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ZOOPLANKTON, ZOOBENTHOS, ZOOPERIPHYTON

Winter Dynamics of the Vertical Distribution of Drifting Invertebrates in a Small Salmon River

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Abstract—Mayfly larvae (Ephemeroptera), Diptera larvae, and adult water mites (Hydracarina) dominated in the winter syrton of a small salmon river. No significant linear dependence of the number of drifters entering the nets on the filtered water volume was found; therefore, we used not the syrton density (ind./m^3), but the data of the actual catches. The vertical distribution of drifting invertebrates of different taxonomic affiliation had its own characteristics. The drift intensity of invertebrates increased in the daytime under conditions of good illumination of the water column. We assume that this fact is indirectly related to the low water temperature, which limits the swimming ability of drift-feeding fish, which, in turn, become more vulnerable to ichthyophagous endothermic predators. Altogether this preconditions fish's predominantly sedentary, secretive lifestyle during daylight hours in winter. In December, most daytime drifters migrated close to the water surface and, in January, on the contrary, they kept near the bottom. The latter may be due to the overwhelming effect of lower daytime air temperatures, since the river channel was not completely covered with ice until mid-February. After a heavy February snowfall, the upper water layers of the river flow turned out to be isolated from the effect of air temperature, and the level of illumination of the water column during the daytime hours corresponded to the period of late twilight. As a result, the fish became less accessible to semiaquatic endothermic predators, the intensity of invertebrate drift in the daytime decreased sharply, and the vertical distribution of drifters along the stream became fairly uniform.

Keywords: invertebrate drift, juvenile salmonids, spatial distribution, winter period

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INTRODUCTION

Changes in the spatial distribution of living organisms over time are an important component of the dynamics of natural populations and communities. Analyzing of the patterns of these changes is an urgent task for a number of biological sciences, including hydrobiology. In light of the basic concepts describing the functioning of flowing ecosystems—the "river continuum concept" (Vannote et al., 1980), the "spot dynamics concept" (Townsend, 1989), as well as the "combined concept" linking them together (Bogatov, 1995)—the spatiotemporal variability of aquatic organism drift is of particular interest. Drift, both random downstream transport and voluntary migration using the drag force of the current, is inherent in all inhabitants of flowing waters, from microorganisms and macroinvertebrates to fish (Müller-Haeckel and Marvanová, 1979; Pavlov and Skorobogatov, 2014; Naman et al., 2016). Drift ensures the dispersal, reproduction, and interaction of conspecifics from isolated river areas and contributes to the weakening and intensification of various forms of competition, the supply of food objects, and aversion to predator pressure. The set of drift objects is described by the term *syrton* (Berner, 1951).

Like any other set of living beings, syrton is characterized by its own spatial structure. The study of it is important to minimize possible damage to fisheries during the operation of water intake facilities associated with the direct destruction of fish larvae and fry migrating downstream, as well as their food objects, which are drifting benthic invertebrates (Tarasov and Tarasova, 1997; Pavlov and Skorobogatov, 2014). The relevance of taking into account the regularities of the vertical distribution of drifters is due to the need to identify the optimal water layers for installing the heads of water intake stations. In addition, information on the vertical distribution of drifting invertebrates is important for a more accurate characterization of the habitats of economically valuable fish (Shubina, 2006). Experimentally, it was proven that in the same river site, juveniles of white-spotted charr and Dolly Varden prefer to keep near the bottom, while juveniles of masu salmon and coho salmon prefer positions near the surface, and in so doing juveniles of white-spotted charr and coho salmon occupies a deepwater area of the site (Zhivoglyadov, 2004). Since the spatial distribution of drift-feeding fish reflects their feeding on syrton, there is an opinion that the very territorial behavior of juvenile salmonids is a competition for microbiotopes that are convenient for the capture and consumption of drifting invertebrates (Chebanova, 2009). Consequently, assessing the vertical distribution of syrton is of particular importance in salmon rivers and streams. Naturally, such interest is paid firstly to pristine watercourses either not affected by anthropogenic load or experiencing a very weak impact (Gorovaya, 2022).

The temporal aspect of drift may be considered at different scales; as a rule, interannual, seasonal, or diel dynamics are analyzed. In temperate and northern latitudes, due to the difficulties in collecting hydrobiological material at negative air temperatures, drift studies are usually limited to the ice-free period.

This study aims to analyze the winter dynamics of the vertical distribution of drifting invertebrates in a typical small salmon river in the southern part of the Russian Far East.

MATERIALS AND METHODS

The material was collected in the middle reaches of the Kedrovaya River, which originates on the slopes of one of the eastern spurs of the Chernye Gory Ridge of the East Manchurian Highlands and flows into the Amur Bay of the Sea of Japan (43°04′41″ N, 131°36′45″ E). The total length of the river is 18 km, the total length of its tributaries is 46 km, and the catchment area is 45 km^2. This river belongs to the category of salmon watercourses, because masu salmon *Oncorhynchus masou* (Brevoort), Dolly Varden *Salvelinus malma* (Walbaum), and whitespotted char *S. leucomaenis* (Pallas) spawns here. The river basin is located in the zone of coniferous–deciduous forests. The climate is monsoonal, so the largest precipitation falls during the warm season. Winters are frosty (reaching –36°C), sunny, and with little snow. During the winter period, 5–7% of the total annual precipitation falls. As a result, the snow cover is relatively thin and does not exceed 0.15 m on average, reaching 0.30 m in ravines (Vasil'ev et al., 1965). The freezing period, as a rule, lasts from the end of the first decade of December to the beginning of April.

In the study area, the soil is mixed, with a predominance of the gravel–pebble fraction; there are relatively few large boulders. Three 24-hr sampling series were carried out, timed to coincide with the dates of new moons (to avoid the effect of moonlight on the nighttime activity of aquatic organisms): December 19–20, 2006, and January 19–20 and February 16–17, 2007. The width of the river on the dates of collection did not exceed 8 m and the depth did not exceed 0.5 m. Throughout the winter, the river was covered with ice, but until mid-February, polynyas were encountered in the areas with the fastest flow. The February series took place a day after a heavy snowfall, due to which the polynyas were hidden under the snow. The water temperature during observations varied from 0.3 to 0.7°C in December, from 0.1 to 0.5°C in January, and from 0.12 to 0.7°C in February. The air temperature varied from –13.9 to –5°C (December), from –19 to –3°C (January), and from –16 to +2.2°C (February).

Drifting aquatic organisms were caught using a portable sampler of original design (Astakhov, 2009, 2012). The device consists of a vertical upright and removable nets fixed one above the other. The height of the mouth of each net is 0.1 m and the width is 0.25 m; the filter cone length is 0.6 m and mesh size is 220 μm. The design allowed one to operate five nets at once, but only three were used in this study (Fig. 1a). During operation, the sampler was installed in a preliminarily prepared ice-hole in such a way that the total height of the three nets (0.3 m) was equal to the flow depth. The flow velocity was measured with a hydrometric meter GR-55 at three water layers corresponding to the position of nets in the river: near the bottom, in the middle layer of the water column, and near the surface. The average daily flow velocities at these water layers were 0.15, 0.28, and 0.45 m/s (December); 0.145, 0.25, and 0.36 m/s (January); and 0.34, 0.445, and 0.66 m/s (February). The duration of the night was defined as the time interval between the end of the evening twilight and the beginning of the morning. During the dark period of the day, the material was taken every hour and, during the daylight, every 2 h. The exposure time of the sampler in the river was 5 min. Immediately after removing the sampler from the ice-hole, it was transferred to a warm room, where the samples were thawed, washed, and fixed with 4% formalin.

All calculations were carried out on the basis of primary data (actual catches of each net for 5 min of exposure, ind.). Syrton density (ind./m^3) was not calculated due to the absence of a significant linear dependence of the number of drifters entering the nets on the volume of water filtered by the nets during exposure (Figs. 1b–1d; all $R^2 < 0.5$). Such a dependence suggests the possibility of standardizing drift samples from different areas and watercourses for further comparison. However, if this relationship is absent, the calculations based on values of ind./m^3 may distort the real picture and hide the really existing differences and regularities (Downes, 2010; Downes and Lancaster, 2010). When visualizing the diel dynamics of drift (Fig. 2), the number of aquatic organisms carried in 1 h through the registration section of each water layer (1.0 × 0.1 m) was used as an indicator of drift intensity.

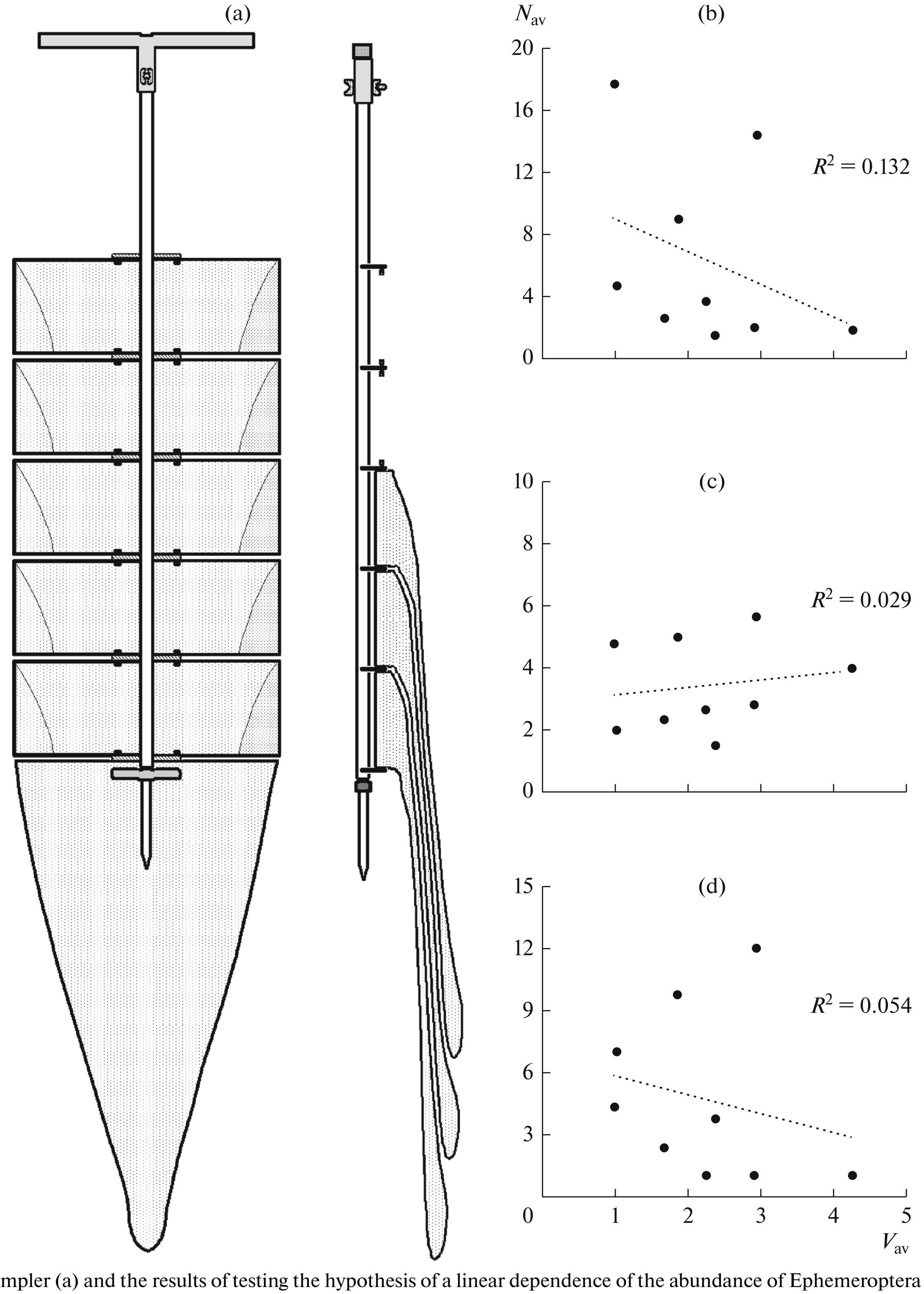

Fig. 1. Sampler (a) and the results of testing the hypothesis of a linear dependence of the abundance of Ephemeroptera (b), Diptera (c), and Hydracarina (d) in catches on the volume of water filtered by nets: $N_{av.}$ is average abundance in the catch, ind., and $V_{av.}$ is the average volume of filtered water, m^3. R^2 is the coefficient of determination, showing how adequate the dependence model is to the primary data (the model is considered unacceptable when $R^2 < 0.5$ and substantial when $R^2 > 0.9$).

Taxa that accounted for ≥15% of the total number of drifters were classified as dominants, those that accounted for 5.0—14.9% were subdominants, and those that accounted for 1.0–4.9% were secondary (Levanidov and Levanidova, 1979).

The Reynolds numbers were calculated to identify further possible relationships between the number of drifters at different water layers and turbulence:

$$\mathrm{Re} = vh\rho/\mu,$$

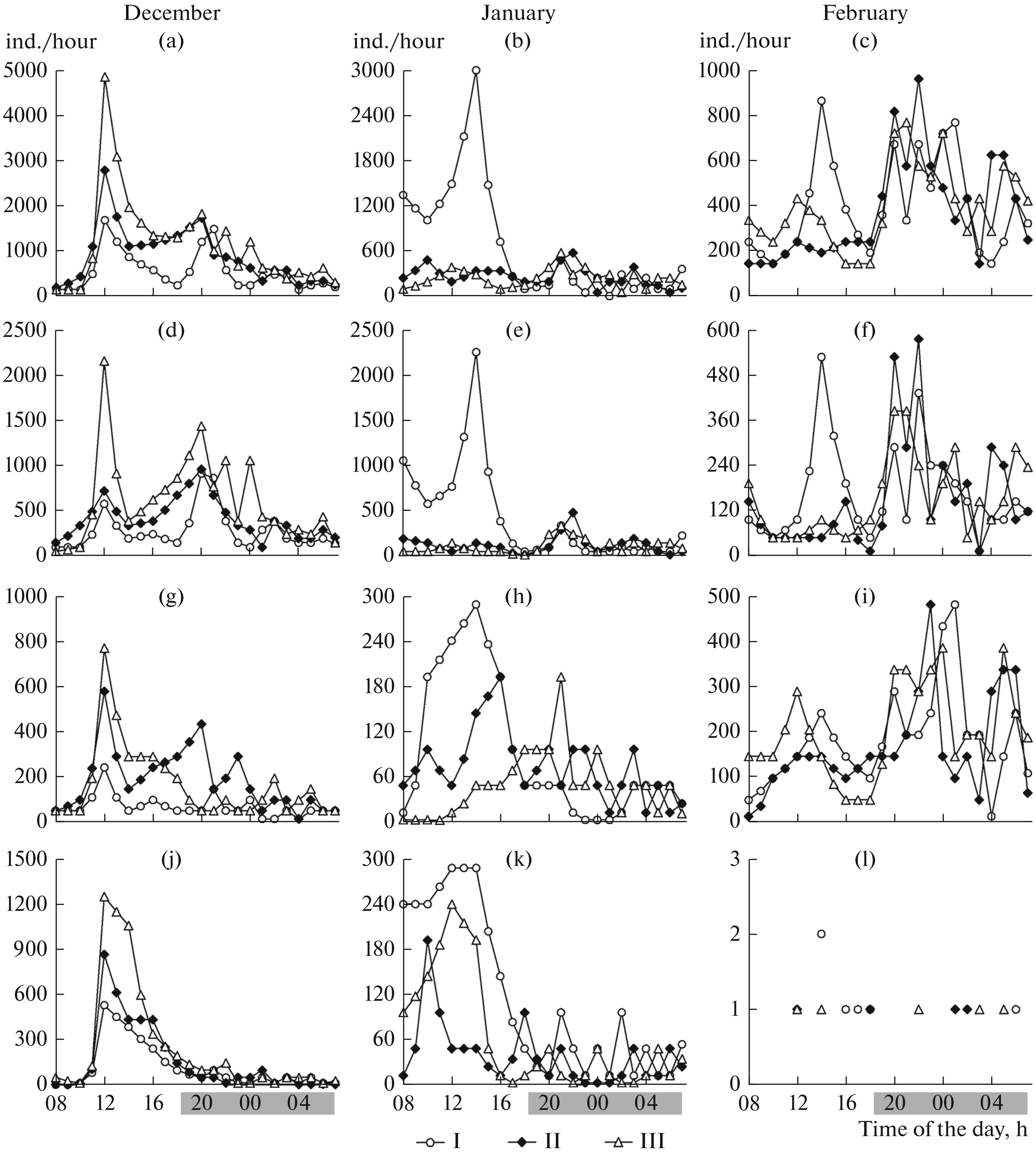

Fig. 2. Intensity of drift of benthic invertebrates at different water layers during the twenty-four hours: all groups (a–c), Ephemeroptera (d–f), Diptera (g–i), and Hydracarina (j–l). I, II, and III are near-bottom, middle and upper water layers. Night hours are highlighted with dark fill along *x* axis. Figure (l) shows primary data.

where *v* is the the average current velocity, m/s; *h* is the water layer height, m; ρ is water density, kg/m^3; and μ is the dynamic coefficient of viscosity (viscosity) of water, Pa · s.

When calculating water density and viscosity water temperature data (t, °C) were used (Statzner et al., 1988). Regression equations based on standard tables of the dependence of water density and dynamic coefficients of water viscosity on temperature (Aleksandrov and Trakhtengerts, 1978; Pavlov et al., 1987) were developed:

$$\rho = 0.00009t^3 - 0.0091t^2 + 0.0682t + 999.839$$

(the dependence is functional ($R^2 = 1$) for the water temperature range of 0.0–8.2°C);

$$\mu = -0.00003t^3 + 0.0017t^2 - 0.0624t + 1.7917$$

(the dependence is functional ($R^2 = 1$) for the water temperature range of 0.0–12.0°C).

Statistical analysis was performed using PAST 4.10 software. The distribution of most of the data did not follow the normal distribution (Shapiro–Wilk test), so statistical comparisons were made on the basis of nonparametric tests (Kruskal–Wallis, Mann–Whitney, Friedman, and Wilcoxon). The Kendall's τ coefficients were calculated to establish possible correlations. The significance level of 0.05 was taken as the cutoff value. All post-hoc comparisons were adjusted with Bonferroni correction.

RESULTS

During most of the winter period, in the Kedrovaya River, representatives of three taxonomic groups of benthic invertebrates (mayflies (Ephemeroptera), dipterans (Diptera), and water mites (Hydracarina)) dominated in syrton, accounting for 85.7% (December), 92.0% (January), and 89.1% (February) of the total number of drifters. Therefore, the vertical distribution of the winter syrton of the river was considered mainly for these three groups. The order Ephemeroptera was the most represented by the larvae of the families Ephemerellidae, Heptageniidae, Baetidae, Leptophlebiidae, and Ameletidae. The order Diptera was represented by the larvae of Chironomidae, Simuliidae, and Limoniidae. Hydracarina (families Sperchontidae, Feltriidae, Aturidae, Lebertiidae, and Torrenticolidae) were presented both by deutonymphs and imagoes. In February, the number of drifting water mites had sharply decreased; they, bypassing the category of subdominants, moved into the category of secondary taxa. It should be noted that, in the winter syrton of the studied river, the group of subdominants in terms of large taxa was presented only once (Oligochaeta, December). Tabulated data on the structural hierarchy of the main taxonomic groups of syrton of the Kedrovaya River were presented in our earlier publication (Bogatov and Astakhov, 2011). The general dynamics of the vertical syrton structure in winter is presented at Fig. 2.

In December, the lowest intensity of the total drift was observed in the near-bottom layer of the water column. The maximum activity of drifters was noted at 12:00 (noon)—at once in all water layers. The abundance of syrton in the upper water layer of the stream exceeded the similar indicators of the middle and near-bottom ones by 1.7 and 2.9 times, respectively. From noon until late evening twilight, drift intensity decreased almost consistently and monotonously both near the surface and near the bottom, although it was slightly increasing at the same time in the middle water layer. At the end of the evening twilight, the syrton abundance in the upper and middle water layers was the same, but it turned out to be 4.5 times lower near the bottom. At the onset of night, the abundance of invertebrates in the near-bottom water layer began to increase; by 21:00, it exceeded values that were observed at upper and middle water layers, where peaks of nighttime activity were recorded at 20:00. After 21:00, invertebrates migrated to the upper and middle water layers again. Statistical analysis refuted the hypothesis about the absence of vertical stratification of syrton during daylight hours in December (Table 1). The diagram (Fig. 2a) made it possible to draw a conclusion about the numerical predominance of daytime migrants in December, which was also evidenced by relative indicators of the total drift (61.6% during the daytime and 38.4% at night). However, the result of the corresponding statistical test did not support this conclusion (Table 1).

The dynamics of the vertical redistribution of the drifters of each of the taxonomic group under study had its own characteristics (Fig. 2).

After the midday drift peak, at which the number of mayflies in the upper water layer of the stream exceeded similar indicators in the middle and near-bottom water layers by 3.0 and 3.8 times, respectively, a significant decrease in their migratory activity followed at 14:00. For the rest of the daylight, the abundance of mayflies in the upper and middle water layers gradually increased. Near the bottom, the intensity of their drift remained low until the end of evening twilight. The night maximum drift of mayflies in all water layers was recorded at 20:00, when their abundance in the upper water layer exceeded by 1.5 times the values recorded for the middle and near-bottom layers, the mayfly abundances in the latter were similar. During the dark period, a decrease in the drifting intensity of mayflies was recorded, accompanied by two relatively small peaks near the surface.

Unlike mayflies, Diptera drifted mainly in the middle water layer. During the midday migration peak, the abundance of these animals here was only 1.3 times lower than the corresponding values in the upper water layer, but exceeded more than twofold a similar indicator in the near-bottom layer. Diptera activity also decreased in all water layers at 14:00; however, the drift intensity did not increase then in the upper water layer—instead it decreased. During the period from 14:00 to 20:00, the numbers of Diptera drifting here has decreased by 6 times. On the contrary, a steady increase in the drift rate was observed in the middle water layer at similar time interval; its maximum was recorded at 20:00. At 21:00, an insignificant peak of Diptera drift activity was recorded in the near-bottom water layer, where the low intensity of their drift persisted from 14:00. At 23:00, the second nocturnal abundance peak of these animals was noted in the middle water layer. Near the surface, the nocturnal drift maximum for Diptera was observed at 02:00.

A statistical evaluation of vertical distribution of mayflies and Diptera along the water column in

Table 1. Results of testing hypotheses about the absence of differences in drift intensity at different layers and in different periods of the twenty-four hours

An object	Grouping	Test	*p*		
			December	January	February
Invertebrates (total)	I-D × II-D × III-D	Friedman	0.001	<0.001	ns
	I-D × II-D	Wilcoxon*	0.004	0.009	«
	I-D × III-D	«	0.035	0.009	«
	II-D × III-D	«	ns	ns	«
	I-N× II-N× III-N	Friedman	0.015	«	«
	I-N × II-N	Wilcoxon*	ns	«	«
	I-N × III-N	«	«	«	«
	II-N × III-N	«	«	«	«
	D × N	Wilcoxon	«	0.001	0.005
Mayflies	I-D × II-D × III-D	Friedman	0.007	<0.001	ns
	I-D × II-D	Wilcoxon*	0.004	0.004	«
	I-D × III-D	«	0.026	0.004	«
	II-D × III-D	«	ns	ns	«
	I-N × II-N × III-N	Friedman	0.004	«	«
	I-N × II-N	Wilcoxon*	ns	«	«
	I-N × III-N	«	0.026	«	«
	II-N × III-N	«	0.044	«	«
	D × N	Wilcoxon	ns	0.027	0.024
Dipterans	I-D × II-D × III-D	Friedman	0.002	0.001	ns
	I-D × II-D	Wilcoxon*	0.018	ns	«
	I-D × III-D	«	0.035	0.019	«
	II-D × III-D	«	ns	0.042	«
	I-N × II-N × III-N	Friedman	0.046	ns	«
	I-N × II-N	Wilcoxon*	0.035	«	«
	I-N × III-N	«	ns	«	«
	II-N × III-N	«	«	«	«
	D × N	Wilcoxon	«	0.045	0.003
Water mites	I-D × II-D × III-D	Friedman	0.001	<0.001	–
	I-D × II-D	Wilcoxon*	ns	0.013	–
	I-D × III-D	«	0.035	0.004	–
	II-D × III-D	«	ns	ns	–
	I-N × II-N × III-N	Friedman	«	«	–
	I-N × II-N	Wilcoxon*	«	«	–
	I-N × III-N	«	«	«	–
	II-N × III-N	«	«	«	–
	D × N	Wilcoxon	0.008	0.001	–

(I) bottom, (II) middle, and (III) upper water layers, respectively; (D) daytime, (N) night; *p*-values > 0.05 correspond to non-significant results and are marked as "ns".

* Post hoc comparisons applying the Wilcoxon test with Bonferroni correction.

December revealed significant stratification not only during the daylight, but also at night (Table 1). Moreover, if, for the daytime post-hoc comparisons, the absence of differences only between the middle and upper water layers was confirmed, then, for the night collections, there were no differences between the middle and near-bottom layers (mayflies), or between the near-bottom and upper, middle, and upper water layers (dipterans). Null hypotheses about the absence of differences in abundance at daytime and nighttime were confirmed for both mayflies and dipterans (Table 1).

The diel maximum of migratory activity of water mites was also observed at 12:00. At this time, 1.4 and 2.4 times more representatives of this group were caught in the upper water layer of the stream than in the middle and lower water layers, respectively. In the afternoon, the overall intensity of Hydracarina drift began to decline steadily. As a result, their abundance at the upper, middle, and near-bottom water layers by 20:00 was 7.7, 5.6, and 9.1% of the corresponding midday values. At night, the drift rates of these animals in the entire water column remained stably low. The hypothesis about the absence of differences between the indicators of drift of water mites at different depths was not confirmed only when considering the results of the daylight samples obtained from the near-bottom and upper water layers. In the daytime, significantly more representatives of this group drifted in the Kedrovaya River than in the dark (Table 1).

In January, the overall pattern of drift changed dramatically: the drift intensity was maximal in the near-bottom water layer. During the daylight hours, the number of aquatic invertebrates drifting here was more than 2.5 times higher than the total number of aquatic organisms migrating in the other two water layers. The daytime peak of drifter activity shifted from noon to 14:00. Moreover, the drift rates in the middle and upper water layers were not related to the formation of this peak (insignificant maxima in the abundance of invertebrates in these water layers were recorded at other hours of the daylight). During the period from 14:00 to 18:00, the intensity of the drift in the near-bottom water layer decreased by more than 20 times; these values corresponded to those observed in the middle and upper water layers. As night began, drift rates increased at all three layers, but only slightly. Nighttime maxima in the near-bottom and upper water layers were recorded at 21:00, on average, at 22:00. The hypothesis about the absence of vertical syrton stratification at night in January did not contradict the test results (Table 1). At the same time, only the differences between the drift indices in the middle and upper water layers turned out to be insignificant for daylight hours (Table 1). Most aquatic organisms migrating in January had daylight activity (Table 1).

The intensity of mayfly migrations varied in close correspondence with the diel dynamics of general drift rates at different depths (Fig. 2e). The daily maximum abundance of these insects at 14:00 was also formed exclusively due to drift in the near-bottom water layer. At the same time, the decrease in drift rates here at 14:00–18:00 turned out to be even more significant (by 47 times). At night, the maximum peak of activity of drifting mayflies was recorded at 22:00 in the middle water layer.

In January, the intensity of Diptera drift was also maximal at 14:00; however, dynamics of the vertical distribution of representatives of this group did not coincide with those of mayflies and all invertebrates. In the near-bottom and middle water layers, the largest number of Diptera drifted at 14:00 and 16:00, respectively. In the upper water layer, the diurnal maximum intensity of drift of these invertebrates was confined to the nighttime (21:00).

Regard must be paid to the lowest numbers of drifting water mites in the middle water layer during the daytime, not in the upper one. Moreover, here, unlike the other two water layers, two peaks of their activity were observed during daylight hours: in the morning (at 10:00) and in the evening before sunset (at 18:00). In the upper water layer, the maximum number of representatives of this group was found at noon, while in the near-bottom layer, this peak looked like a small plateau (12:00–14:00). At night, the intensity of migrations of water mites was relatively low, although two small peaks of their numbers were noted near the bottom.

The hypothesis about the uniformity of the vertical distribution of mayflies, dipterans, and water mites in syrton in January turned out to be correct for the data obtained at night (Table 1). In the daytime, significantly more mayflies and water mites drifted in the near-bottom water layer than in the middle and upper water layers, and significantly more dipterans drifted in the near-bottom and middle water layers than in the upper one (Table 1). Representatives of mentioned taxonomic groups of aquatic organisms preferred drifting during daylight hours (Table 1).

Compared to January, the drift in the near-bottom layer noticeably decreased in February, but the drift rates increased both in the middle and upper water layers. Daytime maxima of the total abundance of invertebrates in these water layers were recorded at noon. Nevertheless, during daylight hours, the most pronounced peak of aquatic organism drift intensity was observed near the bottom at 14:00. However, the mentioned peak of activity was no longer the diurnal maximum, as it was in January. In February the maximum diurnal rate of invertebrate drift was recorded at night (22:00) in the middle water layer. Statistical analysis confirmed the hypothesis about the absence of vertical stratification of syrton in February both in the daytime and in the dark. In February, significantly more aquatic invertebrates drifted in the river at night (Table 1).

In February, the vertical distribution of mayflies in the daytime was similar to that observed in January.

Like a month ago, their migratory activity in the near-bottom water layer exceeded that in the middle and upper water layers, but this difference was less contrasting. In January, the number of mayflies that drifted during daylight hours near the bottom exceeded fivefold the total daytime numbers of these animals in the other two water layers, but in February the corresponding ratio was only 1.1. The daytime maximum of the mayfly numbers in the bottom layer at 14:00 (Fig. 2f) contributed the most to the daylight peak of the total number of all drifters (Fig. 2c). By the beginning of the evening twilight, the drift intensity of mayflies near the bottom decreased more than an order of magnitude compared to the daytime maximum. With the onset of the dark time of the day, the drift of mayflies in the middle water layer in February was the most pronounced, with the night (diurnal) maximum recorded at 22:00.

Dipterans, in contrast to mayflies, had slight preference for drift near the surface during daylight hours. The daytime maximum of their migratory activity was recorded at noon. After 12:00 in the upper water layer and after 14:00 in the near-bottom water layer, a monotonous decrease in their drift rate was observed; by 18:00, their drift was most pronounced in the middle water layer. At night, the activity maxima of the drifting representatives of this group were recorded twice: in the middle water layer at 23:00 and in the near-bottom one at 01:00.

Null hypotheses about the uniformity of the vertical distribution of mayflies and dipterans in syrton in February at different times of the day did not contradict the results of statistical analysis. Most of the mayflies and dipterans migrated at night (Table 1).

In the last month of winter, drifting water mites were found sporadically, which makes it impossible to carry out a statistical assessment of the February drift parameters of these animals (Fig. 2l shows the results of actual catches).

Mayflies were the key group forming total drift in each of the winter months (Fig. 2). *Epeorus* sp. (Heptageniidae) and *Drunella* sp. (Ephemerellidae) larvae constantly dominated, which together accounted for 91.8, 84.5, and 73.1% of all mayflies in December, January, and February, respectively. One important feature of larvae of both *Epeorus* sp. and *Drunella* sp. was that their bodies flattened dorsoventrally. Such a flattened shape increases the susceptibility of aquatic organisms to the action of lifting force in the water flow, especially with increasing flow velocity (Weissenberger et al., 1991). For this reason, the emphasis on the drift of these larvae (model drifters) could contribute to the interpretation of the inversion of the vertical distribution of syrton that occurred in January. Moreover, due to the slowdown in growth processes at low winter temperatures, the average mass of drifting larvae of *Epeorus* sp. (<0.25 mg) and *Drunella* sp. (<0.10 mg) did not actually change during the study period (Kruskal–Wallis test, all $p > 0.05$). Such a constancy of the weight of a drifting object made it possible to exclude the influence of this indicator on the specificity of the transfer of such an object by a water flow. Consequently, the probability of a "pure" assessment of possible correlations between the number of drifters and flow parameters increased in order to identify the leading factor. The average flow velocity, water density, water viscosity, and Reynolds numbers in different months and periods of the day were chosen as such parameters.

According to our calculations, the average water density and viscosity varied within the following limits (day–night): 999.88–999.86 kg/m^3 and 0.001754–0.001771 Pa · s (December), 999.86–999.85 kg/m^3 and 0.001771–0.001782 Pa · s (January), and 999.86–999.85 kg/m^3 and 0.001768–0.001784 Pa · s (February). According to the Reynolds numbers (Table 2), the lowest turbulent exchange was in January. This increased the probability of accumulation of drifting larvae mainly in the near-bottom water layer. However, we failed to establish statistically significant relationships between the number of model drifters at different depths and the mentioned hydraulic parameters (Kendall's τ correlation, all $p > 0.05$).

DISCUSSION

The invertebrate drift in winter is characterized by a minimum intensity in the watercourses of the temperate zone of both the Northern and Southern hemispheres (McLay, 1968; Clifford, 1972; Bogatov and Astakhov, 2011). As a rule, at this season the lowest stream discharge is observed; the processes of growth and development of aquatic organisms are slowed down due to the low temperature of the environment. Low metabolism, which is characteristic of ectotherms in winter, also negatively affects the foraging activity of drift-feeding fish, the main consumers of syrton. Moreover, a low metabolic rate significantly limits the swimming ability of fish in winter, thereby making them more vulnerable to endothermic semi-aquatic predators (Fraser et al., 1993; Heggenes et al., 2018). In the Kedrovaya River, such predators include the grey heron *Ardea cinerea* (Linnaeus), American mink *Neovison vison* (Schreber), and Eurasian otter *Lutra lutra* (Linnaeus). In winter, juvenile fish in salmon rivers mainly switch to nocturnal activity to avoid the risk of predation (Valdimarsson and Metcalfe, 1998; Heggenes et al., 2018), leading a sedentary lifestyle during the day and hiding among the elements of the bottom substrate (Semenchenko, 1977; Esin et al., 2009). Also, at low temperatures, it is more profitable for fish to consume zoobenthos at night directly from the bottom, which excludes energy expenditure on maintaining their position in the flow when feeding on drifters (Heggenes et al. al., 2018). Consequently, for benthic invertebrates, which during the warm season drift mainly at night (Klyuchareva, 1963;

Table 2. Mean values of Reynolds numbers (Re ± SD)

Water layer	December	January	February
III	$\frac{25647 \pm 46}{25408 \pm 57}$	$\frac{20327 \pm 111}{20203 \pm 40}$	$\frac{37318 \pm 158}{36994 \pm 31}$
II	$\frac{15958 \pm 29}{15809 \pm 35}$	$\frac{14116 \pm 77}{14030 \pm 28}$	$\frac{25161 \pm 107}{24943 \pm 21}$
I	$\frac{8549 \pm 15}{8469 \pm 19}$	$\frac{8187 \pm 45}{8137 \pm 16}$	$\frac{19224 \pm 82}{19058 \pm 16}$

Values above the line refer to day hours and those below the line refer to night.

Naman et al., 2016), in winter using nighttime to avoid visually-oriented drift-feeding fish becomes less relevant. In this case, the probability of equalization of the invertebrate drift intensity in daytime and nighttime increases, similar to that in fishless watercourses (Malmqvist, 1988; Flecker, 1992; Douglas et al., 1994).

Indeed, although with the onset of cold weather, more and more drifters prefer migration during daylight hours (Astakhov, 2009; Bogatov and Astakhov, 2011), generally they switched migration patterns from predominantly nocturnal to daytime only in January. The predominance of daytime drift over nighttime one in December turned out to be statistically insignificant. Throughout the winter, some species, such as the larvae of the mayfly *Leptophlebia chocolata* Imanishi (Leptophlebiidae), retain the nocturnal type of drifting usual for them during other seasons of the year. At the same time, amphipods *Gammarus koreanus* Uéno (Gammaridae) and water beetles *Hydraena flavomarginata* Shatr. (Hydraenidae), which during the warm period of the year may drift at any time, have been noted in winter exclusively among nocturnal migrants. Of the other invertebrates, which mainly adhered to the tactics of night drift, the most numerous were the larvae of stoneflies *Taenionema japonicum* Okamoto (Taeniopterygidae) and *Amphinemura* sp. (Nemouridae), as well as copepods *Eucyclops* sp. (Cyclopidae). It should be noted that previously the persistent adherence of Leptophlebia larvae to nocturnal drifting was observed in one of the Canadian watercourses, where also in December, during the light and dark periods, approximately the same number of invertebrates drifted (Clifford, 1972).

The amount of snow precipitation was insignificant during the first two and a half winter months in the river basin, so the snow cover height on the river ice did not exceed 0.10–0.15 m until mid-February, and in the sites with the fastest current there were polynyas with traces of semiaquatic endothermic predators. At the same time, the illumination of the water column was quite high in the daytime. However, a heavy snowfall occurred a day before the date of sampling in February; as a result, all the polynyas were hidden, and the height of the snow cover on the river ice exceeded 0.6 m. This led to a sharp drop in the daytime illumination of the water column to a level that approximately corresponded to the late twilight. Under such conditions, the intensity of daytime drift, which prevailed among the drifters of the Kedrovaya River from mid-January, has also dropped sharply and became lower than the values obtained at nighttime. It is possible that, in this case, the reason for the decrease in the migratory activity of drifters during the daytime could be an increase in the activity of fish, which became less accessible to semiaquatic predators due to deep snow. In contrast to the results obtained at the Bolshaya River (Travina, 2014), the increase in the depth of snow cover on the ice of the Kedrovaya River did not lead to a decrease in the total drift rate of invertebrates. On the contrary, even more drifters were registered in February in the Kedrovaya River compared to January.

The vertical distribution of drifting animals is closely related to the hydraulic structure of the flow (McNair et al., 1997). Obviously, both simple (e.g., current velocity, depth, water density, and water viscosity) and complex (e.g., Reynolds number) hydraulic characteristics are useful in assessing relationships between the structure of aquatic communities and their habitat (Statzner et al., 1988). In particular, as the Reynolds number (which is a sign of the turbulence of a free flow) increases, the turbulent exchange coefficient increases, as does the lifting force acting on particles suspended in the water column. It has been established, that at an average flow velocity of 0.45 m/s, the velocity of ascending water currents reaches 0.012 m/s (Taradina et al., 1997). It is important that the transfer of suspended particles by a water stream depends on its temperature, a factor that changes the water density and viscosity and, hence, its supporting properties. A temperature decrease leads to an increase in the transport capacity of the flow and to an increase in the content of suspended matter along the longitudinal profile (Alekseevsky, 2006). According to experiments, it takes longer to leave the drift and return to the substrate for the larvae of mayflies at 4°C than at 14°C (McLay, 1970).

However, the process of transport of animals by the flow may be influenced by their own behavior and their ability to swim, change their buoyancy, and control their position in space, in addition to their physical properties such as size, shape, specific gravity, and center of gravity (McLay, 1970; Oldmeadow et al., 2010; Pavlov and Skorobogatov, 2014). For example, mayfly nymphs begin to actively leave the drift and settle to the bottom as the speed of the current increases (Elliott, 1971; Allan and Feifarek, 1989). On the contrary, as the current velocity decreases, mayflies of different families not only swim upwards and/or take a “parachuting” pose, but even insert their limbs into the surface tension film in order to increase their time spent in drifting (Campbell, 1985; Allan and Feifarek, 1989).). A stonefly nymph “attaches” its head capsule and antennae to the surface tension film for a similar purpose (Madsen, 1969).

The heterogeneity of the vertical distribution of drifters by depth in the daytime and at night may evidence in favor of the fact that the formation of a syrton is largely determined by the voluntary transition of benthic organisms into the water column (Konstantinov, 1969). This is especially clearly demonstrated by the results of works on relatively deep rivers, where the "sudden" but regular (within the circadian rhythm) appearance of a large number of bottom aquatic organisms near the water surface is difficult to explain only as a consequence of random washout and turbulence. In particular, vertical migrations in mayflies, stoneflies, chironomids, and caddisflies at early stages of development have been proven on the material of the catches in the near-bottom and upper water layers of the Amur River at sections with depths of 10–31 m (Levanidov and Levanidova, 1979). According to these authors, at night at the surface drifted 9, 3 and 4 times, and at the bottom – 4, 2 and 3 times more caddisflies, mayflies, and stoneflies than in the daylight. Moreover, mayflies during the twenty-four hours were more numerous in the upper water layer than in the deep ones, while stoneflies and chironomids showed the opposite trend. The drift of caddisflies during daylight hours was more pronounced in the lower water layer of the river and, at night, in the upper one. In general, in the Amur River, the total intensity of near-bottom drift exceeded that of near-surface drift by about a third. A slightly different picture was obtained by same authors at one of the large river of the Amur River basin. In that river, at sections with depths of 3.5–5 m, the most of benthic invertebrates was caught in the upper water layer, at night, and the number of mayfly larvae from the near-bottom water layer was almost always 4–5 times lower than in the upper layer (Levanidova and Levanidov, 1965).

In the main channel of the Volga River, the number of drifting oligochaetes and amphibiotic insect larvae in the daytime was approximately twice as high near the bottom comparing to that near the surface, while at night the pattern was the opposite (Konstantinov, 1969). As the flow rate decreased during the transition from the main channel to the backwater, the diurnal inversion in the stratification of syrton became more pronounced.

The vertical redistribution through the water column at different periods of the twenty-four hours is performed not only by drifting invertebrates. In the Otava River basin, as a rule, the drift of larval fish from different families was more intense at night near the surface than at medium depth and near the bottom, while the opposite pattern was observed during the daytime (D'Amours et al., 2001).

A statistical analysis of our materials from the Kedrovaya River showed that at the beginning of winter (December) the larvae of mayflies and dipterans preferred to drift in the upper and middle water layers even during daylight hours. This fact is probably associated with a decrease in the swimming ability of drift-feeding fish preconditioned by lowering water temperature; for this reason, fish avoided active foraging during the day, since they became easily accessible by endothermic semiaquatic predators. With a decrease of water and air daytime temperature to the minimum values (January), invertebrates that drifted in the daylight began to concentrate significantly more in the near-bottom water layer. Due to a sharp drop in under-ice illumination due to a significant increase of snow cover height after a heavy snowfall (February), the vertical distribution of invertebrates through the water column throughout the twenty-four hours became quite uniform. Nevertheless, mayfly tended to drift near the bottom during the daytime.

Significant differences in the vertical distribution of syrton depending on the time of day were also found in the Mississippi River (Matter and Hopwood, 1980). At night, the average catches of mayfly larvae from the upper water layer exceeded those from the lower water layer more than twice; on the contrary, the catches of caddisfly larvae were twice as high near the bottom. In the daytime, the larvae of mayflies did not tend to keep in a certain water layer, while the larvae of caddisflies were more common in the lowest water layer. The observed "asymmetric" vertical distribution of drifting representatives of different taxa was explained by the differences in their swimming ability (Matter and Hopwood, 1980). A slightly different conclusion was drawn after summarizing the materials of weekly daytime collections conducted throughout the year in a small river in Italy (Fenoglio et al., 2004). According to these researchers, the vertical stratification of syrton was due to the behavioral characteristics of drifters of different taxonomic groups. For example, water mites are crawling animals, so they tend to drift near the bottom. However, according to other data, obtained during the year from one of the Canadian streams, significantly more water mites were drifting near the surface (Clifford, 1972). In the Kedrovaya River, water mites could prevail both in the upper (December) and near-bottom (January) water layers under different conditions, although such preferences were evident only during daylight hours.

It is worth noting that a tendency to keep at a certain water layer may depend on the stage of the drifter's life cycle. For example, at the larval stage, chironomids may show only a slight tendency to drift near the surface, while at the pupal stage they already significantly dominate in the upper water layer (Clifford, 1972). In later works, it was also shown that chironomid pupae and last instar larvae, drift mainly near the surface (Bogatov and Astakhov, 2013; Astakhov and Bogatov, 2014). Perhaps, in some cases, it is the connection of the vertical structure of the sirton with the share of participation of drifters in it at one stage or another of development that causes the ambiguity of the information given in the literature. According to various researchers, drifting larvae of caddisflies

(Hydropsychidae family) may be associated mainly with the near-bottom water layer (Matter and Hopwood, 1980) or upper water layer (Crisp and Gledhill, 1970; Fenoglio et al., 2004), and the drifting larvae of blackflies tend to drift near the bottom (Clifford, 1972), near the surface (Fenoglio et al., 2004), or they are evenly distributed through the water column (Crisp and Gledhill, 1970). However, the very fact that drifters of one or another taxonomic affiliation, for the most part, have the ability to occupy a certain layer of the water column under the conditions of a particular watercourse, indicates the voluntary nature of their vertical moving and maintaining their position in three-dimensional space.

Obviously, animals with negative buoyancy tend to migrate close to the bottom more often. Nevertheless, under certain circumstances, aquatic organisms, which are traditionally considered to be purely near-bottom migrants, may drift and even dominate in the upper water layer. For example, sturgeon larvae are characterized by negative buoyancy; however, in the first 3 days after hatching, they exhibit positive phototaxis and periodically move upward from the bottom, performing active movements of the posterior part of the body (Gisbert and Williot, 1997). Similar vertical “jumps” are characteristic of the larvae of various fish (Copp et al., 2002; Koporikov and Bogdanov, 2019). In combination with turbulent exchange, this behavior promotes individuals with both positive and negative buoyancy to drift near the watercourse surface (Pavlov and Skorobogatov, 2014). In this case, as the turbulence decreases along the longitudinal profile of the watercourse, an inversion of the vertical distribution of drifters with negative buoyancy, and their concentration in the near-bottom layer of water, should occur in the areas located further and further downstream. This may explain the pronounced predominantly near-bottom drift in the Kedrovaya River observed in the daytime in January. However, this is only a hypothesis. We do not know anything about the intensity of turbulent exchange upstream of the sampling site and about the intravital buoyancy of migrants during the daylight in January. At the same time, one should not exclude the possibility of a direct influence of air temperature on invertebrates drifting near the surface. For example, the daytime temperature of the water column in January did not differ significantly from that in February. However, due to the greater openness of the river channel in January, the degree of the suppressing effect of negative (and significantly lower) air temperature on the total abundance of daytime drifters near the water surface could be much more substantial than immediately after the snowfall in February.

CONCLUSIONS

The use of a sampler, which allows one to differentially catch of drifters within water layers, made it possible to reveal the presence of vertical stratification of the winter syrton in a river section with a depth of only 0.3 m. Verification of the key assumption (rarely tested in drift studies) about the presence of a significant linear dependence of the number of drifters in catches on the volume of water filtered by nets showed the absence of such a dependence. For this reason, only data on actual net catches were used in the calculations. Larvae of mayflies and dipterous insects, as well as water mites, predominated. Drifters of different taxonomic groups were distributed variously through the water column. We assumed that the tendency of a drifter to keep in one or another water layer may depend on its particular life cycle stage. The number of daytime winter drifters increased at good illumination. This may be due to the low foraging activity of drift-feeding fish, which leads a secretive lifestyle during the daylight due to their decreased swimming ability at winter water temperatures, thereby reducing the risk of attack by piscivorous endothermic predators. In general, the tendency of most drifting representatives of a particular taxa to occupy a certain layer of the water column during migrations may indicate the voluntary nature of drifting of these animals.

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COMPLIANCE WITH ETHICAL STANDARDS

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