



Research, Monitoring, and Evaluation of Emerging Issues and Measures to Recover the Snake River Fall Chinook Salmon ESU

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Abstract

The portion of the Snake River fall Chinook Salmon *Oncorhynchus tshawytscha* ESU that spawns upstream of Lower Granite Dam transitioned from low to high abundance during 1992–2014 in association with U.S. Endangered Species Act recovery efforts and other Federally mandated actions. This annual report focuses on (1) numeric and habitat use responses by natural- and hatchery-origin spawners, (2) phenotypic and numeric responses by natural-origin juveniles, and (3) predator responses in the Snake River upper and lower reaches as abundance of adult and juvenile fall Chinook Salmon increased. Spawners have located and used most of the available spawning habitat and that habitat is gradually approaching redd capacity. Timing of spawning and fry emergence has been relatively stable; whereas the timing of parr dispersal from riverine rearing habitat into Lower Granite Reservoir has become earlier as apparent abundance of juveniles has increased. Growth rate (g/d) and dispersal size of parr also declined as apparent abundance of juveniles increased. Passage timing of smolts from the two Snake River reaches has become earlier and downstream movement rate faster as estimated abundance of fall Chinook Salmon smolts in Lower Granite Reservoir has increased. In 2014, consumption of subyearlings by Smallmouth Bass was highest in the upper reach which had the highest abundance of Bass. With a few exceptions, predation tended to decrease seasonally from April through early July. A release of hatchery fish in mid-May significantly increased subyearling consumption by the following day. We estimated that over 600,000 subyearling fall Chinook Salmon were lost to Smallmouth Bass predation along the free-flowing Snake River in 2014. More information on predation is presented in Appendix A.3 (page 51). These findings coupled with stock-recruitment analyses presented in this report provide evidence for density-dependence in the Snake River reaches and in Lower Granite Reservoir that was influenced by the expansion of the recovery program. The long-term goal is to use the information covered here in a comprehensive modeling effort to conduct action effectiveness and uncertainty research and to inform fish population, hydrosystem, harvest, hatchery, and predation and invasive species management RM&E.

Introduction

The Independent Scientific Advisory Board (2015) recently wrote “Understanding density dependence — the relationship between population density and population growth rate—is important for effective implementation of the Columbia River Basin Fish and Wildlife Program, biological opinions, recovery plans, and tribal programs. Information on how density dependence limits fish population growth and habitat carrying capacity is vital for setting appropriate biological goals to aid in population recovery, sustain fisheries, and maintain a resilient ecosystem. Habitat restoration and population recovery actions can be planned and implemented more effectively by understanding mechanisms that cause density dependence in particular cases, such as limited food supply, limited rearing or spawning habitat, or altered predator-prey interactions.”

Management efforts have been implemented in response to listing under the Endangered Species Act (ESA; NMFS 1992) to increase the size of the population and survival of Snake River basin fall Chinook Salmon *Oncorhynchus tshawytscha* (e.g., reduced harvest, Peters et al. 2001; stable minimum spawning flows, Groves and Chandler 1999; summer flow augmentation, Connor et al. 2003b; predator control, Beamesderfer et al. 1996; increased hatchery production and supplementation; improved dam passage structures, Rainey et al. 2006; summer spill operations, CBR 2015). To track changes in attributes of the natural-origin population as abundance increased, Connor et al. (2013) divided the years 1991–2011 into periods of low and high abundance. To track changes in the attributes of spawning, rearing, emigration, and predation in this report, we added the years 2012 through 2014 to the period of record. The low and high abundance periods for adults were set at 1991–1998 and 1999–2014. The low and high abundance periods for juveniles were set at 1992–1999 and 2000–2014. Estimated escapement of

natural- and hatchery-origin spawners upstream of Lower Granite Dam (hereafter, total escapement) increased markedly between the two abundance periods reaching a post-ESA listing high of 51,900 in 2014 (Table 1).

To assist during the monitoring of recovery measures, staff of project 199102900 has collected and analyzed data on adult and juvenile fall Chinook Salmon collected along the lower Snake River upper and lower reaches to the tailrace of Lower Granite Dam (Figure 1) since brood year 1991 (fry emergence year 1992). That project functions in the long-term as a research project by publishing papers to help to answer uncertainty and action effectiveness questions, while reporting interim information on status and trends as the data are collected. Predation by nonnative fishes is one factor that has been implicated in the decline of juvenile Salmonids *O. spp.* in the Pacific Northwest, but it has been scantily studied in the case of Snake River fall Chinook Salmon. The only evaluation of predation on subyearling Snake River fall Chinook Salmon in the Snake River upper and lower reaches was conducted by Nelle (1999). Within the upper reach, Nelle (1999) reported that subyearlings only made up 1.9% and 0.8% of Smallmouth Bass diets by weight in 1996 and 1997, respectively. That study was conducted during the low abundance period soon after the Snake River fall Chinook Salmon ESU was listed under the ESA in 1992. Thus, low abundance of fall Chinook Salmon could explain why Smallmouth Bass consumption rates were relatively low compared to those from studies conducted in the Columbia and Yakima rivers where Salmon abundance was higher (Tabor et al. 1993; Fritts and Pearsons 2004).

TABLE 1. Estimates of escapement of natural- and hatchery-origin adult (≥ 53 cm FL) fall Chinook Salmon from the Snake River basin ESU, 1991–2014. Reference the following for the results: Busack (1991), Cooney (1991), LaVoy (1992, 1993, 1994, 1995), LaVoy and Mendel (1996), Mendel and LaVoy (1997), Mendel (1998, 1999, 2000), Young et al. (2012, unpublished). The means (\pm SD) of the annual estimates (All) and of the abundance period estimates (Low and High) are also given.

Year	Natural	Hatchery	Total
1991	318	253	571
1992	549	111	660
1993	742	195	937
1994	406	186	592
1995	350	267	617
1996	639	260	899
1997	797	195	992
1998	306	610	916
1999	905	890	1,795
2000	1,148	1,410	2,558
2001	5,163	4,382	9,545
2002	2,116	7,231	9,347
2003	3,455	8,974	12,429
2004	2,637	9,773	12,410
2005	4,584	5,340	9,924
2006	3,984	2,501	6,485
2007	2,816	5,538	8,354
2008	2,995	8,930	11,925
2009	4,273	16,412	20,685
2010	7,347	32,417	39,764
2011	8,072	15,508	23,580
2012	11,315	19,048	30,363
2013	20,425	30,813	51,238
2014	13,142	38,758	51,900
All \pm SD	4,103 \pm 4,932	8,750 \pm 11,294	12,854 \pm 15,736
Low \pm SD	513 \pm 196	260 \pm 151	773 \pm 178
High \pm SD	5,899 \pm 5,193	12,995 \pm 11,743	18,893 \pm 16,214

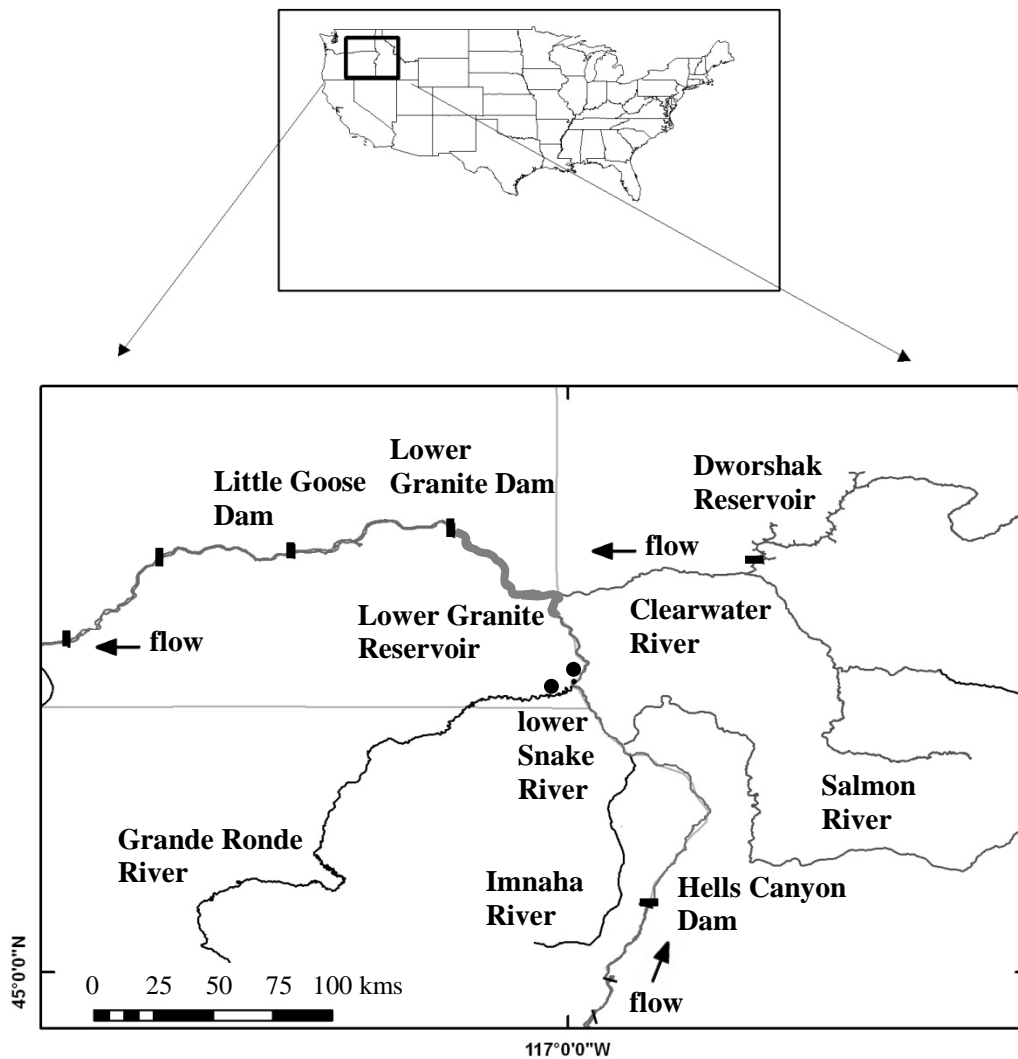


FIGURE 1. The Snake River basin including the free-flowing but regulated Snake River upper (Hells Canyon Dam to Salmon River mouth) and lower (Salmon River mouth to the upper end Lower Granite Reservoir) reaches where natural- and hatchery-origin adults spawned during 1991–2014 and natural-origin fall Chinook Salmon subyearlings were captured, seined and PIT tagged while rearing during 1992–2014. Lower Granite Reservoir and Lower Granite Dam are the first of the impoundments and dams encountered by the fish after they had become smolts during early seaward migration.

The goal of this annual report is to describe how the status and trends in the data collected on fall Chinook Salmon in the Snake River upper (Hells Canyon Dam to the Salmon River mouth) and lower (Salmon River mouth to upper end of Lower Granite Reservoir; Figure 1) reaches provide evidence for density-dependent interactions including an update on the response to predation. The objectives of this report are to summarize information collected on attributes of (1) spawning in riverine habitat, (2) natural-origin juveniles rearing in riverine habitat, (3) natural-origin juveniles emigrating through Lower Granite Reservoir, and (4) seasonal variation in Smallmouth Bass diets and consumption of subyearling Chinook Salmon during rearing in riverine habitat.

Methods

Attributes of Spawning in Riverine Habitat (Protocol ID 2058, Published)

Aerial surveys were scheduled at 7-d to 14-d intervals starting in late October and ending in early December. The number of flights made varied by year. Redds were counted from a helicopter flown about 200 m above the river, which allows observing 100% of the river bottom at depths approximately < 3 m (i.e., shallow water). Potential deep water spawning locations (>3 m) were searched for redds as described in the protocol and by Groves et al. (2013). We tabulated the redd counts by year and reach. We calculated inter-annual mean redd counts by abundance period. To evaluate the evidence for density-dependence during spawning, we plotted the annual numbers of shallow redds counted, number of shallow sites used, deep redds counted, and deep sites used against the corresponding brood year estimates of total escapement (Table 1). Plots were made for the reaches jointly. To assess the plausibility and strength of density-

dependence during spawning, we assumed a log-normal error structure and fit three types of linear models. First, in the following manner we fit a simple linear regression model so that recruitment (R ; e.g., aerial redd counts) increased proportionately and indefinitely (no density-dependence) with increases in total escapement (S):

$$(1) \quad R_{t+1} = \theta_0 + \theta_1 S_t .$$

Secondly, we fit the Beverton-Holt model:

$$(2) \quad R_{t+1} = \frac{\alpha S_t}{1 + (\beta S_t)} ,$$

whereby α measures productivity when the number of spawning adults is near zero (i.e., density-independence), and β measures the strength of density-dependence as the number spawning adults increases. The Beverton-Holt model reaches an asymptote in the number recruits produced at α/β .

Lastly, we fit the Ricker production model expressed as:

$$(3) \quad R_{t+1} = \rho S_t e^{-\delta S_t} ,$$

where ρ is similar to α in the Beverton-Holt and measures density-independent productivity (proportional to fecundity) and δ measures the strength of density-dependence. We used Akaike's Information Criterion (AIC) to pick the model with the best fit.

To evaluate the time of spawning, if redds were counted during a given aerial survey we assigned a spawning date to that survey by subtracting seven days from the flight date. For example, if the first flight was made on 10/21 and 10 redds were counted, the first spawning date would be 10/14. We calculated the first, peak, and last spawning dates as just described and calculated the percentages of the total redd count made on those dates. We calculated inter-annual means for the first, peak, and last spawning dates and for the percentages on those dates by abundance period.

Attributes of Natural-Origin Juveniles Rearing in Riverine Habitat (Protocol ID 2057, DRAFT)

Attributes evaluated during rearing in riverine habitat included apparent abundance of natural-origin subyearlings, timing of fry (< 46-mm FL) presence, and timing of parr (> 45-mm FL; after Connor et al. 2002) dispersal from riverine habitat, parr dispersal size, and parr growth. To collect data on those attributes, we used a beach seine at 11–15 permanent stations located along 142 contiguous kms of the two riverine reaches studied. Large portions of the hatchery smolts released into the river were released without an external mark or fin clip (i.e., unmarked). After hatchery smolts were released upstream of a given seining station, the origin (i.e., natural or hatchery) of each collected unmarked fish was classified based on morphology (overall accuracy 98.7%; Tiffan and Connor 2011). During 1992–2007, we implanted each natural-origin parr ≥ 60 mm long collected during seining in riverine habitat with an 11.5-mm passive integrated transponder (PIT) tag (Prentice et al. 1990a). During 2008–2014, in addition to tagging fish longer than 59 mm with 11.5-mm tags, we also tagged natural-origin parr that were

50–59 mm long with 8.5-mm tags. Natural-origin parr were given 15 min to recover from tagging in an aerated 19-L bucket of river water before release at their capture site.

Mean daily CPUE (natural-origin subyearlings per seine haul) values for each sampling station were adjusted for the presence of natural-origin, spring/summer Chinook Salmon and averaged across sampling stations and weeks within a year to calculate mean annual CPUE (\pm SE) by reach and for reaches combined as an indices of apparent abundance in riverine rearing habitat, where N was the number of station visits. We also calculated mean inter-annual CPUE by abundance period (low abundance period, 1992–1999; high abundance period, 2000–2014; after Connor et al. 2013). To evaluate the evidence for density-dependence during rearing in riverine habitat, mean annual CPUE for the combined reaches was plotted against the corresponding brood year estimates of total escapement (Table 1) and curves were fit to the data as described for redd counts.

The median, minimum and maximum day of year (January 1 = 1) of fry and parr presence were tabulated by reach and year. We calculated inter-annual means from the annual median dates of presence for each abundance period under the premise that dispersal timing into the reservoir became earlier as the median dates of parr presence became earlier. We calculated annual mean and abundance period wet weights (0.1 g) of all natural-origin parr captured in the riverine habitat reasoning that decreases in weight reflected decreases in size at dispersal (and vice versa). We calculated absolute growth rates (g/d) of individual PIT-tagged, natural-origin parr recaptured by beach seine as $(WT2 - WT1) / (Day2 - Day1)$ and used those growth rates to calculate annual mean growth rates for fish recaptured within each year, and inter-annual mean growth rates for each abundance period.

Attributes of Natural-Origin Juveniles Emigrating through Lower Granite Reservoir (Protocol ID 2057, DRAFT)

The basin-wide population of subyearling smolts consists of the aggregate of natural- and hatchery-origin fish produced or released upstream of Lower Granite Reservoir. We modified Method ID 3999 to estimate the daily number of natural-origin, fall Chinook Salmon subyearling smolts that passed Lower Granite Dam each year. We summed the daily estimates made for March through October to estimate seasonal passage abundance. To evaluate the evidence for density-dependence during early seaward migration in the reservoir, we plotted estimated annual passage abundance at the dam against the corresponding brood year estimates of total escapement (Table 1) and curves were fit to the data as described for redd counts..

We also used Method ID 3999 to estimate daily passage abundance of natural-origin subyearlings at Lower Granite Dam that had been PIT tagged in the Snake River reaches. The annual median passage dates for each reach were plotted against year, and the inter-annual means of those medians were calculated by abundance period. Downstream movement rate was calculated for individual, natural-origin subyearlings that had been PIT tagged while rearing in riverine reaches of the Snake River as the elapsed days between release and detection at a point downstream divided by the channel distance in river kms traversed between release and subsequent detection at Lower Granite Dam. Annual means, medians, minimums, and maximums were calculated by reach and abundance period using the downstream movement rates of individual fish.

Seasonal Variation in Smallmouth Bass Diets and Consumption of Subyearling Chinook Salmon during Rearing in Riverine Habitat (Protocol ID 299, Published)

To evaluate predation, we focused on three sections of the free-flowing Snake River that fall within the previously described upper and lower reaches. The lower section was within the lower reach and extended 34 km downstream from the mouth of the Grande Ronde River (Figure 1). The middle section was also in the lower reach and it extended 31 km downstream from the mouth of the Salmon River to the mouth of the Grande Ronde River (Figure 1). The upper section was in the upper reach and it extended 66 km upstream from the mouth of the Salmon River. The upper section encompasses the “upper section” sampled by Nelle (1999), whereas the lower and middle sections combined correspond to the “lower or downstream section” sampled by Nelle (1999).

Sampling was conducted biweekly with angling or electrofishing from late March through early July to document the seasonal changes in Smallmouth Bass abundance, diet, and consumption of subyearlings. Four fixed sampling sites were established in each reach and then sampled through time so as to make recapturing tagged Smallmouth Bass more effective. In addition, random sites were sampled as well to increase our sample sizes for consumption estimates.

Collected Smallmouth Bass >150 mm TL had their stomach contents removed by non-lethal lavage, were measured, Floy tagged, and released. Subsequent recapture information was used to estimate absolute abundance. Catch per unit effort (# Bass/m shoreline) was also calculated. Abundance estimates were ultimately used to expand consumption estimates to generate an estimate of subyearling loss to predation.

Smallmouth Bass stomach contents were identified to major taxonomic group: insects, crustaceans, fish, and other. Fish species and length at ingestion were identified from diagnostic bones and associated regressions (Hansel et al. 1988; Rogers and Burley 1991; Rieman et al. 1991; Vigg et al. 1991; Parrish et al. 2006). Consumption of different prey taxa was expressed as percentages by frequency of occurrence and weight on a seasonal basis.

The consumption of subyearling fall Chinook Salmon was estimated following established, peer-reviewed methods (Rogers and Burley 1991; Rieman et al. 1991; Vigg et al. 1991; Naughton et al. 2004; Parrish et al. 2006). In brief, we first estimated the fresh weight of subyearlings at ingestion. Next, we estimated the meal weight of all prey. Then we input this into an evacuation rate model to determine if the subyearlings were ingested within 24 h of when the Bass was collected. Finally, we estimated total loss as the sum of the number of subyearlings eaten per Bass over all sampling intervals multiplied by the abundance of Bass in our study area.

Results

Attributes of Spawning in Riverine Habitat

A total of 1,712 redds were counted along the Snake River upper reach during 2014 (Table 2), which ranked third for the 24-year period of record for that reach. A total of 1,096 redds were counted along the Snake River lower reach during 2014 (Table 2), which ranked fourth for the 24-year period of record for that reach. A grand total of 2,808 redds were counted along both reaches of the Snake River during 2014 (Table 2), which ranked fourth for the 24-year period of record for the free-flowing Snake River.

Mean inter-annual redd counts were similar between reaches during the low abundance period, whereas the mean inter-annual redd count was 1.47 times higher in the upper reach compared to the lower reach during the high abundance period (Table 2). As such, there was a

large change in the percentage of the total redds counted between reaches and abundance periods with the upper reach supporting the majority of redds during the high abundance period (Table 2).

The Beverton-Holt (AIC = 323.5) and Ricker (AIC = 325.0) models provided similar amounts of information about the shape of the relation between total escapement and aerial redd counts for the reaches combined compared to the linear (AIC = 346.7) model. The gradual slopes of both the stock-recruitment curves provided no evidence for attainment of redd capacity (Figure 2). The Beverton-Holt model provided the best fit (AIC = 178.6) to the data set composed of total escapement and the number of shallow spawning sites used (Linear, AIC = 229.2; Ricker, AIC = 201.7; Figure 3).

The fits to the total escapement and deepwater redd count data were similar between the Beverton-Holt (AIC = 304.2) and Ricker (AIC = 302.8) models, but better than the fit of the linear (AIC = 319.3) model (Figure 4). The Beverton-Holt model (AIC = 168.6) provided the best fit to data collected on the total escapement and the number of deepwater sites used (Linear, AIC = 192.2; Ricker, AIC = 171.0; Figure 5).

There was a 7-d difference between the mean first dates of spawning of the two abundance periods, that was partly caused by starting the aerial surveys early during several years of the high abundance period (Table 3). On average, however, relatively low proportions of the total number of redds counted within each abundance period were counted during on the first date of spawning (Table 3). There was no large difference between the mean peak and last dates of spawning between abundance periods (Table 3). Thus, difference in time of spawning between abundance periods was not a large factor for changes in the attributes of juveniles described later in this report.

TABLE 2. Redd count data collected during aerial surveys (< 3 m deep) and deepwater searches (> 3 m deep) surveys conducted along the Snake River upper and lower reaches, 1991–2014. The inter-annual mean (\pm SE) counts (All) and abundance period mean counts (Low and High) are also given. Data are currently being proofed against those of our cooperators at Idaho Power Company, thus there are some small differences between those presented here and in Groves et al. (2013).

Year	Upper reach			Lower reach			Grand total	Percent by reach	
	Aerial	Deep	Total	Aerial	Deep	Total		Upper	Lower
1991	17		17	24	5	29	46	37.0	63.0
1992	16		16	31	0	31	47	34.0	66.0
1993	14	5	19	46	62	108	127	15.0	85.0
1994	31	6	37	22	8	30	67	55.2	44.8
1995	28	5	33	13	19	32	65	50.8	49.2
1996	49	7	56	22	26	48	104	53.8	46.2
1997	20	4	24	29	5	34	58	41.4	58.6
1998	109	28	137	26	22	48	185	74.1	25.9
1999	225	67	292	48	33	81	373	78.3	21.7
2000	186	42	228	69	49	118	346	65.9	34.1
2001	301	87	388	234	86	320	708	54.8	45.2
2002	533	114	647	345	120	465	1,112	58.2	41.8
2003	675	165	840	443	229	672	1,512	55.6	44.4
2004	685	279	964	533	210	743	1,707	56.5	43.5
2005	662	203	865	380	195	575	1,440	60.1	39.9
2006	452	147	599	244	181	425	1,024	58.5	41.5
2007	482	241	723	232	162	394	1,117	64.7	35.3
2008	761	368	1,129	472	218	690	1,819	62.1	37.9
2009	948	379	1,327	563	205	768	2,095	63.3	36.7
2010	1,110	641	1,751	840	375	1,215	2,966	59.0	41.0
2011	874	521	1,395	1,075	344	1,419	2,814	49.6	50.4
2012	1,016	274	1,290	396	142	538	1,828	70.6	29.4
2013	1,552	332	1,884	1,115	264	1,379	3,263	57.7	42.3
2014	1,129	583	1,712	837	259	1,096	2,808	61.0	39.0
All ± SE									
Low ± SE			42 ± 14	45 ± 9			87 ± 17	55.7 ± 2.8	44.3 ± 2.8
High ± SE			1,002 ± 131	681 ± 103			1,683 ± 228	61.0 ± 1.7	39.0 ± 6.6

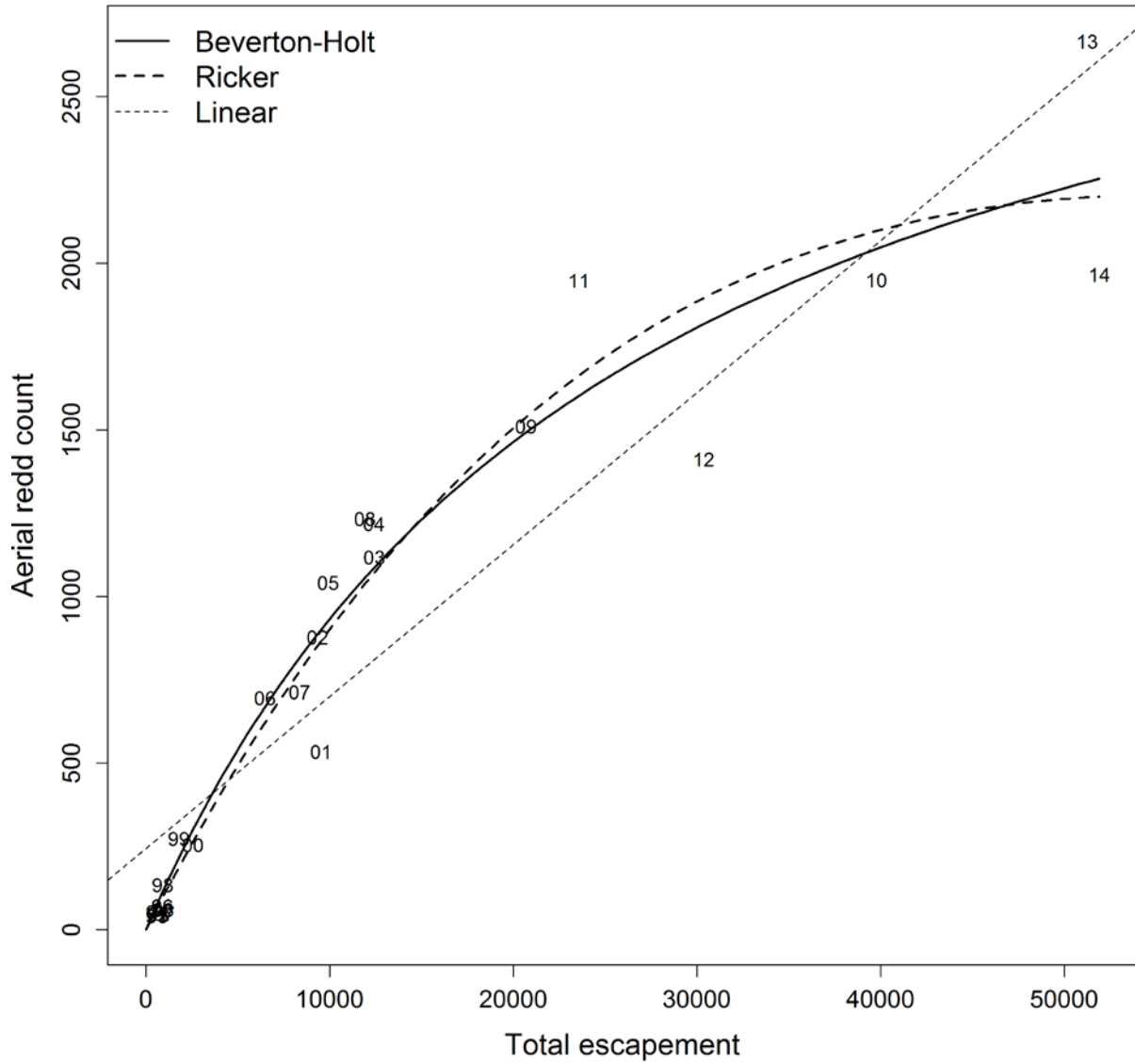


FIGURE 2. The relation between total escapement (Table 1) and the annual counts of shallow (< 3 m deep) redds counted from the air in the Snake River upper and lower reaches combined (Table 2), 1992–2014. The numbers are the last two digits of the calendar year. The parameters (\pm SE) for the Beverton-Holt and Ricker models (of similar fit) were: $\alpha = 1.283\text{e-}01 \pm 1.551\text{e-}02$ and $\beta = 3.765\text{e-}05 \pm 8.541\text{e-}06$; and $\alpha = 1.078\text{e-}01 \pm 8.737\text{e-}03$ and $\beta = 1.799\text{e-}05 \pm 2.223\text{e-}06$.

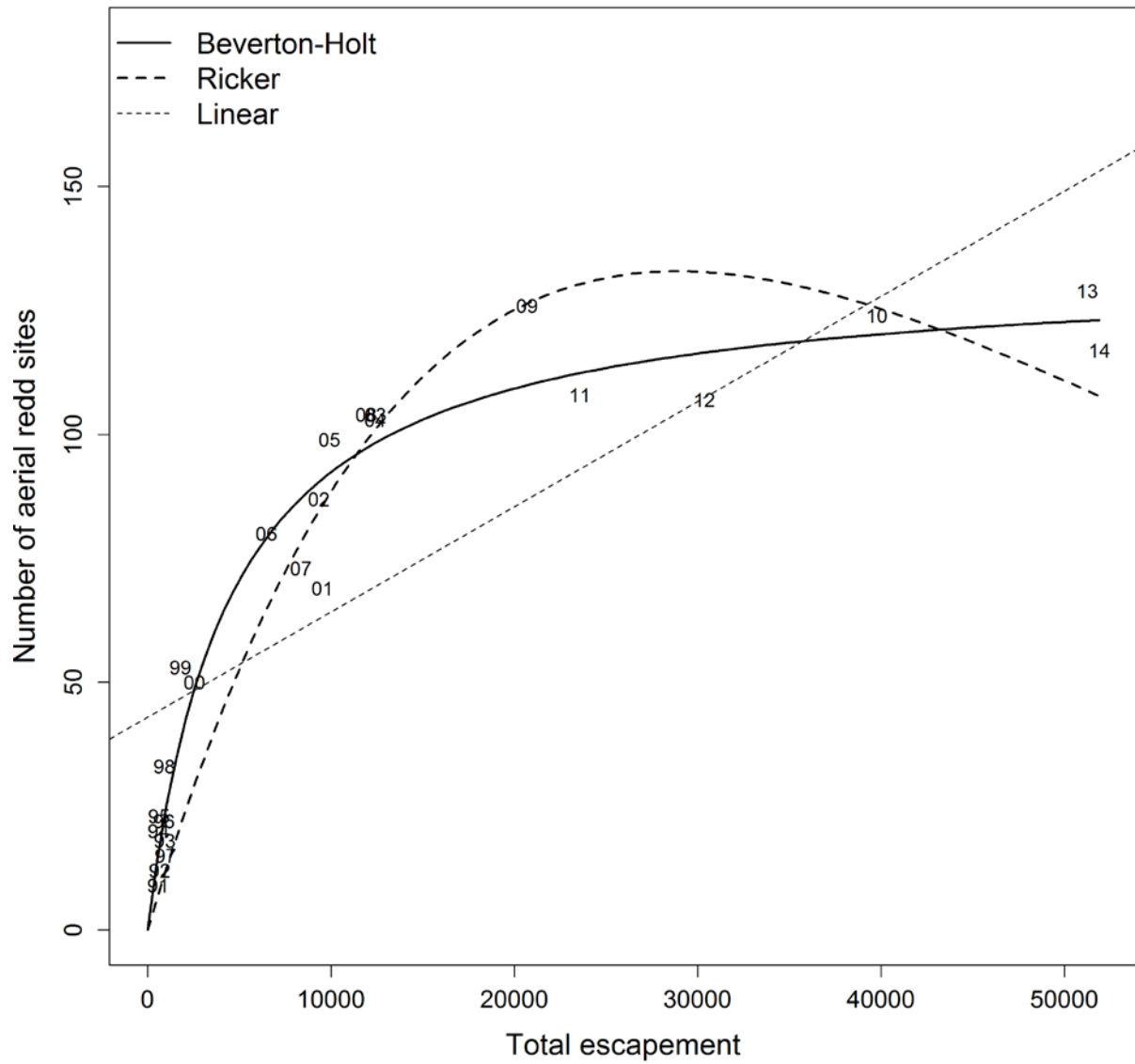


FIGURE 3. The relation between total escapement (Table 1) and the annual number of shallow (< 3 m deep) sites at which redds were counted from the air in the Snake River upper and lower reaches combined, 1992–2014. The numbers are the last two digits of the calendar year. The parameters (\pm SE) for the Beverton-Holt model (the best fit) were $\alpha = 0.0298837 \pm 0.0035989$ and $\beta = 0.0002236 \pm 0.0000342$.

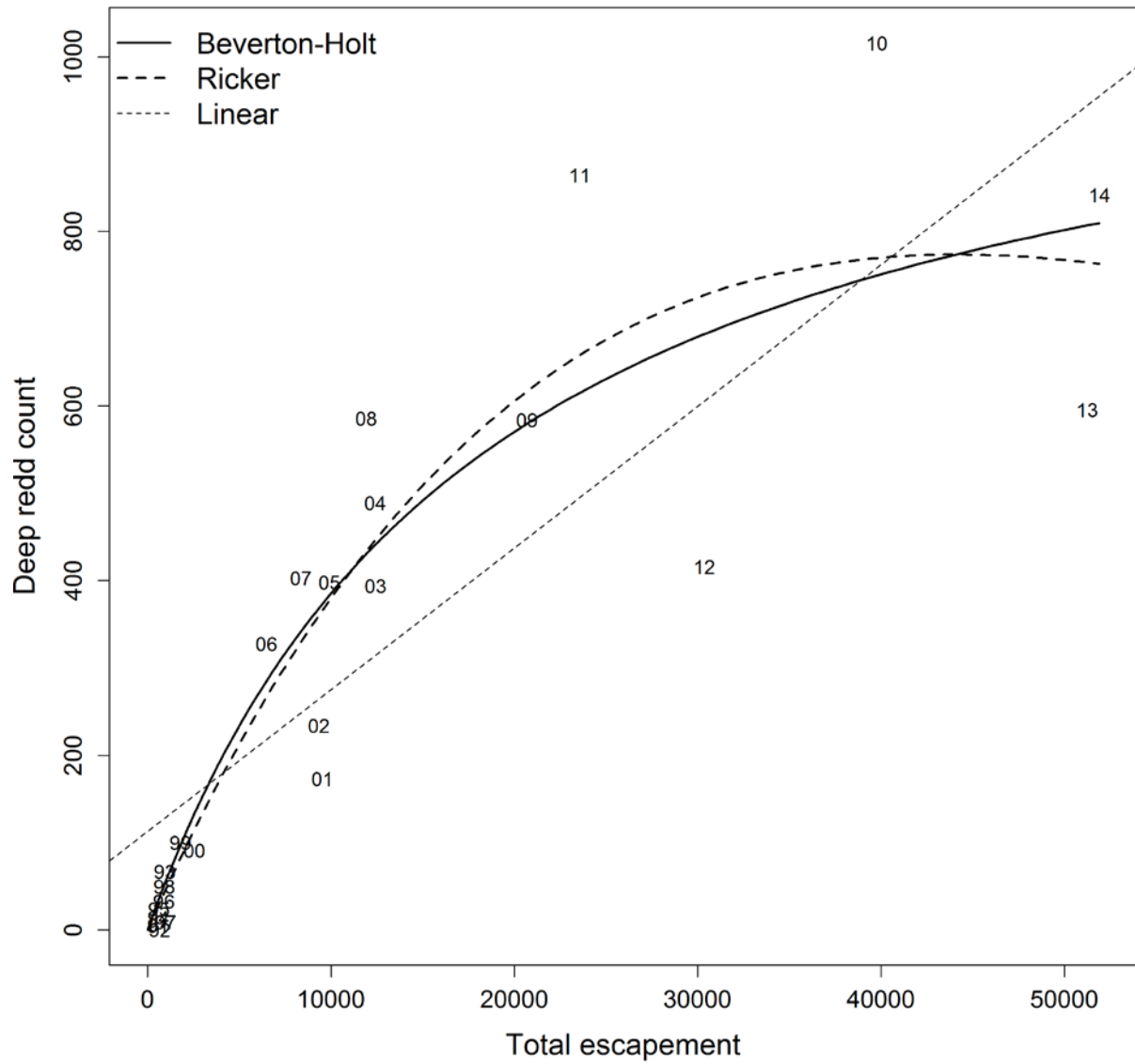


FIGURE 4. The relation between total escapement (Table 1) and the annual counts of deep (> 3 m deep) redds counted underwater in the Snake River upper and lower reaches combined (Table 2), 1992–2014. The numbers are the last two digits of the calendar year. The parameters (\pm SE) for the Beverton-Holt and Ricker models (of similar fit) were: $\alpha = 5.934\text{e-}02 \pm 1.345\text{e-}02$ and $\beta = 5.403\text{e-}05 \pm 2.058\text{e-}05$; and $\alpha = 4.765\text{e-}02 \pm 5.997\text{e-}03$ and $\beta = 2.266\text{e-}05 \pm 3.669\text{e-}06$.

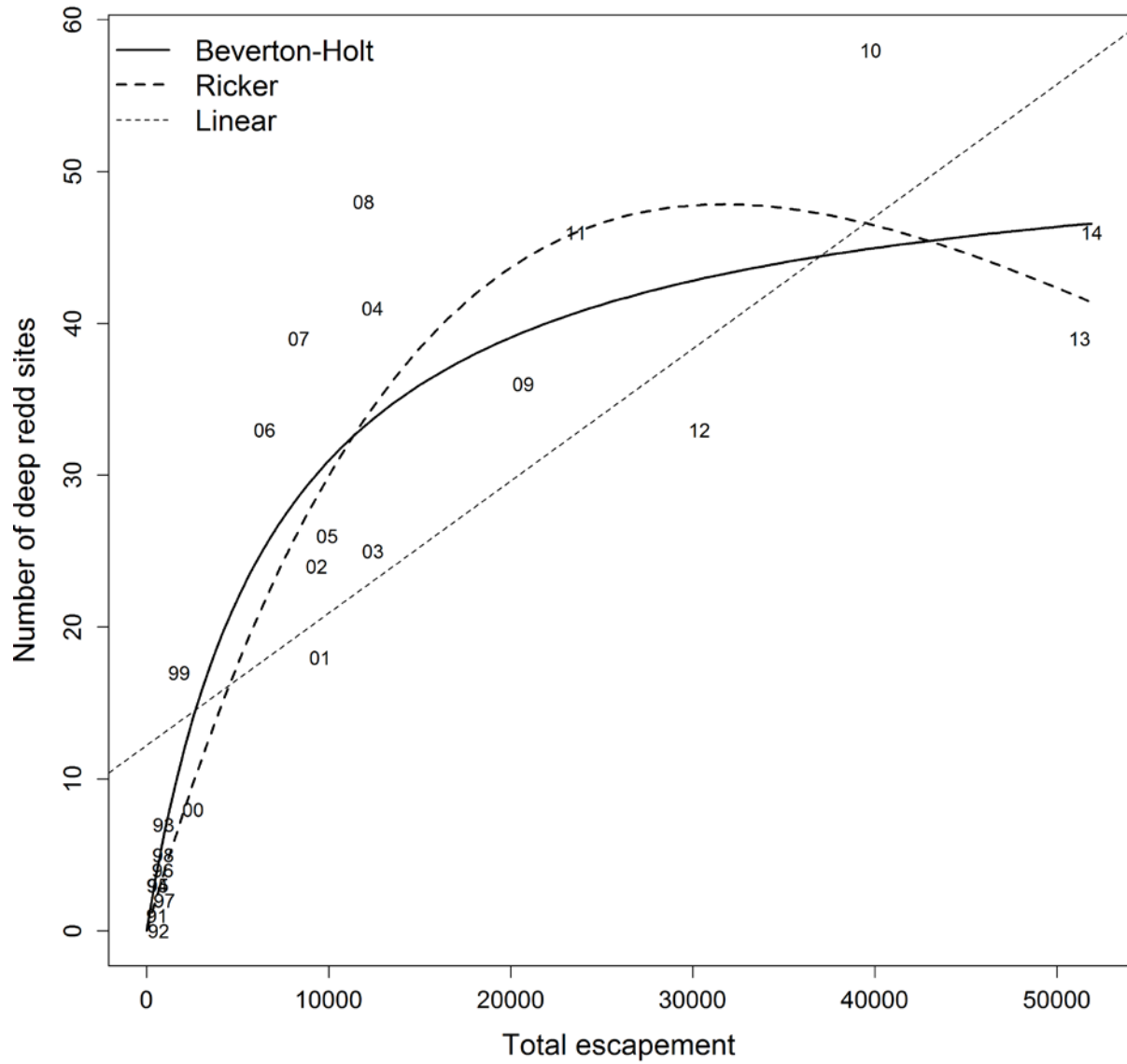


FIGURE 5. The relation between total escapement (Table 1) and the annual number of deep (> 3 m deep) sites at which redds were counted underwater in the Snake River upper and lower reaches combined, 1992–2014. The numbers are the last two digits of the calendar year. The parameters (\pm SE) for the Beverton-Holt model (the best fit) were $\alpha = 0.0074494 \pm 0.0018920$ and $\beta = 0.0001407 \pm 0.0000487$.

TABLE 3. Information from the annual aerial redd surveys made in shallow water (< 3 m) along the Snake River upper and lower reaches including the number of flights made, the spawning date represented by the first flight (Earliest), and the first, peak, and last spawning dates observed including the cumulative percentages (%) of eventual total redd counts made on those dates. The inter-annual mean (\pm SE) counts and percentages (All) and abundance period mean counts and percentages (Low and High) are also given.

Year	Flights		First		Peak		First	
	N	Earliest	Date	%	Date	%	Date	%
1991	9	10/07	10/21	2.4	11/11	26.2	12/02	4.8
1992	8	10/09	10/29	8.9	11/16	40.0	12/05	0.0
1993	8	10/18	10/18	3.3	10/25	30.0	12/06	3.3
1994	8	10/17	10/17	1.8	10/31	31.6	11/28	1.8
1995	8	10/16	10/16	9.8	10/30	43.9	11/20	2.4
1996	8	10/14	10/14	2.8	10/21	36.6	11/25	1.4
1997	8	10/13	10/13	2.0	10/20	32.7	11/24	2.0
1998	8	10/12	10/19	20.7	10/26	31.9	11/23	3.7
1999	9	10/04	10/11	1.8	11/04	43.6	11/30	0.4
2000	9	10/02	10/02	0.4	10/23	31.4	11/21	2.0
2001	10	10/02	10/02	1.8	11/06	41.6	12/03	1.6
2002	7	10/14	10/14	3.4	10/28	33.1	11/25	0.3
2003	7	10/13	10/13	0.4	11/03	37.4	12/01	0.5
2004	8	10/11	10/11	0.1	11/01	40.5	11/29	1.1
2005	9	10/11	10/11	0.8	10/31	33.2	12/05	0.1
2006	6	10/16	10/16	5.0	10/23	39.3	12/04	1.3
2007	8	10/08	10/08	0.1	10/30	39.5	11/26	6.0
2008	8	10/13	10/13	1.9	10/27	46.0	12/01	0.5
2009	8	10/12	10/12	1.2	10/26	46.6	11/30	0.9
2010	4	10/18	10/18	3.2	11/02	51.5	11/29	13.8
2011	5	10/17	10/17	1.7	10/31	47.5	11/28	6.7
2012	4	10/15	10/15	2.4	10/29	68.5	11/26	1.8
2013	4	10/14	10/14	4.8	10/28	74.3	11/27	0.8
2014	4	10/13	10/13	1.9	10/27	53.8	11/24	2.4
All \pm SD		10/12 \pm 5	10/14 \pm 6	3.4 \pm 4.4	10/30 \pm 6	41.7 \pm 11.6	11/29 \pm 5	2.5 \pm 3.0
Low \pm SD		10/14 \pm 4	10/19 \pm 5	6.4 \pm 6.5	10/31 \pm 10	34.1 \pm 5.7	11/28 \pm 6	2.4 \pm 1.5
High \pm SD		10/12 \pm 5	10/12 \pm 5	1.9 \pm 1.5	10/30 \pm 4	54.5 \pm 11.9	11/30 \pm 4	2.5 \pm 3.6

Attributes of Natural-Origin Juveniles Rearing in Riverine Habitat

Mean (\pm 95% C.L.) annual CPUE for natural-origin Snake River fall Chinook Salmon subyearlings along the Snake River upper reach during 2014 was 24.9 ± 13.0 fish per seine haul (Table 4), which ranked eleventh for the 20-year period of record for the upper reach. Mean (\pm 95% C.L.) annual CPUE for natural-origin Snake River fall Chinook Salmon subyearlings along the Snake River lower reach during 2014 was 21.5 ± 4.5 fish per seine haul (Table 4), which ranked seventh for the 23-year period of record for the lower reach. Mean (\pm 95% C.L.) annual CPUE for natural-origin Snake River fall Chinook Salmon subyearlings along the Snake River upper and lower reaches combined during 2014 was 21.9 ± 5.0 fish per seine haul (Table 4), which ranked eighth for the 23-year period of record.

Mean inter-annual CPUE was lower during the low abundance period compared to the high abundance period for the upper reach, lower reach, and the combined reaches (Table 4). The Ricker model provided the best fit ($AIC = 179.7$) to the relation between estimated total escapement and mean annual CPUE calculated jointly between Snake River reaches compared to the linear ($AIC = 192.6$) and Beverton-Holt models ($AIC = 181.8$; Figure 6).

TABLE 4. Mean (\pm 95% C.L.) CPUE (fish per seine haul) for natural-origin fall Chinook Salmon subyearlings along the Snake River upper and lower reaches, 1992–2014. The start and end dates for beach seining, the total number of station visits (N), means (\pm SE) of the annual means (All), and of the abundance period medians (Low and High) are also given.

Year	Upper reach				Lower reach				Combined			
	N	Start	End	CPUE	N	Start	End	CPUE	N	Start	End	CPUE
1992					173	04/01	06/11	3.5 \pm 0.9	173	04/01	06/11	3.5 \pm 0.9
1993					247	04/06	07/20	1.5 \pm 0.3	247	04/06	07/20	1.5 \pm 0.3
1994					249	04/06	07/13	6.0 \pm 1.8	249	04/06	07/13	6.0 \pm 1.8
1995	70	04/07	06/29	8.2 \pm 2.7	199	04/05	07/06	3.3 \pm 0.8	269	04/05	07/06	4.6 \pm 0.9
1996	54	04/18	07/11	0.8 \pm 0.3	145	04/16	07/17	2.2 \pm 0.5	199	04/16	07/17	1.8 \pm 0.4
1997	71	04/24	07/03	0.6 \pm 0.3	167	04/22	07/16	2.5 \pm 0.7	238	04/22	07/16	1.9 \pm 0.5
1998	73	04/15	07/06	4.7 \pm 1.8	149	04/14	07/08	5.2 \pm 1.3	222	04/14	07/08	5.0 \pm 1.1
1999	81	04/08	07/09	8.8 \pm 3.4	171	04/06	07/15	4.2 \pm 0.9	252	04/06	07/15	5.7 \pm 1.2
2000	41	04/06	06/29	31.4 \pm 24.2	98	04/04	07/06	17.5 \pm 5.0	139	04/04	07/06	21.6 \pm 7.8
2001	49	04/06	06/21	11.3 \pm 8.2	140	04/04	07/03	11.1 \pm 3.0	189	04/04	07/03	11.2 \pm 3.1
2002	56	04/04	07/11	29.6 \pm 16.6	160	04/02	07/17	7.8 \pm 1.8	216	04/02	07/17	13.5 \pm 4.6
2003	52	03/27	06/26	40.1 \pm 16.6	146	03/25	07/02	19.7 \pm 4.8	198	03/25	07/02	25.1 \pm 5.7
2004	55	03/25	06/24	90.9 \pm 49.2	150	03/23	06/30	41.8 \pm 11.3	205	03/23	06/30	54.9 \pm 15.6
2005	60	03/31	06/30	88.7 \pm 45.9	199	03/29	07/12	39.7 \pm 8.6	259	03/29	07/12	51.0 \pm 12.6
2006	78	03/31	07/06	7.0 \pm 3.7	216	03/29	07/11	5.8 \pm 1.2	294	03/29	07/11	6.1 \pm 1.3
2007	68	03/29	07/05	65.2 \pm 38.5	144	03/27	07/03	23.1 \pm 5.4	212	03/27	07/05	36.6 \pm 13.0
2008	92	03/27	07/17	34.7 \pm 14.4	169	03/25	07/16	10.2 \pm 2.2	261	03/25	07/17	18.8 \pm 5.4
2009	79	03/26	06/25	25.6 \pm 13.7	155	03/23	07/07	14.5 \pm 5.1	234	03/23	07/07	18.3 \pm 5.7
2010	86	03/25	07/22	20.6 \pm 8.0	187	03/23	07/27	26.7 \pm 5.3	273	03/23	07/27	24.8 \pm 4.4
2011	79	03/31	07/14	20.4 \pm 8.4	161	03/29	07/20	13.8 \pm 3.7	240	03/29	07/20	16.0 \pm 3.7
2012	85	03/28	07/11	49.0 \pm 22.4	178	03/27	08/01	21.2 \pm 4.5	263	03/27	08/01	30.2 \pm 7.9
2013	68	03/28	06/27	65.0 \pm 46.2	145	03/26	07/03	28.8 \pm 6.5	213	03/26	07/03	40.4 \pm 15.3
2014	60	03/27	06/19	24.9 \pm 13.0	133	03/25	07/01	20.5 \pm 4.4	193	03/25	07/01	21.9 \pm 5.0
All \pm SE				31.4 \pm 6.2				14.4 \pm 2.5				18.3 \pm 3.3
Low \pm SE				4.6 \pm 1.8				3.6 \pm 0.5				3.8 \pm 0.7
High \pm SE				40.3 \pm 6.8				20.1 \pm 2.8				26.0 \pm 3.7

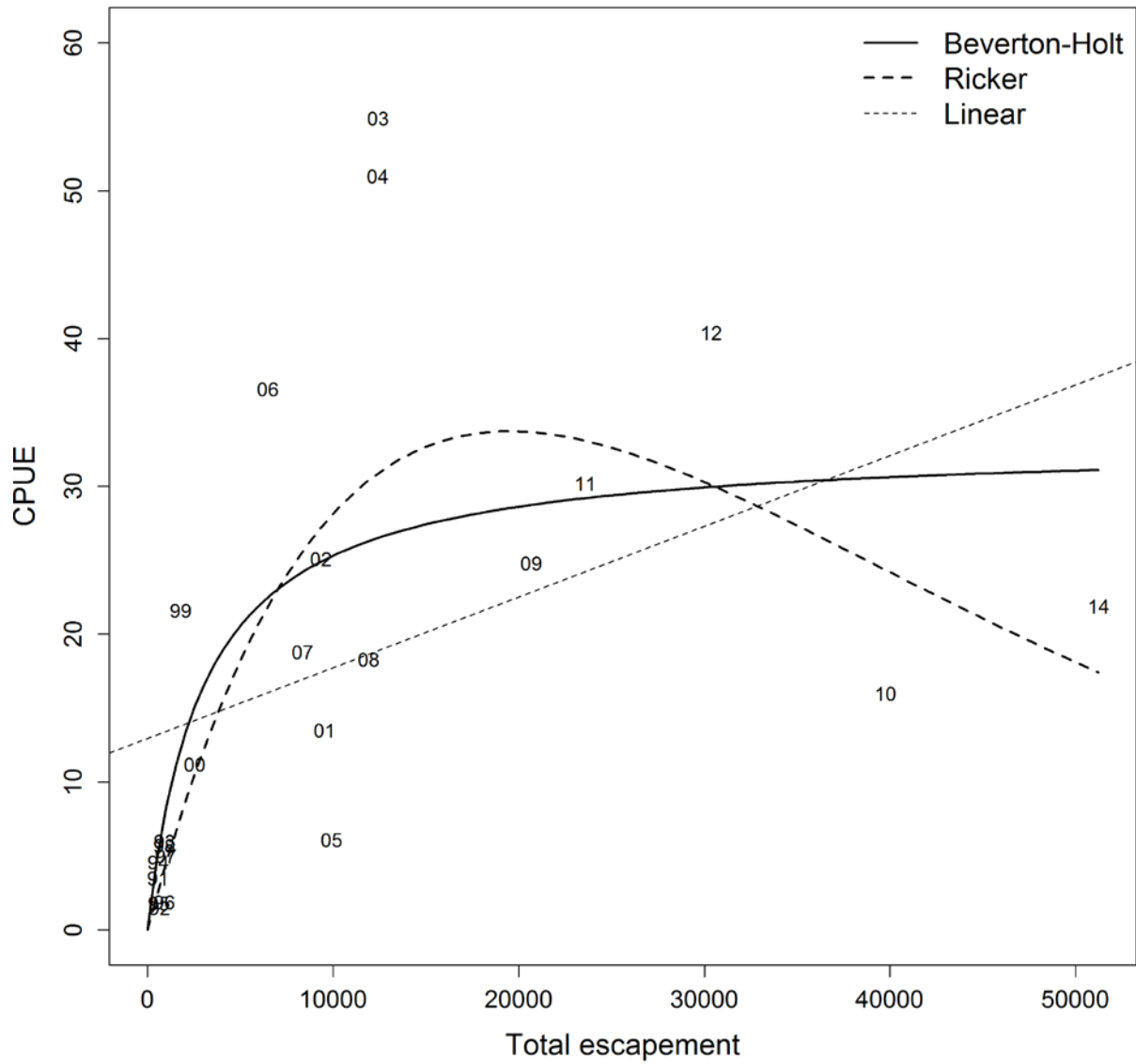


FIGURE 6. The relation between total escapement (Table 1) and inter-annual mean CPUE of natural-origin Fall Chinook Salmon subyearlings along the Snake River upper and lower reaches combined (Table 4), 1992–2014. The numbers are the last two digits of the juvenile sampling year (e.g., 14 = 2014 juveniles produced by spawning in 2013). The parameters (\pm SE) for the Ricker model (the best fit) were $\alpha = 4.698\text{e-}03 \pm 9.492\text{e-}04$ and $\beta = 5.125\text{e-}05 \pm 9.930\text{e-}06$.

Of the life stages evaluated, timing of fry presence has been the most stable across the years 1992–2014 with emergence timing being earlier in the relatively warmer Snake River upper reach than in the relatively cooler Snake River lower reach (Table 5). The median date of parr presence along the shorelines is an indicator of when the number of parr rearing in riverine habitat became less than the number of parr that had begun downstream dispersal into Lower Granite Reservoir. The median date of parr presence along both Snake River reaches generally became earlier as density along the shorelines increased as can be seen by examining the means of the median dates of parr presence for the periods of low (1992–1999) and high (2000–2014) abundance (Table 6).

Mean (\pm SE) wet weight of natural-origin parr in the Snake River upper reach declined from 4.7 ± 0.4 g during the low abundance period to 2.4 ± 0.2 g during the high abundance period, and a similar decline in wet weight of parr was observed in the Snake River lower reach (Table 7). The decline in wet weight of parr was accompanied by a decline in growth in weight in both reaches, but especially in the upper reach (Table 7) where rearing habitat availability and connectivity are relatively low and apparent abundance high (Table 4).

TABLE 5. Timing of fry presence (Sunday's day of year; January 1 = 1) along the Snake River upper and lower reaches, 1992–2014. The means (\pm SE) of the annual medians (All) and of the abundance period medians (Low and High) are also given.

Year	Upper reach				Lower reach			
	<i>N</i>	Median	Min	Max	<i>N</i>	Median	Min	Max
1992					356	117	89	145
1993					199	136	94	171
1994					441	135	93	156
1995	117	113	92	141	257	120	92	155
1996	14	119	105	126	268	126	105	175
1997	1	110	110	110	114	124	110	180
1998	101	109	102	130	322	116	102	165
1999	97	122	94	143	278	122	94	178
2000	683	100	93	135	415	100	93	156
2001	552	119	91	140	1,268	126	91	154
2002	2,289	111	90	153	965	125	90	167
2003	962	103	82	145	1,726	110	82	173
2004	6,123	109	81	144	4,952	123	81	158
2005	5,462	107	86	135	3,786	107	86	156
2006	75	106	85	141	588	134	85	162
2007	4,311	112	84	154	1,771	119	84	154
2008	1,628	118	90	146	1,231	118	83	167
2009	811	109	81	137	1,017	116	81	165
2010	1,572	115	80	157	4,393	115	80	171
2011	1,778	128	86	163	1,408	128	86	191
2012	3,782	120	85	169	2,207	127	85	162
2013	7,874	111	83	146	4,033	118	83	167
2014	1,174	107	82	159	2,755	117	82	166
All \pm SE		112 \pm 2			121 \pm 2			
Low \pm SE		115 \pm 3			125 \pm 3			
High \pm SE		112 \pm 2			119 \pm 2			

TABLE 6. Timing of natural-origin parr presence (Sunday's day of year; January 1 = 1) along the Snake River upper and lower reaches, 1992–2014. The means (\pm SE) of the annual medians (All) and of the abundance period medians (Low and High) are also given.

Year	Upper reach				Lower reach			
	<i>N</i>	Median	Min	Max	<i>N</i>	Median	Min	Max
1992					1,765	138	89	159
1993					2,166	157	101	199
1994					4,348	149	93	191
1995	985	148	99	169	1,408	155	92	183
1996	118	133	105	168	756	147	105	196
1997	119	145	110	166	938	159	110	194
1998	1,078	137	102	186	2,512	151	102	186
1999	1,493	143	101	178	1,647	157	94	192
2000	1,064	114	93	163	1,578	135	93	177
2001	794	123	91	161	3,076	140	91	175
2002	3,013	125	97	181	3,620	146	90	188
2003	4,523	124	82	173	6,821	131	82	180
2004	6,310	123	88	172	11,225	137	88	179
2005	8,119	121	86	170	16,803	135	86	184
2006	1,344	134	85	176	2,658	134	99	176
2007	7,226	119	91	182	7,500	133	84	182
2008	6,610	139	97	195	3,357	146	83	195
2009	3,876	130	88	165	4,706	137	95	186
2010	2,502	129	87	199	9,193	143	87	199
2011	2,237	135	93	184	2,759	149	86	191
2012	4,769	134	106	176	5,791	148	99	190
2013	4,503	125	104	174	7,171	139	83	174
2014	2,484	131	82	159	3,785	138	89	180
All \pm SE		131 \pm 2				144 \pm 2		
Low \pm SE		141 \pm 5				152 \pm 3		
High \pm SE		127 \pm 2				139 \pm 2		

TABLE 7. Mean (\pm SD) wet weights (0.1 g) and absolute growth rates (0.01 g/d) of natural-origin parr rearing along the Snake River upper and lower reaches, 1992–2014. The means (\pm SE) of the annual means (All) and of the abundance period means (Low and High) are also given.

Year	Upper reach				Lower reach			
	<i>N</i>	Weight	<i>N</i>	Growth	<i>N</i>	Weight	<i>N</i>	Growth
1992					1,128	4.2 \pm 2.5	36	0.17 \pm 0.11
1993					1,901	4.2 \pm 3.1	161	0.13 \pm 0.13
1994					3,712	3.8 \pm 2.8	238	0.19 \pm 0.17
1995	606	4.4 \pm 3.2	29	0.28 \pm 0.13	888	4.0 \pm 3.3	35	0.21 \pm 0.11
1996	112	3.8 \pm 2.5	17	0.26 \pm 0.13	714	4.2 \pm 3.4	49	0.20 \pm 0.14
1997	114	6.1 \pm 2.7	20	0.34 \pm 0.10	922	4.7 \pm 3.1	78	0.20 \pm 0.11
1998	981	4.7 \pm 3.0	89	0.25 \pm 0.11	2,145	4.0 \pm 2.8	86	0.18 \pm 0.09
1999	1,489	4.3 \pm 3.0	169	0.30 \pm 0.13	1,642	3.7 \pm 2.8	92	0.24 \pm 0.12
2000	932	4.2 \pm 3.9	61	0.38 \pm 0.11	1,553	3.7 \pm 3.1	45	0.20 \pm 0.10
2001	724	2.0 \pm 1.3	11	0.22 \pm 0.03	2,981	2.6 \pm 1.8	120	0.18 \pm 0.07
2002	3,005	2.1 \pm 1.6	169	0.24 \pm 0.09	3,620	3.1 \pm 2.3	185	0.17 \pm 0.07
2003	4,480	2.5 \pm 1.5	359	0.18 \pm 0.10	6,821	2.5 \pm 1.5	186	0.14 \pm 0.06
2004	4,031	2.2 \pm 1.4	150	0.18 \pm 0.10	10,373	2.6 \pm 1.7	422	0.17 \pm 0.06
2005	7,739	2.1 \pm 1.2	218	0.20 \pm 0.08	15,995	2.4 \pm 1.6	353	0.18 \pm 0.07
2006	1,138	3.4 \pm 1.8	46	0.22 \pm 0.12	2,648	2.7 \pm 1.9	52	0.20 \pm 0.10
2007	7,223	1.7 \pm 1.0	128	0.21 \pm 0.08	7,318	2.9 \pm 1.9	425	0.19 \pm 0.07
2008	5,570	3.2 \pm 2.3	770	0.17 \pm 0.10	3,272	2.9 \pm 2.1	168	0.15 \pm 0.08
2009	3,348	2.2 \pm 1.0	121	0.09 \pm 0.03	4,478	2.5 \pm 1.6	265	0.10 \pm 0.07
2010	1,754	2.3 \pm 1.6	184	0.11 \pm 0.07	8,080	2.4 \pm 1.7	759	0.09 \pm 0.07
2011	1,544	2.1 \pm 1.6	139	0.15 \pm 0.09	2,454	2.5 \pm 1.7	149	0.13 \pm 0.08
2012	3,772	1.9 \pm 1.1	133	0.12 \pm 0.05	4,973	2.9 \pm 1.9	512	0.14 \pm 0.07
2013	2,092	2.0 \pm 1.1	149	0.13 \pm 0.09	5,534	2.7 \pm 1.9	436	0.11 \pm 0.06
2014	1,253	2.4 \pm 1.6	96	0.23 \pm 0.11	2,669	2.5 \pm 1.8	165	0.13 \pm 0.07
All \pm SE		3.0 \pm 0.3		0.21 \pm 0.02		3.2 \pm 0.2		0.17 \pm 0.01
Low \pm SE		4.7 \pm 0.4		0.29 \pm 0.02		4.1 \pm 0.1		0.19 \pm 0.01
High \pm SE		2.4 \pm 0.2		0.19 \pm 0.02		2.7 \pm 0.1		0.15 \pm 0.01

Attributes of Natural-Origin Juveniles Emigrating through Lower Granite Reservoir

Estimated passage abundance for the basin-wide population of natural-origin, subyearling smolts at Lower Granite Dam in 2014 ranked eighth for the 23-year period of record (Table 8) even though total escapement for brood year 2013 ranked first for brood years paired with passage abundance estimates (Table 1; brood year 2014 spawners will produce offspring in 2015). The Beverton-Holt (AIC = 634.7) and Ricker (AIC = 635.1) models provided similar amounts of information about the shape of the relation between total escapement and estimated passage abundance of the basin-wide population of subyearling smolts compared to the linear (AIC = 644.4; Figure 7) model.

The median (\pm SE) date of passage of PIT-tagged, natural-origin subyearling smolts from the Snake River upper reach was later during the low abundance period compared to the high abundance period (Table 9; 6-d difference). The same pattern was observed for smolts that had been PIT tagged as parr in the lower reach, but the difference was greater than was observed for smolts from the upper reach (Table 9; a 13-d difference). In addition to the change in dispersal timing of parr from riverine habitat observed between abundance periods (Table 6), changes in downstream movement rate also contributed to the general shift in passage timing at Lower Granite Dam between abundance periods. Smolts that had been PIT-tagged as parr rearing along the Snake River upper reach moved downstream slower on average during the low abundance period compared to the high abundance period (Table 10; 1.4-km/d difference). A similar shift in rate of downstream movement was observed for smolts that had been PIT tagged as parr in the lower reach, but the difference was not as great as observed for smolts from the upper reach (Table 10; a 0.6-km/d difference).

TABLE 8. Estimated (N^{\wedge} ; 95% lower C.L.; 95% upper C.L.) passage abundance of natural-origin, subyearling fall Chinook Salmon smolts from the basin-wide population at Lower Granite Dam, 1992–2014. The means (\pm SE) of the annual estimates (All) and of the abundance periods (Low and High) are also given. Passage abundance was not estimated from November of year t through the third week of March year $t + 1$ when the Smolt Monitoring Program was not in operation and juvenile fish bypass system was dewatered.

Year	N^{\wedge}	95% Lower C.L.	95% Upper C.L.
1992	13,672	12,236	21,002
1993	15,222	14,593	19,387
1994	15,895	15,165	22,403
1995	82,797	81,367	109,757
1996	36,752	35,725	48,805
1997	298,553	274,731	461,608
1998	130,765	124,893	192,413
1999	303,808	280,765	438,467
2000	585,424	471,100	1,172,425
2001	446,497	406,453	633,339
2002	255,237	216,226	405,064
2003	683,169	663,222	873,430
2004	1,177,956	1,118,431	1,514,057
2005	558,317	481,085	910,945
2006	268,364	257,713	394,865
2007	197,907	120,629	370,693
2008	429,650	398,996	644,548
2009	406,498	385,639	552,105
2010	849,839	809,427	1,235,190
2011	423,120	413,022	547,658
2012	584,172	559,331	825,038
2013	654,498	638,684	942,771
2014	486,446	448,642	763,673
All \pm SE	387,154 \pm 61,306		
Low \pm SE	112,183 \pm 43,656		
High \pm SE	533,806 \pm 64,274		

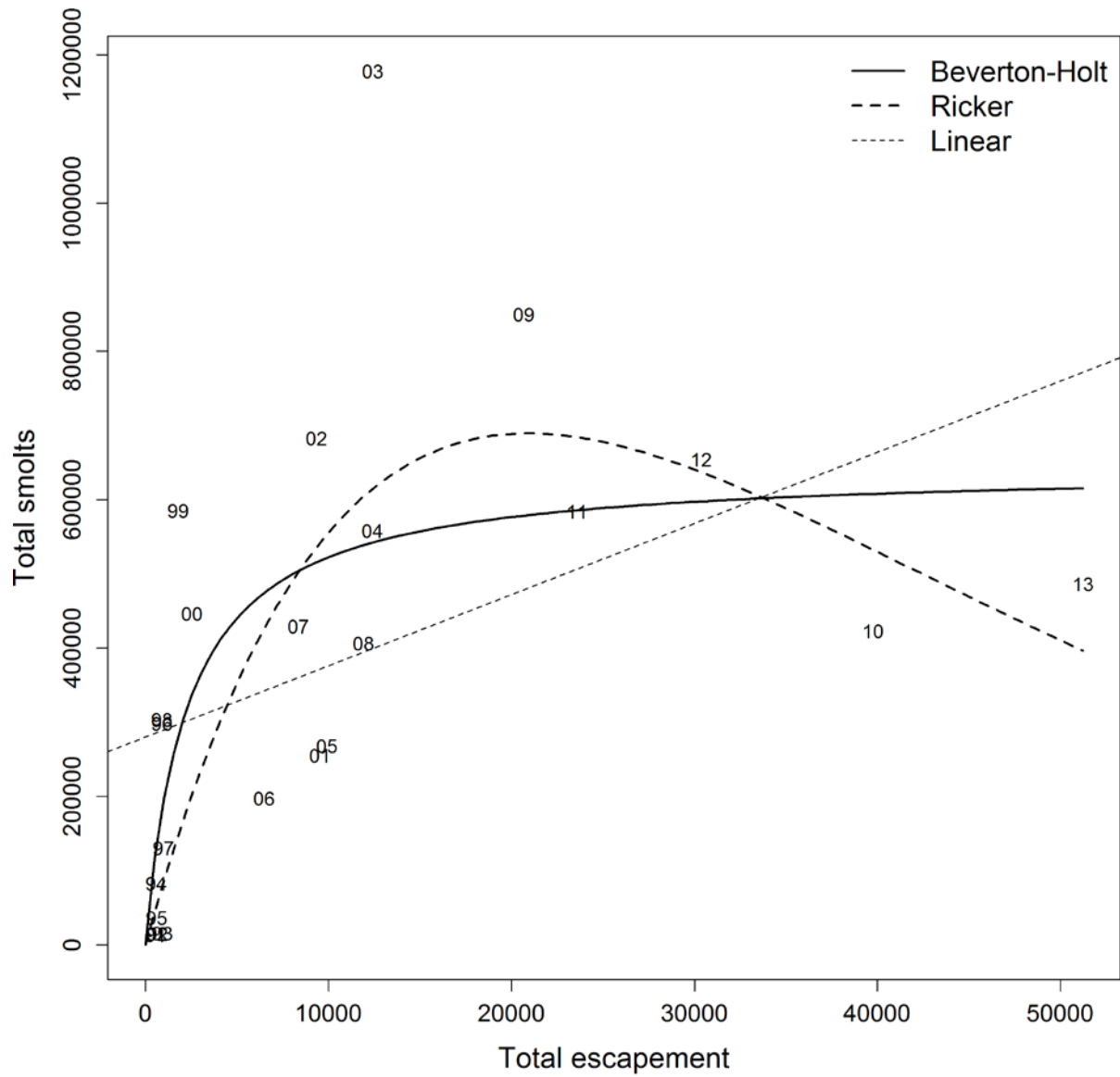


FIGURE 7. The relation between total escapement (Table 1) and estimated annual passage abundance of natural-origin, subyearling smolts from the basin-wide population at Lower Granite Dam (Table 8), 1992–2014. Passage abundance was not estimated from November of year t through the third week of March year $t + 1$. The numbers are the last two digits of the brood year. The parameters (\pm SE) for the Beverton-Holt and Ricker models (of similar fit) were: $\alpha = 2.783\text{e}+02 \pm 1.514\text{e}+02$ and $\beta = 4.327\text{e}-04 \pm 2.823\text{e}-04$; and $\alpha = 8.955\text{e}+01 \pm 1.779\text{e}+01$ and $\beta = 4.778\text{e}-05 \pm 9.298\text{e}-06$.

TABLE 9. Median dates of passage at Lower Granite Dam for natural-origin, subyearling smolts that were PIT tagged along the Snake River upper and lower reaches, 1992–2014. Estimated annual passage abundance (N^{\wedge}) of the PIT-tagged fish, the means (\pm SE) of the annual medians (All), and of the abundance period medians (Low and High) are also given.

Year	Upper reach		Lower reach	
	N^{\wedge}	Median	N^{\wedge}	Median
1992			85	06/22
1993			514	07/22
1994			464	07/17
1995	401	07/18	490	08/02
1996	47	06/29	256	07/18
1997	55	06/20	215	07/16
1998	356	07/07	752	07/11
1999	712	06/26	556	07/27
2000	203	06/19	544	07/02
2001	20	07/10	374	07/07
2002	314	07/01	1,161	07/04
2003	642	06/24	1,697	06/27
2004	337	06/24	2,911	06/24
2005	1,059	06/20	2,941	06/24
2006	335	06/15	410	06/27
2007	238	06/18	1,260	06/25
2008	1,386	07/01	957	07/17
2009	405	06/22	1,032	07/03
2010	263	07/02	2,014	07/12
2011	402	06/17	593	07/12
2012	674	06/25	1,559	07/09
2013	179	07/01	903	07/04
2014	249	07/02	971	07/14
All \pm SE		06/27 \pm 2		07/09 \pm 2
Low \pm SE		07/02 \pm 5		07/17 \pm 4
High \pm SE		06/26 \pm 2		07/04 \pm 2

TABLE 10. Median, minimum, and maximum rates of downstream movement (km/d) for natural-origin parr that were PIT tagged along the Snake River upper and lower reaches and subsequently detected at Lower Granite Dam as subyearling smolts, 1992–2014. The inter-annual means (\pm SE) of the annual medians (All) and of the abundance period medians (Low and High) are also given.

Year	Upper reach				Lower reach			
	<i>N</i>	Median	Min	Max	<i>N</i>	Median	Min	Max
1992					39	3.3	1.1	18.8
1993					248	1.5	0.2	19.7
1994					201	1.5	0.2	13.8
1995	203	3.4	1.1	44.7	239	1.5	0.4	20.3
1996	19	3.7	2.1	43.7	126	1.5	0.4	19.3
1997	24	5.3	1.7	70.5	111	2.0	0.2	21.6
1998	175	3.4	0.5	20.1	384	2.0	0.2	28.3
1999	326	4.7	1.0	35.0	280	2.1	0.4	19.5
2000	72	5.4	2.6	19.9	263	1.9	0.2	13.6
2001	10	3.6	1.3	4.5	185	1.8	0.5	15.0
2002	96	4.6	0.5	25.0	397	2.3	0.2	19.3
2003	304	5.3	2.3	43.7	815	2.5	0.2	29.5
2004	186	5.0	2.9	21.9	1,599	2.6	0.3	21.3
2005	314	6.0	2.9	26.3	673	3.4	0.3	19.7
2006	96	8.0	3.5	58.3	103	3.0	0.6	45.0
2007	37	5.3	3.8	13.5	182	2.8	0.2	15.6
2008	360	5.3	0.6	87.5	211	2.1	0.5	57.0
2009	145	4.9	2.2	29.8	320	2.5	0.3	42.5
2010	72	6.8	2.8	61.7	475	2.9	0.3	58.0
2011	167	7.6	2.4	64.3	233	3.4	0.3	59.0
2012	163	5.0	2.2	59.7	305	2.5	0.2	42.5
2013	33	4.1	2.6	29.2	143	2.3	0.4	21.8
2014	61	5.4	2.1	46.2	198	2.2	0.5	27.3
All \pm SE		5.1 \pm 0.3				2.3 \pm 0.1		
Low \pm SE		4.1 \pm 0.4				1.9 \pm 0.2		
High \pm SE		5.5 \pm 0.3				2.5 \pm 0.1		

Seasonal Variation in Smallmouth Bass Diets and Consumption of Subyearling Chinook Salmon during Rearing in Riverine Habitat

Smallmouth Bass abundance varied seasonally among river sections. Smallmouth Bass abundance in shoreline areas during biweekly sampling intervals ranged from 10,725 to 42,613 in the lower section in the Snake River lower reach, from 26,640 to 35,135 in the middle section in the Snake River lower reach, and from 23,645 to 55,398 in the upper section in the Snake River upper reach.

We captured 2,573 Smallmouth Bass for dietary analysis which ranged in size from 150 mm to 509 mm. Smallmouth Bass diets varied both between reaches and weeks when examined on a percent weight basis (Figure 8). Diets in the lower section were mainly composed of sand rollers and crayfish, while salmonids only comprised a large portion (51%) by weight during the week of 21 April. Diets in the middle section were mainly composed of salmonids through May and then were composed of crayfish for the remaining weeks. Sculpin comprised most of the diet by weight in the upper section from 24 March to 7 April, followed by insects (57%) during 5 May, salmonids (49%) during 19 May, and crayfish (78%) during 2 June. During the week of 19 May, the portion of salmonids in bass diets increased from 3% before a release of hatchery fish to 71% after the release.

Total loss of subyearling Chinook Salmon to Smallmouth Bass predation within our study area in 2014 was estimated to be 603,812 (Table 11). The highest loss was observed in the upper section (403,817 fish) and most of this was influenced by the estimated loss of 200,791 fish following a hatchery release during the week of 19 May. The estimated subyearling loss in the middle section was 134,936 fish. Loss was lowest in the lower section (68,059 fish), which might be due to the abundance of Sand Rollers *Percopsis transmontana* that might alleviate some of the predation pressure on subyearlings.

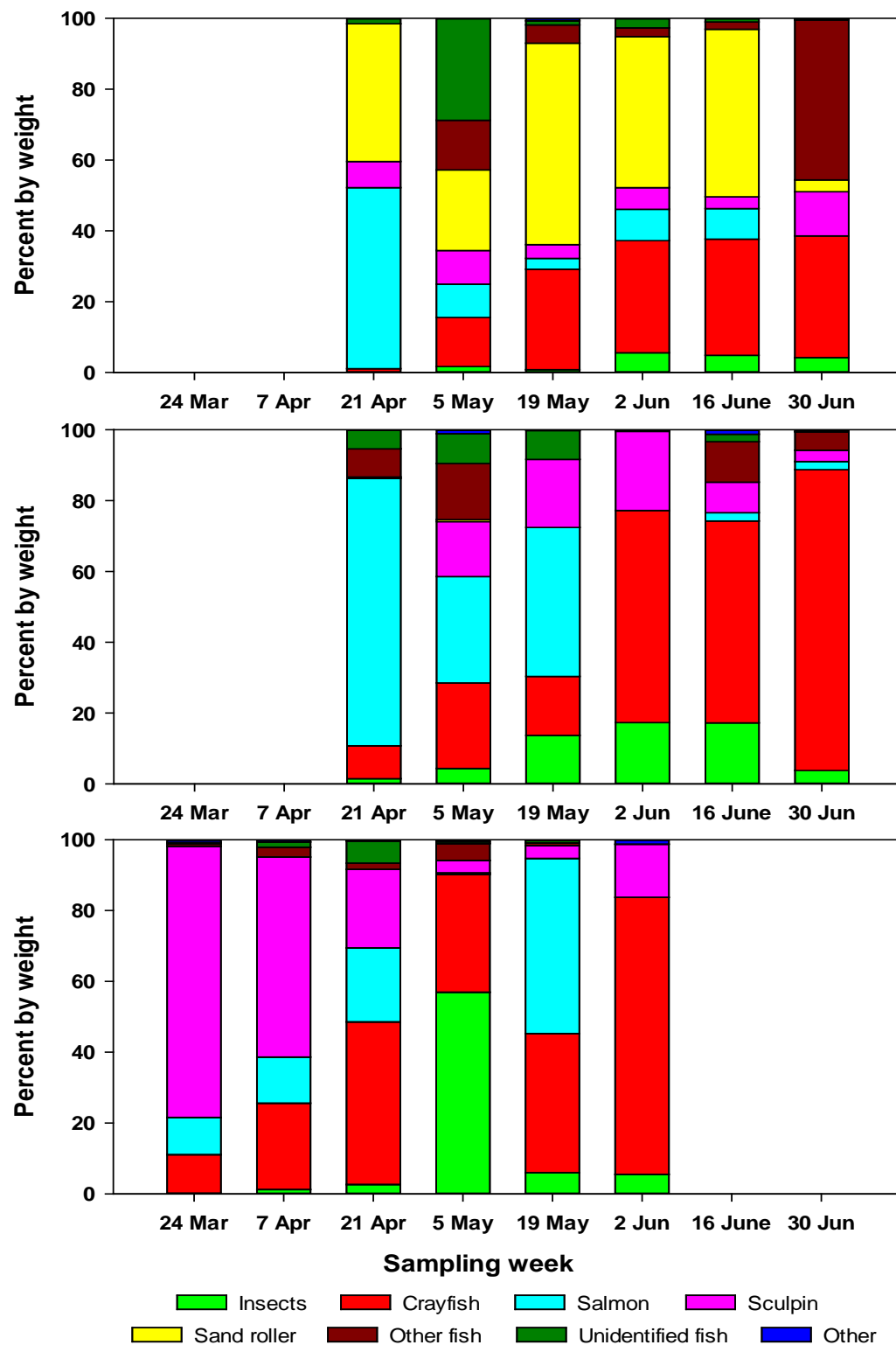


FIGURE 8. Seasonal variation in diet composition (percent weight based on non-empty stomachs) of Smallmouth Bass in the lower section (top panel), middle section (middle panel), and upper section (bottom panel) of the free-flowing Snake River reaches in 2014.

TABLE 11. Estimated losses (95% CI) of juvenile salmonids in the upper, middle, and lower sections of the free-flowing Snake River reaches in 2014.

Week	Salmonids	95% CI	Chinook	95% CI	Subyearling Chinook	95% CI
Lower						
21-Apr	24,442	8,335-102,517	24,155	8,237-101,311	16,908	5,766-70,918
5-May	16,449	4,247-103,810	16,449	4,247-103,810	12,337	3,185-77,858
19-May	12,179	4,213-49,241	11,999	4,151-48,517	11,999	4,151-48,517
2-Jun	4,617	1,704-20,488	4,617	1,704-20,488	4,617	1,704-20,488
16-Jun	22,198	5,509-60,105	22,198	5,509-60,105	22,198	5,509-60,105
30-Jun	0		0		0	
Section Total	79,885		79,418		68,059	
Middle						
21-Apr	86,948	30,723-260,313	85,925	30,361-257,250	60,147	21,253-180,075
5-May	60,979	25,603-170,877	60,979	25,603-170,877	45,734	19,202-128,158
19-May	24,436	8,078-83,819	24,077	7,960-82,586	24,077	7,960-82,586
2-Jun	0		0		0	
16-Jun	4,978	2,325-12,690	4,978	2,325-12,690	4,978	2,325-12,690
30-Jun	11,318	4,144-28,868	0		0	
Section Total	188,659		175,959		134,936	
Upper						
24-Mar	74,483	36,444-168,134	74,483	36,444-168,134	46,924	22,959-105,924
7-Apr	80,678	34,337-210,137	78,270	33,312-203,864	75,922	32,313-197,748
21-Apr	96,904	35,253-278,147	95,764	34,839-274,875	67,035	24,387-192,413
5-May	17,527	8,317-39,573	17,527	8,317-39,573	13,145	6,238-29,679
19-May	200,791	82,802-506,138	200,791	82,802-506,138	200,791	82,802-506,138
2-Jun	0		0		0	
Section Total	470,383		466,835		403,817	
Study Total	738,927		722,212		603,812	

Discussion/Conclusion

Attributes of Spawning in Riverine Habitat

The functional growth relations that we modeled, between total escapement and the number of shallow and deep sites used, were the first of several lines of evidence for density dependence in this report. The functional growth relation between total escapement and the numbers of shallow and deep redds counted provided growing but relatively weak evidence for density dependence as clear maximums were not attained. Together, the four curve fitting exercises for attributes of spawning showed that most of the suitable spawning habitat has been used by spawners, but the habitat has not reached redd capacity. In support of that conclusion, the maximum redd count observed in the Snake River reaches was 3,263 or 1,179 below the estimated redd capacity of 4,442 for the river (Groves et al. 2013). We are questioning the accuracy of our redd counts in recent years, however, because the large numbers of redds are difficult to count from the air especially when redds are superimposed. Superimposition occurs when a new redd is constructed on top of one or more previously constructed redds. In addition to being a source of counting error, that process can dislodge eggs in the previously constructed redds and be the underlying mechanism leading to the Beverton-Holt and Ricker-type recruitment we reported earlier.

In cooperation with staff of the Idaho Power Company who pioneered the use of Unmanned Aerial Systems (UAS) for counting redds, we worked with statisticians from the University of Idaho to design and implement a study to improve monitoring of superimposition and accuracy of our redd counts. That effort will hopefully come to fruition in 2015. For the present, superimposition is likely common in the Snake River reaches at the spawner escapement levels observed in recent years. In 2014, video taken from a UAS was used to determine that

some superimposition occurred at 43% of the sites used along the Snake River reaches, and that heavy superimposition occurred at 28% of the sites used (P. Groves, Idaho Power Company, unpublished data). Continued collection of redd count data will aid in monitoring and managing the recovery of the Snake River fall Chinook Salmon ESU.

Attributes of Natural-Origin Juveniles Rearing in Riverine Habitat and Emigrating through Lower Granite Reservoir

We found that recruitment of natural-origin fall Chinook Salmon subyearlings assessed based on CPUE declined at high total escapements (i.e., overcompensation or Ricker-recruitment). The three most plausible causes of that decline are redd superimposition, egg predation, and juvenile predation. As mentioned, superimposition has only been assessed in 2014. Additional analyses of video footage collected by UAS in earlier years would be informative. White Sturgeon *Acipenser transmontanus* have been observed along the Snake River reaches hovering over redds in both underwater and UAS video footage (P. Groves, Idaho Power Company, unpublished data). That footage provides circumstantial evidence for egg predation. Ongoing research by staff of project 199102900 (described later in this report) has also provided evidence that predation on natural-origin fall Chinook Salmon subyearlings by Smallmouth Bass has increased as total escapement of fall Chinook Salmon spawners has increased. Evidence for density dependent mechanisms, however, is not solely limited to the spawning life stage or predator/prey interactions.

Intra-specific density-dependent mechanisms during rearing in riverine habitat are also evident in this report. Growth rates of natural-origin parr in riverine rearing habitat declined slightly as parr abundance increased. Timing of downstream dispersal into the reservoir was also

earlier and dispersal size decreased between abundance periods. One explanation for the lack of a large difference in parr growth between abundance periods is that the recaptured PIT-tagged natural-origin parr were the larger more competitive members of the riverine population. Such winners could maintain growth under high fish densities if smaller, less competitive conspecific losers dispersed downstream in sufficient numbers to preserve adequate growth conditions for the winners (Reimers 1973; Chandler and Bjornn 1988; Grant and Kramer 1990). This social hierarchy would result in an overall shift to earlier dispersal of the population, and a decrease in the mean size at dispersal with only a slight effect on the growth or size of the winners.

Our results on growth, passage, and size of natural-origin subyearling smolts in Lower Granite Reservoir provided ample evidence for density dependence. In addition to finding evidence for Beverton-Holt and Ricker-type recruitment, smolt growth declined between abundance periods in association with density-dependent changes in size at dispersal from riverine habitat, migrational behavior in the reservoir, and increased concentrations of subyearling smolts in the reservoir as the hatchery program expanded. In turn, time of passage through the reservoir of natural-origin smolts became earlier and smolt size decreased. During the low abundance period, natural-origin smolts also remained in the reservoir later into the summer, which allowed them to experience warmer temperatures and grow to larger sizes. However, during the high abundance period, natural-origin smolts spent more time migrating and less time lingering and feeding resulting in passage through the reservoir before they could benefit from warmer water temperatures that favored growth.

In contrast to our findings on natural-origin parr in riverine habitat, we found little evidence of winners in Lower Granite Reservoir during the high abundance period as there were marked differences between abundance periods not only in smolt growth, but in the presence of

large smolts. This finding raises the question “does density-dependent movement behavior vary between riverine and impounded habitats?” The riverine habitat studied was more structurally complex than the reservoir, and complex habitats can encourage juvenile fish to establish territories for feeding and holding in energetically profitable positions (Fausch 1984; Rosenfeld and Boss 2001; Venter et al. 2008). The presence of some fish with established territories yields greater dispersal of fish without territories (Keeley 2001) as we observed for natural-origin parr in riverine habitat. Natural-origin smolts in the reservoir resided in homogenous habitat with decreased complexity, lower velocities and increased depths, and the shoreline orientation of fish declined (Connor et al. 2003a; Tiffan et al. 2009). The influence of a similar change in habitat complexity on fish behavior was observed in the estuary of the Sixes River, Oregon, where fall Chinook subyearlings switched from antagonistic to schooling behavior when velocities declined during flood tides (Reimers 1968). Moreover, schooling was the most common social behavior displayed by subyearlings rearing in homogenous, low-velocity habitats in the Hanford Reach of the Columbia River, Washington (Tiffan et al. 2010).

Connor et al. (2013) hypothesized that density-dependent schooling behavior played a role in shaping the phenotypic changes observed in natural-origin smolts as they passed downstream in Lower Granite Reservoir. When smolt abundances were low in the reservoir, schools of natural-origin smolts were likely small and widely spaced with little social pressure to move. As discussed by Hoar (1958), a key point in the Keenleyside (1955) definition of a fish school is that “the chief factor common to all schools is a definite mutual attraction between individuals.” Such mutual attraction was likely enhanced between schools of natural-origin and hatchery smolts in the low-velocity reservoir as abundance increased. Furthermore, hatchery smolts in Lower Granite Reservoir tend to migrate more than linger and feed (Connor et al.

2004). Schooling with actively migrating hatchery smolts could intermittently move some natural-origin fish long distances downstream over short periods of time, while sustaining downstream movement in others (e.g., *Salmo salar*; Hansen and Jonsson 1985). This phenomenon referred to as the “pied-piper” effect (Hillman and Mullins 1989) would partly explain our reservoir findings because natural-origin smolts that temporarily or permanently joined schools of hatchery smolts would spend more time migrating, less time feeding, arrive at Lower Granite Dam early, and be exposed to relatively cool seasonal temperatures.

Attributes of Seasonal Variation in Smallmouth Bass Diets and Consumption of Subyearling Chinook Salmon during Rearing in Riverine Habitat

Our results suggest that both Smallmouth Bass abundance and consumption of subyearlings has increased since the 1990s. Our estimates of Smallmouth Bass abundance were much higher than those estimated by Nelle (1999). Our estimates in the lower and middle reaches combined were more than double that reported by Nelle (1999) for bass ≥ 150 mm. There may be a number of reasons for this. First, we marked and recaptured fish at six biweekly intervals at the same time fish were being sampled for consumption. Our use of an open population model produced more robust estimates of abundance, although the wide confidence intervals surrounding the estimates suggest there is room for improvement. In contrast, Nelle (1999) conducted only one mark-recapture event in the fall of 1997, well after his consumption data were collected. Seasonal differences in Smallmouth Bass habitat use and the low effort used to mark and recapture fish may explain the differences in abundance between the two studies. Second, the population of Smallmouth Bass may have increased over time in response to the increase in the subyearling population or other factors such as an increase in productivity low in

the food chain in response to nutrients supplied by carcasses of spawners. Given the differences in how abundances were estimated between the two studies, it would be difficult to confirm this fact definitively.

We also found significantly higher consumption rates and loss of subyearlings in our study compared to that of Nelle (1999). Nelle (1999) found consumption rates ranged from 0 to <0.009 subyearling/Smallmouth Bass/day. By comparison, most consumption rates in our study exceeded 0.05 subyearling/Smallmouth Bass/day. Nelle (1999) estimated total losses of subyearlings to range from 714 to 5,347 during 1996 and 1997 (depending on differing estimation models), whereas our loss estimates for the same section ranged from 68,000 to over 400,000 fish. One reason loss of subyearlings may be higher today is because there are more subyearlings as a result of hatchery supplementation and natural production. However, a large portion of that production is being consumed by Smallmouth Bass.

It is important to recognize the limitations of this study. Estimates of predation losses of juvenile Salmon are sensitive to the size of the predator population. Estimating Smallmouth Bass abundance over 130 km of river is a difficult task and adds uncertainty to estimates. Many models and equations are used to ultimately estimate loss and each has some associated level of error and assumptions. One area of uncertainty that needs to be addressed is how Smallmouth Bass consumption rates change in response to hatchery releases. We suspect that predators are initially swamped, but high feeding rates are likely not sustained through time because hatchery fish tend to quickly disperse downstream. Understanding this would improve our estimates of loss, particularly surrounding a hatchery release.

Adaptive Management & Lessons Learned

Multistage life cycle models provide a powerful framework for understating how each life stage of a population contributes to population growth rate (Moussalli and Hilborn 1986; Brooks and Powers 2007). When used for simulation, multistage models allow the relative effects of density dependence at different life stages to be explored in the context of management actions including Fish Population RM&E, Hydrosystem RM&E, Harvest RM&E, Hatchery RM&E, Predation and Invasive Species Management RM&E. For example, by using a multistage model, Greene and Beechie (2004) found that the importance of habitat restoration to population recovery of Chinook Salmon depended on the mechanisms of density dependence affecting particular life stages.

Multistage models may also be used as an analytical framework to explicitly estimate demographic parameters of a population model. This approach has an advantage over single-stage stock-recruitment models by allowing population growth rates to be partitioned among life stages rather than aggregated over an entire life cycle. Such partitioning allows for estimating 1) stage-specific estimates of density dependence, and 2) stage specific effects of environmental factors or management actions. Zabel et al. (2005) estimated parameters of a multistage model used in the context of a population viability analysis spring/summer Chinook Salmon in the Snake River, but such an approach has yet to be applied to fall Chinook Salmon in the Snake River basin.

Typically, data informing estimates of abundance at particular “check points” in the life cycle dictates the complexity of multistage models that can be fit to data. For fall Chinook Salmon, we will start with a two-stage model that encompasses: 1) upstream passage of

spawners at Lower Granite Dam to the subsequent the downstream passage of their progeny at the Dam, and 2) downstream passage of juveniles at Lower Granite Dam to their subsequent return from the ocean and passage at the Dam 3–5 years later. This approach partitions the life cycle of fall Chinook Salmon both spatially and temporally, which will allow us to fit and compare alternative models with covariates specific to each stage. We are building such a model while participating in the Adaptive Management Implementation Plan process where ideas on model development are shared among the members. Information is also presented at AFS meetings and regional forums to disseminate it and receive useful feedback from peers.

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Appendices

A.1: Data Links

Redd count data: Available:<http://www.fpc.org/>

PIT-tag data: Available:<http://www.ptagis.org/>

Other data is backed up on site and remotely. Inquires can be sent to william_connor@fws.gov or ktiffan@usgs.gov.

A.2: Bibliography of Published Journal Articles (N = 42)

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***A.3: Smallmouth Bass predation on juvenile fall Chinook Salmon in Hells
Canyon of the Snake River, 2014***

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Introduction

Predation by nonnative fishes is one factor that has been implicated in the decline of juvenile Salmonids *Oncorhynchus* spp. in the Pacific Northwest. Smallmouth Bass *Micropterus dolomieu* were thought to have first been stocked into the Snake River basin in the late 1800s to provide angling opportunities (Munther 1970). Smallmouth Bass were actively stocked in the Snake River by the Idaho Department of Fish and Game in 1941, and have become the most abundant predator in the unimpounded Hells Canyon Reach of the Snake River (Nelle 1999) and its lower reservoirs (Zimmerman and Parker 1995). This is a particular concern for Snake River fall Chinook Salmon *O. tshawytscha* subyearlings because their relatively small size and the overlap of their main-stem rearing habitats with that of Smallmouth Bass may make them particularly vulnerable to predation (Curet 1993; Tabor et al. 1993).

Concern over juvenile Salmon predation precipitated a number of large-scale studies to quantify its effect in the late 1980s, 1990s, and early 2000s (Poe et al. 1991; Rieman et al. 1991; Vigg et al. 1991; Fritts and Pearsons 2004; Naughton et al. 2004). In transitional habitat between the Hanford Reach of the Columbia River and McNary Reservoir, juvenile Salmon (presumably subyearlings) were found in 65% of Smallmouth Bass (>200 mm) stomachs and composed 59% of the diet by weight (Tabor et al. 1993). Within the upper portion of Hells Canyon on the Snake River, Nelle (1999) reported that subyearlings only made up 1.9% and 0.8% of Smallmouth Bass diets by weight in 1996 and 1997, respectively. However, this study in the Snake River was conducted soon after Endangered Species Act (ESA) listing of Snake River fall Chinook Salmon (NMFS 1992). During this time, fall Chinook Salmon abundance was at an historic low and may explain why Smallmouth Bass consumption rates were relatively low compared to those from studies conducted in the Columbia and Yakima rivers where Salmon abundance was higher (Tabor et al. 1993; Fritts and Pearsons 2004).

We speculate that predation on subyearlings by Smallmouth Bass in the Snake River may have increased in recent years for several reasons. Since their ESA listing, recovery measures implemented for Snake River fall Chinook Salmon have resulted in a large increase in the juvenile population (Connor et al. 2013). For example, the annual subyearling passage index at Lower Granite Dam, the first dam encountered by fish produced in Hells Canyon, was 18,533 in 1996 but was 960,893 in 2014 (DART 2015). Both Zimmerman (1999) and Naughton et al. (2004) showed that fish can comprise a large portion of Smallmouth Bass diets. Considering that subyearlings probably now make up a larger portion of the forage fish population, it is plausible they should make up a large portion of smallmouth diets. We initiated a study in 2012 to re-examine Smallmouth Bass predation on subyearlings in Lower Granite Reservoir. Our objectives were to 1) describe the seasonal variation in Smallmouth Bass diets during the April-July subyearling rearing and outmigration period, and 2) estimate the abundance of Smallmouth

Bass and quantify their consumption of subyearlings. This report summarizes data collected in 2014.

Study Area

We conducted our study within Hells Canyon between Asotin, Washington (river kilometer [rkm] 234) and Sheep Creek Rapids (rkm 369). The Snake River flows through Hells Canyon in a northwesterly direction through a semi-arid environment of steep canyon walls of basalt. The overall mean gradient in this reach is 1.1 m/km and mean width is 142 m (Nelle 1999). Shoreline substrates consist mainly of bedrock, large boulders, and cobble interspersed with occasional small sandy beaches.

We divided the study area into three reaches for logistical ease of sampling. The lower reach extended from Asotin, Washington, upstream to the mouth of the Grande Ronde River (rkm 272). The middle reach extended from the mouth of the Grande Ronde River upstream to the mouth of the Salmon River (rkm 303). The upper reach extended from the mouth of the Salmon River upstream to Sheep Creek Rapids. The upper reach encompasses the “upper section” sampled by Nelle (1999), whereas the lower and middle reaches combined correspond to the “lower or downstream section” sampled by Nelle (1999).

Methods

Smallmouth Bass collections

We collected Smallmouth Bass in each reach using angling or boat electrofishing. ESA permit restrictions required us to use angling once water temperatures exceeded 18°C.

In 2014, we used the same four fixed-sampling locations within each reach (upper, middle, lower) that we used in 2013. We refer to these as fixed sites, which were chosen to examine site-specific changes in consumption over time. We supplemented the fixed-sampling sites with randomly chosen sites (without replacement) from a pool of river kilometer starting locations delineated to 0.1 km.

Each fixed site sampled by angling in 2014 included both banks of the river and each bank was sampled for about 200-800 m in length for 75 minutes by one boat with 2-3 people. In 2014, sampling was conducted biweekly in the upper section from 24 March to 2 June. Sampling was not continued in the upper reach thereafter because water temperatures became too warm and it was assumed that most juvenile Salmonids had migrated further downstream. Sampling in the lower and middle reaches was conducted from 21 April to 30 June. Daytime electrofishing was conducted in the lower reach from 21 April to 30 June, and in the middle reach from 21 April to 19 June. The shorelines of each site were sampled in a downstream

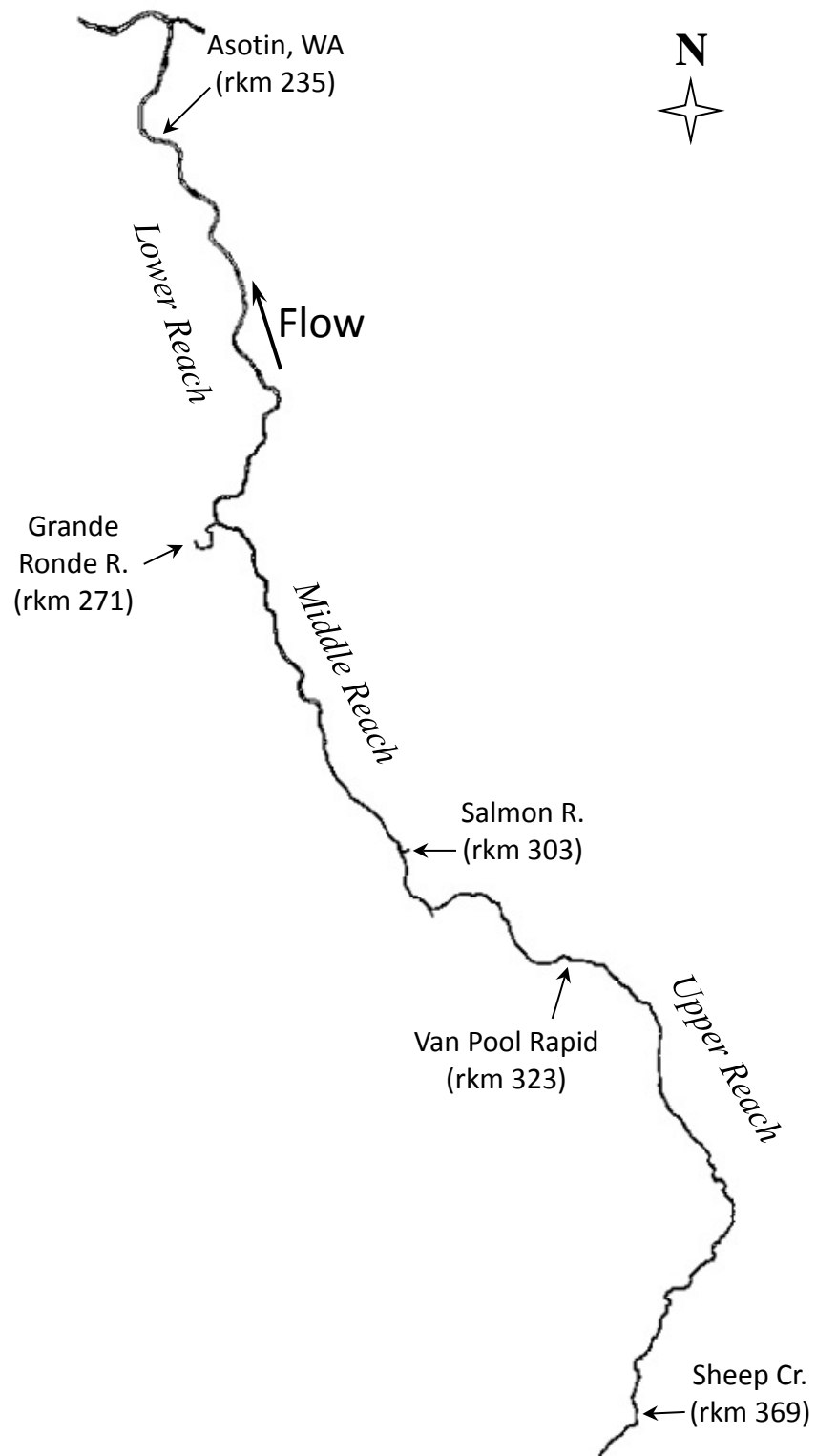


Figure 1. Map of Hells Canyon showing the upper, middle, and lower reaches and other land marks.

direction from the starting point. The time and distance sampled were recorded for each site. Electrofishing output was 400 V DC with 60 pulses per second at 2-4amps. Smallmouth Bass were collected by 1-2 dipnetters. Angling was conducted during all sampling weeks in the upper reach and during the week of 30 June in the lower and middle reaches. In addition to sampling biweekly, we sampled both before and after a hatchery release in the upper reach because hatchery releases in 2013 had a major effect on total Salmonid loss estimates. This was a release of production subyearlings (on 19 May) in the tailrace of Hells Canyon Dam that were reared at the Irrigon Hatchery. Our sampling began prior to the release on 19 May and after the release on 20 May.

All captured Smallmouth Bass were placed in an aerated live well supplied with recirculating water and held no longer than 80 minutes for electrofishing events and 25-80 minutes for angling events before being processed and released. All fish over 150 mm TL were measured then tagged with a unique Floy tag. Weights were measured on about 5 bass at each site. Weights for the remaining bass were estimated from a regression we developed from the length and weight data collected in 2014 along with data collected in 2012 and 2013. The regression was:

$$Wt = 0.000008TL^{3.09} \quad (1)$$

where Wt is the weight (g) and TL is the total length (mm; $N=3,339$, $R^2=0.93$).

At each sampling site, we collected the stomach contents from all Smallmouth Bass using modified non-lethal lavage (Seaburg 1957). The lavage instrument consisted of a 6 mm (¼”) tube connected to a common garden spray nozzle that supplied filtered river water via a wash-down pump installed on the boat. Stomach contents were collected in a 425µm sieve and preserved in 90% ethanol.

Smallmouth Bass abundance

We calculated catch-per-unit-effort (CPUE) for both angling and electrofishing to compare the efficiency of each method. CPUE for each reach and sampling week was calculated as the total number of Smallmouth Bass collected divided by the total sampling time (min). For purposes of CPUE calculations, each fixed location consisted of two sites (one for each bank).

We used an open population mark-recapture model in program MARK (White and Burnham 1999) to estimate weekly abundances of Smallmouth Bass in each reach because we sampled four fixed sites/reach throughout the study (described above). The POPAN parameterization of the Jolly-Seber model (Schwarz and Arnason 1996) was used to derive estimates of abundance for each sampling occasion for each fixed site (both banks pooled). A

fully time-dependent model and models with constant survival and catchability (p) were fit and Akaike's Information Criterion (AIC) was used to determine the best overall model. Because estimates could not be derived for the first and last sampling occasion, we estimated abundances for these time periods in each site by regressing weekly CPUE against weekly abundances (for the weeks where they could be derived) and predicting the first and last abundances from the CPUE estimates. The abundance estimates (and CIs) for the fixed sites were then divided by the number of meters sampled (MS_r) to determine the number of fish per meter of shoreline at each site. The mean bass/m was calculated from all four fixed sites per reach and then extrapolated to the number of total meters of shoreline in each reach.

Diet analysis

Smallmouth Bass diet items were identified to the lowest practical taxon in the laboratory and were placed into four groups: insects, crustaceans, fish, and other. All diet items were then enumerated, blotted for 30 s, and weighed (± 0.001 g). All insects were identified to order and unidentifiable insect parts were not enumerated, but were weighed together as a group. Crustaceans were identified to order and where possible to genus and species. All other prey that could not be assigned to a group were classified as "other" and often consisted of vegetation, rocks, and worms. Ingested fish were identified to lowest possible taxon (usually species) using diagnostic bones (i.e., dentary, cleithrum, opercle; Parrish 2006). Fish remains were soaked in warm water to soften muscle tissue which was then scraped from the bones. Bones were measured with an ocular micrometer mounted in a dissecting scope. We back-calculated fork length at ingestion for individual Salmonid and other prey fish consumed using species-specific bone-length regressions from the literature (Hansel et al. 1988) or to standard length (SL) with regressions developed by this study (Table 1). We used additional regressions to calculate FL from SL, nape to tail lengths, or dorsal standard lengths when necessary (Vigg et al. 1991; Parrish et al. 2006). Fish remains that did not contain diagnostic bones were classified as "unidentified" and were weighed. When a sample only contained unidentifiable fish parts along with a diagnostic bone, we associated all weight to the species identified.

The diet composition of Smallmouth Bass was examined in each reach on a bi-weekly basis. We determined the frequency of occurrence (number of samples with specific prey/number of stomachs examined) and percent diet composition of different prey types based on non-empty stomachs only. These metrics were also calculated for the before and after hatchery release events. We also calculated the maximum relative length of prey fish consumed by Smallmouth Bass (original prey fish FL/bass TL * 100) to determine the size of prey vulnerability.

Table 1. Linear regressions for predicting various measures of fish length based on measurements of diagnostic bones of Chinook Salmon. Regression models take the form of $y=a+bx$, where y is the fish length (mm) to be estimated, a is the intercept, b is the slope, and x is the measure of the diagnostic bone (mm).

Fish length measure	N	a	b	r^2
Cleithrum				
Fork length	31	1.983	7.347	0.96
Standard length	114	-0.408	6.984	0.95
Dentary				
Fork length	30	14.823	7.819	0.83
Standard length	96	13.291	7.499	0.80
Opercle				
Fork length	12	9.844	10.888	0.89
Standard length	29	10.485	9.884	0.80

Consumption

We used a series of regressions to estimate the daily consumption of juvenile Salmonids by Smallmouth Bass (≥ 150 mm) in each reach. Consumption rate (C ; number of Salmonids consumed/bass/day) was calculated as:

$$C = n/N, \quad (2)$$

where n is the number of Salmonids consumed within 24 hours of capture, and N is the total number of bass stomachs examined (including stomachs that were empty). First, we calculated the original weight of each prey fish at ingestion (WI) for each bass stomach sample that contained at least one Salmonid by using length-weight regressions (Vigg et al. 1991, Parrish 2006) with the back-calculated length at ingestion (described above). Next, we calculated meal weight (MW) using an equation similar to Vigg et al. (1991) for individual bass that had prey fish in their stomach where the digested weight was within 90% of WI (WI_{90}):

$$MW = \sum_{i=1}^{np} WI_{90} + O, \quad (3)$$

where np = the number of prey fish in the stomach contents of an individual bass (that were <90% digested) and O is the digested weight of all other prey items (mainly insects and crustaceans) in the sample. We also included all digested weights of prey fish that were not within 90% of original weight in the calculation of E because meal weight has an impact on evacuation rates (Rogers and Burley 1991). We used 90% digestion (after Rogers and Burley 1991) because indigestible parts could remain in the gut of fish for long periods of time. Next, we input MW into an evacuation model developed for Smallmouth Bass digestion rates of Salmonids by Rogers and Burley (1991):

$$E = MW[1 - \exp(-0.005tMW^{-0.29}e^{0.15T}W^{0.023})]^{1.95}, \quad (4)$$

where T is temperature ($^{\circ}\text{C}$; measured at time of sample collection), W is bass weight (g; also taken at time of sample collection), and t is hours (set to 24). If the amount of food projected to be evacuated (E) in 24 h was less than the total digested weight of the meal at the time the bass was collected, then the salmonids were included in the calculation for daily consumption rate (n in equation 2) because they would have been consumed within the past 24 h.

We estimated the total loss of juvenile Salmonids to predation by Smallmouth Bass using a similar equation to Rieman et al. (1991):

$$L_{ir} = \hat{N}_{ir}C_{ir}D_i \quad (5)$$

where L_{ir} is the loss of Salmonid during sampling interval i in reach r , \hat{N}_{ir} represents the bi-weekly abundance estimate of Smallmouth Bass for each reach r , C_{ir} is the consumption rate during sampling interval i for section r (equation 2) and D_i is the number of days in sampling interval i (i.e., 14).

Results

Abundance

Relative abundance.—In 2014, we sampled a total of 161 sites by angling (97 random and 64 fixed site events) and 113 sites by electrofishing (12 random and 101 fixed site events; Table 2). We angled for 6,069 minutes and collected 1,435 bass, most of which were collected in the upper reach. A total of 2,049 minutes were expended electrofishing which collected 1,487 bass. In 2014, 0.73 Smallmouth Bass were collected per minute of electrofishing whereas only 0.24 bass per minute were caught by angling (Table 2).

Table 2. Seasonal catch-per-unit-effort of Smallmouth Bass collected by angling and boat electrofishing in three sections in Hells Canyon of the Snake River, 2014. Effort was calculated from total minutes angled by individual boat or total time electrofishing.

Week beginning	Method	Site Type	Number of sites	Effort (minutes)	Number captured	Number per site	Number per minute
Lower							
4/21/14	EF	Fixed	9	157	40	4.44	0.26
	Angling	Random	4	70	1	0.25	0.01
	EF	Random	2	29	2	1.00	0.07
5/5/14	EF	Fixed	7	132	60	8.57	0.46
5/19/14	EF	Fixed	8	134	86	10.75	0.64
	EF	Random	5	88	90	18.00	1.02
6/2/14	Angling	Fixed	1	31	2	2.00	0.06
	EF	Fixed	8	161	142	17.75	0.88
6/16/14	EF	Fixed	15	332	335	22.33	1.01
	Angling	Random	4	77	18	4.50	0.23
6/30/14	EF	Fixed	1	21	7	7.00	0.33
	Angling	Random	7	195	82	11.71	0.42
Middle							
4/21/14	Angling	Fixed	1	20	37	37.00	1.85
	EF	Fixed	9	139	112	12.44	0.81
	EF	Random	2	29	17	8.50	0.58
5/5/14	EF	Fixed	8	135	122	15.25	0.90
5/19/14	EF	Fixed	8	103	73	9.13	0.71
6/2/14	Angling	Fixed	5	74	0	0.00	0.00
	EF	Fixed	4	53	25	6.25	0.47
6/16/14	EF	Fixed	16	307	266	16.63	0.87
	Angling	Random	6	105	21	3.50	0.20
6/30/14	Angling	Fixed	8	257	37	4.63	0.14
	Angling	Random	6	114	33	5.50	0.29
Upper							
3/24/14	Angling	Fixed	8	540	39	4.88	0.07
	EF	Fixed	4	78	22	5.50	0.28
	Angling	Random	11	236	68	6.18	0.29
	EF	Random	1	17	7	7.00	0.40
4/7/14	Angling	Fixed	9	610	96	10.67	0.16
	EF	Fixed	2	46	14	7.00	0.30
	Angling	Random	24	669	253	10.54	0.38
	EF	Random	2	34	17	8.50	0.50
4/21/14	Angling	Fixed	8	595	164	20.50	0.28
	Angling	Random	8	174	102	12.75	0.59
5/5/14	Angling	Fixed	8	600	84	10.50	0.14
	EF	Fixed	2	53	50	25.00	0.94

Table 2. Continued

	Angling	Random	9	165	43	4.78	0.26
5/19/14	Angling	Fixed	8	600	76	9.50	0.13
	Angling	Random	18	379	97	5.39	0.26
6/2/14	Angling	Fixed	8	558	182	22.75	0.33

Absolute abundance.—The open population models for each fixed site converged on parameters and successfully estimated model parameters. The fully time-dependent model had the lowest *AIC* for most sites and was therefore used to derive abundance estimates. Models with constant capture probabilities were selected for remaining sites. The abundance of Smallmouth Bass ≥ 150 mm was highest in the upper reach during all biweekly sampling occasions with a peak of 55,398 bass during 5 May (Table 3). This estimate was over double the amount of bass during the first sampling occasion (24 Mar). After 5 May, abundances in the upper reach dropped slightly. Bass abundance in the middle reach was relatively similar throughout the study but also peaked during 5 May (35,135). In terms of mean density (bass/m of shoreline) across all sampling weeks, the middle reach (mean = 0.457) was slightly higher than the upper reach (0.449). Abundance estimates in the lower reach steadily increased during the first five sampling weeks (peak abundance = 42,613) followed by a slight decline during the week of 30 June. The mean bass/m of shoreline was lowest (0.376) in the lower reach compared to the other reaches.

Diet

In 2014, we captured 2,922 Smallmouth Bass ≥ 150 mm and examined the gut contents of 2,573 individuals. The mean size at capture was larger during the spring for all reaches (Table 4). Mean sizes were slightly larger in the upper reach and more similar between the lower and middle reaches for most sampling weeks. The largest individuals were captured in the upper reach (up to 509 mm) at the end of March, before sampling began in the middle and lower reaches. Of the bass examined for diet analysis, 76% (1,968/2,573) had some amount of food in their stomachs. Of the bass containing food, 36% (711/1,968) had <0.1 g of food and 3% (65/1,968) had <0.001 g. The percentage of empty stomachs decreased with time for most reaches and the highest percentages were found in the lower reach.

The most common prey found in non-empty stomachs during most weeks (based on frequency of occurrence) was insects (Table 5). Sand rollers were the most common prey during the week of 21 April in the lower reach while sculpin were most common during the week of 24 March in the upper reach. Crayfish were often the second most frequently found prey (range 6–48%). The frequency of occurrence of Salmonids showed a decreasing trend throughout the

Table 3. Estimates of population abundance of Smallmouth Bass ≥ 150 mm TL in study reaches of Hells Canyon in 2014. The lower reach of Nelle (1999) encompassed our middle and lower reaches.

River section	Week	Estimated abundance	95% Confidence intervals	Bass/m of shoreline
Lower	21 Apr	10,725	3,657 - 44,982	0.146
Lower	5 May	17,330	4,474 - 109,372	0.236
Lower	19 May	28,011	9,690 - 113,255	0.381
Lower	2 Jun	38,255	14,118 - 169,756	0.521
Lower	16 Jun	42,613	10,574 - 115,381	0.580
Lower	30 Jun	28,858	10,970 - 75,914	0.393
Mean		27,632	8,914-104,777	0.376
Middle	21 Apr	26,640	9,413 - 79,757	0.423
Middle	5 May	35,135	14,752 - 98,458	0.558
Middle	19 May	31,854	10,531 - 109,264	0.506
Middle	2 Jun	23,114	5,973 - 89,452	0.367
Middle	16 Jun	28,443	13,287 - 72,514	0.451
Middle	30 Jun	27,485	10,065 - 70,108	0.436
Mean		28,778	10,670-86,592	0.457
Upper	24 Mar	23,645	11,569 - 53,376	0.258
Upper	7 Apr	32,512	13,837 - 84,682	0.354
Upper	21 Apr	45,856	16,682 - 131,623	0.500
Upper	5 May	55,398	26,288 - 125,078	0.604
Upper	19 May	42,054	17,342 - 106,007	0.459
Upper	2 Jun	47,815	22,637 - 105,820	0.521
Mean		41,213	18,059-101,098	0.449

Table 4. Seasonal total lengths of Smallmouth Bass collected for diet analysis from study sections of Hells Canyon on the Snake River in 2014.

Week Beginning	<i>N</i>	Mean	SD	Range
Lower				
21 Apr	43	273	58	152-365
5 May	60	212	59	150-349
19 May	176	205	51	150-468
2 Jun	144	179	39	150-427
16 Jun	353	190	48	150-423
30 Jun	89	238	53	157-384
Middle				
21 Apr	166	285	55	161-442
5 May	122	229	45	151-429
19 May	73	220	42	151-306
2 Jun	25	201	43	151-313
16 Jun	287	206	56	150-466
30 Jun	70	243	50	150-431
Upper				
24 Mar	136	338	42	275-509
7 Apr	380	315	41	248-502
21 Apr	266	299	32	221-422
5 May	177	275	47	151-367
19 May	173	181	35	210-392
2 Jun	182	275	37	168-372

Table 5. Seasonal variation in diet composition (percent frequency of occurrence of non-empty stomachs) of Smallmouth Bass in three sections of Hells Canyon on the Snake River in 2014. *N*s indicate the number of Smallmouth Bass with empty and non-empty stomachs.

Week beginning	<i>N</i> (empty)	<i>N</i> (non-empty)	Prey					
			Insects	Crayfish	Salmonid	Sand roller	Sculpin	Other fish
Lower								
4/21/14	24	19	21	11	26	37	11	0
5/5/14	28	31	42	13	13	3	10	3
5/19/14	89	72	31	14	7	26	10	4
6/2/14	29	87	77	24	1	8	7	2
6/16/14	34	181	80	21	3	18	10	1
6/30/14	26	61	64	34	0	3	15	11
Middle								
4/21/14	69	94	57	7	36	0	1	1
5/5/14	48	73	58	11	18	1	19	3
5/19/14	21	52	87	6	8	0	12	0
6/2/14	5	20	75	15	0	0	10	0
6/16/14	6	154	92	32	1	0	14	3
6/30/14	16	52	73	48	2	0	8	4
Upper								
3/24/14	29	91	32	24	21	0	74	2
4/7/14	88	290	70	12	16	0	20	1
4/21/14	40	225	83	22	13	0	13	1
5/5/14	0	177	97	46	2	0	8	1
5/19/14	20	153	84	40	24	0	8	1
Pre-release ^a	6	94	96	22	5	0	9	2
Post-release ^a	14	59	84	53	54	0	8	0
6/2/14	33	136	82	41	0	0	11	0

^aDenotes sampling conducted before (19-May) and after (20-May) a hatchery release of fall Chinook Salmon

study, except in the upper reach where it increased from the hatchery release during the week of 19 May. The hatchery release increased the frequency of occurrence from 5 to 54 %. These are both pooled for the 24% frequency during the 19 May sampling week. The frequency of occurrence of Salmonids in bass diets of the lower reach declined from 26% to 3% by mid-June. No Salmonids were found during the 30 June sampling week. The frequency of occurrence of Salmonids in bass diets in the middle reach declined from 36% to 0% by the week of 2 June, after which a few Salmonids were found in stomachs through the week of 30 June. No Salmonids were found in the upper reach during the 2 June sampling week. Sculpin were frequently found in stomachs in all reaches during all weeks and sand rollers were found in stomachs in the lower reach. Only one sand roller was found in a stomach from the middle reach.

Smallmouth Bass diets varied both between reaches and weeks when examined on a percent weight basis (Figure 2, Tables 6 and 7). Diets in the lower reach were mainly composed of sand rollers and crayfish, while Salmonids only comprised a large portion (51%) by weight during the week of 21 April. Diets in the middle reach were mainly composed of Salmonids through May and then were composed of crayfish for the remaining weeks. Sculpin comprised most of the diet by weight in the upper reach from 24 March to 7 April, followed by insects (57%) during 5 May, Salmonids (49%) during 19 May, and crayfish (78%) during 2 June. During the week of 19 May, the portion of Salmonids in bass diets increased from 3% before a release of hatchery fish to 71% after the release.

Salmonids consumed by Smallmouth Bass were predominantly Chinook Salmon (94%). The remainder comprised unidentifiable (4%), steelhead (1%), or mountain whitefish (1%). Estimated Chinook Salmon length at ingestion ranged from 22 to 137 mm (mean= 60 mm). Steelhead were only found in mid-April and were larger (91-151mm) in size than other Salmonids consumed during this time. Mountain whitefish were only consumed in mid- to late June and were smaller (32-33 mm). All of the unidentifiable Salmonids were consumed before mountain whitefish appeared in the diets and were smaller than the steelhead that were consumed. Therefore, we classified the unidentified Salmonids as Chinook Salmon. The length-frequencies of consumed Chinook Salmon (Figure 3) suggested most were fall Chinook subyearlings. We estimated that the larger size classes in the first four sampling weeks were likely spring Chinook yearlings. Subyearlings comprised the majority of Chinook Salmon consumed (62.5%, 24 March; 96.7%, 7 April; 69.9%, 21 April; 75.0%, 5 May; 100%, all remaining weeks). These percentages were used in the consumption estimates. By the week of 19 May, the larger size class was not apparent but an intermediate size class appeared. We assumed this size class represented the hatchery subyearlings released at Hells Canyon Dam. We made no further attempt to classify subyearling origin (i.e., hatchery or natural). The smallest bass that contained a Salmonid was 152 mm TL. The maximum size of vulnerability (in FL) of Salmonids during 2014 was 50% (mean= 20%) of bass total length.

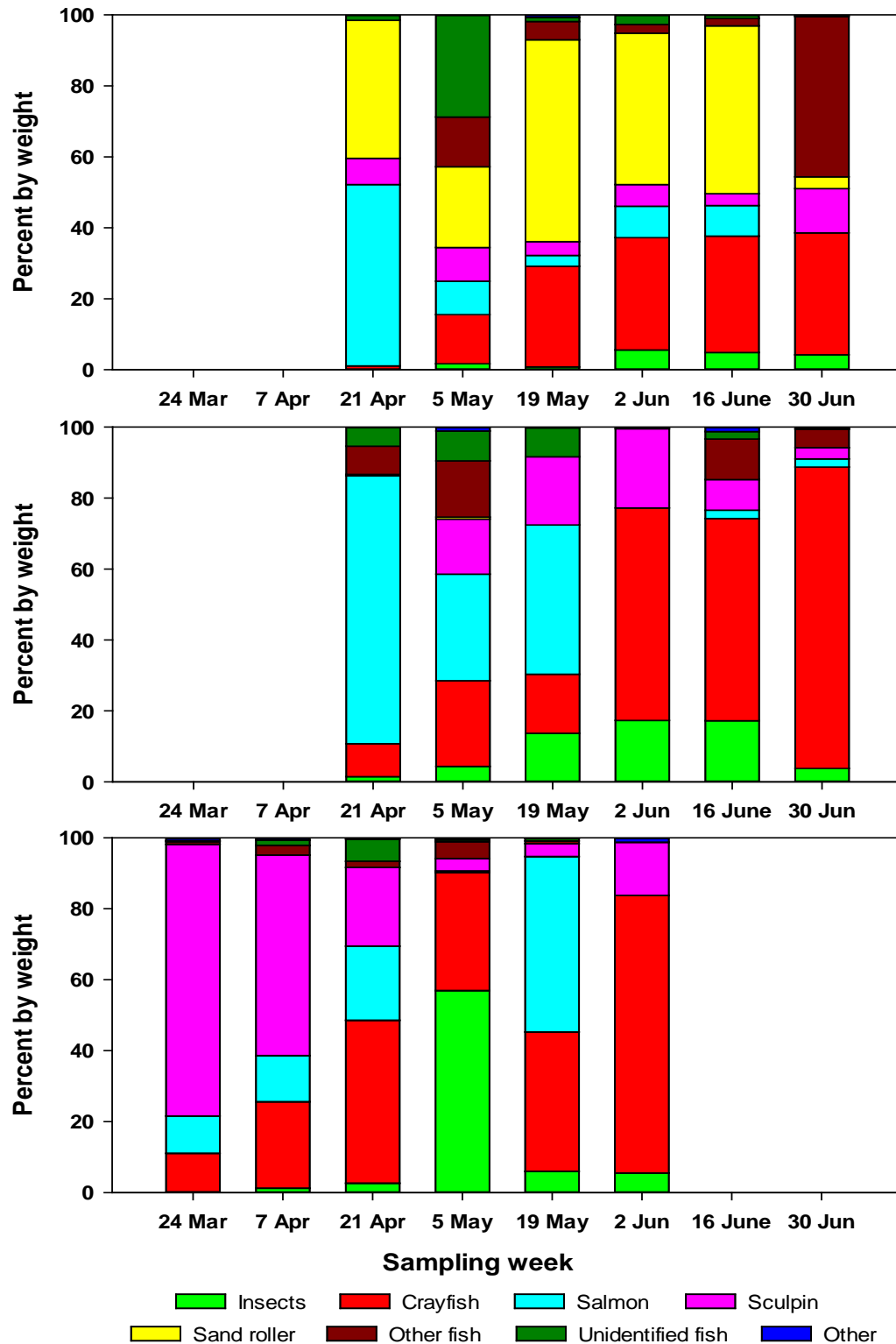


Figure 2. Seasonal variation in diet composition (percent weight based on non-empty stomachs) of Smallmouth Bass in the lower (top panel), middle (middle panel), and upper reaches (bottom panel) of Hells Canyon in 2014.

Table 6. Seasonal variation in diet composition (percent weight based on non-empty stomachs) of Smallmouth Bass in three reaches of Hells Canyon on the Snake River in 2014. *N*s indicate the number of Smallmouth Bass with empty and non-empty stomachs.

Week beginning	<i>N</i> (empty)	<i>N</i> (non- empty)	Prey							
			Insects	Crayfish	Salmonid	Sculpin	Sand roller	Other fish	Unidentified fish	Other taxa
Lower										
4/21/14	24	19	0	1	51	7	39	0	1	0
5/5/14	28	31	2	14	9	10	23	14	29	0
5/19/14	89	72	1	28	3	4	57	5	1	1
6/2/14	29	87	6	32	9	6	43	2	3	0
6/16/14	34	181	5	33	9	3	47	2	1	0
6/30/14	26	61	4	34	0	12	3	45	0	0
Middle										
4/21/14	69	94	1	9	76	0	0	8	5	0
5/5/14	48	73	4	24	30	16	1	16	8	1
5/19/14	21	52	14	17	42	19	0	0	8	0
6/2/14	5	20	17	60	0	22	0	0	0	0
6/16/14	6	154	17	57	2	9	0	11	2	1
6/30/14	16	52	4	85	2	3	0	5	0	0
Upper										
3/24/14	29	91	0	11	11	77	0	1	0	1
4/7/14	88	290	1	24	13	56	0	3	1	1
4/21/14	40	225	3	46	21	22	0	2	6	0
5/5/14	0	177	57	33	0	4	0	5	0	1
5/19/14	20	153	6	39	49	4	0	1	1	0
Pre- release ^a	6	94	16	71	3	6	0	2	1	1
Post- release ^a	14	59	1	24	71	2	0	0	1	0
6/2/14	33	136	6	78	0	15	0	0	0	1

^aDenotes sampling conducted before (19-May) and after (20-May) a hatchery release of fall Chinook Salmon

Table 7. Summary of prey items obtained from all Smallmouth Bass stomachs sampled in Hells Canyon on the Snake River in 2014.

Category	Taxon	Total mass(g)	Percent
Insects	Trichoptera	293.6	73
	Odonata	34.9	9
	Ephemeroptera	34.2	8
	Unidentifiable insect parts	20.5	5
	Diptera	8.9	2
	Plecoptera	8.4	2
	Hymenoptera	1.6	<1
	Orthoptera	1.3	<1
	Lepidoptera	1.1	<1
	Coleoptera	0.3	<1
	Hemiptera	0.2	<1
	Dermaptera	<0.1	<1
	Homoptera	<0.1	<1
Crustaceans	Crayfish	1137.7	100
	Isopoda	0.6	<1
	Amphipoda	0.2	<1
Salmonids	Chinook	661.5	96
	Steelhead	23.1	3
	Unknown	2.5	<1
	Mountain Whitefish	1.6	<1
Other fish	Sculpin spp.	800.7	66
	Sandroller	262.5	22
	Smallmouth Bass	103.4	9
	Sucker spp.	17.1	1
	Peamouth	12.1	1
	Chiselmouth	7.2	1
	Northern Pikeminnow	3.8	<1
	Catfish spp.	1.0	<1
Unidentifiable fish	Parts	65.1	95
	Fry	3.6	5
Other	Egg	6.9	36
	Rock	6.4	34
	Vegetation	2.7	14
	Unknown	1.5	8

Table 7. Continued

Oligochaeta	0.5	2
Reptile	0.4	2
Nematoda	0.2	1
Centipede	0.2	1
Arachnida	0.2	1
Gastropoda	0.1	1
Bivalva	0.1	<1
Hirudinea	<0.1	<1

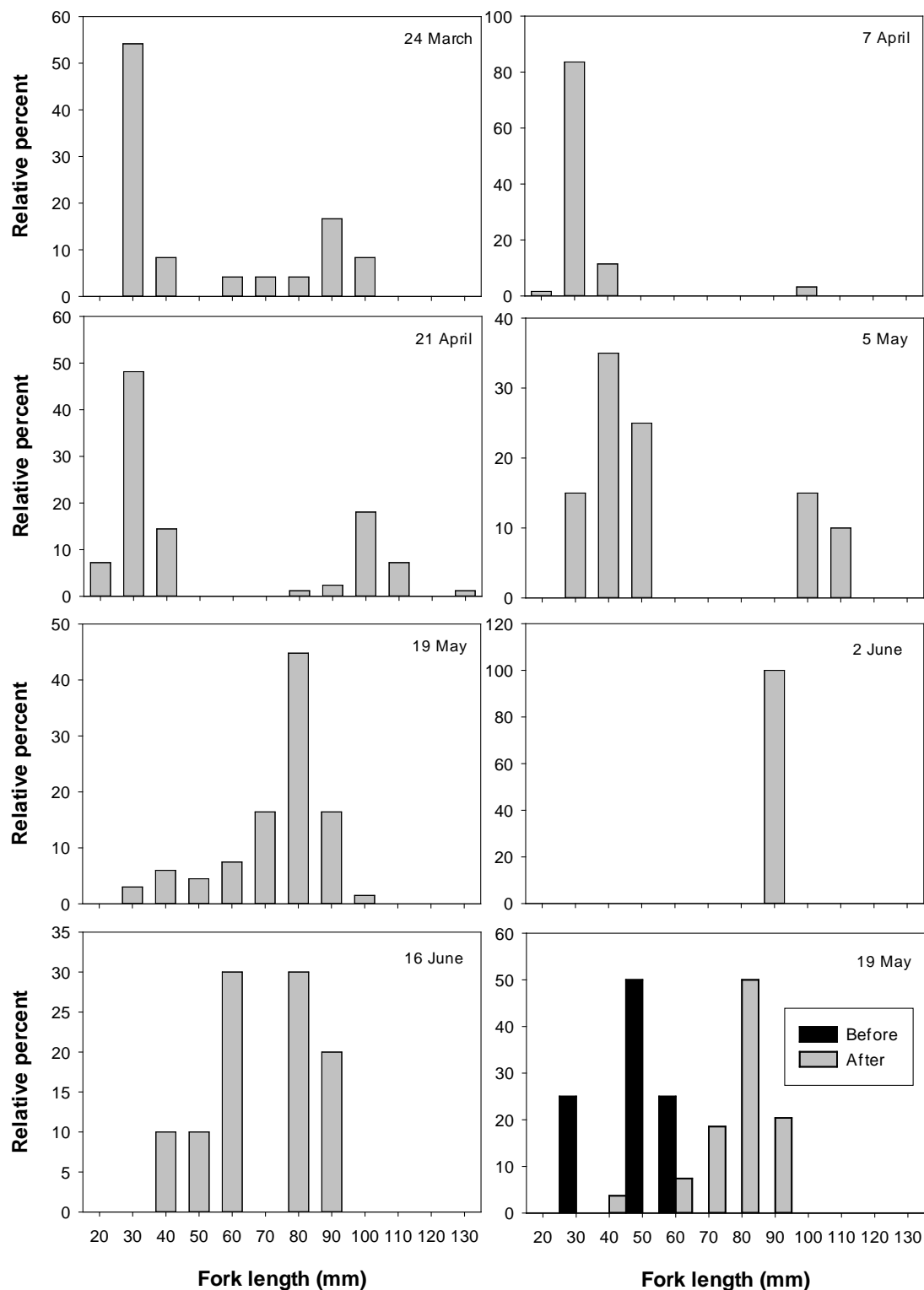


Figure 3. Size distribution of Chinook Salmon consumed by Smallmouth Bass in Hells Canyon on the Snake River by sampling week in 2014. The bottom right panel shows the size distribution in the upper reach of Hells Canyon before (19 May) and after (20 May) hatchery releases of subyearling Chinook Salmon at Hells Canyon Dam.

Consumption and loss

Total estimated loss of Salmonids to Smallmouth Bass predation within our study area was 738,927 individuals (Table 8), of which 81.7% were subyearling Chinook Salmon. Coincident to the abundance estimates, the highest total consumption occurred in the upper reach followed by the middle and lower reaches. In the upper reach alone, 43% of the estimated consumption occurred during the 2-week period beginning 19 May when 200,791 Salmonids were estimated to be consumed. This estimate was influenced by the large release of hatchery fish. The consumption rate estimated before this release was 0.050 Salmonids/bass/day which equates to a daily loss of 2,770 Salmon (Table 9), whereas the post-release consumption rate was 0.730 Salmonids/bass/day which equates to a daily loss of 40,220 Salmonids.

Discussion

Juvenile Salmonids were a major component of Smallmouth Bass diet at times during 2014. This was evident by their high frequency of occurrence (up to 36% in the middle reach) and percentage of the diet (by weight; up to 76% in the middle reach), as well as the high Smallmouth Bass consumption rates (up to 0.341 Salmonids/bass/day in the upper reach) during the spring. This was probably due in part to hatchery releases of subyearlings upstream which was in excess of 1.3 million in 2014. All of the bass predation metrics were high in early spring and decreased significantly through time. We estimated that Chinook Salmon comprised 97.7% of the Salmonids in bass diets and were consumed up to early June in the upper reach and mid-June in the middle and lower reaches. After these times, the abundance of Chinook Salmon declined as fish dispersed downstream out of the study reaches. The downward trend in Salmonid consumption was only interrupted in the upper reach due to hatchery releases, which had a dramatic effect on total loss estimates. Due to the timing of our sampling, we acknowledge that some predation occurred prior to sampling began in each reach, but we assume that consumption was probably lower during these times due to colder water temperatures reducing bass feeding activity.

Subyearlings are probably the Salmonid most vulnerable to Smallmouth Bass predation because of their extended use of shoreline habitats and small size (Sogard 1997; Tiffan et al. 2006). We estimated that 81.7% of all Salmonids consumed by bass were likely subyearlings, and the impacts on larger yearling Chinook Salmon or steelhead were minimal. We found that Smallmouth Bass as small as 152 mm contained subyearlings, which suggests that even small bass may pose a predation threat. Fritts and Pearsons (2006) found that 150-199 mm Smallmouth Bass accounted for 42.9% of the Salmonid consumption in the Yakima River, and that decreasing

Table 8. Estimated losses (95% CI) of juvenile Salmonids in the upper, middle, and lower reaches of Hells Canyon on the Snake River in 2014.

Week	Salmonids	95% CI	Chinook	95% CI	Subyearling Chinook	95% CI
Lower						
21-Apr	24,442	8,335-102,517	24,155	8,237-101,311	16,908	5,766-70,918
5-May	16,449	4,247-103,810	16,449	4,247-103,810	12,337	3,185-77,858
19-May	12,179	4,213-49,241	11,999	4,151-48,517	11,999	4,151-48,517
2-Jun	4,617	1,704-20,488	4,617	1,704-20,488	4,617	1,704-20,488
16-Jun	22,198	5,509-60,105	22,198	5,509-60,105	22,198	5,509-60,105
30-Jun	0		0		0	
Section Total	79,885		79,418		68,059	
Middle						
21-Apr	86,948	30,723-260,313	85,925	30,361-257,250	60,147	21,253-180,075
5-May	60,979	25,603-170,877	60,979	25,603-170,877	45,734	19,202-128,158
19-May	24,436	8,078-83,819	24,077	7,960-82,586	24,077	7,960-82,586
2-Jun	0		0		0	
16-Jun	4,978	2,325-12,690	4,978	2,325-12,690	4,978	2,325-12,690
30-Jun	11,318	4,144-28,868	0		0	
Section Total	188,659		175,959		134,936	
Upper						
24-Mar	74,483	36,444-168,134	74,483	36,444-168,134	46,924	22,959-105,924
7-Apr	80,678	34,337-210,137	78,270	33,312-203,864	75,922	32,313-197,748
21-Apr	96,904	35,253-278,147	95,764	34,839-274,875	67,035	24,387-192,413
5-May	17,527	8,317-39,573	17,527	8,317-39,573	13,145	6,238-29,679
19-May	200,791	82,802-506,138	200,791	82,802-506,138	200,791	82,802-506,138
2-Jun	0		0		0	
Section Total	470,383		466,835		403,817	
Study Total	738,927		722,212		603,812	

Table 9. Estimated consumption rates of Salmonids by Smallmouth Bass ≥ 150 mm (fish/Smallmouth Bass/day) in Hells Canyon on the Snake River in 2014. No distinction was made between hatchery and natural subyearling prey.

Week of	All Salmonids	Chinook			Steelhead	Mountain whitefish
		Combined	Subyearling	Yearling		
Lower						
4/21/14	0.163	0.161	0.113	0.048	0.002	0.000
5/5/14	0.068	0.068	0.051	0.017	0.000	0.000
5/19/14	0.031	0.031	0.031	0.000	0.000	0.000
6/2/14	0.009	0.009	0.009	0.000	0.000	0.000
6/16/14	0.037	0.037	0.037	0.000	0.000	0.000
6/30/14	0.000	0.000	0.000	0.000	0.000	0.000
Middle						
4/21/14	0.233	0.230	0.161	0.069	0.003	0.000
5/5/14	0.124	0.124	0.093	0.031	0.000	0.000
5/19/14	0.055	0.054	0.054	0.000	0.000	0.001
6/2/14	0.000	0.000	0.000	0.000	0.000	0.000
6/16/14	0.013	0.013	0.013	0.000	0.000	0.000
6/30/14	0.029	0.000	0.000	0.000	0.000	0.029
Upper						
3/24/14	0.225	0.225	0.142	0.083	0.000	0.000
4/7/14	0.177	0.172	0.167	0.005	0.005	0.000
4/21/14	0.151	0.149	0.104	0.045	0.002	0.000
5/5/14	0.023	0.023	0.017	0.006	0.000	0.000
5/19/14	0.341	0.341	0.341	0.000	0.000	0.000
Pre-release ^a	0.050	0.050	0.050	0.000	0.000	0.000
Post-release ^a	0.730	0.730	0.730	0.000	0.000	0.000
6/2/14	0.000	0.000	0.000	0.000	0.000	0.000

^aDenotes sampling conducted before (19-May) and after (20-May) a hatchery release of fall Chinook Salmon

relative length of Salmonid prey increased with Smallmouth Bass size. In our study, the maximum relative length of Salmonids ($\text{Salmonid FL/bass TL} * 100$) consumed by 150-199 mm Smallmouth Bass was 37.8% (only slightly lower than our 2013 estimate of 47.2%), suggesting that subyearling susceptibility to predation based on size alone is very high because of the high abundance of small-sized (<200 mm) Smallmouth Bass in Hells Canyon. Conversely, Anglea (1997) found that Smallmouth Bass ranging in size from 250-389 mm had the highest Salmonid consumption in Lower Granite Reservoir in 1994-1995. It is clear that Smallmouth Bass >150 mm pose a substantial predation risk to subyearling fall Chinook Salmon in Hells Canyon as evidenced by our high consumption rates and loss estimates.

Our estimates of Smallmouth Bass consumption rates of juvenile Salmonids are generally much higher than those reported by Nelle (1999), who studied Smallmouth Bass predation of subyearlings in the mid to late 1990s. Nelle (1999) observed the highest consumption rates of subyearlings directly below hatchery release sites and immediately following releases. However, at sites located away from these sites, Nelle (1999) found consumption rate to range from 0 to <0.009 subyearling/Smallmouth Bass/day. By comparison, most consumption rates in the middle and lower reaches exceeded 0.1 subyearling/Smallmouth Bass/day in our study.

There are several possible reasons for the increase in daily consumption rates of subyearlings by Smallmouth Bass that we observed. First, the run size of subyearlings has increased dramatically since 1996. Hatchery supplementation has directly increased the population via annual releases of juveniles and indirectly as a result of increased production from natural spawners (Connor et al. 2013). Nelle (1999) conducted his study in 1996 and 1997 when the subyearling population was at a low level and hatchery supplementation was just beginning in the Snake River. To illustrate, the number of subyearlings that passed Lower Granite Dam during the 1 April to 1 October outmigration was 18,066 fish in 1996 and 97,985 fish in 1997. In 2014, the annual passage index of subyearlings at Lower Granite Dam was 960,893 fish (DART 2015). The large increase in the subyearling population may have made more fish accessible to Smallmouth Bass predators. Interestingly, the consumption of subyearlings was lowest in the lower reach where sand rollers were abundant and often comprised the majority of fish prey in Smallmouth Bass diets. Sand rollers were virtually absent in the middle and upper reaches. This species was absent when Nelle conducted his study in the 1990s but is very abundant today and may be reducing the predation pressure on subyearlings in the lower reach.

Our loss estimates of subyearling fall Chinook Salmon to Smallmouth Bass predation were also significantly higher than those reported by Nelle (1999). Nelle (1999) estimated total losses of subyearlings to range from 714 to 5,347 during 1996 and 1997 (depending on differing

estimation models), whereas our loss estimates ranged from 68,000 to over 400,000 fish. One reason for this is that our abundance estimates of Smallmouth Bass were much higher than those estimated by Nelle (1999). Our estimates in the lower and middle reaches combined were more than double for fish ≥ 150 mm than reported by Nelle (1999). Loss estimates are most sensitive to Smallmouth Bass abundance. The confidence intervals on our estimates are wide suggesting that Smallmouth Bass abundance estimates could be improved. Nonetheless, we believe our multiple mark-recapture approach using an open population model was a more robust approach than the single mark-recapture event that Nelle (1999) used in October, 1997. We also believe that use of an open population model to estimate abundance was more realistic than the simpler, closed model used by Nelle (1999). Finally, we collected Smallmouth Bass abundance data during the same time period when consumption data was collected. Nelle (1999) estimated Smallmouth Bass abundance in the fall and their habitat use may have shifted from that in the spring, which may have influenced his abundance estimates. This is the reason we collected abundance and consumption data concurrently starting in 2013.

One important aspect of our sampling design was that it allowed abundance to be estimated at biweekly intervals. Our results showed increasing trends in abundance within most reaches through the spring, a pattern that is consistent with other studies of Smallmouth Bass abundances (Fritts and Pearsons 2004, Zimmerman and Parker 1995) in the Columbia River Drainage. If the abundances were held constant from estimates derived later in the year (which were higher) then Salmonid loss estimates would have been much higher because consumption rates were much higher earlier in the year. It is unknown if the increases in abundance through time were caused by fish migrating into the reaches, recruitment of fish to the 150-mm minimum size threshold, or just a habitat shift resulting in increased occupancy of shoreline habitats and vulnerability to our gears. It may also be related to temperature-related activity. Smallmouth Bass typically do not become active until water temperatures exceed 10°C (Munther 1970) and therefore are not likely to use shoreline areas to feed prior to fall Chinook Salmon emergence. However, we found Smallmouth Bass actively feeding during late March in the upper reach when daily water temperatures ranged from 7.3 to 7.9°C (mean= 7.7°C), although their abundance in shoreline habitats was low at that time. As temperatures increase seasonally, Smallmouth Bass may become more abundant along shorelines to both feed and spawn. However, Smallmouth Bass abundance did not steadily increase in the middle and lower reaches as it did in the upper reach, perhaps because sampling did not begin until a month later and water temperatures did not increase in the lower and middle reaches as rapidly (Figure 4).

Certain sampling limitations and assumptions may have influenced our results. We used both angling and electrofishing and their use varied by reach. We primarily used angling in the

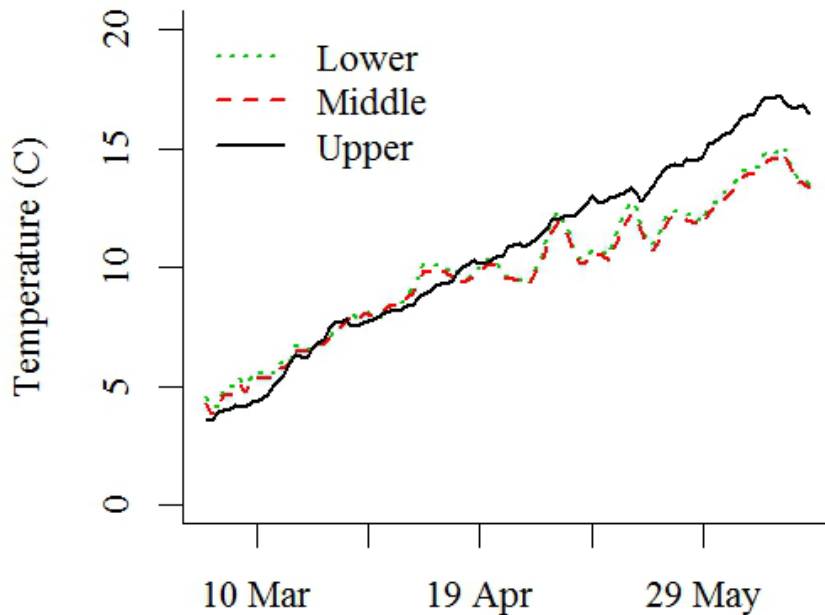


Figure 4. Mean daily water temperatures from three reaches in Hells Canyon on the Snake River, 2014.

upper reach because we were only able to access portions of the reach with our electrofishing boat depending on discharge levels and rapids that could be run safely. We primarily used electrofishing in the middle and lower reaches, which vastly improved our catch rates, because past angling catch rates were often low, particularly during turbid, high-water events. However, each gear may have introduced bias into our results. For example, electrofishing can collect both actively and inactively feeding Smallmouth Bass, but is only effective in shallow water near shore. Differences in habitat use between larger and small fish could influence electrofishing catches and introduce bias. In contrast, angling may be biased toward collecting actively feeding Smallmouth Bass but it can collect them from a range of water depths and distances from shore. The effect of angling bias may be to artificially inflate consumption estimates if collected Smallmouth Bass are those that are actively feeding. It is also possible that the larger fish observed in the upper reach are a product of gear bias because angling has been found to collect a larger size distribution of Smallmouth Bass than electrofishing (Beamesderfer and Rieman 1988). Since a larger size distribution may have been sampled and used to develop abundance estimates, numbers may be skewed low since a representative portion of the smaller size class may not have been incorporated. We did not have adequate data to allow for size covariates in our mark-recapture population estimates.

Another critical assumption was that our sampling sites were representative of the larger study area and that Smallmouth Bass were distributed evenly throughout each reach. This assumption directly affects the accuracy of expanding consumption estimates to estimate subyearling loss over the entire study area. We believe the mix of fixed and random sampling sites that we used in 2014 was the best way to minimize expansion error if this assumption did not hold. The fixed sites allowed us to examine variation in Smallmouth Bass abundance and consumption through time, and the random sites allowed us to determine if consumption was similar to the fixed sites. Quantifying the variation in Smallmouth Bass abundance and consumption due to variation in habitat will allow us to more accurately expand subyearling losses to the entire study area in future years.

Finally, we recognize that large hatchery releases of subyearlings could produce a short-term increase in apparent Smallmouth Bass predation that might artificially increase consumption and loss estimates over the 2-week time intervals between sampling events. This was evident during our evaluation of the hatchery release at Hells Canyon Dam on 20 May. The dramatic increase in consumption rates (0.050 fish/Smallmouth Bass/day to 0.740 fish/Smallmouth Bass/day) during this time shows the magnitude of change in total loss estimates from releasing hatchery fish. We pooled data from both days to derive an estimate for the biweekly loss, but this may not be representative of the entire 2-week interval because hatchery fish may disperse downstream quickly (Smith et al. 2003) and their availability to bass may not be constant. In other words, if prey availability changes temporally following a release, predation rates will likely change as well and must be accounted for. An important question would be how does a hatchery release change bass consumption on a more temporal and spatial scale? Also, can continuous releases (or large releases) of hatchery Chinook Salmon swamp Smallmouth Bass with more prey than they could eat? These questions were posed in the Yakima River where it was determined that the uncertain effects on naturally produced fish may not outweigh the costs of hatchery fish losses, and because predators were also currently swamped by other naturally occurring prey fish (Fritts and Pearsons 2008). They did suggest that predation on hatchery-released Salmonids could be lowered by releasing fish prior to mid-April when bass consumption is lower under cooler temperatures. Earlier releases in Hells Canyon could have similar results. For example, sampling the day after the hatchery release resulted in a consumption rate of 0.730 Salmonids/bass/day in the upper reach. Using the abundance estimate of 55,398 bass resulted in 40,220 Salmonids being consumed that day. Decreasing the evacuation model temperature by 1°C (T in equation 4) decreased that loss estimate to 34,908 Salmonids and decreasing it by 2°C decreased the loss to 32,632 Salmonids. These results may provide fisheries managers with important information for assisting with

hatchery release plans; however, further examination and simulations would be recommended because other factors such as meal size affect evacuation rates. Similar to Vigg et al. (1991), we conclude that temperature is the largest factor in consumption rates of Salmonids by Smallmouth Bass. A more in-depth study on functional or numerical responses of Smallmouth Bass to increased prey numbers (from hatchery releases) and the effects on non-target (natural Salmonids and native fish species) would be beneficial.

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