types cannot be clearly defined, and certain types form a continuum that is difficult to divide into a series of discrete groupings. Nevertheless, the authors gave qualitative characteristics of the malacocoenoses that were thought to be specific for each type of minor water body. Though the book by Beriozkina and Starobogatov remains almost unknown beyond the Russian-speaking community of limnologists, the clear influence of their approach is seen in some of the recent research of malacologists from the former USSR (e.g., [21,22]).

Table 2. The classification of minor water bodies proposed by Beriozkina and Starobogatov [20] (pp. 16–25).

Habitat Type	Subtypes *	Description
I. Temporary (astatic)	(a) severely desiccating (b) ephemeral (c) periodical (d) semipermanent	Habitats with irregular water feeding; the evaporation noticeably exceeds the flow of water into them
II. Permanent or constant (static) minor water bodies	(a) drained reservoirs ** (b) semilotic	Habitats with regular water feeding; not subject to drying
III. Minor springs formed by groundwater	(a) limnocrenes *** (b) rheocrenes (c) helocrenes	Habitats with regular water feeding; not subject to drying out during the warm season of the year
IV. Madide habitats	–	Various moist surfaces (wet stream banks, wet rocks around waterfalls, etc.) with a permanent and very thin water film that does not cover the invertebrates completely
V. Thermal springs	–	Springs with high water temperature (40 . . . 45 °C and more); remain stable throughout the year

Note(s): * As many subtypes of this classification are not represented in the research area and, therefore, are not discussed in this paper, we do not provide definitions for all categories of this scheme. See [20] for further detail. ** Small permanent floodplain lakes, certain small ponds, etc., which are fed mainly by groundwater, are shallow, and cause the terrain to become swampy [20] (p. 20). *** See [8] for more information on these classical spring types.

Modern limnology is completely dependent on statistical analysis and quantitative approaches. Quantitative evidence is considered necessary for any hypothesis or working classification to be accepted. The two approaches outlined above lacked such evidence. Both Klimowicz [12,13] and Beriozkina and Starobogatov [20] developed their typological schemes on a strictly descriptive, qualitative method. These authors simply listed snail species found in water bodies of different types. They then attempted to distinguish some presumably habitat-specific groupings on the basis of these faunal lists. No kind of statistical analysis was applied by these authors, which, perhaps, explains the relative neglect of their classification schemes in the works of subsequent researchers. Another limitation of their typologies is that they are not universal, wherein they are applicable to the temperate regions only.

The main aim of this work is to evaluate the typological scheme of Klimowicz that was modified by Beriozkina and Starobogatov (KBS hereafter) using a modern analytical approach. Since Klimowicz [12,13] based his classification on empirical faunal data collected from water bodies lying within two relatively small areas, we also followed this approach and conducted a malacofaunistic survey of minor water bodies located in a restricted region of Western Siberia. The results of this survey were used as the primary data for the study.

We wish to highlight that the studied area is almost entirely located within a specially protected area—the ”Yugansky” State Nature Reserve—in which economic activity is strictly limited. Therefore, as the ecosystems of this area are free from deep anthropogenic impact, they can be considered background ecosystems in contrast to disturbed ecosystems. Studying these would allow one to reveal the “background” relationships between mollus-can communities and their environment to thus create a benchmark for comparison, which can be useful for the purposes of biomonitoring and assessing the impact of human activity on freshwater communities and ecosystems.

2. Material and Methods

The study area: The primary faunal data were collected by two of the authors (ESB, MVV) in 2010–2018 in the Bolshoy Yugan River basin, Western Siberia, Russia (Figure 1). A small collection of snails from the Bolshoy Yugan basin water bodies was given to us by Dr. Elena A. Zvyagina (”Yugansky” State Nature Reserve). This area belongs to the Ob–Irtysh River drainage basin and is located in the middle taiga landscape zone. According to the current administrative division of Russian Federation, it is located in the Surgutsky district of Khanty-Mansi Autonomous Okrug—Yugra. There are no large cities, dense human population, heavy industry, and developed agriculture in the Bolshoy Yugan River basin. Moreover, a substantial part of the studied area is legally protected as the ”Yugansky” State Nature Reserve. Thus, we considered the freshwater habitats of this area to be virtually pristine.

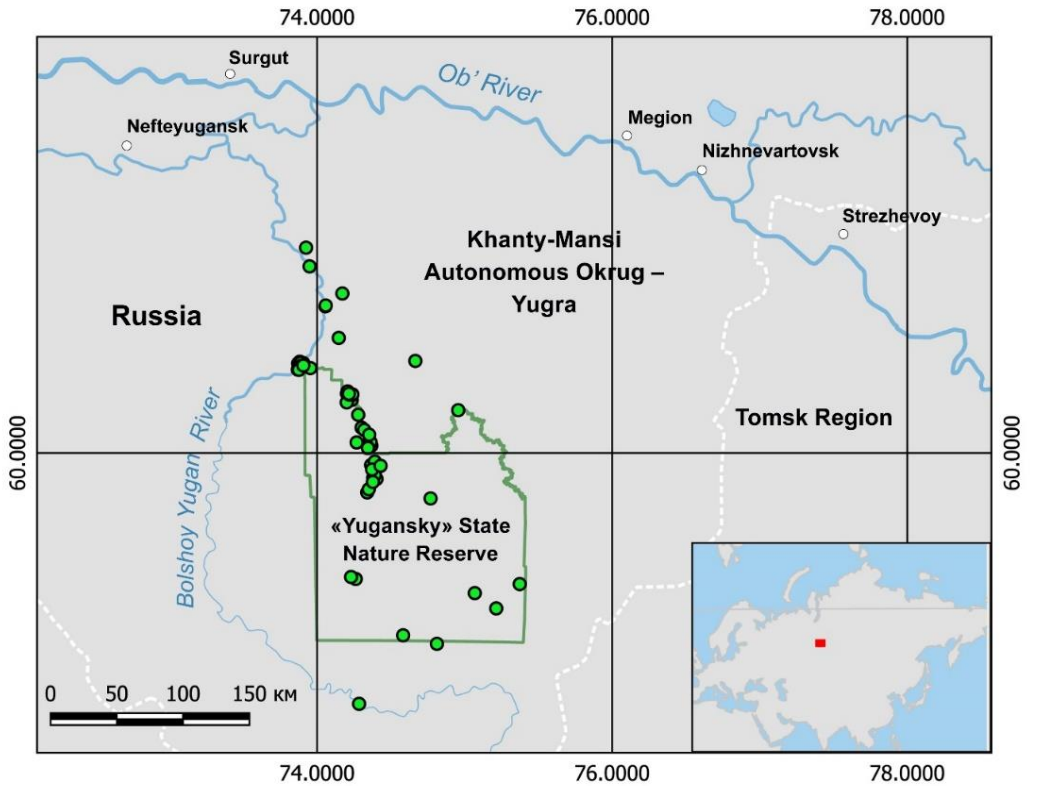

Figure 1. Map of sampling localities of gastropods in minor water bodies of the Bolshoy Yugan River basin. Localities are marked with green circles and correspond to those in Table S1 (Supplementary materials). The axes of the figure show geographic coordinates.

Due to the flat terrain and excessive humidity in the Bolshoy Yugan basin, the riverbeds are very meandering, with many channels and oxbows, and there are numerous floodplain swamps and lakes. Swamps occupy up to a third of the basin area, while the well-drained wooded areas are located in a narrow strip along the watercourses. Sphagnum bogs are confined to the flat sections of watersheds and river terraces. The vast majority of freshwater habitats (over 90%) are located on marshes and wetlands [23–25]. Almost all water bodies are influenced by swamp waters, and all rivers have their sources in swamps. Water bodies, in most cases, have water coloured with humic acids; their shores are usually swampy, and their vegetation is characteristic of swamps.

The geographical position of the Bolshoy Yugan River basin is almost in the centre of one of the largest lowlands on the planet, the West Siberian Plain, which determines its climatic features. The Ural Range serves as a barrier to the path of air masses moving from the west and the East Siberian Upland from the east. The continental climate with excessive moisture is characterized by long severe winters with heavy snowstorms, stable snow cover, and short, often hot, summers. The maximum precipitation occurs in summer. Transitional seasons (autumn and spring) are short, with sharp fluctuations in temperature [23,24].

Gastropod sampling and identification: Snails were collected following the standard methods of sampling of benthic invertebrates [26–28], which were performed by hand, dredge, or scraper, from the bottom substrate or surface of aquatic plants and submerged objects (stones, logs, etc.). A set of basic hydrological variables was assessed during the sampling procedure (the list of these variables is given below). During this work, we tried to take samples from all types of gastropod habitats represented in the river basin. Only part of these types can be classified as "minor water bodies" *sensu* Klimowicz [12,13]. The data collected from these water bodies served as the basis for the subsequent analysis.

In total, 86 localities belonging to various types of minor water bodies were examined, wherein we collected 1851 specimens of aquatic gastropods. All collected materials were deposited in the collections of the Zoological Institute of the Russian Academy of Sciences (St. Petersburg, Russia), the Laboratory of Macroecology and Biogeography of Invertebrates of St. Petersburg State University (St. Petersburg, Russia), and the Russian Museum of Biodiversity Hotspots at the N. Laverov Federal Centre for Integrated Arctic Research of the Ural Branch of the Russian Academy of Sciences (Arkhangelsk, Russia).

Mollusc species were identified using taxonomic guides [29–36] on the basis of conchological and, sometimes, anatomical features. The species nomenclature generally followed MolluscaBase (https://www.molluscabase.org/; accessed on 20 December 2022, with the exception of *Valvata frigida* Westerlund 1873 (family Valvatidae), which we considered a 'good' or valid species [37]; but see [29,30].

The fauna analysis was conducted using the entire set of collected primary data (1851 gastropod specimens from 86 sampled localities), including the samples in which snails were not found. The occurrence of species was calculated as the ratio of the number of habitats in which the species was registered to the total number of habitats sampled during this research. Since we did not assess the snail density during the sampling procedures, the abundance of gastropod species is defined here as the ratio of the number of specimens of each species to the total number of collected individuals (1851), which is expressed as a percentage.

The *a priori* habitat typology: Not all types of minor water bodies included in the Beriozkina and Starobogatov scheme (see Table 2) were represented in the Bolshoy Yugan River basin. For instance, there were no thermal habitats in this area. Therefore, we based schemes on the literature data [12,13,20] and our own field experience, classified the minor water bodies of the studied basin into four main categories, and, thus, obtained a kind of *a priori* habitat typology, which can be viewed as a version of the KBS classification scheme:

1. Temporary stagnant waterbodies and watercourses that dry up during the year for a period of one to several months (Figure 2A–D). In rainy years, they do not dry out completely, only significantly decreasing in size;

2. Small water bodies formed by groundwater (limno-, rheo-, and helocrenes according to [20]) (Figure 2E);

3. The madide habitats. The term (from the Latin "*madidus*"—wet) applies to specific localities: wet banks of reservoirs and streams, which are covered only by a thin water film (Figure 2F). There is an alternative (and extremely rarely used) term for such water bodies—*hydropetra*, introduced by Zernov [2];

4. Minor water bodies of swamps (Figure 3A–D). In the context of this work, by "swamp" we do not mean a single habitat, but a type of landscape. Within a separate swamp massif, numerous different minor habitats (pools, ponds, and streams) can be represented. This category corresponds, more or less, to the category of 'drained' habitats distinguished by Beriozkina and Starobogatov (see Table 2).

Statistical analysis: To test the validity of the *a priori* classification of minor water bodies in the research area, we used the cluster analysis and ordination of habitats and species of freshwater gastropods.

Initially, we prepared a matrix of data on the occurrence of gastropods in 86 habitats (Table S1 in Supplementary material). In accordance with the requirements of multivariate analysis methods [38], the species found in only one habitat and the habitats in which only one species was found (singletons or single values), as well as samples without snails, were omitted from further statistical analysis. For various statistical algorithms, we used only the absence/presence matrix of species, since abundance indicators have significant seasonal variability, usually non-Gaussian distribution, and often do not provide compatibility of the results of individual studies due to the use of different indicators, techniques, and subjective assessments [39].

Multivariate statistical analysis was performed using PAST 4.10 software [38]. As a measure of similarity in cluster analysis, we chose the Dice index, also known as the Sorensen coefficient. It is used for binary (absence/presence) data. A pooling algorithm based on UPGMA (Unweighted Pair Group average Method with Arithmetic mean) was applied. The robustness of the clusterisation was confirmed by bootstrap analysis with 1000 pseudo-samples.

Algorithms of direct and indirect ordination were used to group habitats and species when testing the classification. Nonmetric multidimensional scaling (Nonmetric MDS or NMDS) is an indirect ordination, not taking environmental factors into account, along the abstract axes that reflect the maximum variability in the data structure [38,39]. The method was chosen because it is believed [38–40] that it gives the most adequate results, especially for matrices with strong noise. Another advantage is that the method does not require any *a priori* assumptions about the type of the statistical distribution [39,41]. Dice index was applied.

As a method of direct ordination, we chose Canonical Correspondence Analysis (CCA), which contributes to the interpretation of the results obtained by taking environmental factors into consideration. The method is suitable for studying the influence of a complex of factors that may be dependent on each other. The CCA algorithm solves the problems of both ordination and regression analysis by statistically assessing the order of species and habitats under the influence of external factors [39]. Information on the following environmental factors was used: depth at the sampling sites (in meters); presence and velocity of the current (score: 0, current is absent; 1, low velocity; 2, high velocity); the percentage of submerged plants, wood debris, and forest litter in the composition of substrates; the percentage of detritus, silt, sand, and clay in the bottom substrate.

To assess the variability within habitat groups and between them, we used the One-Way ANOSIM nonparametric test [38,41]. The test makes it possible to assess the significance of differences between two or more groups based on any measure of distance (similarity or difference) [41], and we used the same Dice index. Pairwise ANOSIMs between all pairs of groups are provided as a post-hoc test. When assessing the statistical significance of differences between groups of habitats, we applied the Bonferroni correction [38].

To identify the species that contribute the most to the formation of differences between groups of habitats, the SIMPER method [38,41] implemented in PAST [38] was used. We combined all three groups to perform one overall multi-group SIMPER; to compare these groups, we used the Bray–Curtis dissimilarities based on data on the number of recorded mollusc specimens in various minor water bodies (see Table S2). All possible group pairs were compared. The overall mean difference was calculated using all taxa, while the species-specific differences between habitat groups were calculated for each species separately [38].

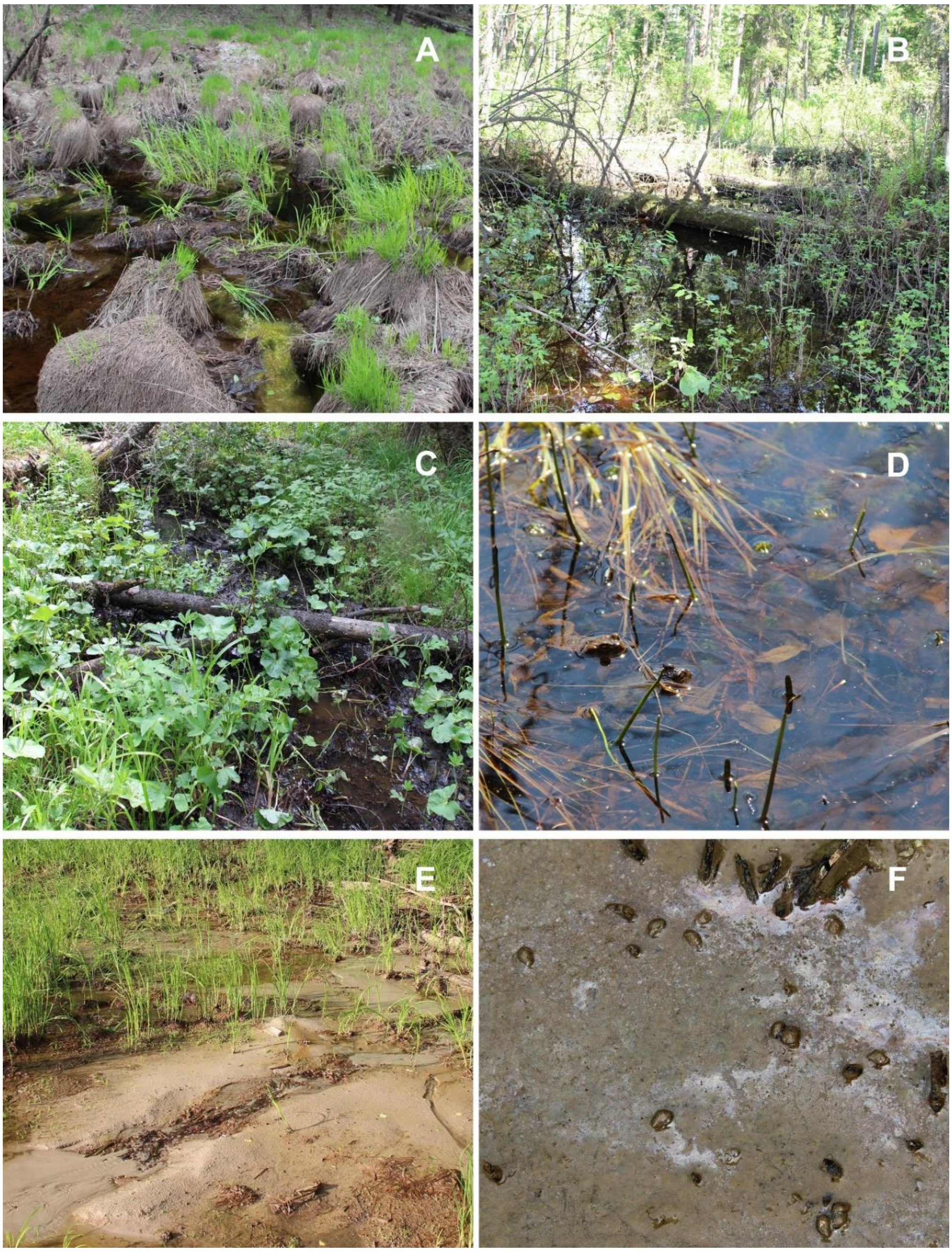

Figure 2. Minor water bodies of the Bolshoy Yugan River basin: (**A**), temporary floodplain puddles between hummocks; (**B**), a temporary pool on the site of a channel that existed in the past; (**C**), a chain of temporary reservoirs stretching along the streambed; (**D**), a puddle with meltwater; (**E**), a spring formed by groundwater on the shore of a bay of the Bolshoy Yugan River; (**F**), a madide habitat, where pond snails of the genera *Ampullaceana* and *Peregriana* are crawling on the wet surface.

Figure 3. Types of swampy habitats of the Bolshoy Yugan River basin. (**A**), a transient type swamp; (**B**), minor water bodies of a raised bog; (**C**), a raised bog; (**D**), an edge of a raised bog.

3. Results

In total, 17 species of freshwater gastropods were registered in the minor water bodies of the Bolshoy Yugan River basin. Amphibiotic snails of the genus *Oxyloma* (family Succineidae) were recorded during our fieldwork as well. Most probably, they belong to the same species, but we are not qualified enough to identify these snails to the species level, so we treated them as *Oxyloma* sp. (Table 3). Most of the found species were pulmonates, while the branchiate gastropods were represented by three species only. Gastropods were found in 67.4% of the sampled habitats. In 20 habitats out of 86 surveyed (23.3%), only one species was recorded. The occurrence of individual snail species was low, with predominant pulmonates *Peregriana dolgini*, 23.3%; *Gyraulus borealis*, 22.1%; *Galba truncatula*, 20.9%; and *Oxyloma* sp., 16.3%. *Valvata confusa*, *Acroloxus lacustris*, and *Gyraulus acronicus* each found in a single locality (see Table 3).

Table 3. Species composition, number of collected specimens, abundance, and occurrence of gastropods in the studied water bodies of the Bolshoy Yugan River basin.

	Species	N	Abundance, %	Occurrence, %
1	*Valvata confusa* Westerlund, 1897	4	0.2	1.2
2	*Valvata frigida* Westerlund, 1873	177	9.6	5.8
3	*Valvata sibirica* Middendorff, 1851	177	9.6	11.6
4	*Acroloxus lacustris* (Linnaeus, 1758)	1	0.1	1.2
5	*Stagnicola saridalensis* (Mozley, 1934)	9	0.5	2.3
6	*Ladislavella terebra* (Westerlund, 1885)	14	0.8	4.7
7	*Galba truncatula* (O. F. Müller, 1774)	340	18.4	20.9
8	*Ampullaceana balthica* (Linnaeus, 1758)	4	0.2	2.3
9	*Ampullaceana fontinalis* (Studer, 1820)	26	1.4	5.8
10	*Ampullaceana intermedia* (Lamarck, 1822)	224	12.1	10.5
11	*Ampullaceana lagotis* (Schrank, 1803)	148	8.0	8.1
12	*Peregriana dolgini* (Gundrizer and Starobogatov, 1979)	150	8.1	23.3
13	*Aplexa hypnorum* (Linnaeus, 1758)	47	2.5	7.0
14	*Bathyomphalus contortus* (Linnaeus, 1758)	72	3.9	10.5
15	*Gyraulus acronicus* (J. B. Férussac, 1807)	5	0.3	1.2
16	*Gyraulus borealis* (Lovén in Westerlund, 1875)	355	19.2	22.1
17	*Gyraulus stromi* (Westerlund, 1881)	29	1.6	8.1
18	*Oxyloma* sp.	69	3.7	16.3
	In total:	1851	100.0	67.4

After the removal of singletons, the final matrix for analysis contained information on the presence/absence of 15 gastropod taxa in 37 minor habitats in the research area (Table S2 in Supplementary Materials).

Regarding the dendrogram of hierarchical cluster analysis obtained using the Dice index as a measure of similarity (Figure 4), only two high-level clusters were reliably distinguished with 100% bootstrap support. The first cluster combined most of the temporary habitats and all swamp water bodies. The second cluster included madide habitats and springs. The classification was not fully accurate, since a few of the temporary habitats were placed in the second cluster, which was contrary to the tendency of these localities to concentrate in the left part of the dendrogram. The allocation of lower-rank clusters had negligible or weak bootstrap support in all cases.

The ordination diagram yielded by Nonmetric MDS (Figure 5) revealed three distinctly separated groups of gastropod habitats corresponding to three types of the *a priori* classification of minor water bodies of the Bolshoy Yugan River basin. Similar to the dendrogram above (see Figure 4), groundwater springs and madide habitats formed a common group. When grouping habitats, the NMDS method also made it possible to visualize the species' habitat preferences in the space of variability scales. For example, groundwater springs and madide water bodies were typically inhabited by the same gastropod species.

When groundwater springs and madide water bodies were tested by one-sided ANOSIM separately, as belonging to distinct groups, the variability within the groups did not differ from the intergroup variability. The value of the R statistic was close to zero ($R = 0.183$, $p = 0.067$, permutation $N = 9999$), which indicated that there were no differences between the groups.

Therefore, in the further analysis, we combined madide habitats and groundwater springs into one group called "madide habitats". At the next stage, we used ANOSIM to test the division of habitats into three groups: temporary, madide, and swampy. The ANOSIM test confirmed the results obtained earlier by clustering and ordination procedures. The intergroup differences that were statistically significant exceeded the intragroup differences. The high positive value of the R statistic ($R = 0.614$, $p = 0.0001$, permutation $N = 9999$) indicated greater similarity within groups than between them. When comparing habitat groups in pairs (post-hoc ANOSIM), all differences between groups were also statistically significant.

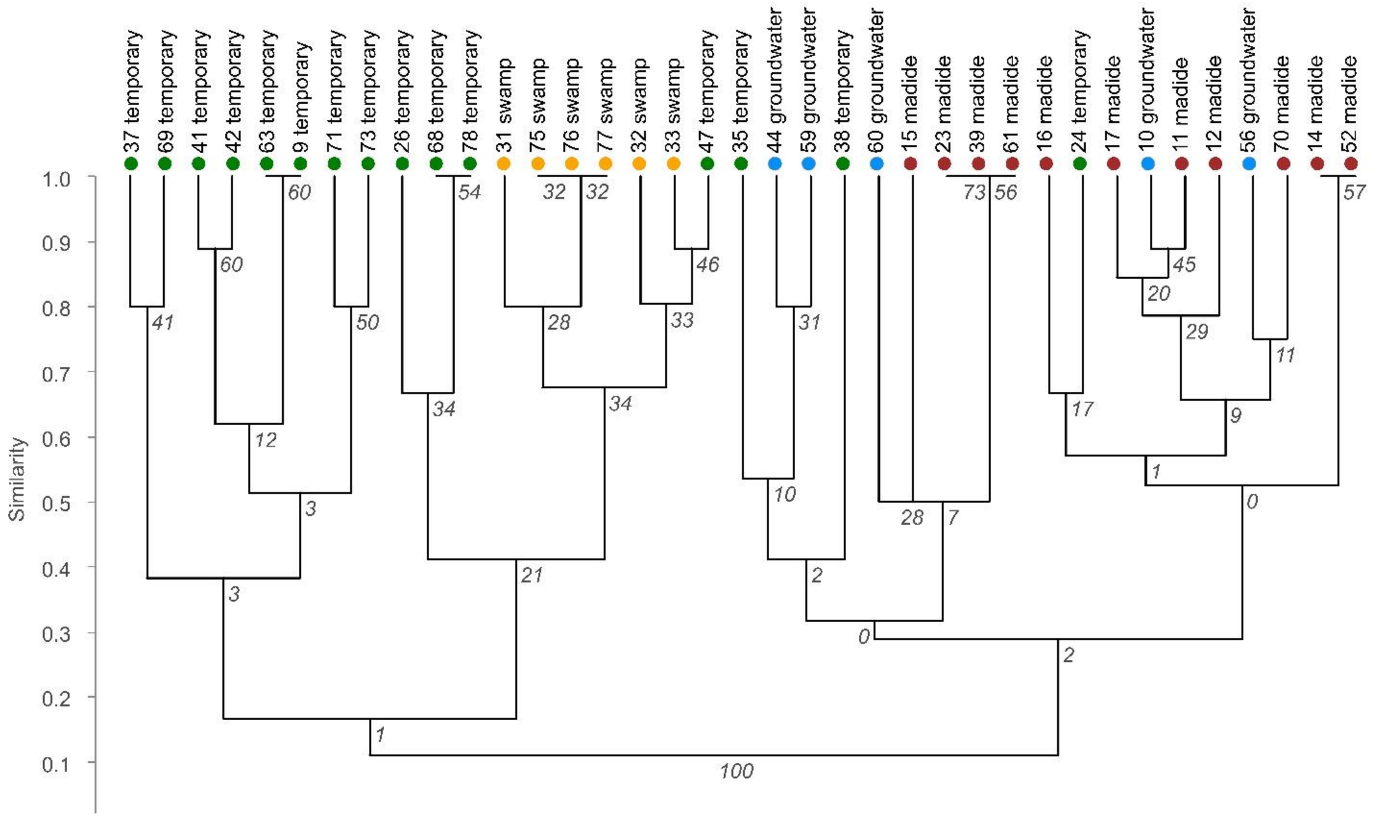

Figure 4. Dendrogram of the similarity of gastropod communities in "minor" habitats of the Bolshoy Yugan River basin. Black numbers near nodes are bootstrap support (BS) values in % (N = 1000). The four habitat types of our *a priori* classification are denoted by different colours: temporary water bodies (green), madide reservoirs (brown), groundwater springs (turquoise), and swamps (orange). The numbers after the coloured symbols correspond to the numbers of localities.

Since ANOSIM showed significant differences between the three habitat groups, we used the SIMPER method to assess which gastropod species were primarily responsible for the observed differences between the groups [41] (Table 4). The molluscs were collected according to the same methodology, wherein almost all were collected by one or two collectors, so we believe that the research effort was approximately the same, and the data obtained can be validly used to determine the contribution of species to the differences between the habitat groups. The overall average dissimilarity was 95.52. The largest contributor was the species *Gyraulus borealis*—18 or 18.84%—with the largest contribution of the species to the total dissimilarity in the temporary water bodies (see Table 4). The SIMPER results showed that species *Gyraulus borealis*, *Valvata sibirica*, *Galba truncatula*, *Ampullaceana intermedia*, *Peregriana dolgini*, *V. frigida*, *Bathyomphalus contortus*, and succineid snails of the genus *Oxyloma* made the greatest contribution to the formation of differences between the habitat groups.

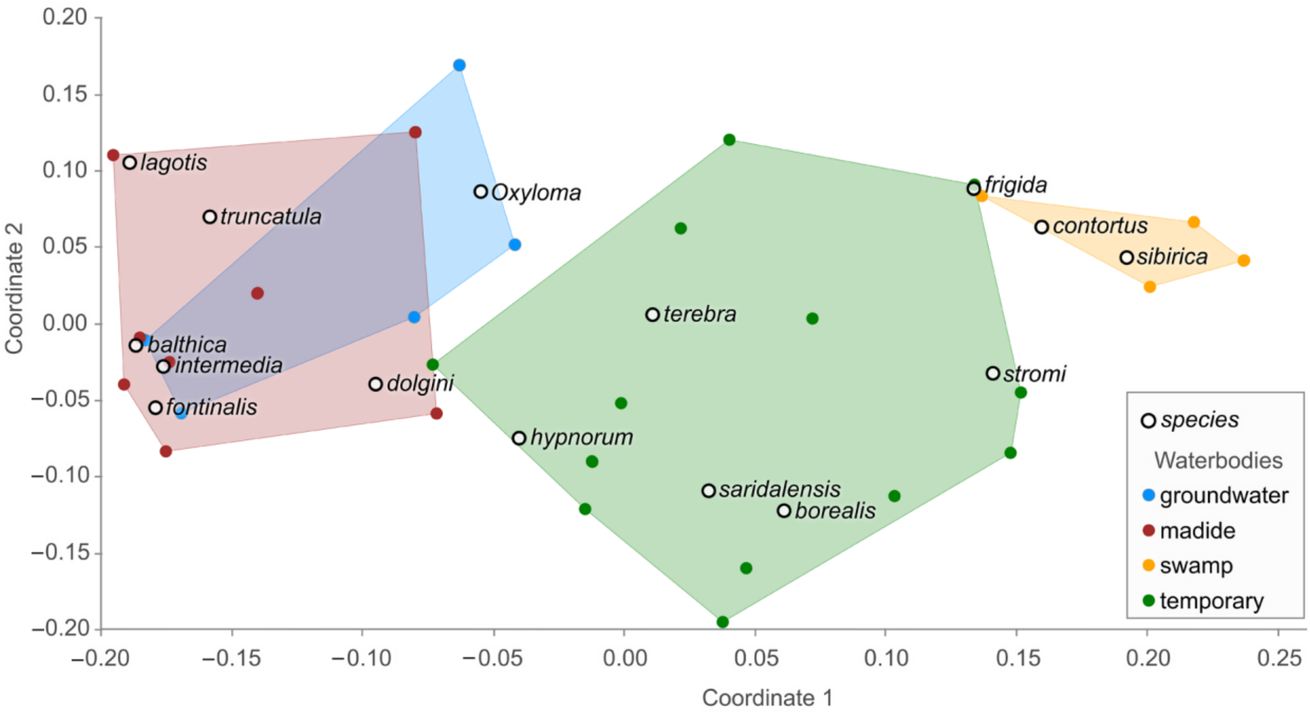

Figure 5. Ordination diagram of nonmetric multidimensional scaling of minor water bodies of the Bolshoy Yugan River basin based on the Dice similarity index. White dots indicate certain snail species: borealis; *Gyraulus borealis*; contortus; *Bathyomphalus contortus*; dolgini; *Peregriana dolgini*; frigida; *Valvata frigida*; hypnorum; *Aplexa hypnorum*; lagotis; *Ampullaceana lagotis*; saridalensis; *Stagnicola saridalensis*; sibirica; *Valvata sibirica*; stromi; *Gyraulus stromi*; terebra; *Ladislavella terebra*; truncatula; *Galba truncatula*; and genus *Oxyloma*.

The positive direction of axis 1 in the CCA ordination diagram (Figure 6) correlated with such factors as depth and the presence of submerged plants, forest litter, and wood debris in the bottom substrate; the negative direction correlated with the concentration of silt, clay, sand, and detritus in the bottom substrate. Axis 2 was largely determined by the presence and velocity of the water current. The three groups of gastropod habitats outlined above were located in the gradient of environmental factors. Each group of habitats had its own characteristic complex of gastropod species.

The reliability of the obtained CCA ordination was confirmed by the eigenvalues, which together explained 62.7% of the variance in the relationship between the occurrence of species and environmental variables for axes 1 and 2; the results were statistically significant (*p*-level 0.001 and 0.009, respectively; Table S3). Correlation coefficients between environmental variables and factor loads (Table S4 in Supplementary material) also supported the reliability of ordination and provided additional information for the interpretation of the main ordination axes of the diagram.

The statistical results presented above indicated the division of all the studied minor reservoirs into three types, which were characterized by the specific features of their hydrology and malacofauna. Table 5 gives a short summary of this *a posteriori* three-part typology. The highest species richness of snails was observed in temporary water bodies; the lowest species richness was observed in swampy habitats. Gastropods were relatively often found in temporary and madide water bodies, whereas, in swamps, they were much rarer. The highest abundance of aquatic snails was observed in madide habitats (Table S5 in Supplementary material).

Table 4. Contribution of individual gastropod species to the formation of differences between habitat groups obtained by SIMPER method.

Taxon	Average Dissimilarity	Contribution, %	Cumulative Contribution to Dissimilarity, %	Habitat Type		
				T	M	S
Gyraulus borealis	18.00	18.84	18.84	17.2	0.125	0
Valvata sibirica	16.92	17.71	36.55	1.73	0	25.2
Galba truncatula	12.28	12.85	49.41	0.6	18.6	0
Ampullaceana intermedia	10.97	11.48	60.89	0.2	13.8	0
Peregriana dolgini	7.731	8.094	68.98	2.73	4.69	0
Valvata frigida	5.619	5.883	74.86	10.1	0	3.67
Oxyloma sp.	5.513	5.772	80.63	0.8	3.06	0.17
Bathyomphalus contortus	5.226	5.471	86.10	1.87	0	7.33
Ampullaceana lagotis	3.389	3.548	89.65	0.067	8.81	0
Aplexa hypnorum	3.103	3.249	92.90	3.07	0	0
Gyraulus stromi	2.747	2.876	95.78	1.6	0.063	0.5
Ladislavella terebra	1.552	1.625	97.40	0.933	0	0
Ampullaceana fontinalis	1.406	1.472	98.87	0	1.56	0
Stagnicola saridalensis	0.725	0.759	99.63	0.6	0	0
Ampullaceana balthica	0.350	0.367	100.00	0	0.25	0
Overall average dissimilarity: 95.52						

Note(s): Abbreviations of habitat types: T, Temporary; M, Madide; S, Swamp minor water bodies.

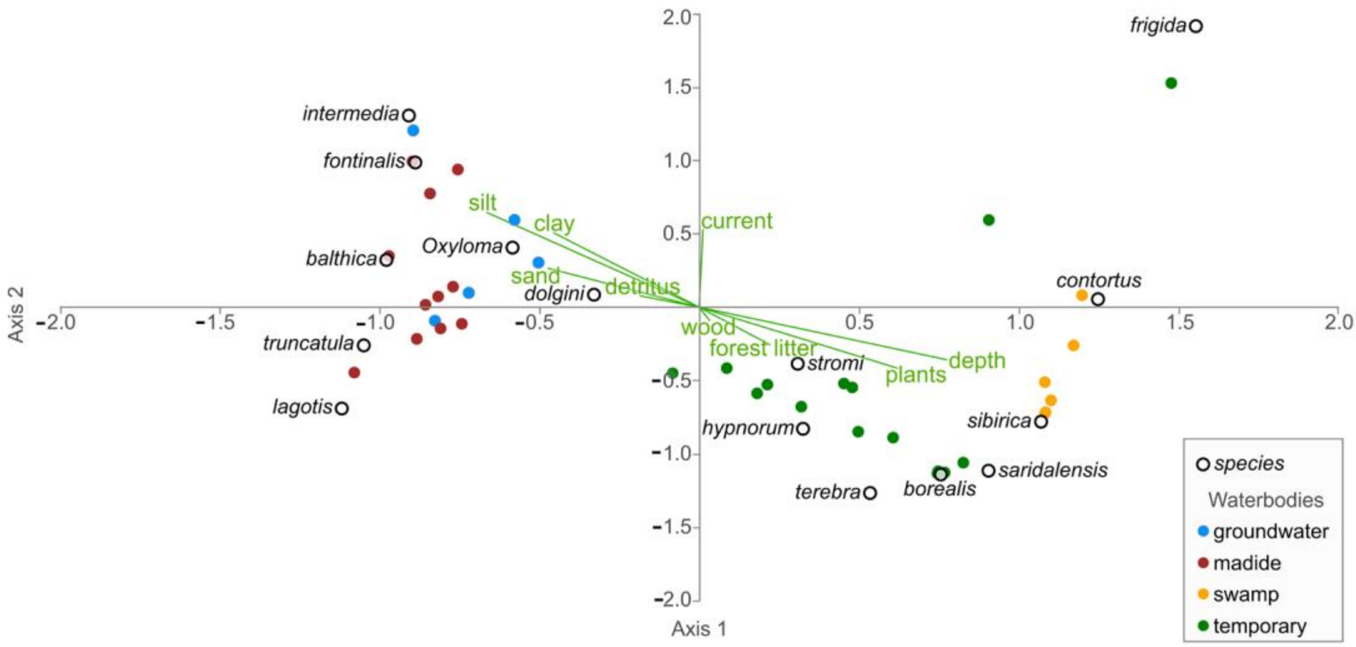

Figure 6. CCA diagram of minor aquatic habitats of the Bolshoy Yugan River basin. The habitat designations were the same as in Figure 4; depth—depth at the sampling sites; current—the presence and velocity of the current. Plants, wood and forest litter –respective concentrations of plants, submerged wood debris, and forest litter in the bottom substrate. Detritus, silt, sand, and clay –respective concentrations of detritus, silt, sand, and clay in the bottom substrate.

Table 5. *A posteriori* classification of the minor water bodies of the Bolshoy Yugan River basin.

Habitat Type	Hydrological Characteristics	Typical Snail Species
Temporary habitats	periodic and/or non-periodic dessication during the year; bottom substrate rich in wood debris and forest litter	*Stagnicola saridalensis*, *Ladislavella terebra*, *Aplexa hypnorum*, *Gyraulus borealis*, *G. stromi*
Madide habitats (including groundwater springs)	a thin film of water on silt and clay, with an admixture of sand and detritus substrates	*Galba truncatula*, *Ampullaceana balthica*, *A. fontinalis*, *A. intermedia*, *A. lagotis*, *Peregriana dolgini*, *Oxyloma*
Swamp habitats (waterbodies watercourses)	high abundance of macrophytes; slow or absent current; stability of hydrological regime throughout the year	*Valvata sibirica*, *Bathyomphalus contortus*

4. Discussion

Despite the efforts of Klimowicz [12,13], Beriozkina and Starobogatov [20], and some other malacologists of the past century (e.g., [11,15,42,43]), the malacofauna of minor water bodies (sensu Klimowicz) remains a relatively understudied object (for counter examples see [17,44–47] and references therein). The present work is a *case study* contributing to the understanding of the suitability of gastropod communities as a tool for freshwater habitat classification. Though the research area is located in the middle part of Western Siberia, the results of our study can be applicable to other parts of Northern, Central, and Eastern Europe, as well as Northern Asia, which are situated within the temperate climate belt.

The species richness of gastropods found in minor water bodies of the Bolshoy Yugan River basin was quite high, which was equal to 39.5% of the total number of gastropod species recorded in this drainage basin [48]. In general, the pulmonates were predominant in the basin of the Bolshoy Yugan River: their portion of the total species richness of gastropods exceeded 60% [48]. In the minor water bodies of the research area, the predominance of pulmonates was even more pronounced, as the pulmonates accounted for 82.4% of all registered species. The branchiate snails were represented by three species only, which all belonged to the same family (Valvatidae). Their abundance was as low as 19.4%, and their occurrence was 12.8% (see Table 3). The predominance of pulmonate snails was probably due to the fact that ecosystems of minor stagnant waterbodies and watercourses with specific prevalent conditions, particularly including oxygen shortage, periodic drying, and freezing, form an environment to which the pulmonates are much better adapted than the gill-breathing snails [20,49].

When classifying minor water bodies by species composition and occurrence of the gastropods inhabiting them, it is important to understand just how specific species complexes are to different types of water bodies. Further, it is important to know whether identified species content is not a random set formed as a result of the decrease in species richness as it separates from a large permanent reservoir, watercourse, drying out, waterlogging, etc. (i.e., under the influence of random causes). According to several independent studies, the species richness of gastropods in the minor water bodies is typically significantly lower than that in the region as a whole and amounts to approximately 40% of the latter figure. On the other hand, certain snail species occur exclusively or almost exclusively in minor stagnant waterbodies and watercourses [11,50,51]. As examples of such species, we would like to mention *Aplexa hypnorum* and *Galba truncatula* [20,32–34]. According to our studies of molluscs in large permanent [48,52] and minor (this study) stagnant waterbodies and watercourses of the Bolshoy Yugan River basin, such species as *Ampullaceana fontinalis*, *A. lagotis*, *Galba truncatula*, and *Peregriana dolgini* were found mainly in minor water objects. *Stagnicola saridalensis*, *Ladislavella terebra*, and *Aplexa hypnorum* were found almost exclusively in temporary reservoirs. Succineids of the genus *Oxyloma* were found only in minor water bodies.

We removed rows and columns from the primary data matrix that were uninformative for multivariate analysis methods. These were the rows and columns with only null values, or with only one non-zero cell (singletons). Events such as a discovery of a species in only one habitat, or a record of a habitat with only one encountered species, may be the result of a narrow specialisation of species to inhabiting certain biotopes, or they may be the result of a random event. Since the identified species composition does not contain highly specialised species and local endemics, the first option is unlikely, especially since we initially considered a limited set of habitats, and the *a priori* classification included four types of minor water bodies. We believe that the most likely causes of single records and negative survey results (species not found) were insufficient research effort and chance events. The use of multivariate statistics algorithms based on the primary matrix of species records in different habitats (without removing null and single values) can lead to an overestimation of the role of species known from single finds; thus, this leads to the instability of the resulting classification and the ambiguity of its practical application. Our goal was to develop the classification of habitats according to the species composition of gastropods on the basis of the most general patterns, rather than random events. The value of such a classification is that the higher it is, the easier it is to use it in practice, i.e., the more it is based on the findings of the most common species. In this regard, our decision to discard noninformative rows and columns (with null values) is quite obvious and does not require further explanation. We attempted to overcome the overestimation of the role of single encounters by including temporal and spatial replicates—in other words, we included new samples in the studied habitats within the study area.

In general, the three types of minor water bodies of the Bolshoy Yugan River basin, which we identified on the basis of the ordination of habitats and gastropod communities, differed significantly from each other in species composition and in patterns of the occurrences of individual species. Only *Gyraulus stromi* and *Oxyloma* were registered in all three types of water bodies, while the number of collected specimens, the species' portion in the total collection, and their occurrence varied considerably across different types of the minor habitats. Apparently, the most favourable habitats for gastropods were found in temporary and madide stagnant waterbodies and watercourses, whereas swampy habitats appeared to be less suitable for aquatic snails (see Table S5 in Supplementary Materials).

Our results showed that, though the *a priori* typology used in our research must be corrected, the very principle at its basis, namely, a correspondence between faunal complexes of gastropods and different types of natural water bodies, remains valid. In our opinion, the KBS typological scheme has an objective basis and may be used for further development and improvement. For example, it would be beneficial to test its validity using the data on bivalve species or by analysing whole molluscan communities (i.e., snails and bivalves). On the other hand, we did not find any grounds for the further division of the three main types into subtypes (as had been proposed by Beriozkina and Starobogatov [20], see Table 2). The very possibility of such a division seems unlikely. Within each of the three identified types of minor water bodies, many various habitats can be distinguished, which provide gastropods with habitats with a similar range of environmental factors. For instance, the category of temporary water bodies embraces such various habitats as puddles left after the spring flood, including very large (several square meters and larger) puddles and those that do not dry up annually; pools near floodplain lakes, under the canopy of the forest, and on the site of a previously existing watercourse; and floodplain channels. We also assigned the short-term puddles with thawed and/or rain-stained waters to this type, despite the fact that snails only rarely could be found in them. In the study area, only in a few such water bodies were recorded with single juvenile individuals of the genus *Gyraulus* (Planorbidae) and terrestrial gastropods, which probably arrived there by accident. The evidence in favour of the separation of each of these groups of small water bodies into a "type" of its own is lacking.

Combining the madide and groundwater spring habitats into a single type (see Table 5) is relatively easy to explain. In most of the studied springs, the snails were absent from the current itself; the living molluscs were found on the wet banks of these springs, which is technically equivalent to the "madide" habitats sensu Beriozkina and Starobogatov [20]. Perhaps, in other regions, where springs themselves are inhabited by molluscs, the differences in the faunal composition between springs and madide habitats would be expressed more clearly. This fact highlights that the application of a given typology, even when supported by a statistical analysis, must be done with a caution while taking into account the regional/local properties of freshwater habitats.

Various gastropod habitats located in lowland and transitional swamps, as well as along the forest–swamp border, were combined into the single category of minor stagnant waterbodies and watercourses of the swamps (see Table 5 and Figure 3). The habitats of this type included in our database varied greatly, but they had at least three characters in common: high macrophyte richness, slow water exchange, and relatively stable hydrological regime. These ecological characteristics of swampy habitats, in combination with some others observed in many swamps (high acidity, low hardness, general mineralisation of water, high content of organic matter, and a lack of oxygen), result in a depleted and taxonomically specific malacofauna [53]. It should be noted that gastropods were nearly absent in the minor habitats within raised watershed bogs, such as lakelets, hollows, and swamp streams [28]. The main factor preventing them from inhabiting these localities is high water acidity, which dissolves the inorganic matter of mollusc shells. In the humid zone of Western Siberia, freshwater molluscs are totally absent from water bodies with pH < 4.0 [54].

Some limitations of the approach to classification applied during this research must be discussed before the conclusions.

The study of the formation of gastropod communities is significantly complicated by the high diversity of minor water bodies, the presence of permanent connections and transitions between the types, and the absence of clear temporal and spatial boundaries between them [11–13,20]. It is also well known that the distribution of freshwater molluscs is governed simultaneously by many factors, and it is not always possible to determine the contribution of each of them [11]. For example, it is quite possible that, during floods, mollusc species that are typical of permanent habitats can penetrate into temporary floodplain habitats flooded with the meltwater, which will add a "riverine" or "lacustrine" quality to their fauna. This can probably explain how temporary habitats were scattered across different clusters in the diagram (see Figure 4).

Another restriction to our *a posteriori* typology is that it is based on a statistical analysis of a presence/absence matrix. The complete absence of molluscs from a stagnant waterbody or watercourse was repeatedly observed during our study, and, in most cases, it is very difficult to understand why the snails avoid that habitat. Obviously, their absence can be explained by factors other than hydrology, for example, those related to the local parameters of water chemistry. In other words, it is not impossible that the separation of only three main categories of habitats in this study reflects the fact that we used a limited set of ecological parameters, which primarily included those related to the physical properties of snail environments. However, the addition of some chemical "dimension" to the analysis may, in our opinion, result in a blurring of category boundaries. The point is that the hydrological and hydrochemical parameters do not correlate in many cases. For instance, the same pH value can be observed in aquatic habitats of very different types and vice versa; water bodies of the same type may have very different values of pH that fluctuate over years and seasons [43]. The same applies to the calcium concentration, as well as to many other chemical parameters of the snails' environment [20,40,43,55]. However, this issue requires further study.

5. Conclusions

Despite the restrictions discussed above, our statistical analysis, by applying several different algorithms, has revealed a fairly good correlation between the basic categories of minor habitats and their snail communities. A substantial difference between the three main types of minor water bodies was noticeable, even without the use of special instruments, analyses, and statistical algorithms. However, the difference in the species composition of snail communities was not so obvious, especially when considering the entire variety of habitats. The use of ordination algorithms allowed us, on the basis of statistically significant results, to build a reliable classification of minor water bodies in the Bolshoy Yugan River basin.

The literature data on the ecological preferences of freshwater snail species and their tendencies to inhabit specific types of habitats are rather heterogeneous, often speculative, and sometimes lack the data for potential confirmation and verification. We conclude that the approach developed by Klimowicz [12,13] is a promising way to improve the existing classification schemes of freshwater habitats, provided that the primary data on mollusc communities are collected from numerous water bodies of different types and are subjected to modern methods of statistical scrutiny.

We believe that, in the future, it would be interesting and useful to test the influence of other environmental parameters on mollusc communities in different types of waterbodies, including consideration of the chemical "dimension". Such studies would be of both fundamental and applied importance.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/w15061178/s1. Table S1. The initial matrix: the presence/absence of gastropod species in 86 habitats. Table S2. The final matrix of data on the occurrence of gastropods in 37 habitats. Table S3. Eigenvalues: the proportion of the explained variance and the achieved significance level (determined by the Monte Carlo method) for each of the CCA ordination axes. Table S4. Pearson correlation coefficients (r) between environmental variables with factor loads. Table S5. Species composition, number of specimens, proportion in the collection, and occurrence of gastropods in various types of minor water bodies of the Bolshoy Yugan River basin.

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