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ARTICLE

Juvenile salmonid growth, survival, and production in a large river floodplain modified by beavers (*Castor canadensis*)

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Abstract: Beavers (*Castor canadensis*) may strongly influence juvenile salmon production by damming spring brooks that are primary rearing habitats on expansive floodplains of large Pacific Rim salmon rivers. We studied three floodplain rearing habitats in the Kwethluk River, Alaska: free-flowing (beaver-free, $n = 3$) and beaver-influenced (below beaver dams, $n = 4$) spring brooks and early-successional beaver ponds ($n = 4$). We analyzed juvenile coho (*Oncorhynchus kisutch*) and Chinook (*Oncorhynchus tshawytschwa*) salmon movement, survival, densities, and growth using a multistate robust capture–mark–recapture design. Survival (46% to 80%) and densities (0.9 fish·m^{-2}) were highest in beaver-free spring brooks. Ponds had lower salmon densities, producing less biomass per unit area than beaver-influenced or beaver-free spring brooks (1.87 ± 0.57 g·m^{-2} vs. 2.98 ± 1.22 and 3.23 ± 0.73 g·m^{-2}). However, ponds covered 2× greater area than either type of spring brook and therefore produced more salmon biomass at the floodplain scale than either type of spring brook (175 kg vs. 149 kg in beaver-influenced spring brooks and 140 kg in beaver-free spring brooks). We conclude that beaver damming of floodplain spring brooks produces bigger juveniles and more total biomass, but spring brooks produce significantly more, albeit smaller, coho and Chinook juveniles. Thus, the presence of beavers on the floodplain increases habitat variation, which provides a larger range of growth opportunities for juvenile salmon.

Résumé : Les castors (*Castor canadensis*) pourraient exercer une forte influence sur la production de saumons juvéniles en construisant des barrages sur des ruisseaux de source qui constituent d'importants habitats de grossissement dans les vastes plaines inondables de grandes rivières à saumons du littoral du Pacifique. Nous avons étudié trois habitats de grossissement de plaine inondable dans la rivière Kwethluk (Alaska), soit des ruisseaux de source à écoulement libre (sans castor, $n = 3$) et influencés par les castors (en aval de barrages de castors, $n = 4$), et des étangs de castors à des stades de succession précoces ($n = 4$). Nous avons analysé les déplacements, la survie, la densité et la croissance de saumons cohos (*Oncorhynchus kisutch*) et quinnats (*Oncorhynchus tshawytschwa*) juvéniles en utilisant un schéma multi-états robuste de capture–marquage–recapture. Le taux de survie (46–80 %) et la densité (0,9 poisson·m^{-2}) étaient les plus élevés dans les ruisseaux de source sans castor. Les étangs présentaient de plus faibles densités de saumons, produisant moins de biomasse par unité de surface que les ruisseaux de source influencés par les castors ou sans castor (1,87 ± 0,57 contre 2,98 ± 1,22 et 3,23 ± 0,73 g·m^{-2}, respectivement). Toutefois, les étangs couvraient des superficies deux fois plus grandes que les deux types de ruisseaux et produisaient donc une plus grande biomasse de saumons à l'échelle de la plaine inondable que l'un ou l'autre des types de ruisseaux de source (175 kg contre 149 kg dans les ruisseaux influencés par les castors et 140 kg dans les ruisseaux sans castor). Nous en concluons que la construction de barrages par les castors dans des ruisseaux de source de plaine inondable produit des juvéniles plus gros et une plus grande biomasse totale, mais que les ruisseaux de source produisent significativement plus de saumons cohos et quinnats juvéniles, bien que ces saumons soient plus petits. Ainsi, la présence de castors dans une plaine inondable accroît la variabilité des habitats, ce qui offre un plus grand éventail de possibilités aux saumons juvéniles. [Traduit par la Rédaction]

Introduction

Large alluvial rivers of the North Pacific Rim have expansive floodplains that provide abundant spawning and rearing habitat for wild salmonid fishes (Whited et al. 2013). In fact, 40% of all wild Pacific salmon are produced in the expansive floodplain rivers of Kamchatka, Russian Federation, with the large floodplain river and lake systems of Alaska and British Columbia making up most of the balance (Augerot 2005). These floodplains are characterized by a shifting habitat mosaic (Stanford et al. 2005) that encompasses a complex network of channels, ponds, and wetlands with attendant riparian vegetation and alluvial aquifers fed by the river. Floodplain spring brooks that flow from groundwater discharge are especially important because they are confluent with the main channel at the downstream end and have protective and productive qualities (Morley et al. 2005; Eberle and Stanford 2010) that often result in high juvenile salmonid densities (4–10 fish·m^{-2}). These qualities can enhance growth and survival of juvenile salmonids compared with the main channel and tributaries (Sommer et al. 2001; Jeffres et al. 2008; Eberle and Stanford 2010). Thus, floodplain spring brooks provide critical nursery habitat for juvenile salmon, especially *Oncorhynchus kisutch* (coho salmon) and *Oncorhynchus tshawytschwa* (Chinook salmon) that typically reside in freshwater 1–2 years prior to seaward migration as smolts (Quinn 2005).

Because rearing space and food control the size and production of stream-rearing salmon juveniles and smolts, and because larger smolts tend to have higher survival rates in the ocean (Holtby et al. 1990; Zabel and Achord 2004), damming of floodplain spring brooks by beavers may influence salmon productivity. Beavers are very efficient in creating and maintaining lentic habitats that would otherwise be free-flowing with abundant and often over-

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hanging riparian vegetation (McDowell and Naiman 1986; Naiman et al. 1988; Smith et al. 1991). Indeed, Malison et al. (2014) found that 80% of the spring brooks of an expansive floodplain of the Kwethluk River, a fifth-order river in western Alaska, were impounded by beavers. The dynamic interplay of dam location (in the parafluvial zone close the main channel or farther from the river in the orthofluvial zone; sensu Stanford et al. 2005) and hydrology resulted in a mosaic of different beaver-modified habitats on the landscape with strong consequences for juvenile salmonid habitat use. Malison et al. (2014) found that salmon were virtually absent from mid- and late-successional ponds in the orthofluvial zone owing to disconnection of migratory pathways from the river channel at base flow, but that early-successional ponds in the parafluvial zone were important rearing habitats. The influence of effects related to ecological engineering of beavers (sensu Naiman 1988) on growth and survival of juvenile salmon has never been examined in expansive floodplain rivers of North America, in spite of the acknowledged importance of these rivers as salmon producers.

A recent review of the effects of beavers on stream fish in low-order streams found that the benefits of beavers are more often cited than negative impacts (Kemp et al. 2012). With respect to salmon, studies in low-order streams have shown that beaver ponding can increase survival (Bustard and Narver 1975; Quinn and Peterson 1996), growth rates (Bustard and Narver 1975; Swales and Levings 1989), and production (Nickelson et al. 1992; Layman and Smith 2001; Pollock et al. 2004) of coho salmon, apparently because food supplies are more robust and the fish are less crowded in beaver ponds. However, other studies of low-order streams have shown that beaver dams impede movement of fishes (Schlosser and Kallemeyn 2000; Mitchell and Cunjak 2007), cause hypoxia by organic matter and sediment retention, and elevate temperatures above thresholds conducive to salmonid growth and survival (Burchsted et al. 2010). It is not clear if beaver damming of spring brooks in the floodplains of larger rivers will have positive or negative effects on juvenile salmonid populations.

In this study, we investigated how beavers influence the growth, survival, and production of juvenile coho and Chinook salmon on an expansive floodplain of the fifth-order Kwethluk River in western Alaska. Herein we hypothesize that the presence of early-successional beaver ponds on fish-accessible spring brooks increases salmon production because abundant lentic food and lower fish densities in the ponds substantially enhance growth in comparison to undammed spring brooks or spring brooks below beaver dams. Thus, we expected that the production potential of the parafluvial zone of the floodplain is higher than it would be if beavers were not present. From our working hypothesis, we made the following predictions: (1) habitat quality (including warmer temperatures and prey availability) will be greater in beaver ponds compared with beaver-free (no dams) and beaver-influenced (downstream of ponds) spring brooks (for distribution of these habitat types on this floodplain river, see Malison et al. 2014); (2) growth and condition of juvenile salmon will be higher in beaver ponds than in beaver-free and beaver-influenced spring brooks; (3) movement rates of juvenile salmon will be higher in beaver-free and beaver-influenced spring brooks than in ponds because spring brooks are more accessible (juveniles cannot get over or through the dams except during flooding); and (4) survival rates will be higher in ponds. Thus, we expected that cumulative production from early-successional ponds would be higher than production from all spring brooks due to increased fish growth rates and the large area covered by early-successional beaver ponds.

Methods

Study floodplain and sampling sites

The study was conducted on the lower floodplain of the Kwethluk River, a tributary of the Kuskokwim River in western Alaska (Fig. 1). The Kwethluk River is in the Yukon Delta National Wildlife Refuge and enters the Kuskokwim River approximately 15 km upstream of Bethel, Alaska. We chose to study the influence of beavers on juvenile salmon production on this unregulated and productive salmon river (Miller and Harper 2012) because beavers are prevalent throughout its floodplain reaches. Beaver ponds vary in age from recently formed ponds found in flood channels that cut through early-successional vegetation (*Salix* spp. and *Alnus* spp.) in the parafluvial zone (annually flooded and scoured) of the river, to >100-year-old ponds persisting in old-growth riparia (*Populus balsamifera* and *Picea glauca*) in the orthofluvial zone (flooded only by overbank discharge, mostly depositional, and generally removed from the main channel network) (Mouw et al. 2013). Moreover, the floodplain is mostly unaltered by humans, although it is an important subsistence-fishing and wood-gathering area.

The 27 km study reach is an expansive anastomosing floodplain that is located between 37 and 64 km above the confluence of the Kwethluk River with the Kuskokwim River. It is gravel–cobble bedded and characterized by a laterally migrating main channel, coupled with anabranching avulsion events that create an intricate network of flood and secondary channels, and gravel bars (as described by Arscott et al. (2002) for gravel bed rivers). Spring brooks occur throughout the floodplain where flood channels located lateral to the main channel network have scoured deep enough to intercept the shallow aquifer (Fig. 2). During base flow, spring brooks are maintained by outflows from the alluvial aquifer that underlies the entire floodplain. Spring brooks may be free-flowing from the source of upwelling to the main channel network (beaver-free spring brooks), or they may be impounded by one or more beaver dams upstream of a flowing section (beaver-influenced spring brooks). We selected study sites on beaver-free spring brooks, beaver-influenced spring brooks, and early successional beaver ponds (Figs. 2 and 3). We did not focus on mid- and late-successional ponds because Malison et al. (2014) showed that salmon are virtually absent from these habitat types. Moreover, we observed that beavers tended to build their dams at upwelling sites, which provided maximum control of pond water volume in relation to dam size.

All five species of Pacific salmon are present in the Kwethluk River: Chinook, coho, sockeye (*Oncorhynchus nerka*), chum (*Oncorhynchus keta*), and pink (*Oncorhynchus gorbuscha*). Other fish species include rainbow trout (*Oncorhynchus mykiss*), Dolly Varden (*Salvelinus malma*), stickleback (*Pungitius pungitius*), Alaska blackfish (*Dallia pectoralis*), and slimy sculpin (*Cottus cognatus*). Round whitefish (*Prosopium cylindraceum*) and pike (*Esox lucius*) are also present but were not found in spring brooks or beaver ponds (Malison et al. 2014). We focused on Chinook and coho salmon because they are abundant and spend 1–2 years rearing in floodplain habitats and thus may be strongly influenced by beavers. Moreover, they are preferred by subsistence fishers and are of great conservation concern in the Yukon–Kuskokwim delta region (Krueger and Zimmerman 2009). Adult Chinook salmon spawn in the main channel network primarily in tail-outs, whereas coho spawn in a nearly all habitats in the main and distributary channels and even spring brooks if they are deep enough. After emergence from natal nests (redds), fry seek shallow-water rearing habitats that contain ample food and restrict predators (Quinn 2005).

Study design

We selected sampling sites to encompass the three habitat types that serve as floodplain nurseries for coho and Chinook salmon in Pacific Rim salmon rivers (e.g., Eberle and Stanford 2010): (*i*) beaver-free spring brooks (i.e., free-flowing from aquifer outflow to main channel); (*ii*) beaver-influenced spring brooks (i.e., lotic reaches downstream from dams that were continually connected to the main channel by gradual release of pond storage and aquifer outflow at the dam site); and (*iii*) early-successional

Fig. 1. The Kwethluk River floodplain study area, a tributary of the Kuskokwim River, located in western Alaska.

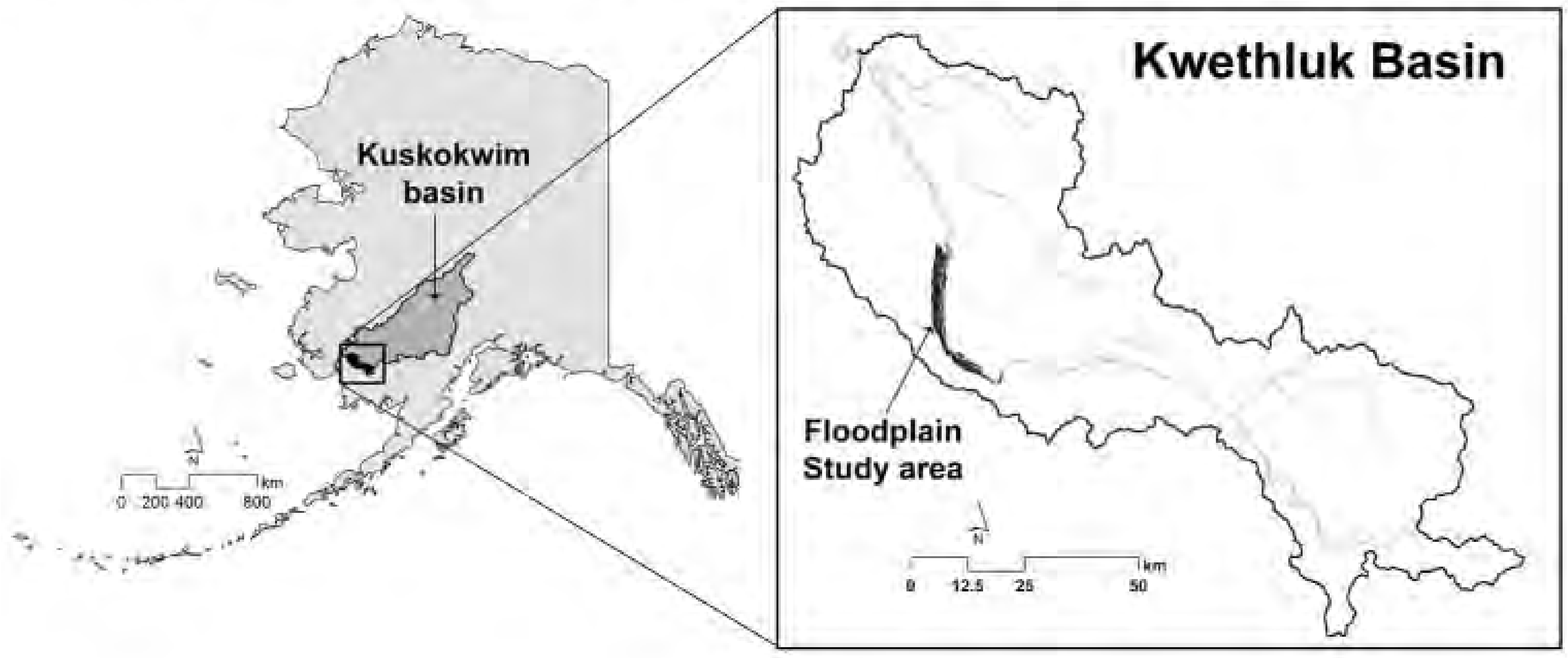
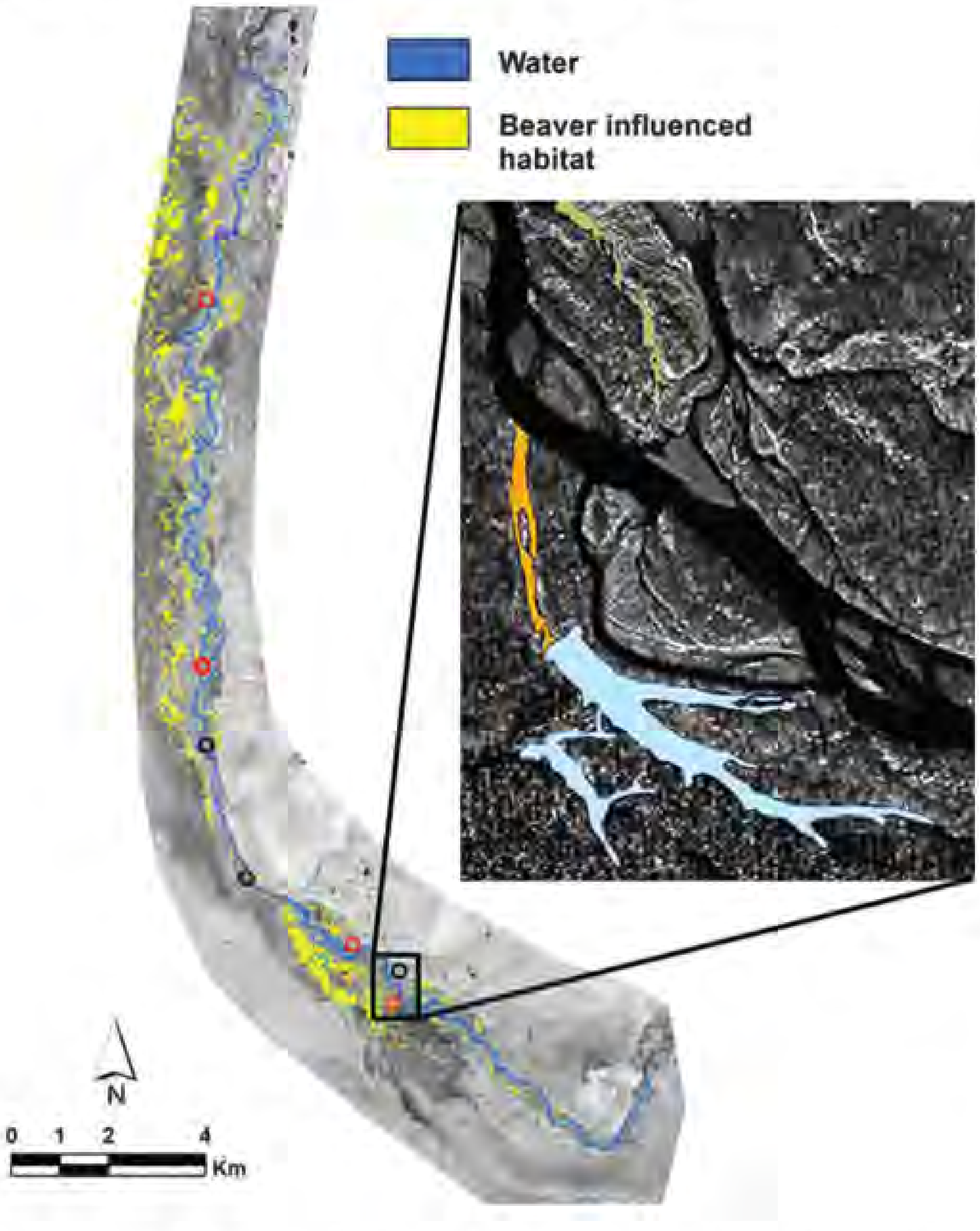


Fig. 2. The 27 km study reach with water (blue) and beaver influenced areas (yellow). Circles mark locations of mark–recapture sites (red, paired ponds and beaver-influenced spring brooks; black, beaver-free spring brooks). The inset illustrates an example of one beaver complex (blue, beaver pond; orange, beaver-influenced spring brook) and a beaver-free spring brook (green).



beaver ponds. For routine sampling, we selected three beaver-free spring brooks and four beaver-influenced spring brooks, each with an early-successional beaver pond upstream. Thus we routinely sampled seven spring brooks throughout their length (50–200 m), of which four were impounded upstream by recent (i.e., 3–5 years since construction) beaver dams (Figs. 2, 3), for a total of 11 sites.

At each of the 11 sampling sites, we measured biophysical metrics leading to robust estimates of juvenile coho and Chinook salmon production at both the habitat and floodplain scale of resolution (see study design overviewed in Fig. 4). To estimate habitat-specific population dynamics, we used mark–recapture methods. For fish larger than 58 mm, we implanted passive integrated transponder (PIT) tags that allowed individual fish to be identified and growth rates to be measured. Over 8100 fish were PIT-tagged, and 32% were recaptured, from which we estimated rates of survival, movement, and growth. Additionally, we tagged fish that did not receive PIT tags with site-specific color-coded elastomer injected into the base of the caudal and anal fins to ensure that a high proportion of the population was marked for population abundance studies. To further elaborate movement, we instrumented two of the four beaver-influenced spring brooks in 2010 and two of the three beaver-free spring brooks in 2011 with PIT-tag detection antennae at their outlets to document PIT-tagged fish emigrating from the "study systems," as well as to provide data on fish moving from ponds to spring brooks.

Movement, growth, and population size data thus obtained allowed us to model salmon production at habitat and floodplain scales of resolution (Fig. 4). We previously determined total area of each habitat type on the entire floodplain using satellite imagery (Malison et al. 2014) to permit scaling up of habitat-specific production estimates to the entire floodplain. In the final analysis, we assessed the influence of beavers in two ways. First, we compared the abundance and growth of the two salmon species in beaver-influenced habitats versus beaver-free spring brooks. Using these data, we modeled and compared habitat-specific and floodplain production. Second, we compared floodplain-scale production of the parafluvial zone with an estimate of the potential production that likely would occur if beavers were not present (i.e., if all parafluvial habitat was composed of free-flowing spring brooks). Per our working hypothesis, we expected that estimated potential production without beavers would be substantially less than the current beaver-dominated system.

Habitat characteristics

At each of the 11 sampling sites, we measured key physical variables that likely influence juvenile salmon population dynamics and production. We monitored water temperature every hour year-round using HOBO pressure transducer data loggers (Onset, Pocasset, Massachusetts, USA; www.onsetcomp.com) and Vemco data loggers (Vemco, Halifax, Nova Scotia, Canada; www.vemco.com) from 2009 to 2011. Temperature loggers were located at fixed positions approximately 1–2 m in depth in ponds and spring brooks. We calculated growing degree-days (GDD) between June and August using the following equation (Elliott 1994; McMaster and Wilhelm 1997): $\text{GDD} = \Sigma[(T_{\text{MAX}} + T_{\text{MIN}})/2] - 4$. We measured dissolved oxygen with an Oakton handheld meter (Waterproof DO 300; Oakton, Vernon Hills, Illinois, USA; www.4oakton.com) during each visit to determine if the sites had sufficient oxygen to minimize stress on the fish. We measured conductivity and pH in ponds and spring brooks with an Oakton handheld meter (Water-

Fig. 3. Study sites located in parafluvial habitats, including (A) beaver-free spring brooks, (B) beaver-influenced spring brooks, and (C) early-successional beaver ponds (embedded in willow and alder). (D) Dams on early-successional ponds range from 1.1 to 2 m in height.

proof pH/CON 10 Series; Oakton, Vernon Hills, Illinois, USA; www.4oakton.com). Site area was measured from satellite imagery collected in 2011 using ArcMap (for detailed methods, see Malison et al. 2014), and on the ground, validation was completed with a handheld Trimble GeoXM 2005 GPS (Trimble, Sunnyvale, California, USA) at a subset of sites.

The effect of habitat type (beaver-free spring brook, beaver-influenced spring brook, or early-successional beaver pond) on GDD, dissolved oxygen, pH, conductivity, and site area was analyzed using one-way analysis of variance (ANOVA; PROC GLM, SAS Institute Inc., Cary, North Carolina, USA). Pairwise comparisons among 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, $\log_{10}$-transformed to meet assumptions of normality and homogeneity of variance prior to statistical analysis. All statistical tests were analyzed in SAS 9.3 and were considered significant when $P < 0.05$.

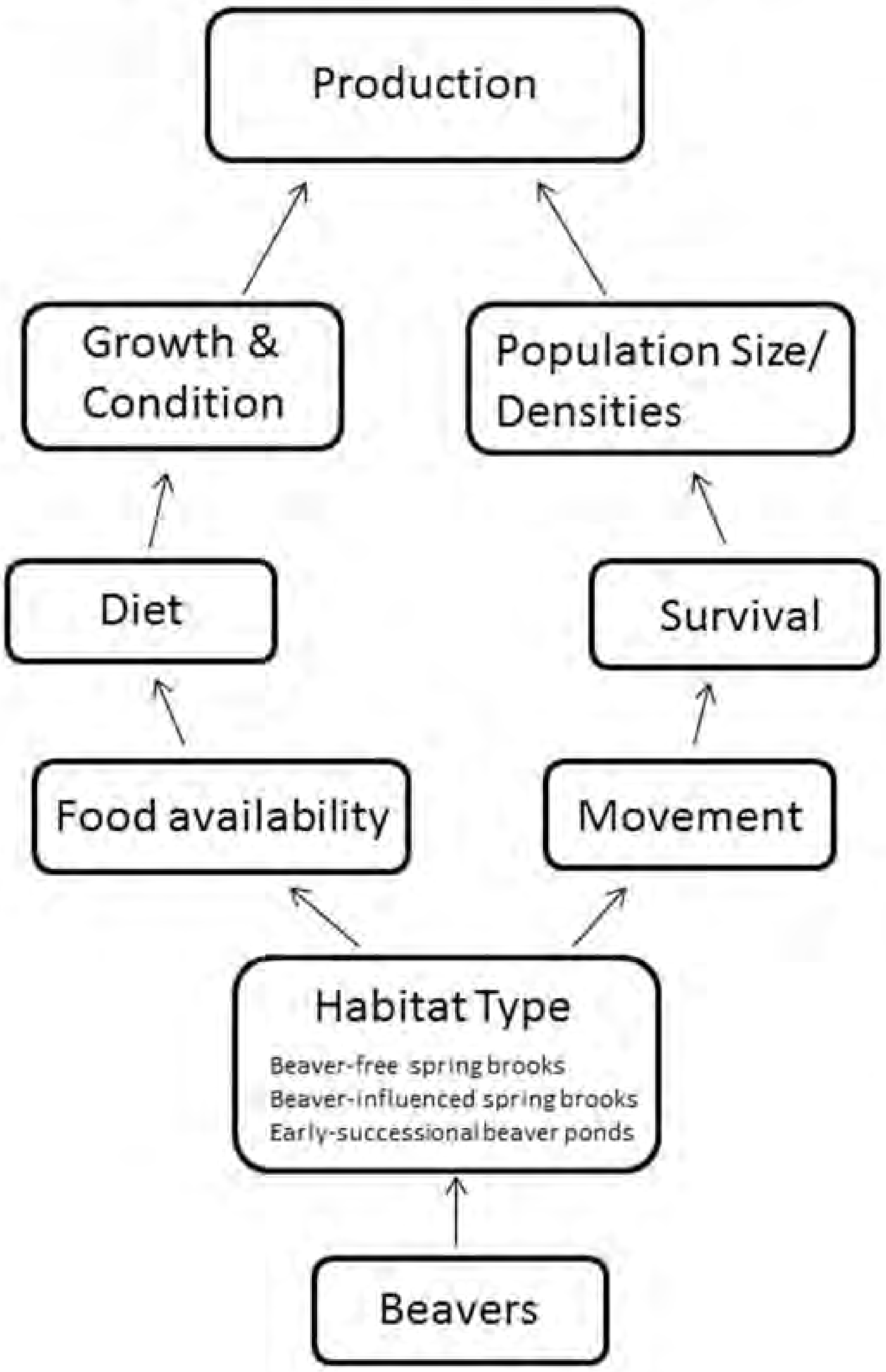
Overwinter survival

We conducted fieldwork in April 2011 to determine if juvenile salmon could overwinter in our study ponds. We drilled holes in four ponds at deep pools and obtained dissolved oxygen profiles with a Hydrolab DS5 sonde (OTT Hydromet, Loveland, Colorado, USA; www.hachhydromet.com). Where possible, we placed two minnow traps baited with salmon roe in the holes overnight. We identified, measured, and weighed all fish and checked for tags (see tagging methods below). Presence of healthy juveniles under the ice (especially individuals tagged in the same habitats the previous fall) indicated overwinter survival. We calculated Fulton's condition factor, *K* (Ricker 1975), for each fish by dividing mass (g) by length (mm) cubed and multiplying by a scalar of 10^5. Spring brooks did not freeze owing to warm groundwater flux.

Prey availability

We sampled allochthonous (terrestrially derived) and autochthonous (aquatically derived) prey resources at each site to investigate potential differences in prey availability because both the amount and composition of available food could influence the caloric content of fish diets and growth rates (Probst et al. 1984; Pope et al. 2001). We used floating traps (four 0.348 m^2 opaque pans at each site) to measure the inputs ($mg{\cdot}day^{-1}{\cdot}m^{-2}$) of invertebrates, once per month (June–September) for period of 2–5 days at each site. We sorted and preserved samples in ethanol in the field and later identified individuals to family and then dried them at 60 °C to obtain measures of biomass. Total site input ($g{\cdot}day^{-1}$) was calculated by extrapolating input values to the entire habitat (pond or spring brook) by multiplying by total site area. Allochthonous inputs by habitat type and time were analyzed using mixed ANOVA (IBM SPSS Statistics 22, Armonk, New York, USA). Data for the month of August were removed from the analysis because of missing data points. All flux data met the assumptions of the mixed-effects analysis and total input data were $\log_{10}$-transformed to meet assumptions. Pairwise comparisons among the least squares means for habitat type were assessed using Tukey's HSD. Invertebrates were also classified as either terrestrial or aquatic (flying adults of aquatic taxa) to determine

Fig. 4. Flow diagram of study design used to determine the influence of beavers on production of juvenile coho and Chinook salmon from the parafluvial zone of the Kwethluk River.



whether there were more terrestrial prey in beaver ponds. We analyzed the relative abundance of taxa at each site with nonmetric multidimensional scaling (NMDS) (Kruskal and Wish 1978) to evaluate differences among habitat types with the program PC-ORD (version 6; MjM Software Design, Gleneden Beach, Oregon, USA; www.pcord.com). We excluded rare taxa (relative values, <5%) from the data set to reduce skewness in the data. We used multiresponse permutation procedures (MRPP) to test for significant differences in community composition by habitat category.

To compare biomass of benthic macroinvertebrates between beaver-free and beaver-influenced spring brooks, we sampled the benthos from three riffles once per month using a kick net (125 μm, 0.25 m^2 metal frame). Replicate samples were collected from three riffles selected from each spring brook reach by disturbing the bed sediments for 1 min. Each sample was then sorted in the field for 1 h, or until no more specimens were visible. Most samples were completely sorted, with a similar effort exerted for each sample, and both large and small individuals were collected (as small as zooplankton). We sampled drifting prey in spring brooks by deploying three drift nets in riffles overnight once per month at each site (0.10 m diameter opening, 125 μm mesh). Drift nets were placed in riffles distributed along the length of each spring brook, and velocity at the net opening was measured to calculate volume of water sampled in each net. All samples were sorted at the site for up to 1 h, or until no more macroinvertebrates were visible, and then preserved in ethanol. In the laboratory, the samples were identified, dried, weighed, and recorded as dry mass per taxon. The effect of habitat type on mean total benthic and drift biomass was analyzed using *t* tests.

To determine composition of prey in ponds, we collected three replicate sweep net samples once per month using a D-net. We swept a D-net through vegetation and along logs in the pond for 1 min for each replicate. Each sample was sorted in the field for 1 h, or until no more specimens were visible, and samples were preserved in ethanol until identified, dried, and weighed in the lab.

Fish diets

To determine how diets related to prey availability and to determine food availability, we examined the amount of food consumed (biomass of fish diets) and the composition of prey in diets three times per site in 2010 (for four paired beaver ponds and spring brooks) and four times per site in 2011 (for three beaver-free spring brooks). We collected diet samples from a subset of the fish collected during mark–recapture sampling events each month (see below). Twenty coho (59–117 mm) and Chinook (61–87 mm) were sampled per site in 2010, and 20 coho (58–114 mm) were sampled per site in 2011. Nonlethal stomach-content samples were collected via lavage (stomach-flushing). Gut contents for each site were pooled into a composite sample and preserved in ethanol. In the laboratory, we identified individuals to order or family. Identified samples were then dried at 60 °C and weighed for biomass (g). Taxa were categorized as either terrestrial or aquatic, with aerial stages of aquatic insects categorized as aquatic to differentiate prey by origin, and percent composition by number and biomass were calculated.

The effect of habitat type and time on fish diet biomass was also analyzed using ANOVA, and pairwise comparisons among the least squares means for habitat type were assessed using Tukey's HSD for the months of July, August, and September. We used NMDS to evaluate differences among habitat types in the composition of fish diets, following the same methods described for prey availability.

Population dynamics

To compare juvenile salmon population dynamics in the parafluvial habitats, we measured movement (Ψ), apparent survival (ϕ), and population sizes (N) per the study design for mark–recapture sampling described above. Juvenile salmon were sampled at each of the 11 sites using minnow traps baited with salmon roe placed in film canisters with small holes (ensuring an attraction scent but leaving eggs unavailable for consumption) and soaked for 2 h (to standardize catch per effort) during each sampling session. We placed traps throughout each site at approximately 5 m intervals. Sites were sampled during three consecutive days monthly from June–September over 2 years (beaver-influenced habitats in 2010 and beaver-free spring brooks in 2011) to recover previously marked fish and to mark with PIT tags a proportion of new unmarked fish. All fish caught were measured (fork length), weighed, and checked for tags after being anesthetized with MS-222. We implanted juvenile coho and Chinook greater than 58 mm with 12 mm HDX or FDX PIT tags into the abdominal cavity (ORFID, Portland, Oregon, USA; www.oregonrfid.biz). We implanted up to 300 individuals (randomly netted from the entire sample per site) on each sampling day with PIT tags, depending on the number of individuals captured. Any coho and Chinook 58 mm or larger that did not receive a PIT tag (because we did not have enough tags for every fish) was implanted with a site-specific visual implant elastomer (VIE) mark on the caudal fin (Northwest Marine Technology, Shaw Island, Washington, USA; www.nmt.us). Both young-of-the-year (YOY) and age-1+ fish were tagged.

Table 1. $\Delta\mathrm{AIC}_c$ results for models used to estimate apparent survival (ϕ), movement (Ψ), and population sizes (N) for the four beaver complexes (sites 1–4) and three beaver-free spring brooks (sites 5–7).

	$\Delta\mathrm{AIC}_c$ values by site			
	Site 1 (BU) [p(g)c(se)N(gt)]	Site 2 (SB) [p(g)c(g,se)N(gt)]	Site 3 (LB) [p(g,se)c(g,se)N(gt)]	Site 4 (AB) [p(g)c(g,se)N(gt)]
ϕ(gt)Ψ(g)	**0**	**0**	*	**0**
ϕ(g)Ψ(gt)	−8.3	−7.8	−26.1	−85.4
ϕ(g)Ψ(g)	−29.6	−7.9	−22.6	−121.0
ϕ(gt)Ψ(null)	−125.2	−8.6	**0**	*
ϕ(g)Ψ(null)	−155.3	−16.6	−34.0	−119.4
ϕ(null)Ψ(gt)	−27.2	−6.2	−49.2	−112.5
ϕ(null)Ψ(g)	−49.4	−6.3	−46.4	−141.9
	$\Delta\mathrm{AIC}_c$ values by site			
	Site 5 (CR) [p(g)c(se)N(t)]	Site 6 (CT) [p(g)c(se)N(t)]	Site 7 (NN) [p(se)c(se)N(t)]	
ϕ(t)Ψ(t)	**0**	**0**	**0**	
ϕ(t)Ψ(null)	−21.3	**0**	**0**	
ϕ(null)Ψ(t)	−13.1	−46.6	−5.5	

Note: The top model for "nuisance" variables (detection probability (p) and recapture probability (c)) is listed below each site in brackets. For each complex, this selection of nuisance variables was used to run different combinations of survival (ϕ) and movement (Ψ) parameters, varying by group (g), sampling session (se), and time (t). Bold text indicates the best model for each site. Asterisks indicate that models contained at least some parameters that could not be estimated due to extremely high standard errors, resulting in model rejection.

We monitored the emigration of fish from spring brooks into the river using PIT-tag antennae HDX readers (model LF HDX RFID; ORFID, Portland, Oregon, USA) placed at the mouth of two of the four beaver-influenced spring brooks in 2010 and two of the three beaver-free spring brooks in 2011. The antenna systems were installed in June and operated continuously through September. Portions of the spring brooks not encompassed by the antenna were blocked with mesh panels. Antennae ran continuously except for 23 days in 2010 due to flooding. Though flooding also occurred in 2011, the antennae remained operable. It is possible that some emigration was missed during flooding, which could bias survival rates low. For each site, we modeled survival as constant over time, varying over time, varying by group (i.e., pond or spring brook), or varying by group and time (see Table 1).

Survival and movement of fish in the seven "study systems" were analyzed separately and by sampling month in Program MARK (White and Burnham 1999) using all PIT-tagged individuals and the multistate robust closed capture model. Study systems were composed of either two (beaver-free systems, n = 3) or three (beaver-influenced complexes, n = 4) states. All complexes included the main channel (state C) and a spring brook (either beaver influenced or not, state B), and beaver complexes included a third state — a beaver pond at the top of the spring brook (state A). The main channel (i.e., "the river") was a state where we measured fish immigration rates into the river but they were no longer recaptured. We used a multistate robust closed capture model because movement occurred between the states (i.e., between ponds and spring brooks and between spring brooks and the river). Within a study system, each fish had a capture history representing its location during each sampling event. We fixed survival (Φ) and recapture probability (c) within the river at zero because we did not tag or capture fish in the main channel network (Φ: C:C = 0; c of C:C = 0). Because we did not detect movement of tagged fish returning from the river into ponds or from the river into spring brooks (i.e., once fish left a study system, they did not come back), these movement rates were fixed at zero (Ψ C to A = 0 and Ψ C to B = 0). Movement directly between the ponds and the river (i.e., paths not utilizing the dam and downstream spring brook) was fixed at zero (Ψ A to C = 0) because we assumed that this pathway was closed. We followed the strategy of Zabel and Achord (2004) by analyzing the detection (p) and recapture (c) probabilities before modeling survival and movement rates. By doing so, we first set the structure of these "nuisance" parameters for each of the seven study systems and then focused on investigating which models with parameters of interest, survival (ϕ) and movement (Ψ), ranked the highest. To examine the contribution of different combinations of parameters to model fit, we compared alternative models comprising various combinations of variables using Akaike's information criterion corrected for sample size (AIC_c) to select the top model for each system. In general, we compared models of the parameters varying by group (pond vs. spring brook) or by session so that parameters varied over time during open sessions but were constant during the closed period. Again, we selected the best model using the criteria listed above (for models, see Table 1).

We calculated monthly population estimates for each of the 11 sites with Schnabel population estimates made using all fish at least 58 mm in length captured at each site (i.e., all PIT-tagged and batch-marked individuals large enough to receive a PIT tag combined). To incorporate survival rates into the Schnabel estimate, we assumed that PIT-tagged and batch-marked juvenile coho and Chinook in the same site had similar survival rates. We used the site-specific survival rates calculated in Program MARK to determine the number of previously marked fish that should be included at the beginning of each month in the Schnabel estimate (because ignoring mortality in the Schnabel estimate would overestimate population sizes). We calculated site-specific densities by dividing Schnabel population estimates by site area.

Fish growth and condition

We measured growth rates by measuring the length and biomass of fish captured in successive mark–recapture sampling events. Growth rates were calculated for individual coho and Chinook salmon by age class (age 0 and age 1+) for each sample time period and presented as percent daily growth in both length and mass. For each sampling date and site, we calculated Fulton's condition factor as described in the methods for overwinter survival. We checked for any length bias in our condition factor before proceeding with analysis. The effect of habitat type on percent daily growth rates was analyzed using ANOVA, and pairwise comparisons among the least squares means for habitat type were assessed using Tukey's HSD.

Habitat-specific and floodplain production

We estimated the amount of biomass produced in each site from June–August. We calculated the mean biomass accumulated per individual (g) by taking the mean of the biomass accumulated for individuals tagged in June and recaptured in August for each site. We then multiplied mean accumulated biomass by August population estimates for each site to calculate site-specific production (in kilograms). To extrapolate production estimates to the entire parafluvial zone of the floodplain, we multiplied mean biomass produced per unit area for each habitat type by the total area of early-successional beaver ponds, beaver-influenced spring brooks, and beaver-free spring brooks in the parafluvial zone (quantified from satellite imagery; see Malison et al. 2014).

In addition to the biomass produced per habitat type, an understanding of the number of individuals that reared in each habitat type is important. Due to differences in accessibility (i.e., ponds are more difficult for fish to enter than free-flowing spring brooks), the importance of higher growth rates in ponds may be negligible if few fish rear in pond habitats. To determine the abundance of individuals rearing in the entire parafluvial zone, we used September densities (from each site, multiplied by site area) to determine the abundance of juvenile salmon by habitat type for the entire parafluvial zone. We used September densities because the population in the fall represents the number of individuals that will overwinter. We viewed the abundance of individuals as an important proxy for floodplain production because patterns in biomass accumulation may be substantially different from the number of individuals produced.

Lastly, we estimated potential floodplain production of juvenile coho and Chinook if beavers were absent and all spring brooks were free-flowing. We used satellite imagery in ArcMap to delineate channel courses (i.e., previous spring brook flow paths) through existing beaver ponds and calculated spring brook areas that would be present had they not been dammed by beavers (~45% of the area remains as spring brooks if ponds are not present). We used density and growth measurements from the beaver-free spring brooks to estimate potential floodplain production without beavers.

Results

Habitat characteristics

All habitats exhibited similar temperatures, dissolved oxygen, pH, and conductivity, and none of these variables were deemed limiting to salmon growth and survival. In any case, all mark–recapture sites exhibited optimal temperatures for growth during the summer months (ranging between 6 and 12 °C; Brett 1952), but ponds generally had the highest temperatures (8–12 °C vs. 7–10 °C for beaver-free spring brooks). GDDs varied slightly for mark–recapture habitats between June and August (though not significantly, $F_{[2,7]} = 3.37$, $P = 0.0945$), with beaver ponds being 1.3 times warmer than beaver-free spring brooks (Tukey's HSD, $P = 0.0851$). Dissolved oxygen, pH, and conductivity were similar for all habitat types ($F_{[2,6]} < 3.30$, $P > 0.1078$). We were surprised that ponds did not exert much control on the biophysical conditions in beaver-influenced spring brooks (downstream of dams). However, as noted above, both habitats were substantially influenced by upwelling groundwater, which equalized these variables. However, habitat area varied significantly by habitat type ($F_{[2,8]} = 7.57$, $P = 0.0143$), with beaver ponds having 8.4 times the area as beaver-free spring brooks (Tukey's HSD, $P = 0.0144$) and 2.5 times the area as beaver-influenced spring brooks (Tukey's HSD, $P = 0.0607$).

Overwinter survival

In April 2011, all ponds and spring brooks were ice-covered, except for the groundwater effluent zones in some spring brooks. Ice on beaver ponds was 0.65 to 0.90 m thick, and two of the four ponds were frozen to the bottom in the locations where we drilled. The other two ponds had water, with depths varying between 0.42 and 0.83 m, and mean dissolved oxygen concentrations indicated that oxygenated water was upwelling under the ice (56.2% ± 9.1% and 7.3 ± 1.2 mg·L^{-1} and 77.4% ± 1.5% and 10.0 ± 0.3 mg·L^{-1} for the two sites). Very likely, all of the ponds were ice-free at the points of groundwater outflows, and salmonids are known to survive a few centimetres into favorable conditions within substrata. In any case, we documented juvenile salmon overwinter survival in the two ponds with open water underneath the ice. We captured a total of 27 coho, 42 Chinook, and three sockeye salmon in these two ponds. Of the 27 coho, seven were tagged in the same sites in the summer and fall of 2010. Of the 42 Chinook, nine were tagged in 2010. Fish condition was slightly lower for juvenile coho and Chinook captured during the winter compared with fish sampled at the same sites during the summer and fall of 2010 (0.93 ± 0.02 vs. 1.10 ± 0.02 for coho and 0.95 ± 0.03 vs. 1.10 ± 0.05 for Chinook). All spring brooks were either ice-free or flowing under the ice (because groundwater temperatures were always well above freezing), and therefore, we assumed that survival was not limited by physical conditions.

Prey availability

Aerial food resources varied by habitat type on a unit area basis ($F_{[2,8]} = 11.866$, $P = 0.004$, partial $\eta^2 = 0.748$). Beaver-free spring brooks received 2.1× higher fluxes (mg·m^{-2}·day^{-1}) of invertebrates than beaver ponds (Fig. 5A; $P = 0.003$) and 1.4× higher fluxes of invertebrates than beaver-influenced spring brooks (Fig. 5A; $P = 0.051$). There was no effect of time on invertebrate flux ($F_{[2,11]} = 1.142$, $P = 0.344$, partial $\eta^2 = 0.125$) and no interaction between habitat type and time on invertebrate flux ($F_{[4,11]} = 0.179$, $P = 0.946$, partial $\eta^2 = 0.043$). After extrapolating to the area of complete habitat units (i.e., entire ponds or spring brooks), there were also significant differences in total inputs (g·day^{-1}) by habitat type ($F_{[2,8]} = 7.028$, $P = 0.017$, partial $\eta^2 = 0.637$). However, in contrast to fluxes, beaver ponds had 4.4× higher total inputs of invertebrates than beaver-free spring brooks (Fig. 5B; $P = 0.014$). There was no effect of time on invertebrate inputs ($F_{[2,11]} = 1.340$, $P = 0.290$, partial $\eta^2 = 0.143$) and no interaction between habitat type and time on invertebrate inputs ($F_{[4,11]} = 0.268$, $P = 0.894$, partial $\eta^2 = 0.063$). Aerial inputs were dominated by adult Diptera (true flies, both aquatic and terrestrial), collembolan (springtails), adult Trichoptera (caddisflies), adult Tipulidae (crane flies), Hemipterans (true bugs), and Coleoptera (beetles). Inputs into beaver-free spring brooks were comprised of 1.2 to 1.3× higher proportions of aquatically derived invertebrates than beaver-influenced spring brooks and beaver ponds, though the only significant difference by habitat type occurred in July ($F_{[2,8]} = 5.34$, $P = 0.0336$; for June, August, and September, $F_{[2,8]} \leq 3.94$, $P \geq 0.0645$). The aerial input composition was similar for all habitat types (NMDS ordination; $A = 0.017$, $P > 0.129$).

Overall mean total biomass of benthic prey was similar between beaver-free and beaver-influenced spring brooks ($t = -2.05$, $P = 0.1692$), although beaver-free spring brooks had, on average, 2.8× greater biomass (but sample variance was high). Some qualitative differences occurred in the community structure of benthic prey between the two spring brook types, with some mayflies and stoneflies being more predominant in beaver-free spring brooks (for NMDS results, see Malison et al. 2014). Benthic samples were generally dominated by Chironomidae, Platyhelminthes, and Oligochaeta. The biomass of drifting prey was low in all samples and similar in beaver-free vs. beaver-influenced spring brooks (0.028 ± 0.033 mg·m^{-3} vs. 0.025 ± 0.025 mg·m^{-3}; $Z = -0.5303$, $P = 0.5959$). Drift samples contained organisms from both falling inputs and benthic samples, but the predominant taxa were all aquatic, including larval Chironomidae and larval Trichoptera, cladocerans, Oligochaeta (worms), and Ostracoda. Sweep net samples collected

Fig. 5. Flux and inputs of aerial invertebrate biomass into floodplain habitats. (A) Mean (±1 SE) flux (mg·m^{-2}·day^{-1}) of invertebrates into pan traps in four beaver ponds (BP), four beaver-influenced spring brooks (BSB), and three beaver-free spring brooks (SB) during four sampling periods (June, July, August, and September). (B) The same data as given in (A) but mean total input calculated by scaling flux values to the entire area of each site and averaging by habitat type.

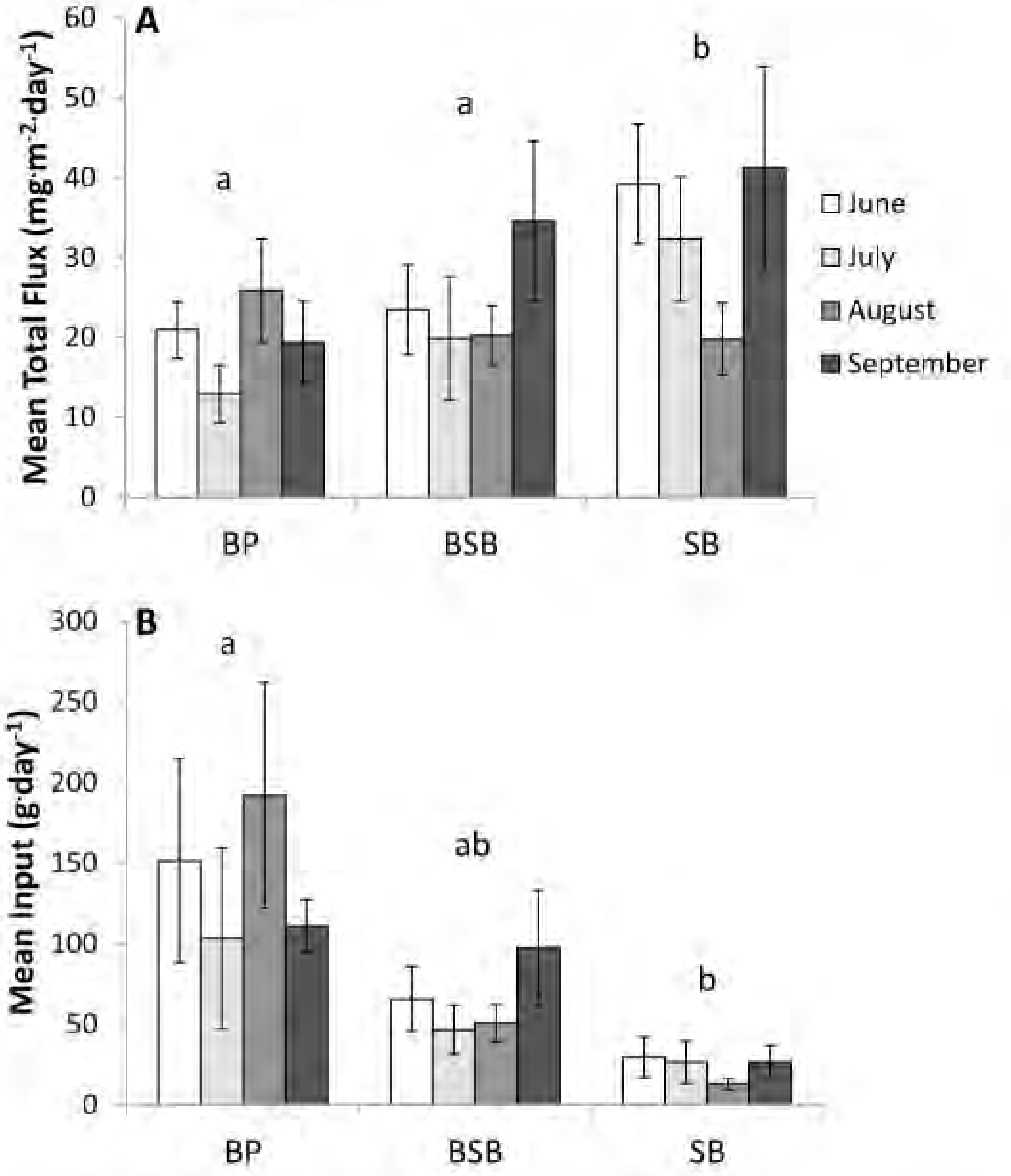


Fig. 6. Mean composition of juvenile coho and Chinook diets by habitat type (BP, beaver pond; BSB, beaver-influenced spring brook; SB, beaver-free spring brook).

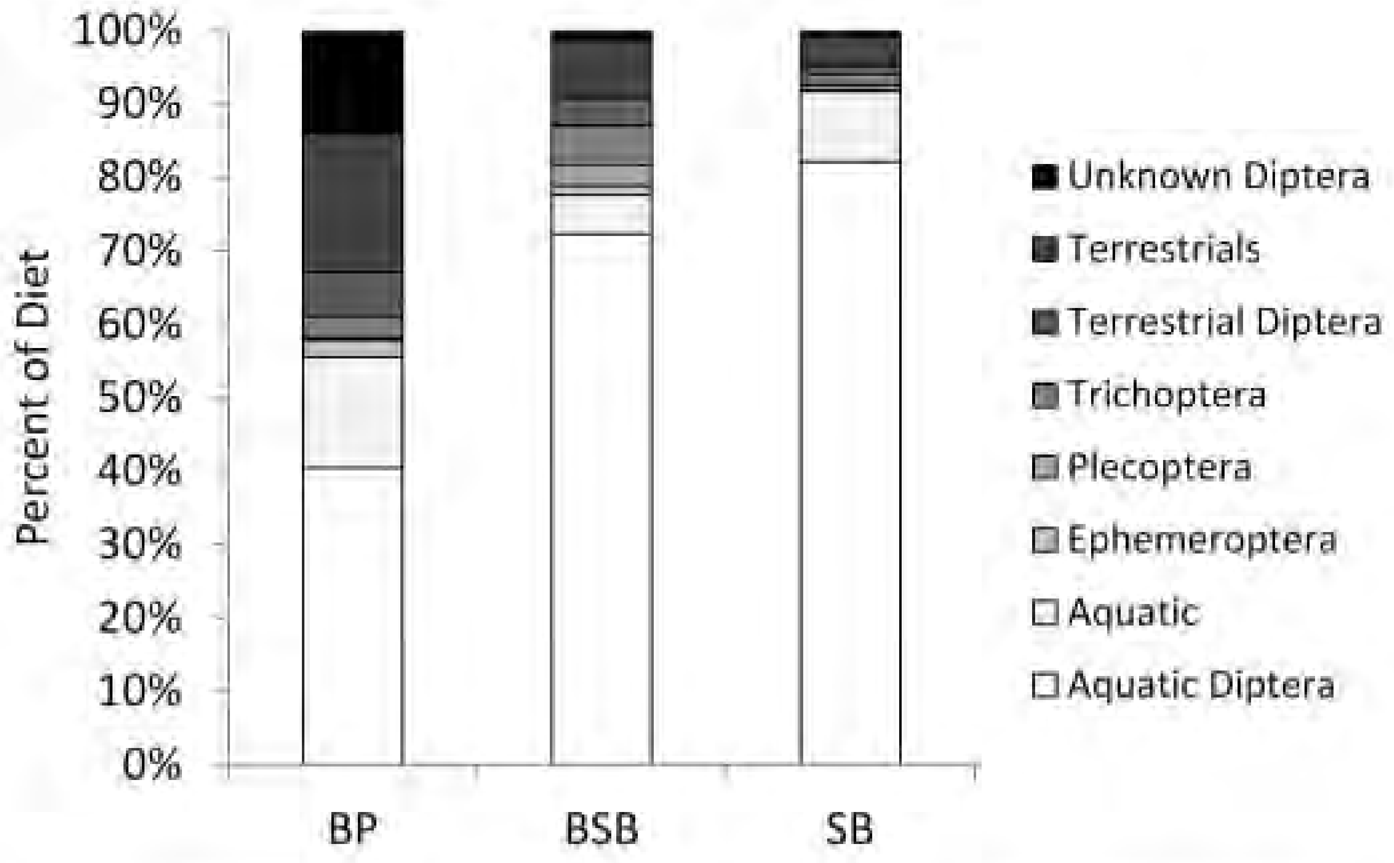
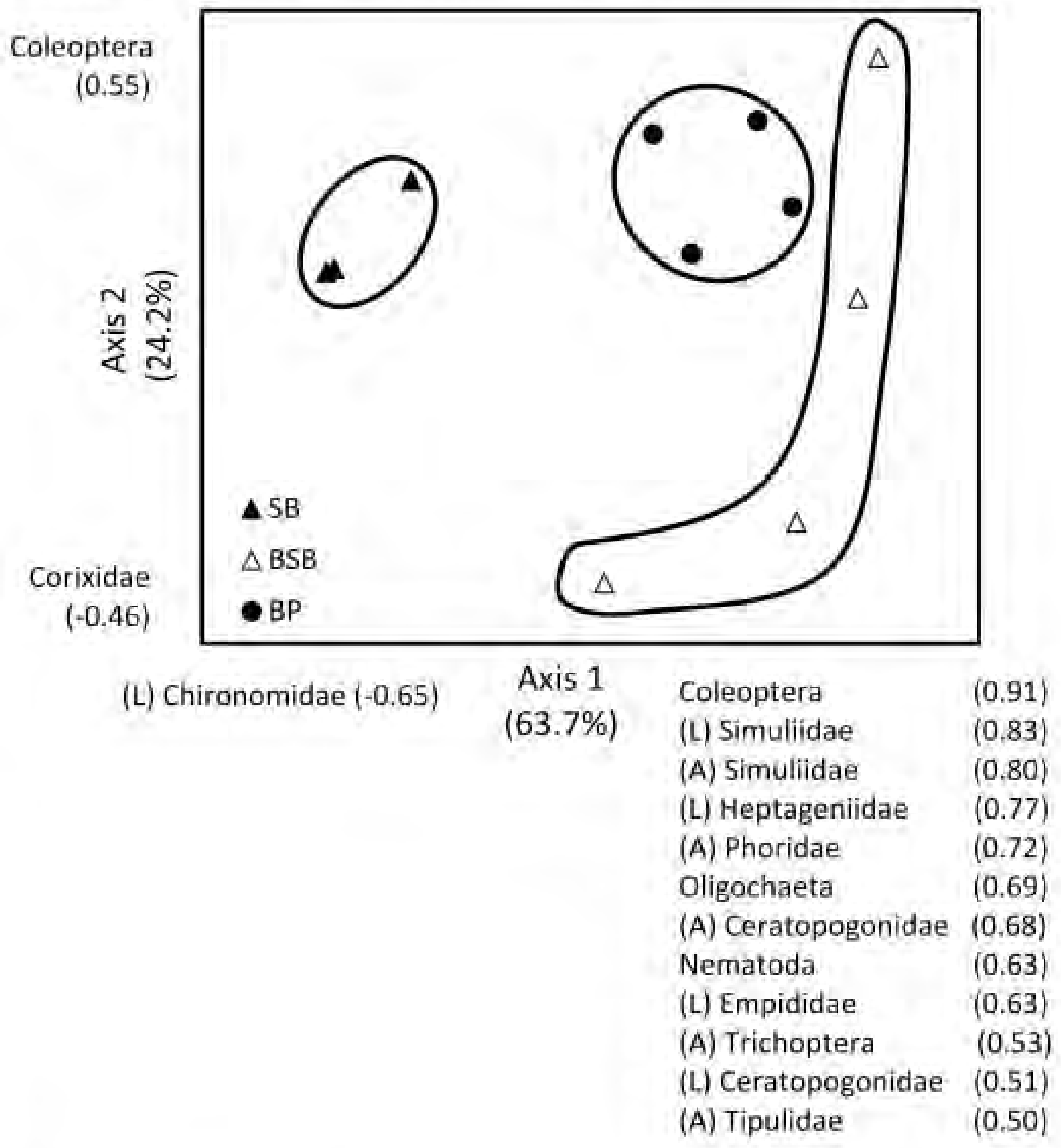


Fig. 7. Ordination plot obtained by nonmetric multidimensional scaling of the relative abundance of macroinvertebrates in diets of juvenile coho residing in beaver-free spring brooks (SB), beaver-influenced spring brooks (BSB), and beaver ponds (BP). Site position in diet space is shown relative to axes 1 and 2, and diets in the three habitat types were significantly different. Numbers in parentheses next to axis titles represent the percent variation explained by each axis. Relative importance of each taxon is indicated by ranking of Pearson correlation coefficients between taxon, and each axis as given below the ordination plot. Aerial (A) and larval (L) forms of macroinvertebrates were present in the diets.



from within ponds contained, on average, 96% (±0.02%) aquatic organisms (i.e., taxa entering ponds from aerial inputs were underrepresented in sweep samples) and had different species compositions compared with both types of spring brooks (for NMDS results, see Malison et al. 2014). Dominant invertebrate taxa within the ponds included Chironomidae (nonbiting midges), cladocerans and copepods (small crustaceans), and gastropoda (snails), with Ostracoda (small crustacean) and Trichoptera making up slightly less of the samples.

Fish diets

Diet samples from juvenile coho and Chinook in all habitat types had a similar biomass of prey in all months ($F_{[2,8]} < 4.16$, $P > 0.0644$). The occurrence of empty fish stomachs was rare in all sampling sites. Although the mean total biomass of diets was similar, strong differences in the origin (aquatic vs. terrestrial) of diets by habitat type may have contributed to differences in growth rates. Terrestrially derived taxa made up a greater proportion of diets in beaver ponds, and aquatically derived taxa made up greater proportions of diets in beaver-free spring brooks (Fig. 6). Sixty percent of diet items of pond fish were aquatically derived each month compared with 84% and 92% of prey items being from aquatic sources in beaver-influenced and beaver-free spring brooks, respectively. The composition of prey in fish diets also differed by habitat type. The NMDS ordination of mean relative abundance of 41 taxa groups found in diets yielded a solution that represented 87.8% of the total variation among sites on two axes (Fig. 7). Diets from sites in different habitat categories were significantly separated in community ordination space (MRPP, $A = 0.335$, $P = 0.0006$). Beaver pond diet composition was different from beaver-influenced spring brook diet composition ($P = 0.024$), but diets from these two habitat types were still more similar to each other than to beaver-free spring brook diets ($P < 0.010$). Habitats were most strongly separated in diet composition space along axis 1, which explained 63.7% of the variation. Larval Chironomidae were predominant in beaver-free spring brook diets, whereas Coleoptera, Simuliidae, Heptageniidae, Phoridae, Oli-

Fig. 8. Movement rates (percentage of marked fish that moved) of juvenile salmon (coho and Chinook data pooled) among habitat types based on mark–recapture data obtained in the four beaver complexes and one spring brook site. (A) Mean (±1 SE) movement rates from ponds to beaver-influenced spring brooks (BP to BSB) and from beaver-influenced spring brooks into ponds (BSB to BP). (B) Mean (±1 SE) movement rates with sites pooled by habitat type (solid diamonds, from ponds to beaver-influenced spring brooks (BP to BSB); from beaver-influenced spring brooks to ponds (BSB to BP); from beaver-influenced spring brooks to the river (BSB to river) averaged over the sampling period; open symbols, from beaver-free spring brooks to the river (SB to river) over three time periods (diamond, June–July (no fish moved); circle, July–August; square, August–September). Asterisks indicate sites with PIT-tag antennae; emigration data from these sites were used to parameterize the models in Program MARK.

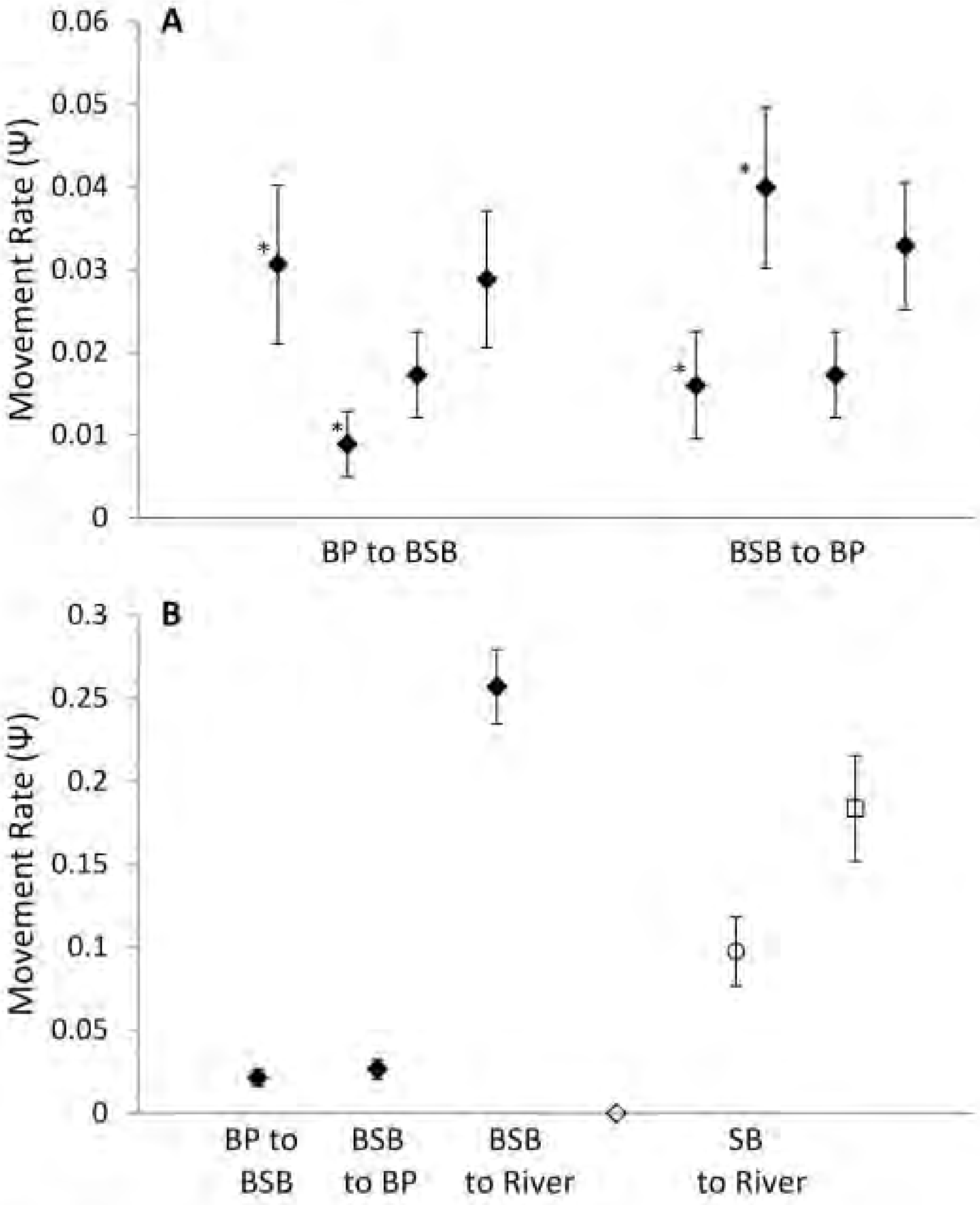
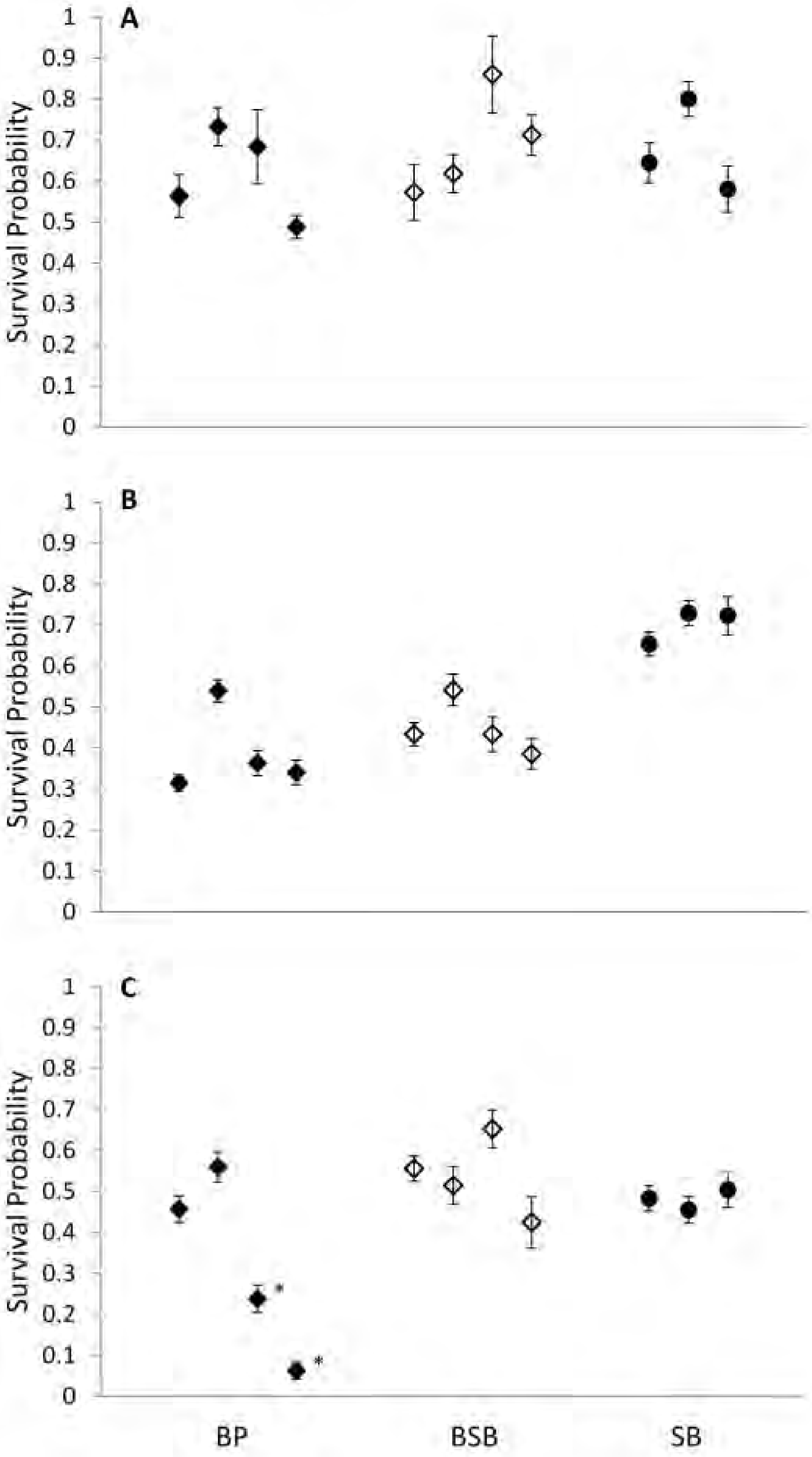


Fig. 9. Survival rates (±1 SE) of juvenile coho salmon in beaver ponds (BP, solid diamonds), beaver-influenced spring brooks (BSB, open diamonds), and beaver-free spring brooks (SB, solid circles) for three time periods: (A) June–July, (B) July–August, and (C) August–September. An asterisk (*) indicates survival rates that may be underestimates due to emigration.



gochaeta, Ceratopogonidae, Nematoda, Empididae, Trichoptera, and Tipulidae were associated more strongly with beaver pond and beaver-influenced spring brook diets. Corixidae and Coleoptera most strongly drove separation in diet space along axis 2, which represented 24.2% of the variation.

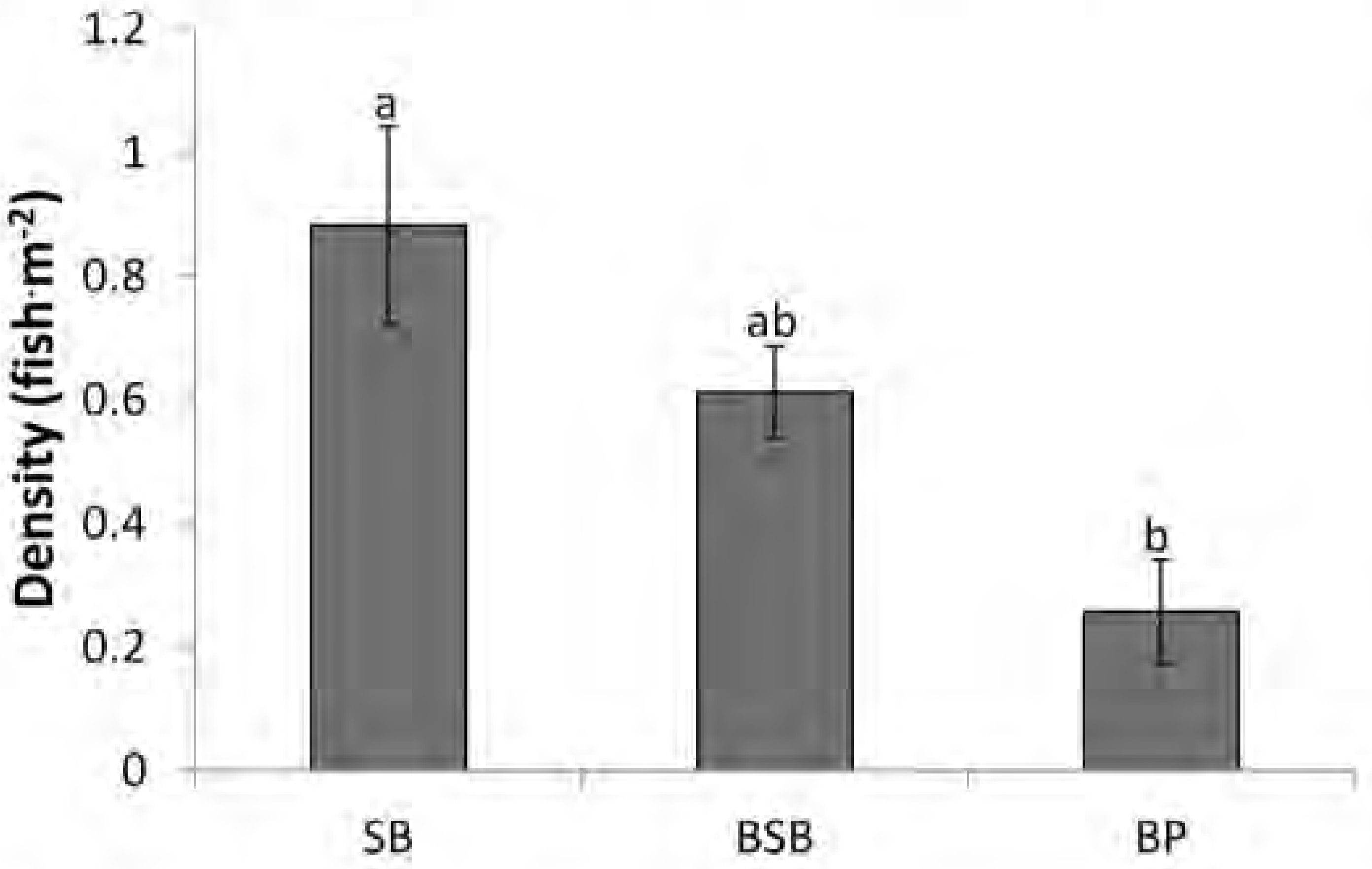
Population dynamics

Model selection results are presented for the four beaver-dominated study systems and the three beaver-free systems (free-flowing spring brooks) (Table 1). The top model was $\phi(gt)\Psi(g)$ for three of the beaver systems, $\phi(gt)\Psi(\text{null})$ for one beaver system, and $\phi(t)\Psi(t)$ for the beaver-free spring brooks (where ϕ = survival, Ψ = movement, g = group (pond or spring brook), t = time, null = constant).

Movement rates varied by study system but were similar from ponds to spring brooks and from spring brooks to ponds ($t = -0.66$, $P = 0.5367$; Figs. 8A, 8B). Emigration varied over time for the beaver-free spring brook, increasing from a very low rate to a level similar to that estimated for beaver-influenced spring brooks by the end of the season (Fig. 8). However, the best models for the beaver system did not include movement varying over time (see Table 1), so the same value represented emigration each month (see Fig. 8). We did observe a general increase in emigration rates over the course of the sampling season in the beaver systems.

Survival rates were similar among habitat types from June to July and from August to September, except for two beaver ponds (Fig. 9). It is unclear why two of the beaver ponds had very low survival estimates from August to September (Fig. 9C), but emigration was not directly measured at these sites. It is likely that emigration from these sites was higher than at the other sites, which would result in biased low apparent survival rates (Fig. 9C). From July to August, the beaver-free spring brooks exhibited higher survival rates than both beaver habitats. However, the survival rates for the beaver habitats are likely biased low during

Fig. 10. Mean (±1 SE) juvenile coho and Chinook density in September for all juveniles large enough to be tagged (pit-tagged and elastomer tagged) for beaver-free spring brooks (SB), beaver-influenced spring brooks (BSB), and early-successional beaver ponds (BP).



this time due to missed emigration when antennae were inoperable because of flooding for 23 days.

We divided population estimates by habitat area and presented data as densities to compare different habitat types. The density of tagged coho and Chinook differed significantly by habitat type ($F_{[2,8]}$ = 9.09, P = 0.0087), with higher densities present in beaver-free spring brooks than in early-successional beaver ponds (Tukey's HSD, P = 0.0074; Fig. 10).

Fish growth and condition

In total, slightly more than 8100 juvenile coho and Chinook were PIT tagged at the 11 sites. Growth rates were calculated from individuals tagged at each site originally in June and recaptured in August (spring brooks, n = 136; beaver-influenced spring brooks, n = 140; ponds, n = 176). Habitat type had a significant effect on percent daily growth rates (in length and mass) for YOY coho growing between June and August (Figs. 11A, 11B; $F_{[2,8]}$ = 11.68, P = 0.0042, and $F_{[2,8]}$ = 16.89, P = 0.0013, respectively). The greatest difference in YOY coho growth rates in percent daily length was between beaver ponds and beaver-influenced spring brooks (1.6× higher in beaver ponds; Tukey's HSD, P = 0.0034), and although not significant, rates were 1.3× faster in beaver ponds than in beaver-free spring brooks (Tukey's HSD, P = 0.0605). For percent daily mass, YOY coho in beaver ponds grew faster than YOY coho in both beaver-influenced and beaver-free spring brooks (Tukey's HSD, $P \leq 0.0069$). Percent daily growth rates were similar in length and mass for age-1+ coho by habitat type, largely due to high variance in growth rates in beaver-free spring brooks (Figs. 11A, 11B; $F_{[2,8]} \leq 2.86$, $P \geq 0.1371$). A key finding concerning growth was that YOY coho were of similar size in June but grew faster in beaver ponds, resulting in September sizes of pond fish being 10–15 mm longer than in both types of spring brook fish (Fig. 12; $F_{[2,8]}$ = 19.68, P = 0.0008).

Growth of YOY Chinook followed patterns similar to coho, but data are only presented from July to August (juveniles were not large enough to tag until July). Growth rates (percent daily, in length and mass) differed significantly for YOY Chinook from July to August (Figs. 11A, 11B; length, $F_{[2,3.74]}$ = 20.18, P = 0.0099; mass, $F_{[2,8]}$ = 6.49, P = 0.0212), with Chinook in beaver ponds growing significantly faster than those in beaver-influenced spring brooks (Tukey's HSD, P = 0.0134 and 0.0171, length and mass, respectively).

The size and condition of fish going into winter are important because they influence the decision of when to smoltify for coho (at age 1+ or age 2+) and may influence the survival of both species. There was no relationship between condition and size of fish for any site, probably because of the small size range of fish in this study. By the end of the growing season (just before winter), the condition of coho was not statistically significantly different among habitat types ($F_{[2,8]}$ = 3.14, P = 0.0983), but coho in ponds did have 2%–3% higher condition factors than coho in both types of spring brooks. The condition of Chinook was similar for all habitat types in September ($F_{[2,8]}$ = 0.28, P = 0.7656).

Habitat-specific and floodplain production

Accumulation of juvenile coho and Chinook biomass per square metre was generally higher for beaver-free spring brooks and beaver-influenced spring brooks than for beaver ponds, although the difference was not statistically significant (2.98 ± 2.11 g·m^{-2} and 3.23 ± 1.46 g·m^{-2} vs. 1.87 ± 1.14 g·m^{-2}, respectively; $F_{[2,8]}$ = 0.857, P = 0.4601). By extrapolating habitat-specific biomass accumulation to the entire parafluvial zone of the floodplain, the total production of juvenile coho and Chinook biomass between June and August was highest in beaver ponds (175 kg in total, 2.9 kg·day^{-1}) compared with either type of spring brook habitat (beaver-free, 140 kg in total, 2.3 kg·day^{-1}; beaver-influenced, 149 kg in total, 2.5 kg·day^{-1}) due to higher growth rates and greater pond area. Nonetheless, the combined areas of both types of spring brooks produced greater total biomass of juvenile salmon compared with the ponds. In total for the parafluvial zone, we estimated that the three habitat types produced 463 kg of juvenile salmon biomass (7.7 kg·day^{-1}) between June and August. In contrast, juvenile coho and Chinook salmon were most abundant (highest densities) in beaver-free spring brooks and were least abundant in early-successional beaver ponds habitat; whereas beaver-influenced spring brooks were intermediate. Juvenile coho and Chinook salmon were almost 2× more abundant in beaver-free spring brook habitat (~41 400) than in beaver ponds (~24 100) and almost 1.5× more abundant in beaver-free spring brooks than in beaver-influenced spring brooks (~20 500).

Without beavers, all off-channel floodplain habitats would be free-flowing spring brooks and accessible to juvenile salmon as natal habitat. We estimated that the total production of juvenile coho and Chinook biomass would be 13% lower (403 kg in total, 6.7 kg·day^{-1}, vs. 463 kg in total, 7.7 kg·day^{-1}) in the parafluvial zone of the floodplain if beavers were absent. In contrast, if beavers were absent on the floodplain, we estimate that almost 1.5× more individuals would be able to rear in parafluvial habitats (~119 300 vs. 93 800), because densities were 1.5 to 3.5× higher in beaver-free spring brooks than in beaver-influenced spring brooks and ponds. These numbers increase substantially (119 300 to 370 000) if orthofluvial spring brooks are also available as natal habitat (Malison 2013).

Discussion

This study supported our hypotheses that the presence of early-successional beaver ponds on fish-accessible spring brooks increases salmon production because abundant lentic food and lower fish densities in the ponds substantially enhance growth in comparison to undammed spring brooks or spring brooks below beaver dams. Indeed, growth rates for YOY coho and Chinook were higher in early-successional beaver ponds than in spring brooks, and patterns were similar for age-1+ coho. Additionally, the ponds provided the same quantity of rearing habitat as both types of spring brooks (beaver-free and beaver-influenced) combined. Increased growth rates and the large habitat area of ponds corresponded with a slightly higher biomass of juvenile salmon being produced in the parafluvial zone than if beavers were absent from the floodplain. However, in spite of higher growth rates in the ponds, the number of juveniles rearing in ponds was limited, resulting in pond densities being 3× lower per unit area than spring brook densities. Surprisingly, high survival rates did not correspond with low densities and were actually similar among all habitat types in June and July, with the lowest rates observed

Fig. 11. Mean (±1 SE) growth for age-0 and age-1+ coho in (A) percent daily length and (B) percent daily mass, and for age-0 Chinook in (C) percent daily length and (D) percent daily mass for four beaver ponds (BP), four beaver-influenced spring brooks (BSB), and three beaver-free spring brooks (SB) based on fish recaptured during June to August.

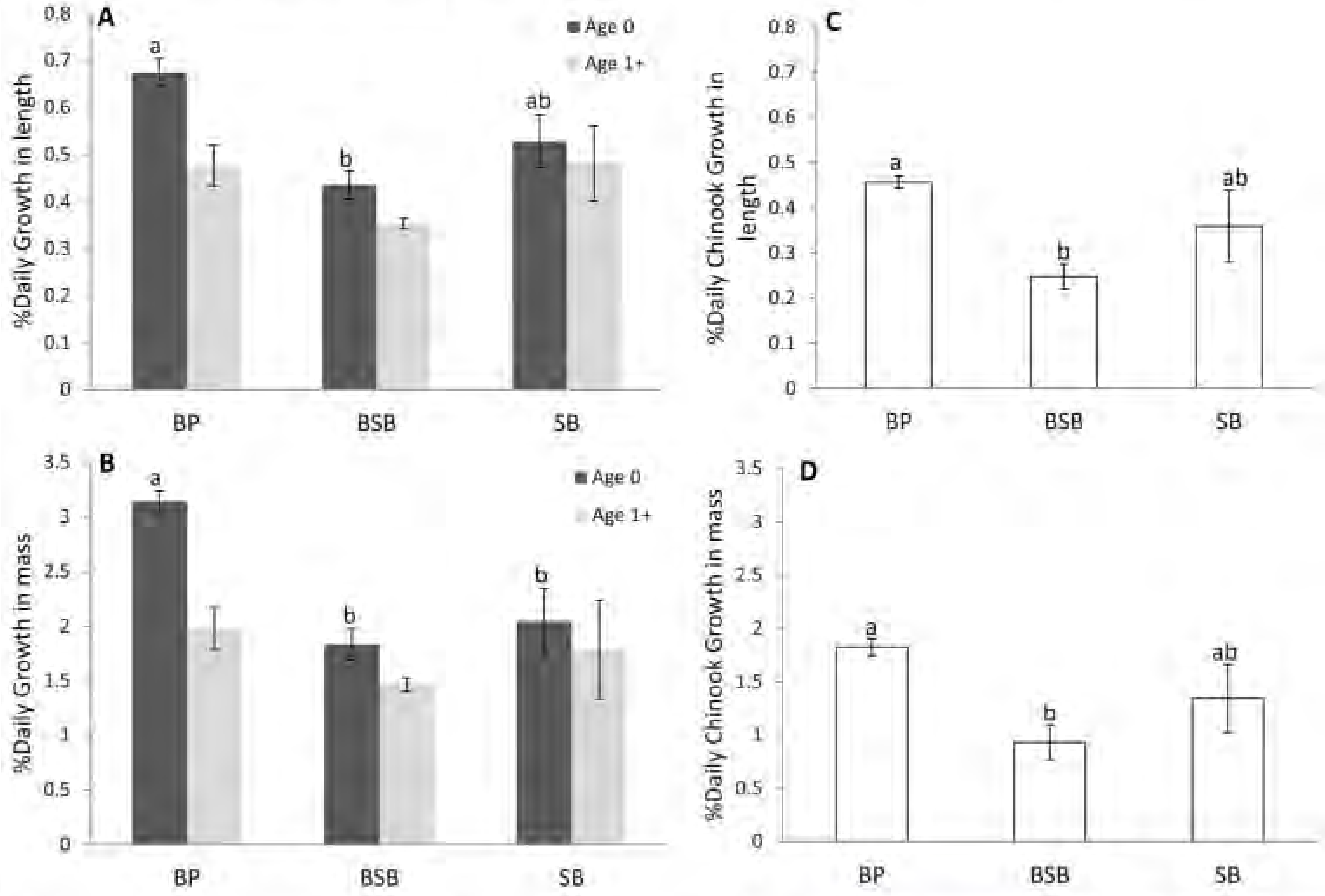
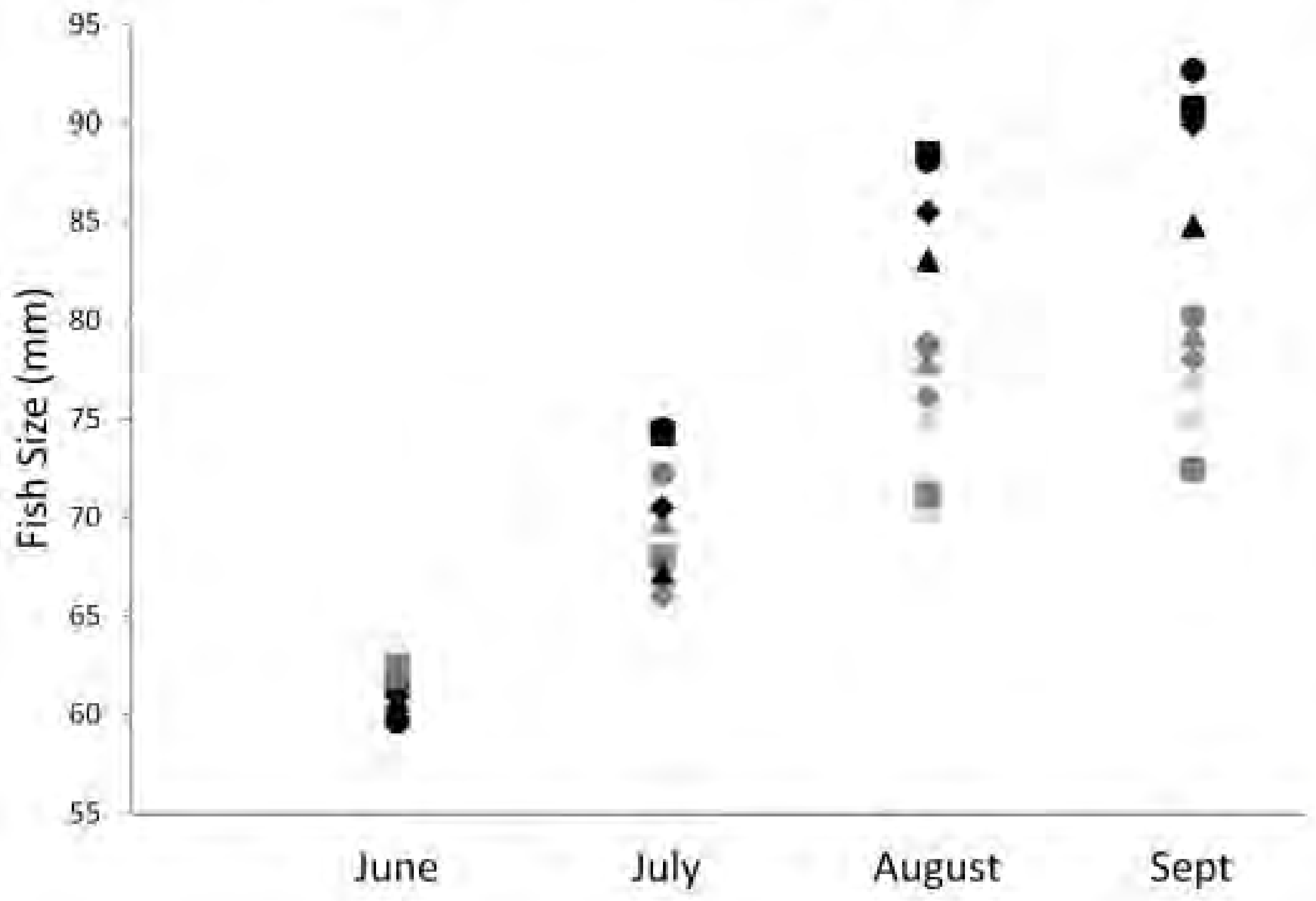


Fig. 12. Length of age-0 coho by habitat type from June to September (black symbols, beaver ponds; dark grey symbols, beaver-influenced spring brooks; light gray symbols, spring brooks). Different symbols within each color group represent individual sites. YOY were about the same size in June but grew faster over the summer in beaver ponds than in the spring brooks.



between August and September in the two beaver ponds that froze solid in April of 2011. We did document individuals surviving in some ponds under the ice during the winter, suggesting that ponds with deep pools and effluent groundwater are suitable overwintering habitat.

The differences that we observed in growth rates by habitat type could have a variety of mechanistic explanations. Reduced competition and decreased energy expenditure has resulted in increased growth rates for Atlantic salmon (*Salmo salar*) in both lakes and beaver ponds (Hutchings 1986; Sigourney et al. 2006). As with Atlantic salmon, coho and Chinook display territorial behavior, and similar mechanisms may be driving the observed differences in growth rates (Chapman 1966), with lower pond densities resulting in decreased competition and stimulated growth rates. In fact, Malison (2013) found that growth rates were the same in early-successional ponds and spring brooks when juvenile salmon were held at identical densities in enclosures. Lower densities likely occurred in ponds for two reasons: (*i*) fewer YOY were able to find pathways into ponds and (*ii*) ponding greatly increases habitat area. Indeed, a similar number of age-1+ coho were captured from spring brooks and ponds (3142 vs. 3258), but over threefold more age-0 coho were caught in spring brooks than in beaver ponds (10 009 vs. 2971) (Malison 2013). The marginally warmer temperatures in beaver ponds could also have contributed to increasing growth rates (Brett et al. 1969). It is likely that a combination of the above mechanisms, as well as the lower maintenance costs of lentic environments, contributed to the increased growth rates in ponds (Enders et al. 2003).

Fewer fish combined with greater inputs of food resources could have resulted in less competition in the ponds, which also would promote higher growth rates, especially for YOY salmon, which had 1.5 to 3.5× higher densities in spring brooks. Other studies have found that increased prey resources promote increased growth of juvenile salmon in beaver ponds (Peterson 1982). Ponds received up to 4× as much allochthonous prey inputs as spring brooks per unit area, though the composition was similar for all habitat types. Furthermore, the availability of benthic prey was on average 2.8× greater in beaver-free spring brooks than in beaver-influenced spring brooks. Although the biomass of diet samples was similar by habitat type, it is possible that variation in the time of sample collection and the composite sampling technique introduced error that masked any differences. We did find differences in the composition of diets by habitat type that might relate to food quality. Chironomidae dominated diets of fish in beaver-free spring brooks, which exhibited intermediate growth rates, whereas multiple prey taxa dominated diets of beaver pond fish, which grew the fastest. Furthermore, aquatically derived taxa made up greater proportions of beaver-free spring brook diets, whereas terrestrial taxa were more important in pond diets.

In any case, by the end of the summer, YOY coho in beaver ponds were 10–15 mm larger than coho in beaver-free and beaver-influenced spring brooks, which could have important implications for migratory survival. Survival during the time that smolts first enter the ocean is an important determinant of subsequent adult populations (Zabel and Achord 2004; Quinn 2005). In fact, larger parr and smolts have been shown to have higher overwinter (Zabel and Achord 2004) and higher marine (Holtby et al. 1990) survival rates. Rearing in ponds may therefore result in a survival advantage for more individuals. If so, then a greater proportion of the salmon produced in ponds may return as adults to spawn than those produced in spring brooks. Consequently, the greater numbers of smolts rearing in spring brooks may not be as important as the larger individuals produced in ponds. Nonetheless, larger smolts do not always have consistently higher survival rates (Holtby et al. 1990), and it is questionable whether higher survival rates for pond fish would make up the difference of greater numbers rearing in spring brooks. Tracking the return of adult salmon tagged as juveniles in known freshwater habitats would provide the necessary information to determine if any differences in marine survival occurred in relation to freshwater rearing habitat.

Survival and movement strongly influenced habitat-specific population sizes and densities. We expected that patterns in survival and growth rates would be higher in ponds, but all ponds and beaver-influenced spring brooks exhibited similar survival rates to beaver-free spring brooks between June and July, and half of the ponds were similar to beaver-free spring brooks from August to September. We suspect that survival rates for beaver-influenced habitats from July to August were biased low because of flooding and incapacitated PIT-tag antennae that missed emigration for 23 days. It is less clear why two ponds had extremely low survival rates from August to September. We expect that these sites experienced higher emigration rates than the sites where emigration was measured. Interestingly, these sites were also the shallowest pond habitats and were frozen solid in drilling locations during winter sampling. It may be possible that salmon emigrated in much greater numbers from these shallow pond rearing habitats, suggesting that pond depth and groundwater connection could predict whether ponds can be used for overwintering habitat.

We found that salmon densities varied with habitat type, although higher growth rates did not always correspond with the lowest densities. Using population estimates from all juvenile coho and Chinook large enough to tag (>58 mm), we found that densities were highest in beaver-free spring brooks, intermediate in beaver-influenced spring brooks, and lowest in early-successional beaver ponds. If small YOY (too small to tag) were also included in the estimate, this relationship may change and would result in densities being the highest in beaver-influenced spring brooks. Beaver-free spring brooks had higher growth rates and higher densities than beaver-influenced spring brooks when only fish large enough to tag were considered, but if the large number of YOY were included, the much higher densities in beaver-influenced spring brooks could explain why growth rates were lower in this habitat type.

We determined that beavers may increase production from the parafluvial zone in terms of biomass by increasing growth rates, but they may also limit the total number of individuals that rear in the parafluvial zone. We estimated that if ponds and beaver-influenced spring brooks were present as beaver-free spring brooks, 1.5 to 2× more individuals would rear on the floodplain. However, to make a more robust estimate of what production might be like without beavers, we need to have a much better understanding of how rearing habitat availability would change if beavers were not present (i.e., exactly how much area would be covered by spring brooks if dams were absent). Additionally, we need a better understanding of whether rearing habitat availability is actually a limiting factor for juvenile salmon production on the floodplain. The presence of ponds (that rear lower densities of juveniles) may not limit production if juvenile salmon densities are not at carrying capacity. It seems unlikely that rearing habitats are saturated at the current level of escapement for both coho and Chinook on the Kwethluk River because escapement levels have declined by 12 to 15× over the past 9 years (Miller and Harper 2012). Moreover, densities at Kwethluk were on par with or lower than densities observed in other very productive large salmon rivers (Murphy et al. 1986, 1989; Eberle and Stanford 2010), which suggests minimal concern for density dependence in relation to likely negative effects of spring brook conversion to beaver ponds.

We determined that the presence of beavers and ponds results in a trade-off, ponds grow larger fish, but fish are more abundant in spring brooks. If all spring brooks in the parafluvial zone were free-flowing at the floodplain scale, then production would potentially exceed the existing beaver-influenced system because greater numbers can rear in spring brooks. Even stronger differences in production may exist when the entire floodplain, with both parafluvial and orthofluvial zones included, is considered. In beaver-free floodplains such as the Kol and Krutogorova rivers in western Kamchatka, Russia, juvenile salmon are able to rear in spring brooks spanning the floodplain from the parafluvial zone to the orthofluvial zone far from the main channel of the river (Stanford et al. 2002). The spring brooks in beaver-free systems are extremely important spawning habitats and rearing areas because they tend to be quite large with dependable flows and good access to riparian food resources (Eberle and Stanford 2010). Whereas in a beaver-dominated floodplain such as the Kwethluk River, late-successional beaver complexes in the orthofluvial zone seem disconnected physically and ecologically (Malison et al. 2014). Thus, beavers may reduce juvenile salmon production at the floodplain scale (i.e., including both parafluvial and orthofluvial zones), even though they stimulate biomass production in the parafluvial zone, if they block significant amounts of orthofluvial rearing habitat. Beavers alter floodplain hydrology and change the mosaic of floodplain habitats (Mouw et al. 2013; Malison et al. 2014), strongly influencing the resources available for juvenile salmon and consequently salmonid population dynamics.

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