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Prey Availability, Consumption, and Quality Contribute to Variation in Growth of Subyearling Chinook Salmon Rearing in Riverine and Reservoir Habitats

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NOTE

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Abstract

We examined prey availability, prey consumed, and diet energy content as sources of variation in growth of natural fall Chinook Salmon *Oncorhynchus tshawytscha* subyearlings rearing in riverine and reservoir habitats in the Snake River. Subyearlings in riverine habitat primarily consumed aquatic insects (e.g., Diptera, Ephemeroptera, Trichoptera), of which a high proportion was represented by adult, terrestrial forms. In the reservoir, subyearlings also consumed aquatic insects but also preyed heavily at times on nonnative lentic amphipods *Corophium* spp. and the mysid *Neomysis mercedis*, which were absent in riverine habitats. The availability of prey was typically much higher in the reservoir due to *N. mercedis* often composing over 90% of the biomass, but when this taxon was removed from consideration, biomass estimates were more often higher in the riverine habitat. Subyearling diets during 2009–2011 were generally 17–40% higher in energy in the riverine habitat than in the reservoir. Observed growth in both length and weight were significantly higher in the riverine habitat than in the reservoir. Little is known about how temporal and spatial changes in the food web in large river landscapes influence populations of native anadromous fishes. Our results provide a glimpse of how the spread and establishment of nonnative prey species can reduce juvenile salmon growth in a large river impoundment, which in turn can affect migration timing and survival.

Juvenile Pacific Salmon occupy a variety of rearing and migratory habitats in freshwater that ideally should provide adequate opportunity for growth to ensure timely progression through developmental life stages, high survival, and successful ocean entry. This is particularly true for fish with an ocean-type life history (Gilbert 1912; Healey 1991) that must grow rapidly to emigrate seaward, undergo smoltification, and enter the ocean in their first summer of life as subyearlings (age 0). Ocean-type fall-run Chinook Salmon *Oncorhynchus tshawytscha* (hereafter

"subyearlings" unless otherwise noted) in the Snake River employ a transitory rearing strategy as subyearlings whereby parr gradually move downstream through a continuum of shoreline habitats before becoming pelagic, migratory smolts (Connor et al. 2003b; Coutant and Whitney 2006). Given that many rivers in the northern hemisphere are highly modified, Chinook Salmon subyearlings, must often rear and move through riverine and impounded habitats, which potentially differ in the prey and fish communities they support (Rondorf et al. 1990; Sommer et al. 2001; Naiman et al. 2012). Therefore, there is the potential for growth opportunity to differ between riverine and reservoir habitats that may ultimately affect population attributes such as emigration timing, fish size, and survival.

Relatively few studies have examined differences in food resources for migratory juvenile salmon that transition between riverine and impounded habitats. In the Columbia River, Rondorf et al. (1990) compared the diets of Chinook Salmon subyearlings collected in the riverine Hanford Reach and McNary Reservoir. They found that subyearlings rearing in riverine habitats primarily consumed energy-rich adult trichopterans, whereas in reservoir habitats lower-energy cladoceran zooplankton and other insects such as dipterans composed the majority of the subyearling diet. They concluded that subyearlings foraging in McNary Reservoir may reap a reduced energetic benefit because of the small prey, such as *Daphnia*, that they feed on. Similarly, Koehler et al. (2006) found that subyearlings rearing in Lake Washington primarily consumed chironomid pupae and zooplankton that had a lower energy density than adult chironomids and terrestrial insects commonly consumed in streams and rivers (e.g., McCarthy et al. 2009). However, if abundant enough, lower quality prey may still support good growth if consumed in sufficient quantities.

Therefore, differences in both the quantity and quality of prey between riverine and reservoir habitats are important if they influence juvenile salmon food consumption and growth.

Past studies suggest that prey resources for juvenile salmon in lower Snake River reservoirs may be limited. Muir and Coley (1996) found that one-third of yearling Chinook Salmon arriving at Lower Granite Dam—the first dam encountered during downstream dispersal and seaward migration—had empty stomachs. Similarly, Curet (1993) showed that subyearlings rearing in Lower Granite Reservoir were feeding only slightly above maintenance levels and had poor growth. More recently, Connor et al. (2013) showed that subyearling growth in riverine habitats has been relatively high and stable over the last 20 years but has declined in reservoir habitats over the last decade. It is plausible that differing prey resources between riverine and reservoir habitats explain growth variation in the Snake River subyearlings, and should be cause for concern if they also reflect reservoir food web changes brought about by shifting thermal regimes or invasion by nonnative prey (Naiman et al. 2012).

In this paper, we explore diet and growth differences of Chinook Salmon subyearlings rearing in riverine and reservoir habitats in the Snake River. Our objectives were to compare the (1) seasonal variation in prey availability and prey consumed by subyearlings rearing in riverine habitats and downstream reservoir habitats in the lower Snake River, (2) energy content of the diets consumed by subyearlings in the two rearing habitats, and (3) absolute growth of the subyearlings in the two rearing habitats.

METHODS

Study area.—We conducted our study during 2009–2011 in riverine and reservoir portions of the lower Snake River (an 8th order river) in southeastern Washington. Our riverine study area extended 38 river kilometers (rkm) from rkm 272 downstream to rkm 234 (the Snake River mouth = rkm 0). This stretch of riverine habitat supports rearing subyearlings produced by spawning within its boundaries, as well as subyearlings that disperse downstream from upstream riverine habitats. The river transitions from a free-flowing to a fully impounded state beginning at rkm 234; Lower Granite Reservoir extends from there downstream to Lower Granite Dam at rkm 173. Subyearlings that inhabit the reservoir shorelines are composed solely of fish that disperse downstream from upstream riverine spawning areas. Within the reservoir, we collected data between rkm 222 and rkm 187. In both riverine and reservoir habitats, fish rear as parr (about 45–85 mm) along shorelines from April through June before moving off shore to become pelagic smolts (>85 mm).

Prey availability sampling.—We collected drift samples to describe the relative abundance of prey available to subyearlings over time in riverine habitat and the reservoir from 12 April to 23 June 2010, and from 12 April to 28 June 2011. During each biweekly sampling, we tried to collect three samples at 4-h in-

tervals throughout a 24-h period (i.e., 0600, 1000, 1400, 1800, 2200, 0200, and 0600 hours) for a total of 21 samples. At each time interval, one sample was collected as close to shore as possible, one was collected off shore at the limit of wadeable depth (about 1.2 m), and the third sample was collected at a midpoint between the nearshore and offshore samples. The drift net was made of 153-μm mesh and was 2 m long; it tapered from a 58×40-cm rectangular opening (attached to a metal frame) to a 10-cm diameter cod end that was attached to a collection bucket. Inside the metal frame, we attached a General Oceanics flowmeter to later calculate the volume of water filtered. Each drift sample was collected by lowering the net frame into the water so that there was about a 5-cm gap between the water surface and the top of the net that captured floating insects. Where adequate flow existed, the net was held stationary in the flow for 2 min. Where there was insufficient flow (typically in the reservoir), the net was walked in an upstream direction for 2 min. After each sample was collected, the net was washed down from the outside into the collection bucket and then the sample was preserved in 90% ethanol.

Drift samples were first sorted to remove invertebrates. Of the three samples collected during each time interval, invertebrates were only identified from the midpoint sample. Invertebrates were identified to the lowest practical taxon, enumerated, and then dried at 60°C for 24 h to obtain a dry weight of each taxon. These weights were then summed to obtain a total dry weight for the sample. The invertebrates from each sample that was sorted, but not identified, were dried and weighed collectively to obtain a total dry sample weight. The biomass (dry mg/m^3) of each drift sample was calculated by dividing the sample dry weight by the volume of water filtered by each sample. For each sample period, a mean biomass was calculated from all 21 samples collected within a 24-h period.

Prey consumption sampling.—To evaluate the prey consumed, we used a beach seine to collect, anesthetize, and measure FL (1.0 mm) and weight (0.1 g) of subyearling parr in riverine and reservoir shoreline habitats. Sampling was done concurrent to drift sampling in 2010 and 2011 (as described by Connor et al. 2002). On each sampling occasion, we attempted to collect 15 fish at 4-h intervals throughout a 24-h period (i.e., 0600, 1000, 1400, 1800, 2200, and 0200 hours) to better characterize the diel feeding of subyearlings. We used nonlethal lavage to remove stomach contents (i.e., stomach and esophagus) with 96% efficiency (Tiffan et al. 2012). Our lavage instrument was a 30-mL syringe with a 100-μl pipette tip affixed to the end. Fish had their stomachs flushed into a 153-μm sieve with distilled water. Stomach contents were then preserved in 90% ethanol.

Stomach contents were sorted and individual taxa were identified to Family and then dried (24 h at 60°C) and weighed (±0.00001 g dry). In 2010, the stomach contents of all fish were identified, but in 2011 the contents of only 5 of the 15 fish per time interval were identified. Diet compositions for each sampling date were summarized by the proportion of each prey based on dry weight.

We examined selection of each prey taxon consumed by subyearlings in relation to its relative abundance in the drift using the linear food selection index (*L*; Strauss 1979). This index is simply the unweighted difference in proportions:

$$L = r_i - p_i, \qquad (1)$$

where r_i is the proportion of prey item i in the gut, and p_i is the proportion of the same prey item in the environment. The index ranges from -1 to $+1$, positive values indicating preference and negative values indicating avoidance or inaccessibility. For each sampling occasion, we calculated separate *L*s using prey weight.

Diet energy content analyses.—We determined the energetic importance of each major prey taxon to subyearling diets by first determining the energy density (J/g wet) of prey either empirically or from the literature (Table 1). Empirical energy density was determined for the mysid *Neomysis mercedis* and the amphipod *Corophium* spp. with a Parr 6300 bomb calorimeter. We multiplied the proportion of each prey taxon in the diet by its energy density and divided the product by the weighted mean energy density from all the prey taxa in the diet for each sampling trip. This yielded the proportional energetic contribution of each major prey taxon to the diet.

Measuring absolute growth.—We collected subyearlings for analyzing absolute growth by beach seining during 2009–2011 that was separate from the seining conducted to collect data on prey availability, prey consumed, and diet energy content. Each year we began collecting fish in riverine habitat beginning at the onset of fry emergence in late March. Five permanent stations were sampled in one day almost every week by set-

ting the seine 1–3 times, depending on beach length. Sampling ended when the natural subyearlings had dispersed offshore and downstream (typically by early July). In the reservoir, beach seining was conducted 2–3 d each week from late April through late July. Systematic sample sites were not established in the reservoir; however most sampling took place at four locations spread throughout the reservoir. Subyearlings were weighed and measured, implanted with passive integrated transponder (PIT) tags (Prentice et al. 1990) and released after a 15-min recovery period at their site of capture (as described by Tiffan and Connor 2011). Water temperature along the shoreline was measured at the time of release.

Recaptures of tagged fish during subsequent seining provided data for calculating absolute growth rates for both FL and weight. We calculated absolute growth rate in length (mm/d) for individual recaptured fish as $(\text{Length}_2 - \text{Length}_1)/(\text{Day}_2 - \text{Day}_1)$. We assumed linear growth in length (after Ostrovsky 1995) because the elapsed number of days between tagging and recapture was relatively short (maximum = 52 d) and the size range of subyearlings was relatively narrow (52–102 mm). To account for allometric growth in weight, we used a standardized mass-specific growth rate (*Gs*) equation (Sigourney et al. 2008), which was derived as follows:

$$Gs = \left(W_t^b - W_0^b\right)(bt)^{-1}, \qquad (2)$$

where W_0 is the mass at the start of the growth interval, W_t is the mass at the end of the growth interval, and b is the allometric growth rate exponent. We used a value of 0.2828 for b as estimated for juvenile Atlantic Salmon *Salmo salar* by Sigourney et al. (2008). Because some fish did not have either

TABLE 1. Energy densities of subyearling fall Chinook Salmon prey that were used in diet comparisons. Asterisks indicate a mean value was calculated from values provided in the sources listed.

Prey	Energy density (J/g wet)	Source
Amphipoda (*Corophium* spp.)	2,675	This study
Coleoptera (adults)	6,090*	Ciancio et al. (2007); McCarthy et al. (2009)
Diptera (Chironomid larvae, pupae)	3,248*	Beauchamp et al. (2004); Gray (2005); Pizzul et al. (2009); James et al. (2012)
Diptera (adults)	4,229*	Gray (2005); Koehler et al. (2006); McCarthy et al. (2009)
Ephemeroptera (nymphs)	3,665	James et al. (2012)
Homoptera (adults)	4,347[a]	Kolok and Rondorf (1987)
Neomysis mercedis	3,825	This study
Trichoptera (larvae, pupae)	4,312*	McCarthy et al. (2009); Pizzul et al. (2009)
Trichoptera (adults)	5,495*	Gray (2005); Koehler et al. (2006); McCarthy et al. (2009)
Zooplankton	2,252	Luecke and Brandt (1993)
Other	3,368–4,484[b]	

[a] Calculated from a caloric value of 5,200 Kcal (dry) and an assumed moisture content of 0.8.
[b] Average of the major taxa by year and rearing habitat (after Beauchamp et al. 2004).

a release or recapture weight, we used separate length–weight regressions to estimate the weights for these fish in riverine habitat (Weight $= 0.000004 \times FL^{3.2252}$, where $N = 717$ and $R^2 = 0.98$) and in the reservoir (Weight $= 0.000006 \times FL^{3.1355}$, where $N = 301$ and $R^2 = 0.96$).

For each year, we calculated seasonal means for subyearlings by rearing habitat for six variables including FL at initial capture, weight at initial capture, mean temperature between initial capture and recapture ($[°C_1 + °C_2] /2$), number of days fish were at large between initial capture and recapture, growth in FL, and growth in weight. We used two-sample t-tests ($\alpha = 0.05$) to compare the seasonal mean growth rates between rearing habitats within each year. We did not conduct analysis of variance (ANOVA) because we were primarily interested in differences between habitats within each year and not differences across years. In all analyses, we only used fish that were at large for more than 8 d between tagging and recapture to avoid any bias associated with short-term tagging effects on growth (Prentice et al. 1990).

RESULTS

Seasonal Variation in Prey Availability and Consumption

The biomass of prey in the drift varied seasonally and was typically lower in riverine habitat than in the reservoir (Table 2). However, the higher biomass of prey in the reservoir was largely due to the presence of *N. mercedis*, which generally accounted for over 90% of the biomass (Table 2). When this taxon was excluded, drift biomass was more often higher in the riverine habitat than in the reservoir (Table 2). It is noteworthy that *N. mercedis* and *Corophium* spp., being lentic species, were never collected in riverine drift samples, but only in the reservoir.

To evaluate prey consumed, we collected a total of 1,052 subyearlings (means ranged 48.0– 66.7 mm FL [SD, 2.7–11.2] and 0.9 to 3.7 g [SD, 0.2–2.1]) in the riverine habitat, and in the reservoir we collected 1,626 subyearlings (49.4–64.2 mm FL [SD, 3.5–7.5] and 1.1–2.8 g [SD, 0.4–1.1]).

Prey in the diet of subyearlings differed between the two habitats and varied seasonally (Figure 1). In 2010,

TABLE 2. Summary of drift invertebrate biomass in riverine and reservoir habitats of the Snake River in 2010 and 2011. N_{I+W} refers to the number of drift samples for which invertebrates were both identified and weighed, and N_W refers to the number of drift samples for which invertebrates were only weighed.

| Habitat	Date	N_{I+W}	N_W	Mean invertebrate biomass (dry mg/m³)	*N. mercedis* percentage of drift biomass (%)	Mean invertebrate biomass without *N. mercedis* (dry mg/m³)
				2010		
Riverine	12 Apr	5	9	23.7		23.7
Reservoir	13 Apr	7	9	476.8	<0.1	476.5
Riverine	20 Apr	9	14	31.2		31.2
Reservoir	27 Apr	8	13	10.9	97	0.3
Riverine	04 May	7	14	6.0		6.0
Reservoir	11 May	8	13	1.6	91	0.1
Riverine	18 May	7	14	1.9		1.9
Reservoir	25 May	7	14	4.6	91	0.4
Riverine	01 Jun	7	14	3.0		3.0
Reservoir	08 Jun	7	14	83.1	99	0.6
Riverine	15 Jun	7	14	2.0		2.0
Reservoir	23 Jun	7	14	93.4	98	1.4
				2011		
Riverine	12 Apr	4	8	1.3		1.3
Reservoir	12 Apr	7	14	31.8	99	0.3
Riverine	26 Apr	7	14	2.2		2.2
Reservoir	26 Apr	7	14	4.4	94	0.3
Riverine	10 May	7	14	2.8		2.8
Reservoir	10 May	7	14	6.2	92	0.5
Riverine	23 May	4	8	1.8		1.8
Reservoir	23 May	7	14	15.3	93	1.1
Riverine	14 Jun	7	14	2.5		2.5
Reservoir	14 Jun	7	14	12.8	98	0.3
Riverine	28 Jun	7	14	2.7		2.7
Reservoir	28 Jun	7	14	11.1	62	4.2
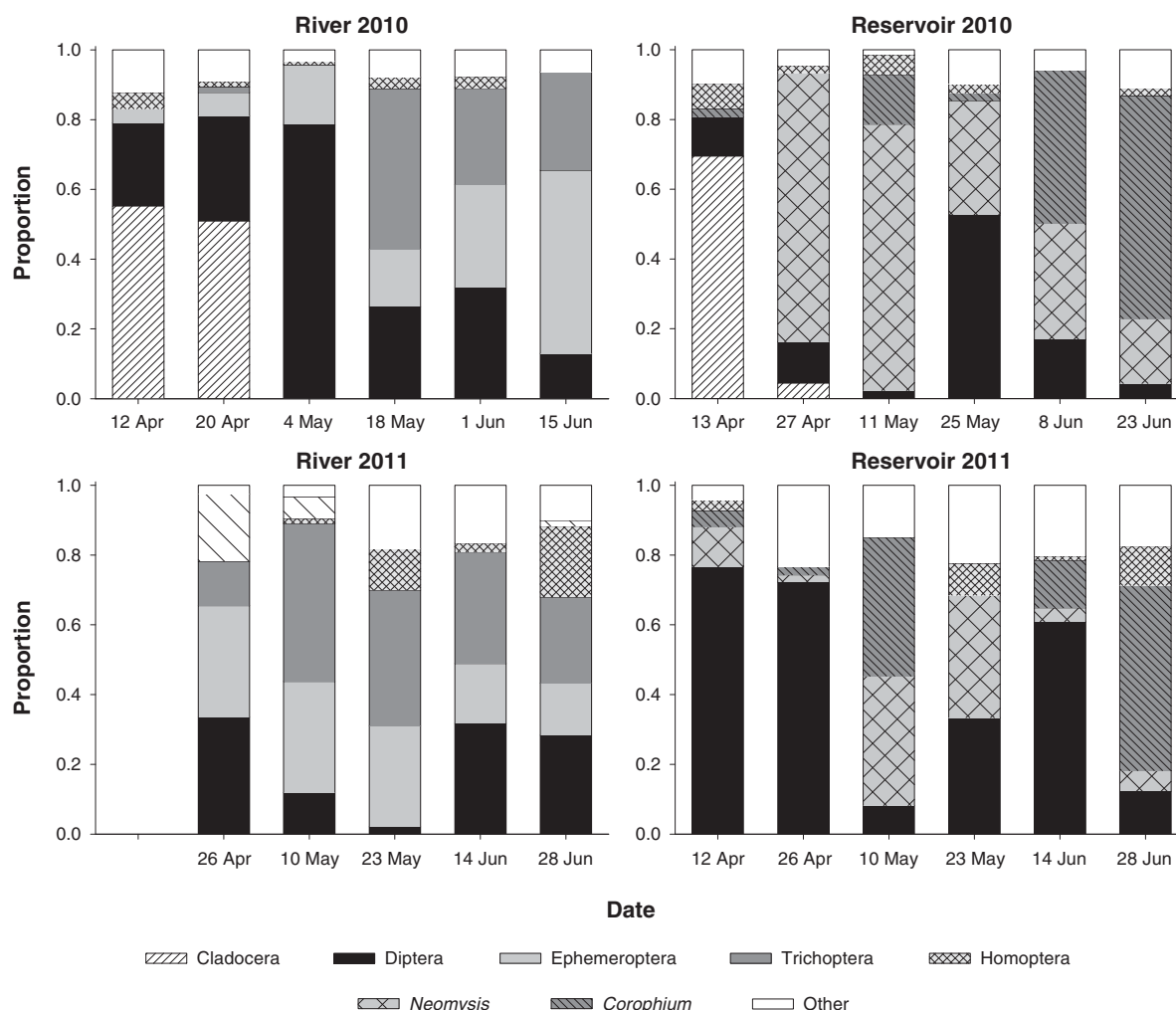
FIGURE 1.   Proportion by weight of different prey taxa in the diets of subyearling Chinook Salmon rearing in riverine and reservoir habitats in the Snake River in 2010 and 2011.

cladoceran zooplankton composed large proportions (0.51–0.55) of the diet in riverine habitat in April (Figure 1). Thereafter, dipterans (primarily chironomids) were consistently preyed upon throughout the rearing season (proportion range, 0.13–0.79), but their importance declined from early May through late June as the importance of ephemeropterans and trichopterans increased (combined proportion range, 0.04–0.8; Figure 1).

In the reservoir in 2010, cladoceran zooplankton were also important subyearling prey in early April (proportion = 0.7; Figure 1). *N. mercedis* was present in the diet throughout the rearing season and was the most important prey (proportion range, 0.33–0.77) in the diet from late April through mid May (Figure 1). Dipterans were also consumed throughout the season but only composed a significant portion (proportion = 0.53) of the diet in late May. During the remainder of the rearing season, *Corophium* spp. was the most important prey (proportion range, 0.44–0.64) in subyearling diets (Figure 1).

Patterns in subyearling consumption and prey importance were different in riverine habitat in 2011 than in 2010. In 2011, cladoceran zooplankton were not important in subyearling diets (Figure 1); however, no diet samples were examined in early April. Dipterans composed one-third of the diet in late April, declined to almost zero by late May, and then increased again to compose almost one-third of the diet in June. Ephemeropterans (proportion range, 0.15–0.32), and trichopterans (proportion range, 0.13–0.45) were seasonally important earlier in the rearing season and generally composed a larger portion of the diet than in 2010 (Figure 1). Homopterans (mainly leaf hoppers and aphids) were present during much of the season and were most important (proportion = 0.2) in late June.

In the reservoir in 2011, dipterans were generally more important in the diets of reservoir-rearing subyearlings than in 2010 and at times composed the majority of the diet (Figure 1). *N. mercedis* and *Corophium* spp. were consumed to a lesser extent in 2011 (Figure 1) but at times were important
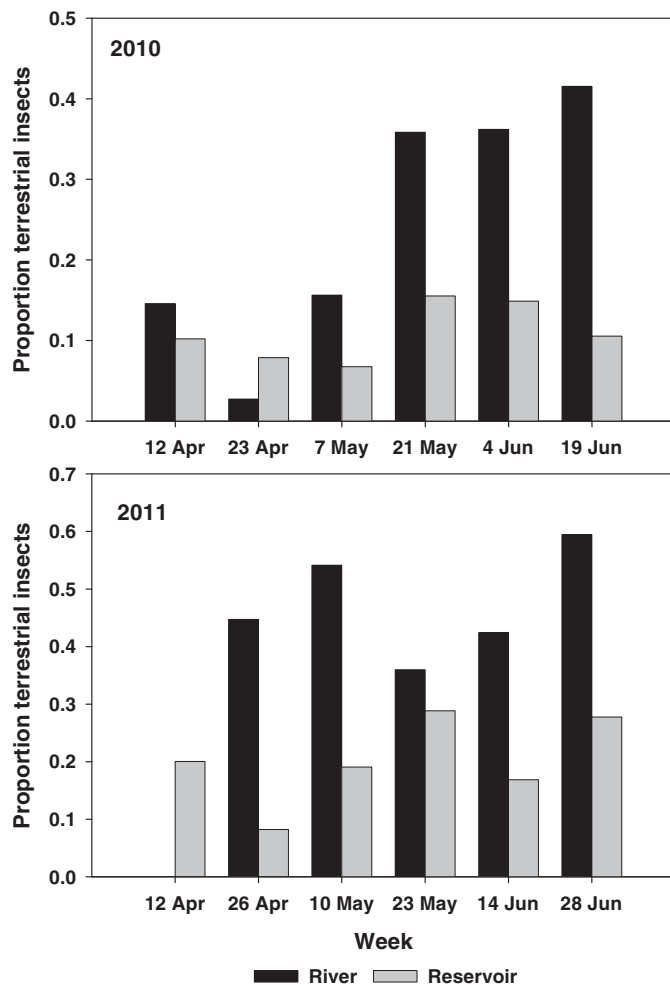
FIGURE 2.   Proportion (based on dry weight) of subyearling Chinook Salmon diets composed of terrestrial insects in riverine and reservoir habitats of the Snake River during 2010 and 2011.

contributors to the diet (*N. mercedis* proportion = 0.37; *Corophium* spp. proportion = 0.4).

In both 2010 and 2011, the proportions of terrestrial insects in subyearling diets were higher in riverine habitat than in the reservoir (Figure 2). The main terrestrial prey consumed by subyearlings in the riverine habitat were dipterans, homopterans, and trichopterans, whereas in the reservoir terrestrial prey was primarily represented by dipterans and homopterans. Terrestrial insects consumed in the riverine habitat were mainly of aquatic origin (88% in 2010 and 56% in 2011), whereas terrestrial insects consumed in reservoir habitats were primarily of terrestrial origin (73% in 2010 and 68% in 2011).

Although subyearlings consumed a wide variety of prey, they only showed selection for a relatively small subset of taxa (Table 3). Dipterans (primarily chironomids) were the most commonly selected prey in riverine and reservoir habitats in both years. In riverine habitat in 2010, subyearlings switched from selecting dipterans early in the rearing season to selecting trichopterans and ephemeropterans from mid May through June.

However, subyearlings showed selection for these taxa throughout the season in riverine habitats in 2011 (Table 3). These selections were also reflected in subyearling diets (Figure 1). In riverine habitats in 2011, subyearlings also showed selection for eggs (presumably from fish), homopterans, and coleopterans.

In the reservoir, *Corophium* spp. were at times strongly selected for by subyearlings in both years in addition to dipterans, homopterans, and trichopterans (Table 3). Because of their high abundance and the way the selection index is calculated, selection was always negative for *N. mercedis* despite being heavily preyed upon by subyearlings (Table 3; Figure 1).

Diet Energy Content

The importance of prey as reflected by their composition in the diet and the linear selection index did not necessarily reflect their energetic importance in subyearling diets. In the riverine habitat during 2010, subyearlings only obtained about 43% of their ingested energy from cladoceran zooplankton in April, in spite of their prevalence in the diet (Figures 1 and 3). Dipterans consistently contributed to the energy intake, peaking at 77% in early May 2010 (Figure 3). From mid May through mid June, 2010, riverine-rearing subyearlings obtained most of their energy from ephemeropterans and trichopterans, the latter comprising 25–32% terrestrial forms. In the reservoir in 2010, *N. mercedis* contributed 78–80% of dietary energy in late April through mid May and 22–36% of the dietary energy during the remainder of the rearing season. As *N. mercedis* declined in subyearling diets in June, they were replaced by *Corophium* spp., which contributed 39–60% of dietary energy in that month.

In 2011, subyearlings rearing in riverine habitat obtained most of their energy from aquatic and terrestrial insects, of which trichopterans consistently provided the largest portion (13–53%; Figure 3). Other energetically important taxa included dipterans, empheropterans, coleopterans, and homopterans. All of the coleopterans and homopterans in subyearling diets were adults of terrestrial origin. In the reservoir in 2011, dipterans (primarily chironomids) contributed more energy to subyearling diets than they did in 2010 (Figure 3). *N. mercedis* and *Corophium* spp. also contributed large portions of consumed energy, particularly in May (75%) and June (54%).

Weighted mean energy densities of subyearling diets were 11–38% higher in riverine habitats than in reservoir habitats during five of six bi-weekly sampling events in 2010 and were 17–40% higher in the river than in the reservoir during all sampling events in 2011 (Table 4).

Absolute Growth

We collected growth information from 541 recaptured PIT-tagged subyearlings during 2009–2011. Subyearlings in the riverine habitat and the reservoir were similar in FL and weight, experienced similar temperatures during shoreline rearing, and were at large between tagging and recapture for similar durations (Table 5). Despite the similarities in these factors that affect growth, mean growth in both FL and weight

TABLE 3. Prey most strongly selected by subyearling fall Chinook salmon rearing in riverine and reservoir habitats in the Snake River in 2010 and 2011. Only linear food selection index values (*L*) greater than 0.1 are listed in parentheses after each taxon. *L* was calculated based on prey weights. Taxa are abbreviated: Dip = Diptera, Eph = Ephemeroptera, Tri = Trichoptera, Hom = Homoptera, Neo = *Neomysis mercedis*, Cor = *Corophium* spp., Col = Coleoptera.

Date	Habitat	Taxon (*L*)
	2010	
12–14 Apr	Riverine	Dip (0.238)
13–15 Apr	Reservoir	Dip (0.112)
20–22 Apr	Riverine	Dip (0.300)
27–29 Apr	Reservoir	Dip (0.116), Neo (–0.183)
4–6 May	Riverine	Dip (0.686)
11–13 May	Reservoir	Cor (0.109), Neo (–0.127)
18–20 May	Riverine	Tri (0.400), Eph (0.121)
25–27 May	Reservoir	Dip (0.490), Neo (–0.535)
1–3 Jun	Riverine	Tri (0.165), Eph (0.165)
8–10 Jun	Reservoir	Cor (0.438), Dip (0.170), Neo (–0.546)
15–17 Jun	Riverine	Tri (0.179), Eph (0.172)
23–25 Jun	Reservoir	Cor (0.638), Neo(–0.788)
	2011	
12–14 Apr[a]	Reservoir	Dip (0.765), Neo (–0.868)
26–28 Apr	Riverine	Dip (0.133), Col (0.133), Tri (0.108)
26–28 Apr	Reservoir	Dip (0.721), Neo (–0.937)
10–12 May	Riverine	Tri (0.453), Dip (0.119)
10–12 May	Reservoir	Cor (0.394), Neo (–0.474)
23 May	Riverine	Tri (0.374), Eph (0.266), Eggs (0.153), Hom (0.108)
23–25 May	Reservoir	Dip (0.323), Neo (–0.549)
14–16 Jun	Riverine	Eph (0.237), Dip (0.120), Eggs (0.104)
14–16 Jun	Reservoir	Dip (0.607), Cor (0.134), Neo (–0.931)
28–30 Jun	Riverine	Eph (0.177), Dip (0.149), Tri (0.144)
28–30 Jun	Reservoir	Cor (0.439), Tri (0.113), Dip (0.110), Neo (–0.310)

[a]An insufficient number of subyearlings (*N* = 2) was collected from the river on 12 April 2011.

TABLE 4. Weighted mean energy density of diets of subyearling Chinook Salmon rearing in riverine and reservoir habitats in the Snake River, 2010–2011.

Date	Riverine diet energy density (J/g wet)	Reservoir diet energy density (J/g wet)	River versus reservoir difference (%)
		2010	
12–13 April	2,927	2,633	11
20–27 April	2,804	3,690	32
4–11 May	3,474	3,674	6
18–25 May	4,311	3,542	22
1–8 June	4,085	3,301	24
15–23 June	4,185	3,036	38
		2011	
12 April[a]		3,483	
26 April	4,455	3,405	31
10 May	4,652	3,331	40
23 May	4,423	3,773	17
14 June	4,302	3,373	28
28 June	4,269	3,208	33

[a]An insufficient number of subyearlings (*N* = 2) was collected from the river on 12 April 2011.

TABLE 5.   Summary (means ± SD) of information collected on PIT-tagged subyearlings recaptured during rearing in riverine and reservoir habitats in the Snake River during 2009–2011. Metrics shown are the seasonal mean FL at initial capture, weight at initial capture, temperature for the time fish were at large, number of days at large between initial capture and recapture, and absolute growth rates in FL and weight. Means are reported ± SD except for temperature which is reported ± SE. Growth in both FL and weight (WT) varied significantly between subyearlings rearing in riverine and reservoir habitats in 2009 ($P_{\text{FL and WT}} <$ 0.0001), 2010 ($P_{\text{FL}} = 0.03$; $P_{\text{wt}} < 0.0001$), and 2011($P_{\text{FL and WT}} < 0.0001$).

Year	Habitat	N	FL (mm)	Weight (g)	Temperature (°C) [a]	Days at large	Observed growth (mm/d)	Observed growth[b] (g/d)
2009	Riverine	70	56.1 ± 5.7	2.0 ± 0.7	12.6 ± 0.2	17.2 ± 5.8	0.78 ± 0.26	0.05 ± 0.017
2009	Reservoir	23	62.2 ± 3.8	2.5 ± 0.6	14.3 ± 0.2	14.3 ± 2.3	0.49 ± 0.18	0.03 ± 0.013
2010	Riverine	246	54.1 ± 4.8	1.7 ± 0.5	12.2 ± 0.1	17.7 ± 6.8	0.69 ± 0.20	0.05 ± 0.014
2010	Reservoir	96	56.5 ± 5.9	1.9 ± 0.8	12.2 ± 0.1	19.3 ± 6.7	0.64 ± 0.17	0.04 ± 0.011
2011	Riverine	65	56.7 ± 7.3	2.2 ± 1.0	12.9 ± 0.2	18.1 ± 5.8	0.91 ± 0.22	0.06 ± 0.012
2011	Reservoir	41	56.1 ± 5.8	2.0 ± 0.8	12.1 ± 0.2	17.0 ± 5.5	0.49 ± 0.16	0.03 ± 0.014

[a]Mean ± SE.
[b]The number of estimated weights used in growth calculation in riverine habitats was 5 in 2009, 36 in 2010, and 4 in 2011. The number of estimated weights used in growth calculations in the reservoir was 0 in 2009, 10 in 2010, and 11 in 2011.
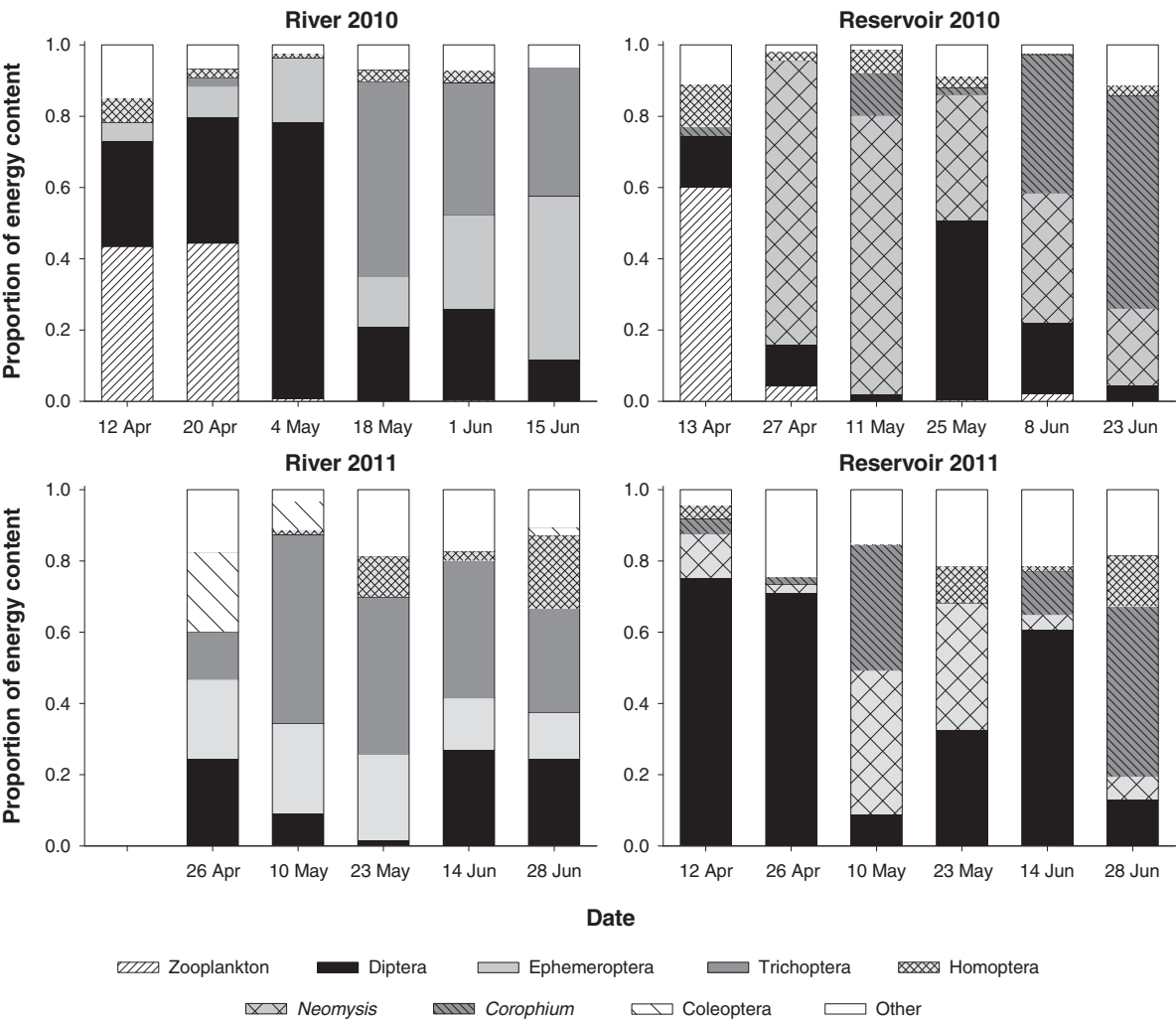

FIGURE 3.   Proportion of energy contribution (J/g wet) of different prey taxa to the diets of subyearling Chinook Salmon rearing in riverine and reservoir habitats in the Snake River in 2010 and 2011.

was significantly higher in riverine habitat than in the reservoir in all years (Table 5).

DISCUSSION

Our results show that differences in growth opportunity exist between riverine and reservoir rearing habitats and explain differences in subyearling diet and growth. Prey quality and availability, suitability of foraging and resting habitat, and temperature all interact to influence food consumption and conversion of that food to tissue (i.e., growth). Subyearlings rearing in the riverine habitat consumed more energy-rich prey and grew faster than in the reservoir in all years despite similarities in fish sizes, rearing temperatures, and time at large. Both subyearling selectivity for certain prey and food web differences between riverine and reservoir habitats help explain these results.

Subyearlings are opportunistic feeders and feed on a wide variety of prey (Rondorf et al. 1990; Merz 2001; Koehler et al. 2006) but also show preference for certain taxa, such as dipterans, regardless of rearing habitat (Dauble et al. 1980; Muir and Emmett 1988; Merz 2001). The differences in selection and composition of subyearling diets between riverine and reservoir rearing habitats was not unexpected given that invertebrate communities differ between lotic and lentic environments. Prey in the riverine habitat was predominated by lotic species of dipterans, ephemeropterans, and trichopterans, which is consistent with findings from the unimpounded Hanford Reach of the Columbia River where subyearlings prey heavily on these taxa (Becker 1973; Dauble et al. 1980; Rondorf et al. 1990). In contrast, *Corophium* spp. and *N. mercedis* were prominent in subyearling diets in the reservoir in addition to common taxa such as dipterans and other aquatic and terrestrial insects. *Corophium* spp. is an estuarine, tube-dwelling benthic amphipod that is used heavily by subyearlings and other Pacific salmon juveniles in the lower Columbia River and its estuary (Kirn et al. 1986; Kolok and Rondorf 1987; Muir and Emmett 1988). *Corophium* spp. expanded its range upstream into the Snake River (presumably via barges) soon after Lower Granite Dam was completed in 1975 (Dorband 1980), but was still not prominent in subyearling diets as late as the early 1990s (Curet 1993). In recent years, *Corophium* spp. has apparently become abundant enough in Lower Granite Reservoir to compose the majority of the subyearling diet, at times.

N. mercedis is another recent invader of Lower Granite Reservoir that has become established and is heavily preyed upon by subyearlings. Interestingly, Koehler et al. (2006) did not document much subyearling consumption of *N. mercedis* in Lake Washington where they are abundant (Murtaugh 1983). *N. mercedis* is a lentic, estuarine mysid that has expanded its distribution upstream (probably via barges) from the Columbia River estuary into Columbia and Snake River reservoirs (Haskell and Stanford 2006; Tiffan et al. 2012). *N. mercedis* was not reported in the diets of subyearlings rearing in Lower Granite Reservoir as of 1992 (Curet 1993), nor in many of the benthic surveys

of the reservoir conducted by personnel from the University of Idaho in the 1990s (e.g., Bennett et al. 1995). However, today *N. mercedis* is very abundant in reservoir rearing habitats as evidenced by their constituting the majority of drift biomass and prominence in subyearling diets. Spring and early summer aerial densities of *N. mercedis* in subyearling rearing areas estimated from beam trawling averaged 142 mysids/m^2 in 2011 and 2012 and maximum densities exceeded 400 mysids/m^2 (U.S. Geological Survey, unpublished data). At this time, little is known about the ecology of this relatively large prey (about 13 mm TL) in Lower Granite Reservoir and what long-term effects the population might have on the reservoir food web that subyearlings and other juvenile salmonids rely on. However, they are known planktivores (Murtaugh 1981, 1983; Haskell and Stanford 2006) and may reduce the availability of zooplankton for subyearlings in early spring.

The differences in subyearling diets between riverine and reservoir rearing habitats are important because of the energy they provide for growth. High-energy density diets allow for higher conversion efficiency and growth (Stewart and Ibarra 1991; Koehler et al. 2006), which explains the greater subyearling growth rates we observed in the river. Subyearling diets in the river were higher in energy and changed seasonally reflecting the availability and selection of different prey through time. The higher energy density of riverine diets was largely due to the consumption of prey, such as trichopterans, and the greater proportion of terrestrial forms, which are lower in water content and, thus, higher in energy (Ciancio et al. 2007; McCarthy et al. 2009; James et al. 2012). In contrast, subyearling diets in the reservoir were often composed of large portions of *N. mercedis* and *Corophium* spp., which have a lower energy density than many insects, particularly adult forms. The empirical energy densities we derived for *N. mercedis* (3,825 J/g) and *Corophium* spp. (2,675 J/g) were slightly higher than, but close to, the values derived by others for mysids, 3,553 J/g (Rudstam 1989), 3,550 J/g (Gray 2005), 3,475J/g (James et al. 2012), and for related amphipods, 2,547 J/g (Ciancio et al. 2007) and 2,464 J/g (James et al. 2012). The relatively low energy density of *Corophium* spp. contributed to the low energy density of subyearling diets in the reservoir, particularly when they composed a greater portion of the diets. In contrast, *N. mercedis* was energetically intermediate in the range of prey consumed by subyearlings. This contributed to the higher energy density diets observed in the reservoir in late April and early May in 2010 when they composed the majority of the diet.

It is somewhat paradoxical that the apparent higher biomass of prey in the reservoir, which was largely due to the presence of *N. mercedis*, was insufficient to produce higher subyearling growth rates. Although subyearlings in the reservoir often fed heavily on *N. mercedis*, they also fed on other taxa, suggesting that they may pass over more abundant prey to forage on more preferred taxa. This is the reason selection was always negative for *N. mercedis*. In addition, *N. mercedis* may not have

been as functionally available as other prey because adults can be over 13 mm TL (Haskell and Stanford 2006), which may be too large for small subyearling parr to ingest until they grow larger. Also, *N. mercedis*, being a benthic invertebrate, may have been less noticeable to subyearlings that are more surface-oriented in their feeding (Tiffan et al. 2010). Finally, competition with other native resident fishes and juvenile salmonids, which are abundant in the reservoir (Tiffan and Connor 2012) may have limited the amount of prey available to subyearlings.

We recognize that our results and interpretations are subject to the assumptions we made and the limitations of our sampling. As with many dietary studies, diet and drift composition reflect sampling frequency (2-week intervals in our study), which may not adequately represent prey consumption and drift at a finer temporal scale. We assumed that subyearling diet composition was representative of the intervening time between sampling occasions. We also assumed that the literature values of invertebrate moisture contents needed to convert from dry prey weight to wet energy density were representative of our prey. Consequently, we only considered studies that provided moisture content information. We also recognize that differences in subyearling foraging costs between riverine and reservoir habitats may influence net energy gained from prey that would result in differential growth. It could be argued that fish rearing in the river expend less energy foraging by taking advantage of higher prey delivery rates and using optimal foraging strategies (e.g., Fausch 1984; Hill and Grossman 1993). In contrast, fish rearing in the reservoir may expend more energy and experience reduced growth if they have to actively swim and search low-velocity waters for prey, as was shown for Yellow Perch *Perca flavescens* by Rennie et al. (2005). Although constant swimming can be 4.7 times less costly than complex swimming maneuvers, such as those associated with drift feeding (Boisclair and Tang 1993; Hughes and Kelly 1996), subyearlings would still need to use complex swimming to capture prey in the reservoir, which would add to their foraging costs.

The differential growth that we observed in subyearlings rearing in riverine and reservoir habitats is important because it may be expressed in differential migration timing and survival. Connor and Tiffan (2012) found that parr growth was the most influential factor for predicting subyearling survival in the Snake River. Fish that can grow quickly to a large size can migrate earlier under higher flows and cooler temperatures and consequently have higher migration rates and survival (Connor et al. 2003a, 2003b; Smith et al. 2003). The growth opportunity of rearing habitats that ultimately affects subyearling migration and survival is influenced in part by prey resources that are a product of the underlying food web. Reservoirs can facilitate invasion by nonnative species with unknown consequences to the food web (Havel et al. 2005; Johnson et al. 2008). The prominence of nonnative prey like *Corophium* spp. and *N. mercedis* in the reservoir food web seems to be a recent phenomenon, and such changes raise questions regarding the food web's capacity to support juvenile salmon and ongoing recovery efforts (Naiman et al. 2012). Future research is needed to more fully explore the long-term effects of reservoir food web changes on subyearling consumption and growth, and competition for food with native species and conspecifics whose abundance may increase through natural or anthropogenic means.

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