

Effects of habitat and internal prey subsidies on juvenile coho salmon growth: implications for stream productive capacity

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Abstract – To evaluate the effects of habitat, foraging strategy (drift vs. limnetic feeding) and internal prey subsidies (downstream transport of invertebrate drift between habitats) on fish production, we measured the growth of juvenile coho salmon confined to enclosures in flowing (pond inlets and outlets) or standing water (centre of pond) habitats in a constructed river side-channel. The effects of habitat and foraging strategy on fish growth were mediated primarily through habitat effects on prey abundance. Invertebrate drift biomass was nearly an order of magnitude higher at pond inlets relative to outlets. Drift-feeding coho in inlet enclosures grew 50% faster than drift-feeding coho at pond outlets or limnetic feeding coho in the centre of ponds, suggesting that elevated drift at inlets was sufficient to account for higher inlet growth rates. Forty per cent of prey biomass in stomachs was terrestrial in origin. These results indicate that, in addition to dependence on external terrestrial subsidies, streams with alternating slow and fast water (i.e., pool-riffle) sequences are also characterised by internal prey subsidies based on transport of drifting invertebrates from refuge habitats (high velocity riffles) to habitats more suitable for drift-feeding predators (e.g., pools), which may result in higher maximum fish growth in systems where internal subsidies are large. Restoration of small streams to maximise productive capacity for pool-rearing salmonids will require a better understanding of the length and interspersion of habitats that maximises both internal prey subsidies and available rearing habitat for juvenile salmon.

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Introduction

Streams typically include a mosaic of high- and low-velocity environments that permit different foraging strategies. Small lakes, natural impoundments, or ponds formed by beaver dams or side-channel sloughs constitute much of the productive habitat in many drainages (e.g., Sharma & Hilborn 2001; Pollock et al. 2004). At a smaller spatial scale within flowing reaches, pools, riffles and backwaters provide a range of velocity environments that allow a variety of foraging strategies (Nielsen 1992). Contrasting biophysical constraints in flowing- and still-water micro and mesohabitats influence prey availability and the

type of foraging strategies that fish adopt, and therefore the associated energetic costs and benefits that affect fish growth. Drift-feeding fish swim stationary relative to the stream bed while feeding on suspended invertebrates, whereas fish in side-channel ponds, sloughs, or backwater pools swim through the water column in search of suspended or benthic prey (henceforth known as ‘limnetic’ feeding). These contrasting strategies should result in different growth rates depending on habitat-specific differences in swimming costs, prey abundance and encounter rates, and the energetic benefits of prey acquisition (e.g., Werner & Hall 1979; Grant & Noakes 1987; Nielsen 1992; Nakano & Furukawa-Tanaka 1994; Grossman

et al. 2002). Understanding the relative production benefits of foraging strategies that take place in flowing- versus standing-water micro and mesohabitats nested within a riverine landscape is important both for understanding the drivers of fish production in undisturbed streams, and for optimising the design of habitat restoration projects (e.g., Roni et al. 2006; Rosenfeld et al. 2008).

In addition to foraging strategy, fish growth will also be affected by local prey abundance, both of which may differ between habitats (Nielsen 1992; Cellot 1996; Leung et al. 2009). It is now widely recognised that prey abundance is strongly influenced by external subsidies from adjacent ecosystems, such as inputs of terrestrial energy (e.g., leaves and invertebrates) that contribute significantly to fish growth and production in streams (e.g., Wipfli 1997). However, there may also be significant flows of energy and prey between habitats within an ecosystem (e.g., from riffles to downstream pools; Waters 1965), such that high prey production in one habitat can subsidise predator production in the adjacent one (Finlay et al. 2002). This may be especially true in streams, where directional flow imposes a longitudinal spatial structure on prey production, transport, and depletion that is absent in purely lentic habitats.

In this study, we assessed the energetic consequences of habitat and foraging strategy by measuring summer growth and diet of juvenile coho salmon (*Oncorhynchus kisutch*) feeding limnetically in the centre of ponds or drift feeding at pond inlets and outlets. Coho salmon are widespread in streams of coastal North America, and juveniles adopt a variety of foraging strategies and habitats ranging from drift feeding in river mainstems to limnetic feeding in side channel ponds and lakes (e.g., Swales & Levings 1989). Because they rear in both flowing and still-water environments, juvenile coho are ideal for studying the consequences of drift versus limnetic feeding in different habitats. Measuring habitat-specific patterns of prey abundance and fish growth in serially arranged slow- and fast-water habitats also provides a basis for understanding how fish production is influenced by internal subsidies of prey transported by flowing water.

The first objective of this study was to evaluate the contribution of differences in prey abundance to differences in growth experienced by fish in higher-velocity habitats, where fish drift-feed, versus low-velocity habitats, where fish forage limnetically. Based on earlier studies that demonstrated higher prey availability and growth rates of drift-feeding fish relative to fish foraging in still-water microhabitats (e.g., Nielsen 1992), our expectation was that drift-feeding fish would experience higher prey abundance (biomass, $\text{mg}\cdot\text{m}^{-3}$) and growth than limnetic feeding

fish. Our second objective was to evaluate the dependence of fish growth on terrestrial inputs and internal prey subsidies. We then use insights from our experiment to develop a conceptual framework for predicting the effect of channel structure (length and interspersed pool habitats) on prey abundance and productive capacity for juvenile salmonids, based on the spatial structure of prey production, transport and depletion imposed by directional flow in streams.

Methods

Study site

Experiments were performed in enclosures built in a constructed side channel on the floodplain of Chapman Creek (UTM 448100E 5478100N), a large coastal stream on the Sunshine Coast of British Columbia 50 km north of the city of Vancouver, Canada. Chapman Creek has an average bankfull channel width of 20 m and a summer low flow of approximately $0.30 \text{ m}^3\cdot\text{s}^{-1}$. Juvenile coho salmon, steelhead trout (*Oncorhynchus mykiss*), cutthroat trout (*Oncorhynchus clarki*) and Chinook salmon (*Oncorhynchus tshawytscha*) are present in mainstem and side channel habitats. Both wild and hatchery-reared coho spawn in the side channel, which is colonised through *in situ* natural reproduction and immigration of juvenile fish from the mainstem.

The side channel was constructed in an abandoned river meander, and consists of a series of six ponds (each 30–90 m long, 7–18 m wide, 0.9–1.6 m maximum depth; Fig. 1) separated by steep riffles (3–6% gradient) 10 m in length, and was designed as a rough analogue of the beaver pond habitat that was once abundant on coastal floodplains (Pollock et al. 2004). A 12-inch-diameter pipe with a bottom-draw intake buried in the bed of Chapman Creek diverted an average flow of $0.05 \text{ m}^3\cdot\text{s}^{-1}$ into the side channel. Adult coho spawn in riffles and gravel placed at the tailout of ponds (top of riffles). Water velocities at pond inlets (below riffles) and outlets (above riffles) were fast enough for fish to drift feed (Table 1), while velocities in the main body of ponds were slow ($0\text{--}3 \text{ cm}\cdot\text{s}^{-1}$), and fish would forage by slowly swimming through the water column in search of surface, benthic, or suspended prey (i.e., limnetic feeding). Riparian vegetation surrounding the ponds was a mix of mature second growth conifer and alder with an understory of immature alder growing on pond banks.

Ponds had large quantities of logs and root wads added during construction to provide cover and habitat structure. Herons were observed feeding in the ponds, a beaver was also resident, as were larger (15–20 cm) juvenile steelhead and cutthroat trout at low densities.

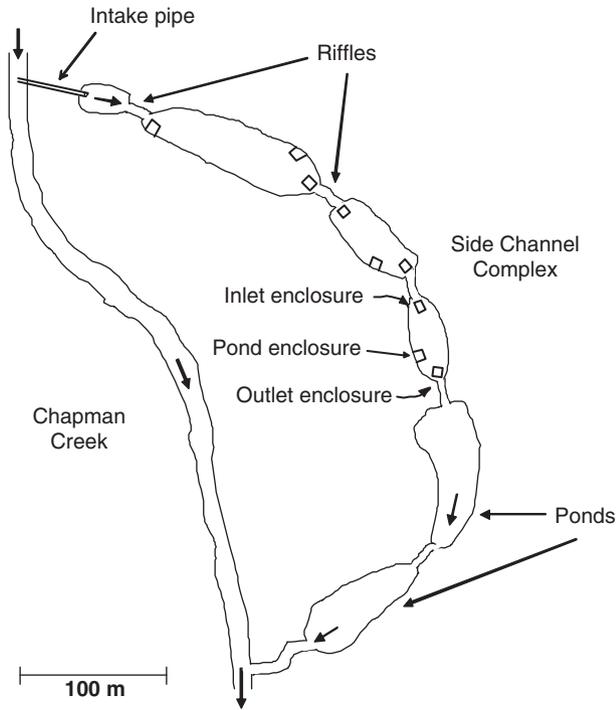


Fig. 1. Schematic diagram illustrating the study site and experimental design. Scale is approximate (width of ponds is exaggerated to show detail).

Experimental design

To determine how growth rates differ between drift versus limnetic feeding fishes, we placed enclosures in three different habitats: pond inlets (drift feeding), the main body of ponds (limnetic feeding) and pond outlets (drift feeding; Fig. 1), providing the main experimental contrast in foraging strategies, prey community and serial location of habitats. Enclosures were 2 by 2 m, and built of 6-mm square wire screen extending above the water surface and buried beneath the channel substrate to prevent escape of stocked fish. The 6-mm mesh was permeable to all but the largest drifting invertebrates (e.g., Zimmerman & Vondracek 2006). Enclosures were held upright by steel re-enforcing rods driven into the substrate, and the buried mesh skirt was sealed against the channel bed using bags filled with gravel. Screens on enclosures were cleaned with a brush daily or every second day to prevent clogging and maintain flow of water and invertebrates.

To characterise differences in physical habitat between inlet, outlet and pond enclosures, we measured

depth and velocity (at 20% and 80% of total depth) at 40-cm intervals along two transects perpendicular to flow in each enclosure, using a Marsh–McBirney model 2000 flow meter. Maximum depth in enclosures ranged from 34 cm in inlet enclosures to 83 cm in pond enclosures; velocities were the highest in inlet and outlet enclosures, and negligible in pond enclosures (Table 1). Current velocities inside and outside of enclosures were fast enough for fish to drift feed at inlets and outlets, but not in the main body of ponds (Table 1). Vertical velocity gradients [the difference in velocity at 20% and 80% of water column depth divided by distance between the two points; an index of the potential for fish to scan large volumes of water while swimming at low velocities (Hayes & Jowett 1994; Smith et al. 2005)] were also the greatest at inlet enclosures (Table 1). Dominant substrate at inlet enclosures was cobble and boulder, pond enclosures had predominantly fine sediment and organic substrate, and outlet enclosures were predominantly gravel. Water temperature in the side channel averaged 16.8 °C during the experiment (temporal range 13.2–20.1 °C).

Three replicates of each enclosure type were placed as blocks in three separate ponds (total of nine enclosures; Fig. 1). To minimise density-dependent effects in enclosures and ensure that fish growth accurately reflected the maximum growth rate potential of each habitat, fish were stocked at low densities (0.75 fish m⁻²) relative to ambient densities in ponds (2–3 fish m⁻², estimated by mark-recapture). Each enclosure was stocked on 27 July 2004 with three juvenile coho (49.2 ± 0.7 mm SD fork length, 1.34 ± 0.07 g SD wet weight) individually marked with coloured elastomer injections (Northwest Marine Technology, Shaw Island, WA, USA). Fish were recaptured halfway through the experiment on 10 August using minnow traps, weighed and measured to the nearest 0.01 g and 1 mm, respectively, and returned unharmed. Final fish collection took place from 1 to 4 September (average duration of 37 days) using minnow traps and electrofishing. Daily instantaneous growth rates of fish (per cent per day) were calculated as $\{[\log_e(\text{final weight}) - \log_e(\text{initial weight})]/\text{duration}\} \times 100$ (Ricker 1975).

Limnetic-feeding fish confined to pond enclosures and drift-feeding fish in inlet and outlet enclosures were observed to forage similarly to fish outside of enclosures. Although the 2 × 2 m enclosures may have

Habitat	Maximum depth (cm)	Average depth (cm)	Maximum velocity (cm)	Average velocity (cm)	Vertical velocity gradient (cm·s ⁻¹ ·cm ⁻¹)
Inlet	34 ± 4	27 ± 2	20.3 ± 9.7	5.2 ± 1.3	0.67 ± 0.42
Pond	83 ± 16	56 ± 14	1.0 ± 0	0.2 ± 0.1	0.01 ± 0.01
Outlet	46 ± 16	25 ± 9	8.0 ± 3.6	4.5 ± 2.4	0.09 ± 0.03

Table 1. Physical characteristics of enclosures in inlet, pond and outlet habitats.

restricted normal movement of limnetic fish, average prey resource abundance inside of pond enclosures should have been equal to or greater than prey abundance outside of enclosures, because of the much lower density of fish stocked in enclosures relative to external densities in ponds.

Dominance rank of fish in enclosures was assigned based on final size of fish within an enclosure. As fish were initially stocked at equal sizes (± 0.7 mm SD), and juvenile coho are known to be extremely aggressive and quickly establish dominance hierarchies (Chapman 1962) that are exclusively size-based (Young 2003), it is reasonable to attribute differences in final size to dominance rank rather than other factors (e.g., variation in intrinsic growth rate). Casual observations during the experiment confirmed strong dominance hierarchies of fish inside enclosures. Relative sizes of individually marked fish collected at the middle and end of the experiment were invariant, indicating that size-based dominance hierarchies within enclosures were stable over time.

To determine the relative availability of prey for drift versus limnetic feeding fish, we measured invertebrate abundance in the drift, in the pond water column, as aerial drop onto the water surface, and in benthic samples in all enclosure types. Invertebrate drift was collected in each inlet and outlet enclosure ($N = 6$) on two occasions (4 and 17 August 2004, total $N = 12$) using 250- μ m mesh drift nets with a 17.5 \times 17.5 cm opening set between 10:00 and 16:30 (average set duration 4.7 ± 0.3 h). To characterise prey available to limnetic-feeding fish in the water column, a drift net was used as a plankton tow to sample the water column of each of the three ponds containing enclosures ($N = 3$ samples on each of 4 and 17 August). Plankton tows were taken from ponds rather than enclosures to minimise disturbance in enclosures and maximise the volume of water sampled (each sample consisted of three replicate tows of 3–5 m length). Aerial drop was sampled using black plastic trays (28 cm wide by 34 cm long) floating on the water surface adjacent to enclosures. Trays were filled with 1.5–2 l of water containing 10 ml of surfactant (liquid soap) to facilitate trapping of invertebrates by reducing surface tension (Wipfli 1997; Allan et al. 2003). Four replicate trays were left in place over two separate 7-day sampling intervals during the experiment (3–10 August and 16–23 August; $N = 8$ samples). Abundance of benthic prey was assessed with a single benthic invertebrate sample randomly collected from each enclosure ($N = 9$) at the end of the experiment, using a 17.5 \times 17.5 cm Surber sampler to a substrate depth of 2 cm in inlet and outlet enclosures, and a core sampler to collect sediment substrate to a depth of 1 cm in pond enclosures. All invertebrate samples were preserved in 5% formalin.

Benthic invertebrate and drift samples were sorted from detritus in the laboratory at 16 \times magnification and preserved in 70% ethanol. Most aquatic invertebrates were identified to genus using Merritt & Cummins (1984), with the exception of chironomids, which were identified to subfamily, and terrestrial invertebrates, which were identified to family. Invertebrate length was measured to the nearest 0.05 mm using a binocular microscope equipped with a drawing tube that projected images of invertebrates onto a digitising pad (Roff & Hopcroft 1986), and invertebrate biomass (dry weight) was then estimated using published length–weight regressions for aquatic (Meyer 1989; Benke et al. 1999; Sabo et al. 2002) and terrestrial invertebrates (Edwards 1966; Gowing & Recher 1984; Sample et al. 1993). Invertebrate abundance in the drift and water column of the pond was expressed as $\text{mg}\cdot\text{m}^{-3}$ (total biomass divided by water volume filtered by a net), benthic biomass was expressed as $\text{g}\cdot\text{m}^{-2}$ and aerial drop was expressed as $\text{mg}\cdot\text{m}^{-2}\cdot\text{h}^{-1}$.

To determine fish diet associated with different habitats and foraging strategies, as well as the overall dependence of fish production on external terrestrial subsidies, we used a gastric lavage (Foster 1977; Meehan & Miller 1978) to sample stomach contents of coho. Five fish were collected from each inlet, outlet and centre of three separate ponds (outside of enclosures to minimise disturbance) between 12:00 and 17:00 on 5, 9 and 11 August (total $N = 45$, 15 from each habitat type) using minnow traps or dip nets. Stomach contents were preserved in 70% ethanol in the field, and later digitised to estimate biomass as described above.

Although some studies have demonstrated that drift abundance and consumption are higher at night, including dusk and dawn (e.g., Elliott 1973), other studies have detected primarily daytime drift consumption by juvenile salmonids (e.g., Allan 1981; Sagar & Glova 1988; Dedual & Collier 1995). As juvenile coho in our side channel habitats fed continuously throughout the day and were not observed to feed at night (Rosenfeld, personal observation), we considered day drift samples to be most representative of average prey abundance. Day drift samples may somewhat underestimate prey consumption at dusk and dawn, but this bias is likely small when integrated over a full day because of the much longer duration of daytime feeding (12 h in our study).

Data analysis

To test for hypothesised differences in growth between drift versus limnetic feeding fishes, we used analysis of variance (ANOVA) to determine the effect of habitat (three levels – inlet, outlet, or pond

enclosure) on daily growth rate of coho in enclosures ($N = 21$; 78% of fish were recovered from enclosures at the end of the experiment), with fish rank (three levels – dominant, intermediate or subordinate) as an additional variable to control for the strong effects of dominance on growth. To assess differences in prey availability for drift versus limnetic feeding fishes, we tested for a habitat effect (inlet vs. outlet vs. pond enclosures) on drift and benthic invertebrate abundance separately using *t*-tests (for inlet vs. outlet drift) and ANOVA (for comparing inlet with outlet drift and zooplankton, and for comparing benthic biomass between habitats; $N = 6$ drift or zooplankton samples from each habitat type; $N = 3$ benthic samples from each habitat type). Dependent variables in *t*-tests or ANOVA met assumptions of normality and equal variance at $P = 0.05$, which was assessed using the Shapiro–Wilke statistic (SAS Institute 1989) and frequency histograms. Any *t*-tests with unequal variances were analysed using the Satterthwaite method (SAS Institute 1989). Nonparametric tests were used when assumptions of normality and homogeneity of variance could not be met through data transformation.

To determine the importance of terrestrial prey subsidies to juvenile coho, we calculated the proportion of terrestrial prey biomass in stomach contents of fish. To determine the relative quality of terrestrial subsidies (in terms of prey size), we used a Wilcoxon signed rank test to assess differences in mean prey size between terrestrial and aquatic invertebrates in the drift, drop and stomach contents. To assess whether fish differentially selected prey of terrestrial origin, we used a Wilcoxon rank sum test to compare the proportion of terrestrial invertebrates in stomach contents to the proportion in the drift.

It is possible that individual fish in side channel habitats forage in a variety of habitat types rather than specialising as drift or limnetic feeders, and that habitat differences associated with our enclosures are artificial, i.e., due to confinement. To determine whether diets of unconfined fish in inlets, outlets and the centre of ponds differed, and to assess whether fish appeared to specialise in different habitat types and foraging modes, we performed correspondence analysis of stomach content samples ($N = 45$). We ordinated untransformed abundance data so as to reflect differences in both taxonomic composition and absolute abundance of different prey (Jackson 1993).

Results

Fish growth and prey abundance in different habitats

The prediction of higher growth rate for drift feeding fish was only partially supported. Growth rates of drift

feeding fish in inlet enclosures were significantly higher than limnetic feeding fish in pond enclosures (ANOVA, $F_{2,16} = 15.7$, $P < 0.0002$), but drift-feeding fish in outlet enclosures had similar growth rates to those in pond enclosures ($P = 0.65$; Fig. 2). Fish production in inlet enclosures (increase in weight of all three fish combined) was roughly double that in pond or outlet enclosures (Fig. 2), and fish rank within an enclosure also accounted for substantial variation in growth (ANOVA, $F_{2,16} = 14.0$, $P < 0.0003$, significant difference between all ranks $P < 0.02$; Fig. 2). Size distributions of fish were skewed in all enclosures (Fig. 2), indicating that dominant coho were capable of monopolising prey resources even in the 4-m² still-water pond enclosures.

The prediction of higher invertebrate prey abundance in the water column for drift feeding fish was ambiguously supported. While drift in inlet enclosures was an order of magnitude higher than drift in outlet enclosures (*t*-test with unequal variances, $t_{1,6} = 3.96$, $P < 0.0096$; Fig. 3), biomass of invertebrates from the water column of ponds (plankton tows) was so variable that it was not significantly different from either zero (Fig. 3, central bar; $t_{1,6} = 1.44$, $P = 0.21$) or inlet or outlet drift ($F_{2,15} = 1.49$, $P = 0.26$). High variation (low confidence) in plankton biomass estimates from ponds was due to the small number of invertebrates collected per sample (mean of 8 ± 3 in zooplankton tows, compared with 800 ± 470 in inlet and 190 ± 150 in outlet drift samples), and the presence of a relatively small number of high biomass terrestrial invertebrates in some tows (e.g., small flies or spiders). Low numbers and high variability in zooplankton samples were partly a consequence of the low volume of water sampled in relatively short zooplankton tows. Removing one high biomass plankton replicate containing an adult fly decreased the mean biomass threefold in plankton tows (Fig. 3, centre left bar), and excluding all terrestrial invertebrates (Fig. 3, centre right bar) generated a mean

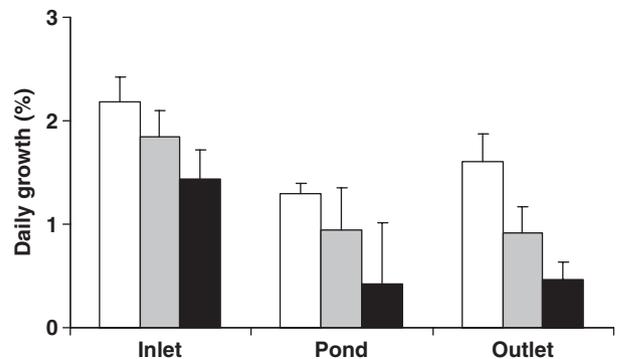


Fig. 2. Daily growth rate (per cent of body weight per day) of dominant (open bars), sub-dominant (grey bars) and subordinate (black bars) juvenile coho in inlet, outlet and pond enclosures. Error bars represent one standard deviation.

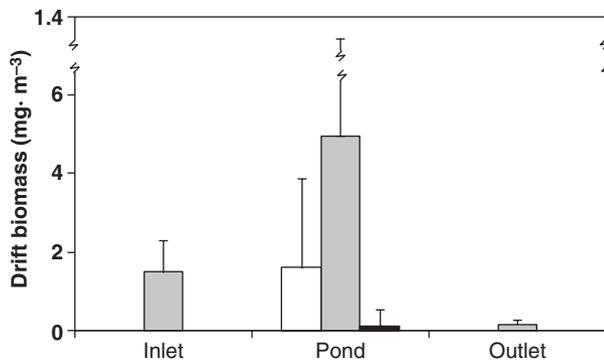


Fig. 3. Concentration of invertebrates in the water column at the centre of ponds and in the drift at pond inlets and outlets. The white bar in the centre shows concentration in pond habitat with one outlier replicate plankton tow removed, and the dark bar shows concentration in pond habitat with plankton only.

biomass similar to outlet drift samples. Despite higher inlet drift biomass, abundance of invertebrates in inlet and outlet drift samples was similar (9.3 ± 4.5 and 8.3 ± 4.2 individuals·m⁻³ respectively), reflecting the smaller size of drifting invertebrates (primarily zooplankton) at pond outlets.

Benthic invertebrate biomass in enclosures was variable [824 ± 651 (SD) mg·m⁻² at inlet enclosures, 1614 ± 1371 (SD) mg·m⁻² at pond enclosures and 227 ± 105 (SD) mg·m⁻² at outlet enclosures] with no significant differences between habitat types (ANOVA, $F_{2,6} = 1.9$, $P = 0.23$), despite the highest benthic biomass in the fine organic substrate of pond enclosures. Benthic biomass was unrelated to growth rate of juvenile coho.

Total biomass of invertebrates in the aerial drop was also extremely variable (4.39 ± 3.33 mg·m⁻²·h⁻¹), as observed by others (e.g., Wipfli 1997). Large adult caddis flies contributed a disproportionate 58% of the total biomass of aerial drop, despite constituting only 6.8% of total numbers. Aerial drop biomass with adult caddis flies excluded was 2.2 ± 3.0 mg·m⁻²·h; this is likely a more realistic estimate of aerial drop inputs, as adult caddis flies were found in only one of 45 stomach samples, probably because adult caddis flies were nocturnally active when coho were not observed to forage.

Terrestrial invertebrates accounted for 40% of total prey biomass in coho stomachs ($N = 45$; Fig. 4), but the proportion of terrestrial invertebrates in stomach contents did not differ significantly between habitats (Kruskal–Wallis Test, $\lambda_2^2 = 2.8$, $P < 0.24$). The proportion of terrestrial invertebrates in stomachs tended to be higher than the proportion in the drift (Fig. 4; Wilcoxon Rank Sum Test, $S = 260$, $P < 0.09$), suggesting some level of selectivity for prey of terrestrial origin, which were on average larger than aquatic prey. Terrestrial invertebrates accounted for only 28% of the biomass in aerial drop (with the balance from flying

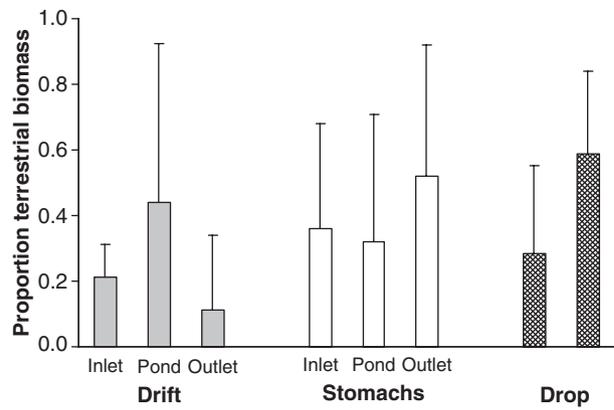


Fig. 4. Proportion of terrestrial invertebrate biomass in the drift, in the stomach contents of juvenile coho collected from different habitats and in aerial drop [including all prey captured in drop trays (left hatched bar); and aerial drop with caddis fly adults removed (far right hatched bar; see text for explanation)]. Error bars represent one standard deviation.

adults of aquatic insects), with the contribution of terrestrial invertebrates increasing to 59% of aerial drop when adult caddis flies were excluded from the analysis (far right bar in Fig. 4).

Average biomass of individual terrestrial prey was up to an order of magnitude higher than aquatic prey in drift and stomach samples (Fig. 5; Wilcoxon Signed Rank Test, $S = 314$, $P < 0.0001$), but not in the aerial drop (Wilcoxon Signed Rank Test, $S = -8$, $P < 0.31$). Average individual prey size was the largest in aerial drop, and intermediate in stomach samples (Kruskal–Wallis Test, $\lambda_2^2 = 39.8$, $P < 0.0001$), highlighting the greater size and associated energy value of aerial drop and prey of terrestrial origin.

Ordination of fish stomach contents showed substantial separation in diet between habitats, particularly between inlet fish and fish in outlets and ponds, which showed considerable overlap (Fig. 6). Inlet fish scored high on dimension 2, which was negatively correlated with *Camptocercus* sp. (the dominant zooplankton in ponds) and positively correlated with several dominant drift taxa (Simuliidae, Baetidae, nonchironomid dipteran larvae), supporting the inference that individual fish in the side-channel were specialising on particular habitats and associated foraging strategies.

Discussion

In this study, we examined the effect of habitat and associated foraging strategy and prey abundance on growth rate of juvenile coho salmon, and tested whether drift feeders experience higher growth than limnetic feeders in ponds. We predicted that energy intake and prey abundance would be higher for drift-feeding fishes, resulting in higher growth rates. Concordance of our results with these predictions

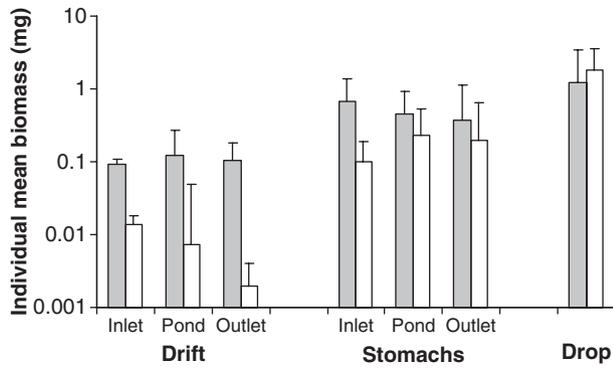


Fig. 5. Mean individual biomass of terrestrial (filled bars) and aquatic (open bars) invertebrates in the drift, stomach contents of coho, and aerial drop. Note vertical axis is a log scale. Error bars represent one standard deviation.

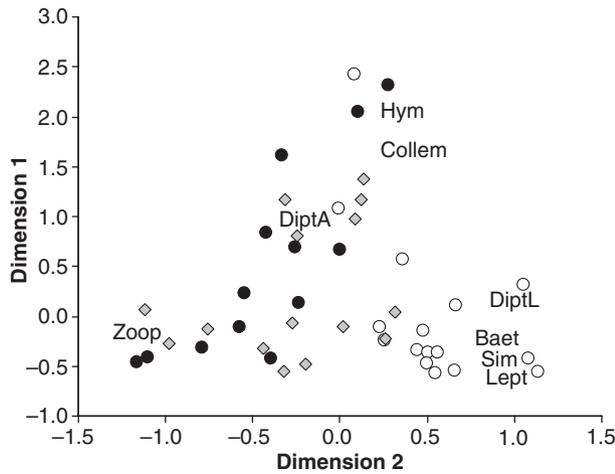


Fig. 6. Ordination of stomach contents of fish collected from pond inlets (open circles), pond outlets (filled circles) and pond centres (filled diamonds) in taxonomic space. Dimension 2 is negatively correlated with the dominant zooplankton taxon in the ponds (Zoop) and positively correlated with common riffle-dwelling taxa [blackfly larvae (Sim), mayfly larvae (Baet, Lept) and nonchironomid dipteran larvae (DiptL)]. Dimension 1 is correlated with nonchironomid dipteran adults (DiptA), ants and wasps (Hym), and Collembolans (Collem).

was equivocal. Both prey abundance and growth rates were indeed higher for drift-feeding fish at pond inlets, but drift-feeding fish at pond outlets experienced similar prey abundance and growth as limnetic fish in the centre of ponds.

The relative profitability of the drift foraging strategy clearly depends on spatial context. The reason for this is apparently straightforward – drift-feeding fish deplete prey passing by in the water column, so that concentrations of invertebrates are reduced towards the downstream end of a pool (e.g., Hayes et al. 2007). Consequently, dominant fish typically hold station at the head of a pool where drift is the highest (e.g., Hughes 1992; Elliott 2002a; Rosenfeld

et al. 2005). A single pond with its upstream riffle in our side channel habitat can be visualised as equivalent to a riffle-pool sequence in a typical stream, with the length and width of the pool exaggerated to become a pond. While the observation of longitudinal prey depletion in the direction of flow is apparently trivial, it has significant implications for the effects of pool and riffle length and spacing on productive capacity, as discussed later.

Our empirical measurements of higher drift at inlets suggest that elevated drift is the most parsimonious cause of accelerated growth for inlet drift feeders. Alternative mechanisms for higher growth of drift feeders relative to limnetic feeders could include lower swimming costs per volume of water searched [i.e., velocity refuges associated with habitat complexity (Hayes & Jowett 1994) may allow drift feeding fish to scan an equivalent volume of water with lower energy expenditures]. However, the order of magnitude higher drift biomass at inlets relative to outlets appears sufficient to account for higher inlet growth. This inference is supported by Nielsen (1992), who similarly observed that elevated growth of drift-feeding coho relative to nonterritorial floaters was associated with higher prey abundance, and Wilzbach et al. (1986), who found that trout growth was positively correlated with drift density. Bioenergetic modelling of the costs and benefits of drift versus limnetic foraging would be one approach for separating the effects of prey abundance versus swimming costs on realised growth rates (e.g., Rosenfeld & Taylor 2009), but space limitations and parameter uncertainty preclude this application here.

The large proportion of terrestrial prey in the diet of drift and limnetic foraging coho clearly demonstrates the importance of external terrestrial subsidies to juvenile salmon in small water bodies. This conclusion is supported by similar observations from many other studies (e.g., Nielsen 1992; Wipfli 1997; Allan et al. 2003; Romaniszyn et al. 2007), and the quality of terrestrial prey is further enhanced by their larger individual size.

Drift distance, useable habitat and internal prey subsidies: implications for fish growth

As availability of prey appears to be the primary driver of observed differences in growth between slow- and fast-water habitats (this study and Nielsen 1992), the factors that influence the spatial distribution of prey abundance in streams deserve further consideration. Prey biomass in the water column is a function of inputs (prey recruitment from the benthos and aerial drop) and depletions (prey consumption by fish or deposition in slow water; Martin & Knight 1989; Hayes et al. 2007). Realised prey concentration at any

point in a stream will therefore be the outcome of spatial variation in prey recruitment and prey consumption. Recruitment of invertebrates to the drift will depend on benthic production as well as the hydraulic forces that entrain invertebrates and maintain them in suspension (Elliott 1971; Lancaster et al. 1996). If all habitats suitable for fish are occupied, then spatial variation in consumption of drift will be driven by the exclusion of fish from hydraulically harsh stream habitats that are beyond their performance limits (e.g., high-velocity riffle habitats where drifting prey experience a refuge from fish predation). Streams should therefore have high spatial variation in abundance of suspended prey, resulting from local depletion of prey in hydraulically benign habitats that are suitable for fish (e.g., ponds in our study, or pools in a more

typical stream channel; Fig. 7), and high drift concentrations in fast-water habitats that are refuges from fish predation (typically turbulent riffles that will also have higher prey recruitment to the drift, e.g., the riffles between ponds in our study).

In effect, streams are characterised by internal prey subsidies resulting from accumulation of drifting invertebrates in refuge habitats (e.g., riffles), and subsequent physical transport to habitats more suitable for predators (e.g., stream pools or ponds; Harvey et al. 2006; Rosenfeld & Taylor 2009). While the importance of external terrestrial energy subsidies that cross ecosystem boundaries is well documented (Polis et al. 1997; Kawaguchi et al. 2003; Baxter et al. 2005), the same process at a smaller scale within an ecosystem can also result in local elevation of

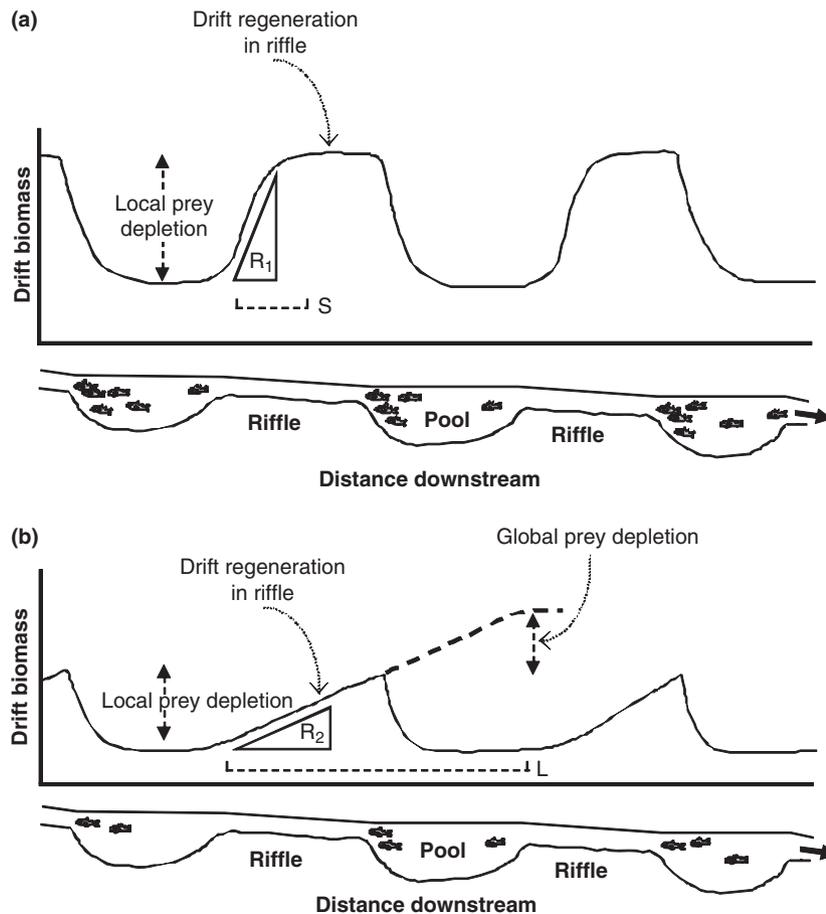


Fig. 7. A schematic diagram illustrating hypothetical changes in invertebrate drift abundance ($\text{mg}\cdot\text{m}^{-3}$) as a function of downstream distance along a stream profile. Fish are present in pools, but excluded from riffles because of higher velocities. The upper panel (a) illustrates a scenario where fish locally deplete drifting invertebrates in pool habitat, which quickly regenerates to a high drift concentration in riffle habitat in the absence of predation. The steep slope of the drift concentration curve in riffles indicates a high recruitment rate (production; R_1) of drift from the benthos, and the rapid asymptote indicates a short average drift distance (S). The lower panel (b) represents a scenario where the rate of production of drift in riffle habitat (R_2) is approximately one-third of that in the first scenario, while average drift distance is tripled (L). In both scenarios, asymptotic drift concentrations should be equivalent, but an average drift distance that exceeds riffle length in the second scenario prevents drift from reaching its maximum potential (bold broken line) before entering the downstream pool. In the second scenario, consumption of drift and short riffle lengths lead to global as well as local prey depletion by fish. Number of fish in pools indicates hypothesised effects of drift dynamics on fish abundance.

production in subsidised habitats (Finlay et al. 2002). These internal subsidies, in conjunction with the ability of territorial fish to monopolise resources, can be hypothesised to result in higher localised production and maximum fish growth in subsidised habitats than might be realised in lentic habitats where the directional physical transport processes that drive internal spatial subsidies are largely absent, and where unimpeded movement of fish consumers facilitates energy flow between adjacent habitats rather than movement of prey (Schindler & Scheuerell 2002). Higher production of fish in subsidised habitats is illustrated by the higher growth and production of fish in our inlet enclosures downstream of riffles.

The distance that invertebrates drift in streams is a key parameter controlling drift concentration and the strength of internal subsidies. Assuming that the rate of depletion of drift (i.e., by settling) equals the rate of recruitment (entry into the water column), equilibrium biomass of drifting invertebrates in the absence of fish predation (i.e., in a high velocity riffle) will be a function of the rate of recruitment of invertebrates from the benthos and average residence time of drifting invertebrates in the water column (Elliott 1971, 2002b):

$$\text{drift conc.} = \text{recruitment/depth} \cdot \text{time in suspension} \quad (1)$$

However, the residence time of invertebrates in the water column is proportional to drift distance,

$$\text{time in suspension} = \text{drift distance/velocity} \quad (2)$$

so that drift concentration will increase with average drift distance, but should not increase downstream beyond the average drift distance, as illustrated in Fig. 7. If average drift distance is longer than the length of a riffle, then biomass will increase longitudinally throughout the riffle. The longitudinal rate of increase in drift (i.e., slope of the increasing drift biomass line downstream of pools in Fig. 7) will depend on the recruitment (production) rate of invertebrates from the benthos, while the maximum asymptotic drift biomass remains dependent on average drift distance, e.g., if average drift distance is infinite (drifting prey never return to the substrate), then drift concentrations will increase continuously in a downstream direction. Correlation of drift concentration with riffle lengths up to 12 m (Hansen & Closs 2007) supports this simple conceptual model.

Consumption by fish (Wilzbach et al. 1986) as well as settling (Martin & Knight 1989) reduces average drift distance when drift enters a pool occupied by fish. If consumption is assumed to be greatest at the

upstream end of a pool, then drift concentration will decrease as a negative exponential function of distance below the head of a pool,

$$\text{drift conc.} = \text{recruitment/depth} \cdot \text{time in suspension} \cdot (a \cdot e^{-b(\text{distance below head of pool})}), \quad (3)$$

where a and b are constants. The downstream rate of drift depletion through fish consumption (e^{-b}) is unclear; however, in a typical stream with relatively short pools, bioenergetic estimates of consumption by juvenile trout indicate that a large proportion of the invertebrate prey subsidy entering a pool from the upstream riffle is consumed over a relatively short distance (e.g., a pool length of 3–4 m; Leung et al. 2009). Equivalent growth of fish in pond and outlet enclosures in our study supports the inference that most of the prey subsidy from the upstream riffle was likely consumed by fish in our much longer (30–90 m) side-channel ponds, i.e., predation in the main body of the pond eliminated any prey subsidy before it reached the outlet.

The impact of fish on prey abundance will be further mediated by the proportion of stream habitat that is usable (i.e., the foraging arena *sensu* Walters & Juanes 1993), which will in turn be a function of the performance tolerances of a species and channel structure (Rosenfeld et al. 2007; note that from this perspective, the size of the foraging arena (Walters & Juanes 1993) is driven by physical constraints on the performance limits of fish rather than risk of predation.) In fast, shallow, or high-gradient streams with very low pool frequency, only a small proportion of stream habitat will be usable by pool-rearing salmonids. Fish in usable habitat will be essentially donor-controlled; while fish can locally deplete drift in pools, they will have no impact on stream-average drift abundance, and growth rates of dominant fish will therefore be density independent. In contrast, if a large proportion of stream habitat is usable, fish will be able to globally deplete prey abundance (Fig. 7b), and growth rates of even dominant fish will be density dependent (e.g., Jenkins et al. 1999).

Hypothesised effects of channel structure on productive capacity

Understanding how channel structure affects internal prey subsidies and productive capacity is central to optimising the design of restoration and enhancement projects, and for understanding variation in habitat capacity of natural streams. Although expert opinion (e.g., Johnston & Slaney 1996, Table 5) and conceptual models (e.g., Poff & Huryn 1998) suggest maximum production with pool area in the range of 40–50% of

stream habitat, the specific length and spacing of pools and riffles that maximise internal prey subsidies and production of drift-feeding salmonids remain unknown (Poff & Huryn 1998).

As described earlier, average drift distance is a key parameter for optimising the tradeoff between maximising usable area for pool-rearing salmonids and maximising drift concentrations entering pools. If average drift distances are short, then drift concentrations will asymptote over a short distance, and short riffles will be sufficient to maximise both subsidies entering pool habitat and the area of usable habitat (i.e., pools). If drift distances are longer than natural riffle lengths, then there becomes an increasingly costly tradeoff between designing long riffles to maximise invertebrate drift entering pools, and loss of usable habitat for pool-rearing salmonids. At the other extreme, a very high proportion of pool habitat at a reach scale (as with our side-channel ponds; Fig. 1) will maximise available habitat for pool-rearing salmonids, but minimise internal subsidies. The rate of depletion of drift through consumption will similarly influence optimal pool length; pools that are longer than the distance over which fish effectively deplete drift should have lower production per unit area and smaller average fish size than shorter pools. Pool length in our side channel habitat (30–90 m), for example, almost certainly exceeded the distance over which fish deplete incoming drift.

Studies indicate that average invertebrate drift distances can be fairly short, ranging from 3 to 10 m in small streams at modal velocities of 30 cm s^{-1} (Elliott 1971, 2002b), suggesting that riffles as short as 3–5 m may be sufficient to maximise drift, although Hansen & Closs (2007) found drift to increase linearly with riffle length up to 12 m in a small stream. However, drift distance also increases with water velocity (Elliott 1971; Lancaster et al. 1996), and longer riffles will be required to achieve maximum drift concentration in higher-velocity habitats. Drift distances and recruitment from the benthos can also be expected to increase with velocity at higher stream discharge (O'Hop & Wallace 1983). Because high discharge events likely elevate and homogenise drift concentrations throughout the channel (Leung et al. 2009), habitat unit length should be engineered for medium or lower flows that are likely to represent the dominant (or most food-limited) conditions that drift-feeding fish experience while rearing. The shorter habitat units in smaller streams relative to large rivers, in conjunction with a higher proportion of lower-velocity habitats within the performance range of juvenile salmonids (Rosenfeld et al. 2007) would therefore be expected to maximise internal prey subsidies and support higher densities of drift-feeding fishes. This prediction is largely consistent with the

highest reach-average densities of juvenile salmonids commonly occurring in smaller streams (Mundie 1974; Rosenfeld et al. 2000). The tendency of large woody debris or other obstructions to shorten riffles and increase the frequency of pools (Montgomery et al. 1995) would also be expected to increase net internal prey subsidies.

The above discussion applies primarily to pool-rearing salmonids such as juvenile coho salmon. For drift-feeding fish whose juveniles are adapted to faster water habitats [e.g., Atlantic salmon (*Salmon salar*) and steelhead trout], there will be greater overlap between habitats that generate prey (e.g., riffles, runs, and cascades) and habitats that are usable, and the dynamics of internal prey subsidies may be less relevant to optimising channel design for these species. The unifying prediction across species is that there should be an optimal channel design that maximises production based on habitat composition and the interspersion distance of usable habitat (e.g., pools) and less suitable habitat that generates invertebrate prey (e.g., riffles), and this optimal configuration will likely differ between species as a function of their velocity preferences. Careful consideration should be given to the fact that optimising channel structure for one species may negatively affect species with contrasting habitat preferences (e.g., Reeves et al. 1993), and single versus multi-species objectives need to be clear when designing restoration projects or managing fish habitat. Our discussion has also focused on summer-rearing habitat; the optimal proportion of pool habitat may increase if hydraulic refuges for overwinter survival limit a population (Poff & Huryn 1998). Similarly, we consider channel structure effects on productive capacity in the absence of predation risk, and the optimal proportion of pool and riffle habitats will also depend on how vulnerability to aquatic and terrestrial predators differs between habitat types (i.e., Harvey 1991; Lonzarich & Quinn 1995).

Our enclosure experiment highlights the importance of prey abundance and foraging strategy to fish production, and the linkage between spatial variation in prey abundance and fish growth. However, despite the enormous quantity of research on stream rearing salmonids and their habitat associations, stream ecologists still lack a definitive understanding of the relationship between channel structure, prey production and habitat capacity for drift-feeding fishes (Poff & Huryn 1998). A better understanding of the factors that influence production of invertebrate drift and their sensitivity to management actions (e.g., Mundie 1974; Shearer et al. 2003; Romaniszyn et al. 2007; Saunders & Fausch 2007) would benefit the optimisation of channel restoration design. Ultimately, experiments contrasting fish growth and production

in channels with different pool and riffle frequencies and configurations are needed to determine the effects of usable habitat area versus habitat adjacency and internal prey subsidies on production of drift-feeding fishes.

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