Identification of Freshwater Zooplankton Functional Groups Based on the Functional Traits of Species

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Abstract—Information on the functional traits of the most widespread species of freshwater zooplankton (Rotifera, Cladocera, and Copepoda) in European Russia was collected and analyzed. Our database includes 355 species described by four traits, namely, the maximum body length, trophic group, feeding type, and movement type. Cluster analysis based on Gower’s functional distances shows that freshwater zooplankton can be classified into 19 groups with different ecological roles. The characteristics of each functional group identified are presented. We believe it to be fundamentally important to build a unified classification using all available data and traits applicable to all three main taxonomic groups of zooplankton. Comparison with the existing ecological zooplankton classification proposed by Yu.S. Chuikov has demonstrated a number of advantages of our approach. Several ecological groups in Chuikov’s classification are represented by more fractional categories in our classification. Our system of functional groups can be used in studies of the structure of zooplankton communities based on direct cluster analysis and ordination or based on functional distances between samples. To calculate the functional similarity between species, one can use our database of traits, which is contained in the Appendix. Analysis based on functional groups gives a better understanding of the community structure than conventional ordination, which takes into account only the taxonomic affiliation of species. The approach used for functional group identification can be useful in assessing the functional diversity and identifying patterns in the dynamics of freshwater zooplankton communities. The database of functional traits of zooplankton can be used to check the relationship of functional traits with environmental variables.

Keywords: zooplankton, rotifers, crustaceans, functional traits, European Russia

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INTRODUCTION

Functional groups of organisms associated with their role in the ecosystem are actively used in various areas of community ecology. In the structural and functional classifications of higher plants, subdivision into groups is based on growth form and qualitative low-varying morphological characteristics of plants (Zlobin, 2012). The most common classifications are those of Ch. Raunkiaer (Raunkiaer, 1937), including five life forms and based on the location of the renewal buds and the availability of adaptations for experiencing an unfavorable season of the year, and the system of I.G. Serebryakov (1962), which includes four divisions and eight types of life forms of plant. Another approach is based on the classification of plants according to their ecological strategies (Onipchenko, 2014). In this case, the most common version is based on two classifications. The two-component classification is split into r- and K-strategists and is based on the relative costs of reproduction or maintaining the viability of adults; it goes back to the studies of J. MacLeod, as well as R. MacArthur and E. Wilson and is applied to both plants and animals (Mirkin and Naumova, 2012). The Ramenskii–Grime three-component CSR classification (Ramenskii, 1935; Grime, 1977) is based on the reaction to stress and community disturbance and applies almost exclusively to plants.

In hydrobiology, systems of functional groups are also used. In particular, a morphological and functional classification of phytoplankton was developed and ecological groups of phytoplankton were identified based on the study of the functional traits of algae (Reynolds et al., 2002; Padisak et al., 2009). Functional groups were identified taking into account the physiological, morphological, and ecological characteristics, based on which certain phytoplankton groups can potentially dominate or subdominate in a certain type of water body.

Traditionally, in Russian hydrobiology, the study of aspects of the functional organization of zooplankton communities was associated with the study of the trophic structure of zooplankton and the classification of aquatic animals according to their place in food chains (Chuikov, 1978). Groups of species with relatively
homogeneous feeding type were identified (Chuikov, 1981). The analysis of functional complexes (Smirnov, 1971) later allowed combining the trophic and topical classifications of aquatic invertebrates (Chuikov, 1981). As a result, ecological (functional) groups of zooplankters were identified based on the movement type and feeding type (Chuikov, 1981, 2000; Krylov, 2005). Attempts to adapt the Ramenski–Grime system of ecological strategies for Cladocera have also been made (Romanovskii, 1989), but this classification has not become widely used.

Functional groups of species are actively used for the analysis of the structure of communities. In many cases, analyses based on functional groups provide a better understanding of the structure of a community than traditional ordination, which takes into account only the taxonomic affiliation of species. For example, a number of studies on the relationship between biodiversity and ecosystem functioning show that the ecological role of the present species is more important than just the number of taxa (Walker, 1991; Tilman et al., 1997; Symstad et al., 2000).

Zooplankton organisms play an important role in the structure and functioning of freshwater ecosystems, providing energy flows to higher trophic levels (Krylov, 2005). Nevertheless, the approach to the analysis of the structure of zooplankton communities based on functional groups is relatively rarely used due to the lack of a sufficiently detailed classification of organisms. The available classifications are either based on particular traits (Chuikov, 1981, 2000), or cover only one of the three main systematic groups of zooplankton (Romanovsky, 1989; Benedetti et al., 2016).

The aim of this study was the development of a functional classification for three groups of freshwater zooplankton: Rotifera, Cladocera, and Copepoda. A database of traits for the most widespread freshwater zooplankton species in European Russia was compiled and used to calculate functional distances between species, and cluster analysis was performed. The cluster analysis allowed us to substantiate the selection of 19 functional groups of zooplankton.

MATERIALS AND METHODS

An approach based on the functional traits of species was used for the construction of the system of functional groups of freshwater zooplankton (Litchman et al., 2013). Functional traits are any morphological, physiological, or phenological characteristics that determine the niche and competitive abilities of individuals (Geber and Griffen, 2003; Violle et al., 2007), the ecological role of a species, its interaction with other species, and the environment (Diaz and Cabido, 2001).

The database of functional traits of freshwater zooplankton was compiled based on one quantitative trait—the maximum body size—and three qualitative traits: trophic group (two categories: predator, non-predator), feeding type (six categories: capture, primary filtration, secondary filtration, vertication, suction, gathering), and type of locomotion (three categories: swimming, crawling, attachment). The values of traits were obtained from manuals for identification, monographs, and scientific articles (Rylov, 1948; Kutikova, 1970, 2005; Smirnov, 1971, 1976; Sushchenya, 1975; Monakov, 1976, 1998; Chuikov, 1981, 2000; Borutsky et al., 1991; Korovichkiny, 2004; Krylov, 2005; Kotov and Stifter, 2006; Opredelitel’..., 2010; Kotov, 2013; Stoyko et al., 2016; Kotov and Bekker, 2016; Bledzki and Rybak, 2016; Korovichkiny, 2018).

The database for 355 species of freshwater zooplankton is presented in the supplementary material to this article.

For the maximal formalization of the identification of functional groups of zooplankton species, hierarchical cluster analysis was used. Cluster analysis in the community ecology is traditionally used to construct similarity dendrograms among samples, which is constructed based on similarity indices between samples (Pesenko, 1982). In the present study cluster analysis was used for the classification of species; therefore, the first step in our analysis was calculation of the functional similarity between species. The functional similarity was calculated using Gower’s index (Gower, 1971):

$$ S_{ij} = \frac{\sum_{u=1}^{K} s_{uij} \cdot \sum_{u=1}^{K} \delta_{uij}}{\sum_{u=1}^{K} \sum_{u=1}^{K} \delta_{uij}}, \quad (1) $$

where $S_{ij}$ is the general similarity between species $i$ and $j$, $s_{uij}$ is the similarity between species $i$ and $j$ by trait $u$, and $\delta_{uij}$ is an indicator that comparison based on the trait and between species $i$ and $j$ is possible (it is equal to 1 if comparison is possible, otherwise it is equal to 0). If all comparisons are possible, $\sum_{u=1}^{K} \delta_{uij}$ will be equal to the number of traits $K$, otherwise this sum will be equal to the number of traits for which comparison is possible. If a comparison is not possible for any of the traits, the similarity is considered uncertain.

Quantitative, categorical, and alternative traits are distinguished when calculating Gower’s index. For quantitative traits, the similarity is calculated on the basis of the difference in trait values, divided by the range of variation of this trait in all species involved in the study:

$$ s_{uij} = 1 - \frac{|t_{ui} - t_{uj}|}{t_{u}^{\text{max}} - t_{u}^{\text{min}}}, \quad (2) $$

where $t_{ui}$ is the initial non-normalized value of the $u$-th trait in species $i$ and $t_{u}^{\text{max}}$ and $t_{u}^{\text{min}}$ are the maximum and minimum values of the trait $u$ in all species. In the present study, the similarity according to for-
mula (2) was calculated for a single quantitative trait, the maximum body size.

For categorical traits, the similarity $S_{uij}$ is equal to 1 if the values of this trait for the species coincide, otherwise the similarity is 0. Alternative traits comprise a special category of traits. These traits indicate the presence or absence of a certain characteristic. At the same time, it is believed that, in the presence of this characteristic in two species, their similarity by the alternative trait is 1, the presence of the characteristic in one species and the absence in the other corresponds to zero similarity, and in the absence of the characteristic in both species, their comparison is considered impossible ($\delta_{uij} = 0$). For traits of all types, comparisons are impossible in the absence of data on the value of the trait for at least one of the compared species. In the present study, we used the three categorical traits with categories that were not mutually exclusive. For example, there are zooplankton species capable of using several types of food. From a technical point of view, each category was considered as a separate alternative trait.

Gower’s index is the average value of the similarity between the two species for all traits, with the similarity being normalized to the range (0, 1). For the adjustment of the contribution of categories of qualitative traits to the total sum of 1, they were given weights corresponding to the number of the categories within the separate traits. Thus, each of the six feeding types received a weight of 1/6, the three locomotion types received a weight of 1/3, etc.

Using Gower’s index, the similarity matrix among all species was calculated and it was converted into a distance matrix by subtracting all values from one. The resulting distance matrix was used in the conventional way for the construction of the similarity dendrogram using the Ward’s method. For the determination of the optimal number of clusters, the approach based on the average silhouette width of the clusters was used (Yakimov et al., 2016).

RESULTS

The constructed dendrogram includes 355 species of zooplankton (202 species of Rotifera, 102 species of Cladocera, and 51 species of Copepoda). The naupliar and copepodite stages of Copepoda, as well as rotifers of the order Bdelloida, were considered as separate taxonomic categories.

For the formalization of the choice of the number of groups of zooplankton species, various classification options were tested (from 2 to 355 groups). Within each potential classification, the silhouette width was calculated for each species, reflecting the degree of reliability of the species belonging to the cluster (Rousseeuw, 1987; Yakimov et al., 2016). The best classification is the one for which the average silhouette width is maximized. The graph of the dependence of the average silhouette width on the number of clusters is shown in Fig. 1. The optimal number of clusters was 19 (marked with a vertical bold line).

The final dendrogram is shown in Fig. 2. Nineteen functional groups of zooplankton were identified on the final dendrogram. The first level of the hierarchical classification separates predatory from nonpredatory species. At the next level, predators are separated into a branch of obligate predators (three groups), as well as a branch of optional predators (four groups). Nonpredators, in turn, are separated into two branches according to the type of locomotion: swimming—crawling (six groups) and only swimming or attached species (seven groups).

The summary characteristics of the 19 allocated functional groups are shown in Table 1. The full composition of the groups is provided in the Appendix (https://doi.org/10.35885/1684-7318-2020-3-290-306.suppl). Now we will characterize each functional group.
Group 1 includes large predators (0.85–4 mm) capable of swimming and crawling. This includes the Copepoda from the genera *Macrocyclops*, *Megacyclops*, and *Mesocyclops leuckarti* as well as the necrophage *Pseudochydorus globosus*. The feeding type is capture.

Group 2 includes only one, the largest (up to 7 mm) representative of freshwater predatory zooplankton *Leptodora kindtii* which has a swimming type of locomotion. The feeding type is capture.

Group 3 includes smaller predators (0.6–3 mm), with the swimming type of locomotion. These are representatives of the copepod crustaceans from the genera *Acanthocyclops*, *Cyclops*, *Diacyclops*, and *Thermocyclops*; crustaceans *Polyphemus pediculus* and *Bythotrehpes longimanus*; and the rotifer *Bipalpus hudsoni*. The feeding type is capture.

Group 4 consists of rotifers with a mixed feeding type, with the swimming type of locomotion. These are *Dieranophorus grandis*, *Trichocerca capucina*, *Trichocerca pusilla*, *Trichocerca stylata*, and the rotifers *Notommata*. The feeding type is suction.

Group 5 contains only copepods with a mixed feeding type and the floating and crawling locomotion type. This group includes representatives of the genera *Eucyclops*, *Microcyclops*, *Paracyclops*, *Cryptocyclops bicolor*, *Ectocyclops phaleratus*, *Macrocylops distinctus*, and *Metacyclops gracilis*. The feeding type is gathering.

Group 6 includes copepods with a mixed feeding type and the swimming type of locomotion. The feeding type is capture (*Cyclops scutifer* and *Cyclops vici-nus*) and capture and primary filtration (genera *Eurytemora* and *Heterocope*, and copepod stages *Calanoida* and *Cyclopoida*).

Group 7 includes rotilers with a mixed diet with the swimming type of locomotion. This group includes representatives of the genera *Ascomorpha*, *Asplanchna*, *Asplanchnopus*, *Gastropus*, and *Ploesoma*. The feeding type is capture and suction.

Groups 8—19 consist of nonpredatory species feeding on bacterio- and phytoplankton and detritus.

Group 8 includes cladocerans with the swimming and crawling types of locomotion. These are representatives of the families *Ilyocryptidae* and *Macrotrici-dae*. The feeding type is gathering.

Group 9 consists of cladocerans with the swimming and crawling type of locomotion. This group includes representatives of the families *Chydoridae*, *Eurycercidae*, and *Ophryoxidae*. The feeding type is secondary filtration.

Group 10 is the largest group, and it includes rotifers with both the swimming and crawling types of locomotion. This group includes representatives of the genera *Brachionus*, *Colurella*, *Dipleuchlanis*, *Euchla-nis*, *Eudactylota*, *Epiphanes*, *Lepadella*, *Lophocharis*, *Mytilina*, *Platyas*, *Pompholyx*, *Proales*, *Squatinella*, *Testudinella*, *Trichotria*, and *Wolga*. The feeding type is verification.

Group 11 consists only of rotifers of the genus *Lecane* with the swimming and crawling type of locomotion. The feeding type is vertication and suction.

Group 12 contains rotifers with the swimming and crawling type of locomotion. This group includes representatives of the genera *Cephalodella*, *Eosphora*, *Monommata*, *Pleurotrocha*, *Scari-dium*, *Taphrocampa*, and *Trichocerca*, as well as rotifers of the order *Bdelloida* (including the genera *Dissotrocha* and *Rotaria*). The feeding type is suction.

Group 13 contains only rotifers of the genus *Synchaeta* with the swimming type of locomotion. The feeding type is capture and suction.

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**Fig. 2.** Dendrogram of the hierarchical clustering of zooplankton species considering the functional traits. Separate functional groups are marked with rectangles.
Group 14 includes rotifers of the genera *Anuraeopsis*, *Filinia*, *Hexarthra*, *Kellicottia*, *Keratella*, *Notholca*, and *Polyarthra*, with the swimming locomotion type. The feeding type is vertication.

Group 15 includes the largest representatives of the genera *Daphnia* and *Gigantodiaptomus* (3.5–6 mm), with only the swimming type of locomotion. The feeding type is primary filtration.

Group 16 contains smaller cladocerans and copepods (less than 2.9 mm) from the genera *Bosmina*, *Bosminopsis*, *Ceriodyaphnia*, *Daphnia*, *Diaphanosoma*, *Holopedium*, *Limnosida*, *Moina*, and *Eudiaptomus* and the naupliar stages of copepods with the swimming type of locomotion. The feeding type is primary filtration.

Group 17 includes cladocerans, primary filter feeders, with the swimming and attached type of locomotion. This group includes members of the genera *Scapholeberis*, *Simocephalus*, *Megafenestra aurita*, and *Sida crystallina*. The feeding type is primary filtration.

Group 18 consists of rotifers of the genera *Collotheca*, *Conochilus*, *Conochiloides*, with the swimming and attachment type of locomotion. The feeding type is vertication.

Group 19 contains the rotifers *Lacinularia ismai-loviensis* and *Sinantherina socialis* with the attachment type of locomotion. The feeding type is vertication.

**DISCUSSION**

This study is focused on the development of a classification of freshwater zooplankton species in the European part of Russia, which is sufficiently detailed for further use in studies of the structure of zooplankton communities. Information was collected for four functional traits for 355 species of rotifers, copepods, and cladocerans. We believe it is fundamentally important to build a unified classification for all three main taxonomic groups. That is why the authors investigated four universal traits (Litchman et al., 2013), despite the fact that many aspects of the physiology and life cycle are not covered by our traits. Here, the authors proceeded from considerations of data availability and the applicability of traits for the three main taxonomic groups.

An analysis of the literature compiled showed that the main limitation is the lack of descriptions of traits at the species level. A similar remark was made by the authors of the classification of copepods in the Medi-
terranean Sea into functional groups (Benedetti et al., 2016).

It is known that a number of traits are characteristic for certain groups of freshwater zooplankton (rotifers, cladocerans, and copepods). Thus, there are traits associated with the life cycle of zooplankters, for example, the “spawning strategy” (when eggs emerge from the egg sac separately or whole egg sacs are torn off) (Benedetti et al., 2016). However, this trait is specific, since it is only inherent in copepods, and it cannot be applied to other taxonomic groups of zooplankton. Another specific trait is the type of rotifer maxillo-bulbous complex, which determines the feeding strategy (Obertegger et al., 2011). This functional trait underlies the taxonomy of this group, but is not applicable to crustaceans.

In this article, the classification of functional groups of zooplankton is constructed on the basis of hierarchical cluster analysis with the calculation of the functional similarity between species and the optimal division of the dendrogram into clusters. Most of the identified functional groups contain representatives of one taxonomic group of zooplankton (Rotifera, Cladocera, Copepoda), which includes species from different families and genera. However, the dendrogram shows conservatism at the genus level. Thus, group 2 is formed by the predatory cladocerans L. kindtii. The allocation of a separate functional group for this crustacean is due to its maximum body size, the largest among all the zooplankters studied. Also, separate functional groups are characteristic of rotifers of the genera Lecane (group 11) and Synchaeta (group 13) due to their two feeding types: vertical feeding. Thus, Lecane and capture and suction for Synchaeta. In a number of functional groups, the presence of different taxonomic groups of zooplankton was noted. For example, group 1 includes carnivorous cladocerans and copepods, while group 3 includes carnivorous rotifers, cladocerans, and copepods. Groups 15 and 16 contain cladocerans and copepods from the primary filter feeders. The differences between the latter are due to the size of the zooplankters.

The main functional classification of zooplankton applied in Russian studies is the classification of planktonic invertebrates by Chuikov (1981, 2000). It identified ten ecological groups based on the analysis of the feeding types and movement type of zooplankters. The classification of functional groups created by the authors of this article has some common features with the classification by Chuikov. Thus, both classifications distinguish separate functional (ecological) groups for attached rotifers of the genus Sinantherina and attached-swimming cladocerans from the genera Sida and Simeocephalus. A group of actively swimming predators from rotifers, cladocerans, and copepods (group 3) is also distinguished in both classifications. At the same time, there are also significant differences. The classification of the authors of this article is based on four functional traits and includes 19 functional groups. Several ecological groups in the classification by Chuikov are represented by more fractional categories in our classification. Thus, in the classification by Chuikov, swimming primary filter feeders from the cladocerans and copepods and floating rotifers, i.e., obligate verticators, are included in one ecological group. In the classification of the authors of the article, they are represented by different functional groups. The same applies to swimming—crawling gatherers from the cladocerans of the families Ilyocryptitae and Macrotricidae and copepods of the genera Eucyclops and Microcyclops. It can be stated that the classification created by the authors of this article has a more in-depth analysis of the functional characteristics of zooplankton.

The system of functional groups developed by the authors of this article can be applied in studies of the structure of zooplankton communities in several ways. First, functional groups can be used in cluster analysis and ordination methods as structural units, replacing species. In this case, before the main stage of the analysis, it is necessary to sum the abundances of species of the corresponding functional groups. Second, multidimensional methods for analyzing the structure of a community can be performed based on the functional distances between samples, which are a generalization of conventional indices, taking into account the functional similarity between species (Pavoine and Ricotta, 2014). In this case, it is impossible to use ordination methods based on the method of principal components, which directly use the matrix of abundances (species or functional groups), but methods based on the analysis of principal coordinates and nonmetric scaling, operating based on the distance matrix between objects, can be used (Legendre, P. and Legendre, L., 2012). For the calculation of the functional similarity between species, the database of functional traits, which is presented in the supplementary material, can be used (https://doi.org/10.35885/1684-7318-2020-3-290-306.suppl).

CONCLUSIONS

The information collected on the functional traits of the most widespread species of freshwater zooplankton (Rotifera, Cladocera, and Copepoda) in European Russia can be useful for assessing the functional diversity of zooplankton communities. The importance of such information was pointed out in a number of studies (Vogt et al., 2013, Pomerleau et al., 2015). One of the complex and unsolved problems of modern ecology is the determination of the influence of environmental factors on the formation of certain traits of planktonic organisms. The database of functional traits can be used to test whether traits are associated with environmental variables (Barton et al., 2013). This knowledge can be used for the prediction of possible rearrangements of the zooplankton com-
The identification and description of the functional groups of zooplankton should improve our understanding of the ecological roles of zooplankton in ecosystems (Benedetti et al., 2016). The use of the functional approach will provide a deeper understanding of the mechanisms determining the composition and structure of zooplankton communities.

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COMPLIANCE WITH ETHICAL STANDARDS

Conflict of interest. The authors declare that they have no conflict of interest.

Statement on the welfare of animals. All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

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