Aquat Sci (2017) 79:689–703
DOI 10.1007/s00027-017-0529-0

Aquatic Sciences

RESEARCH ARTICLE

Decoupled reciprocal subsidies of biomass and fatty acids in fluxes of invertebrates between a temperate river and the adjacent land

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Received: 20 June 2016 / Accepted: 24 March 2017 / Published online: 5 April 2017
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Abstract Streams and riparian areas are tightly coupled through reciprocal trophic subsidies, and there is evidence that these subsidies affect consumers in connected ecosystems. Most studies of subsidies consider only their quantity and not their quality. We determined the bidirectional exchange of organisms between the Kowie River and its riparian zone in South Africa using floating pyramidal traps (to measure insect emergence) and pan traps (to capture infalling invertebrates). The exchanges of biomass were variable spatially (three sites) and temporally (four seasons), with emergence declining about two orders of magnitude between summer (169–1402 mg m^{-2} day^{-1}) and winter (3–28 mg m^{-2} day^{-1}) across all sites, while invertebrate infall declined by a much smaller range from summer (413–679 mg m^{-2} day^{-1}) to winter (11–53 mg m^{-2} day^{-1}). Conversely, the absolute flux of physiologically important highly unsaturated fatty acids contained in the emergent and infalling arthropods peaked at comparable values in summer (emergence = 0.3–18 mg m^{-2} day^{-1} and infall = 0.3–3 mg m^{-2} day^{-1}) and declined less in winter (emergence = 0.01–0.5 mg m^{-2} day^{-1} and infall = 0.01–0.03 mg m^{-2} day^{-1}). During some seasons, there was no net flux of essential fatty acids, but there was generally a net flow of highly unsaturated fatty acids from river to land, even when land-to-river inputs dominated by biomass. Thus, qualitative net fluxes of biomass were decoupled from net fluxes of qualitatively key nutrients, establishing the importance of considering both the quality and the quantity of trophic subsidies.

Keywords Reciprocal subsidies · Aquatic insect emergence · Infalling invertebrates · Invertebrate rain · Polyunsaturated fatty acids · Kowie River · South Africa

Introduction

Rivers and adjacent riparian habitats are coupled through reciprocal trophic cross-subsidies. Spatial cross-subsidies occur when biological matter (e.g. detritus and invertebrates) moves from one habitat (donor or source) to another (recipient or sink), thereby potentially altering the productivity of the recipient system (Polis et al. 1997; Nakano and Murakami 2001). Early theorists proposed that the net flow of energy is from more productive to less productive systems (e.g. Vannote et al. 1980; Polis and Hurd 1996; Polis et al. 1997). Contemporary studies therefore focused on the 'more productive' systems and addressed terrestrial inputs to aquatic food webs, although some ecologists have also quantified the flow of energy from aquatic to terrestrial systems (e.g. Paetzold et al. 2005). Such studies moved the view of energy flow as coarsely unidirectional to a more nuanced model of bidirectional aquatic–terrestrial connectivity. Subsidies from streams to riparian landscapes occur when adult aquatic insects emerge or the remains of stream animals and plants are washed to the shore (Richardson and Sato 2015) or removed by consumers. Falling leaf litter, pollen, fruits, seeds and terrestrial invertebrates (Richardson and Sato 2015), termed 'infall' or 'organic rain', may move from land to water. The uni- and bi-directional perspectives both equate energy with matter, and assume

Electronic supplementary material The online version of this article (doi:10.1007/s00027-017-0529-0) contains supplementary material, which is available to authorized users.

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