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= AQUATIC FLORA AND FAUNA =

Landscape—Zonal Distribution of Blackflies (Diptera: Simuliidae) in the Ob-Irtysh River Basin (Overview)

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Abstract—The blackfly distribution patterns along the meridional profile for the Ob-Irtysh River basin area have been analyzed with the use of long-term quantitative data. Ninety-six species of nine genera, comprising approximately 60% of the fauna in Siberia and the Far East, are recorded. The spatial pattern formation in the blackfly zonal structures is revealed. There are significant differences between blackfly populations in highland and lowland landscapes. In the highlands, the communities confined to different altitudinal belts are formed. In the lowland of the basin, three community zonal types—steppe, taiga—forest, and tundra—are identified. Significant climatic factors affecting the heterogeneity of the blackflies in the Ob-Irtysh River basin have been estimated.

Keywords: blackflies, Simuliidae, community, space distribution, Ob-Irtysh River basin **DOI:** 10.1134/S1995082918020177

INTRODUCTION

The analysis of taxocenes at a certain stage of knowledge about them requires a consideration of the geographical distribution and identification of the zonal groups and the factors causing them. Synecological and biogeographic studies are generally performed with comparative volumetric materials using formalized methods [38].

Blackflies (Diptera, Simuliidae) are considered amphibiotic insects, being the basis of the macrozoobenthos in lotic waters. All amphibionts exist under dual conditions; the spatial distribution mainly depends on both aquatic environments, which provide conditions for most of ontogenesis, and terrestrial ecosystems, where the important life cycle stage comes once the species of both sexes have met and the imago is involved in the distribution. The regulatory mechanisms of formation of the populations of the amphibionts in the river systems were studied in a range of reported works [7, 45, 47, 50, 51]. However, the interconnection between the aquatic and terrestrial ecosystems is insufficiently investigated [44].

The Ob-Irtysh basin is one of the largest basins in Russia. Its area is of 3662.5 thousand km²; the water resources comprise 19228 km² per year. It extends from the Altai Mountains to the Kara Sea shores [10]. The greatest tributary of the Ob River is the Irtysh River, which rises in the Mongol Altai Range and flows through the upland and lowland landscapes in northeast Kazakhstan and Western Siberia. At the preimaginal stages, blackflies are developed; in numerous streams of the huge Ob–Irtysh basin; their imago is often assigned to main bloodsuckers. The first information reports on the bloodsucking diptera in the Ob River area are present in the monograph [4]. In the subsequent years, information for the taiga area on the Yamal Peninsula, the taiga and steppe landscapes in the Irtysh River and Ob River areas, and the Altai Mountains were obtained. The surveys were carried out by different methods. The use of a formalized method could enhance the comparability of the results.

The objective of the survey is to examine the blackfly distribution throughout the zonal allotment and the altidudinal belts, analyzing the composition and the structure of the communities and estimating the significanse of the factors that govern the climate with the use of formalized methods, supplemented with the example observed in the Ob-Irtysh basin.

MATERIALS AND METHODS

The long-term quantitative data obtained by the authors and from the literature sources for 29 regions in Western Siberia and northeastern Kazakhstan are used (Fig. 1). The geographical coordinates of the surveys are $48^{\circ}-74^{\circ}$ N and $65^{\circ}-87^{\circ}$ E. The zonal division scheme based on the plant cover was used [35].

All the data were reduced to a common standard [14, 32, 34]. The structure of the species predomi-

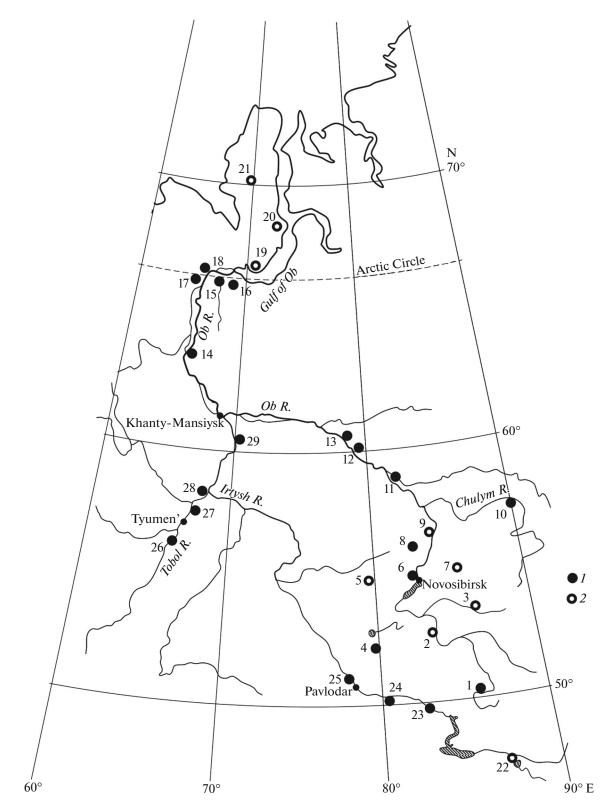


Fig. 1. Mapping scheme of survey areas. Upper Ob River Area: (1) Yst'-Koksa settlement, Verkh-Uimon settlement (Uimon Depression, Katun' River and its trubutaries) [5]; (2) Cherga settlement and Shebalino village (Cherga Depression, Katun' River, Cherga River, Ulus-Cherga River, and tributaries) [31]; (3) Artybash settlement (Teletskaya Depression, Lake Teletskoe, tributaries, and Biya River) [8]. Karasuk-Burla drainless system: (4) Karasuk town (Karasuk River and outflow streams of lakes) [4, 28]; (5) Krasnoozerskoe settlement and village of Polovinnoe (Karasuk River and small tributaries and outflow streams of lakes) [26, 28]. Middle Ob River Area: (6) Novosibirsk city (Ob River, Berd'River, Inya River, Izdrevaya River, Shadrikha River, Sharapka River, Zyryanka River, El'tsovka River, and Chik River) [4, 21, 26]; (7) Maslyanino settlement, Suenga village, and Verkh-Iki village (Salair Mountain Ridge, Berd' River, and small tributaries) [4, 20]; (8) Kolyvan' town and settlement of Skala (Chaus River and small tributaries) [21, 26]; (9) Viuny settlement and Boyarka village (Krutikha River, Viuny River, Kashlam River, and streams running off the cutoff meanders) [26]; (10) Kopylovka village, Oskolkovo village, and Asino town (Ob River, Chulym River, Yuksa River, Chichka-Yul River, and small tributaries) [4, 20]; (11) settlement of Molchanovo (Ob River, Tagan River, Kaimas River, small tributaries, and outflow streams of lakes) [6]; (12) village of Nazino (Ob River, Tagan River, and outflow streams of the Ob River) [11, 23]; (13) village of Aleksandrovskoe (Ob River and small tributaries) [11]. Lower Ob River Area: (14) village of Oktyabr'skoe (Ob River and small tributaries) [4]; (15) settlement of Toi-Pugola (Polui River and tributaries) [24]; (16) settlement of Zelenyi Yar (Polui River and tributaries) [24]; (17) settlements of Kharp and Krasnyi Kamen' (Sob' River, Shuchia River, and tributaries) [22]; (18) town of Labytnangi (Ob River, Sob' River, and tributaries) [22]. Gulf of Ob area: (19) Yamal Peninsula, settlement of Yar-Sale (Yuribei River, nameless brooks, and outflow streams of bogs and lakes) [18]; (20) Yamal Peninsula, Kamennyi Cape (Nurmaykha River and small rivers on the Middle Yamal Peninsula eastern seashore) [9, 18]. Lake Neito drainless system: (21) Yamal Peninsula, Lake Neito (nameless brooks and rivers) [9, 18]. Upper Irtysh River Area: (22) Eastern Kazakhstan, settlement of Katon-Karagai (Irtysh River, Lake Markakol', and tributaries) [29]; (23) Eastern Kazakhstan, city of Ust'-Kamenogorsk (Irtysh River and tributaries) [14, 39]. Middle Irtysh River Area: (24) northern Kazakhstan, city of Semipalatinsk (Irtysh River and tributaries) [14]; (25) northern Kazakhstan, city of Pavlodar (Irtysh River, Selety River, Olenty River, Karasu River, and Shiderty River, [13, 14, 17]. Lower Irtysh River Area: (26) town of Yalutorovsk (Tobol River and Iset' River) [19]; (27) city of Tyumen (Tobol River and Tura River) [19, 37]; (28) city of Tobolsk (Tobol River) [19]; (29) village of Demianskoe (Irtysh River, Dimianka River, and tributaries) [19, 23]. (1) Data from literary sources; (2) sample collections of the authors.

nance was assessed for the ranked traits [27, 30] with the use of the Engelman modified scale [46]. The species were classified as follows: dominants (40-100%), subdominants (12.5-39.9%), recedents (1.3-12.4%), and subrecedents (<1.3%) ranked with four, three, two, and one scores, respectively. River biotope zoning was considered in the context of the Illies and Botosaneanu classification [48]. The blackflies were identified up to species according to the modern system of the family Simuliidae [43].

The dates were mathematically processed with the use of one of the methods for cluster analysis and factor analysis in zoogeography [33], which were successfully tested on the blackflies [30, 49]. The population rank indicators and the matrix of the species composition similarity coefficients calculated with the Sorensen–Chekanovskii similarity index [25] were used as the bases for estimation.

In order to interpret the typological structure and assess the significant terrestrial factors affecting the blackfly zonal distribution, data on the long-term climate averages were used. They included the average monthly air temperatures of the coldest and warmest months in a year, the temperature sums for the air of constant temperature of $>10^{\circ}$ C, the number of days a year with average daily air temperature $>10^{\circ}$ C, the duration of the nonfrost period, and the average annual percipitaion [1].

RESULTS

The taxonomic composition of blackflies in the Ob-Irtysh River basin includes 96 species of nine genera: *Gymnopais, Helodon, Prosimulium, Cnephia, Greniera, Metacnephia, Simulium, Stegopterna*, and *Sul*-

INLAND WATER BIOLOGY Vol. 11 No. 3 2018

cicnephia representing 2, 2, 6, 1, 1, 7, 72, 2, and 3 species, respectively. The genus *Simulium*, involving 75% of the whole composition, is represented by ten subgenera: *Boophthora*, *Boreosimulium*, *Byssodon*, *Eusimulium*, *Hellichiella*, *Montisimulium*, *Nevermannia*, *Schoenbaueria*, *Simulium* s. str., and *Wilhelmia*— including 1, 4, 2, 2, 5, 5, 10, 6, 33, and 4 species, respectively.

Five classes with an intraclass species similarity of 40-60% and interclass relationship of 18-32% were identified in the zonal blackfly distribution (Fig. 2).

The communities of the blackfly spatial pattern along the meridional profile in the Altai highland areas (the Upper Ob River area and the Upper Irtysh River area) are assigned to class I of 49% species similarity. The communities involve 59 species of seven genera: Gymnopais, Helodon, Prosimulium, Cnephia, Metacnephia, Simulium, and Sulcicnephia-represented by 2, 2, 5, 1, 4, 42, and 3 species, respectively; the genus *Simulium* is represented by eight subgenera. In the mountain-steppe landscapes, the blackflies of all the genera are recorded. The species of the genera *Gymnopais* and *Cnephia* are absent in the forest-steppe landscapes, while in the taiga midaltitude mountains there are no representatives of the genus Gymnopais. The species of one genus Simulium are only found in lower altitude mountains. The presence of the species of the genus Sulcicnephia and the species of the subgenera Montisimulium and Wilhelmia and the species group bezzi of the genus Simulium (s. str.) should be noted. The species diversity is higher in the mountain forest-steppe and middle-mountain taiga landscapes (28–29 species) when compared to that in the mountain steppe and low-altitude mountains (24 and 17 species, respectively). In the blackfly population of the taiga midaltitude mountains, the species Helodon alpestris (Dorogostaisky, Rubtsov & Vlasenko), Simulium malyschevi Dorogostaisky, Rubtsov & Vlasenko, and S. murmanum Enderlein are dominants, while the species Prosimulium tridentatum Rubtsov and Simulium decimatum Dorogostaisky, Rubtsov & Vlasenko are identified to sodominants. In the waters of the foothill and lower altitude mountain belt, the species S. ornatum Meigen and S. longipalpe Beltvukova develop on a mass scale, while the populations of S. reptans (Linnaeus) and S.(Wilhelmia) equinum (Linnaeus) increase at a lower rate. In the forest-steppe belt, the species S. ornatum is the dominant; the subdominants are S. malvschevi Dorogostaisky, Rubtsov & Vlasenko and S. alajense Rubtsov. The blackfly cenoses in the mountain steppe significantly vary in composition; species Metacnephia edwardsiana (Rubtsov), Simulium decimatum, S. malyschevi, S. murmanum Enderlein, and S. curvans (Rubtsov & Carlsson) may dominate depending on the slope exposure affecting the flow of water.

The mountain regions of the Upper Irtysh River area are assigned to the Southern Altai Province (Eastern Kazakhstan), where the above listed species coexist with representatives of the subgenus *Montisimulium*, confined to the mountain systems of Central Asia [29, 36, 40].

The foothills of the Altai Mountains are situated adjacent to the zonal forest steppe in the Upper Ob River Area, where a decrease in the total blackfy diversity can be observed. The blackflies of 18 species from seven subgenera of the genus Simulium are identified in the communities. The communities of the subzonal allotments differ in composition and structure. Thus, the representative of the steppe complex S. (Boophthora) erythrocephala De Geer is predominant among the eight recorded species in the southern forest steppe; the species S. (Nevermannia) angustitarse (Lundström) and S. (s.str.) rostratum (Lundström) are numerous. In the subzone of the northern forest steppe, blackflies of 13 species are recorded; species S. longipalpe and S. (Byssodon) maculatum (Meigen) are predominant. The species of two biotope groups inhabiting streams of different size categories and hydrological conditions can be observed. In smalland medium-sized streams, S. noelleri Friederichs, S. longipalpe, and S. erythrocephala (having two generations a year) tend to develop, while S. (Byssodon) maculatum) and S. (Schoenbaueria) pusillum Fries (of one generation) develop in the large Ob River.

The Irtysh River basin, compared to the Ob River basin, is characterized by a sparse river network and lower flow, which is caused by the amount of precipitation and the hyperarid environments. The mid- and partially upstream Irtysh River is confined to the arid steppe grasslands in northern and eastern Kazakhstan, where the blackflies are represented by 26 species of the genus *Simulium*, *Montisimulium*, *Wilhelmia*, and the species of *Simulium* group *bezzi*, distributed in Central Asia and the Mediterranean, are recorded in the streams of the mountain-steppe and mountain-taiga landscapes in the Irtysh River area [29, 40, 41, 43].

The blackfly communities in the steppe zone and the southern forest-steppe subzone in the Ob-Irtysh River basin are assigned to class II of 40% species similarity. The communities of the drainless Kulunda herb—bunchgrass steppe (the interfluve between the Ob River and the Irtysh River) are assigned to separate class III, since they differ from those in the Baraba southern forest steppe in composition (13 and 8 species, respectively) and structure. In the interfluve area, the portion of the species *Simulium ornatum*, *S. noelleri*, and *S. rostratum*, developing in the slow water flows running off the ponds and floodplain lakes, often drying out in the summer months, is significantly higher.

The blackfly communities of the taiga landscapes in the middle Ob River area and the lower Irtysh River area, which are assigned to class IV, are diverse in composition; there are 32 species of 5 genera (one species in all four genera *Prosimulium*, *Cnephia*, *Greniera*, and Stegopterna, while the genus Simulium is represented by 28 species). In addition, the genus Simulium is represented by eight sugenera. The species similarity within the class can reach 47%. In the northern and middle taiga subzones, the communities are poorer in species diversity (16-17 species) when compared to that in the southern taiga subzone (25 species); the difference can be expressed as 30%. In the taiga water flows, the species of the subgenus Schoenbaueria are predominant, while Simulium (s. str.) and rather infrequent Eusimulium are assigned to subdominants. The portion of Simulium longipalpe in the multispecies communities tends to decrease from the south to the north, while the portion of S. (Schoenbaueria) pusillum evolving in the medium- and small-sized streams tends to increase. The species S. maculatum is developed on a mass scale in the large Ob River. The blackfly communities in the northern forest steppe and the subtaiga zone are assigned to class IV for taiga communities based on the composition and structure similarities between the species dominants.

In the lower Ob River area, the northern taiga is situated adjacent to the forest tundra, which is characterized by severe waterlogging and the presence of numerous lakes with outflowing streams. In the forest-tundra blackfly community, 30 species of three genera (Prosimulium, Metacnephia, and Simulium represented by 2, 3, and 25 species, respectively) are recorded. The genus Simulium of these genera is represented by seven subgenera (Boreosimulium, Byssodon, Eusimulium, Hellichiella, Nevermannia, Schoenbaueria, and Simulium s. str.). The genera Simulium s. str. (8 species), Schoenbaueria (5 species) Boreosimulium (4 species), and Nevermannia (4 spe-

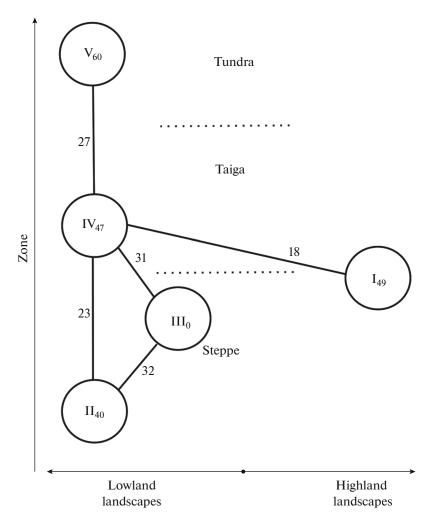


Fig. 2. Spatial and typological structure of blackflies in the Ob-Irtysh River basin. Classes: (I) blackfly communities located in spots 1-3, (II) spots 22-25, (III) spot 4, (IV) spots 5-18 26-29, and (V) spots 19-21. The figures of the numbers of classes are the species similarity (%) between the blackfly communities within the classes; the figures at the lines connecting the classes represent the community similarity between the classes.

cies) are predominant, in total comprising 70% of the whole composition. *Simulium (Schoenbaueria) pusil-lum* is assigned to the dominants, while *S. (Nevermannia) vernum* Macquart and *S. (Sch.) subpusillum* Rubtsov are assigned to the subdominants. The forest-tundra blackfly population is more similar to the northern taiga population in the genus *Simulium* total contribution to the key composition and structure.

The tundra subarctic communities of blackflies on the Yamal Peninsula are assigned to class V of a high intraspecific similarity (60%). They are represented by 25 species of five genera. Nineteen species of them (76%) are classified to the genus *Simulium*: *Simulium* (s. str.) and the subgenus *Schoenbaueria* represented by five species each, *Nevermannia* and *Boreosimulium* represented by three species each, *Hellichiella* represented by two species, and *Byssodon* represented by one species. In addition, the species of the genus *Metacnephia* represented by three species and the genera

INLAND WATER BIOLOGY Vol. 11 No. 3 2018

Prosimulium, *Cnephia*, and *Stegopterna* represented by one species each are recorded. In the shrubby-tundra subzone, 23 species of blackflies are recorded, while seventeen species are identified in the moss-lichen tundra. In the tundra water streams, blackflies of the subgenera *Schoenbaueria* and *Nevermannia* are developed on a mass scale.

The correlations with the use of common factors affecting the climate were revealed throughout the landscape–zonal distribution in the Ob-Irtysh River basin. The recorded factors of the terrestrial invironments can explain 46% of the blackfly measured dispersion (see Table 1.). The average annual precipitation has the most significant impact (37%), while the average annual duration of the nonfrost period is at least as important (10%). The dispersion of 18-22% can be explained by the the rate of warming up and heat absorbed by the water in the warmest summer month.

Factor	Recorded dispersion, %
Average annual precipitaion, mm	3
Number of days a year with constant aver- age daily air temperature $>10^{\circ}C$	22
Average July air temperature, °C	22
Average January air temperature, °C	18
Average annual temperature sum >10°C	18
Average annual duration of the nonfrost period	10
All the factors	46

 Table 1. Significant climate factors affecting blackfly population heterogeneity in Ob-Irtysh River basin

The data on the significant abiotic environmental factors affecting the blackfly distribution in the altitudinal belts and along the longitudinal river profile were previously obtained. The dateset items included the true altitude of the location (44.2%), the water temperature (24.7%), the phyto component (13.7%), the granulometric composition of a substrate (6.5%), the seasonal period (4.5%), the stream size (1.9%), and the river velocity (0.3). A multivariant assessment of the relationship based on the factor correlation proved a total dispersion of 51% [31].

DISCUSSION

Studying the diversity of amphibionts like the rest of the macrozoobenthos, based on the principles of region and basin systems, can allow us to gain a more profound understanding of the taxocenes in the spatial and temporal dimensions [15].

The history of studying blackflies in the Ob-Irtysh basin has spanned approximately 50 years. It is connected with the development of regions in Western Siberia and the adjacent territories of Kazakhstan. If the first monograph report included information on 58 species [4], the current system of Simuliidae [43] in the Ob-Irtysh River basin has identified 96 species, accounting for synonyms, which comprise approximately 60% of the whole fauna of blackflies in Siberia and the Far East [21]. The increase in the number of the species by 38 species (66%) can be explained by the enhancement of the regional surveys in northern and southern Western Siberia and the northern and eastern Kazakhstan.

The highland and lowland blackfly communities are distinctly divided in a common spatial distribution pattern. In the lowland part, three types of zonal groups—steppe, taiga-forest, and tundra—can be observed. The biogeography requires analyzing the spatial patterns of the terrestrial ecosystems in the north—south direction. The tundra and taiga-forest communities are different in taxon composition at the levels of genera (*Prosimulium* and *Metacnephia*) and subgenera (*Boreosimulium* and *Hellichiella*). The representatives of the genus *Simulium*, especially its three subgenera *Schoenbaueria*, *Simulium* s. str., and *Eusimulium*, tend to increase from the north toward the south. In the subzonal taiga allotments, the communities are unequal; the northern- and central-taiga communities are more homogeneous in composition; they have more similarity when compared to the southtaiga communities enriched by the species from the forest steppe.

The forest steppe in the Ob River Area is characterized by high-grade relief differentiation affecting the density of the river network, hydrodynamic properties, and typical climate chracteristics [12]. The communities of the northern forest steppe and the subtaiga zone are more similar to that in the southern taiga than to the extremely poor southern forest-steppe communities in the interfluve area between the Ob River and the Irtysh River. In the interfluve area, the sparse river network, the unsteady flow regime, and the summer steady low water level do not advantage blackfly development [28]. With the existing difference, blackflies of the genus *Simulium* are predominant in the Ob River area, comprising 70% of the total composition.

A tendency to increase species diversity within the zonal allotments in the southern subzones, when compared to that in the northern subzones, is observed. This can be explained by drifting the blackfly larvae downstream and their successful developing in intrazonal biotopes, a kind of passage for species penetration into the adjacent areas [38]. In addition, the ecological valence of the dominant species when taking into account their heterotopic character can be accomplished [3]. The principle of the biotope change, associated with the stream size and the surface relief on the lowland, remains the same [2, 42, 49], which can be easily observed in species of the genus Simulium. The preferential distribution of the species Simulium s. str., Schoenbaueria, and Nevermannia of the genus *Simulium* in the Ob River Area, comprising 54% of all the basin fauna, is associated with the existing hydrodynamic conditions of the lowland streams, caused by the regional geomorphology.

In the area profile from the foothills in the Altai Mountains to the lowlands of Western Siberia, the biotope replacement from the hyporitral zone to the potamal can be observed throughout the lowland, which contributes to blackflies of the genus *Simulium* evolving. According to ecological characteristics, the lowland communities of blackflies in the taiga-forest, forest-steppe, and steppe landscapes are predominantly represented by the eurybionts adapted to a wide range of temperatures, the laminar flow, and the finegravel bottom with accumulative admixtures. In the communities in tundra toward steppe, the substitution of the species group *venustum* (*S. truncatum* and *Simulium longipalpe*) by the *bezzi* and *ornatum Simulium* s. str. groups confined to the warm areas can be observed. In taiga communities, the species *Schoenbaueria*, as typical representatives of the boreal blackfly complex, are predominant [21, 36].

In addition to the species penetrating from south to north through intrazonal biotopes, the distribution of the stenotopic and psychrophilic species of the subgenus Boreosimulium out of taiga and forest-tundra bounds is limited, excluding Simulium (B.) baffinense Twinn, possibly reaching the southern taiga through the extrazonal biotopes. Species of the subgenus Hellichiella, with few exceptions (Simulium (H.) barabense Rubtsov), do not go beyond the subtaiga bounds. All of them are classified to the subarctic or boreal blackfly complexes in the Holarctic [36, 40, 43]. The group of the boreo-montane species is represented by the stenobionts of the genera Gymnopais, Helodon, Prosimulium, and Metacnephia, distributed in the zonal subarctic and mountain-taiga landscapes, which is caused by the analogy of the natural climatic and hydrodynamic conditions.

Therefore, zonal communities (on the placors, the flat interfluves in the zonal environments), intrazonal communities, and extrazonal communities (in nonzonal environments) are clearly defined in the spatial distribution patterns of blackflies in the Ob-Irtysh River basin.

An analysis of the basin system has proven that the amount of precipitation, annually comprising 1000 mm on average for Western Siberia, is significant in the surface-water occurrence. The progressive decrease in the precipitation in the west—east and north—south directions according to the zonal distribution and the surface relief change is observed [10]. Most presipitation falls in summer months in the Altai Mountain regions. It can often cause flash floods, contributing to blackfly larva migration into the Ob River and further downstream migrating.

It should be noted that the macrodistribution of the blackfly population in the Ob-Irtysh basin is not at varience with the conceptions related to the river ecosystem function. Thus, continuity with the highland and lowland community replacement and the successive formation of the zonal groups is observed. In addition, there are communities of "ecological spots" shaped under the hydrodynamic conditions changing in the intrazonal areas [7, 16, 51]. On the scale of river basin and integrated landscapes, the structural changes in the blackfly communities of the subzonal allotments can be observed. The given spatial distribution structure of the blackfly communities (Fig. 2) shows the intraclass relations at a rather high level and the interclass relations at a low level, which can prove the presence of zonal groupings and the degree of their isolation.

CONCLUSIONS

The 96 species of nine genera are recorded in the Ob-Irtysh basin. They comprise approximately 60% of fauna in Siberia and the Far East. The blackfly-population spatial distribution pattern along the meridional profile is revealed. High intraclass and relatively low interclass similarities in certain zonal groupings are identified. There are significant differences between the blackfly populations in the highland and lowland landscapes in the Ob-Irtysh basin. In the highlands, communities confined to different altitudinal belts are formed. In the lowland of the basin, there are three types of zonal groupings with different composition and structure: steppe, taiga-forest, and tundra are observed. With respect to the zonal distribution of the blackflies in the Ob-Irtysh River basin, the certain correlations with taking into account the changes in the factors affecting the climate are defined. The factor for the average annual precipitation (37%) is considered the most significant; the least significant factor is the duration of the nonfrost period (10%). The dispersion of 18-22% can be explained by the the rate of warming up and the heat absorbed by the water in the warmest summer month.

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