GENERAL PATTERNS OF MACROZOOBENTHOS DISTRIBUTION IN TWO RIVERS BASINS OF THE KHABAROVSKY KRAI (FAR EAST OF RUSSIA)

Lada V. Vorobjeva[1,*], Elena S. Chertoprud[2]

[1]*All-Russian Research Institute of Fishery and Oceanography, Russia*
**e-mail: vorobjeva.lada@yandex.ru*
[2]*A.N. Severtsov Institute of Ecology and Evolution of the RAS, Russia*

Received: 02.06.2023. Revised: 28.07.2023. Accepted: 17.08.2023.

This article analyses the distribution patterns of macrozoobenthos in watercourses of the basins of the River Bajal and River Anyuy (Khabarovsky Krai, Russia) on the territories of the Bajal Sanctuary and Anyuy National Park. The distance-based linear models (DistLM) method was used to estimate the proportion of distribution of macroinvertebrates explained by the factors considered in the study (river basin, current velocity, substrate, channel width, temperature, pH). All of these factors contributed significantly, together explaining about one-third of the variability of macroinvertebrate distribution. The main explanatory factors were river basin and substrate (9.3% and 10.5%, respectively), as well as the current velocity (5.7%). Based on the cluster analysis, eight statistically significant groups of samples on the basis of similarity of taxonomic composition were identified. A set of indicator taxa was determined for each group and their indicator values were found. Using the Kruskal-Wallis analysis, the environmental factors significantly differing between the obtained groups and subgroups were singled out. There are well-defined patterns in the confinement of taxonomic complexes to certain habitats. Local environmental factors are the strong filter influencing the formation of taxonomic communities. The factor of belonging to the river basin also plays a significant role in the formation of invertebrate communities, which should be considered in the planning of monitoring studies on a large spatial scale. However, the distinguished groups and subgroups are characterised by a low level of internal similarity. Only about a quarter of the total species number belongs to indicator taxa, and samples do not form discrete clusters with obvious hiatus on the ordination diagram. The longitudinal distribution of macroinvertebrates for each river can be characterised as a punctuated gradient.

Key words: community, environmental factor, freshwater macroinvertebrates, Russian Far East, watercourse

Introduction

Understanding the patterns of the community formation and their interaction with the environment is necessary for successful planning of environmental monitoring and conservation activities. Ecosystems of Protected Areas are not or slightly disturbed by anthropogenic activity, so they can play the role of reference sites for assessing the degree of disturbance during monitoring studies. One of the key questions of community ecology is whether communities exist as discrete units or form an entire continuum. The first scenario assumes that species groups respond to changes in environmental factors in a similar way, forming closely related groups. In the second case, the species response is individual. A more detailed discussion of the problem is given by Ipatov & Kirikova (1997). The history of this concern goes back about a hundred years (Clements, 1916; Gleason, 1926), but the problem remains controversial (e.g. Heino et al., 2003; Heino, 2005; Merovich & Petty, 2010; Tolonen et al., 2016).

The paramount importance of local environmental factors in the formation of freshwater macroinvertebrate communities is often highlighted in the literature (Pardo & Armitage, 1997; Beisel et al., 1998; Doisy & Rabeni, 2001; Johnson et al., 2004; Costa & Melo, 2008; Korte, 2010; Kubosova et al., 2010; Silva et al., 2014). Environmental factors are a system of filters that allow only those taxa of the regional fauna that have suitable biological and morphological features to colonise a habitat. Factors influencing the community formation in rivers represent a hierarchical system, in which macroscale factors affect conditions at lower hierarchical levels. Altogether, four main levels of the factor scale are distinguished, namely watershed basin, watercourse, watercourse section, and habitat (Poff, 1997; Dallas, 2007a; Heino et al., 2012; Grönroos et al., 2013).

The effects of environmental factors acting at various spatial scales, as well as the interactions between local communities, are the subject of the metacommunity concept (Leibold et al., 2004). A metacommunity is defined as a set of local communities in different areas, united by certain patterns of distribution of species composition. On a large spatial scale, differences in the taxonomic composition of communities can be explained by the limited dispersal abilities of organisms. On the contrary, on a small scale, differences between the fauna of various habitats can be smoothed out by the movement effect of organisms, that is, the fauna from neighbouring habitats can partially mix and merge (the phenomenon of «mass effect»).

In studies of river ecosystems, an important spatial unit is the watershed. Within a basin, the influence of barriers to the dispersal of organisms is thought to be minimised, since dispersal within one is more likely than between different basins. Thus, the structure of communities within a watershed is mainly determined by abiotic environmental factors, which increases its predictability (Heino & Mykrä, 2008; Heino et al., 2017). The effect of such filters is the largest at the mesoscale (metres and tens of metres), where the structure of communities is not affected by either the «mass effect» smoothing the differences, or the limited dispersal abilities of species (Heino et al., 2017; Chertoprud, 2021). Habitat studies at the mesoscale allow a comprehensive analysis of the river ecosystem (Brunke et al., 2001). A clear classification of habitats is important for the research design, which makes the selection of sampling sites not random (Kubosova et al., 2010).

Four groups of aquatic organisms have been identified, which differ in the correlation between their spatial distribution and the heterogeneity of environmental conditions, namely weak passive dispersers with aquatic adult specimens (Oligochaeta, Hirudinea, Gastropoda, Bivalvia, Aranea, Crustacea), weak aerial dispersers with flying adults (Ceratopogonidae, Chironomidae), intermediate aerial dispersers with flying adults (Ephemeroptera, Plecoptera, Megaloptera, Trichoptera, Diptera: Tipuloidea, Tabanidae, Empididae), and strong aerial dispersers with flying adults (Odonata, Heteroptera: Corixidae, Coleoptera: Dytiscidae). Environmental factors to the greatest extent determine the distribution pattern of strong aerial dispersers (up to 80% of variations), while dispersal barriers explain a small proportion of variability (5% of variations). For weak passive dispersers with aquatic adults, only 50% of variation was explained by environmental factors. Mixed influence of environmental factors and dispersal barriers were responsible for 30% and 10%, respectively (Heino, 2013a). Therefore, actively dispersing organisms that are able to select the most suitable conditions are usually confined to specific habitats, while passive dispersers are more likely to demonstrate a random distribution (Grönroos et al., 2013; Heino, 2013b).

This research presents an original approach to the analysis of distributional patterns of organisms based on the example of macrozoobenthos of two Far Eastern rivers (Khabarovsky Krai, Russia). The first task was to assess the contribution of environmental factors to the overall variability in the distribution of organisms. The second task was to check whether it is possible to identify statistically significant classes of communities in the absence of an a priori hypothesis of their existence. Environmental factors determining the habitat type were the main focus of the research. Finally, in the case of reliable identification of community types, the third task was to identify indicator taxa and typical life forms for each of them.

Material and Methods

Study Area

The research has been carried out during the field work in the study area of two rivers located in the Far East, namely the River Anyuy and the River Bajal (Fig. 1). The River Anyuy flows through the territory of the Anyuy National Park (Nanaysky district of the Khabarovsky Krai). The study area was located in the taiga zone, on the western slopes of the Sikhote-Alin mountain range, at an altitude of 50–250 m a.s.l. The River Bajal flows through the territory of the Bajal Sanctuary (Solnechny district of the Khabarovsky Krai). It is the right tributary of the River Amgun in its lower reaches. Both rivers belong to the Amur River Basin.

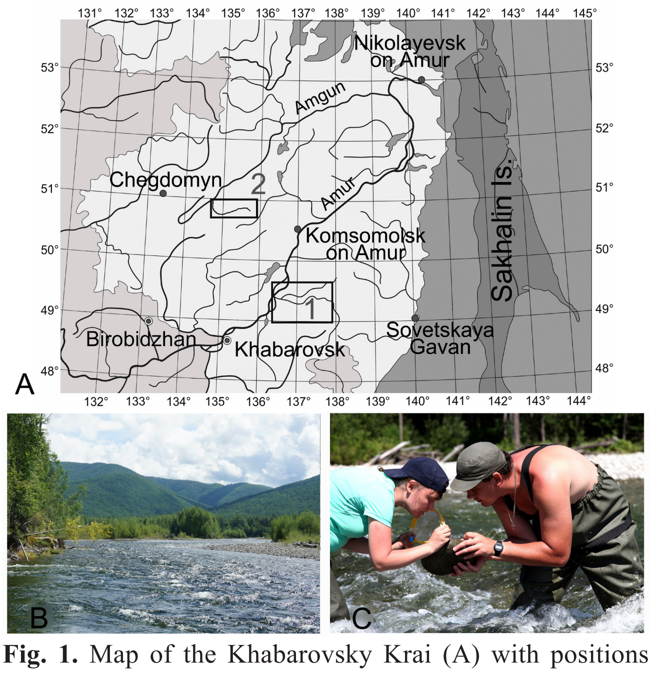

Fig. 1. Map of the Khabarovsky Krai (A) with positions of basins of River Anyuy (1) and River Bajal (2) (black squares). B – middle course of River Bajal (B). C – sampling process on intense flow (C). Authors of the photos: B – I.N. Nikonova, C – E.S. Chertoprud.

Sampling Methods

Samples were collected in August 2016 (River Anyuy) and August 2018 (River Bajal) (Fig. 1). Sampling stations covered both the main rivers of the basins and the mouth zones of some of their tributaries. At each station, the following factors were considered: altitude, sediment type, channel width, depth, water temperature, mineralisation (PPM), acidity (pH), and current velocity. At each station, environmental variables such as water temperature (°C), pH, and total mineralisation (PPM) were measured with a portable multiparameter water quality device YIERYI 5 in 1 (Italy). The current velocity was measured manually using a floating object with standard mass and measuring the distance travelled by it per unit of time. The area of a sample was approximately 1500 cm^2. At each sampling station, three samples were collected and then combined into one complex sample.

While taking quantitative samples, stones of an average size of 15–20 cm were lifted from the bottom, while a hydrobiological net was placed under the rock to avoid the loss of organisms. Samples from pebbles (average size: 3–6 cm) and loose soils (plant detritus and silty sand) were taken with a hydrobiological scraper. All organisms were selected from the substrate with tweezers and preserved in 90% ethanol. A total of 31 quantitative samples were taken in the Bajal River basin, and 80 quantitative samples were taken in the Anyuy River basin.

Most organisms have been identified up to the species level. However, in some cases, larval stages could only be identified up to the genus or family level. We used mainly the following taxonomic literature: Tsalolikhin (1997, 2000, 2001, 2004), Leley (2006), Teslenko & Zhiltsova (2009). Insect life forms were determined according to Merrit et al. (2019), molluscs and oligochaetes were characterised according to Chertoprud (2021) and our own expert assessment, amphipod *Gammarus koreanus* according to Astakhov & Skriptsova (2020).

Statistical Analysis

To identify the groups of samples based on the similarity of taxonomic composition, a hierarchical cluster analysis has been carried out using the group-average link. The similarity profile analysis (SIMPROF) procedure was used to assess the statistical significance of the selected groups. Non-metric multidimensional scaling (nMDS) was used to visualise the location of samples based on taxonomic similarity. The table with data on the relative abundance of taxa in the samples was used for the analysis. The data were square-root transformed. The sample similarity matrix was calculated based on the Bray-Curtis similarity index. All the methods described by Clarke et al. (2014).

To identify the environmental factors that contributed most to explain the sample distribution, the distance-based linear models (DistLM) method was used, together with the selection of step-wise factors and the AICc criterion (Anderson et al., 2008). Additionally, a non-parametric Kruskal-Wallis test was performed to determine the environmental factors that differed significantly for the selected groups of samples (Glantz, 2012). The canonical analysis of principal co-ordinates (CAP) was used to cross-validate the groups obtained in the cluster analysis. In the process of cross-validation, a random sample was selected and the ability of the model to correctly classify it according to a priori division into groups was checked. Thus, the higher percentage of the correct classification corresponded to the more reliable identification of groups.

For each group of samples obtained in the course of the cluster analysis, indicator taxa were identified by calculating the IndVal index (Legendre & Legendre, 2012). The index combined the assessment of taxon specificity for the analysed group (the frequency of occurrence of the taxon outside the given group) and fidelity (the frequency of occurrence of the taxon in samples within the group). The IndVal value could range from 1 to 100. The maximum indicator value of a taxon was observed, when it was found in all samples of the group. All statistical analyses were performed using PRIMER v7 (PRIMER-e, Quest Research Limited, New Zealand) and PAST 4.06b software (Hammer et al., 2001).

Results

Taxonomical composition of macrozoobenthos

In the Bajal River basin and the Anyuy River basin, 216 invertebrate taxa were found and identified to species, groups of species or genus levels. Oligochaetes (families Tubificidae and Enchytraeidae), bivalves (family Euglesidae) and dipterans (family Psychodidae and, in certain cases, Limoniidae) have been identified to the family level, while black flies (subfamily Simuliinae) to the subfamily level. Amphibiotic insects were the predominant group among macroinvertebrates in the surveyed watercourses of the Khabarovsky Krai. They accounted for more than 90% (201 taxa) of the species richness among the observed hydrobionts. A total of 89 taxa, including 86 insects, have been found in the Bajal River basin. The Anyuy River basin can boast a diversity of 184 taxa including 171 insects.

Factors regulating the spatial distribution of organisms

The following factors were considered in the DistLM analysis: river basin, substrate, temperature (°C), channel width (m), depth (m) and water flow velocity (m/s) at the sampling site, pH, mineralisation (PPM). The contribution of only six factors to the variability in macroinvertebrate distribution was statistically significant ($p < 0.001$) (Table 1). The total proportion of explained variance was about 32%, with the following key factors explaining the largest proportion of variability: substrate (about 10.5%), river basin (about 9%), and water flow velocity (5.7%). Thus, about one-third of the variability in the distribution of aquatic organisms is associated with the environmental factors included in the analysis. The remaining unexplained variability appears to be due both to factors not included in the analysis and to stochastic processes in the aquatic ecosystem.

Classification of community types

The cluster analysis identified five statistically significant groups of samples (indicated by the black branches, three of which (№1, №2, and №3 in Fig. 2) were, in turn, divided into two subgroups each. Five samples with rare variants of the macrozoobenthos composition, which have not been included in any of the clusters, were combined into a separate group №6. Thus, eight statistically significant relatively independent clusters were identified with an internal similarity level from 37% (№2B) to 4% (№4) (Fig. 2). Group №6 was not included in the subsequent analysis, not being statistically significant.

Table 1. Significant factors ($p < 0.001$) determined variability in the spatial distribution of macroinvertebrates (results of Sequential test of DistLM using AICc criterion, selection procedure of predictor variables: step-wise, with comparison to full model, selection procedure: all specified)

Factor	*Prop.	**Cumul.
River basin	0.09314	0.09314
Water flow velocity (m/s)	0.05711	0.15026
Substrate	0.10489	0.25515
Channel width (m)	0.02952	0.28466
Temperature (°C)	0.01957	0.30423
pH	0.01532	0.31955
R^2 for best model (selection procedure: step-wise)	0.31955	
AICc for best model (selection procedure: step-wise)	978.87	
R^2 for full model (selection procedure: all specified)	0.33183	
AICc for full model: (selection procedure: all specified)	981.77	

Note: *Prop. – contribution to the explained variability; **Cumul. – cumulative explained distribution.

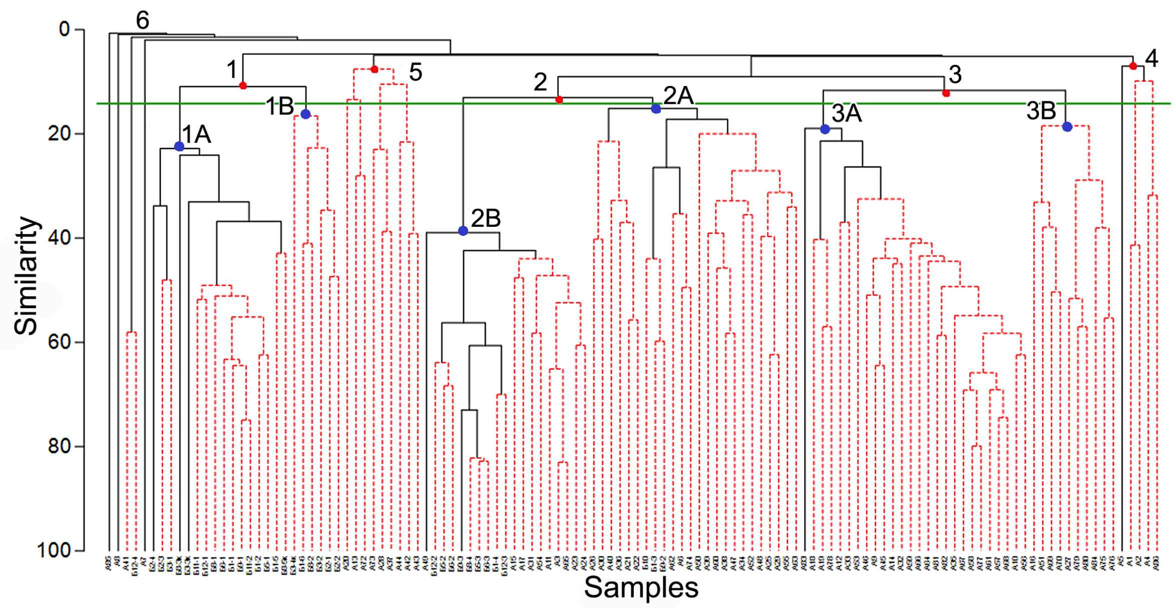

Fig. 2. Dendrogram for hierarchical clustering (group-average link method, Bray-Curtis similarity index) of macrozoobenthos taxonomical structure from samples of various water courses of the Bajal River basin and Anyuy River basin. Main sample groups are marked. Red points – groups with internal similarity level of about 10% and less; blue points – subgroups with internal similarity level > 11%; red dashed branches – groups with no evidence from SIMPROF for the significant clustering structure; black branches – statistically significant groups according to SIMPROF.

A CAP cross-validation procedure has been performed for each level of clustering. In all selected groups (except group №6), 80–100% of samples were classified correctly (Table 2). For the first level of clustering, the first squared canonical correlation is 0.93857, p-value < 0.001. For the second level of clustering, the first squared canonical correlation is 0.9335, p-value < 0.001.

The nMDS plot (Fig. 3) illustrates the interposition of sample groups according to the results of the second level of clustering. Highly similar samples are located closer to each other and form dense point clouds. The identified community types are relatively clear-cut and specific in species structure. However, it is noticeable that the groups of samples belonging to different communities are not discrete. Different point clouds merged smoothly into each other, and there are no clear gaps (hiatuses) between them.

The influence of the river basin factor on the distribution of macrozoobenthos is shown separately (Fig. 4). Samples from the Bajal River basin and Anyuy River basin form two almost non-overlapping groups of points (except one point from Anyuy River basin), highlighting the faunal specificity of these two areas. The absence of a hiatus between the point clouds indicates the gradual nature of the faunal change.

Table 2. Results of CAP cross-validation procedure for samples classification identified on the basis of hierarchical clustering analysis

First level of clustering		
Groups or subgroups	Number of samples	Correct cross-validation (%)
1	22	90.91
2	43	100.00
3	36	91.67
4	6	80.00
5	9	88.89
6	5	40.00
Second level of clustering		
1A	16	93.75
1B	6	100.00
2A	24	100.00
2B	19	100.00
3A	26	88.46
3B	10	100.00
4	6	80.00
5	9	88.89
6	5	40.00

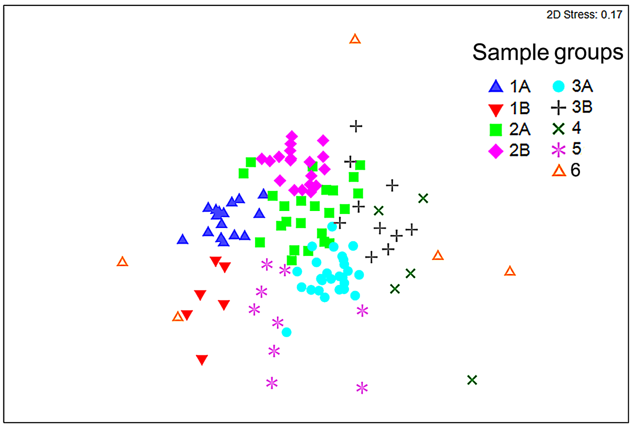

Fig. 3. nMDS ordination of the samples from water cources of the Khabarovsky Krai (Russian Far East), based on Bray-Curtis similarity index and factored with division of the second level of cluster analysis.

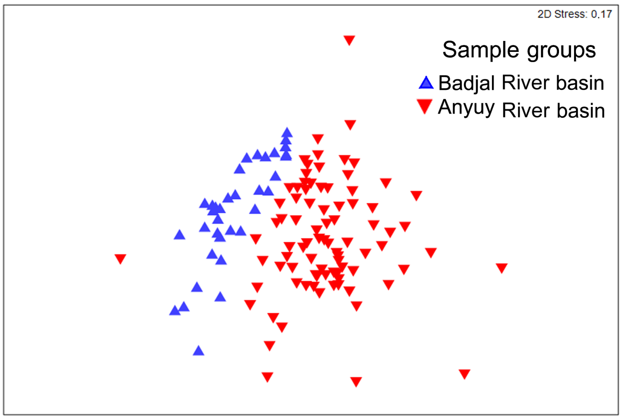

Fig. 4. nMDS ordination of the samples located in watercourses of Khabarovsky Krai (Russian Far East), based on Bray-Curtis similarity index and factored with the rivers basin.

Definition of key environmental factors and indicator taxa for different community types

The Kruskal-Wallis test was performed to assess whether there were significant differences in environmental factors between the selected groups of samples corresponding to the community types. The results of the Kruskal-Wallis test for the second level of clustering are shown in Table 3, and the selected indicator taxa are presented in Table 4. A total of 147 reliable indicator taxa with an indicator value of > 20 (IndVal > 20) were identified for the distinguished communities.

It is shown that the distribution of macroinvertebrates is not random. Selected samples are divided into groups (communities) based on the species (taxonomic) structure. The Kruskal-Wallis test showed that the abiotic factors are significantly different between the distinguished community types. For each type, a set of significant indicator taxa was identified indicating the presence of specific species complexes associated with specific habitats.

Table 3. Values of environmental factors that determine differences between samples patterns on the second level of clustering (Kruskal-Wallis test)

Factor		Groups and subgroups								
		1A	1B	2A	2B	3A	3B	4	5	6
Temperature (°C)	Median	12.00	11.00	13.00	12.00	12.50	14.00	21.00	13.00	16.00
	H	35.43								
	Chi-squared	34.66								
	p-value	< 0.001								
Channel width (m)	Median	9.00	5.00	10.00	10.00	2.50	50.00	20.00	7.00	10.00
	H	45.65								
	Chi-squared	45.02								
	p-value	< 0.001								
Depth (m)	Median	0.15	0.45	0.55	0.40	0.30	2.00	1.00	0.50	0.50
	H	44.81								
	Chi-squared	44.06								
	p-value	< 0.001								
Current velocity (m/s)	Median	0.12	0.02	0.35	0.60	0.20	0.20	0.10	0.10	0.30
	H	59.31								
	Chi-squared	57.94								
	p-value	< 0.001								
pH	Median	7.90	7.90	8.20	8.00	8.00	7.95	8.40	8.10	8.30
	H	18.14								
	Chi-squared	17.61								
	p-value	≈ 0.020								
Mineralisation (PPM)	Median	20.00	20.00	19.50	16.00	16.00	19.00	26.00	18.00	21.00
	H	16.45								
	Chi-squared	16.19								
	p-value	≈ 0.036								
River basin	Bajal	16	6	3	9	0	0	0	0	1
	Anyuy	0	0	21	10	26	10	5	9	4
Substrate	Stones	14	0	18	16	6	1	1	1	0
	Pebbles	2	0	0	0	0	0	0	0	0
	Snags	0	0	5	1	8	1	1	1	0
	Detritus	0	1	1	1	9	7	2	1	2
	Macrophytes	0	0	0	1	2	1	0	0	1
	Sand	0	5	0	0	0	0	0	1	2
	Silt	0	0	0	0	1	0	1	5	0

Discussion

The macroinvertebrate fauna of the freshwaters of the Russian Far East has been relatively well studied (Haritonov & Malikova, 1998; Makarchenko et al., 2005; Tiunova, 2007, 2009; Makarchenko et al., 2008; Tiunova & Korotenko, 2008; Yavorskaya, 2008; Teslenko, 2009, 2014; Tiunova & Gorovaya, 2011; Zasypkina, 2011, 2018; Teslenko et al., 2014; Potikha, 2015; Orel, 2016; Potikha & Vshivkova, 2016). A number of published data are devoted to the functional and spatial structure of macrozoobenthos communities, in particular, to the trophic structure (Kocharina & Khamenkova, 2003; Tiunova, 2006; Labay, 2007), their distribution in the watercourse of the rivers (Potikha, 2011; Labay et al., 2019), including confinement to microhabitats (Tiunova, 2008) and peculiarities of benthos composition in watercourses of various types and assessment of their water quality (Yavorskaya, 2015, 2016, 2021). One of the most recent attempts to classify macrozoobenthos communities in the Khabarovsky Krai is presented in Chertoprud et al. (2020). According to this classification, communities are identified on the basis of dominance structure and a priori limited to previously distinguished habitats.

For the macrozoobenthos of the studied areas, the environmental factors considered in the analysis explained about 30% of the variability in distribution. The main regulating factors were river basin and substrate type (about 10% of the explained distribution per factor), and flow velocity (about 5.7%). The low proportion of explained variability of the macroinvertebrate distribution is a typical phenomenon for river ecosystems, at least within a single basin (Sandin, 2003; Heino & Mykra, 2008; Kubosova et al., 2010; Heino et al., 2012, 2014; Silva et al., 2014). The composition of macroinvertebrate species complexes in rivers is hardly predictable due to frequent flood events leading to the habitat destruction and, as a consequence, their secondary colonisation by organisms. Another factor that determines the low predictability of the composition of river communities is the high number of rare species. The higher percentage of rare species in the river fauna correspond to the lower percentage of explained variability in the distribution of organisms (Heino & Mykra, 2008).

Table 4. Macrozoobenthos indicator taxa of samples patterns on the second level of clustering, identified on the basis of the IndVal index (values > 20)

Groups and subgroups	Taxon	IndVal	p-value	Character of movement	Functional feeding group
1A	*Ameletus cedrensis* Potikha, 1985	66.12	< 0.0001	Swimmers; clingers	Scrapers; collectors-gatherers (detritus. diatoms)
	Suwallia sp. Ricker, 1943	62.15	< 0.0001	Clingers	Predators (engulfers)
	Mesocapnia sp. Rauser, 1968	49.02	< 0.0001	Clingers	Shredders-detritivores
	Rhitrogena putoranica (Kluge, 1980)	38.86	< 0.0001	Clingers	Scrapers; facultative collectors-gatherers
	Brachypsyche sp. Schmid, 1952	37.91	< 0.0001	Climbers; sprawlers; clingers	Shredders-detritlvores
	Pictetiella asiatica Zwick & Levanidova, 1971	36.54	< 0.0001	Clingers	Predators (engulfers)
	Drunella triacantha Tshernova, 1949	34.54	< 0.0001	Clingers; sprawlers	Scrapers; facultative predators; facultative collectors-gatherers
	Ephemerella dentata Bajkova, 1967	30.81	< 0.0001	Swimmers; clingers at rest	Collectors-gatherers; scrapers
	Rhithrogena hirasana Imanishi, 1935	24.41	< 0.0001	Clingers	Scrapers; facultative collectors-gatherers
	Ephemerella aurivillii Bengtsson, 1908	24.37	0.0004	Swimmers; clingers at rest	Collectors-gatherers; scrapers
1B	*Tipula salisetorum* Siebke, 1870	79.84	< 0.0001	Burrowers in plant detritus	Obligate shredders-detritivores
	Micropsectra sp. Kieffer, 1908	68.50	< 0.0001	Sprawlers	Collectors-gatherers
	Siphlonurus immanis Kluge, 1985	56.87	< 0.0001	Swimmers; climbers at rest	Collectors-gatherers
	Oreodytes sp. (larvae) Seidlitz, 1887	33.33	0.0031	Swimmers; climbers at rest	Predators (piercers)
	Chaetocladius sp. Kieffer, 1911	33.33	0.0023	Sprawlers	Collectors-gatherers
	Lumbriculus variegatus (Muller, 1774)	33.33	0.0025	Burrowers	Collectors-gatherers
	Arctopelopia griseipennis (Wulp, 1858)	28.47	0.0033	Sprawlers	Predators (engulfers)
	Polypedilum gr. *nubeculosum*	25.06	0.0026	Burrowers	Collectors-gatherers. predators (engulfers)
	Heterotrissocladius gr. *marcidus*	20.44	0.0114	Sprawlers; borrowers	Collectors-gatherers scrapers
2A	*Epeorus* gr. *pellucidus*	49.72	< 0.0001	Clingers	Scrapers; facultative collectors-gatherers
	Glossosoma sp. Curtis, 1834	29.17	< 0.0001	Clingers (turtle shell case)	Obligate scrapers
	Pagastia orientalis Chernovskij, 1949	26.16	< 0.0001	Sprawlers	Collectors-gatherers; scrapers
	Optioservus kubotai Nomura, 1958	24.91	0.0002	Clingers	Scrapers (larvae); collectors-gatherers (adults)
	Drunella lepnavae Tshernova, 1949	23.47	< 0.0001	Clingers; sprawlers	Scrapers; facultative predators; facultative collectors-gatherers
	Neophylax ussuriensis Martynov, 1914	23.04	< 0.0001	Clingers	Obligate scrapers
	Brachycentrus americanus (Banks, 1899)	21.34	0.0003	Clingers	Shredders-herbivores
	Atherix ibis (Fabricius, 1798)	20.37	< 0.0001	Sprawlers-burrowers	Predators (piercers)
	Ephemerella kozhovi Bajkova, 1967	20.06	0.0003	Swimmers; clingers at rest	Collectors-gatherers; scrapers
2B	Simuliinae spp.	73.30	< 0.0001	Clingers	Filter feeders; collectors
	Epeorus maculatus Tshernova, 1949	56.37	< 0.0001	Clingers	Scrapers
	Orthocladius sp. van der Wulp, 1874	25.58	< 0.0001	Sprawlers; burrowers	Collectors-gatherers
3A	*Gammarus koreanus* Fabricius, 1775	52.85	< 0.0001	Sprawlers	Shredders-detritivores, predators
3B	*Baetis* gr. *vernus*	78.56	< 0.0001	Swimmers; clingers / climbers at rest	Collectors-gatherers; facultative scrapers
	Baetis fuscatus Linnaeus, 1761	40.44	< 0.0001	Swimmers; clingers / climbers at rest	Collectors-gatherers; facultative scrapers
	Ephemerella zapekinae Bajkova, 1967	39.36	< 0.0001	Swimmers; clingers at rest	Collectors-gatherers; scrapers
	Diura sp. Billberg, 1820	37.62	< 0.0001	Clingers	Predators (engulfers)
4	*Juga nodosa* (Westerlund, 1897)	75.42	< 0.0001	Sparwlers	Collectors-gatherers
	Ecdyonurus abracadabrus Kluge, 1983	40.00	0.0017	Clingers	Scrapers; facultative collectors-gatherers
	Labiobaetis atrebatinus (Eaton, 1870)	4000	0.0019	Swimmers; clingers / climbers at rest	Collectors-gatherers; facultative scrapers
	Drunella cryptomeria (Imanishi, 1937)	34.90	0.0005	Clingers; sprawlers	Scrapers; facultative predators; facultative collectors-gatherers
	Microtendipes gr. *pedellus*	34.42	0.0023	Clingers (net spinners)	Filter feeders; collectors; gatherers
	Baetis ussuricus Kluge, 1983	29.56	0.0024	Swimmers; clingers / climbers at rest	Collectors-gatherers; facultative scrapers
	Rheopelopia ornata (Meigen, 1838)	25.38	0.0087	Sprawlers	Predators (engulfers and piercers)
	Radix sp. Montfort, 1810	23.72	0.0080	Sparwlers	Collectors-gatherers
5	Tubificidae spp.	45.52	< 0.0001	Burrowers	Collectors-gatherers
	Euglesidae spp.	37.57	< 0.0001	Burrowers	Filter feeders
	Paratendipes albimanus (Meigen, 1919)	33.33	0.0005	Burrowers (tube builders)	Collectors-gatherers
	Chrysops sp. Meigen, 1803	22.22	0.0056	Sprawlers-burrowers	Predators (piercers)
	Anabolia servata (McLachlan, 1880)	20.70	0.0043	Climbers-sprawlers	Shredders-detritivores; facultative collectors-gatherers

The strong majority of hydrobionts encountered in the research are amphibiotic insects with a flying imago capable to the active dispersion. A considerable influence of abiotic environmental factors on spatial distribution is typical for these organisms. Indeed, groups of samples corresponding to individual habitat types were identified (Fig. 3). However, these groups are not clearly separated from each other, smoothly passing from one to another, and some even overlap to a considerable extent. The substrate type was the main abiotic factor explaining most of the variability in the distribution of organisms. The key role of sediment type for macrozoobenthos has been noted previously (Pardo & Armitage, 1997; Dallas, 2007b; Chertoprud, 2021). The river flow velocity was the second important abiotic factor. It has been shown that the composition of hydrobionts differs significantly between habitats with fast and slow flow and habitats with no flow (Rabeni et al., 2002). Macroinvertebrates reach the highest species richness in fast flowing habitats (Rabeni et al., 2002), which is consistent with the data from the present research. The optimal current velocity for benthic fauna is 0.11–0.50 m/s (Korte, 2010). Under such conditions, the most diverse species complexes are formed, with functional feeding groups represented by scrapers, gatherers, shredders and predators. In this research, samples from subgroup №2A of the habitat with a median flow velocity of 0.35 m/s showed the highest taxonomic richness.

Clustering of the samples revealed five statistically significant groups differing in composition and quantitative characteristics of the macrozoobenthos. Three of these groups were not homogeneous within themselves, and each of them was therefore divided into two subgroups. Thus, the eight main blocks of samples obtained in this way correspond to individual community types. Brief descriptions of habitats, faunistic characteristics in the context of the literature data and the relevance of the identified communities with the previously proposed classifications are presented below.

Group №1 is entirely within the Bajal River basin. These samples are collected from the coldest and the shallowest areas with a slow current velocity on stony and silty substrates. At the second clustering level, this group is divided into subgroup №1A and subgroup №1B.

Samples from subgroup №1A are collected in a habitat characterised by a lower median depth and higher water flow velocity than in subgroup №1B. The substrate types are represented by stones (including small pebbles) and snags. The described habitat is presented on hard substrates in the shore shallow zone of rivers and streams from the Bajal River basin. The species richness subgroup №1A is 61 taxa. According to its description, subgroup №1A corresponds to the habitat «shore areas of accumulated gravel» with a predominance of Ephemeroptera larvae from genus *Ameletus* Eaton, 1865 (Takemon, 1997), and is also comparable to the habitat «shore area of stream and drain» (Tiunova, 2008). An important role of *Ameletus* mayflies on shore gravels has also been reported for rivers on Sakhalin Island (Labay, 2007). In this community, functional feeding groups are represented by scrapers, collectors-gatherers, and to a lesser extent shredders-detritivores and predators. In terms of the movement type, the majority of species are clingers, which is indicative of the predominance of stony substrates.

In subgroup №1B, the median flow velocity and water temperature are the lowest of all the habitats covered in this study. Samples from subgroup №1B included mainly sandy substrate and plant detritus and placed on soft substrates in streams of the Bajal River basin. The species richness is 39 taxa. This habitat corresponds to the «stream side with groundwater inflow» according to Tiunova (2008), with species of the family Tipulidae as the predominant group of hydrobionts. The main indicator taxon of subgroup №1B, *Tipula salisetorum* Siebke, 1870, is a typical cold-water species (Chebanova, 2008). The functional feeding groups are dominated by collector-gatherers, as well as shredders-detritivores and predators, while in terms of the movement type the groups are represented by burrowers, sprawlers and swimmers. Such a composition is typical for soft sediments.

Group №2, marked with the highest flow velocity among all the groups, includes samples from both Anyuy River basin and Bajal River basin. This entire group of samples corresponds to the zone of «accumulated stones in a riffle of high flow», i.e. stony substrates on riffles with fast flow, where the community included species of the genus *Epeorus* Eaton, 1881 and the subfamily Diamesinae (Takemon, 1997). In the studied streams of the Khabarovsky Krai, this group was divided into two subgroups with different flow velocities.

In samples of subgroup №2A, the substrates were represented by stones and snags. The species richness is 108 taxa. The habitat is mainly represented in the watercourses of the Anyuy River basin, with only three samples from the Bajal River basin. This habitat with slightly slower waterflow (compared to subgroup №2B) corresponded to the Chertoprud et al. (2020) classification, i.e. stony substrates at medium to fast flow (0.4–0.7 m/s), with dominance of *Epeorus* gr. *pellucidus*. In terms of functional feeding group composition, this community is close to subgroup №1A, where scrapers and collector-gatherers prevail, while some predators and shredders-detritivores are also presented. Clingers dominate in terms of movement type, but there are also sprawlers (Diptera larvae), which live on the surface of rocks and in the cavities between them.

The median and average flow velocity of the samples in subgroup №2B is the highest among all the groups of the second clustering level (subgroup №2A is the second in terms of flow velocity). This subgroup includes samples from both river basins. The species richness is 88 taxa. This community corresponds to chimaroritral (Chertoprud et al., 2020) and includes habitat of «stone patch on an intense stream roll» (Tiunova, 2008). These are stony areas with an intense flow (0.7–1.0 m/s), with a high abundance of Simuliidae larvae. The community may also include *Epeorus* (*Iron*) *maculatus* Tshernova, 1949 (Tiunova, 2008). Functional feeding groups are represented by sedentary filter feeders (family Simuliidae), which is typical for rivers and streams with fast currents, as well as scrapers and collectors-gatherers. Groups of movement type include sprawlers living in the fouling film on stones (*Orthocladius* sp.) and clingers.

Group №3 includes samples with an average value of temperature, depth, and velocity flow. It entirely refers to the Anyuy River basin. Among all the groups, it has the highest proportion of plant detritus and snags in substrates, and stones, macrophytes and silt are found less.

Subgroup №3A is characterised by the smallest median channel width among all second-level cluster groups. Samples from subgroup №3A were mainly collected on plant detritus, snags and stones. The species richness is 82 taxa. Subgroup №3A corresponds to the gammarocrenal community, the main type of crenal communities of the Khabarovsky Krai with a dramatic dominance of *Gammarus* sp. Fabricius, 1775 (Chertoprud et al., 2020). *Gammarus koreanus* Ueno, 1940, which belongs to the shredders-detritivores and facultative predators in terms of functional feeding groups and sprawlers in terms of the movement types, is the only important indicator species in this community.

Subgroup №3B has the highest median and average stream channel width and depth. Substrates were represented mostly by plant detritus. The species richness is 44 taxa. In terms of characteristics, this community is close to phytoritral and eurypal (Chertoprud et al., 2020); it is located on the shore edge in the lower reaches of the River Anyuy. Functional feeding groups include predators and collectors-gatherers. The movement types are represented by swimmers and clingers, which also corresponds to the phytal and ripal habitat structure, according to Chertoprud et al. (2020).

Group №4 refers entirely to the Anyuy River basin. It is a small group of samples characterised by a wide and deep channel, the highest median water temperature, mineralisation and pH values among all the groups. Substrates are represented by stones, snags, plant detritus and silt. The species richness is 42 taxa. This community with relatively warm and slowly flowing waters corresponds to the malacoripal (Chertoprud et al., 2020) with a dominance of Gastropoda species. The habitats were mainly found in the River Alima, a tributary of the River Anyuy. Functional feeding groups mainly include scrapers and collectors-gatherers, with presence of some predators. In terms of movement types organisms are represented by clingers, swimmers and sprawlers. The diversity of indicator taxa and their life forms reflects the variability of substrates.

Group №5 is also related to the Anyuy River basin, mainly to small streams. Samples from this group are characterised by a low median and average flow velocity and the highest proportion of silty substrates among all the groups. The species richness is 56 taxa. This community combines the features of eupelal, epipelal, and crenopelal according to Chertoprud et al. (2020). Functional feeding groups are represented by filter feeders, collectors-gatherers, shredders-detritivores and predators. Groups of movement types are mostly sprawlers and burrowers, which is typical for silty substrates.

In the macrozoobenthos distribution, a considerable part of the variability is also explained by the river basin factor. Within a river basin, barriers to the macroinvertebrate dispersal are weak. Therefore, local abiotic factors, such as substrate and flow velocity, have a predominant influence on community structure (Heino & Mykra, 2008). The high significance of the river basin factor for the macrozoobenthos of the Far Eastern rivers can be explained both by the unaccounted differences in the environment conditions of basins and by their geographical distance from each other. It is shown that the influence of the river basin increases as distance between the compared geographical areas expands (Heino et al., 2014, 2017).

The river continuum concept (RCC) (Vannote et al., 1980) suggests that the physical factors, such as width, depth, flow velocity, flow volume, and temperature in a river system represent a continuous gradient changing in a regular manner from the headwater to the river mouth. The longitudinal gradient of the community composition is observed in accordance with the environmental changes. Headwater streams are often shadowed by riparian vegetation, which reduces the autotrophic production. Coarse particulate organic matter of allochthonous origin is a predominant food source and the proportion of shredders and collectors is high in the benthic communities. With increasing of stream size, the importance of allochthonous organic matter reduces, like the shading of the channel. It leads to an increase in primary production including algae attached to hard surfaces and proportion of scrapers feeding on said algae is maximised in midsized rivers. As one moves towards the river mouth, the role of autotrophic organic matter decreases, fine particulate organic matter predominates as a food resource, and collectors become the dominant functional feeding group in invertebrate communities.

In the surveyed streams, elements of the river continuum are observed. The indicator taxa for the subgroup №3B with the highest median depth and channel width, corresponding to the sections of the lower reaches of the River Anyuy and some of its tributaries are represented by a high proportion of collectors. It conforms to the description of benthic communities in large rivers in RCC. Samples of subgroup №3A, taken mainly from small tributaries of the River Anyuy with their indicator taxon *Gammarus koreanus* being predominantly shredder, correspond to headwater streams in RCC. Among the indicator taxa in group №2 (midsized rivers), scrapers are widely represented, which also conforms to RCC. However, in case of the continual longitudinal changes, the similarity of communities at adjacent stations would be higher than in general for the entire river or for the river network. In the surveyed streams, it should be noted that spatially close samples are not always more similar taxonomically than spatially distant ones. For example, many neighbouring samples, collected in the Bajal River channel, are included in different subgroups (№1A and №2A). Subgroup №2B, characterised by the highest internal similarity, includes samples from both river basins. Other groups also include samples from different streams. It is usual for rivers, when the composition of hydrobionts differs less in similar habitats of neighbouring rivers, than in different habitats within the same watercourse (Doisy & Rabeni, 2001; Dallas, 2007b; Costa & Melo, 2008).

Townsend (1989) noted that the river continuum concept is not universally applicable worldwide. Townsend (1989) proposed the concept of patch dynamics, based on the notion of the mosaic nature of the river bottom and the importance of disturbances in the formation of communities. Disturbance refers to any event that results in the removal of organisms from habitats and opens up the possibility for subsequent colonisation, such as flood. The constant process of drifting and colonisation of substrates is called «continuous redistribution of benthos». In the process of recolonisation, the key role is played by patches of the channel, in which organisms can survive during a high disturbance, i.e. refugia (e.g. near the banks and in backwaters in general). The location of refugia patches is random, and in general stochastic processes play a large role in the formation of communities in streams and rivers. Bogatov (1995) proposed a concept combining RCC and patch dynamics. It is noted that, although refugia in the riverbed are located randomly, their number and diversity naturally increase from the headwater to the ritral. At the same time, the diversity of organisms increases, too. Probably, the high biodiversity in ritral, noted in RCC, is explained by the high number of refugia. Indeed, in the surveyed watercourses, the largest number of taxa was noted in the subgroup of samples belonging to the ritral (№2A). It is noted that the continuum is usually quickly restored after disturbances due to organisms recolonising habitats from refugia.

Perry & Schaeffer (1987) indicated the existence of a longitudinal gradient in the composition of communities in rivers, but this gradient is not continuous. It is interrupted by abrupt changes. These changes can be triggered by tributaries, geological discontinuities, or land use factors. Such communities can differ sharply in composition from neighbouring ones. Thus, the distribution of the benthos is characterised as a punctuated gradient. According to the riverine ecosystem synthesis (RES) (Thorp et al., 2006), the distribution of species from the headwater to the mouth reflects the functional process zones (FPZ) to a higher extent than the spatial position along the longitudinal dimension of the rather network. FPZ refers to large hydrogeomorphic patches formed by catchment geomorphology and flow characteristics. Both short-term and long-term variability and predictability of environmental conditions differ among types of hydrogeomorphic patches both within and among rivers. The formation of communities is predominantly influenced by stochastic processes associated with hydraulics (flow velocity, turbulence, and substrate mobility), droughts and floods.

In the explored streams, 50 taxa have been identified as relatively strong significant indicators (IndVal > 20) for the respective communities. This is only a quarter of the totally identified taxonomical richness. Within the selected sample groups, the similarity level is relatively low (from about 4% to about 37%). The high variability of structure is typical for river benthic communities (Merovich & Petty, 2010). The continual distribution has been observed for macroinvertebrate communities in many river systems (Rabeni et al., 2002; Heino et al., 2003, 2014; Tolonen et al., 2016), even in the case of discrete changes in environment conditions (Merovich & Petty, 2010).

Thus, this study revealed the existence of relatively distinct species complexes of hydrobionts corresponding to habitats differing in substrate type and flow velocity. However, the low proportion of indicator taxa for these habitats indicates a mixture of species composition from neighbouring habitats. Organisms respond individually to changes in environmental conditions, resulting in a continuous distribution of macrozoobenthos (Merovich & Petty, 2010). Environmental factors serve as an important ecological filter that allows only species with certain adaptations to exist in habitats (Poff, 1997). In macroscale studies covering several large river systems, a significant proportion of community variability is explained by the river basin factor (Heino et al., 2017).

It should be noted that some elements of the river continuum, in terms of Vannote et al. (1980) concept, exist in surveyed streams. At the same time, abrupt changes between neighbouring communities can be observed as well as a relatively high degree of taxonomical similarity between reaches with similar environmental conditions from different streams. The distribution of macroinvertebrates thereby can be characterised as a punctuated gradient described by Perry & Schaeffer (1987). In spite of patchiness of the river bottom and a high significance of stochastic factors in the formation of stream communities, there is a well-defined pattern in distribution of macroinvertebrates.

Conclusions

Studies carried out in the pristine environment, undisturbed or minimally disturbed by anthropogenic activity, such as the natural reserves, are essential for understanding the natural patterns of ecosystem functioning. This understanding is necessary for a correct assessment of the ecosystem condition during monitoring studies by comparison with reference conditions. Analysis of the distribution of macroinvertebrate communities of two Far Eastern rivers basins on the territories of the Bajal Sanctuary and Anyuy National Park shows that the distribution of organisms does not correspond completely to either continuity or discreteness. Well-defined statistically significant groups of samples based on taxonomical similarity have been discovered as well as environmental factors corresponding to these groups. A complex of indicator taxa has been also determined for each group. Local abiotic factors such as substrate type and water flow velocity strongly influence the formation of species complexes. In addition, the factor of the river basin itself played an important role, as supported by the differences between samples from the Anyuy and the Bajal river basins. However, the obtained groups are characterised by a high internal variability and do not form discrete clusters with obvious hiatus on the ordination diagram. Longitudinal patterns of distributions partly conform to the river continuum concept; however, abrupt changes of taxonomical composition between the neighbouring samples can be noticed. Thus, the longitudinal distribution of macroinvertebrates for each river can be characterised as a punctuated gradient. When planning monitoring studies of aquatic ecosystems based on macrozoobenthos, the variability of hydrobionts communities at different scales must be taken into account.

Acknowledgements

The authors are grateful to the staff of the Joint Directorate of State Natural Reserves and National Parks of Khabarovsk Territory (Russia) for their assistance in organising expeditionary studies. We are grateful to Mikhail V. Chertoprud (Associate Professor of Lomonosow Moscow State University, Russia) and Dmitry M. Palatov (Senior Researcher of the A.N. Severtsov Institute of Ecology and Evolution of the RAS, Russia) for taxonomical identification of the macroinvertebrates from the Anyuy River basin; Irina N. Nikonova (Senior Specialist of the All-Russian Federal Research Institute of Fisheries and Oceanography, Russia) for the photographs; Nikolay A. Aseyev (Researcher of Institute of Higher Nervous Activity and Neurophysiology of RAS, Russia); and Anna M. Evseyeva (Moscow, Russia), Irina N. Nikonova, Ivan S. Reshetov (Tambov, Russia), Matvey V. Roshin (Researcher of Institute of Higher Nervous Activity and Neurophysiology of RAS, Russia) for support within sampling in the Anyuy River basin and Bajal River basin.

Supporting Information

The primary data on the zoobenthos samples and environmental factors (Electronic Supplement. Data on the abundance of zoobenthos organisms in samples and the values of environmental factors) may be found in the **Supporting Information**.

References

Anderson M.J., Gorley R.N., Clarke K.R. 2008. *PERMANOVA+ for PRIMER: Guide to Software and Statistical Methods.* Plymouth: PRIMER-E. 214 p.

Astakhov M.V., Skriptsova A.V. 2020. Potential of utilization of allochthonous invertebrates by *Gammarus koreanus* Uéno (Amphipoda). *Transactions of Papanin Institute for Biology of Inland Waters RAS* 92(25): 28–38. DOI: 10.47021/0320-3557-2021-28-40 [In Russian]

Beisel J.N., Usseglio-Polatera P., Thomas S., Moreteau J.C. 1998. Stream community structure in relation to spatial variation: the influence of mesohabitat characteristics. *Hydrobiologia* 389(1–3): 73–88. DOI: 10.1023/A:1003519429979

Brunke M., Hoffmann A., Puscha M. 2001. Use of Mesohabitat-Specific Relationships Between Flow Velocity And River Discharge to Assess Invertebrate Minimum Flow Requirements. *Regulated Rivers: Research and Management* 17(6): 667–676. DOI: 10.1002/rrr.626

Bogatov V.V. 1995. Combined conception of functioning river ecosystems. *Bulletin of the Far Eastern Branch, Russian Academy of Sciences* 3: 51–61. [In Russian]

Chebanova V.V. 2008. *Benthos of salmon rivers in Kamchatka.* Moscow: VNIRO. 172 p. [In Russian]

Chertoprud M.V. 2021. Main Classes of Rheophilic Macroinvertebrates Communities and Their Regional Variability in Eurasia. *Inland Water Biology* 14(5): 555–572. DOI: 10.1134/S2079086411030017

Chertoprud M.V., Chertoprud E.S., Vorob'eva L.V., Palatov D.M., Tsyganov A.N., Reshetov I.S., Kovacheva N.P. 2020. Macrozoobenthic Communities of the Piedmont and Lowland Watercourses of the Lower Amur Region. *Inland Water Biology* 13(1): 51–61. DOI: 10.1134/S1995082920010046

Clarke K.R., Gorley R.N., Somerfield P.J., Warwick R.M. 2014. *Change in Marine Communities: An Approach to Statistical Analysis and Interpretation, 3rd ed.* Plymouth: PRIMER-E. 262 p.

Clements F.E. 1916. *Plant Succession. An Analysis of the Development of Vegetation*. Washington: Carnegie Institution. 512 p.

Costa S.S., Melo A.S. 2008. Beta diversity in stream macroinvertebrate assemblages: among-site and among-microhabitat components. *Hydrobiologia* 598(1): 131–138. DOI: 10.1007/s10750-007-9145-7

Dallas H.F. 2007a. The effect of biotope-specific sampling for aquatic macroinvertebrates on reference site classification and the identification of environmental predictors in Mpumalanga, South Africa. *African Journal of Aquatic Science* 32(2): 165–173. DOI: 10.2989/AJAS.2007.32.2.8.205

Dallas H.F. 2007b. The influence of biotope availability on macroinvertebrate assemblages in South African rivers: implications for aquatic bioassessment. *Freshwater Biology* 52(2): 370–380. DOI: 10.1111/j.1365-2427.2006.01684.x

Doisy K.E., Rabeni C.F. 2001. Flow conditions, benthic food resources, and invertebrate community composition in a low-gradient stream in Missouri. *Journal of the North American Benthological Society* 20(1): 17–32. DOI: 10.2307/1468185

Glantz S.A. 2012. *Primer of Biostatistics. 7th ed*. McGraw-Hill. 312 p.

Gleason H.A. 1926. The individualistic concept of the plant association. *Bulletin of the Torrey Botanical Club* 53(1): 7–26. DOI: 10.2307/2479933

Grönroos M., Heino J., Siqueira T., Landeiro V.L., Kotanen J., Bini L.M. 2013. Metacommunity structuring in stream networks: roles of dispersal mode, distance type, and regional environmental context. *Ecology and Evolution* 3(13): 4473-4487. DOI: 10.1002/ece3.834

Hammer Ø., Harper D.A.T., Ryan P.D. 2001. PAST: Paleontological Statistics Software Package for Education and Data Analysis. *Palaeontologia Electronica* 4(1): 1–9.

Haritonov A.Yu., Malikova E.I. 1998. Odonata of the Russian Far East: a summary. *Odonatologica* 27(3): 375–381.

Heino J. 2005. Metacommunity patterns of highly diverse stream midges: gradients, chequerboards, and nestedness, or is there only randomness?. *Ecological Entomology* 30(5): 590–599. DOI: 10.1111/j.0307-6946.2005.00728.x

Heino J. 2013a. Does dispersal ability affect the relative importance of environmental control and spatial structuring of littoral macroinvertebrate communities?. *Oecologia* 171(4): 971–980. DOI: 10.1007/s00442-012-2451-4

Heino J. 2013b. Environmental heterogeneity, dispersal mode, and co-occurrence in stream macroinvertebrates. *Ecology and Evolution* 3(2): 344–355. DOI: 10.1002/ece3.470

Heino J., Grönroos M., Soininen J., Virtanen R., Muotka T. 2012. Context dependency and metacommunity structuring in boreal headwater streams. *Oikos* 121(4): 537–544. DOI: 10.1111/j.1600-0706.2011.19715.x

Heino J., Ilmonen J., Paasivirta L. 2014. Continuous variation of macroinvertebrate communities along environmental gradients in northern streams. *Boreal Environment Research* 19(1): 21–38.

Heino J., Muotka T., Mykrä H., Paavola R., Hämäläinen H., Koskenniemi E. 2003. Defining macroinvertebrate assemblage types of headwater streams: implications for bioassessment and conservation. *Ecological Applications* 13(3): 842–852. DOI: 10.1890/1051-0761(2003)013[0842:DMATOH]2.0.CO;2

Heino J., Mykrä H. 2008. Control of stream insect assemblages: roles of spatial configuration and local environmental factors. *Ecological Entomology* 33(5): 614–622. DOI: 10.1111/j.1365-2311.2008.01012.x

Heino J., Soininen J., Alahuhta J., Lappalainen J., Virtanen R. 2017. Metacommunity ecology meets biogeography: effects of geographical region, spatial dynamics and environmental filtering on community structure in aquatic organisms. *Oecologia* 183(1): 121–137. DOI: 10.1007/s00442-016-3750-y

Ipatov V.S., Kirikova L.A. 1997. *Phytocenology*. Saint Petersburg: Saint Petersburg State University. 316 p. [In Russian]

Johnson R.K., Goedkoop W., Sandin L. 2004. Spatial scale and ecological relationships between the macroinvertebrate communities of stony habitats of streams and lakes. *Freshwater Biology* 49(9): 1179–1194. DOI: 10.1111/j.1365-2427.2004.01262.x

Kocharina S.L., Khamenkova E.V. 2003. Structure of the bottom invertebrate communities in the some streams of the Tauj River basin (the Magadan Region). In: *Vladimir Ya. Levanidov's Biennial Memorial Meetings*. Vol. 2. P. 96–106. [In Russian]

Korte T. 2010. Current and substrate preferences of benthic invertebrates in the rivers of the Hindu Kush-Himalayan region as indicators of hydromorphological degradation. *Hydrobiologia* 651(1): 77–91. DOI: 10.1007/s10750-010-0291-y

Kubosova K., Brabec K., Jarkovsky J., Syrovatka V. 2010. Selection of indicative taxa for river habitats: a case study on benthic macroinvertebrates using indicator species analysis and the random forest methods. *Hydrobiologia* 651(1): 101–114. DOI: 10.1007/s10750-010-0280-1

Labay V.S. 2007. Distribution of bentos in the lower ritrale of the River Poronai under the influence of some abiotic environmental factors. *Proceedings of the Sakhalin branch of VNIRO* 9: 184–206. [In Russian]

Labay V.S., Novoselova A.I., Berezova O.N., Sharlay O.B., Shpilko T.S., Nikitin V.D., Prokhorov A.P. 2019. Macrobenthos of the crenal and rithral zones of a typical «salmon» river in northeastern Sakhalin Island (on example of the Dagi River). *Izvestiya TINRO* 196(1): 138–154. DOI: 10.26428/1606-9919-2019-196-138-154 [In Russian]

Legendre P., Legendre L. 2012. *Numerical ecology*. 3rd ed. Amsterdam: Elsevier B.V. 990 p.

Leibold M.A., Holyoak M., Mouquet N., Amarasekare P., Chase J.M., Hoopes M.F., Holt R.D., Shurin J.B., Law R., Tilman D., Loreau M., Gonzalez A. 2004. The metacommunity concept: a framework for multi-scale community ecology. *Ecology Letters* 7(7): 601–613. DOI: 10.1111/j.1461-0248.2004.00608.x

Leley A.S. (Ed). 2006. *Key to the insects of Russian Far East. Vol. 6. Part 4: Diptera and Siphonaptera*. Vladivostok: Dalnauka. 936 p. [In Russian]

Makarchenko E.A., Makarchenko M.A., Zorina O.V., Sergeeva I.V. 2005. Preliminary data on fauna and taxonomy of chironomids (Diptera, Chironomidae) of the Russian Far East. In: *Vladimir Ya. Levanidov's Biennial Memorial Meetings*. Vol. 3. P. 394–420. [In Russian]

Makarchenko E.A., Makarchenko M.A., Zorina O.V., Yavorskaya N.M. 2008. Preliminary data on chironomid fauna (Diptera, Chironomidae) of the Amur river basin. In: *Freshwater ecosystems of the Amur River basin*. Vladivostok: Institute of Biology and Soil Sciences, FEB RAS. P. 189–208. [In Russian]

Merovich G.T., Petty J.T. 2010. Continuous response of benthic macroinvertebrate assemblages to a discrete disturbance gradient: consequences for diagnosing stressors. *Journal of the North American Benthological Society* 29(4): 1241–1257. DOI: 10.1899/09-164.1

Merrit R.W., Cummins K.W., Berg M.B. (Eds.). 2019. *An introduction to the aquatic insects of North America*. Dubuque: Kendall Hunt. 1481 p.

Orel O.V. 2016. Fauna of non-biting midges of subfamily Chironominae (Diptera, Chironomidae) of the Russian Far East. In: *Freshwater Life*. Vol. 2. Vladivostok: Dalnauka. P. 185–196. [In Russian]

Pardo I., Armitage P.D. 1997. Species assemblages as descriptors of mesohabitats. *Hydrobiologia* 344(1–3): 111–128. DOI: 10.1023/A:1002958412237

Perry J.A., Schaeffer D.J. 1987. The longitudinal distribution of riverine benthos: A river dis-continuum?. *Hydrobiologia* 148(3): 257–268. DOI: 10.1007/BF00017528

Poff N.L. 1997. Landscape filters and species traits: towards mechanistic understanding and prediction in stream ecology. *Journal of the North American Benthological Society* 16(2): 391–409. DOI: 10.2307/1468026

Potikha E., Vshivkova T. 2016. The caddisfly faunas (Insecta, Trichoptera) of Protected Natural Areas in southern Far East Russia. *Zoosymposia* 10: 357–383. DOI: 10.11646/zoosymposia.10.1.33

Potikha E.V. 2011. Dynamic of benthos biomass and density in small rivers in the Central Sikhote-Alin. In: *Vladimir Ya. Levanidov's Biennial Memorial Meetings*. Vol. 5. P. 425–446. [In Russian]

Potikha E.V. 2015. A Taxonomic List of the Mayflies, Stoneflies and Caddisflies (Insecta: Ephemeroptera, Plecoptera and Trichoptera) of the Sikhote-Alin Biosphere Reserve. *Achievements in the Life Sciences* 9(1): 22–31. DOI: 10.1016/j.als.2015.05.004

Rabeni C.F., Doisy K.E., Galat D.L. 2002. Testing the biological basis of a stream habitat classification using benthic invertebrates. *Ecological Applications* 12(3): 782–796. DOI: 10.1890/1051-0761(2002)012[0782:TTBBOA]2.0.CO;2

Sandin L. 2003. Benthic macroinvertebrates in Swedish streams: community structure, taxon richness, and environmental relations. *Ecography* 26(3): 269–282. DOI: 10.1034/j.1600-0587.2003.03380.x

Silva D.R.O., Ligeiro R., Hughes R.M., Callisto M. 2014. Visually determined stream mesohabitats influence benthic macroinvertebrate assessments in headwater streams. *Environmental Monitoring and Assessment* 186(9): 5479–5488. DOI: 10.1007/s10661-014-3797-3

Takemon Y. 1997. Management of biodiversity in aquatic ecosystems: dynamic aspects of habitat complexity in stream ecosystems. In: T. Abe, S.A. Levin, M. Higashi (Eds.): *Biodiversity: an ecological perspective*. New York: Springer-Verlag. P. 259–275.

Teslenko V.A. 2009. Stoneflies (Plecoptera) of the Russian Far East: diversity and zoogeography. *Aquatic Insects* 31(1): 693–706. DOI: 10.1080/01650420902812230

Teslenko V.A. 2014. New records of stoneflies (Plecoptera) for the Bureya and Zeya rivers basins. In: *Vladimir Ya. Levanidov's Biennial Memorial Meetings*. Vol. 6. P. 654–659. [In Russian]

Teslenko V.A., Matafonov P.V., Matafonov D.V. 2014. To the stonefly fauna (Insecta, Plecoptera) of Upper Amur River basin (Transbaikalia). In: *Vladimir Ya. Levanidov's Biennial Memorial Meetings*. Vol. 6. P. 660–669. [In Russian]

Teslenko V.A., Zhiltzova L.A. 2009. *Key to the stoneflies (Insecta, Plecoptera) of Russia and adjacent countries. Imagines and nymphs*. Vladivostok: Dalnauka. 382 p. [In Russian]

Thorp J.H., Thoms M.C., Delong M.D. 2006. The riverine ecosystem synthesis: biocomplexity in river networks across space and time. *River Research and Applications* 22(2): 123–147. DOI: 10.1002/rra.901

Tiunova T.M. 2006. Trophic Structure of Invertebrate Communities in Ecosystems of Salmon Rivers in the Southern Far East. *Russian Journal of Ecology* 37(6): 419–425. DOI: 10.1134/S1067413606060099

Tiunova T.M. 2007. Current knowledge of the mayfly fauna (Ephemeroptera) in the Far East of Russia and adjacent territories. *Euroasian Entomological Journal* 6(2): 181–194. [In Russian]

Tiunova T.M. 2008. Composition and the structure of zoobenthos communities of microbiotopes in the metarhithral of small foothill river the temperate-cold-water type. In: *Vladimir Ya. Levanidov's Biennial Memorial Meetings*. Vol. 4. P. 31–45. [In Russian]

Tiunova T.M. 2009. Biodiversity and distribution of mayflies (Ephemeroptera) in the Russian Far East. *Aquatic Insects* 31(1): 671–691. DOI: 10.1080/01650420902800581

Tiunova T.M., Gorovaya E.A. 2011. Mayfly fauna (Insecta, Ephemeroptera) of the Low Amur and its left bank tributaries. In: *Vladimir Ya. Levanidov's Biennial Memorial Meetings*. Vol. 5. P. 522–539. [In Russian]

Tiunova T.M., Korotenko G.A. 2008. Mayflies (Insecta: Ephemeroptera) of northern Sikhote-Alin (the ecology-faunistic review and value in feeding of fishes. *Izvestiya TINRO* 154: 165–188. [In Russian]

Tolonen K.E., Leinonen K., Marttila H., Erkinaro J., Heino J. 2016. Environmental predictability of taxonomic and functional community composition in high-latitude streams. *Freshwater Biology* 62(1): 1–16. DOI: 10.1111/fwb.12832

Townsend C.R. 1989. The patch dynamics concept of stream community ecology. *Journal of the North American Benthological Society* 8(1): 36–50. DOI: 10.2307/1467400

Tsalolikhin S.J. (Ed.). 1997. *Key to freshwater invertebrates of Russia and adjacent lands*. Vol. 3: Arachnids. Lower insects. St. Petersburg: Zoological Institute RAS. 439 p. [In Russian]

Tsalolikhin S.J. (Ed.). 2000. *Key to freshwater invertebrates of Russia and adjacent lands*. Vol. 4: Dipteran insects. St. Petersburg: Nauka. 998 p. [In Russian]

Tsalolikhin S.J. (Ed.). 2001. *Key to freshwater invertebrates of Russia and adjacent lands*. Vol. 5: Higher insects. St. Petersburg: Nauka. 825 p. [In Russian]

Tsalolikhin S.J. (Ed.). 2004. *Key to freshwater invertebrates of Russia and adjacent lands*. Vol. 6: Molluscs. Polychaetes. Nemerteans. St. Petersburg: Nauka. 528 p. [In Russian]

Yavorskaya N.M. 2008. Chironomid larvae (Diptera, Chironomidae) from several rivers of the Amur basin and rivers of the Tatar Strait continental coast. *Izvestiya TINRO* 152: 201–214. [In Russian]

Vannote R.L., Minshall G.W., Cummins K.W., Sedell J.R., Cushing C.E. 1980. The River Continuum Concept. *Canadian Journal of Fisheries and Aquatic Sciences* 37(1): 131–137. DOI: 10.1139/f80-01.

Yavorskaya N.M. 2015. Community structure of benthic invertebrates of the Levaya River (Amur River basin) (Khabarovsk territory). *Amurian Zoological Journal* 7(1): 14–19. [In Russian]

Yavorskaya N.M. 2016. Structure of zoobenthos in the left-bank tributaries of the Lower Amur (Khabarovsk Territory). *Regional Problems* 19(4): 40–45. [In Russian]

Yavorskaya N.M. 2021. Zoobenthos of salmon rivers in the Anyuysky National Park (Khabarovsky Region, Russia). *Amurian Zoological Journal* 13(2): 183–201. DOI: 10.33910/2686-9519-2021-13-2-183-201 [In Russian]

Zasypkina I.A. 2011. Caddisflies (Insecta, Trichoptera) in the north of the Far East of Russia. In: *Vladimir Ya. Levanidov's Biennial Memorial Meetings*. Vol. 5. P. 187–198. [In Russian]

Zasypkina I.A. 2018. An annotated check-list of Stoneflies (Insecta, Plecoptera) of the family Capniidae from the northern part of the Russian Far East. *Euroasian Entomological Journal* 17(2): 92–99. DOI: 10.15298/euroasentj.17.2.03 [In Russian]

ОБЩИЕ ЗАКОНОМЕРНОСТИ РАСПРЕДЕЛЕНИЯ МАКРОЗООБЕНТОСА В БАССЕЙНАХ ДВУХ РЕК ХАБАРОВСКОГО КРАЯ (ДАЛЬНИЙ ВОСТОК РОССИИ)

Л. В. Воробьева[1,*], Е. С. Чертопруд[2]

[1]*Всероссийский научно-исследовательский институт рыбного хозяйства и океанографии, Россия*
**e-mail: vorobjeva.lada@yandex.ru*
[2]*Институт проблем экологии и эволюции имени А.Н. Северцова РАН, Россия*

В данной работе проанализированы закономерности распределения макрозообентоса водотоков в бассейнах рек Баджал и Анюй (Хабаровский край, Россия) на территориях Баджальского заказника и Анюйского национального парка. С помощью процедуры DistLM (distance-based linear models) проведена оценка доли распределения макробеспозвоночных, объясненной учтенными в работе факторами (бассейн, скорость течения, субстрат, ширина русла, температура, pH). Все эти факторы вносили достоверный вклад, суммарно объясняя около трети распределения макробеспозвоночных. Основными объясняющими факторами были водосборный бассейн и субстрат (9.3% и 10.5% соответственно), а также скорость течения (5.7%). На основании кластерного анализа выделены восемь достоверных групп проб по признаку сходства таксономического состава. Выявлены четкие закономерности приуроченности таксономических комплексов к определенным биотопам. Локальные экологические факторы являются сильным фильтром, влияющим на формирование таксономических сообществ. Значимую роль в формировании сообществ играет и фактор принадлежности к бассейну реки, что следует учитывать при планировании мониторинговых исследований крупного пространственного масштаба. Однако выделенные группы и подгруппы характеризуются низким уровнем внутреннего сходства; около четверти общего числа видов относятся к таксонам-индикаторам, пробы не образуют дискретных кластеров на диаграмме ординации. Продольное распределение макробеспозвоночных для каждой реки можно охарактеризовать как прерывистый или «пунктирный» градиент.

Ключевые слова: водоток, Дальний Восток России, пресноводные макробеспозвоночные, сообщество, фактор среды