Acta Biologica Sibirica
Vol 8 (2022): Acta Biologica Sibirica, 521–529
Articles

The role of waterfalls in the structure of macroinvertebrate communities of the Tevenek River (Lake Teletskoye basin, Northeastern Altai)

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Extreme waterfall conditions cause partition of aquatic ecosystems of waterfall streams into discrete zones. To assess the features of aquatic ecosystems that function in waterfall streams, macroinvertebrate communities of the Tevenek River (Lake Teletskoye basin, Northeastern Altai) were examined above and below the waterfall. The diversity, abundance, and biomass of macroinvertebrates were higher above than below the barriers. *Gammarus korbuensis* showed the most significant decrease in number (from 3.1 to 2.3 thousand ind./m2) probably due to the intensive use of amphipods as food for fish living in Lake Teletskoye. An additional factor in favor of the high species richness of macroinvertebrates in the upper reaches is the geomorphology of the waterfall river valley that contributes to the formation of more diverse conditions above the waterfalls. Hydrobiological studies of waterfall streams can help to understand the restructuring of benthic communities divided as a result of the human impact.

Acta Biologica Sibirica 8: 521–529 (2022)

doi: 10.14258/abs.v8.e32

http://journal.asu.ru

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Academic editor: A. Matsyura | Received 24 August 2022 | Accepted 14 September 2022 | Published 11 November 2022

http://zoobank.org/CFAC16D2-A217-4564-90F5-1400C2B68902

Citation: Yanygina LV, Shipunov PA (2022) The role of waterfalls in the structure of macroinvertebrate communities of the Tevenek River (Lake Teletskoye basin, Northeastern Altai). Acta Biologica Sibirica 8: 521–529. https://doi.org/10.14258/abs.v8.e32

Keywords

Taxonomic diversity, macroinvertebrates, disconnectivity, natural barrier, river, waterfall

Introduction

Today, anthropogenic factors have an apparent influence on the structures and functions of many ecosystems, including those of freshwater strongly affected by multiple disturbances (Li et al. 2019). In this regard, among the challenging ecological tasks is the identification of the drivers of the dynamics of aquatic ecosystems and development of methods for their assessment. Modern approaches for assessing the ecological state of rivers are largely based on the Reference Condition Approach (RCA), according to which "health" of any ecosystem is determined by the degree of deviation of its characteristics from those specific for the natural undisturbed state (Bowman and Somers 2005; Bailey et al. 2014). This approach is the basis for environmental monitoring of water bodies in Europe, the USA, Canada, Australia, and many other countries (Stoddard et al. 2016). However, the use of modern approaches is impossible without understanding the patterns of changes in various characteristics of diverse undisturbed ecosystems influenced by natural factors.

Despite growing interest in river ecology and numerous studies of diverse river ecosystems, little attention is still paid to streams with waterfalls (Baker et al. 2017). The reason for poor knowledge of these ecosystems is that in the above waterfall regions it is difficult to access (Rackemann 2012; Clayton and Pearson 2016) and a small proportion of such streams in the river net. High waterfalls hinder the migration of large predators (primarily fish) upstream, thus creating more favorable habitats for invertebrates in the upper reaches, as well as maintaining the continuity of substances and energy flow downstream. Further study of such disconnected rivers may be very useful to understand the peculiarities of the restructuring of benthic communities separated as a result of anthropogenic activity.

Since rapid flow and turbulence of mountain streams cause poor plankton development, the use of macroinvertebrate communities as indicators of the ecological state of rivers becomes a priority. The purpose of this work is to assess the role of waterfalls in the structure of macroinvertebrate communities of the Tevenek River (Teletskoye Lake basin, Northeastern Altai). The main hypothesis is that waterfalls limit fish migration upstream, resulting in the appearance of macroinvertebrate communities with higher density in the river sections above waterfalls.

Material and methods

The material for this work was collected in the Tevenek River, a tributary of Lake Teletskoye (Northeastern Altai). The Tevenek is a small river. Its length is 12 km, the average water discharge is 0.5 m3/s, the total catchment area is 24 km2. The river flows from the taiga marshes and in the upper reaches it runs through a shallow valley composed of loose rocks. In the middle course, the river flows through a deep rocky gorge, in some sites with sharp bottom gradients forming a cascade of waterfalls, the highest of which reaches 5 meters. In the low reaches, the channel slopes decrease, and at the mouth the river forms several shallow channels with a sandy pebble bottom and a low flow velocity (Resources 1966). In the middle reaches, the riverbed is mainly composed of large boulders, in the upper and lower ones – of pebbles. The river banks in the upper and lower reaches are flat and covered with mixed forest, while in the middle reaches they are steep and rocky.

To collect bottom macroinvertebrates at each site (above and below waterfalls), 10 replicate samples were taken with a Surber sampler (0.2x0.2 m frame). Multihabitat sampling was carried out at each sampling site to represent different microhabitats equally. Zoobenthos samples were washed through a nylon net with a mesh size of 350x350 microns. The macroinvertebrates were picked out of each sample and fixed with 70% ethyl alcohol. In the laboratory, all species were identified at the species level if it was possible, except for Oligochaeta, Simuliidae, and Chironomidae, not identified in more detail. In total, more than 4,500 macroinvertebrate specimens were collected and identified.

When assessing the frequency of occurrence, we used the following scale: the most common species - those met in more than 50% of samples, frequently occurring – 20–50%, infrequently occurring – 1–20%, rarely occurring – less than 1% (Bakanov 1987). To estimate the β diversity for each site (above and below the waterfalls), Whittaker's species turnover index was calculated ($\beta W = (\gamma - \alpha)/\alpha$, where γ is the total number of species at the site, α is the average number of species for the same site). Discriminant analysis was performed to reveal differences in taxonomic structure between sites above (N 51.83312°; E 87.36499 ° DD) and below (N 51.79165°; E 87.32191°DD) waterfall. The non-parametric Mann-Whitney U test was used to assess the statistical significance of differences between samples considered significant at $p < 0.05$. Data analysis was performed with Statistica 6.0.

Results

The research allowed to identify 41 species of macroinvertebrates found in the Tevenek River, among which 16 species were of the order Ephemeroptera, 6 species of the order Plecoptera and 8 species – of the order Trichoptera. About 40% of the species (17 species) were marked once and classified as rare for this region. Interestingly, the number of rare species in the upper (9 species) and lower (8 species) sections of the river differed insignificantly. Macroinvertebrate communities above waterfalls were represented by 31 species, while below were only 22. The average number of species in each sample taken from above and below waterfalls made up 12.0±1.3 and 8.9±1.1, respectively (Fig. 1). The Shannon species diversity index both above and below the waterfalls varied widely (0.4–2.8 bits/ind.) and did not differ significantly at different sites (Mann-Whitney test, $p=0.97$).

Above and below-waterfall sites, macroinvertebrate communities were similar by the most frequently encountered species, among which *Gammarus korbuensis*, *Rhyacophila sibirica* and *Oulimnius* sp. dominated. Significant differences in the occurrence of mayflies of the genera *Baetis* (90% above and 10% below waterfalls) and *Ameletus* (40% and 10%, respectively), dipteran *Hexatoma* (60% and 10%) and caddisflies *Lepidostoma* (50% and 10%) were recorded. Some species frequently noted above waterfalls (*Isoperla*, *Taeniopteryx*, *Dicranota*, *Planaria*, and *Simuliidae*) were not observed in low river sections. Differences in the occurrence of common species, as well as a high proportion of rare species in the community structure, provided low similarity in the species composition of macroinvertebrates in the study areas. Despite the similarity of the main abiotic factors (shading of both sections of the river with forest, rocky bottom, similar hydrochemical indicators (Table 1), the Jacquard similarity coefficient appeared to be only 32.5%. Discriminant analysis showed a significant difference in macroinvertebrate structure above and below waterfalls (Wilks' $\lambda=0.14$, $F=7.04$ $p<0.0026$). Differences in relative numbers of *Antocha vitripennis*, *Ecdyonurus joernensis*, *Epeorus pellucidus*, *Hexatoma bicolor*, *Planaria* sp., and *Rhodobaetis* sp. made the greatest contribution to the differences between the sites.

Analysis of Whittaker's species turnover indices demonstrated a higher β-diversity of macroinvertebrate communities in the upper reaches (1.75) than in the low sections (1.46). Not only the species richness, but also the invertebrate density tended to decrease at sites below waterfalls. Above waterfalls, the average number of macroinvertebrates was 7.4± 1.2, while below – only 4.3± 0.8 thousand ind. /m2. In low sections, the decrease in number was mainly due to the reduced density of amphipods *Gammarus korbuensis* (from 3.2± 0.4 to 2.3± 0.7 thousand ind./m2). The number of *Oulimnius* sp. beetles decreased from 1.2±0.3 to 0.56±0.2 thousand ind./m2 and oligochaetes – from 0.9± 0.3 to 0.3± 0.1 thousand ind./m2.

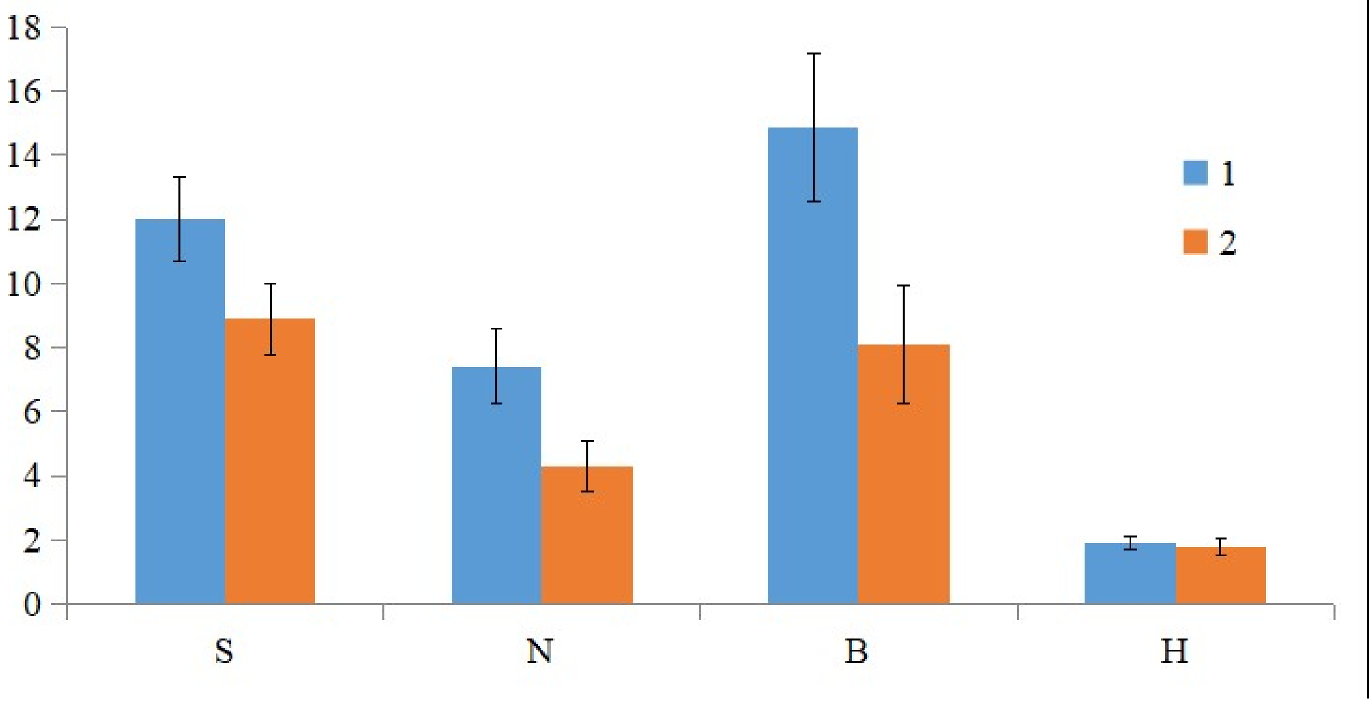

Figure 1. *Structural characteristics of the benthic communities of Tevenek River above (1) and below (2) waterfalls (S – the average number of species in a sample, abundance, thousand ind./m2, B – biomass, g/m2, H – the Shannon species diversity index (bits/ind.).*

Parameter	Above waterfalls	Below waterfalls
Depth, m	0.261	0.143
Temperature, C	14.89	13.39
Electrical conductivity, mcm/cm	93.9	84
Mineralization, g/l	0.076	0.07
pH	7.81	7.65
ORP, mV	189	187
Chlorophyll, mcg/l	6.9	4.6
Oxygen saturation, %	95.6	93.6
Oxygen, mg/l	9.66	9.78
Blue-green algae, cl/m	1498	1376

Table 1. *Environmental characteristics of sampling sites*

Compared to the upper reaches, the most substantial changes in macroinvertebrate structure in the lower ones were manifested in lowered total biomass of zoobenthos (Mann-Whitney test, $p=0.028$). The average biomass of zoobenthos above waterfalls reached 14.9±2.3, whereas below – only 8.1±1.8 g/m2. The decrease in biomass was caused not only by a reduction in the number of macroinvertebrates, but also by a lower average weight of individuals in most microhabitats.

The trophic structure of macroinvertebrate communities above and below waterfalls was generally similar (Fig. 2). The increase in the proportion of gatherers identified above was associated with a greater proportion of oligochaetes in the community structure.

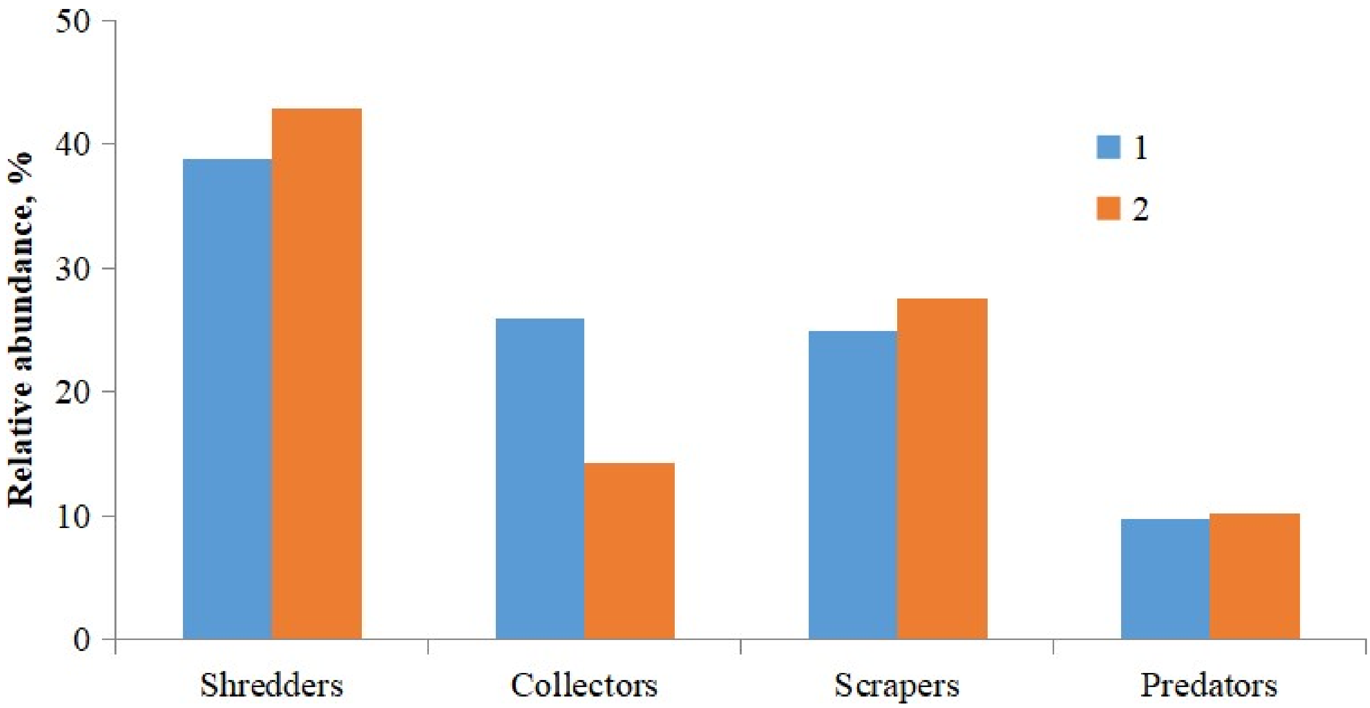

Figure 2. *Trophic structure of macroinvertebrate communities from Tevenek River (1 – above the waterfalls, 2 – below the waterfalls).*

Discussion

Waterfalls create barriers for animal migration upstream, which contributes to fragmentation of species ranges. In studies of the role in spatial distribution of animals, the greatest attention is traditionally paid to fish. These studies suggest that most fish species cannot even overcome a half-meter river threshold, but salmon are able to jump over rifts and waterfalls up to three meters (Fitzsimons and McRae 2007). Higher barriers become an insurmountable obstacle for most fish and create fishless areas in the upper reaches of waterfall streams, thus being favorable for macroinvertebrate communities, for which fish are large active predators. Above waterfalls, the absence of fish is considered one of the main reasons for higher density of macroinvertebrates compared to below-waterfall pools (Baker et al. 2017). The most essential differences in density are observed for large and actively swimming species due to selective feeding of intensively hunting fish. In the Tevenek River, the number of macroinvertebrates above the waterfalls was 1.5 times higher than below. The number of amphipod shrimp *Gammarus korbuensis*, the main food component of benthic fish from Lake Teletskoye, decreased most significantly (Holomuzki and Hoyle 1990). This suggests that fish macroinvertebrate eating plays the leading role in species number above and below waterfalls. Some studies conducted in various regions (March et al. 2002; Covich et al. 2009; Baker et al. 2017) are evidence of more active eating of large fast-swimming macroinvertebrates (especially shrimps) below waterfalls. Differences in zoobenthos biomass above and below barriers allow us to roughly estimate the fish diet in the mouth of the Tevenek River that is useful for elaboration of recommendations on the rational use of fish resources of Lake Teletskoye. The use of river estuaries by fish for feeding leads to a reduction in macroinvertebrate density (especially their biomass) because of overeating (Blaber and Whitfield 1977). However, in the low reaches of the river, reduction was observed in abundance and biomass as well as in species richness of communities. A higher species richness of macroinvertebrates above waterfalls was also mentioned in the study of the Morato River, southern Brazil (Jonck and Aranha 2010). However, in other studies, similar dependence was not found at all (Baker et al. 2017). Therefore, more research is required to understand the characteristics of the formation of the bottom community above and below waterfalls as well as the influence of spatial and environmental factors on macroinvertebrates in different sections of the waterfall rivers. Among factors of the homogenization of taxonomic composition of macroinvertebrates is their drift downstream, which contributes to species replenishment of the pool in low river sections and increases the similarity of taxonomic composition above and below waterfalls. The drift in the Tevenek river was passive and active. The number of drifting organisms reached 46 ind / m3 (Rudneva 1995).

Despite this, the similarity in the species composition of macroinvertebrates from two sites turned out to be low (the Jacquard coefficient of 32.5%). When comparing pools separated by waterfalls on the Morato River, the similarity coefficient (36.5%) was also low (Jonck and Aranha 2010). This indicates a gap in the biological connectivity of discrete zones of waterfall rivers.

Waterfalls prevent upstream migration as fish as macroinvertebrates that may cause fauna depletion in the upper reaches. This barrier is particularly essential for homotopic hydrobionts (Jonck and Aranha 2010; Baker et al. 2017). Amphibiotic insects are able to colonize areas above waterfalls during the imaginal phase. Hence, waterfalls are not significant limiting barriers to their spread. The differences in the composition of macroinvertebrate communities on the Tevenek River above and below waterfalls were mainly due to rare amphibiotic insect species, and therefore physical barriers are highly unlikely to be the main drivers of such differences.

Differences in the species richness of Tevenek macroinvertebrates above and below waterfalls are likely induced by differences in habitat conditions associated with the geomorphological features of waterfall streams. Waterfalls limit the rate of base-level lowering, which leads to the formation of more gentle valleys and more stable hydrological conditions above waterfalls (May et al. 2017). This contributes to the retention in the channel and prevents catastrophic flood-induced drifts, thus forming spatially more diverse and more stable habitats. The Whittaker's species turnover index increases with growing differences in the community structure and generally reflects the diversity of habitat conditions at the study sites (Koleff et al. 2003, Tuomisto 2010). In the Tevenek River, with similar values of α-diversity, the indicators of β and γ-diversity are higher above waterfalls, supporting the assumption of a greater heterogeneity of habitat conditions there. At the same time, the falls in the channel practically did not affect the trophic structure of the benthic communities. The high level of river shading by a forest canopy along with a rapid flow predetermine poor phytoperiphyton in both river sections, resulting in a low proportion of scrapers in the bottom community structure. At the same time, deciduous forest along riverbanks are the source of a constant supply of detritus into the channel that contributes to the formation of a high proportion of shredders at both in sites above and below waterfalls.

Conclusion

Thus, waterfalls are essential in fragmenting benthic communities. Despite current-induced drift from the upper sections of the river and limited movement of organisms upstream, macroinvertebrates with greater diversity and density appear mostly not below but above waterfalls. Due to migration obstructions by large predators (primarily fish) and hydromorphological features of waterfall rivers, more favorable conditions for macroinvertebrate habitat are created in sites above waterfalls. This makes it possible to consider the upper sections of waterfall rivers as priority areas for biodiversity conservation.

Acknowledgements

The research was supported by RSF (project No. 22-24-00757).

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