

Export of Biomass and Metals from Aquatic to Terrestrial Ecosystems via the Emergence of Dragonflies (Insecta: Odonata)

O. N. Popova^{a, *}, A. Yu. Haritonov^{a, †}, O. V. Anishchenko^{b, **}, and M. I. Gladyshev^{b, c, ***}

^a*Institute of Systematics and Ecology of Animals, Siberian Branch, Russian Academy of Sciences, ul. Frunze 11, Novosibirsk, 630091 Russia*

^b*Institute of Biophysics, Siberian Branch, Russian Academy of Sciences, Akademgorodok, Krasnoyarsk, 660036 Russia*

^c*Siberian Federal University, pr. Svobody 79, Krasnoyarsk, 660041 Russia*

*e-mail: *popova-2012@yandex.ru, **hydrakr@rambler.ru, ***glad@ibp.ru*

Received September 13, 2015; in final form, October 05, 2015

Abstract—Long-term monitoring of the abundance and spatial distribution of 18 widespread species of Odonata has made it possible to assess their contribution to the export of aquatic productivity that entered the Barabinsk forest-steppe ecosystem. The annual emergence of Odonata varies from 0.8 to 4.9 g/m² of the land area and from 2.3 to 13.3 g/m² of the water area, which is 4–5 times larger than that in Diptera. The total flux of organic matter from water to terrestrial ecosystems remains relatively stable (sixfold interannual variability) irrespective of large interannual variations in the abundance of separate species (e.g., 42-fold interannual variability in *Libellula quadrimaculata*). The metal content was determined in nine Odonata species. Export of metals by dragonflies decreases in the series K > Na > Mg > Ca > Fe > Zn > Cu > Mn > Pb > Ni > Cr > Cd. Therefore, odonates appear to be quantitatively and qualitatively important providers of aquatic resources to the forest-steppe landscape of Western Siberia.

Keywords: Odonata, long-term ecological monitoring, emergence, abundance, biomass, metals, Barabinsk forest steppe, Western Siberia

DOI: 10.1134/S1995425516040090

INTRODUCTION

The principle of the existence of any ecosystem is based on the permanent movement of fluxes of organic matter, energy, and information in trophic chains (Lekyavichus, 1986; Alimov, 2000). The transfer of matter along the gradient of an abiogenic runoff, i.e., from terrestrial to water ecosystems, has been studied most deeply, while its transfer against the gradient of the runoff has been studied rather fragmentarily (Gratton and Vander Zanden, 2009). Amphibiotic insects (whose preimaginal phases develop in water, while imagoes have a terrestrial mode of life) are one of the main biogenic factors of the return of many chemical elements from topographic lowlands (water bodies) to plakor areas (Baxter et al., 2005; Ballinger and Lake, 2006; Gratton and Vander Zanden, 2009). In some landscapes, the export of aquatic resources during the emergence of amphibiont insects may be comparable to the productivity of terrestrial insects or even be higher (Gratton and Vander Zanden, 2009).

Although a conceptual model generalizing all reliable data on the flux of aquatic resources via the emergence of amphibiotic insects has been proposed quite

recently (Gratton and Vander Zanden, 2009), it has a number of limitations: (1) it is not intended for making predictions with respect to specific areas or regions; (2) the calculated mean values of dispersion of aquatic insects from the shore are underestimated, being no more than 100 m; and (3) the basic volume of data was obtained from watercourses. According to this generalization, Diptera constitute 60–99% of the emerging biomass, followed by Ephemeroptera, Plecoptera, and Trichoptera in decreasing order, and Odonata ranks last (Gratton and Vander Zanden, 2009).

At the same time, due to a number of biological and ecological features, odonates are of substantial interest for productive ecology. First, over the period of larval development in a water body (from several months to several years), a significant reserve of organic matter in terms of amount and quality accumulates in the body of larvae. Second, the morphophysiological organization and mode of life of odonate imagoes determine their high mobility: they can disperse tens of kilometers (some species even hundreds of kilometers) from native water bodies (Haritonov and Popova, 2011a, 2011b), thereby contributing to dispersion of organic matter over a large land area. Third, Odonata colonize almost all types of

[†] Deceased.

freshwater bodies, and a greater portion of species inhabit temporary water bodies, such as ditches, puddles, and bogs (Clark and Samways, 1996; Harabis and Dolny, 2010; Haritonov and Popova, 2011a). Thus, in some landscapes, e.g., in steppes, where a greater part of water bodies are temporary puddles and boggy areas, and in areas with high fluctuations of the level of water content (e.g., Barabinsk forest steppe), odonates may also be a quantitatively important group of amphibiotic insects. Therefore, the main purpose of our research was to assess the export of water ecosystem productivity by dragonflies to terrestrial cenoses in a specific landscape, namely, the Barabinsk forest steppe in the southeast of Western Siberia.

In addition to the export of organic carbon, representing a source of food for terrestrial consumers, the biomass that is exported from water ecosystems also contains other nutrient and toxic elements, e.g., heavy metals (HMs). HMs may accumulate in higher levels of trophic chains, thereby posing potential danger for human health (Zhou et al., 1998; Gladyshev et al., 2009). The content of HMs is generally determined in amphibiotic insect larvae to monitor the water quality (Nummelin et al., 2007; Lavilla et al., 2010; Corbi and Froehlich, 2010; Corbi et al., 2011); however, there are limited data on HMs (Scheuhammer et al., 1997; Nummelin et al., 2007; Boron and Mirosławski, 2009; Burghelca et al., 2011). There are single studies that estimate export of metals, including nonessential metals, by amphibiotic insects, including Odonata, to the land area (Currie et al., 1997). Therefore, the second purpose of our research was to measure the metal content in odonate imagoes and assess the export of metals by emerging dragonflies in a specific landscape. In our work, we did not seek to reveal the largest possible number of chemical elements and focused only on elements that are the most significant for the ecosystem, both from the general biological and toxicological points of view: K, Na, Ca, Mg, Fe, Cu, Zn, Mn, Ni, Cr, Pb, and Cd.

MATERIALS AND METHODS

Study site. The studies were carried out in the southeast of Western Siberia, in the Barabinsk forest steppe, in the basin of Lake Chany. The climate of the region is continental. The average temperature of the coldest month, i.e., January, is about -20°C , and the average temperature of the hottest month, i.e., July, is over $+18^{\circ}\text{C}$. The frostless vegetation period is short, being 112 days, on average. The annual amount of precipitation is about 350 mm; the relative air humidity is about 50–60%. The rainiest month is July. The average annual wind velocity is about 5 m/s. The annual solar radiation is about 4000 MJ/m^2 (*Prirodnye...*, 1963). The plain landscapes alternate with ridges and islets occupied by birch and birch–aspen forests with the undergrowth of bird cherry, brier, and other bushes. A greater part of the area is presented by a

flood-meadow and meadow-solonchak forest steppe, plowlands, and fallows. The Barabinsk forest steppe is the most depressed (so-called Chany depression) and, accordingly, boggiest area in the forest steppe of Western Siberia and is distinguished by a high water-reserve level (30% of the total area) and an unstable water regime (*Prirodnye...*, 1963).

The investigated place is in Novosibirsk oblast, ($54^{\circ}32'–54^{\circ}39' \text{ N}$ and $78^{\circ}06'–78^{\circ}19' \text{ E}$), occupies the area of 272 km^2 , and is adjacent to the northeastern shore of Lake Malye Chany. The areas of different biotopes were calculated using satellite images in the Image 2010 Terra Metrics system, as well as 1-km scale maps and aerial photographs, and we also measured distances and angles directly in situ. As a result, it was established that the water-covered area—lakes, rivers, ponds, ditches, puddles, and bogs (including reed beds)—is 82 km^2 , of which only 69 km^2 serve as a habitat for odonate larvae (further referred to as an odonatogenic water area). Odonate larvae are absent or their number is very low outside the odonatogenic water area, namely, in bitter lakes (2 km^2) and water body sites without aquatic vegetation (11 km^2) (Popova and Haritonov, 2012). Within the land area (190 km^2), we selected seven biotopes, in which quantitative samples of imagoes were regularly performed: (1) wet lowland meadows (87 km^2), (2) steppe meadows and fallows (61 km^2), (3) tillage (19 km^2), (4) birch and birch–aspen groves (8 km^2), (5) shrubs (11 km^2), (6) shelterbelts (3.5 km^2), and (7) earth roads (0.5 km^2).

Object of research. The Barabinsk forest steppe is inhabited by 42 of the 68 odonate species generally known for the forest steppe of Western Siberia (Popova, 2007). To calculate products exported by odonates to the terrestrial ecosystems under study, we sampled 18 mass and middle-abundance species, which constitute 95–98% of both the abundance and biomass of dragonflies: suborder Zygoptera—*Coenagrion lunulatum* (Charpentier, 1840), *C. armatum* (Charpentier, 1840), *C. pulchellum* (V.d. Linden, 1823), *Enallagma cyathigerum* (Charpentier, 1840), *Erythromma najas* (Hansemann, 1823), *Lestes dryas* Kirby, 1890, *L. sponsa* (Hansemann, 1823), *L. virens* (Charpentier, 1825), and *Sympecma paedisca* (Brauer, 1877); suborder Anisoptera—*Aeshna mixta* Latreille, 1805, *A. serrata* Hagen, 1856, *Leucorrhinia pectoralis* (Charpentier, 1825), *L. rubicunda* (Linnaeus, 1758), *Libellula quadrimaculata* Linnaeus, 1758, *Sympetrum danae* (Sulzer, 1776), *S. flaveolum* (Linnaeus, 1758), *S. sanguineum* (Müller, 1764), and *S. vulgatum* (Linnaeus, 1758).

Quantitative samples of imagoes and their methods. In total, we performed 16721 quantitative samples in the land area over the period of 31 years from 1980 to 2010, in which 614120 Odonata imagoes were recorded. The counts were performed every year throughout the entire flying period of Odonata, i.e., from May to October. There is a brief description of

four methods of imago sampling that we applied and that are generally accepted in the population ecology of insects, including dragonflies (Kozhanchikov, 1961; Paliy, 1970; Popova and Haritonov, 2012, 2014a; Corbet 1952, 1999; Parr, 1972; Conrad et al., 1999; Bried and Ervin, 2006).

Capture—Mark—Recapture. This sampling method is the main one, since it provides the most reliable results on the density of odonate population and is applicable to all investigated species (Popova and Haritonov, 2010, 2014; Corbet, 1952; Parr, 1972). On the sampling site with certain area a (from 2000 to 15000 m², depending on the mobility of the species), odonate imago individuals in the number of M were caught for several hours (usually in the morning) using an air net; each individual was marked with red water-resistant paint directly after capture, followed by its immediate release. On the next day, n individuals were repeatedly caught, with m previously marked individuals being present among them. The abundance N (ind./m²) was calculated by formula:

$$N = [M \times (n + 1)/(m + 1)]/a. \quad (1)$$

Belt transect (route). This method is generally used for recording odonates from suborder Anisoptera and represents visual sampling on a belt with a predetermined length and a predetermined width. During sunny weather without strong winds, the observer goes along the belt on foot or by transport with a velocity of about 4 km/h and counts all odonates (species and number of individuals) that fly up or cross the sampling belt by recording the information on a voice recorder. In our research, the transects almost completely coincided with earth roads and also crossed all the biotopes under study. A total of eight transects were used, with a length from 1375 to 5750 m and a width of 2 m each. Accordingly, the maximum area of the sampling belt was 5750 m × 2 m = 11500 m². Samples were taken on the transects every two to ten days throughout the season. The results of sampling on transects and counts based on marking and recapture were rather similar (Haritonov and Popova, 2011a).

Entomological net mowing the grass. This method is generally applied for recording odonates of suborder Zygoptera. While moving forward on the site, the observer makes one sweep by a net once per step. Provided that the diameter of the net ring was 30 cm, every 100 sweeps covered the area of 30 m². The number of the collected individuals was multiplied by 2, since simultaneous calculations established that the net captured no more than a half of individuals present on the site being mowed, while about a half of them managed to fly away or dispersed aside, being knocked down by the net or grass stalks.

Capture during timed fifteen-minute intervals. Capturing the insects by an air-net during a certain time interval is one of the standard methods to determine the relative abundance of insects (Paliy, 1970). The

method can be applied for recording all Odonata. We generally used it for studying the biotopical confinement of species and the seasonal and diurnal dynamics of their abundance. Odonates were caught with a net on a site of about 500 m² for 15 minutes. While moving slowly along the perimeter of the site and then along and across the site, the observer carefully examined the grass stand and the space above it and methodically and sequentially caught all detected damselflies (both sitting and flying ones) and put them into a closing vessel.

Selecting the time and place for sampling took into account the features of odonate life activity: response to weather conditions, diurnal and seasonal activity, biotopical preferences, and flying capabilities. All sampling sites were more or less evenly distributed over the seven main biotopes in the area under study. The counts based on capture—mark—recapture methods and entomological mowing and capture during timed intervals were made on 74 sampling sites with 3–12 times for each of them per season.

Estimating the abundance of odonates involved all four methods of sampling, since each of them has its own taxonomic, biotopical, and functional specifics and is different in the accuracy of final results and in use efficiency.

To calculate the wet weight, 30–70 living juvenile individuals (males and females) per individual were weighed and the average wet weight with an accuracy of ±1–20 mg was determined. To calculate the dry weight, the same insects were dried at a temperature of 80°C for 24 h, followed by their weighing with an accuracy of ±0–6 mg.

After recording and identification, most of the caught individuals were released back to the natural environment and a small number of individuals were used for morphometry, weighing, and chemical analysis.

The period of mass emergence (PME, days/year) of each species was determined by monitoring the abundance of imagoes on the sampling sites located in the vicinity of the near-shore area that is overgrown with helophytes, hygrophytes (water edge plants), and hygrophytes and serves as a zone for odonate emergence. In addition, we used the above-described method of imago capture for 15 min. By the beginning of the PME, we assumed the date when the species was presented in a number of no less than three individuals in sampling and its relative abundance reached 5% of the total number of individuals in sampling (Pesenko, 1982), while by the end of the PME we assumed the date when the species was presented in a number of less than three individuals in sampling, and its relative abundance was less than 5%, respectively. Using the data of all the near-shore sites, we calculated the average duration of the PME for each species and for each year. The long-term annual average duration of the

PME over the period from 1980 to 2010 was then calculated.

The lifetime of imagoes (LTI) of each species was measured by two methods. (1) *Imago mark*, which makes it possible to establish the ecological LTI (Gavrilov and Gavrilova, 1991). Individual and data-specific marks were put on the wings of young imagoes soon after their emergence, but not before cuticle hardening, and the marked individuals were then monitored over the period of the flying season during local and route counts (Pajunen 1962; Ubukata, 1981; Bennett and Mill, 1995). (2) *Content in cages*, which makes it possible to determine the physiological (species) LTI (Gavrilov and Gavrilova, 1991). The newly emerged imagoes were placed into a $1 \times 1 \times 1$ m cage covered with a fine-meshed screen. Plant branches were attached to the cage bottom as roosts for odonates. The cages with odonates were located in a well-ventilated room under natural lighting. The odonates were fed with different insects and spiders once a day. For each individual, the time interval from the date of its emergence to the date of its death in the cage was assumed to be its lifetime. The LTI values obtained by these two methods were rather similar.

Calculation of Imago Emergence

The quantitative estimate of the emergence of odonate imagoes included a calculation of the abundance, biomass, and Haritonov's coefficient. All calculations were first made separately for each species and for each year (season) on the basis of all the performed quantitative samples. The number of samples per year varied from 394 to 850. All the following calculations provide an opportunity to estimate the emergence of Odonata imagoes per unit of the study land area. To estimate the emergence from unit of the water area being studied, we used the coefficient equal to the ratio of the land area to the odonatogenic water area: $190/69 \text{ km}^2 = 2.75$.

The average annual abundance of each species, N_{YS} ($1 \times 10^6 \text{ ind./km}^2$ or ind./m^2), within the entire investigated area was calculated by the following formula:

$$N_{YS} = \sum_{i=1}^7 N_{Si} A_i / \sum_{i=1}^7 A_i \quad (2)$$

That is, the average abundance of species S within biotope i (from the total of seven biotopes) was first calculated; for this purpose, the average annual density of the population in the biotope, N_{Si} ($1 \times 10^6 \text{ ind./km}^2 = \text{ind./m}^2$), was multiplied by the biotope area A_i (km^2 or m^2); the abundances of all seven biotopes were then summed up and this sum was

divided into the entire area under study, $\sum_{i=1}^7 A_i = 190 \text{ km}^2$.

The total average annual abundance, N_Y ($1 \times 10^6 \text{ ind./km}^2 = \text{ind./m}^2$), made up the sum of average annual abundances, N_{YS} , of all 18 odonate species.

The average annual abundance reflects only a portion of the entire number of dragonflies that emerged from water bodies, since the period of emergence is elongated for several weeks and even months and generally exceeds the average duration of individual imago life. As a result, several sets (fluxes) of imagoes of the same species consistently pass through the same territory during the season.

Therefore, the annual emergence of the species, i.e., the number of individuals of the species of Odonata that emerged to the study land area over the whole year, E_S ($\text{ind./m}^2 \text{ year}$), was calculated by the following formula:

$$E_S = N_{YS} R_S \quad (3)$$

where N_{YS} is the average annual abundance of the species, R_S (year^{-1}) is the coefficient of renewability of fluxes of the species imago. This coefficient was introduced in odonate ecology by A. Yu. Haritonov and was calculated by the following formula:

$$R_S = D_S / L_S$$

where D_S is the duration of the period of mass emergence of species S per year (days/year) and L_S is the lifetime of imago (days) of the species under consideration (S); their calculations are given above.

The total annual emergence of the odonate population, E_Y ($\text{ind./m}^2 \text{ year}$), makes up the sum of the total annual emergences E_S of all 18 species.

The total annual emergence biomass of the odonate population, B_Y ($\text{g/m}^2 \text{ year}$) or $\text{t/(km}^2 \text{ year)}$), was calculated by the following formula:

$$B_Y = \sum_{S=1}^{18} E_S B_S \quad (4)$$

where E_S is the annual emergence and B_S is the average biomass of species S.

Determination of Metal Content in Odonate Imagoes

To determine the total content of metals, preliminarily dried samples were ground in an agate mortar and then held at 105°C until they reached constant weight. The samples (0.2–0.6 g) were digested by heating in a mixture of nitric and perchloric acids (1 : 1) and diluted to 15 mL by distilled water. To determine Ca and Mg, the samples were diluted in the ratio of 1 mL of LaCl_3 solution (the mass concentration of La was 20 g/L) and 8 mL of distilled water per 1 mL of ashed sample. The calibration standards also contained the necessary addition of LaCl_3 .

Concentrations of Na and K were determined on a FLAPHO-4 flame photometer (Carl Zeiss, Jena) in

Table 1. Odonate emergence in the investigated land area, Barabinsk forest steppe, Western Siberia

Species	Abundance, ind./(m^2 year)		Wet biomass, mg/(m^2 year)		Dry biomass, mg/(m^2 year)	
	$M \pm m$	min–max	$M \pm m$	min–max	$M \pm m$	min–max
<i>Coenagrion armatum</i>	1.55 ± 0.16	0.53–3.96	47 ± 5	16–120	14 ± 1	5–36
<i>Coenagrion lunulatum</i>	2.86 ± 0.7	0.40–20.30	91 ± 25	13–650	32 ± 9	4–220
<i>Coenagrion pulchellum</i>	1.14 ± 0.08	0.40–2.12	34 ± 2	12–64	10 ± 1	4–19
<i>Enallagma cyathigerum</i>	5.79 ± 0.85	0.62–26.83	197 ± 29	21–912	67 ± 10	7–322
<i>Erythromma najas</i>	1.35 ± 0.23	0.35–7.36	6 ± 1	2–31	19 ± 3	5–103
<i>Lestes dryas</i>	0.64 ± 0.06	0.16–1.63	30 ± 3	8–7	79 ± 1	2–23
<i>Lestes sponsa</i>	3.00 ± 0.17	1.00–5.30	129 ± 7	43–228	39 ± 2	13–69
<i>Lestes virens</i>	0.63 ± 0.06	0.24–1.45	18 ± 2	7–42	6 ± 1	2–13
<i>Sympecma paedisca</i>	1.87 ± 0.09	0.46–2.66	58 ± 3	14–83	19 ± 1	5–27
<i>Aeshna mixta</i>	0.12 ± 0.01	0.03–0.20	52 ± 4	13–88	16 ± 1	4–28
<i>Aeshna serrata</i>	0.15 ± 0.01	0.08–0.29	119 ± 7	58–222	37 ± 2	18–69
<i>Leucorrhinia pectoralis</i>	0.45 ± 0.04	0.10–0.87	89 ± 7	21–170	27 ± 2	6–53
<i>Leucorrhinia rubicunda</i>	0.46 ± 0.05	0.09–1.20	86 ± 10	16–224	26 ± 3	5–69
<i>Libellula quadrimaculata</i>	1.12 ± 0.18	0.12–5.00	356 ± 59	38–1600	95 ± 16	10–430
<i>Sympetrum danae</i>	1.20 ± 0.07	0.50–2.12	108 ± 7	45–191	32 ± 2	13–57
<i>Sympetrum flaveolum</i>	1.94 ± 0.17	0.38–3.88	204 ± 18	40–407	64 ± 6	12–128
<i>Sympetrum sanguineum</i>	0.22 ± 0.02	0.03–0.56	25 ± 3	3–64	8 ± 1	1–20
<i>Sympetrum vulgatum</i>	2.96 ± 0.21	0.68–7.22	447 ± 32	103–1090	130 ± 9	30–318
Total	27.47 ± 2.09	9.99–77.59	2147 ± 132	843–4856	650 ± 40	252–1493

M , mean value for 31 years; m , standard error of mean; min, minimum value; and max, maximum value.

the propane-air flame (GOST 30503-97 and GOST 30504-97). Ca and Mg were determined by the atomic absorption method in the air-acetylene flame using a Solaar M5 spectrophotometer (Thermo Electron, United States) (GOST 26570-95 and GOST 30502-97) and Fe, Mn, Zn, Cu, Cr, Ni, Cd, and Pb were determined by an AAS Kvant-2A photometer (GOST 30692-2000). The detection limits (mg/L) were 0.1 for Na and K, 0.001 for Ca, 0.0005 for Mg, 0.003 for Fe, Ni, Pb, and Co, 0.002 for Cr, 0.0006 for Cu, 0.001 for Mn, and 0.0003 for Zn and Cd. Single Element Standards (Ural'skii Zavod Khimreaktivov (Ural Reagent Plant)) were used for the instruments calibrations. The samples were analyzed ones and, included 20 individuals of *S. paedisca*, 4 individuals of *L. rubicunda*, 54 individuals of *E. cyathigerum*, 33 individuals of *E. najas*, 4 individuals of *L. quadrimaculata*, 2 individuals of *A. serrata*, 7 individuals of *S. vulgatum*, and 10 individuals of *S. flaveolum*. The metal content in *L. dryas* species was revealed in two samples consisting of 45 males and 40 females.

Statistical Analysis

To calculate the basic statistical parameters, we used the Statistica software package, version 9 (Stat-Soft, United States).

RESULTS

Over the entire period of investigation, i.e., from 1980 to 2010, the total average annual abundance of the odonate population, N_Y , varied in a rather wide range, being from 3.0 (in 2010) to 23.2 ind./ m^2 (in 1988), at the average value being 8.3 individuals/ m^2 .

Tables 1–2 provide long-term annual average values on odonate emergence, E_Y , expressed through abundance and biomass. These values are well correlated with the average annual abundance, N_Y , and, therefore, the minimum and maximum values of emergence that are given in the tables correspond to 2010 and 1988, respectively.

One can distinguish the following ecological trends of the investigated species and their long-term annual average values. The lifetime L_S varied from 10 (*Coenagrion armatum*, *C. lunulatum*, and *C. pulchellum*) to 20 days (*Aeshna mixta* and *A. serrata*); the duration of the period of mass emergence, D_S , varied from 30 (*Coenagrion* spp. and *Leucorrhinia* spp.) to 60 days (*Aeshna* spp., *Sympetrum danae*, *S. flaveolum*, *Enallagma cyathigerum*, and *Sympecma paedisca*). The value of Haritonov's size coefficient, R_S , varied from 2.5 (*Leucorrhinia pectoralis* and *L. rubicunda*) to 4 (*E. cyathigerum*, *S. paedisca*, and *S. flaveolum*),

Table 2. Odonate emergence from the odonatogenic water area, Barabinsk forest steppe, Western Siberia

Species	Abundance, ind./(m^2 year)		Wet biomass, mg/(m^2 year)		Dry biomass, mg/(m^2 year)	
	$M \pm m$	min–max	$M \pm m$	min–max	$M \pm m$	min–max
<i>Coenagrion armatum</i>	4.27 \pm 0.44	1.45–10.86	128 \pm 13	43–326	38 \pm 4	13–98
<i>Coenagrion lunulatum</i>	7.85 \pm 2.15	1.14–55.70	252 \pm 69	36–1780	86 \pm 24	12–610
<i>Coenagrion pulchellum</i>	3.13 \pm 0.22	1.10–5.82	94 \pm 7	33–174	28 \pm 2	10–52
<i>Enallagma cyathigerum</i>	15.91 \pm 2.33	1.69–73.70	541 \pm 79	57–2506	191 \pm 28	20–884
<i>Erythromma najas</i>	3,70 \pm 0.63	0.96–20.23	156 \pm 26	40–850	52 \pm 9	13–283
<i>Lestes dryas</i>	1.76 \pm 0.17	0.45–4.48	83 \pm 8	21–210	25 \pm 2	6–63
<i>Lestes sponsa</i>	8.25 \pm 0.47	2.75–14.56	355 \pm 20	118–626	107 \pm 6	36–189
<i>Lestes virens</i>	1.74 \pm 0.16	0.66–3.98	51 \pm 5	19–116	16 \pm 1	6–36
<i>Sympecma paedisca</i>	5.13 \pm 0.26	1.27–7.32	159 \pm 8	39–227	51 \pm 3	13–73
<i>Aeshna mixta</i>	0.32 \pm 0.02	0.08–0.55	142 \pm 10	35–243	45 \pm 3	11–76
<i>Aeshna serrata</i>	0.43 \pm 0.03	0.21–0.79	329 \pm 19	165–611	103 \pm 6	52–191
<i>Leucorrhinia pectoralis</i>	1.24 \pm 0.10	0.29–2.40	246 \pm 20	58–480	76 \pm 6	18–150
<i>Leucorrhinia rubicunda</i>	1.28 \pm 0.14	0.25–3.31	237 \pm 27	46–616	73 \pm 8	14–189
<i>Libellula quadrimaculata</i>	3.09 \pm 0.51	0.33–13.90	982 \pm 163	110–4410	258 \pm 43	30–1180
<i>Sympetrum danae</i>	3.31 \pm 0.21	1.38–5.85	298 \pm 18	124–526	89 \pm 6	37–158
<i>Sympetrum flaveolum</i>	5.35 \pm 0.46	1.05–10.68	562 \pm 49	110–1122	176 \pm 15	35–352
<i>Sympetrum sanguineum</i>	0.60 \pm 0.07	0.07–1.55	69 \pm 8	8–176	21 \pm 2	3–54
<i>Sympetrum vulgatum</i>	8.15 \pm 0.59	1.88–19.87	1230 \pm 89	283–3001	358 \pm 26	83–875
Total	75.50 \pm 5.74	27.53–213.28	5912 \pm 363	2321–13347	1793 \pm 110	705–4108

M, mean value for 31 years; *m*, standard error of mean; min, minimum value; and max, maximum value.

which, on average, corresponds to the number of emergence peaks per year. The average wet weight per individual varied from 29 (*Lestes virens*) to 47 mg (*Lestes dryas*) in species of suborder Zygoptera and from 90 (*S. danae*) to 771 mg (*A. serrata*) in Anisoptera. The average dry weight of one individual varied from 9 to 14 mg in species of suborder Zygoptera and from 27 to 241 mg in Anisoptera, provided that the species set was the same. In all species the moisture content in bodies was rather similar, being on average, $69.0 \pm 0.5\%$; therefore, their dry weight was well correlated with their wet weight. The quantitative share of species (the percentage of species individuals of the total number of individuals of all species) varied from 0.5% (*A. mixta*) to 19.4% (*E. cyathigerum*); the mass share (the weight of species individuals of the total weight of individuals of all species) varied from 0.9% (*L. virens*) to 21.3% (*S. vulgatum*) both in wet and dry weight.

Eleven of the 18 species had a rather high abundance (the annual number of individuals that emerged in the land area), and their total long-term annual average quantitative share was 90% of the long-term annual average abundance of all the 18 species: *Enallagma cyathigerum* (19.4%), *Lestes sponsa* (11.4%), *Sympetrum vulgatum* (11.3%), *Coenagrion lunulatum* (8.3%), *Sympecma paedisca* (7.8%), *S. flaveolum*

(7.4%), *C. armatum* (6.0%), *S. danae* (4.9%), *Coenagrion pulchellum* (4.8%), *Erythromma najas* (4.5%), and *Libellula quadrimaculata* (3.8%). Of these 11 species, seven species (total share 62.2%) belong to suborder Zygoptera, and four species (total share 27.4%) belong to suborder Anisoptera (*L. quadrimaculata* and three species of the genus *Sympetrum*). The other seven of the 18 species had a low abundance (their individual shares are less than 3%) and were 10% in total.

Eleven of the 18 species had a rather high biomass (annual biomass of individuals that emerged in the land area), and their total long-term annual average share was 87.2% of the biomass of all 18 species: *Sympetrum vulgatum* (21.3%), *Libellula quadrimaculata* (14.8%), *S. flaveolum* (9.5%), *Enallagma cyathigerum* (8.6%), *Lestes sponsa* (6.3%), *Aeshna serrata* (6.2%), *S. danae* (5.5%), *Leucorrhinia pectoralis* (4.4%), *Leucorrhinia rubicunda* (4.1%), *Coenagrion lunulatum* (3.5%), and *Sympecma paedisca* (3%). Of these 11 species, seven species (total share 65.8%) belong to suborder Anisoptera and four species (total share 21.4%) belong to suborder Zygoptera (*C. lunulatum*, *E. cyathigerum*, *L. sponsa*, and *S. paedisca*). These 11 species provide about 87% of biomass export. The other seven of the 18 species had a low biomass (their

individual shares were less than 3%) and were 12.8% in total.

In nine Odonata species belonging to two suborders, Anisoptera (five species) and Zygoptera (four species), we measured the content of 12 chemical elements and calculated their export to the land area; of these elements, eight (Cr, Mn, Fe, Ni, Cu, Zn, Cd, and Pb) belong to trace elements, in particular, to heavy metals (HMs), and four (K, Na, Ca, and Mg) belong to macroelements (MEs). All 12 investigated elements, except for lead and cadmium, belong to biologically important elements, or essential elements. The content of metals in the investigated odonate imagoes (a total of ten samples were studied) is given in Table 3. The concentration of Co in the investigated samples was below the method detection limit. On average, the content of HMs in nine Odonata species decreases in the row Fe > Zn > Cu > Mn > Pb > Ni > Cr > Cd, and the content of MEs decreases in the row K > Na > Mg > Ca; the content of MEs in both odonate suborders and of HMs in suborder Anisoptera decreases in the same rows as in the whole order; in turn, the distribution of heavy metals in suborder Zygoptera is somewhat different: Fe > Zn > Cu > Mn > Ni > Cd > Cr, with no Pb revealed. The content of elements varied between different species both qualitatively (a set of elements) and quantitatively (concentration of elements) (Table 3). In all nine investigated Odonata species, we revealed all the four macroelements and four (Fe, Cu, Zn, and Mn) of the eight investigated heavy metals. Each species amounts to five (*S. paedisca*) to seven (*E. najas* and *L. quadrimaculata*) HMs. Six of the 12 elements revealed in odonates have rather high concentrations in most of the investigated species. Thus, four HMs were 99% of the total concentration of all the eight HMs for nine species: Fe 50%, Zn 37%, Cu 9%, and Mn 3%. Two MEs were 93% of the total concentration of four MEs for nine species: K 70% and Na 23%.

The total content of all the investigated metals is approximately the same both in different odonate species and in different suborders (Table 3), while the content of separate elements varies rather significantly between species of the same suborder, family, and even genus (Table 3). Thus, *A. serrata* was characterized by the largest content of Cu, Zn, Mn, Ni, Cd, and Ca, *S. paedisca* by the largest content of Fe, *S. flaveolum* by the largest content of Cr, and *L. dryas* and *E. cyathigerum* by the largest content of K, Na, and Mg. Nickel was not revealed in *L. rubicunda* and *S. flaveolum*; however, we revealed Pb only in these species, with its content having an 18-fold variation: from 0.49 in *S. flaveolum* to 8.81 µg/g of dry weight in *L. rubicunda*. Cd was not found in *S. paedisca* and *S. flaveolum*. Finally, Cr was revealed only in *E. najas*, *L. quadrimaculata*, and *S. flaveolum*. Significant differences in the content of metals were found in two species belonging to the same genus *Sympetrum*: unlike *S. flaveolum*, *S. vulgatum* had no Pb and Cr;

however, the content of Ni and Cd was revealed in it, which is absent in *S. flaveolum*, and the content of Cu and Mn in *S. vulgatum* was twice as high as that in *S. flaveolum*.

The data on metal content and Odonata emergence were used for calculating the export of metals (Tables 4, 5) to the land area and from the water area (µg/m² year). For this purpose, the metal content (µg/g of dry weight) (Table 3) was multiplied by the value of dry biomass of dragonflies of the respective species (mg/(m² year)) (Tables 1 and 2). For 18 species, the export of HMs was 175.31 and the export of MEs was 10638.55, the total of the revealed metals being 10813.86 µg/(m² year). Export of HMs by Odonata decreases in the row Fe > Zn > Cu > Mn > Pb > Ni > Cr > Cd, while export of MEs decreases in the row K > Na > Mg > Ca. Among the nine investigated species, the maximum export of metals was recorded in representatives of suborder Anisoptera: Cu, Zn, Mn, K, and Mg in *S. vulgatum*, Fe, Ni, Cd, Na, and Ca in *L. quadrimaculata*, Pb in *L. rubicunda*, Cr in *S. flaveolum*, and Cd in *A. serrata* (Tables 4 and 5). Among Zygoptera species, the species *E. cyathigerum* is the absolute leader with respect to export of metals, except for Pb and Cr, which are absent in *E. cyathigerum* (Tables 4 and 5).

DISCUSSION

Thirty-one-year studies of the seasonal and interannual dynamics of the abundance of odonate imagoes, as well as their spatial distribution and migration, have made it possible to estimate the export of biomass (organic matter) and metals from water bodies to the Prichanov area of the Barabinsk forest steppe by these insects. The emergence of the investigated odonate population was rather significant, reaching 27.5–213.3 individuals/m² of the water area per year. For comparison, the annual emergence of odonates from temporary water bodies of South Carolina (United States) was 0.8–8.4 (Leeper and Taylor, 1998) and 98 individuals from 1 m² of the water area from minor rivers of Palawan Island (Philippines) (Freitag, 2004).

Biomass export from the unit water area by odonates was 2.3–13.3 g/(m² year) of wet weight and 0.7–4.1 g/(m² year) of dry weight, which is 4–5 times larger than that in representatives of Diptera: 1.25 g/(m² year) of wet weight or 0.45 g/(m² year) of dry weight for mosquitos (Culicidae) (Gladyshev et al., 2011) and 0.35 g/(m² year) of dry weight for culicomorphous insects (suborder Nematocera: Chironomidae, Ceratopogonidae, and Chaoboridae) (Djomina, 2014).

In some odonate species, the amplitude of interannual fluctuations of abundance was very high, while in other species it was very low. For instance, the maximum abundance was different from the minimum one by 51 times in *C. lunulatum*, by 43 times in *E. cyathigerum*, and by 42 times in *L. quadrimaculata*,

Table 3. Metal content in odonates ($\mu\text{g/g}$) in the Barabinsk forest steppe, Western Siberia

Suborder	Species	Heavy metals								Sum of HMs	Macroelements				Sum of MEs
		Fe	Cu	Zn	Mn	Ni	Pb	Cr	Cd		K	Na	Ca	Mg	
Zygoptera	<i>Sympetma paedisca</i>	172.37	13.30	95.75	8.16	0.391	0.000	0.000	0.000	289.97	7950	2850	146	716	11662
	<i>Lestes dryas</i>	141.00	24.00	94.35	6.96	0.212	0.000	0.128	0.000	266.64	15100	4700	95	1224	21119
	<i>Enallagma cyathigerum</i>	146.72	24.14	96.58	7.54	0.423	0.000	0.136	0.000	275.54	15100	5030	90	1223	21443
	<i>Erythronma najas</i>	144.86	23.20	93.09	7.22	0.444	0.000	0.062	0.301	269.18	11270	2950	74	941	15235
Mean	Dry weight	151.24	21.16	94.94	7.47	0.368	0.000	0.075	0.082	275.33	3883	101	1026	17365	
Anisoptera	<i>Aeshna serrata</i>	170.66	38.61	117.05	17.55	0.465	0.000	0.404	0.000	344.74	10690	3310	258	968	15226
	<i>Leucorrhinia rubicunda</i>	153.65	19.62	96.49	7.06	0.000	8.813	0.053	0.000	285.69	12740	3300	79	1094	17213
	<i>Libellula quadrimaculata</i>	137.86	21.13	105.58	7.05	0.433	0.000	0.157	0.517	272.73	10520	4280	112	1005	15917
	<i>Sympetrum vulgatum</i>	88.68	31.77	93.42	6.27	0.248	0.000	0.046	0.000	220.43	9040	3010	44	884	12978
	<i>Sympetrum flaveolum</i>	74.32	16.27	107.61	2.82	0.000	0.493	0.000	0.878	202.39	11330	4120	99	956	16505
Mean	Dry weight	125.03	25.48	104.03	8.15	0.229	1.861	0.279	0.132	265.20	3604	118	981	15567	
Mean value for nine species	Dry weight	136.68	23.56	99.99	7.85	0.291	1.034	0.188	0.110	269.70	3728	111	1001	16367	
	\pm error	11.24	2.57	2.75	1.32	0.062	0.974	0.106	0.041	13.60	815	21	54	1090	
Minimum value		74.32	13.30	93.09	2.82	0.000	0.000	0.000	0.000	202.39	2850	44	716	11662	
Maximum value		172.37	38.61	117.05	17.55	0.465	8.813	0.878	0.404	344.74	5030	258	1224	21443	
Mean value for nine species	*Wet weight	42.32	7.29	30.96	2.43	0.090	0.320	0.058	0.034	83.50	1154	34	310	5067	

* Divided by coefficient 3.23, based on the average moisture of 69%. HMs are heavy metals and MEs are macroelements.

Table 4. Metal export by odonates to the investigated land area ($\mu\text{g}/(\text{m}^2 \cdot \text{year})$), Barabinsk forest steppe, Western Siberia

Suborder	Species	Heavy metals								Sum of HMs	Macroelements				Sum of MEs
		Fe	Cu	Zn	Mn	Ni	Pb	Cr	Cd		K	Na	Ca	Mg	
Zygoptera	<i>Sympetma paedisca</i>	3.28	0.25	1.82	0.16	0.007	0.000	0.000	0.000	5.51	151.05	54.15	2.77	13.60	221.58
	<i>Lestes dryas</i>	1.27	0.22	0.85	0.06	0.002	0.000	0.000	0.001	2.40	135.90	42.30	0.86	11.02	190.07
	<i>Enallagma cyathigerum</i>	9.83	1.62	6.47	0.51	0.028	0.000	0.000	0.009	18.46	1011.70	337.01	6.03	81.94	1436.68
	<i>Erythromma najas</i>	2.75	0.44	1.77	0.14	0.008	0.000	0.006	0.001	5.11	214.13	56.05	1.41	17.88	289.47
Sum for Zygoptera		17.13	2.53	10.91	0.86	0.045	0.000	0.006	0.011	31.48	1512.78	489.51	11.07	124.44	2137.80
Anisoptera	<i>Aeshna serrata</i>	6.31	1.43	4.33	0.65	0.017	0.000	0.000	0.015	12.76	395.53	122.47	9.55	35.82	563.36
	<i>Leucorrhinia rubicunda</i>	4.00	0.51	2.51	0.18	0.000	0.229	0.000	0.001	7.43	331.24	85.80	2.05	28.44	447.54
	<i>Libellula quadrimaculata</i>	13.10	2.01	10.03	0.67	0.041	0.000	0.049	0.015	25.91	999.40	406.60	10.64	95.48	1512.12
	<i>Sympetrum vulgatum</i>	11.53	4.13	12.15	0.82	0.032	0.000	0.000	0.006	28.66	1175.20	391.30	5.72	114.92	1687.14
<i>Sympetrum flaveolum</i>		4.76	1.04	6.89	0.18	0.000	0.032	0.056	0.000	12.95	725.12	263.68	6.34	61.18	1056.32
Sum for Anisoptera		39.69	9.12	35.90	2.50	0.090	0.261	0.105	0.037	87.70	3626.49	1269.85	34.30	335.84	5266.48
Sum for nine Odonata species		56.82	11.64	46.81	3.36	0.135	0.261	0.111	0.048	119.18	5139.27	1759.36	45.36	460.28	7404.27
*Total for 18 species		88.84	15.31	64.99	5.10	0.189	0.672	0.122	0.072	175.31	7492.55	2423.20	72.15	650.65	10638.55

* Calculated for total dry weight ($0.650 \text{ g}/(\text{m}^2 \cdot \text{year})$) of all the investigated species (according to Table 1). HMs are heavy metals and MEs are macroelements.

Table 5. Metal export by odonates from the odonotogenic water area ($\mu\text{g}/(\text{m}^2 \text{ year})$), Barabinsk forest steppe, Western Siberia

Suborder	Species	Heavy metals								Sum of HMs	Macroelements				Sum of MEs
		Fe	Cu	Zn	Mn	Ni	Pb	Cr	Cd		K	Na	Ca	Mg	
Zygoptera	<i>S. paedisca</i>	8.79	0.68	4.88	0.42	0.020	0.000	0.000	0.000	14.79	405.45	7.45	36.52	594.76	
	<i>L. dryas</i>	3.53	0.60	2.36	0.17	0.005	0.000	0.003	0.000	6.67	377.50	2.38	30.60	527.98	
	<i>E. cyathigerum</i>	28.02	4.61	18.45	1.44	0.081	0.000	0.026	0.000	52.63	2884.10	17.19	233.59	4095.61	
	<i>E. najas</i>	7.53	1.21	4.84	0.38	0.023	0.000	0.003	0.016	14.00	586.04	3.85	48.93	792.22	
	Sum for Zygoptera	47.87	7.10	30.53	2.41	0.129	0.000	0.032	0.016	88.08	4253.09	30.86	349.64	6010.57	
Anisoptera	<i>A. serrata</i>	17.58	3.98	12.06	1.81	0.048	0.000	0.042	0.000	35.51	1101.07	26.57	99.70	1568.28	
	<i>L. rubicunda</i>	11.22	1.43	7.04	0.52	0.000	0.643	0.004	0.000	20.86	930.02	5.77	79.86	1256.55	
	<i>L. quadrimaculata</i>	35.57	5.45	27.24	1.82	0.112	0.000	0.133	0.041	70.37	2714.16	28.90	259.29	4106.59	
	<i>S. vulgatum</i>	31.75	11.37	33.44	2.25	0.089	0.000	0.016	0.000	78.92	3236.32	15.75	316.47	4646.12	
	<i>S. flaveolum</i>	13.08	2.86	18.94	0.50	0.000	0.087	0.155	0.000	35.62	1994.08	17.42	168.26	2904.88	
	Sum for Anisoptera	109.19	25.10	98.72	6.88	0.249	0.730	0.288	0.103	241.27	9975.65	94.41	923.58	14482.42	
	Sum for nine Odonata species	157.06	32.19	129.25	9.29	0.378	0.730	0.135	0.304	329.35	14228.74	125.27	1273.23	20492.99	
	*Total for 18 species	245.07	42.24	179.28	14.07	0.522	1.854	0.197	0.337	483.57	20667.91	199.02	1794.79	29346.03	

* Calculated for total dry biomass ($1.793 \text{ g}/(\text{m}^2 \text{ year})$) of all the investigated species (according to Table 2). HMs are heavy metals and MEs are macroelements.

while only by 3.6 times in *A. serrata*, by 4.2 times in *S. danae*, by 5.3 times in *C. pulchellum* and *L. sponsa*; the other species had an average difference between the maximum and minimum abundances from 6 times to 21 times. For all the odonate population, the maximum flux of abundance was different from the minimum one only by 8 times, including a small difference for suborder Anisoptera (5 times) and Zygoptera (9 times). Therefore, the total flux of organic matter from aquatic to terrestrial ecosystems remains relatively stable in spite of interannual variations in the abundance of separate species. In addition, emergence expressed through biomass had a lower (sixfold) amplitude of interannual fluctuations.

The abundance of odonates is directly associated with the level of water content in the area: during the rise of water level, the number of water bodies increases and habitat conditions for larvae improve in them, which leads to an increase in the abundance of dragonflies, and the opposite picture is observed during the fall of water level. Therefore, lake natural cycles inherent in Western Siberia on the whole are extremely important for Odonata. The aquatic ecosystems of the Barabinsk forest steppe are characterized by an unstable water regime; Lake Chany is a demonstrative indicator of manifestation of transgressive–regressive phases of territorial wetting. Chany is a so-called pulsing lake that has several cycles of water level fluctuations, with the maximum cycle being about 100 years and the minimum cycle being 2–4 years, and a number of intermediate cycles (*Pulsiruyushchee ozero Chany*, 1982; *Ekologiya ozera Chany*, 1986). It was previously established that the abundance of populations of the overwhelming majority of the investigated odonate species is strongly related to the water balance of Lake Chany (Popova and Haritonov, 2010). Thus, 14 of the 18 investigated species have significant correlation coefficients, which range from 0.4 to 1, and only four species have insignificant correlation coefficients (in the range from 0.1 to 0.3). The maximum value of the coefficient ($r = 0.9$) was recorded in *L. quadrimaculata*; like in most other species its abundance may be maximal 1–2 years after the water reaches the maximum level (Popova and Haritonov, 2010).

It is important to note that the maximum migration activity of odonates is observed during years characterized by the largest abundance. Thus, mass migrations have been recorded for some Baraba species (*L. quadrimaculata*, *Leucorrhinia pectoralis*, *L. rubicunda*, *Sympetrum danae*, *S. flaveolum*, *S. vulgatum*, and *Aeshna mixta*); i.e., a great number of individuals are observed to be expelled from overpopulated habitats; under these conditions, the absolute majority of migrants die, and only a few of them migrate to new areas (Kharitonov and Popova, 2011). Another variety of the migration activity of odonates is mass reproductive wanderings of dragonflies, including *Sympetrum danae* and *S. vulgatum* in

Baraba (Popova and Haritonov, 2014b). Such dispersion strategies of odonates optimize the abundance of populations, especially in areas with an unstable level of water content, and increase the intensity of export of chemical elements and organic matter from eutrophic water bodies.

The basic emergence (72.5%) was provided by eight species, which were leading both with respect to abundance and with respect to biomass: four Anisoptera species (*L. quadrimaculata*, *S. flaveolum*, *S. vulgatum*, and *S. danae*) and four Zygoptera species (*C. lunulatum*, *E. cyathigerum*, *L. sponsa*, and *S. pae-discia*). These are broad-range species. On the investigated territory, they occurred in a wide range of biotopes. Apparently, the habitat versatility of the species is one of the leading factors of its widespread occurrence and the high density of its spatial distribution, which has already been emphasized by other authors (Harabiš and Dolný, 2010).

In some works, odonate larvae occupy the last positions (with respect to their abundance to a greater extent and with respect to their biomass to a lesser extent due to their large sizes) among other amphibionts. This estimate is quite objective when the matter concerns watercourses in which amphibiotic insects are usually dominated by Diptera, Trichoptera, Plecoptera, or Ephemeroptera. However, when we consider semiflowing and, in particular, standing (temporary) water bodies, this estimate appears to be wrongly underestimated due to the application of inadequate methods with respect to odonates, since large sizes of larvae, their high motility, and reaction rate are not taken into account in this case, and it is also not considered that the spatial distribution of odonate larvae is equally of a random and aggregated nature.

In our studies the emergence of dragonflies was estimated based on an investigation of the imago population. A large number of imago samples (16721 samples over 31 years) leveled the irregularity in the spatial distribution of individuals. It is impossible to perform such a great number of larval samples for the same purposes due to their high labor and time requirements compared with adult insect samples. In addition, our calculations of odonate emergence were based not just on the average annual abundance (which is, in turn, averaged over all the investigated biotopes), which reflects only a portion of the entire biomass of odonates that emerged from a water body, but also on application of Haritonov's coefficient R_S , which takes into account the renewability of fluxes of organic matter. It was initially calculated as the ratio of the period of mass emergence (D_S) per year to the lifetime of imago of this species (L_S). On the whole, the value of this coefficient was species-specific and varied from 2 to 4 in different species. We further paid attention to the fact that these estimated values of the coefficient coincided almost completely with the number of emergence peaks and imago flight peaks for

each species and for each year. The two latter events are closely related in the life of odonates: mass emergence of the species is usually followed by the mass flight of this species on the same or next day.

Of course, the influx of emerging odonates and other insects is much smaller than primary terrestrial productivity. For example, the long-term annual average maximum emergence of odonates in Prichanov area (283.6 t/year in dry weight) was only about 0.04% of terrestrial plant productivity (643900 t/year). The latter was calculated based on data on the terrestrial productivity of forb-grass-reed bogs (2092 g/m²) (Kosykh, 2009) and steppified forb-grass-graminaceous meadows (430 g/m²) (Titlyanova, 2007) in the Barabinsk forest steppe, as well as on data on terrestrial productivity of broad-leaved forests and shrubs (19000 g/m²) (Pokarzhevskii, 1985) in the forest and forest-steppe zones; the areas occupied by these plant associations on the investigated forest-steppe site were also taken into account. It is interesting that the same share (0.04%) was obtained during the emergence of the insects in the near-shore area of Lake Michigan (MacKenzie and Kaster, 2004).

If we assume the secondary terrestrial productivity (namely, first-order consumers) to be a unit of comparison, the influx of aquatic resources that enter terrestrial ecosystems during emergence of amphibiotic insects may be 3 times higher than the influx of productivity of herbivorous insects (Gray, 1989). Unfortunately, we have no data on the productivity of terrestrial insects on the study site of the Barabinsk forest steppe. However, we can make formal comparison, irrespective of the territory, if we apply an index such as the carbon percentage of dry weight: Odonata 52–54% (our data), Coleoptera 37–56%, Lepidoptera 44–57%, and Hymenoptera 47–57% (Pokarzhevskii, 1985). That is, on average, carbon concentrations are 4–5% higher in odonates than those in terrestrial beetles, butterflies, and Hymenoptera.

In our research the total content of both all metals and separate elements in suborder Zygoptera (275.3 µg/g of dry weight per 1 averaged Zygoptera species for all metals) was almost the same as that in suborder Anisoptera (265.2 µg/g of dry weight per 1 averaged Anisoptera species for all metals) (Table 3). Although, a priori, Anisoptera had been assumed to prevail in concentration (both total and with respect to separate elements) of metals, which is due to the specific character of the movement of dragonfly larvae: in addition to the ability to move by feet along a substrate or by swimming, which is inherent in all Odonata larvae, larvae of suborder Anisoptera can make reactive movements based on the vacuum-pump principle, i.e., when water is first soaked into the rectum through the rectal orifice and is then discharged outwards under the head. During these movements, in addition to water-dissolved oxygen, other elements may enter the insect organism, including HMs, while the organ-

ism of larvae of suborder Zygoptera may acquire chemical elements only together with food. It should also be noted that, except for the general type of diet for all Odonata (obligate predators), larvae of these suborders are significantly different by their appearance and sizes (on the average, Anisoptera larvae are of a larger size than Zygoptera larvae) and biotopical confinement (Anisoptera larvae are included in phytophilous, near-bottom, and benthic communities, while Zygoptera larvae are included only in phytophilous communities).

The interspecific differences in the total content of all metals were insignificant: the minimum and maximum values were 202.4 (*S. flaveolum*) and 344.7 (*A. serrata*) µg/g of dry weight for HMs and 11 662 (*S. paedisca*) and 21 443 (*E. cyathigerum*) µg/g of dry weight for MEs (Table 3). The species specificity was clearly revealed in preferential accumulation of separate elements by some Odonata species or, on the contrary, in their absence in other species. Such differences may hardly be associated with food composition, since Odonata larvae are practically opportunistic predators: they consume any living animal feed they can physically cope with. In some cases, elective metal accumulation by species may be due to the local concentration of metals in water bodies. For instance, the recorded maximum of Pb in *L. rubicunda*, whose concentration is below the analytical detection limit in most cases, may indicate local pollution or selectivity in metal accumulation by this species, which requires further research. In any case, Pb exported by some Odonata species may be dangerous for swimming birds that nest on lake shores in the Barabinsk forest steppe. However, the content of Pb in the dragonflies investigated by us does not exceed the maximum level (10 µg/g of dry weight) established for feed of pets: rodents, poultry, and fish (*Mineral tolerance...*, 2005). According to other sources, Pb concentration in feed at a rate of less than 100 µg/g of dry weight does not influence birds breeding (cit. by Eeva and Lehtikoinen, 1996).

The content of Cd, Ca, Cr, Co, Cu, Fe, Mg, Mn, and Ni in odonates in the Barabinsk forest steppe also does not exceed the maximum level established for poultry and rodents feeding (*Mineral tolerance...*, 2005), except for insignificant potassium excess (the established norm is 10 mg/g of dry weight). Nickel concentrations of over 300 mg/kg of dry weight in a diet were observed to cause a decrease in growth rate in newly hatched chickens. Dietary Cd concentrations of 20 mg/kg of dry weight caused kidney lesions and anemia in mallard ducklings (cit. by Eeva and Lehtikoinen, 1996).

On average, the Odonata representatives investigated by us contained more HMs than *Coenagrion puella* (suborder Zygoptera) at the national park in Poland (Boron and Miroslawski, 2009): the content of Fe and Cu was three times higher and the content of Cu and Mn was almost two times higher. Specifically,

the Cd concentration in the odonate imago in the Barabinsk forest steppe was 20 times lower than the established background value for *C. puella*. However, on the HM-polluted site of the industrial area (Boron and Mirosławski, 2009), the content of most of elements in odonates exceeds that in Odonata in the forest-steppe zone of Western Siberia. In one of the Canadian lakes in the northwest of the province of Ontario, the content of this element is also observed to have increased in emerged odonates (by 3 times) after the experimental addition of Cd (Currie et al., 1997), compared with the average value obtained by us for dragonflies in the Barabinsk forest steppe. The content of metals in the Odonata species investigated by us does not generally exceed that in bugs (Hemiptera) in Canadian and Finnish water bodies (Scheuhammer et al., 1997; Nummelin et al., 2007) and in beetles (Coleoptera) in Canadian water bodies (Scheuhammer et al., 1997). Odonates in Western Siberia contain more Fe, Zn, Ni, Pb, and Cd than beetles of Dytiscidae family in the background area in Spain (Burghelea et al., 2011). The average content of Pb in Odonata representatives collected in the Barabinsk forest-steppe area is almost twice as high as that in bugs of Gerridae family (water striders) and beetles of Gyrinidae family (gyrinids) in water bodies of Canada (Scheuhammer et al., 1997) and six times higher than in beetles of Dytiscidae family (diving beetles) in Spanish rice fields (Burghelea et al., 2011), which is determined by the elevated concentration of this element in the body of *L. rubicunda* (Table 3). However, the recorded maximum content of Pb does not exceed the concentration of this element in *Coenagrion puella* inhabiting the contaminated territory of Verkhnesilizski industrial area (Poland) (Borona and Mirosławski, 2009) and in bugs of Notonectidae family in water bodies and wetlands of Canada (Scheuhammer et al., 1997).

Studies of the specificity of metal accumulation by different species and taxa of aquatic insects were carried out during the exposure of larvae in water with HM additions (Tollet et al., 2009). It was found that larvae of *Pachydiplax longipennis* and *Erythemis simplicicollis* (Anisoptera: Libellulidae) are more tolerant to HM effects than other aquatic invertebrates and can accumulate very large concentrations of Pb, Cd, and Cu (>1000 µg/g of dry weight); in addition, the larvae are more sensitive to Cu accumulation than to Pb and Cd accumulation, which the authors explain by the ability of aquatic insects to quickly accumulate copper (Tollet et al., 2009). This feature is possibly determined by the quicker interaction of copper with metal-binding proteins. It was experimentally shown (Poteat and Buchwalter, 2014; Poteat et al., 2015) that the rate and efficiency of accumulation of dissolved HMs by larvae of caddisflies, mayflies, and stoneflies are determined by their body size and mass and phylogeny (at the level of orders). In addition, a large variability in HM accumulation was recorded between species of the same family or even the same genus. It is assumed

that such differences may also be associated with different feed sources. For instance, mayflies belonging to the same genus may be different in regards to the type of their diet (Poteat et al., 2015).

The amount (µg/(m² year)) of HMs exported by odonates in the Barabinsk Steppe to the land area or from the water area decreases in the sequence Fe > Zn > Cu > Mn > Pb > Ni > Cr > Cd, while the amount of macroelements decreases in the sequence K > Na > Mg > Ca (Tables 4 and 5). The average content of metals in odonates decreases in the same row (see above). However, the content of metal and its export do not always have direct correlations (the above-described analogy with the abundance and biomass of odonates may also be observed, i.e., when the abundance of the species may be low, while the extracted biomass may be high). For instance, among the nine investigated species, the highest Fe concentration was revealed in *S. paedisca* (172.4 µg/g of dry weight), while the lowest concentration was found in *S. flaveolum* (74.3), which, on the other hand, makes a larger contribution (4.8 µg/(m² year) in dry weight) to the export of Fe than *S. paedisca* (3.3) does; in turn, the largest contribution with respect to export of Fe is made by *L. quadrimaculata* species (13.1), which occupies the intermediate position with respect to Fe content among other species (137.8 µg/g). Here, a positive correlation between the exported biomass and the export of metals is observed: a larger odonate biomass (which is generally characteristic of Anisoptera species) involves the export of a larger amount of metals contained in them. Accordingly, the above-described proportion with respect to the contribution of the two suborders to the export of water productivity remains the same: the total volume of organic matter exported by representatives of suborder Anisoptera is two times higher than that exported by representatives of suborder Zygoptera, including the export of metals, which is three times higher in representatives of Anisoptera than that in representatives of Zygoptera.

During the experimental addition of cadmium chloride to the lake ecosystem, the export of Cd from bottom sediments by aquatic insects was estimated by (Currie et al., 1997). The work being cited used literature data on the productivity of the investigated insect groups. It was shown that potential export of Cd by odonate imagoes may be from 0.0019 to 4.4 µg/(m² year) during their minimum and maximum productivity, respectively. The value of export of Cd was 3.3 µg/(m² year) for Diptera imagoes and from 0.3 to 2.9 for Ephemeroptera. Therefore, the value of Cd export from 1 m² of the water area, that is made by odonates in the Barabinsk forest steppe, is 21 times lower than the maximum export of this metal by odonates in the Canadian lake (Currie et al., 1997).

According to the 5-point scale of ecological indices on the content of chemical elements in different food links (1 point-relative well-being, 2 points-risk,

3 points-crisis, 4 points-disaster, and 5 points-catastrophe), the Barabinsk forest steppe is classified as an ecological risk zone; the Baraba soils have a middle level of content of macro- and trace elements (Il'in and Syso, 2001). The three basic types of Barabinsk soil, namely, chernozems, meadow–chernozem soils, and solonchic soils, have the following average content of heavy metal: Cu 24.1, Zn 70.6, Mn 775, Ni 39.3, Pb 19.7, Cr 95.1, and Cd 0.17, total 1023.97 mg/kg; these values only slightly exceed the state soil standards (Il'in and Syso, 2001). On average, 86.5 $\mu\text{g}/\text{m}^2$ of these metals annually enter Barabinsk landscapes through odonate emergence. Although we deal with different dimensions (mg/kg of soil in one case and $\mu\text{g}/\text{m}^2$ in the other case), one can still make an approximate estimate on odonate contribution (taking into account the ways Odonata utilizes through food chains) to the total content of these metals in the investigated locality. This contribution is quantitatively small, being only 0.01%, and is possibly not that important for biogeocenosis in general; however, it is essential for a toxicological assessment of feeding of higher-order consumers whose diet includes odonates. For instance, as was already noted above (Tollet et al., 2009), and also according to our data, odonates as aquatic insects can accumulate large concentrations of Pb, Cd, and Cu.

CONCLUSIONS

The presented research on biomass and metal export by odonates from aquatic to terrestrial ecosystems, which was conducted not just in the near-shore zone of a water body, but on a larger territory (272 km²) that also includes the water area and land area, is almost unprecedented in the world scientific literature.

Over the entire period of research, i.e., from 1980 to 2010, the total average annual abundance of the odonate population in the Barabinsk forest steppe in Western Siberia varied in a rather wide range from 3.0 to 23.2 individuals/m², with the average value being 8.3 individuals/m².

Irrespective of large interannual variations of the abundance of separate species (e.g., 51-fold interannual variability in *Coenagrion lunulatum*), the general flux of organic matter from aquatic to terrestrial ecosystems remains relatively stable (sixfold interannual variability).

The maximum total emergence of odonates (283.6 t/year in dry weight) was only 0.04% of the total terrestrial primary (plant) productivity; however, it is comparable to flux of terrestrial secondary productivity, namely, productivity of first-order consumers (herbivorous insects). The export of biomass by odonates from the odonatogenic water area ($\text{g}/(\text{m}^2 \text{ year})$) was 2.3–13.3 (at an average value of 5.9 ± 0.4) in wet

weight and 0.7–4.1 (1.8 ± 0.1) in dry weight, which is 4–5 times higher than that in Diptera representatives.

The content of metals ($\mu\text{g}/\text{g}$) in Barabinsk forest-steppe odonates and their export ($\mu\text{g}/(\text{m}^2 \text{ year})$) from water bodies to the land area decreases in the sequence $\text{K} > \text{Na} > \text{Mg} > \text{Ca} > \text{Fe} > \text{Zn} > \text{Cu} > \text{Mn} > \text{Pb} > \text{Ni} > \text{Cr} > \text{Cd}$.

The content of metals in Barabinsk forest-steppe odonates does not exceed the maximum level established for feeds of pets (rodents, birds, and fish).

We revealed selectivity in the accumulation of elements by different odonate species (even those belonging to the same genus), which is likely due to genetic factors (species affiliation) rather than to food composition.

There are almost no differences in metal accumulation at the level of suborders, except for Pb, which was present only in odonates of the suborder Anisoptera. However, due to their large biomass, the total volume of organic matter exported by representatives of suborder Anisoptera is two times larger than that exported by representatives of suborder Zygoptera; specifically, the volume of metals exported by representatives of the first suborder is three times larger than that exported by representatives of the second suborder.

The obtained high values of dragonflies emergence from water bodies in the Barabinsk forest steppe, together with their high migration activity, ecological plasticity, and ability to colonize a wide range of types of water bodies (especially numerous temporary water bodies), show a significant contribution of Odonata to fluxes of water productivity, including metals, to the land area and also confirm the export of these products at significant distances from the emergence sites.

ACKNOWLEDGMENTS

The study was supported by the Federal Fundamental Scientific Research Program for 2013–2020, projects nos. VI.51.1.9 and 51.1.1.

REFERENCES

- Alimov, A.F., *Elementy teorii funktsionirovaniya vodnykh ekosistem* (Elements of the Theory of Functions of Aquatic Ecosystems), St. Petersburg: Nauka, 2000.
- Ballinger, A. and Lake, P.S., Energy and nutrient fluxes from rivers and streams into terrestrial food webs, *Mar. Freshwater Res.*, 2006, no. 57, pp. 15–28.
- Baxter, C.V., Fausch, K.D., and Saunders, W.C., Tangled webs: reciprocal flows of invertebrate prey link streams and riparian zones, *Freshwater Biol.*, 2005, no. 50, pp. 201–220.
- Bennett, S. and Mill, P.J., Pre- and post-maturation survival in adults of the damselfly *Pyrrhosoma nymphula* (Zygoptera: Coenagrionidae), *J. Zool.*, 1995, no. 235, pp. 559–575.

- Bried, J.T. and Ervin, G.N., Note to abundance patterns of dragonflies along a wetland buffer, *Wetlands*, 2006, vol. 26, no. 3, pp. 878–883.
- Boroń, M. and Mirosławski, J., Using insects (damselflies: azajre damselfly, *Coenagrion puella*) as biomarkers of environmental pollution, *Fresenius Environ. Bull.*, 2009, vol. 18, no. 7, pp. 1219 – 1225.
- Buckner, J.S. and Hagen, M.M., Triacylglycerol and phospholipid fatty acids of the silverleaf whitefly: composition and biosynthesis, *Arch. Insect Biochem. Physiol.*, 2003, no. 53, pp. 66–79.
- Burghelca, C.I., Zaharescu, D.G., Hoodac, P.S., and Palanca-Soler, A., Predatory aquatic beetles, suitable trace elements bioindicators, *J. Environ. Monit.*, 2011, vol. 13, pp. 1308–1315.
- Clark, T.E. and Samways, M.J., Dragonflies (Odonata) as indicators of biotope quality in the Kruger National Park, South Africa, *J. Appl. Ecol.*, 1996, no. 33, pp. 1001–1012.
- Conrad, K.F., Willson, K.H., Harvey, I.F., Thomas, C.J., and Sherratt, T.N., Dispersal characteristics of seven odonate species in an agricultural landscape, *Ecography*, 1999, vol. 22, pp. 524–531.
- Corbet, P.S., An adult population study of *Pyrhosoma nymphula* (Sulzer): (Odonata: Coenagrionidae), *J. Anim. Ecol.*, 1952, vol. 21, pp. 206–222.
- Corbet, P.S., *Dragonflies: Behavior and Ecology of Odonata*, Colchester: Harley Books, 1999.
- Corbi, J.J. and Froehlich, C.G., Bioaccumulation of metals in aquatic insects of streams located in areas with sugar cane cultivation, *Quim. Nova*, 2010, vol. 33, no. 3, pp. 644–648.
- Corbi, J.J., Froehlich, C.G., Trivinho-Strixino, S., and dos Santos, A., Evaluating the use of predatory insects as bioindicators of metals contamination due to sugarcane cultivation in neotropical streams, *Environ. Monit. Assess.*, 2011, vol. 177, pp. 545–554.
- Currie, R.S., Fairchild, W.L. and Muir, D.C.G., Remobilization and export of cadmium from lake sediments by emerging insects, *Environ. Toxicol. Chem.*, 1997, vol. 16, no. 11, pp. 2333–2338.
- Djomina, I.V., Role of culicomorph insects (Diptera, Nematocera) in formation of the matter and energy flows through the “water-air” border of the floodplain lakes of the Volga River (Saratov oblast), *Cand. Sci. (Biol.) Dissertation*, Saratov, 2014.
- Eeva, T. and Lehikoinen, E., Growth and mortality of nestling great tits (*Parus major*) and pied flycatchers (*Ficedula hypoleuca*) in a heavy metal pollution gradient, *Oecologia*, 1996, vol. 108, pp. 631–639.
- Ekologiya ozera Chany* (Ecology of the Chany Lake), Novosibirsk: Nauka, 1986.
- Freitag, H., Composition and longitudinal patterns of aquatic insect emergence in small rivers of Palawan Island, the Philippines, *Int. Rev. Hydrobiol.*, 2004, no. 89, pp. 375–391.
- Gavrilov, L.A. and Gavrilova, N.S., *Biologiya prodolzhitel'nosti zhizni. Kolichestvennye aspekty* (Biology of Life Duration: Quantitative Aspects), Moscow: Nauka, 1991.
- Gladyshev, M.I., Kharitonov, A.Yu., Popova, O.N., Sushchik, N.N., Makhutova, O.N., and Kalacheva, G.S., Quantitative estimation of dragonfly role in transfer of essential polyunsaturated fatty acids from aquatic to terrestrial ecosystems, *Dokl. Biochem. Biophys.*, 2011, vol. 438, no. 1, pp. 141–143.
- Gladyshev, M.I., Sushchik, N.N., Anishchenko, O.V., Makhutova, O.N., Kalachova, G.S., and Gribovskaya, I.V., Benefit-risk ratio of food fish intake as the source of essential fatty acids vs. heavy metals: a case study of Siberian grayling from the Yenisei River, *Food Chem.*, 2009, vol. 115, pp. 545–550.
- GOST (State Standard) 26570-95: *Interstate Standard. Fodder, Mixed Fodders, and Mixed Fodder Sources. Flame-Photometric Analysis of Calcium Content*, Minsk: Mezghos. Sovet Standart., Metrol., Sertifikats., 1995.
- GOST (State Standard) 30503-97: *Interstate Standard. Fodder, Mixed Fodders, and Mixed Fodder Sources. Flame-Photometric Analysis of Sodium Content*, Minsk: Mezghos. Sovet Standart., Metrol., Sertifikats., 1997.
- GOST (State Standard) 30504-97: *Interstate Standard. Fodder, Mixed Fodders, and Mixed Fodder Sources. Flame-Photometric Analysis of Potassium Content*, Minsk: Mezghos. Sovet Standart., Metrol., Sertifikats., 1998.
- GOST (State Standard) 30502-97: *Interstate Standard. Fodder, Mixed Fodders, and Mixed Fodder Sources. Flame-Photometric Analysis of Magnesium Content*, Minsk: Mezghos. Sovet Standart., Metrol., Sertifikats., 1998.
- GOST (State Standard) 30692-2000: *Interstate Standard. Fodder, Mixed Fodders, and Mixed Fodder Sources. Flame-Photometric Analysis of Cooper, Lead, Zink, and Cadmium Content*, Minsk: Mezghos. Sovet Standart., Metrol., Sertifikats., 2000.
- Gratton, C. and Vander Zanden, M.J., Flux of aquatic insect productivity to land: comparison of lentic and lotic ecosystems, *Ecology*, 2009, no. 90, pp. 2689–2699.
- Gray, L.J., Emergence production and export of aquatic insects from a tallgrass prairie stream, *Southwest. Nat.*, 1989, no. 34, pp. 313–318.
- Harabis, F. and Dolny, A., Ecological factors determining the density-distribution of Central European dragonflies (Odonata), *Eur. J. Entomol.*, 2010, no. 107, pp. 571–577.
- Haritonov, A. and Popova, O., Spatial displacements of Odonata in south-west Siberia, *Int. J. Odonatol.*, 2011, vol. 14, no. 1, pp. 1–10.
- Il'in, V.B. and Syso, A.I., *Mikroelementy i tyazhelye metally v pochvakh i rasteniyakh Novosibirskoi oblasti* (Trace Elements and Heavy Metals in Soil and Plants of Novosibirsk Oblast), Novosibirsk: Sib. Otd., Ross. Akad. Nauk, 2001.
- Kharitonov, A.Yu. and Popova, O.N., Migrations of dragonflies (Odonata) in the south of the West Siberian plain, *Entomol. Rev.*, 2011, vol. 91, no. 4, pp. 411–419.
- Kosykh, N.P., Biological productivity of bogs in forest-steppe zone, *Vestn. Tomsk. Gos. Pedagog. Univ.*, 2009, no. 3 (81), pp. 87–90.
- Kozhanchikov, I.V., *Metody issledovaniya ekologii nasekomykh* (Analysis Methods of Insect Ecology), Moscow: Vysshaya Shkola, 1961.
- Lavilla, I., Rodríguez-Liñares, G., Garridob, J., and Bendicho, C., A biogeochemical approach to understanding the accumulation patterns of trace elements in three

- species of dragonfly larvae: evaluation as biomonitors, *J. Environ. Monit.*, 2010, vol. 12, pp. 724–730.
- Leeper, D.A. and Taylor, B.E., Insect emergence from a South Carolina (USA) temporary wetland pond, with emphasis on the Chironomidae (Diptera), *J. North Am. Benthol. Soc.*, 1998, no. 17, pp. 54–72.
- Lekyavichus, E., Information status of an ecosystem, in *Ekologicheskii prognoz* (Ecological Forecast), Moscow: Mosk. Gos. Univ., 1986, pp. 157–163.
- MacKenzie, R.A. and Kaster, J.L., Temporal and spatial patterns of insect emergence from a Lake Michigan coastal wetland, *Wetlands*, 2004, no. 24, pp. 688–700.
- Mineral Tolerance of Animals*, Washington, DC: Natl. Acad. Press, 2005, 2nd ed.
- Pajunen, V.I., Studies on the population ecology of *Leucorhinia dubia* V. D. Lind. (Odonata, Libellulidae), *Ann. Zool. Soc.*, 1962, vol. 24, no. 4, pp. 1–79.
- Palii, V.F., *Metodika izucheniya fauny i fenologii nasekomykh* (Analysis Method of Fauna and Phenology of Insects), Voronezh: Tsentr.-Chernozem. Knizh. Izd., 1970.
- Parr, M.J., Comparative studies of Coenagriid (Odonata) population ecology, *Proc. XIII Int. Entomological Congr., Moscow, August, 1968*, St. Petersburg, 1972, vol. 1, pp. 540–541.
- Pesenko, Yu.A., *Printsipy i metody kolichestvennogo analiza v faunisticheskikh issledovaniyakh* (Principles and Methods of Quantitative Analysis in Faunistic Studies), Moscow: Nauka, 1982.
- Pokarzhevskii, A.D., *Geokhimicheskaya ekologiya nazemnykh zivotnykh* (Geochemical Ecology of Terrestrial Animals), Moscow: Nauka, 1985.
- Popova, O.N., The dragonflies of forest-steppe in West Siberia: fauna, ecology, biology, in *Odonata: Biology of Dragonflies*, Tyagi, B.K., Ed., Madurai, India: Sci. Publ, 2007, pp. 89–104.
- Popova, O.N., The dragonfly larva population (Odonata) in a temporal water pond, *Euroasian Entomol. J.*, 2010, vol. 9, no. 2, pp. 239–248.
- Popova, O.N. and Haritonov, A.Yu., Population dynamics and migration in the dragonfly *Libellula quadrimaculata* L., 1758 (Odonata, Libellulidae), *Euroasian Entomol. J.*, 2010, vol. 9, no. 2, pp. 231–238.
- Popova, O.N. and Haritonov, A.Yu., Estimation of the carry-over of substances by dragonflies from water bodies to land in the forest-steppe of West Siberia, *Contemp. Probl. Ecol.*, 2012, vol. 5, no. 1, pp. 34–39.
- Popova, O.N. and Haritonov, A.Yu., Disclosure of Biotopical Groups in the Population of the Dragonfly *Coenagrion armatum* (Charpentier, 1840), *Contemp. Probl. Ecol.*, 2014a, vol. 7, no. 2, pp. 175–181.
- Popova, O.N. and Haritonov, A.Yu., Mass reproductive wandering of dragonflies of the genus *Sympetrum* (Odonata, Libellulidae), *Entomol. Rev.*, 2014b, vol. 94, no. 1, pp. 21–28.
- Poteat, M.D. and Buchwalter, D.B., Phylogeny and size differentially influence dissolved Cd and Zn bioaccumulation parameters among closely related aquatic insects, *Environ. Sci. Technol.*, 2014, vol. 48, pp. 5274–5281.
- Poteat, M.D., Jacobus, L.M., and Buchwalter, D.B., The importance of retaining a phylogenetic perspective in traits-based community analyses, *Freshwater Biol.*, 2015, vol. 60, pp. 1330–1339.
- Prirodnye usloviya i estestvennye resursy SSSR: Zapadnaya Sibir'* (Nature Conditions and Resources of Soviet Union: Western Siberia), Rikhter, G.D., Ed., Moscow: Akad. Nauk SSSR, 1963.
- Pul'siruyushchee ozero Chany* (Pulsating Chany Lake), Leningrad: Nauka, 1982.
- Scheuhammer, A.M., McNicol, D.K., Mallory, M.L., and Kerekes, J.J., Relationships between lake chemistry and calcium and trace metal concentrations of aquatic invertebrates eaten by breeding insectivorous waterfowl, *Environ. Pollut.*, 1997, vol. 96, no. 2, pp. 235–241.
- Titlyanova, A.A., Pure primary productivity of grassy and boggy ecosystems, *Sib. Ekol. Zh.*, 2007, vol. 5, pp. 763–770.
- Tollett, V.D., Benvenuti, E.L., Deer, L.A., and Rice, T.M., Differential toxicity to Cd, Pb, and Cu in dragonfly larvae (Insecta: Odonata), *Arch. Environ. Contam. Toxicol.*, 2009, vol. 56, pp. 77–84.
- Ubukata, H., Survivorship curve and annual fluctuation in the size of emerging population of *Cordulia aenea amurensis* Selys (Odonata: Corduliidae), *Jpn. J. Ecol.*, 1981, no. 31, pp. 335–346.
- Wang, Y., Lin, D.S., Bolewicz, L., and Connor, W.E., The predominance of polyunsaturated fatty acids in the butterfly *Morpho peleides* before and after metamorphosis, *J. Lipid Res.*, 2006, no. 47, pp. 530–536.
- Zhou, H.Y., Cheung, R.Y.H., Chan, K.M., and Wong, M.H., Metal concentrations in sediments and tilapia collected from inland waters of Hong Kong, *Water Res.*, 1998, vol. 32, pp. 3331–3340.

Translated by D. Zabolotny