

ARTICLE

Trophic Interactions and Consumption Rates of Subyearling Chinook Salmon and Nonnative Juvenile American Shad in Columbia River Reservoirs

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Abstract

We used a large lampara seine coupled with nonlethal gastric lavage to examine the diets and estimate consumption rates of subyearling Chinook Salmon *Oncorhynchus tshawytscha* during July and August 2013. During August we also examined the diet and consumption rates of juvenile American Shad *Alosa sapidissima*, a potential competitor of subyearling Chinook Salmon. Subyearling Chinook Salmon consumed *Daphnia* in July but switched to feeding on smaller juvenile American Shad in August. We captured no juvenile American Shad in July, but in August juvenile American Shad consumed cyclopoid and calanoid copepods. Stomach evacuation rates for subyearling Chinook Salmon were high during both sample periods (0.58 h^{-1} in July, 0.51 h^{-1} in August), and daily ration estimates were slightly higher than values reported in the literature for other subyearlings. By switching from planktivory to piscivory, subyearling Chinook Salmon gained greater growth opportunity. While past studies have shown that juvenile American Shad reduce zooplankton availability for Chinook Salmon subyearlings, our work indicates that they also become important prey after *Daphnia* abundance declines. The diet and consumption data here can be used in future bioenergetics modeling to estimate the growth of subyearling Chinook Salmon in lower Columbia River reservoirs.

We studied the diet and consumption of subyearling Chinook Salmon *Oncorhynchus tshawytscha* and juvenile American Shad *Alosa sapidissima* in a large, warm, Columbia River reservoir during periods of anticipated species overlap. Subyearling Chinook Salmon (hereafter subyearlings) are more reliant on main-stem habitats than are other juvenile salmon (Coutant and Whitney 2006), migrating later in the season with peak emigration in

June and July (DART 2016). Subyearlings are the progeny of “upriver bright” Chinook Salmon that historically spawned throughout the upper main-stem Columbia and Snake rivers, but today spawn in two areas: above the confluence with the Snake River to Priest Rapids Dam on the Columbia River and from Lower Granite Dam to Hells Canyon Dam on the Snake River (Norris et al. 2000; Figure 1).

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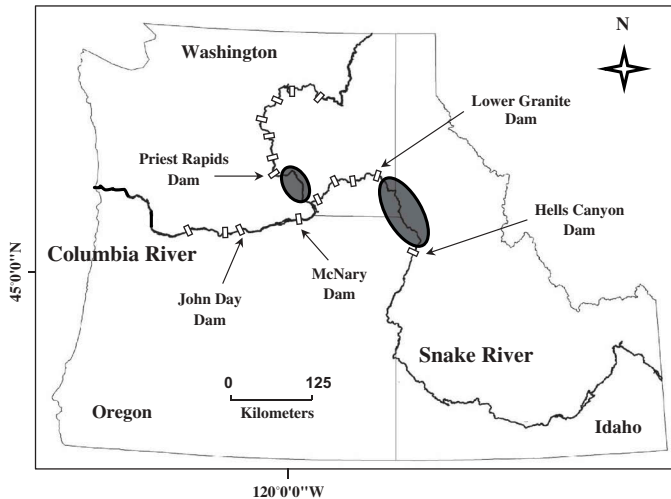


FIGURE 1. The Columbia River basin depicting natural reproduction areas (shaded ovals) for upriver bright Chinook Salmon and sampling area (shaded rectangle) in John Day Reservoir just upstream from John Day Dam.

The presence of subyearlings overlaps with juvenile American Shad in the lower Columbia River during July and August (DART 2016). American Shad are nonindigenous to the Columbia River basin (Smith 1895), and an abundance of juveniles (age 0) has the potential to reduce growth of subyearlings through competition for food (Independent Scientific Advisory Board 2011). Roughly 500,000 American Shad spawn in John Day Reservoir annually (Hinrichsen et al. 2013), and they are highly fecund (400,000 eggs per female). Juvenile American Shad are abundant and reduce *Daphnia* biomass and production in the lower Columbia River (Haskell et al. 2013). *Daphnia* are also important prey for subyearlings (Craddock et al. 1976; Rondorf et al. 1990) in the lower Columbia River, but it is unknown whether their diet overlaps with shad, and if so, whether diet overlap results in reduced fitness (i.e., reduced growth) of subyearlings.

Currently, consumption estimates for subyearlings are not available due in part to the logistical challenges of sampling pelagic fishes in large rivers such as the Columbia River. Previously, fish for diet analysis were collected from bypass structures and holding tanks at dams where food could have been digested or regurgitated before stomach sampling. This practice introduced uncertainty regarding diel gut fullness and feeding chronology (e.g., Muir and Emmett 1988). Moreover, some of the Chinook Salmon populations that produce subyearlings are listed under the U.S. Endangered Species Act (ESA) (e.g., Snake River fall Chinook Salmon: NMFS 1992), and traditional, lethal sampling to obtain diet information is restricted. Empirical estimates of consumption rates derived from diel sampling could be used as inputs in future bioenergetics modeling to estimate the

growth of subyearlings and evaluate potential reductions in fitness resulting from competition with juvenile American Shad.

Given the potential for competition and its implications for reductions in fitness, we studied subyearling Chinook Salmon and juvenile American Shad diets and consumption rates in John Day Reservoir when their emigrations overlapped temporally. The specific objectives of this research were to compare the diet of subyearlings and juvenile American Shad and empirically estimate the consumption and evacuation rates of the two species.

METHODS

Study Area

John Day Dam impounds John Day Reservoir (Figure 1). The reservoir is 122 km long, has a mean depth of 14 m, and does not thermally stratify. Like other main-stem Columbia River reservoirs, John Day Reservoir is operated as a “run-of-the-river” reservoir and has little storage capacity. It has a mean water retention time of 9.0 d (2008–2015 range: 7.1–10.3 d), the longest of the lower Columbia River reservoirs. We collected fish for diet and empirical consumption estimation between river kilometers (rkm) 350.2 and 353.7. We chose this area because of its proximity to John Day Dam (rkm 348), which offered shelter from strong westerly winds and rough water that are prevalent in summer and preclude sampling by boat in much of the reservoir.

Lampara Seining

A rapidly repeatable, active, live-capture method was essential for sampling diel patterns in gut fullness for ESA-listed species. We used a 305-m-long lampara seine and a 7.3-m boat to collect fish from pelagic habitats in John Day Reservoir. The lampara seine is a surface encircling net consisting of two 91.4-m wings and a 22.9-m bunt section. The mesh gradually reduces from 127 mm (stretch mesh) at the end of the wings to 6.3 mm (delta mesh) at the bunt. The lead line is shorter than the float line and becomes the floor of the net as the wings are retrieved. The lead line weighs 189 g/m, is 30.5 m deep at the bunt, and tapers to the float line at the end of each wing section. The net effectively fishes to a maximum depth of about 21 m at the bunt, based on readings from depth loggers deployed on the lead line. The net was deployed in a large circle by paying out one of the wings, followed by the bunt section, then the other wing. When the net was fully deployed, the circle was closed and both wings were retrieved simultaneously onto two hydraulically operated drums, reducing the net area, and concentrating the fish in the bunt section. Sampling transects were established perpendicular to the current at 0.16-km intervals within the sample area and were randomly selected with replacement from all possible transects. The lampara seine was then deployed on a selected transect within the thalweg. The seine was redeployed

on the same transect until the desired number of fish were collected.

We sampled fish during July 21–24 and August 11–14, 2013, to coincide with the expected migration overlap of subyearling Chinook Salmon and juvenile American Shad. During each sample period we attempted to collect the stomach contents from at least 15 of each species every 4 h within a 24-h period. Sampling of the first 4-h period was repeated to calculate a “closure” correction factor when gut fullness values from the first and last samplings were not equal (Elliott and Persson 1978; Eggers 1979; Boisclair and Leggett 1988; Boisclair and Marchand 1993) so that seven collections were completed over a 24-h cycle. Due to logistical constraints and rough weather, we did not complete all the time blocks sequentially, but occasionally completed them on another day within the 3-d sample period. We handled and counted a general subsample of juvenile American Shad to decrease the holding time and handling stress experienced by subyearlings when both species were captured in the seine.

Upon capture, subyearlings and American Shad were identified (Page and Burr 1991), anesthetized with buffered MS-222 (tricaine methanesulfonate), measured to the nearest millimeter FL, and weighed to the nearest 0.1 g, and their stomach contents collected via nonlethal lavage. The lavage instrument was a 30-mL syringe affixed with a 100- μ L pipette tip inserted into the esophagus to the head of the stomach. Using distilled water, the contents of each stomach were backflushed into a 63- μ m-mesh sieve and washed into a Whirl-Pak plastic bag, immediately frozen on dry ice, and then stored at -80°C until analysis. To measure the effectiveness of our stomach lavage method, we froze five lavaged subyearlings from each time block for subsequent dissection in the laboratory.

Laboratory Analysis

In the laboratory, stomach contents collected from Chinook Salmon subyearlings and juvenile American Shad via lavage were completely thawed and each prey item was identified to the lowest practical taxon (order or lower) following Pennak (1989) and Edmondson (1959). After identification and enumeration, stomach contents were placed in a 63- μ m-mesh sieve, and the blotted wet weight was measured. The contents were then dried for 24 h at 60°C and weighed. Subyearlings that were sacrificed in the field after lavage were partially thawed to dissect and examine the stomachs for any remaining food, which, if any, was removed and processed as described above. We determined both the blotted wet and dry weights of stomach contents when possible to facilitate comparison of our results to those from other studies.

Data Analysis

Lavage efficiency.—Lavage efficiency (E) for each subyearling Chinook Salmon was calculated as the dry weight (g) of pumped stomach contents (P) divided by the

sum of the weight of P and the leftover (L) dry weight after dissection, multiplied by 100.

$$E = \left(\frac{P}{P + L} \right) \times 100. \quad (1)$$

To minimize error associated with blotting and weighing (wet) small numbers of zooplankton, we determined their dry weight in calculating lavage efficiency. When the total number of zooplankton in a sample was fewer than 15, we estimated the dry weight using species- and sex-specific equations developed by Culver et al. (1985) for estimating weight from length. We used a mean standard length of 0.9 mm for *Daphnia* and assumed that all *Daphnia* in our study area were nonovigerous *D. retrocurva* (Haskell et al. 2006). We expressed the overall lavage efficiency (OE) of all fish as:

$$OE = \frac{\sum P_i}{\sum (P + L)_i} \times 100. \quad (2)$$

Daily Ration.—We used the weights of stomach contents and fish to obtain the relative gut fullness (F_t) of each subyearling and juvenile American Shad as follows:

$$F_t = G_t / W_t \times 100, \quad (3)$$

where G_t = the blotted dry wet weight of stomach contents and W_t = the wet weight of fish following Boisclair and Leggett (1988) and Principe et al. (2007). Evacuation rate, R , was calculated from the greatest decrease in median gut fullness between successive 4-h time blocks from a 24-h consumption field trial:

$$R = \frac{(\ln \hat{F}_{t+1} - \ln \hat{F}_t)}{T}, \quad (4)$$

where T is equal to the time in hours between sampling successive time blocks t and $t + 1$, which varied in field collections from 2.85 to 5.20 h. We combined our evacuation rates with others from the literature (Sagar and Glova 1988; Principe et al. 2007; Benkwitt et al. 2009) to develop a linear regression model to predict evacuation rate over a broad range of temperatures for subyearlings.

Following the model of Eggers (1979), we calculated daily ration, D , as:

$$D = \bar{F}_t \times R \times 24 + (S_{24} - S_0), \quad (5)$$

where $\bar{F}_t$ = the mean of F_t values of all fish collected in a 24-h trial, and S_{24} and S_0 in $(S_{24} - S_0)$, the closure correction, are the final and initial median gut fullness values, respectively, collected in a 24-h trial. We used empty stomachs to calculate individual (F_t) and mean gut fullness ($\bar{F}_t$) values, but not in the calculation of evacuation rates (R). Diel trends in

subyearling Chinook Salmon and juvenile American Shad gut fullness were examined using mean gut fullness values and 95% confidence intervals; however, in August medians and ranges were used for subyearlings because sample sizes were small (<10). We compared the feeding rate of subyearlings in our study to others using a standard allometric relationship for C_{max} (Hanson et al. 1997), where:

$$C_{max} = 0.303 * W^{-0.275} \quad (6)$$

to account for the effects of body size on consumption at optimal water temperatures (Stewart and Ibarra 1991).

RESULTS

During the first sampling period (July 21–24), we conducted 18 lampara seine hauls and collected 311 subyearling Chinook Salmon and 162 adult American Shad, but no juvenile American Shad. The median catch of subyearlings was three per seine haul (range: 0–90), and we collected no fish in 33% of the sets. During the second sampling period (August 11–14), we collected 31 subyearlings and many juvenile American Shad in 28 seine hauls but did not count them all to reduce holding time and handling stress on subyearlings.

The overall lavage efficiency was 73% and the mean efficiency was 81%. Of the 47 subyearlings euthanized to evaluate stomach lavage efficiency, seven contained no contents when stomachs were initially pumped nor when dissected and were removed from efficiency analysis. Of the 40 remaining fish containing measurable contents (either the pumped or leftover), 32 were from the July sampling period and eight were from August. Individual efficiencies were greater than 90% for 27 fish, but ranged from 83.6% to 0.01% for the remaining 13 fish. The mean lavage efficiency of subyearlings ($n = 32$) pumped in July was 80.0% (dry weight) and 83.9% in August ($n = 8$). In July, lower efficiencies resulted from retention of dipteran parts and small numbers of *Daphnia* after lavage. During August, two fish had less than 100% efficiency: one retained a single dipteran, and the other retained one juvenile American Shad and one dipteran.

Diet and Length

In July, subyearlings averaged 118 mm FL (range: 95–142 mm) and 20.1 g (range: 10.1–34.1 g), and diets were composed of 97.7% *Daphnia* spp. with small percentages of other zooplankton taxa (Table 1). In August, subyearlings averaged 125 mm FL (range: 103–155 mm) and 20.0 g (range: 10.3–37.9 g), and their diets consisted of 71.4% juvenile American Shad (Table 1). The mean length of juvenile American Shad in the stomachs of subyearlings was 24.4 mm FL (range: 11–40 mm) and were significantly smaller than those collected concurrently in the lampara seine; those samples averaged 64.0 mm FL (range: 48–90 mm) and 2.7 g (range: 1.0–7.0 g). The percentage of empty stomachs for

TABLE 1. Proportion of prey taxa by number collected from subyearling Chinook Salmon during July 21–24, 2013, and those collected from both subyearling Chinook Salmon and juvenile American Shad during August 11–14, 2013.

Prey taxa	July 21–24	August 11–14	
	Subyearling Chinook Salmon	Subyearling Chinook Salmon	Juvenile American Shad
Calanoid copepods	0.02	2.04	20.06
<i>Americorophium</i> spp.	0.12	4.08	0.09
Cyclopoid copepods	0.22	2.04	73.77
<i>Daphnia</i> spp.	97.69	2.04	0.95
Dipteran larvae and pupae	0.44	6.12	0.23
Juvenile American Shad	< 0.01	71.43	0.00
<i>Neomysis mercedis</i>	0.02	8.16	0.03
Other prey items	1.22	0.00	0.40

subyearlings in our study changed from 3.3% (3 of 91) in July to 19.4% (6 of 31) in August. During August, all six of the empty stomachs occurred during daylight, and three of these occurred during the sample period at 1500 hours. In August juvenile American Shad were predominately planktivorous, feeding on cyclopoid and calanoid copepods, and less than 1% of their diet consisted of *Neomysis mercedis*, *Americorophium* spp., and dipterans (Table 1).

Gut Fullness, Evacuation Rate, and Daily Ration

Diel trends in gut fullness for subyearlings varied between July when they were planktivorous and August when they were predominately piscivorous (Figure 2). During July, mean gut fullness ranged from 0.21% to 1.57% of body weight (BW; wet) as feeding increased throughout the day. Gut fullness peaked in the evening (1740 hours) and minimum gut fullness was observed near midnight (Figure 2). During August subyearlings exhibited low gut fullness after midnight and throughout the day and a crepuscular peak of 1.14% of BW at dusk (2031 hours; Figure 2). Diel trends in gut fullness indicated that juvenile American Shad fed during both day and night. Mean gut fullness ranged from a minimum of 0.98% BW at noon to 2.43% BW at midnight but was variable throughout the diel cycle. Gut fullness values peaked at midnight indicating the greatest period of feeding was from 2000

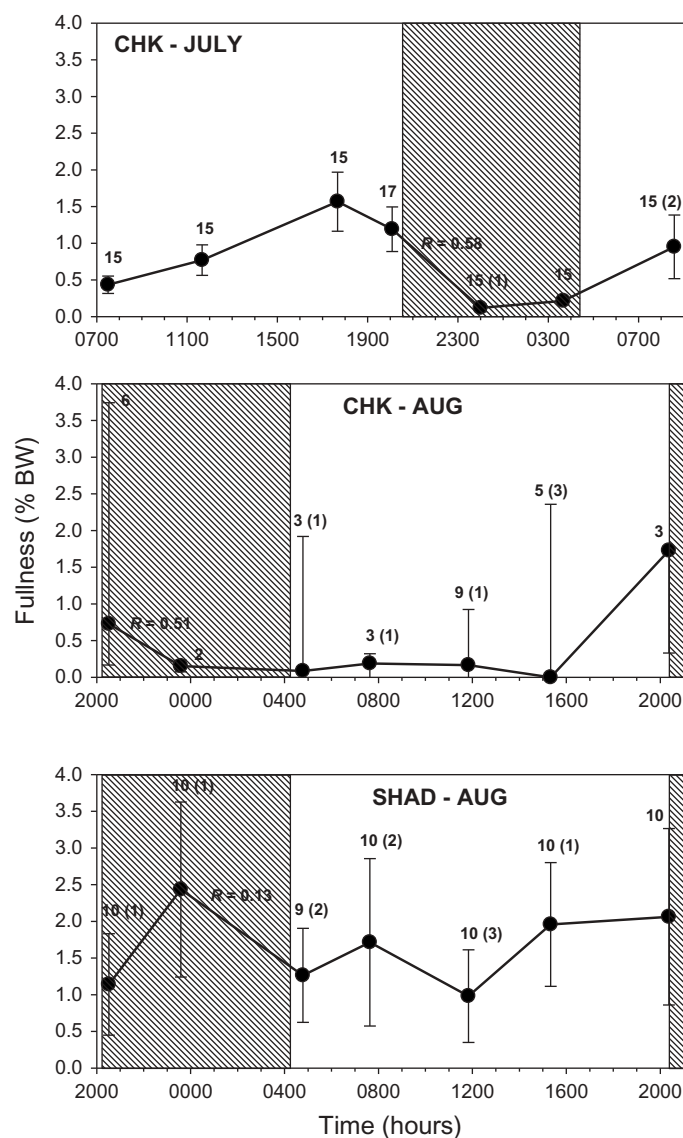


FIGURE 2. Change in gut fullness over a 24-h cycle in empirical consumptions trials conducted in John Day Reservoir during July and August 2013. Solid circles represent mean values and error bars represent 95% confidence intervals in the top panel (CHK; subyearling Chinook Salmon) and bottom panel (SHAD; juvenile American Shad). In the middle panel, solid circles represent medians and error bars are ranges. Sample sizes are shown above the points, and numbers in parentheses are the number of fish with empty stomachs. Shading indicates periods of darkness and the evacuation rates (R) are shown within the time interval for which they were calculated.

hours to midnight followed by a period of digestion and nonfeeding that occurred from midnight to dawn.

Evacuation rates for subyearlings ranged from 0.58 h^{-1} at 20.78°C in July to 0.51 h^{-1} at 22.02°C in August (Table 2). The regression developed from these and other evacuation rates for subyearlings (Figure 3) took the form:

$$R = 0.006595 \times e^{0.2131 \times T}, \quad (7)$$

where $R^2 = 0.89$, $N = 9$, $P < 0.001$, and the residual SE = 0.3415. For subyearlings, daily ration was 11.0% of BW in July and 8.5% of BW in August. For juvenile American Shad, daily ration was 5.6% of BW in August.

DISCUSSION

Subyearling Chinook Salmon shifted from feeding on *Daphnia* at a high consumption rate in July to feeding on juvenile American Shad at a moderately high rate in August. We found minimal diet overlap between subyearlings and juvenile American Shad in August, but overlap in July was unknown due to a lack of juvenile American Shad samples. In August, the lampara seine captured larger juvenile American Shad ($>47 \text{ mm FL}$), but the mesh size limited our catch of smaller juvenile American Shad that subyearlings were consuming. Juvenile American Shad predominately fed on copepods, and we found no evidence that they were consuming *Daphnia* as has been previously reported in John Day Reservoir. The shift from planktivory to piscivory by subyearling Chinook Salmon was consistent with changes in the diel foraging pattern but also with observed ontogenetic shifts in foraging in other systems (Breck 1993; Arrington et al. 2002; Vinson and Angradi 2011). Although the cost of foraging on juvenile American Shad might be modestly higher than on *Daphnia*, switching to prey having a higher energy density is beneficial.

Our evacuation rates were relatively similar for subyearlings collected in July and August but were higher than those reported for other fish (He and Wurtsbaugh 1993). However, our evacuation rate estimates for subyearlings were not unexpected given the high temperatures under which we carried out our sampling. The subyearlings we sampled were migrating under thermal regimes near or beyond their critical thermal maximum of 20.9°C (Plumb and Moffitt 2015).

In our study, Chinook Salmon subyearlings fed at a relatively high rate on large, high-energy, fish prey to grow while compensating for the higher metabolic demands of warmer water temperature in August. Compared with a standard allometric relationship for $C_{\max}$, we found that subyearlings were feeding at 83% of $C_{\max}$ during July and 64% of $C_{\max}$ during August. Other studies estimating subyearling daily ration generally reported lower $C_{\max}$ values (Table 3). With subyearlings ranging from 5.9 to 16.1 g, Benkwitt et al. (2009) estimated daily rations ranging from 2.0% to 4.3% BW with fish feeding from 17% to 37% of $C_{\max}$. Sagar and Glova (1988) reported a daily ration of 8.3% BW for 4-g fish feeding at 40% of $C_{\max}$. The larger daily rations (33% BW) reported by Principe et al. (2007) for 2.4-g subyearlings led them to conclude that these fish were feeding beyond maximum consumption, a phenomenon that does not often occur in the wild (Armstrong and Schindler 2011).

TABLE 2. Sampling date, number of fish sampled, number of empty stomachs, mean water temperature, mean fish weight, mean gut fullness ($\bar{F}_t$), evacuation rate per hour (R), Eggers correction closure ($S_{24} - S_0$), and daily ration (D) of subyearling Chinook Salmon during July 21–24, 2013, and those collected from subyearling Chinook Salmon and juvenile American Shad during August 11–14, 2013.

Date	Number sampled	Number of empty stomachs	Water temperature (°C)	Mean weight (g)	$\bar{F}_t$ (g/g, wet weight)	R (h ⁻¹)	$S_{24} - S_0$	D (% BW)
Subyearling Chinook Salmon								
Jul 21	107	3	20.78	20.1	0.0076	0.58	0.0037	11.0
Aug 11	30	6	22.02	20.0	0.0062	0.51	0.0100	8.5
Juvenile American Shad								
Aug 11	69	10	22.02	2.7	0.0166	0.13	0.0054	5.6

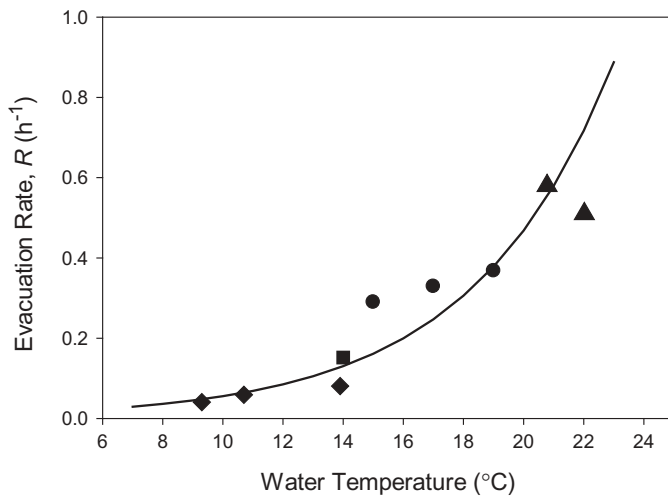


FIGURE 3. Regression derived from water temperatures and evacuation rates of subyearling Chinook Salmon from Benkwitt et al. (2009; diamonds), Sagar and Glova (1988; square), Principe et al. (2007; circles), and this study (triangles).

Our lavage efficiency of 73% was less than that reported by Meehan and Miller (1978) for juvenile Coho Salmon *O. kisutch* (96.4%) and Cutthroat Trout *O. clarkii* (84.0%) but not for Rainbow Trout *O. mykiss* (56.2%). They attributed decreases in efficiency to larger fish (Cutthroat Trout and Rainbow Trout > 150 mm), which in turn consumed larger prey, including crayfish *Astacus* sp., sculpins *Cottus* sp., and stoneflies *Acroneturia* sp., that were more difficult to remove by lavage. The size range of subyearlings on which we carried out gastric lavage was small (91–133 mm FL), but despite notable differences in prey sizes between sampling periods, there was only a small difference in lavage efficiency.

Two aspects of our sampling methodologies could have affected our evacuation rate and daily ration estimates. First, the use of stomach contents instead of complete digestive tracts in our sampling could have decreased gut fullness and subsequent daily ration estimates for both fishes (Boisclair and Marchand 1993). Future studies estimating evacuation rates from empirical gut fullness values should incorporate the use

TABLE 3. Previous studies of evacuation rate and daily ration for subyearling Chinook Salmon with the estimated theoretical $C_{\max}$ and % $C_{\max}$ values provided for comparison.

Study	Water temperature (°C)	Wet weight (g)	Daily ration, D (% BW)	Evacuation rate, R (h ⁻¹)	Theoretical $C_{\max}$ (% BW)	$C_{\max}$ (%)
Sagar and Glova (1988)	14	4	8.3	0.15	20.7	40.1
Principe et al. (2007)	15	2.4	33.3	0.29	23.8	139.7
Principe et al. (2007)	17	2.4	27.5	0.33	23.8	115.6
Principe et al. (2007)	19	2.4	30.7	0.37	23.8	129.0
Benkwitt et al. (2009)	9.3	5.9	3.3	0.04	18.6	17.8
Benkwitt et al. (2009)	10.7	6.5	6.7	0.06	18.1	36.9
Benkwitt et al. (2009)	12.7	12.6	2.9	0.18	15.1	19.4
Benkwitt et al. (2009)	13.1	16.1	2.5	0.17	14.1	17.4
Benkwitt et al. (2009)	13.9	6	5.4	0.08	18.5	29.2
This study (July 24)	20.8	20.1	11.0	0.58	13.3	82.9
This study (August 14)	22.0	20.0	8.5	0.51	13.3	64.0

of complete digestive tracts when possible, though this precludes the use of lavage. Although we could have lethally sampled juvenile American Shad, we surmised that our comparisons between the two species would be limited if we were comparing daily rations based on stomach contents (subyearlings) to those using complete digestive tracts (juvenile American Shad); thus, we only examined the stomach contents for both species. Second, although the individual lavage efficiencies of most subyearlings were greater than 90%, the overall efficiency was about 75% (dry weight) of stomach contents. Therefore, the actual daily ration and evacuation rates for subyearlings could have been slightly higher given a constant evacuation rate.

Our overall sample sizes for subyearlings feeding in August were modest ($n = 31$) due to the difficulty of collecting fish. During this time period, the number of subyearlings was diminishing (DART 2016). Although ours is the first formal study of subyearling Chinook Salmon during this time, Parsley et al. (2011) collected 13 subyearlings in John Day Reservoir that were also feeding on juvenile American Shad (>75% by weight). We believe that our results of piscivory on juvenile American Shad are representative of the larger population of subyearlings in John Day Reservoir during this time.

By switching from planktivory to piscivory, subyearlings likely derive an energetic benefit from juvenile American Shad presence in the Columbia River. The empirical consumption rates estimated here provide a critical underpinning for future bioenergetics work estimating the growth of subyearlings. Future bioenergetics work coupled with laboratory functional response experiments could be used to further examine growth repercussions of zooplankton reductions mediated by juvenile American Shad on later-migrating Chinook Salmon subyearlings.

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