

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/301537994>

Predation by Northern Pikeminnow and Tiger Muskellunge on Juvenile Salmonids in a High-Head Reservoir: Implications for Anadromous Fish Reintroductions

Article in *Transactions of the American Fisheries Society* · May 2016

DOI: 10.1080/00028487.2015.1131746

CITATIONS

11

READS

298

6 authors, including:



Mark Sorel

National Oceanic and Atmospheric Administration

4 PUBLICATIONS 28 CITATIONS

[SEE PROFILE](#)



Adam G. Hansen

Colorado Parks and Wildlife

37 PUBLICATIONS 209 CITATIONS

[SEE PROFILE](#)



Kristin Connelly

Washington State University

11 PUBLICATIONS 47 CITATIONS

[SEE PROFILE](#)



David Beauchamp

Western Fisheries Research Center, US Geological Survey, Seattle

135 PUBLICATIONS 4,295 CITATIONS

[SEE PROFILE](#)

Some of the authors of this publication are also working on these related projects:



1. ecological effects of hatchery-reared fish stocking on lake and reservoirs ecosystems. [View project](#)



Evaluación de los Recursos Ícticos del lago Nahuel Huapi, ANPCyT PICT 25722 [View project](#)



Predation by Northern Pikeminnow and Tiger Muskellunge on Juvenile Salmonids in a High-Head Reservoir: Implications for Anadromous Fish Reintroductions

Mark H. Sorel, Adam G. Hansen, Kristin A. Connelly, Andrew C. Wilson, Erin D. Lowery & David A. Beauchamp

To cite this article: Mark H. Sorel, Adam G. Hansen, Kristin A. Connelly, Andrew C. Wilson, Erin D. Lowery & David A. Beauchamp (2016) Predation by Northern Pikeminnow and Tiger Muskellunge on Juvenile Salmonids in a High-Head Reservoir: Implications for Anadromous Fish Reintroductions, Transactions of the American Fisheries Society, 145:3, 521-536, DOI: [10.1080/00028487.2015.1131746](https://doi.org/10.1080/00028487.2015.1131746)

To link to this article: <http://dx.doi.org/10.1080/00028487.2015.1131746>



Published online: 19 Apr 2016.



Submit your article to this journal [↗](#)



View related articles [↗](#)



View Crossmark data [↗](#)

ARTICLE

Predation by Northern Pikeminnow and Tiger Muskellunge on Juvenile Salmonids in a High-Head Reservoir: Implications for Anadromous Fish Reintroductions

Mark H. Sorel,^{*1} Adam G. Hansen,² Kristin A. Connelly, Andrew C. Wilson, and Erin D. Lowery³

Washington Cooperative Fish and Wildlife Research Unit, School of Aquatic and Fishery Sciences, University of Washington, Box 355020, Seattle, Washington 98195-5020, USA

David A. Beauchamp

U.S. Geological Survey, Washington Cooperative Fish and Wildlife Research Unit, School of Aquatic and Fishery Sciences, University of Washington, Box 355020, Seattle, Washington 98195-5020, USA

Abstract

The feasibility of reintroducing anadromous salmonids into reservoirs above high-head dams is affected by the suitability of the reservoir habitat for rearing and the interactions of the resident fish with introduced fish. We evaluated the predation risk to anadromous salmonids considered for reintroduction in Merwin Reservoir on the North Fork Lewis River in Washington State for two reservoir use-scenarios: year-round rearing and smolt migration. We characterized the role of the primary predators, Northern Pikeminnow *Ptychocheilus oregonensis* and tiger muskellunge (Northern Pike *Esox lucius* × Muskellunge *E. masquinongy*), by using stable isotopes and stomach content analysis, quantified seasonal, per capita predation using bioenergetics modeling, and evaluated the size and age structures of the populations. We then combined these inputs to estimate predation rates of size-structured population units. Northern Pikeminnow of FL ≥ 300 mm were highly cannibalistic and exhibited modest, seasonal, per capita predation on salmonids, but they were disproportionately much less abundant than smaller, less piscivorous, conspecifics. The annual predation on kokanee *Oncorhynchus nerka* (in biomass) by a size-structured unit of 1,000 Northern Pikeminnow having a FL ≥ 300 mm was analogous to 16,000–40,000 age-0 spring Chinook Salmon *O. tshawytscha* rearing year-round, or 400–1,000 age-1 smolts migrating April–June. The per capita consumption of salmonids by Northern Pikeminnow having a FL ≥ 200 mm was relatively low, due in large part to spatial segregation during the summer and the skewed size distribution of the predator population. Tiger muskellunge fed heavily on Northern Pikeminnow, other nonsalmonids, and minimally on salmonids. In addition to cannibalism within the Northern Pikeminnow population, predation by tiger muskellunge likely contributed to the low recruitment of larger (more piscivorous) Northern Pikeminnow, thereby decreasing the risk of predation to salmonids. This study highlights the importance of evaluating trophic interactions within reservoirs slated for reintroduction with anadromous salmonids, as they can be functional migration corridors and may offer profitable juvenile-rearing habitats despite hosting abundant predator populations.

The construction of large dams has extirpated Pacific salmon (Rainbow Trout) from 45% of their historic habitat in the western contiguous United States, which has contributed to the decline of *Oncorhynchus* spp. and steelhead *O. mykiss* (anadromous

*Corresponding author: marks6@uw.edu

¹Present address: National Marine Fisheries Service, Northwest Fisheries Science Center, 2725 Montlake Boulevard East, Seattle, Washington 98112, USA.

²Present address: Colorado Parks and Wildlife, 317 West Prospect Road, Fort Collins, Colorado 80526, USA.

³Present address: Seattle City Light, Environmental Affairs and Real Estate Division, 700 Fifth Avenue, Suite 3200, Post Office Box 34023, Seattle, Washington 98104, USA.

Received September 3, 2015; accepted December 7, 2015

many populations (Beechie et al. 2006; Sheer and Steel 2006; McClure et al. 2008). To combat salmon declines and reopen historically accessible habitats above dams that cannot be feasibly removed, reintroductions of anadromous salmonids using trap-and-haul methods are increasingly being proposed as part of relicensing agreements with regulating agencies. These methods involve trapping returning adults below the dams and releasing them into the watershed above, then trapping downstream-migrating smolts at or upstream from the dams and releasing them below these barriers. This strategy, which reintroduces salmon into high-elevation habitat above dams, can help conserve anadromous salmonids by enhancing life history diversity, abundance, productivity, and spatial structure, and may provide a refuge from the effects of climate change and development (McElhany et al. 2000; Bilby and Mollet 2008; Schindler et al. 2008; Anderson et al. 2014).

Reintroductions may aid conservation efforts; however, there may be significant risks and constraints. Risks include homogenization of population structures, depletions of source populations, and the spread of disease (Viggers et al. 1993; Williamson and May 2005; Eldridge and Naish 2007). If these risks are not prohibitive, then potential constraints include the lack of adequate passage around remaining barriers, suitable spawning habitat, and conditions that support the survival of juveniles and adults in the face of changing climate and land use (Beechie et al. 2006; Ferguson et al. 2007; Schaller and Petrosky 2007; Bilby and Mollet 2008; Sanderson et al. 2009a; Anderson et al. 2014).

One key uncertainty surrounding reintroductions above high-head dams is how storage reservoirs will affect the production of anadromous salmonids. Habitats and food webs in storage reservoirs contain new hybrid communities of resident fishes and altered thermal and flow regimes from their historic state (Naiman et al. 2012). Lentic conditions and interactions with resident fish could either undermine or support a successful reintroduction of salmonids by influencing the survival, growth, behavior, and distribution of reintroduced fish (Pess et al. 2011; Carey et al. 2012). Use of the reservoir by juvenile salmonids as either a migration corridor or year-round rearing habitat will influence the strength of these potential interactions.

Migration through storage reservoirs, which generally have little flow, can disorient smolts and may subject them to predation by lentic piscivores. Collection efficiencies in surface collectors on the Baker, Cowlitz, and Deschutes rivers average 19–91%, indicating that residualization and mortality of smolts within reservoirs could significantly undermine the success of a reintroduction (Al-Chokhachy 2013).

Juvenile anadromous fish produced in tributaries may use reservoirs for rearing if quality habitat and food are available (Lowery and Beauchamp 2010; Bourret et al. 2014). Sockeye Salmon *O. nerka* typically require lentic habitat for rearing, whereas other Pacific salmon species use lentic habitats to varying degrees (Burgner 1991). Of these, juvenile Chinook Salmon *O. tshawytscha* most consistently rear in lentic habitats,

such as in North Fork Reservoir on the Clackamas River, reservoirs on the upper Willamette River, Snake River, and Columbia River, Lake Washington, and other lakes and reservoirs in the Pacific Northwest (Connor et al. 2002; Koehler et al. 2006; Lowery and Beauchamp 2010; Naiman et al. 2012; Monzyk et al. 2013; Bourret et al. 2014). Juvenile Coho Salmon *O. kisutch* sometimes rear in lentic habitats such as in Cultus Lake in British Columbia, the Chignik Lakes in Alaska, and Mesachie Lake on Vancouver Island (Foerster and Ricker 1953; Swain and Holtby 1989; Ruggerone and Rogers 1992). Juvenile steelhead primarily use lotic habitat for feeding and rearing (Everest and Chapman 1972; Bisson et al. 1988; Lowery and Beauchamp 2010), whereas adfluvial Rainbow Trout commonly rear in lakes. When planning new reintroductions above high-head dams, it is reasonable to assume that juveniles from one or more species of anadromous salmonids would use the reservoir habitat for rearing if conditions are favorable for growth and survival. Thus, evaluating factors (e.g., thermal structure and predation) that could limit these processes is an important step in determining reintroduction feasibility.

Merwin Reservoir, on the North Fork Lewis River in Washington State, is being evaluated for potential reintroduction of salmonids. The operating utility, PacifiCorp Energy, proposed the reintroduction of steelhead, Coho Salmon, and spring Chinook Salmon, which were extirpated by the construction of Merwin Dam in 1931. Beginning in 2010, a reintroduction of the same suite of species, using trap-and-haul methods, was implemented in Swift Reservoir, located upstream from Merwin Reservoir on the North Fork Lewis River (Figure 1). A floating surface collector above Swift Dam went into operation in 2012 to improve downstream transport, and a similar strategy is proposed for Merwin Reservoir after evaluating potential ecological constraints on tributary and reservoir rearing. Successful reintroductions of salmonids in these reservoirs and their tributaries would be important for broader conservation efforts of anadromous fishes in the Lewis River basin and Columbia River basin as a whole.

One potential constraint on successful reintroduction of salmonids in Merwin Reservoir is predation. In the late 1950s and 1960s, an experimental introduction of hatchery Coho Salmon fry in Merwin Reservoir resulted in high growth rates but low survival, and predation was hypothesized as the cause for low survival (Hamilton et al. 1970). Northern Pikeminnow *Ptychocheilus oregonensis* were the most abundant predator of juvenile salmon, with a mark-recapture estimate of 350,000 fish of FL \geq 200 mm in 1961, but the population has not been assessed since (Hamilton et al. 1970). Additionally, the Washington Department of Fish and Wildlife (WDFW) began stocking approximately 1,400 tiger muskellunge (Northern Pike *Esox lucius* \times Muskellunge *E. masquinongy*) annually in 1995 to limit the population of Northern Pikeminnow and provide a sport fishery, but the efficacy of this program has not been evaluated. The primary objective of this study was to estimate the magnitude of

predation mortality on current resident salmonids and predict potential predation impacts on reintroduced juvenile anadromous salmonids. A secondary objective was to evaluate the impact of tiger muskellunge on the Northern Pike minnow and salmonid populations. This information addresses the uncertainty regarding the role of predation within reservoirs on the feasibility of successful reintroductions of anadromous salmonids.

We characterized the spatiotemporal dimensions of the thermal environment and the abundance, distribution, size and age structure, and diets of Northern Pike minnow and tiger muskellunge in Merwin Reservoir. We examined the food-web structure of Merwin Reservoir through stable isotope analysis and data on seasonal and size-specific diet compositions of top predators to identify potential prey and ontogenetic shifts in predatory behavior. These data were used as inputs for bioenergetics model simulations to estimate the consumption of resident salmonids and alternative prey fish species by Northern Pike minnow, and of Northern Pike minnow and salmonids by tiger muskellunge. We used the results from the bioenergetics simulations to infer likely predation rates on reintroduced anadromous salmonids under different scenarios regarding

prolonged reservoir rearing versus migration through the reservoir by subyearling and yearling fish.

METHODS

Study site.—Merwin Reservoir is located in southwestern Washington on the North Fork Lewis River, a tributary of the lower Columbia River at river kilometer 140 (Figure 1). This oligotrophic reservoir is approximately 23.3 km long (PacifiCorp 2004) and has a maximum depth of 73 m and a mean depth of 31 m (PacifiCorp, unpublished data), a mean Secchi disk depth of roughly 5 m, and <0.02 mg/L total phosphorus (PacifiCorp and Cowlitz PUD 2004a; Table A.1 in the Appendix). Thermal stratification in Merwin Reservoir begins in May and peaks in August; rapid destratification occurs during October, and the water column becomes isothermal in November.

Catches in nets and other sampling gear set in Merwin Reservoir were dominated by Northern Pike minnow, Largescale Suckers *Catostomus macrocheilus*, sculpins *Cottus* spp., and Pumpkinseed *Lepomis gibbosus*; but kokanee (lacustrine Sockeye Salmon), Coastal Cutthroat Trout *O. clarkii clarkii*,

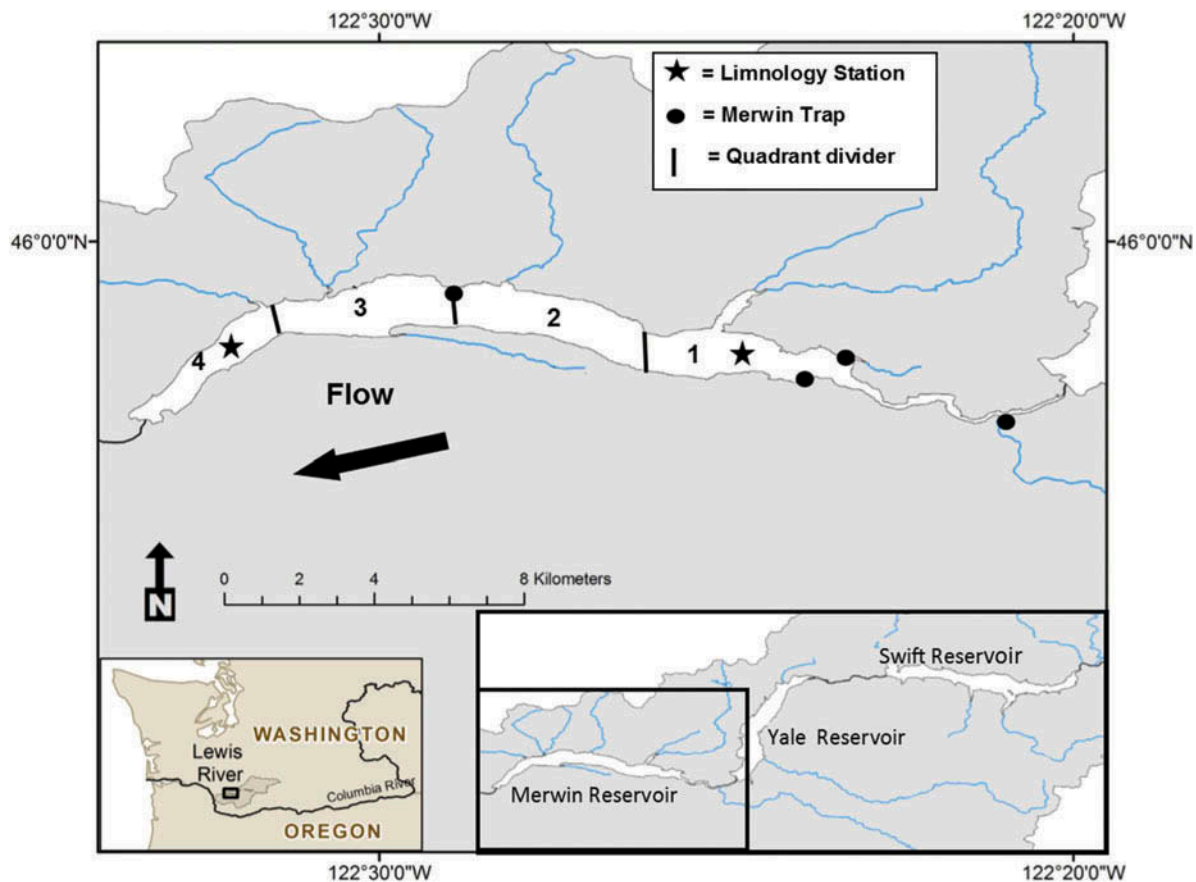


FIGURE 1. Merwin Reservoir on the North Fork Lewis River in Washington State showing limnology stations, Merwin trap locations, and quadrant delineations.

Rainbow Trout, Coho Salmon, tiger muskellunge, Threespine Stickleback *Gasterosteus aculeatus*, and Largemouth Bass *Micropterus salmoides* were present at low to moderate levels (Table A.2). The kokanee population is supplemented annually with approximately 100,000 hatchery fingerlings and yearlings, in addition to recruitment from the upstream Yale Reservoir and minimal natural production in tributaries (PacifiCorp and Cowlitz PUD 2004b, 2014).

Fish sampling.—Fish were sampled in June, late July, and November of 2013 to obtain biological samples and to characterize seasonal depth distributions and size structures. Sinking monofilament gill nets with variable stretched mesh (5.1, 6.4, 7.6, 8.9, 10.2, 11.4, 12.7, and 15.2 cm) were set perpendicular to shore for approximately 24 h. Nets were fished in three depth strata: 1–15 m, 16–30 m, and >30 m (Figure 1). Additional samples were gathered opportunistically during other sampling events using Merwin traps (Hamilton et al. 1970; Lynch 1993).

We identified, sexed, and counted fish by species and recorded FL (mm) and wet weights (WW; g) in the field. Whole dissected stomachs for stomach contents analysis, scales from the preferred body region for age and growth analysis, fin tissue for stable isotope analyses, and some whole bodies were collected in the field, placed on ice, and later frozen for preservation until analysis in the laboratory. Fish were handled and released or euthanized according to University of Washington Institutional Animal Care and Use Committee protocol 3286-21.

Size distribution of Northern Pikeminnow.—To account for sex-specific differences in growth and survival, separate adjusted length distributions for male and female Northern Pikeminnow caught in Merwin traps were combined with those caught in gill nets. The length-frequency distributions of fish captured in gill nets were adjusted for effort by mesh size, size-dependent encounter probability (Spangler and Collins 1992), and gill-net size-selectivity (Hansen et al. 1997) to estimate unbiased size distributions. Catches from Merwin traps were adjusted for the probability of encounter. We compared adjusted length distributions between this study and the 1958–1963 study by Hamilton et al. (1970) using gill-net data from similar mesh sizes and Merwin traps set in similar areas to test whether the size structure of Northern Pikeminnow had changed, which would potentially change the predation risk to juvenile salmonids.

Survival and abundance of tiger muskellunge.—Using stocking records and a catch-curve analysis, we constructed an age-structured population estimate for tiger muskellunge. Since 2004, fish have been reared at Ringold Springs Hatchery, Washington, at a constant water temperature of approximately 16°C (Richard French, WDFW, personal communication), and an average of 1,411 fish (range, 500–2,220) have been stocked at age 1 in April–June (WDFW, unpublished data). The large FL at

which tiger muskellunge are stocked (range, 293–333 mm; mean = 319 mm; SE = 4.1 mm) and the cool surface water temperatures and seemingly abundant forage base of small Northern Pikeminnow in spring suggest that stocking mortality is negligible (Carline et al. 1986; Mather and Wahl 1989; Szendrey and Wahl 1996; Wahl 1999).

Annual survival for age-1–10 tiger muskellunge (the range of ages observed) was estimated with a catch-curve analysis (Miranda and Bettoli 2007). We used cleithra-based ages and the observed size distribution to estimate the age structure of the population and an annual survival rate of 71%.

Bioenergetics model inputs.—Bioenergetics models are energy balance equations that operate on a daily time step and estimate the feeding rate (percent of maximum theoretical consumption; % C_{max}) and consumption rate (g of prey/d) needed to achieve the growth observed by different age-classes of consumers over the time interval of the simulation. These estimates depend on the energy densities of predators and prey and species-specific parameters that describe the temperature-dependent and allometric effects of body mass on consumption, metabolism, and waste (Hanson et al. 1997). Energy densities of predators (6,703 J/g for Northern Pikeminnow and 3,600 J/g for tiger muskellunge) and prey were taken from literature values and held constant across the growing season in the absence of empirical measurements from this study (see Table 1). We collected field data on growth, seasonal diet composition, and thermal experience (daily temperature experienced by the consumer) to construct a set of inputs specific to models for Northern Pikeminnow (Petersen and Ward 1999) and tiger muskellunge (Bevelhimer et al. 1985) in Merwin Reservoir.

TABLE 1. Energy density (J/g) of predators and prey items of Northern Pikeminnow and tiger muskellunge.

Prey	Energy density (J/g)	Reference
Zooplankton	1,950	D. A. Beauchamp, unpublished data
Terrestrial insects	5,000	Lowery and Beauchamp (2010)
Aquatic insects	3,400	Hansen et al. (1997)
Salmonids	5,200	Lowery and Beauchamp (2010)
Sculpins	4,305	Mazur (2004)
Northern Pikeminnow	6,703	Peterson and Ward (1999)
Tiger muskellunge	3,598	Bevelhimer et al. (1985)
Largescale Sucker	3,641	Bryan et al. (1996)
Pumpkinseed	4,186	Selch and Chipps (2007)
Signal crayfish	3,318	Mazur (2004)
Plant matter	1,435	Peterson and Ward (1999)

Thermal experience and depth distribution.—Seasonal thermal experiences of different size-classes of Northern Pikeminnow and tiger muskellunge were estimated using thermal profiles and depth-distribution patterns inferred from catches in gill and trap nets (Beauchamp et al. 2007; Table 2). Temperature profiles were recorded monthly from April to November at 1-m intervals from the surface to 30 m and every 2 m thereafter down to 60 m at two limnology stations (Figure 1). Relative catches at different depths in different seasons were used to calculate the average daily thermal experiences for each species and size-class of consumer.

Stable isotope analysis.—Stable isotopes provide an integrative signal of diet, providing a valuable complement to and corroboration for stomach content analysis. We used stable isotopes to identify the length at which Northern Pikeminnow transition to piscivory, in order to delineate size-classes for calculating diet composition. We examined $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for a range of sizes of Northern Pikeminnow and tiger muskellunge and representative samples of different guilds of potential prey (Vander Zanden and Rasmussen 1999; McIntyre et al. 2006). Fin tissue from fish and muscle tissue from Asian clams *Corbicula fluminea* and signal crayfish *Pacifastacus leniusculus* were placed on ice in the field and then frozen within 12 h for storage (Sanderson et al. 2009b). Samples were dried at 60°C for 48 h and homogenized with mortar and pestle, and 0.4–0.6 mg of material from each sample were then analyzed by the University of Washington IsoLab using a Costech Elemental Analyzer, Conflo III, MAT253, for continuous flow-based measurement of solid organic material (Fry et al. 1992). The reference material was Vienna Pee Dee belemnite for carbon and atmospheric N_2 for nitrogen.

Diet composition and energy density of prey.—We analyzed the seasonal diets for different sizes of Northern Pikeminnow

and tiger muskellunge as inputs for the bioenergetics model (Table 3). Stomach contents were identified under a dissecting microscope to species for prey fish and to taxonomic order for invertebrates, and lengths of prey fish were measured or reconstructed from diagnostic bones (Hansel et al. 1988). We calculated diet proportions by blotted WW for two size-classes of Northern Pikeminnow (200–299 mm and ≥ 300 mm FL), the breakpoint reflecting a transition to piscivory based on $\delta^{15}\text{N}$ signatures (Chipps and Garvey 2007). One set of seasonal diet proportions was calculated for all sizes of tiger muskellunge given their similarity in diet across sizes and the limited number of nonempty stomachs obtained. The energy densities of prey items were taken from published literature values (Table 1).

Age and growth of Northern Pikeminnow.—We measured the age and growth of Northern Pikeminnow from scales to obtain annual growth increments for bioenergetics simulations (Table 4). Fork length at age was back-calculated using the Fraser–Lee method with a biological intercept of zero (FL range: 34–560 mm, $N = 101$, $R^2 = 0.97$, $P < 0.001$; Isely and Grabowski 2007). Growth in length was characterized by a von Bertalanffy growth function fit to length-at-age data using the back-calculated length at final annulus for each fish (von Bertalanffy 1938). A likelihood ratio test using the “vblrt” function in the “fishmethods” package in R (Nelson 2014) indicated that a sex-specific von Bertalanffy growth model described the length-at-age data significantly better than a single model for both sexes ($\chi^2 = 12.88$, $\text{df} = 3$, $P < 0.005$). While scales often underestimate ages of Northern Pikeminnow > 350 mm, opercles were analyzed for a subset of individuals to corroborate the scale-based ages and reduce this bias by identifying older annuli on > 350 -mm fish (Takata et al. 2007). The von Bertalanffy growth parameters fit for females were $L_\infty = 786.64$ mm, $K = 0.0665$, and $t_0 = -2.0139$ ($N = 34$).

TABLE 2. Thermal experiences of Northern Pikeminnow and tiger muskellunge in bioenergetics simulations.

Date	Simulation day	Thermal experience (°C)		
		Northern Pikeminnow (200–299 mm)	Northern Pikeminnow (≥ 300 mm)	Tiger muskellunge
Apr 1	1	7.7	8.3	8.3
May 15	45	11.5	12.3	12.3
Jun 30	89	15.6	16.7	16.7
Jul 19	109	17.8	19.1	19.1
Aug 15	135	18.8	20.1	20.1
Sep 18	168	18.6	19.3	19.3
Oct 10	190	17.5	17.6	17.6
Nov 18	228	12.5	12.7	12.7
Dec 15	255	5.8	5.8	5.8
Jan 1	270	5.5	5.5	5.5
Mar 1	330	6.0	6.3	6.3
Mar 31	365	7.7	8.3	8.3

TABLE 3. Diet proportions of two size-classes of Northern Pikeminnow, and tiger muskellunge. *n* = number of nonempty stomachs, ZOOP = zooplankton, TERR INS = terrestrial insects, AQUA INS = aquatic insects, KOK = kokanee, COT = sculpin, NPM = Northern Pikeminnow, CRAY = signal crayfish, PLANT = plant matter, L SUC = Largescale Sucker, PUM = Pumpkinseed.

Day	Season	<i>n</i>	ZOOP	TERR INS	AQUA INS	KOK	COT	NPM	CRAY	PLANT	L SUC	PUM
Northern Pikeminnow (200–299 mm)												
45	Spring	23	0.71	0.05	0.10	0.00	0.03	0.00	0.09	0.02	0.00	0.00
135	Summer	9	0.88	0.00	0.11	0.00	0.00	0.00	0.00	0.01	0.00	0.00
225	Fall	12	0.11	0.00	0.00	0.00	0.26	0.00	0.00	0.63	0.00	0.00
Northern Pikeminnow (≥300 mm)												
45	Spring	11	0.01	0.00	0.09	0.00	0.00	0.43	0.45	0.02	0.00	0.00
135	Summer	29	0.00	0.00	0.07	0.14	0.09	0.19	0.51	0.00	0.00	0.00
225	Fall	26	0.08	0.04	0.00	0.28	0.14	0.10	0.28	0.08	0.00	0.00
Tiger muskellunge												
45	Spring	10	0.00	0.00	0.00	0.00	0.00	0.80	0.00	0.00	0.10	0.10
135	Summer	15	0.00	0.00	0.07	0.07	0.00	0.65	0.01	0.00	0.20	0.00
225	Fall	4	0.00	0.00	0.00	0.00	0.00	0.75	0.00	0.00	0.25	0.00

TABLE 4. Bioenergetics inputs of initial and final length and weight, and output of percent maximum consumption (%*C*_{max}), and annual consumption of all prey (total), kokanee, Northern Pikeminnow, sculpins, and signal crayfish by individual male and female Northern Pikeminnow of ages 3–14. Energy densities for the consumers were held constant at 6,703 J/g.

Age (years)	Initial FL (mm)	Initial weight (g)	Final weight (g)	%C _{max}	Annual consumption (g)				
					Total	Kokanee	Northern Pikeminnow	Sculpins	Signal crayfish
Male Northern Pikeminnow									
3	208	94	137	60	1,290	0	0	90	21
4	236	137	188	57	1,622	0	0	116	26
5	263	188	258	57	2,060	0	0	144	34
6	288	258	335	55	2,480	0	0	182	42
7	311	335	421	25	1,481	0	0	215	640
8	333	421	515	24	1,708	223	316	126	739
9	354	515	617	23	1,939	256	366	144	839
10	373	617	724	23	2,170	289	417	163	940
11	392	724	837	23	2,401	323	468	182	1,041
12	409	837	954	22	2,630	356	519	201	1,140
13	425	954	1,075	22	2,856	389	570	219	1,239
14	440	1075	1,197	22	3,078	421	620	238	1,336
Female Northern Pikeminnow									
3	223	115	180	62	1,602	0	0	107	25
4	259	180	259	60	2,107	0	0	146	34
5	293	259	387	28	1,456	0	0	189	625
6	325	387	518	26	1,784	224	305	126	768
7	354	518	667	25	2,139	271	379	152	923
8	382	667	831	25	2,504	322	457	181	1,082
9	408	831	1,009	24	2,873	375	537	211	1,243
10	432	1,009	1,198	23	3,244	428	619	241	1,404
11	455	1,198	1,396	23	3,614	482	701	272	1,565
12	476	1,396	1,601	23	3,978	535	783	302	1,724
13	496	1,601	1,811	22	4,337	587	864	331	1,880
14	515	1,811	2,025	22	4,687	639	944	360	2,033

Corresponding parameters for the male model were $L_{\infty} = 689.23$, $K = 0.0599$, and $t_0 = -3.0117$ ($N = 38$).

Fork length at age was converted to WW at age using separate FL–WW relationships developed for individuals having a FL < 300 mm and ≥ 300 mm due to the inability of a single power function to fit WW measurements over the entire range of observed FLs. The FL to WW relationship for Northern Pikeminnow with FL < 300 mm was $WW = 0.00001162 \times FL^{2.9790}$ ($N = 2,941$; range, 34–299 mm; adjusted $R^2 = 0.972$; $P < 0.001$). The relationship for individuals having a FL ≥ 300 mm was $WW = 0.000001511 \times FL^{3.3480}$ ($N = 354$; range, 300–574 mm; adjusted $R^2 = 0.974$; $P < 0.001$).

Spawning losses were calculated by subtracting the average gonadosomatic index ($100 \times$ gonad mass/body mass) of spent fish from that of ripe fish in the spring, and were phased in over two age-classes for bioenergetics model simulations to represent an increase in the proportion of mature fish. Spawning losses were 3.9% of body mass for age-3–14 males, 6% for age-3 females, and 8.9% for age-4–14 females.

Age and growth of tiger muskellunge.—Annual growth increments for bioenergetics simulations of tiger muskellunge were determined with age-to-length and WW–length relationships (Table 5). Age was determined using standard cleithra-aging procedures for one parent species, Northern Pike (Euchner 1988), and corroborated for several individuals with blank wire tags inserted at the hatchery in various locations on their bodies to indicate their brood year. We used the proportional linear relationship of cleithra length to TL derived for the other parent species, Muskellunge, to back-calculate TL at age (Harrison and Hadley 1979). A von Bertalanffy growth curve was fit to TL at age ($K = 0.389$, $L_{\infty} = 1023.9$, $t_0 = 0.00$), and TL was converted to FL with the relationship $FL = 0.959(TL) - 0.654$ (Gaygusuz et al. 2006). Fork length at age was then converted to WW at age with the

equation $WW = 0.0000003702 \times FL^{3.4787}$ ($N = 62$; range, 324–975 mm; adjusted $R^2 = 0.988$; $P < 0.001$).

Bioenergetics modeling simulations of seasonal predation by Northern Pikeminnow.—The Wisconsin bioenergetics model fit daily per capita consumption, starting April 1, to satisfy the observed growth of an average Northern Pikeminnow from each age-class and sex over an annual cycle (Hanson et al. 1997). Per capita consumption demands were expanded to separate age-structured populations of 1,000 Northern Pikeminnow of the 200–299-mm and ≥ 300 -mm size-classes, based on age-frequency distributions and assuming an even sex ratio (Isely and Grabowski 2007). We then used estimates of resident salmonid consumption to gauge potential predation on reintroduced anadromous salmonids.

Estimating predation on reintroduced salmonids.—To estimate maximum potential predation on reintroduced anadromous salmonids, we assumed that all predation on resident kokanee would switch to anadromous fish once they were reintroduced. Thus, the monthly biomass of kokanee that was consumed from April 1 to March 30 based on bioenergetics simulations was divided by the estimated monthly WW of an age-0 Chinook Salmon that adopted a reservoir-rearing strategy year-round, to estimate how many individuals could be lost to predation. We simulated the monthly mass of individual age-0 Chinook Salmon using a bioenergetics model, assuming that they would have similar depth distributions as kokanee and would therefore share similar thermal experiences, based on observations of Chinook Salmon in North Fork Reservoir on the Clackamas River (Lowery and Beauchamp 2010). This assumption also suggested that they would have similar overlap with predatory Northern Pikeminnow, supporting our use of kokanee as a surrogate to estimate predation on anadromous salmonids in the reservoir. We assumed a diet of zooplankton and insects for Chinook Salmon and a feeding rate of 93% C_{\max} , as informed by observations of age-1 Chinook

TABLE 5. Bioenergetics inputs of initial and final length and weight, and output of percent maximum consumption (% C_{\max}), total consumption, and growth efficiency by individual tiger muskellunge. Energy densities for the consumers were held constant at 3,600 J/g.

Age (years)	Initial FL (mm)	Initial weight (g)	Final weight (g)	Growth (g)	% C_{\max}	Total consumption (g)	Growth efficiency (%)
1	316	184	1,116	932	48.85	2,213	42.13
2	531	1,116	2,592	1,475	40.28	4,772	30.92
3	676	2,592	4,159	1,568	35.74	7,049	22.24
4	774	4,159	5,545	1,385	33.01	8,798	15.74
5	841	5,545	6,652	1,107	31.29	10,060	11.01
6	886	6,652	7,486	834	30.18	10,944	7.62
7	917	7,486	8,092	606	29.44	11,553	5.24
8	938	8,092	8,521	430	28.95	11,971	3.59
9	952	8,521	8,821	300	28.62	12,255	2.45
10	961	8,821	9,029	208	28.40	12,448	1.67

Salmon that residualized in the upstream Swift Reservoir following releases in 2013. Fish in this simulation grew from 0.36 g (35 mm) on April 1 to 45 g (155 mm) on November 15, after which their mass was held constant through March 30 to simulate reduced prey supply and growth during winter. The mass that Chinook Salmon smolts achieved in this simulation was at the upper end of the length distribution of yearling smolts that outmigrated from the Columbia River and survived at least 30 d in the marine environment (Tomaro et al. 2012). To bound the uncertainty surrounding our numerical consumption estimate, we also simulated the magnitude of predation on a smaller, typical reservoir-rearing, Chinook Salmon that achieved a mass of only 18 g (120 mm), which is at the lower end of the length distribution of yearling smolts that survived at least 30 d in the marine environment (Tomaro et al. 2012). A different predation scenario was used to simulate potential predation on migrating age-1 smolts.

Some juvenile stream-type Chinook Salmon smolts might only use the reservoir as a migration corridor after rearing in tributaries. Therefore, we estimated the potential predation impact of Northern Pikeminnow on their survival during the spring out-migration period. As before, population-level consumption demand of kokanee by Northern Pikeminnow was divided by the mass of individual stream-type Chinook Salmon; however, we restricted these simulations to April through June, spanning the months for peak out-migration (PacifiCorp and Cowlitz PUD 2004b). We used the same potential average smolt sizes (18 g and 120 mm; 45 g and 155 mm), which were held constant for the 3-month simulations.

Our estimates of predation on age-0 or age-1 Chinook Salmon represent the maximum on either age-class, because the same consumption by Northern Pikeminnow was used to estimate losses in both scenarios. However, we might expect that this overall consumption rate would be partitioned among the two age-classes of anadromous salmonids as well as resident salmonids, so the realized predation should be lower than our estimates. Our estimates of predation by size-structured units of 1,000 predators contain all the major variability related to seasonal and size-specific diets, consumption rates, and relative abundance of each size per age-class. The estimates can be multiplied by however many thousands of predators of that size range that are in the population (or however many might be prescribed in different predation scenarios) to generate full population-level predation estimates.

Estimating predation by tiger muskellunge on Northern Pikeminnow.—Thermal experience, size-specific diet composition, and growth estimates were fed into a bioenergetics model coded in Microsoft Excel to determine annual consumption rates for each age-class of tiger muskellunge (Bevelhimer et al. 1985). Individual consumption demands were then expanded by the respective abundance estimates of each age-class to determine the population-level consumption. For predator size-classes of age 1 and ages 2–10, we used the biomass of Northern

Pikeminnow consumed by tiger muskellunge and the lengths of Northern Pikeminnow found in stomachs to estimate the number and size distribution of prey consumed.

RESULTS

Seasonal Distribution and Thermal Experience of Northern Pikeminnow

During stratification from May to October, the epilimnion was approximately 8 m deep, the metalimnion ranged roughly 8–18 m, and the hypolimnion was ≥ 18 m (Figure 2). The epilimnion warmed from 14°C to 16°C in May to 22–24°C in August, and the hypolimnion warmed from 5°C to 6°C in April to 15–18°C in October, when fall turnover occurred.

Depth distribution of Northern Pikeminnow varied by season. Most Northern Pikeminnow and especially those having a FL ≥ 300 mm occupied warmer surface waters nearshore in 0–15-m depths during strongly thermally stratified periods (June–September), but were deeper during isothermal conditions in November (Figures 2, 3). The CPUE of the larger fish was significantly greater in 0–15-m depths (4.8 fish/net) than in deeper depths (0.3 fish/net) in spring–summer (two-sided *t*-test: *df* = 18, *t* = 5.11, *P* < 0.001). This pattern reversed as the reservoir became isothermal in November, and CPUE was higher in 16–30-m depths (5.7 fish/net) than in 0–15-m depths (1.5 fish/net), although this difference was not significant (two-sided *t*-test: *df* = 3, *t* = 1.89, *P* = 0.155). The CPUE of Northern Pikeminnow with a FL of 200–299 mm was also significantly higher at 0–15-m depths (24.3 fish/net) during summer stratification, but a sizeable number also occupied the 15–30-m depth (13.4 fish/net; two-sided *t*-test: *df* = 14, *t* = 3.42, *P* = 0.004). Northern Pikeminnow with a FL of 200–299 mm exhibited the same distribution pattern as fish ≥ 300 mm in November, and the CPUE in 16–30-m depths (15 fish/net) was not significantly

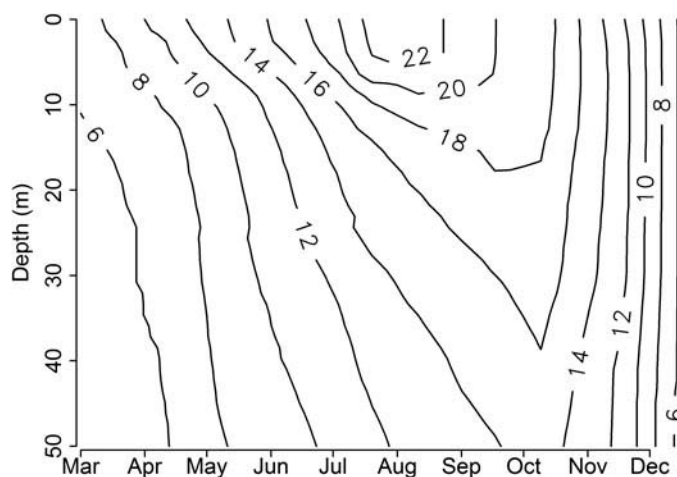


FIGURE 2. Isoclines of average water temperature (°C) in Merwin Reservoir in 2014.

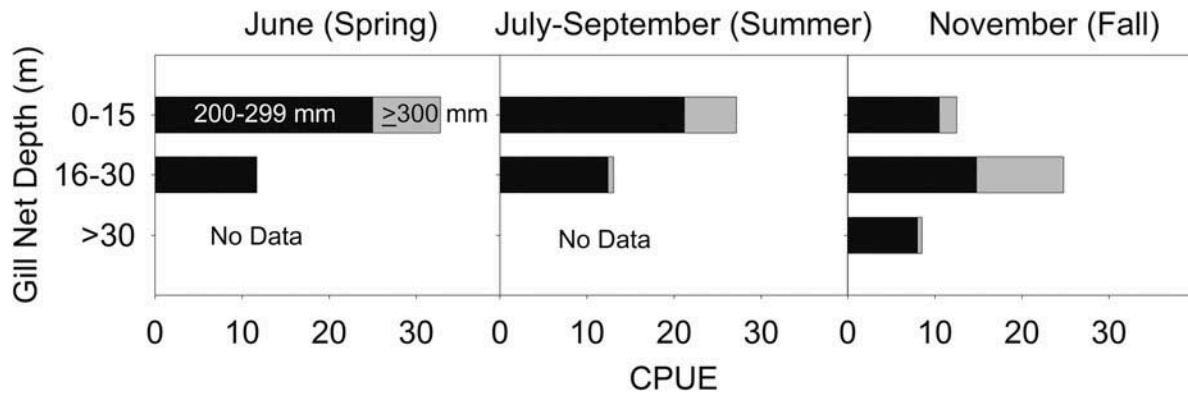


FIGURE 3. Catch per unit effort for two sizes of Northern Pikeminnow by depth and season. Black bars: 200–299 mm FL; gray bars: ≥ 300 mm FL.

higher than in 0–15-m depths (10.4 fish/net; two-sided t -test: $df = 3$, $t = 0.65$, $P = 0.561$). Tiger muskellunge remained in the epilimnion in spring–summer and were found in somewhat deeper water in fall, similar to that of large Northern Pikeminnow.

Although not significant, the CPUE of Northern Pikeminnow with a FL ≥ 300 mm in gill nets appeared greater in the lower half (quadrants 3–4; 6 fish/net) than in the upper half of the reservoir (3.1 fish/net) during sampling in August–September 2014 (two-sided t -test: $df = 6$, $t = 2.08$, $P = 0.083$). The CPUE of Northern Pikeminnow with a FL of 200–299 mm during summer was significantly higher in the lower half of the reservoir (27.1 fish/net) than in the upper half (17.8 fish/net; two-sided t -test: $df = 58$, $t = 2.79$, $P = 0.007$). This pattern suggests that predation rates are higher in the lower half of the reservoir in summer.

Stable Isotopes and Diet Composition

Stable isotopes.—Northern Pikeminnow became increasingly piscivorous and reliant on benthically derived energy as they increased in size (Figure 4). The trophic position of medium-sized Northern Pikeminnow (200–299 mm) suggested that they fed primarily on a mix of pelagic and benthic invertebrates and increasing proportions of benthic fish or signal crayfish. The isotopic signatures for large Northern Pikeminnow having a FL ≥ 300 mm suggested that they consumed a combination of pelagic and benthic fish and signal crayfish.

Stable isotope analysis suggested that tiger muskellunge fed on a mix of pelagically and bentholithorally derived carbon and increased by nearly one trophic level (typically represented by a $\sim 3.4\%$ increase in $\delta^{15}\text{N}$; Minagawa and Wada 1984; Hussey et al. 2014) over the range of 450–1,050 mm in FL (Figure 4). Thus, stable isotope patterns indicated that tiger muskellunge initially consumed invertebrate-feeding fish, but progressed to consuming partially piscivorous fish as they grew.

Stomach content analysis.—Northern Pikeminnow exhibited seasonal and ontogenetic shifts in diet composition and increasingly relied on prey fish as their size increased, in

agreement with the stable isotope patterns. The spring and summer diets of 200–299-mm Northern Pikeminnow contained 72–88% zooplankton and smaller proportions of sculpins, signal crayfish, insects, and plant matter, but no salmonids were detected (Table 3). Diets of Northern Pikeminnow having a FL ≥ 300 mm contained primarily fish and signal crayfish. During spring, signal crayfish (45%) and smaller Northern Pikeminnow (43%) were the predominant prey. During summer, signal crayfish still represented 51% of the diet, but Northern Pikeminnow declined to 19%, whereas sculpins (9%) and kokanee (14%) increased. The diet proportions of sculpins (14%) and kokanee (28%) continued to increase during fall,

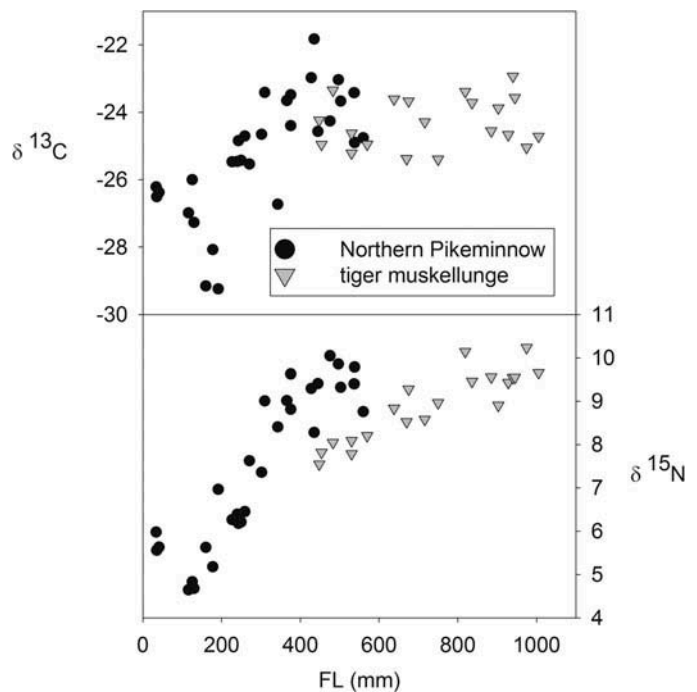


FIGURE 4. Stable isotope values for $\delta^{13}\text{C}$ (upper panel) and $\delta^{15}\text{N}$ (lower panel) of individual Northern Pikeminnow and tiger muskellunge as a function of FL.

while signal crayfish (29%) and smaller Northern Pikeminnow (10%) declined.

The maximum FL of prey fish consumed increased with the FL of Northern Pikeminnow (Figure 5). Kokanee were the largest prey fish consumed and occasionally exceeded 50% of the predator's FL when reconstructed from diagnostic bones. Four 100–150-mm kokanee were found in the guts of 300–399-mm Northern Pikeminnow, and six 200–325-mm kokanee were observed in predators having a FL ≥ 400 mm. As prey, the average FL of Northern Pikeminnow eaten by 300–399-mm conspecifics was 143 mm (range, 143–144; $N = 2$) and 164 mm for ≥ 400 -mm predators (range, 101–252 mm; $N = 10$).

The diet composition of tiger muskellunge remained relatively constant from spring through fall, and was corroborated by stable isotopes. Northern Pikeminnow were the largest component (65–80% of diet across seasons) followed by Largescale Suckers (10–25%), while kokanee, Pumpkinseed, signal crayfish, and aquatic insects represented smaller proportions (Table 3). Only one salmonid (FL = 451 mm) was found in the stomach of a tiger muskellunge, a 920-mm fish captured in September. Tiger muskellunge consumed a wide size range (57–394 mm) of Northern Pikeminnow; the majority of prey fish were approximately 40% of the consumer's FL, and a smaller secondary mode of prey fish were $<20\%$ of the predator's length (Figure 5). Tiger muskellunge at age 1 and FL > 300 mm began feeding on Northern Pikeminnow having a FL ≥ 200 mm. The mean FL of Northern Pikeminnow consumed was not significantly different between age-1 (152 ± 49 mm [mean \pm SD]) and age-2–10 tiger muskellunge

(195 ± 97 mm) (t -test: $df = 19$, $t = -1.354$, $P = 0.192$). The mean FL of Northern Pikeminnow consumed was also not significantly different among spring (181 ± 76 mm), summer (182 ± 92 mm), and fall (163 ± 81 mm) (one-factor ANOVA: $F = 0.087$, $df = 21$, $P = 0.917$).

Size distribution.—The length frequency distributions of male and female Northern Pikeminnow were skewed toward smaller (200–299 mm FL) individuals and exhibited a decrease in modal FL from 1958–1963 to 2013–2014 (Figure 6). Fish with a FL of 200–299 mm represented 83% of the Northern Pikeminnow ≥ 200 mm in the present study. Males in the present study were significantly smaller on average than in the earlier (Hamilton et al. 1970) study ($\chi^2 = 192$, $df = 80$, $P < 0.001$) as were females ($\chi^2 = 336$, $df = 224$, $P < 0.001$). Additionally, the current female size structure was significantly larger than that for males ($\chi^2 = 240$, $df = 160$, $P < 0.001$).

Tiger muskellunge abundance.—The population abundance of tiger muskellunge based on stocking records and the fitted 71% annual survival rate (adjusted $R^2 = 0.554$, $N = 6$, $P = 0.05$) was 5,362 fish. We expanded individual consumption demands by this population abundance estimate as well as a size-structured population of 1,000 tiger muskellunge for comparison with Northern Pikeminnow.

Population-Level Consumption Demand of Northern Pikeminnow

Total monthly consumption of salmonids and other fishes by Northern Pikeminnow was highly influenced by the size

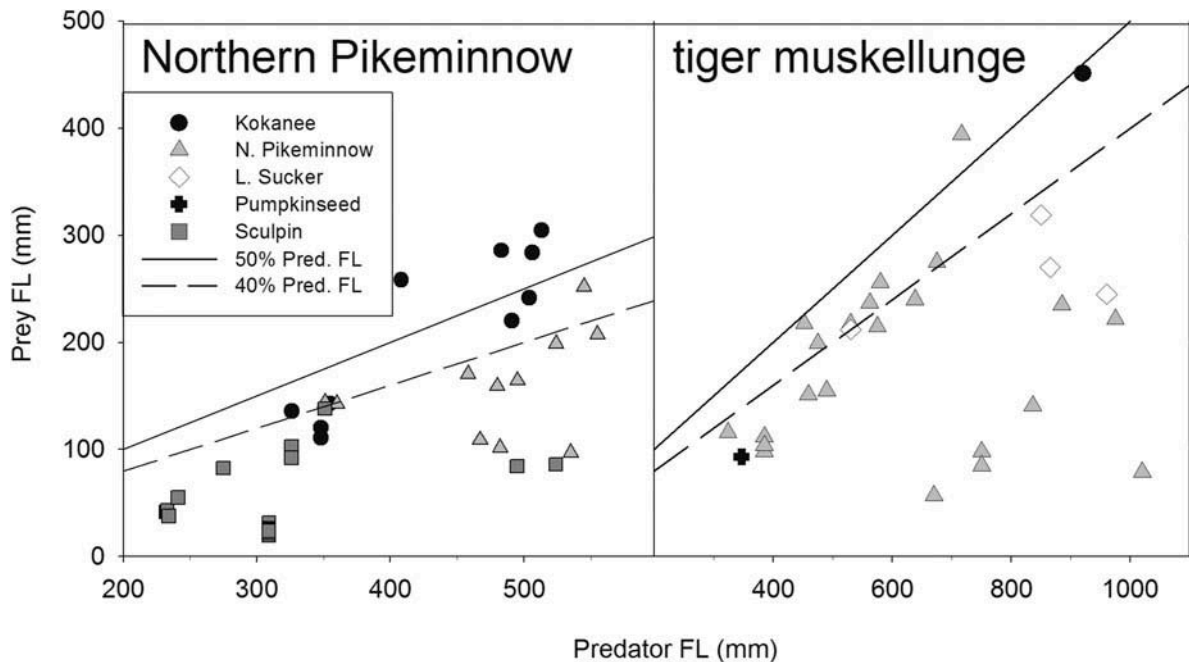


FIGURE 5. The relationship between Northern Pikeminnow and tiger muskellunge predator FLs and prey fish FLs. Reference lines represent 40% and 50% of predator FLs. Note that the scales of the x-axes of the two panels are different.

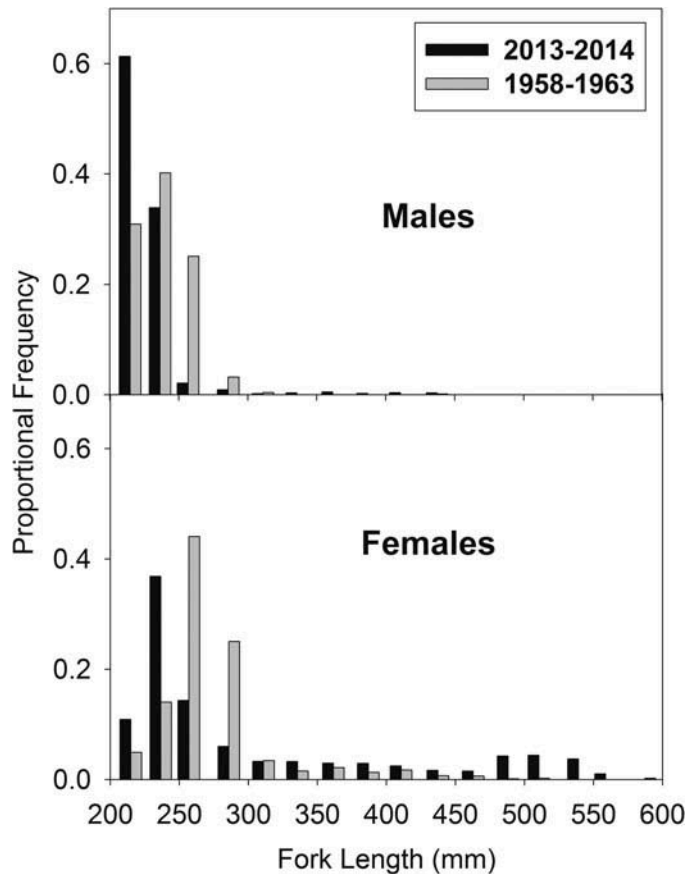


FIGURE 6. Length frequency distributions of male and female Northern Pikeminnow in 2013–2014 and in 1958–1963 (Hamilton et al. 1970). The mesh sizes of the gill nets used in the present study are larger than those used in the earlier study. The data from the Hamilton et al. (1970) study were included in the 2013–2014 distribution to best characterize the current size distribution of the population.

structure and abundance of the population, as well as the thermal regime, which influenced metabolic rates and spatial overlap with salmonids. Overall consumption increased as the water warmed in spring, and fish consumption was high from June through October (Figure 7). Consumption demand was very low in winter, when water temperature limited metabolic rates. The feeding rate of 200–299-mm Northern Pikeminnow was 55–65% C_{max} , but declined to 22–25% C_{max} for the size-class having a FL ≥ 300 mm (Table 4). Consumption by a size-structured population of 1,000 Northern Pikeminnow with a FL of 200–299 mm over the entire year totaled 1,069 kg of zooplankton (peak in August), 382 kg of plant matter (peak in October), and 159 kg of sculpins (peak in October) (Figure 7). Consumption by 1,000 Northern Pikeminnow having a FL ≥ 300 mm over the entire year totaled 1,118 kg of crayfish (peak in August), 557 kg of Northern Pikeminnow (peak in June), and 384 kg of salmonids (peak in October).

Dividing monthly consumption demand of resident salmonids by the corresponding monthly mass of an age-0,

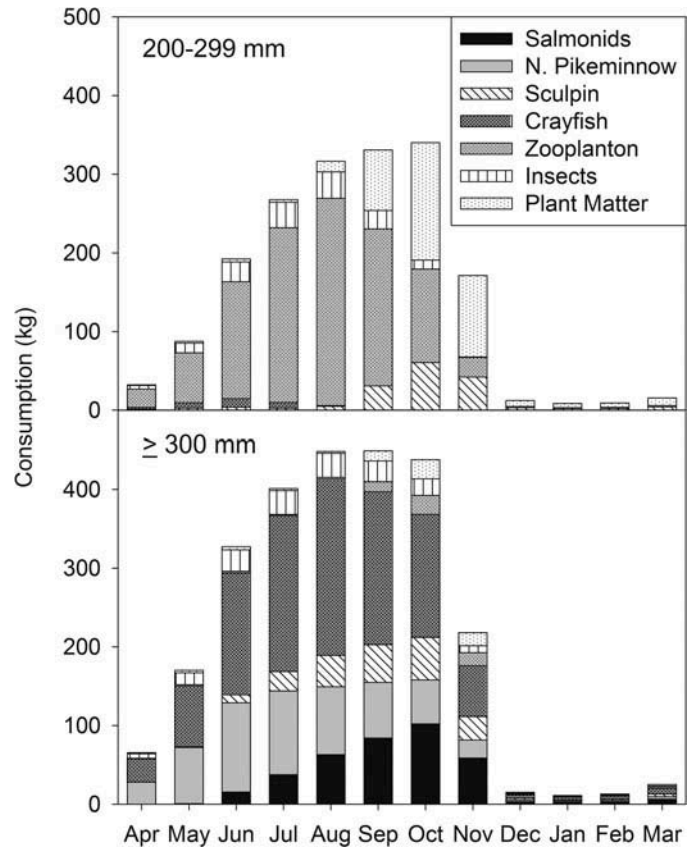


FIGURE 7. Modeled monthly biomass of prey consumed by size-structured populations of 1,000 Northern Pikeminnow having FL of 200–299 mm and FL ≥ 300 mm.

reservoir-rearing stream-type Chinook Salmon that reached 18 g (120 mm) by November and summing across months provided an estimate of 39,250 Chinook Salmon consumed from April 1 to March 31 by a size-structured population of 1,000 Northern Pikeminnow having a FL ≥ 300 mm (Figure 8). The equivalent predation mortality if Chinook Salmon reached a mass of 45 g (150 mm in FL) by November was 16,022 fish annually. Our estimates of potential predation on age-1 Chinook Salmon smolts simply migrating through the reservoir was considerably less than on age-0 fish assumed to rear in the reservoir year-round.

Salmonid consumption by a size-structured population of 1,000 large Northern Pikeminnow during peak months of smolt out-migration in April–June was only 17 kg (Figure 7). This biomass was equivalent to 969 salmon smolts weighing 18 g each, or 388 smolts weighing 45 g each (Figure 8). These numerical estimates of smolt consumption were driven in large part by the lack of salmonids observed in Northern Pikeminnow diets during spring and low overall consumption rates due to cold water in spring.

Cannibalism on smaller Northern Pikeminnow by 1,000 predators having a FL ≥ 300 mm was 557 kg, which was equivalent

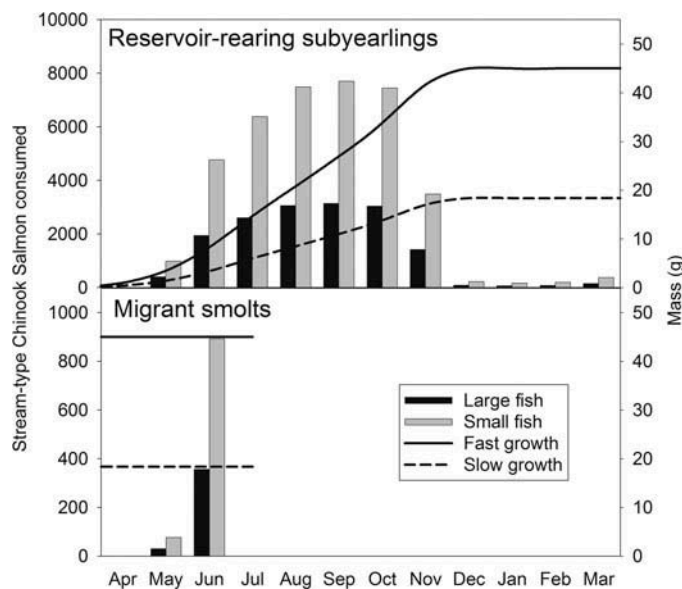


FIGURE 8. Two estimates for the monthly body mass (lines) of Chinook Salmon: a fast-growth scenario where age-0 fish reach a mass of 45 g (155 mm) by the end of the growing season, and a slow-growth scenario where they reach a mass of 18 g (120 mm). Bars represent potential numerical consumption of juvenile Chinook Salmon by a size-structured population unit of 1,000 large (≥ 300 mm FL) Northern Pikeminnow. Numerical consumption estimates were created by dividing biomass consumed by the monthly body mass of the prey fish. Bars represent alternative scenarios rather than being additive. The top panel shows a scenario where age-0 Chinook Salmon use the reservoir for year-round rearing, and the bottom panel represents a scenario where smolts only use the reservoir as a migration corridor in spring. The primary y-axes have different scales in the two panels.

to 1,862 Northern Pikeminnow having a FL of 200–299 mm and 9,311 fish < 200 mm based on the length distribution of cannibalized individuals and a FL–WW regression (Figures 5, 7). Thus, every Northern Pikeminnow having a FL ≥ 300 mm ate an average of 11 smaller conspecifics per year.

Population-Level Consumption Demand of Tiger Muskellunge

We estimated that the population of tiger muskellunge (FL range, 316–970 mm) consumed 27,252 Northern Pikeminnow having a FL ≥ 300 mm, 138,875 having a FL of 200–299 mm, and 240,470 having a FL < 200 mm over the course of a year (Figure 9). The equivalent consumption by a size-structured population unit of 1,000 tiger muskellunge was 5,296 Northern Pikeminnow ≥ 300 mm, 25,967 fish of 200–299 mm, and 45,141 fish < 200 mm FL. Thus, every tiger muskellunge ate an average of 86 Northern Pikeminnow per year, and their per capita predation impact was approximately eight times that of Northern Pikeminnow ≥ 300 mm.

DISCUSSION

Northern Pikeminnow and tiger muskellunge consumed a modest amount of salmonids, but their predation also affected

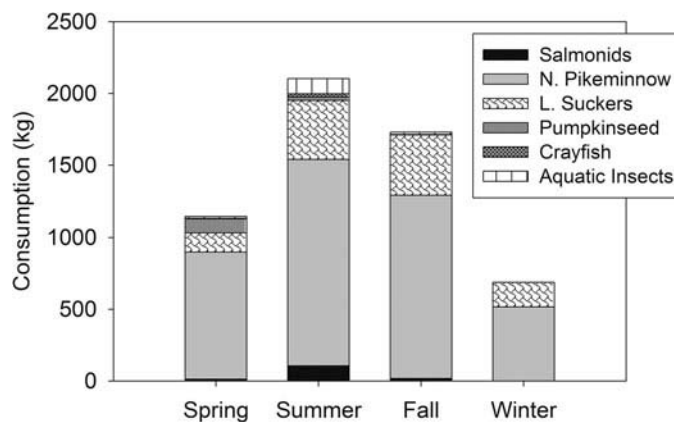


FIGURE 9. Seasonal biomass of prey consumed by an age-structured population of 5,362 tiger muskellunge. Tiger muskellunge did not consume much salmonid biomass when alternative prey types were available.

the recruitment of larger piscivorous Northern Pikeminnow. Predation by large Northern Pikeminnow and tiger muskellunge on smaller Northern Pikeminnow contributed to an attenuated size structure that reduced predation pressure on salmonids. Our simulations indicated that a unit population of 1,000 large Northern Pikeminnow could consume approximately 16,000–40,000 age-0, spring Chinook Salmon rearing in the reservoir year-round based on their current feeding rate, consumption of resident salmonids, and the size distribution of the population. The likely magnitude of predation mortality during a hypothetical age-1 salmon smolt out-migration in spring was 400–1,000 smolts per 1,000 large Northern Pikeminnow, suggesting that Merwin Reservoir would function as a migration corridor without imposing undue predation mortality. These estimates could be expanded to the population level with robust abundance estimates of Northern Pikeminnow. Two factors that significantly reduced predation rates on salmonids by Northern Pikeminnow were a partial thermal refuge from predation and the truncated size structure of the predator population.

Thermal stratification created a partial predation refuge from Northern Pikeminnow for salmonids during the peak growing season, and cold water in destratified periods metabolically reduced predation during early spring, fall, and winter. However, consumption of salmonids increased in summer relative to spring, suggesting that thermal stratification only partially segregated Northern Pikeminnow from kokanee. The crucial assumption that Chinook Salmon would exhibit a depth distribution and diel vertical migration similar to those of kokanee, to minimize their overlap with Northern Pikeminnow, is based on observations in North Fork and Lookout Point reservoirs (Lowery and Beauchamp 2010; Monzyk et al. 2013) and is supported by differences in the temperature-dependent growth potential curves for Chinook Salmon (Stewart and Ibarra 1991; Plumb and Moffitt 2015) and Northern Pikeminnow (Petersen and Ward 1999).

The other major factor limiting predation on salmonids was the size distribution of the Northern Pikeminnow population. The vast majority of the population was <300 mm in FL and fed predominantly on invertebrates, sculpins, and plant matter, with seemingly no consumption of salmonids. Despite their lack of piscivory on salmonids or other limnetic fish in this study, the smaller Northern Pikeminnow could conceivably be important predators on Chinook Salmon fry during winter or spring when salmon fry are more bentholithorally oriented; however, Northern Pikeminnow consumption rates would be thermally constrained during that period. The high mortality rate of 200–299-mm Northern Pikeminnow inferred from the catch curve was unusual, given that mortality is generally low for fish of this relatively large size. Cannibalism and predation by tiger muskellunge accounted for a portion of this mortality based on our bioenergetics simulations and the length distributions of Northern Pikeminnow in diets, and may explain the decrease in modal FL of the Northern Pikeminnow population between the 1960s and the present. This predation-driven mortality of 200–299-mm Northern Pikeminnow potentially reduced predation rates on salmonids in this system by reducing recruitment of larger piscivores.

While the size distribution of the Northern Pikeminnow clearly suggested that there was significant mortality for 200–299-mm fish, the size distribution may have been biased due to size-selective sampling (Beamesderfer and Rieman 1988). However, we attempted to account for the potential bias in size-selective sampling via published correction methods and managed this uncertainty by estimating size-structured predation rates per 1,000 predators separately for Northern Pikeminnow > 300 mm, thus insulating this analysis from the uncertainty in relative abundance of small versus large Northern Pikeminnow.

Another source of uncertainty in our study was the use of kokanee as a surrogate for evaluating potential predator–prey interactions between Northern Pikeminnow and juvenile Chinook Salmon. Both stream-type Chinook Salmon in the Clackamas and Willamette rivers and ocean-type Chinook Salmon in Lake Washington often initially occupy littoral habitats upon entering lakes or reservoirs before shifting into limnetic habitats later in the spring (Koehler et al. 2006; Lowery and Beauchamp 2010; Monzyk et al. 2013). Utilization of the littoral zone in spring would increase the spatiotemporal overlap of fry with Northern Pikeminnow at a size when they would be highly vulnerable to predation. The predators might therefore respond differently to this size and spatial distribution of salmonid prey than to the contemporary population of salmonids in the reservoir, which could affect mortality. A shift toward consumption of salmonids by the abundant smaller size-class of Northern Pikeminnow could lead to higher predation rates than those estimated in this study. Petersen and Ward (1999) found that Northern Pikeminnow consumed a greater proportion of salmonids in the forebay of John Day Dam than in the main reservoir,

suggesting that higher predation rates may also occur in the Merwin Dam forebay in response to a smolt out-migration. However, predation rates would be metabolically depressed by cold water during this period of potential overlap in spring. Large-scale, experimental releases of Chinook Salmon fry into tributaries of Merwin Reservoir would effectively address this uncertainty by enabling direct observation of the distribution (timing and extent of reservoir entry, offshore migration, and out-migration) and behavior (schooling and diel vertical migration) of juvenile salmon and the response by predators in this watershed.

Despite uncertainty, this study suggests that predation losses of juvenile Chinook Salmon are likely to occur, but are reduced by the skewed size distribution of the Northern Pikeminnow population and their spatial mismatch during thermal stratification. Further evaluation of habitat use by reintroduced salmonids, response by predators, and the abundance of predators would increase the precision of predation mortality estimates on the introduced salmonids. Continued monitoring of the abundance, size distribution, vertical and horizontal distribution, and diet of the predator populations will be highly beneficial for guiding salmonid management.

This study highlights the importance of evaluating trophic interactions within reservoirs slated for salmonid reintroduction, as they can be functional migration corridors and may offer profitable juvenile-rearing habitat, despite the reservoirs hosting abundant predator populations. Reservoirs should be evaluated on an individual basis for physical environment, fish behavior, and predator demographics to determine whether predation risk to salmonids will preclude or limit the success of the reintroduction. This information is significant given the tremendous conservation potential of reintroducing Pacific salmon above high-head dams into quality high-elevation habitat amid declines in salmonid populations and habitat degradation in lower portions of the watershed.

ACKNOWLEDGMENTS

This research was funded by PacifiCorp Energy, the U.S. Geological Survey, the School of Aquatic and Fisheries Science at the University of Washington, and the Washington Lakes Protection Association. C. Clark was instrumental in planning and execution of field and laboratory work. S. Burgess, K. Ellis, A. Fuller, D. Lombardo, I. Vincent, and numerous others also conducted field and laboratory work. Collaboration with R. Al-Chokhachy, H. Bowen, and C. Clark provided valuable information on the lotic habitat in the basin, and expert local knowledge was provided by F. Shrier and J. Doyle. This manuscript benefited greatly from comments by T. Quinn, R. Zabel, J. Breck, and several anonymous reviewers. The Washington Cooperative Fish and Wildlife Research Unit is jointly sponsored by the U.S. Geological Survey, the University of Washington, the Washington Departments of Ecology, Fish and Wildlife, and

Natural Resources, and the Wildlife Management Institute. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

REFERENCES

- Al-Chokhachy, R. A. 2013. A review of existing data to anadromous fish reintroduction, collection and transport of anadromous fish above hydro-power/dam facilities. U.S. Geological Survey, draft report, Bozeman, Montana.
- Anderson, J. H., G. R. Pess, R. W. Carmichael, M. J. Ford, T. D. Cooney, C. M. Baldwin, and M. M. McClure. 2014. Planning Pacific salmon and steelhead reintroductions aimed at long-term viability and recovery. *North American Journal of Fisheries Management* 34:72–93.
- Beamesderfer, R. C., and B. E. Rieman. 1988. Size selectivity and bias in estimates of population statistics of Smallmouth Bass, Walleye, and Northern Squawfish in a Columbia River reservoir. *North American Journal of Fisheries Management* 8:505–510.
- Beauchamp, D. A., D. Wahl, and B. M. Johnson. 2007. Predator–prey interactions. Pages 765–842 in C. S. Guy and M. J. Brown, editors. *Analysis and interpretation of inland fisheries data*. American Fisheries Society, Bethesda, Maryland.
- Beechie, T., E. Buhle, M. Ruckelshaus, A. Fullerton, and L. Holsinger. 2006. Hydrologic regime and the conservation of salmon life history diversity. *Biological Conservation* 130:560–572.
- Bevelhimer, M. S., R. A. Stein, and R. F. Carline. 1985. Assessing significance of physiological differences among three esocids with a bioenergetics model. *Canadian Journal of Fisheries and Aquatic Sciences* 42:57–69.
- Bilby, R. E., and L. A. Mollet. 2008. Effect of changing land use patterns on the distribution of Coho Salmon (*Oncorhynchus kisutch*) in the Puget Sound region. *Canadian Journal of Fisheries and Aquatic Sciences* 65:2138–2148.
- Bisson, P. A., K. Sullivan, and J. L. Nielsen. 1988. Channel hydraulics, habitat use, and body form of juvenile Coho Salmon, steelhead, and Cutthroat Trout in streams. *Transactions of the American Fisheries Society* 117:262–273.
- Bourret, S. L., B. P. Kennedy, C. C. Caudill, and P. M. Chittaro. 2014. Using otolith chemical and structural analysis to investigate reservoir habitat use by juvenile Chinook Salmon *Oncorhynchus tshawytscha*. *Journal of Fish Biology* 85:1507–1525.
- Bryan, S. D., C. A. Soupir, W. G. Duffy, and C. E. Freiburger. 1996. Caloric densities of three predatory fishes and their prey in Lake Oahe, South Dakota. *Journal of Freshwater Ecology* 11:153–161.
- Burgner, R. L. 1991. Life history of Sockeye Salmon *Oncorhynchus nerka*. Pages 3–117 in C. Groot and L. Margolis, editors. *Pacific salmon life histories*. University of British Columbia Press, Vancouver.
- Carey, M. P., B. L. Sanderson, K. A. Barnas, and J. D. Olden. 2012. Native invaders: challenges for science, management, policy and society. *Frontiers in Ecology and the Environment* 10:373–381.
- Carline, R. F., R. A. Stein, and L. M. Riley. 1986. Effects of size at stocking, season, Largemouth Bass predation and forage abundance on survival of tiger muskellunge. Pages 151–167 in G. E. Hall, editor. *Managing muskies: a treatise on the biology and propagation of Muskellunge in North America*. American Fisheries Society, Special Publication 15, Bethesda, Maryland.
- Chippis, S. R., and J. E. Garvey. 2007. Quantitative assessment of food habits and feeding patterns. Pages 473–514 in C. Guy and M. Brown, editors. *Analysis and interpretation of freshwater fisheries data*. American Fisheries Society, Bethesda, Maryland.
- Connor, W. P., W. L. Burge, R. Waite, and T. C. Bjornn. 2002. Juvenile life history of wild fall Chinook Salmon in the Snake and Clearwater rivers. *North American Journal of Fisheries Management* 22:703–712.
- Euchner, R. B. 1988. Collection, preparation and use of Northern Pike (*Esox lucius*) cleithra for age determination. Ministry of Environment and Parks, Recreational Fisheries Branch, Report PCE 20, Fort St. John, British Columbia.
- Eldridge, W. H., and K. A. Naish. 2007. Long-term effects of translocation and release numbers on fine-scale population structure among Coho Salmon (*Oncorhynchus kisutch*). *Molecular Ecology* 16:2407–2421.
- Everest, F. H., and D. W. Chapman. 1972. Habitat selection and spatial interaction by juvenile Chinook Salmon and steelhead in two Idaho streams. *Journal of the Fisheries Research Board of Canada* 29:91–100.
- Ferguson, J. W., B. P. Sandford, R. E. Reagan, L. G. Gilbreath, E. B. Meyer, R. D. Ledgerwood, and N. S. Adams. 2007. Bypass system modification at Bonneville Dam on the Columbia River improved the survival of juvenile salmon. *Transactions of the American Fisheries Society* 136:1487–1510.
- Foerster, R. E., and W. E. Ricker. 1953. The Coho Salmon of Cultus Lake and Sweltzer Creek. *Journal of the Fisheries Research Board of Canada* 10:293–319.
- Fry, B., W. Brand, F. J. Mersch, K. Tholke, and R. Garritt. 1992. Automated analysis system for coupled $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ measurements. *Analytical Chemistry* 64:288–291.
- Gaygusuz, Ö., Ç. Gürsoy, M. Özuluğ, A. Serhan Tarkan, H. Acipinar, G. Bilge, and H. Filiz. 2006. Conversions of total, fork and standard length measurements based on 42 marine and freshwater species (from Turkish waters). *Turkish Journal of Fisheries and Aquatic Sciences* 6:79–84.
- Hamilton, J. A. R., L. O. Rothfus, M. W. Erho, and J. D. Remington. 1970. Use of a hydroelectric reservoir for rearing of Coho Salmon (*Oncorhynchus kisutch*). *Washington Department of Fisheries Research Bulletin* 9.
- Hansel, H. C., S. D. Duke, P. T. Lofy, and G. A. Gray. 1988. Use of diagnostic bones to identify and estimate original lengths of ingested prey fishes. *Transactions of the American Fisheries Society* 117:55–62.
- Hansen, M. J., C. P. Madenjian, J. H. Selgeby, and T. E. Helsel. 1997. Gillnet selectivity for Lake Trout (*Salvelinus namaycush*) in Lake Superior. *Canadian Journal of Aquatic and Fisheries Science* 54:2483–2490.
- Hanson, P. C., T. B. Johnson, D. E. Schindler, and J. F. Kitchell. 1997. Fish bioenergetics 3.0. University of Wisconsin Sea Grant Institute, Technical Report WISCU-T-97-001, Madison.
- Harrison, E. J., and W. F. Hadley. 1979. A Comparison of the use of cleithra to the use of scales for age and growth studies. *Transactions of the American Fisheries Society* 108:452–456.
- Hussey, N. E., M. A. MacNeil, B. C. McMeans, J. A. Olin, S. F. Dudley, G. Cliff, S. P. Winter, S. T. Fennessy, and A. T. Fisk. 2014. Rescaling the trophic structure of marine food webs. *Ecology Letters* 17:239–250.
- Isely, J. J., and T. B. Grabowski. 2007. Age and growth. Pages 187–228 in C. S. Guy and M. J. Brown, editors. *Analysis and interpretation of inland fisheries data*. American Fisheries Society, Bethesda, Maryland.
- Koehler, M. E., K. L. Fresh, D. A. Beauchamp, J. R. Cordell, and C. A. Simenstad. 2006. Diet and bioenergetics of lake-rearing juvenile Chinook Salmon in Lake Washington. *Transactions of the American Fisheries Society* 135:1580–159.
- Lowery, E. D., and D. A. Beauchamp. 2010. Baseline food web assessment of the upper Clackamas River basin prior to reintroduction of Bull Trout. Final Report to the Upper Clackamas Bull Trout Working Group, Washington Cooperative Fish and Wildlife Research Unit, Report WACFWRU-010-02, Seattle.
- Lynch, J. M. 1993. Evaluation of the Merwin trap as a means of Northern Squawfish *Ptychocheilus oregonensis* control in the Columbia River. Master's thesis. University of Washington, Seattle.
- Mather, M. E., and D. H. Wahl. 1989. Comparative mortality of three esocids due to stocking stressors. *Canadian Journal of Fisheries and Aquatic Sciences* 46:214–217.
- Mazur, M. 2004. Linking visual foraging with temporal prey distribution to model trophic interactions in Lake Washington. Doctoral dissertation. University of Washington School of Aquatic and Fisheries Sciences, Seattle.

- McClure, M. M., S. M. Carlson, T. J. Beechie, G. R. Pess, J. C. Jorgensen, S. M. Sogard, S. M. Sogard, S. E. Sultan, D. M. Holzer, J. Travis, B. L. Sanderson, M. E. Power, and R. W. Carmichael. 2008. Evolutionary consequences of habitat loss for Pacific anadromous salmonids. *Evolutionary Applications* 1:300–318.
- McElhany, P., M. H. Ruckelshaus, M. J. Ford, T. C. Wainwright, and E. P. Bjorkstedt. 2000. Viable salmon populations and the recovery of evolutionary significant units. NOAA Technical Memorandum NMFS-NWFSC-42.
- McIntyre, J. K., D. A. Beauchamp, M. M. Mazur, and N. C. Overman. 2006. Ontogenetic trophic interactions and benthic–pelagic coupling in Lake Washington: evidence from stable isotopes and diet analysis. *Transactions of the American Fisheries Society* 135:1312–1328.
- Minagawa, M., and E. Wada. 1984. Stepwise enrichment of ^{15}N along food chains: further evidence and the relation between $\delta^{15}\text{N}$ and animal age. *Geochimica et Cosmochimica Acta* 48:1135–1140.
- Miranda, L. E., and P. W. Bettoli. 2007. Mortality. Pages 229–278 in C. S. Guy and M. J. Brown, editors. *Analysis and interpretation of inland fisheries data*. American Fisheries Society, Bethesda, Maryland.
- Monzyk, F. R., R. Emig, J. D. Romer, and T. A. Friesen. 2013. Life-history characteristics of juvenile spring Chinook Salmon rearing in Willamette Valley reservoir. U.S. Army Corps of Engineers, Portland District, Willamette Valley Project, Portland, Oregon.
- Naiman, R. J., J. R. Alldredge, D. A. Beauchamp, P. A. Bisson, J. Congleton, C. J. Henny, N. Huntly, R. Lamberson, C. Levings, E. Merrill, W. Pearcy, B. Rieman, G. Ruggerone, D. Scarnecchia, P. E. Smouse, and C. C. Wood. 2012. Developing a broader scientific foundation for river restoration: Columbia River food webs. *Proceedings of the National Academy of Sciences of the USA* 109:21202–21207.
- Nelson, A. G. 2014. fishmethods: fishery science methods and models in R. R package version 1.7–0. Available: <http://CRAN.R-project.org/package=fishmethods>. (March 2016).
- PacifiCorp. 2004. Final license application exhibit A – description of project. PacifiCorp, Merwin Hydroelectric Project, FERC Project 935, Portland, Oregon.
- PacifiCorp and Cowlitz PUD (Public Utility District). 2004a. Water quality monitoring and assessments study. PacifiCorp and Cowlitz PUD, Final Technical Report, Portland, Oregon and Longview, Washington.
- PacifiCorp and Cowlitz PUD (Public Utility District). 2004b. Report on life history, habitat requirements, and distribution of aquatic analysis species (AQU 1). PacifiCorp and Cowlitz PUD, Final Technical Report, Portland, Oregon and Longview, Washington.
- PacifiCorp and Cowlitz PUD (Public Utility District). 2014. Lewis River hatchery and supplementation plan. PacifiCorp and Cowlitz PUD, FERC Projects 935, 2071, 2111, and 2213, Portland, Oregon and Longview, Washington.
- Pess, G. R., P. M. Kiffney, M. C. Liermann, T. R. Bennett, J. H. Anderson, and T. P. Quinn. 2011. The influences of body size, habitat quality, and competition on the movement and survival of juvenile Coho Salmon during the early stages of stream recolonization. *Transactions of the American Fisheries Society* 140:883–897.
- Petersen, J. H., and D. L. Ward. 1999. Development and corroboration of a bioenergetics model for Northern Pikeminnow feeding on juvenile salmonids in the Columbia River. *Transactions of the American Fisheries Society* 128:784–801.
- Plumb, J. M., and C. M. Moffitt. 2015. Re-estimating temperature-dependent consumption parameters in bioenergetics models for juvenile Chinook Salmon. *Transactions of the American Fisheries Society* 144:323–330.
- Ruggerone, G. T., and E. R. Rogers. 1992. Predation on Sockeye Salmon fry by juvenile Coho Salmon in the Chignik Lakes, Alaska: implications for salmon management. *North American Journal of Fisheries Management* 12:87–102.
- Sanderson, B. L., K. A. Barnas, and A. M. W. Rub. 2009a. Nonindigenous species of the Pacific Northwest: an overlooked risk to endangered salmon? *Bioscience* 59:245–256.
- Sanderson, B. L., C. D. Tran, H. J. Coe, V. Pelekis, E. A. Steel, and W. L. Reichert. 2009b. Nonlethal sampling of fish caudal fins yields valuable stable isotope data for threatened and endangered fishes. *Transactions of the American Fisheries Society* 138:1166–1177.
- Schaller, H. A., and C. E. Petrosky. 2007. Assessing hydrosystem influence on delayed mortality of Snake River stream-type Chinook Salmon. *North American Journal of Fisheries Management* 27:810–824.
- Schindler, D. E., X. Augerot, E. Fleishman, N. J. Mantua, B. Riddell, M. Ruckelshaus, J. Seeb, and M. Webster. 2008. Climate change, ecosystem impacts, and management for Pacific salmon. *Fisheries* 33:502–506.
- Selch, T. M., and S. R. Chipps. 2007. The cost of capturing prey: measuring Largemouth Bass (*Micropterus salmoides*) foraging activity using glycolytic enzymes (lactate dehydrogenase). *Canadian Journal of Fisheries and Aquatic Sciences* 64:1761–1769.
- Sheer, M. B., and E. A. Steel. 2006. Lost watersheds: barriers, aquatic habitat connectivity, and salmon persistence in the Willamette and lower Columbia River basins. *Transactions of the American Fisheries Society* 135:1654–1669.
- Spangler, G. R., and J. J. Collins. 1992. Lake Huron fish community structure based on gill-net catches corrected for selectivity and encounter probability. *North American Journal of Fisheries Management* 12:585–597.
- Stewart, D. J., and M. Ibarra. 1991. Predation and production by salmonine fishes in Lake Michigan, 1978–88. *Canadian Journal of Aquatic and Fisheries Science* 48:909–922.
- Swain, D. P., and L. B. Holtby. 1989. Differences in morphology and behavior between juvenile Coho Salmon (*Oncorhynchus kisutch*) rearing in a lake and in its tributary stream. *Canadian Journal of Aquatic and Fisheries Science* 46:1406–1414.
- Szendrey, T. A., and D. H. Wahl. 1996. Size-specific survival and growth of stocked Muskellunge: effects of predation and prey availability. *North American Journal of Fisheries Management* 16:395–402.
- Takata, H. K., M. J. Reesman, G. E. Reed, L. D. Layng, and T. A. Jones. 2007. Development of a system-wide predator control program: indexing fisheries evaluations. Report to the Bonneville Power Administration, Project 1990-077-00, Portland, Oregon.
- Tomaro, L. M., D. J. Teel, W. T. Peterson, and J. A. Miller. 2012. When is bigger better? Early marine residence of middle and upper Columbia River spring Chinook Salmon. *Marine Ecology Progress Series* 452:237–252.
- Vander Zanden, M. J., and J. B. Rasmussen. 1999. Primary consumer $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ and the trophic position of aquatic consumers. *Ecology* 80:1395–1404.
- Viggers, K. L., D. B. Lindenmayer, and D. M. Spratt. 1993. The importance of disease in reintroduction programs. *Wildlife Research* 20:687–698.
- von Bertalanffy, L. 1938. A quantitative theory of organic growth. *Human Biology* 10:181–213.
- Wahl, D. H. 1999. An ecological context for evaluating the factors influencing Muskellunge stocking success. *North American Journal of Fisheries Management* 19:238–248.
- Williamson, K. S., and B. May. 2005. Homogenization of fall-run Chinook Salmon gene pools in the Central Valley of California, USA. *North American Journal of Fisheries Management* 25:993–1009.

Appendix: Additional Information for Merwin Reservoir

TABLE A.1. Limnological and morphometric characteristics of Merwin Reservoir (PacifiCorp 2004 and unpublished data; PacifiCorp and Cowlitz PUD 2004).

Characteristic	Value
Surface area (km ²)	15.7
Length (km)	23.3
Mean depth (m)	31
Maximum depth (m)	73
Mean Secchi disk depth transparency (m)	~5
Water residence time (d)	118.4
Total phosphorus (mg/L)	<0.02
Trophic status	Oligotrophic
Months stratified	May–Oct
Top of thermocline (m)	~8
Ice cover	None
Range of surface temperatures (°C)	5–23
Maximum surface elevation (m above mean sea level)	73

TABLE A.2. Relative abundance and primary habitat of fish species present in Merwin Reservoir.

Species	Abundance	Habitat
Kokanee <i>Oncorhynchus nerka</i>	High ^a	Limnetic
Rainbow Trout and steelhead <i>O. mykiss</i>	Moderate ^a	Littoral and limnetic
Coastal Cutthroat Trout <i>O. clarkii clarkii</i>	Rare	Littoral and limnetic
Juvenile Coho Salmon <i>O. kisutch</i>	Rare ^a	Littoral and limnetic
Juvenile Chinook Salmon <i>O. tshawytscha</i>	Rare ^a	Littoral and limnetic
Northern Pikeminnow <i>Ptychocheilus oregonensis</i>	High	Benthopelagic
Largescale Suckers <i>Catostomus macrocheilus</i>	High	Benthic
Sculpins <i>Cottus</i> spp.	Moderate	Benthic (limnetic as fry)
Threespine Stickleback <i>Gasterosteus aculeatus</i>	Rare	Littoral and limnetic
Tiger muskellunge <i>Esox lucius</i> × <i>E. masquinongy</i>	Moderate ^a	Littoral
Pumpkinseed <i>Lepomis gibbosus</i>	High	Littoral
Largemouth Bass <i>Micropterus salmoides</i>	Rare	Littoral

^a Hatchery-supplemented population.

APPENDIX REFERENCES

PacifiCorp. 2004. Final license application exhibit A – description of project. PacifiCorp, Merwin Hydroelectric Project, FERC Project 935, Portland, Oregon.

PacifiCorp and Cowlitz PUD (Public Utility District). 2004. Water quality monitoring and assessments study. PacifiCorp and Cowlitz PUD, Final Technical Report, Portland, Oregon and Longview, Washington.

Downloaded by [Adam G. Hansen] at 17:18 20 April 2016