



Export of aquatic productivity, including highly unsaturated fatty acids, to terrestrial ecosystems via Odonata



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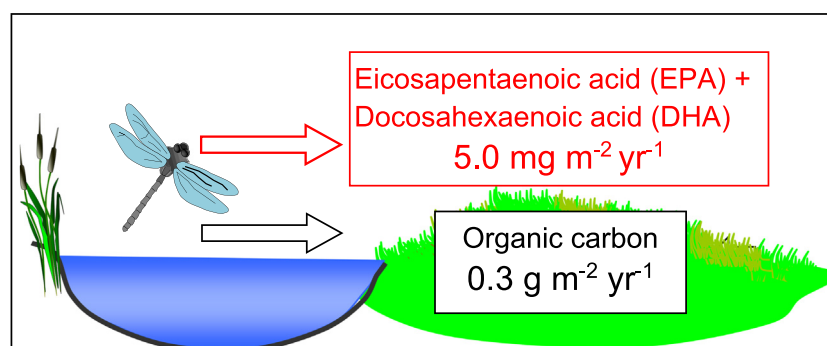
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HIGHLIGHTS

- We measured abundance and emergence of odonates in forest-steppe during 31 years.
- Odonates bring organic carbon to the land, which is equal to land insect production.
- Highly unsaturated fatty acids (HUFA) were measured in biomass of odonates.
- Odonates subsidize essential HUFAs in land as many as all other amphibiotic insects.

GRAPHICAL ABSTRACT



ARTICLE INFO

Article history:

Received 12 November 2016

Received in revised form 24 December 2016

Accepted 3 January 2017

Available online xxx

Editor: D. Barcelo

Keywords:

Amphibiotic insect emergence

Aquatic subsidy

Eicosapentaenoic acid

Docosahexaenoic acid, forest-steppe

ABSTRACT

Based on 31-year field study of the abundance and biomass of 18 species of odonates in the Barabinsk Forest-Steppe (Western Siberia, Russia), we quantified the contribution of odonates to the export of aquatic productivity to surrounding terrestrial landscape. Emergence varied from 0.8 to 4.9 g of wet biomass per m² of land area per year. Average export of organic carbon was estimated to be 0.30 g·m⁻²·year⁻¹, which is comparable with the average production of herbivorous terrestrial insects in temperate grasslands. Moreover, in contrast to terrestrial insects, emerging odonates contained high quantities of highly unsaturated fatty acids (HUFA), namely eicosapentaenoic acid (20:5n-3, EPA), and docosahexaenoic acid (22:6n-3, DHA), which are known to be essential for many terrestrial animals, especially for birds. The export of EPA + DHA by odonates was found to be 1.92–11.76 mg·m⁻²·year⁻¹, which is equal to an average general estimation of the export of HUFA by emerging aquatic insects. Therefore, odonates appeared to be a quantitatively and qualitatively important conduit of aquatic productivity to forest-steppe ecosystem.

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1. Introduction

Nutrient inputs from terrestrial landscapes into aquatic ecosystems have been studied since the middle of 20th century (e.g., Likens et al., 1970; Nakano et al., 1999; Pace et al., 2004). However, aquatic

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ecosystems may be important sources of energy and nutrients for surrounding terrestrial habitats (McCarty, 1997; Ben-David et al., 1998; Nakano and Murakami, 2001; Ballinger and Lake, 2006; Gratton and Vander Zanden, 2009). A large part of aquatic productivity is exported to the surrounding terrestrial landscape via aquatic insect emergence (e.g., Baxter et al., 2005; Gratton and Vander Zanden, 2009).

Generalizations of field data on the insect emergence demonstrated that most part of biomass exported from aquatic ecosystems to the adjacent terrestrial zone occurs mostly <10 m from the water and decreases exponentially to 100–500 m (e.g., Delettre and Morvan, 2000; Gratton and Vander Zanden, 2009; Richardson et al., 2010; Muehlbauer et al., 2014). Much of the above data were from streams, in which adult Diptera made up 60–99% of emergent biomass, whereas the rest being primarily adult Ephemeroptera, Plecoptera and Trichoptera. Meanwhile, such taxa as Odonata were believed to be of the least importance (Baxter et al., 2005). However, large insects that are strong fliers, such as dragonflies, may move further inland than average (Gratton and Vander Zanden, 2009).

Odonata and their habitats, small ponds and temporary pools, are not currently the focus of the measurements of fluxes of aquatic productivity to terrestrial ecosystems. However, Odonata, as mentioned above, are strong fliers and thereby can potentially contribute significantly to the inland dispersal of aquatic productivity. Indeed, Conrad et al. (1999) calculated exponential decay curve for odonate dispersal with zero point of about 800 m, i.e. 8 times more distant than the average value 100 m used by Gratton and Vander Zanden (2009). Moreover, regular migrations of dragonflies up to 18 km from the nearest water body occurred, and sometimes dragonfly migration may exceed 50 km (Kharitonov and Popova, 2011). Besides having comparatively high dispersal ability, odonates occupy almost all types of freshwater habitats, and most species inhabit ephemeral water bodies, such as pans, pools, bogs, others (Clark and Samways, 1996; Harabis and Dolny, 2010; Kharitonov and Popova, 2011). Naturally, these ephemeral water bodies must exist long enough to do aquatic development of odonates possible. Thus, in some landscapes, for instance, in semiarid steppe, where most water bodies are ephemeral pools and bogs, odonates may be a quantitatively important group of amphibiotic insects (i.e., insects that initially live in water as larvae but live on land as adults). Therefore, the first aim of our study was to estimate a flux of aquatic productivity to terrestrial ecosystems via odonates in the Barabinsk forest-steppe zone in the south of West Siberia. In contrast to previously published data (Kharitonov and Popova, 2011; Popova and Kharitonov, 2012), we aimed to take into account annual abundance of all dominant odonate species for the period of 1980–2010, and to use a novel set of formulas for a quantification of their emergence. Calculations of the emergence were based on the annual abundance and some other ecological traits of species, including a coefficient of renewability, introduced in the present work.

In some landscapes, the flux of aquatic productivity via emerging amphibiotic insects can be comparable with productivity of terrestrial insects or even higher (Gratton and Vander Zanden, 2009). In addition to the quantitative importance of emerging insects for terrestrial consumers, the biomass exported from aquatic ecosystems has important qualitative peculiarities. In the last few decades, highly unsaturated fatty acids (HUFA) have come to be recognized as biochemicals of physiological importance for animals at all trophic levels, including humans (Arts et al., 2001). Eicosapentaenoic acid (20:5n-3, EPA), and docosahexaenoic acid (22:6n-3, DHA) are known to be the most physiologically important HUFAs. EPA is known to be the biochemical precursor in the synthesis of endohormones, eicosanoids, namely the 3-series prostaglandins and thromboxanes, and the 5-series leukotrienes, which initiate anti-inflammatory reactions, are active vasodilators and inhibitors of platelet aggregation, and provide anti-allergic response, respectively (Simopoulos, 2000; Wall et al., 2010). DHA can control synthesis of eicosanoids by inhibiting a key enzyme, cyclooxygenase (Norris and Dennis, 2012). In addition, DHA is the major fatty acid in structural

lipids of neural cells, for instance, it composes 30% of total retinal fatty acids and 20% of those of brain tissues (SanGiovanni and Chew, 2005; McNamara and Carlson, 2006; Bazan, 2009). The above physiological roles of EPA and DHA have been demonstrated primarily in mammals, but it is highly likely that they are similar in other vertebrates and also in invertebrates (Heckmann et al., 2008; Fronte et al., 2008; Ahlgren et al., 2009). For instance, a deficiency of EPA and DHA in diet decreased learning ability of birds (Fronte et al., 2008). Besides the above importance for neural tissues, DHA is believed to be essential for phospholipids of high-frequency contraction pectoral muscles of actively flying birds, because DHA-containing phospholipids are conformational cofactors for the functional assembly of membrane protein complexes of mitochondria (Infante et al., 2001).

Among organisms in the biosphere, some taxa of microalgae, unlike higher plants, can synthesize high amounts of EPA and DHA de novo (Heinz, 1993; Cohen et al., 1995; Harwood, 1996; Tocher et al., 1998). Therefore, aquatic ecosystems play the unique role in the biosphere as the principal source of HUFA for most animals, including inhabitants of terrestrial ecosystems (Gladyshev et al., 2009, 2013). Emerging amphibiotic insects, whose aquatic larvae obtain EPA and DHA from aquatic food webs, are one of the principal sources of HUFA export from aquatic to terrestrial ecosystems (Gladyshev et al., 2009). It is important to emphasize that unlike amphibiotic insects, most terrestrial insects have no EPA and DHA in their biomass or contain only trace amounts of the HUFA (Stanley-Samuelson et al., 1988; Buckner and Hagen, 2003; Wang et al., 2006; Rumpold and Schluter, 2013; Barroso et al., 2014; Sanchez-Muros et al., 2014; but see Nor Aliza et al., 2001; Cakmak et al., 2007). Thus, fluxes of emergent amphibiotic insects to land may be important conduits not only of carbon, but also of essential HUFA into terrestrial systems (Gladyshev et al., 2009, 2013; Hixson et al., 2015; Twining et al., 2015). However, practically all data on HUFA content in amphibiotic insects are for larvae. Thus, the second aim of our study was to measure HUFA content in odonate imagoes and to estimate export of these essential biochemicals via odonate emergence in a natural landscape. In summary, we aimed to answer the question whether aquatic subsidies via odonates are compare with that for other insects, and thus odonates might be overlooked as an aquatic-terrestrial linkage.

2. Materials and methods

2.1. Study area

The study was carried out from 1980 to 2010 in vicinity of the Chany Research Biological Station (Institute of Systematics and Ecology of Animals of Siberian Branch of Russian Academy of Sciences) in the central part of Barabinsk Forest-Steppe (54°32'–54°39' N, 78°06'–78°19' E, Fig. 1). This area of 272 km² has an elevation of 105–115 m above mean sea level and is adjacent to the southeastern shore of the Chany Lake (Fig. 1), which is the largest lake in Western Siberia.

The regional climate is continental. The mean temperature of the hottest month, July, is higher than 18 °C, while in the coldest one, January, it is around –20 °C. The mean annual precipitation is about 350 mm, with relative moisture around 50–60%. Rains peaked in July. The mean annual wind speed is around 5 m·s⁻¹. The annual radiation is around 4000 MJ·m⁻² (Western Siberia, 1963).

Within the study area of 272 km² (Fig. 1), areas of different habitats, calculated using Image 2010 TerraMetrics, maps of 1 km scales, aero photographs and direct measurements of distances and angles in the studied locations, are as follows. Water bodies' area (lakes, rivers, pans, puddles, pools, ditches and bogs, including reed beds) is 82 km². Except brackish and salt lakes (2 km²) and water bodies without aquatic plants (11 km²), all the other water area, 69 km², is the habitat of odonates (Popova and Kharitonov, 2012). Terrestrial area, 190 km², is represented by habitats, listed in Table 1. Sample sites were located in all the types of habitats (Fig. 1).

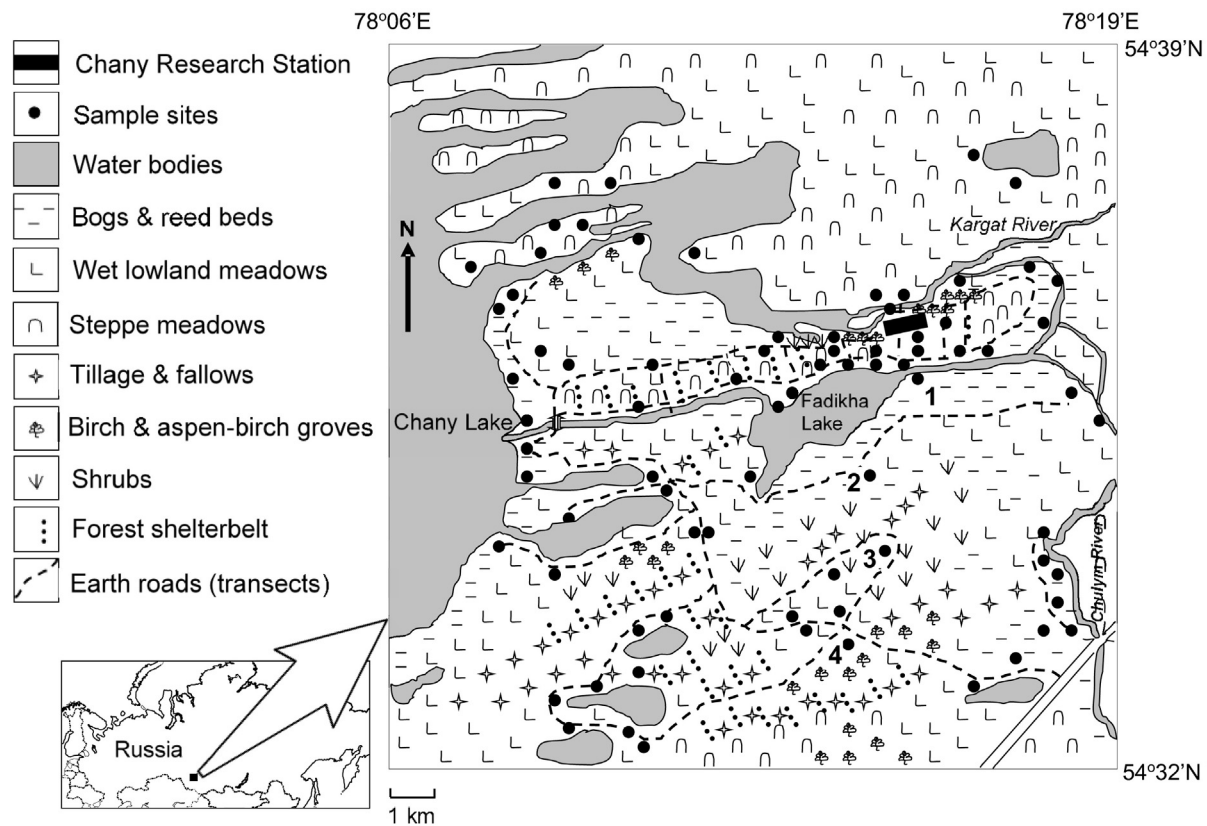


Fig. 1. Map of studied area. 1–4 – sites for estimation of odonates spatial distribution (see text for details).

2.2. Imago abundance measurements

For aquatic insect sampling emergence traps are used conventionally. However, in contrast to small insects, large insects, odonates, are often underestimated by the traps (Poepperl, 2000; MacKenzie and Kaster, 2004; Davis et al., 2011; Wesner, 2012; Schriever et al., 2014). Therefore, our main odonate sampling method, capture-mark-recapture, was as follows. In a given square (usually $1 \cdot 10^4 \text{ m}^2$) of a sample site, during a certain time span (usually from 08:00 h to 14:00 h) all individuals were caught, got color marks on wings and were released. The number of captured and marked individuals, M , was recorded. The next day, in the same square, during the same time span, n individuals were captured, including m individuals marked the day before. Then the abundance, N ($\text{ind.} \cdot \text{m}^{-2}$), was calculated as follows:

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

where a is area (m^2) of the square. During the study, M and n varied from 300 to 500 individuals, and m varied from 1 to 12 individuals. Thus, n/m ratio varied from 500 to 25. The capture-mark-recapture method was suitable for all studied species.

Table 1
Area (km^2) of studied terrestrial habitats.

Habitat	Area
Wet lowland meadows	87
Steppe meadows	61
Tillage and fallows	19
Shrubs	11
Birch and aspen-birch groves	8
Forest shelterbelts	3.5
Earth roads	0.5

The second method, primarily suitable for species of suborder Anisoptera, was belt transect counting. A collector moved near midday at ca. 4 km per hour and registered all dragonflies which took off or crossed the transect (earth road) using a dictaphone. The transect length usually was ca. 350 m and the width 2 m, thus the transect area was 700 m^2 . All the earth roads, given in Fig. 1, were used as transects. The belt transect method gave the density estimations, similar to those, obtained by the capture-mark-recapture method (Haritonov and Popova, 2011). Therefore, average annual abundance values, calculated below, included data from both methods. These methods are conventional in the population ecology of insects, including odonates (Corbet, 1952, 1999; Conrad et al., 1999; Rouquette and Thompson, 2005; Bried and Ervin, 2006; Popova and Haritonov, 2014).

Sampling was carried out for 31 years, from 1980–2010, from May to October (flight period of odonates). Using methods of capture-mark-recapture, each of 74 sites (Fig. 1) were sampled 3–8 times per each year (season). Sampling by the transect method was carried out every 2–10 days throughout each season. Overall, during 1980–2010, 6422 quantitative samplings were done, and 386,863 odonate individuals were recorded.

It is worth mentioning, that all the captured specimens were released after recording and identification, except for a comparatively small number of individuals, used for weight measurements and biochemical analyses, described below. To prevent individuals from damaging each other and to keep them alive following release, during sampling they were collected in containers, filled with crumpled filter paper.

2.3. Spatial distribution measurements

To estimate spatial distribution, four sample sites, located at different distances from a water body, the Fadikha Lake, were chosen. Site 1 was situated at 100 m from shore of the lake in reed beds, site 2 was

situated at 1 km from this shore in a wet lowland meadow, site 3 was at 2.7 km from the shore in shrubs and site 4 was at 4 km from the lake in a birch grove (Fig. 1). Site 4 was also at 3 km from a small salt lake (Fig. 1, southeastern corner of the map), but in this lake, there were no the accounted mass odonate species. Moreover, at sites 2–4, odonate species, marked at shore of the Fadikha Lake (site 1), were often caught. There were no temporary water bodies, which may additionally supply emerged odonates, in neighborhood. Thus, we used the distance from the Fadikha Lake shore as the attributes of these sites. These sites were simultaneously sampled in 1980–1990 (i.e., during 11 years) and thereby were chosen for estimation of spatial distribution of odonates along a distance from lake shore. Pair comparison of average annual abundance at the sites for each year were done. Thus, number of pairs was 11.

2.4. Biomass measurements

To measure wet weight (WW), samples of 30–70 young (freshly emerged) males and females of each species were weighed. The specimens were weighed individually. Then, to obtain dry weight (DW), these samples were dried at 80 °C for 24 h until constant weight and weighed. The measurements of freshly emerged odonates were done to take into account flux of aquatic productivity only, rather than biomass, obtained during feeding in terrestrial ecosystems.

2.5. Emergence duration measurements

Duration of mass emergence (days per year) for each species was determined in the course of the imago abundance measurements at sample sites, situated at shoreline of water bodies (Fig. 1), based on the method of the captures during 15-minute intervals. Using this method, a collector moved steadily along the perimeter of a 500 m² square, and then across the square, which took 15 min, and caught all the sitting and flying odonates (primarily Zygoptera) with a handle net. Each site was sampled every 3–7 days. The mass emergence recording period was started when there were at least 3 individuals of a given species in the sample, and if their relative abundance was at least 5% of all individuals in the sample (Pesenko, 1982). Accordingly, mass emergence recording period was completed when there were <3 individuals of the given species in the sample, and their relative abundance was <5%. Average value of duration of the period mass emergence for each species for each year was calculated using data for all sites. Then, the general average duration of the period mass emergence for each species for all years, 1980–2010, was calculated.

2.6. Imago lifespan measurements

Lifespans for each species were measured by placing freshly emerged imagoes in a cage 1 × 1 × 1 m, exposed in an aired room. The caged imagoes were fed daily with live midges. The lifespan (days) was recorded as the time from the emergence to death in the cage.

2.7. Emergence rate calculations

Emergence was estimated for 18 abundant species of a total of 42 species, found in the studied area (Popova, 2007). The other 24 species were rare, i.e., constituted <5% of the total abundance and biomass of Odonata. These 18 abundant species were: suborder Zygoptera, *Enallagma cyathigerum* (Charpentier, 1840), *Erythromma najas* (Hansemann, 1823), *Coenagrion lunulatum* (Charpentier, 1840), *Coenagrion armatum* (Charpentier, 1840), *Coenagrion pulchellum* (V.d. Linden, 1823), *Lestes dryas* Kirby, 1890, *Lestes sponsa* (Hansemann, 1823), *Lestes virens* (Charpentier, 1825), *Sympetrum paeidisca* (Brauer, 1877); suborder Anisoptera, *Libellula quadrimaculata* Linnaeus, 1758, *Leucorrhinia rubicunda* (Linnaeus, 1758), *Leucorrhinia pectoralis*

(Charpentier, 1825), *Sympetrum flaveolum* (Linnaeus, 1758), *Sympetrum vulgatum* (Linnaeus, 1758), *Sympetrum danae* (Sulzer, 1776), *Sympetrum sanguineum* (Müller, 1764), *Aeshna serrata* Hagen, 1856, *Aeshna mixta* Latreille, 1805.

Emergence was calculated basing on imago abundance, biomass and renewability. Average annual abundances were calculated using all samples, obtained in a year by all three methods. Number of samples, n , used for the calculations of average annual abundances, varied from 394 to 850. As mentioned above, the sum of n for 31 years was 16,721. Average abundance of each species for each year for the whole study area, N_{YS} ($1 \cdot 10^6$ ind. · km⁻² or ind. · m⁻²) was calculated as follows:

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

where N_{Si} ($1 \cdot 10^6$ ind. · km⁻²) is average annual abundance of species S in terrestrial biotope i , A_i (km²) is area of habitat i . As mentioned above, 7 terrestrial habitats were studied, and the total studied area, $\sum_{i=1}^7 A_i = 190$ km². Total average annual abundance, N_Y ($1 \cdot 10^6$ ind. · km⁻² = ind. · m⁻²), was calculated as sum of N_{YS} for all 18 species.

To calculate annual emergence of odonates using the above data on their abundance, we need to take into account that during the period of emergence (May–October) emergence intensity varies abruptly and is species-specific. Although single individuals may emerge in any day of the period, most part of odonates emerge synchronously within very short time spans of several days, when sharp peaks of emergence occur. These time spans of peak emergence, which can happen once or several times per season, are designated as periods of mass emergence (measuring of their duration is described above). Thus, to calculate annual emergence, i.e., the number of individuals of each species, appeared at the studied area during a given year, E_S (ind. · m⁻² · year⁻¹), it is necessary to introduce a special species-specific coefficient:

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

where R_S (year⁻¹) is Haritonov's coefficient of renewability for given species S , defined as follows:

$$R_S = D_S / L_S \quad (4)$$

where D_S is duration of period of mass emergence (day · year⁻¹) of given species S per year, and L_S is lifetime of imago (day) of given species S . Thereby, Haritonov's coefficient gives number of mass emergence events per year.

Total annual emergence, E_Y (ind. · m⁻² · year⁻¹), was calculated as sum of E_S for all 18 species.

Annual total emergence biomass, B_Y , (g · m⁻² · year⁻¹) was calculated as follows:

$$B_Y = \sum_{S=1}^{18} E_S \cdot B_S \quad (5)$$

where B_S is average biomass of species S , published elsewhere (Popova and Kharitonov, 2012).

The above calculations of emergence were done per unit of the studied land area. In the text, all the data are presented per units of land area, except cases, where 'water area' is added. To calculate the emergence from unit of water area, we used land/water area ratio, which was equal to 190 km²/69 km² = 2.75.

2.8. Fatty acid and organic carbon analysis

In contrast to the above measurements, carried out from 1980 to 2010, fatty acids (FA) were measured only in 2009 and in 2016. We suppose that for the aims of estimation of average flux of HUFA from water to land, probable inter-annual variations in FA content of odonates are negligible. For 9 abundant species (see below) we took from 5 to 20

individuals for each sample, depending on their size. Number of samples, $n = 2$ for *L. dryas* and $n = 1$ for all other species in 2009, and $n = 3$ for all species in 2010. The samples were weighed and placed in chloroform:methanol mixture (2:1, v/v) and kept at $-20\text{ }^{\circ}\text{C}$ until further lipid analysis, like in our previous study (Sushchik et al., 2013). In the laboratory, the samples were mechanically homogenized with glass beads, and lipids were simultaneously extracted with three portions of 3 ml of chloroform–methanol (2:1, v/v). Then the solvents were roto-evaporated under vacuum, and the lipid extracts were derivatized to form fatty acid methyl esters (FAMES) with a methanolic solution of sulphuric acid (20:1, v/v) at $85\text{ }^{\circ}\text{C}$ during 2 h as described elsewhere (Gladyshev et al., 2010). A gas chromatograph equipped with a mass spectrometer detector (GC–MS, model 6890/5975C; Agilent Technologies, Santa Clara, USA) and with a 30 m long, 0.25 mm internal diameter capillary column HP-FFAP was used for FAME analysis. The temperature program started from $120\text{ }^{\circ}\text{C}$ that was maintained for 3 min, then increased at $5\text{ }^{\circ}\text{C min}^{-1}$ to $180\text{ }^{\circ}\text{C}$ with 10 min isothermally, followed by $5\text{ }^{\circ}\text{C min}^{-1}$ to $230\text{ }^{\circ}\text{C}$, and finally the isothermal regime was held for 30 min. The injector temperature was $220\text{ }^{\circ}\text{C}$, and helium was the carrier gas with a flow rate of 1 ml min^{-1} . Mass spectrometric conditions are given elsewhere (Gladyshev et al., 2014). The peaks were identified comparing their retention time and mass spectra to those in the integrated data base (NIST-2005, USA) and to those of available authentic standards (Sigma-Aldrich, USA). We used the common standard that contains 37 components (CRM47885) and some others those contained FAME mixtures, such as 47085-U and 47080-U, and individual FAMES, such as 04872 and CRM47563. Additionally for FAMES that were not available as commercial standards, we used our previous identification data that were based on specific derivatizing procedures with following GS-MS (Gladyshev et al., 2010; Sushchik et al., 2013). The FAMES were quantified according to the peak area of the internal standard, nonadecanoic acid (19:0), the solutions of which were added to samples prior to the lipid extraction.

The same number of samples as for lipid analyses were collected for organic carbon analyses. Organic carbon measurements of odonates were done with a Flash EA 1112 NC Soil/MAS 200 elemental analyzer (ThermoQuest, Milan, Italy). The calibration curves for the elemental analyzer were generated using aspartic acid and standard soil reference material (ThermoQuest, Milan, Italy).

2.9. Statistical analyses

Standard errors (SE), Kolmogorov-Smirnov one-sample test for normality D_{K-S} , Student's t -test for dependent samples and one-way ANOVA with Tukey HSD post hoc test were calculated conventionally, using STATISTICA software, version 9.0 (StatSoft, Inc., Tulsa, OK, U.S.A.). Only normally distributed data were used for ANOVA.

3. Results

3.1. Annual abundance

Total average annual abundance of odonates, N_Y , varied considerably through the studied period (Fig. 2). Maximum annual abundance, $23\text{ ind.}\cdot\text{m}^{-2}$, occurred in 1988, and minimum abundance, $3\text{ ind.}\cdot\text{m}^{-2}$, was found in 2010 (Fig. 2). The data suggest a downward trend in abundance from year 2001.

3.2. Spatial distribution

Abundance of the studied species of odonates increased significantly in shrub and grove habitats, situated at 2–4 km from the lake shore compared to that in shore and meadow habitats (Fig. 3). Evidently, odonates easily flight several kilometers away from place of their emergence and accumulate in preferable types of habitats.

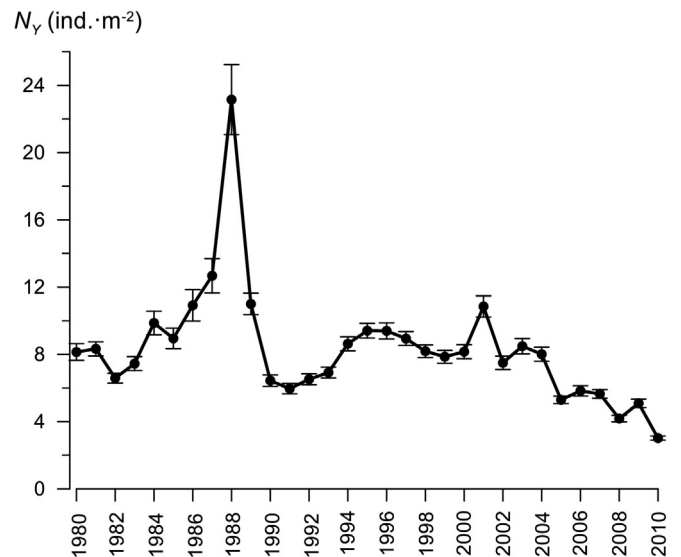


Fig. 2. Total average annual abundance, N_Y , of odonates in Barabinsk Forest–Steppe (West Siberia, Russia). Horizontal bars represent standard deviations.

3.3. Ecological traits of species

Average duration of period of mass emergence, D_s , of odonates species varied about two-fold, from 30 days (*Coenagrion armatum*, *C. lunulatum*, etc.) to 60 days (*Sympetrum paedisca*, etc.) (Table 2). Average lifespan of imagoes, L_s , ranged from 9.9 days (*C. lunulatum*) to 20.3 days (*Aeshna mixta*) (Table 2). Values of the dimensionless Haritonov's coefficient of renewability, R_s , varied from 2.50 (*Leucorrhinia pectoralis* and *L. rubicunda*) to 4.00 (*Sympetrum flaveolum*) (Table 2). This means that the studied species on average had from two to four events of mass emergence per summer. Average percentage of each species in total odonates' abundance varied insignificantly during the studied period and ranged from 0.5% (*Aeshna mixta*) to 19.4% (*Enallagma cyathigerum*) (Table 2). Average percentage of each species in total odonates' biomass

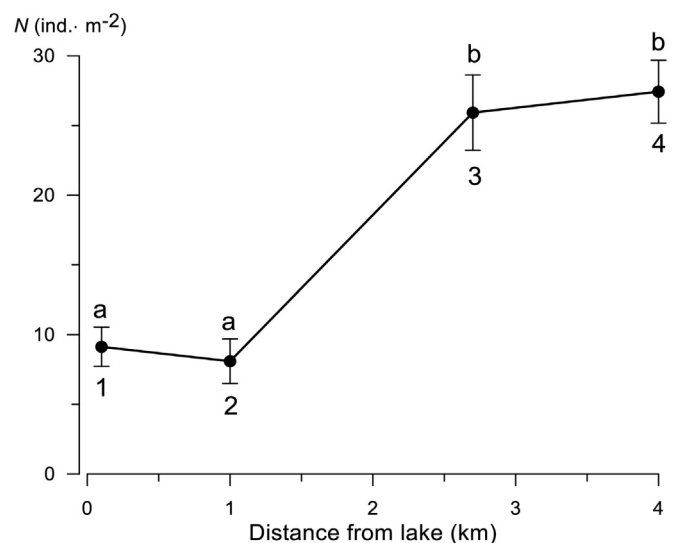


Fig. 3. Mean abundance (N) of odonates in 1980–1990 at four sample sites in Barabinsk forest–steppe (see Fig. 1): 1 – shore of the Fadikha Lake, 2 – wet lowland meadow, 3 – shrubs, 4 – birch grove. Horizontal bars represent standard deviations. Means labelled with the same letter are not significantly different at $P < 0.05$ after Student's t -test for dependent samples (number of pairs, $n = 11$).

Table 2

Ecological traits of odonate species (mean values for 31 years \pm SE): D_S – duration of period of mass emergence, L_S – lifespan, R_S – Haritonov's coefficient of renewability; percentage of species in total odonates' abundance (NP) and biomass, wet weight (WWP). Barabinsk Forest–Steppe (West Siberia, Russia), May–October 1980–2010.

Species	D_S , day \cdot year $^{-1}$	L_S , day	R_S , year $^{-1}$	NP, %	WWP, %
Suborder Anisoptera					
<i>Aeshna mixta</i>	60 \pm 0	20.3 \pm 0.4	2.96 \pm 0.02	0.5 \pm 0.1	2.7 \pm 0.3
<i>Aeshna serrata</i>	60 \pm 0	20.2 \pm 0.5	2.98 \pm 0.02	0.6 \pm 0.1	6.2 \pm 0.6
<i>Leucorrhinia pectoralis</i>	30 \pm 0	12.1 \pm 0.2	2.50 \pm 0.02	1.8 \pm 0.2	4.4 \pm 0.4
<i>Leucorrhinia rubicunda</i>	30 \pm 0	12.1 \pm 0.2	2.50 \pm 0.02	1.8 \pm 0.2	4.1 \pm 0.4
<i>Libellula quadrimaculata</i>	40 \pm 0	13.1 \pm 0.3	3.04 \pm 0.03	3.8 \pm 0.4	14.8 \pm 1.5
<i>Sympetrum danae</i>	60 \pm 0	17.2 \pm 0.4	3.48 \pm 0.03	4.9 \pm 0.4	5.5 \pm 0.4
<i>Sympetrum flaveolum</i>	60 \pm 0	15.1 \pm 0.4	4.00 \pm 0.03	7.4 \pm 0.6	9.5 \pm 0.6
<i>Sympetrum sanguineum</i>	50 \pm 1	16.7 \pm 0.3	2.98 \pm 0.03	0.9 \pm 0.1	1.3 \pm 0.2
<i>Sympetrum vulgatum</i>	50 \pm 0	16.9 \pm 0.4	2.96 \pm 0.03	11.3 \pm 0.8	21.3 \pm 1.2
Suborder Zygoptera					
<i>Coenagrion armatum</i>	30 \pm 0	10.1 \pm 0.3	2.97 \pm 0.02	6.0 \pm 0.5	2.2 \pm 0.2
<i>Coenagrion lunulatum</i>	30 \pm 0	9.9 \pm 0.3	3.03 \pm 0.02	8.3 \pm 1.5	3.5 \pm 0.7
<i>Coenagrion pulchellum</i>	30 \pm 0	10.2 \pm 0.3	2.96 \pm 0.03	4.8 \pm 0.5	1.8 \pm 0.2
<i>Enallagma cyathigerum</i>	60 \pm 0	15.1 \pm 0.3	3.98 \pm 0.03	19.4 \pm 1.4	8.6 \pm 0.7
<i>Erythromma najas</i>	50 \pm 0	14.3 \pm 0.4	3.51 \pm 0.03	4.5 \pm 0.3	2.4 \pm 0.2
<i>Lestes dryas</i>	40 \pm 0	13.4 \pm 0.5	2.98 \pm 0.04	2.4 \pm 0.2	1.5 \pm 0.1
<i>Lestes sponsa</i>	40 \pm 0	13.2 \pm 0.4	3.04 \pm 0.04	11.4 \pm 0.5	6.3 \pm 0.3
<i>Lestes virens</i>	40 \pm 0	13.3 \pm 0.4	3.02 \pm 0.03	2.4 \pm 0.2	0.9 \pm 0.1
<i>Sympecma paedisca</i>	60 \pm 0	15.2 \pm 0.6	3.98 \pm 0.02	7.8 \pm 0.6	3.0 \pm 0.2

(wet weight) also had small inter-annual variations and ranged from 0.9% (*Lestes virens*) to 21.3% (*Sympetrum vulgatum*) (Table 2).

3.4. Fatty acids and organic carbon

In all samples of nine Odonate species, 69 fatty acids were identified. Contents of the target fatty acids, EPA and DHA, are given in (Table 3). Contents of DHA in all species were approximately 100-fold lower, than those of EPA. Most species had similar contents of EPA, while *E. cyathigerum* and *E. najas* had significantly higher contents, than those of the other species (Table 3). Since the 9 species studied for fatty acid contents composed >70% of total biomass (Table 2), we used their EPA and DHA contents (Table 3) as a proxy for sum all odonates species biomass in the studied area. Thus, assuming the 9 species composed 100% of Odonate biomass, using their proportions (WWP, Table 2) and EPA and DHA contents (Table 3), the weighted average contents of EPA and DHA in Odonate biomass were calculated to be 2.39 and 0.01 mg \cdot g $^{-1}$ WW, respectively.

Contents of organic carbon per wet weight of odonate species varied in a small range: ANOVA gave insignificant differences (Table 3). Therefore, for following calculations, we used the mean content of organic carbon for all species (Table 3), 142 mg \cdot g $^{-1}$ WW.

Moisture content in species varied in a small range, had normal distribution. Average value of moisture was 71.0 \pm 0.7%.

Table 3

Mean values (\pm standard errors) of contents of eicosapentaenoic (EPA) and docosahexaenoic (DHA) fatty acids (mg \cdot g $^{-1}$, wet weight) and organic carbon (C, mg \cdot g $^{-1}$, wet weight) in bodies of adult Odonates in the Baraba forest-steppe zone in the south of West Siberia, June–August 2009 and 2016. Means labelled with the same letter are not significantly different at $P < 0.05$ after Tukey HSD post hoc test for ANOVA. When ANOVA is insignificant, letter labels are absent. Number of samples, $n = 5$ for *L. dryas* and $n = 4$ for all other species.

Species	EPA	DHA	C
<i>Aeshna serrata</i>	1.99 \pm 0.21 ^{AC}	0.01 \pm 0.00 ^{AB}	158 \pm 7
<i>Enallagma cyathigerum</i>	4.15 \pm 0.21 ^B	0.02 \pm 0.01 ^{AB}	165 \pm 16
<i>Erythromma najas</i>	3.77 \pm 0.20 ^B	0.02 \pm 0.00 ^{AB}	155 \pm 12
<i>Lestes dryas</i>	2.28 \pm 0.05 ^{AC}	0.03 \pm 0.00 ^A	127 \pm 3
<i>Leucorrhinia rubicunda</i>	2.26 \pm 0.04 ^{AC}	0.02 \pm 0.00 ^{AB}	128 \pm 7
<i>Libellula quadrimaculata</i>	1.75 \pm 0.06 ^A	0.00 \pm 0.00 ^B	130 \pm 12
<i>Sympecma paedisca</i>	2.63 \pm 0.15 ^C	0.01 \pm 0.00 ^{AB}	154 \pm 11
<i>Sympetrum flaveolum</i>	2.14 \pm 0.09 ^{AC}	0.02 \pm 0.00 ^{AB}	138 \pm 15
<i>Sympetrum vulgatum</i>	2.18 \pm 0.13 ^{AC}	0.02 \pm 0.01 ^{AB}	129 \pm 3

3.5. Emergence

Ranges and average values of odonate emergence and concomitant biochemical fluxes are given in Table 4. Emergence, expressed both as number of individuals and their biomass, and concomitant fluxes of organic C and HUFA, which correlated with annual abundance, N_Y . Therefore, maximum and minimum values of all emergence parameters (Table 4) occurred in 1988 and 2010, respectively, that is in the years of maximum and minimum annual abundance (Fig. 2). Emergence, expressed as number of individuals, E_Y , varied about 8-fold between years, while the emergence, expressed as biomass, B_Y , and its biochemical parameters, C_Y , EPA_Y , DHA_Y and $EPA_Y + DHA_Y$, varied only about 6-fold (Table 4).

4. Discussion

During 31 years of observations, emerging odonates provided a considerable flux of aquatic productivity to the studied forest-steppe area. This flux, i.e., abundance of odonates, varied about 8-fold between years. Similarly, in a temporary wetland pond in South Carolina, emergence of odonates varied about 10-fold during two years (Leeper and Taylor, 1998). The main driver of the annual variations of odonate emergence in the Barabinsk forest-steppe is believed to be the water level of the Chany Lake, which is a measure of the relative water supply of the whole region. The correlation coefficient between the annual

Table 4

Odonate total annual emergence as number of individuals, E_Y (ind. \cdot m $^{-2}$ \cdot year $^{-1}$), and biomass, B_Y (g \cdot m $^{-2}$ \cdot year $^{-1}$, wet weight) and concomitant fluxes of organic carbon (C_Y , g \cdot m $^{-2}$ \cdot year $^{-1}$) and the essential polyunsaturated fatty acids, eicosapentaenoic (EPA_Y , mg \cdot m $^{-2}$ \cdot year $^{-1}$) and docosahexaenoic (DHA_Y , mg \cdot m $^{-2}$ \cdot year $^{-1}$): min. – minimum, max. – maximum and av. – average. Barabinsk Forest–Steppe (West Siberia, Russia), 1980–2010.

Emergence	From water area			To land area		
	Min.	Max.	Av.	Min.	Max.	Av.
E_Y	27.5	213.4	75.5	10.0	77.6	27.5
B_Y	2.3	13.3	5.9	0.8	4.9	2.1
C_Y	0.33	1.89	0.84	0.11	0.70	0.30
EPA_Y	5.50	31.79	14.10	1.91	11.71	5.02
DHA_Y	0.02	0.13	0.06	0.01	0.05	0.02
$EPA_Y + DHA_Y$	5.52	31.92	14.16	1.92	11.76	5.04

population abundance of odonates and the lake water level was ca. 0.9 (Haritonov and Popova, 2011).

Quantitatively, emergence from water area in our forest-steppe study system of 27–213 ind. · m⁻² · year⁻¹, was significantly greater than that in a wetland in South Carolina, 0.8–8.4 individuals per m² of water area per year (Leeper and Taylor, 1998). However, in Philippine streams annual emergence of odonates was up to 98 individuals per m² of water area (Freitag, 2004), which falls within the range of the annual emergence found in our study.

A decrease of abundance with distance from donor water body edge, common for most amphibiotic insects (Gratton and Vander Zanden, 2009; Sabo and Hagen, 2012; Muehlbauer et al., 2014; Dreyer et al., 2015) evidently is not true for the studied odonate species. The fact, that odonates can fly away up to 50 km from water bodies of their emergence and accumulate in preferable habitats, shrubs, birch and aspen-birch groves, forest shelterbelts, was described earlier (Kharitonov and Popova, 2011; Popova and Kharitonov, 2012). In this paper, we quantified this fact comparing odonates abundance at given distances from the donor lake for several years. Thus, adult odonates appeared to inhabit the entire forest-steppe area (Fig. 1), rather than narrow strips around water bodies. Therefore, we calculate the aquatic subsidy via odonate emergence for the whole studied territory.

As mentioned, odonates are often regarded as quantitatively insignificant compared to the abundance of other emergent insects, Diptera (Chironomidae), Trichoptera and Ephemeroptera (Baxter et al., 2005). However, we argue that the flux of aquatic productivity should be estimated in biomass (organic carbon) units, rather than as number of individuals. Gratton and Vander Zanden (2009) estimated global insect deposition rate to land next to a body of water within 100 m from shore as 0.008–0.83 g C m⁻² year⁻¹. In our study, odonates gave 0.11–0.70 g C per year per m⁻² of all studied land area, rather than that near shore. Thus, the contribution of odonates to the aquatic carbon deposition to land is close to the highest value of the global estimation for all insects.

The high contribution of odonates to the water-land fluxes was also reported for some other habitats. For instance, although odonates in a Lake Michigan coastal wetland constituted a small percentage of total abundance of emergent insects, <10%, they provided a major contribution to the emergent biomass due to their large size (MacKenzie and Kaster, 2004). Similarly, in temporary ponds in mixed coniferous-deciduous forest (Ontario, Canada) damselflies were important contributors to the emergent insect flux and provided 83% of concomitant organic carbon flux, even though they represented only 0.004% of collected individuals (Schriever et al., 2014). In forest ponds, carbon flux due to emergent odonates, has been estimated as 2.8 g C m⁻² per year (Schriever et al., 2014), which is close to our maximum value, measured in the Barabinsk forest-steppe. In contrast, in a Lake Michigan coastal wetland annual emergence of odonates was up to ~0.5 g of dry weight from m² of water area (MacKenzie and Kaster, 2004), that is lower than the minimum value of year emergence, found in our study, 0.7 g DW · m⁻². However, the cited authors (MacKenzie and Kaster, 2004) remarked, that the large insects, odonates, avoided traps, used in their study. Thus, the biomass of emergent odonates might be underestimated by emergence trap measurements, which generally designed for small insects (Wesner, 2012; Schriever et al., 2014). Indeed, in some studies of emergence odonates were not analyzed because of the low number of species caught in emergence traps (Poepperl, 2000; Davis et al., 2011).

In our study, odonate emergence was estimated via measurements of abundance of adults, rather than based on trap measurements. For our estimations, we used Haritonov's coefficient of renewability, R_5 (year⁻¹) which represents the number of events of mass emergence per year. Values of Haritonov's coefficients, obtained in our study for different species in different years, were from 2 to 4. Therefore, each studied species of odonates had 2–4 periods of mass emergence during the year. It is worth noting, that Haritonov's coefficient was calculated from imago lifespan, L_5 and duration of mass emergence D_5 , that is

independently calculated from observations of number of measured annual periods of mass emergence of species. However, the independently calculated values always coincided with the number of observed periods of mass emergence.

The flux of aquatic productivity to terrestrial ecosystems via emergent insects may be comparable with daily aboveground production of terrestrial arthropods in surrounding terrestrial habitats (Gray, 1989). Unfortunately, there are no data on production of terrestrial insects in our study system. Nevertheless, we can use an estimation of production of herbivorous insects in temperate grasslands of 0.19–0.40 g C m⁻² year⁻¹ (Gratton and Vander Zanden, 2009) as a proxy. Based on that, the flux of organic carbon due to odonate emergence to the studied forest-steppe, 0.11–0.70 g C m⁻² year⁻¹, appeared to be quite comparable with previous estimations of the production of terrestrial insects.

Odonates in our studied area are known to be consumed by abundant insectivorous birds, namely Passeriformes (up to 64% of the diet), and by some other vertebrate and invertebrate predators (Tchernyshov, 1981; Prokofieva, 2004; Popova and Kharitonov, 2012). In other locations, odonates are also known to be the actively preferred prey of aerial insectivore birds (McCarty and Winkler, 1999; Mengelkoch et al., 2004). Thus, the emergent aquatic insects likely are an important component of the diets of terrestrial insectivorous predators, especially of birds (Dodson et al., 2016). For example, aquatic prey from a Japanese stream accounted for 25.6% of the annual total energy demand of the entire forest bird assemblage (Nakano and Murakami, 2001).

Moreover, besides their high quantity, which is equal or even higher, than production of terrestrial insects, emergent aquatic insects appear to provide higher nutritional quality for terrestrial vertebrate predators, especially for birds, in terms of HUFA contents. As known, many birds, including Passeriformes, have especially high EPA and DHA requirements (Maillet and Weber, 2006, 2007; Klaiman et al., 2009; Rodríguez-Turiénzo et al., 2010). Direct experimental evidence on a key importance of food with high contents of EPA and DHA for growth and development of chicks of aerial insectivores, Tree Swallow (*Tachycineta bicolor*, order Passeriformes) were recently obtained by Twining et al. (2016). As mentioned, most terrestrial insects do not contain the physiologically essential HUFA, EPA and DHA in their biomass (Buckner and Hagen, 2003; Wang et al., 2006; Rumpold and Schluter, 2013; Barroso et al., 2014; Sanchez-Muros et al., 2014), therefore, they may not satisfy the biochemical requirements of birds. In contrast to terrestrial insects, the studied odonates had high content of EPA in their biomass, 8.24 mg · g⁻¹ DW, and also contained DHA, 0.03 mg · g⁻¹ DW. These contents are lower, than that of imago of some other amphibiotic insects, Chironomidae, 17.8 and 0.3 mg · g⁻¹ DW, respectively (Gladyshev et al., 2009). However, the average EPA content in odonates was higher, than that of imago of Culicidae, 6.60 mg · g⁻¹ DW, but the average DHA content in odonates was lower, than that of Culicidae, 0.17 mg · g⁻¹ DW (Sushchik et al., 2013). Therefore, odonate imagoes have a median nutritive value for birds and other vertebrates in terms of HUFA content compared with previously studied taxa of emergent insects. However, comparatively large odonates may be the prey that is more profitable for birds which forages on insects in the air column, because they are more visible (McCarty and Winkler, 1999).

The flux of EPA + DHA via odonate emergence in the studied forest-steppe was 1.92–11.76 g · m⁻² · year⁻¹. Average global estimation of the HUFA flux from aquatic to terrestrial ecosystems via insect emergence is 2.5–11.8 mg · m⁻² · year⁻¹ (Gladyshev et al., 2009). Thus, odonates exported a similar quantity of EPA and DHA to the studied terrestrial ecosystem as all emergent insect species in an 'average' ecosystem. In addition, as seen in other studies, cited above, large odonates gave a major contribution to the total emergent biomass (MacKenzie and Kaster, 2004). It is worth noting, that the above global approximation of the flux of HUFA appeared to be well confirmed by our present study of the natural landscape.

Most studies of subsidies from water bodies to land focus on organisms and food webs within several meters of shore (Muehlbauer et al., 2014). However, the behavior of specific emergent taxa may affect subsidy distance (Muehlbauer et al., 2014). Indeed, odonates are strong flyers, and can disperse at distances of several kilometers from their native water bodies. Thus, odonates can transfer considerable amounts of aquatic productivity, including essential biochemicals, beyond the riparian zone to whole terrestrial ecosystems.

Acknowledgements

This work was supported by the Russian Federal Fundamental Scientific Research Program, projects No. VI.51.1.9 and No. VI.51.1.1, by Federal Tasks of Ministry of Education and Science of the Russian Federation for Siberian Federal University and was partly supported by the Council on grants from the President of the Russian Federation for support of leading scientific schools (grant NSh-9249.2016.5). We are grateful to anonymous Reviewers for their kind help to improve the manuscript.

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