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ZOOPLANKTON, ZOOBENTHOS, AND ZOOPERIPHYTON

Distribution of Amphibiotic Insects of Different Trophic Groups in Mountainous and Steppe Rivers of Western Tuva

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Abstract—The distribution of preimaginal stages of amphibiotic insects (mayflies, stoneflies, caddisflies, and black flies) in the running waters of the mountain-steppe landscapes of western Tuva has been investigated. The basin of the Hemchik River is 500–2200 meters above sea level. The taxonomic composition and spatial distribution are determined; high-mountain, middle-mountain and low-mountain plain types of communities are detailed. The trophic structure of amphibiotic communities is analyzed along the ecological profiles from the upper to the lower reaches of the rivers.

Key words: amphibiotic insects, taxonomic and trophic structures, spatial distribution, mountains and steppe, rivers of Western Tuva.

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INTRODUCTION

Tuva is located on the northern boundary of Central Asia. This region includes tundra, tundra–taiga, and steppe arid biocenoses, which allows a comparison of the diversity and structure of taxocenes in the gradient of environmental factors. Amphibiotic insects are widespread due to their different adaptations at preimaginal stages of development. In running waters they constitute >50% of the population, sometimes reaching 99% of the total biomass and density [6, 7]. In hydrocenoses they are considered macrozoobenthos, which includes mayflies, caddisflies, stoneflies, and two-winged flies. The authors studied black flies (Diptera and Simuliidae) as typical dwellers of running waters. In watercourses, amphibionts adapt to existence on different substrates: periphyton, stony, and soft grounds. The surface of stones is inhabited mainly by mixed periphytic and benthic communities [19]. Mayflies and stoneflies have a smooth flat oblong body and move actively on the substrate surface in search of food and refuge for their existence. Caddisflies and black flies are less mobile and have an apparatus for fixating onto the substrate surface. Except for this apparatus for fixation, different groups of insects are characterized by different feeding modes reflecting the diversity of hydrocenoses components.

The faunistic composition of aquatic animals in riverine and lacustrine systems has been studied in most of the territory of Tuva and in some regions of Mongolia [1, 3–5, 11, 12, 14, 16]. However the western part of Tuva has been insufficiently studied. The Khemchik River Basin is contiguous with southeastern Altai, Western Sayan, and the Great Lakes Depression in Central Asia, which allows us to compare the fauna of adjacent territories and find the distribution patterns of taxa in the mountains of southern Siberia.

The aim of the work is to study the taxonomical composition and spatial distribution of amphibiotic insects in streams of the Khemchik River Basin and analyze the structure of the macrozoobenthos communities.

MATERIALS AND METHODS

The samples were collected in the Khemchik River Basin and in the upper part of the Sayano-Shushinskoye reservoir located in the Ulug-Khem River Basin (Upper Yenisei). A total of 15 watercourses were studied (Fig. 1). Samples were collected in ecological profiles of the landscape from the upper to the lower reaches of the rivers. A 10-m portion of the river was investigated at each site, ≥5 samples were collected, and the data were averaged. Amphibiotic insects at the preimaginal stages were collected manually and with a hydrobiological net.

Insects were identified by species according to the modern keys [2, 4, 5, 17, 22]. Amphibiontic communities were classified by their location in zonal hydrological subdivisions of the longitudinal profile of the

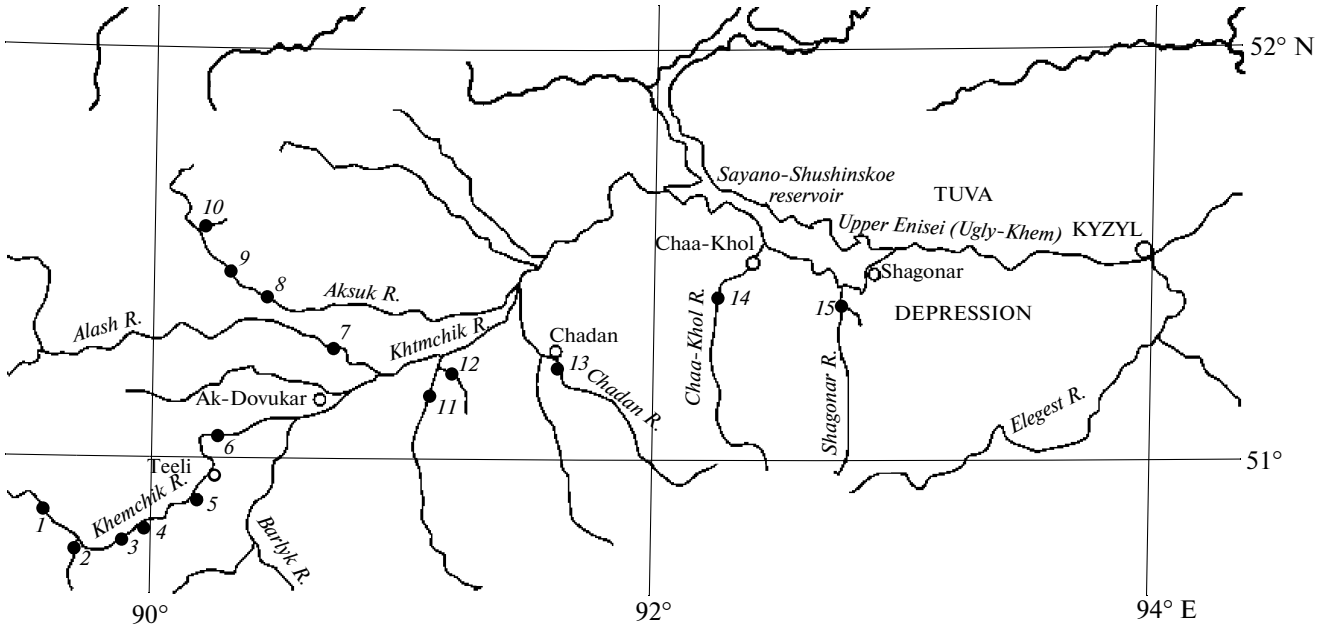

Fig. 1. Sites of sampling: (*1*) Khemchik River upstream the Chinge-Khem River inflow, (*2*) the Chinge River, (*3*) Khemchik River upstream the settlement of Bai-Tal, (*4*) canal of the Khemchik River near the settlement of Bai-Tal, (*5*) soil-reclamation canal upstream the settlement of Teeli, (*6*) Khemchik River between the settlements of Teeli and Ak-Dovukar, (*7*) the Alash River, (*8*) the Aksuk River (middle course), (*9*) upper reach of the Aksuk River, (*10*) nameless stream (a tributary of the Aksuk River), (*11*) the Chyrgaky River, (*12*) the Shemi River, (*13*) the Chadan River, (*14*) the Chaa-Khol River, and (*15*) the confluence of the Torgalyk and Shagonar Rivers.

rivers according to Illies and Botosaneanu [28]. The distribution of communities was analyzed using indices of abiotic and biotic factors: the altitude of the locality above sea level, water temperature, current velocity, granulometric composition of the ground, electrical conductivity of water, and substrate fouling. Parameters of temperature, pH, and total water mineralization estimated by an integrated index of electrical conductivity [25] were registered with the help of an Anion 7051 portable analyzer produced by Infraspak-Analit (Novosibirsk). For a proper comparison of the results and to obtain true values of the measured parameters, the regime of automatic temperature compensation with a recalculation to 25°C was used. The ground composition was determined using the following size characteristics: >50-cm boulders; 20–50-cm stones; 5–20 cm large gravel, 0.2–5-cm small gravel, and <0.2 cm sand, silt, and clay.

RESULTS

In the Khemchik River Basin, 25 species of mayflies (Ephemeroptera), 6 stoneflies (Plecoptera), 11 caddisflies (Trichoptera), 24 black flies (Diptera, Simuliidae)—a total of 66 species—have been registered.

The insects under study at their preimaginal stages were found in all investigated watercourses located in different altitude and vegetative zones. Landscape and biotopic characteristics of the streams are presented in Table 1. The streams in the Khemchik River Basin

Table 1. Landscape–biotopic characteristics of western Tuva watercourses

Region of studies	Vegetative zone	Altitude above sea level, m	Water temperature, °C	Water electroconductivity, μCm/cm	Hydrobiological zone
Upper reach of the Khemchik River	Tundra	>1900	7–9	10–20	Epirhithral
	Taiga	1300–1900	8–10	30–120	Epirhitral
	Taiga	900–1300	10–12	50–70	Metarhithral
	Mountain steppe	900–1200	10–14	50–100	Metarhithral
Middle course of the Khemchik River	Steppe	500–900	11–14	300–350	Metarhithral
Upper reach of the Ulug-Khem River	Steppe	500–600	13–18	200–400	Metarhithral, hyporhithral

belong to the rhithral with distinctly expressed epi- and metarhithral zones, and streams with hyporhithral features are located in the lower reach of the profile on flat low mountainous parts and well-warmed elements of relief, but their boundaries are not well-expressed [13].

The taxonomical composition, with a relative abundance and distribution of the studied groups of amphibiotic insects along ecological profiles, are presented in Table 2. Mayflies are represented well in the taiga epirhithral of the upper reaches of the Khemchik River and the steppe metarhithral with elements of hyporhithral in the upper reach of the Ulug-Khem River, which corresponds to 48 and 36% of the total number of species found. The taiga and steppe taxocenes of mayflies differ by their total number of species, amounting to 17 and 14, correspondingly. Differences are also manifested at the level of background species. Thus, in the mountainous taiga streams, *Epeorus maculates*, *Rhithrogena cava*, *Baetis pseudotermicus*, and *Ephemerella lepnevae* were numerous. Significant changes in biotopic conditions lead to a reorganization of the taxocenes structure in portions of the rivers running through low mountainous steppe parts. *Epeorus maculates* and *Ephemerella lepnevae*, which are numerous on stone soils in the upper reaches of the profile, disappear, and *Epeorus pellucidus* and *Ephemerella nuda* appear. In spite of differences in the taxonomical composition of mayflies in the studied biotopes, species occurring both in the taiga and steppe parts of the profile were found (altogether in 4–5 biotopes), including *Rhithrogena cava* and *Baetis pseudotermicus*.

A comparison of the taxonomical composition of mayflies in the Khemchik River Basin with those of adjacent territories has revealed a large faunistic similarity with those in the Tuva Depression (60%) and Mongolia (52%) and the least similarity was found to be with those from the Todzha Depression (35%).

Stoneflies are not numerous and occur occasionally, which is explained by an early emergence of imago and the absence of the larvae of most species in the period of sampling. The species composition of stone flies in the mountainous-taiga and steppe streams differs greatly. *Triznaka longidentata* it is more frequent in the upper reaches of the rivers.

The diversity of caddisflies in the Khemchik River Basin is low. Three species were registered in the taiga epirhithral and mountaineous-steppe metarhithral. Their number increased to 8 in the upper reach of the Ulug-Khem River. The species *Brachicentrus americanus* and *Apatania crymophila* belong to background species and were registered in 4–5 biotopes differing by many biotopic indices. In the plain–steppe, taxocenes of caddisflies *Rhyacophila sibirica*, *Glossoma intermedium*, and *Halesus tesselatus* were marked in the rank of common species. The similarity between the species composition of caddisflies in the Khemchik River and those of the adjacent territories is less expressed than of mayflies and is 38% with Mongolia, 33% with the Tuva Depression, and 17% with the Todzha Depression.

Black flies are comparable with mayflies in regard to the number of taxa. The basis of the fauna is formed by the species belonging to the genera *Cnetha*, *Gnus*, and *Simulium*. They comprise 46% of the species known in western Tuva. As for the distribution along the landscape–ecological profile, a gradual increase in the number of black flies is registered from the tundra and taiga to steppe streams (from 4 to 13 species, correspondingly). At the same time, the differences in the composition and structure of black-fly taxocenes were traced in some biotopes of the profile. Simultaneously, the species inhabiting several types of biotopes were registered. Thus, on the whole, the tundra and taiga streams in the upper basin of the Khemchik River are similar in their compositions of black flies. This similarity is manifested in the presence of *Helodon alpestris* being an absolutely dominant species in mountainous areas. Streams in the middle mountainous part of the Khemchik River, which is a taiga and mountain-steppe metarhithral, have similar amounts of the species of the genus *Gnus* (*G. corbis*, *G. decimatum*, and *G. albipes*) and differ in the structure of taxocenes. In the taiga part, black flies *Gnus albipes* dominate; in the mountain-steppe part, *Archesimulium vulgare* dominate. At the same time, the whole slope–transitory part of the profile is a continuum for the habitation of black flies *Helodon alpestris*, *Gnus corbis*, *G. decimatum*, *Metacnephia crassifistula*, and *Archesimulium vulgare*. The middle course of the Khemchik River has a well-expressed steppe character. Accumulative processes occur in streams, resulting in the appearance of species adapting to such conditions and replacing dominant species (*Simulium reptans* and *S. promorsitans*). The upper course of the Ulug-Khem River, which is considered the upper zone of the Sayano-Shushenskoye reservoir, is characterized by a total reorganization in the structure of black-fly communities. *Cnetha pugetensis* and *Tetisimulium alajense* were dominant species there.

A comparison of the taxonomical composition of black flies in the Khemchik River Basin and adjacent territories testifies to their large similarity: 75% with the fauna of black flies in the Ubsunur Depression (the territory of Tuva), 64% with those in the Tuva Depression, 54% with those in southeastern Altai (basins of the Chuya and Bashkaus rivers), and 44% with those in Western Sayan (the Abakan River Basin). A lower similarity was found with the fauna of the Todzha Depression and Mongolia (32 and 38%, correspondingly).

The existence of watercourses determines biotopic relations between different groups and species of aquatic organisms. Certain trophic relations characterizing a functional component of hydrocenosis are established [8, 23]. In the course of studies of the rheophilous complex of amphibiotic insects in the Khemchik River Basin, a primary analysis of the trophic structure was

Table 2. Taxonomica composition and trophic characteristic of amphibiontic insects in western Tuva watercourses

Species	Khemchik River					Ulug-Khem River	Trophic characteristic
	Upper reach				Middle course	Upper reach	
	I	II	III	IV	V	VI	
Mayflies (Ephemeroptera)							
Epeorus aesculatus Iman. (?)	–	–	1	–	–	–	Collectors
E. Maculates Tsh. (?)	1	3	–	–	–	–	Scrapers
E. (*Belovius*) *pellucidus* Brod.	–	–	–	–	1	1	Collectors
E. sp.	–	1	–	–	–	–	Collectors
Rhithrogena (*Cinygmula*) *cava* Ulmur	–	3	1	1	1	2	Scrapers
R. (*C.*) *grandifolia* Tsh. (?)	1	–	–	–	1	1	Collectors
R. (*C.*) *hirasana* Iman. (?)	–	–	1	–	–	1	Collectors
R. (*C.*) *kurensis* (Bajk.)	–	–	–	–	1	–	Collectors
R. (*C.*) *putoranica* Kluge	–	1	–	–	–	–	Collectors
R. sibirica Brod.	–	1	–	–	–	–	Collectors
Amaletus inopinatus Eatn.	–	1	–	1	1	–	Collectors
Baetis (*Acentrella*) *bicaudatus* Dod.	–	1	–	–	–	–	Collectors
B. (*A.*) gr. *lapponicus*	1	–	1	–	–	–	Collectors
B. (*A.*) *sibiricus* Kazl.	–	1	–	–	–	–	Collectors
B (*A.*) sp.	–	–	–	1	–	1	Collectors
B. fuscatus L.	–	–	–	–	1	–	Collectors
B. oreophilus Kluge	–	2	–	–	–	–	Collectors
B. pseudothermicus Kluge	–	3	1	–	2	2	Collectors
Ephemerella (*Ephemerella*) *aurivillii* Beng.	1	–	1	–	–	1	Collectors
E. (*Ephemerella*) *kozhovi* Bajak	–	1	–	–	1	–	Collectors
E. (*E.*) *mucronata* Bgtn. (?)	1	–	–	–	–	–	Collectors
E. (*Torlea*) *nuda* Tsh.	–	–	–	–	–	3	Collectors
E. (*T.*) *ignata* Poda	–	–	–	1	–	–	Collectors
E. (*D.*) *lepnevae* Tsh.	–	3	–	–	–	–	Collectors
E. (*Drunella*) *triacantha* Tsh.	–	–	1	1	–	1	Predators
Stone flies (Plecoptera)							
Arcynopteryx altaica Zap.-Dulk.	1	–	1	–	–	–	Predators
Diura sp.	–	1	–	–	–	–	Predators
Triznaka longidentata Rauser	–	1	–	–	–	–	Predators
Amphinemura borealis Mart.	–	–	–	–	1	–	Shredders
Pictetiella asiatica Zw. et Lev.	–	–	–	–	1	1	Predators
P. (?) sp.	–	1	–	–	1	–	Predators
Caddisflies (Trichoptera)							
Rhyacophila egijnica Schm.	–	–	–	–	–	1	Predators
R. sibirica Mcl.	–	–	–	–	2	2	Predators
*Brachicentrus americanu*s Banks	–	2	1	2	1	1	Filterers
Apatania crymophila Mcl.	–	1	1	2	1	1	Scrapers
Asynarchus lapponicus Zett.	–	–	–	–	–	1	Filterers
Ecclisomyia digitata Mart.	1	–	–	–	–	–	Filterers
Glossoma altaica Mart.	–	–	–	–	–	1	Filterers

Table 2. (Contd.)

Species	Khemchik River					Ulug-Khem River	Trophic characteristic
	Upper reach				Middle course	Upper reach	
	I	II	III	IV	V	VI	
G. intermedium Klap.	–	–	–	–	–	2	Scrapers
Goera sp.	–	–	–	1	–	–	Scrapers
Halesus tesselatus Ramb	–	–	–	–	–	2	Scrapers
Mystrophora sp.	–	1	–	–	–	–	Scrapers
Black flies (Diptera)							
Prosimulium hirtipes (Fries)	1	–	–	–	–	–	Filterers
P. pecticrassum Rubz.	1	1	1	–	–	–	Filterers
Helodon alpestris (Dor., Rubz. et Vlas.)	3	2	1	–	–	–	Filterers
Metacnephia crassifistula (Rubz.)	1	1	1	–	–	–	Filterers
M. edwardsiana (Rubz.)	1	–	1	–	–	–	Filterers
M. kirjanovae (Rubz.)	1	1	–	–	–	2	Filterers
Cnetha bicornis (Dor., Rubz. et Vlas.)	–	–	–	1	1	2	Filterers
C. cornifera Yank.	–	1	–	1	–	–	Filterers
C. curvans (Rubz. et Carls.)	–	–	–	–	1	–	Filterers
C. pugetensis (Dyar et Shan.)	–	–	–	–	–	3	Filterers
C. verna (Macq.)	–	–	–	1	1	1	Filterers
Gnus acrotrichum (Rubz.)	–	–	–	–	2	1	Filterers
G. albipes Rubz.	–	–	3	2	2	2	Filterers
G. corbis (Twinn)	1	3	2	2	2	–	Filterers
G. decimatum (Dor., Rubz. et Vlas.)	–	2	1	1	2	1	Filterers
G. saccatum Rubz.	–	–	–	–	1	–	Filterers
Tetisimulium alajense (Rubz.)	–	–	–	2	2	3	Filterers
T. latimentum (Rubz.)	–	–	–	2	1	1	Filterers
Odagmia ornata (Mg.)	–	–	–	–	1	2	Filterers
Archesimulium vulgare (Dor., Rubz. et Vlas.)	1	1	2	3	1	2	Filterers
Simulium aemulum Rubz.	–	–	–	–	–	1	Filterers
S. flavidum (Rubz.)	–	–	1	1	2	–	Filterers
S. reptans (L.)	–	–	–	–	3	–	Filterers
S. promorsitans Rubz.	–	–	–	2	3	–	Filterers

Note: (I) tudra, epirhithral, (II) taiga, epirhithral, (III) taiga, metarhithral, (IV) mountain steppe, metarhithral, (V) steppe, metarhithral, (VI) steppe, metarhithral-hyporhithral; (1) solitary (<1.3% in the dominance structure), (2) common (1.3–12.4%), (3) numerous (>12.5%); "?" identification was made according to juvenile larvae that did not allow us to identify the species reliably.

conducted with due regard for general information on the trophity of some amphibiotic species.

The trophic specialization predetermines many morphological adaptations and the species position in the ecosystem: its ecomorph and a living form. In the considered case, the types of living forms depend on the current velocity and the presence of stony ground [18].

In the studied watercourses, the larvae of mayflies form a large part of the rheophilic population: 84% of the total abundance of amphibionts. Predatory mayflies are represented by one species (*Ephemerella (Drunella) triacantha* Tsh). The base of the population is formed by the larvae of mayflies algophages-scrapers (*Epeorus maculates* and *Rhithrogena cava*), which consume only diatom algae prevailing in periphyton of mountainous and premountainous watercourses [10]. The share of species with a combined feeding mode (*Baetis pseudothermicus*, *B. oreophilus*, *B. sibiricus* and

Ephemerella nuda) is also notable. Their diet consists of detritus and diatom and filamentous algae.

Nymphs of stone flies comprise 10% of the total abundance. Their predatory and secluded way of life predetermined morphological types subdivided by N.F. Sinichenkova [18] into 10 living forms. In the Tuva watercourses, only predatory litophilic cryptobionts (5 species) and phytosapro-phytophilic cryptobiont (1 species) were registered.

Larvae of caddis flies are not numerous, they share only 3% of the rheophilic benthos. They are considered as highly ecologically differentiated amphibionts using a large trophic base for feeding [9]. In watercourses of the Khemchik River Basin both predatory species (*Brachicentrus americanus* and *Rhyacophila sibirica*) and phytophagous species with specific algophagous species, scrapers of diatoms from stony substrates (*Halesus tesselatus* and *Glossoma intermedium*). All abovementioned species belong to the category of common species in the structure of domination. The use of the classification of living forms of stone flies [18] for the description of rheophilic caddis flies allows us to refer them to lithophilous cryptobionts.

In the Khemchik River Basin the larvae of black flies can constitute up to 30% of the total abundance in the upper taiga part of the profile decreasing to ≤10% towards the steppe landscape. Larvae of black flies belong mainly to passive filter-feeders with the mouth apparatus adapted to capturing food objects in a water flow. Among exceptions we should distinguish specialized scrapers of the genus *Gymnopais* not found in the Khemchik River Basin but registered earlier in the Alash River (a left tributary of the Khemchik) [16]. In watercourses of the taiga belt larvae of black flies belonging to the genera *Helodon* and *Prosimulum* with the combined mode of feeding were found in the great amount. Their ration included detritus, algae, larvae of juvenile black flies and chironomid larvae. The authors registered ≤8 semi-destroyed head capsules of chironomid larvae and ≤3 of black flies larvae in intestines of larvae of black flies *P. pecticrassum*. These biotopes are also inhabited by larvae of black flies *Metacnephia kiryanovi*, *Gnus corbis*, *G. albipes* and *Archesimulium vulgare* belonging to typical filter-feeders with the ration of detritus and algae. With the decrease of the altitude of the landscape and increase of watercourses on submountainous plains only black flies –filter-feeders were developing.

The trophic structure of the amphibiotic communities in mountainous and steppe rivers of western Tuva is presented below. The group of collectors is numerous (22 species) and they have a 33% share in the total amphibiont abundance. The basis of this trophic group is formed by may flies. Collectors-filterers are represented mainly by black flies (24 species) and some caddis flies (4 species). In the trophic structure they make up 42%. The group of predators includes 5 species of stoneflies, 2 species of caddis flies and 1 species of may flies (total 12%). Scrapers are less representative: 2 species of may flies and 5 species of caddis flies (total 11%). The group of shredders is the smallest and includes only 1 species of stoneflies (2%).

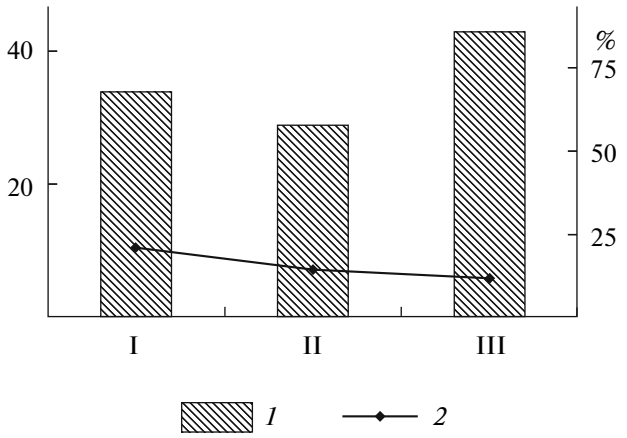

Fig. 2. Distribution of amphibiotic insects along the landscape–ecological profiles in rivers of western Tuva: (I) high-mountain type of communities, (II) middle-mountain, (III) low-mountain plain; (*1*) number of species and (*2*) portion of predatory species, %.

DISCUSSION

The Tuva territory includes altitude and vegetative zones from tundra to dessert steppe on a relatively small area that makes possible to carry out studies during a short time interval and smooth away the factor of time. For the Khemchik River Basin, data on distribution and structure of the communities of amphibiotic insects with respect to the landscape and ecological profiles have been obtained broken down into three types of communities: high-mountainous, medium-mountainous, and low-mountainous (Fig. 2). All these types were registered for each of the considered amphibiotic groups. High-mountainous river portions have low species diversity. The communities consist of a limited number of species; some species can be referred to as eudominants, like black flies. The most distinct differences are manifested in the structure of amphibiotic communities between the medium-mountain taiga and low-mountain steppe watercourses, which is caused by changes in abiotic and biotic characteristics. Thus, in the upper and middle courses of rivers, erosive processes occur; accumulative processes take place in the low reaches. Rivers in the taiga epirhithral are characterized by stony ground, a cascade current, low temperature and electroconductivity caused by their proximity to the river heads, and the absence of sources of biogenic pollution. Among caddisflies and black flies in the upper reaches of rivers, dominant and subdominant (taiga epirhitral) species from stenotopic oxyphilic rheophils are distinguished. In the middle course of rivers

(metarhithral), the communities are reorganized sequentially according to the gradient of the main environmental factors. With a slight decrease in the number of species, the structure of communities becomes more complex and an increase in the number of accompanying species and a reduction of dominant species, a polydominant structure, are observed. Low reaches of rivers are located in submountainous steppe plains, where the decline of the land gradient leads to a decrease in the current velocity, a rise in the water temperature, and an intensification of the accumulative processes stimulating the accumulation of sediments and salts washed out of the grounds and anthropogenic wastes. In these parts of the profile, the total reorganization of communities of amphibiotic animals easily seen in mayflies, caddisflies, and black flies is observed.

The spatial distribution and taxonomical composition of amphibionts is closely dependent on the physico-geographical conditions in the territory under study. Thus, the high similarity (>50%) of the taxonomical composition of amphibiotic insects in the Khemchik River Basin with adjacent territories is explained by the dominant mountainous landscapes of southern, central, and western regions of Tuva. The aridity of these territories determines the biotopic characteristics of the rivers and the structure of insect communities. Tundra and mountainous taiga landscapes of Western Sayan and the Todzha Depression are characterized by a great amount of precipitation in the summer; the biotopic parameters of the watercourses and taxonomical composition differed from the Khemchik River Basin. The originality of biotopic conditions in the watercourses of western Tuva affects the taxonomical composition and structure of the communities in each group of amphibiotic animals differently adapted to assimilation in the living space.

Problems of trophity are presented in one of the divisions of ecology of the preimaginal stages of amphibiotic insects related to the morphological and behavioral features of the considered taxa. The feeding of amphibiotic larvae was classified according to Cummins [26]. The data on trophity of amphibionts in surface waters of Russia mainly concern mayflies, caddisflies, stoneflies, and dragonflies. Black flies, except for some of them, are only mentioned by their presence in samples [2, 6, 8, 9, 20, 21].

The leading group in the trophic structure of the amphibiotic insect communities in the rivers of western Tuva is made up of collector–filterers and collector–gatherers (74% of the total species composition). The role of filter–feeders was more important than was described in the literature sources [6]. This is probably because the taxonomic composition of black flies was not taken into account in earlier analyses of the trophic structure. The portion of predators, scrapers, and shredders in the total trophic structure amounted to 26%; all of them were found, as a rule, in the upper portions of the profiles.

The main food resource in mountain and submountain watercourses is detritus and algae (mainly diatoms) included in the diet of the most amphibiotic insects [10, 23, 27]. The role of protozoans and bacteria is less notable. Among black flies and caddis flies, there are species and genera with a combined mode of feeding and predation [24, 25].

Among black flies, the combined mode of feeding is typical for representatives of some genera of the subfamily Prosimuliinae. Thus, in the Khemchik River Basin—in streams of the mountain tundra and on the upper boundary of the taiga zone—black flies belonging to genera *Helodon* and *Prosimulium* develop. They are capable of passively catching larger food than just algae and detritus, e.g. larvae of chironomids and larvae of juvenile black flies. Larvae of black flies of the mentioned genera are large (up to 10–13 mm long) and they can become active predators, including engaging in cannibalism [28, 29]. The consumption of food rich in calories gives them an opportunity to finish their preimaginal development in the shortest time (for two months from the mid-June until mid-August) at low water temperatures (≤10°C). The transition of larvae to a combined mode of feeding makes the additional feeding of larvae on blood for maturation and laying eggs unnecessary. In the midmountain–taiga rivers, black flies of the genera *Metacnephia*, *Gnus*, and *Archisimulium* are abundant and larvae of the species of the genera *Helodon* and *Prosimulium* also occur. The filtrating apparatus (premandible) of the larvae of *Metacnephia kiryanovae* has a finer structure, and the number of rays is 2 and 3 times more than in *Helodon alpestris* and *Prosimulium pecticrassum*, correspondingly [15, 16, 22]. The content of the intestine of larvae of *Metacnephia kiryanovae* is fine and soft and does not contain chitin remains of animals; imago does not refer to the number of bloodsuckers. In larvae of *Gnus corbis* and *Archesimulium vulgare*, the number of rays of premandibles is 1.5–2 times less than in *Metacnephia kiryanovae*, but greater than in *Helodon alpestris* and *Prosimulium pecticrassum*. Imago of *Gnus corbis* and *Archesimulium vulgare* belong to bloodsuckers and often attack humans in search of blood.

The comparison of filtering elements of the mouth apparatus of larvae and the distribution of species along ecological profiles allow us to note that the trophic specialization of black fly larvae depends on the ecological niche and availability of the food resource of a certain size category. This regularity has been established for many aquatic organisms [27]. As far as black flies are concerned, the larvae of the genus *Gymnopais* inhabiting the upper portions of the catchment area are specialized in scraping the available periphyton from the surface of stones; larvae of the genera *Helodon* and *Prosimulium* become detritozoophages; and larvae of the genera *Metacnephia*, *Gnus, Archesimulium, Tetisimulium, Odagmia*, and *Simulium* are phytodetritophages. Thus, according to their mode of feeding, larvae of black flies are scrapers and filter-feeders;

according to their nutrition ration, they are distinguished as phytophages, phytodetritophages, and detritozoophages. The redistribution of both the taxonomical composition and the trophic structure of the black fly taxocenes is observed along the landscape–ecological profiles. In the tundra biotopes, scrapers and detritozoophages are found; in the taiga streams, detritizoophages and phytodetritophages are abundant. Low-mountain and submountain–plain parts of the basin are inhabited by typical phytodetritophages.

On the whole, the amphibiotic animals of western Tuva are characterized by successive changes in the trophic structure of communities from the catchment area to the lower reaches of rivers caused by general tendencies in the ecology of rheophils. The main spectrum of the organic matter utilization includes algae and detritus, which evidences the participation of larvae in the biological purification of running waters. The work does not consider in detail the food relations of predators, but it is necessary to mention the relationship between predatory and nonpredatory amphibionts in the Khemchik River Basin. (Fig. 2). On the whole, predators amount to 17% in the basin. Scrapers, gatherers, and predators are presented in the upper reaches of the basin on stony-boulder ground in the tundra and taiga rivers at low water temperatures. The share of predators is maximal (21%). In lower reaches, at active sedimentation processes and higher temperatures, phytodetritophages are numerous, but the portion of zoophages decreases to 12%.

CONCLUSIONS

In the watercourses of Tuva, the communities of amphibiotic insects, including black flies, caddisflies and stoneflies, are characterized by heterogeneity in the longitudinal profile of the rivers. High-mountain, middle-mountain, and low-mountain types of communities are well distinguished. The redistribution in the structure of domination conditioned by the gradient of biotopic characteristics in the altitude-zonal regime is observed. Trophic characteristics of the communities also undergo changes. A gradual replacement of ways to catch food, from scraping to predation in the upper reaches to collecting in the lower reaches, is caused by changes in the food base in watercourses. The larvae of amphibiotic insects feed on algae, detritus, and small insects, selecting their food objects according to a size category.

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