Preliminary estimation of the export of omega-3 polyunsaturated fatty acids from aquatic to terrestrial ecosystems in biomes via emergent insects

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Abstract

For future estimating of potential limitation of some terrestrial consumers by food quality in global scale, the water-land fluxes of essential polyunsaturated fatty acids (PUFA), eicosapentaenoic acid (20:5n-3, EPA) and docosahexaenoic acid (22:6n-3, DHA), with the biomass of emergent aquatic insects in several biomes were estimated. The water /land area ratios for each biome were calculated by dividing the water area of each biome by its terrestrial area. Data on insect emergence from water bodies (g of dry mass m^{-2} $year^{-1}$), were generalized and averaged for each biome.From available data, EPA and DHA contents (mg g^{-1} dry mass), in the biomass of emergent aquatic insects were calculated first so that annual fluxes of PUFA to land area via aquatic insect emergence could be estimated for each biome. A high variability of PUFA fluxes occurred between the biomes, ranging from 0.04 to 4.39 mg$\cdot$$m^{-2}$$\cdot$$year^{-1}$. In this study, the aquatic PUFA supply to land area appeared to be significantly lower than that of a previous global average estimate. This finding indicates that a putative limitation of some terrestrial consumers by food quality, namely by the supply of aquatic PUFA, may be more severe than was previously determined.

Key words: eicosapentaenoic acid, docosahexaenoic acid, aquatic-terrestrial subsidies, food quality, water/land area ratio

1. Introduction

Matter and energy exchange between terrestrial and aquatic ecosystems, often designated 'reciprocal subsidies', has appeared as one of the hot topics in ecology in recent decades (Baxter

et al., 2005; Ballinger and Lake, 2006; Gratton and Vander Zanden, 2009; Richardson et al., 2010; Bartels et al., 2012; Schulz et al., 2015; Schindler and Smits, 2017). Terrestrial subsidies for aquatic ecosystems, primarily governed by gravity, are commonly examined, while fewer works have focused on counter-gravitational biogenic flows from aquatic ecosystems (Baxter et al., 2005; Ballinger and Lake, 2006; Gratton and Vander Zanden, 2009; Epanchin et al., 2010; Bartels et al., 2012; Schulz et al., 2015). One of the main biogenic flows of matter and energy from water to land is provided by emerging aquatic (amphibiotic) insects. The flux of emergent aquatic insects can be comparable or even can exceed the production of terrestrial insects in the surrounding landscape (Gray, 1989; Bartrons et al., 2013). Thus, in many locations, emergent aquatic insects are an important or even principal food supply for many terrestrial consumers, especially for spiders and birds (Nakano and Murakami, 2001; Sanzone et al., 2003; Baxter et al., 2005; Paetzold et al., 2005; Epanchin et al., 2010; Richardson et al., 2010; Schulz et al., 2015).

The quantitative contribution of emergent insects to food webs of a given terrestrial ecosystem is determined by many ecological factors, such as the productivity of aquatic ecosystems and water/land area ratios (ecosystem geometry) (Gratton and Vander Zanden, 2009; Bartrons et al., 2013). Currently, there are several global average estimates of emergence based on local measurements (Baxter et al., 2005; Gladyshev et al., 2009) but only one calculation for a particular landscape (Bartrons et al., 2013). However, specific knowledge of the interrelations of aquatic and terrestrial ecosystems in particular landscapes is necessary to manage these systems for protection of biodiversity and functionality (Ballinger and Lake, 2006; Gratton and Vander Zanden, 2009).

In addition to the quantitative importance for surrounding land ecosystems, the contribution of emergent aquatic insects to terrestrial food webs was recently recognized as being based on their high quality relative to terrestrial food sources (Gladyshev et al., 2009, 2013; Marcarelli et al., 2011; Hixson et al., 2015; Twining et al., 2015; Schindler and Smits, 2017). Currently, food quality is conventionally determined using elemental stoichiometric ratios and amino acid and lipid content and composition (e.g., Anderson et al., 2004; Muller-Navarra, 2008; Marcarelli et al., 2011). Among lipids, long-chain polyunsaturated fatty acids (LC-PUFA) of the omega-3 family, such as eicosapentaenoic acid (20:5n-3, EPA) and docosahexaenoic acid (22:6n-3, DHA), are of key physiological importance for most animals. Indeed, EPA is a biochemical precursor of signalling molecules (endohormones), which control the cardiovascular system, allergic and inflammatory reactions, etc., while DHA regulates the synthesis of endohormones and is the main structural fatty acid of membranes in the brain and retina cells as well as in those of mitochondria in high-frequency contraction skeletal muscles (Simopoulos,

2000; Infante et al., 2001; Lauritzen et al.,2001; Heckmann et al., 2008; Ahlgren et al., 2009; Wall et al., 2010; Norris and Dennis, 2012).

The parent acid of omega-3 family, alpha-linolenic acid (18:3n-3, ALA), is synthesized only by plants, while animals cannot do it, because they (except the nematode *Caenorhabditis elegans*) do not have key enzymes, delta-15/omega-3 desaturases (Sperling et al., 2003; Sayanova et al., 2006; Uttaro, 2006; Lands, 2009; Alloatti et al., 2011; Zhou et al., 2011). Terrestrial vascular plants cease their synthesis of omega-3 acids on the 18-carbon ALA, which is the main constituent of membranes of chloroplasts, i.e., stores primarily in green parts of plants (Heinz, 1993; Sayanova et al., 2006). In general, animals, including humans, can convert the parent alpha-linolenic acid, obtained from plants, to physiologically important long-chain EPA and DHA (Stark et al., 2008). Strictly herbivorous terrestrial animals, which consume green parts of plants, evidently can satisfy their ~~own~~ physiological requirements in the long-chain PUFA by the conversion of ALA only (Wood et al., 2008; Kang et al., 2010; Kouba and Mourot, 2011). Specifically, herbivorous terrestrial insects use LC-PUFA primarily as precursors of signalling molecules, eicosanoids, and thereby synthesize them in small quantities, on the level of vitamin requirements (Stanley and Kim, 2014). ~~However, some omnivorous and carnivorous animals cannot cover their physiological requirements in EPA and DHA via the conversion of ALA, thereby they must obtain these essential long-chain PUFA from food (Davis & Kris-Etherton, 2003; Green et al., 2004; Abba et al., 2005; Wall et al., 2010; Twining et al., 2016; 2018; Hadley et al., 2017). Meanwhile in terrestrial ecosystems there are no considerable sources of EPA and DHA for such animals (Gladyshev et al., 2013; Hixson et al., 2015; Twining et al., 2015).~~ In contrast, some omnivorous and carnivorous terrestrial animals deposit appreciable amounts of EPA and DHA in their specific tissues that are unlikely supported only by the products of ALA conversion (Davis & Kris-Etherton, 2003; Green et al., 2004; Abba et al., 2005; Wall et al., 2010; Twining et al., 2016; 2018; Hadley et al., 2017). The direct food sources of EPA and DHA may be of crucial importance for such animals, although terrestrial production is known to be poor in these compounds (Gladyshev et al., 2013; Hixson et al., 2015; Twining et al., 2015).

In contrast to terrestrial vascular plants, some taxa of microalgae are capable of synthesizing large amounts of EPA and DHA (Harwood, 1996; Uttaro, 2006; Ruiz-Lopez et al., 2012). EPA and DHA are transferred through aquatic food chains to organisms of progressively higher trophic levels and are then exported to terrestrial ecosystems via vectors such as emerging aquatic insects (Gladyshev et al., 2009, 2013). Emerging aquatic insects were found to be the high-quality food regarding LC-PUFA contents, which support significantly better conditions of

some insectivorous birds and spiders compared to terrestrial insects (Twining et al., 2016; 2018; Fritz et al., 2017).

Thus, aquatic insects subsidize terrestrial ecosystems with ~~unique molecules,~~ the omega-3 LC-PUFA, which are ~~essential~~ crucial for many physiological processes in some terrestrial animals. The magnitude of these subsidies is poorly known, and the published information remains scattered. Recently, an attempt was made to estimate the export of EPA and DHA from water to land via emergent insects on a global scale (Gladyshev et al., 2009).This coarse estimation gave at least a potential for situations in which there may be a shortage of LC-PUFA for some terrestrial consumers, insectivore rodents (Gladyshev et al., 2009). Nevertheless, it was concluded that to obtain more reliable quantitative estimates data on LC-PUFA fluxes from particular aquatic ecosystems to surrounding terrestrial ecosystems in specific landscapes (biomes) are desirable (Gladyshev et al., 2009).

Then, several direct measurements of the EPA and DHA fluxes in several locations were completed, using quantifications of the emergence and PUFA contents in the emergent biomass (Gladyshev et al., 2011a, b; Borisova et al., 2016; Martin-Creuzburg et al., 2017; Moyo et al., 2017; Popova et al., 2017). To make their local case study data more applicable in a general (worldwide) context, the authors compared data, obtained in their studies with the coarse preliminary estimation of average global PUFA flux made by Gladyshev et al. (2009). However, such comparisons are not conclusive, and more specific estimations of average EPA and DHA fluxes in different types of biomes are desirable (Gladyshev et al., 2009; Schindler and Smits, 2017). Thus, the paper aims to compile a global picture of the LC-PUFA subsidies, their potential size and distribution across biomes.

2. Material and methods

2.1. Calculation of water/land area ratio

The water/land area ratios in biomes (Olson et al., 2001) were calculated using data from Feng et al. (2016, Table 3 of the reference) and dividing the water area (km^2) of each biome by its terrestrial area (km^2).

2.2. Data on emergence

To calculate emergence, the available data from the literature in the Web of Science Core Collection were taken. Only reports on emergence calculated in mass, dry mass (DM) or organic carbon units from square metres of a water body for the emergence period (year^{-1}) for all or dominant emergent taxa were considered. If the same water body was sampled in different years, or closely situated and ecologically similar water bodies from the same landscape were sampled, then the mean overall reported values of the emergence were calculated and used for further meta-analysis, as in similar studies (Bartels et al., 2012).

2.3. Determining the biome

To attribute the water bodies where the emergence was measured to a biome, the resource http://worldmap.harvard.edu/maps/6046/ was used. Additionally, to specify the biome, the descriptions of geomorphology and vegetation in relevant papers were considered.

2.4. Generalization of PUFA contents in emergent insects

Available data on EPA and DHA contents (mg g^{-1} of dry mass) were extracted from the Web of Science Core Collection. These data were obtained based on an extraction of total lipids by a chloroform (dichloromethane):methanol mixture and gas chromatography (GC) of fatty acids methyl esters (FAME) and internal standards, i.e., they represented quantitative (mg g^{-1} biomass) EPA and DHA estimates (for details, see, e.g., Sushchik et al., 2013). In addition, we included our unpublished data in the analysis, obtained by the above methods (GC of FAME and internal standard), described in detail elsewhere (Sushchik et al., 2013). Since all the data on PUFA contents in emergent aquatic insects were obtained by similar fatty acid analysis methods, they were comparable with each other and with our unpublished data.

When collecting the data for calculating the median PUFA content in emergent insect biomass from the relevant literature and unpublished data, we considered species composition of emergent aquatic insects published in the insect emergence literature (Section*2.2 Data on emergence*). In most cases, Chironomidae dominated the species composition (up to ~ 90% of the biomass of emergent insects), while the remaining species composition consisted of primarily Ephemeroptera, Plecoptera, Trichoptera, and Odonata (Brittain and Lillehammer, 1978; Jackson and Fisher, 1986; Stagliano et al., 1998; Rolauffs et al., 2001; Baxter et al., 2005; MacKenzie, 2005; Paetzold et al., 2005; Rundio and Lindley, 2012; Jonsson and Stenroth, 2016; Yuen and Dudgeon, 2016; Salvarina et al., 2017). In some locations, rather than Chironomidae, Diptera such as Culicidae, Simuliidae and Chaoboridae were the dominant taxa (Whiles and Goldowitz,

2001; Sushchik et al., 2013; Martin-Creuzburg et al., 2017; Salvarina et al., 2017). Finally, we collected all published data for PUFA contents in imago of Chironomidae (measured in 4 case studies in 4 locations) and in imago ofEphemeroptera, Plecoptera, Trichoptera, Culicidae, Chaoboridae and miscellaneous insects (each taxa was measured in 1 case study in 1 location) and calculated their median value to determine their principal contribution to the biomass of emergent insects in most locations. The median for all taxa was used for the following calculation to estimate the PUFA fluxes from water to land via the emergent insects.

2.5. Statistics

Descriptive statistic for biomes with number of data $n \geq 3$, Kolmogorov-Smirnov one-sample test for normality D_{K-S}, standard errors SE, coefficient of variation *CV*, Student's *t*-tests and one-way ANOVA were calculated conventionally, using STATISTICA software, version 9.0 (StatSoft, Inc., Tulsa, OK, USA).

3. Results

Data on insect emergence from the surface of water bodies (g DM m^{-2} year^{-1}) were available only for 8 biomes (Table 1). The highest value of emergence was reported for a South African river (tropical and subtropical moist broadleaf forests biome) (Table 1). A high value of emergence was also reported for a desert creek (deserts and xeric shrublands biome) (Table 1). However, only single observations were available from these two biome types.

For three biomes with number of data $n \geq 3$ descriptive statistics was calculated (Table 1). All data for these three biomes had normal distribution. In biome Tropical and Subtropical Moist Broadleaf Forests average value of emergence was higher, than those for biomes Temperate Broadleaf and Mixed Forests and Temperate Grasslands, Savannas and Shrublands (Table 1). Nevertheless, because of a high coefficient of variation, which value was nearly 100%, average value of emergence in Tropical and Subtropical Moist Broadleaf Forests did not differ significantly from those of two other biomes according to Student's *t*-tests and one-way ANOVA.

The sum of EPA and DHA in the biomass of imago of emergent insects varied from 7.96 to 33.7 mg·g^{-1} of dry mass, with median value 11.4 mg·g^{-1} (Table 2).

Among the 13 biomes, apart from mangroves, the highest water/land area ratio was characteristic of the tundra biome (Table 3). The tropical and subtropical coniferous forests

biome had the lowest ratio (Table 3). Multiplying the values of the water/land area ratios (Table 3) by the respective values of emergence from the water area (Table 1), values of emergence were obtained for each biome (Table 3). Then, using the median value of EPA+DHA contents in the biomass of emergent insects (Table 2), fluxes of these PUFA from aquatic ecosystems in the biomes were calculated (Table 3). The highest emergence and concomitant PUFA flux values were characteristic of tropical and subtropical moist broadleaf forests (Table 3). Surprisingly, the deserts and xeric shrublands biome also had high emergence and concomitant PUFA flux values, while the minimum values were in the temperate coniferous forests biome (Table 3). Data on 6 biomes were absent (Table 3).

4. Discussion

The main findings of this study are follows. The first generalization of LC-PUFA contents in imago of emergent aquatic insects was done and ~4-fold variations of the reported values, from ~8 to ~34 mg·g^{-1} DM was found (Table 2). Most likely, when more samples are analysed throughout the world, the range of variations will be expanded. Indeed, variations of EPA+DHA contents in the benthic larvae of aquatic insects were ~10-fold (Makhutova et al., 2016). Besides, the average LC-PUFA flux to land area was found to vary from 0.04 to 4.39 mg·m^{-2}·year^{-1} across numerous biomes. According to previous estimations, the average global flux of EPA+DHA by emergent insects could be from 2.5 to 11.8 mg·m^{-2}·year^{-1} (Gladyshev et al., 2009).

Since our calculations gave the lower LC-PUFA supply, the putative limitation of some terrestrial consumers by these essential biochemical compounds (Gladyshev et al., 2009) may be more severe than was previously thought. ~~These terrestrial consumers, which seem be limited by a shortage of supply of aquatic EPA and DHA, are some insectivore birds.~~ For instance, insectivore birds that evolve with access to aquatic insects seem to be limited by a shortage of supply of aquatic EPA and DHA. Twining et al. (2018) found that tree swallow (*Tachycineta bicolor*, Passeriformes) cannot cover their LC-PUFA demands by the synthesis from dietary ALA ~~precursor~~ and ~~thereby must~~ obtain most EPA and DHA from the direct food sources, aquatic insects. Thus, terrestrial insects, which contain no detectable quantities of EPA and DHA in their biomass (Stanley-Samuelson et al., 1988; Rumpold and Schluter, 2013; Barroso et al., 2014; Sanchez-Muros et al., 2014), would not compensate dietary needs of tree swallows and other aerial insectivores with similar niches with respect to LC-PUFA (Twining et al., 2018). Besides the birds, insectivorous rodents may be limited by the putative aquatic LC-PUFA shortage, as well as wolf spiders (Fritz et al., 2017).

Meanwhile, the paper recognizes the lack of reliable information on the global demand of terrestrial consumers in EPA and DHA and relative contribution of their synthesis from ALA precursor vs the flux from aquatic ecosystems, as well as the fraction of the aquatic production of LC-PUFA which is transferred to land consumers.

Among biomes, the highest emergence and concomitant PUFA flux values were found in tropical and subtropical moist broadleaf forests. On the one hand, this seems to be reasonable, considering the comparatively high biological productivity and humidity of this biome. On the other hand, the high estimate was evidently due to only one extremely high value of emergence obtained from South African river, but in other locations of this biome the values of emergence were approximately an order of magnitude lower (Table 1). Thus, additional studies are necessary to confirm this preliminary estimate.

Calculating the emergence to land area, we used the water/land area ratio and uniformly distributed the aquatic biomass through the whole biome territory. However, many authors reported that the flux of aquatic productivity decays exponentially and is deposited within ~100 m inland from the shore (Delettre et al., 2000; Gratton and Vander Zanden, 2009; Bartrons et al., 2013; Korobushkin, 2014; Muehlbauer et al., 2014; Korobushkin et al., 2016; Schindler and Smits, 2017). Nevertheless, there are several circumstances that justify our assumption of the uniform distribution of emergent insects. First, large insects, such as odonates, are strong fliers and can move several kilometres from waterbodies inside terrestrial habitat (Gratton and Vander Zanden, 2009; Popova et al., 2017). Second, when terrestrial birds, which visit waterbodies and riparian zones to consume emergent insects, return to their inland nest sites, they transport aquatic productivity for several kilometres, providing spatial integration of the aquatic subsidies (e.g., Epanchin et al., 2010; Schindler and Smits, 2017). In addition, even if the spatial extent of emergent insects is within several metres from the edge of the water, the overall spatial extent of the exchange in many landscapes may be high because of the dendritic form of drainage networks and meander bends of waterbodies, which provide substantial overlap of the deposition areas (Sabo et al., 2012). Indeed, Bartrons et al. (2013) used detailed geographical information for the state of Wisconsin to determine that approximately 20% of the total land area of Wisconsin falls within 100 m of a lake or stream. Assuming the aquatic insect deposition is within 100 m inland from the shore, using detailed geographical data on the area of lakes and rivers and estimating the emergence based on benthic insect production, Bartrons et al. (2013) calculated the total annual insect emergence in the state of Wisconsin as 6,800 metric tons of organic carbon (C).It is worth noting, that ~20% of the total land area of Wisconsin falls within 100 m of a lotic or lentic waterbody (Bartrons et al. 2013).Now let's determinethe emergence in Wisconsin using our more coarse way of calculations. Taking the area of Wisconsin as 169639

km^2 and the total water area in this state as 10950 km^2 (Table 2 in Bartrons et al., 2013) and taking 1 g C = 2.75 g DM (Alimov, 1989), the emergence in Wisconsin was 0.12 g DM · m^{-2} · $year^{-1}$. Wisconsin is in the temperate broadleaf and mixed forests biome. According to our calculations, the average emergence to land area in this biome was 0.119 g DM · m^{-2} · $year^{-1}$ (Table 4). Here, we see good similarity between the calculations, based on detailed geographical information for the actual landscape, the state of Wisconsin (Bartrons et al., 2013), and our global-scale calculations, which are inevitably based on a number of simplifications and assumptions. Hence, more work on actual landscapes based on fine-scale geographical information (e.g., Bartrons et al., 2013; Popova et al., 2017) are desirable to specify the areal flux of aquatic productivity via emergent insects.

5. Conclusions

The study demonstrated the high variability of the aquatic LC-PUFA fluxes via emergent insects among biomes and gave a benchmark for future studies in particular landscapes. The present calculations give lower values of the aquatic PUFA flux to land area than were previously determined. Thus, taking into account the sparse but clear evidence of the possible limitation of some terrestrial consumers by a shortage of essential PUFA, the quantification of EPA and DHA fluxes via emergent aquatic insects for actual landscapes is believed to be important for theoretical and applied ecology.

Acknowledgements

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Table 1

Insect emergence from the water surfaces (g DM m^{-2} year^{-1}) in biomes. Accounted (dominant) taxa: D – Diptera, Ch – Chironomidae, C – Culicidae, E – Ephemeroptera, O – Odonata, P – Plecoptera, T – Trichoptera, W – whole community.

Water body	Taxa	Emergence	Reference
Tundra			
lake (61° N 9° E)	W	0.1[a]	Brittain and Lillehammer, 1978
creek (59°20′ N 158°40′ W)	E, P, T	0.4	Francis et al., 2006
Average		**0.3**	
Boreal Forests/Taiga			
bog (61°41' N, 24°06' E)	Ch	1.1[b]	Paasivirta et al., 1988
lake (65°36' N, 17°00' W)	Ch	1.9	Dreyer et al., 2015
Average		**1.5**	
Temperate Coniferous Forests			
lake (47° N 121° W)	Ch	0.2[c]	Sherk and Rau, 1992
lake (52°50′ N 93°14′ E)	Ch	0.2	Borisova et al., 2016
Average		**0.2**	
Temperate Broadleaf and Mixed Forests			
streams (47° N 15° E)	E, P, T	4.3[d]	Jackson and Fisher, 1986
streams & springs (51° N 10° E)	W	3.2[e]	Jackson and Fisher, 1986
river (45° N 74° W)	W	6.2[f]	Jackson and Fisher, 1986
lake (59° N 18° E)	Ch	1.9[g]	Jackson and Fisher, 1986
lake (56°N 12°E)	W	1.3[a]	Woollhead, 1994
wetland pond (33° N 81° W)	Ch	1.1[h]	Leeper and Taylor, 1998
wetland pond (32°52′ N 87° 26′ W)	Ch	1.5[b]	Stagliano et al., 1998
stream (54°N 10°E)	D, T, E	1.7	Poepperl, 2000
brook (51°N 6°E)	Ch	10.4[b]	Rolauffs et al., 2001
stream (42°43′ N 141°36′ E)	W	1.2[i]	Nakano and Murakami, 2001
wetland (44° N 87° 39′ W)	O, E	0.5	MacKenzie and Kaster, 2004
salt marsh (43°N 70°W)	Ch	0.2[h]	MacKenzie, 2005
river (46° N 12°30′ E)	P, E, Ch	6.3	Paetzold et al., 2005
stream (38°N 81°W)	Ch, P, T	3.7[j]	Johnson et al., 2013
lake (51°48′ N 39°22′ E)	W	2.4	Silina, 2016
lakes (47°45′ N 9°01′ E)	W	1.6[k]	Martin-Creuzburg et al., 2017 Salvarina et al., 2017
Average ± SE (standard error)		**3.0±0.7**	
Coefficient of variation (%)		**23.3**	
Temperate Grasslands, Savannas and Shrublands			
wetland (40°N 106°W)	D, Ch	1.2[b]	Whiles and Goldowitz, 2001
lakes & wetlands (54°35′ N 78°10′ E)	O	0.9	Gladyshev et al., 2011a
lakes & wetlands (53°43′ N 77°51′ E)	C	0.5	Gladyshev et al., 2011b
lakes (51°N 46°E)	W	0.2[l]	Djomina et al., 2016
Average ± SE		**0.7±0.2**	
Coefficient of variation (%)		**28.6**	
Mediterranean Forests, Woodlands and Scrubs			
creek (36°04′ N 121°35′ W)	Ch, E, P	6.6[b]	Rundio and Lindley, 2012
Tropical and Subtropical Moist Broadleaf Forests			
stream (2°S 29°E)	W	2.2[m]	Jackson and Fisher, 1986
rivers (10°N 119°E)	W	2.1[h]	Freitag, 2004
streams (22°30′ N 114°E)	W	0.9	Yuen and Dudgeon, 2016
river (33°S 27°E)	D, E, T, O	101[b]	Moyo et al., 2017
Average ± SE		**26.5±24.8**	

Coefficient of variation (%)		93.6	
Deserts and Xeric Shrublands			
creek (33°N 111°W)	Ch, E, T	23.1	Jackson and Fisher, 1986

[a] recalculated using energy equivalent 1 g DM = 23 kJ (Alimov, 1989).

[b] average calculated from the authors' data.

[c] average value calculated from Table 2 of the reference.

[d] average for two Austrian streams from Table 5 of the reference.

[e] average for three German streams & springs from Table 5 of the reference.

[f] average for two Canadian rivers from Table 5 of the reference.

[g] Sweden lake from Table 5 of the reference.

[h] recalculated using an average specimen dry mass 150 µg (Stagliano et al., 1998).

[i] recalculated from Fig. 1C of the reference.

[j] recalculated from authors' data on secondary production in forested stream using their emergence/production ratio.

[k] average value calculated for three lakes from data of the two papers.

[l] average value calculated from Table 3 of the reference.

[m] average for Zaire stream from Table 5 of the reference.

Table2
Contents of the sum of eicosapentaenoic and docosahexaenoic fatty acids (EPA+DHA, $mg \cdot g^{-1}$ of dry mass) in the biomass of imago of emergent aquatic insects.

Taxa	Water body	EPA+DHA	Reference
Chironomidae	The Yenisei River	18.1	Gladyshev et al., 2009
Chironomidae	Lake Oiskoie	11.9	Borisova et al., 2016
Chironomidae	Lake Mindelsee	16[1]	Martin-Creuzburg et al., 2017
Chironomidae	Lake Shira	10.1	Makhutova et al., 2017
Ephemeroptera	Lake Oiskoie	11.3	our data
Plecoptera	The Yenisei River & Lake Oiskoie	11.4	our data
Trichoptera	The Yenisei River	9.4	our data
Odonata	Wetlands & pools	7.98	Gladyshev et al., 2011a
Culicidae	Wetlands & pools	7.96[2]	Gladyshev et al., 2011b
Chaoboridae	Lake Mindelsee	33.7	Martin-Creuzburg et al., 2017
Miscellaneous	Lake Mindelsee	13[1]	Martin-Creuzburg et al., 2017
Median		11.4	

[1]median value, approximated from Fig. 3 of the reference.
[2]calculated from Table 1 of the reference.

Table 3

Ratio of water/land area for each biome (W/L), calculated from Table 3 of Feng et al., (2016), insect emergence to land area (g DM m^{-2} year^{-1}) in the biomes and concomitant flux of the sum of eicosapentaenoic and docosahexaenoic fatty acids (EPA + DHA, mg m^{-2} year^{-1}): nd – no data.

Biome	W/L	Emergence	EPA+DHA
Tundra	0.076	0.023	0.26
Boreal Forests/Taiga	0.057	0.086	0.98
Temperate Broadleaf and Mixed Forests	0.040	0.119	1.36
Temperate Coniferous Forests	0.016	0.003	0.04
Temperate Grasslands, Savannas and Shrublands	0.016	0.011	0.13
Deserts and Xeric Shrublands	0.006	0.130	1.48
Montane Grasslands and Shrublands	0.013	nd	nd
Tropical and Subtropical Moist Broadleaf Forests	0.015	0.385	4.39
Tropical and Subtropical Coniferous Forests	0.004	nd	nd
Tropical and Subtropical Dry Broadleaf Forests	0.013	nd	nd
Tropical and Subtropical Grasslands, Savannas and Shrublands	0.007	nd	nd
Flooded Grasslands and Savannas	0.050	nd	nd
Mediterranean Forests, Woodlands and Scrubs	0.008	0.052	0.60
Mangroves	0.098	nd	nd