Freshwater Biology

Freshwater Biology (2014) **59,** 1229–1246 doi:10.1111/fwb.12343

Beavers (*Castor canadensis*) influence habitat for juvenile salmon in a large Alaskan river floodplain

RACHEL L. MALISON, MARK S. LORANG, DIANE C. WHITED AND JACK A. STANFORD
Flathead Lake Biological Station, The University of Montana, Polson, MT, U.S.A.

SUMMARY

Our aim was to determine how beavers affect habitats and food resources for juvenile salmon in the Kwethluk River in western Alaska.

1. Habitat modification by beavers was quantified using 3 years of satellite imagery to assess the amount and spatial distribution of potential juvenile rearing habitat. Macroinvertebrate community composition and juvenile salmon abundance in beaver ponds, spring brooks with and without upstream beaver dams, and main channel shorelines were quantified to determine beaver influence. Presence of beaver dams and time-series measures of water levels were used to assess hydrological connectivity and fish access between the sites and the river as modified by beavers.
2. Of the off-channel aquatic habitat, 87.5% was altered by beavers damming spring brooks. All beaver-free and beaver-influenced juvenile salmon habitats had similar physical characteristics [by non-metric multidimensional scaling (NMDS) ordination], indicating that all are suitable as juvenile salmon rearing habitat.
3. Aquatic macroinvertebrate community composition differed between beaver ponds and spring brooks (by NMDS ordination) with differences driven by larval stoneflies in spring brooks compared to cladocerans, copepods and freshwater clams in beaver ponds.
4. Chinook (*Oncorhynchus tshawytscha*) and coho (*O. kisutch*) salmon were predominant in all habitat types except late-successional ponds. Total fish species and salmon species richness was 2–3× higher, the proportion of young-of-the-year salmon was over 50% compared to <5%, and densities of juvenile salmon were 5–7× higher in spring brooks and early-successional ponds compared to late-successional ponds.
5. Early-successional ponds had high hydrological synchrony values (closely tracking water fluctuations in the main channel), while mid- and late-successional ponds, being farther from the main channel and with more dams blocking flow paths, had lower and highly variable synchrony values. Almost no movement of juvenile salmon occurred past dams at base flow. However, summer and autumn flooding mediated movement past dams, allowing individuals to 'escape' or enter early-successional ponds.
6. Beavers reduced habitat connectivity and added variability to macroinvertebrate assemblages within habitats by damming floodplain spring brooks. Nonetheless, juvenile salmon were able to effectively inhabit and move between early-successional ponds and spring brooks in the Kwethluk River, although the presence of beaver dams strongly limited the use of late-successional ponds on the large alluvial river floodplain.

Keywords: Alaska, *Castor canadensis*, Kwethluk River, large river floodplain, salmon movement

Correspondence: Rachel L. Malison, Flathead Lake Biological Station, The University of Montana, 32125 Bio Station Lane, Polson, MT 59860-6815, U.S.A. E-mails: rachel.malison@umontana.edu/wilkrach@gmail.com

Introduction

Large animals, especially herbivores such as moose, elk (Collins & Helm, 1997; Beschta, 2003; Butler & Kielland, 2008) and beavers (*Castor canadensis*), have the ability to strongly modify habitats and influence the availability of resources for other organisms (Naiman, 1988; Jones, Lawton & Shachak, 1994; Naiman & Rogers, 1997). Beavers are well known to shape the physical environment by cutting vegetation and building dams that impound small streams and create ponds. In low-order streams, beaver damming results in lentic habitats with altered nutrient and carbon cycles (Francis, Naiman & Melillo, 1985; Naiman, Manning & Johnston, 1991; Naiman *et al.*, 1994), increased nutrient availability (Wilde, Youngberg & Hovind, 1950; Naiman & Melillo, 1984; Pinay & Naiman, 1991), altered fluxes of organic matter, sediment and heat (Naiman, Melillo & Hobbie, 1986; Naiman *et al.*, 1994; Rosell *et al.*, 2005) and increased overall biocomplexity (Naiman & Rogers, 1997; Gurnell, 1998; Wright, Jones & Flecker, 2002; Rosell *et al.*, 2005).

Most of our understanding of the effects of beavers on lotic processes and organisms comes from studies of low-order streams that are generally considered preferred beaver habitats (Beier & Barrett, 1987; Suzuki & Mccomb, 1998; Pollock *et al.*, 2004). However, beavers are also ubiquitous inhabitants of large North American rivers (Naiman, Johnston & Kelley, 1988). Beavers have the potential to substantially impound and regulate the flow and exchange of surface and ground water in the low-gradient flood channel networks of larger rivers (Gurnell, 1998). For example, based on observations of beaver activity in the Bow River in the Canadian Rocky Mountains, Rutten (1967) suggested that dams standing for decades in low-gradient floodplains have the ability to confine the main channel and reduce floodplain complexity as sediments are deposited over time. Despite the generally observed substantial influence of beavers on large floodplain rivers, the extent and process of floodplain impoundment and water regulation by beavers and their influence on the distribution and abundance of aquatic organisms have not been examined in detail.

Large alluvial river floodplains are characterised by a shifting habitat mosaic (Stanford, Lorang & Hauer, 2005) that encompasses a variety of habitat types and rates of change that may be influenced by beavers. Off-channel habitats include an array of spring brooks, ponds and wetlands that occur at base flows within the network of abandoned flood channels (Bayley, 1995; Brown, 1997; Petry, Bayley & Markle, 2003; Stanford *et al.*, 2005). Because flood channels scour the bed and intercept the water table, spring brooks develop in abandoned channels, making them ideal sites for the construction of beaver dams that create ponds. As part of a project to compare physical features of salmon rivers around the North Pacific Rim (Luck *et al.*, 2010; Whited *et al.*, 2013), we observed that in North American rivers native beavers routinely dam floodplain spring brooks and create massive pond complexes throughout the parafluvial (area of active scour near the main channel) and orthofluvial (area of deposition farther from the main channel) zones of many expansive floodplains. Understanding how extensively beavers can modify large alluvial river floodplains, and how the resulting suite of beaver ponds may differ in physical characteristics based on their location in the floodplain and successional stage (see Mouw *et al.*, 2013), is important because habitat quality is a critical controlling influence on the distribution and abundance of biota. In this study, we were particularly interested in the influence of beaver ponding on the ecology of juvenile salmon.

The potentially strong influence of floodplain impoundment by beavers may be expected to strongly influence prey (macroinvertebrates) and consumer (salmon and other fishes) communities by creating lentic habitats in areas that would otherwise be lotic. Macroinvertebrate community composition, richness and diversity have been shown to be altered by beaver activities in low-order stream systems (Mcdowell & Naiman, 1986; Smith *et al.*, 1989; Hammerson, 1994). Impounded sections of low-order streams also have greater numbers and sizes of fish (Hanson & Campbell, 1963; Leidholt Bruner, Hibbs & Mccomb, 1992; Schlosser, 1995), although in other cases reduced habitat quality has negatively affected fish habitat use (e.g. low oxygen levels, Burchsted *et al.*, 2010). How strongly the presence of beaver dams and ponds influences the composition and distribution of juvenile salmon and their food resources on an alluvial river floodplain should depend on the amount of habitat dammed and the degree to which habitat quality differs.

In addition to altering habitat quality, beavers may change the physical and hydrological connectivity of floodplain habitats, which in turn may strongly influence juvenile salmon movement and habitat use. In the absence of beavers, off-channel habitats, including spring brooks, are very important rearing areas for juvenile salmon (Morley *et al.*, 2005; Eberle & Stanford, 2010). However, access to off-channel rearing habitats could be limited if beaver dams block fish movement and limit physical connectivity (Schlosser & Kallemeyn, 2000; Mitchell & Cunjak, 2007). Despite the potential for limited movement, many studies have shown that the movement of adult and juvenile fish does occur past beaver dams, especially at higher flows (Bryant, 1983; Murphy *et al.*, 1989; Schlosser, 1995). Both the magnitude and patterns of flooding could determine when dammed habitats are inundated and accessible, and whether or not juvenile salmon can utilise these habitats for rearing and then leave the habitats to migrate to the ocean. Thus, understanding how beavers influence the hydrological dynamics of a floodplain system is critical in determining whether juvenile salmon distributions may be influenced by beavers.

We present the first analysis of beaver influences on an expansive floodplain of a large alluvial (gravel-bed) river. Our study site was the Kwethluk River in western Alaska, a typical example of a North American floodplain river that is known to be an important salmon producer (Miller & Harper, 2012). Specifically, we addressed the following questions: (i) What proportion of the floodplain is influenced by beavers, what types of habitats are present, and has the influence of beavers been relatively constant over the last decade? (ii) How do different habitat types vary in physical characteristics and habitat qualities that may be important for salmon production? (iii) How does the composition of macroinvertebrate forage items and fishes differ by habitat type? (iv) Do different habitat types vary in physical and hydrological connectivity, and does this influence habitat use and movement of juvenile salmon?

Methods

Study area

The Kwethluk River (3787-km^2 catchment area) is a fifth-order tributary of the Kuskokwim on the west coast of Alaska. The Kwethluk River enters the Kuskokwim River just above the tidally influenced lower reach, *c.* 15 km upstream of Bethel, Alaska. It is protected from development and flow regulation by inclusion within the Yukon Delta National Wildlife Refuge. We chose to study the influence of beavers in this floodplain landscape because beavers are prevalent in the river drainage. In fact, beavers have been present in Alaska since the early Holocene (Robinson *et al.*, 2007), and their long-term presence has resulted in altered successional pathways of riparian vegetation in the floodplain (Mouw *et al.*, 2013).

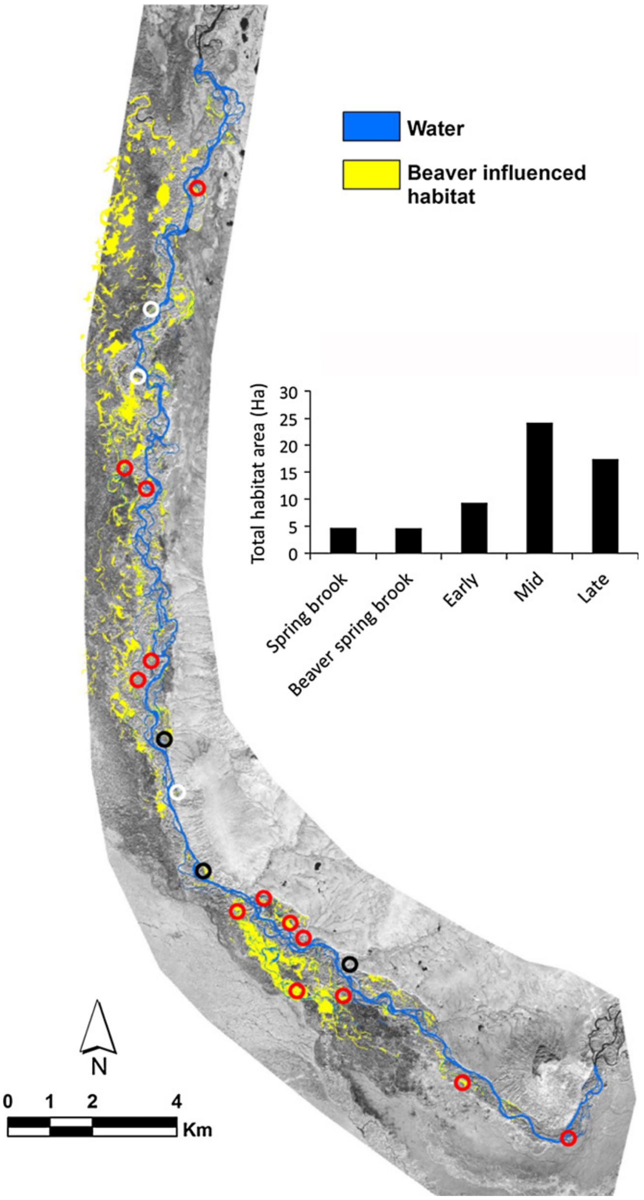

Fig. 1 Beaver-modified habitat in the lower floodplain of the Kwethluk River is highlighted in yellow, and the main (base flow) channel network is highlighted in blue. Red circles show locations of 13 beaver pond complexes where individual sites were sampled. Black circles show locations of beaver-free spring brooks, and white circles show an additional 3 beaver complexes sampled for fish. The inset gives total habitat area of the five primary habitat types in 2011.

The study reach is an expansive anastomosing floodplain located between 37 and 64 km (from Three-Step to Elbow Mountain) above the confluence of the Kwethluk River with the Kuskokwim (Fig. 1). The floodplain is underlain by an extensive alluvial aquifer that maintains a robust riparian zone, in this case mainly composed of willow (*Salix* spp.), alder (*Alnus* spp.) and cottonwood (*Populus balsamifera*), with white spruce (*Picea glauca*) as the climax riparian species (Mouw *et al.*, 2013). The floodplain has a laterally migrating main channel, which coupled with frequent occurrences of anabranching avulsions (mediated by gravel bar and drift wood deposition) creates a complex channel network of primary, secondary and tertiary channels that flow continuously (as described by Arscott *et al.*, 2002 generally for gravel-bed rivers). Flood channels disconnect from the main river during base flow conditions owing to levee formation from wood jamming and sediment accretion at upstream ends (Lorang & Hauer, 2006). Spring brooks form in abandoned flood channels from upwelling ground water during base flow and remain free flowing (beaver-free spring brook) or are dammed by beavers. Dammed spring brooks form ponds that often have multiple dams and ponds in a downstream sequence to the main channel confluence or, alternatively, have one or two dams and ponds that feed a spring brook to the river confluence (beaver-influenced spring brook, Fig. 2).

Our floodplain reach ends at Three-Step Mountain where the river switches to torture meander morphology due to tidally induced backwater effects in the main Kuskokwim River. The change in elevation from the top of the 27-km study reach to the bottom is about 68 m, resulting in an overall floodplain slope of 0.0025. The floodplain is surrounded on both sides by permafrost tundra (*c.* 3 m higher in elevation). The river generally experiences spring (snowmelt) and autumn (rain events) flooding that can inundate the entire floodplain or at lower levels simply activate some portion of the flood channel network.

Fig. 2 (a) Aerial view of the main river (top) and dammed (circled) off-channel habitats. (b) Beaver-free spring brooks, (c) beaver-influenced spring brooks (with upstream dam), (d) early-successional beaver ponds (embedded in willow and alder), (e) mid-successional beaver ponds (embedded in meadow) and (f) late-successional beaver ponds (embedded in spruce forest) are present on the floodplain. White dots in some pictures are floats attached to minnow traps.

Spatial and temporal habitat composition

To measure spatial modification of the floodplain by beavers, we quantified the types, amount and distribution of aquatic habitats in the entire study reach from Quickbird satellite multispectral imagery for 2004, 2008 and 2011. Pixels associated with waterbodies were classified and delineated using Definiens Developer (version 8.6; Definiens, Westminster, CO, U.S.A.; www.ecognition.com) and Erdas Imagine (version 9.3; Intergraph, Norcross, GA, U.S.A.; www.geospatial.intergraph.com) software. Following delineation, habitat patches (i.e. ponds, spring brooks and main channel shallow shorelines) were manually demarcated using heads-up digitising (manually drawing polygons around features) in Arc/Map (version 10; ESRI, Redlands, CA, U.S.A.; www.esri.com) for each year, following similar methods used by Whited *et al.* (2013). We classified three types of beaver ponds (early-, mid- and late-successional) based on the dominant vegetation surrounding ponds. Ponds were classified as early-successional if they were embedded in willow/alder (*Salix* and *Alnus* spp. – see Mouw *et al.*, 2013). Ponds were classified as mid-successional if they were embedded in meadows and as late-successional if embedded in spruce forest (*P. glauca*). Image classifications were validated from field observations of these habitats at specific study sites.

We analysed temporal variation in floodplain habitats with three images, for a total of two time steps between 2004–08 and 2008–11. We calculated the amount of area in the following cover type classes for both time steps: restored spring brooks (following dam blow out, i.e. dam present in the first image, but not in the second), recently dammed spring brooks (free flowing in first image, dammed in the second), new spring brooks with dams (spring brook not present in first image, but present and dammed in second) and new free-flowing spring brooks (present only in the second image and not dammed). Classifications were made by visual inspection of the imagery and confirmed for a portion of the 2011 image through a field survey.

Habitat characteristics

We compared physical characteristics among different types of beaver ponds (early-, mid- and late-successional) and among different types of spring brooks (beaver-free or beaver-influenced). We selected a subset of each habitat type identified in the satellite image for study and refer to individual study 'sites'. We selected six early-, four mid- and three late-successional beaver pond sites, as well as three beaver-free and four beaver-influenced spring brook sites along the length of the floodplain. It is common for multiple ponds and a beaver-influenced spring brook to be present and connected in one area, which we call a 'complex'. Four beaver-influenced spring brooks were located in the same complexes as four early-successional ponds, resulting in the 17 beaver-influenced sites being located within 13 complexes. Thus, we had a total of 20 study sites, located within 16 study areas on the floodplain (13 beaver complexes and three beaver-free spring brooks, Fig. 1).

Site area and perimeter were measured from satellite imagery using Arc/Map and on the ground validation was completed by walking the perimeter of the site with a handheld Trimble GeoXM 2005 GPS (Trimble, Sunnyvale, CA, U.S.A.) for a subset of sites. Conductivity and pH were measured in ponds and spring brooks with an Oakton handheld meter (Waterproof pH/CON 10 Series; Oakton, Vernon Hills, IL, U.S.A.; www.4oakton.com) because these metrics typically vary significantly between groundwater and surface water sources. Width and depth were measured on cross-sectional transects every 10 m along the length of each spring brook site. At 100 locations (every 1 m) along each spring brook, a rock was randomly selected and its size and embeddedness was measured (Davis *et al.*, 2001). We monitored water temperature hourly at each site year-round using HOBO and Vemco data loggers from 2006 to 2011 (Vemco, Halifax, NS, Canada; www.vemco.com). Cumulative degree days were calculated by summing the mean daily temperatures for each site above 0 degrees. Mean diel change in temperature was calculated by subtracting the minimum temperature from the maximum temperature for each day and taking the average for the study period.

Multivariate techniques were used to test for differences in physical habitat characteristics by pond type and spring brook type. Site characteristics were analysed using non-metric multidimensional scaling (NMDS) (Kruskal & Wish, 1978) with the program PC-ORD (version 6; MjM Software Design, Gleneden Beach, OR, U.S.A.; www.pcord.com) because NMDS does not require linear relationships between variables. Metrics used in the pond analysis included cumulative degree days, mean diel change in temperature, vegetation type, site area and perimeter, mean conductivity and mean pH. Metrics used in the spring brook analysis included cumulative degree days, mean substratum embeddedness and size, mean width and depth and mean pH and conductivity. We used multiresponse permutation procedures (MRPP) to test for significant differences in variable composition by habitat type (Mielke & Berry, 2001), following the methods outlined in Peck (2010).

Macroinvertebrates

We collected samples of macroinvertebrates at a subset of the habitat sites including four early-, three mid- and three late-successional beaver ponds as well as four beaver-influenced and three beaver-free spring brooks for a total of 17 sites. At each pond site, we collected three replicate samples by sweeping a D-net (125-μm mesh) through vegetation, along logs and over the substratum for 1 min. In spring brooks, three replicate samples were obtained from riffles selected systematically from each site by disturbing bed sediments within a 0.25-m^2 area for 1 min (upstream of a 125-μm kick mesh net). All samples from ponds and spring brooks were sorted in the field for 1 h or until no more specimens were visible; samples were preserved in ethanol until identified to order or family in the laboratory.

We used NMDS (Kruskal & Wish, 1978) to identify possible patterns in macroinvertebrate taxonomic composition among the five habitat types. Mean abundance of each taxon was computed for each site by averaging the abundance values from the three replicate samples in each site. We used relative abundance values for taxa for all NMDS ordinations because of high variation in raw values. We excluded rare taxa (relative values <5%) from the data set to reduce skewness in the data. The heterogeneous zero-rich response matrix was analysed using the Sorensen distance measure. We used MRPP to test for significant differences in community composition by habitat type (Mielke & Berry, 2001), following the methods outlined in Peck (2010).

Fish composition and juvenile salmon density

In 2006, we conducted a preliminary study to determine the density of juvenile salmon in beaver-free spring brooks ($n = 5$) and main channel shallow shorelines ($n = 5$) by electrofishing, and in early- ($n = 4$), mid- ($n = 4$) and late-successional ($n = 3$) ponds by depletion minnow trapping. Depletion sampling was conducted in known areas and population estimates made using a regression of catch to previous total catch (Zippin, 1958). Between 2009 and 2011, we sampled to determine how fish species richness and composition, and the size distributions and condition of juvenile salmon, varied by habitat type by sampling 16 beaver complexes and three beaver-free spring brooks. We sampled entire beaver complexes rather than just individual sites to increase our sample size and to allow for potential detection of fish movement (see below). The 16 beaver complex sites included the same sites sampled for habitat characteristics, as well as two additional early-successional and one late-successional beaver complex (Fig. 1). Each habitat was sampled once a month during June–September using minnow traps placed throughout the habitat at *c.* 5-m intervals. To standardise trapping effort, baited traps were submersed for 2 h and were removed in the order deployed. Captured fish were held in buckets with aerators. Fish were identified and measured and a subset was weighed. For each sampling date and site, we calculated Fulton's condition factor, K (Ricker, 1975), for each fish by dividing weight (g) by length (mm) cubed and multiplying by a scalar of 10^5.

The effect of habitat type on juvenile salmon density, total fish species richness, salmon richness, condition and proportion of young of the year was analysed using one-way analysis of variance (ANOVA) (PROC GLM; SAS Institute Inc., Cary, NC, U.S.A.). Pairwise comparisons between the least-squares means for habitat type were assessed using Tukey's honestly significant difference (HSD). All data sets were tested for normality and, where necessary, 1og_{10}-transformed to meet the assumptions of normality and homogeneity of variance prior to statistical analysis.

Physical connectivity

Distance and the number of dams may influence the ability of juvenile salmon to move in to different habitat types. We measured physical connectivity among sites relative to the active channel network from the Quickbird satellite imagery (as described above) using five metrics: (i) upstream aquatic distance along the shortest flow path from the site to the main channel, (ii) downstream distance of the shortest flow path, (iii) perpendicular distance (closest straight line distance to the main channel), (iv) number of upstream dams (along the shortest flow path) and (v) number of downstream dams (along the shortest flow path). Juvenile salmon could enter or leave rearing habitats by following aquatic flow paths upstream or downstream of the site (from the main channel), or if overland flooding occurred by moving perpendicularly to access a site.

The effect of pond type on all three physical connectivity distance metrics was analysed using one-way ANOVA. All data were log-transformed to meet parametric assumptions prior to analysis. Pairwise comparisons between the least-squares means for habitat type were assessed using Tukey's HSD. Because data for the number of upstream and downstream dams violated parametric assumptions, we used a nonparametric Kruskal–Wallis test. *Post hoc* multiple comparisons were made after the Kruskal–Wallis tests. Because five comparisons of physical connectivity were made, a Bonferroni correction factor was used to determine the significance at $P < 0.01$ (0.05/5).

Hydrological connectivity

The hydrological connectivity of habitats to the main channel may influence juvenile salmon movement because some habitats may constitute a sink or trap as the hydrology of the channel–floodplain system varies in relation to discharge. We monitored the changes in site-stage height relative to changes in the main channel with HOBO pressure transducer data loggers (Onset, Pocasset, MA, U.S.A.; www.onsetcomp.com). Loggers were anchored on the bed in 13 of the study sites (two main channel, two spring brook, four early-successional, three mid-successional and two late-successional ponds). Year-round hourly changes in habitat-stage height were determined from pressure data and accuracy was checked by coherence of logger data with visual measurements on staff gauges. Although water depth data spanned the period 2006–11, data were only available for every logger between 17 October to 14 December 2007 and 14 May to 27 September 2008, and these data were used for water fluctuation analyses.

Synchrony analysis was used to assess the seasonal patterns in beaver pond hydrodynamics in relation to the river. Temporal coherence, or synchrony, measures the similarity between a pair of sampling sites (e.g. Soranno *et al*., 1999; Kling *et al*., 2000; Karaus, Alder & Tockner, 2005; Patoine & Leavitt, 2006). Synchrony was calculated as the Pearson product–moment correlation coefficient (r) between time series of data for each site paired with the main channel (sites responding similarly to the main channel will have high values, close to 1). To avoid bias from differences in ranges of water-level fluctuations, all time-series data were Z-transformed to standardise variances (Rusak *et al*., 1999). Plots of daily fluctuations and normalised depth plots were used to visually investigate the patterns in water-level fluctuations.

Juvenile salmon movement

We conducted an elastomer tagging study from 2009 to 2011 to find whether juvenile salmon could move past beaver dams. Nine of the sixteen beaver complexes (described above) were sampled for the movement study because they contained at least 2 (and up to 6) adjacent habitats separated by dams (either multiple ponds or early-successional pond/s and a beaver-influenced spring brook), for a total of 32 discrete sampling habitats. Salmon 55 mm or larger were implanted with visual implant elastomer (VIE) tags (Northwest Marine Technology, Shaw Island, WA, U.S.A.; www.nmt.us) in the caudal and anal fins to allow the recognition of tagged individuals moving between discrete habitat units each month. VIE tags have been applied to a wide variety of small fish without compromising their growth, survival or behaviour (Bailey *et al*., 1998; Hale & Gray, 1998; Garcia *et al*., 2004; Walsh & Winkelman, 2004; Kano, Shimizu & Kondou, 2006). Movement rates were calculated as a percentage (the number of fish that moved from one habitat to another out of the total number tagged in the original habitat).

Results

Spatial and temporal habitat composition

Of the entire off-channel aquatic habitat, 87.5% was comprised of ponds and beaver-influenced spring brooks in 2011 (Fig. 1). Mid- and late-successional pond habitats made up the majority of off-channel habitats (38 and 27%, respectively), with early-successional ponds making up the next largest portion (15%, Fig. 1). Spring brooks made up 11% of the total off-channel habitat, but half of them were located downstream of beaver dams (i.e. beaver-influenced, Fig. 1). The smallest portion included parafluvial ponds (0.9%, see Crete, 2012) and backwaters (1.5%). Beaver-free and beaver-influenced spring brooks and early-successional beaver ponds were located in the parafluvial zone, while mid- and late-successional ponds occurred farther from the main channel in the active and passive orthofluvial zones (Fig. 3).

Over almost a decade, there was little temporal variation in the total amount of beaver-modified habitat. The percentage of off-channel habitat modified by beavers generally increased with 70.9% dammed in 2004, 81.7% in 2008 and 80.2% in 2011 (Table 1). The total number of dams in the study reach was 369 in 2004, 414 in 2008 and 373 in 2011. However, some of these differences could be due to the variation in imagery leaf cover or discharge between years (August 2004 versus October 2008). The habitat change that did occur between 2004 and 2011 was predominantly within the parafluvial zone due to channel avulsions that altered the path of the main channel (see Fig. S1). In fact, little change occurred

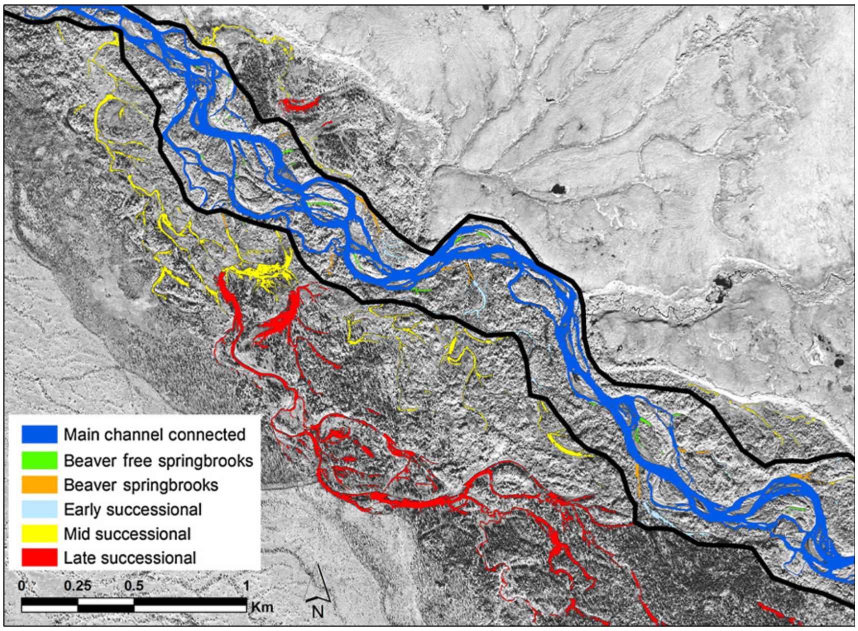

Fig. 3 Distribution of the predominant off-channel habitats of the Kwethluk River floodplain.

in the orthofluvial zone and there was no change in the amount or location of mid- and late-successional beaver ponds (see Fig. S1).

From 2004 to 2008, 7.8% of all off-channel aquatic habitats changed (i.e. new spring brooks formed, new dams were built, spring brooks were restored). The damming of existing spring brooks (i.e. brooks free flowing in 2004 but dammed by 2008; 3.42 ha, 64%) followed by the formation of new spring brooks (1.4 ha, 25%) made up most of the change. Dammed spring brooks blowing out (0.3 ha, 6%) and newly formed spring brooks being dammed (0.2 ha, 5%) contributed much less to habitat change. From 2008 to 2011, slightly less of the total off-channel aquatic habitat changed (5.1%). During this period, the dominant habitat change (40%, 1.6 ha) was caused by the restoration of dammed spring brooks (i.e. dams blew out) but almost as much habitat change (1.2 ha) was composed of existing and newly formed spring brooks being dammed (0.6 ha, 15% and 0.6 ha, 14%, respectively). Despite these dynamics, there was little cumulative change in total amount of each habitat type over time.

Table 1 Area and percentage of total for habitats influenced by beavers on the Kwethluk River floodplain and analysed for temporal change based upon the classification of multispectral imagery from the Quickbird satellite obtained in August 2004, October 2008 and September 2011

	2004		2008		2011	
Habitat type	Area (ha)	%	Area (ha)	%	Area (ha)	%
Main channel connected	172.5	71.6	190.9	71.5	219.3	77.5
Beaver-influenced	48.6	20.2	62.2	23.3	51.0	18.0
Beaver-free parafluvial	13.6	5.6	8.4	3.2	4.2	1.5
Beaver-free orthofluvial	6.4	2.6	5.5	2.1	8.4	3.0
Total aquatic	241.1		267.0		282.9	
Total aquatic off-channel	68.6		76.1		63.6	
Percentage off-channel influenced by beavers		70.9		81.7		80.2

Habitat characteristics

Physical habitat characteristics were similar among different stages of ponds, suggesting that all types of ponds should be equally suitable for juvenile salmon. The NMDS ordination of seven site characteristics yielded a solution that represented 98.5% of the total variation among sites on two axes, but ponds in different habitat categories (early-, mid- and late-successional ponds) were not significantly separated in habitat space (MRPP, $A = -0.0642$, $P = 0.772$). Habitat characteristics were also similar among the two types of spring brooks, with the NMDS solution representing 93.9% of the total variation on 1 axis and no separation of spring brook type in habitat space (MRPP, $A = -0.0096$, $P = 0.467$).

The presence of ponds and spring brooks provided a wide range of thermal habitats for aquatic organisms with temperatures between 4 and 15 °C available on the floodplain during a given day during the ice-free period. Over the course of 1 year, there was a marginally significant difference in degree days between successional stages of beaver ponds, with early-successional ponds generally warmer than mid- and late-successional ponds (734 ± 56 versus 581 ± 141 and 607 ± 153 DD, respectively; $F_{2,12} = 3.233$, $P = 0.075$). However, there was no difference in growing degree days by spring brook type for a portion of the year (274 ± 36 versus 304 ± 57 DD, respectively; $t_4 = 2.776$, $P = 0.486$).

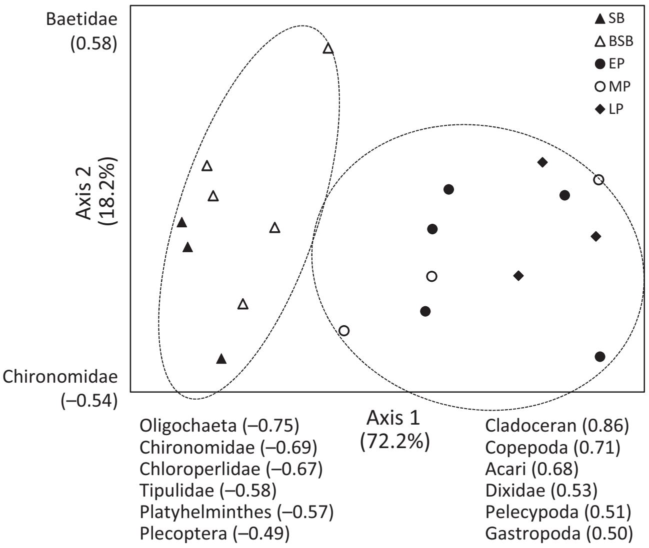

Fig. 4 Non-metric multidimensional scaling (NMDS) ordination plot of relative abundance of macroinvertebrates [beaver-free spring brooks: SB ($n = 3$), beaver-influenced spring brooks: BSB ($n = 4$), early-successional beaver ponds: EP ($n = 4$), mid-successional beaver ponds: MP ($n = 3$), late-successional beaver ponds: LP ($n = 3$)]. Site position in species ordination space is shown relative to axes 1 and 2. Circles enclose groups of sites that were significantly different based on multiresponse permutation procedure analysis by habitat type. Data in the plot are mean relative abundance by site, and percentage of total variation explained by each axis is given in parentheses. Pearson's correlation coefficients between taxa and the axes are given.

Macroinvertebrate and fish community composition

Assemblage composition of macroinvertebrates differed across habitat types (Fig. 4). The NMDS ordination, based on the relative abundances of 35 taxa groups, yielded a solution that represented 90.4% of total variation among sites on two axes (Fig. 4). Sites in different habitat categories were significantly separated in community ordination space (MRPP, $A = 0.231$, $P < 0.001$), with all beaver ponds significantly different from both types of spring brooks ($A \geq 0.159$, $P \leq 0.029$). There was no significant difference among types of beaver ponds ($A \leq 0.028$, $P \geq 0.217$) or among types of spring brooks ($A = 0.012$, $P = 0.347$), although there was some separation in species space by spring brook type (see Fig. 4). Habitat types most strongly separated along axis 1, which explained 72.2% of the variation in assemblage structure. *Oligochaeta*, *Chironomidae*, *Chloroperlidae*, *Tipulidae*, *Platyhelminthes* and larval stoneflies (see Fig. 4 for correlation values) were more predominant in spring brook habitats than in beaver ponds. Small crustaceans, *Acari*, *Dixidae*, *Pelecypoda* and gastropods had higher relative abundance in beaver ponds than in spring brooks.

Fish species composition varied by habitat type (Fig. 5). Coho (*Oncorhynchus kisutch*) salmon were dominant in both types of spring brooks and early- and mid-successional ponds (65-79%), while Chinook (*Oncorhynchus tshawytscha*) salmon were found in the greatest proportions in early-successional ponds (28%) followed by beaver-influenced spring brooks (22%). Late-successional ponds had greater proportions of Alaska blackfish (*Dallia pectoralis*, 27%) and ninespine stickleback (*Pungitius pungitius*, 28%) compared to all other habitats (0–1%). Total species richness and salmon richness varied significantly by habitat type ($F_{4,26} = 5.11$, $P = 0.004$ and $F_{4,26} = 6.99$, $P < 0.001$). Both types of spring brooks and early-successional ponds had double the number of fish species compared to late-successional ponds (7 ± 0, 6.4 ± 1.7, 6.3 ± 1.6 versus 3 ± 1.2; Tukey's HSD, $P < 0.034$). Spring brooks, early- and mid-successional ponds had significantly more salmon species than late-successional ponds (4.3 ± 0.6, 4.1 ± 1.0, 3.9 ± 1.0, 3.3 ± 1.0 versus 1.3 ± 1.5; Tukey's HSD, $P < 0.004$).

Densities of juvenile salmon varied strongly by habitat type ($F_{4,17} = 15.23$, $P < 0.0001$; Fig. 6a). Spring brooks and early-successional ponds had higher juvenile salmon densities than mid- and late-successional ponds (Tukey's HSD, $P < 0.004$). Spring brooks had significantly higher densities and early-successional ponds had marginally higher densities than main channel habitats (Tukey's HSD, $P < 0.002$ and $P = 0.079$, respectively). The percentage of young of the year (fish less than 70 mm) also varied by habitat type (Fig. 6b; $F_{4,23} = 11.56$, $P < 0.0001$). Spring brooks had higher proportions than mid- and late-successional ponds (Tukey's HSD, $P \leq 0.0224$), and early-successional ponds had higher proportions than late-successional ponds (Tukey's HSD, $P < 0.001$).

The condition of juvenile coho and Chinook salmon was highly variable by habitat type and over time, but there was no significant difference in mean condition of coho or Chinook by habitat type for the entire season ($F_{4,19} = 0.84$, $P = 0.517$ and $F_{4,18} = 0.67$, $P = 0.618$). However, coho in late-successional ponds and spring brooks did exhibit the largest drop in condition by September.

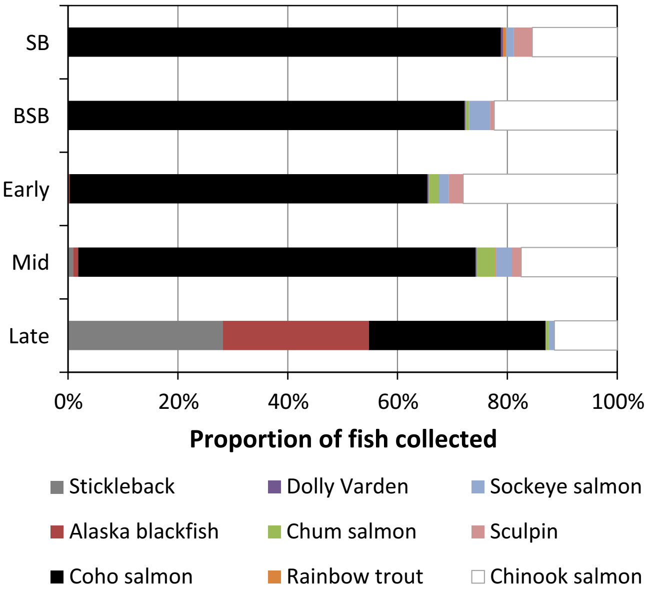

Fig. 5 Fish species composition by habitat type (SB = beaver-free spring brooks, BSB = beaver-influenced spring brooks and early, mid and late representing successional stage of the beaver ponds sampled). Species included stickleback (*Pungitius pungitius*), Alaska blackfish (*Dallia pectoralis*), coho salmon (*Oncorhynchus kisutch*), Dolly Varden (*Salvelinus malma*), chum salmon (*Oncorhynchus keta*), rainbow trout (*Oncorhynchus mykiss*), sockeye salmon (*Oncorhynchus nerka*), slimy sculpin (*Cottus cognatus*) and Chinook salmon (*Oncorhynchus tshawytscha*).

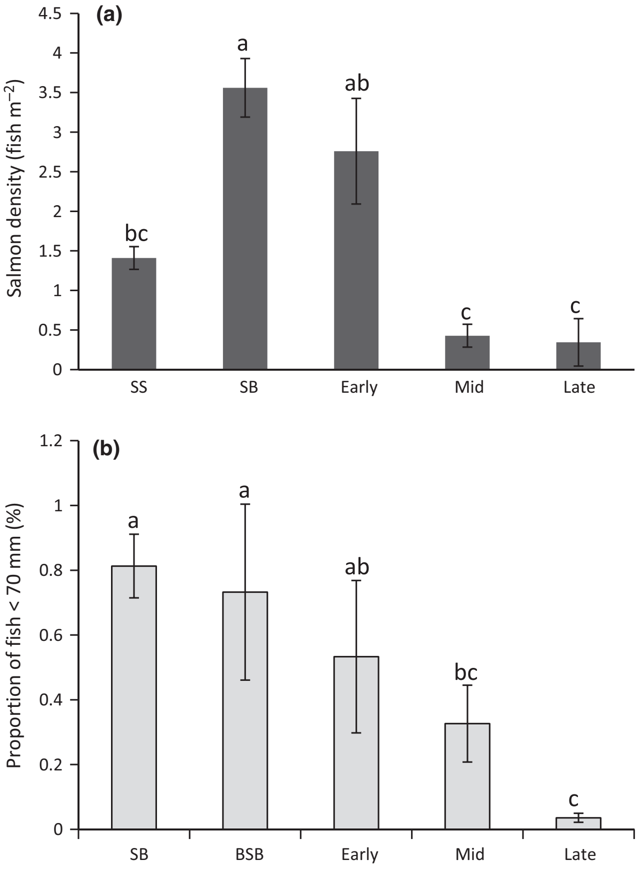

Fig. 6 (a) Mean (±1 SE) juvenile salmon density and (b) proportion of coho and Chinook salmon that were young of the year (out of total including all young of the year and age 1+ or 2+) among primary habitat types (SS = main channel shallow shore, SB = beaver-free spring brooks, BSB = beaver-influenced spring brooks and early, mid and late represent successional stage of the beaver ponds sampled).

Connectivity and juvenile salmon movement

Physical connectivity, or the length of pathways that juvenile salmon could follow to enter and rear in sites, varied significantly by habitat type ($F_{2,14} > 11.04$, $P < 0.001$). Both mid- and late-successional ponds were marginally farther from the main channel in the upstream direction than early-successional ponds (557 ± 99 and 1462 ± 244 m versus 248 ± 59 m; Tukey's HSD, $P < 0.036$). Late-successional ponds were significantly farther from the main channel than both early- and mid-successional ponds in the downstream direction (2406 ± 508 versus 502 ± 300 m and 148 ± 58 m; Tukey's HSD, $P < 0.011$). There was a significant difference in the number of dams present between sites and main channel in the downstream direction (1.5 ± 0.7 versus 1 ± 0 versus 16 ± 6 for early-, mid- and late-successional ponds, respectively; $\chi^2_{2,N=14}$, $P = 0.004$), with both early- and mid-successional ponds having fewer dams than late-successional ponds ($P \leq 0.004$). There was a marginally significant difference in the number of dams between sites and the main channel in the upstream direction (0.1 ± 0.1 versus 1.6 ± 0.6 versus 4 ± 1.8 for early-, mid- and late-successional ponds, respectively; $\chi^2_{2,N=14}$, $P = 0.022$), with early-successional ponds having fewer dams than both mid- and late-successional ponds ($P \leq 0.040$).

Hydrological connectivity varied by habitat type and with distance of the site from the main channel. Spring brooks and early-successional ponds consistently had high synchrony values (0.53 ± 0.13 and 0.54 ± 0.14), reflecting the close tracking of daily water-level fluctuations in the main channel (Fig. 7a,b). Variation in spring brook fluctuations (two peak events, Fig. 7a) may have been caused by avulsions or the formation of debris jams. Variation in early-successional pond depth was probably due to water retention by the dams during flood events and subsequent dam repair and building activities by beavers (Fig. 7b). Mid- and late-successional ponds exhibited comparatively high variation (0.17 ± 0.57 and 0.21 ± 0.72) in synchrony values, probably associated with beaver activities and the greater

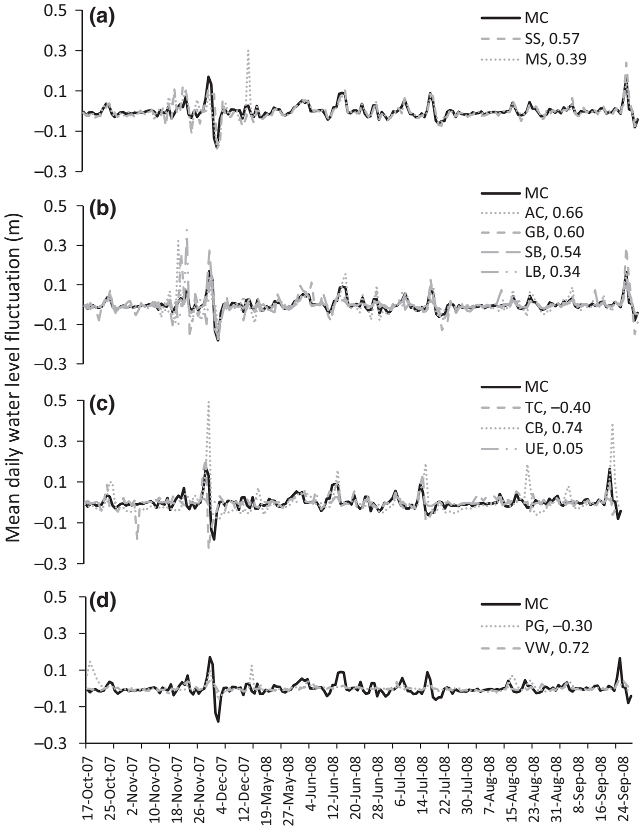

Fig. 7 Daily water-level changes of (a) spring brooks, (b) early-successional beaver ponds, (c) mid-successional beaver ponds and (d) late-successional beaver ponds relative to water-level changes for the main channel (MC, black line in all panels). Synchrony values (correlation of water level relative to the main channel) for each site are listed next to each site in the legends.

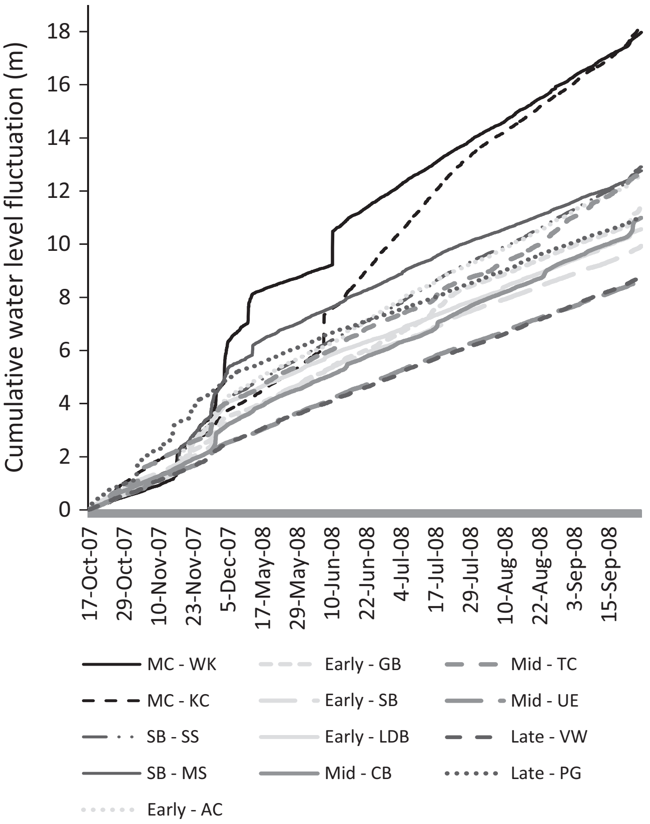

Fig. 8 Cumulative water-level change over the study period for each habitat type. Cumulative change was calculated as the sum of the absolute values of depth changes measured each hour. Main channel habitats shown in black, beaver-free spring brooks in dark grey, early-, mid- and late-successional ponds in light, medium and dark grey, respectively.

distances separating the sites from the main channel (Fig 7c,d). There was no significant difference in synchrony by habitat type due to high variation in the synchrony values of mid- and late-successional ponds ($F_{3,8} = 0.87$, $P = 0.494$). Cumulative water-level change (sum of the absolute values of depth changes recorded each hour) ranged from 8.6 to 12.6 m for pond habitats and from 12.8 to 12.9 m for spring brooks, as compared to 18.2 m for the main channel of the river (Fig. 8), showing that beaver dams in flood channels buffered flow dynamics compared to the main channel.

Normalised depth plots illustrate differences in flood pulse response by habitat type and floodplain position (Fig. 9). Main channel sites exhibited fast increases and declines in depth as flood waters pulsed through the system and were closely tracked by rising and falling limbs in spring brook habitats (MS, SS, BS in grey, Fig. 9a,b). In contrast, the ponding behind beaver dams prolonged the flood pulse (Fig. 9c,d). Early-successional ponds responded faster and more strongly to the flood pulse than mid- and late-successional ponds, illustrating a greater degree of connectivity to the main channel. Additionally, floodplain position influenced flood response. Note in particular in Fig. 9a that the flood wave passing through the upstream main river site (KC) lagged 1–2 days behind the flood wave for the most downstream main river site (WK). This illustrates a fact common to alluvial floodplains but one that is infrequently documented: downstream areas of the floodplain flood before upstream areas. This apparently occurs because the expansive alluvial aquifers are typically losing channels at the upstream end and gaining channels on the downstream end and hence the floodplain subsurface has to fill to capacity before overland flooding can occur (except perhaps in very sudden spates, see Helton *et al*., 2014). This phenomenon is enhanced on the Kwethluk River owing to the beaver ponds that impound nearly all of the flood channels.

The only movement of juvenile salmon past dams was detected in early-successional pond complexes. No

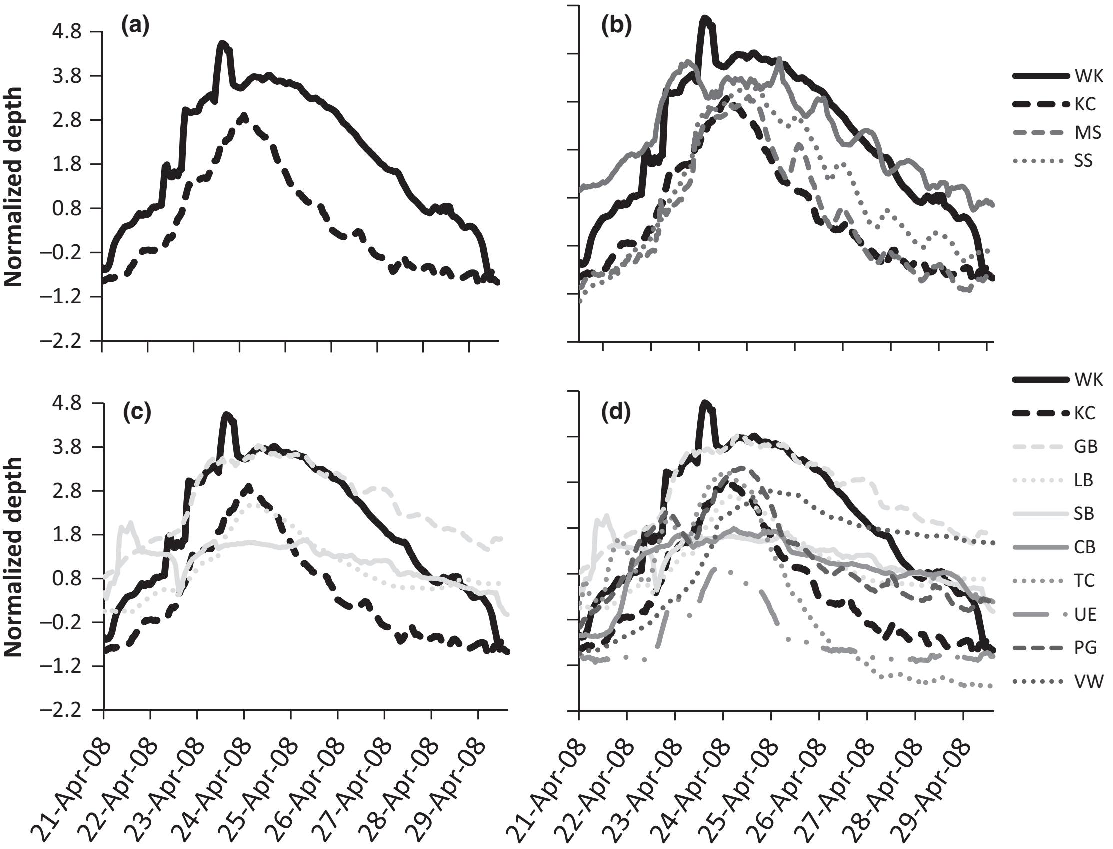

Fig. 9 Normalised depth plots for 1 week in April 2008. (a) Two main channel sites in different floodplain positions (black lines, WK = downstream site, KC = upstream site), (b) close tracking of main channel fluctuations by spring brook sites (dark grey), (c) differences in water-level fluctuations between early-successional beaver pond sites (light grey) compared to the main channel sites and (d) differences in stage height between all successional stages of beaver ponds and the main channel (early-successional = light grey, mid-successional = medium grey and late-successional = dark grey).

tagged salmon were detected moving past dams in mid-successional pond complexes, and too few salmon were present in late-successional ponds to tag. Within the early-successional complexes, we documented almost no movement past beaver dams when the river remained near base flow. Only 3 of 8229 (0.04%) elastomer tagged individuals moved between ponds and spring brooks and this was detected following the one minor flood event. Very low movement rates of individuals between separate beaver ponds within the same complexes occurred at the same time (i.e. past dams, 0.12%, from 8 coho and 2 Chinook). During this time, we did detect slightly higher movement rates between unique spring brooks within a complex where no dams blocked potential movements (0.4%, 39/1020 coho and Chinook).

Ponds were discrete units during baseflow (the white boundary in Fig. 10), but at high flows, there were many potential paths for fish to leave or enter ponds (arrows in Fig. 10). During a season with multiple flood events, we detected higher movement rates, suggesting that flooding mediates movement in and out of beaver ponds. Prior to large floods, we documented 25 of 1762 marked individuals moving (1.4%; 15 fish from ponds into spring brooks and 10 from spring brooks into ponds). Following flooding, we documented an additional 95 fish (of 5102, 1.9%) move between habitat types. Fish ‘escaped’ beaver ponds (49), but a surprising number of fish (46) moved in the opposite direction, upstream from spring brooks into ponds. It is likely that movement rates were even higher (we could not sample every pathway). Despite the ability of salmon to leave beaver ponds during flooding, many fish stayed in the ponds to overwinter. Recapture rates during the flood ranged from 16 to 35% in August and remained as high as 22% (range: 1–22%) in beaver ponds in September.

Discussion

By modifying the physical connectivity and hydrological dynamics of floodplain habitats, beavers have the poten-

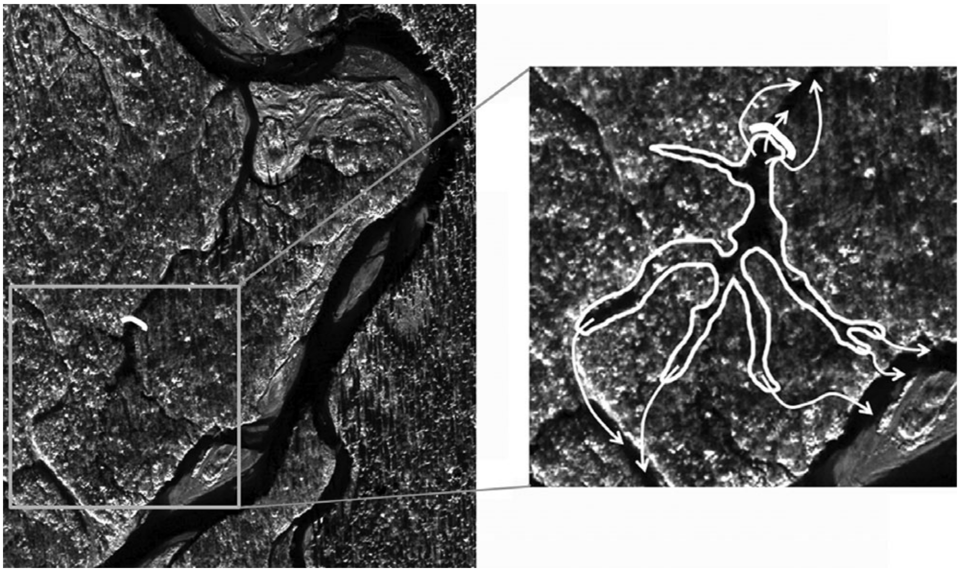

Fig. 10 A section of the study reach illustrating a beaver complex with an early-successional beaver pond and beaver-influenced spring brook below (between the pond and the main channel). At low flow, movement between pond and spring brook was limited (i.e. fish stayed within the white pond boundary), but at high flow fish were able to move between the two habitats. The white shape at the downstream end of the pond boundary shows the location of the beaver dam, and arrows indicate potential pathways of connectivity for juvenile salmon at high flow.

tial to strongly influence juvenile salmon populations. Beaver ponds are characteristically different habitats than lotic streams and spring brooks (Naiman *et al.*, 1988), and the presence of ponds introduces a fundamentally different habitat type for use by macroinvertebrates and juvenile salmon. Beaver-modified habitats occupied 87% of all aquatic off-channel area in the Kwethluk River floodplain. Modified habitat included beaver-influenced spring brooks and early-, mid- and late-successional beaver ponds. Despite the presence of different types of ponds, habitat characteristics of all ponds were very comparable, suggesting all provided rearing habitats of similar quality. However, different successional stages of ponds differed from each other and from spring brooks in their hydrological and physical connectivity to the main channel. Reduced connectivity to late-successional pond habitat resulted in a large portion of the floodplain having very low densities of juvenile salmon (and often no salmon at all). By reducing connectivity to a large portion of the off-channel floodplain habitat, the presence of beaver ponds and dams strongly influenced the habitat use and distribution of juvenile salmon.

We documented little temporal change in the total amount of habitat influenced by beavers, but the location of individual spring brooks and ponds shifted, especially in the parafluvial zone. Hence, beavers are influencing the shift component of the shifting habitat mosaic (sensu Stanford *et al.*, 2005). Within 6% of the parafluvial zone, new habitat types were created due to flood-driven processes that blew out beaver dams and created new spring brooks for beavers to dam. However, little change occurred in the orthofluvial zone compared to documented channel avulsions in the main channel and parafluvial zone. If beavers act to confine the main channel over time, as suggested by Rutten (1967), then the levee effect of extensive dam complexes would decrease lateral connectivity in large floodplains and potentially increase channel incisement. This effect could reduce the power of flood waters across the floodplain and potentially confine the erosive power of the main channel network within the parafluvial zone. Reducing the river's ability to avulse and cut through new sections of the floodplain could be a positive feedback mechanism promoting additional development of late-successional beaver complexes and late-successional species like *P. glauca*. Indeed, Mouw *et al.* (2013) found that about 65% of the Kwethluk River floodplain area was comprised of *P. balsamifera* galleries and *P. glauca* forest.

The presence of beaver ponds on the floodplain strongly influenced the composition of macroinvertebrate communities, important prey items for juvenile salmon. Many studies have found that beaver ponding changes macroinvertebrate communities (Mcdowell & Naiman, 1986; Smith *et al.*, 1989; Hammerson, 1994) and it is not surprising that macroinvertebrate composition was significantly different between ponds and spring brooks on the floodplain. However, it is interesting that the composition of macroinvertebrates in different successional stages of ponds was quite similar. This suggests that food resources for juvenile salmon are similar in all ponds, regardless of their location on the floodplain. In comparison with ponds, spring brooks were dominated by more larval Diptera and Plecoptera taxa. Furthermore, food resources upwelling in alluvial spring brooks (Stanford *et al*., 2005) could provide additional resources, resulting in spring brooks having the capacity to support greater densities of juvenile salmon.

By changing the availability of freshwater rearing habitats, beavers have the ability to strongly influence the distribution of juvenile salmon on the floodplain. Both total fish and salmonid species richness was lower in mid- and late-successional ponds as compared to early-successional ponds and spring brooks. Furthermore, densities of juvenile salmon were lowest in late-successional ponds in the passive orthofluvial zone, illustrating the fact that habitat connectivity influences juvenile salmon distributions. In addition to altering juvenile salmon distributions in general, we also observed differences in the distribution of individual salmon species. As expected, higher proportions of coho salmon occurred in early-successional ponds and spring brooks. Coho fry are typically found in pools and off-channel habitats, including beaver ponds (Sedell, Yuska & Speaker, 1984; Murphy *et al*., 1989; Swales & Levings, 1989; Leidholt Bruner *et al*., 1992). More surprisingly, we also found higher proportions of Chinook salmon in some beaver ponds, including age 1+ Chinook (up to 107 mm; R. L. Malison, pers. comm.), despite the fact that Chinook generally occupy different habitat types than Coho (i.e. river versus off-channel habitats, Stein, Reimers & Hall, 1972; Murphy *et al*., 1989). The presence of ponds may influence the life history of Chinook, resulting in some Chinook rearing in fresh water for longer than the typical 0–1 summers (Quinn, 2005).

Altered physical connectivity of off-channel habitats may help explain juvenile salmon distributions on the floodplain. Beavers can be detrimental to fish populations by blocking fish movements (Schlosser & Kallemeyn, 2000; Mitchell & Cunjak, 2007). It is clear from our work that while some habitats behind dams are not utilised (late-successional ponds), others are heavily used by juvenile salmon (early-successional ponds). The early-successional complexes, where juvenile salmon densities were higher, were located in the parafluvial zone and only had one or a few dams between the sites and main channel. In contrast, the mid- and late-successional ponds in which we detected lower densities (or no salmon) were typically located farther away from the main channel behind multiple dams. It is clear that juvenile salmon can pass beaver dams to enter early-successional pond rearing habitat (because adult salmon do not spawn in the ponds), but late-successional ponds may have too many dams blocking fish passage for these habitats to be used for rearing.

Variation in the hydrological connectivity of different habitats will determine whether juvenile salmon are able to pass over dams to access rearing habitat in different portions of the floodplain. Spring brooks and early-successional ponds exhibited higher synchrony with the main channel compared to mid- and late-successional ponds, which were highly variable. This reflects the fact that spring brooks and early-successional ponds were more strongly connected to the main channel, quickly becoming inundated during flooding. We expected that synchrony would be lower for mid- and late-successional ponds because of their location in the orthofluvial zone. However, these sites exhibited both high and low synchrony values, probably a result of variation in site position relative to the main channel and beaver activity. For example, the mid-successional site with the highest synchrony value was located below a bend of the main river, while the mid-successional site with a negative synchrony value was located downstream of a tundra tributary and had a very active beaver population (that was observed repairing and rebuilding the dam on multiple occasions). By repairing and building dams, beavers are able to raise pond levels even as the main channel drops and these activities seem to be reflected in patterns of daily water-level fluctuations and normalised depth plots for the ponds. Beaver dams also hold back and slowly release water after the river and spring brooks have already receded, which may increase their potential as juvenile salmon rearing habitat compared to spring brooks that would dry up without the ponds and pond maintenance by the beavers. Water storage varied with pond type and location, creating a dynamic template of water levels that could influence the amount of habitat available for juvenile salmon rearing and site accessibility (for example when ponds are inundated, upstream pathways are present for fish movement). The storage of more water in the floodplain through summer and in to the winter could also have important consequences for overwinter habitat for aquatic organisms (Malison, 2013).

The movement of juvenile salmon past dams varied according to habitat type and was mediated by flooding. Reflecting their higher connectivity with the main channel, early-successional ponds tended to fill even during small flood events, providing more opportunities for juvenile salmon to move in. We expect that it would take much larger flood events to inundate the floodplain sufficiently for juvenile salmon to utilise late-successional pond habitat. Such large floods might connect late-successional ponds, but would have devastating effects on early-successional ponds, most likely removing them from the floodplain. In the case of such a large flood event, late-successional ponds might become survival refuges for both beavers and salmon. Despite the ability of juvenile salmon to enter early-successional pond rearing habitats, movement rates past dams separating early-successional ponds from beaver-influenced spring brooks were extremely low at base flow. We documented the movement of more individuals between ponds and spring brooks in both directions during flood events, which suggests that salmon are not trapped once they enter the ponds (also see Malison, 2013), as long as natural flow regimes (including flood events) occur.

By damming significant amounts of off-channel floodplain habitats, beavers may affect the production of juvenile salmon. Spring brooks have been shown to be among the most important rearing habitats for juvenile salmon (Eberle & Stanford, 2010). In large alluvial rivers such as the Krutogorova River (Kamchatka, Russia), where Eurasian beavers have never existed and North American beavers have not been introduced (Halley, Rosell & Saveljev, 2012), floodplains are very complex with dynamic channels and alluvial spring brooks are full (up to 5 fish per m^2, often including three or more salmonid species) of juvenile salmonids throughout the parafluvial and orthofluvial zones (Stanford *et al.*, 2002). In contrast to the Krutogorova River, over 80% of the spring brooks in the Kwethluk River have been dammed on the floodplain, which may result in portions of off-channel habitat generally being lost to use by juvenile salmon. However, beavers are a natural part of the landscape and have been present in Alaska since the early Holocene (Robinson *et al.*, 2007) allowing them to evolve together with salmon. Although we have shown that juvenile salmon can and do use pond habitats, especially early-successional ponds, it remains unclear as to how this modified landscape might influence the growth, survival and overall production of juvenile salmon on a large alluvial river floodplain. If early-successional ponds stimulate the growth and production of juvenile salmon by reducing competition in larger rearing areas, then the overall impact of beavers on juvenile salmon could be positive. However, if substantial habitat that would otherwise be full of juvenile salmon (as is the case in the Krutogorova) is lost from the orthofluvial zone, then the overall influence of beavers on juvenile salmon could be negative.

Acknowledgments

The authors thank N. Banish, Z. Crete, A. DelVecchia, N. Hoeme, D. Kaus, B. Kent, J. Lewis, J. Malison, E. Powell, D. Stone and R. Wohler, for assistance in field research. W. Ferris provided laboratory assistance. Tyler Tappenbeck and Jake Chaffin conducted exploratory work in the Kwethluk and laid the groundwork making this study possible. Dan Gillikin and the Yukon Delta National Wildlife Refuge, USFWS, were collaborators and provided logistical support and funding. Dr. Lisa Eby and two anonymous referees provided comments that greatly strengthened this paper. Funding for this study was provided in part by the Gordon and Betty Moore Foundation as a part of the Salmonid Rivers Observatory Network Project at FLBS. This research was also supported by the NSF EPSCoR Large River Ecosystem Fellowship under Grant # EPS-0701906 and the Montana Institute on Ecosystems PhD Fellowship by the NSF EPSCoR Program Grant # EPS-1101342 at The University of Montana.

References

Arscott D.B., Tockner K., Van Der Nat D. & Ward J.V. (2002) Aquatic habitat dynamics along a braided alpine river ecosystem (Tagliamento River, Northeast Italy). *Ecosystems*, **5**, 802–814.

Bailey R.E., Irvine J.R., Dalziel F.C. & Nelson T.C. (1998) Evaluations of visible implant fluorescent tags for marking coho salmon smolts. *North American Journal of Fisheries Management*, **18**, 191–196.

Bayley P.B. (1995) Understanding large river floodplain ecosystems. *BioScience*, **45**, 153–158.

Beier P. & Barrett R.H. (1987) Beaver habitat use and impact in Truckee River basin, California. *Journal of Wildlife Management*, **51**, 794–799.

Beschta R.L. (2003) Cottonwoods, elk, and wolves in the Lamar Valley of Yellowstone National Park. *Ecological Applications*, **13**, 1295–1309.

Brown A.G. (1997) Biogeomorphology and diversity in multiple-channel river systems. *Global Ecology and Biogeography Letters*, **6**, 179–185.

Bryant M.D. (1983) The role of beaver dams as coho salmon habitat in southeast Alaska streams. In: *Proceedings of the Olympic Wild Fish Conference. Fisheries Technology Program, Peninsula College, Port Angeles, Washington* (Eds J.M. Walton & D.B. Houston), pp. 183–192.

Burchsted D., Daniels M., Thorson R. & Vokoun J. (2010) The river discontinuum: applying beaver modifications to baseline conditions for restoration of forested headwaters. *BioScience*, **60**, 908–922.

Butler L.G. & Kielland K. (2008) Acceleration of vegetation turnover and element cycling by mammalian herbivory in riparian ecosystems. *Journal Of Ecology*, **96**, 136–144.

Collins W.B. & Helm D.J. (1997) Moose, Alces alces, habitat relative to riparian succession in the boreal forest, Susitna River, Alaska. *Canadian Field-Naturalist*, **111**, 567–574.

Crete Z.J. (2012) *The Ecology of Parafluvial Ponds on a Salmon River*. Master of Science, The University of Montana, Missoula, MT.

Davis J.C., Minshall G.W., Robinson C.T. & Landres P. (2001) *Monitoring Wilderness Stream Ecosystems*. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Ogden, UT, p. 137.

Eberle L.C. & Stanford J.A. (2010) Importance and seasonal availability of terrestrial invertebrates as prey for juvenile salmonids in floodplain spring brooks of the Kol River (Kamchatka, Russian Federation). *River Research and Applications*, **26**, 682–694.

Francis M.M., Naiman R.J. & Melillo J.M. (1985) Nitrogen fixation in subarctic streams influenced by beaver (*Castor canadensis*). *Hydrobiologia*, **121**, 193–203.

Garcia A.P., Connor W.P., Milks D.J., Rocklage S.J. & Steinhorst R.K. (2004) Movement and spawner distribution of hatchery fall chinook salmon adults acclimated and released as yearlings at three locations in the Snake River basin. *North American Journal of Fisheries Management*, **24**, 1134–1144.

Gurnell A.M. (1998) The hydrogeomorphological effects of beaver dam-building activity. *Progress in Physical Geography*, **22**, 167–189.

Hale R.S. & Gray J.H. (1998) Retention and detection of coded wire tags and elastomer tags in trout. *North American Journal of Fisheries Management*, **18**, 197–201.

Halley D.J., Rosell F. & Saveljev A. (2012) Population and distribution of Eurasian beavers (*Castor fiber*). *Baltic Forestry*, **18**, 168–175.

Hammerson G.A. (1994) Beaver (*Castor canadensis*) ecosystem alterations, management and monitoring. *Natural Areas Journal*, **14**, 44–57.

Hanson W.D. & Campbell R.S. (1963) The effects of pool size and beaver activity on distribution and abundance of warm-water fishes in a north Missouri stream. *American Midland Naturalist*, **69**, 137–149.

Helton A.M., Poole G.C., Payn R.A., Izurieta C. & Stanford J. (2014) Relative influences of the river channel, floodplain surface, and alluvial aquifer on simulated hydrologic residence time in a montane river floodplain. *Geomorphology*, **205**, 17–26.

Jones C.G., Lawton J.H. & Shachak M. (1994) Organisms as ecosystem engineers. *Oikos*, **69**, 373–386.

Kano Y., Shimizu Y. & Kondou K. (2006) Status-dependent female mimicry in landlocked red-spotted masu salmon. *Journal of Ethology*, **24**, 1–7.

Karaus U., Alder L. & Tockner K. (2005) "Concave Islands": habitat heterogeneity of parafluvial ponds in a gravel-bed river. *Wetlands*, **25**, 26–37.

Kling G.W., Kipphut G.W., Miller M.M. & O'brien W.J. (2000) Integration of lakes and streams in a landscape perspective: the importance of material processing on spatial patterns and temporal coherence. *Freshwater Biology*, **43**, 477–497.

Kruskal J.B. & Wish M. (1978) *Multidimensional Scaling*. Sage Publications, Beverly Hills, CA.

Leidholt Bruner K., Hibbs D.E. & Mccomb W.C. (1992) Beaver dam locations and their effects on distribution and abundance of coho salmon fry in two coastal Oregon streams. *Northwest Science*, **66**, 218–223.

Lorang M.S. & Hauer F.R. (2006) Fluvial geomorphic processes. In: *Methods in Stream Ecology* (Eds F.R. Hauer & G.A. Lamberti), pp. 145–168. Academic Press, New York, NY.

Luck M., Maumenee N., Whited D., Lucotch J., Chilcote S., Lorang M. *et al.* (2010) Remote sensing analysis of physical complexity of North Pacific Rim rivers to assist wild salmon conservation. *Earth Surface Processes and Landforms*, **35**, 1330–1343.

Malison R.L. (2013) *Ecology of Juvenile Salmon in large floodplain rivers: The Influence of Habitat Modification by Beavers (Castor canadensis) on salmon growth and production*. PhD Thesis, University of Montana, Missoula, MT.

Mcdowell D.M. & Naiman R.J. (1986) Structure and function of a benthic invertebrate stream community as influenced by beaver (*Castor canadensis*). *Oecologia*, **68**, 481–489.

Mielke P.W. Jr & Berry K.J. (2001) *Permutation Methods: A Distance Function Approach*, Springer Series in Statistics. Springer, New York, NY, 344 p.

Miller S.J. & Harper K.C. (2012) Abundance and Run Timing of Adult Pacific Salmon in the Kwethluk River, Yukon Delta National Wildlife Refuge, Alaska, 2011. In: Fisheries Data Series Report Number 2012-3 (Eds U.S. Fish and Wildlife Service) Alaska Fisheries Data Series Report Number 2012-3, Soldotna, Alaska.

Mitchell S.C. & Cunjak R.A. (2007) Stream flow, salmon and beaver dams: roles in the structuring of stream fish communities within an anadromous salmon dominated stream. *Journal of Animal Ecology*, **76**, 1062–1074.

Morley S.A., Garcia P.S., Bennett T.R. & Roni P. (2005) Juvenile salmonid (*Oncorhynchus* spp.) use of constructed and natural side channels in Pacific Northwest rivers. *Canadian Journal of Fisheries and Aquatic Sciences*, **62**, 2811–2821.

Mouw J.E.B., Chaffin J.L., Whited D.C., Hauer F.R., Matson P.L. & Stanford J.A. (2013) Recruitment and successional dynamics diversify the shifting habitat mosaic of an Alaskan floodplain. *River Research and Applications* **29**, 671–685.

Murphy M.L., Heifetz J., Thedinga J.F., Johnson S.W. & Koski K.V. (1989) Habitat utilization by juvenile Pacific salmon (*Oncorhynchus*) in the glacial Taku River, southeast Alaska. *Canadian Journal of Fisheries and Aquatic Sciences*, **46**, 1677–1685.

Naiman R.J. (1988) Animal influences on ecosystem dynamics. *BioScience*, **38**, 750–752.

Naiman R.J., Johnston C.A. & Kelley J.C. (1988) Alteration of North American streams by beaver. *BioScience*, **38**, 753–762.

Naiman R.J., Manning T. & Johnston C.A. (1991) Beaver population fluctuations and tropospheric methane emission in boreal wetlands. *Biogeochemistry*, **12**, 1–15.

Naiman R.J. & Melillo J.M. (1984) Nitrogen budget of a subarctic stream altered by beaver (*Castor canadensis*). *Oecologia*, **62**, 150–155.

Naiman R.J., Melillo J.M. & Hobbie J.E. (1986) Ecosystem alteration of boreal forest streams by beaver (*Castor canadensis*). *Ecology*, **67**, 1254–1269.

Naiman R.J., Pinay G., Johnston C.A. & Pastor J. (1994) Beaver influences on the long-term biogeochemical characteristics of boreal forest drainage networks. *Ecology*, **75**, 905–921.

Naiman R.J. & Rogers K.H. (1997) Large animals and system-level characteristics in river corridors: implications for river management. *BioScience*, **47**, 521–529.

Patoine A. & Leavitt P.R. (2006) Century-long synchrony of fossil algae in a chain of Canadian prairie lakes. *Ecology*, **87**, 1710–1721.

Peck J.E. (2010) *Multivariate Analysis for Community Ecologists: Step-by-Step Using PC-ORD*. MjM Software Design, Gleneden Beach, OR.

Petry P., Bayley P.B. & Markle D.F. (2003) Relationships between fish assemblages, macrophytes and environmental gradients in the Amazon River floodplain. *Journal of Fish Biology*, **63**, 547–579.

Pinay G. & Naiman R.J. (1991) Short-term hydrological variation and nitrogen dynamics in beaver created meadows. *Archive fur Hydrobiologie*, **123**, 187–205.

Pollock M.M., Pess G.R., Beechie T.J. & Montgomery D.R. (2004) The importance of beaver ponds to coho salmon production in the Stillaguamish River Basin, Washington, USA. *North American Journal of Fisheries Management*, **24**, 749–760.

Quinn T.P. (2005) *The Behavior and Ecology of Pacific Salmon and Trout*. University of Washington Press, Seattle, WA.

Ricker W.E. (1975) Computation and interpretation of biological statistics for fish populations. *Fisheries Research Board of Canada Bulletin*, **191**, 1–382.

Robinson S., Beaudoin A.B., Froese D.G., Doubt J. & Clague J.J. (2007) Plant macrofossils associated with an early Holocene beaver dam in interior Alaska. *Arctic*, **60**, 430–438.

Rosell F., Bozser O., Collen P. & Parker H. (2005) Ecological impact of beavers *Castor fiber* and *Castor canadensis* and their ability to modify ecosystems. *Mammal Review*, **35**, 248–276.

Rusak J.A., Yan N.D., Somers K.M. & Mcqueen D.J. (1999) The temporal coherence of zooplankton population abundances in neighboring North-temperate lakes. *American Naturalist*, **153**, 46–58.

Rutten M.G. (1967) Flat bottom glacial valleys, braided rivers and beavers. *Geologie en mijnbouw*, **46e**, 356–360.

Schlosser I.J. (1995) Dispersal, boundary processes, and trophic-level interactions in streams adjacent to beaver ponds. *Ecology*, **76**, 908–925.

Schlosser I.J. & Kallemeyn L.W. (2000) Spatial variation in fish assemblages across a beaver-influenced successional landscape. *Ecology*, **81**, 1371–1382.

Sedell J.R., Yuska J.E. & Speaker R.W. (1984) Habitats and salmonid distribution in pristine sediment rich river valley systems: South Fork Hoh and Queets River, Olympic National Park. In: *Fish and Wildlife Relationships in Old Growth Forests* (Eds W.R. Meehan, T.R. Merrel & T.A. Hanley), pp. 33–46. American Institute of Fishery Research Biologists, Morehead City, NC.

Smith M.E., Driscoll C.T., Wyskowski B.J., Brooks C.M. & Cosentini C.C. (1989) Modification of stream ecosystem structure and function by beaver (*Castor canadensis*) in the Adirondack Mountains, New York. *Canadian Journal of Zoology*, **69**, 55–61.

Soranno P.A., Webster K.E., Riera J.L., Kratz T.K., Baron J.S., Bukaveckas P.A. *et al.* (1999) Spatial variation among lakes within landscapes: ecological organization along lake chains. *Ecosystems*, **2**, 395–410.

Stanford J.A., Gayeski N.J., Pavlov D.S., Savvaitova K.A. & Kuzishchin K.V. (2002) Biophysical complexity of the Krutogorova River (Kamchatka, Russia). *Verhandlungen Internationale Vereinigung fur Theoretische und Angewandte Limnologie*, **28**, 1354–1361.

Stanford J.A., Lorang M.S. & Hauer F.R. (2005) The shifting habitat mosaic of river ecosystems. *Verhandlungen Internationale Vereinigung fur Theoretische und Angewandte Limnologie*, **29**, 123–136.

Stein R.A., Reimers P.E. & Hall J.D. (1972) Social interaction between juvenile coho (*Oncorhynchus kisutch*) and fall Chinook salmon (*O. tshawytscha*) in Sixes River, Oregon. *Journal of the Fisheries Research Board of Canada*, **29**, 1737–1748.

Suzuki N. & Mccomb W.C. (1998) Habitat classification models for beaver (*Castor canadensis*) in the streams of the central Oregon Coast Range. *Northwest Science*, **72**, 102–110.

Swales S. & Levings C.D. (1989) Role of off-channel ponds in the life cycles of coho salmon (*Oncorhynchus kisutch*) and other juvenile salmonids in the Coldwater River, British Columbia. *Canadian Journal of Fisheries and Aquatic Sciences*, **46**, 232–242.

Walsh M.G. & Winkelman D.L. (2004) Anchor and visible implant elastomer tag retention by hatchery rainbow trout stocked into an Ozark stream. *North American Journal of Fisheries Management*, **24**, 1435–1439.

Whited D.C., Kimball J.S., Lorang M.S. & Stanford J.A. (2013) Estimation of juvenile salmon habitat in Pacific Rim rivers using multiscalar remote sensing and geospatial analysis. *River Research and Applications*, **29**, 135–148.

Wilde S.A., Youngberg C.T. & Hovind J.H. (1950) Changes in composition of ground water, soil fertility, and forest growth produced by the construction and removal of beaver dams. *Journal of Wildlife Management*, **14**, 123–128.

Wright J.P., Jones C.G. & Flecker A.S. (2002) An ecosystem engineer, the beaver, increases species richness at the landscape scale. *Oecologia*, **132**, 96–101.

Zippin C. (1958) Removal method of population estimate. *Journal of Wildlife Management*, **22**, 83–90.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Time series of the position of main channel network at base flow from 2004 to 2011, illustrating a very active channel in the parafluvial zone due to the occurrence of avulsions and only very minor changes in the orthofluvial zone where mid- and late-successional ponds are located.

(Manuscript accepted 24 January 2014)