

# Stream salmonids as opportunistic foragers: the importance of terrestrial invertebrates along a stream-size gradient

J. Syrjänen, K. Korsu, P. Louhi, R. Paavola, and T. Muotka

**Abstract:** Terrestrial invertebrates have been reported to be positively selected by stream salmonids. We assessed the importance of terrestrial and aquatic invertebrates to salmonid diets in 25 streams in Finland, with the hypothesis that terrestrial prey would be important in only the smallest forest streams. Several measures of prey availability were used, including proportional abundance in benthic or drift samples, compared with a trait-based approach, to predict diet composition. Across all 25 streams in autumn, blackfly and caddis larvae were the most important prey items. Terrestrial invertebrates were of moderate importance in all streams, including the smallest. Pure availability predicted diet best and provided, in most cases, a significant fit with the observed diet. In a quantitative literature review, the mean proportion of terrestrial prey in salmonid diets was 17%, being highest for the largest fish ( $\geq 15$  cm). Species of the genus *Salmo* consumed significantly less terrestrials than did other salmonid genera. The proportion of terrestrial prey was highest in streams flowing through deciduous forests, but it was only weakly correlated with channel width.

**Résumé :** On a signalé que les salmonidés d'eau courante font une sélection positive des invertébrés terrestres. Nous évaluons l'importance des invertébrés terrestres et aquatiques dans les régimes alimentaires de salmonidés dans 25 cours d'eau de Finlande avec comme hypothèse que les proies terrestres ne devraient être significatives que dans les plus petits cours d'eau forestiers. Nous avons utilisé plusieurs mesures de disponibilité des proies, en particulier l'importance proportionnelle dans les échantillons de benthos ou de dérive, par comparaison aux méthodes basées sur les traits, pour prédire la composition du régime alimentaire. Sur l'ensemble des 25 cours d'eau en automne, les larves de mouches noires et de phryganes constituent les proies individuelles les plus importantes. Les invertébrés terrestres sont d'importance moyenne dans tous les cours d'eau, y compris les plus petits. La simple disponibilité est la meilleure variable prédictive du régime et permet, dans la plupart des cas, un ajustement significatif avec le régime observé. Dans une revue quantitative de la littérature, la proportion moyenne de proies terrestres dans les régimes de salmonidés est de 17 % et elle est maximale chez les poissons les plus grands ( $\geq 15$  cm). Les espèces du genre *Salmo* consomment significativement moins de proies terrestres que les autres genres de salmonidés. La proportion de proies terrestres est maximale dans les cours d'eau qui traversent des forêts décidues; elle n'est que faiblement corrélée à la largeur du chenal.

[Traduit par la Rédaction]

## Introduction

Dietary composition and prey selectivity of stream-dwelling salmonids have been addressed in numerous studies that have typically focused on one fish species in a particular stream or stream system, often at just one sampling time (Cada et al. 1987; Miyasaka et al. 2003; Baxter et al. 2004). Generalizations of the determinants of salmonid diets have proved difficult, owing to, for example, spatially and temporally variable taxonomic composition of prey assemblages in streams. Thus far, the most systematic efforts for a generalization have been produced by Rader (1997) and De Crespín De Billy and

Usseglio-Polatera (2002) in an attempt to explain and predict salmonid diets based on the relative vulnerability of benthic invertebrates to fish predation. Their models were thus based on invertebrate traits known, or assumed, to be of importance to prey selection by salmonids.

Salmonid fishes are traditionally considered visually hunting, day-active, sit-and-wait predators that feed on invertebrates drifting in the water column (Elliott 1973; Fraser and Metcalfe 1997). They select foraging sites to minimize energy costs and maximize the availability of drifting prey per unit time (Nakano and Kaeriyama 1995; Young et al. 1997). They may also attack epibenthic prey, particularly in darkness

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(Nakano and Furukawa-Tanaka 1994; Kreivi et al. 1999), but this strategy is considered of moderate importance. However, when drift is reduced experimentally, epibenthic foraging may become the predominant foraging mode (Nislow et al. 1998). The choice of a foraging strategy is also contingent on the social status of a fish, with less dominant (and usually smaller) fish feeding disproportionately from the benthos (Nakano et al. 1999). This may cause strong intra- and inter-population variation in salmonid diets (e.g., Bridcut and Giller 1995), further complicating any generalizations based simply on prey availability in the drift. Salmonids are also size-selective predators, feeding disproportionately on the largest and (or) most conspicuous prey items (Allan 1981; Meissner and Muotka 2006). One aspect of this behavior is selective feeding on terrestrial invertebrates that fall on the water surface. While floating downstream, these prey are highly conspicuous and vulnerable to attacks by drift-feeding fish (Nakano et al. 1999). On the other hand, prey availability in streams is often limited (Johnson et al. 2006), potentially driving fish towards omnivorous feeding. Indeed, several studies have shown that salmonids are opportunistic foragers, with diets closely reflecting the composition of benthic and (or) drift samples (Allan 1981; Bres 1986; Esteban and Marchetti 2004). Benthic invertebrate densities in boreal streams decline to their annual minimum during summer (Poff and Huryn 1998), whereas availability and activity of riparian invertebrates often peaks at the same time, potentially causing fish to focus strongly on terrestrial prey during summer. Such a seasonally variable importance of terrestrial invertebrates to salmonid diets has recently been detected in many fish populations (e.g., Kawaguchi and Nakano 2001; Nakano and Murakami 2001).

The importance of terrestrial prey to salmonids may also depend on stream width, with greatest importance in small headwater streams. There are at least two potential, not mutually exclusive, mechanisms causing such a pattern. First, in small, heavily shaded streams, the riparian canopy often extends over the entire channel, thus delivering terrestrial prey over the entire stream surface. Food webs in such streams, as also in lakes with undeveloped riparian forests, are heavily subsidized by inputs of terrestrial prey, although this riparian subsidy may exhibit strong seasonality (Nakano and Murakami 2001; Francis and Schindler 2009). As the river gets wider, terrestrial invertebrates will fall on a smaller proportion of the stream surface, contributing relatively less to the prey base. Second, even if the input of terrestrial prey to salmonid food base remains constant with increasing channel width, relative terrestrial contribution to diet may still decline if benthic invertebrate production increases downstream. Also, not only the mere presence of riparian vegetation but, even more importantly, the riparian vegetation type affects the availability of terrestrial prey, with deciduous trees providing more terrestrial subsidies to stream fish than coniferous trees (Wipfli 1997; Allan et al. 2003).

We analyzed prey availability for and use by brown trout (*Salmo trutta*) in 25 streams, spanning a size gradient from small (2–3 m wide) headwater streams to fifth-order rivers (up to 80 m wide) in central and northern Finland. Most of our data represent late summer – early autumn conditions (late August to mid-September), but we also include corresponding early summer (early June) data for seven streams. These two

seasons represent the periods of the fastest growth of brown trout in boreal forest streams (e.g., Korsu et al. 2009). Further, we evaluated the ability of Rader's (1997) model to predict the diet of brown trout in our study streams, adjusting the model to site-specific conditions by estimating prey abundance in each stream. We specifically assessed the importance of terrestrial invertebrates to trout diets across a stream-size gradient. Finally, to place our results in a wider perspective, we extracted data from literature on the use of terrestrial prey by salmonid fishes in relation to stream size and other explanatory variables (fish size and genus; riparian vegetation type).

## Materials and methods

### Study streams and field protocol

We divided the 25 study streams into three size groups: small (mean channel width < 3.5 m,  $n = 10$ ), medium-sized (4–12 m,  $n = 8$ ), and large (>20 m,  $n = 7$ ) streams (Table 1), roughly corresponding to first- to second-order, third-order, and fourth- to fifth-order streams, respectively. One of the medium-sized streams and four of the large streams were lake outlets. The sampling site in each stream consisted mainly of stony riffles, covering an area of 100–1000 m<sup>2</sup>. Water quality was good to excellent (see Table 1), and the stream channels were hydro-morphologically unmodified or only slightly modified. Riparian forests were mainly mixed, with 2–10 m high deciduous trees (alder, *Alnus* spp.; birch, *Betula* spp.; and bird cherry *Prunus padus*) and willows (*Salix* spp.) and 5–20 m high coniferous trees (spruce, *Picea abies*; pine, *Pinus sylvestris*). In early autumn (August to September), we sampled all 25 streams for both trout and benthic organisms; seven of the streams (six small and one medium-sized) were also sampled for drift. To assess seasonal variability in trout diets, we sampled some of the streams (five small and two medium-sized) also in the early summer (early June). Brown trout reproduce naturally in all of the study streams, and although stocking is practiced in some of the streams, about 95% of fish were wild-born (based on fin condition; J. Syrjänen, personal observation). Trout populations in the small streams are generally resident, but in the medium-sized and large streams they are partly lake-migrating (Saraniemi et al. 2008; Syrjänen and Valkeajärvi 2010). We collected trout of mainly 11–22 cm in total length (ages 1 to 3) with a backpack electrofishing gear (GeOmega FA3, pulsed direct current 50 Hz, 350–700 V). We then anaesthetized the fish with carbon dioxide and flushed their stomachs with 3–4 dL of water. This method is nondetrimental to fish, removing more than 95% of stomach contents (Light et al. 1983; Sotiropoulos et al. 2006). Number of fish collected per stream varied between 14 and 48. After full recovery from anesthesia, we released the fish to their site of capture. Kreivi et al. (1999) showed that in late summer the feeding of age-1 trout in a sub-arctic Finnish river peaked at 0600 to 0900 h. Therefore, to ascertain that gut contents would represent recent feeding, we conducted all fish sampling between 1000 and 1400 h.

We measured prey availability in benthos by collecting kick net samples (0.30 mm mesh size) from the same reach just before fish sampling. When collecting a sample, substrate in front of the net was disturbed to the depth of 5–10 cm for 30 s. We measured prey availability in drift using polyvinyl chloride (PVC) tubes fitted with a 1 m long net (11 cm diameter, net mesh size 0.30 mm, 5–10 nets per

**Table 1.** Location, size, selected water chemistry characteristics, and density of brown trout (individuals per 100 m<sup>2</sup>) in the 25 study streams in Finland.

Stream	Latitude (N)	Longitude (E)	Mean channel width (m)	Stream order	pH	Total P (µg·L <sup>-1</sup> )	Trout density
<b>Small</b>							
Hirvasjoki	62°30′	25°42′	3.8	2	7.0	13	5
Kiertojoki	61°59′	26°03′	1.7	2	6.2	5	36
Kölniönpuro	62°15′	25°40′	1.6	2	7.0	12	11
Särkioja	65°40′	28°11′	3.0	2	6.0	NA	40
Ukonoja	65°44′	27°45′	2.6	2	5.8	NA	60
Kostonlamminoja	65°36′	28°02′	1.5	2	7.2	11	62
Virsuoja	65°22′	27°39′	2.6	2	6.4	18	68
Jelestimänjoki	66°12′	29°32′	3.0	3	NA	NA	NA
Koivupuro	65°46′	27°50′	2.1	1	NA	NA	NA
Raatepuro	66°15′	29°40′	2.8	2	7.3	9	5
<b>Medium</b>							
Arvajanjoki	61°41′	25°10′	12	3	6.6	4	145
Könkköjoki	62°14′	25°16′	7.0	3	6.4	19	30
Rutajoki	61°59′	25°59′	8.0	3	6.8	9	35
Saajoki	61°59′	25°24′	4.3	3	6.1	16	24
Loukusanjoki	65°35′	27°57′	6.7	3	6.7	12	12
Ohtaoja	65°36′	28°03′	6.0	3	7.5	22	NA
Porontimanjoki	66°12′	29°21′	7.0	3	7.3	9	4
Rääpysoja	65°40′	28°21′	7.0	3	6.7	16	NA
<b>Large</b>							
Huopanankoski	63°33′	25°02′	20	4	6.9	12	20
Muuramenjoki	62°08′	25°41′	19	4	6.9	9	28
Ripatinkoski	61°36′	26°40′	20	5	7.0	5	72
Siikakoski	62°37′	26°21′	80	4	7.0	6	56
Simunankoski	62°23′	26°11′	42	5	7.1	7	54
Kitkajoki	66°15′	29°28′	40	4	7.3	7	15
Kuusinkijoki	66°17′	29°54′	45	4	7.2	17	45

**Note:** NA, no data available.

stream). The drift samplers operated for 3–4 h before fish sampling, just above the area to be electrofished. To calculate drift densities, we measured current velocity at the mouth of each net at the beginning and end of a sampling period. At each site where drift was collected, we positioned some of the nets 3–5 cm above the substratum, thus sampling subsurface drift, while others were positioned so that they intersected water surface, thus sampling mainly surface drift (aerial stages of aquatic insects and terrestrial invertebrates). We collected three to five kick net and drift samples at each site. We identified invertebrates mainly to genus level and counted their numbers in the laboratory. Counts of individuals were used in all analyses. We pooled the numbers of prey used by trout across all individuals in each stream, as well as numbers of prey available across all samples in each stream. Thus, each stream produced one data point.

**Prey selectivity by trout**

We grouped prey taxa into eight functionally and (or) taxonomically similar groups that dominated (by numbers) in the benthic–drift samples and trout diet: baetid mayfly nymphs (Baetidae), nonpredatory stonefly nymphs (mainly families Leuctridae and Nemouridae), case-bearing caddis larvae (Trichoptera), net-spinning caddis larvae (Trichoptera),

midge larvae (Chironomidae), blackfly larvae (Simuliidae), adult stages of aquatic insects, and terrestrial invertebrates. These eight groups comprised 79% of prey use (by numbers) in early summer and 75% in early autumn. We compared prey availability with prey consumption using Chesson’s (1983) preference index ( $\alpha$ ) calculated for each of the eight prey groups in each stream:

$$\alpha = \left(\frac{r_i}{n_i}\right) \left(\sum_{j=1}^m \frac{r_j}{n_j}\right)^{-1}$$

where  $r$  is the proportion of prey type  $i$  in the diet,  $n$  is the proportion of prey type  $i$  in a benthic–drift sample, and  $m$  is the number of prey categories included in the analysis. The index was calculated separately for benthic and drift samples (when available). We tested the index values for each stream size category (small, medium, large) by one-sample  $t$  test against neutral selectivity, estimated as  $1/m$ , where  $m$  is the number of prey categories included. To reduce the risk of type I error, we set the alpha level a priori at  $\alpha = 0.01$ .

**Correlations between prey use and availability: test of Rader’s model**

Rader (1997) classified aquatic invertebrates based on 11

traits that determine their availability to salmonid fishes: benthic exposure, body size, and nine categories describing drift propensity (intentional drift, habitat, flow exposure, mobility, drag index, drift distance, emergence behavior, ovipositing behavior, and diel activity). Rader (1997) assigned each prey type to each of these categories, using scores from 0 to 9, and then summed the subtotal group scores. For final group scores, subtotal scores were weighted by multipliers depending on the abundance of each prey (see next section for details). Taxonomically, Rader's prey groups were insect genera or families and larger clusters for other aquatic invertebrates. To test the applicability of Rader's model to our data, we used exactly the same prey groups and scores as Rader (1997) for all prey taxa that occurred in both our data and in his classification. Four of the prey taxa observed in this study (leeches, Hirudinea; the cased caddis family Goeridae and genus *Sericostoma*, the isopod *Asellus aquaticus*) were not included in Rader's classification. We therefore asked four experienced benthic invertebrate ecologists to provide their independent scores for these taxa for each of the eight traits used by us (see below) and then used a consensus scoring in data analysis (see online Supplemental Table S1<sup>1</sup>).

We used Spearman rank correlations to test for the correspondence between trout diet and several measures of prey availability to examine whether a trait-based approach would predict diet better than assuming that consumption was proportional to prey availability in benthic or drift samples: (i) diet composition (proportional abundance of each prey type) vs. Rader's (1997) scores; (ii) diet vs. Rader's scores combined with site-specific abundance in benthic samples; (iii) diet vs. relative abundance in benthos; (iv) diet vs. Rader's scores combined with site-specific abundance in drift samples; and (v) diet vs. relative abundance in drift. However, we focused on only those eight of Rader's original traits that characterize aquatic life forms—stages, excluding three (emergence behavior, ovipositing behavior, diel activity) that characterize adult stages of aquatic insects. We used Rader's original abundance categories based on regional abundance (obtained from literature) in (i) and Rader's multipliers (0.5, 1.0, 1.2, 1.5) for scores based on abundance in (i), (ii), and (iv). We estimated average subtotal scores (ASS) for the eight traits included and only for the taxonomic categories that occurred in our data. We used ASS in (i), (ii), and (iv) to determine the multiplier values. We included site-specific abundance (ii, iv) to mimic Rader's generalized abundance classification. Thus, we categorized each prey type into one of three abundance classes (abundant, common, rare) based on their abundance in stream benthos (ii) or drift (iv). A prey category was determined abundant if its proportion in availability samples was more than 20%, common if it was 3%–20%, and rare if it was less than 3%. Following Rader's (1997) final (total) scoring, we multiplied subtotal scores by 0.5 (rare taxa), 1.0 (common and abundant taxa with scores less than mean ASS), 1.2 (common taxa with scores exceeding mean ASS), or 1.5 (abundant taxa with scores exceeding mean ASS). To avoid the strong impact on correlations by a large number of zeros, as well as the many ties caused by rare taxa (Esteban and Marchetti 2004), we only included taxa that comprised more than 0.1% of the mean use and

availability across all streams in each season. The total number of taxonomic categories thus included was 18 (early summer) or 30 (early autumn). We considered correlations significant at  $\alpha < 0.01$ .

We used nonmetric multidimensional scaling (NMDS) ordination to summarize and compare visually patterns in trout diet vs. benthic samples based on their taxonomic composition. We ran NMDS in an autopilot mode, letting the program choose the best ordination solution (i.e., solution with the lowest stress value) from 100 separate runs of real data using PC-ORD software (McCune and Mefford 1999). We then used Procrustes analysis with ProTest to test for pairwise concordance between the two ordination configurations. Procrustean fitting was based on the least-squares criterion, which minimizes the sum of the squared residuals ( $m^2$ ) between two ordinations, using the  $m^2$  statistic as the measure of association. Low values of  $m^2$  indicate strong concordance between availability (benthic samples) and use (stomach samples) across study streams. ProTest extends Procrustes analysis by providing a permutation test for the significance of the Procrustean fit (Peres-Neto and Jackson 2001). ProTest randomly permutes original observations in one matrix so that each site can be assigned any of the values attributed to other sites. The  $m^2$  statistic is recalculated for each permutation, and the proportion of the statistic smaller than or equal to the observed value provides the significance level of the test. We used the program ProTest (Jackson 1995) with 9999 permutations. Because of sample size limitations, we only conducted these analyses for the early autumn samples. We used multi-response permutation procedure (MRPP) to analyse differences in community composition among stream-size classes, separately for dietary and benthic samples. MRPP is a nonparametric method for testing differences in assemblage structure between a priori defined groups. The null hypothesis of no difference among groups was tested by a Monte Carlo procedure with 1000 permutations.

### The importance of terrestrial invertebrates to salmonid diets: a quantitative review

To quantify the general importance of terrestrial invertebrates to the diet of stream salmonids, we performed a literature survey on studies published between 1973 and 2009 using Biological Abstracts and Google Scholar. We used various combinations of the following key words: trout, salmon, charr, food, feeding, diet, foraging, prey, predation, and terrestrial. We obtained additional papers by examining reference lists of the original articles and by including our own data (this study) to the final database. We considered individual streams as data points (replicates). For each study, we recorded the percentage of terrestrial (aquatic adult insects not included) invertebrates in the diet of salmonids, as well as several explanatory variables, if available. As we initially suspected that terrestrial prey would be important for salmonids mainly in small streams, we included channel width as a primary explanatory variable in our analysis. In addition, we used fish size class, salmonid genus, and riparian vegetation type as additional explanatory variables. We divided channel width into four size classes: <3, 3–8, 8–20, >20 m. Fish total length was divided into three size classes: <80, 80–149,

<sup>1</sup>Supplementary data are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/f2011-118>.



and  $\geq 150$  mm. Salmonids were classified in three genera: *Salmo*, *Oncorhynchus*, and *Salvelinus*. Riparian vegetation type was classified into four categories: deciduous forest, coniferous forest, mixed forest, and open canopy (streams bordered by bush, grass, or open bank). If a study included information on several fish size classes, fish genera, and (or) riparian vegetation type, we included each as a separate data point. We only included summer months (June to August in the Northern Hemisphere; December to February in the Southern Hemisphere) in our data. In data analysis, we set channel width (four levels), vegetation type (four levels), fish size (three levels), and fish genus (three levels) as factorial variables. We analysed the statistical significance of each factor to the proportion of terrestrials in salmonid diets using generalized least squares model (GLS) (gl function in nlme library) available in the free software R 2.11.1 (R Development Core Team 2010). Because of data limitations, we only included two-way interactions in the maximal model and used manual model simplification (partial  $F$  tests) to obtain the minimal adequate model. We set the significance level at  $\alpha = 0.05$  and arcsine-transformed the proportion of terrestrial items used by fish to better meet the assumption of normality. To deal with data heteroscedasticity, VarIdent function, allowing groups to have different variance (Pinheiro and Bates 2000), was fitted in the model.

## Results

### Prey use and selectivity by trout

The total number of fish sampled was 297 in June and 878 in August–September. The proportion of fish with empty stomachs was 1% in June (range 0% to 9%) and 7% in early autumn (range 0% to 31%). Nine brown trout had ingested other fish (mainly sculpin).

Across all 25 streams (ten small, eight medium-sized, and seven large streams) in early autumn, blackfly larvae and case-bearing and net-spinning caddis larvae (in order of importance) were the most important prey groups in trout diet (Fig. 1), whereas larval stages of baetid mayflies, net-spinning caddis, and chironomid midges dominated the benthos. Drift was generally dominated by baetid, chironomid, and blackfly larvae, and to a lesser degree, and in small streams only, by terrestrial invertebrates (Supplemental Table S2<sup>1</sup>). Differences in diet related to stream size were obvious, however. In small streams, diet was dominated by terrestrial invertebrates, blackfly larvae, and case-bearing caddis larvae. Only chironomid larvae deviated from random selection in both benthic and drift samples, being significantly under-represented in the diet of trout ( $P < 0.001$ ). Five of the prey groups present in drift samples were significantly under-represented in the diet, whereas none were significantly over-represented (Fig. 1a). In medium-sized streams, only cased caddis larvae were significantly over-represented ( $P = 0.004$ ), whereas baetid mayfly, stonefly, and chironomid larvae were under-represented in the diet (all  $P < 0.01$ ) (Fig. 1c). In large streams, trout used mostly caddis larvae and blackfly larvae. Baetids and midge larvae were significantly under-represented in trout diet (both  $P < 0.01$ ) (Fig. 1e). In early summer (five small and two medium-sized streams), the most important prey group in trout diet, as well as in benthic and drift samples, was larval blackflies. In small streams, no prey type was over-

represented, but chironomid and blackfly larvae in both drift and benthos, and terrestrial invertebrates in drift, were significantly under-represented (all  $P < 0.005$ ) (Fig. 1b). In medium-sized streams, low sample size prevented statistical comparisons, but trout seemed to use chironomid larvae and terrestrial invertebrates less than expected in these streams (Fig. 1d).

In the NMDS ordination plots, a stream-size gradient was evident, for both benthos and trout diet (Fig. 2). The  $m^2$  statistic (0.713;  $P = 0.012$ ) indicated that the two ordinations were strongly concordant (i.e., trout gut contents resembled closely benthic communities in their taxonomic composition). According to MRPP, the difference in taxonomic composition between stream size classes was significant for the diet samples ( $A = 0.052$ ,  $P = 0.011$ ), whereas it was somewhat weaker for the benthic samples ( $A = 0.042$ ,  $P = 0.061$ ).

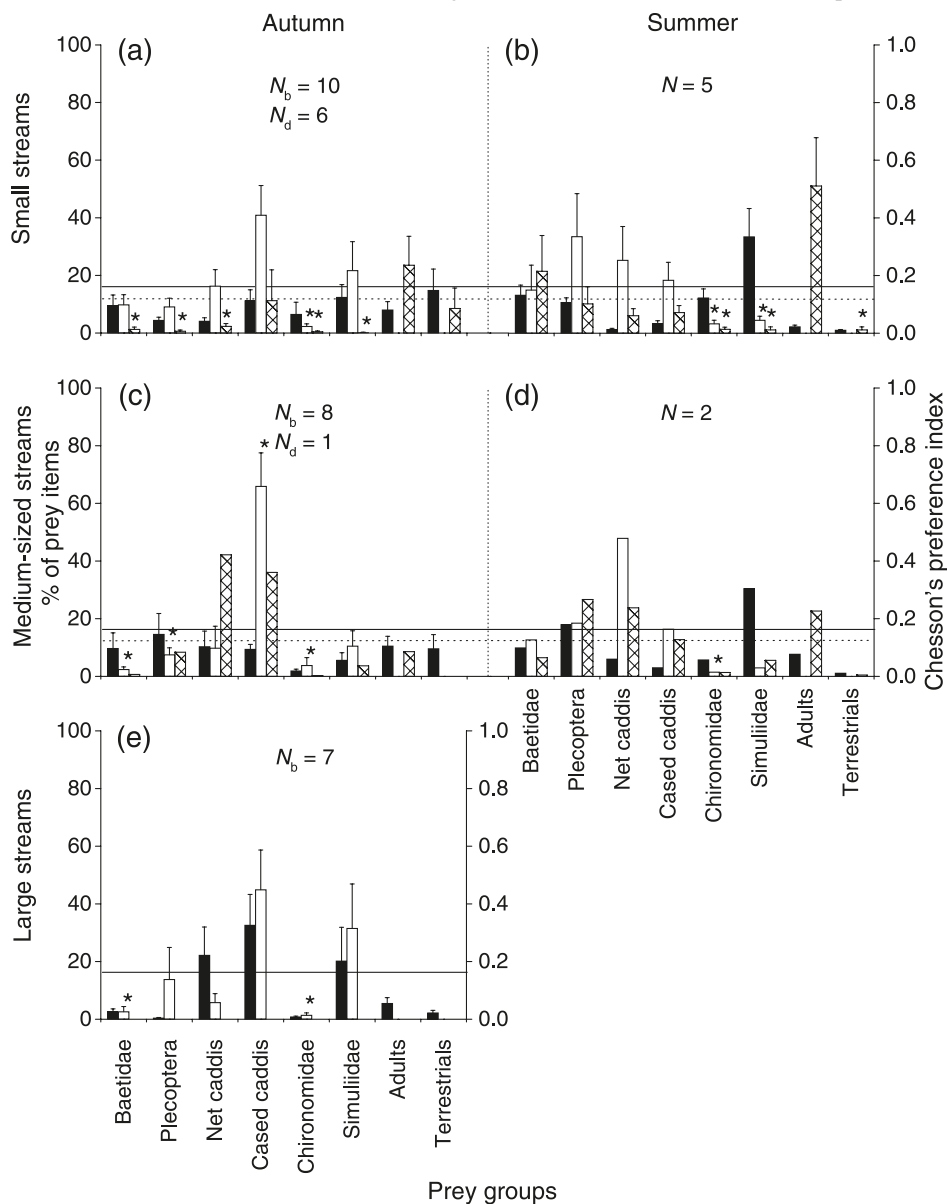
The percentage of terrestrial items in trout guts was 1.1% ( $\pm 1$  standard error, SE = 0.2%) in small and 1.1% ( $\pm 0.1\%$ ) in medium-sized streams in early summer. In early autumn, the corresponding figures were 14.8% ( $\pm 7.4\%$ ) for small, 9.6% ( $\pm 4.9\%$ ) for medium-sized, and 2.2% ( $\pm 0.9\%$ ) for large streams. In the early autumn data, the proportion of terrestrial invertebrates in brown trout diet across the 25 streams was weakly, though nonsignificantly, negatively related to channel width ( $r^2 = 0.142$ ,  $P = 0.063$ ). The most important groups of terrestrial prey in trout diet were ants (Formicidae, mainly non-winged), aphids (Aphididae), spiders (Araneae), insect caterpillars (mainly Lepidoptera), and a combined group of sawflies, wasps, and bees (Hymenoptera other than ants).

### Correlations between prey use and availability

Rader's (1997) model with eight invertebrate traits predicted the prey use by brown trout moderately weakly in the early summer (Table 2). For small streams, the average Spearman correlation across all five streams in the June samples was 0.446, one of the five correlations being significant ( $P = 0.002$ ). The correspondence with the observed diet was consistently lower when Rader's scores were combined with site-specific abundance in either benthic (mean  $r_s = 0.409$ ; number of significant correlations = 1/5) or drift (0.348 and 1/5, respectively) samples. Pure availability produced the best predictions of trout diet (benthic samples: mean  $r_s = 0.761$ , number of significant correlations = 5/5; drift samples: 0.671 and 4/5, respectively). Number of mid-sized streams sampled in June was only two, but correlations showed the same pattern as for small streams, with pure proportional abundance providing the best fit with trout diet (Table 2).

Rader's model was even less successful in predicting the early autumn prey use, average correlations between trout diet and unmodified Rader's scores, or scores combined with site-specific abundances, ranging between 0.150 and 0.374. Less than one-third of the correlations were significant (Table 2). By contrast, pure availability provided a significant fit with the observed diet in 67%–100% of cases, average correlations ranging from 0.512 (drift abundances in a mid-sized stream) to 0.654 (drift abundances in a small stream). Furthermore, closely similar results were obtained irrespective of how availability was defined, reflecting the fact that the taxonomic composition of benthos and drift correlated significantly ( $P < 0.01$ ) on both seasons, with 64% of all stream-specific correlations being significant (Table 2).

**Fig. 1.** Trout mean use (% of all prey items; black bars) of and mean selectivity vs. benthos (open bars) and selectivity vs. drift (hatched bars) for the eight most important prey types in small (*a*, *b*), medium-sized (*c*, *d*), and large (*e*) streams in early autumn and early summer. Sample sizes for each comparison (selectivity in relation to benthic samples,  $N_b$ ; selectivity in relation to drift samples,  $N_d$ ) are indicated in each figure. For diet samples, each stream provided one data point, and the number of streams included is the same as for  $N_b$ . Error bars indicate one standard error of the mean. Solid line shows the level of random feeding (or neutral selectivity) in relation to proportional availability in benthos; dotted line shows the relation to drift. Asterisks indicate significant difference ( $P < 0.01$ ; one-sample  $t$  test) from neutral selectivity.

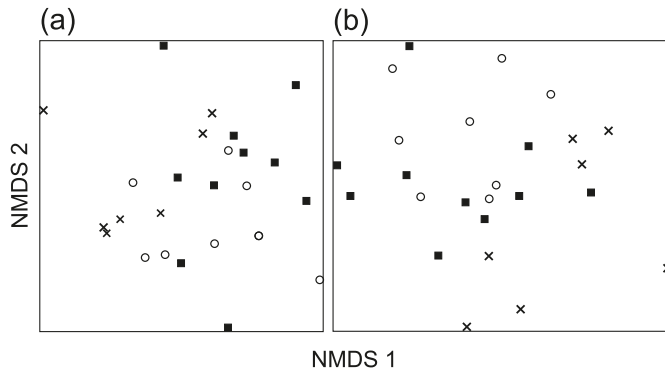


### Terrestrial invertebrates in salmonid diets: a quantitative review

We found 41 articles (Supplemental Appendix S1<sup>1</sup>) where the proportion of terrestrial food consumed by stream salmonids was given (or could be calculated based on information presented); overall, these studies produced 95 data points. Adding our own data (17 data points from this paper and 10 from K. Korsu, unpublished data), the sample size increased to 122, representing stream-living populations of three salmonid genera: *Salmo*, *Oncorhynchus*, and *Salvelinus* from four continents: Europe ( $n = 51$  studies), North America (43), Japan (12), and New Zealand (16). The overall mean proportion of terrestrial prey in salmonid diets was 17%. All other

explanatory variables but stream size (see Fig. 3a) differed significantly among the levels included (Table 3). Thus, fish size was strongly related to the proportion of terrestrial prey in salmonid diets, with the percentage increasing from the mean of 12% in the smallest (<80 mm) to 25% in the largest ( $\geq 150$  mm) size class (Fig. 3b). Representatives of the genus *Salmo* consumed the least terrestrials (mean of 9%), whereas the percentage was considerably higher in *Oncorhynchus* (27%) and *Salvelinus* (23%) (Fig. 3c). The percentage of terrestrial prey was highest in streams flowing through deciduous forests (30%), intermediate in mixed forests (13%), and lowest in coniferous forests and non-woody vegetation (11% both) (Fig. 3d). Only one interaction was significant

**Fig. 2.** NMDS (nonmetric multidimensional scaling) ordination diagrams for the benthic samples (a) (final stress for two-dimensional solution: 0.170) and trout stomach samples (b) (stress: 0.151) in the 25 streams sampled in early autumn. Squares are for small streams, open circles for medium-sized streams, and crosses for large streams. For stream size definitions, see text.



(vegetation type  $\times$  salmonid genus), reflecting the fact that a great majority of studies including *Salmo* species were conducted in strongly forested (mainly mixed forests) watersheds. Also, the interaction between riparian vegetation type and stream width bordered at significance ( $F_{[1,118]} = 2.93$ ,  $P = 0.089$ ), possibly indicating that stream width was only important in relatively small streams with mainly deciduous canopies.

The effect of stream width was obscured by the surprisingly low importance of terrestrial items in the smallest streams (i.e., <3 m wide). Thus, the percentage of terrestrials in fish diet was only 14%, on average, in the smallest streams, while it was much higher (21%) in the second-smallest stream size class (3 to 8 m), and 19% even in streams of 8 to 20 m in width (Fig. 3a). Focusing on streams wider than 3 m, a distinct size gradient was established, with the proportion of terrestrial prey in fish diet decreasing with increasing stream size ( $F_{[1,85]} = 45.43$ ,  $P < 0.001$ ). However, in linear regression, this gradient bordered at significant for the largest fish only (Fig. 4), as also indicated by a significant channel width  $\times$  fish size interaction (for data excluding the smallest streams) ( $F_{[1,85]} = 12.48$ ,  $P < 0.001$ ); that is, the largest fish included proportionally more terrestrial invertebrates in their diet in relatively small streams, while no such pattern was evident for smaller fish.

## Discussion

### Prey availability for and prey use and selectivity by brown trout

The use of different prey types by brown trout largely paralleled prey availability, resulting in a diet dominated by blackfly larvae, case-bearing caddis larvae, and terrestrial invertebrates in small streams grading to a diet dominated by case-bearing and net-spinning caddis larvae in large streams. Seasonally, a gradient from blackfly-dominated diet in early summer to terrestrial invertebrates and case-bearing caddis larvae in early autumn was detected. This pattern of prey use closely tracks seasonal variation of benthic communities in boreal streams (Malmqvist 1994; Erkinaro and Erkinaro 1998). Overall, brown trout was a highly opportunistic forager,

feeding on most prey types present, roughly proportional to their availability. Prey selectivity, however, differed slightly from prey use; trout showed a weak overall selectivity for caddis larvae, a rather strong under-representation of chironomid larvae, and a weaker under-representation of baetid mayfly and, in some cases, blackfly larvae. These patterns of selectivity likely reflect size-selective feeding by brown trout, a behavior repeatedly reported for salmonids (e.g., Allan 1981; Bechara et al. 1993; Meissner and Muotka 2006). Case-bearing and net-spinning caddis larvae are among the largest prey types present in boreal streams, and in experimental studies, trout have significantly reduced densities of these prey, while chironomids may even benefit from the presence of trout (Englund et al. 1999; Meissner and Muotka 2006). As chironomid larvae are usually among the smallest prey types available, they may be of little importance to fish longer than 10 cm, but may still be of high value to age-0 fish, particularly as these start exogenous feeding after emergence from the gravel (Keeley and Grant 1997; Steingrímsson and Gíslason 2002). Larval blackflies are also relatively small, but because of their high availability in early summer and preference for exposed microhabitats (Meissner et al. 2009), they may be a seasonally important component of salmonid diets.

The observation that trout behave as an opportunistic forager was also reflected in the fact that pure prey availability, estimated from either benthic or drift samples, produced very high correlations with trout diets. Benthic biomass in our study area declines to a minimum in mid- to late summer (Haapala et al. 2001), and prey availability, particularly that of large invertebrate prey, is much higher in early summer (Kreivi et al. 1999; see also Utz and Hartman 2006); yet, correlations between use and availability were even higher in early summer. It thus appears that very simple behavioral rules (e.g., focus on most abundant prey, prefer the largest prey) regulate trout foraging, and more sophisticated models including behavioural traits of invertebrates may not be needed in most cases. Furthermore, we feel that any model explaining trout diets must include terrestrial invertebrates, while many of the traits included in Rader's (1997) or De Crespín De Billy and Usseglio-Polatera's (2002) models are not readily adjustable to terrestrial prey (or adult stages of aquatic insects). Also, these models are largely based on the latest instars of aquatic insects, while ontogenetic changes in behavioural traits may lead to wide variation in the predation risk encountered by a prey species during its aquatic life.

Interestingly, correlations between trout diet vs. benthos and diet vs. drift were about the same order. Thus, trout seemed to sample these partly overlapping prey communities quite extensively. Trout frequently ingested prey that rarely enter the drift (e.g., cased caddis larvae). Our study thus supports the view that brown trout feed directly off the bottom more often than is commonly believed. Most previous studies suggesting this have been based on evidence from just one or a few salmonid populations in lakes (Tremblay and Magnan 1991; Venne and Magnan 1995) or streams (e.g., Angradi and Griffith 1990; Kreivi et al. 1999; Amundsen et al. 2000), and our data with 25 streams provide thus far the strongest observational evidence of the potential importance of epibenthic feeding in genus *Salmo*. In several studies, salmonids have been shown to feed on benthos when drift is depleted (Nislow et al. 1998; Nakano et al. 1999). However,

**Table 2.** Spearman rank correlation coefficients (mean and range) for five streams in the early summer (June) and 25 streams in early autumn (August–September).

Season	Stream size	<i>n</i>	Type of correlation	Mean	Range	No. of significant correlations
Summer	Small	5	R	0.446	0.175–0.679	1
		5	RB	0.409	0.109–0.752	1
		5	B	0.761	0.712–0.828	5
		5	RD	0.348	0.080–0.603	1
		5	D	0.671	0.432–0.805	4
		5	BD	0.643	0.564–0.779	4
Autumn	Small	10	R	0.233	0.054–0.518	1
		10	RB	0.370	0.205–0.675	1
		10	B	0.625	0.458–0.892	8
		6	RD	0.324	0.166–0.637	2
		6	D	0.654	0.400–0.889	4
		6	BD	0.508	0.110–0.825	3
	Medium	8	R	0.150	–0.048–0.276	0
		8	RB	0.231	–0.044–0.391	0
		8	B	0.556	0.368–0.676	7
	Large	7	R	0.200	0.044–0.604	1
		7	RB	0.374	0.201–0.599	2
		7	B	0.606	0.496–0.782	7

**Note:** R = prey use vs. Rader’s scores for eight invertebrate traits and abundance (based on original regional abundance categories); RB = prey use vs. Rader’s scores for the eight traits, combined with site-specific abundance in benthos; B = prey use vs. pure availability (proportional abundance) in benthos; RD = prey use vs. Rader’s scores for the eight traits combined with site-specific abundance in drift; D = prey use vs. pure availability in drift; and BD = prey abundance in benthos vs. prey abundance in drift. Correlations are based on proportional abundances of prey taxa in benthic, drift, or diet samples. Correlations are considered significant at  $\alpha < 0.01$ .

these observations were made in daylight, and as drift-feeding salmonids are visual foragers, they are likely to be severely impaired at low light levels (Fraser and Metcalfe 1997; Young et al. 1997). Case-bearing caddis, as well as many terrestrial invertebrates, are relatively large and conspicuous prey and may therefore be detected even at very low light levels, using perhaps cues other than vision (e.g., hydrodynamic cues). It is known that salmonids forage preferentially at night, but feed also during the daylight hours to satisfy their daily energy needs (Orpwood et al. 2006). We find it hard to find any other explanation but epibenthic feeding for the frequent selectivity for such rarely drifting prey as case-bearing caddis larvae (see also Forrester et al. 1994). At present, however, this hypothesis is based on correlation and must be corroborated by experiments and direct behavioral observations of individual fish, at all times of day and on different seasons representing different prey availabilities.

Terrestrial invertebrates in salmonid diets

Our finding of a relatively low amount of, and lack of selectivity for, terrestrial invertebrates in the diet of brown trout led us to suspect that the current doctrine about the great importance of terrestrial prey to salmonids may be biased, reflecting the fact that most studies showing this have been conducted in small streams with heavily forested canopies. Terrestrial invertebrate prey are often larger than aquatic prey (see Romaniszyn et al. 2007; Rosenfeld and Raeburn 2009). This, however, is not always the case; for example, Meissner and Muotka (2006) showed that while terrestrial prey were, on average, among the largest prey types available for brown trout in a Finnish forest stream, they ranged a large

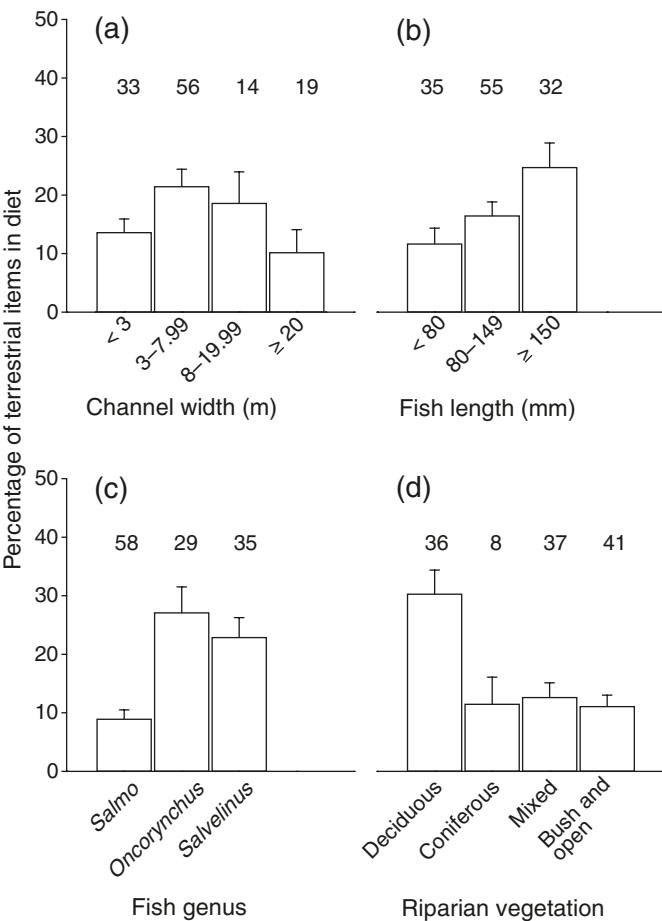
size gradient and were generally about the same size or even smaller than the largest benthic invertebrates (i.e., predatory invertebrates, particularly perlotid stonefly larvae and rhyacophilid caddis larvae). Therefore, we do not believe that the fact that we measured numbers of prey instead of biomass caused any serious bias to our results. Clearly, however, the quantitative literature survey showed that our results may be more of an exception than a general pattern, as the meta-analysis distinctly corroborated the importance of terrestrial invertebrates to salmonids. Not surprisingly, terrestrial prey increased in importance with fish size and in streams with mainly deciduous riparian canopy. A more interesting observation was that the use of terrestrial prey was only weakly correlated with channel width. This was contrary to our expectation, particularly as the use of terrestrial prey peaked at channels of 3–8 m, not in the narrowest ones. This seems to suggest that the effective range of terrestrial prey input from the riparian canopy may be wider than commonly believed, and the riparian subsidy of stream food webs may not, therefore, be restricted to headwater systems but may prove to be important also in larger rivers.

Another interesting observation stemming from our quantitative review was that the use of terrestrial invertebrates was size-dependent, as the largest fish included proportionally more terrestrial invertebrates in their diet than did smaller fish. Such a relationship has also been documented in several previous studies (e.g., Montori et al. 2006; Dineen et al. 2007). This pattern can be caused by at least two mechanisms: (i) salmonids defend feeding territories, with larger fish usually occupying the best drift-feeding positions; then, if terrestrial prey are the largest prey type available in the

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**Fig. 3.** Mean ( $\pm 1$  standard error, SE) proportion of terrestrial invertebrates in salmonid diets in relation to channel width (a), fish size (b), salmonid genus (c), and riparian vegetation type (d). Numbers above each bar indicate the sample size (number of streams included in each category).



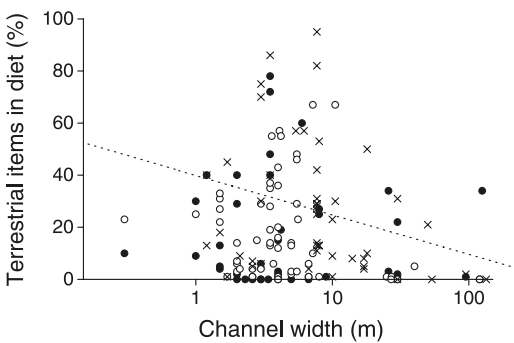
**Table 3.** Generalized least squares model for the proportion of terrestrial invertebrates in the diet of salmonid fishes based on a quantitative literature survey.

Source of variation	$F_{[df]}$	$P$
Vegetation	11.48 <sub>[1,120]</sub>	<0.001
Channel width	0.05 <sub>[1,120]</sub>	0.820
Fish length	6.65 <sub>[1,120]</sub>	0.011
Salmonid genus	18.48 <sub>[1,120]</sub>	<0.001
Vegetation $\times$ genus	10.09 <sub>[1,118]</sub>	0.002
Vegetation $\times$ channel width	2.93 <sub>[1,118]</sub>	0.089
Vegetation $\times$ fish length	0.01 <sub>[1,118]</sub>	0.987
Channel width $\times$ fish length	0.27 <sub>[1,118]</sub>	0.606
Channel width $\times$ genus	2.63 <sub>[1,118]</sub>	0.107
Fish length $\times$ genus	1.24 <sub>[1,118]</sub>	0.267

**Note:** All variables were included in the model as factorial, and VarIdent function, allowing heterogeneity of variances, was fitted in the model. All main effects and two-way interactions are reported.

drift, the large, dominant fish will disproportionately ingest these profitable prey items. Alternatively, (ii) size-specific differences in the use of terrestrial prey may be explained by gape limitation, with smaller fish being unable to ingest the largest invertebrate prey (Gowan 2007). Both of these hy-

**Fig. 4.** Relationship between channel width and the proportion of terrestrial invertebrates in salmonid diets, separately for each fish length class (<80, 80–149,  $\geq 150$  mm). Solid circles are for fish shorter than 80 mm, open circles for fish of 80–149 mm, and crosses for fish equal or longer than 150 mm. The overall relationship (all fish size classes combined) was nonsignificant, and linear regression bordered significance only for the largest fish length class ( $r^2 = 0.078$ ,  $P = 0.055$ ).



potheses are based on terrestrial prey being, on average, larger than aquatic prey. Thus, one explanation for the relatively low proportion of terrestrial invertebrates in trout diet in our field survey might have been that terrestrial and aquatic prey did not differ appreciably in size and that brown trout in our streams seemed to be feeding relatively intensively on epibenthic invertebrates.

The most surprising finding of our review was that salmonid genera differed vastly, with *Salmo* ingesting terrestrial items much less frequently than did the other two genera. This may reflect different habitat preferences and (or) foraging strategies in different species. For example, Korsu et al. (2010) observed age-1 brook trout (*Salvelinus fontinalis*) to select primarily slow-flowing pool sections, while brown trout of the same age preferred riffles. Such species-specific differences in habitat use may cause different salmonid species to encounter partly differing prey assemblages. Terrestrial invertebrates drifting on the water surface in pools should be highly visible for fish, but the more turbulent flow in riffles may render surface-drifting (i.e., terrestrial) invertebrates less easily detectable. Unfortunately, studies comparing the foraging behavior and prey selectivity of *Salmo* spp. with those of other salmonids are surprisingly rare. In one of the few exceptions, Mookerji et al. (2004) showed that while Atlantic salmon (*Salmo salar*) preferred aquatic insects, brook trout fed mainly upon terrestrial invertebrates.

Allan et al. (2003) proposed that deciduous trees are of better food quality for herbivores than are coniferous trees, and thus deciduous riparian forests should deliver more invertebrates to streams. Our findings, and those of Romero et al. (2005), support this assertion, as the proportion of terrestrial prey in trout diets was higher in streams draining deciduous forests. Similarly, the use of terrestrial prey by fish was much higher in lakes with intact riparian forest than in developed, open-shore lakes in North America (Francis and Schindler 2009).

As most studies of salmonid diets are conducted in later summer or autumn, they may miss the most important season for parr growth in boreal streams, that is, spring and early summer. The total food intake of parr is often highest in early summer (Allan 1981; Kreivi et al. 1999), presumably because

of the high availability of aquatic prey then. This was also indirectly reflected in our study, where the contribution of riparian invertebrates to the early summer diet of brown trout was minimal. Thus, studies focusing on mid- to late summer diets alone may provide a biased estimate of the importance of terrestrial prey to salmonid diets. Indeed, Nakano and Murakami (2001) reported the proportion of terrestrial prey to be 23%–57% of the total annual energy intake of four salmonid species (no *Salmo* species included) in a Japanese forest stream. Although riparian invertebrates were not strongly preferred by brown trout in our study, they can still be of critical importance for the overwintering success of trout. For example, terrestrial invertebrates may be a key component of trout diet in late September, when many riparian invertebrates are still active but large-sized benthic prey are scarce. Overall, the proportional importance of terrestrial invertebrates compared with aquatic prey in trout diet seems to follow a similar seasonal pattern in boreal streams draining conifer-dominated forests and more southern, deciduous forest streams (Romero et al. 2005, Romaniszyn et al. 2007), being low in winter and spring, low to moderate in summer, and relatively high in late summer and autumn.

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## References

- Allan, J.D. 1981. Determinants of diet of brook trout (*Salvelinus fontinalis*) in a mountain stream. *Can. J. Fish. Aquat. Sci.* **38**(2): 184–192. doi:10.1139/f81-024.
- Allan, J.D., Wipfli, M.S., Caouette, J.P., Prussian, A., and Rodgers, J. 2003. Influence of streamside vegetation on inputs of terrestrial invertebrates to salmonid food webs. *Can. J. Fish. Aquat. Sci.* **60**(3): 309–320. doi:10.1139/f03-019.
- Amundsen, P.-A., Gabler, H., Herfindal, T., and Riise, L.S. 2000. Feeding chronology of Atlantic salmon parr in subarctic rivers: consistence of nocturnal feeding. *J. Fish Biol.* **56**(3): 676–686. doi:10.1111/j.1095-8649.2000.tb00765.x.
- Angradi, T.R., and Griffith, J.S. 1990. Diel feeding chronology and diet selection of rainbow trout (*Oncorhynchus mykiss*) in the Henry's Fork of the Snake River, Idaho. *Can. J. Fish. Aquat. Sci.* **47**(1): 199–209. doi:10.1139/f90-022.
- Baxter, C.V., Fausch, K.D., Murakami, M., and Chapman, P.L. 2004. Fish invasion restructures stream and forest food webs by interrupting reciprocal prey subsidies. *Ecology*, **85**(10): 2656–2663. doi:10.1890/04-138.
- Bechara, J.A., Moreau, G., and Hare, L. 1993. The impact of brook trout (*Salvelinus fontinalis*) on an experimental stream benthic community: the role of spatial and size refugia. *J. Anim. Ecol.* **62**(3): 451–464. doi:10.2307/5194.
- Bres, M. 1986. A new look at optimal foraging behavior: rule of thumb in the rainbow trout. *J. Fish Biol.* **29**(Suppl. sA): 25–36. doi:10.1111/j.1095-8649.1986.tb04996.x.
- Bridcut, E.E., and Giller, P.S. 1995. Diet variability and foraging strategies in brown trout (*Salmo trutta*): an analysis from subpopulations to individuals. *Can. J. Fish. Aquat. Sci.* **52**(12): 2543–2552. doi:10.1139/f95-845.
- Cada, G.F., Loar, J.M., and Sale, M.J. 1987. Evidence of food limitation of rainbow and brown trout in southern Appalachian soft-water streams. *Trans. Am. Fish. Soc.* **116**(5): 692–702. doi:10.1577/1548-8659(1987)116<692:EOFLOR>2.0.CO;2.
- Chesson, J. 1983. The estimation and analysis of preference and its relationship to foraging models. *Ecology*, **64**(5): 1297–1304. doi:10.2307/1937838.
- De Crespín De Billy, V., and Usseglio-Polatera, P. 2002. Traits of brown trout prey in relation to habitat characteristics and benthic invertebrate communities. *J. Fish Biol.* **60**(3): 687–714. doi:10.1111/j.1095-8649.2002.tb01694.x.
- Dineen, G., Harrison, S.S.C., and Giller, P.S. 2007. Diet partitioning in sympatric Atlantic salmon and brown trout in streams with contrasting riparian vegetation. *J. Fish Biol.* **71**(1): 17–38. doi:10.1111/j.1095-8649.2007.01441.x.
- Elliott, J.M. 1973. The food of brown and rainbow trout (*Salmo trutta* and *S. gairdneri*) in relation to the abundance of drifting invertebrates in a mountain stream. *Oecologia*, **12**(4): 329–347. doi:10.1007/BF00345047.
- Englund, G., Sarnelle, O., and Cooper, S.D. 1999. The importance of data-selection criteria in meta-analyses of stream predation experiments. *Ecology*, **80**(4): 1132–1141. doi:10.1890/0012-9658(1999)080[1132:TIODSC]2.0.CO;2.
- Erkinaro, H., and Erkinaro, J. 1998. Feeding of Atlantic salmon, *Salmo salar* L., parr in the subarctic River Teno and three tributaries in northernmost Finland. *Ecol. Freshw. Fish.* **7**(1): 13–24. doi:10.1111/j.1600-0633.1998.tb00168.x.
- Esteban, E.M., and Marchetti, M.P. 2004. What's on the menu? Evaluating a food availability model with young-of-the-year Chinook salmon in the Feather River, California. *Trans. Am. Fish. Soc.* **133**(3): 777–788. doi:10.1577/T03-115.1.
- Forrester, G.E., Chace, J.G., and McCarthy, W. 1994. Diel and density-related changes in food consumption and prey selection by brook charr in a New Hampshire stream. *Environ. Biol. Fishes*, **39**(3): 301–311. doi:10.1007/BF00005131.
- Francis, T.B., and Schindler, D.E. 2009. Shoreline urbanization reduces terrestrial insect subsidies to fishes in North American lakes. *Oikos*, **118**(12): 1872–1882. doi:10.1111/j.1600-0706.2009.17723.x.
- Fraser, N.H.C., and Metcalfe, N.B. 1997. The costs of becoming nocturnal: feeding efficiency in relation to light intensity in juvenile Atlantic salmon. *Funct. Ecol.* **11**(3): 385–391. doi:10.1046/j.1365-2435.1997.00098.x.
- Gowan, C. 2007. Short term cues used by foraging trout in a California stream. *Environ. Biol. Fishes*, **78**(4): 317–331. doi:10.1007/s10641-006-9099-z.
- Haapala, A., Muotka, T., and Markkola, A.-M. 2001. Breakdown and macroinvertebrate and fungal colonization of alder, birch and willow leaves in a boreal forest stream. *J. N. Am. Benthol. Soc.* **20**(3): 395–407. doi:10.2307/1468037.
- Jackson, D.A. 1995. PROTEST: a PROcrustean Randomization TEST of community environment concordance. *Ecoscience*, **2**: 297–303.
- Johnson, R.L., Blumenshine, S.C., and Coghlan, S.M. 2006. A bioenergetic analysis of factors limiting brown trout growth in an Ozark tailwater river. *Environ. Biol. Fishes*, **77**(2): 121–132. doi:10.1007/s10641-006-9059-7.
- Kawaguchi, Y., and Nakano, S. 2001. Contribution of terrestrial invertebrates to the annual resource budget for salmonids in forest and grassland reaches of a headwater stream. *Freshw. Biol.* **46**(3): 303–316. doi:10.1046/j.1365-2427.2001.00667.x.
- Keeley, E.R., and Grant, J.W. 1997. Allometry of diet selectivity in juvenile Atlantic salmon (*Salmo salar*). *Can. J. Fish. Aquat. Sci.* **54**(8): 1894–1902. doi:10.1139/cjfas-54-8-1894.
- Korsu, K., Huusko, A., and Muotka, T. 2009. Does the introduced brook trout (*Salvelinus fontinalis*) affect growth of the native

- brown trout (*Salmo trutta*)? *Naturwissenschaften*, **96**(3): 347–353. doi:10.1007/s00114-008-0482-9. PMID:19050841.
- Korsu, K., Huusko, A., and Muotka, T. 2010. Invasion of north European stream by brook trout: hostile takeover or preadapted habitat niche segregation? *Biol. Invasions*, **12**(5): 1363–1375. doi:10.1007/s10530-009-9553-x.
- Kreivi, P., Muotka, T., Huusko, A., Mäki-Petäys, A., Huhta, A., and Meissner, K. 1999. Diel feeding periodicity, daily ration and prey selectivity in juvenile brown trout in a subarctic river. *J. Fish Biol.* **55**(3): 553–571. doi:10.1111/j.1095-8649.1999.tb00699.x.
- Light, R.M., Adler, P.H., and Arnold, D.E. 1983. Evaluation of gastric lavage for stomach analyses. *N. Am. J. Fish. Manage.* **3**(1): 81–85. doi:10.1577/1548-8659(1983)3<81:EOGLFS>2.0.CO;2.
- Malmqvist, B. 1994. Preimaginal blackflies (Diptera: Simuliidae) and their predators in a central Scandinavian lake outlet stream. *Ann. Zool. Fenn.* **31**: 245–255.
- McCune, B., and Mefford, M.J. 1999. PC-ORD. Multivariate analysis of ecological data. Version 4.0. MjM Software, Gleneden Beach, Ore., USA.
- Meissner, K., and Muotka, T. 2006. The role of trout in stream food webs: integrating evidence from field surveys and experiments. *J. Anim. Ecol.* **75**(2): 421–433. doi:10.1111/j.1365-2656.2006.01063.x. PMID:16637995.
- Meissner, K., Juntunen, A., Malmqvist, B., and Muotka, T. 2009. Predator–prey interactions in a variable environment: responses of a caddis larva and its blackfly prey to variations in stream flow [online]. *Ann. Zool. Fenn.* **46**: 193–204. Available from <http://www.sekj.org/PDF/anz46-free/anz46-193.pdf> [accessed 2 June 2011].
- Miyasaka, H., Nakano, S., and Furukawa-Tanaka, T. 2003. Food habit divergence between white-spotted charr and masu salmon in Japanese mountain streams: circumstantial evidence for competition. *Limnology*, **4**(1): 1–10. doi:10.1007/s10201-002-0088-4.
- Montori, A., Tierno De Figueroa, J.M., and Santos, X. 2006. The diet of the brown trout *Salmo trutta* (L.) during the reproductive period: size-related and sexual effects. *Int. Rev. Hydrobiol.* **91**(5): 438–450. doi:10.1002/iroh.200510899.
- Mookerji, N., Weng, Z., and Mazumder, A. 2004. Food partitioning between coexisting Atlantic salmon and brook trout in the Sainte-Marguerite River ecosystem, Quebec. *J. Fish Biol.* **64**(3): 680–694. doi:10.1111/j.1095-8649.2004.00333.x.
- Nakano, S., and Furukawa-Tanaka, T. 1994. Intra- and interspecific dominance hierarchies and variation in foraging tactics of two species of stream-dwelling charrs. *Ecol. Res.* **9**(1): 9–20. doi:10.1007/BF02347237.
- Nakano, S., and Kaeriyama, M. 1995. Summer microhabitat use and diet of four sympatric stream-dwelling salmonids in a Kamchatkan stream. *Fish. Sci.* **61**: 926–930.
- Nakano, S., and Murakami, M. 2001. Reciprocal subsidies: dynamic interdependence between terrestrial and aquatic food webs. *Proc. Natl. Acad. Sci. U.S.A.* **98**(1): 166–170. doi:10.1073/pnas.98.1.166. PMID:11136253.
- Nakano, S., Fausch, K.D., and Kitano, S. 1999. Flexible niche partitioning via a foraging mode shift: a proposed mechanism for coexistence in stream-dwelling charr. *J. Anim. Ecol.* **68**(6): 1079–1092. doi:10.1046/j.1365-2656.1999.00355.x.
- Nislow, K.H., Folt, C., and Seandel, M. 1998. Food and foraging behavior in relation to microhabitat use and survival of age-0 Atlantic salmon. *Can. J. Fish. Aquat. Sci.* **55**(1): 116–127. doi:10.1139/f97-222.
- Orpwood, J.E., Griffiths, S.W., and Armstrong, J.D. 2006. Effects of food availability on temporal activity patterns and growth of Atlantic salmon. *J. Anim. Ecol.* **75**(3): 677–685. doi:10.1111/j.1365-2656.2006.01088.x. PMID:16689950.
- Peres-Neto, P.R., and Jackson, D.A. 2001. How well do multivariate data sets match? The advantages of a Procrustean superimposition approach over the Mantel test. *Oecologia*, **129**(2): 169–178. doi:10.1007/s004420100720.
- Pinho, J.C., and Bates, D.M. 2000. Mixed-effects models in S and S-PLUS. Springer-Verlag, New York.
- Poff, N.L., and Huryn, A.D. 1998. Multi-scale determinants of secondary production in Atlantic salmon (*Salmo salar*) streams. *Can. J. Fish. Aquat. Sci.* **55**(S1): 201–217. doi:10.1139/d98-013.
- R Development Core Team. 2010. A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. ISBN 3-900051-08-9. Available from <http://www.r-project.org> [accessed 2 June 2011].
- Rader, R.B. 1997. A functional classification of the drift: traits that influence invertebrate availability to salmonids. *Can. J. Fish. Aquat. Sci.* **54**(6): 1211–1234. doi:10.1139/f97-025.
- Romanisyn, E.D., Hutchens, J.J., and Wallace, J.B. 2007. Aquatic and terrestrial invertebrate drift in southern Appalachian mountain streams: implications for trout food resources. *Freshw. Biol.* **52**(1): 1–11. doi:10.1111/j.1365-2427.2006.01657.x.
- Romero, N., Gresswell, R.E., and Li, J.L. 2005. Changing patterns in coastal cutthroat trout (*Oncorhynchus clarki clarki*) diet and prey in a gradient of deciduous canopies. *Can. J. Fish. Aquat. Sci.* **62**(8): 1797–1807. doi:10.1139/f05-099.
- Rosenfeld, J.S., and Raeburn, E. 2009. Effects of habitat and internal prey subsidies on juvenile coho salmon growth: implications for stream productive capacity. *Ecol. Freshw. Fish.* **18**(4): 572–584. doi:10.1111/j.1600-0633.2009.00372.x.
- Saraniemi, M., Huusko, A., and Tahkola, H. 2008. Spawning migration and habitat use of adfluvial brown trout, *Salmo trutta*, in a strongly seasonal boreal river. *Boreal Env. Res.* **13**: 121–132.
- Sotiropoulos, J.C., Nislow, K.H., and Ross, M.R. 2006. Brook trout, *Salvelinus fontinalis*, microhabitat selection and diet under low summer stream flows. *Fish. Manage. Ecol.* **13**(3): 149–155. doi:10.1111/j.1365-2400.2006.00487.x.
- Steingrímsson, S.Ó., and Gíslason, G.M. 2002. Body size, diet and growth of landlocked brown trout, *Salmo trutta*, in the subarctic River Laxa, North-East Iceland. *Environ. Biol. Fishes.* **63**(4): 417–426. doi:10.1023/A:1014976612970.
- Syrjänen, J., and Valkeajärvi, P. 2010. Gillnet fishing drives lake-migrating brown trout to near extinction in the Lake Päijänne region, Finland. *Fish. Manage. Ecol.* **17**(2): 199–208. doi:10.1111/j.1365-2400.2010.00738.x.
- Tremblay, S., and Magnan, P. 1991. Interactions between two distantly related species, brook trout (*Salvelinus fontinalis*) and white sucker (*Catostomus commersoni*). *Can. J. Fish. Aquat. Sci.* **48**(5): 857–867. doi:10.1139/f91-102.
- Utz, R.M., and Hartman, K.J. 2006. Temporal and spatial variation in the energy intake of brook trout (*Salvelinus fontinalis*) population in an Appalachian watershed. *Can. J. Fish. Aquat. Sci.* **63**(12): 2675–2686. doi:10.1139/f06-152.
- Venne, H., and Magnan, P. 1995. The impact of intra- and interspecific interactions on young-of-the-year brook charr, in temperate lakes. *J. Fish Biol.* **46**(4): 669–686. doi:10.1111/j.1095-8649.1995.tb01103.x.
- Wipfli, M.S. 1997. Terrestrial invertebrates as salmonid prey and nitrogen sources in streams: contrasting old-growth and young-growth riparian forests in southeastern Alaska, U.S.A. *Can. J. Fish. Aquat. Sci.* **54**(6): 1259–1269. doi:10.1139/f97-034.
- Young, M.K., Rader, R.B., and Belish, T.A. 1997. Influence of macroinvertebrate drift and light on the activity and movement of Colorado River cutthroat trout. *Trans. Am. Fish. Soc.* **126**(3): 428–437. doi:10.1577/1548-8659(1997)126<0428:IOMDAL>2.3.CO;2.