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Aquatic Terrestrial Linkages Along a Braided-River: Riparian Arthropods Feeding on Aquatic Insects

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ABSTRACT

Rivers can provide important sources of energy for riparian biota. Stable isotope analysis ($\delta^{13}C$, $\delta^{15}N$) together with linear mixing models, were used to quantify the importance of aquatic insects as a food source for a riparian arthropod assemblage inhabiting the shore of the braided Tagliamento River (NE Italy). Proportional aquatic prey contributions to riparian arthropod diets differed considerable among taxa. Carabid beetles of the genus *Bembidion* and *Nebria picicornis* fed entirely on aquatic insects. Aquatic insects made up 80% of the diet of the dominant staphylinid beetle *Paederidus rubrothoracicus*. The diets of the dominant lycosid spiders *Arctosa cinerea* and *Pardosa wagleri* consisted of 56 and 48% aquatic insects, respectively. In contrast, the ant *Manica rubida* fed mainly on terrestrial sources. The proportion of aquatic insects in the diet of lycosid spiders changed seasonally, being related to the seasonal abundance of lycosid spiders along the stream edge. The degree of spatial and seasonal aggregation of riparian arthropods at the river edge coincided with their proportional use of aquatic subsidies. The results suggest that predation by riparian arthropods is a quantitatively important process in the transfer of aquatic secondary production to the riparian food web.

Key words: boundary; Carabidae; food web; Formicidae; Lycosidae; riparian; stable isotopes; Staphylinidae; subsidy.

INTRODUCTION

Ecosystem dynamics are rarely confined to a particular habitat and the spatial flow of matter and organisms between habitats can substantially affect local population, community, and food web dynamics (Polis and others 1997). The exchange of energy and nutrients between the river channel and its riparian zone is an important process in lotic ecosystems (Ward 1989; Naiman and Décamps 1997; Fisher and others 1998; Helfield and Naiman 2001). Whereas the role of allochthonous inputs (for example, leaf litter) as an energy source for aquatic biota in rivers is widely recognized (Fisher and Likens 1973; Vannote and others 1980; Wallace and others 1999), less is known about the energy flow from aquatic to terrestrial systems. However, reciprocal flows of matter and organisms from the stream into the riparian zone can be important energy sources to terrestrial consumers (Power and Rainey 2000; Nakano and Murakami 2001; Naiman and others 2002; Sabo and Power 2002). These spatial subsidies seem to be particularly important for consumers living in less productive habitats that receive inputs from adjacent habitats of higher production (Bustamante and others 1995; Polis and Hurd 1996; Stapp and Polis 2003).

In braided rivers, the primary channel splits into several channels that flow around low productivity areas of exposed gravel. These gravel banks are colonized by carnivorous riparian arthropods, pri-

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marily spiders, staphylinid beetles, ground beetles, and ants (Manderbach and Hering 2001; Framenau and others 2002; Sadler and others 2004). The strong productivity gradient (river to gravel bank), combined with a predator dominated arthropod community, suggests the importance of aquatic subsidies for the ground-dwelling arthropods of gravel banks. For instance, gut analysis of riparian ground beetles in a braided river indicated a high proportion of aquatic insects (Hering and Plachter 1997). Recent stable isotope studies from other rivers showed that riparian spiders (Collier and others 2002; Sanzone and others 2003) and grasshoppers (Bastow and others 2002) can also feed extensively on aquatic resources. However, we need to extend our knowledge of aquatic subsidies from a small subset of consumers to entire communities to estimate prey fluxes from the river to the riparian zone. The contribution of emerged aquatic insects to bird diets has been quantified for a riparian forest bird assemblage (Nakano and Murakami 2001). To estimate aquatic prey fluxes through different pathways of the riparian food web (ground predators versus aerial predators), we also need to quantify the role of aquatic insects as a food source for entire riparian arthropod assemblages. This requires a quantitative knowledge of the use of aquatic insects for all dominant riparian arthropods and their relative dominance in the assemblage. The role of aquatic subsidies for riparian consumers can also vary strongly among seasons (Nakano and Murakami 2001). Therefore, we need to understand the interrelationship between seasonal changes in aquatic subsidies and the spatio-temporal distribution of riparian arthropods along the river edge.

Natural abundances of stable isotopes have been successfully applied to assess flows of nutrients and matter across the aquatic terrestrial interface (for example, Ben-David and others 1998; Thorp and others 1998). As the turnover time for stable isotopes in small arthropods can be relatively short (Tieszen and others 1983; Ostrom and others 1997), stable isotopes also can be used to detect seasonal changes in the food sources of an animal. Stable isotope methods in ecosystem studies have the advantage over traditional methods in that they reveal an integrated feeding history of an animal and what source of food is actually used for tissue growth (Rounick and Winterbourn 1986). We used stable isotope analysis to examine aquatic–terrestrial feeding linkages for the dominant taxa of a riparian arthropod assemblage.

In the present study, we addressed the following primary questions: Do dominant riparian arthropods differ in their proportional consumption of aquatic insects, and does this change seasonally? Is the degree of seasonal and spatial aggregation of riparian arthropod taxa along the land–water interface related to the respective contribution of aquatic insects to their diets? Does riparian arthropod predation represent a quantitatively important pathway in the transformation of secondary aquatic production to the terrestrial food web?

METHODS

Study Site

Extensive studies of riparian arthropods along five braided rivers (Switzerland and Italy) exhibited similar community composition, spatial distributions and densities of riparian arthropods (Uhlmann 2001; A. Paetzold, unpublished data). For the detailed investigation of trophic linkages across the aquatic–terrestrial interface in this study, we selected the site that was least modified by human activities. The riparian arthropod assemblage along the stream edge consisted mainly of lycosid spiders (Lycosidae), ground beetles (Carabidae), rove beetles (Staphylinidae), and ants (Formicidae).

The study was conducted from April to October 2002 along a 400 m gravel bank of a side-channel in a braided reach of the Tagliamento River. The Tagliamento River is a seventh order gravel-bed river located in NE-Italy (46°N, 12°30'E) with a catchment of 2580 km^2 (see detailed description in Ward and others 1999; Tockner and others 2003). The river corridor is fringed by continuous riparian woodland (Gurnell and others 2001). The Tagliamento River is characterized by a flashy flow regime, with highest average discharge in autumn by torrential rains and smaller peak flows in spring from snowmelt runoff (Arscott and others 2002). Despite local water abstraction and a channelized downstream section, the river retains an essentially pristine morphological character and flood dynamics (Ward and others 1999). The active flood plain width was 0.8 km in the island-braided reach. The reach included a complex channel network and exposed gravel bars represented the largest proportion of the landscape cover (van der Nat and others 2002).

The 400-m gravel bank of the study section represented the dominant type of river-riparian interface along the entire braided-river corridor (Petts and others 2000). The channel had an average width of 20 m at low water level and comprised pool, run, riffle, and backwater sections.

The gravel bar was up to 60 m wide and bordered by riparian forest on the upslope side. It included steep (eroding) and shallow (depositional) banks. Ground cover was predominantly gravel along the stream edge with sand and patches of grass and woody vegetation in higher, less frequently flooded habitats. Woody vegetation consisted of *Populus nigra* and various willow species (Karrenberg and others 2003).

Sampling for Isotope Analysis

Samples of riparian arthropods and their potential aquatic and terrestrial food sources were collected in April, June, August, and October 2002 for isotope analysis. Samples of primary aquatic and terrestrial producers were taken for background information. Primary terrestrial producers of the gravel bar included leaves from the two dominant riparian trees (*P. nigra, Salix* spp.*)* in April, June, and August, and grass (*Calamagrostis* spp., Poaceae) in June and August. For primary aquatic producers, we sampled periphyton in April, June, and October from randomly selected stones in the river. Ground-dwelling riparian arthropods were collected within 1 m of the stream edge at randomly selected locations along the study section. Dominant riparian taxa present in the different seasons were sampled and identified to genus, subgenus or species level.

We sampled late-instar larvae of the most abundant aquatic insect taxa, using a 500-µm kick net, as potential aquatic food sources for riparian arthropods. The late-instar larva of an insect reflects its isotopic composition at the time of emergence when it is most prone to predation by riparian arthropods. These larvae were sampled at ten randomly selected locations in the river channel and identified to family level. Ephemeroptera (mayflies) included specimens of Heptageniidae and Baetidae. Diptera (trueflies) comprised Chironomidae and Limoniidae, and Plecoptera (stoneflies) included Chloroperlidae and Leuctridae. Trichoptera (caddisflies) comprised specimens of Hydropsychidae and Rhyacophilidae.

Aquatic insect taxa were grouped according to their isotopic signals. The Heptageniidae and Baetidae were designated as grazers because their isotopic signal was more similar to periphyton, considering isotopic fractionation. The other taxa were more different from periphyton but similar in their isotopic signals. Therefore, we grouped them as primarily detritivorous insects. Large predators, such as stoneflies in the family Perlidae, were excluded from the analysis because they were larger than most riparian arthropods. At least ten specimens of each family were used for isotope analysis.

We inferred possible terrestrial food sources of riparian arthropods indirectly from predaceous ground-dwelling arthropods living far from the stream (terrestrial arthropods) because it can be assumed that they integrated isotope signals from a wide variety of terrestrial food sources that are often unknown, small, and difficult to sample in the field. To test our assumption that the terrestrial arthropods reflected the isotopic signal of terrestrial prey, we checked for similarity in carbon isotopic signatures of predaceous terrestrial arthropods with a primary terrestrial consumer on the gravel bar (the grasshopper *Sphingonotus caerulans*, Caelifera, Acrididae) and terrestrial vegetation, considering isotopic fractionation. Predaceous terrestrial arthropods were sampled from the ground at randomly selected locations at a distance of more than 50 m from the stream edge, directly adjacent to the riparian forest, concurrently with riparian arthropods. We grouped the terrestrial arthropods by taxon and size class to infer potential terrestrial food sources for the different riparian arthropod taxa more specifically because taxon-specific foraging behavior and predator size mostly determine the potential prey. Therefore, we grouped the terrestrial predators into small beetles (body length < 10 mm, similar in size to *Bembidion* spp. and *Paederidus rubrothoracicus*), large beetles (body length >10 mm, similar in size to *Nebria picicornis*), lycosid spiders (comparable to *Pardosa wagleri*), and ants. Small beetles comprised the staphylinid *Paederus limnophilus* and carabids of the taxa: *Bembidion lampros*, *Asaphidion flavipes*, *Poecilus* spp., and *Lionychus quadrillum*. Large beetles comprised carabids of the taxa: *Cicindela* spp., *Carabus cancellatus*, *Broscus cephalotes*, and *Calathus* spp. Terrestrial ants included Myrmicinae and Formicinae, and lycosid spiders included mainly specimens of the genus *Pardosa*. Indirect inference of terrestrial prey for the large lycosid spider *Arctosa cinerea* was not possible because no similar sized ground-dwelling spiders were found in the terrestrial habitat. All collected terrestrial arthropods represented potential terrestrial prey for *A. cinerea*.

Sampling for Seasonal Abundance along the Stream Edge

We collected quantitative riparian arthropod samples concurrently with samples for isotope analyses. Arthropods were collected from nine randomly chosen plots along the water's edge in each season.

Arthropods were sampled from the ground within standard sized quadrats (1 m^2) using aspirators and forceps and were identified alive. During collection, all loose stones, gravel and debris were removed from the sampling plots up to a sediment depth of 10–20 cm. Frequent taxa were identified to genus or species, and less frequent taxa to family or genus. For the dominant lycosid spider, *P. wagleri*, size classes were noted (body length < 0.5 mm, 0.5–1.0 mm) and *A. cinerea* (Araneae: Lycosidae) were grouped as juveniles and adults. At least ten specimens of each of the dominant taxa and size classes were collected for determination of average dry mass.

Sampling for Aquatic Insect Emergence

Aquatic insect emergence was sampled every six weeks from the middle of April until the end of October 2002. On each sampling date four emergence traps placed randomly along the stream edge (water depths 1–10 cm) remained in place for 12 days. We used pyramidal emergence traps with a square base of 0.25 m^2. Foamed plastic bars fixed at the ground frame allowed traps to float on the water surface while they were anchored with rebars at a fixed location. Traps were covered with a white mesh (500 μm) and had a collecting head (ecoTech GmbH, Bonn, Germany) at the top, filled with water and some drops of surfactant. Samples were preserved in 70% ethanol. Emerging insects were determined to family and classified as morphospecies (sensu Derraik and others 2002) to obtain a better estimate of biomass. Ten individuals of each morphospecies were dried and weighed to estimate average dry weight.

Sampling for Lateral Distribution

Samples for the lateral distribution of riparian arthropods across the gravel bank were collected in April, June, and September 2001. Arthropods were sampled from the ground within standard-sized quadrats as described above. Samples were taken in four strata defined by the distance from the water's edge (0–1 m, 1–2 m, 2–5 m, 5–30 m). In each season, we randomly selected 16 sampling sites within each of the first two strata, 8 within the third stratum (2–5 m), and 24 within the fourth stratum (5–30 m). Arthropods were stored in 70% ethanol and identified to family.

Sample Processing and Analysis

Samples for isotope analysis were frozen shortly after sampling, except for riparian arthropods which were held in containers for at least one day to allow time for gut clearance. Animals were identified in the laboratory, rinsed and then freeze-dried. Several individuals (5–10) of each taxon were ground into fine powder to obtain a homogenized composite sample, except for the large carabid *N. picicornis* and the spider *A. cinerea* which were analyzed individually. Periphyton was treated with 10% HCL for decarbonation before isotope analysis (Schubert and Nielsen 2000).

Carbon and nitrogen isotopic composition was measured using a ThermoQuest NC 2500 elemental analyzer connected via an open split to a Micromass mass spectrometer (Isoprime). International standards used for calibration were NBS 19, IAEA-CO-8, IAEA-N-1, IAEA-N-2, and IAEA-NO-3; laboratory standards were EA-NAC1 (NaHCO3), EA-UREA-1, and a coastal sediment. Results are reported in the δ notation: $\delta^{13}C$ (‰) = $\{^{13}C/^{12}C_{\mathrm{sample}}/^{13}C/^{12}C_{\mathrm{standard}}-1\} \times 1000$ for carbon and $\delta^{15}N$ (‰) = $\{^{15}N/^{14}N_{\mathrm{sample}}/^{15}N/^{14}N_{\mathrm{standard}}-1\} \times 1000$ for nitrogen, and expressed relative to VPDB and air, respectively.

Estimating Food Sources

We used linear mixing models, as reported in Phillips and Gregg (2001), to estimate the amount of aquatic insects in the diet of riparian arthropod predators. This model includes the isotopic variances of the sources (prey) and the consumer (predators), resulting in more reliable estimates of food sources and their standard errors (Phillips and Gregg 2001). We used dual isotope, three-source mixing models except when negative values for one source were found. Negative values for one source indicate that this food source was not utilized by the consumer. In the latter case, we used single isotope ($\delta^{13}C$), two-source mixing models. Isotopic signatures of the aquatic insects were adjusted to account for fractionation. We assumed a trophic fractionation of 3.4‰ for $\delta^{15}N$ and 0.4‰ for $\delta^{13}C$ (Minagawa and Wada 1984; Peterson and Fry 1987; Oelbermann and Scheu 2002; Post 2002). Because the amount of terrestrial organisms in the diet of riparian predators was inferred from isotope signals of similar predators with a terrestrial diet no adjustment for fractionation was needed.

Data Analysis

All statistical tests were performed with SYSTAT 10.0 (SPSS 2000) using (ln + 1) transformed data to control for heteroscedacity. We used ANOVA to determine differences in the abundance of riparian arthropod taxa among the four lateral

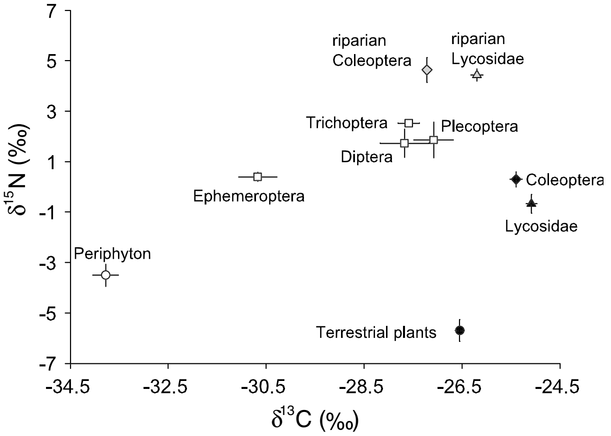

Figure 1. Natural $\delta^{13}C$ and $\delta^{15}N$ values (mean ± SE) of periphyton (n = 12), aquatic insects (open symbols), riparian arthropods (grey symbols), terrestrial plants and terrestrial arthropods (black symbols). Aquatic insects (open squares) were grouped as Ephemeroptera (Heptageniidae and Baetidae, n = 15), Trichoptera (Hydropsychidae and Rhyacophilidae, n = 12), Plecoptera (Chloroperlidae and Leuctridae, n = 5), and Diptera (Chironomidae and Limoniidae, n = 6). Riparian and terrestrial arthropods were grouped as riparian Coleoptera (Carabidae and Staphylinidae n = 86), riparian lycosid spiders (n = 38), terrestrial Coleoptera (Carabidae and Staphylinidae, n = 28), and terrestrial lycosid spiders (n = 10). Terrestrial plants include *Salix, Populus,* and *Calamagrostis* of the riparian zone (n = 18). Each replicate is a composite sample of 5–10 individuals.

strata in different seasons. If season had a significant influence on the lateral distribution of riparian arthropods, we performed an ANOVA for each season separately. Seasonal differences in the abundance of riparian taxa were analyzed with a one-way ANOVA. We report Bonferroni adjusted P-values for all pairwise comparisons. For calculation of the mixing models and their standard errors, we used the Excel spreadsheet, isoerror1_04, provided by the U.S. Environmental Protection Agency (2001).

RESULTS

Food Sources of Riparian Arthropods

Values of $\delta^{13}C$ showed a clear separation between aquatic and terrestrial primary producers and consumers (Figure 1). $\delta^{15}N$ and $\delta^{13}C$ values indicated that beetles and lycosid spiders collected more than 50 m from the stream edge (terrestrial) relied entirely on a terrestrial diet. Aquatic insects of the orders Trichoptera, Diptera, and Plecoptera (detritivores) were similar in their isotopic signal and different from Ephemeroptera (grazers). The diet of riparian arthropods collected at the stream edge consisted mostly of detritivorous aquatic insects. All taxa of the Carabidae, the staphylinid *P. rubrothoracicus*, and the heteropteran *Saldula* were very similar in their $\delta^{13}C$ composition to aquatic insects (detritivores), when considering fractionation (Figure 2a, b). In particular, the different carabid taxa of the genus *Bembidion* were highly similar in their isotopic signals, indicating similar composition in diet. The $\delta^{15}N$ values of the larger-sized riparian predators *N. picicornis* and *A. cinerea* were about the same as for the smaller riparian arthropods. Based on the isotopic mixing model, the dominant riparian carabid species of the genus *Bembidion* and *N. picicornis* as well as the heteropteran of the genus *Saldula* fed entirely on aquatic insects, mostly detritivores (>80%) (Figure 3). The staphylinid *P. rubrothoracicus* also fed predominantly on aquatic insects (80%), whereas the diet of lycosid spiders *A. cinerea* and *P. wagleri* consisted of 56 and 48% on average of aquatic insects, respectively. In contrast, the diet of the ant *Manica rubida* from nests close to the stream edge consisted predominantly of terrestrial sources. The ants from nests near the stream showed a similar isotopic composition to ants from nests at larger distances from the stream (Figure 2a).

Seasonal changes in the use of aquatic food sources occurred in lycosid spiders (Figure 4). In early summer, spiders obtained most of their body tissue from terrestrial arthropods. The proportion of terrestrial sources in the tissue of *P. wagleri* was lowest in April (26%), whereas it comprised 97% in June. From late summer to autumn, the proportion of terrestrial food sources decreased from about 75% to an average of 45%. The proportion of terrestrial sources in the tissue of *A. cinerea* was lowest in August (18%) followed by April (39%).

Seasonal Abundance along the Stream Edge

Distinct seasonal changes in the abundance of riparian arthropods occurred along the stream edge. The abundance of *Bembidion* spp. (Carabidae) was highest in spring and autumn (F = 11.70, df = 3, 32, $P < 0.001$), whereas the abundance of the lycosid spider *P. wagleri* was significantly higher in summer than in April and October (F = 17.45, df = 3, 32, P = 0.003; Figure 5a). The abundance of the large carabid *N. picicornis* was highest in April (F = 7.82, df = 3, 32, P = 0.01; Figure 5b). The large lycosid spider *A. cinerea* was mainly present in June, being absent from the stream edge in April and August. Ground beetles dominated the biomass

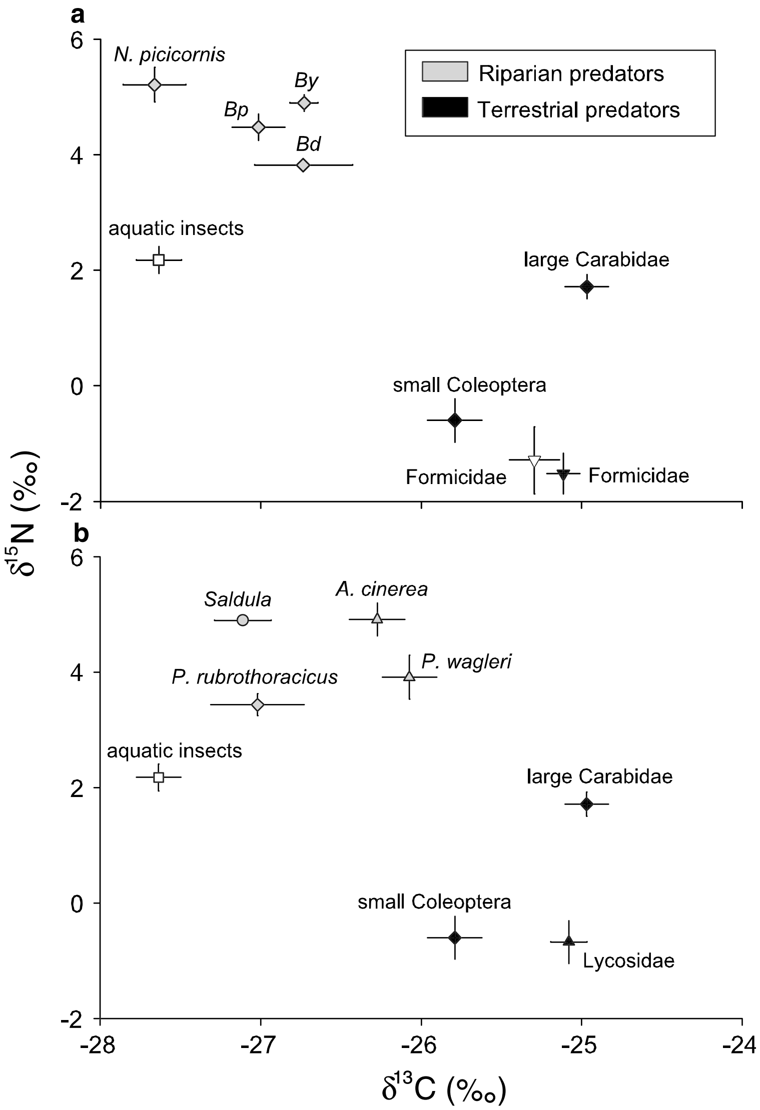

Figure 2. Natural δ^{13}C and δ^{15}N values (mean ± SE) of riparian arthropods, comparable terrestrial arthropods, and aquatic insects (including Plecoptera, Trichoptera, Diptera, $n = 23$) as potential food sources. Each replicate is a composite sample of 5–10 individuals, except for *N. picicornis* and *A. cinerea* ($n = 1$ individual). Symbols indicate different riparian and terrestrial arthropod orders: Diamonds are beetles (Coleoptera), triangles down are ants (Formicidae), triangles up are lycosid spiders (Araneida, Lycosidae), and the circle indicates bugs (Heteroptera). **a** Riparian Carabidae, Formicidae, and comparable terrestrial taxa: *N. picicornis* ($n = 32$) similar in size to large terrestrial Carabidae ($n = 16$), *Bp: Bembidion punctulatum* ($n = 17$), *Bd: Bembidion decorum* ($n = 8$), *By: Bembidioneteolitzkya* (*Bembidion ascendens/ fasciolatum*, $n = 17$) similar in size to small terrestrial Coleoptera (Staphylinidae and Carabidae, $n = 12$); riparian Formicidae (*M. rubida*, $n = 10$); terrestrial Formicidae ($n = 18$). **b** Riparian Lycosidae, Staphylinidae (Coleoptera), Heteroptera and comparable terrestrial taxa: *P. wagleri* ($n = 18$) comparable to terrestrial Lycosidae ($n = 10$); *A. cinerea* ($n = 20$) with potential terrestrial prey (large Carabidae, small Coleoptera, and Lycosidae) *P. rubrothoracicus* ($n = 12$), and *Saldula* ($n = 2$) similar in size to small Coleoptera.

of the riparian arthropod assemblage in April and October, whereas lycosid spiders dominated in June and August (Figure 5c). The abundance of ants and the staphylinid *P. rubrothoracicus* along the shoreline varied between 1.0–2.6 individuals/m^2 and 0.2–3.2 individuals/m^2, respectively. In August, when *P. rubrothoracicus* was most abundant, it contributed 10.3 mg/m^2 (7.6%) to the riparian arthropod biomass.

Seasonal Emergence

Biomass and taxonomic composition of aquatic insect emergence varied among seasons (Figure 6). Average emergence over the entire period (April–October) was 30.2 ± 7.0 mg m^{-2} d^{-1}. Plecoptera formed a large part of emerging biomass in April (21%) whereas Ephemeroptera dominated in August and October (66 and 71% respectively). Abundance of emerging aquatic insects was highest in April (94.6 ± 8.1 individuals m^{-2} d^{-1}) and October (114.7 ± 70.5 individuals m^{-2} d^{-1}) and lowest in June (20.1 ± 9.8 individuals m^{-2} d^{-1}) followed by August (33.0 ± 10.1 individuals m^{-2} d^{-1}). Abundance was dominated by Diptera, particularly Chironomidae (midges) and Empididae throughout the sampling period.

Lateral Distribution of Riparian Arthropods

Carabids had highest abundances immediately at the stream edge (0–1m) in all seasons (Figure 7a; $F = 29.29$, $df = 3, 180$, $P < 0.001$). Staphylinids showed highest abundances 0–2 m from the stream edge (Figure 7b; $F = 13.79$, $df = 3, 180$, $P < 0.001$). Spiders showed a significantly higher abundance

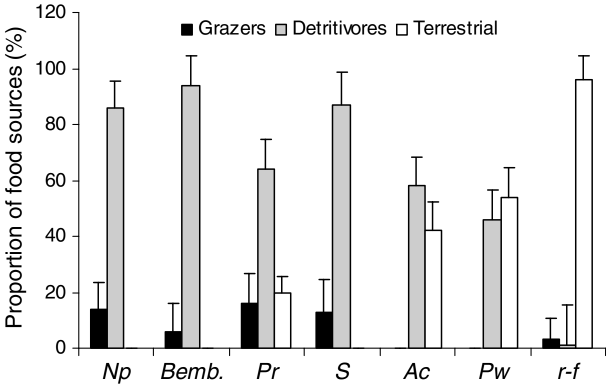

Figure 3. Relative proportion (mean ± SE) of aquatic insects (grazers, detritivores) and terrestrial food sources in the diet of riparian arthropods, based on isotope data. *Np*: *N. picicornis* (*n* = 32), *Bemb.*: *Bembidion* spp (*n* = 42), *Pr*: *P. rubrothoracicus* (*n* = 12), *S*: *Sadula* spp.(*n* = 2), *Ac*: *A. cinerea* (*n* = 20), *Pw*: *P. wagleri* (*n* = 18), r-f: riparian Formicidae (*M. rubida*, *n* = 10).

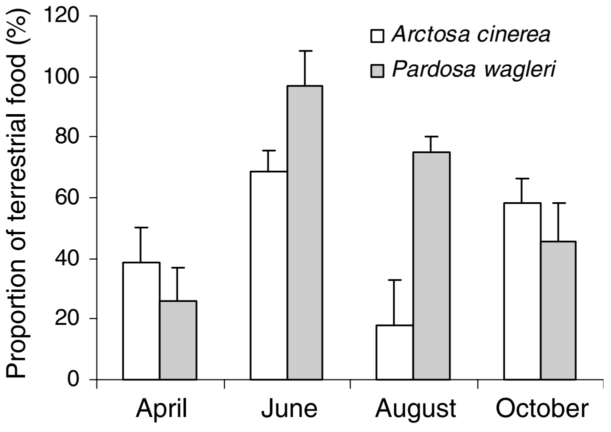

Figure 4. Relative proportions (mean ± SE) of the body tissue derived from terrestrial food sources of the two dominant Lycosidae (Araneae) in different seasons, based on stable isotope data.

close to the stream edge only in June (Figure 7c; *F* = 15.36, *d*f = 3, 60, *P* < 0.001). Spiders were more evenly distributed across the riparian zone in April and September, although with lowest abundances 5–30 m from the stream margin. There was no significant difference in abundance of ants with distance from the stream edge (Figure 7d).

DISCUSSION

Food Sources

Our study demonstrated that the riparian arthropod community along a braided river bank was dominated by carnivores that were mainly fueled by energy of aquatic origin. However, the proportion of aquatic insects in the diet differed among taxa and changed seasonally. Gut analysis of carabids along the channel edge of a similar gravel bed river (Isar River, Germany) showed that most of their diet (89%) also consisted of aquatic insects (Hering and Plachter 1997). Ground dwelling spiders along two New Zealand streams and in an intermittent Sonoran desert stream (SW USA) obtained around 55 and 68% of their body carbon from aquatic insects, respectively (Collier and others 2002; Sanzone and others 2003). The differences in the proportional use of aquatic insects by certain riparian arthropods along different rivers are likely to be influenced by the availability of terrestrial resources versus aquatic inputs. For instance, the higher proportion of aquatic food sources in the spiders of the Sonoran desert stream might be explained by the high productivity gradient between the stream and its riparian zone (Jackson and Fisher 1986; Sanzone and others 2003). The proportion of aquatic food sources in the diets of the ground beetles *N. picicornis* and *Bembidion* spp. can be as low as 34% along small alpine streams (Hering and Plachter 1997). Along these streams the proportion of terrestrial organisms in the surface drift and the availability of terrestrial prey species on the gravel bank were much higher than along an adjacent braided-river bank (Hering and Plachter 1997). The low productivity and organic matter content of the exposed gravel could explain the strong reliance of the riparian arthropod community on aquatic inputs along the Tagliamento River.

Ground-dwelling carnivorous arthropods can obtain aquatic food sources either by preying on living adults of aquatic insects or by scavenging on dead insects that float on the surface drift and become stranded along the stream edge. Aquatic insects that mainly emerge directly from the water surface, such as mayflies, are not easily available for ground-dwelling arthropods whereas insects that emerge on land, such as many stoneflies (A. Paetzold, personal observation), are particularly prone to predation. Thus, the relatively low proportion of grazing aquatic insects (mayflies) in the diet of riparian arthropods can be explained by predominant feeding on insects that emerge on land (for example, stoneflies). Gut analysis of *N. picicornis* at the Isar River has shown that its diet consisted mainly of stonefly nymphs and adults (Hering and Plachter 1997). The consumption of primarily detritivorous aquatic insects by riparian arthropods represents a feedback cycle of terrestrial derived energy: Terrestrial leaves that enter the stream are consumed by detrivorous aquatic insects

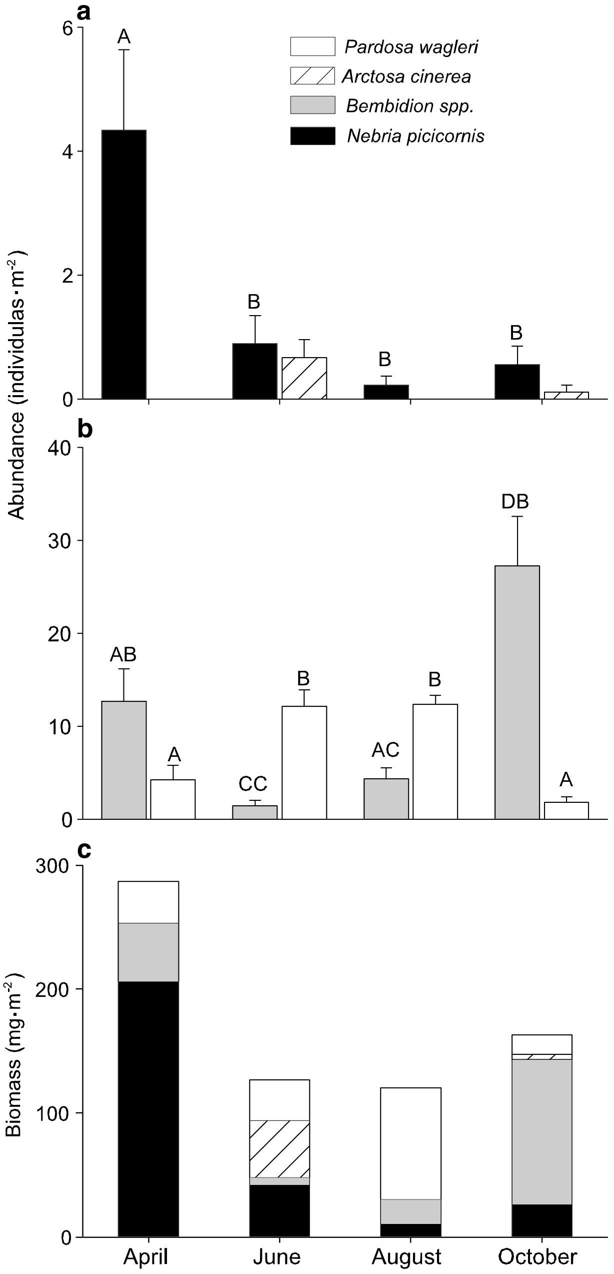

Figure 5. Abundance (mean ± SE) and biomass (mean) of the most common riparian Carabidae and Lycosidae in different seasons in 2002, **a** small taxa (body length < 10 mm), **b** large taxa (body length > 10 mm), **c** biomass. Entirely different letters show significant differences among seasons within each taxon ($P < 0.05$).

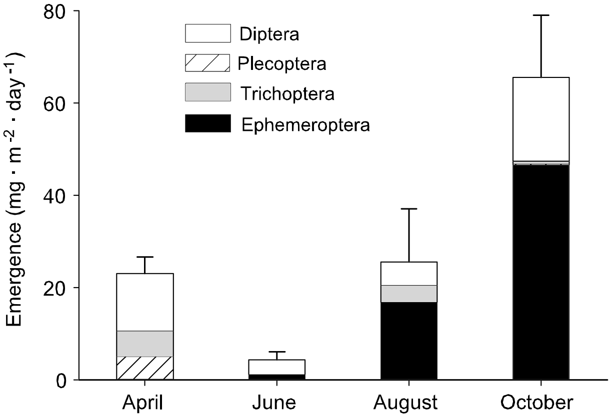

Figure 6. Biomass (mean ± SE) of aquatic insect emergence in different seasons in 2002, separated by taxonomic orders.

that transfer some of this energy back into the terrestrial system during emergence. Thereby, aquatic insects transform terrestrial leaves into high quality food for riparian consumers.

We also observed strong seasonal changes in the use of aquatic insects by the entire riparian arthropod assemblage. The overall use of aquatic insects by arthropods along the stream edge was highest in spring and autumn because ground beetles dominated the riparian arthropod assemblage during these months. Abundance of emerging aquatic insects near the stream edge was highest also in spring and autumn. This relationship suggests that the use of aquatic insects by riparian arthropods might be coupled to the emergence pattern of aquatic insects. Seasonal shifts in aquatic–terrestrial fluxes generally appear to control the seasonal efficiency of spatial subsidies (Nakano and Murakami 2001). The high abundance of carabids in spring and autumn also could be explained by the life cycle patterns of the dominant carabid taxa, *N. picicornis* and *Bembidion* spp. *N. picicornis* generally emerges in spring and early summer (Manderbach and Plachter 1997) and most *Bembidion* species are spring breeders with emergence in autumn (Hering and Plachter 1997). These life cycle patterns might be adaptations to the seasonal availability of emerging aquatic insects and to interspecific competition. However, not all coexisting arthropods received most of their aquatic subsidies when emergence was highest (for example, *A. cinerea*). This contrast indicates that the importance of aquatic subsidies can also be controlled by the life history of coexisting riparian consumers.

Subsidy Effect on Spatial and Seasonal Aggregations

Recent studies demonstrated that terrestrial consumers that are subsidized by aquatic resources aggregate at the land–water interface (Polis and Hurd 1996; Sanzone and others 2003; Stapp and Polis 2003). We found that the degree of spatial and seasonal aggregation of riparian arthropods at

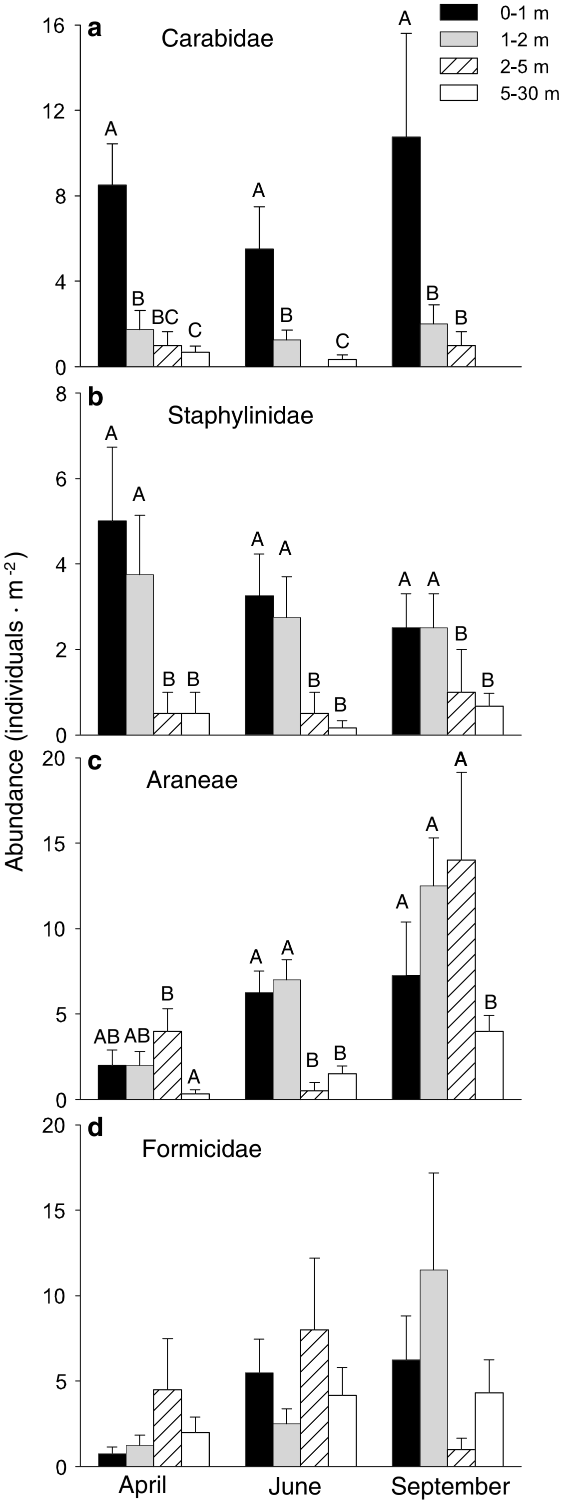

Figure 7. Abundance (mean ± SE) of Carabidae (**a**), Staphylinidae (**b**), Araneae (**c**), and Formicidae (**d**) at different distances from the water's edge in 2001. Entirely different letters show significant differences among distance-classes for each season ($P < 0.05$).

the river edge coincided with the proportional contribution of aquatic insects to their diets. Carabids, that had an entirely aquatic diet, peaked in abundance at the stream edge (0–1 m), where the highest availability of aquatic food sources can be expected. For instance, Hering (1995) observed a steep decline in the abundance of potential aquatic food items for riparian arthropods beyond 1m from the stream. Staphylinids, with a proportion of 80% aquatic insects in their diet, showed highest abundance 0–2 m from the stream edge, and ants with a mainly terrestrial diet showed no clear spatial aggregation. Seasonal aggregations of riparian spiders also coincided with a seasonally higher proportion of aquatic insects in their body tissue, considering the turnover time of stable isotopes. Turnover time of stable isotopes in arthropods seems to be short. In a diet switching experiment, the $\delta^{13}C$ and $\delta^{15}N$ values of a ladybird beetle showed a shift of more than 75% in the direction of the new diet after 6 and 21 days, respectively (Ostrom and others 1997). This time-lag must be considered in the interrelationship between the seasonal aggregation of riparian arthropods and their seasonal use of aquatic insects. Therefore, the seasonal shift in isotope signals of arthropods reflected predominantly dietary changes from the previous season. For example, the aggregation of *A. cinerea* along the stream edge in June resulted in a shift in their stable isotope signatures towards aquatic food sources in August. The interrelationship between the proportional use of aquatic subsidies and the spatial aggregation of riparian arthropods indicates a tight linkage between aquatic subsidies and the spatio-temporal structure of the riparian arthropod assemblage. This interrelationship suggests that the spatial and seasonal distribution of riparian arthropods is controlled by their reliance on aquatic subsidies. However, the spatio-temporal distribution of riparian arthropods might be also controlled by other factors, such as interspecific competition or abiotic conditions (for example, humidity, temperature), which then determine the use of aquatic food sources by different riparian arthropods. Further experimental studies are needed to understand the mechanisms causing these interrelationships.

Transfer of Aquatic Production by Riparian Arthropod Predation

Based on the seasonal biomass of the dominant riparian arthropod taxa, the proportion of aquatic insects in their diets, and their average consumption rate, the total consumption of aquatic insects by the ground dwelling riparian arthropod assemblage along the river edge can be estimated. Using an average daily consumption of their own body weight for ground beetles (Thiele 1977) and 10% of their body weight for spiders (Foelix 1996) the estimated daily aquatic insect consumption along the river edge by riparian arthropods was 0.12 g m^{-1} of river edge during the period from April to October. In comparison, average aquatic insect emergence in the channel of the Tagliamento River was about 0.03 g m^{-2} day^{-1} during the same time period. This corresponds to an average daily emergence of 0.30 g m^{-1} of river edge (average channel width: 20 m). Thus, average consumption along the river edge by riparian arthropods was 40% of the total average aquatic insect emergence. This is a very coarse estimate based on standard assumption of consumption rates and does not include variation of aquatic insect emergence across the channel. Further, aquatic insects that float on the water surface, for example, after egg deposition, might have been an additional food source for riparian arthropods. Jackson and Fisher (1986) estimated a daily aquatic insect emergence of 0.08 g m^{-2} day^{-1} over an entire year in a highly productive Sonoran desert stream and a return rate of aquatic insect biomass to the stream of only 3%. They suggested because of this low return rate that most of the emerging aquatic insects were preyed upon a variety of terrestrial insectivores. Our study provides evidence that ground predation by riparian arthropods can be an important process in the transformation of secondary aquatic insect production to terrestrial food webs.

Most of the ground predation seems to happen directly along the shoreline where riparian predators tend to aggregate, many aquatic insects emerge, and floating organisms accumulate. Thus, a high ratio of shoreline to stream area promotes a high ratio of riparian arthropod predators to emerging aquatic insects resulting in a high energy flux to the terrestrial habitat. Braided rivers are characterized by a high ratio of shoreline length per area flood plain. In the braided section of the Tagliamento River, shoreline length can be as high as 214 m ha^{-1}, which corresponds to 16.3 km per river-kilometer (van der Nat and others 2002). Another important landscape parameter that can influence the exchange rate among habitats might be the boundary permeability between the habitats (Wiens and others 1985; Polis and others 1997; Cadenasso and others 2003). Along gravel banks, the boundary between land and water is relatively open for cross habitat movements of aquatic insects that crawl on the shore for emergence, and their ground-dwelling predators. For instance, lycosid spiders can walk on the water surface (Foelix 1996) and ground beetles can swim on the water surface and are able to stay submerged for considerable time periods (Thiele 1977). Thus, ground predation on aquatic insects is likely to be a particularly important process in the aquatic–terrestrial energy transfer along braided rivers.

Riparian arthropods can further facilitate the transfer of instream biomass to higher trophic levels of terrestrial consumers (Jackson and Fisher 1986). Carabids and spiders are important food source for lizards, bats, shrews, and birds (Thiele 1977; Forster and Forster 1999). Kolb (1958) showed that carabids form a large part of the diet of the mouse-eared bat *Myotis myotis*. Many riparian arthropods might transfer aquatic biomass into the terrestrial habitat by seasonal habitat movements, such as the riparian lycosid *A. cinerea* that moves away from the stream edge for winter diapause (Framenau and others 1996).

In conclusion, our study suggests that predation by ground dwelling arthropods is a quantitatively important pathway in the transformation of aquatic secondary production to the riparian food web. Taxonomic composition and seasonal dynamics of the consumer assemblage can substantially affect this process. River regulation and alteration of riparian zones might change this energetic transfer. Identifying possible effects on this important process could be helpful for a river management that aims to maintain or restore important ecological functions of rivers and their riparian zones. A good indicator for the energy transfer from the river to its riparian zone might be the importance of aquatic food sources for entire riparian arthropod communities.

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REFERENCES

Arscott DB, Tockner K, van der Nat D, Ward JV. 2002. Aquatic habitat dynamics along a braided Alpine river ecosystem (Tagliamento River, Northeast Italy). Ecosystems 5:802–14.

Bastow JL, Sabo JL, Finlay JC, Power ME. 2002. A basal aquatic-terrestrial trophic link in rivers: algal subsidies via shore-dwelling grasshoppers. Oecologia 131:261–8.

Ben-David M, Hanley TA, Schell DM. 1998. Fertilization of terrestrial vegetation by spawning salmon: the role of flooding and predator activity. Oikos 83:47–55.

Bustamante RH, Branch GM, Eekhout S. 1995. Maintenance of an exceptional intertidal grazer biomass in South Africa: subsidy by subtidal kelp. Ecology 76:2314–29.

Cadenasso ML, Pickett STA, Weathers KC, Jones CG. 2003. A framework for a theory of ecological boundaries. BioScience 53:750–8.

Collier KJ, Bury S, Gibbs M. 2002. A stable isotope study of linkages between stream and terrestrial food webs through spider predation. Freshwater Biol 47:1651–9.

Derraik JGB, Closs GP, Dickinson KJM, Sirvid P, Barratt BIP, Patrick BH. 2002. Arthropod morphospecies versus taxonomic species: a case study with Araneae, Coleoptera, and Lepidoptera. Conserv Biol 16:1015–23.

Fisher SG, Grimm NB, Martí E, Holmes RM, Jones Jr. JB. 1998. Material spiralling in stream corridors: a telescoping ecosystem model. Ecosystems 1:19–34.

Fisher SG, Likens GE. 1973. Energy flow in Bear Brook, New Hampshire: an integrative approach to stream ecosystem metabolism. Ecol Monogr 43:421–39.

Foelix RF. 1996. Biology of spiders, 2nd edition. Oxford: Oxford University Press.

Forster R, Forster L. 1999. Spiders of New Zealand and their worldwide kin. Dunedin, New Zealand: University of Otago Press.

Framenau V, Dietrich M, Reich M, Plachter H. 1996. Life cycle, habitat selection and home ranges of Arctosa cinerea (Fabricius, 1777) (Araneae: Lycosidae) in a braided section of the upper Isar (Germany, bavaria). Revue Suisse de Zoologie vol. hors serie:223–34.

Framenau V, Manderbach R, Baehr M. 2002. Riparian gravel banks of upland and lowland rivers in Victoria (south-east Australia): arthropod community structure and life-history patterns along a longitudinal gradient. Aust J of Zool 50:103–23.

Gurnell AM, Petts GE, Hannah DM, Smith BPG, Edwards PJ, Kollmann J, Ward JV, Tockner K. 2001. Riparian vegetation and island formation along the gravel-bed Fiume Tagliamento, Italy. Earth Surf Proc Land 26:31–62.

Helfield JM, Naiman RJ. 2001. Effects of salmon-derived nitrogen on riparian forest growth and implications for stream productivity. Ecology 82:2403–9.

Hering D. 1995. Nahrung und Nahrungskonkurrenz von Laufkäfern und Ameisen in einer nordalpinen Wildflussaue. Arch Hydrobiol Suppl 101:439–53.

Hering D, Plachter H. 1997. Riparian ground beetles (Coeloptera, Carabidae) preying on aquatic invertebrates: a feeding strategy in alpine floodplains. Oecologia 111:261–270.

Jackson JK, Fisher SG. 1986. Secondary production, emergence, and export of aquatic insects of a Sonoran desert stream. Ecology 67:629–38.

Karrenberg S, Kollmann J, Edwards PJ, Gurnell AM, Petts GE. 2003. Patterns in woody vegetation along the active zone of a near-natural Alpine river. Basic Appl Ecol 4:157–66.

Kolb A. 1958. Nahrung und Nahrungsaufnahme bei Fledermäusen. Zeitschrift für Säugetierkunde 23:84–95.

Manderbach R, Hering D. 2001. Typology of riparian ground beetle communities (Coleoptera, Carabidae, *Bembidion* spec.) in Central Europe and adjacent areas. Arch Hydrobiol 152:583–608.

Manderbach R, Plachter H. 1997. Lebensstrategie des Laufkäfers *Nebria picicornis* (FABR. 1801) (Coleoptera, Carabidae) an Fliessgewässern. Beiträge der Gesellschaft für Ökologie 3:17–27.

Minagawa M, Wada E. 1984. Stepwise enrichment of ^{15}N along food chains: Further evidence and the relation between d^{15}N and animal age. Geochimi Cosmochim Ac 48:1135–40.

Naiman RJ, Bilby RE, Schindler DE, Helfield JM. 2002. Pacific salmon, nutrients, and the dynamics of freshwater and riparian ecosystems. Ecosystems 5:399–417.

Naiman RJ, Décamps H. 1997. The ecology of interfaces: riparian zones. Ann Rev Ecol Syst 28:621–58.

Nakano S, Murakami M. 2001. Reciprocal subsidies: Dynamic interdependence between terrestrial and aquatic food webs. P Nat Acad Sci USA 98:166–70.

Oelbermann K, Scheu S. 2002. Stable isotope enrichment (d15N and d13C) in a generalist predator (*Pardosa lugubris*, Araneae: Lycosidae): effects of prey quality. Oecologia 130:337–44.

Ostrom PH, Colunga-Garcia M, Gage SH. 1997. Establishing pathways of energy flow for insect predators using stable isotope ratios: field and laboratory evidence. Oecologia 109:108–13.

Peterson BJ, Fry B. 1987. Stable isotopes in ecosystem studies. Ann Rev Ecol Syst 18:293–320.

Petts GE, Gurnell AM, Gerrard AJ, Hannah DM, Hansford B, Morrissey I, Edwards PJ, Kollmann J, Ward JV, Tockner K, Smith BPG. 2000. Longitudinal variations in exposed riverine sediments: a context for the ecology of the Fiume Tagliamento, Italy. Aquat Conserv 10:249–66.

Phillips DL, Gregg JW. 2001. Uncertainty in source partitioning using stable isotopes. Oecologia 127:171–79.

Polis GA, Anderson WB, Holt RD. 1997. Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. Ann Rev Ecol Syst 28:289–316.

Polis GA, Hurd SD. 1996. Linking marine and terrestrial food webs: Allochthonous input from the ocean supports high secondary productivity on small islands and coastal land communities. Am Nat 147:396–423.

Post DM. 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology 83:703–18.

Power ME, Rainey WE. 2000. Food webs and resource sheds: towards spatially delimiting trophic interactions. In: Hutchings MJ, John EA, Stewart AJA, Eds. The ecological consequences of environmental heterogeneity. Cambridge, UK: Blackwell Science. pp 291–314.

Rounick JS, Winterbourn MJ. 1986. Stable carbon isotopes and carbon flow in ecosystems. BioScience 36:171–77.

Sabo JL, Power ME. 2002. River-watershed exchange: Effects of riverine subsidies on riparian lizards and their terrestrial prey. Ecology 83:1860–69.

Sadler JP, Bell D, Fowles A. 2004. The hydroecological controls and conservation value of beetles on exposed riverine sediments in England and Wales. Biol Conser 118:41–56.

Sanzone DM, Meyer JL, Marti E, Gardiner EP, Tank JL, Grimm NB. 2003. Carbon and nitrogen transfer from a desert stream to riparian predators. Oecologia 134:238–50.

Schubert CJ, Nielsen B. 2000. Effects of decarbonation treatments on d^{13}C values in marine sediments. Mar Chem 72:55–59.

Stapp P, Polis GA. 2003. Marine resources subsidize insular rodent populations in the Gulf of California, Mexico. Oecologia 134:496–504.

Thiele HU. 1977. Carabid beetles in their environments. Berlin: Springer.

Thorp JH, Delong MD, Greenwood KS, Casper AF. 1998. Isotopic analysis of three food web theories in constricted and floodplain regions of a large river. Oecologia 117:551–63.

Tieszen LL, Boutton TW, Tesdahl KG, Slade NA. 1983. Fractionation and turnover of stable carbon isotopes in animal tissues: implications for d^{13}C analysis of diet. Oecologia 57:32–7.

Tockner K, Ward JV, Arscott DB, Edwards PJ, Kollmann J, Gurnell AM, Petts GE, Maiolini B. 2003. The Tagliamento River: a model ecosystem of European importance. Aquat Sci 65:239–53.

Uhlmann V. 2001. Die Uferzoozönosen in natürlichen und regulierten Flussabschnitten. Diplomarbeit, ETH Zürich.

U.S. Environmental Protection Agency 2001. Exel spreadsheet, Isoerror1_04. http://www.epa.gov/wed/pages/models/isotopes/isoerror1_04.htm.

van der Nat D, Schmidt AP, Tockner K, Edwards PJ, Ward JV. 2002. Inundation dynamics in braided floodplains: Tagliamento River, Northeast Italy. Ecosystems 5:636–47.

Vannote RL, Minshall GW, Cummins KW, Sedell JR, Cushing CE. 1980. The river continuum concept. Can J Fish Aquat Sci 37:130–7.

Wallace JB, Eggert SL, Meyer JL, Webster JR. 1999. Effects of resource limitation on a detrital based ecosystem. Ecol Monogr 69:409–42.

Ward JV. 1989. The four-dimensional nature of lotic ecosystems. J N Am Benthol Soc 8:2–8.

Ward JV, Tockner K, Edwards PJ, Kollmann J, Bretschko G, Gurnell AM, Petts GE, Rossaro B. 1999. A reference river system for the Alps: the 'Fiume Tagliamento'. Regulated River 15:63–75.

Wiens JA, Clifford S, Gosz JR. 1985. Boundary dynamics: a conceptual framework for studying landscape ecosystems. Oikos 45:421–7.