Science of the Total Environment 577 (2017) 174–182

Contents lists available at ScienceDirect

Science of the Total Environment

journal homepage: www.elsevier.com/locate/scitotenv

Cross-ecosystem fluxes: Export of polyunsaturated fatty acids from aquatic to terrestrial ecosystems via emerging insects

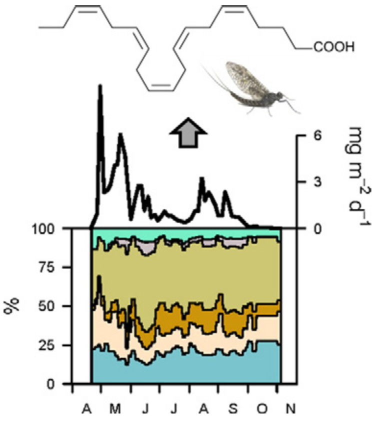
Dominik Martin-Creuzburg *, Carmen Kowarik, Dietmar Straile

Limnological Institute, University of Konstanz, Mainaustrasse 252, 78464 Konstanz, Germany

HIGHLIGHTS

- Export of PUFA via emerging aquatic insects was studied in a midsize lake.
- Aquatic insects contained high concentrations of essential PUFA.
- In total, 80.5 mg PUFA were exported per square meter and year.
- Chironomidae contributed most to total PUFA export.
- *Chaoborus* contributed most to the export of EPA, ARA, and especially DHA.

GRAPHICAL ABSTRACT



ARTICLE INFO

Article history:
Received 31 August 2016
Received in revised form 30 September 2016
Accepted 20 October 2016
Available online 31 October 2016

Editor: D. Barcelo

Keywords:
Aquatic-terrestrial coupling
Chaoborus
Chironomidae
Docosahexaenoic acid
Eicosapentaenoic acid
Insect emergence
Resource subsidies

ABSTRACT

Cross-ecosystem fluxes can crucially influence the productivity of adjacent habitats. Emerging aquatic insects represent one important pathway through which freshwater-derived organic matter can enter terrestrial food webs. Aquatic insects may be of superior food quality for terrestrial consumers because they contain high concentrations of essential polyunsaturated fatty acids (PUFA). We quantified the export of PUFA via emerging insects from a midsize, mesotrophic lake. Insects were collected using emergence traps installed above different water depths and subjected to fatty acid analyses. Insect emergence from different depth zones and seasonal mean fatty acid concentrations in different insect groups were used to estimate PUFA fluxes. In total, 80.5 mg PUFA m^{-2} yr^{-1} were exported, of which 32.8 mg m^{-2} yr^{-1} were eicosapentaenoic acid (EPA), 7.8 mg m^{-2} yr^{-1} were arachidonic acid (ARA), and 2.6 mg m^{-2} yr^{-1} were docosahexaenoic acid (DHA). While Chironomidae contributed most to insect biomass and total PUFA export, *Chaoborus flavicans* contributed most to the export of EPA, ARA, and especially DHA. The export of total insect biomass from one square meter declined with depth and the timing at which 50% of total insect biomass emerged was correlated with the water depths over which the traps were installed, suggesting that insect-mediated PUFA fluxes are strongly affected by lake morphometry. Applying a conceptual model developed to assess insect deposition rates on land to our insect-mediated PUFA export data revealed an average total PUFA deposition rate of 150 mg m^{-2} yr^{-1} within 100 m inland from the shore. We propose that PUFA export can be reliably estimated using taxon-specific information on emergent insect biomass and seasonal mean body PUFA concentrations of adult insects provided here. Our data indicate that insect-mediated PUFA fluxes from lakes are substantial, implying that freshwater-derived PUFA can crucially influence food web processes in adjacent terrestrial habitats.

---

* Corresponding author.
E-mail addresses: Dominik.Martin-Creuzburg@uni-konstanz.de (D. Martin-Creuzburg), Carmen.Kowarik@uni-konstanz.de (C. Kowarik), Dietmar.Straile@uni-konstanz.de (D. Straile).

http://dx.doi.org/10.1016/j.scitotenv.2016.10.156
0048-9697/

1. Introduction

The flow of energy and nutrients across ecosystem boundaries can crucially influence the productivity of adjacent habitats (Polis and Hurd, 1996; Nakano and Murakami, 2001; Gratton and Vander Zanden, 2009). Reciprocal resource subsidies can be mediated by various pathways. Aquatic ecosystems are inherently linked to terrestrial ecosystems by the discharge of terrestrial matter from the catchment areas and by organic matter input from near-shore vegetation (e.g. leaf litter). Terrestrial subsidies, including the human-caused input of nutrients, are well-known to support the productivity of freshwater ecosystems (Conley et al., 2009; Schindler, 2012), albeit the relative importance of autochthonous versus allochthonous organic matter for freshwater food web processes is still a matter of debate (Carpenter et al., 2005; Pace et al., 2007; Brett et al., 2009). The ecological relevance of aquatic organic matter for terrestrial food webs has been also recognized (Polis et al., 1997; Henschel, 2004; Richardson et al., 2010; Kautza and Sullivan, 2016). Emerging aquatic insects represent one important pathway by which freshwater-derived organic matter can enter terrestrial food webs (Gratton and Vander Zanden, 2009). Stable isotope studies revealed that emerging insects can significantly contribute to the nutrition of riparian predators, such as spiders, birds, and bats (Kato et al., 2004; Baxter et al., 2005; Paetzold et al., 2005; Burdon and Harding, 2008). Aquatic insects dying after mass emergence are often deposited in adjacent terrestrial ecosystems, thereby influencing terrestrial invertebrate communities (Hoekman et al., 2011). Potential effects of resource subsidies on food web processes and trophic cascades have been suggested to depend on the quantity of the subsidy and the trophic level at which the subsidies enter the adjacent food web (Leroux and Loreau, 2008). Moreover, it has been argued that the quality of subsidies may influence recipient food webs and ecosystem processes (Marcarelli et al., 2011). A meta-analysis quantifying reciprocal subsidies between freshwater and terrestrial ecosystems revealed that freshwater ecosystems generally receive higher subsidies than terrestrial ecosystems, albeit the contribution of these subsidies to animal carbon in recipient food webs was similar, suggesting that aquatic subsidies are of higher quality (Bartels et al., 2012). Differences in the nutritional quality of aquatic and terrestrial subsidies have been suggested to be due to differences in elemental stoichiometry (Bartels et al., 2012). However, they may also result from differences in the biochemical nutrient composition of aquatic and terrestrial subsidies.

Algae and terrestrial plants differ considerably in their capacity to synthesize polyunsaturated fatty acids (PUFA). In contrast to many algae, higher plants are mostly incapable of synthesizing PUFA with >18 carbon atoms (Harwood, 1996; Sayanova and Napier, 2004; Hixson et al., 2015). Consequently, aquatic primary producers are often rich in long-chain PUFA, such as arachidonic acid (ARA; 20:4n-6), eicosapentaenoic acid (EPA; 20:5n-3), and docosahexaenoic acid (DHA; 22:6n-3), while most terrestrial plants contain merely C18-PUFA, such as linoleic acid (LIN; 18:2n-6) and α-linolenic acid (ALA; 18:3n-3). Although some soil microorganisms are capable of synthesizing C20-PUFA, terrestrial PUFA production is presumably low (Gladyshev et al., 2009; Gladyshev et al., 2013). The long-chain PUFA synthesized by algae are distributed in the aquatic food web and transferred to higher trophic levels (Kainz et al., 2004; Persson and Vrede, 2006; Strandberg et al., 2015). Consequently, aquatic and terrestrial animals often differ fundamentally in their PUFA composition (Hixson et al., 2015). Aquatic insects, for instance, generally contain much higher concentrations of C20 and C22 PUFA than terrestrial insects (Hanson et al., 1985; Stanley, 2000). Thus, emerging aquatic insects may provide a crucial pathway by which freshwater-derived PUFA are transported to the land (Gladyshev et al., 2009).

Long-chain PUFA are known to crucially influence animal physiology; they are indispensable as structural components of cell membranes, are involved in regulating various membrane properties and serve as precursors for eicosanoids, important signaling molecules in reproduction and the immune system (Stanley, 2000; Stillwell and Wassall, 2003; Schlotz et al., 2016). The C18 PUFA LIN and ALA are commonly considered to be essential for all animals, albeit a few insect species seem to be capable of synthesizing LIN de novo (Blomquist et al., 1991). In general, animals have limited capacities to synthesize C20 and C22 PUFA from their respective C18 precursors LIN and ALA, giving rise to the various beneficial effects of dietary long-chain PUFA on animal performance. It is well-established that the dietary supply with long-chain PUFA, such as ARA, EPA, and DHA, can substantially improve somatic growth and reproduction of freshwater zooplankton (Müller-Navarra et al., 2000; von Elert, 2002; Martin-Creuzburg et al., 2010). PUFA requirements of insects may differ between species (Beenakkers et al., 1985; Canavoso et al., 2001) and it is tempting to speculate that PUFA-requirements of insects are linked to their aquatic or terrestrial lifestyle. In contrast to aquatic insects, which encounter long-chain PUFA at least in their larval diet, terrestrial insects may rely more on their capacity to synthesize long-chain PUFA from dietary precursors (LIN and ALA). Whether these differences in fatty acid profiles are adaptive to the respective environment (Hanson et al., 1985) and whether aquatic and terrestrial insects differ in their susceptibility to dietary PUFA deficiencies remains to be tested.

The substantial differences in fatty acid profiles between aquatic and terrestrial insects may result in severe differences in food quality for terrestrial predators in near-shore habitats. Riparian predators may benefit from consuming emerging aquatic insects not only because they represent a temporarily abundant food source but also because they provide high amounts of long-chain PUFA and thus are of higher food quality than terrestrial prey. Recently, it has been shown that Tree Swallow chicks feeding on a PUFA-rich diet grow faster and are in better condition than chicks feeding on a diet deficient in long-chain PUFA. Tree Swallows are naturally foraging on a mixture of aquatic and terrestrial insects and it has been proposed that Tree Swallows are timing breeding to coincide with the peak abundance of PUFA-rich aquatic insects (Twining et al., 2016). Although aquatic ecosystems have been recognized as the principal source of long-chain PUFA potentially supporting even terrestrial food webs (Gladyshev et al., 2009; Gladyshev et al., 2013), further studies are required investigating insect-mediated PUFA fluxes from aquatic to terrestrial ecosystems.

Here, we quantified the export of PUFA via emerging insect from a mid-size, mesotrophic lake. Insects were collected from April to November using emergence traps installed above different water depths and subjected to fatty acid analyses. The export of insect biomass from different depths zones and seasonal mean body PUFA concentrations in different insect groups were used to estimate PUFA fluxes.

2. Material and methods

2.1. Study site and sampling

The study was conducted in 2015 on Lake Mindelsee, a midsize ($1.02\ km^2$), mesotrophic lake with a maximum depth of 13 m situated in the western Lake Constance region. Most of the littoral zone of the lake is covered by reed, except for the southern part, which is bordered by forest. Emergence traps were installed above different water depths. A transect consisting of four traps was installed above 1, 3, 5, and 7 m water depth (2, 10, 28, and 36 m distance to shore, respectively); additional four traps were installed around the deepest part of the lake (distance to shore 200–220 m). The traps were assumed to cover different depth zones, i.e. 0–2, 2–4, 4–6, 6–8, and 8–13 m, respectively. Each trap consisted of four floatable tubes covering an surface area of $0.36\ m^2$, a pyramid-shaped construction of struts covered with extra fine mosquito net (mesh size ~500 μm), and a beaker with a narrowing opening that allowed the insects to enter but prevented them to get out again. The traps were emptied twice a week (i.e. beakers were exchanged and insects on the inside of the net were collected using an exhauster) between April 20th and November 4th. The collected insects were transported to the laboratory, snap-frozen, assigned to different