

Evidence of energy and nutrient transfer from invasive pink salmon (*Oncorhynchus gorbuscha*) spawners to juvenile Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) in northern Norway

Kathy Dunlop¹  | Antti P. Eloranta^{2,3} | Erik Schoen⁴ | Mark Wipfli⁵ |
Jenny L.A. Jensen⁶ | Rune Muladal⁷ | Guttorm N. Christensen⁶

¹Institute of Marine Research, Tromsø, Norway

²Department of Biological and Environmental Science, University of Jyväskylä, Jyväskylä, Finland

³Norwegian Institute for Nature Research, Trondheim, Norway

⁴Institute of Arctic Biology, University of Alaska Fairbanks, Fairbanks, AK, USA

⁵U.S. Geological Survey, Alaska Cooperative Fish and Wildlife Research Unit, Institute of Arctic Biology, University of Alaska Fairbanks, Fairbanks, AK, USA

⁶Akvaplan-niva AS, Fram Centre, Tromsø, Norway

⁷Naturtjenester i Nord, Tromsø, Norway

Correspondence

Kathy Dunlop, Institute of Marine Research, 9007 Tromsø, Norway.
Email: katherine.mary.dunlop@hi.no

Funding information

FRAM - High North Research Centre for Climate and the Environment. Terrestrial Flagship.

Abstract

Recent large influxes of non-native Pacific pink salmon (*Oncorhynchus gorbuscha*) to North European rivers have raised concern over their potential negative impacts on native salmonids and recipient ecosystems. The eggs and carcasses of semelparous pink salmon may provide a significant nutrient and energy subsidy to native biota, but this phenomenon has not been widely documented outside the species' native distribution. We analysed the stomach contents and stable isotope values ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) in muscle and liver tissues of juvenile Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) to determine whether these native salmonids utilise marine-derived nutrients and energy provided by pink salmon eggs and carcasses in the subarctic river system Vesterelva, northern Norway. Although egg foraging and assimilation of marine-derived nutrients in fish body tissues were found to be minor at the population level, a few juvenile salmon and trout had recently eaten large quantities of pink salmon eggs. Some of these individuals also had high $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values, indicating a long-term diet subsidised by marine-derived nutrients and energy from pink salmon eggs. Hence, our study provides novel evidence that the eggs of invasive pink salmon may provide an energetic, profitable food resource for juvenile native fish. More research is needed to understand the broader ecological implications for fishes and other biota in river ecosystems invaded by pink salmon.

KEYWORDS

egg predation, marine-derived nutrients, non-native salmonids, resource subsidy, stable isotope analysis, subarctic river

1 | INTRODUCTION

Invasions by non-native species are among the major global threats to biodiversity and natural structure and function of both terrestrial

and aquatic ecosystems (Early et al., 2016; Rahel & Olden, 2008). Besides predation and competition with native species that utilise overlapping habitat and food resources, non-native species can alter fundamental ecosystem processes via, for example, altered nutrient

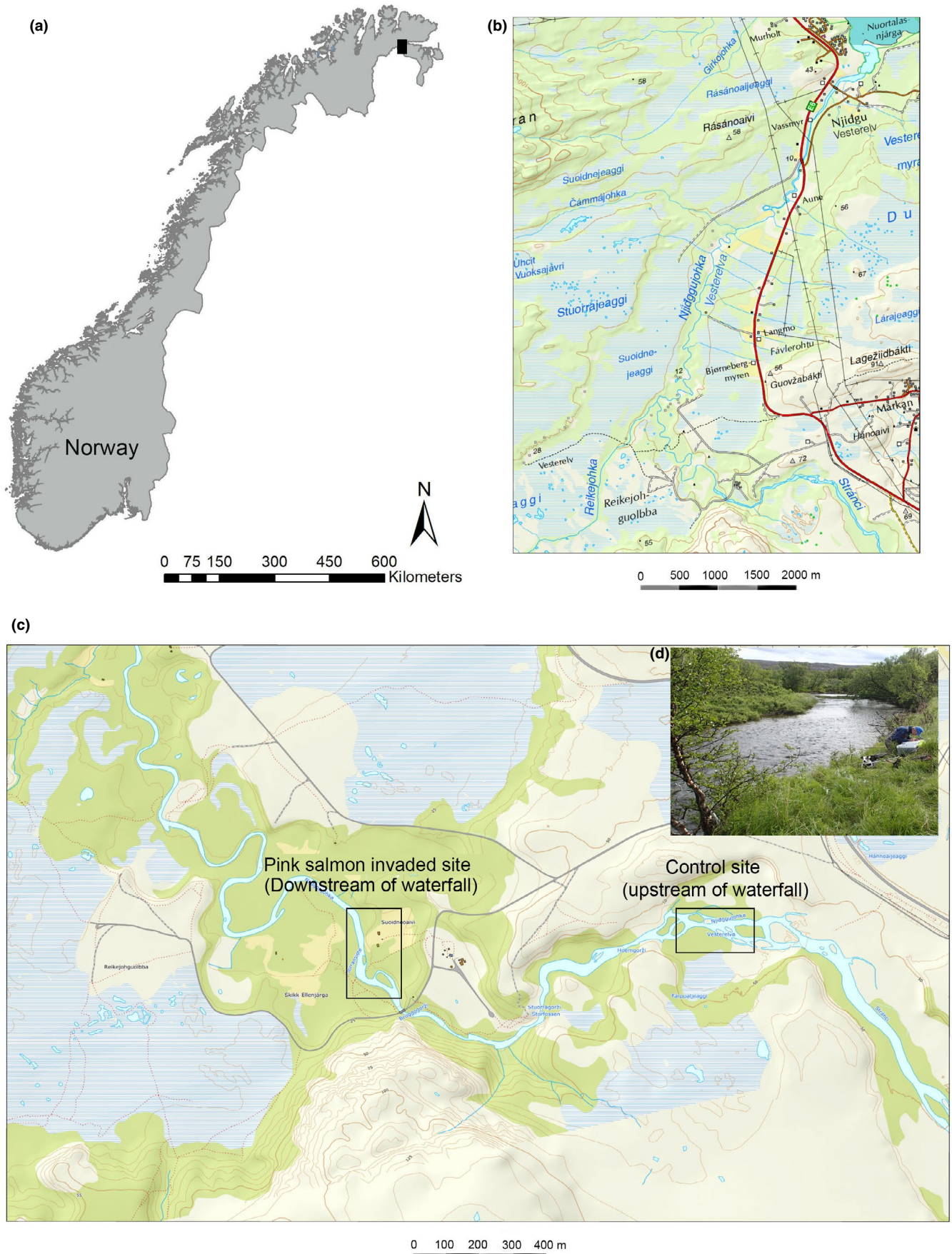


FIGURE 1 Map illustrating the position of Vesterelva in (a) Troms og Finnmark county, northern Norway and (b) in relation to Varangerbotn, Nesseby Municipality. Map (c) depicts the position of the study site invaded by Pacific pink salmon (WGS84: 70.118659, 28.505109) downstream of the waterfall (70.115514, 28.506976) and the control study site upstream of the waterfall (70.116457, 28.530815). Image (d) shows a section of Vesterelva river downstream of the waterfall that was invaded by pink salmon in July 2019. Maps (b) and (c) extracted from www.norgeskart.no

cycling and food-web dynamics (David et al., 2017; Jo et al., 2017). Some non-native species migrate between distinct ecosystems to complete their life cycles. This is the case with anadromous fishes whose juvenile stages rely heavily on riverine ecosystems, but whose adult stages spend one or multiple years feeding in the sea prior to returning to their natal rivers to spawn (Jonsson & Jonsson, 2009). Hence, non-native anadromous fishes may have particularly widespread and complex impacts across multiple connected ecosystems (Schindler et al., 2003).

Pink salmon (*Oncorhynchus gorbuscha*) is an anadromous and semelparous species native to the northern Pacific. Pink salmon fry generally emerge from the spawning gravel during spring, migrate directly to the sea and feed in the ocean for roughly 18 months before returning as mature fish to the river to spawn and die (Heard, 1991). Pink salmon generally spawn in the lower reaches of rivers that are periodically influenced by marine water (Heard, 1991), although in some rivers they migrate >200 km inland (e.g., Rine et al., 2016). During spawning, the female excavates a depression (or redd) in the gravel, where she lays between 1,200 and 1,900 eggs, which she subsequently covers with a gravel layer (Heard, 1991; McNeil & Ahnell, 1964).

Pink salmon were first introduced to Europe in coastal north-eastern Russia between 1956 and 1957 (Sandlund et al., 2019), and Russian stocking programmes continued until 1999 (Zubchenko et al., 2004). Following this introduction, pink salmon catches began to be recorded in neighbouring Finnmark County, northern Norway, in the 1960s (Bjerknes & Vaag, 1980). An increase in pink salmon number has occurred in northern Norway over the past 20 years, and peaks in numbers were experienced in both 2017 and 2019 (Moe et al., 2018; Sandlund et al., 2019). During each of these peak years, an estimated tens of thousands of pink salmon migrated into rivers along the Norwegian coast, with 70%–80% of these pink salmon entering rivers in the Varanger region (R. Muladal, Naturtjenesteri Nord, unpublished data). This sudden rise in the numbers of pink salmon has led to concern over the ecological effect of the species on freshwater and marine ecosystems (Sandlund et al., 2019). A primary concern regarding the introduction of pink salmon is potential negative interactions with native freshwater fishes, such as Atlantic salmon (*Salmo salar*), brown trout (*Salmo trutta*) and Arctic charr (*Salvelinus alpinus*). Potential interactions include competition over spawning sites, the spread of diseases, oxygen depletion in rivers from the decomposition of adult carcasses, competition for food between pink salmon fry and juvenile native fish, and hybridisation with native salmonids (Hindar et al., 2020; Sandlund et al., 2019). Knowledge is, however, currently limited on the nature and impacts of these interactions (Hindar et al., 2020; Jonsson & Jonsson, 2018).

The large body of research conducted on the ecological role of Pacific salmon in their native range (e.g., Quinn, 2018; Schindler et al., 2003; Wipfli & Baxter, 2010) provides a valuable resource to identify and estimate the impact of potential interspecific interactions between pink salmon and other salmonids in invaded areas. Pacific salmon runs deliver nutrients and energy to numerous coastal Pacific freshwater ecosystems (Cederholm et al., 1999; Gende et al., 2004). The marine-derived nutrients (MDN) and energy provided by Pacific salmon eggs and carcasses increase production of low trophic levels (biofilm and freshwater and terrestrial invertebrates; Wipfli et al., 1998; Wipfli et al., 1999) and provide a direct food source to juvenile salmonids (Bilby et al., 1998; Cederholm et al., 1999; Wipfli et al., 2003).

Salmonid eggs have a particularly high energy density (7–12 kJ/g wet mass), higher than aquatic invertebrates, which in general provide 3–5 kJ/g wet mass (Armstrong, 2010; Cummins & Wuycheck, 1971). This makes salmon eggs a highly profitable food source in freshwater ecosystems. There is considerable evidence of stream-resident salmonids feeding on Pacific salmon eggs from the Pacific Northwest United States (Bilby et al., 1998; Wipfli, 2009), Alaska (Denton et al., 2010; Scheuerell et al., 2007), and the North American Great Lakes, where pink, Chinook (*Oncorhynchus tshawytscha*), and coho salmon (*O. kisutch*) have been introduced (Johnson et al., 2016). In a tributary of Salmon River (NY), juvenile Atlantic salmon and brown trout, species native to the tributaries of the Great Lakes, were observed to feed on Pacific salmon eggs (Johnson et al., 2016; Johnson & Ringler, 1979; Stauffer, 1971). Age-2 and older brown trout fed heavily on coho salmon eggs in the fall (Stauffer, 1971) and eggs constituted >90% of the diets of young brown trout (Johnson & Ringler, 1979). Further studies in tributaries of Salmon River found that Pacific salmon eggs and carcass tissue represented an important dietary component to subyearling Atlantic salmon in both the fall and spring (Johnson et al., 2016). Juvenile Atlantic salmon have also been observed to feed on the eggs of pink salmon in the rivers Indera and Pulonga, Kola Peninsula, north-eastern Russia (Rasputina et al., 2016). The consumption of pink salmon eggs has been observed to increase the growth and condition of juvenile fish and is thought to have the potential to enhance overwintering survival (Johnson et al., 2009, 2016; Johnson & Ringler, 1979).

In light of these findings, the main objective of this study was to determine whether native juvenile Atlantic salmon and brown trout are feeding on eggs and assimilated MDN of introduced Pacific pink salmon in northern Norway. This work specifically examines the importance of pink salmon eggs compared to other food items in the diets of Atlantic salmon and brown trout and examines the assimilation of MDN into fish tissue. Stomach contents analysis (SCA) was used to quantify the

TABLE 1 Summary of stomach content (SCA) and stable isotope (SIA) data from juvenile Atlantic salmon and brown trout sampled during and after pink salmon spawning

Period	Site	Species	Fork length (mm)	Weight (g)	N _{SCA}	N _{SIA}	SIA muscle tissue		SIA liver tissue	
							$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)
During	Invaded	Salmon	83.1 ± 6.3	9.4 ± 1.4	18	22	-27.30 ± 0.24	7.76 ± 0.17	-28.18 ± 0.29	7.05 ± 0.18
During	Invaded	Trout	73.3 ± 6.1	7.9 ± 1.7	24	27	-27.30 ± 0.16	7.21 ± 0.10	-28.22 ± 0.18	6.19 ± 0.16
During	Control	Salmon	93.4 ± 3.3	9.4 ± 0.9	10	10	-27.22 ± 0.29	7.44 ± 0.21	-28.09 ± 0.31	6.43 ± 0.20
During	Control	Trout	86.6 ± 6.0	9.8 ± 2.5	11	12	-27.18 ± 0.19	6.93 ± 0.13	-27.75 ± 0.16	5.73 ± 0.16
After	Invaded	Salmon	67.6 ± 4.7	4.4 ± 0.8	30	30	-27.23 ± 0.21	7.62 ± 0.10	-28.20 ± 0.21	6.99 ± 0.14
After	Invaded	Trout	73.1 ± 7.8	6.0 ± 1.5	9	9	-27.29 ± 0.45	7.50 ± 0.12	-27.98 ± 0.49	6.35 ± 0.10
After	Control	Salmon	95.4 ± 10.1	8.5 ± 2.6	12	12	-27.88 ± 0.46	7.26 ± 0.22	-28.79 ± 0.72	6.82 ± 0.57
After	Control	Trout	79.0 ± 9.3	7.6 ± 3.0	8	8	-27.47 ± 0.46	7.19 ± 0.19	-28.70 ± 0.44	6.00 ± 0.26

Note: Fork length, weight, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ are given as mean values ± SE.

most recent, ingested diet, while stable isotope analysis (SIA) of nitrogen ($\delta^{15}\text{N}$) and carbon ($\delta^{13}\text{C}$) was used to evaluate the long-term transfer and assimilation of MDN from pink salmon eggs and carcasses to body tissues of native Atlantic salmon and brown trout. For this, the stomach contents and $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of both species were compared between two study periods (i.e., during versus after pink salmon spawning) and two study sites (i.e., invaded versus uninvaded control river section). In addition, stable isotopes were also analysed in two fish body tissues (i.e. muscle versus liver) with contrasting isotopic turnover rates. The potential foraging of Atlantic salmon and brown trout on pink salmon eggs and carcasses was expected to be reflected as enriched, marine $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values (a) following pink salmon spawning, (b) in invaded site as compared to an uninvaded control site, and (c) in liver tissue as compared to muscle tissue SIA values. While the muscle tissue reflects the consumer diet over the past few weeks or months, the liver tissue with a faster turnover rate typically reflects the assimilated diet over the past few days (e.g. Guelinckx et al., 2007).

Moreover, the MDN transfer to Atlantic salmon and brown trout is expected to depend on the individuals' size, with small individuals likely unable to eat relatively large-sized eggs due to gape limitation (Armstrong et al., 2010). Therefore, the contribution of pink salmon eggs to diet and the transfer of MDN was examined across a range of juvenile salmonid sizes. Finally, an estimate is provided of the energy made available to native juvenile salmonids from pink salmon eggs in the study river in northern Norway. Combined, this work represents one of the first published studies in Northern Europe to examine the ecological effect of MDN subsidies from the introduced pink salmon on commercially and recreationally important native salmonids and freshwater food webs.

2 | MATERIAL AND METHODS

2.1 | Area description

The study was conducted in the River Vesterelva in eastern Troms and Finnmark county, northern Norway. Vesterelva is ca. 19.6 km long and drains to the innermost part of the Varangerfjord (70°N,

28°E) (Figure 1a,b). The river has an average width of 7 m and an annual mean flow of 2.5 m³/s. Native salmonids, Atlantic salmon, brown trout and Arctic charr, spawn in the River Vesterelva during the October to November period, that is after non-native Pacific pink salmon that spawns in late summer (August). A small waterfall with a fish ladder is located ca. 8.9 km upstream from the sea and allows native salmonids to pass further upstream. It is known from anadromous fish counting using snorkelling studies in 2017 and catches in 2017 and 2019 that no pink salmon were observed above the waterfall and ladder. These barriers were too steep for pink salmon to transcend and therefore separated the upstream control site that was uninvaded by pink salmon and the otherwise comparable site invaded by pink salmon downstream of the waterfall (Figure 1c). The river is slow flowing and meanders over gravel substratum with a few areas with somewhat more rapid water and coarser substratum below the waterfall. The riparian zone below the waterfall is heavily vegetated primarily by birch (*Betula* spp.) and willow (*Salix* spp.), and surrounded by rocky terrain, birch forest and some farmed land in the lower stretches. The river above the waterfall runs through rocky terrain with sparse vegetation and has a mix of gravel and coarse riverbed substratum. Native fish species observed during fieldwork were primarily Atlantic salmon and brown trout, and three-spined sticklebacks (*Gasterosteus aculeatus*) were also seen downstream and upstream of the waterfall. In late summer 2017 and 2019, some of the highest densities of pink salmon in Norway were recorded in Vesterelva.

2.2 | Fish capture and sampling

Brown trout and Atlantic salmon juveniles were collected using a portable backpack electrofishing gear system on the 23–24 August 2019 (during pink salmon spawning) and 25–26 September 2019 (after pink salmon spawning). Electrofishing sampling was conducted within a ~300-m stretch of river in and around the invaded site (Figure 1c,d) where pink salmon were observed to spawn downstream of the waterfall. During the spawning period of pink salmon,

many pink salmon were observed to be spawning in the impacted region and the timing was unsuitable for the spawning of native salmonids. Native salmonids were also sampled in the uninvaded control site with similar substratum above the waterfall (Figure 1c). The densities of juvenile Atlantic salmon and brown trout have not been quantified in the river stretches above and below the waterfall. However, based on knowledge of the river morphology, information from fishers and our observations and sampling efforts during electrofishing, densities appeared to be similar in the invaded and uninvaded control sites. In the time period during pink salmon spawning, 22 Atlantic salmon and 27 brown trout juveniles were sampled in the invaded river section ($n = 49$) and 10 Atlantic salmon and 12 brown trout in the control site ($n = 22$). After spawning, 30 Atlantic salmon and nine brown trout were sampled in the invaded site ($n = 39$) and 12 Atlantic salmon and eight brown trout in the control site ($n = 20$; Table 1). The majority of these juvenile fish, particularly brown trout, were caught close to the riverbank. The fish were kept in a 10 L bucket and euthanised prior to sampling by an overdose (5 ml/L) of 2-phenoxy-ethanol (EC No 204-589-7; SIGMA Chemical Co.).

During the August sampling, stomach contents were collected from larger fish (>55 mm fork length, F_L) by gastric lavage, due to the advantages it provides in immediately stopping digestion and preserving stomach contents for easier identification. This technique becomes difficult and less effective on smaller fish, and thus fish under 55 mm were not lavaged. For lavaged fish, filtered stream water was injected into fish stomachs using a 10-ml syringe assembly, forcing stomach contents out of the fishes' mouths (Meehan & Miller, 1978). Stomach contents and associated water were preserved in Whirl-pak® plastic bags with an equal or greater volume of 96% ethanol for later analysis in the laboratory. The fish were thereafter frozen and dissected in the laboratory to ensure stomachs were completely emptied. Smaller individuals collected during August and all fish collected during the September sampling were frozen within 1.5 hr after euthanasia and dissected later in the laboratory.

2.3 | Stomach content analysis (SCA)

Fish stomach contents were analysed using two approaches. During pink salmon spawning, a detailed mass-based approach was used for the SCA of the large size class of fish ($F_L > 55$ mm) to compare the diet proportions by mass and ration size between the invaded and control sites. A second rapid volumetric approach was applied to characterise overall dietary patterns for fish with a $F_L < 55$ mm during the spawning period. The rapid volumetric method was also used to analyse the stomach contents of all fish sampled in September, after the pink salmon spawning. Both approaches are appropriate for food web and energy flow studies (Chipps & Garvey, 2007); however, the resulting diet composition estimates were not directly comparable. Thus, we restricted our analysis to quantitative comparisons between sampling strata analysed using the same approach.

The detailed mass-based diet analysis was based on measurements of individual prey items identified in each stomach content sample. Prey items were identified to family and classified as aquatic or terrestrial, with aquatic insects further subdivided into aquatic juveniles or winged adults. Intact prey items were measured for body length (mm), and the lengths of partially digested prey were estimated based on intact items of the same taxon that appeared similar in size (Wipfli, 1997). Intact salmon eggs were measured for diameter (mm), and the diameters of collapsed egg membranes that remained in one piece were estimated. The dry masses of invertebrate prey items and salmon eggs were estimated using published taxon-specific length-mass relationships. The wet masses of prey fish found in salmonid stomachs were estimated using a length-mass relationship for salmonids captured in this study:

$$M = 0.00856F_L^{3.06}$$

where M is wet mass (mg) and F_L is fork length (mm) ($n = 128$, $r^2 = .98$, $p < .00001$). Dry masses of prey fish were estimated by multiplying wet masses by a literature value of 25.5% dry matter for juvenile Atlantic salmon (Jonsson & Jonsson, 2003). Diet composition was calculated in terms of proportions by mass pooled across all fish, and the frequency of occurrence of each prey type in fish stomachs was calculated to evaluate the degree of specialisation on particular prey (Chipps & Garvey, 2007). The ration size of each fish was calculated as the total energy (J) of the reconstructed stomach contents, divided by fish mass (g wet) to allow for comparison of energy intake among differently sized consumers (Armstrong et al., 2010). Linear models were run to test whether ration sizes were affected by the individuals' size (i.e., fork length), species identity (salmon versus trout), sampling site (invaded versus control), and presence-absence of eggs in individuals' stomach contents. The full model was specified as:

$$\text{Ration size} = \text{ForkLength} + \text{Species} + \text{Site} + \text{EggsInStomach} + \epsilon.$$

where ϵ is the error term. Model selection was performed by stepwise removal of terms to minimise AIC_c , using the dredge function in the MuMIn v. 1.42.1 package (Barton, 2016) in R (R Core Team, 2018).

For the rapid volumetric diet analysis, the total stomach fullness was visually estimated on a percentage scale ranging from empty (0%) to full (100%). The prey items were identified to species, genus or family level and their relative contribution to the total fullness was estimated following the relative-fullness method (Amundsen & Sánchez-Hernández, 2019). Diet composition was calculated in terms of proportions by volume (Chipps & Garvey, 2007).

2.4 | Stable isotope analysis

Fresh samples of muscle and liver tissue were dissected from a subsample of Atlantic salmon ($n_{\text{muscle}} = 74$; $n_{\text{liver}} = 65$) and brown trout ($n_{\text{muscle}} = 56$; $n_{\text{liver}} = 54$) caught in both study sites and periods (Table 1). In addition, pink salmon eggs ($n = 7$) and muscle

tissue of adult pink salmon ($n = 5$) caught in Vesterelva in July 2019 were collected to obtain reference SIA data of MDN. For graphical illustration of the river food web and reference SIA data of typical freshwater and terrestrial food sources for native salmonids, qualitative samples of aquatic ($n = 110$) and terrestrial ($n = 47$) invertebrates were collected in both study sites before (15 July 2019) and after (26–27 September 2019) pink salmon spawning, with a 500- μm kick net and a sweep net, respectively. Both aquatic and terrestrial invertebrate samples were identified to the lowest feasible taxonomic level and cleaned from detritus and other unwanted material prior to storage in Eppendorf tubes. Only the soft body tissue was dissected from molluscs and case-building trichopteran larvae.

The nonpreserved tissue samples were kept frozen at -20°C prior to freeze-drying and homogenisation into fine powder. From each sample, 0.300–0.800 mg of powder was weighed and encapsulated into a tin cup prior to final analysis at the University of Jyväskylä, Finland, conducted using a FlashEA 1112 elemental analyser (Thermo Fisher Scientific Corporation) coupled to a Thermo Finnigan DELTAplus Advantage mass spectrometer. Stable nitrogen and carbon isotope ratios are expressed as delta values ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, respectively) relative to the international standards for nitrogen (atmospheric nitrogen) and carbon (Vienna Pee Dee Belemnite). Pike (*Esox lucius*) white muscle tissue with known isotopic composition was used as an internal working standard and inserted in each run after every five samples. In each run, standard deviation of the internal standard was $<0.25\%$ for $\delta^{15}\text{N}$ and 0.13% for $\delta^{13}\text{C}$.

The SIAR (Stable Isotope Analysis in R, version 4.2; Parnell et al., 2010) isotopic mixing model was used to estimate the relative reliance of Atlantic salmon and brown trout on marine (i.e., MDN), freshwater and terrestrial food sources. The SIAR model was run separately for the consumer (i.e., Atlantic salmon and brown trout) muscle and liver SIA data as input data. The commonly used trophic fractionation factors of $3.4 \pm 1.0\%$ for $\delta^{15}\text{N}$ and $0.4 \pm 1.3\%$ for $\delta^{13}\text{C}$ were used (Post, 2002). The marine, freshwater and terrestrial baselines ("sources") were calculated as the mean $\pm$ SD $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of all pink salmon and of selected invertebrate samples obtained from both study sites and periods, including terrestrial Hemiptera and Brachycera and aquatic Ephemeroptera and Trichoptera larvae. For obtained SIAR estimates, nonoverlapping 95% Bayesian credibility intervals are interpreted as significant differences between study sites, periods and fish tissue types.

Linear models were run to test whether the fish muscle and liver $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values were affected by the species identity (salmon versus trout), sampling site (invaded versus control), period (during versus after pink salmon spawning), and individuals' size (i.e., fork length). To account for the potential contrasting ontogenetic dietary shifts of salmon and trout, a two-way interaction between species and fork length was also included in the full model:

$$Y = \text{Species} + \text{Site} + \text{Period} + \text{ForkLength} + \text{Species:ForkLength} + \epsilon.$$

where Y is the individual's $\delta^{15}\text{N}$ or $\delta^{13}\text{C}$ value and ϵ is the error term. The models were run separately for fish muscle and liver SIA data.

Model selections for the SCA and SIA data were performed by stepwise removal of terms to minimise AIC, using the dredge function in the MuMIn v. 1.42.1 package (Barton, 2016) in R (R Core Team, 2018). The best final models are summarised in Table 2. Finally, paired t test was used to test whether the fish liver tissue was consistently enriched in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ as compared to the muscle tissue, indicating a recent shift of individual fish to increased reliance on MDN. Moreover, if some individuals had eaten eggs based on SCA, their SIA values were visually inspected to evaluate whether egg foraging had only been incidental or a long-term feeding strategy as indicated by elevated $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values. All statistical analyses were performed using R computing program v. 3.5.1 (R Core Team, 2018).

2.5 | Energy availability from eggs

Eggs were collected from a single mature pink salmon female in the lower reaches of Vesterelva on 20 August 2019. The female still retained her silver colouring indicating that she had not yet initialised spawning. The eggs were oven-dried at 50°C until a constant dry mass was achieved and then homogenised by grinding. The energy density of the eggs (kJ/g wet mass) was determined using a bomb calorific method using an IKA calorimeter C6000 in isoperibol mode. Individual egg content (kJ) was used to calculate the energy made available to Atlantic salmon and brown trout that had fed on pink salmon eggs. In addition, to estimate the potential energy subsidy to the river food web from pink salmon eggs, the mean energy content of an individual pink salmon egg was multiplied by the number of eggs produced per pink salmon female (1,200–1,900 eggs; Heard, 1991). The number of pink salmon entering and spawning in Vesterelva during the study period was estimated from pink salmon catches recorded in 2017 and 2019 and snorkelling counts from 2017 (Berntsen et al., 2020; R. Muladal, unpublished data). The snorkelling studies followed the Norwegian standard for "visual registration of anadromous salmonids in watercourses." In summary, this involved a single diver travelling with the passive flow of the river, while recording the number, species, sex and size of each anadromous fish observed within the defined river stretch. The energy provided by eggs from each individual female was further multiplied by the estimated range of female pink salmon in Vesterelva in 2019.

3 | RESULTS

3.1 | Fish stomach contents

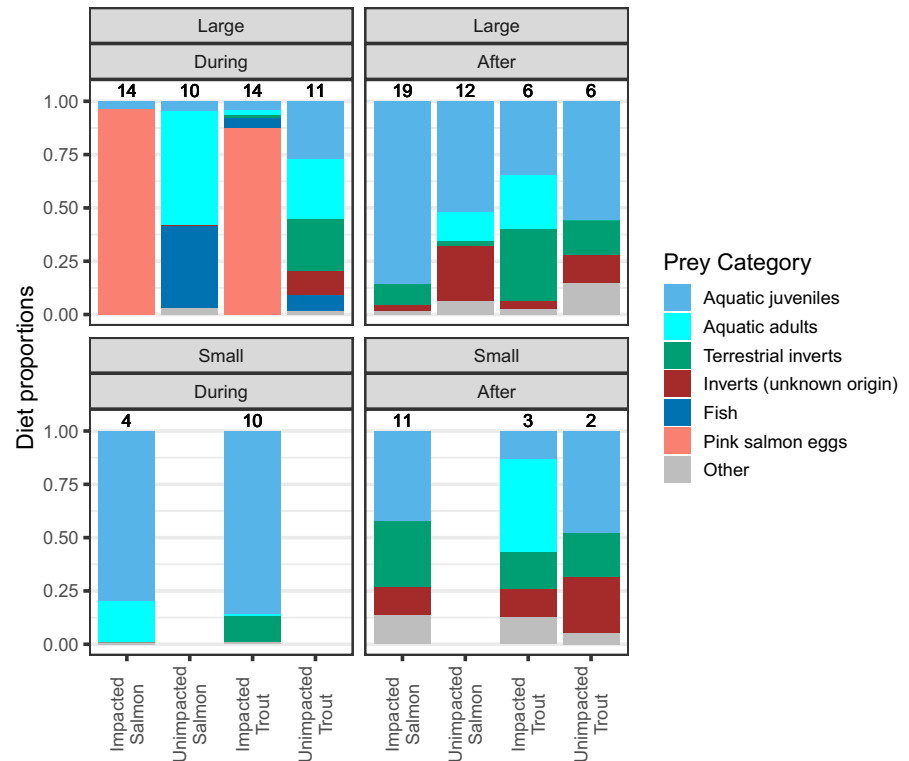
During the pink salmon run in August, pink salmon eggs were consumed by some larger juvenile Atlantic salmon ($n = 2$) and brown trout ($n = 3$) in the invaded site, whereas neither species consumed

TABLE 2 Summary of the most supported (lowest AIC) final models for the effects of individual's size (fork length, mm), sampling period (before versus during pink salmon spawning), site (invaded versus control site) and species identity (Atlantic salmon versus brown trout) on $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of fish muscle and liver tissues, and on the ration size of juvenile native salmonids

	Parameter	Estimate	SE	t-value	p	-95% CI	+95% CI
<i>Muscle $\delta^{15}\text{N}$</i>	Intercept	6.967	0.193	36.09	<.001	6.584	7.349
	ForkLength	0.007	0.002	3.31	.001	0.003	0.011
	Period	0.151	0.101	1.50	.137	-0.049	0.351
	Site	-0.325	0.105	-3.11	.002	-0.532	-0.118
	Species	-0.235	0.100	-2.35	.020	-0.434	-0.037
<i>Liver $\delta^{15}\text{N}$</i>	Intercept	5.614	0.235	23.89	<.001	5.148	6.080
	ForkLength	0.016	0.002	6.40	<.001	0.011	0.020
	Period	0.302	0.123	2.46	.015	0.059	0.546
	Site	-0.586	0.127	-4.60	<.001	-0.839	-0.334
	Species	-0.636	0.122	-5.22	<.001	-0.878	-0.395
<i>Liver $\delta^{13}\text{C}$</i>	Intercept	-29.010	0.333	-87.00	<.001	-29.671	-28.350
	ForkLength	0.010	0.004	2.55	.012	0.002	0.018
<i>Ration size</i>	Intercept	26.40	15.23	1.734	.0895	-4.235	57.033
	EggsInStomach	674.43	47.67	14.148	<.001	578.530	770.329

Note: The final model predicting ration size included only the additional binary factor of egg consumption (0 = no eggs, 1 = eggs in stomach contents). Standard error (SE), t- and p-values, as well as 95% confidence intervals (CI) for each parameter are shown, with significant parameters highlighted in bold ($p < .05$).

FIGURE 2 The diet composition of juvenile Atlantic salmon and brown trout during and after the pink salmon spawning period, at invaded (downstream) and control (upstream) site. Data shown are for the large (fork length ≥ 55 mm) and small (fork length < 55 mm) size classes of each species. Diet proportions were calculated in terms of mass for large fish during the spawning run (top left panel) and in terms of volume for all other panels. Numerals above bars indicate the number of fish sampled



eggs in the control site (Figure 2). However, in general pink salmon eggs were an uncommon prey item found in the stomachs of only 14% of large (>55 mm FL) juvenile Atlantic salmon and 20% of large juvenile brown trout in the invaded site (Table S1). However, due to

their large size, pink salmon eggs dominated the overall diet composition of both species in terms of mass, comprising 96% and 87% of the diet of all large Atlantic salmon and brown trout, respectively (Figure 2). The fish with eggs in their stomachs were all >80 mm in

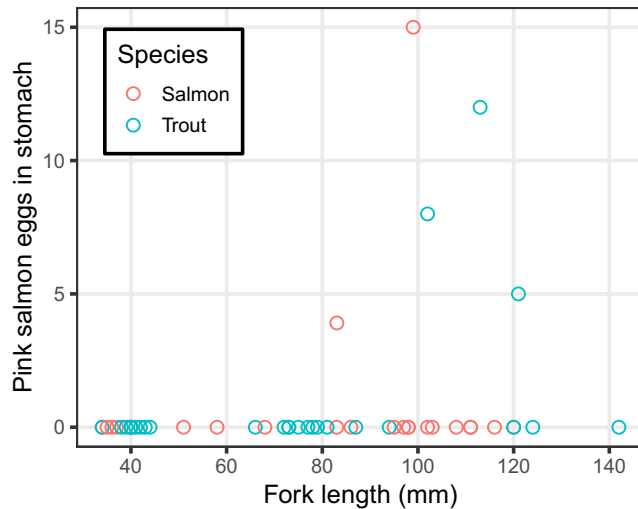


FIGURE 3 Numbers of intact pink salmon eggs identified in stomach contents of juvenile Atlantic salmon and brown trout captured downstream of a barrier to pink salmon migration during August 2019. Numerous additional fragments of egg membranes were not quantified

F_L (Figure 3). Aquatic invertebrates comprised most of the remainder diets of >55 mm Atlantic salmon and brown trout. Juvenile aquatic insects comprised (by volume) 80% and 85% of the diets of small Atlantic salmon and brown trout, respectively, by volume at the downstream invaded site. By contrast, in the upstream control site, pink salmon eggs were not present in fish stomachs (Figure 2). Large Atlantic salmon had mainly eaten adult aquatic insects and fish, whereas large brown trout had preyed upon immature and adult aquatic insects. No small fish were sampled for stomach contents at the control site during the spawning run.

After spawning, no pink salmon eggs were observed in juvenile salmon and brown trout stomachs, and the diet composition of both species was more similar between the invaded and control sites and between the large and small size classes (Figure 2). At the invaded downstream site, the diets of salmon (both size classes combined) were composed of immature aquatic insects, terrestrial insects and other food items. Adult and immature aquatic invertebrates and terrestrial invertebrates also largely featured in the diets of trout. At the uninhabited upstream site, salmon also fed predominantly on aquatic invertebrates, but here adult aquatic insects and invertebrates of unknown origin constituted a greater proportion of the diet, whereas terrestrial insects featured less compared to the invaded site. The diets of trout sampled upstream were composed primarily of aquatic juvenile invertebrates, as well as other prey and terrestrial insects (17%).

Consumption of pink salmon eggs during spawning increased the ration of the larger size class (>55 mm FL) of juvenile Atlantic salmon and brown trout by 1–2 orders of magnitude (Figure S1). The most parsimonious model of ration size included only a positive effect of egg consumption ($AIC_c = 0$; Table 2). A model including egg consumption and a negative effect of fork length received somewhat less support from the data ($AIC_c = 1.28$), indicating that larger fish

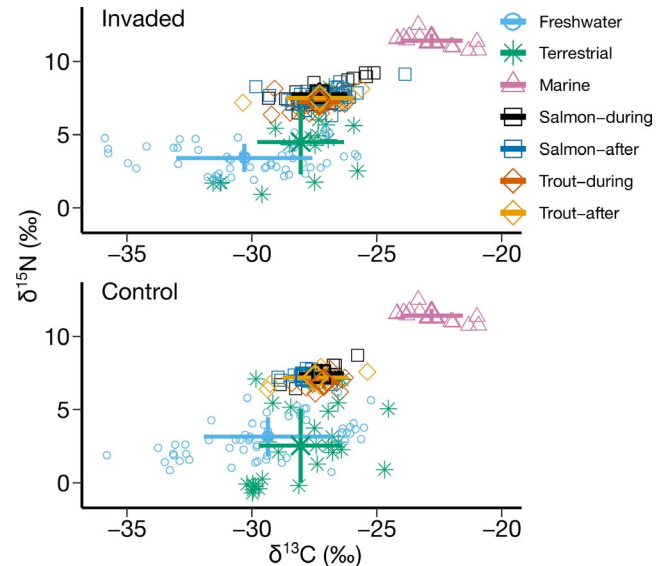


FIGURE 4 Stable isotope biplots showing the individual and mean $\pm$ SD $\delta^{13}C$ and $\delta^{15}N$ values of Atlantic salmon and brown trout muscle tissue sampled during and after pink salmon spawning, as well as the $\delta^{13}C$ and $\delta^{15}N$ values of freshwater, terrestrial and marine food resources. Biplots for invaded downstream and control upstream sites are shown

had relatively smaller ration sizes, in proportion to their body mass. Models including species and sampling site received relatively little support from the data ($AIC_c > 2$), indicating that these factors did not strongly influence ration size. Within the invaded site, the fish with eggs in their stomachs had a 31-times greater mean and 86-times greater median ration than fish that did not eat eggs (large size classes of both species combined). The mean $\pm$ SD ration size of fish that consumed eggs was 701 ± 323 J dietary energy/g fish wet mass versus. only 22.4 ± 38.8 J/g for fish that did not eat eggs. Overall, the mean ration size of juvenile salmonids was 4.7-times greater in the invaded site than in the control site. However, these mean values were highly skewed by the small numbers of fish that consumed eggs, and the median ration size was actually 19% smaller in the invaded site. Comparing only the fish that did not eat eggs, fish at the invaded site had 27% smaller mean (38% smaller median) ration size than fish at the control site (Figure S1).

3.2 | Stable isotope analyses

Pink salmon eggs and muscle tissue had markedly higher $\delta^{15}N$ and $\delta^{13}C$ values as compared to the freshwater and terrestrial food resources, as well as to the body tissues of juvenile Atlantic salmon and brown trout (Figure 4). Terrestrial invertebrates had on average 1.3–2.3‰ higher $\delta^{13}C$ and 0.9–1.0‰ lower $\delta^{15}N$ values than aquatic benthic invertebrates, but in general they showed large variation and overlap in $\delta^{15}N$ and $\delta^{13}C$ values, unlike the distinct marine resources.

Based on the linear models, the individual's size, species and sampling site all had significant effect on $\delta^{15}N$ of fish muscle and liver tissue (Table 2). Both species shifted to a higher trophic position

FIGURE 5 Ontogenetic (size-related) shifts in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of salmon (black) and trout (white) muscle and liver tissue. The lines indicate linear regression curves, with shading depicting 95% confidence intervals. Individuals with eggs in the stomach are highlighted in red

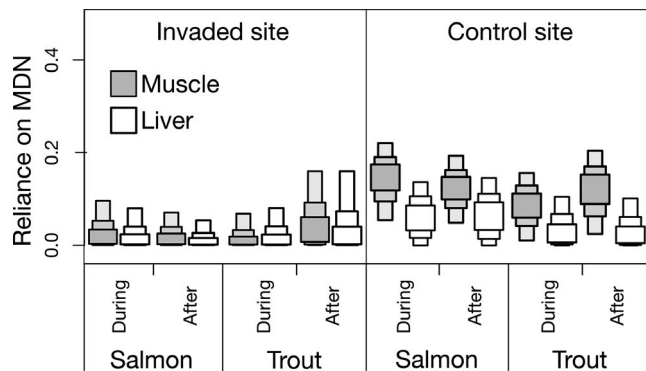
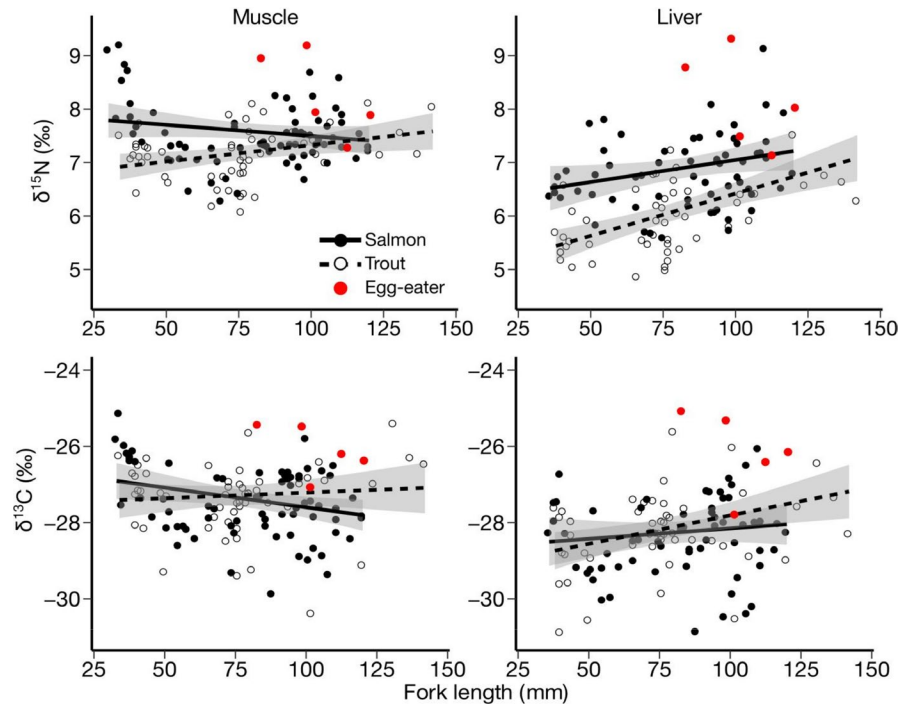


FIGURE 6 Reliance of Atlantic salmon and brown trout on marine-derived nutrients (MDN) in invaded (downstream) and control (upstream) sites in Vesterelva during and after the pink salmon spawning period. The estimates are based on results from a three-source (i.e., marine, terrestrial and freshwater) SIAR stable isotope mixing model run using either fish muscle or liver $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values as the consumer input data. The boxes indicate 95%, 75% and 50% Bayesian credibility intervals

(increased $\delta^{15}\text{N}$) with increasing length (Table 2, Figure 5), possibly indicating higher reliance of large individuals on MDN sources. A few small (<40 mm) Atlantic salmon also had elevated muscle $\delta^{15}\text{N}$ values, which likely reflects maternal "signals" of these young-of-the-year fish, and not true external foraging on MDN sources in the river. Fish in the invaded downstream site were on average more enriched in ^{15}N as compared to fish in the control site. Moreover, salmon occupied on average a higher trophic position than brown trout. The fish liver $\delta^{15}\text{N}$ values were also higher following pink salmon spawning. No evidence for significant two-way interaction between species and individual's size was found. Contrary to $\delta^{15}\text{N}$, no evidence for significant effects of species, sampling site or period on fish $\delta^{13}\text{C}$

values were found, but instead only a slight positive effect of individual's size on liver $\delta^{13}\text{C}$ (Table 2, Figure 5).

Contrary to the results of linear models, the SIAR estimates indicated in general only a minor reliance of Atlantic salmon and brown trout on MDN as compared to freshwater and terrestrial food resources (Figure 6). Contrary to the expectation, the SIAR estimates based on fish liver tissue indicated lower reliance on MDN as compared to estimates based on fish muscle $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values. However, as indicated by the overlapping 95% Bayesian credibility intervals, no significant differences were found in MDN reliance between the study sites, periods, fish species or the two fish tissue types.

The liver tissue with a faster isotopic turnover rate was for most fish individuals depleted in ^{15}N and ^{13}C as compared to the muscle tissue (see Supplementary Figure S2 for graphical illustration and results of paired *t* tests). Only a very few individuals showed a recent shift to a food resource with higher $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ value, indicating potential utilisation of MDN sources following pink salmon spawning.

3.3 | Energy content of eggs

Pink salmon eggs ($n = 30$) sampled in Vesterelva had a mean $\pm$ SD energy content of 9.85 ± 0.06 kJ/g wet mass, a value within the range published for mature salmon of the genus *Oncorhynchus* (8.5–11.2 kJ/g wet mass) (Armstrong, 2010; Crossin et al., 2003). Based on snorkelling surveys and official catch statistics an estimated total of 2,200 pink salmon entered Vesterelva in 2019 (Berntsen et al., 2020; R. Muladal, unpublished data). An estimated 60%–80% of these pink salmon were removed prior to spawning, leaving 440–880 pink salmon to spawn in the river. Assuming equal numbers of males and

females, between 220 and 440 pink salmon females were estimated to have spawned in Vesterelva in 2019 (R. Muladal, unpublished data). With each of these females producing 1,200–1,900 eggs, pink salmon in Vesterelva in 2019 could have contributed 0.3 to 0.9 million kJs of energy in egg deposits to the river in addition to the decomposing carcasses. Some of this energy will return to the marine environment when juveniles hatch and migrate to the sea.

4 | DISCUSSION

During recent years, large runs of introduced pink salmon have resulted in increased public and management concerns about their potential negative impacts on native salmonids and the well-being of river ecosystems in northern Europe (Hindar et al., 2020). Our study from Vesterelva in northern Norway demonstrates that pink salmon eggs can provide a highly profitable energy-dense food resource for some individuals of native juvenile Atlantic salmon and brown trout. However, stomach content and stable isotope data indicate that the population-level reliance on marine-derived nutrients (MDN) from pink salmon eggs in the study river is currently generally low.

During pink salmon spawning, stomach content analysis (Figures 2 and 3) revealed that pink salmon eggs (4–15 eggs per stomach) were featured as a dietary component for some larger juvenile Atlantic salmon ($n = 2$) and brown trout ($n = 3$). Atlantic salmon juveniles are opportunistic visual feeders that exploit both drifting and benthic prey (Amundsen et al., 1999; Johansen et al., 2010; Wańkowski & Thorpe, 1979). Benthic feeding on invertebrates is known to be an important foraging strategy of Atlantic salmon parr in the nearby rivers Tana and Reisa (Sánchez-Hernández et al., 2017). The prevalence of benthic feeding in juvenile Atlantic salmon is known to increase towards fall in August and September (Gabler & Amundsen, 1999), and to also occur more frequently at night (Amundsen et al., 2000, 2001). Atlantic salmon parr may therefore have been active benthic feeders at the time when they discovered and fed on the pink salmon eggs on the riverbed or suspended in the stream water in August 2019. Atlantic salmon parr quickly learn to consume novel prey items, and if readily available, these new items can become an important dietary component (Egglishaw, 1967; Reiriz et al., 1998). The primary dietary components of juvenile brown trout known from rivers across Norway are benthic aquatic insects (Sánchez-Hernández & Cobo, 2018), and the pink salmon eggs may have been easily discovered by individuals of this species. Salmon eggs are also not completely novel dietary items to parrs of both species as predation on the eggs of native anadromous salmonids have been documented in a number of European streams (Aymes et al., 2010; Näslund et al., 2015). The spawning stock of native salmonids (Atlantic salmon, brown trout and Arctic charr) in Vesterelva is estimated to be 500–700 individuals (R. Muladal, unpublished data). Native salmonids, and thereby their consumed salmonid eggs, could potentially have been discovered in the stomach contents of juveniles in the period after pink salmon spawning but none were found present.

In Alaska, juvenile coho salmon and other stream fishes primarily feed on drifting sockeye salmon (*O. nerka*) eggs in the water column, rather than buried eggs in the gravel. Drifting eggs become available during spawning, most often when a female spawner digs up an existing redd and dislodges the previously spawned eggs (Moore et al., 2008). This process of redd superimposition causes a disproportionate increase in egg availability with increasing spawner abundance, so that small increases in spawners after the spawning habitat becomes saturated can drive large increases in egg subsidies to stream fishes. During 2019, approximately 1,500 pink salmon were removed from Vesterelva, presumably before they could spawn, so it is likely that redd superimposition was minimal and few of the spawned pink salmon eggs were dislodged to drift. Alternatively, if pink salmon were removed after spawning, then the removals could potentially have increased redd superimposition by preventing females from defending their redds. If drift feeding is an important mechanism by which juvenile Atlantic salmon and brown trout feed on eggs, it is then likely that the availability of egg subsidies to these consumers would be higher in future years if such removals were scaled back or the numbers of spawners continued to increase.

Pink salmon eggs were only found in the stomachs of 18%–20% of the larger ($F_L > 55$ mm) juvenile Atlantic salmon and brown trout during spawning in the river section invaded by pink salmon. These findings are comparable to the 18% of Atlantic salmon (F_L 79–127 mm) and 20% of brown trout (F_L 78–140 mm) that fed on eggs from spawning native salmonids in a coastal stream in Sweden in 2013 (Näslund et al., 2015). Näslund et al. (2015) found that egg predation substantially increased closer to a spawning site, a relationship that was not investigated in the current study. Juvenile salmonids in the uninvaded upstream river section showed no egg feeding but larger salmon and trout had preyed on small fish, likely on sticklebacks. Piscivory is common in salmonids and particularly on three-spined sticklebacks (Sánchez-Hernández et al., 2017; Vik et al., 2001). In addition to fish, juvenile salmon fed on adult aquatic insects in the control section, whereas trout fed on a combination of immature and adult aquatic and terrestrial insects. After spawning, no eggs or fish predation was observed at either site, potentially indicating that both eggs and fish were only easily available in the summer. Terrestrial insects and immature aquatic insects featured more in the diets of juvenile salmonids in Vesterelva after spawning in both river sections. In the River Tana, invertebrates originating from the riparian vegetation are commonly found in brown trout diets (Johansen et al., 2005).

Although only two Atlantic salmon had eaten pink salmon eggs, a few more individuals also had slightly elevated $\delta^{15}\text{N}$ values (Figure 5) indicating potential egg foraging earlier in the season. Alternatively, some large juveniles may also have elevated $\delta^{15}\text{N}$ values due to piscivorous foraging on small fish (most likely sticklebacks) as indicated by the stomach contents data (Figure 2). Recent piscivorous foraging by juvenile Atlantic salmon may also explain their slightly higher trophic position as suggested by the liver $\delta^{15}\text{N}$ values. As discussed below, foraging on small fish or on predatory invertebrates may also explain the relatively high $\delta^{15}\text{N}$ values of some juvenile fish in the

upstream control site and not true higher reliance on MDN as suggested by the results from the SIAR isotopic mixing model (Figure 6).

Size partitioning influences juvenile salmonid diets and the maximum, minimum and optimal size of prey is determined by the gape size (Johnson et al., 2016; Wańkowski & Thorpe, 1979), as seen for predators feeding on invertebrates (Gabler & Amundsen, 1999) and eggs (Armstrong et al., 2010; Johnson et al., 2016; Näslund et al., 2015). The pink salmon eggs consumed in this study were 6.0–6.2 mm in diameter, and the smallest Atlantic salmon and brown trout feeding of eggs in this study had a F_L of 83 mm and 102 mm, respectively. This may provide an indication of the size range of juvenile Atlantic salmon and brown trout capable of feeding on pink salmon eggs in northern Norwegian rivers. However, subyearling Atlantic salmon as small as 70 mm long consumed the eggs of introduced Pacific salmon (Chinook, coho and steelhead salmon) that ranged between 5.3 and 7.2 mm in diameter in Salmon River, NY (Johnson et al., 2016). Similarly, juvenile coho salmon consumed sockeye salmon eggs in the Bristol Bay region of Alaska after reaching roughly 70 mm F_L (Armstrong et al., 2010). Salmonid eggs are high in energy content and the maximum $\pm$ SD daily energy intake provided by pink salmon eggs to salmonids in Vesterelva was 9.85 ± 0.06 kJ/g wet mass. Pink salmon eggs therefore provided approximately three times the energy intake of invertebrates (mean 3.54 kJ/g wet mass) and twice that of fish (mean 4.50 kJ/g wet mass) based on energy contents reported by McCarthy et al. (2009) and Cummins and Wuycheck (1971). The energy provided to juvenile Atlantic salmon and brown trout from the eggs of native salmonids that spawn in the late summer and early fall have been considered to potentially provide energy to increase winter survival (Finstad et al., 2005; Huss et al., 2008). However, the effects of egg predation on overwintering survival of native salmonids may be minor due to the early spawning period of pink salmon. A deeper understanding of the broader effects of increased MDN and energy intake from pink salmon requires further studies using bioenergetic modelling (e.g., Scheuerell et al., 2007).

Our stable isotope data indicate large individual variation in trophic position ($\delta^{15}\text{N}$) and carbon source ($\delta^{13}\text{C}$) among juvenile Atlantic salmon and brown trout in River Vesterelva, with some individuals being specialised on either freshwater ($\delta^{13}\text{C}$ below -30‰) or terrestrial ($\delta^{13}\text{C}$ above -28‰) prey resources. However, no consistent ontogenetic shifts in carbon sources were evident, especially if the smallest individuals ($F_L < 40$ mm) with maternal SIA signals were omitted. In contrast, the shift towards a higher trophic position with increasing size indicates increased reliance on MDN or piscivorous foraging for large juveniles ($F_L > 80$ mm). These results support our hypothesis that foraging on pink salmon eggs might be particularly evident among and advantageous for large juveniles that are capable of efficient egg ingestion and likely also competitively dominant over smaller individuals.

We found only minor support for increased reliance of native salmonid populations on MDN following pink salmon spawning. Although a few juvenile salmon and trout had eaten eggs and showed elevated $\delta^{15}\text{N}$ or $\delta^{13}\text{C}$ values indicating assimilation of MDN, there were no evident population-level shifts to elevated $\delta^{15}\text{N}$ or

$\delta^{13}\text{C}$ values following pink salmon spawning. The same pattern was observed when comparing SIA values of fish from the control site and the invaded downstream site or the fish muscle and liver tissues, with the latter indicating more recent assimilated diet. Besides seldom egg foraging, the somewhat higher $\delta^{15}\text{N}$ values of salmon likely resulted from frequent consumption of small fish (i.e., three-spined sticklebacks) which were less commonly found in trout stomachs (Figure 2). The potentially more frequent predation on small fish or on predatory invertebrates with elevated $\delta^{15}\text{N}$ values, or starvation-induced ^{15}N -enrichment of fish body tissues (Hertz et al., 2015 and references therein), may have introduced bias on our estimates of MDN reliance which was seemingly higher in the upstream control site. Overall, the estimated minor reliance of juvenile native salmonids on MDN can be explained by several ecological, environmental and methodological issues. Firstly, our study river Vesterelva is a relatively pristine and productive ecosystem likely providing sufficient aquatic and terrestrial food resources for juvenile native salmonids, contrary to, for example, dammed and/or more oligotrophic and cold mountainous river ecosystems (e.g., Koshino et al., 2013) that could respond more strongly to MDN subsidies. Secondly, our latter sampling in September occurred soon after pink salmon spawning and thus there may not have been enough time for nutrients from pink salmon carcasses to be transferred to juvenile native salmonids and other riverine biota. The transfer and assimilation of MDN are also slowed down by cold water and decreased primary and secondary production in autumn. In fact, it might be that MDN transfer to fish and other biota could be most pronounced or more easily detected in spring following decomposition of pink salmon carcasses during winter (Rinella et al., 2012). Thirdly, a large proportion of pink salmon was removed from Vesterelva as a joint effort of local fishers and environmental authorities. This has evidently decreased MDN transfer from pink salmon eggs and carcasses to the river ecosystem, with potential influence also on our SCA and SIA results.

This study is part of a project examining the pathways of MDN transport from pink salmon to freshwater ecosystems in northern Norway and represents some of the first published work on the ecological effects of pink salmon in Norway. The opportunistic nature and limited resources of this first study meant that an individual river system was studied. Future studies of the effects of MDN on freshwater ecosystems might examine effects on oligotrophic river ecosystems that are not targeted for pink salmon removals and where MDN effects are likely more pronounced, given their inherently nutrient-limited nature. In addition, the role of pink salmon eggs in the overwintering survival of native salmonids requires further quantification with a bioenergetic analysis or confirmation with a tagging study.

Salmon eggs have a high energetic value, higher than that provided by invertebrates (Scheuerell et al., 2007), and represent, alongside carcasses, a pathway for the transfer of MDN and energy to riverine ecosystems. Compared to the large body of research on the roles and impacts of MDN and energy from Pacific salmon in their native range, significantly less is known about pathways of transport and its importance in European rivers (Jonsson

& Jonsson, 2003; Näslund et al., 2015). The large pink salmon runs now entering rivers in northern Norway represent a significant increase in the input of MDN, and we currently know little about the potential ecological effects. This study begins to address this broad question and demonstrates that pink salmon egg predation by juvenile Atlantic salmon and brown trout is a pathway for the transport of MDN to the river ecosystem in northern Norway. It has been suggested that the consumption of eggs can boost the energy reserves and thus the potential chances of survival of juvenile salmonids as they enter overwintering. Indeed, in spite of relatively low pink salmon spawner densities compared to North American systems, we found that a small number of large juvenile native salmonids had pink salmon eggs in their stomachs as well as enriched isotopic values. This suggests that they had assimilated substantial amounts of MDN into their body tissues and potentially gained an advantage in overwinter survival. However, our results also showed that MDN had low incorporation into the tissues of the studied fish populations overall, indicating that the energy-rich eggs are not yet a major diet item for most juvenile salmonids at our study site, potentially due to the large-scale removals of pink salmon from the river during 2019. Yet, pink salmon are now naturalised in Norwegian rivers and are most likely here to stay and will continue to provide an energy-rich food source to large juvenile native salmonids.

ACKNOWLEDGEMENTS

We are grateful for the assistance of Mikko Kiljunen and Nina Honkanen for running SIA samples, and Eva Thorstad for valuable comments on an earlier draft of the manuscript. We would also like to thank Ottar Store (Nesseby herreds hunting and fishing association) and Grzegorz Wierzbinski (Naturtjenesteri Nord) for assistance in the field and sharing local knowledge. The reviews provided by two anonymous reviewers were gratefully received and helped to improve the manuscript. The project was funded by the Fram Centre Terrestrial Flagship. Any use of trade, firm or product names is for descriptive purposes only and does not imply endorsement by the U.S. government.

CONFLICT OF INTEREST

It is confirmed that as far as the authors are aware no conflict of interest exists regarding this manuscript.

DATA AVAILABILITY STATEMENT

All data included in this paper are available on Mendeley Data.

ORCID

Kathy Dunlop  <https://orcid.org/0000-0002-2397-1841>

REFERENCES

- Amundsen, P.-A., Bergersen, R., Huru, H., & Heggberget, T. G. (1999). Diel feeding rhythms and daily food consumption of juvenile Atlantic salmon in the River Alta, northern Norway. *Journal of Fish Biology*, 54, 58–71. <https://doi.org/10.1111/j.1095-8649.1999.tb00612.x>
- Amundsen, P.-A., Gabler, H. M., Herfindal, T., & Riise, L. S. (2000). Feeding chronology of Atlantic salmon parr in subarctic rivers: Consistency of nocturnal feeding. *Journal of Fish Biology*, 56, 676–686. <https://doi.org/10.1111/j.1095-8649.2000.tb00765.x>
- Amundsen, P.-A., Gabler, H. M., & Riise, L. S. (2001). Intraspecific food resource partitioning in Atlantic salmon (*Salmo salar*) parr in a subarctic river. *Aquatic Living Resources*, 14, 257–265. [https://doi.org/10.1016/S0990-7440\(01\)01127-5](https://doi.org/10.1016/S0990-7440(01)01127-5)
- Amundsen, P.-A., & Sánchez-Hernández, J. (2019). Feeding studies take guts - critical review and recommendations of methods for stomach contents analysis in fish. *Journal of Fish Biology*, 95, 1364–1373. <https://doi.org/10.1111/jfb.14151>
- Armstrong, J. B. (2010). Comment on "Egg consumption in mature Pacific salmon (*Oncorhynchus* spp.)". *Canadian Journal of Fisheries and Aquatic Sciences*, 67, 2052–2054. <https://doi.org/10.1139/F10-127>
- Armstrong, J. B., Schindler, D. E., Omori, K. L., Ruff, C. P., & Quinn, T. P. (2010). Thermal heterogeneity mediates the effects of pulsed subsidies across a landscape. *Ecology*, 91, 1445–1454. <https://doi.org/10.1890/09-0790.1>
- Aymes, J. C., Larrieu, M., Tentelier, C., & Labonne, J. (2010). Occurrence and variation of egg cannibalism in brown trout *Salmo trutta*. *Naturwissenschaften*, 97, 435–439. <https://doi.org/10.1007/s00114-010-0656-0>
- Barton, K. (2016). *MuMIn: Multi-model inference*. R package version 1.42.1. Retrieved from <https://CRAN.R-project.org/package=MuMIn>
- Berntsen, H. H., Sandlund, O. T., Thorstad, E. B., & Fiske, P. (2020). *Pukkellaks i Norge, 2019*. NINA Rapport 1821 : Norwegian Institute for Nature Research. <https://hdl.handle.net/11250/2651741>
- 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, USA. *Canadian Journal of Fisheries and Aquatic Sciences*, 55, 1909–1918. <https://doi.org/10.1139/f98-094>
- Bjerknes, V., & Vaag, A. B. (1980). Migration and capture of pink salmon, *Oncorhynchus gorbuscha* Walbaum in Finnmark, North Norway. *Journal of Fish Biology*, 16, 291–297. <https://doi.org/10.1111/j.1095-8649.1980.tb03706.x>
- Cederholm, C. J., Kunze, M. D., Murota, T., & Sibatani, A. (1999). Pacific salmon carcasses: Essential contributions of nutrients and energy for aquatic and terrestrial ecosystems. *Fisheries*, 24, 6–15. [https://doi.org/10.1577/1548-8446\(1999\)024<0006:PSC>2.0.CO;2](https://doi.org/10.1577/1548-8446(1999)024<0006:PSC>2.0.CO;2)
- Chipp, S. R., & Garvey, J. E. (2007). Assessment of diets and feeding patterns. In C. S. Guy & M. L. Brown (Eds.), *Analysis and interpretation of freshwater fisheries data* (pp. 473–514). American Fisheries Society.
- Crossin, G. T., Hinch, S. G., Farrell, A. P., Whelley, M. P., & Healey, M. C. (2003). Pink salmon (*Oncorhynchus gorbuscha*) migratory energetics: Response to migratory difficulty and comparisons with sockeye salmon (*Oncorhynchus nerka*). *Canadian Journal of Zoology*, 81, 1986–1995. <https://doi.org/10.1139/z03-193>
- Cummins, K. W., & Wuycheck, J. C. (1971). Caloric equivalents for investigations in ecological energetics. *Internationale Vereinigung für Theoretische und Angewandte Limnologie: Mitteilungen*, 18, 1–158. <https://doi.org/10.1080/05384680.1971.11903918>
- David, P., Thébault, E., Anneville, O., Duyck, P. F., Chapuis, E., & Loeuille, N. (2017). In A. Bohan David, J. Dumbrell Alex & F. Massol (Eds.), *Networks of invasion: A synthesis of concepts* (pp. 1–60). Academic Press.
- Denton, K. P., Rich, H. B., Moore, J. W., & Quinn, T. P. (2010). The utilization of a Pacific salmon *Oncorhynchus nerka* subsidy by three populations of charr *Salvelinus* spp. *Journal of Fish Biology*, 77, 1006–1023. <https://doi.org/10.1111/j.1095-8649.2010.02746.x>
- Early, R., Bradley, B. A., Dukes, J. S., Lawler, J. J., Olden, J. D., Blumenthal, D. M., ... Tatem, A. J. (2016). Global threats from invasive alien species in the twenty-first century and national response capacities. *Nature Scientific Communications*, 7, 12485. <https://doi.org/10.1038/ncomms12485>

- Egglishaw, H. J. (1967). The food, growth and population structure of salmon and trout in two streams in the Scottish Highlands. *Freshwater Salmon Fisheries Research, Scotland*, 38, 1–32.
- Finstad, B., Økland, F., Thorstad, E. B., Bjørn, P. A., & McKinley, R. S. (2005). Migration of hatchery-reared Atlantic salmon and wild anadromous brown trout post-smolts in a Norwegian fjord system. *Journal of Fish Biology*, 66, 86–96. <https://doi.org/10.1111/j.0022-1112.2005.00581.x>
- Gabler, H. M., & Amundsen, P.-A. (1999). Resource partitioning between Siberiansculpin (*Cottus poecilopus* Heckel) and Atlantic salmon parr (*Salmo salar* L.) in a sub-Arctic river, northern Norway. *Ecology of Freshwater Fish*, 8, 201–208. <https://doi.org/10.1111/j.1600-0633.1999.tb00071.x>
- 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. <https://doi.org/10.1080/02705060.2004.9664522>
- Guelinckx, J., Maes, J., Van Den Driessche, P., Geysen, B., Dehairs, F., & Ollevier, F. (2007). Changes in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in different tissues of juvenile sand goby *Pomatoschistus minutus*: A laboratory diet-switch experiment. *Marine Ecology Progress Series*, 341, 205–215. <https://doi.org/10.3354/meps341205>
- Heard, W. R. (1991). Life history of pink salmon. In C. Groot & L. Margolis (Eds.), *Pacific salmon life histories*, (119–230). University of British Columbia Press.
- Hertz, E., Trudel, M., Cox, M. K., & Mazumder, A. (2015). Effects of fasting and nutritional restriction on the isotopic ratios of nitrogen and carbon: A meta-analysis. *Ecology and Evolution*, 5, 4829–4839. <https://doi.org/10.1002/ece3.1738>
- Hindar, K., Hole, L. R., Kausrud, K., Malmstrøm, M., Rimstad, E., & Velle, G. (2020). Assessment of the risk to Norwegian biodiversity and aquaculture from pink salmon (*Oncorhynchus gorbuscha*). *Scientific Opinion of the Panel on Alien Organisms and Trade in Endangered Species (CITES)*. VKM report 2020:01, ISBN: 978-82-8259-334-2, ISSN: 2535-4019. Norwegian Scientific Committee for Food and Environment (VKM).
- Huss, M., Byström, P., & Persson, L. (2008). Resource heterogeneity, diet shifts and intra-cohort competition: Effects on size divergence in YOY fish. *Oecologia*, 158, 249–257. <https://doi.org/10.1007/s00442-008-1140-9>
- Jo, I., Fridley, J. D., & Frank, D. A. (2017). Invasive plants accelerate nitrogen cycling: Evidence from experimental woody monocultures. *Journal of Ecology*, 105, 1105–1110. <https://doi.org/10.1111/1365-2745.12732>
- Johansen, M., Elliott, J. M., & Klemetsen, A. (2005). Relationships between juvenile salmon, *Salmo salar* L., and invertebrate densities in the River Tana, Norway. *Ecology of Freshwater Fish*, 14, 331–343. <https://doi.org/10.1111/j.1600-0633.2005.00107.x>
- Johansen, M., Thorstad, E. B., Rikardsen, A. H., Koksvik, J. I., Ugedal, O., Jensen, A. J., ... Næsje, T. F. (2010). Prey availability and juvenile Atlantic salmon feeding during winter in a regulated subarctic river subject to loss of ice cover. *Hydrobiologia*, 644, 217–229. <https://doi.org/10.1007/s10750-010-0118-x>
- Johnson, J. H., Chalupnicki, M. A., Abbett, R., & Verdoliva, F. (2016). Predation on Pacific salmonid eggs and carcasses by subyearling Atlantic salmon in a tributary of Lake Ontario. *Journal of Great Lakes Research*, 42, 472–475. <https://doi.org/10.1016/j.jglr.2015.12.004>
- Johnson, J. H., Nack, C. C., & Chalupnicki, M. A. (2009). Predation by fall-fish (*Semotilus corporalis*) on Pacific salmon eggs in the Salmon River, New York. *Journal of Great Lakes Research*, 35, 630–633. <https://doi.org/10.1016/j.jglr.2009.08.001>
- Johnson, J. H., & Ringler, N. H. (1979). Predation on Pacific salmon eggs by salmonids in a tributary of Lake Ontario. *Journal of Great Lakes Research*, 5, 177–181. [https://doi.org/10.1016/S0380-1330\(79\)72144-7](https://doi.org/10.1016/S0380-1330(79)72144-7)
- Jonsson, B., & Jonsson, N. (2003). Migratory Atlantic salmon as vectors for the transfer of energy and nutrients between freshwater and marine environments. *Freshwater Biology*, 48(1), 21–27. <https://doi.org/10.1046/j.1365-2427.2003.00964.x>
- Jonsson, B., & Jonsson, N. (2009). A review of the likely effects of climate change on anadromous Atlantic salmon, *Salmo salar*, and brown trout, *Salmo trutta*, with particular reference to water temperature and flow. *Journal of Fish Biology*, 75, 2381–2447. <https://doi.org/10.1111/j.1095-8649.2009.02380.x>
- Jonsson, N., & Jonsson, B. (2018). Comment on “The pink salmon invasion: A Norwegian perspective” (Mo et al, Norwegian perspective) (Mo A Norwegian perspective) (Mo. *Freshwater Biology*, 48, 21–27. <https://doi.org/10.1111/jfb.13814>
- Koshino, Y., Kudo, H., & Kaeriyama, M. (2013). Stable isotope evidence indicates the incorporation into Japanese catchments of marine-derived nutrients transported by spawning Pacific Salmon. *Freshwater Biology*, 58, 1864–1877. <https://doi.org/10.1111/fwb.12175>
- McCarthy, S. G., Duda, J. J., Emlen, J. M., Hodgson, G. R., & Beauchamp, D. A. (2009). Linking habitat quality with trophic performance of steelhead along forest gradients in the South Fork Trinity River watershed, California. *Transactions of the American Fisheries Society*, 138, 506–521. <https://doi.org/10.1577/T08-053.1>
- McNeil, W. J., & Ahnell, W. H. (1964). *Success of pink salmon spawning relative to size of spawning bed material*. : US Fish and Wildlife Service. Special Scientific Report, Fisheries 469.
- Meehan, W. R., & Miller, R. A. (1978). Stomach flushing: Effectiveness and influence on survival and condition of juvenile salmonids. *Journal of the Fisheries Board of Canada*, 35, 1359–1363. <https://doi.org/10.1139/f78-212>
- Moe, T. A., Thorstad, E. B., Sandlund, O. T., Berntsen, H. H., Fiske, P., & Uglem, I. (2018). The pink salmon invasion: A Norwegian perspective. *Journal of Fish Biology*, 93, 5–7. <https://doi.org/10.1111/jfb.13682>
- Moore, J. W., Schindler, D. E., & Ruff, C. P. (2008). Habitat saturation drives thresholds in stream subsidies. *Ecology*, 89, 306–312. <https://doi.org/10.1890/07-1269.1>
- Näslund, J., Aldvén, D., & Závorka, L. (2015). Eggs from anadromous adults provide marine-derived nutrients to Atlantic salmon and brown trout parr in late autumn—observations from a Swedish coastal stream. *Environmental Biology of Fishes*, 98, 2305–2313. <https://doi.org/10.1007/s10641-015-0436-y>
- Parnell, A. C., Inger, R., Bearhop, S., & Jackson, A. L. (2010). Source partitioning using stable isotopes: Coping with too much variation. *PLoS One*, 5, e9672. <https://doi.org/10.1371/journal.pone.0009672>
- Post, D. M. (2002). Using stable isotopes to estimate trophic position: Models, methods, and assumptions. *Ecology*, 83, 703–718. [https://doi.org/10.1890/0012-9658\(2002\)083\[0703:USITET\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2002)083[0703:USITET]2.0.CO;2)
- Quinn, T. P. (2018). *The behavior and ecology of Pacific salmon and trout* (pp. 1–547). University of Washington Press.
- R Core Team (2018). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. <https://www.R-project.org/>
- Rahel, F. J., & Olden, J. D. (2008). Assessing the effects of climate change on aquatic invasive species. *Conservation Biology*, 22, 521–533. <https://doi.org/10.1111/j.1523-1739.2008.00950.x>
- Raspoutine, E. N., Shustov, Y. A., & Tyrkin, I. A. (2016). Eggs of pink salmon (*Oncorhynchus gorbuscha*) as additional nontraditional food of juvenile Atlantic salmon (*Salmo salar*) in rivers of the Kola Peninsula. *Russian Journal of Biological Invasions*, 7, 294–296. <https://doi.org/10.1134/S2075111716030115>
- Reiriz, L., Nicieza, A. G., & Braña, F. (1998). Prey selection by experienced and naive juvenile Atlantic salmon. *Journal of Fish Biology*, 53, 100–114. <https://doi.org/10.1111/j.1095-8649.1998.tb00113.x>
- Rine, K. M., Wipfli, M. S., Schoen, E. R., Nightengale, T. L., & Stricker, C. A. (2016). Trophic pathways supporting juvenile Chinook and coho salmon in the glacial Susitna River, Alaska: Patterns of freshwater, marine, and terrestrial food resource use across a seasonally dynamic

- habitat mosaic. *Canadian Journal of Fisheries and Aquatic Sciences*, 73, 1626–1641. <https://doi.org/10.1139/cjfas-2015-0555>
- Rinella, D. J., Wipfli, M. S., Stricker, C. A., Heintz, R. A., & Rinella, M. J. (2012). Pacific salmon (*Oncorhynchus* spp.) runs and consumer fitness: Growth and energy storage in stream-dwelling salmonids increase with salmon spawner density. *Canadian Journal of Fisheries and Aquatic Sciences*, 69, 73–84. <https://doi.org/10.1139/f2011-133>
- Sánchez-Hernández, J., & Cobo, F. (2018). Examining the link between dietary specialization and foraging modes of stream-dwelling brown trout *Salmo trutta*. *Journal of Fish Biology*, 93, 143–146. <https://doi.org/10.1111/jfb.13672>
- Sánchez-Hernández, J., Gabler, H. M., & Amundsen, P.-A. (2017). Prey diversity as a driver of resource partitioning between river-dwelling fish species. *Ecology and Evolution*, 7, 2058–2068. <https://doi.org/10.1002/ece3.2793>
- Sandlund, O. T., Berntsen, H. H., Fiske, P., Kuusela, J., Muladal, R., Niemelä, E., ... Zubchenko, A. V. (2019). Pink salmon in Norway: The reluctant invader. *Biological Invasions*, 21, 1033–1054. <https://doi.org/10.1007/s10530-018-1904-z>
- Scheuerell, M. D., Moore, J. W., Schindler, D. E., & Harvey, C. J. (2007). Varying effects of anadromous sockeye salmon on the trophic ecology of two species of resident salmonids in southwest Alaska. *Freshwater Biology*, 52, 1944–1956. <https://doi.org/10.1111/j.1365-2427.2007.01823.x>
- 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. [https://doi.org/10.1890/1540-9295\(2003\)001\[0031:PSATEO\]2.0.CO;2](https://doi.org/10.1890/1540-9295(2003)001[0031:PSATEO]2.0.CO;2)
- Stauffer, T. M. (1971). *Salmon eggs as food for stream salmonids and sculpins*. Ann Arbor, MI: Michigan Department of Natural Resources. Report 233.
- Vik, J. O., Borgstrøm, R., & Skaala, Ø. (2001). Cannibalism governing mortality of juvenile brown trout, *Salmo trutta*, in a regulated stream. *Regulated Rivers: Research & Management*, 17, 583–594. <https://doi.org/10.1002/rrr.647>
- Wańkowski, J. W. J., & Thorpe, J. E. (1979). Spatial distribution and feeding in atlantic salmon, *Salmo salar* L. juveniles. *Journal of Fish Biology*, 14, 239–247. <https://doi.org/10.1111/j.1095-8649.1979.tb03515.x>
- Wipfli, M. S. (1997). Terrestrial invertebrates as salmonid prey and nitrogen sources in streams: Contrasting old-growth and young-growth riparian forests in southeastern Alaska, USA. *Canadian Journal of Fisheries and Aquatic Sciences*, 54, 1259–1269. <https://doi.org/10.1139/f97-034>
- Wipfli, M. S. (2009). Food supplies of stream-dwelling salmonids. *American Fisheries Society Symposium*, 70, 1–14.
- Wipfli, M. S., & Baxter, C. V. (2010). Linking ecosystems, food webs, and fish production: Subsidies in salmonid watersheds. *Fisheries*, 35, 373–387. <https://doi.org/10.1577/1548-8446-35.8.373>
- 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. <https://doi.org/10.1139/cjfas-55-6-1503>
- 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. [https://doi.org/10.1577/1548-8659\(2003\)132<0371:MSIFES>2.0.CO;2](https://doi.org/10.1577/1548-8659(2003)132<0371:MSIFES>2.0.CO;2)
- Wipfli, M. S., Hudson, J. P., Chaloner, D. T., & Caouette, J. P. (1999). Influence of salmon spawner densities on stream productivity in southeast Alaska. *Canadian Journal of Fisheries and Aquatic Sciences*, 56, 1600–1611. <https://doi.org/10.1139/f99-087>
- Zubchenko, A. V., Veselov, A. E., & Kalyuzhin, S. (2004). *Pink Salmon (Oncorhynchus gorbuscha): Problems in acclimatization in Europe, North Russia*. Polar Research Institute of Marine Fisheries and Oceanography (PINRO) (In Russian).

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Dunlop K, Eloranta AP, Schoen E, et al. Evidence of energy and nutrient transfer from invasive pink salmon (*Oncorhynchus gorbuscha*) spawners to juvenile Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) in northern Norway. *Ecol Freshw Fish*. 2020;00:1–14. <https://doi.org/10.1111/eff.12582>