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THE IMPORTANCE AND SEASONAL VARIATION OF TERRESTRIAL
INVERTEBRATES AS PREY FOR JUVENILE SALMONIDS ON THE KOL RIVER
FLOODPLAIN, KAMCHATKA, RUSSIAN FEDERATION

By

Lorri Christine Eberle
B.A., University of North Carolina, Chapel Hill, 2002

Thesis
presented in partial fulfillment of the requirements
for the degree of

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in Division of Biological Sciences, Organismal Biology and Ecology

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Approved by:

Dr. David A. Strobel, Dean
Graduate School

Dr. Jack Stanord, Chair
Flathead Lake Biological Station
Division of Biological Sciences

Dr. Lisa Eby
Wildlife Biology

Dr. F. Richard Hauer
Flathead Lake Biological Station
Division of Biological Sciences

Eberle, Lorri C., M.S., Spring 2007

Biological Science

The Importance and Seasonal Variation of Terrestrial Invertebrates as Prey for Juvenile Salmonids on the Kol River Floodplain, Kamchatka, Russia

Committee Chair: Dr. Jack Stanford

Fluxes of energy and resources from one system to another across an interface can play a major role in the structure and function of the food web of the receiving system. Floodplain spring brooks have a particularly high interface value and host high densities of juvenile fish likely seeking refuge from predators, high velocity water, and stressful temperatures. We propose that one potential reason that these systems are able to support such high densities of fish is related to prey subsidies coming from the neighboring terrestrial system (i.e. terrestrial invertebrates).

We examined terrestrial invertebrate inputs into spring brooks and their use as prey by salmonids in two spring brook habitats from May- October 2006 on the Kol River flood plain in Kamchatka, Russia. Benthic and drifting invertebrates, terrestrial invertebrate inputs, terrestrial invertebrate communities and fish diet were analyzed to assess the seasonal and spatial variation in the terrestrial invertebrate subsidy. Sites were selected that are representative of two different vegetation types: early and late succession.

Biomass of benthic and drifting invertebrates was low for both sites and annual average of terrestrial inputs was $22.2 \pm 0.1 \text{ mg}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$. Terrestrial invertebrates were most important to the diets of coho salmon with as much as 68% of their diet being terrestrial in origin, whereas on average only 13% of the Dolly Varden diet was terrestrial.

Terrestrial invertebrates were most important in the fall at both sites. However, in the spring, an unlikely prey item caused a spike in the terrestrial percentage at the early succession site. The Curculionidae larva (order: Coleoptera) which live in the catkins of willows were found to be far more abundant in the species of willow that exists only in early succession. This study links terrestrial prey items to floodplain succession, and demonstrates for the first time the seasonal variation in the terrestrial invertebrate subsidy in the floodplain habitats. By highlighting the link between terrestrial and aquatic systems, the results of this study raise concerns in dealing with riparian management and salmonid production and conservation.

Key words: allochthonous inputs, terrestrial invertebrates, resource subsidy, forest-stream ecotone, food webs, stream ecology, salmonids, Kamchatka

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Introduction

Ecological interfaces, or ecotones, are the places where “structural or functional system properties change discontinuously in space or time” (Naiman & Decamps 1997), and these places are unique in their interactions with the neighboring systems. The subsidies of resources from neighboring systems at such interfaces can even help to support higher than expected densities of both producers and consumers in the recipient habitats. Even habitats with extremely low primary productivity are actually able to support relatively high levels of consumers because of subsidies from more productive donor habitats. In these cases, the system cannot support itself with in situ production and is dependent on allochthonous resources for sustainability (e.g. Polis & Hurd 1995; Polis et al. 1997a; Polis et al. 1997b).

Flood plains in particular are an interesting place to study the dynamics of the flow of resources between systems. According to the river continuum concept (Vannote et al. 1980), the importance of allochthonous materials decreases as you move downstream because the ecosystem perimeter to area ratio generally decreases. However, this theory may not hold true when considering flood plains. The nature of the physical processes that form flood plains create large areas where these interfaces occur. This ratio of ecosystem perimeter to its area has been positively correlated to the flow of resources between the systems (Polis & Hurd 1995), and the constant migration of river channels on flood plains helps to increase this perimeter to area ratio. The natural oscillations of floodplain processes result in a high level of biocomplexity known as the “shifting habitat mosaic” (Stanford et al. 2005). This patchwork of habitats represents an array of environments and niches that can support rich varieties of both terrestrial and aquatic inhabitants which can be at least partially attributed to the strong links between the terrestrial and aquatic systems (Stanford et al. 2005).

Riparian plants often provide important nutrient and energy subsidies to streams and rivers, and studies of allochthonous leaves and wood have shown that these subsidies may determine the composition aquatic food webs (Vannote et al. 1980; Cummins et al. 1989; Gregory et al. 1991). However, allochthonous leaves and wood are not a direct food source for predators such as fish. Indeed, dependence of aquatic consumer species

on direct inputs of invertebrates from riparian forests has only recently been quantified (Fausch et al. 2002).

On the Kol River flood plain in Kamchatka, Russia the springbrook habitats that occur in disconnected flood channels (*sensu* Stanford et al. 2005) serve as nurseries for salmonids and may have particularly high densities of juvenile salmonid fishes (Fig. 1). Juvenile fish may be seeking refuge from predators, high velocity water, or stressful temperature regimes (Stanford et al. 2005). One potential reason that these springbrook systems are able to support such high densities could be related to prey subsidies coming from the neighboring terrestrial system (i.e. terrestrial invertebrates).

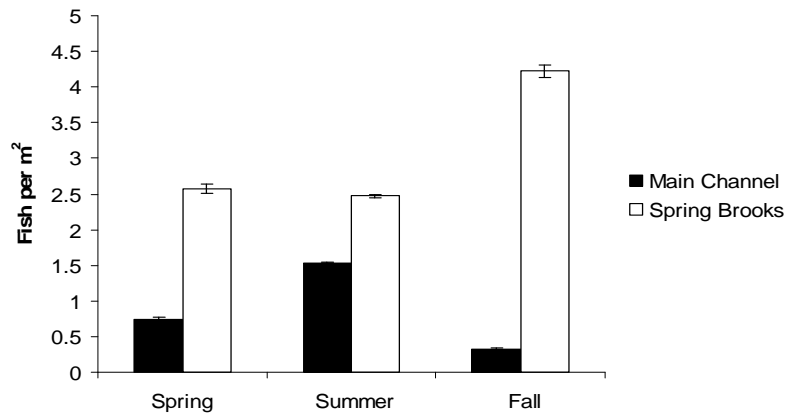


Fig. 1 Densities of fish for the 2005 season in the Kol main channel and spring brook study sites for the Salmonid River Observatory Network (Stanford, unpublished data). Estimates based on 3-pass electroshock fish removal. Bars represent one standard deviation of the mean.

A study by Southwood (1961) demonstrated that vegetation can influence the species composition and abundance of associated invertebrates, and others have demonstrated the importance of terrestrial invertebrates as prey for fish (see Hunt 1975; Mason & Macdonald 1982; Cloe & Garman 1996; Wipfli 1997; Allen et al. 2003). Additionally, the role of terrestrial invertebrates in mutual trophic interactions between stream and forest ecosystems (Nakano & Murakami 2001) and the potential for trophic cascades controlled by terrestrial invertebrate inputs into streams (Nakano et al. 1999a) have been demonstrated for a headwater stream in Japan. However, the effect that riparian vegetation has on the flow of these resources along seasonal and successional

gradients is still poorly understood (Baxter et al. 2005). Insect phenology or subtle changes in humidity, temperature, and weather can affect invertebrate activity over relatively short periods of time. Therefore, the flux of inputs of terrestrial invertebrates and the subsequent availability to fish as prey can vary greatly with the seasons (Baxter et al. 2005). These temporal and spatial dynamics related to terrestrial prey subsidies in aquatic systems are an important but missing link in our understanding of the relationship between terrestrial and aquatic systems.

Herein, I examined temporal variations of terrestrial insects in the diets of salmonids living in the riparian fringe habitats of the Kol River flood plain. Most of the studies of terrestrial subsidies of aquatic food webs have been conducted on small, headwater streams like the Horonai experimental stream in Japan, and to my knowledge, only one other study (Romero et al. 2005) has looked at the differences of terrestrial invertebrate inputs along a seasonal gradient. This study is one of the first to evaluate the seasonality of terrestrial prey subsidies in the context of floodplain habitats along successional gradients.

The objectives of this study were to (i) quantify seasonal variations of terrestrial and aquatic prey in the diets of juvenile salmonids in two springbrook habitats on the Kol River Floodplain in Kamchatka, Russia between June and October 2006, (ii) quantify seasonal availability of terrestrial and aquatic prey both within the stream and falling into the stream from the terrestrial habitat, and (iii) determine differences in terrestrial insect community assemblages in association with two different forest successional stages.

Study Site

The Kol River is a west-flowing river on the southern end of the Kamchatka Peninsula, Russia (Fig. 2). It originates in the central Kamchatka range at an elevation of approximately 2000m, and it flows westward to the Sea of Okhotsk. A research camp, operated by the Wild Salmon Center is located approximately 12km upstream from the Sea of Okhotsk (N53 49.506 E15603712), and at this point the river is 7th order, characterized by an expansive, gravel-bed floodplain. All six species of Pacific Salmon reside in the Kol, but runs are dominated by pink salmon (*Oncorhynchus gorbusha*), some 5-7 million on even years and approximately 500,000 on odd years. The Kol River

catchment has no year-round inhabitants, but a new pipeline road allows limited access. Nonetheless, the river system is completely intact ecologically and has been formally designated as a salmon protected area. For this reason, the Kol was chosen as one of a suite of study sites in the Salmonid Rivers Observatory Network (SaRON) for the purpose of comparing and contrasting the ecology of pristine salmon rivers around the Pacific Rim.



Fig.2 Kamchatka Peninsula, showing the location of the Kol River at the star (<http://encarta.msn.com>)

The Kol receives inputs from snowmelt throughout the summer that create flood pulses that cut and fill alluvium to produce a complex channel network consisting of a patchwork of interconnected riparian and aquatic habitats (Figs. 3a,c). Spring brooks that occur in old flood channels make up 83.21 hectares of the total floodplain area, whereas the main channel area in the Kol floodplain encompasses 325.35 hectares, based on estimations from satellite imagery and habitat classification at base flow of the river. This study was conducted on two spring brooks in the Kol River flood plain. The spring brooks were functionally similar, occurring as upwelling ground water in flood channels that are plugged by gravel and wood levees at the upstream end but connected to the main channel at the downstream ends. However, the spring brooks existed in two different forest types. Hollywood spring brook (Figs. 3a,b) had a more open canopy and riparian vegetation dominated by willows (*Salix spp.*), representative of an earlier stage in the forest succession trajectory (~20 years old). The second, Fuzzy spring brook (Figs. 2c,d) had a dense, mixed canopy of willow and alder (*Alnus spp.*) and more herbaceous vegetation, typical of a later forest succession stage (~80 years). Hollywood had a mix of

the two common willow species (one which dominates early in succession and the other dominates late in succession). However, Fuzzy, being in a late succession stage forest, lacked the early succession willow species (Morris, unpublished data). The vegetation at both sites was in peak foliage between late June and early July, with the leaves beginning to senesce in early to mid- September.

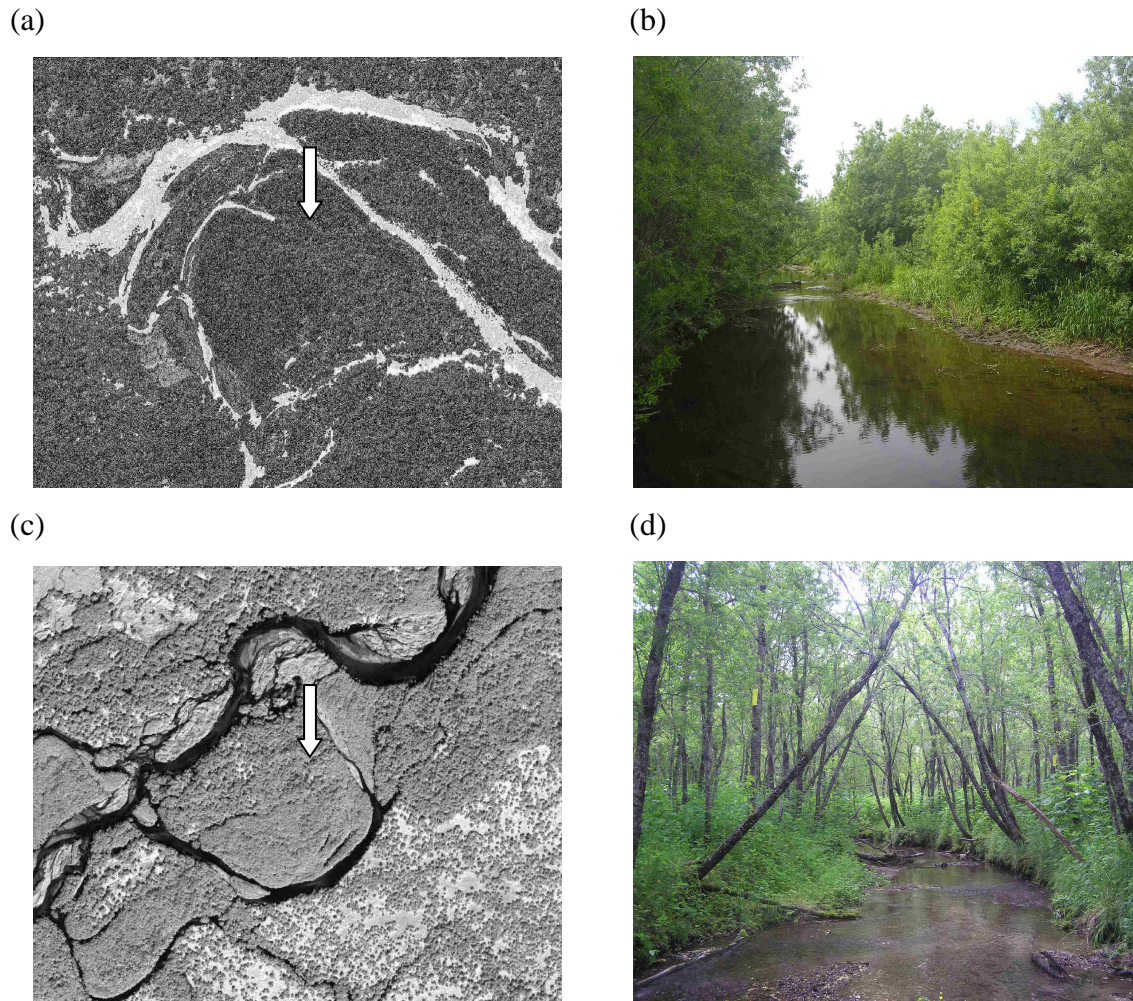


Figure 3 (a-d) Figure (a) Hollywood spring brook viewed from a Quickbird multispectral image. Figure (b) photo of Hollywood spring brook; Figure (c) Quickbird image of fuzzy spring brook located approximately 1 km upstream from the view in figure (a). Figure (d) photo of Fuzzy spring brook. Quickbird image was obtained on July 29, 2004. Arrows designate spring brook locations.

Both spring brook sites hosted a variety of fish species, including Dolly Varden charr (*Salvelinus malma*), coho salmon (*Oncorhynchus kisutch*), masu salmon

(*Oncorhynchus masou*), chinook salmon (*Oncorhynchus tshawytscha*), white-spotted charr (*Salvelinus leucomaenis*), pink salmon (*Oncorhynchus gorbusha*), chum salmon (*Oncorhynchus keta*), sockeye salmon (*Oncorhynchus nerka*), three-spine stickleback (*Gasterosteus aculeatus*), nine-spine stickleback (*Pungitius pungitius*), and lamprey (*Lethenteron japonicum*). However, this study focused primarily on the most abundant springbrook species, coho and Dolly Varden.

The study sites were comparable 50-80m reaches that incorporated one or more riffle, run and pool sequences. Each study reach encompassed approximately 35% of the total spring brook length. The head of both spring brooks typically connect with the main channel at the upper end during higher flows and remain disconnected during lower flows. This can cause the spring brook to connect and disconnect from the main channel multiple times throughout the year. However, this study was conducted in June-October 2006 which proved to be a low water year, and both sites were fed only by upwelling groundwater throughout the study period. The low water in the main channel also created habitats in the main channel that resembled spring brook and off-channel habitats with lower velocities, and more refugia, making the main channel more accessible for juvenile fish than in the previous three years. Furthermore, during 2003-2005 Dolly Varden, chum, pink, coho and sockeye salmon were observed spawning in these channels. However, this year there were no spawners found at either site, potentially due to the extremely low flows experienced in the 2006 season. The presence of spawning salmon in the spring brooks and the potential feeding on eggs by juvenile salmonids could cause significant differences in the diets of fish, particularly in the fall. Our study could serve as an interesting baseline as a comparison to fish diets on years when spawners are present.

Methods

Objective (i) Quantify seasonal variations of terrestrial and aquatic prey in the diets of juvenile salmonids.

Fish Diet Analysis

Seasonal changes in the invertebrate prey composition in fish diets were examined seven times per site between June and October 2006. Fish were collected

using an electrofishing backpack unit between 10:00am and 1:00pm. Fish were held in buckets on the river edge, separated into species and measured (mm) and weighed (g). Non-lethal gut content samples were collected via lavage with a modified 5mL plastic pipette from 28-76 individuals per sample period from both coho and Dolly Varden with fork lengths of 30-165mm. These fish included both young of year and sub-adults. Gut contents were also collected on any other incidental species caught during electrofishing.

Contents were funneled into a labeled collecting jar and preserved in dilute Formalin until sorted and identified. Stomach flushing allowed the collection of stomach contents from a large number of fish while keeping fish mortality to a minimum. All fish were allowed to recover in the bucket before being transferred back to the stream. In the lab, stomach contents were sorted with a microscope at 20x magnification and measured with a micrometer to the nearest millimeter. Individuals were identified to the lowest taxonomic level possible (typically family) and categorized as either terrestrial or aquatic in origin. Only individuals with exclusively terrestrial life stages were counted as terrestrial. Aerial stages of aquatic insects were categorized as aquatic. Terrestrial invertebrate prey was presented as the dry-mass fraction of total dry mass invertebrate prey per fish. Fractions of terrestrial prey for individual fish were then averaged over sampling date and site.

Additionally, relative condition factors were calculated for all fish that were collected and lavaged using Fulton's condition factor (K) (eds. Moyle & Cech 2004), such that $K=(W \cdot L^{-3}) \cdot 10^3$ where W is weight in grams, L is length in millimeters and 10^3 is a scaling factor.

Objective (ii) Quantify seasonal availability of terrestrial and aquatic prey both within the stream and falling into the stream from the terrestrial habitat.

Terrestrial invertebrate inputs to the stream

Abundance and composition of invertebrates falling into the stream were measured using floating surface-pan traps. Although we recognize the limitations associated with this method (see Wipfli 1997), it is a commonly used method and currently lacks an effective alternative. Furthermore, this method was met with increased

difficulty on the Kol River due to the significant bear activity and frequent destruction of traps.

Four 12 x 14 inch (0.108m²), opaque, plastic, surface-pan traps per site were deployed 3 times between June and October 2006 (more were attempted but the traps were destroyed by bears). The traps were filled with a saturated salt solution and a few drops of vegetable glycerin which served as an odorless surfactant to aid in trapping insects. The traps were attached to the stream bank with wooden stakes and deployed for a period of 5 days and 5 nights. Upon collection samples were filtered and concentrated in a bolus net and preserved in dilute formalin until identification. Terrestrial inputs are presented as mg/day/m², and aerial forms of aquatic insects were not included in this estimate.

Benthic Invertebrates

Availability of aquatic prey was estimated two times during the study period via benthic invertebrate collections using a Stanford-Hauer kicknet (250 µm). Samples were collected from 3-5 randomly selected riffle locations within the stream reach. A 0.25m² metal frame was placed on the stream bottom with the net just downstream, and the substrate was disturbed for 1 minute. The sample was then filtered with the bolus net and preserved in dilute formalin. In the lab the entire sample was macro-picked for large and rare individuals. Then 1/24 portions of the sample were picked with a microscope at 20x magnification until at least 200 individuals had been counted and identified.

Drifting Invertebrates

In order to assess the availability of prey drifting in the water column drift nets were deployed on 6/29/06 and 6/30/06 to examine the potential prey available to fish in the drift. Four drift nets (0.25 m × 0.45 m opening, 125-µm mesh) were deployed per site 3 times per 24 hours: once at dawn, noon, and dusk (true night drift was not collected due to bear activity and river navigation difficulties). These times were chosen because prey availability is difficult to ascertain from drift samples and these different sample times would provide a range of estimates. Dusk and dawn drifts were expected have the highest abundance and diversity of organisms due to behavioral nocturnal drifting of macroinvertebrates. The noon drift was expected to be lower in abundance and diversity.

Drift nets were deployed in the middle of the riffle, usually mid channel, or in such a way to receive the largest inflow with two nets at the top of the reach and two nets at the bottom of the study reach. Nets were suspended in the water column slightly above the stream bottom to prevent insects from crawling into the net. Also, the top lip of the net was set to extend just above the surface of the water to catch insects that were drifting on the surface. Nets were deployed for approximately 20 minutes each, and exact time of deployment and removal was recorded. Point velocity measurements were taken immediately upstream from the net during the deployment, and the depth of water flowing into the net was recorded (net bottom to water surface) in order to estimate the volume of water flowing through the net over the recorded time.

Upon removal, collected samples were carefully removed from the drift net with special attention to animals that may be clinging to the net. The sample was then concentrated in a bolus net and preserved in a labeled vial with dilute Formalin. In the lab, the entire sample was macro-picked for any large and rare individuals. Then a 50% sub-sample was micro-picked with a microscope, and the individuals were sorted, enumerated, dried and weighed. Biomass of drifting invertebrates is presented as $\text{mg}\cdot\text{m}^{-3}$.

Objective (iii) Assess differences in terrestrial insect community assemblages in association with two different forest successional stages.

Invertebrates associations with riparian vegetation

Sticky traps were deployed to determine relative diversity of terrestrial insects and community assemblages in association with the different vegetation types. Five yellow sticky traps per site were deployed for a period of five days, four times throughout the season. Traps were hung at a uniform height (~3m) from randomly selected trees along the stream bank. Although there are issues with sticky traps being a potential attractant for certain species, they were useful to estimate catch per unit area at each site.

Sweep net samples also were collected to estimate relative diversity and abundance of terrestrial insects. The sweep samples were collected for seven minutes five times per site throughout the season. Attempts were made to ensure that samples were taken at approximately the same time of day and under similar weather conditions (aside from unavoidable seasonal variations). Any large leaves collected in the sweep

were inspected for insects and then discarded. The samples were labeled and preserved in dilute Formalin until they were sorted and enumerated, and individuals were dried and weighed.

In order to assess the association of the willow catkin-dwelling Curculionidae larvae (order: coleoptera) with different willow species, willow catkins were collected from the stream bank and inspected for larva. Catkins were collected from the ground at Hollywood spring brook (where both species of willow coexist) from inside a randomly placed 0.25 m² square frame for a total of 21 separate collections. In the lab, the catkins were divided by species and checked for evidence of larvae. The presence of “larval tunnels” was counted as evidence of larvae. In this case it is presumed that the larva had crawled out already.

Additionally, catkins were floated in a bucket of water and observed, in order to determine the mode of deposition into the stream of the Curculionidae larva,. Thirty-eight large willow catkins collected randomly from trees at Hollywood spring brook were placed in a bucket of river water. Daily counts were made of the number of larvae that crawled out of the catkins and fell to the bottom (presumably what would be available to fish). After two weeks, all catkins were collected and examined for larva remaining inside.

Sample Analysis

All aquatic and terrestrial invertebrates were identified to the lowest taxonomic level possible (typically family) using Merritt and Cummins' *Introduction to the Aquatic Insects of North America, How to Know the Insects* (eds. Bland and Jaques), *Borror and DeLong's Introduction to the Study of Insects* (eds. Triplehorn and Johnson), and McCafferty's *Aquatic Entomology*. However, difficulties with identification of partially digested prey items and identification of certain Diptera families prevented this taxonomic resolution in some cases. A reference collection including each invertebrate species was compiled, preserved and sent to Dr. Ruslan Butovsky, a Russian invertebrate specialist from Moscow State University, for identification confirmation.

Individual invertebrate biomass estimates were acquired through collections of live invertebrates. Individuals (often from benthos or sweep samples) were enumerated,

dried for 24 hours at 60°C, and weighed to the nearest 0.1mg. Biomass for individuals that could not be collected in large enough numbers for weighing were estimated via published length- weight regressions (Rogers et al. 1977; Meyer 1989; Sample et al. 1993; Burgherr & Meyer 1997; Benke et al. 1999). Dry mass estimates (calculated or measured) were used in the diet, terrestrial input, benthic macroinvertebrate and drift components of this study.

For fish diet, terrestrial invertebrates are presented as a fraction of total invertebrate dried biomass. Fish with completely empty stomachs (rare) were excluded from the analysis. All aerial forms of aquatic insects were considered aquatic. Unidentifiable invertebrates or those of unknown origin (mostly Diptera) were included in the total biomass, but were not attributed to the terrestrial or aquatic category. At times this subset comprised 29% of the diets but on average comprised only 10% of the diet. Terrestrial-dwelling forms of aquatic invertebrates were not included in the estimates of terrestrial invertebrate inputs into the stream which is presented as $\text{mg}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$.

Statistical Analysis

Proportion of terrestrial invertebrates in fish diets, terrestrial invertebrates falling into the stream, drifting invertebrates and benthos were analyzed with one-way ANOVA and *t*-tests. All statistical tests were two-tailed. Arcsine square-root transformations for proportional data and Log_{10} transformations for exact values were performed in order to standardize variances and improve normality where necessary to meet the assumptions of ANOVA and *t*-tests. For all tests, alpha was set at 0.05 for statistical significance.

Results

Fish diet analysis

Juvenile coho and Dolly Varden both ate a variety of prey items that included both terrestrial and aquatic organisms from 16 different orders of invertebrates. The mean dry mass of total prey ingested per fish by both species across both sites was 13.9 ± 0.02 mg (mean \pm 1 standard error). When averaged across both sites, for the entire season, approximately 46% of the ingested prey for coho was of terrestrial origin and 41% was aquatic in origin (the remaining 13% was prey that could not be attributed to

aquatic or terrestrial origin with the given level of taxonomic resolution). On the other hand, only 13% of Dolly Varden prey was of terrestrial origin and 80% was aquatic (Fig. 4).

We tested for cohort differences within species between young of year and sub-adults using independent sample *t*-tests and found no significant difference except for coho on two sampling dates. On August 25, 2006 in Fuzzy spring brook and September 25, 2006 in Hollywood spring brook the young of year coho ate a significantly smaller proportion of terrestrial invertebrates than the older fish ($p=0.004$ and $p<0.001$ respectively). Ultimately, the most significant differences were between the coho and Dolly Varden species, regardless of cohort.

The fraction of terrestrial invertebrates found in the diets varied significantly between the two species, as coho diet comprised of a significantly larger proportion of terrestrial invertebrates (0.46 ± 0.02 , $n=617$) than Dolly Varden (0.13 ± 0.01 , $n=367$) when averaged over the entire study period for both sites and compared with an independent sample *t*-test ($p<.001$).

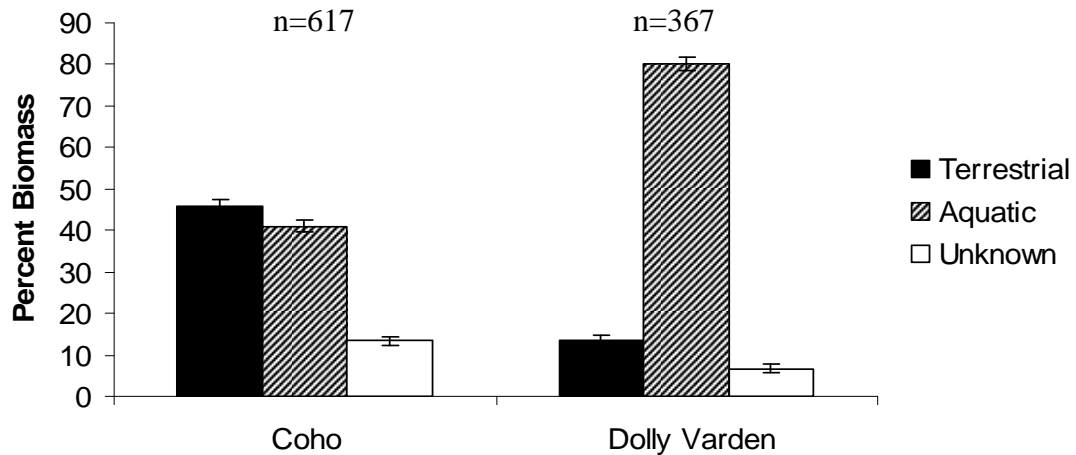


Fig. 4 Average percent biomass of invertebrate prey for all sampling dates Hollywood and Fuzzy spring brooks, June- October 2006. Bars represent one standard error of the mean.

The fraction of terrestrial invertebrates found in the diets of coho varied significantly between the two sites. Coho in Hollywood spring brook had a significantly

higher fraction of terrestrial invertebrates in their diet in the spring (0.56 ± 0.07 , $n=28$) than coho in Fuzzy spring brook in the spring (0.14 ± 0.05 , $n=28$) ($p < .001$). On the other hand, in the summer Fuzzy coho had significantly higher terrestrial fraction in their diets (0.39 ± 0.03 , $n=130$) when compared to Hollywood (0.25 ± 0.03 , $n=133$) ($p=0.001$). Terrestrial percentages were highest for both sites in the fall, but there was no significant difference in coho diets between the two sites in the fall (Fig. 5).

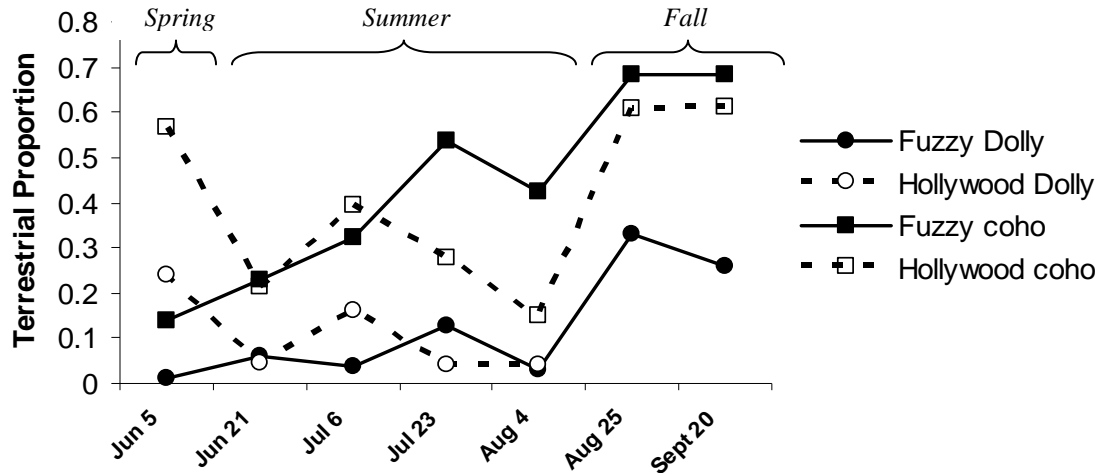


Fig 5 Proportion of fish diet composed of terrestrial invertebrates for individual sampling dates for Fuzzy spring brook coho and Dolly Varden and Hollywood spring brook coho and Dolly Varden.

Results also suggest a seasonal variation in the fraction of diet that is composed of terrestrial invertebrates for coho. In Hollywood, in the spring and fall, terrestrial invertebrates made up over 56% (0.56 ± 0.07) of the invertebrate diet on average, whereas in the summer only about 25% (0.25 ± 0.03) of the diet was composed of terrestrial invertebrates (Fig. 6a). However, the seasonal variation at Hollywood did not demonstrate a significant difference. On the other hand, Fuzzy spring brook had a lower percentage in the summer and the highest was in the fall with over 60% of the diet being terrestrial invertebrates during that time. Each of the three seasons at Fuzzy was significantly different from the other (Fig. 6b).

For both sites, fall was the season with the highest terrestrial subsidy to the diet (Fuzzy 0.68 ± 0.04 , $n=86$ and Hollywood 0.61 ± 0.03 , $n=135$) (Fig. 5). The greatest difference between the two sites occurred in the spring when fuzzy coho had a diet composed of

14% (0.14 ± 0.05 , $n=28$) terrestrial invertebrates and Hollywood coho diets were 56% terrestrial ($0.56 \text{ SE}=0.07$, $n=28$). The higher percentages of terrestrial invertebrates in the spring-time diet at Hollywood spring brook can be attributed almost entirely to the catkin-dwelling Curculionidae larva (order: Coleoptera). The terrestrial portion was comprised almost entirely of Curculionidae, 92% for coho and 98% for Dolly Varden. However, Curculionidae did not play a major role in the diet of fish at Fuzzy Spring brook.

The diets of Dolly Varden did not differ significantly between sites or season as aquatic invertebrates were the primary food source at all times for this species (see Figs. 6c,d).

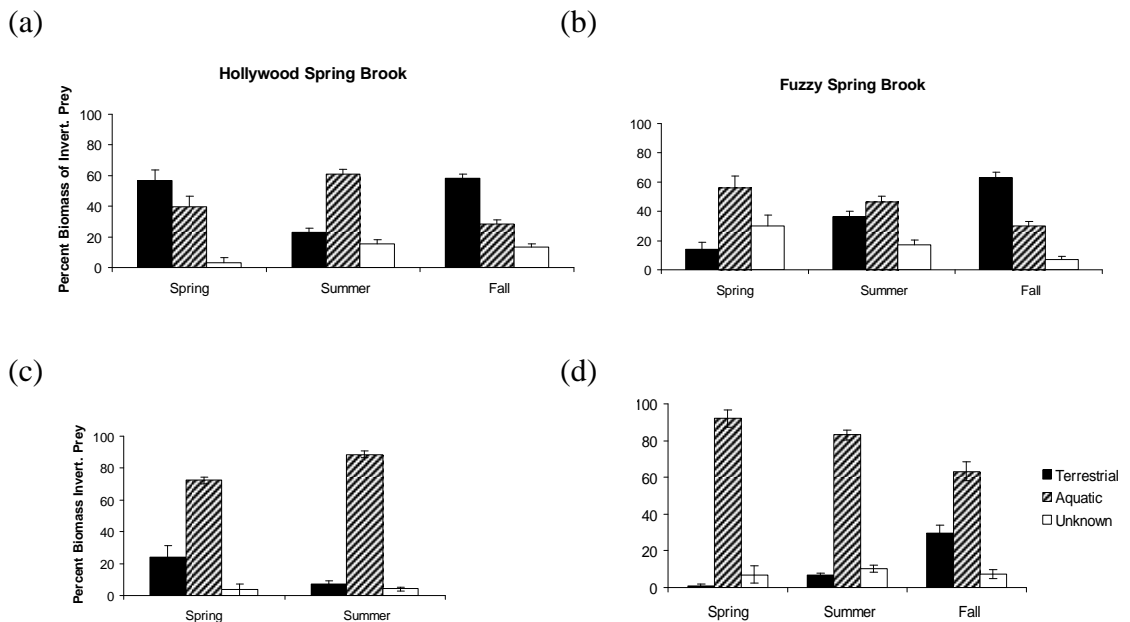


Fig. 6(a-d) Percent Biomass of Invertebrate Prey in (a) coho in Hollywood spring brook, (b) coho in Fuzzy spring brook, (c) Dolly Varden in Hollywood springbrook, (d) Dolly Varden in Fuzzy Spring brook. (note: No Dolly Varden were found in Hollywood spring brook in the fall sampling). Bars represent one standard error of the mean.

Analysis of Fulton's relative condition index suggests that both species of fish are most robust in the summer. Although, robustness appears to be lower in the spring and fall, fish appear to be doing well in the spring brooks and are equally or more robust at the end of the season as at the beginning (Fig. 7).

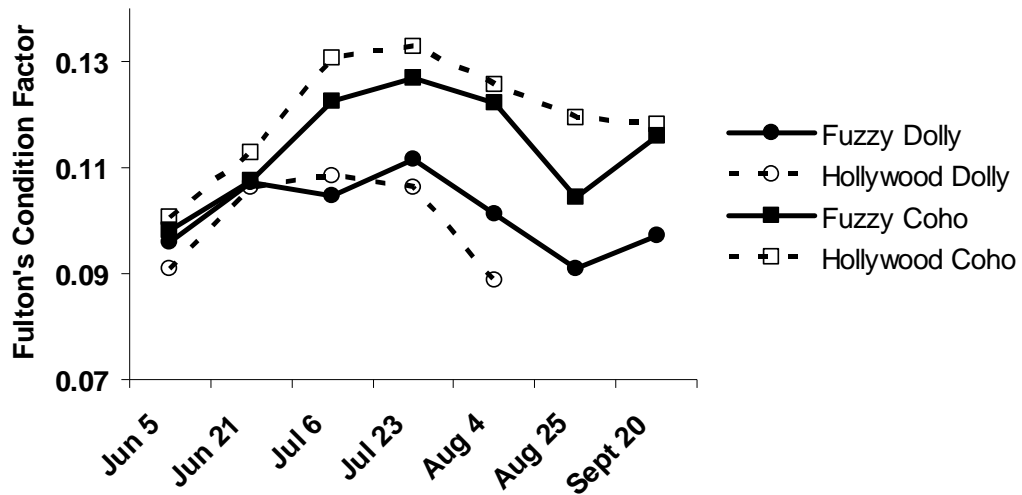


Fig. 7 Fulton's relative condition index for Coho and Dolly Varden in Fuzzy and Hollywood spring brooks, such that $K=(W \cdot L^{-3}) \cdot 10^3$ where W is weight in grams, L is fish fork length in mm, and 10^3 is a scaling factor.

Fish in the main channel were sampled on only one occasion on August 16, but results suggest that diets for main channel fish are primarily aquatic. Main channel coho diet was composed of significantly less terrestrial invertebrates (0.16 ± 0.01 , $n=34$) as compared to coho during the closest sample period at the two spring brook sites (0.64 ± 0.003 , $n=101$) ($p < .001$), and Dolly Varden collected in the main channel consumed 100% aquatic prey (Fig. 8).

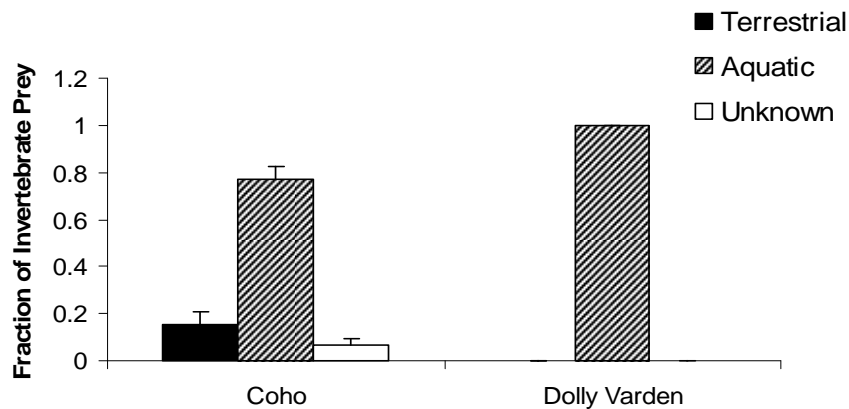


Fig. 8 Fraction of invertebrate prey in coho, Dolly Varden collected in the main channel on August 16, 2006. Bars represent one standard error of the mean.

Although the primary focus of this study was on coho and Dolly Varden we did collect gut contents on any of the alternative species that were caught during the sampling of Fuzzy and Hollywood spring brooks. Sockeye, Cherry, and Chum salmon all appear to be consuming primarily terrestrial invertebrates, although, sample sizes should be noted. White-spotted charr appear to be consuming more terrestrial invertebrate, however, the sample size (n=2) is inadequate to make accurate generalizations (Fig. 9).

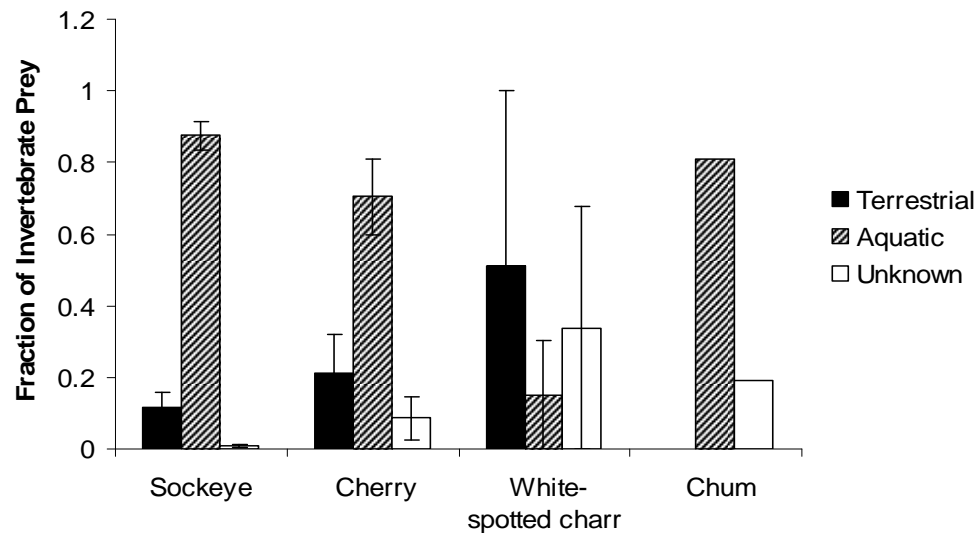


Figure 9 Average fraction of invertebrate prey in sockeye salmon (n=44), cherry salmon (n=8), white-spotted charr (n=2), and chum salmon (n=1) for all sampling events June-October 2006.

Terrestrial invertebrate inputs

Representatives from eleven orders of invertebrates were found in the float pan traps. Diptera was the most abundant Order making up 44.2% of the total biomass captured. Of all invertebrate taxa captured in the float pan traps 62% were of terrestrial origin and 28% were aquatic in origin (remaining could not be classified as terrestrial or aquatic at the given taxonomic resolution).

The estimates suggest peaks for terrestrial invertebrate inputs at both sites occurring in July, and comparison between sites suggests slightly higher inputs at Fuzzy for all three sampling dates. However, these differences were not found to be significant. No significant differences were encountered between sites or sampling dates (Fig. 10). The estimated dry biomass of terrestrial invertebrate inputs into the stream averaged over

the entire season for both sites is $22.2 \pm 0.8 \text{ mg}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$ (mean \pm 1 standard error of the mean). This estimate excludes aerial forms of aquatic invertebrates.

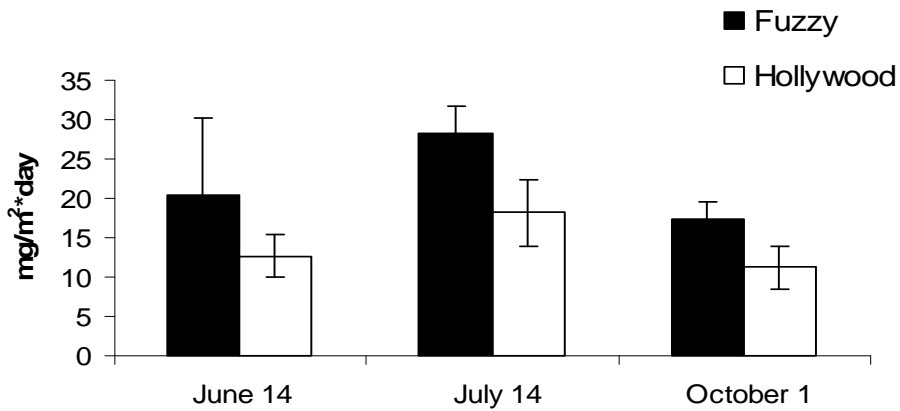


Fig. 10 Estimates of terrestrial invertebrate falling from the canopy into Hollywood spring brook (early succession site) and Fuzzy spring brook (late succession site). Bars represent one standard error of the mean.

Benthic Invertebrates

Benthic invertebrate biomass was less than $26,000 \text{ mg}/\text{m}^2$ for both sites in spring and summer, and Fuzzy spring and summer and Hollywood summer benthic biomass was below $4,620 \text{ mg}/\text{m}^2$. Estimates of benthic invertebrates suggest greater benthic biomass in Fuzzy in June and greater in Hollywood in September (Fig. 11). However, no significant differences were found between sites or seasons.

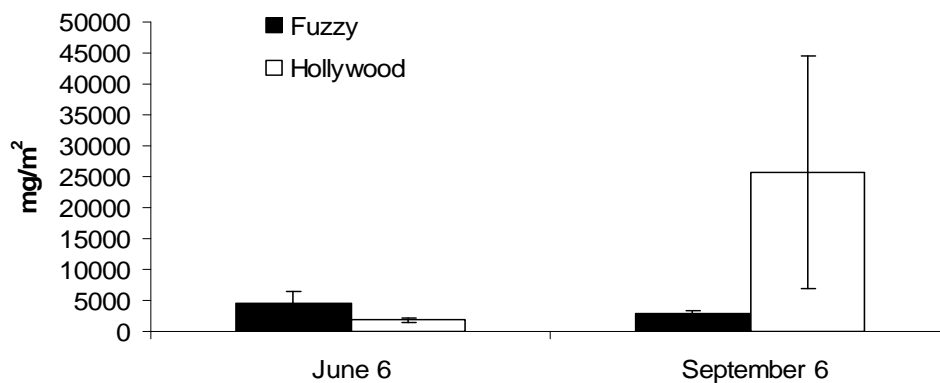


Fig. 11 Biomass of benthic invertebrates during two dates at Hollywood and Fuzzy Spring brooks. Bars represent one standard error of the mean.

Drifting Invertebrates

Estimates suggest that the average drifting biomass at dawn is lower for Fuzzy spring brook ($0.313 \pm 0.17 \text{ mg/m}^3$, mean \pm standard error) than for Hollywood ($1.03 \pm 0.25 \text{ mg/m}^3$). Fuzzy also had a lower drift ($0.33 \pm 0.27 \text{ mg/m}^3$) than Hollywood ($0.76 \pm 0.35 \text{ mg/m}^3$) for the dusk drift. However, differences between the two sites and between the sampling times were not significant (Fig. 12).

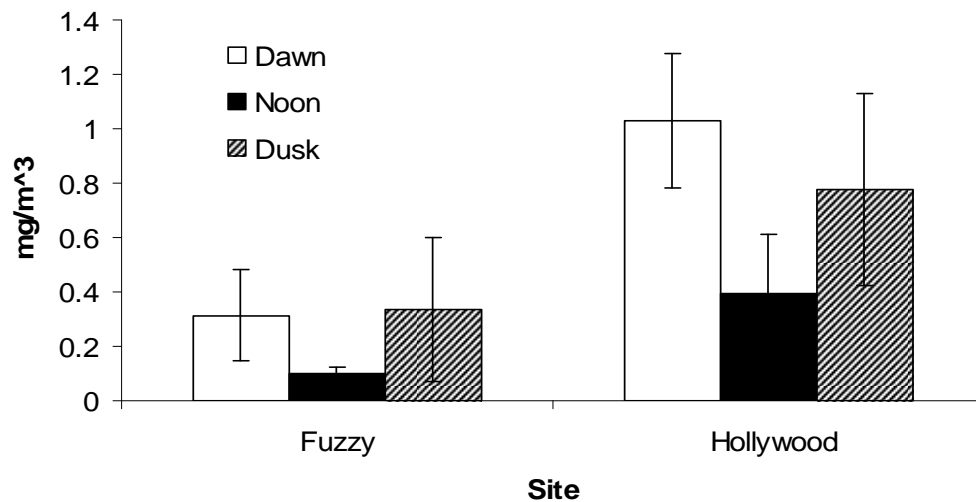


Fig. 12 Biomass of drifting invertebrates ($\text{mg} \cdot \text{m}^{-3}$) at Hollywood and Fuzzy spring brooks sampled at dawn, noon, and dusk. Error bars represent one standard error of the mean.

Terrestrial invertebrate association with riparian vegetation

Of all invertebrate taxa collected in sweep nets or sticky traps, 93% were found at both sites (and most of the taxa that were found at only one of the sites were rare), suggesting no significant differences in the terrestrial invertebrate communities of the two sites. However, significant differences were found in the abundance of invertebrates caught at the two sites. Abundance of invertebrates caught in the sticky traps and sweep nets was consistently higher at the early succession site, Hollywood spring brook, throughout the season (Figs. 13a,b).

Of all collected taxa, 33.8% were present each of the four sample types: float pans, fish diets, sweep sample, and sticky traps. Of that 26.9% of the taxa were aquatic in origin and 61.5% were terrestrial. Another 6.5% of taxa were found in sweep and

sticky traps, but did not occur in the diet (however, all but one of these taxa were found in the float pans implying that they are reaching the water surface, but were not eaten by the fish), and 2.6% of all terrestrial taxa were found in diet, but not in the sweep samples (see Appendix A).

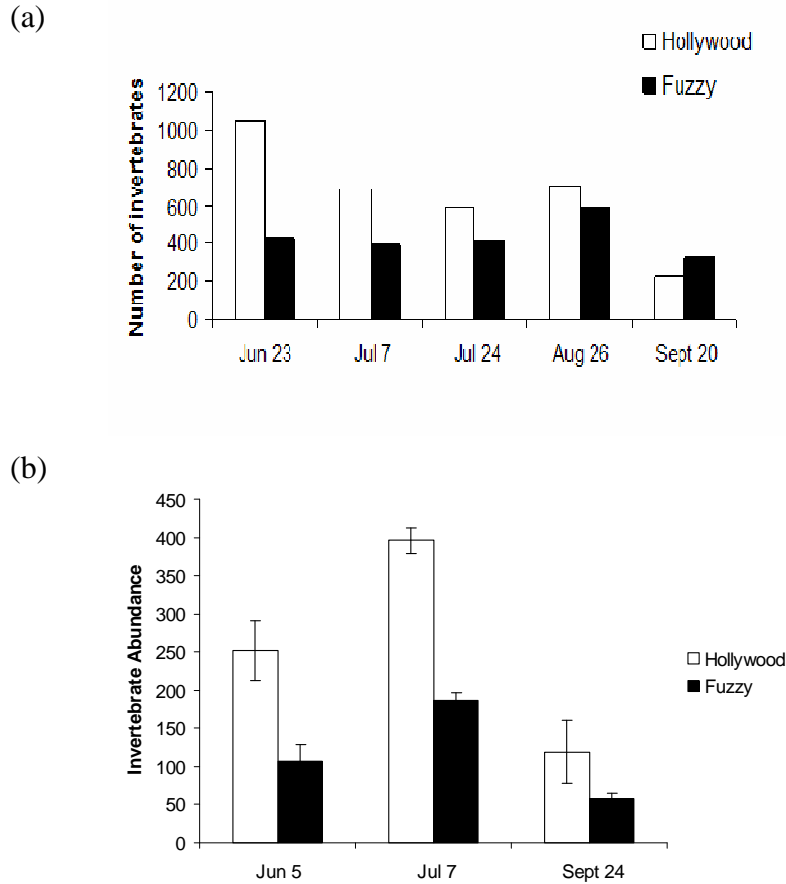


Fig. 13(a-b) Abundance of invertebrates caught by (a) sweep samples (n=1 per site and date) and (b) sticky traps (n=5 per site and date) at Hollywood and Fuzzy spring brooks. Bars represent one standard error of the mean.

The abundance of Curculionidae larvae that live in the willow catkins also varied significantly between the sites. The early succession willow species (only present at Hollywood) is much more likely to host the larva (71.5% larval presence) than the late succession willow species (31.8% presence). Additionally, of the early succession willow catkins that did not have evidence of the larva most were immature and smaller than 15mm which is potential too small for the larva. Both of the willow species are

present earlier in succession (e.g. Hollywood spring brook), but only the late succession species persists later in succession (Fuzzy spring brook) (Morris, unpublished data), and this difference showed up in the fish diets. The larva was an important part of the spring coho diet at Hollywood spring brook, where the larva made up 92% of the terrestrial portion for coho and 98% for Dolly Varden, but it did not play a significant role at Fuzzy spring brook (Figs. 6a-d).

In the experiment where we placed catkins in a bucket of river water, we found that after one week, all 38 of the catkins remained floating on the surface, but 28 Curculionidae larvae were found on the bottom of the bucket. After two weeks, only 5 of the catkins had become saturated and sunk to the bottom of the bucket, and when the catkins were cut open and examined we found an additional 68 larva that remained in the catkins.

The local spring time estimate for Curculionidae inputs to Hollywood spring brook is 23.5 mg/m^2 . However, this is probably an underestimation as it assumes that catkins that have the larva only have one larva, whereas many catkins have more than one larva in them and sometimes as many as five per catkin.

Discussion

Terrestrial invertebrates are an important subsidy to the diet of juvenile salmonids in the spring brooks on the Kol floodplain, and they contribute a significant energy supply during the growing season of these young fish. Our results suggest that this subsidy is especially important in the fall when terrestrial invertebrates make up 60-70% of the diet for coho. Also, the spring when terrestrial invertebrates were a significant food source at only one of the sites, the terrestrial proportion was attributed almost entirely to one unlikely prey item, the catkin-dwelling Curculionidae larva (Fig. 14). These results provide a good example of how floodplain successional



Fig. 14 Curculionidae larva in a willow catkin

patterns can influence the feeding habits of fish, further strengthening the link between terrestrial and aquatic environments. This prey item is of particular interest because the larva's inhabitation in willow catkins does not suggest it would be available as prey for fish. Additionally, our experiment demonstrated that the larvae continue to thrive within the catkin long after the catkin has fallen into the water (larvae appear to survive until they crawl out of the catkin and into the water). This suggests that the larva could be providing a steady food source long after the catkins have fallen into the water.

One of the sites, Hollywood, has a forest that is characteristic of earlier succession stages (~20 years) which has a mix of two willow species. On the other hand, Fuzzy spring brook has much older riparian forest (~80 years) with a forest community representative of a later succession stage when one of the willow species has died out (Fig. 15; Morris, unpublished data). Interestingly, the early succession willow species that dies out in the later successional stages is much more likely to host Curculionidae larva.

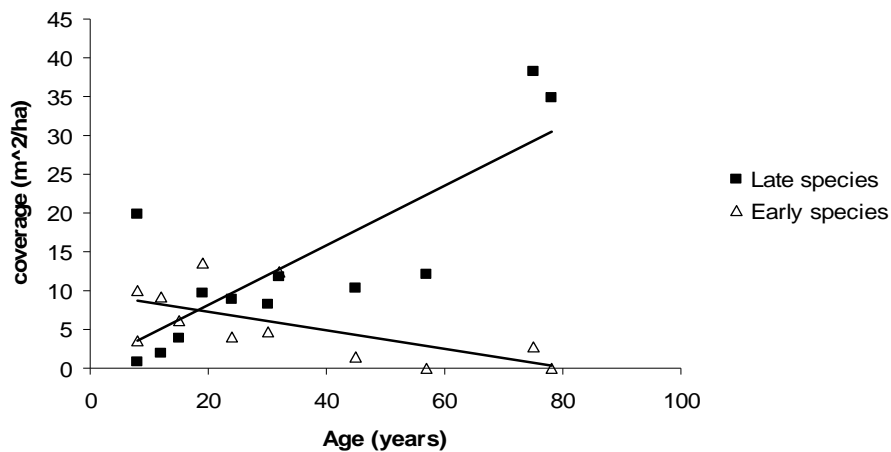


Fig. 15 Willow coverage across succession on the Kol floodplain in Kamchatka Russia. Late species ($y = 0.3846x + 0.477$, $r^2 = 0.6396$) and Early species ($y = -0.1186x + 0.3992$, $r^2 = 0.3992$) (Morris, unpublished data).

One potential reason that the larvae do not inhabit the late succession willow species could be the difference in the width of the catkin pithe, because the early succession species has a wider pithe than the late. However, this study did not further investigate the nature of the species associations. The difference in the forest community structure with respect to succession had a significant impact on the feeding of the fish

within those sites. Curculionidae played a major role in the diets of fish at Hollywood in the spring where both willow species are present, whereas fish were much more dependent on aquatic invertebrates at Fuzzy in the spring, where the Curculionidae were not as abundant in the willows. The differences in the abundance of this species suggest a link between the heterogeneity of riparian vegetation with respect to floodplain succession and the variation in the feeding of fish.

Moreover, a study by Kawaguchi (2003) experimentally reduced terrestrial invertebrate inputs into a stream, which resulted in a dramatic increase in salmonid emigration. This study coupled with a study by Kawaguchi and Nakano (2001), which links riparian vegetation type to spatial heterogeneity in terrestrial invertebrate inputs and fish biomass suggest that local distribution and abundance of salmonids could be at least partially controlled by heterogeneity in terrestrial invertebrate subsidies, and that vegetation type could influence local and seasonal abundance of salmonids. Correlations between the variation of the terrestrial invertebrate inputs and the variation of fish densities merit further investigation and could help to explain the movement of fish in and out of spring brooks throughout the season.

The results of our study also demonstrate a partitioning of resources among coexisting species, as terrestrial invertebrates appear to be much more important to coho than to Dolly Varden in both Hollywood and Fuzzy spring brooks. These differences are due, at least partially, to differences in foraging behavior and microhabitat use between the coho and Dolly Varden (Nakano & Kaeriyama 1995) and can help account for their coexistence. This partitioning of resources coupled with the terrestrial invertebrate subsidy may help explain why these shallow fringe environments are preferred habitat for many juvenile salmonids.

We also found significant seasonal variation in the use of this subsidy as a prey for juvenile fish. Terrestrial invertebrates were most important in the fall at both sites and were also significantly more important in the spring at Hollywood spring brook where we found significant inputs of Curculionidae larva. Additionally, the fact that 93.5% of all invertebrate taxa collected in sweep nets and sticky traps were also found in the diets of fish suggests that the fish are taking full advantage of all of the available invertebrates.

Comparison of Fulton's relative condition factor suggests that fish the most robust in the summer, and all fish at both sites were equally if not more robust at the end of the season as they were at the beginning (Fig. 8). However, although the apparent decrease in robustness from summer to fall could suggest decreasing condition, the results of the condition index are confounded due to the migration of fish in and out of the spring brooks. We cannot assume that the fish sampled in one season are the same fish sampled in the next. In addition, the natural growth of the fish could result in a normal rise and fall in the condition index as fish increase in length or increase in girth as they grow.

We were not able to detect significant seasonal or site difference in the input of terrestrial invertebrates into the streams because our sampling tools were repeatedly destroyed by bears which severely limited the number of sampling events and the number of replications we were able to obtain per sampling event. However, the seasonal differences in the presence of terrestrial invertebrates in the diets of fish could suggest potential seasonal differences in the inputs of this subsidy.

Nonetheless, estimates of terrestrial invertebrate inputs are comparable to estimates on the headwater streams of the deciduous River Nethy drainage in Scotland (spring 21.2, summer 26.8, fall 19.5 $\text{mg}\cdot\text{d}^{-1}\cdot\text{m}^{-2}$) (Birdcut 2000). On the other hand, they are much lower than those reported for third order, deciduous forest streams of the eastern U.S. (spring 5-78, summer 50-450, fall 20-50 $\text{mg}\cdot\text{d}^{-1}\cdot\text{m}^{-2}$) (Cloe & Garman 1996) and the deciduous headwater stream in Japan studied by Nakano and Murakami (2001) (spring 14, summer 63.3, fall 74 $\text{mg}\cdot\text{d}^{-1}\cdot\text{m}^{-2}$) (see Baxter et al. 2005 for a review). However, it should be noted that these sites represent much warmer biomes with longer growing seasons, where we might expect greater inputs of terrestrial invertebrates.

The low estimates for drifting invertebrate biomass and benthic invertebrates, could suggest a simple lack of invertebrates in the stream, or that invertebrates are consumed by fish before they can be caught in the nets. However, it is important to note that the low biomass estimates do not necessarily suggest a lack of productivity in these sites. Some invertebrates, such as chironomids, have a particularly fast turnover time that could result in benthic productivity not being accurately reflected in benthic samples. In any case, the low biomass of drifting invertebrates coupled with high densities of fish could suggest a dependency on an external subsidy. The importance of terrestrial

invertebrates is further supported by the fact that often the aquatic invertebrates that are preferable aquatic prey items are nocturnal and therefore potentially less available while fish are feeding (Nakano et al. 1999b).

This study was not intended to be a comparison of spring brooks to main channel, however, our data suggests that terrestrial invertebrates may not be as important to fish in the main channel (Fig. 8), and studies that link canopy cover to terrestrial invertebrate inputs into streams suggests less terrestrial inputs into main channel environments (Baxter et al. 2005). A comparison between diets of fish in spring brooks to main channel fish merits further investigation and could further emphasize the importance of spring brooks as nurseries for juvenile fish and crucial sites for salmonid production.

Conclusion

By demonstrating that terrestrial invertebrates are an important food source for spring brook salmonids, this study highlights an important link between terrestrial and aquatic systems in floodplain habitats. In addition, we further define that link by describing the seasonal variation in the terrestrial invertebrate subsidy and linking it to riparian vegetation types that correspond to varying stages of succession on the Kol River. These findings raise important concerns when dealing with the management of riparian areas particularly in floodplains with regard to salmonid production.

This study supports the understanding that spring brooks are important habitats to salmonid production, and by evaluating the link between the terrestrial and aquatic habitats, it highlights the importance of habitat interfaces as vital habitats for salmonid production and priorities for conservation. Our results also emphasize the importance of quality habitat by demonstrating the functional role of the habitat in providing food sources which help to maintain the abundance and diversity of salmonids. Furthermore, understanding the link between the terrestrial and aquatic habitats is crucial to the implementation of proper management practices and conservation. This study demonstrates how the quality and type of riparian habitat and the related management practices could have major implications for within-stream feeding behavior and juvenile salmon production.

Degradation of riparian systems and the introduction of exotic species can cut off the flow of energy and resources which can have devastating effects on both the aquatic and terrestrial communities (Polis et al. 1997a; Baxter 2004). Changes in the terrestrial or aquatic community assemblages could have significant impacts of the flow of resources between the systems, and without an understanding of that flow of resources the impacts of habitat degradation on food webs could be much greater than we would expect. In the case of the salmonids on the Kol River, if the terrestrial invertebrate subsidy was cut off, it could have devastating effects on the salmon production of that river. This critical understanding of the flow of energy between two systems demonstrates how disturbances and management practices in one system could have major impacts on neighboring systems, and it emphasizes the importance of maintaining connectivity not just within a system but also between neighboring systems.

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Appendix A. List of invertebrate taxa and presence of invertebrate taxa in collections of different sampling techniques and definition as terrestrial, aquatic or unknown

| | Taxa | sweep | sticky | float | diet | Terr./Aqua. |
|---------------|-----------------------|--------------|---------------|--------------|-------------|--------------------|
| Arachnida | Acari | | | x | x | A |
| Arachnida | daddy long legs | x | | | x | T |
| Arachnida | Spiders | x | x | x | x | T |
| Coleoptera | Cantharidae | x | | x | x | T |
| Coleoptera | Carabidae | x | | x | x | T |
| Coleoptera | coleoptera unknown | x | x | | x | U |
| Coleoptera | Curculionidae | x | x | x | x | T |
| Coleoptera | Dytiscidae | | | | x | A |
| Coleoptera | Hydrophilidae | | | | x | A |
| Coleoptera | Scolytidae | | | x | x | T |
| Coleoptera | Staphylinidae | x | x | x | x | T |
| Collembola | Collembola | | | x | x | U |
| Copepoda | Copepoda | | | | x | A |
| Diptera | Anthomyiidae | x | | x | X | T |
| Diptera | Axyiidae | x | x | x | x | T |
| Diptera | Bibionidae | x | x | x | x | T |
| Diptera | Ceratopogonidae | x | x | x | x | A |
| Diptera | Chironomid | x | x | x | x | A |
| Diptera | Culicidae | x | x | x | x | A |
| Diptera | diptera unknown | x | x | x | x | U |
| Diptera | Dixidae | | | | x | A |
| Diptera | Dolichopodidae | x | x | x | x | U |
| Diptera | Empididae | x | x | x | x | U |
| Diptera | Lauxaniidae | x | | x | x | T |
| Diptera | Lonchoptera | x | x | x | x | T |
| Diptera | Muscidae | x | x | x | x | T |
| Diptera | Mycetophilidae | x | x | x | x | T |
| Diptera | Phoridae | x | | x | x | T |
| Diptera | Pipunculidae | x | | | x | T |
| Diptera | Rhagionidae | x | x | x | x | T |
| Diptera | Sciaridae | x | | | x | T |
| Diptera | Sciomyzidae | x | x | | x | T |
| Diptera | Sepsidae | x | | | x | T |
| Diptera | Simulidae | x | | | x | A |
| Diptera | Sphaeoceridae | x | | | | T |
| Diptera | Stratiomyiidae | | | x | x | T |
| Diptera | Tabanidae | x | x | | x | A |
| Diptera | Tipulid | x | x | x | x | A |
| Ephemeroptera | Baetidae | | | x | x | A |
| Ephemeroptera | Ephemerellid | | | | x | A |
| Ephemeroptera | Ephemeroptera unknown | x | | x | x | A |
| Ephemeroptera | Heptegeniidae | | | | x | A |

| | | | | | | | |
|---------------|------------------------------|---|---|---|---|---|---|
| Ephemeroptera | Siphonuridae | | | | | x | A |
| Hemiptera | Anthocoridae | x | x | x | x | | T |
| Hemiptera | Cicada | | x | x | x | | T |
| Hemiptera | Cicadellidae(leaf hopper) | x | x | x | x | | T |
| Hemiptera | Hemiptera | x | x | x | x | | T |
| Hemiptera | Psyllidae | x | x | x | x | | T |
| Hemiptera | Reduviidae | x | x | x | x | | T |
| Hemiptera | Aphidae | x | | x | x | | A |
| Hymenoptera | Braconidae | | | | | x | T |
| Hymenoptera | Cecidomyidae | | | x | | | T |
| Hymenoptera | Cynipidae | | | x | | | T |
| Hymenoptera | Hymenoptera | | x | | | x | T |
| Hymenoptera | Ichneumonid | x | x | x | x | | T |
| Hymenoptera | Scelionidae | | | x | | | T |
| Hymenoptera | Tenebrionidae | | | | | x | T |
| Hymenoptera | Tenthredinidae | x | x | x | x | | T |
| Lepidoptera | Caterpillar | x | | x | x | | T |
| Lepidoptera | Moth | x | x | x | x | | T |
| Nematoda | Nematoda | | | | | x | A |
| Oligochaeta | Oligochaeta | | | | | x | U |
| Ostracoda | Ostracoda | | | | | x | A |
| Plecoptera | Capniidae | x | x | x | x | | A |
| Plecoptera | Chloroperlidae | x | x | x | x | | A |
| Plecoptera | Nemouridae | | | | | x | A |
| Plecoptera | Plecoptera unknown | | | | | x | A |
| Psocoptera | Psocoptera | | | | | x | T |
| Trichoptera | Brachycentridae | | | | | x | A |
| Trichoptera | Glossosomatid | | | | | x | A |
| Trichoptera | Hydropsychidae | | | | | x | A |
| Trichoptera | Lepidostomatidae | | | | | x | A |
| Trichoptera | Leptoceridae | | | | | x | A |
| Trichoptera | Limnephilidae | | | x | x | | A |
| Trichoptera | Rhyacophilidae | | | x | | | A |
| Trichoptera | Trichoptera | x | x | x | x | | A |
| Unknown | unknown Larva (#49) | x | | x | x | | U |