

Varying effects of anadromous sockeye salmon on the trophic ecology of two species of resident salmonids in southwest Alaska

MARK D. SCHEUERELL^{*1}, JONATHAN W. MOORE^{*†}, DANIEL E. SCHINDLER^{*†} AND CHRIS J. HARVEY[‡]

^{*}School of Aquatic and Fisheries Sciences, University of Washington, Seattle, WA, U.S.A.

[†]Department of Biology, University of Washington, Seattle, WA, U.S.A.

[‡]National Marine Fisheries Service, Northwest Fisheries Science Center, Seattle, WA, U.S.A.

SUMMARY

1. Anadromous salmon transport marine-derived nutrients and carbon to freshwater and riparian ecosystems upon their return to natal spawning systems. The ecological implications of these subsidies on the trophic ecology of resident fish remain poorly understood despite broad recognition of their potential importance.

2. We studied the within-year changes in the ration size, composition and stable isotope signature of the diets of two resident salmonids (rainbow trout, *Oncorhynchus mykiss*; Arctic grayling, *Thymallus arcticus*) before and after the arrival of sockeye salmon (*Oncorhynchus nerka*) to their spawning grounds in the Bristol Bay region of southwest Alaska.

3. Ration size and energy intake increased by 480–620% for both species after salmon arrived. However, the cause of the increases differed between species such that rainbow trout switched to consuming salmon eggs, salmon flesh and blowflies that colonized salmon carcasses, whereas grayling primarily ate more benthic invertebrates that were presumably made available because of physical disturbances by spawning salmon.

4. We also observed an increase in the $\delta^{15}\text{N}$ of rainbow trout diets post-salmon, but not for grayling. This presumably led to the observed increase in the $\delta^{15}\text{N}$ of rainbow trout with increasing body mass, but not for grayling.

5. Using a bioenergetics model, we predicted that salmon-derived resources contributed a large majority of the energy necessary for growth in this resident fish community. Furthermore, the bioenergetics model also showed how seasonal changes in diet affected the stable isotope ratios of both species. These results expand upon a growing body of literature that highlights the different pathways whereby anadromous salmon influence coastal ecosystems, particularly resident fish.

Keywords: diet subsidy, marine-derived, stable isotope, nitrogen, bioenergetics

Correspondence: Mark Scheuerell, National Marine Fisheries Service, Northwest Fisheries Science Center, 2725 Montlake Boulevard East, Seattle, WA 98112, U.S.A.

E-mail: mark.scheuerell@noaa.gov

¹Present address: Mark Scheuerell, National Marine Fisheries Service, Northwest Fisheries Science Center, 2725 Montlake Blvd E, Seattle, WA 98112, U.S.A.

Introduction

The flux of organisms, materials and energy across ecosystem boundaries strongly influences the structure and dynamics of various food webs (Polis, Anderson & Holt, 1997; Polis, Power & Huxel, 2004). For example, some plants and generalist predators link above- and below-ground terrestrial ecosystems

(Scheu, 2001). Marine detritus may support nearshore terrestrial scavengers and predators, such as spiders (Polis & Hurd, 1995) and mammals (Roth, 2002; Carlton & Hodder, 2003). In lakes, much of the carbon in zooplankton and fish is derived from the surrounding terrestrial ecosystem (Pace *et al.*, 2004). Terrestrial invertebrates from riparian areas can enhance the diets and abundance of fish in streams (Kawaguchi, Taniguchi & Nakano, 2003) while, reciprocally, aquatic insects may determine the spatial distribution and density of riparian predators (Baxter, Fausch & Saunders, 2005).

For coastal areas surrounding the North Pacific Ocean, anadromous salmon (*Oncorhynchus* spp.) link marine, estuarine, freshwater and riparian ecosystems through the annual upstream spawning migration of adults and the downstream migration of juveniles toward the ocean (Levy, 1997; Naiman *et al.*, 2002; Schindler *et al.*, 2003). Because adult salmon gain >95% of their biomass at sea, the nutrients and carbon transported upstream in adults represent substantial subsidies that contribute to the production of periphyton, macroinvertebrates and fish (e.g. Kline *et al.*, 1990; Bilby *et al.*, 1998; Wipfli, Hudson & Caouette, 1998; Chaloner & Wipfli, 2002; Wipfli *et al.*, 2003; Mitchell & Lamberti, 2005). Terrestrial wildlife, such as birds, mammals and insects also consume salmon eggs and carcasses (Cederholm *et al.*, 1989; Willson, Gende & Marson, 1998; Gende *et al.*, 2002). Largely through the action of bears (*Ursus arctos* Linnaeus, *U. americanus* Pallas), salmon carcasses are transported into riparian areas where their nutrients ultimately make their way into vegetation (Ben-David, Hanley & Schell, 1998; Hilderbrand *et al.*, 1999; Helfield & Naiman, 2006). Spawning adult salmon also create large physical disturbances that modify bottom substrata and displace invertebrates (Peterson & Foote, 2000; Moore, Schindler & Scheuerell, 2004). Juvenile salmon (smolts) rearing in fresh water also transport nutrients back to the sea (Moore & Schindler, 2004; Scheuerell *et al.*, 2005) and provide food subsidies to marine mammals and fish upon their entry into the estuary and ocean (Wood *et al.*, 1993; Orr *et al.*, 2004). Thus, anadromous salmon have been called 'keystone species' because of their integral role in coastal ecosystems (Willson *et al.*, 1998; Helfield & Naiman, 2006).

Salmon acquire enriched signals of both carbon and nitrogen stable isotopes while in the ocean and then

carry those distinct marine signatures with them upon their return to fresh water (Kline *et al.*, 1990). Because returning adult salmon seldom feed in fresh water, their unique isotopic signature is preserved, allowing researchers to trace the flow of salmon-derived nutrients through food webs to various freshwater and terrestrial organisms (e.g. Kline *et al.*, 1990; Bilby, Fransen & Bisson, 1996; Hilderbrand *et al.*, 1996; Ben-David, Flynn & Schell, 1997; Chaloner *et al.*, 2002; Helfield & Naiman, 2002). Some studies have shown that salmon can account for 30–75% of the nitrogen source in freshwater ecosystems (Naiman *et al.*, 2002). Fish such as sculpin (*Cottus* spp.), char (*Salvelinus* spp.) and trout (*Oncorhynchus* spp.), that reside in streams used by spawning adult salmon, often have high stable isotope ratios indicating the accumulation of marine-derived nutrients (Kline *et al.*, 1990, 1993; Chaloner *et al.*, 2002). Furthermore, the experimental addition of carcasses has shown seasonal increases in the growth rates of juvenile salmonids (Wipfli *et al.*, 2003). Nevertheless, differences among species in the trophic pathways by which resident fish acquire salmon-derived resources, and ontogenetic changes in their importance, remain poorly understood.

Here, we expand upon earlier studies and compare the trophic ecology of two resident stream fish before and after anadromous sockeye salmon (*Oncorhynchus nerka* Walbaum) arrive to spawn in southwest Alaska. We use data on the mass and energy content of food eaten by fish as inputs to a bioenergetics model to evaluate the impact of anadromous salmon on the growth potential of both resident species. We then use the bioenergetics model to predict how short-term changes in the stable isotope ratios of the diet of the resident fish would change their stable isotope signatures. We also consider a wide range of fish sizes to examine how the importance of marine-derived subsidies changes with age and growth.

Methods

Study site

We studied the diet, energy intake and stable isotope signatures of resident rainbow trout (*Oncorhynchus mykiss* Walbaum) and Arctic grayling (*Thymallus arcticus arcticus* Pallas) during summer 2001, from four streams that drain into Lake Nerka (59°34'N, 158°59'W), part of the Wood River catchment that

ultimately flows into Bristol Bay in southwest Alaska (for details see Moore *et al.*, 2004). In the streams studied (Lynx Creek, Hidden Lake Creek, Little Togiak River and Elva Creek), anadromous sockeye salmon (*O. nerka*) all spawn after 1 August (Rogers & Rogers, 1998), which thus marks the time when salmon eggs and carcasses become available for consumption by resident stream fish. Therefore, we divided our samples into two time periods: 'before' (26 June–21 July) and 'after' (13–30 August) the salmon arrived.

Field and laboratory protocols

We sampled resident fish with stick seines and angling, depending on fish size, stream flow and water depth. We caught a total of 28 rainbow trout and 31 grayling before salmon arrived and 24 rainbow trout and 23 grayling after the arrival of salmon, with no significant differences in the mean length or mass of the 'before-' or 'after-salmon' groups for either species (two-way ANOVA, species: $F_{1,87} = 1.2$, $P = 0.28$; time: $F_{1,87} = 0.11$, $P = 0.74$). Following collection, we transferred the fish to a 20-L holding container and anaesthetized them with a 50 ppm solution of MS-222 (tricaine methane sulphonate). Once fish lost their righting response (after 5–10 min), they were tagged with a unique alpha-numeric visual implant tag to ensure that the same fish was not sampled more than once. Next, we recorded their length and mass before sampling their diets via gastric lavage. The stomach contents of each fish were flushed into a 300 µm sieve, backwashed into individual sample jars and then preserved with 95% ethanol for later identification, counting and stable isotope analysis.

To assess the stable isotope composition of resident fish, we drew approximately 250 µL of blood from the caudal vein of each individual, using a sterile, 20-gauge hypodermic needle attached to a 1-mL syringe. Blood was then transferred to an individual vial containing 7 µL of Heparin as an anticoagulant and the vial placed on ice. In the laboratory, we spun each blood sample in a centrifuge for 5 min to separate the plasma and cell constituents, transferred the lighter plasma portion to a second vial with a pipette and then froze all samples for later isotopic analysis. We chose to analyse blood, because we had planned to measure the isotopic signature in both the cellular and

Table 1 List of dietary items found in resident rainbow trout and Arctic grayling and their associated energy densities (kJ g⁻¹ wet mass) and mean δ¹⁵N (‰) values

Diet item	Taxon	Energy density	δ ¹⁵ N
Salmon eggs	<i>Oncorhynchus nerka</i>	7.8*	11.0
Salmon flesh	<i>Oncorhynchus nerka</i>	1.3 [†]	10.7
Mayflies	Ephemeroptera	4.7	4.4
Stoneflies	Plecoptera	3.6	6.5
Caddisflies	Tricoptera	3.6	5.9
Beetles	Coleoptera	3.6	6.6
True flies	Diptera	2.6	6.6
Larval blowflies	Diptera: Calliphoridae	4.3	12.5
Snails	Gastropoda	1.8	5.4

Energy densities for salmon eggs and flesh come from Hendry & Berg (1999); all others come from Cummins & Wuycheck (1971).

*This value represents the energy density of eggs obtained during the 'spawning' phase and is less than the values obtained during the 'coastal' or 'freshwater entry' stages.

[†]This value represents the average energy density of soma obtained during the 'spawning' and 'death' phases and is less than the values obtained during the 'coastal' or 'freshwater entry' stages.

plasmid portions, which have relatively long and short turnover times, respectively. However, because of resource constraints we could only analyse the cellular portion. Furthermore, a recent study on fish shows that δ¹⁵N values in blood and muscle show similar responses to shifts in diet (Miller, 2006).

We sorted dietary items into coarse taxonomic groups (Table 1) and placed them into aluminium weighing boats. We then recorded the wet mass of the total sample of each diet type for each fish, dried the samples for 48 h at 70 °C and then recorded the dry mass. For each of the diet categories, we then selected four to 10 samples for stable isotope processing. Although there were no significant effects of species or time period on the mean mass of the sampled fish (two-way ANOVA, species: $F_{1,87} = 1.2$, $P = 0.28$; time: $F_{1,87} = 0.11$, $P = 0.74$), we estimated the total ration for each fish as the sum of all prey items corrected for fish mass (g of diet per g of fish mass) to account for any size-related differences in consumption. We took the energy density (i.e. energy per unit mass) of each prey item from the literature (Table 1) and applied these values to the wet mass of each category to derive the total energy intake. We assigned any unidentifiable portion of the dietary items (<6% in all cases) to the other categories in direct proportion to those observed.

Stable isotope analyses

For each of the dietary items, we transferred the dried sample to 7.5-mL vials, ground it to a fine powder with a glass rod that had been cleaned in ethanol and then placed *c.* 1 mg into small tin capsules. For the blood samples, we dried cell constituents for 48 h at 70 °C. We then pulverized the dried blood with a glass rod as above, before transferring *c.* 1 mg of the sample to a tin capsule, using a fine-tipped forceps that had been cleaned with ethanol. We sent all samples to the UC-Davis Stable Isotope Facility (3112 Plant and Environmental Sciences Bldg, Davis, CA, U.S.A.) where they analysed all samples with a Europa Hydra (Europa Scientific, Cambridge, U.K.) 20/20 continuous flow isotope ratio mass spectrometer. The machine precision is within 0.5% of the natural standard for nitrogen.

We concentrated on the stable isotopes of nitrogen, because salmon are enriched in the heavier isotope (¹⁵N) because of their foraging and growth in the ocean and, therefore, it serves as a useful tracer of salmon-derived nitrogen in freshwater food webs (Kline *et al.*, 1990, 1993). We expressed nitrogen stable isotope values on the δ scale, where the per mille difference from the standard is:

$$\delta^{15}\text{N} = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 1000, \quad (1)$$

and *R* corresponds to the ratio of ¹⁵N : ¹⁴N in the sample and standard (Peterson & Fry, 1987). The standard for nitrogen is atmospheric nitrogen gas, which has a $\delta^{15}\text{N} = 0$ by definition (Peterson & Fry, 1987).

Bioenergetics model

We modelled fish growth using the bioenergetics models presented by Hanson *et al.* (1997). For rainbow trout, we employed the parameter set from Railsback & Rose (1999), as modified from Hanson *et al.* (1997), except for the excretion and egestion equations. For those functions, we used eqn 1 and the corresponding parameter values from Hanson *et al.* (1997) because we did not have information on the proportion of digestible material in the different prey items. We utilized the bioenergetics parameters for Arctic grayling from Jones *et al.* (2003).

Model inputs included average daily water temperatures, prey proportions and energy densities and daily ration sizes. Temperatures were daily averages

across all four study streams and we assumed constant stream discharge and fixed the activity multiplier at 1.3 (Railsback & Rose, 1999). Mean daily rations were used to estimate consumption rates of both species; we estimated average daily ration for the time periods before and after salmon began spawning by taking observed mass of stomach contents and multiplying by 2.5, based on the temperature-dependent salmonid evacuation rates observed by He & Wurtsbaugh (1993). We then solved for the parameter *P*, the proportion of maximum consumption (*C*_{max}) for a given body size and temperature (Kitchell, Stewart & Weininger, 1977). For modelling simplicity, we assumed that the stomach content masses and prey proportions observed were indicative of a full 24-h diet (i.e. there was no diel variation).

We modelled daily trout and grayling growth under two scenarios: one in which diet proportions and daily ration followed observed patterns before and after the salmon spawning period (Figs 1 & 2) and a second in which diet proportions and daily ration remained at the pre-salmon conditions for the entire model period; these conditions represent what was observed and what might have occurred had salmon not been present. Initial masses of simulated rainbow trout and grayling were both 100 g. We began our model runs on 1 July, with 1 August as the transition point at which salmon entered the modelled system and ended the runs on 15 September, for a total time period of 76 days.

We coupled a stable isotope dynamic model to the bioenergetics model, following the method of Harvey

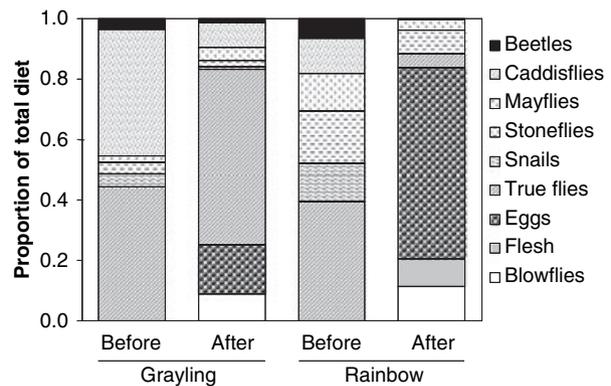


Fig. 1 Diet proportions of Arctic grayling and rainbow trout before and after the arrival of anadromous sockeye salmon. Larval blowflies (Diptera: Calliphoridae) are listed separately from other true flies.

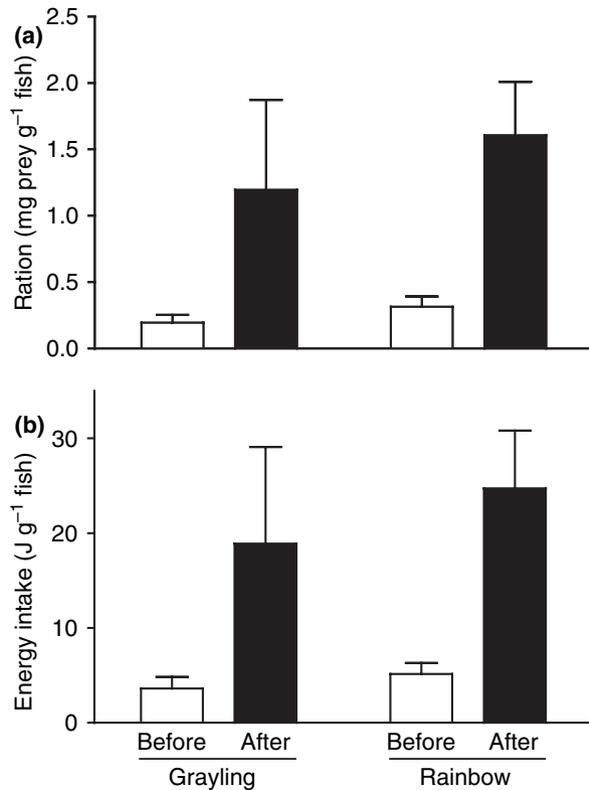


Fig. 2 Mean (+SD) ration size (a) and energy intake (b) of Arctic grayling and rainbow trout before and after the arrival of anadromous sockeye salmon on their spawning grounds.

et al. (2002). Growth estimates from the bioenergetics model, in terms of wet biomass on day t (B_t), were used to estimate the fish's $\delta^{15}\text{N}$ on day t (δ_t) via a stable isotope dilution equation:

$$\delta_t = [\delta_{t-1}B_{t-1} + (B_t - B_{t-1})(\delta_{\text{diet}} + \Delta)]/B_t - m[\delta_{t-1} - (\delta_{\text{diet}} + \Delta)], \quad (2)$$

where δ_{t-1} is the $\delta^{15}\text{N}$ of the fish on day $t-1$, δ_{diet} is the $\delta^{15}\text{N}$ of the diet (Table 1) with the contribution of each prey species weighted according to its occurrence in fish diets, Δ is the trophic fractionation of nitrogen ($\Delta = 3.4\text{‰}$; Minigawa & Wada, 1984) and m is a dimensionless metabolic turnover constant ($m = 0.0005$; Harvey *et al.*, 2002). We used the model to predict the integrated $\delta^{15}\text{N}$ of entire rainbow trout and Arctic grayling, based on diet observations and employing variability of delta values of predator and prey. We ran both species' models 500 times; in each run, initial fish δ -values were drawn randomly from distributions derived from field observations. Daily prey δ -values were also drawn randomly from empirically derived distributions. We also used

two-sample t -tests to compare the final stable isotope distributions from the two diet scenarios (i.e. with or without salmon present) to determine if the distributions were distinct, and we conducted power analysis to estimate the number of samples that would be required to detect a salmon effect on isotopic signature.

Results

We observed large shifts in the dietary composition of both rainbow trout and grayling after anadromous salmon arrived on their spawning grounds (Fig. 1). Beforehand, grayling consumed primarily larval dipterans (41%) and caddisflies (39%) with the remaining prey items constituting <6% each. Subsequently, grayling ate primarily larval dipterans (58%), but salmon eggs (16%) and larval blowflies (Diptera: Calliphoridae) (8%) also appeared in their diets. Before salmon arrived, rainbow trout also consumed largely dipterans (39%) along with similar proportions of caddisflies (11%), mayflies (12%) and stoneflies (18%). After the arrival of salmon, rainbow trout diets shifted to consist primarily of salmon eggs (64%), larval blowflies (Diptera: Calliphoridae) (11%) and salmon flesh (9%). Interestingly, both species ate some snails before salmon arrived (4% and 13% for grayling and rainbow trout, respectively), but snails dropped from their diets entirely after salmon arrived in the streams.

We found significant increases in the ration sizes and total energy intake for both species coincident with changes in their diet composition (Table 2; Fig. 2). Grayling ration size increased from $0.19 \pm 0.060 \text{ mg g}^{-1}$ (mean \pm SE) to $1.2 \pm 0.67 \text{ mg g}^{-1}$, while rainbow trout ration size increased from $0.32 \pm 0.076 \text{ mg g}^{-1}$ to $1.6 \pm 0.41 \text{ mg g}^{-1}$ (Fig. 2a). Similarly,

Table 2 ANOVA results comparing the changes in ration size (top) and energy intake (bottom) for grayling and rainbow trout (species) before and after the arrival of salmon on the spawning grounds (time). The sample size equals 106 in each case

Response	Factor	SS	d.f.	F	P-value
Ration size	Species	0.81	1	0.30	0.58
	Time	15	1	5.6	0.020
	Species \times time	0.24	1	0.089	0.77
Energy intake	Species	156	1	0.26	0.61
	Time	3489	1	5.8	0.019
	Species \times time	53	1	0.088	0.77

energy intake for grayling rose from $3.6 \pm 1.2 \text{ J g}^{-1}$ to $19 \pm 10 \text{ J g}^{-1}$ after the arrival of salmon, while energy intake for rainbow trout increased from $5.1 \pm 1.2 \text{ J g}^{-1}$ to $25 \pm 5.7 \text{ J g}^{-1}$ (Fig. 2b). We did not detect any significant effect of species or a species-by-time interaction (Table 2).

As the dietary composition of the resident fish shifted after the arrival of salmon, we also found differences in the stable isotope signature ($\delta^{15}\text{N}$) of their entire diets (Table 3; Fig. 3). For grayling, there were no changes over time (means of $6.3 \pm 0.63\text{‰}$ and $7.4 \pm 0.64\text{‰}$ for before and after, respectively), reflecting their continued reliance on aquatic invertebrates. For rainbow trout, however, we observed a significant increase in $\delta^{15}\text{N}$ from $6.1 \pm 0.43\text{‰}$ to $10.3 \pm 0.44\text{‰}$ after salmon resources were available, and fish switched to consuming primarily salmon eggs, salmon flesh and larval terrestrial blowflies with $\delta^{15}\text{N}$ values of 11.0, 10.7 and 12.5‰, respectively (Table 1). We found no change in dietary $\delta^{15}\text{N}$ with fish body

Table 3 ANCOVA results comparing the change in $\delta^{15}\text{N}$ of the diets for grayling and rainbow trout (species) before and after the arrival of salmon on the spawning grounds (time). Body size (mass) is the covariate. The overall model has a sample size of 106

Factor	SS	d.f.	F	P-value
Species	2.1	1	0.43	0.52
Time	21	1	4.3	0.043
Mass	7.4	1	1.5	0.23
Species × time	76	1	15	0.00022
Species × mass	0.76	1	0.15	0.70
Time × mass	0.20	1	0.040	0.84

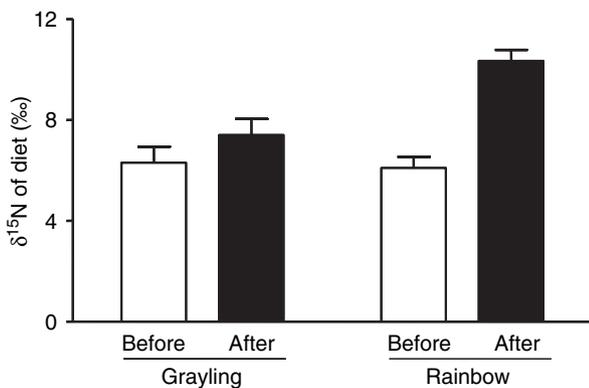


Fig. 3 Mass-weighted isotopic signature (mean + SD) of the entire diets for Arctic grayling and rainbow trout before and after the arrival of anadromous sockeye salmon.

mass or any significant interactions between species and body mass or time period and body mass (Table 3).

A lack of significant shift in the $\delta^{15}\text{N}$ of grayling diets was matched by a non-significant change in the stable isotope signature of grayling blood with increasing body mass (Fig. 4). On the other hand, the $\delta^{15}\text{N}$ of rainbow trout blood did show a significant increase with fish mass (linear regression, $R^2 = 0.33$, $F = 12.4$, $P = 0.0018$; Fig. 4), presumably resulting from their preference for salmon-derived resources with correspondingly high $\delta^{15}\text{N}$ values. Even if we exclude the four data points corresponding to fish >1500 g, the regression is still significant ($R^2 = 0.21$, $F = 9.16$, $P = 0.0047$). The overall high $\delta^{15}\text{N}$ for rainbow trout (maximum = 14.6‰) indicates heavy reliance on salmon-derived resources.

Our bioenergetics modelling demonstrated a strong effect of anadromous salmon on the growth rates of these resident fish (Fig. 5). Using the observed dietary proportions and ration sizes, we predicted that grayling would grow from 100 to 192 g in 76 days, nearly doubling their size in just 2.5 months. However, when we assumed that their ration size and energy intake would not change (e.g. in the absence of anadromous salmon), grayling growth was much less, such that they only gained 31 g over the same time period. For rainbow trout, we found a similar pattern. Using the empirically-derived ration size and diet composition, they grew from 100 to 183 g in 76 days. When we ignored their switch to salmon-derived resources and

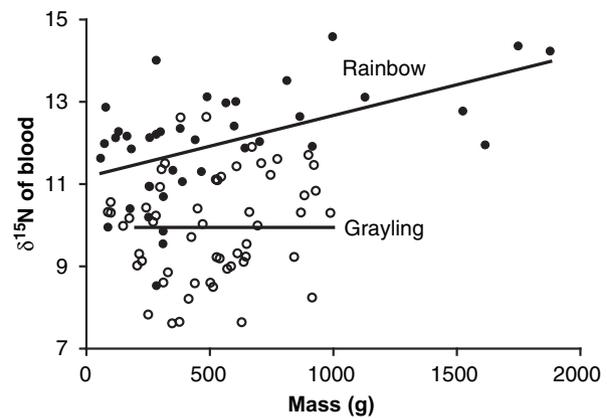


Fig. 4 Changes in the $\delta^{15}\text{N}$ signature of the blood from rainbow trout (closed circles) and Arctic grayling (open circles) with increasing fish mass. The regression line for Arctic grayling had a non-significant slope (see Results) and is therefore plotted as the mean. Data are for all sampling periods.

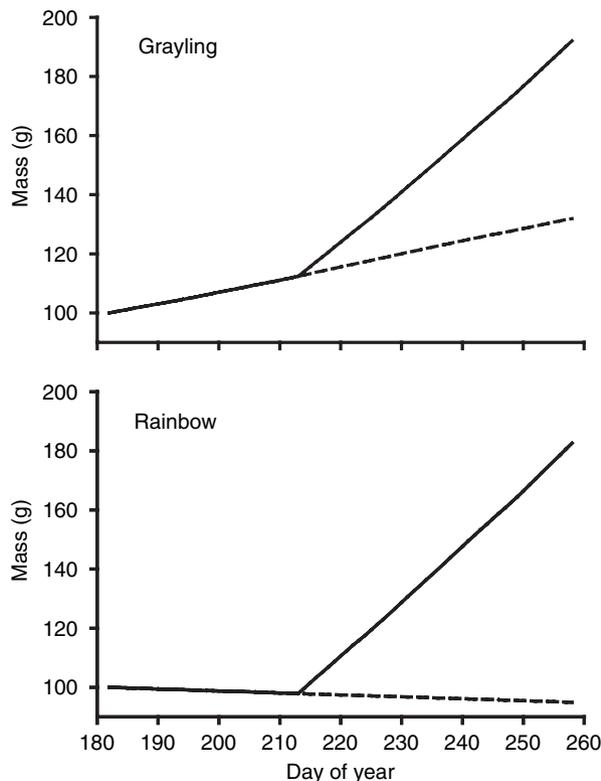


Fig. 5 Differences in the modelled growth trajectories for Arctic grayling and rainbow trout for two different diet scenarios. In the first (solid line), fish eat invertebrates until 1 August and then eat a mix of invertebrates and salmon-derived resources according to the observed diet proportions (see Fig. 1). In the second case, fish continue to eat invertebrates after 1 August as if no salmon resources were available (dashed line).

assumed that they simply continued to consume the same pre-salmon diet, rainbow trout actually lost 5 g over the same period.

The bioenergetics model also showed how shifts in diet by grayling and rainbow trout would affect their integrated stable isotope signatures (Fig. 6). Using the observed diet data as inputs, grayling demonstrated very little change in the mean $\delta^{15}\text{N}$ of their body tissues, increasing from 9.9 to just 10.3‰, but the difference was significant ($t = 8.22$, $P < 0.0001$). The $\delta^{15}\text{N}$ signature of rainbow trout, however, rose from 11.2 to 12.3‰ over the same growing period – also a significant change ($t = 16.2$, $P < 0.0001$). In the absence of salmon-derived resources, the model predicted that neither grayling nor rainbow trout would show any significant change in $\delta^{15}\text{N}$ over time (Fig. 6).

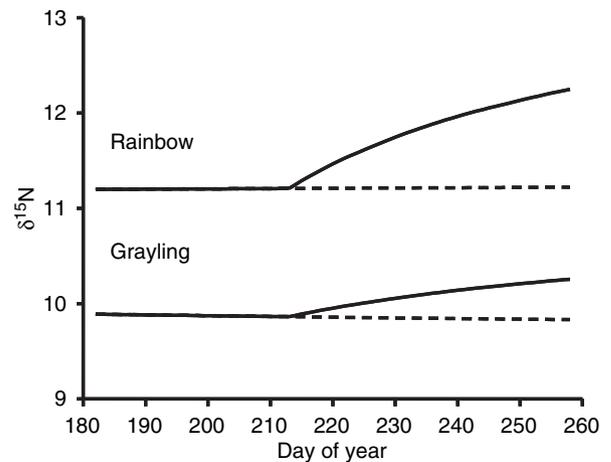


Fig. 6 The $\delta^{15}\text{N}$ signature for grayling and rainbow trout versus fish size as predicted from the bioenergetics model.

Discussion

Our results show obvious short- and long-term effects of anadromous sockeye salmon on resident stream fish. Following the arrival of salmon on their freshwater spawning grounds, the diets of resident grayling and rainbow trout shifted to include direct salmon resources and indirect subsidies, significantly increasing the total mass and energy content of their food intake over a few weeks. These salmon-derived resources represented not only an increase in food quantity, but also an increase in food quality because of the relatively high energy densities of salmon eggs and larval blowflies that feed on salmon carcasses (Table 1). The bioenergetics model suggested that these additional salmon-derived resources contributed a large proportion of the necessary energy for growth in both grayling and rainbow trout. Thus, while anadromous sockeye salmon spend only about 1 month on the spawning grounds in the Wood River system (Rogers & Rogers, 1998), their presence creates a pulse in food availability, with clear positive effects on the resident fish.

Previous work has also shown a variety of positive impacts of subsidies derived from adult salmon on various species of juvenile salmonids. Bilby *et al.* (1998) demonstrated that the additions of coho salmon (*Oncorhynchus kisutch* Walbaum) carcasses to small streams in southwestern Washington led to increased density and body condition of juvenile coho and steelhead (*O. mykiss*), and that eggs and salmon flesh dominated the diets of those fish during the 1 month

they were available. Following the addition of salmon carcasses to small experimental stream channels in southeast Alaska, Wipfli *et al.* (2003) found significant increases in the growth rates of juvenile cutthroat trout (*Oncorhynchus clarkii* Richardson) and Dolly Varden (*Salvelinus malma* Walbaum). Furthermore, in their artificial stream reaches without any salmon resources, juvenile coho salmon (*O. kisutch*) actually lost 16% of their body mass over the 9 week experiment – similar to our prediction from the bioenergetics model for rainbow trout based on the ‘no salmon’ scenario. Recently, Wilzbach *et al.* (2005) found that additions of chinook salmon (*Oncorhynchus tshawytscha* Walbaum) carcasses had some positive effect on the growth rates of young rainbow and cutthroat trout, but only in stream reaches where the riparian vegetation had been cut. Our study builds upon this growing body of evidence and is novel in three ways. First, while it did not involve experimental manipulations, it did occur in a natural ecosystem with a native fish community and all of the important organisms that affect the availability of salmon resources, including the sockeye salmon themselves, brown bears (*U. arctos*) and gulls (*Larus glaucescens* Naumann) (Quinn & Buck, 2000; Gende, Quinn & Willson, 2001). We also made use of naturally occurring live and dead salmon rather than adding carcasses experimentally. This is very important because salmon are more than simple bags of nutrients, but rather serve as ecosystem engineers via the large disturbance of sediments and benthic invertebrates (Moore *et al.*, 2004; Moore, 2006) while altering the foraging behaviour of stream fish (M.D. Scheuerell, J.W. Moore, D.E. Schindler, pers. obs). Secondly, we examined explicitly the composition, energy density, ration sizes and stable isotope composition of the diets of resident fish before and after anadromous salmon arrived. Thirdly, we then combined that information with a bioenergetics model to illustrate how changes in observed rations could affect the growth and stable isotope signature of two important members of the fish community, as would be expected in areas with drastically reduced runs of salmon (e.g. the Columbia River basin; Scheuerell *et al.*, 2005).

The apparent differences in dietary composition between grayling and rainbow trout (Fig. 1) illustrate four important pathways through which anadromous salmon positively affect stream communities. First, stream-resident fish directly consume the eggs

and carcasses of salmon. Secondly, a wide variety of benthic macroinvertebrates, including mayflies (Ephemeroptera), stoneflies (Plecoptera), caddisflies (Tricoptera) and true flies (Diptera), colonize carcasses within the stream and feed off of them directly (Wipfli *et al.*, 1998; Reimchen *et al.*, 2003; Winder *et al.*, 2005). Additionally, terrestrial blowflies (Diptera: Calliphoridae) will lay their eggs on carcasses stranded on gravel bars or the shoreline, with an average of 35 000 larval blowflies per sockeye salmon carcass typically devouring it within a week (Meehan, Seminet-Reneau & Quinn, 2005). Some of those larval blowflies are then washed into the streams and rivers because of floods or disturbance by bears, where they serve as food resources for fish (Cederholm *et al.*, 1989; Meehan *et al.*, 2005). Thirdly, nutrients from decomposing carcasses can increase stream primary productivity, subsequently leading to a greater biomass of the benthic invertebrates that fish feed upon (Wipfli *et al.*, 1998; Minakawa & Gara, 1999; Chaloner & Wipfli, 2002). Fourthly, nest-digging by adult salmon dislodges benthic invertebrates that are subsequently consumed by fish (Peterson & Foote, 2000).

Our results suggest that the direct consumption pathway is more important to rainbow trout, given the high proportion of eggs and flesh in their diets after the arrival of salmon. Grayling, in contrast, seemed to benefit most from the indirect production of macroinvertebrates. Earlier studies highlighted the positive responses of Arctic river food webs to fertilization, resulting in increased growth rates of grayling (Deegan & Peterson, 1992; Deegan *et al.*, 1999). Furthermore, physical disturbance of the substratum during excavation of redds (nests) by female salmon dislodges benthic invertebrates (Minakawa & Gara, 2003; Moore *et al.*, 2004). In an earlier study in the Wood River system, Peterson & Foote (2000) found that redd digging by sockeye salmon increased the drift of potential prey, and juvenile coho salmon had significantly higher numbers of chironomid larvae in their diets compared with pre-spawning conditions. In our case, grayling also appear to have exploited the increased invertebrate drift following the arrival of sockeye salmon. Furthermore, grayling from the Bristol Bay region of Alaska are among the largest at a given age of any population across their entire range (Northcote, 1995), perhaps in part because of the consistently high densities of spawning salmon.

The different diets of grayling and rainbow trout had disparate effects on their stable isotope signatures. Over the life cycle, the importance of salmon-derived resources to rainbow trout was evident in their increasing $\delta^{15}\text{N}$ signature with body size (Fig. 4). As a result of isotopic fractionation of nitrogen at each trophic level, a predator should, on average, be 3.4‰ higher than its prey base (Minigawa & Wada, 1984). Thus, each year when rainbow trout consume large quantities of ^{15}N -enriched salmon eggs, carcasses and larval blowflies, the $\delta^{15}\text{N}$ signature of their bodies also shifts upwards as the heavier isotope ^{15}N is subsequently transferred throughout the body. Therefore, as fish grow larger, they would require larger amounts of isotopically unique food to shift their stable isotope signature away from that indicating a reliance on salmon (i.e. high $\delta^{15}\text{N}$). Another hypothesis to explain the increase in dietary $\delta^{15}\text{N}$ of rainbow trout with increasing size is that larger fish feed on prey that are themselves feeding higher in the food web (e.g. on other fish). However, we found no effect of fish size on the $\delta^{15}\text{N}$ of the diet (Table 3), indicating that small fish consume salmon-derived resources in similar proportion to large fish. Grayling, on the other hand, did not show a systematic increase in their $\delta^{15}\text{N}$ signature with size, because of their tendency to continue eating invertebrates rather than switching to direct salmon resources. Regardless of size, both of these species would probably have much lower $\delta^{15}\text{N}$ signatures in the absence of salmon altogether. Kline *et al.* (1990) found that stream-dwelling rainbow trout upstream of a waterfall that blocked salmon access had $\delta^{15}\text{N}$ values about 5‰ lower than those fish below the anadromous barrier. In a later study, $\delta^{15}\text{N}$ values of rainbow trout, coastrange sculpin (*Cottus aleoticus* Gilbert), Dolly Varden (*S. malma*) and ninespine stickleback (*Pungitius pungitius* Linnaeus) from a lake without anadromous salmon were also 4.0–4.8‰ lower than those from a lake with salmon (Kline *et al.*, 1993).

As stable isotopes become increasingly popular for studying the energy and nutrient sources of organisms, data should be interpreted cautiously. Stable isotopes such as nitrogen are best used as long-term integrators of diet composition (Robinson, 2001), because consumers are not necessarily in isotopic equilibrium with their diets because of time lags related to trophic level, tissue turnover times and growth rates (Harvey *et al.*, 2002; Miller, 2006). For

example, Hesslein, Hallard & Ramlal (1993) noted from laboratory experiments that muscle in fast-growing broad whitefish (*Coregonus nasus* Pallas) had not reached isotopic equilibrium with their diet after 1 year although, interestingly, Miller (2006) found that muscle in relatively slow-growing Pacific herring (*Clupea pallasii* Valenciennes) did so after about 6 months. Further, the measurement of stable isotopes from a variety of tissues, as an indicator of recent and past consumption by fish, has shown very little difference in the rate of change between blood and muscle (Hesslein *et al.*, 1993; MacAvoy, Macko & Garman, 2001; Miller, 2006). These two tissues are commonly used to represent relatively fast and slow turnover times in mammals and birds (Tieszen *et al.*, 1983; Hobson & Clark, 1992; Cerling *et al.*, 2007). Given that blood has a tissue turnover time of approximately 1 month (Tieszen *et al.*, 1983), our post-salmon isotope samples for rainbow trout should show very little indication of their recent shift toward increased salmon-derived resources. Rather, direct diet measurements and time-integrated models were necessary. Over the long-term, however, the general increase in $\delta^{15}\text{N}$ of larger rainbow trout showed the effects of successive seasonal switches to salmon-derived resources.

Nitrogen stable isotopes offer a picture of the average diet composition, but we observed considerable variation in diet composition, mass and energy content over a relatively short time period. This variation includes individual differences in fish foraging behaviour, related to prey abundance and intra- and interspecific competition (Hughes, 1992; Merrick, Hershey & McDonald, 1992; Hughes, 1998; O'Brien, Barfield & Sigler, 2001; Railsback *et al.*, 2005). Therefore, parsing out the amount of variation caused by individual differences in diet versus the effects of species and organism size is indeed important. For example, our bioenergetics model predicted a significant difference in the final $\delta^{15}\text{N}$ of both rainbow trout and grayling between the pre- and post-salmon conditions. While our data indicated that we might expect a change for rainbow trout, we found no systematic change in the $\delta^{15}\text{N}$ of grayling with body size (Fig. 4). However, the power of the statistical tests was low. In order to be 95% sure of not committing a type-II error (i.e. failing to recognize that the populations are different), we would need 52 samples of rainbow trout and 194 samples of grayling.

This study took place in an area with very large runs of anadromous salmon – approximately one million adult sockeye salmon ‘escape’ the Bristol Bay fishery each year and spawn in the Wood River system (Hilborn *et al.*, 2003). In other regions, such as southwest Canada and the northwest U.S.A., however, runs of anadromous salmon have declined considerably over the past 50 years (Gresh, Lichatowich & Schoonmaker, 2000; Schoonmaker *et al.*, 2003). The import of marine-derived nutrients and carbon into these freshwater and riparian ecosystems is now several orders of magnitude less than it was historically and the impacts on the biota could be substantial (Gresh *et al.*, 2000; Scheuerell *et al.*, 2005). Indeed, reductions in marine subsidies have led to decreased productivity in food webs with subsequent negative effects on juvenile salmonids (Bilby *et al.*, 1998; Minakawa & Gara, 1999; Wipfli *et al.*, 2003).

Efforts to rehabilitate depleted salmon runs are now supported by policies to restore properly functioning biogeochemical cycles (Lackey, 2003; Wipfli, Hudson & Caouette, 2004). Although the addition of inorganic fertilizers can increase the productivity of streams and lead to better conditions for salmon (Johnston *et al.*, 1990; Wilson *et al.*, 2003), they do not contain the carbon-based proteins and lipids found in salmon carcasses that are important for invertebrates, mammals, birds and fish (Wipfli *et al.*, 1998; Chaloner & Wipfli, 2002; Gende *et al.*, 2002, 2004). Artificial carcass analogues, often made from hatchery fish, offer some promise because their chemical composition is similar to salmon carcasses (Wipfli *et al.*, 2004). Nevertheless, our results highlight the direct importance of salmon to the trophic ecology of resident fish. Furthermore, we must not forget that live salmon do more than simply import nutrients and carbon. They also act as ‘ecosystem engineers’ by physically disturbing streambeds, mobilizing sediments, reducing periphyton abundance and displacing benthic invertebrates (Moore *et al.*, 2004; Moore, 2006). Our study demonstrates the large changes in composition, size, energy content and stable isotope signature of the diets of resident fish following the arrival of anadromous salmon, thereby highlighting the importance of different trophic pathways for moving salmon-derived resources to various resident species. This further justifies the need to consider explicitly all aspects of the fish community (e.g. species, size, age) when evaluating the entire spectrum of benefits that

Pacific salmon provide to freshwater and surrounding riparian ecosystems.

Acknowledgments

This is a contribution of the Alaska Salmon Program at the University of Washington, funded by the National Science Foundation and the Bristol Bay salmon processing industry. We thank Anne Carlson, Brandon Chasco, Tessa Francis, Ray Hilborn, Jennifer Jones, Wendy Palen, Laura Payne, Jennifer Scheuerell and Bob Scheuerell for help with fish collections and sample processing. Tessa Francis also provided additional stable isotope data for invertebrates. Stable isotope samples were processed with funding to MDS from the Ford Foundation. John Williams, Rich Zabel, Alan Hildrew and two anonymous reviewers provided helpful comments on earlier versions of the manuscript.

References

- Baxter C.V., Fausch K.D. & Saunders W.C. (2005) Tangled webs: reciprocal flows of invertebrate prey link streams and riparian zones. *Freshwater Biology*, **50**, 201–220.
- Ben-David M., Flynn R.W. & Schell D.M. (1997) Annual and seasonal changes in diets of martens: evidence from stable isotope analysis. *Oecologia*, **111**, 280–291.
- Ben-David M., Hanley T.A. & Schell D.M. (1998) Fertilization of terrestrial vegetation by spawning Pacific salmon: the role of flooding and predator activity. *Oikos*, **83**, 47–55.
- Bilby R.E., Fransen B.R. & Bisson P.A. (1996) Incorporation of nitrogen and carbon from spawning coho salmon into the trophic system of streams: evidence from stable isotopes. *Canadian Journal of Fisheries and Aquatic Sciences*, **53**, 164–173.
- Bilby R.E., Fransen B.R., Bisson P.A. & Walter J.K. (1998) Response of juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead (*Oncorhynchus mykiss*) to the addition of salmon carcasses to two streams in southwestern Washington, U.S.A. *Canadian Journal of Fisheries and Aquatic Sciences*, **55**, 1909–1918.
- Carlton J.T. & Hodder J. (2003) Maritime mammals: terrestrial mammals as consumers in marine intertidal communities. *Marine Ecology – Progress Series*, **256**, 271–286.
- Cederholm C.J., Houston D.B., Cole D.L. & Scarlett W.J. (1989) Fate of coho salmon (*Oncorhynchus kisutch*) carcasses in spawning streams. *Canadian Journal of Fisheries and Aquatic Sciences*, **46**, 1347–1355.

- Cerling T.E., Ayliffe L.K., Dearing M.D., Ehleringer J.R., Passey B.H., Podlesak D.W., Torregrossa A.M. & West A.G. (2007) Determining biological tissue turnover using stable isotopes: the reaction progress variable. *Oecologia*, **151**, 175–189.
- Chaloner D.T. & Wipfli M. (2002) Influence of decomposing Pacific salmon carcasses on macroinvertebrate growth and standing stock in southeastern Alaska streams. *Journal of the North American Benthological Society*, **21**, 430–442.
- Chaloner D.T., Martin K.M., Wipfli M.S., Ostrom P.H. & Lamberti G.A. (2002) Marine carbon and nitrogen in southeastern Alaska stream food webs: evidence from artificial and natural streams. *Canadian Journal of Fisheries and Aquatic Sciences*, **59**, 1257–1265.
- Cummins K.W. & Wuycheck J.C. (1971) Caloric equivalents for investigations in ecological energetics. *Mitteilungen der Internationale Vereinigung für Theoretische und Angewandte Limnologie*, **18**, 1–158.
- Deegan L.A. & Peterson B.J. (1992) Whole-river fertilization stimulates fish production in an Arctic tundra river. *Canadian Journal of Fisheries and Aquatic Sciences*, **49**, 1890–1901.
- Deegan L.A., Golden H.E., Harvey C.J. & Peterson B.J. (1999) Influence of environmental variability on the growth of age-0 and adult Arctic grayling. *Transactions of the American Fisheries Society*, **128**, 1163–1175.
- Gende S.M., Quinn T.P. & Willson M.F. (2001) Consumption choice by bears feeding on salmon. *Oecologia*, **127**, 372–382.
- Gende S.M., Edwards R.T., Willson M.F. & Wipfli M.S. (2002) Pacific salmon in aquatic and terrestrial ecosystems. *BioScience*, **52**, 917–928.
- Gende S.M., Quinn T.P., Willson M.F., Heintz R. & Scott T.M. (2004) Magnitude and fate of salmon-derived nutrients and energy in a coastal stream ecosystem. *Journal of Freshwater Ecology*, **19**, 149–160.
- Gresh T., Lichatowich J. & Schoonmaker P. (2000) An estimation of historic and current levels of salmon production in the northeast Pacific ecosystem: evidence of a nutrient deficit in the freshwater systems of the Pacific Northwest. *Fisheries*, **25**, 15–21.
- Hanson P.C., Johnson T.B., Schindler D.E. & Kitchell J.F. (1997) *Fish Bioenergetics 3.0*. University of Wisconsin Sea Grant Institute, Madison, WI.
- Harvey C.J., Hanson P.C., Essington T.E., Brown P.B. & Kitchell J.F. (2002) Using bioenergetics models to predict stable isotope ratios in fishes. *Canadian Journal of Fisheries and Aquatic Sciences*, **59**, 115–124.
- He E. & Wurtsbaugh W.A. (1993) An empirical model of gastric evacuation rates for fish and an analysis of digestion in piscivorous brown trout. *Transactions of the American Fisheries Society*, **122**, 717–730.
- Helfield J.M. & Naiman R.J. (2002) Salmon and alder as nitrogen sources to riparian forests in a boreal Alaskan watershed. *Oecologia*, **133**, 573–582.
- Helfield J.M. & Naiman R.J. (2006) Keystone interactions: salmon and bear in riparian forests of Alaska. *Ecosystems*, **9**, 167–180.
- Hendry A.P. & Berg O.K. (1999) Secondary sexual characters, energy use, senescence, and the cost of reproduction in sockeye salmon. *Canadian Journal of Zoology*, **77**, 1663–1675.
- Hesslein R.H., Hallard K.A. & Ramlal P. (1993) Replacement of sulfur, carbon, and nitrogen in tissue of growing broad whitefish (*Coregonus nasus*) in response to a change in diet traced by $\delta^{34}\text{S}$, $\delta^{13}\text{C}$, and $\delta^{15}\text{N}$. *Canadian Journal of Fisheries and Aquatic Sciences*, **50**, 2071–2076.
- Hilborn R., Quinn T.P., Schindler D.E. & Rogers D.E. (2003) Biocomplexity and fisheries sustainability. *Proceedings of the National Academy of Sciences*, **100**, 6564–6568.
- Hilderbrand G.V., Hanley T.A., Robbins C.T. & Schwartz C.C. (1999) Role of brown bears (*Ursus arctos*) in the flow of marine nitrogen into a terrestrial ecosystem. *Oecologia*, **121**, 546–550.
- Hilderbrand G.V., Farley S.D., Robbins C.T., Hanley T.A., Titus K. & Servheen C. (1996) Use of stable isotopes to determine diets of living and extinct bears. *Canadian Journal of Zoology*, **74**, 2080–2088.
- Hobson K.A. & Clark R.G. (1992) Assessing avian diets using stable isotopes. 2. Factors influencing diet-tissue fractionation. *Condor*, **94**, 189–197.
- Hughes N.F. (1992) Selection of positions by drift feeding salmonids in dominance hierarchies: model and test for Arctic grayling (*Thymallus arcticus*) in sub-Arctic mountain streams, interior Alaska. *Canadian Journal of Fisheries and Aquatic Sciences*, **49**, 1999–2008.
- Hughes N.F. (1998) A model of habitat selection by drift-feeding stream salmonids at different scales. *Ecology*, **79**, 281–294.
- Johnston N.T., Perrin C.J., Slaney P.A. & Ward B.R. (1990) Increased juvenile salmonid growth by whole-river fertilization. *Canadian Journal of Fisheries and Aquatic Sciences*, **47**, 862–872.
- Jones N.E., Tonn W.M., Scrimgeour G.J. & Katapodis C. (2003) Productive capacity of an artificial stream in the Canadian Arctic. *Canadian Journal of Fisheries and Aquatic Sciences*, **60**, 849–863.
- Kawaguchi Y., Taniguchi Y. & Nakano S. (2003) Terrestrial invertebrate inputs determine the local abundance of stream fishes in a forested stream. *Ecology*, **84**, 701–708.
- Kitchell J.F., Stewart D.J. & Weininger D. (1977) Applications of a bioenergetics model to yellow perch (*Perca flavescens*) and walleye (*Stizostedion vitreum vitreum*).

- Journal of the Fisheries Research Board of Canada*, **34**, 1922–1935.
- Kline T.C. Jr., Goering J.J., Mathisen O.A. & Poe P.H. (1990) Recycling of elements transported upstream by runs of Pacific Salmon: I. $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ evidence in Sashin Creek, southeastern Alaska. *Canadian Journal of Fisheries and Aquatic Sciences*, **47**, 136–144.
- Kline T.C. Jr., Goering J.J., Mathisen O.A. & Poe P.H. (1993) Recycling of elements transported upstream by runs of Pacific Salmon: II. $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ evidence in the Kvichak River Watershed, Bristol Bay, southwestern Alaska. *Canadian Journal of Fisheries and Aquatic Sciences*, **50**, 2350–2365.
- Lackey R.T. (2003) Nutrient addition to restore salmon runs: considerations for developing environmental protection policies and regulations. In: *Nutrients in Salmonid Ecosystems: Sustaining Production and Biodiversity* (Ed. J. Stockner), pp. 283–285. American Fisheries Society Symposium 34, Bethesda, MD.
- Levy S. (1997) Pacific salmon bring it all back home. *BioScience*, **47**, 657–660.
- MacAvoy S.E., Macko S.A. & Garman G.C. (2001) Isotopic turnover in aquatic predators: quantifying the exploitation of migratory prey. *Canadian Journal of Fisheries and Aquatic Sciences*, **58**, 923–932.
- Meehan E.P., Seminet-Reneau E.E. & Quinn T.P. (2005) Bear predation on Pacific salmon facilitates colonization of carcasses by fly maggots. *American Midland Naturalist*, **153**, 142–151.
- Merrick G.W., Hershey A.E. & McDonald M.E. (1992) Salmonid diet and the size, distribution, and density of benthic invertebrates in an Arctic lake. *Hydrobiologia*, **240**, 225–233.
- Miller T.W. (2006) Tissue-specific response of $\delta^{15}\text{N}$ in adult Pacific herring (*Clupea pallasii*) following an isotopic shift in diet. *Environmental Biology of Fishes*, **76**, 177–189.
- Minakawa N. & Gara R.I. (1999) Ecological effects of a chum salmon (*Oncorhynchus keta*) spawning run in a small stream of the Pacific northwest. *Journal of Freshwater Ecology*, **14**, 327–335.
- Minakawa N. & Gara R.I. (2003) Effects of chum salmon redd excavation on benthic communities in a stream in the Pacific northwest. *Transactions of the American Fisheries Society*, **132**, 598–604.
- Minigawa M. & Wada E. (1984) Stepwise enrichment of ^{15}N along food chains: further evidence and the relation between $\delta^{15}\text{N}$ and animal age. *Geochimica et Cosmochimica Acta*, **48**, 1135–1140.
- Mitchell N.L. & Lamberti G.A. (2005) Responses in dissolved nutrients and epilithon abundance to spawning salmon in southeast Alaska streams. *Limnology and Oceanography*, **50**, 217–227.
- Moore J.W. (2006) Animal ecosystem engineers in streams. *BioScience*, **56**, 237–246.
- Moore J.W. & Schindler D.E. (2004) Nutrient export from freshwater ecosystems by anadromous sockeye salmon (*Oncorhynchus nerka*). *Canadian Journal of Fisheries and Aquatic Sciences*, **61**, 1582–1589.
- Moore J.W., Schindler D.E. & Scheuerell M.D. (2004) Disturbance of freshwater habitats by anadromous salmon in Alaska. *Oecologia*, **139**, 298–308.
- Naiman R.J., Bilby R.E., Schindler D.E. & Helfield J.M. (2002) Pacific salmon, nutrients, and the dynamics of freshwater and riparian ecosystems. *Ecosystems*, **5**, 399–417.
- Northcote T.G. (1995) Comparative biology and management of Arctic and European grayling (Salmonidae, *Thymallus*). *Reviews in Fish Biology and Fisheries*, **5**, 141–194.
- O'Brien W.J., Barfield M. & Sigler K. (2001) The functional response of drift-feeding Arctic grayling: the effects of prey density, water velocity, and location efficiency. *Canadian Journal of Fisheries and Aquatic Sciences*, **58**, 1957–1963.
- Orr A.J., Banks A.S., Mellman S., Huber H.R., DeLong R.L. & Brown R.F. (2004) Examination of the foraging habits of Pacific harbor seal (*Phoca vitulina richardsi*) to describe their use of the Umpqua River, Oregon, and their predation on salmonids. *Fishery Bulletin*, **102**, 108–117.
- Pace M.L., Cole J.J., Carpenter S.R., Kitchell J.F., Hodgson J.R., Van de Bogert M.C., Bade D.L., Kritzberg E.S. & Bastviken D. (2004) Whole-lake carbon-13 additions reveal terrestrial support of aquatic food webs. *Nature*, **427**, 240–243.
- Peterson D.P. & Foote C.J. (2000) Disturbance of small-stream habitat by spawning sockeye salmon. *Transactions of the American Fisheries Society*, **129**, 924–934.
- Peterson B.J. & Fry B. (1987) Stable isotopes in ecosystem studies. *Annual Review of Ecology and Systematics*, **18**, 293–320.
- Polis G.A. & Hurd S.D. (1995) Extraordinarily high spider densities on islands: flow of energy from the marine to terrestrial food webs and the absence of predation. *Proceedings of the National Academy of Sciences of the U.S.A.*, **92**, 4382–4386.
- Polis G.A., Anderson W.B. & Holt R.D. (1997) Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. *Annual Review of Ecology and Systematics*, **28**, 289–316.
- Polis G.A., Power M.E. & Huxel G.R. (2004) *Food Webs at the Landscape Scale*. The University of Chicago Press, Chicago, IL.
- Quinn T.P. & Buck G.B. (2000) Scavenging by brown bears, *Ursus arctos*, and glaucous-winged gulls, *Larus*

- glaucescens*, on adult sockeye salmon, *Oncorhynchus nerka*. *Canadian Field Naturalist*, **114**, 217–223.
- Railsback S.F. & Rose K.A. (1999) Bioenergetics modeling of stream trout growth: temperature and food consumption effects. *Transactions of the American Fisheries Society*, **128**, 241–256.
- Railsback S.F., Harvey B.C., Hayse J.W. & LaGory K.E. (2005) Tests of theory for diel variation in salmonid feeding activity and habitat use. *Ecology*, **86**, 947–959.
- Reimchen T.E., Mathewson D., Hocking M.D., Moran J. & Harris D. (2003) Isotopic evidence for enrichment of salmon-derived nutrients in vegetation, soil, and insects in riparian zones in coastal British Columbia. In: *Nutrients in Salmonid Ecosystems: Sustaining Production and Biodiversity* (Ed. J. Stockner), pp. 59–69. American Fisheries Society Symposium 34, Bethesda, MD.
- Robinson D. (2001) Delta ¹⁵N as an integrator of the nitrogen cycle. *Trends in Ecology & Evolution*, **16**, 153–162.
- Rogers D.E. & Rogers B.J. (1998) *Spawning Ground Surveys in the Wood River Lakes*. Alaska Salmon Program, Technical Report No. FRI-UW-9803, University of Washington, Seattle, WA.
- Roth J.D. (2002) Temporal variability in arctic fox diet as reflected in stable-carbon isotopes; the importance of sea ice. *Oecologia*, **133**, 70–77.
- Scheu S. (2001) Plants and generalist predators as links between the below-ground and above-ground system. *Basic and Applied Ecology*, **2**, 3–13.
- Scheuerell M.D., Levin P.S., Zabel R.W., Williams J.G. & Sanderson B.L. (2005) A new perspective on the importance of marine-derived nutrients to threatened stocks of Pacific salmon (*Oncorhynchus* spp.). *Canadian Journal of Fisheries and Aquatic Sciences*, **62**, 961–964.
- Schindler D.E., Scheuerell M.D., Moore J.W., Gende S.M., Francis T.B. & Palen W.J. (2003) Pacific salmon and the ecology of coastal ecosystems. *Frontiers in Ecology and the Environment*, **1**, 31–37.
- Schoonmaker P.K., Gresh T., Lichatowich J. & Radtke H.D. (2003) Past and present Pacific salmon abundance: bioregional estimates for key life history stages. In: *Nutrients in Salmonid Ecosystems: Sustaining Production and Biodiversity* (Ed. J. Stockner), pp. 33–40. American Fisheries Society Symposium 34, Bethesda, MD.
- Tieszen L.L., Boutton T.W., Tesdahl K.G. & Slade N.A. (1983) Fractionation and turnover of stable carbon isotopes in animal tissues: implications for $\delta^{13}\text{C}$ analysis of diet. *Oecologia*, **57**, 32–37.
- Willson M.F., Gende S.M. & Marson B.H. (1998) Fishes and the forest. *BioScience*, **48**, 455–462.
- Wilson G.A., Ashley K.I., Land R.W. & Slaney P.A. (2003) Experimental enrichment of two oligotrophic streams rivers in south coastal British Columbia. In: *Nutrients in Salmonid Ecosystems: Sustaining Production and Biodiversity* (Ed. J. Stockner), pp. 149–162. American Fisheries Society Symposium 34, Bethesda, MD.
- Wilzbach M.A., Harvey B.C., White J.L. & Nakamoto R.J. (2005) Effects of riparian canopy opening and salmon carcass addition on the abundance and growth of resident salmonids. *Canadian Journal of Fisheries and Aquatic Sciences*, **62**, 58–67.
- Winder M., Schindler D.E., Moore J.W., Johnson S.P. & Palen W.J. (2005) Do bears facilitate transfer of salmon resources to aquatic macroinvertebrates? *Canadian Journal of Fisheries and Aquatic Sciences*, **62**, 2285–2293.
- Wipfli M.S., Hudson J. & Caouette J. (1998) Influence of salmon carcasses on stream productivity: response of biofilm and benthic macroinvertebrates in southeastern Alaska, U.S.A. *Canadian Journal of Fisheries and Aquatic Sciences*, **55**, 1503–1511.
- Wipfli M.S., Hudson J.P. & Caouette J.P. (2004) Restoring productivity of salmon-based food webs: contrasting effects of salmon carcass and salmon carcass analog additions on stream-resident salmonids. *Transactions of the American Fisheries Society*, **133**, 1440–1454.
- Wipfli M.S., Hudson J.P., Caouette J.P. & Chaloner D.T. (2003) Marine subsidies in freshwater ecosystems: Salmon carcasses increase the growth rates of stream-resident salmonids. *Transactions of the American Fisheries Society*, **132**, 371–381.
- Wood C.C., Hargreaves N.B., Rutherford D.T. & Emmett B.T. (1993) Downstream and early marine migratory behavior of sockeye salmon (*Oncorhynchus nerka*) smolts entering Barkley Sound, Vancouver Island. *Canadian Journal of Fisheries and Aquatic Sciences*, **50**, 1329–1337.

(Manuscript accepted 16 May 2007)