



Ecology and movement of juvenile salmonids in beaver-influenced and beaver-free tributaries in the Trøndelag province of Norway

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Abstract

There is concern that expanding beaver (*Castor fiber*) populations will negatively impact the important economic, recreational and ecological resources of Atlantic salmon (*Salmo salar*) and sea trout (*Salmo trutta*) populations in Europe. We studied how beaver dams influenced habitat, food resources, growth and movement of juvenile Atlantic salmon and trout on three paired beaver-dammed and beaver-free (control) tributaries of important salmon rivers in central Norway. Lotic reaches of beaver-dammed and control sites were similar in habitat and benthic prey abundance, and ponds were small (<3,000 m²). Though few juvenile salmonids were detected in ponds, trout and salmon were present in habitats below and above ponds (comprising 9%–31% and 0%–57% of the fish collected respectively). Trout dominated control sites (79%–99%), but the greatest proportion of Atlantic salmon were upstream of beaver ponds (0%–57%). Growth rates were highly variable, with no differences in growth between lotic reaches of beaver-dammed and control sites. The condition and densities of juvenile salmon and trout were similar in lotic reaches of beaver-dammed and control sites, though one beaver-dammed site with fine sediment had very few juvenile salmonids. Beaver dams did not block the movement of juvenile salmonids or their ability to use upstream habitats. However, the degree of repeated movements and the overall proportion of fish moving varied between beaver-dammed and control sites. The small scale of habitat alteration and the fact that fish were able to move past dams makes it unlikely that beaver dams negatively impact the juvenile stage of salmon or trout populations.

KEYWORDS

Atlantic salmon, beaver ponds, Eurasian beaver, rearing habitat, salmonid movement, trout

1 | INTRODUCTION

Atlantic salmon (*Salmo salar*) and sea trout (*Salmo trutta*) are an important economic, recreational and ecological resource in rural areas of the European Atlantic and Baltic seaboard, from northern Norway

to Spain (Butler, Radford, Riddington, & Loughton, 2009; Elliott, 1989; Hendry & Cragg-Hine, 2003; Radford, Hatcher, & Whitmarsh, 1991). More than 400 rivers in Norway have populations of Atlantic salmon which account for approximately 25% of the world's healthy populations (Hindar, Hutchings, Diserud, & Fiske, 2011). Both

Atlantic salmon and sea trout are exposed to a number of threats in the ocean and in freshwater. In the ocean, fish farming, sea lice infections and exploitation are among the most important threats, while in freshwater, river regulation, migration barriers, acid precipitation, pollution from industry and agriculture, escapees from fish farms and infections from the parasite *Gyrodactylus salaris* have all affected salmon populations negatively (Aas, Einum, Klemetsen, & Skurdal, 2011; Forseth et al., 2017). The Atlantic salmon is listed in annexes II and V of the European Union's Habitats Directive as a species of European importance (Elliott, Lyle, & Campbell, 1997; Hendry & Cragg-Hine, 2003; Jonsson & Jonsson, 2003; Lyle & Elliott, 1998). It is important to understand the different factors that can influence the production of salmonids because they have experienced population declines over much of their range in recent years (Hendry & Cragg-Hine, 2003; Youngston & Hay, 1996).

Both Eurasian (*Castor fiber*) and North American beavers (*Castor canadensis*) are known to be engineers of freshwater habitats. By cutting vegetation and building dams, beavers can alter fluvial processes and system hydrology, creating new habitats that can increase biocomplexity (Anderson, Paszkowski, & Hood, 2015; Girit, Gorkyca, & Sobucki, 2016; Gurnell, 1998; Law, Mclea, And, & Illby, 2016; Naiman & Rogers, 1997; Rosell, Bozser, Collen, & Parker, 2005; Wright, Jones, & Flecker, 2002). This results in altered nutrient and carbon cycles (Francis, Naiman, & Melillo, 1985; Naiman, Manning, & Johnston, 1991; Naiman, Pinay, Johnston, & Pastor, 1994), increased nutrient availability (Naiman & Melillo, 1984; Pinay & Naiman, 1991) and altered fluxes of organic matter, sediment and heat (Naiman, Melillo, & Hobbie, 1986; Naiman et al., 1994; Rosell et al., 2005). Though beavers are not commonly listed as a threat to salmonid populations in Norway, and there is potential for beavers to have positive effects on salmonid populations (based on research in North America—see below), there is concern in Europe that expanding beaver populations may negatively influence salmonid populations by altering fundamental freshwater habitat characteristics.

In low-order streams in North America, beaver ponds provide benefits to many species of salmonids (Kemp, Worthington, Langford, Tree, & Gaywood, 2012). The presence of beaver ponds covering larger areas with abundant food resources can benefit juvenile salmon by increasing survival rates (Bustard & Narver, 1975; Quinn & Peterson, 1996), growth rates (Bustard & Narver, 1975; Malison, Eby, & Stanford, 2015; Swales & Levings, 1989) and production (Layman & Smith, 2001; Nickelson, Nicholas, et al., 1992; Pollock, Pess, Beechie, & Montgomery, 2004). By increasing habitat complexity, ponds have been found to allow greater spatial resource partitioning with positive effects on steelhead density, survival and production (Wathen, Allgeier, Bouwes, Pollock, & Jordan, 2018). Other recent work has also shown that beaver dams can buffer diel summer temperature extrema and create thermal refugia (Weber et al., 2017). Fewer studies have shown that North American beaver dams can have negative impacts on fishes when sediment and organic matter retention results in hypoxia or when temperatures are elevated above conducive levels (Burchsted, Daniels, Thorson, & Vokoun, 2010). In respect to fish movement, the results are mixed.

While some studies suggest that beaver dams may seasonally alter movement patterns of fishes (Mitchell & Cunjak, 2007; Schlosser & Kallemeyn, 2000), other studies have shown that juvenile and adult salmonids have the ability to negotiate multiple North American beaver dams or beaver dam analogs (Bouwes et al., 2016; Lokteff, Roper, & Wheaton, 2013).

Though a large body of knowledge exists in North America regarding the interaction of *C. canadensis* and Pacific salmonids, relatively little is known about how Eurasian beavers may influence Atlantic salmon and trout populations. All *S. trutta* juveniles rear in freshwater, but some adults are anadromous sea trout, while others remain in freshwater as resident fish their entire lives (Klemetsen et al., 2003). Because the ecology of the two beaver species differs in some respects (Collen & Gibson, 2001) and Atlantic salmon have very complex life histories (Thorstad, Whoriskey, Rikardsen, & Aarestrup, 2011) compared to most Pacific salmonids (but not *O. mykiss*, Quinn, 2005), caution is required in using North American beaver literature when considering potential Eurasian beaver effects on Atlantic salmon and trout (Collen, 1997). Juvenile Atlantic salmon and trout may use off-channel and tributary habitats differently than Pacific salmonids, which could change how strongly beavers are able to influence salmonid populations. Increased lentic habitat would likely benefit juvenile trout more so than juvenile Atlantic salmon because of their stronger affinity for pool environments (Heggenes, Bagliniere, & Cunjak, 1999; Heggenes & Saltveit, 1990). However, high densities of juvenile Chinook have been found rearing in beaver ponds in Alaska (Malison, Lorang, Whited, & Stanford, 2014), even though they are considered to favour faster flowing water like Atlantic salmon. It is not clear how strongly movement of juvenile salmon and trout might be limited by the presence of dams, especially since juvenile Atlantic salmon have been considered fluvial residents that exhibit overall restricted movements (Armstrong, Kemp, Kennedy, Ladle, & Milner, 2003; Hesthagen, 1988; Symons & Heland, 1978).

Beavers and salmonids coexisted in Norwegian watersheds for millennia, since the end of the last Ice Age, prior to Eurasian beavers becoming largely extirpated in Europe due to hunting by the 17th century. Eurasian beavers were reduced to ~1,200 individuals in eight known, scattered populations in the early 20th century (Halley & Rosell, 2003). Now, after three decades of recovery, natural spread and reintroductions (Halley & Rosell, 2003; Halley, Rosell, & Saveliev, 2012), there is a recent estimated minimum population of 1.3 million individuals, now found in all countries of the former natural range in Europe excluding Portugal, Moldova and the southern Balkans (Halley, Rosell, & Saveliev, in prep). The species has been reclassified as Least Concern by the IUCN. The expansion and planned reintroductions of beavers to rivers holding important anadromous salmon and trout populations are causing considerable concern in Atlantic and Baltic seaboard regions because the impact of beaver dams on these fishes is unknown. Despite the documented positive effects of beavers on stream fishes in North America, a continuing concern in the European Atlantic and Baltic seaboard is that beaver dams will block fish movements and remove available habitat (Arts,

Fischer, & van der Wal, 2013; Berthelsen, 2008; Collen, 1997; Collen & Gibson, 2001; Halley et al., 2009; Halley & Lamberg, 2001; Kemp, Worthington, & Langford, 2010; Kesminas, Leliuna, & Rymantus, 2006; Nolet & Rosell, 1998; Parker & Rosell, 2003; Rudzite, 2005; Salmon & Trout Association, 2008).

The goal of this study was to determine how beaver dams influenced the ecology of juvenile Atlantic salmon and trout in tributaries of important salmon and trout rivers in the Trøndelag province of Norway, as well as to collect empirical data on movement rates of juvenile salmonids in sites with and without dams. Based on relationships between *C. canadensis* and juvenile Pacific salmon, we predicted that the presence of dams would (a) alter freshwater habitat characteristics, food availability and fish diets, (b) alter fish distribution and species composition, (c) that growth and condition of juvenile salmon and trout would be highest in beaver ponds compared to lotic reaches of beaver-influenced and beaver-free control sites and (d) that movement rates would be lower in beaver-influenced sites because dams would limit movement. Overall, we expected that the presence of beaver ponds on tributaries would influence how freshwater habitats are used by juvenile salmon and trout.

2 | MATERIAL AND METHODS

2.1 | Study area

We conducted this study in 2014 in the Trøndelag province of Norway. Study sites were located on tributaries of two larger rivers, the Stjørdal River (4 sites, Figure 1) and the Orkla River (2 sites; Figure 1; see Table 1). The Stjørdal River (63°25'N; 10°49'E) has a catchment area of 2,130 km² and a mean annual flow of 79 m³/s. Anadromous salmonids have access to 57 km of river, up to the Nustad waterfall in Meråker, and the estimated total weight of females spawning was 10,000 kg in 2016 (Forseth & Fiske, 2018). The Orkla River (63°18'N; 9°49'E) has a 3,092 km² catchment and a mean annual flow of 70 m³/s. Anadromous salmonids have access to 90 km of river before waterfalls block upstream habitat from use, and an estimated 14,000 kg of female salmon returned to spawn in 2016 (Forseth & Fiske, 2018). Both rivers drain into the sea via Trondheimsfjord and are managed for hydropower (the Orkla since 1983; see Hvidsten et al., 2015). These rivers are among the most important river systems for Atlantic salmon and sea trout angling in the world (e.g., the Orkla is usually among the top four Norwegian rivers by catch weight and number of salmon caught, Statistics Norway, 2013). These watersheds further provide an ideal setting for this research as beaver recolonisation is not yet complete and there are many unoccupied streams that provide control sites. In fact, while surveying salmon habitat for suitable sites, we only observed a handful of dams in total in four different watersheds. Both rivers flow through landscapes heavily modified by humans and are impacted by development, agriculture and grazing, culverts, etc., that limit the amount of off-channel (water outside of, but connected to the main channel, e.g., springs, secondary and tertiary channels)

rearing habitat, and the quality of tributary spawning and rearing habitat.

Study sites were located on three paired tributaries of the Stjørdal and Orkla rivers. No data on spawner abundances are available, but we estimate that all tributaries receive small numbers of returning adult spawners (<100/year). Tributary pairs were in close proximity, with similar physical characteristics, except that one of each pair had a beaver dam and pond and the other provided a beaver-free control (Figure 2; Table 1). The Stjørdal N. sites were located on the north side of the Stjørdal on the Råelva (63°30'38.6"N; 11°05'21.5"E; with beavers) and the Hofstadelva (63°29'35.4"N; 11°05'55.3"E; no beaver control; Figure 2). The Stjørdal S. sites were located on the south side of the Stjørdal on the Holmsbekken (63°26'59.3"N; 11°03'48.6"E; with beavers) and Hemrasbekken (63°27'21.8"N; 11°05'36.6"E; no beaver control). The Orkla beaver site was located on the Leirbekken (63°15'54.0"N; 9°47'58.5"E), and the control site was on the Sola (63°12'51.3"N; 9°47'14.0"E; Figure 2). Stjørdal N. sites had stream gradients between 1% and 2%, while all other sites had stream gradients <1%. All sites had similar riparian vegetation with grey alder (*Alnus incana*), goat willow (*Salix caprea*), common birch (*Betula pubescens*), silver birch (*B. pendula*) and bird cherry (*Prunus padus*) being the most common.

2.2 | Study design

Each study site was sampled from July to October of 2014, except for the Stjørdal N. pair where sampling started in August when land access was granted. In each site, we measured habitat characteristics and sampled fish communities. Each beaver site was sampled primarily in two different habitat types: lotic reaches below dams (Below Pond) and within the pond (Pond; Figure 3). Additional tagging (for movement) and sampling of fish distributions occurred in the upstream lotic reaches above ponds (Above Pond; Figure 3), except for the Stjørdal N. pond where there was a small lake just upstream (from a quick-clay slide). Each beaver-free site was sampled along a similar length of stream reach to determine how fish communities and movement differed in sites without dams.

2.3 | Sampling

2.3.1 | Habitat

At each site, we collected data on a number of habitat characteristics that could influence fish populations. We calculated mean width and depth by taking measurements at multiple transects along the length of the wetted channel (at each point that the stream changed size). We calculated habitat area by summing the area of each measured polygon (width × length between transects). Beaver ponds at the Stjørdal sites were smaller and were mapped by hand, measuring pond width every 2 m. The Orkla pond was large and open, allowing us to calculate pond area from imagery online (kart.finn.no). We

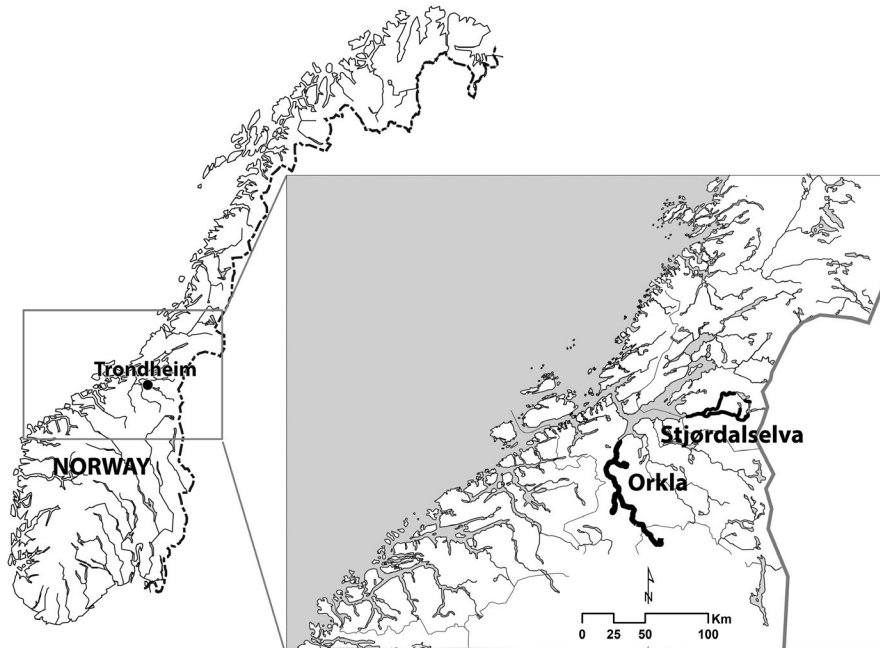


FIGURE 1 Map of the study area and focal rivers in the Trøndelag province of Norway

TABLE 1 Characteristics of paired beaver-influenced and beaver-free habitats

	Stjørdal North		Stjørdal South		Orkla	
	Beaver	No beaver	Beaver	No beaver	Beaver	No beaver
Lotic reach length (m)	90	90	100	140	110	120
Lotic reach width (m)	2.8 ± 1.1	3.8 ± 1.6	1.7 ± 0.5	1.5 ± 0.6	4.3 ± 2.1	6.0 ± 1.9
Lotic reach depth (m)	0.3 ± 0.1	0.4 ± 0.2	0.2 ± 0.1	0.1 ± 0.1	0.2 ± 0.1	0.4 ± 0.1
Lotic reach substrate size (cm)	27.4 ± 25.8	14.2 ± 15.6	1.5 ± 7.6	16.7 ± 22.2	21.1 ± 26.1	9.4 ± 24.4
Lotic reach substrate %embeddedness	21.4 ± 32.2	14.2 ± 26.2	8.3 ± 24.1	26.9 ± 34.3	30.6 ± 35.4	14.8 ± 31.5
Dam height (m)	1.2	—	1	—	1	—
Dam length (m)	7.4	—	8.4	—	19	—
Pond area (m ²)	1,044	—	1,364	—	2,966	—
Pond length (m)	120	—	85.5	—	140	—
Pond width (m)	8.7 ± 1.8	—	16.0 ± 7.2	—	31.0 ± 18.4	—
Max pond depth (m)	>2.0	—	>2.0	—	>2.0	—
Distance from river (km)	8.9	6.3	1.1	1.1	0.025	0.14

Note: Beaver-influenced habitats include both the impounded areas above dams and the lotic flowing reaches below the dams.

conducted substrate surveys at each lotic site by randomly selecting a rock every 1m along the study reach and measuring its size and percent embeddedness (Davis, Minshall, Robinson, & Landres, 2001). Beaver pond substrate was not formally surveyed because all pond substrate was a fine mud/silt material. We deployed temperature loggers at all six sites for one year (HOBO Pendant temp/light UA-002-64 and HOBO Temp H08-001-02, Onset Computer Corporation, Bourne, MA, USA; www.onsetcomp.com) and recorded temperature every hour. At beaver sites, temperature loggers were placed in the lotic reach downstream of the pond. We calculated growing degree-days (GDD) between June and August using the

following equation (Elliott, 1994; McMaster & Wilhelm, 1997): $GG = \sum [T_{MAX} + T_{MIN}] / 2 - 4$. Data were analysed for the time period of 20 September 2014 until 7 April 2015 for 3 beaver sites and 2 control sites because the Stj. S. control site logger was lost in a flood and another logger had an error and stopped logging on 7 April 2015.

The effect of habitat type on stream width, depth, substrate characteristics and stream temperature was analysed using two-sample *t* tests after testing if data met assumptions of normality and homogeneity of variance. All statistical tests (except for nonmetric multidimensional scaling, below) were analysed in R version 3.5.2 and were considered significant when $p < .05$.

FIGURE 2 Study sites (a) Stjørdal North Beaver, (b) Stjørdal North Control, (c) Stjørdal South Beaver, (d) Stjørdal South Control, (e) Orkla Beaver and (f) Orkla Control. Red arrows show the locations of visible PIT-tag antennae

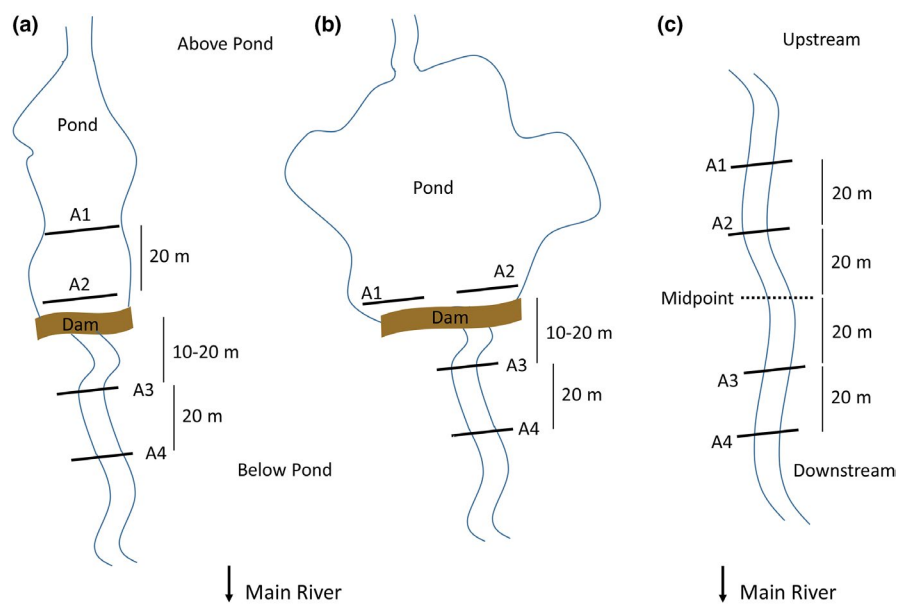
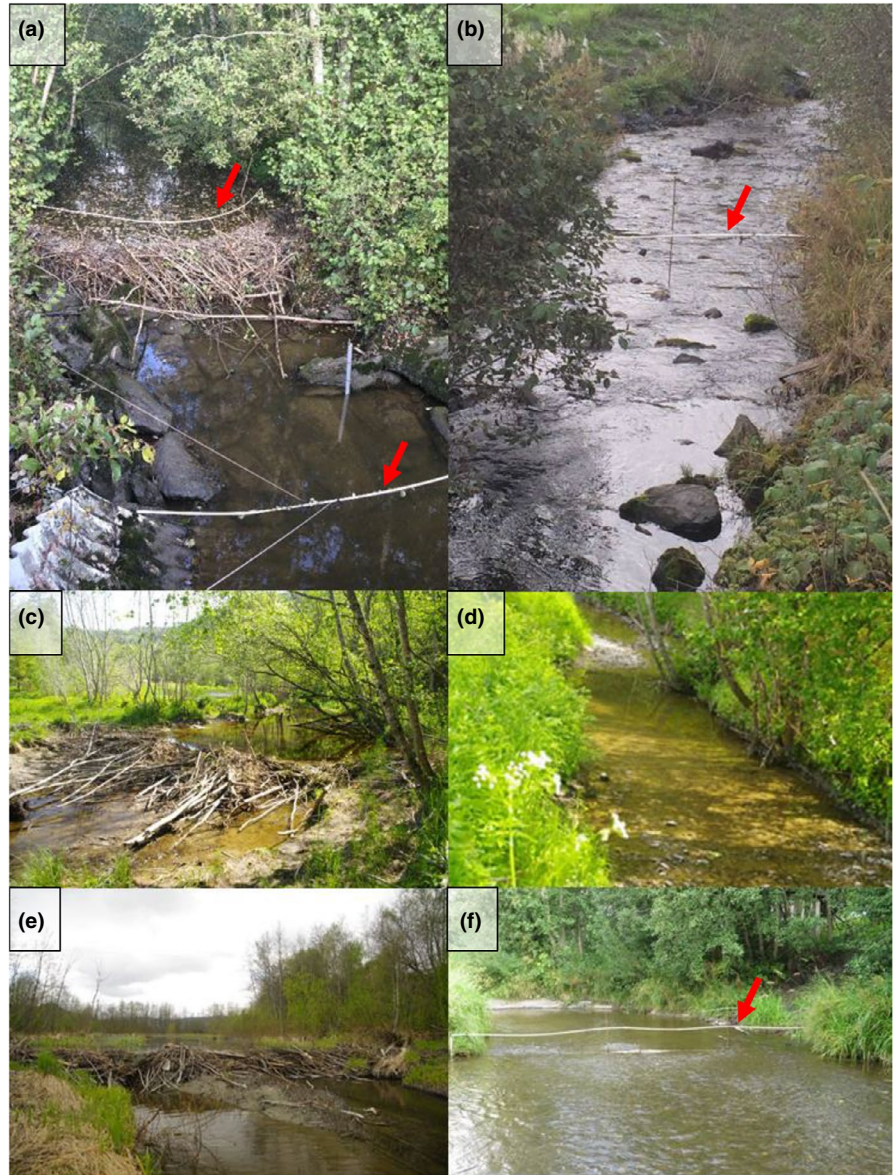


FIGURE 3 Diagram of PIT-tag antennae placement on (a) Stjørdal North and South beaver sites, (b) the Orkla beaver site and (c) all control sites

2.3.2 | Prey availability and fish diets

At each site, we sampled autochthonous (within the stream) and allochthonous (falling into the stream) prey resources and salmonid diets because differences in prey availability could influence fish habitat use and fish population dynamics. To compare the number of benthic invertebrates between beaver-influenced and control sites, we sampled benthos from three riffles at each site in September using a D net and metal frame (0.25 m²). Replicate samples were collected from each riffle by disturbing the bed sediments within the metal frame for one minute. We picked each sample in the field for one and a half person-hours and preserved macroinvertebrates in ethanol. In the laboratory, most samples were identified to family, or further to genus and species when size allowed (except for acari, oligochaeta, ostracoda, nematoda and copepods) and counted. The effect of habitat type on total benthic invertebrate counts was analysed using a two-sample *t* test. We analysed the relative abundance of taxa at each site with nonmetric multidimensional scaling (NMDS; Kruskal & Wish, 1978) to evaluate differences among habitat types with the program PC-ORD (version 7; MjM Software Design, Gleneden Beach, Oregon, USA; www.pcord.com). We excluded rare taxa from the data set (relative values, <5%) and/or combined them with higher order levels, to reduce skewness in the data. We used multiresponse permutation procedures (MRPP) to test for significant differences in community composition by habitat type.

We used floating traps (four 0.4-m² opaque pans at each site) to measure the inputs (individuals/day) of adult invertebrates (both aquatic and terrestrial in origin) in September for a period of 2–4 days at each site (pond, beaver-influenced lotic site, control site). We picked all individuals from each trap and preserved samples in ethanol in the field. Samples were identified and counted in the laboratory. Adult Ephemeroptera, Plecoptera, Trichoptera and Diptera were most often identified to family, but only to order if family could not be confirmed, while other groups were not identified past class or order (e.g. Ostracoda). Site input was calculated by dividing the number of insects falling into the stream by the number of days each trap ran. Allochthonous inputs by habitat type were analysed using one-way analysis of variance (ANOVA; R version 3.5.2). We analysed the relative abundance of taxa at each site with nonmetric multidimensional scaling as described above for benthic samples.

We examined the amount and composition of prey in salmonid diets to determine if diets varied by habitat type. We collected diet samples from a subset of the fish collected in September during mark–recapture sampling. A composite sample was collected from a total of twenty fish, comprised of both Atlantic salmon (74–133 mm) and trout (68–170 mm), at each site, except for the Stjørdal S. beaver site where no salmonids were captured in September. We collected stomach-content samples nonlethally using gastric lavage. Samples were preserved in ethanol and identified and counted in the laboratory. The effect of habitat type on fish diet was analysed using a two-sample *t* test. We used NMDS to evaluate differences among habitat types in the composition of fish diets, following the same methods described for prey availability.

2.3.3 | Fish sampling

Lotic reaches below and above beaver ponds, beaver-free reaches and the shallow edges of beaver ponds were sampled using a backpack electrofisher (Paulsen FA-3, exponential pulses of 700 V, 70 Hz; Paulsen, Norway). We primarily sampled each beaver pond using collapsible minnow traps because minnow traps have been used to successfully catch juvenile pacific salmon (Malison, Eby, & Stanford, 2015; Malison et al., 2014; DreamTM Ørekyteteine m 2 innganger, DreamTM, Norway). Minnow traps were placed in ponds for 2–24 hr and were baited with salmon flesh. All captured fish were placed in live wells in the stream until they were processed. Fish were anaesthetised with Benzoak vet 200 mg/ml (1–1.5 ml/10 L). Fish were anaesthetised for <2 min, until they started to turn over. Fish were identified, measured for fork length and weighed. Individuals over 80 mm were implanted with a HDX 12-mm passive integrated transponder (PIT) tag (12.0 mm × 2.12 mm HDX ISO, Oregon RFID, Oregon, USA; www.oregonrfid.com). Fish were held long enough to determine that they fully recovered from drugging and handling prior to being released back throughout the study reach. We also did some exploratory electrofishing at pond edges and detected the presence of PIT-tagged salmonids in ponds using PIT-tag antennae (see below).

We sampled three times a month from July to September and twice in October using a capture–mark–recapture design, to measure growth and estimate survival in the lotic reaches of beaver and control sites. Instantaneous growth rates were calculated for fish recaptured at each site for each monthly sampling period using the equations:

$$G = 100 \times (\log_e L_2 - \log_e L_1) (T_2 - T_1)^{-1},$$

$$G = 100 \times (\log_e W_2 - \log_e W_1) (T_2 - T_1)^{-1}$$

where L_x is the fork length (mm) at time T_x , W_x is the weight (g) at time T_x , and T is measured in days, representing the number of days between tagging and recapture or between recapture events (Busacker, Adelman, & Goolish, 1990). Unfortunately, we could not estimate survival for a number of reasons: (a) overall too few fish were tagged and recaptured (often none or only 1–2 were recaptured per site per monthly sampling period), (b) some sites had no recaptures of salmon or trout in any months, (c) large flood events or the presence of spawning adults prevented repeated capture–mark–recapture sampling at other sites, and (d) we could not measure emigration from the sites because we did not have enough antennae to place at the end of the reaches (see Table 2 for a sampling summary). The combination of these factors resulted in too poor of a data set to conduct a robust capture–mark–recapture analysis.

Instead of capture–mark–recapture methods, we used depletion sampling once a month (July–October) at each site to estimate population sizes and calculate salmon and trout densities in the lotic sections of beaver and beaver-free sites. We fished each reach three times, over a short time period (starting the next pass when the water cleared). Fish from previous passes were held in live wells until

TABLE 2 Summary of tagged and recaptured trout and salmon captured for each site during capture–mark–recapture sampling events (MR) in July (J MR1-3), August (A MR1-3), September (S MR1-3) and October (O MR1-2)

		July			August			September			October		Total	Individual recapture rate
		MR1	MR2	MR3	MR1	MR2	MR3	MR1	MR2	MR3	MR1	MR2		
Stj S.	# Newly tagged trout	8	5	5	5	5	2	30	12	3	14	6	95	
Control	# Recaptured trout (prev. tagged)				5	3	0	7	1	0	8	2	26	(18/95, 19%)
	Trout recaptures each month (%)				(8/18, 44%)			(8/30, 27%)			(10/75, 13%)			
	# Newly tagged salmon	0	0	0	1	1	0	0	0	0	1	0	3	
	# Recaptured salmon (prev. tagged)							2	0	0	1	0	3	(2/3, 67%)
	Salmon recaptures each month (%)							(2/2, 100%)			(1/2, 50%)			
Stj S.	# Newly tagged trout	4	0	0	0	0	–	4	–	–	3	–	11	
Beaver	# recaptured trout (prev. tagged)				0	0	–	0	–	–	0	–	0	
	Trout recaptures each month (%)						0			0		0	0	
	# Newly tagged salmon	0	0	0	0	0	–	0	–	–	0	–	0	
	# Recaptured salmon (prev. tagged)				0	0	–	0	–	–	0	–	0	
	Salmon recaptures each month (%)						0			0		0	0	
Stj N.	# Newly tagged trout	–	–	–	59	46	51	50	10	5	23	–	244	
Control	# Recaptured trout (prev. tagged)							29	6	7	8	–	50	(49/244, 20%)
	Trout recaptures each month (%)							(42/156, 27%)			(8/221, 4%)			
	# Newly tagged salmon	–	–	–	2	3	7	3	0	1	4	–	20	
	# Recaptured salmon (prev. tagged)							3	0	2	1	–	6	(6/20, 30%)
	Salmon recaptures each month (%)							(5/12, 42%)			(1/16, 6%)			
Stj N.	# Newly tagged trout	27	7	4	3	–	–	50	7	–	18	–	116	
Beaver	# Recaptured trout (prev. tagged)				4	–	–	14	2	–	12	–	32	(26/116, 22%)
	Trout recaptures each month (%)				(4/38, 11%)			(16/41, 39%)			(12/98, 12%)			
	# Newly tagged salmon	0	0	0	0	–	–	2	0	–	0	–	2	
	# Recaptured salmon (prev. tagged)					–	–	0	0	–	1	–	1	(1/2, 50%)
	Salmon recaptures each month (%)						0			0	(1/2, 50%)			
Orkla	# Newly tagged trout	10	10	3	5	1	1	17	0	3	19	8	77	
Control	# Recaptured trout (prev. tagged)				2	0	1	1	1	0	2	2	9	(8/77, 10%)
	Trout recaptures each month (%)				(3/23, 13%)			(2/30, 7%)			(4/50, 8%)			
	# Newly tagged salmon	1	1	0	8	2	0	10	1	2	4	1	30	
	# Recaptured salmon (prev. tagged)				1	0	0	2	0	0	0	1	4	(4/30, 13%)
	Salmon recaptures each month (%)				(1/2, 50%)			(2/12, 17%)			(1/25, 4%)			

(Continues)

TABLE 2 (Continued)

		July			August			September			October			Individual recapture rate
		MR1	MR2	MR3	MR1	MR2	MR3	MR1	MR2	MR3	MR1	MR2	Total	
Orkla	# Newly tagged trout	2	1	0	4	3	1	5	2	—	27	—	45	
Beaver	# Recaptured trout (prev. tagged)	0	0	0	0	0	0	0	0	—	0	—	0	
	Trout recaptures each month (%)						0			0		0	0	
	# Newly tagged salmon	3	2	2	3	4	0	16	4	—	19	—	53	
	# Recaptured salmon (prev. tagged)				1	0	0	3	0	—	5	—	9	(8/53, 15%)
	Salmon recaptures each month (%)				(1/7, 14%)			(3/14, 21%)			(5/34, 15%)			

Note: Dashes indicate that sampling was not conducted for the respective site on the respective sampling day. Total recaptures reflect the total number of recaptures caught each month. The individual recapture rate reflects the total number of individuals that were recaptured at least once during the entire sampling period.

all electrofishing passes were completed and then all fish were processed. Both sites in the Orkla were sampled completely for all four months. The Stjørðdal N. pair was only sampled in September and October. The Stjørðdal S. pair was not sampled in October because adult salmon and trout were present in the streams. Furthermore, if too few salmonids were caught in previous months, three pass depletion sampling was discontinued and one pass of electrofishing was completed (i.e., Stjørðdal S. beaver site). Stream sections were not blocked off with nets; however, in all but one site an obstacle (e.g., waterfall, beaver dam, stream reconstruction) blocked at least one end of each reach and during portions of the summer stream segments were isolated on both ends when the channel dried in places in one site. Population sizes could be underestimated because reaches were not completely blocked off during electrofishing.

To measure movement rates of PIT-tagged salmonids, we placed four pass-through PIT-tag antennae (built from double looped 10 gauge stranded wire and placed in plastic tubing) and one HDX Multi-Antenna Reader at each study site (Oregon RFID, Oregon, WA, USA; www.oregonrfid.com; Figure 3). The reader and antennae were powered by a battery bank of deep-cycle marine batteries charged by a solar panel. Antennae size varied by location, with the largest antennae being 6.5 m long by 50 cm high. All antennae were held vertically in the water column by rebar as pass-through antennae to increase tag read distance, which ranged from 20 to 50 cm on each side of the antennae. In beaver-influenced sites, two antennae were placed below the beaver dam and two were placed above the beaver dam (Figure 3a,b). The Stjørðdal N. and S. Beaver ponds were narrow enough above the dam to place antennae 1 (A1) upstream of antennae 2 (A2) within the pond (Figure 3a), whereas the Orkla Beaver pond was much wider so A1 and A2 were placed side by side (Figure 3b). Below the dam antennae 3 (A3) was placed upstream of antennae 4 (A4) for all beaver sites (Figure 3a,b). In control sites, we selected a mid-point of the stream at a similar distance from the mouth of the tributary where the dam on the paired beaver site was located (Figure 3c). Two antennae were placed downstream from this point (A3&4) and two

antennae upstream of this point (A1&2, Figure 3c). This design allowed us to compare movement rates along reaches with and without dams. The four antennae at each site covered a distance of 60–80 m.

Pit-tag antennae were deployed at all sites in July 2014, except for the Stjørðdal N. control site where the antennae were deployed in August 2014. All antennae ran continuously until removal between 14 and 18 October 2014, excluding time periods when batteries had to be removed from the field for charging (solar panels failed to continuously charge) or when flood events damaged antennae and readers. The total number of hours of active data collection was recorded for each site. One large flood event at the Stjørðdal S. beaver site inundated the PIT-tag reader and damaged it beyond repair on 17 August, resulting in a gap of 27 days while we waited for a new reader. At other sites, antennae systems went off intermittently due to power issues. Because there were gaps in time where moving fish were not tracked, the measured movement rates are likely biased low. Beaver-influenced site antennae ran for a total of 40–68 days (on average 54 days) and control site antennae ran for 47–49 days (on average 48 days). Because different numbers of fish were tagged at each site, the percentage of individual fish exhibiting different movement behaviours at each site were analysed.

To measure fish movement, we tagged individual salmonids upstream and downstream of the Stjørðdal S. and Orkla beaver ponds and upstream and downstream of the antennae in the control sites. Fish were only tagged below the beaver pond at the Stjørðdal N. site because there was a lake just upstream of the beaver pond and we did not capture any salmonids between the pond and the lake. We calculated movement rates for fish that exhibited different movement behaviours. From upstream to downstream, fish could (a) stay above the study reach, that is, they were tagged upstream and never were detected in A1 or A2 or any point downstream, (b) approached A1 using the upstream study reach habitat, (c) approached mid-reach (A2) or the dam, that is, were detected in A2 but did not move past the dam or mid-reach, (d) moved and stayed downstream past mid-reach or downstream past the dam, (e) moved downstream and back upstream again, and from downstream to upstream, fish

could (f) move upstream past the dam or mid-reach and back down again, (g) moved and stayed upstream, (h) approached mid-reach or the dam, that is were detected in A3 but did not move upstream, (i) approached A4 using only the downstream study reach habitat, or (j) stayed downstream of the study reach and were never detected in an antennae or anywhere upstream. The percentage of fish that exhibited each behaviour are presented, as well as overall mean movement or lack of movement rates. Percentages are calculated by tagging location, that is, the percent of fish that approached A2 from upstream is the number that approached A2 divided by the total number tagged upstream. We also tracked the timing of fish movements to see whether there were any differences by site in the timing of movement or attempted movements.

The effect of habitat type (pond, upstream and downstream beaver-influenced site, control site) on total fish species richness and salmonid species richness was analysed using ANOVA, and Tukey HSD was used to determine significant differences between variables. The effect of habitat on fish growth, condition and movement rates was analysed using two-sample *t* tests, except Welch two-sample *t* tests were used for the following movement categories: multiple movements up and downstream, multiple movements down and upstream, and stayed above the reach (due to unequal variance).

Population estimates were made in the program MicroFish (3.0, <http://www.microfish.org/>), which calculates maximum-likelihood population estimates and capture probabilities using electrofishing removal data for each fish species. When few fish (≤ 6 individuals captured in total over all three passes) were caught, maximum-likelihood estimates could not be made and the actual number of fish caught was used to calculate densities. In the cases, where depletion was nondescending and fewer than 30 fish were captured, then the actual number of fish caught was also substituted for an estimate (Riley & Fausch, 1992; Utz & Hartman, 2009). Fish density per site was calculated as the population estimate divided by the wetted area (m^2). The effect of habitat type on fish density was analysed using a two-sample *t* test for salmon and Welch two-sample *t* test for trout (due to unequal variance).

3 | RESULTS

3.1 | Habitat

Beaver-influenced and control site lotic reaches had similar widths ($t_4 = -0.5551, p = .6084$) and depths ($t_4 = -0.7318, p = .5049$). The beaver ponds were all $< 3,000 m^2$, relatively small compared to the large complexes found in North America that can cover multiple hectares (Naiman, Johnston, & Kelley, 1988). There was no difference in mean or median substrate size or % embeddedness by habitat type ($t_4 = 0.3988, p = .7104$; $t_4 = 0.7091, p = .5174$; and $t_4 = 0.2340, p = .8264$), though one beaver site (Stj. S beaver) was dominated by mud and silt, with a median substrate size of 0.006 cm. There was also no difference in GDD by habitat type (116.3 ± 8.2 vs. $135.9 \pm 45.1, t_3 = -0.7969, p = .4838$).

3.2 | Prey availability and diet

A similar number of macroinvertebrates were collected in the stream samples of both beaver-influenced and control sites (223 ± 127 vs. 380 ± 126 individuals; $t_4 = -1.5231, p = .2024$), but the composition of benthic samples varied by habitat type. The NMDS ordination, based on the relative abundance of 34 taxa groups, represented 88% of the total variation among sites on two axes. Benthic communities in beaver-influenced reaches were significantly separated in community ordination space from communities in control sites ($A = 0.4859, p = .0226$). The strongest separation in habitat types occurred along axis 1, explaining 75.7% of the variation in assemblage structure. Plecoptera (-0.873), adult Hydraenidae (-0.871), Perlodidae (-0.852), Tipulidae (-0.850), Perlidae (-0.810), Psychodidae (-0.694), Chloroperlidae (-0.645), Heptageniidae (-0.602), Glossosomatidae (-0.591), *Limnius volckmari* (-0.575), Sericostomatidae (-0.564), Hydropsychidae (-0.562), Dixidae (-0.543), Nemouridae (-0.525), Goeridae (-0.524) and adult Elmidae (-0.514) were most strongly associated with control sites, while *Ephemera* (0.842), Chironomidae (0.826), Limnephilidae (0.796), Hirudinea (0.762), Oligochaeta (0.703), larval Dytiscidae (0.703) and Ostracoda (0.629) were most strongly associated with beaver-influenced reaches.

A similar amount of allochthonous invertebrate prey inputs also fell into beaver ponds, beaver-influenced streams and control streams (33.1 ± 25.8 vs. 23.4 ± 7.4 vs. 28.8 ± 12.5 individuals/day; $F_{2,6} = 0.241, p = .793$). However, there were differences in the composition of the invertebrate prey inputs by habitat type. The NMDS ordination, based on the relative abundance of 29 taxa groups, yielded a solution that represented 92.7% of the total variation among sites on two axes. Samples from inputs falling into beaver ponds and beaver-influenced sites were significantly separated in community ordination space from control sites ($A = 0.1024, p = .0569$). The strongest separation in habitat types occurred along axis 1, which explained 85.5% of the variation in assemblage structure. Adult Chironomidae (-0.964) and Psocoptera (-0.596) were most strongly associated with beaver sites, while Collembola (0.794), adult Psychodidae (0.633), Coleoptera (0.558), terrestrial larvae (0.495), adult Empididae (0.489), adult Phoridae (0.479), adult Cecidomyiidae (0.478) and adult Tipulidae (0.475) were most strongly associated with control sites.

Interestingly, the composite diet samples from the two beaver-influenced sites contained significantly more prey items than the composite diet samples from the control sites (370 ± 28 vs. 147 ± 37 individuals; $t_3 = 7.1745, p = .0056$).

3.3 | Fish metrics

3.3.1 | Species composition and richness

The presence of beaver dams altered fish distribution and species composition (Figure 4). No trout or salmon were captured in any of

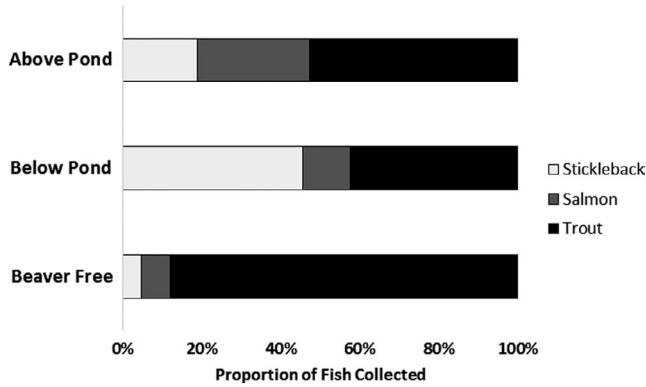


FIGURE 4 Species composition in three of the four habitat types sampled at each site (above pond, below pond and beaver-free control sites). Beaver ponds are not included because salmonids were not captured effectively in the ponds

the beaver ponds. However, a small number of individuals (8 of 208 tagged) were detected by pond antennae for multiple hours or days (see movement and antennae data below) and additional salmonids passed through the ponds, suggesting that our methods were not effective in capturing the small numbers present. Trout (*S. trutta*) almost exclusively dominated tributaries with no beavers (79%–99%)

and salmon made up only a small proportion (0%–16%, depending on the site). In contrast, trout were much less prevalent in the below pond and above pond lotic reaches of beaver-occupied tributaries (9%–31%), except for one higher gradient site where they predominated both above (100%) and below the pond (98%). The greatest proportion of juvenile Atlantic salmon were found in the above pond stream reaches (0%–57%) and a smaller proportion were present downstream of the ponds (0.1%–34%). Stickleback were captured in beaver ponds and also made up large proportions of the fish community below beaver ponds (0%–90%). Stickleback were present to a lesser degree in above pond (0%–45%) and beaver-free reaches (0%–14%). Freshwater flounder were also present in some sites but we did not collect them so they were not included. There was no difference in total species richness or salmon species richness by habitat type ($F_{3,8} = 0.182, p = .906$ and $F_{3,8} = 0.667, p = .596$).

3.3.2 | Recapture rates

In total for the six sites, 588 trout and 108 salmon were tagged over the four sampling months (Table 2). Recapture rates varied by species, month and site, overall ranging from 0% to 22% for trout and

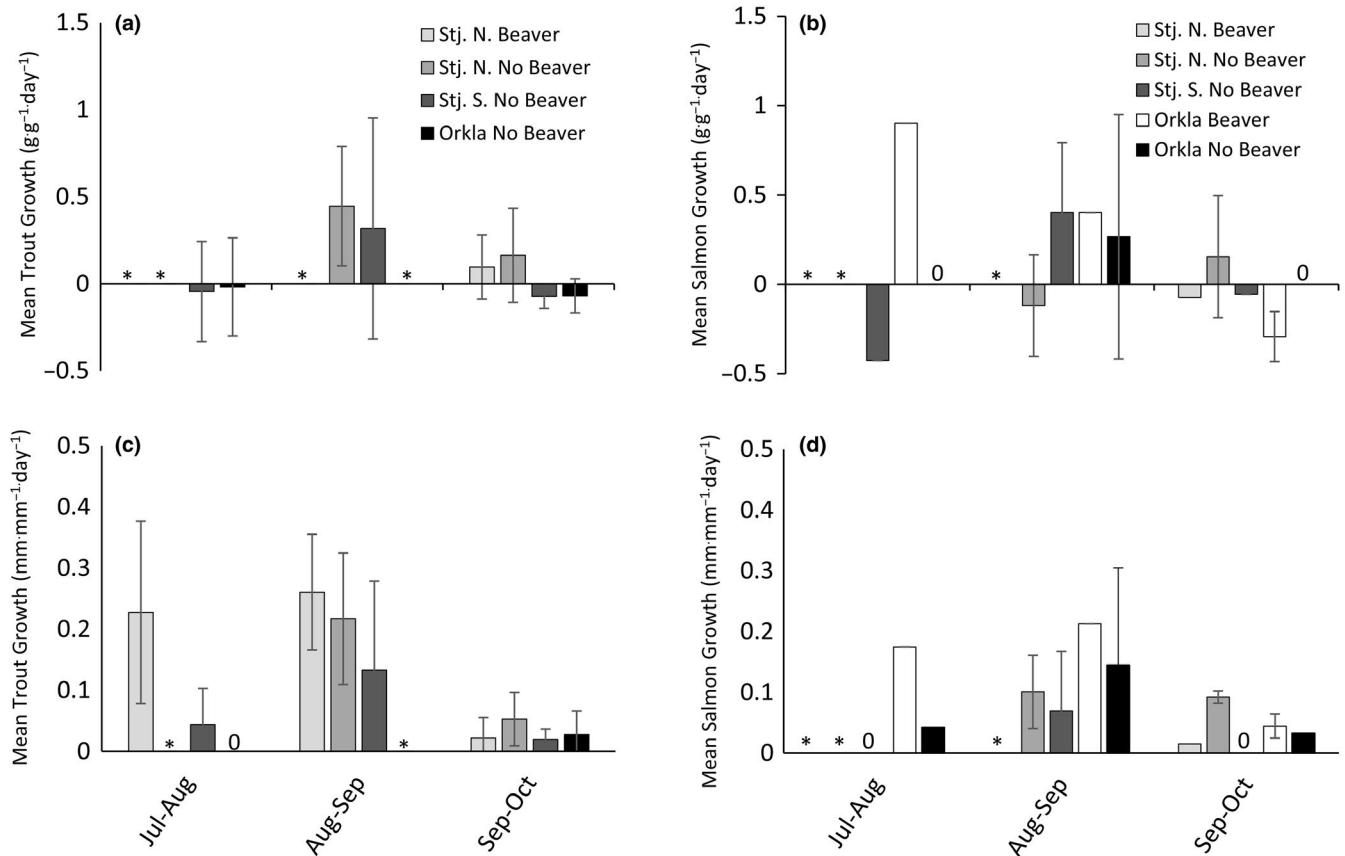


FIGURE 5 Mean ($\pm 1SD$) instantaneous growth rate of juvenile PIT-tagged trout (a and c) and Atlantic salmon (b and d) in weight and length for all sites where individual fish were recaptured between the time periods July–August, August–September and September–October. * indicates data points where no fish were recaptured and growth rates could not be measured. Zeros indicate that growth rates were measured to be zero. Very few fish (0–2 most common) were recaptured and measured at each site for growth each time period. Only four data points are based on over 10 individuals

0%–67% for salmon (Table 2). The vast majority of fish were only recaptured once (70.4%), twice (19.9%) or three times (6.1%), with a few recaptured four or more times (3.6%).

3.3.3 | Growth and condition

There were no consistent differences in trout or salmon growth between habitat types (Figure 5). Often very few fish (sites without error bars indicate only one fish) or no fish (sites with *) were recaptured. There was no significant difference in growth (for weight or length) between habitat types for juvenile salmon from September to October ($t_3 = -1.870$, $p = .1582$ and $t_3 = -0.3227$, $p = .7681$, for weight and length respectively). For all other time periods, growth data were only available for one or no beaver-influenced sites. Of note, growth rates in the Stjørødal South beaver-free site (site with highest densities, see below) varied from lowest to highest compared to other sites depending on the time period for trout. Salmon growth rates at this site were lower or fell within the range of growth rates measured in other sites depending on the time period.

Condition factors were calculated for all age 0 trout and age 1 salmon and trout. Condition was similar in control sites and both the downstream and upstream lotic reaches of beaver-influenced sites ($F_{2,6} \leq 3.468$, $p \geq .0998$; age 0 trout: 1.11 ± 0.01 vs. 1.18 ± 0.02 vs. 1.19 ± 0.06 ; age 1 salmon: 1.08 ± 0.05 vs. 1.14 ± 0.05 vs. 1.16 ± 0.02 ; age 1 trout: 1.16 ± 0.01 vs. 1.10 ± 0.02 vs. 1.19 ± 0.04 , mean \pm SE respectively for each habitat type). Age 0 salmon condition was similar in control sites and the downstream reaches of beaver-influenced sites, but too few were present in the upstream reaches of beaver-influenced sites to analyse ($t_2 = 0.5072$, $p = .6624$; 1.19 ± 0.07 vs. 1.15 ± 0.01 respectively). The condition of all salmonids varied each month, but there was no pattern of decreasing or increasing condition over the sampling season.

3.3.4 | Movement

Out of the 759 individuals tagged in total for the six sites, 492 (65%) were detected by the PIT-tag antennae. Detection rates ranged from 39% to 79% of the total fish tagged at each site (Stj. N. Control 70% (190/272), Stj. N. Beaver 48% (57/118), Stj. S. Control 65% (64/98), Stj. S. Beaver 39% (18/46), Orkla Control 65% (70/107) and Orkla Beaver 79% (93/118)). Overall, a significantly greater proportion of individuals crossed the mid-point of the study reach in control sites without beavers compared to the proportion of individuals that crossed beaver dams (Figure 6a; $t_4 = -4.3518$, $p = .01214$). Similarly, a significantly greater proportion of individuals approached, but did not cross, the dam in beaver-influenced sites, compared to the proportion of fish that approached but did not cross mid-reach in control sites (Figure 6a; $t_4 = 4.232$, $p = .01335$). A similar proportion of fish remained either above or below the study reach and did not attempt to

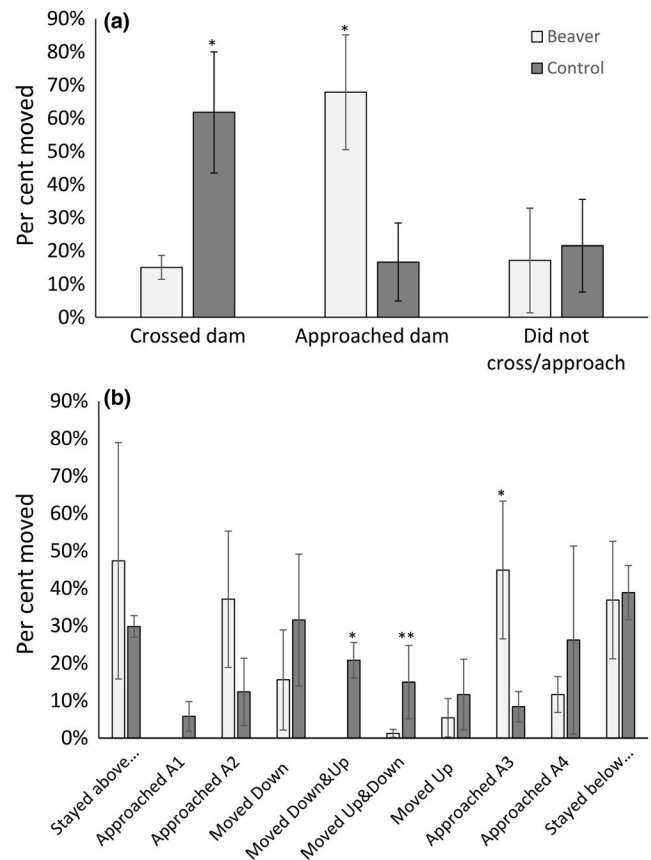


FIGURE 6 (a) Mean (± 1 SE) overall movement rates and (b) mean (± 1 SE) movement rates for each portion of the study reach, for juvenile salmonids in control and beaver-influenced sites. * indicates statistical significance, ** indicates marginal statistical significance.

move in both the beaver-influenced and control sites (Figure 6a; $t_4 = -0.3669$, $p = .7323$). The biggest difference in movement rates by habitat type was due to individual fish making multiple movements up and down the study reach in control sites compared to beaver-influenced sites where dams limited multiple movements (Figure 6b). Significantly more fish made multiple movements down and then back up the reach in control versus beaver sites (Figure 6b; $t_2 = -7.5528$, $p = .0171$). In contrast, there was no significant difference in proportion of fish that made multiple movements up and then back down in control versus beaver sites (Figure 6b; $t_{2,049} = -2.4075$, $p = .1347$). Significantly, more fish approached (but did not pass) the dam from downstream in beaver sites than those fish that approached mid-reach from downstream and turned around in control sites (Figure 6b, $t_4 = 3.355$, $p = .0284$). There was no difference in the proportion of fish that moved down the study reach once or moved up the study reach once in both control and beaver-influenced sites ($t_4 < 0.7820$, $p > .3616$). Thus, the presence of beaver dams does not block the movement of fish, rather the dams seem to limit the degree of repeated movements (Figure 6b).

The degree of individual fish movement or attempted movement varied strongly by habitat, site and over time (Figure 7). There is

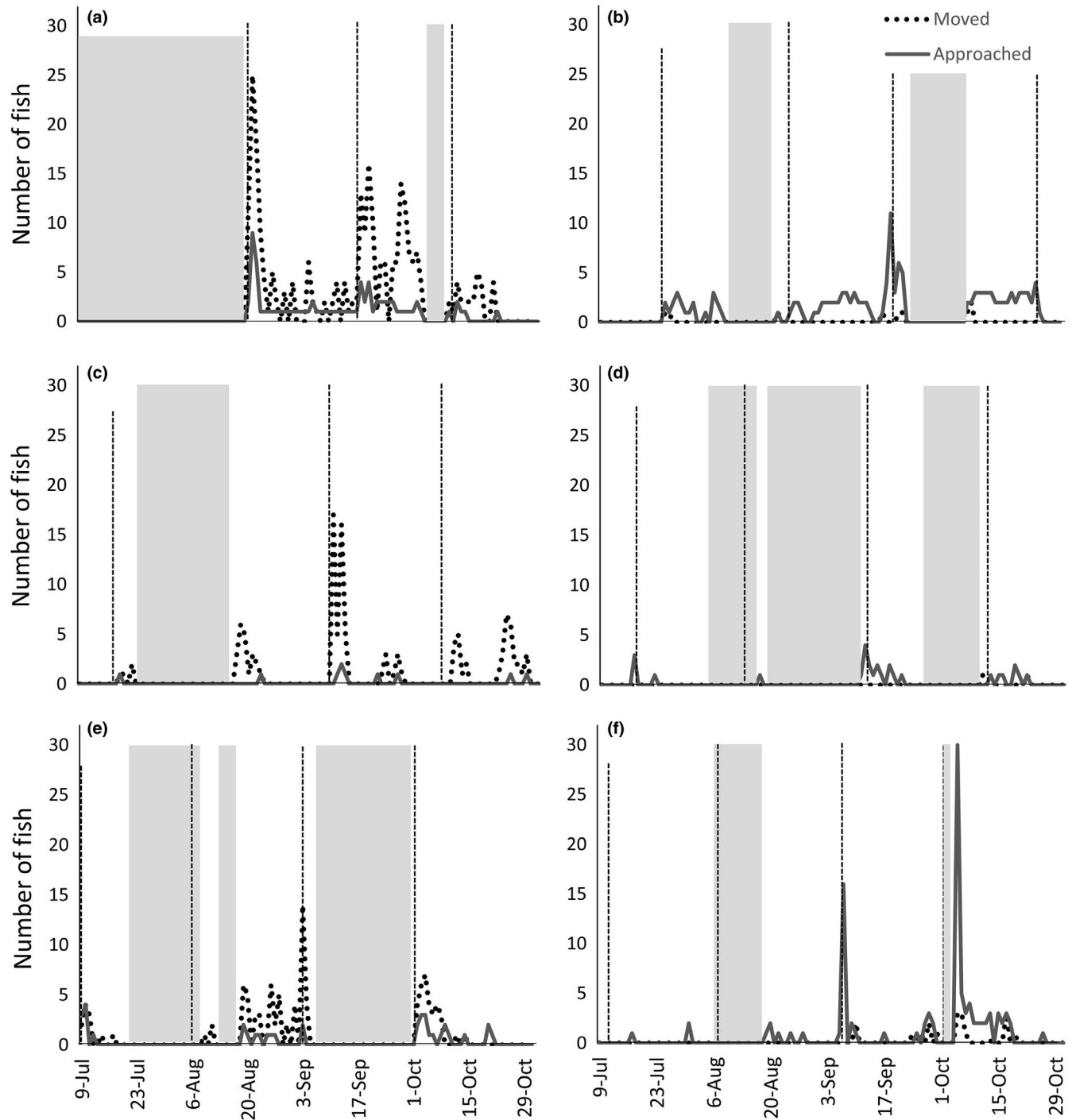


FIGURE 7 The number of individual fish that moved through the reach and the number of fish that approached mid-reach or the beaver dam but did not move over time for (a) Stj. N. Control, (b) Stj. N. Beaver, (c) Stj. S. Control, (d) Stj. S. Beaver, (e) Orkla Control and (f) Orkla Beaver. Dotted black line represents the number of fish that moved up or down the study reach on a given day. Solid dark grey line represents the number of fish that approached the dam or mid-reach, but did not move up or down the reach. Thin vertical dotted lines represent sampling and tagging dates. Grey shaded areas show when PIT-tag readers were not operational (due to reasons like flooding, lack of power, etc.)

a clear difference, with many more fish moving up and down the reach over time in control sites (Figure 7a,c,e) and many more fish approaching the dams but not moving past them over time in the beaver-influenced sites (Figure 7b,d,f). Unsurprisingly, strong peaks in detected movement commonly occurred at every site on the days

when capture and tagging occurred. Overall movement rates are likely even higher than those measured because readers were not continuously operational throughout the season due to uncontrollable events like floods and problems recharging battery banks (see grey highlighted areas, Figure 7).

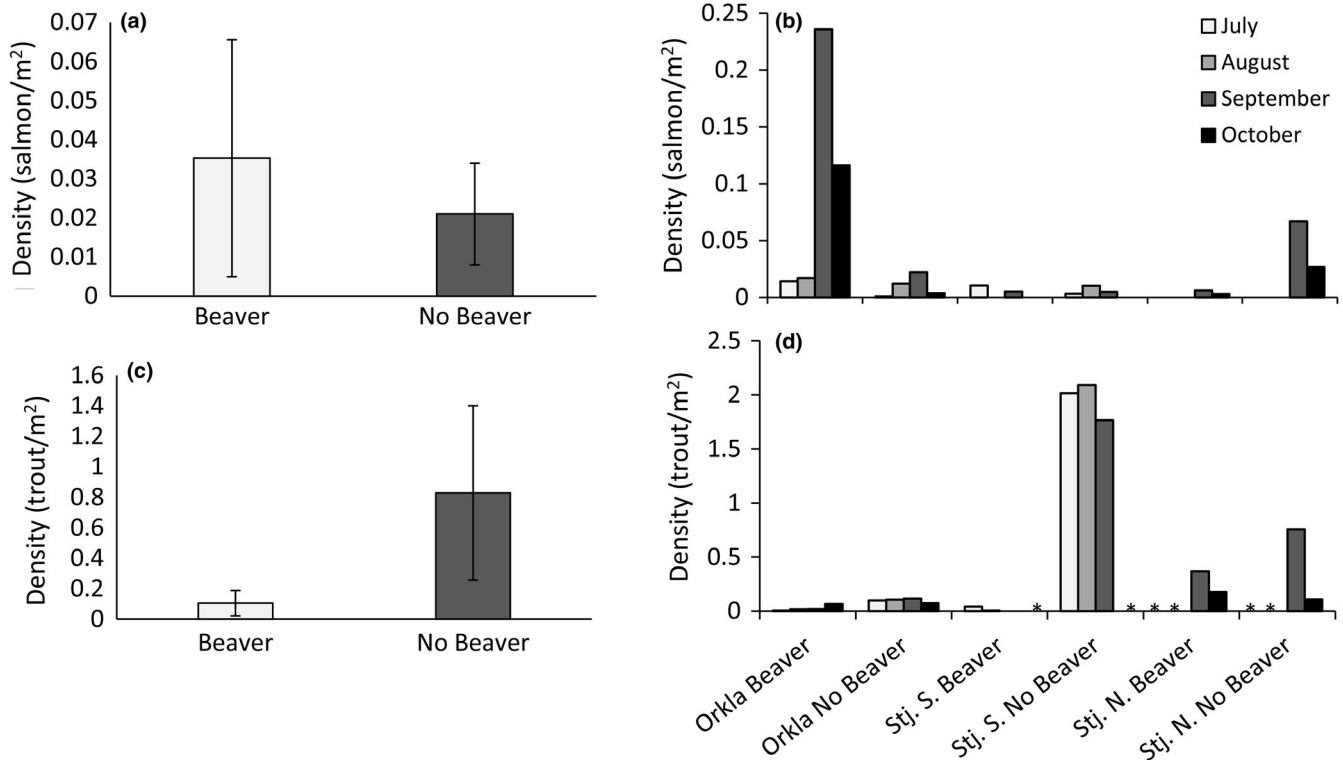


FIGURE 8 Mean ($\pm 1SE$) juvenile fish density for (a) Atlantic salmon and (c) trout in the lotic reaches of beaver-influenced and beaver-free sites and density of juvenile (b) Atlantic salmon and (d) trout for each site in July, August, September and October. * indicates sampling periods where fish were not sampled, not zero densities

Although we did not capture salmonids in the beaver ponds, it was likely because so few fish were present in the ponds that our methods were not effective. Some individuals were present in the ponds long enough to move from the above pond lotic reach to or past the beaver dam (25 ind. total), or to move from the downstream lotic reach up into the pond (21 ind. total). Additionally, eight of the individuals tagged at beaver sites (out of the 282) were detected in the pond antennae for multiple hours or over the course of numerous days. Of these, the individual that spent the least amount of time in the pond was detected on 3 different days, for up to 6 hr at a time and the individual that spent the longest amount of time in a pond was detected for 11 continuous days for up to 24 hr at a time.

3.3.5 | Density

The total number of fish sampled in depletion sampling events was much higher than in capture-mark-recapture sampling because age 0 fish were included in the samples. There was no significant difference in juvenile salmon density by habitat type ($t_4 = 0.4326$, $p = .6876$), with densities being generally very low in the lotic sections of both beaver-influenced and beaver-free sites (Figure 8a,b). However, there was some variation by site and time period. Trout densities varied strongly between control sites and were highest in the Stjørdal South beaver-free site in all months sampled. Interestingly, salmon densities strongly increased within the Orkla

beaver site in September and October (Figure 8b). Densities of juvenile trout were an order of magnitude higher than salmon densities (Figure 8b,d) and there was no significant difference in trout densities by habitat type (Figure 8; $t_{2,0853} = -1.251$, $p = .3331$).

4 | DISCUSSION

The presence of beaver dams altered habitat use by juvenile salmon and trout over small spatial scales, but the dams did not block juvenile salmonid movement. Tagged individuals of both species were recorded moving through beaver ponds, with small numbers of salmonids being detected for multiple hours or days by antennae in the ponds. Additionally, both species were able to move past dams and used lotic reaches above and below the beaver ponds. Trout were generally less prevalent in beaver-influenced tributaries and salmon were most abundant in the above pond reaches. However, it is not clear if the higher abundance of juvenile salmonids above beaver ponds is due to adults successfully passing the dams and spawning upstream, or if juveniles are moving upstream (or both). Despite differences in habitat use, the presence of beaver dams did not influence the growth or condition of juvenile trout and salmon or food availability in the lotic reaches of beaver-influenced tributaries compared to control sites.

The strongest apparent influence of beaver dams was the limited use of beaver ponds as juvenile salmonid rearing habitats. No



FIGURE 9 Photographs of the Stjørødal North Beaver site during low (a) and high (b) water, illustrating how the dam is blown out in large rain events and fish passage is obviously possible

juvenile salmonids were captured in the ponds, but a small number (8 of 208) tagged outside of the ponds were detected for multiple hours or days in the ponds after having moved in from lotic reaches. The small number of fish detected in the pond for hours or days (3.8%) suggests that the ponds may not be an important rearing habitat. In addition to the minnow trapping that may have been ineffective, we did not capture any individuals when electrofishing the shallow reaches of the ponds or observe any individuals swimming in the ponds. Despite this, we cannot say for certain that there was not a resident subset of juvenile salmonids living within the pond that were never captured and tagged. If indeed the ponds are not preferred rearing habitat, this is in strong contrast to the use of beaver ponds by juvenile Pacific salmonids. High densities of juvenile Chinook and coho have been found rearing in beaver ponds in Alaska (Malison et al., 2014) and Sigmourney, Letcher, and Cunjak (2006) measured higher growth rates of juvenile Atlantic salmon in a beaver pond in Canada. However, that pond was formed after salmon parr were already present in June and there was likely not time for substantial deposition of mud. This study appears to be the first to have searched for the species in established beaver ponds. In Europe, juvenile trout are considered to have greater affinities for ponds than Atlantic salmon (Heggenes et al., 1999; Heggenes & Saltveit, 1990), but we did not observe any trout using the beaver

ponds either. Understanding exactly how extensively juvenile salmonids use beaver ponds as rearing habitat would require additional antennae at both the inlet and outlet of the ponds (which was not possible in this study) and additional sampling effort within the ponds themselves.

The beaver dams did not block the movement of juvenile fish in either the upstream or downstream direction. Rather, there were reduced repeated movements by individual fish at beaver sites, with significantly more fish repeatedly moving up and down the study reach in control sites. However, a similar number of fish moved upstream or downstream once, and a similar number of individuals stayed in the upstream or downstream reaches without attempting movement in both beaver-influenced and control sites. Thus, dams may act as structural features that modify daily home ranges, but not as permanent barriers to fish movement. In contrast, it is possible that less movement occurs in the vicinity of the dams because the fish do not need to move as much in the more complex habitat of the ponds (Wathen et al., 2018).

Because habitats both below and above the ponds were still used by juvenile trout and salmon, and the total area of impacted stream bed is small, the overall impact of these ponds seems quite small. Although the beaver dams can look like impassable barriers, many opportunities for fish movement occur. Fish were documented moving even when there was no visible flow path, possibly using the spaces within the dams. Additionally, heavy rain events frequently occur in the Trøndelag Province of Norway. Dams are frequently broken in such events or the ponds fill to the extent that water runs around the dams, or flows in a continuous stream which fish can swim through, over it (Figure 9; R. Malison & D. Halley, personal observations). Thus, the dams may seem to be an obstacle, but they are present in very dynamic systems.

The presence of beaver dams and ponds had no effect on the mean growth, condition or density of juvenile salmonids rearing in lotic stream reaches. However, there was a large amount of variation in site characteristics and associated fish densities. The Stjørødal S. control site had the greatest density of juvenile salmonids (primarily age 0 trout) and the Stjørødal S. beaver site had the lowest densities. Higher densities at this control site may be a result of spawning gravel additions to the study reach in previous years. Sea trout also actively spawned in this reach, so the study was conducted at or near the redds. Despite having the highest densities, the Stjørødal S. control site did not have the lowest growth rates. Rather, growth rates were highly variable, falling below, similar or among the highest measured at other sites. In contrast, the Stjørødal S. beaver site had the worst stream-bed conditions, very few salmonids and no recaptures. Interestingly, the number of salmon captured increased over fourfold from July and August to September and October and the number of trout captured increased almost fourfold from September to October in the Orkla beaver site. These tributary sites, and their beaver ponds, could play a role as habitat refugia in winter months. Beaver ponds are well known to be important winter refugia for Pacific salmon (Bustard & Narver, 1975; Nickelson, Rodgers,

Johnson, & Solazzi, 1992; Swales, Lauzier, & Levings, 1986). The ponds may also be an important benefit to populations of Atlantic salmon and trout rearing in tributaries, especially as downstream refugia for more abundant populations located above beaver ponds. This means the ponds could have more positive benefits to juvenile salmonids that we were not able to measure.

This study was largely conducted and funded because of the uncertainty in how interactions between North American beavers and Pacific salmon may differ from those between Eurasian beavers and Atlantic salmon and trout. At small scales, the impact of beaver dams will depend on how much habitat is altered, if the salmon or trout can move past the dams and if upstream habitat is lost. In this respect, the impact of dams from Eurasian beavers on freshwater rearing habitat will likely be smaller because they build small dams which fish can move over or around and the actual amount of inundated habitat is smaller. At larger scales, the cumulative impacts of all dams need to be considered. Interestingly, it is generally uncommon to see beaver dams in the salmon rivers of the Trøndelag province. For example, in a survey of suitable beaver habitat on the lower Stjørdal River drainage, only nine dams were found in 2015 on 105 km of bankside (i.e., 52.5 km of river; Halley & Svartaas, 2015). In contrast, in only 27 km on the Kwethluk River in Alaska there were up to 414 individual beaver dams present between 2004 and 2011 (Malison et al., 2014). It is not clear if this difference in beaver activity is due to differences between the two beaver species (e.g., Eurasian beavers live in bank burrows more frequently and/or just build fewer dams) or if the lack of complex unaltered floodplain habitats and more constricted tributaries do not provide the same opportunities for habitat damming by Eurasian beavers.

Currently, the presence of beaver dams on tributaries of large salmon rivers in the Trøndelag province has a low potential to negatively impact the juvenile stages of stream salmonid populations because beaver dams do not limit overall movement or prevent the use of other habitats downstream and upstream of the ponds. Additionally, the dams are quite small and they are frequently inundated or broken in large rain events, providing ample opportunities for fish passage. Lastly, the presence of the dams and ponds in the landscape is quite rare in comparison with many areas in North America. It seems therefore unlikely that expanding beaver populations will negatively affect the juvenile stages of salmon and trout populations in the Trøndelag province due to the small spatial scale of habitat modification combined with the lack of major changes to the ecology, habitat use and movement of juvenile salmon and trout caused by the presence of beaver dams and ponds. However, there is potential for the influence of beavers to change following successful reintroductions or establishment of robust beaver populations and continued consideration of their impacts should be evaluated if a change in dam-building behaviour, population sizes or the magnitude of their influence on the landscape occurs. Additionally, this work was conducted in a small geographic area within a country that stretches from 58 to 71°N, with over 400 salmon rivers and more than 1,000 sea trout rivers. It is possible that the influence of beavers in other

parts of Norway or Scandinavia may be different. Reintroduction decisions should carefully consider all factors influencing a river system before reintroductions are made (Malison, Kuzishchin, & Stanford, 2016), including the potential positive effects of beaver ponds on biodiversity that would benefit other species of conservation importance (Stringer & Gaywood, 2016).

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DATA AVAILABILITY STATEMENT

Data have not been shared and are not publically available.

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