Food–web implications of reintroducing anadromous salmonids in reservoirs on the North Fork Lewis River, Washington

Mark Henry Sorel

A thesis
submitted in partial fulfillment of the
requirements for the degree of

Master of Science

University of Washington
2015

Committee:
David A. Beauchamp, Chair
Thomas P. Quinn
Richard W. Zabel

Program Authorized to Offer Degree:
School of Aquatic and Fishery Sciences

University of Washington

Abstract

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Mark Henry Sorel

Chair of Supervisory Committee:
Professor David A. Beauchamp
School of Aquatic and Fishery Sciences

Reintroductions using active transport (trap–and–haul) of anadromous salmonids around impassable high–head dams are being proposed with increasing frequency in the Pacific Northwest. Such reintroductions have already begun or are proposed above three dams on the North Fork Lewis River in Washington State. Spring Chinook Salmon *Oncorhynchus tshawytscha* and Coho Salmon *O. kisutch* have been observed rearing in several lakes and reservoirs elsewhere, raising the question of the potential for reservoir habitat to contribute to smolt production in the Lewis River. To determine whether the Lewis River Reservoirs can support reintroduced populations of juvenile salmonids, we evaluated prey supply and consumption demand of resident fishes to estimate the carrying capacity for planktivores. We also evaluated the potential predation impact of Northern Pikeminnow *Ptychocheilus* *oregonensis* on reintroduced anadromous salmonids in Merwin Reservoir, in response to concern that predation by the large population of native piscivores could undermine the reintroduction effort. To achieve these objectives, we examined the thermal regime, food–web structure, invertebrate abundance and distribution, and fish abundance and distribution in a spatiotemporally explicit manner in each reservoir. We then quantified trophic interactions with bioenergetics and population modeling. In all three reservoirs on the North Fork Lewis River, estimates of prey supply suggested that a moderate surplus of food was available to support the addition of juvenile anadromous salmonid consumption demand. The preliminary estimates for the abundance of sub-yearling salmonids that could be supported ranged 130,000–330,000 for each of the individual reservoirs; however, investigation into the behavior and growth of juvenile anadromous salmonids in the reservoirs would refine these estimates. Estimates of predation rates on resident salmonids were used to infer potential predation rates on reintroduced anadromous salmonids rearing year–round or migrating through Merwin Reservoir. We found that per–capita predation rates by Northern Pikeminnow were relatively low due to non–overlapping distributions during much of the growing season and the size structure of the predator population. The annual predation of Kokanee *Oncorhynchus nerka* by a size–structured population of 1,000 Northern Pikeminnow ≥ 300 mm was analogous to predation losses of 16,000–40,000 sub–yearling spring Chinook rearing in Merwin Reservoir year–round. Estimated salmonid consumption by 1,000 Northern Pikeminnow during peak smolt out–migration (April–June), if directed solely at migrating smolts, was analogous to 400–1,000 yearling spring Chinook Salmon (18–45 g each). These results can help managers set goals for the ongoing and proposed reintroductions of anadromous salmonids in the Lewis River that are desirable to stakeholders and realistic given the constraints of habitat, food supply, and predation losses.

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Acknowledgements

I’d like to thank my advisor Dave Beauchamp for giving me this project and guiding me along the way. Additionally, I’d would like to thank my main funding source, PacifiCorp Energy, for providing me the opportunity to complete this master’s program and thesis. Funding was also provided by the Dave Lamb Memorial Scholarship, issued by the Washington Lakes Protection Association.

I am extremely thankful for all the help I received from my colleagues in the Beauchamp lab and at SAFS. Adam Hansen, Kristin Connelly, and Casey Clark contributed tremendously to planning, data collection in the field and lab, analysis, and reporting. Erin Lowery also helped conceive and implement the project, and was a mentor to me in the lab. Andrew Wilson collected Tiger Muskellunge data in the lab for his undergraduate capstone research project. Ida Vincent, Ava Fuller, Kayla Ellis, Shelby Burgess and numerous others also conducted significant amounts of work on this project.

I’d also like to thank my collaborators from outside of SAFS. I have learned tremendously from, and enjoyed working with Robert Al–Chokhachy, Chad Gebroski and Sarah O’Neil from USGS Rocky Mountain Research Center, and Heather Bowen and Chris Clark from Montana State University. Frank Shrier, Jeremiah Doyle, Chris Karchesky, Mark Ferraiolo, and James Samagaio from PacifiCorp assisted with sample and data collection, and shared expert local knowledge.

I’d like to acknowledge my other committee members, Tom Quinn and Rich Zabel for their guidance and contribution to my thesis and education. Finally, a huge thank you to my parents Ed and Emily, sisters Nina and Lucie, and to my partner Kristin Connelly for supporting and encouraging me. I couldn’t have done it without them.

Introduction

Reintroductions are a valuable conservation and restoration tool; although, many of those attempted are not successful. In the past, comprehensive ecological baseline studies and post–introduction evaluations have rarely accompanied such projects, so factors affecting success are poorly understood and opportunities for insight have been missed (Sarrazin and Barbault 1996). Since the early 1990s, there has been an exponential increase in the number of published post-reintroduction case studies evaluating the factors that contributed to the success or failure of the reintroduction; however, pre-reintroduction feasibility studies are still lacking (Armstrong and Seddon 2008). There are many considerations when planning and managing a reintroduction. Habitat and species composition are often dramatically changed following the extirpation of a species, and the factors that caused a localized extinction may still exist. The study of these factors can help identify why many reintroductions fail, and distinguish opportunities for successful ones. Reintroductions of anadromous salmonids above high–head dams are being proposed in the Pacific Northwest with increasing frequency, necessitating supporting habitat and food web studies to ensure the reintroduction is both feasible and likely to succeed.

Approximately 74% of Washington State's electricity comes from hydropower (U.S. Department of Energy 2015). The widespread construction of high–head hydroelectric dams on tributaries of the Columbia River in the 20th century blocked passage of anadromous fish into parts of their historic habitat, contributing to declines in salmon returns, and dependence on hatchery production (Fulton 1968). All licenses issued by the Federal Energy Regulatory Commission (FERC) to operate hydroelectric dams require an evaluation of the impact on fish and a commitment to mitigate for any negative effects of the dam by the operating entity. While some dams are being razed because their adverse impact on fish outweigh their contribution to society (Loomis 1996), other dams continue to provide valuable services such as renewable energy, water for irrigation, flood control, and recreation. An emerging solution to the dilemma between the benefits of high–head dams and the harm they cause to anadromous fish is the reintroduction of these species above the dams using trap–and–haul. If successful, this emerging strategy has the potential to increase the natural production of salmon, significantly aiding conservation and enhancement efforts. However, there are challenges and significant uncertainty associated with recreating runs of anadromous fish above dams.

While designing infrastructure to allow fish to bypass high head dams is one hurdle to reintroduction, other potential limitations could prevent establishment of anadromous populations (Anderson et al. 2014). The physical habitats and biological communities above dams are much changed from their pre–development states in ways that significantly affect the life cycles of anadromous fish. Perhaps the most dramatic example is when significant portions of historic spawning and rearing habitat in rivers and tributaries are inundated and transformed into reservoirs. Dramatic changes in the physical environment, such as an altered thermal regime and the creation of a limnetic zone that supports the production of zooplankton, accompany reservoir formation. Often a suite of non–native lentic species are introduced to provide fishing opportunities, and native species that were previously marginalized to pool habitats can increase dramatically due to the altered flow regime and serve as predators or competitors of juvenile salmonids (Sanderson et al. 2009, Carey et al. 2012). Considerable uncertainty surrounds predictions of potential growth and survival for juvenile anadromous salmonids reintroduced into these hybrid food webs (Naiman et al. 2012).

The reintroduction of anadromous salmonids in storage reservoirs represents an opportunity to study the ability of a species to survive and thrive in an altered environment.

Many rivers have been impacted by humans in some way throughout the range of Pacific Salmon and trout, which has contributed to the decline of many populations. Altered habitats may still be quality habitats, however. In the case of using trap–and–haul to reintroduce anadromous salmonids above high–head dams, engineering solutions and a bit of human intervention has the potential to re–open large quantities of habitat to imperiled salmonid populations. There may be many opportunities to recover at–risk species and increase biodiversity through minor modification and engineering of previously altered environments to reestablish ecosystem function (Rosenzweig 2003). It is important to study these types of conservation efforts, and the habitat requirements of species we hope to conserve, in order to identify the most important factors to consider when planning such ecosystem re–connectivity projects.

Potential constraints on reintroductions of anadromous salmonids include poor quality habitat, carrying capacity, and predatory and competitive interactions with other species and populations (Anderson et al. 2014). There must be habitat to support both spawning adults and rearing juveniles. Juveniles of different species prefer different thermal and flow environments, and food must be present to support their growth and survival. The physical space for rearing and the available prey resources are generally shared with multiple species leading to potential competitive interactions. Predation is another interaction that could limit the survival of juveniles.

I was fortunate to have the opportunity to examine factors influencing the potential for successful reintroduction of anadromous salmonids in a series of three reservoirs on the North Fork Lewis River in Southwest Washington State. The North Fork Lewis River is a tributary of the lower Columbia River at river km 140. Three high–head dams were constructed without fish passage in 1931–1958 which extirpated anadromous salmonids from the upper watershed and decimated many of the runs below the dams (PacifiCorp and Cowlitz 2004). The series of dams created three storage reservoirs, Swift, Yale and Merwin.

The three anadromous salmonid populations which are slated to be reintroduced into the upper North Fork Lewis River, spring Chinook Salmon *O. tshawytscha*, Coho Salmon *O. kisutch*, and Steelhead Trout *O. mykiss*, were all severely impacted by the damming of the river. Spring and fall Chinook Salmon runs declined following the construction of the dams and spring Chinook Salmon completely disappeared from trap catches at Merwin Dam by the mid–1950's (PacifiCorp and Cowlitz 2004). Spring Chinook from nearby basins were brought to the Lewis River to recreate a run, which has persisted and is supplemented with significant hatchery production. The fall Chinook Salmon run is a native Lewis River stock and persists with little hatchery supplementation. Both spring and fall Chinook Salmon runs on the Lewis River are considered to be "healthy" by the Washington Department of Fish and Wildlife (WDFW) based on escapement trends. The spring Chinook Salmon population in the Lewis River is considered a hatchery stock and is not part of the Endangered Species List "threatened" Lower Columbia River Evolutionarily Significant Unit (ESU). There are two runs of Coho Salmon in the Lewis River, "early" (Type S) and "late" (Type N), both of which have been supplemented with fish from adjacent basins in the past. Today, these Coho Salmon populations are heavily hatchery supplemented, and natural production is believed to account for 5–10% of the total adult escapement. WDFW has designated Coho Salmon in the Lewis River as "depressed," based on a declining trend in escapement over a number of years. Lower Columbia River Coho Salmon are not currently listed under the ESA, because no natural populations could be identified. Winter and summer Steelhead Trout populations in the Lewis River are considered to be of native origin but have likely interbred with fish that have been released or strayed into the Lewis River from other rivers in the past. Steelhead Trout populations in the Lewis River are also heavily supplemented with hatchery production, and natural production is believed to account for roughly 7% of adult escapement to the North Fork. WDFW considers Steelhead in the Lewis River to be “depressed” due to loss of habitat above the dams. Naturally spawned Steelhead Trout in the Lower Columbia River ESU, which includes the North Fork Lewis River, are listed as threatened. The goal of the reintroduction of these populations above the dams is to establish self–sustaining runs.

The current operating utility, PacifiCorp Energy, began reintroducing spring Chinook Salmon, Coho Salmon, and Steelhead Trout above the uppermost Swift Dam in 2010 as part of their relicensing agreement with FERC. Adult fish are collected below Merwin Dam and released above Swift Dam, and juveniles are trapped at Swift Dam with a floating surface collector and released below Merwin Dam. One of the first major studies on the potential for anadromous salmonid reintroduction in the Upper Lewis River watershed utilized Ecosystem Diagnosis and Treatment (EDT) models to estimate the productive capacity of the habitat for anadromous salmonids (Mobrand 2004). The study found that 71–93% (across species) of the capacity for production of juvenile salmon and steelhead was in the Swift Reservoir Basin which is connected to the vast majority of lotic habitat. They found that 7–22% of the capacity for juvenile production was in the Yale Reservoir Basin, and 0–9% was in the Merwin Reservoir basin. This finding led to the decision to implement the ongoing trap–and–haul program that bypasses the lower two reservoirs, Yale and Merwin. PacifiCorp’s efforts have opened 188 km of stream and reservoir habitat to support spawning, rearing, and migration of anadromous salmonids.

PacifiCorp will convene with stakeholders and regulators to decide whether to implement reintroductions in Merwin and Yale Reservoirs by 2016. The decision of whether to invest in reintroducing anadromous salmonids in the lower two reservoirs or to focus resources on habitat restoration elsewhere in the basin will be based on a number of factors, including the degree to which each of the reservoir basins can support juvenile anadromous salmonid rearing. While the EDT results highlighted the limited habitat suitable for salmonids in the Yale and Merwin Reservoir basins, they did not account for species interactions and zooplankton production in the reservoirs. These factors could have a major impact on juvenile salmonid production in these basins, necessitating further study before a reintroduction decision is reached for Yale and Merwin Reservoirs. In addition, examining these factors within Swift will allow for creation of a carrying capacity estimate, to help inform management and production goals for that reservoir.

The three reservoirs differ in fish species assemblage, and limnological and morphometric characteristics. Swift is the uppermost and largest reservoir, with the greatest water residence time (PacifiCorp, *unpublished data*). Of the three reservoirs, it is the only one without Kokanee *O. nerka* or Northern Pikeminnow *Ptychocheilus oregonensis* (PacifiCorp and Cowlitz 2004). Yale Reservoir and Merwin Reservoir, the middle and lowermost impoundments, are more similar in size; however, Yale maintains significantly cooler temperatures than Merwin during the summer, and contains Bull Trout *Salvelinus confluentus* whereas Merwin does not. Merwin is the warmest reservoir and has a large population of Northern Pikeminnow, in addition to populations of Tiger Muskellunge *Esox Lucius x E. masquinongy*, Pumpkinseed Sunfish *Lepomis macrocheilus*, and a small number of Largemouth Bass *Micropterus salmoides*.

Different species of anadromous salmonids exhibit varying affinities to and uses of reservoir habitats. Sockeye Salmon *O. nerka* almost always rear in lentic habitat, whereas other species of Pacific Salmon rear in lentic habitats to varying degrees. Juvenile Chinook Salmon consistently rear in lentic habitats in North Fork Reservoir on the Clackamas River, several reservoirs on the upper Willamette River, reservoirs on the Snake River, Lake Quinault, Lake Washington, and other lakes and reservoirs (Connor et al. 2005; Koehler et al. 2006; Lowery and Beauchamp 2010; Monzyk et al. 2013, R. Tabor, U.S. Fish and Wildlife Service, unpublished data). Juvenile Coho Salmon also use lentic habitats, such as in the Chignik Lakes in Alaska and Mesachie Lake on Vancouver Island (Swain and Holtby 1989; Ruggerone and Rogers 1992). Juvenile Steelhead Trout primarily use lotic habitat for feeding and rearing (e.g. Everest and Chapman 1972; Bisson et al. 1988; Lowery and Beauchamp 2010) but Rainbow Trout *O. mykiss* commonly rear in lakes. Reservoirs offer warmer temperatures and abundant zooplankton prey and can provide growth advantages for juveniles over rearing in tributaries as reported for fall Chinook Salmon in Lake Washington (Koehler et al. 2006) and spring Chinook Salmon in the Middle Fork Willamette River (Monzyk et al 2013) and Upper Clackamas River (Lowery and Beauchamp 2010) in Oregon. It is reasonable to assume that juveniles from one or more species of anadromous salmonids might use reservoir habitat for rearing, in addition to migrating through it on the way to the marine environment. Thus, determining whether the reservoir is favorable for growth and survival, and evaluating the factors (e.g. thermal structure and prey availability) that could limit these processes is an important step when planning new reintroductions above dams. Another factor that could limit survival is predation.

In the late 1950s and 1960s, an experimental introduction of hatchery Coho Salmon fry conducted in Merwin Reservoir resulted in high growth rates but low survival, and predation was hypothesized to be the cause for the low survival (Hamilton et al. 1970). Northern Pikeminnow were identified as the most abundant predator of juvenile salmon in Merwin Reservoir during that study. As part of the study, Hamilton et al. used mark–recapture techniques to estimate that there were roughly 350,000 ≥ 200 mm Northern Pikeminnow (presumed to be predatory) in 1961, but the population has not been assessed since. Additionally, WDFW began stocking approximately 1,300 large juvenile (~300 mm FL) Tiger Muskellunge annually in 1995 to limit the population of Northern Pikeminnow and provide a sport fishery, but the efficacy of this program has not been formally evaluated. The duration and magnitude of predation on salmonids by Northern Pikeminnow in Merwin Reservoir is unknown.

Northern Pikeminnow predation on juvenile salmonids has been well studied in run–of–the–river reservoirs (Petersen and Ward 1999, Zimmerman and Ward 1999), but our understanding of these interactions in lakes and storage reservoirs is much more limited. One of the recurring themes in the existing literature on this subject is that Northern Pikeminnow tend to be much more abundant than piscivorous salmonids in lakes, but have significantly lower per–capita consumption rates of juvenile salmonids due to their non–overlapping distributions during much of the growing season (Eggers 1978, Ricker 1941, Hamilton et al. 1970). Northern Pikeminnow tend to occupy shallow and nearshore waters during spring–summer, whereas salmonids are often deeper in the water column during the day and ascend to feed only at night during these seasons. Northern Pikeminnow are common throughout the range of Pacific salmon and trout, and their interaction with juvenile salmonids is a major consideration for many conservation and management actions (Monzyk et al. 2012).

Research questions and objectives

Chapter 1) What is the availability of rearing habitat and seasonal food supply to support juvenile anadromous salmonids rearing in the reservoirs on the Lewis River, on top of the existing consumption demand of resident fish? To answer this question, we estimated how much prey was consumed by resident planktivores, and the biomass and production of available prey resources accessible to planktivorous salmonids. We then compared this consumption demand to prey supply to evaluate how close the current resident planktivore populations were to the carrying capacity of each reservoir. If there was surplus prey resources available, we estimated approximately how many juvenile anadromous salmonids could be added without exceeding the maximum sustainable rate of prey exploitation.

Chapter 2) Would predation on juvenile salmon by Northern Pikeminnow preclude the establishment of reintroduced populations in the lowermost Merwin Reservoir, where a large predatory population was identified in the 1960s? In order to answer this question, we evaluated the current rates of predation on resident salmonids by different sizes of Northern Pikeminnow in each season. We characterized the abundance and size distribution of the Northern Pikeminnow population, to determine the absolute and relative predation impact of different size classes of the predator population. Predation rates on resident salmonids were converted to the analogous number of reintroduced anadromous salmonids that would be consumed under two scenarios, when they reared in the reservoir year–round, and when they used the reservoir solely as a migration corridor in spring. We also evaluated the consumption of Northern Pikeminnow by cannibals and predation by Tiger Muskellunge, to determine the effect on the size distribution and abundance of Northern Pikeminnow.

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Chapter 1 — Prey supply and consumption demand by resident and reintroduced anadromous salmonids in three reservoirs on the North Fork Lewis River, Washington

Abstract

Reintroductions of anadromous salmonids using trap–and–haul to pass fish around formerly impassable dams are being proposed with increasing frequency in the Pacific Northwest. Reintroduction has already begun or is proposed above three dams on the North Fork Lewis River in Washington State. Spring Chinook Salmon *Oncorhynchus tshawytscha* and Coho Salmon *O. kisutch* (two of three proposed species for reintroduction) have been observed rearing in several lakes and reservoirs elsewhere, raising the question of the potential for reservoir habitat to contribute to smolt production in the Lewis River. To determine whether the Lewis River Reservoirs can support reintroduced populations of juvenile salmonids, we evaluated prey supply and consumption demand of resident fishes to estimate the carrying capacity for planktivores. *Daphnia* first bloomed in spring and remained at moderate levels with a smaller secondary peak in fall before declining to low levels in November. Zooplankton densities were highest in the epilimnion, but warm epilimnetic temperatures and summer fish distributions suggested that salmonids had limited access to the epilimnion during peak stratification. The primary resident planktivores, Kokanee *O. nerka* and hatchery–reared Rainbow Trout *O. mykiss* were both highly dependent on *Daphnia* spp. for food with secondary reliance on insects based on stable isotope and diet analysis. In all three reservoirs, consumption demand exceeded 50% of *Daphnia* biomass during at least one month during the growing season. Less conservative estimates of prey supply suggested that a moderate surplus of food was available to support the addition of juvenile anadromous salmonid consumption demand in all three reservoirs. The

preliminary estimates for the abundance of sub-yearling salmonids that could be supported ranged 130,000–300,000; however, further investigation into the behavior and growth of juvenile anadromous salmonids in the reservoirs would refine these estimates. These results can help managers select fish assemblages that are desirable to stakeholders and realistic given the constraints of habitat and food supply, with a calculated risk of overshooting carrying capacity.

Introduction

Reintroductions of extirpated anadromous salmonids above formerly impassable dams are being proposed with increasing frequency as part of Federal Energy Regulatory Commission (FERC) relicensing agreements, requiring feasibility studies of such undertakings. While designing infrastructure to allow fish to bypass high head dams is one hurdle to reintroduction, other potential limitations could prevent establishment of anadromous populations (Anderson et al. 2014). The physical habitats and biological communities above dams are fundamentally changed from their pre–development states in ways that significantly affect the life cycles of anadromous fish.

Perhaps the most dramatic example is when significant portions of historic spawning and rearing habitat in rivers and tributaries are inundated and transformed into reservoirs. Dramatic changes in the physical environment accompany reservoir formation, such as an altered thermal regime and the creation of a limnetic zone that supports the production of zooplankton. Often a suite of non–native lentic species are introduced to provide fishing opportunities, and native species that were previously marginalized to pool habitats can increase dramatically due to the altered flow regime and serve as predators or competitors of juvenile salmonids (Sanderson et al. 2009, Carey et al. 2012). Considerable uncertainty surrounds predictions of potential growth and survival for juvenile anadromous salmonids reintroduced into these hybrid food webs (Naiman et al. 2012).

A reservoir's ecological function with regard to anadromous salmonids could vary depending on the amount and quality of accessible lotic habitat. If significant lotic habitat is intact in tributaries, then the reservoir may only serve as a migration corridor. However, if the majority of former tributary and mainstem habitat has been inundated or remains blocked by other dams, then reservoir habitat must support significant production in order to warrant reintroduction. To justify reintroduction in systems with little lotic habitat, or in cases where expected production in tributaries is slight, the production potential of reservoir habitat should be quantified. The question of the capacity of storage reservoirs to produce juvenile salmon smolts will likely be asked for a number of systems as more dams are evaluated for relicensing in the Pacific Northwest in the next 20 years, with major implications for conservation and restoration of Pacific salmon and trout *Oncorhynchus spp.*

The North Fork Lewis River in southwest Washington State is a tributary of the lower Columbia River. Three high–head dams were constructed without fish passage during 1931–1958 which extirpated anadromous salmonids from the upper watershed and decimated many of the stocks below the dams (PacifiCorp and Cowlitz 2004a). The current operating utility, PacifiCorp Energy, began reintroducing spring Chinook Salmon *O. tshawytscha*, Coho Salmon *O. kisutch*, and Steelhead Trout *O. mykiss* above the uppermost Swift Dam in 2010 as part of their relicensing agreement with FERC. They will convene with stakeholders to decide whether to implement reintroductions downstream in Merwin and Yale Reservoirs by 2016. The decision on whether to invest in reintroducing anadromous salmonids in the lower two reservoirs or to focus resources on habitat restoration elsewhere in the basin will be based on a number of factors, including the degree to which each of the reservoirs can support juvenile anadromous salmonid rearing. An estimate of the capacity of Swift Reservoir, where the reintroduction is underway, will also help inform management and production goals for that reservoir. Understanding the mechanisms underlying successful reintroduction of anadromous salmonids in the Lewis River would inform other restoration and conservation efforts in the Columbia River Basin and in the Pacific Northwest region in general.

Different species of anadromous salmonids exhibit varying affinities to and uses of reservoir habitats. Sockeye Salmon *O. nerka* almost always rear in lentic habitat, whereas other species of Pacific Salmon rear in lentic habitats to varying degrees. Juvenile Chinook Salmon consistently rear in lentic habitats in North Fork Reservoir on the Clackamas River, several reservoirs on the upper Willamette River, reservoirs on the Snake River, Lake Quinault, Lake Washington, and other lakes and reservoirs (Connor et al. 2005; Koehler et al. 2006; Lowery and Beauchamp 2010; Monzyk et al. 2013, R. Tabor, U.S. Fish and Wildlife Service, unpublished data). Juvenile Coho Salmon also use lentic habitats, such as in the Chignik Lakes in Alaska and Mesachie Lake on Vancouver Island (Swain and Holtby 1989; Ruggerone and Rogers 1992). Juvenile Steelhead Trout primarily use lotic habitat for feeding and rearing (e.g. Everest and Chapman 1972; Bisson et al. 1988; Lowery and Beauchamp 2010) but Rainbow Trout *O. mykiss* commonly rear in lakes. Reservoirs offer warmer temperatures and abundant zooplankton prey and can provide growth advantages for juveniles over rearing in tributaries as reported for fall Chinook Salmon in Lake Washington (Koehler et al. 2006) and spring Chinook Salmon populations in the Middle Fork Willamette River (Monzyk et al 2013) and Upper Clackamas River (Lowery and Beauchamp 2010) in Oregon. It is reasonable to assume that juveniles from one or more species of anadromous salmonids might use reservoir habitat for rearing. Thus, determining whether the reservoir is favorable for growth and survival, and evaluating the factors (e.g. thermal structure and prey availability) that could limit these processes is an important step when planning new reintroductions above dams.

We aimed to quantify the current consumption demand of resident salmonids in each reservoir, as well as the available prey supply during the growing season. These measures were compared, and the capacity of each reservoir to support the addition of juvenile anadromous salmonids were evaluated based on quantity (or absence) of available prey resources.

Methods

To assess the capacity of the reservoirs on the Lewis River to support additional salmonids, we examined the annual progression of vertical temperature profiles, seasonal cycles of zooplankton production and distribution, and consumption demand of the existing resident planktivore community. The fish communities of each reservoir were sampled and stable isotope analysis was used to evaluate the trophic structures of the food webs. We measured seasonal depth distribution, diets, growth, and abundance of key planktivore populations in each reservoir and used bioenergetics models to estimate their monthly consumption demand. Ultimately, planktivore consumption demand was compared to prey supply to evaluate the availability of food to support reintroduced populations of age–0 salmonids. We assumed that the carrying capacity of a reservoir had been reached if the current consumption demand exceeded 50% of the prey supply in any month of the growing season. We divided any surplus prey that could have been consumed without exceeding this arbitrary estimate of maximum sustainable prey exploitation by the consumption demand of individual ag–0 salmonids to estimate how many additional sub-yearlings could be supported in each reservoir. These estimates could be added to expected production from lotic habitats to evaluate the feasibility of reintroductions, and weigh the costs against the benefits.

Study site — All three reservoirs on the North Fork Lewis River (Swift, Yale and Merwin) are oligotrophic and steep sided (Table 1). Swift Reservoir is the uppermost, deepest and largest of the three reservoirs (mean depth = 45 m, maximum depth = 101 m, penstock depth = 37 m) and is connected to approximately 188 km of upstream lotic habitat accessible to anadromous fish (Table 1). Yale Reservoir, the middle impoundment, is the smallest of the three (mean depth = 31 m; maximum depth = 79 m; penstock depth = 27 m) and has 23.5 km of accessible tributary habitat. Merwin Reservoir is the lowermost and is slightly shallower than Yale Reservoir but with deeper penstocks (mean depth = 31 m, maximum depth = 73 m, penstock depth = 54 m), and has just 6 km of accessible lotic habitat.

Thermal stratification in all three reservoirs begins in May and peaks in August; rapid destratification occurs during October, and the water column becomes isothermal in November. The hypolimnion in Swift and Yale Reservoirs remains at a roughly constant temperature throughout the year; however, the hypolimnion in Merwin Reservoir warms significantly during the summer, presumably due to mixing caused by the inflow from Yale Reservoir and water withdrawal through the deeply placed penstocks (Hamilton et al 1970).

Fish sampling — We deployed short term gill nets for 30 minutes to 24 hours in Swift, Yale and Merwin Reservoirs in June–November 2013 and May–November 2014 to obtain biological samples and information on relative abundance and seasonal depth distribution of resident fishes. We only set gill nets for short periods in Swift and Yale Reservoirs to reduce the risk of harming Bull Trout *Salvelinus confluentus* which are listed as threatened under the Endangered Species Act. Creel sampling and trolling were also used to sample fish. A limited amount of midwater trawling was conducted in June and August 2013, but was restricted to the epilimnion due to submerged standing timber in all three reservoirs.

We identified, sexed, and counted fish by species and recorded a subset of fork lengths (FL; mm) and wet weights (g) in the field. Stomachs were collected for diet analysis, scales from the preferred region were taken for age and growth analysis, and fin tissue was sampled for stable isotope analysis, placed on ice in the field, and later frozen for preservation and analysis in the laboratory. Fish were handled and released or euthanized according to UW–IACUC protocol #3286–21.

Hydroacoustics — Mobile hydroacoustic surveys were conducted in June, August, and November 2013 to evaluate the abundance and depth distribution of small limnetic fishes in each reservoir. The hydroacoustics system used for all surveys consisted of two multiplexed split–beam 200 kHz transducers towed in side–looking (12.8° full beam angle) and down–looking (6.8° full beam angle) orientations. The transducers were connected to a Biosonics DE–6000 scientific echosounder with the following data acquisition parameters: bottom threshold = 70 m, ping rate = 2–3 pps, pulse width = 0.3 ms, and target strength detection threshold = –65 dB.

Quantitative surveys of fish abundance and distribution in August consisted of 15–18 zigzag transects across, and one long transect along the center axis of each reservoir (Figure 1). Qualitative surveys in June and November consisted of fewer (5–15) loose zigzag transects across, and one transect along the center axis of each reservoir to examine the vertical distribution of fishes. A portion of each of the surveys was repeated during daylight, dusk, and night to evaluate diel vertical migrations, and to more accurately estimate average daily thermal experience for bioenergetics models.

The abundance of Kokanee and the distribution of limnetic fishes were estimated from hydroacoustic survey data using standard echo counting techniques (Beauchamp et al. 1997; Beauchamp et al. 2009) with EchoView 5.4 software (Myriax Pty. Ltd.). All targets in Yale and Merwin Reservoirs within the main target strength modes corresponding with expected fish lengths (30–275 mm in Yale Reservoir; 30–400 mm in Merwin Reservoir) were assumed to be Kokanee, given that the composition of angler catches was nearly 100% Kokanee in Yale Reservoir (with one account of a Bull Trout hooked) and 80% Kokanee in Merwin Reservoir. The other approximately 20% of angler catches in Merwin Reservoir consisted of larger hatchery–reared Rainbow Trout, and an occasional Northern Pikeminnow. Catches in mid–water trawls were 92% age–0 Kokanee in Yale Reservoir. It is likely that some Three-spine Stickleback, pelagic sculpins, and other fish species were allocated to Kokanee population estimates. However, this creates a conservative population estimate for the purpose of comparing zooplankton consumption demand/supply, as all planktivore species draw from the same zooplankton resources.

Targets measured by the side–looking transducer were used to estimate fish densities within the upper 20 m of the water column over a range of 0–40 m from the survey vessel; however, side–aspect target strengths cannot be reliably converted to fish lengths. Therefore, the observed densities of side–aspect targets represented the total within a range of sizes, and were used to estimate depth distributions for thermal experience calculations, but not size–specific densities for abundance and age–structure calculations.

Fish target strengths measured by the downlooking transducer were converted to fork lengths based on Love's (1977) equation, and used to estimate size–specific target densities. Size–specific target density estimates were calculated for each 5–m depth interval. Targets were summed within specific size modes in the target strength frequency distribution that corresponded with the expected lengths of each size class of fish, and the sums were divided by the volume of water examined by the acoustic beam to calculate density. Targets outside the range of strengths associated with Kokanee were assumed to be background noise caused by debris and noise (if smaller), or branches of standing timber and large piscivorous fish (if larger).

Abundance and survival — Abundances of age 0–2 Kokanee were estimated by expanding density estimates from quantitative hydroacoustic surveys by water volumes in the corresponding depth layers. Assuming constant recruitment and survival between years and age classes as a simplifying assumption, we fit annual survival starting with the abundance of age–0 fish, such that the abundances of ages 1 and 2 Kokanee summed to the pooled abundance estimate for these age classes. We used annual survival rates to allocate the estimated abundance of age 1–2 Kokanee to each age class. Daily population abundances for the rest of the year were calculated using daily survival rates, derived with the exponential relationship: survival = $e^{(-rt)}$, where r = instantaneous mortality rate, and t = time.

In Swift Reservoir, Kokanee were not present, and hydroacoustic surveys could not reliably estimate the abundance and survival of the primary planktivore, Rainbow Trout due to their nearshore and surface orientation. Instead, we relied on stocking and catch data to estimate the abundance and age structure of Rainbow Trout. Catches from the main reservoir were composed entirely of trout from the current year's stocking event, based on scale and length frequency analysis. We modeled consumption demand for a single cohort of 50,000 hatchery–reared Rainbow Trout with zero mortality from stocking (June 1st) to the end of November. By not incorporating mortality, this approach provided a maximum possible estimate of the consumption demand by Rainbow Trout. The total fish abundance in August estimated by hydroacoustics was 40,500 fish 20–200 mm, and 9,800 fish 200–400 mm. The low number of Rainbow Trout sized targets observed suggested that some may have been undetectable due to a nearshore or surface orientation. However, given that there were < 50,000 total fish observed by hydroacoustics in August, and the majority of these fish appeared to be < 200 mm, our estimate of the consumption demand of 50,000 hatchery–reared Rainbow Trout was likely a reasonable approximation of the consumption demand of all planktivorous fishes in Swift Reservoir.

Bioenergetics model inputs — Bioenergetics models are energy balance equations that are commonly used to estimate the feeding rate (% of maximum theoretical consumption; C_{max}) and the consumption rate (g of prey/d) needed to achieve the growth observed by different age classes of consumers, while accounting for variability in body size, thermal experience, and diet of the consumer (Ney 1993). The models operate on a daily time step which enables simulations to track processes with high temporal resolution. 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). We collected field data on growth, seasonal diet composition, and thermal experience (daily temperature experienced by the consumer) to construct a set of model inputs specific to each planktivore population. We used stable isotope analysis to corroborate the diet composition data.

Temperature profiles and thermal experience — Temperature profiles were recorded monthly from April to November at 1–m intervals from the surface to 30 m and every 2 m over 30–60 m at two limnology stations located at 1/3 and 2/3 of the length of each reservoir (Figure 1), and measurements were averaged between stations. Temperature profiles recorded by PacifiCorp in the late fall and winter months were used to complete the characterization of the seasonal thermal regime (PacifiCorp 1999, PacifiCorp and Cowlitz 2004b). Vertical temperature profiles (Figure 2) were combined with depth distribution of pelagic fish in each reservoir from hydroacoustics (Figures 3–5) to calculate time– and depth–weighted thermal experience for bioenergetics simulations (Beauchamp et al. 2007; Table 2).

Stable isotope analysis — We characterized the food web structure of Swift, Yale and Merwin Reservoirs with stable isotopes to identify key trophic pathways supporting or potentially limiting juvenile salmonids and other abundant resident fish likely to overlap in time and space with juvenile salmon (McIntyre et al. 2006). Stable isotope values of fin tissue provide an integrative signal of diet over several months to a year (depending on the growth rate of the consumer), providing a valuable complement to the instantaneous snapshot of diet composition provided by stomach content analysis. Tissue from representative samples of benthic invertebrates, terrestrial insects, zooplankton, planktivores, benthic feeding fishes, and piscivores were immediately placed on ice in the field and then frozen within 12 h for storage (Table A1, Vander Zanden and Rasmussen 1999). Zooplankton were identified to genus, and muscle tissue was removed from snails, Asian Clams *Corbicula fluminea*, and Signal Crayfish *Pacifastacus leniusculus*. For fish samples, caudal fin tissue was clipped from three individuals within each 50–mm size class of each population. Samples were then dried at 60 °C for 48 h, homogenized with mortar and pestle, and 0.4–0.6 mg of material was weighed in aluminum capsules for analysis. Isotope samples were analyzed by the University of Washington IsoLab using a Costech Elemental Analyzer, Conflo III, MAT253 for continuous flow based measurement of solid organic material. The reference material was Vienna Pee Dee belemnite for carbon and atmospheric N_2 for nitrogen.

Diet Composition and Energy Density of Prey — Seasonal diet analysis was conducted for key pelagic species to provide input data for bioenergetics modeling and to evaluate trophic interactions between resident and anadromous fishes. Diet composition was evaluated for a range of sizes of the primary pelagic planktivores in each reservoir. We identified stomach contents under a dissecting microscope to taxonomic order for invertebrates, and calculated diet proportions by wet weight (Chipps and Garvey 2007). The energy densities of prey items were taken from literature values (Table 3).

Age and Growth — A fish's mass at the beginning and ending dates of bioenergetics simulations were estimated based on scale analysis and observations of length and weight. Hatchery–reared Rainbow Trout and yearling Chinook Salmon were weighed at the hatchery before stocking in Swift Reservoir (PacifiCorp and Cowlitz 2014) and again during sampling at the end of the growing season in November, providing an estimate of growth over this interval. Growth intervals for yearling Chinook were used to generate feeding rates (p–values or $\%C_{max}$) which were then used to simulate the growth and consumption demand of sub-yearlings. Length–at–age for Kokanee was back–calculated from scale measurements using the Fraser–Lee method (Isely and Grabowski 2007). Images and measurements of scales were recorded with Image–Pro© digital image–analysis software and a digital camera mounted on a dissecting microscope [1.6–3.2x magnification]. Kokanee lengths were converted to weight based on weight–FL regressions for Yale Reservoir (N = 36, range = 46–281 mm; $r^2 = 0.996$, $P < 0.001$):

$$\text{Weight} = 0.00000198 * \text{FL}^{3.3259}$$

and Merwin Reservoir (N = 179, range = 91–400 mm; $r^2 = 0.964$, $P < 0.001$):

$$\text{Weight} = 0.0000263 * \text{FL}^{2.868}$$

Seasonal size frequency distributions were examined to partition growth, and thus fitted consumption estimates, into fast– and slow–growth seasons. The age–1 Kokanee captured in Merwin Reservoir in November 2013 had a mean fork length of 279 mm, equal to the mean back–calculated length at second annulus for the previous year's cohort. Assuming approximately equal growth conditions between years, this suggested that the majority of annual growth occurred before 1 December, consistent with cycles of zooplankton abundance. Therefore, we allocated 90% of annual growth in mass to the period between April 1 and November 30. Given that the thermal regimes and zooplankton cycles followed similar progressions between reservoirs, we allocated growth in this manner for all of our simulation (Table 4).

Zooplankton — We measured the monthly densities of crustacean zooplankton in each reservoir to estimate the food supply available for resident and reintroduced anadromous salmonids. We conducted oblique tows with a Clarke–Bumpus sampler fitted with a 153µm mesh conical net at depths that represented the epilimnion, metalimnion, and hypolimnion during stratification and similar depths during spring and fall at both limnology stations in each reservoir (Figure 1). We identified and enumerated > 50 crustacean zooplankton in subsamples of each tow, and measured the body length of the first 30 individuals of each genus encountered in each subsample using Image–Pro© digital image–analysis software. *Daphnia* spp. were the most abundant zooplankter and the most significant prey item for juvenile salmonids during the growing season, so we focused our analysis on their abundance and distribution. *Daphnia* were measured from the top of the helmet to the base of the tail spine, and body length (BL; mm) was converted to wet mass (WM; µg) with the equation $WM = 50 * BL^{2.88}$ (Kuns and Sprules 2000). Standing stock biomass was then calculated by multiplying the density of *Daphnia* by the mean wet mass, and expanding based on the volume of water within each corresponding depth layer (PacifiCorp *unpublished data*). The number of *Daphnia* eggs was also enumerated in each sample to estimate zooplankton production rates with the egg–ratio method (Kuns and Sprules 2000). We were not able to estimate production in November without data on zooplankton density in December.

Consumption demand to prey supply ratio and carrying capacity calculation — The Wisconsin Bioenergetics Model (Hanson 1997) parameterized for Rainbow Trout (Rand et al. 1993), Kokanee (Beauchamp et al. 1989), and Chinook Salmon (Stewart and Ibarra 1991) were used to estimate consumption demand. The bioenergetics models fit the daily per–capita consumption needed to satisfy the observed growth of an average individual from each population and age class. Simulations started at the beginning of the growing season (April 1) for Kokanee in Yale and Merwin Reservoirs, and June 1 (approximate stocking date) for Rainbow Trout in Swift Reservoir (Table 4). Simulations ended at the conclusion of the fast–growing season on November 30, or at spawning. In each reservoir, per–capita consumption by salmonids was expanded to the population–level which reflected the abundance, size distribution, and seasonal consumption by each age class of consumer. Population–level consumption was compared to prey supply to evaluate potential food limitations.

The monthly ratio of consumption demand to prey supply was examined to estimate carrying capacity. We designated consumption demand = 50% of prey supply in the single month of greatest prey demand/supply ratio during the growing season as a conservative estimate for carrying capacity, because the remaining 50% of the biomass could absorb additional sources of mortality and produce future generations of *Daphnia* (Beauchamp et al. 1995; Baldwin et al. 2000). Ratios of consumption demand/supply of *Daphnia* were created using both standing stock biomass as a lower estimate of prey supply, and a greater estimate of food supply which included standing stock biomass plus production within depths thermally accessible to salmonids. Using only the standing stock biomass throughout the growing season represents the lowest, most restrictive estimate of food supply, because production by *Daphnia* can provide significant additional biomass. *Daphnia* standing stock biomass plus production was used to represent greater (but still conservative) estimates of carrying capacity, again assuming that carrying capacity was exceeded when the demand/supply ratio was > 50% in any month of the growing season. To simulate the ratio of prey demand and supply assuming salmonids were thermally excluded from the epilimnion during stratification (July–September in Swift and Yale Reservoirs, July–October in Merwin Reservoir), we additionally compared consumption demand to prey supply below the epilimnion (meta– and hypolimnion) in these months.

For the month with the greatest demand/supply ratios, the difference between resident salmonid's consumption demand and 50% of prey supply was divided by the consumption demand of individual age–0 salmonids to estimate the number of additional sub-yearling salmonids that could have been supported in each reservoir for a year. We used the estimate of prey supply that included standing stock biomass and production but was restricted to the meta– and hypolimnion during stratification as our best estimate for these calculations, as it created a moderate estimate of carrying capacity by including *Daphnia* production but excluding epilimnetic prey during stratification. Consumption demand of age–0 spring Chinook Salmon in Swift Reservoir was estimated with a bioenergetics simulation using the feeding rate (p–value or C_{max}) observed for age–1 fish during the growing season (104%) and an estimated starting mass of 0.2 g on April 1. Age–0 Kokanee were used as a surrogate for estimating the consumption demand of a sub-yearling salmon in Yale and Merwin Reservoirs. We believe that Kokanee are a reasonable surrogate for Chinook Salmon because both species feed on *Daphnia* in the limnetic zone and exhibit diet vertical migrations (Koehler et al. 2006; Lowery and Beauchamp 2010).

Results

Relative abundance of fishes — The primary pelagic planktivores captured by anglers and our sampling in Swift Reservoir were hatchery–reared Rainbow Trout and Chinook Salmon smolts (Table 5). Swift Reservoir is stocked with approximately 50,000 hatchery–reared Rainbow Trout of catchable size (200–250 mm) each spring (PacifiCorp and Cowlitz 2014). Stocking has historically occurred in April, but has been delayed until early June since 2013 in order to avoid interactions with outmigrating anadromous salmonid smolts. Several thousand hatchery–reared yearling Chinook Salmon smolts were released in tributaries of Swift Reservoir in 2013 and 2014 as part of the reintroduction (F. Shrier, PacifiCorp Energy, Personal Communication). Rather than migrating out in late spring and early summer as anticipated, some of these fish were captured in the reservoir through fall. Three-spine Stickleback *Gasterosteus acouleatus* were the other planktivore observed in 2013 and 2014. A relatively small population of adfluvial Bull Trout resides in Swift Reservoir, which consume invertebrates as juveniles before becoming highly piscivorous as adults.

Kokanee *Oncorhynchus nerka* were the primary pelagic planktivore captured in Yale Reservoir in 2013 and 2014 (Table 5). The population of Kokanee in Yale Reservoir is self–sustaining and spawns in October at age 3 (after their third growing season) in Cougar Creek, a tributary of the upper portion of the reservoir (Figure 1; PacifiCorp and Cowlitz 2004a). Other planktivores in Yale Reservoir included Three-spine Stickleback and juvenile sculpins *Cottus spp*. There is also a small population of adfluvial Bull Trout.

Kokanee were the primary pelagic planktivore in Merwin Reservoir in 2013 and 2014 (Table 5). Approximately 45,000 Kokanee are stocked annually as fingerlings in fall, and 48,000 as yearlings in spring (PacifiCorp and Cowlitz 2014). Natural production of Kokanee is considered minimal from Merwin Reservoir’s tributaries, although most mature at age 3 and attempt to spawn in September–October. The primary source of natural recruitment of Kokanee into Merwin Reservoir is considered to be entrainment from Yale Reservoir (PacifiCorp and Cowlitz 2004a). Northern Pikeminnow *Ptychocheilus oregonensis* are abundant in Merwin Reservoir and can be planktivorous as juveniles and piscivorous as adults; however, they generally occupy nearshore habitats during spring and warmer shallower water in the limnetic zone during the summer, thus reducing the likelihood of predation on or competition with salmon (Brown and Moyle 1981). The consumption demand of the Northern Pikeminnow population is examined in detail in the other chapter, and is therefore not covered here.

Thermal experience and depth distribution of pelagic planktivores — Thermal regimes and stratification have a large effect on metabolic rates driving consumption demand, and vertical distribution of fish, as well as rates of zooplankton production. Epilimnetic temperatures in Swift and Yale Reservoirs fluctuated between 13–14°C in May, and 22–23°C in August. The hypolimnion remained at approximately 5°C throughout the year. Epilimnetic temperatures were slightly warmer in Merwin Reservoir at 14–16°C in May and peaking at 22–24°C in July and August. Unlike Swift and Yale Reservoirs, the hypolimnion in Merwin Reservoir warmed from 5–6°C in April to 15–18°C in October.

Stratification strongly influenced the vertical distributions of salmonids during summer. Epilimnetic temperatures exceeded the thermal preferences of salmonids during peak summer stratification in all three reservoirs, but the metalimnion remained useable year–round (Figure 2).

In general, fish occupied the upper 40 m of the water column in Swift Reservoir during daylight in spring–fall (Figure 3). During dusk and night, most fish were in the upper 0–15 m of the water column in spring and fall, and from 10–30 m during summer. A similar seasonal pattern was observed for Kokanee in Yale and Merwin Reservoirs; however, fish in Merwin Reservoir were more shallowly distributed in spring and fall, and deeply distributed in summer than in Yale Reservoir (Figures 4&5). We expect that Chinook Salmon would exhibit similar patterns of seasonal depth distribution and diel vertical migrations as Kokanee (e.g. Lowery and Beauchamp 2010). In Yale Reservoir at night, fish were distributed at 5–40 m during spring and fall, but were more concentrated at 15–30 m during the summer. In Merwin Reservoir, nighttime fish distribution was bimodal in spring and fall with a larger mode at 0–10 m and a smaller mode at 20–40 m. However, fish were distributed in a single deeper mode at 20–50 m in the summer in Merwin Reservoir. The deeper fish distributions observed in August relative to June in all three reservoirs suggests decreased access to epilimnetic prey resources during the peak of summer stratification.

Stable isotope analysis — Stable isotope analysis clarified the trophic levels and relative dependence on pelagic and benthic energy pathways of the species and size classes of organisms within the reservoir food webs, and corroborated our identification of the key pelagic planktivore populations. Organisms representing bentho–littoral energy pathways such as snails and small Largescale Suckers *Catostomus macrocheilus* were enriched in $\delta\ ^{13}C$ and organisms representing pelagic energy pathways such as filter–feeding Asian Clams *Corbicula fluminea* and *Daphnia* were depleted of $\delta\ ^{13}C$ in all three reservoirs (Figures 6–8). Stable isotopes signatures varied within and among species, size classes, trophic levels, and reservoirs according to position in and structure of each food web.

Three-spine Sticklebacks and Chinook and Coho Salmon were the most dependent on pelagically derived nutrients in Swift Reservoir, while Rainbow Trout exhibited more benthic influence (Figure 6). Larger sculpin also appeared to rely on pelagic nutrients, but could have been feeding on consumers of limnetically–derived detritus. Kokanee were the primary pelagic planktivores in Yale and Merwin Reservoirs (Figures 7 and 8). Kokanee showed the greatest dependence on pelagic prey of all fish in Yale Reservoir as evidenced by their $\delta^{15}N > 3‰$ above zooplankton and $\delta^{13}C$ values similar to *Daphnia* and other zooplankton. Small Northern Pikeminnow also relied on pelagic prey to a large degree in Merwin Reservoir. Secondary consumers (i.e., invertivores) were enriched in $\delta\ ^{15}N$ relative to primary consumers, and piscivores were further enriched relative to invertivores. The results of stable isotopes were largely corroborated by stomach contents analysis.

Diet analysis — Stomach contents of age 0–2 Kokanee, age–1 hatchery–reared Rainbow Trout, and age–1 Chinook Salmon (the primary pelagic planktivores based on relative abundance and stable isotope analysis) all exhibited similar seasonal trends in the proportions of zooplankton and insects consumed (Table 6). Cladocerans (including mostly *Daphnia*) represented 54–68% of diets in spring, with immature aquatic insects (10–36%) contributing most of the remainder. Cladocerans increased to 76–100% of diets during summer when they were more available, and 86–89% in fall. Overall, *Daphnia* was the most common prey consumed, which emphasized the focus on *Daphnia* abundance and distribution as a determining factor in carrying capacity. Copepods represented < 2% of stomach contents across species and seasons examined in Swift and Merwin Reservoirs, but were somewhat more prevalent in diets of Kokanee in Yale Reservoir (6–16%). *Holopedium gibberum* a cladoceran encased in a gelatinous shell, were common in zooplankton samples from Yale Reservoir (mean = 3.5/L, SE

= 2.1/L in the epilimnion), and Swift and Merwin Reservoirs to a lesser degree, but were rare in diets. Terrestrial insects represented a small proportion of diets (mean = 5.0%, SE = 1.5%) compared to aquatic insects (mean = 11.5%, SE = 3.5%), and both were most common in spring followed by fall. Rainbow Trout diets suggested a higher reliance on zooplankton (59–100% spring–fall) than expected based on their isotope values. However, only four samples of rainbow trout diets were analyzed to represent the summer season and some sampling occurred during the peak of a *Daphnia* bloom, so the results of stomach contents analysis likely underrepresented the true proportion of benthic invertebrates in their summer diet composition. Although rainbow trout had nearly doubled in weight since release, the isotopic signature of their hatchery feed (enriched in δ^{15}N and δ^{13}C) may have influenced their values, further contributing to their seemingly benthic signature.

Zooplankton — A strong late spring peak in *Daphnia* occurred in all reservoirs between May and July, with a smaller secondary peak in September–October **(**Figure 9**)**. In general, moderate to high densities of *Daphnia* (2.5–26 per L) persisted in the epilimnion and metalimnion throughout the growing season in all three reservoirs. Densities in the epilimnion were generally twice that of the metalimnion, and hypolimnetic densities were always below 1 *Daphnia* /L with the exception of May–August in Merwin Reservoir.

Daphnia standing stock biomass followed similar patterns as density in all three reservoirs but was somewhat less variable across months, while *Daphnia* production was highly variable and did not follow the same progression as density. The dampening of the fluctuation in *Daphnia* biomass relative to density resulted from the inverse relationship between average individual mass and density, due to increased production of smaller individuals when density increased (Figure 8). Production varied widely among months from a fraction to an order of magnitude greater than standing stock biomass (Figures 10–12). Many months of high production translated into increases in biomass the following month (and vice versa) as expected; however, significant production did not always translate into increased biomass. This could have been a result of a few different potential sources of error in our estimates of production. Monthly sampling events were too far apart to capture all the dynamics of egg ratios which are notoriously variable across short intervals, we did not account for entrainment out of reservoirs, and our egg–production model did not incorporate information on *Daphnia* age–structure (Lynch 1982; Brett et al 1992). Despite these potential sources of bias, we feel that our estimates of production are reliable for the purpose of estimating carrying capacity.

Kokanee abundance — Kokanee were approximately half as abundant in Merwin Reservoir as in Yale Reservoir, but annual survival rates were similar. We estimated that the annual survival rate for Kokanee in Yale Reservoir was 35% and that in August there were 396,262 age–0, 139,847 age–1, and 49,354 age–2 Kokanee. We estimated that the annual survival rate for Kokanee in Merwin Reservoir was 32% and that in August there were 189,937 Age–0, 60,105 Age–1, and 19,020 Age–2 Kokanee.

Resident planktivore consumption demand to prey supply ratios and carrying capacity — Resident pelagic planktivores fed at moderate to high levels relative to their potential maximum in all three reservoirs (59–123% C_{max}; Table 4), while their consumption demand fluctuated based on ambient water temperatures and average fish size (Figures 10–12). Kokanee in Merwin Reservoir had the highest feeding rate (92–123% C_{max} across age classes from April through November), while hatchery–reared Rainbow Trout in Swift Reservoir were intermediate at 78% C_{max}, as were Kokanee in Yale Reservoir which ranged 59–86% C_{max} (Table 4). Consumption demand on *Daphnia* by the planktivore populations in all three reservoirs started at moderate levels in April–June (20–34 MT/month), peaked in August–October (33–55 MT/month), then declined with decreasing water temperatures (Figures 10–12).

The ratio of consumption demand by Rainbow Trout to prey supply in Swift Reservoir started low in June and increased through September (Figure 10). Consumption demand to *Daphnia* supply ratios were < 10% of standing stock biomass in June (prior to stratification and with all depth layers summed) but increased in July–September once stratification was established. Consumption demand was 21% of the most conservative estimate of prey supply, biomass within the meta– and hypolimnion (epilimnion thermally inaccessible) in July, and increased to 56% in August and 96% in September. However, consumption demand was < 30% of biomass in all months examined if the whole water column was considered. The demand/supply ratio if production was also included was < 30% in the meta– and hypolimnion and < 15% in the whole water column in all months examined. Biomass was 5–10 times greater than consumption demand in October–November. These ratios suggest that a moderate amount of surplus prey would be available to support additional demand if production is considered in addition to biomass. There was a surplus of approximately 9 MT of *Daphnia* biomass and production in the meta– and hypolimnion in September, the month of highest demand/supply ratios, which could have been consumed without exceeding the 50% carrying capacity cutoff according to our simulations. Dividing this biomass by the estimated consumption demand of a sub-yearling spring Chinook Salmon in Swift Reservoir yielded an estimate of roughly 150,000 juvenile salmon that could have been supported during their first year by the surplus prey in the month of greatest prey demand/supply ratio.

Simulated consumption demand of Kokanee in Yale Reservoir exceeded *Daphnia* standing stock biomass plus production in April and May, as *Daphnia* did not begin to bloom until June (Figure 10). Consumption demand in June was 61% of biomass but only 16% of biomass plus production. During peak thermal stratification from July through September, consumption demand was 39–122% of biomass in the meta– and hypolimnion or 22–37% of biomass plus production. Across the entire water column from July through September, consumption demand was 22–65% of biomass or 7–15% of biomass plus production. Simulated consumption was 66–70% of the biomass in October–November and 17% of biomass plus production in October (production data not available for November). These ratios suggest that a moderate amount of surplus prey would be available during the summer growing season to support additional demand in Yale Reservoir if production is considered in addition to standing stock biomass. The surplus biomass and production of *Daphnia* in the meta–and hypolimnion in September, the month of highest demand/supply ratio during the summer growing season, without exceeding 50% of prey supply was roughly 14 MT. Dividing this by the consumption demand of an individual age–0 Kokanee (as a surrogate for a sub-yearling salmon) yielded an estimate of an additional 330,000 fish that could have been supported in the reservoir through their first year.

In April, before the major bloom of *Daphnia* was established, our simulated consumption demand for Kokanee in Merwin Reservoir was 143% of standing stock biomass of *Daphnia* but only 8% of biomass plus production (Figure 12). The consumption demand to prey supply ratio dropped significantly when the spring *Daphnia* bloom was established in May, and was < 15% of biomass in May–June. Consumption demand increased and prey supply began to decrease in July–August, with demand–supply ratios increasing to 33–36% of biomass in the meta– and hypolimnion, and 20–28% in the whole water column. Consumption demand began to outstrip prey supply in September–October when it was 94–125% of biomass and 37–65% of biomass plus production in the meta– and hypolimnion. The demand/supply ratio in September–October, when *Daphnia* in the entire water column was included, was 41–57% biomass and 18–22% biomass plus production. Simulated prey demand was approximately twice biomass in November. Overall, Merwin also offers a moderate surplus of prey resources from April through September. Dividing surplus biomass and production in the meta– and hypolimnion in September, the month of highest demand/supply ratios during the summer growing season, by the consumption demand of an individual age–0 Kokanee yielded an estimate of 130,000 additional sub-yearling fish that could have been supported in the reservoir for their first year.

Discussion

Our simulations indicated that all three reservoirs offered a moderate surplus of *Daphnia* to support consumption demand by reintroduced anadromous salmonids but a significant portion of prey production was also consumed by resident pelagic planktivores. Swift Reservoir had ample prey resources available from May through August, as well as in October–November, suggesting that fish would have access to plenty of food during the critical stages of reservoir entry in spring, and again in late summer/fall when storing energy before winter. Early spring prey resources were limiting in Yale Reservoir; however, if fish survived through spring, there was surplus food to support growth during the summer and early fall. Merwin Reservoir contained abundant surplus prey resources in spring–summer, suggesting that reintroduced fish would experience good growth conditions throughout the growing season. Further evaluation of the distribution and behavior of anadromous salmonids in storage–reservoirs is needed to better understand their timing and degree of reservoir rearing, behavior in reservoirs, and potential for competitive interactions with resident fish.

Our estimates of monthly consumption demand are approximate and our simulations only address the expected likelihood of food limitation occurring at some point during the growing season. Without estimates of monthly growth, potential variation in feeding rates become less certain among months in response to prey supply. For instance, prey supply was limited in September but less limited in August and October in Swift Reservoir. Under this scenario, we would expect that fish actually fed at a slightly higher rate in August and October and a lower rate in September than was estimated using a single growth increment between spring and fall.

Our estimates of the number of sub-yearling Chinook that could be supported in their first year is likely conservative given that the consumption demand to prey supply ratios only approached 50% for one or two month during the growing season in each reservoir. Thus fish could make it through a month of low food availability with a minor decrease in growth and survival, while multiple consecutive months of limiting prey would indicate a more significant bottleneck to production. More refined evaluations of carrying capacity could be constructed to simulate specific reintroduction scenarios.

Uncertainty in our simulations is captured in the different scenarios of prey supply. Standing stock biomass represents a snapshot of the prey supply when sampled, but fails to account for *Daphnia* production which can exceed the standing stock biomass by an order of magnitude over the course of a month. The assumption that prey resources in the epilimnion are inaccessible during stratification is supported by the distribution of Kokanee near the thermocline at night in summer. We expect that Chinook Salmon would have a similar depth distribution in summer to Kokanee, so would also have limited access to the epilimnion during peak stratification. However, daytime and crepuscular distributions suggest that some Kokanee schooled in the epilimnion during the day or conducted brief feeding forays into the epilimnion at dusk, so the exclusion of all epilimnetic prey from supply scenarios likely underestimates carrying capacity. Rainbow Trout in Swift Reservoir also appeared to forage in the epilimnion in summer to a lesser degree than in the metalimnion based on their distribution. Therefore, the greater estimate of prey supply that includes production and standing stock biomass, and the negatively–biasing measure of excluding all epilimnetic prey during stratification provides a good middle–ground scenario in our opinions. Managers may look to other scenarios for higher or lower estimates as needed. However, all of our simulations are conservative given the restriction of consumption to demand to 50% of prey supply.

Exceeding the carrying capacity of the reservoir for pelagic planktivores would reduce growth, survival, and production of smolts. Even in a month of high prey availability, fish can only consume a limited amount of prey dictated by the volume of their stomachs and their digestion rate. In months of low prey availability they are limited by the rate at which they can capture prey (as a function of their size–dependent foraging abilities and prey densities), and anti–predation behaviors limiting their ability to forage at certain times of day or at certain depths (Stockwell and Johnson 1999; Koski and Johnson 2002; Hardiman et al. 2004). Significant prey shortages during the growing season would hinder their ability to acquire enough energy to effectively fight disease and survive. Furthermore, food limitation and size–dependent predation risk promotes risk–taking behavior which increases predation mortality (Biro et al. 2005). Zabel and Achord (2004) found that the length of juvenile Chinook Salmon in the Salmon River basin had a strong effect on survival to outmigration on a within population basis, but not across multiple populations. However, they suggested that there may have been size–dependent survival advantages at subsequent life stages. Growth during the early marine phase for Chinook Salmon in Puget Sound and for those from the Mid– and Upper Columbia

River in the Pacific Ocean strongly affects survival, whereas no effect of freshwater growth was found (Duffy and Beauchamp 2011, Tomaro et al 2012). However, juvenile Chinook Salmon from California's Central Valley that were the larger and faster–growing individuals at marine entry exhibited greater survival during years when overall survival to adulthood was lower for their cohort (Woodson et al. 2013). Thus larger sized smolts could experience better survival during outmigration and later life stages, especially in years when conditions were poor in the marine environment.

Cycles of zooplankton production resulted in moderate to high densities and biomass of *Daphnia* during spring which persisted throughout the growing season, suggesting that hydroelectric–project water operations did not severely undermine prey production. Our estimates of production were imprecise and likely suffered from the infrequency of sampling. However, the production estimates still provided a reliable approximation for evaluating the prey supply available to satisfy planktivore consumption demand. The conservative nature of the 50% of prey supply cutoff for carrying capacity allows for some error.

Diet and stable isotope analyses revealed that salmonids in these reservoirs depend on zooplankton and specifically *Daphnia* during the growing season, as expected, while insects provided a significant supplementary source of energy when *Daphnia* were less abundant. Fluctuations in water level, often resulting from drawdown, can alter littoral–benthic macroinvertebrate communities' species composition, productivity, and timing of prey production (e.g. Furey et al. 2009). Altered insect supply during key growing months could positively or negatively impact carrying capacity depending on how the invertebrate community is affected by water operations. The dynamics of insect production in the Lewis River reservoirs warrants more investigation, especially if reservoirs begin to experience increased fluctuation in water level during the growing season to deal with droughts and trends in climate change.

Vertical distributions of fish are influenced by a number of factors including prey density and distribution, temperature, and predation risk. The relatively shallow distribution of Rainbow Trout in Swift Reservoir was likely driven by the higher prey densities at shallower depths and their tolerance of warm water. The diel vertical migration that they exhibited may have been to avoid overlap with piscivorous Bull Trout during the light hours of the day. The diel vertical migration exhibited by Kokanee in Merwin and Yale Reservoirs is a well–known behavior for this species (Eggers 1978; Levy 1987). The deeper distribution of Kokanee in Merwin Reservoir compared to Yale Reservoir during peak stratification provided some refuge from predation by the abundant but shallowly distributed Northern Pikeminnow. This deep distribution was also likely reinforced by warmer temperatures and higher *Daphnia* densities in the meta– and hypolimnion. The diel vertical migration and daytime schooling exhibited by Kokanee in Yale Reservoir represents a compromise that reduces their risk of predation by the visual predators, Northern Pikeminnow and Bull Trout, while maximizing food consumption and growth efficiency (Clark and Levy 1988).

To refine this evaluation of the growth environment and carrying capacity for juvenile anadromous salmonids in the Reservoirs of the Lewis River, monitoring of zooplankton and planktivores should continue. Our analysis relied on a single year of zooplankton and planktivore abundance data; however, significant inter–annual variability in these factors is likely. For example, average *Daphnia* density in May–August in Lake Washington varied between <1 and 16 individuals per liter between 1977 and 2002, with an overall decreasing trend (Winder and Schindler 2004). Variability as well as long–term trends, perhaps resulting from climate change, should be considered when evaluating the feasibility of and planning anadromous salmonid reintroductions.

Test releases of stream–type Chinook and Coho Salmon fry in tributaries and monitoring of naturally produced individuals in Swift Reservoir could be used to examine their habitat use and growth within the basin. Test releases would provide an opportunity to examine the timing and degree to which fry move into reservoirs to rear, versus remaining in tributaries year–round. Their behavior, distribution, and growth in reservoirs could then be examined explicitly as the resident salmonids were investigated in this study. Preliminary snorkel surveys of the littoral zone in Swift Reservoir in May 2014 detected Coho Salmon fry ubiquitously around the perimeter, suggesting that naturally produced salmon fry are already entering Swift Reservoir in spring. Furthermore, salmon fry density in Swift Reservoir is likely to increase as the reintroduced populations become more established. Monitoring anadromous salmonids rearing in reservoirs throughout the growing season with additional targeted sampling will help to better understand their behavior and distribution to refine estimates of carrying capacity.

Our analysis will aid stakeholders and agencies in setting realistic goals for the production of resident and reintroduced anadromous fish as terms of FERC relicensing agreements, thus maximizing the benefit of the natural resource for user groups and conservation efforts. Our scenarios (including or excluding *Daphnia* production and epilimnetic prey) bound potential carrying capacities, allowing managers to aim for a fish assemblage based on their chosen risk of overshooting prey supply. Quantifying the surplus prey resources available to support the addition of reintroduced anadromous salmonids rearing in storage reservoirs aids managers and stakeholders in making challenging decisions about how to allocate resources for restoration and enhancement that operate within the capacity and constraints of the natural environment. We hope these results are helpful to managers of the Lewis River as well as other systems where similar questions exist, and that our approach can be replicated to help inform future proposed reintroductions and FERC relicensing negotiations.

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Tables

Table 1. Physical characteristics and the lengths of tributary habitat accessible to anadromous salmonids in Swift, Yale and Merwin Reservoirs.

	Swift	Yale	Merwin
Surface area (km^2)[a]	18.3	14.9	15.7
Length (km)	14.4	12.4	14.5
Mean depth (m)[a]	45	31	31
Max depth (m)[a]	101	79	73
Mean Secchi depth transparency (m)	5.75	7.5	5
Water residence time (d) [b]	380.9	112.6	118.4
Total phosphorus (mg/L)[c]	<0.02	–	<0.02
Trophic status	Oligotrophic	Oligotrophic	Oligotrophic
Months stratified	May–Oct.	May–Oct.	May–Oct.
Depth of thermocline (m)	5–15	5–15	~8
Range of surface temps. (°C)	22–4	23–5	24–5
Accessible tributary habitat (km)[d]	188	23.5	6

a. PacifiCorp, unpublished data
b. F. Shrier, PacifiCorp Energy, *personal communication*
c. PacifiCorp and Cowlitz 2004b
d. Al–Chokhachy et al. 2013

Table 2. Thermal experience of pelagic planktivore consumption demands in Swift, Yale, and Merwin Reservoirs.

		Thermal experience (°C)		
Date	Simulation Day	Swift	Yale	Merwin
1–Apr	1	6.6	5.6	7.8
18–May	49	10.8	8.2	11.9
30–Jun	89	14.3	9.5	13.5
19–Jul	109	14.7	11.7	15
15–Aug	135	15.1	12.5	16.2
17–Sep	167	14.6	14	17
13–Oct	193	9.1	11.5	17.3
15–Nov	225	8.2	8	12.7
15–Dec	255	5.9	5.9	5.8
1–Jan	270	5.2	5.4	5.9
1–Mar	330	4.5	4.9	6.1
31–Mar	365	6.6	5.6	7.8

Table 3. Energy density (Joules/gram) of prey items consumed by pelagic planktivores. An indigestible fraction of 17% was assessed on all invertebrate prey consumed (Beauchamp et al. 2007).

Day	Daphnia	Copepod	Terrestrial insects	Aquatic insects
1	1950[a]	2260	5000	3400
365	1950	2260	5000	3400

a. Luecke & Brandt 199; Stockwell et al. 1999

Table 4. Starting and ending dates and consumer weights used in bioenergetics simulations, and outputs of consumption rate (%Cmax) and consumption in biomass. The abbreviation RBT_h = hatchery–reared Rainbow Trout.

Reservoir	Spp.	Age	% C_{max}	Start date	End Date	Initial fork length (mm)	Initial wt. (g)	Final wt. (g)	Growth (g)	Consumption (g)	Daphnia Consumption (g)
Swift	RBT_h	1	78%	1–Jun	20–Nov	258	200.0	362.0	162	3,499	3,149
	Chinook	0	104%	1–Apr	30–Nov	25	0.2	30.5	30.3	331	299
Yale	Kokanee	0	86%	1–Apr	30–Nov	25	0.1	40.6	41	288	234
		1	74%	1–Apr	30–Nov	163	45	143.5	98	1,227	952
		2	59%	1–Apr	30–Oct	236	154	219	64	1,498	1,124
Merwin	Kokanee	0	123%	1–Apr	30–Nov	25	0.3	81.1	81	867	729
		1	92%	1–Apr	30–Nov	190	90	253.0	163	2,794	2,194
		2	100%	1–Apr	30–Sep	279	271	498	227	4,186	3,121

Table 5. Relative abundance of fish species observed in sampling conducted in this study and predominant summer crustacean zooplankton found in each reservoir. Blanks indicate that the species was absent in that reservoir.

	Swift	Yale	Merwin
Northern Pikeminnow		Moderate	High
Largescale Sucker	High	High	High
Kokanee		High	High
Rainbow Trout	High	Rare	Moderate
Coastal Cutthroat Trout	Rare	Rare	Rare
Bull Trout	Rare	Rare	
Tiger Muskie			Moderate
Sculpins	Moderate	Moderate	Moderate
Three-spine Stickleback	Moderate	Rare	Rare
Mountain Whitefish	Rare		
Largemouth Bass			Rare
Juvenile Coho Salmon	Rare		Rare
Juvenile Chinook Salmon	Moderate		
Predominant summer zooplankton	*Daphnia*	*Daphnia*	*Daphnia*

Table 6. Seasonal diet proportions for invertebrate feeding salmonids captured in Swift, Yale and Merwin Reservoirs in 2013–2014. The abbreviations CHK = spring Chinook Salmon, RBT$_h$= hatchery–reared Rainbow Trout, and KOK = Kokanee. The abbreviations Cladoc. = Cladocerans, Copep. = Copepods, Terr. ins. = Terrestrial insects, and Aqua. ins. = Aquatic insects.

					Prey items (proportion in diet)				
Location	Spp.	Size Class	Season	N	Cladoc.	Copep.	Terr. ins.	Aqua. ins.	Fish
Swift	CHK	100–299	Spr	4	0.546	0.000	0.100	0.104	0.250
Swift	CHK	100–299	Sum	7	1.000	0.000	0.000	0.000	0.000
Swift	CHK	100–299	Fall	11	0.855	0.000	0.009	0.136	0.000
Swift	RBT$_h$	200–399	Spr	10	0.593	0.000	0.046	0.360	0.000
Swift	RBT$_h$	200–299	Sum	4	0.999	0.001	0.000	0.000	0.000
Swift	RBT$_h$	200–399	Fall	13	0.893	0.002	0.049	0.056	0.000
Yale	KOK	0–299	Spr	14	0.684	0.084	0.043	0.189	0.000
Yale	KOK	0–299	Sum	14	0.755	0.162	0.000	0.083	0.000
Yale	KOK	100–199	Fall	17	0.879	0.062	0.059	0.000	0.000
Merwin	KOK	0–399	Spr	17	0.536	0.018	0.202	0.243	0.000
Merwin	KOK	200–399	Sum	11	0.908	0.001	0.018	0.073	0.000
Merwin	KOK	100–399	Fall	13	0.857	0.000	0.043	0.100	0.000

Figures

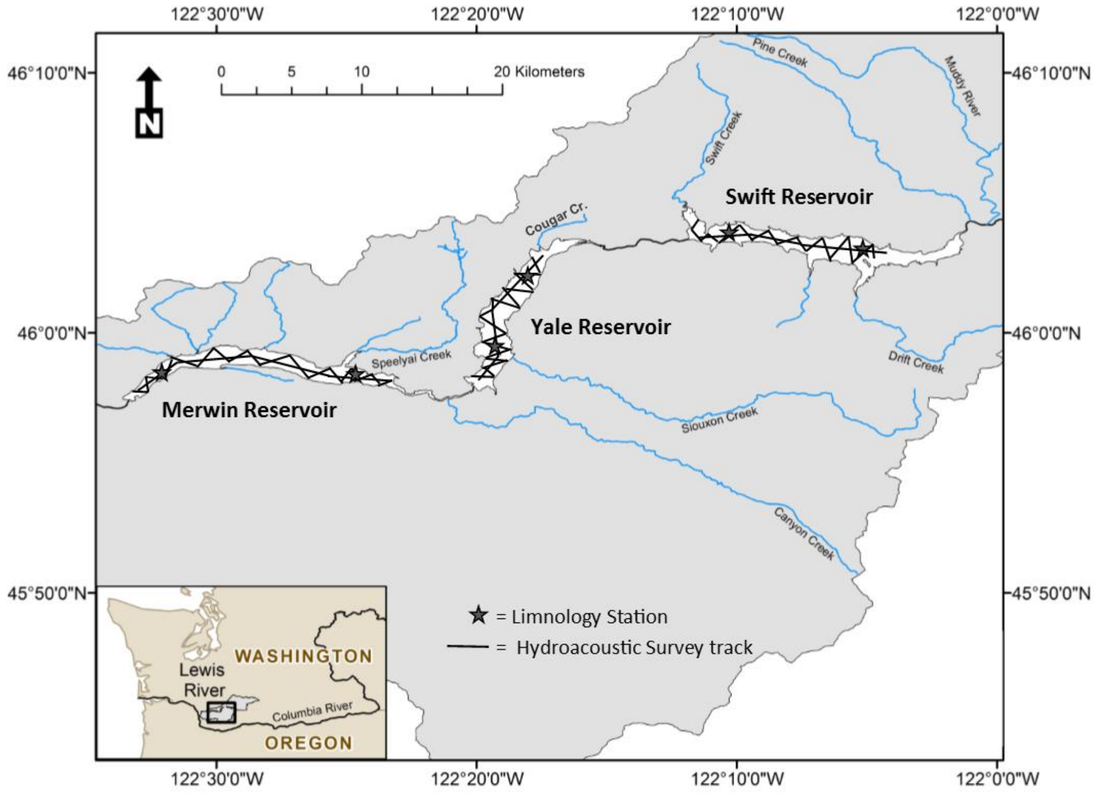

Figure 1. Map of North Fork Lewis River Reservoirs. Stars show location where temperature and zooplankton were sampled. Lines represent hydroacoustic survey tracks.

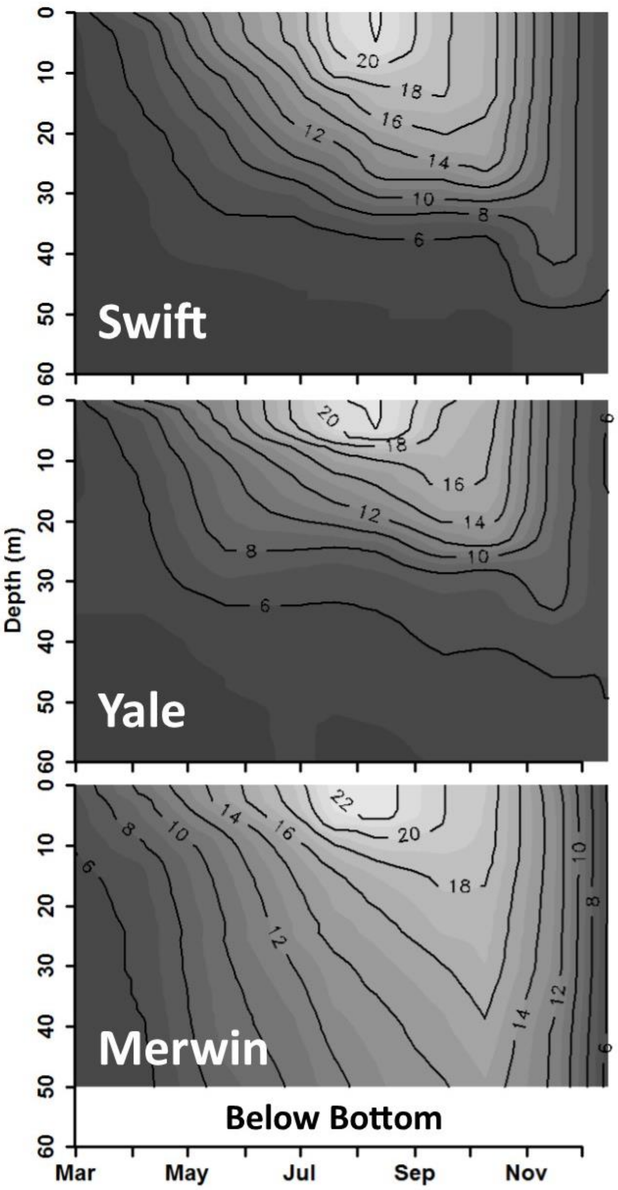

Figure 2. Isoclines of average water temperature (°C) in Swift, Yale, and Merwin Reservoirs in 2013.

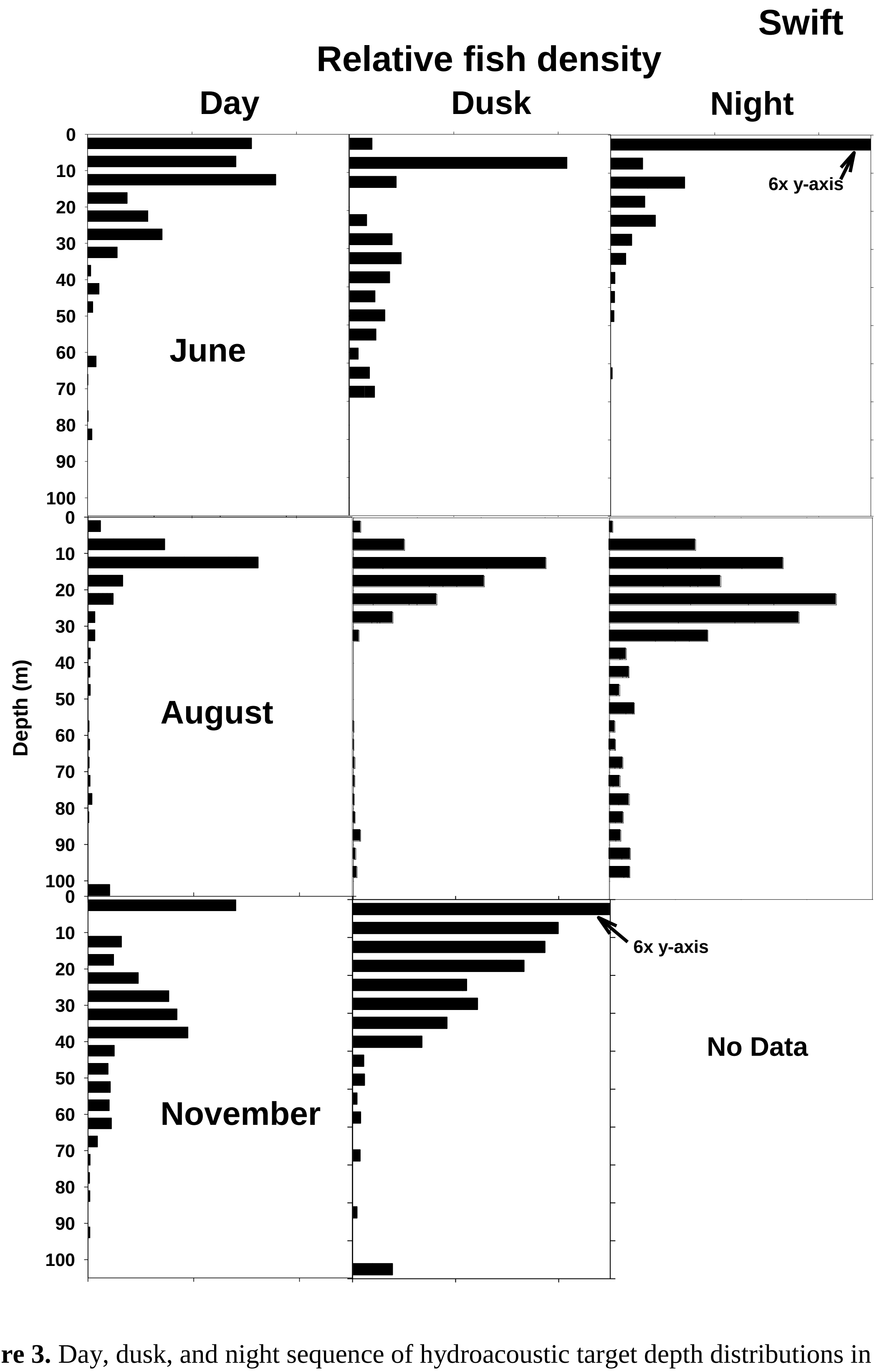

Figure 3. Day, dusk, and night sequence of hydroacoustic target depth distributions in June, August, and November 2013 in Swift Reservoir.

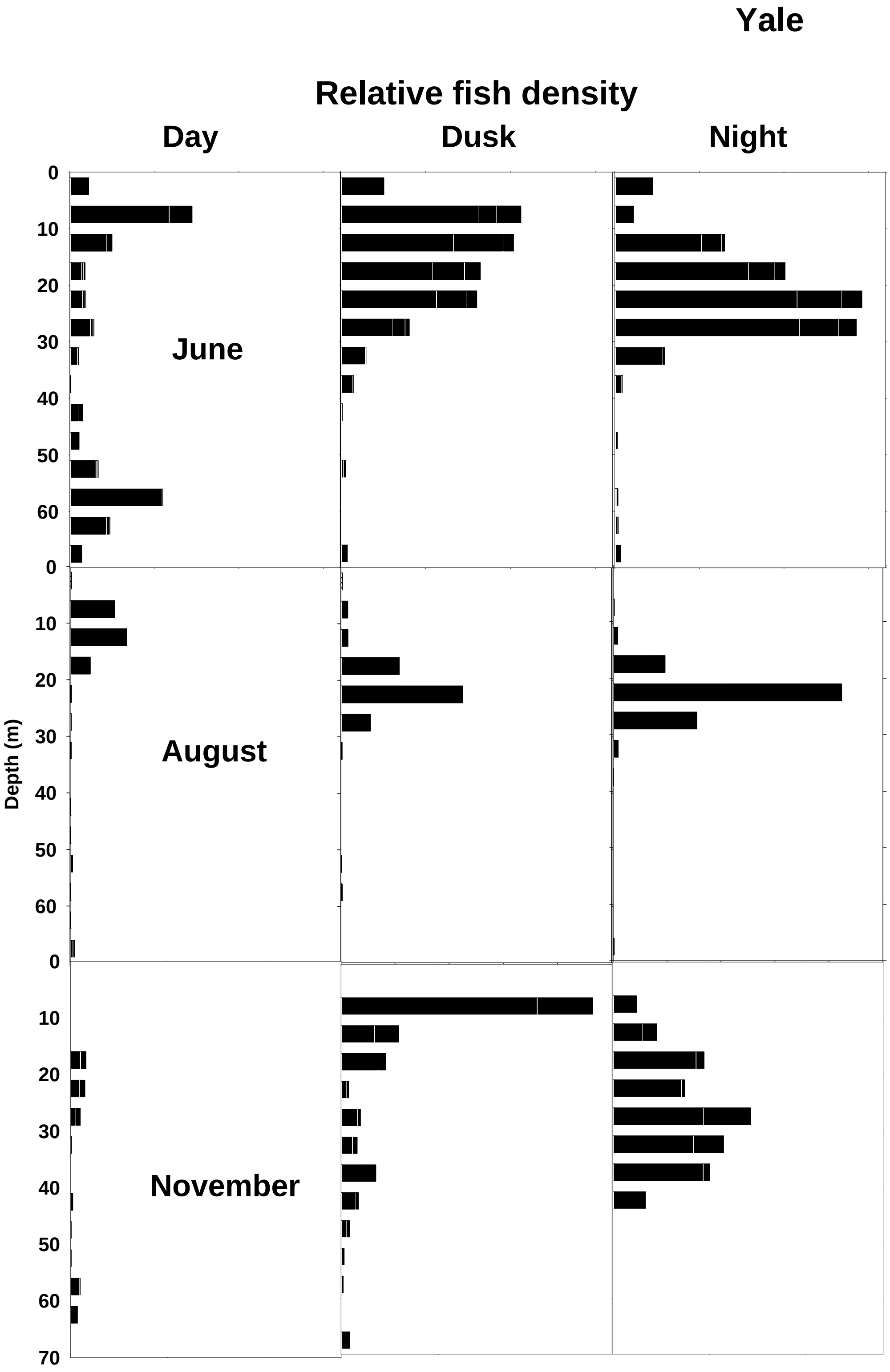

Figure 4. Day, dusk, and night sequence of hydroacoustic target depth distributions in June, August, and November 2013 in Yale Reservoir.

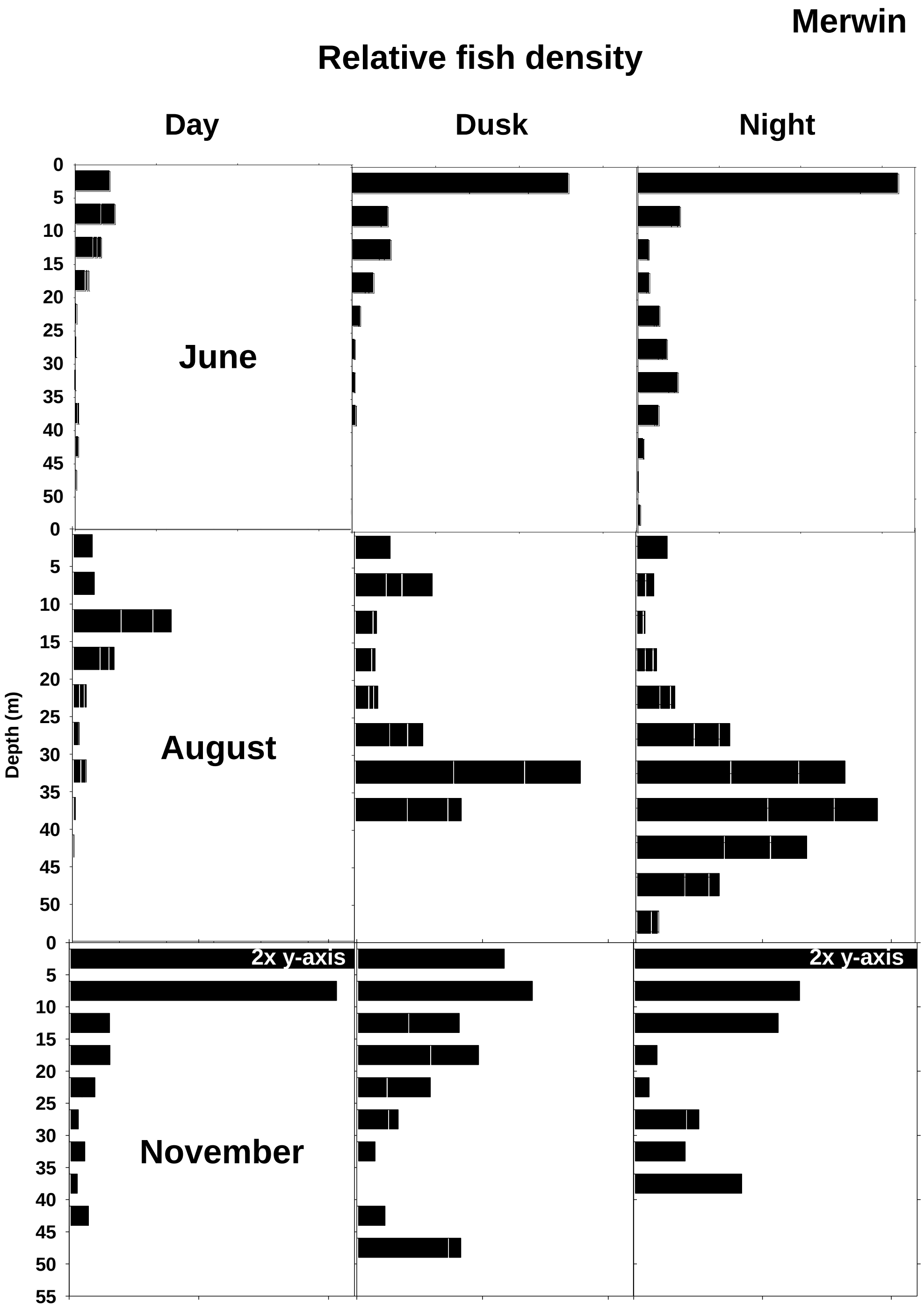

Figure 5. Day, dusk, and night sequence of hydroacoustic target depth distributions in June, August, and November 2013 in Merwin Reservoir.

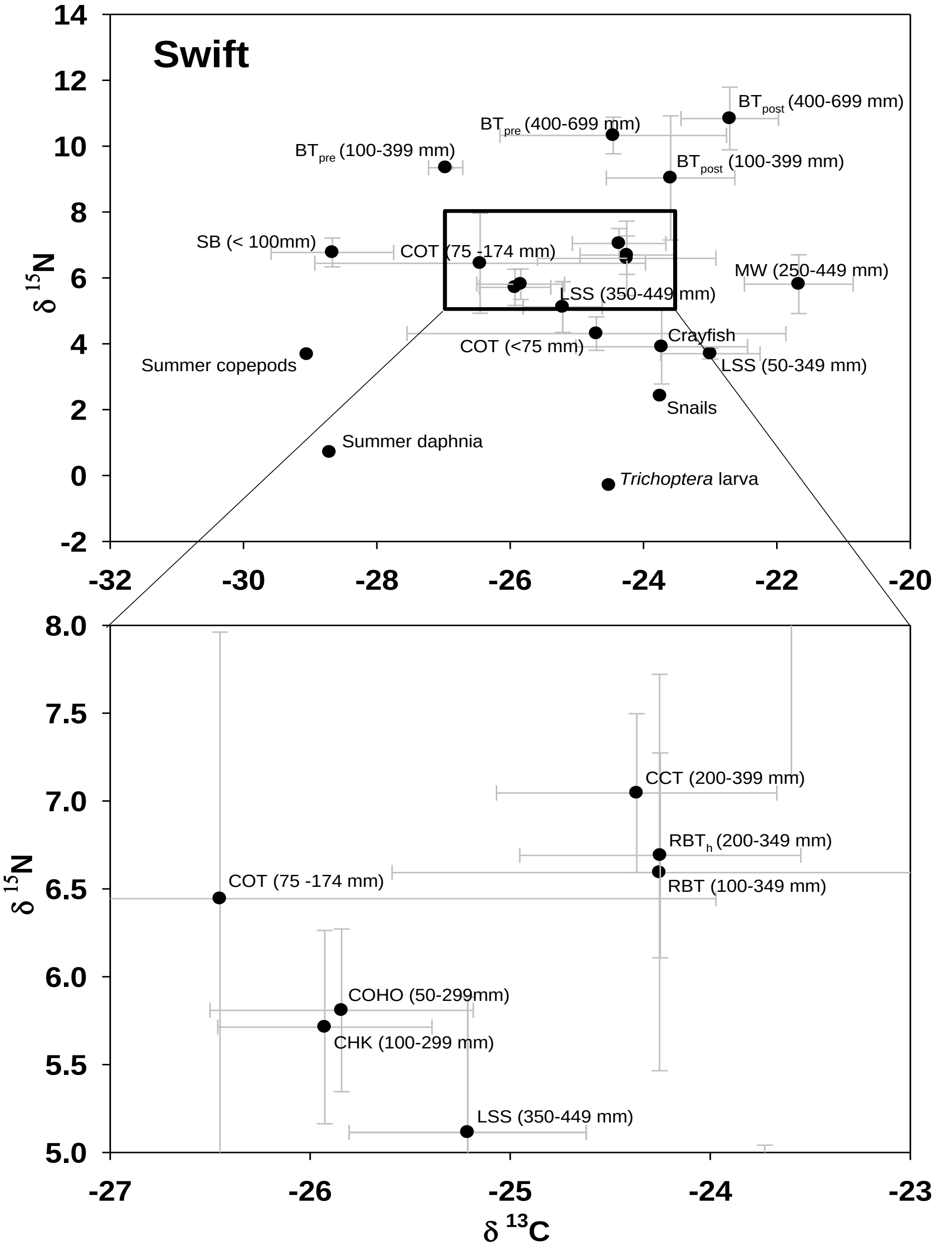

Figure 6. Average δ^{15}N and δ^{13}C values for organisms sampled in Swift Reservoir. Error bars represent 2 SE. Abbreviations BT$_{pre}$ = Bull Trout sampled in 2010 before significant reintroduction of anadromous salmonids, BT$_{post}$ = Bull Trout sampled in 2013–2014 after the reintroduction had begun, CCT = Coastal Cutthroat Trout, CHK = spring Chinook Salmon, COHO = Coho Salmon, COT = Sculpin, LSS = Largescale Sucker, MW = Mountain Whitefish,

RBT = rainbow trout, RBT$_h$ = hatchery–reared Rainbow Trout, and SB = Three-spine Stickleback.

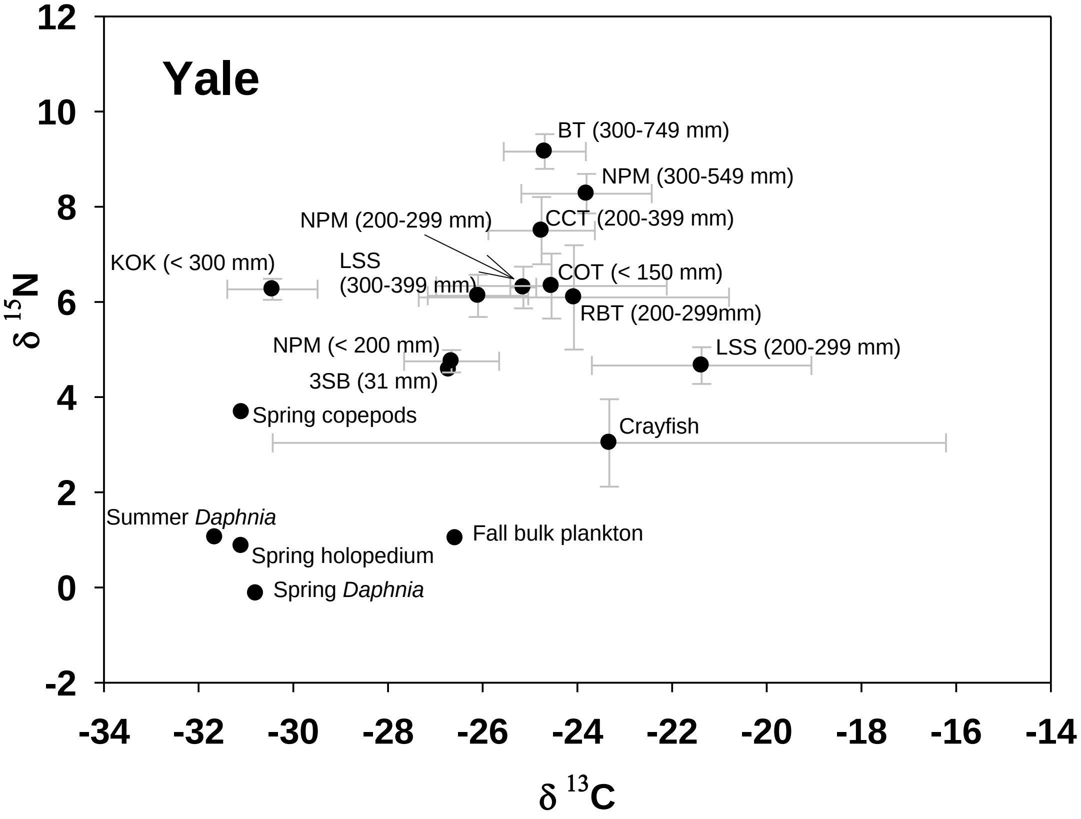

Figure 7. Average δ 15N versus δ 13C for organisms sampled in Yale Reservoir. Error bars represent 2 SE. BT = Bull Trout, CCT = Coastal Cutthroat Trout, COT = Sculpins, KOK = Kokanee, LSS = Largescale Sucker, NPM = Northern Pikeminnow, RBT = Rainbow Trout, and SB = Three-spine Stickleback. Bulk plankton consists of the contents of a vertical plankton net tow, without separating organisms by genus.

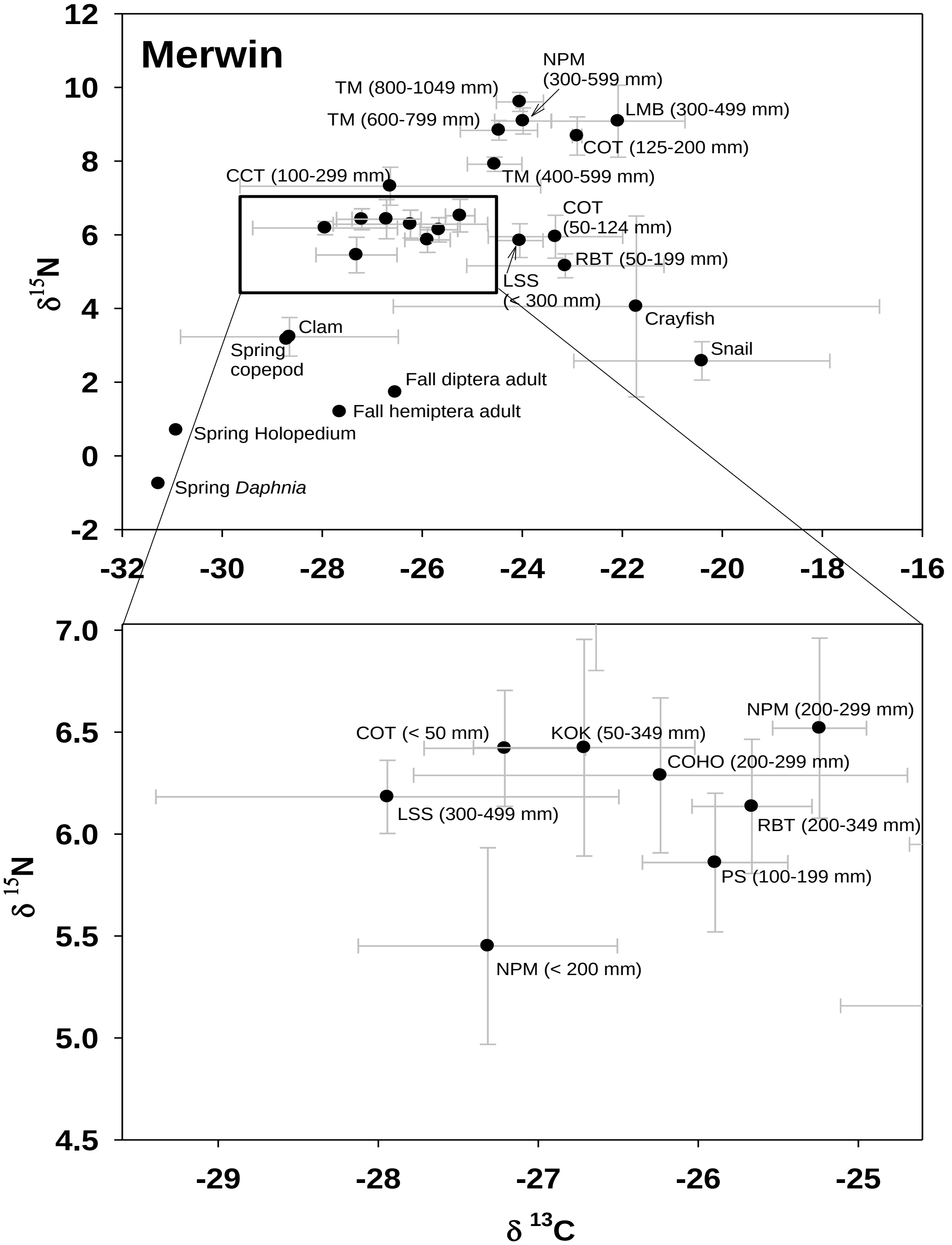

Figure 8. Average δ^{15}N and δ^{13}C for organisms sampled in Merwin Reservoir. Error bars represent 2 SE. Abbreviations CCT = Coastal Cutthroat Trout, COHO = Coho Salmon, COT = Sculpins, Crayfish = Signal Crayfish, KOK = Kokanee, LMB = Largemouth Bass, LSS = Largescale Sucker, NPM = Northern Pikeminnow, RBT = Rainbow Trout, PS = Pumpkinseed Sunfish, Snail = Juga Snail, and TM = Tiger Muskie.

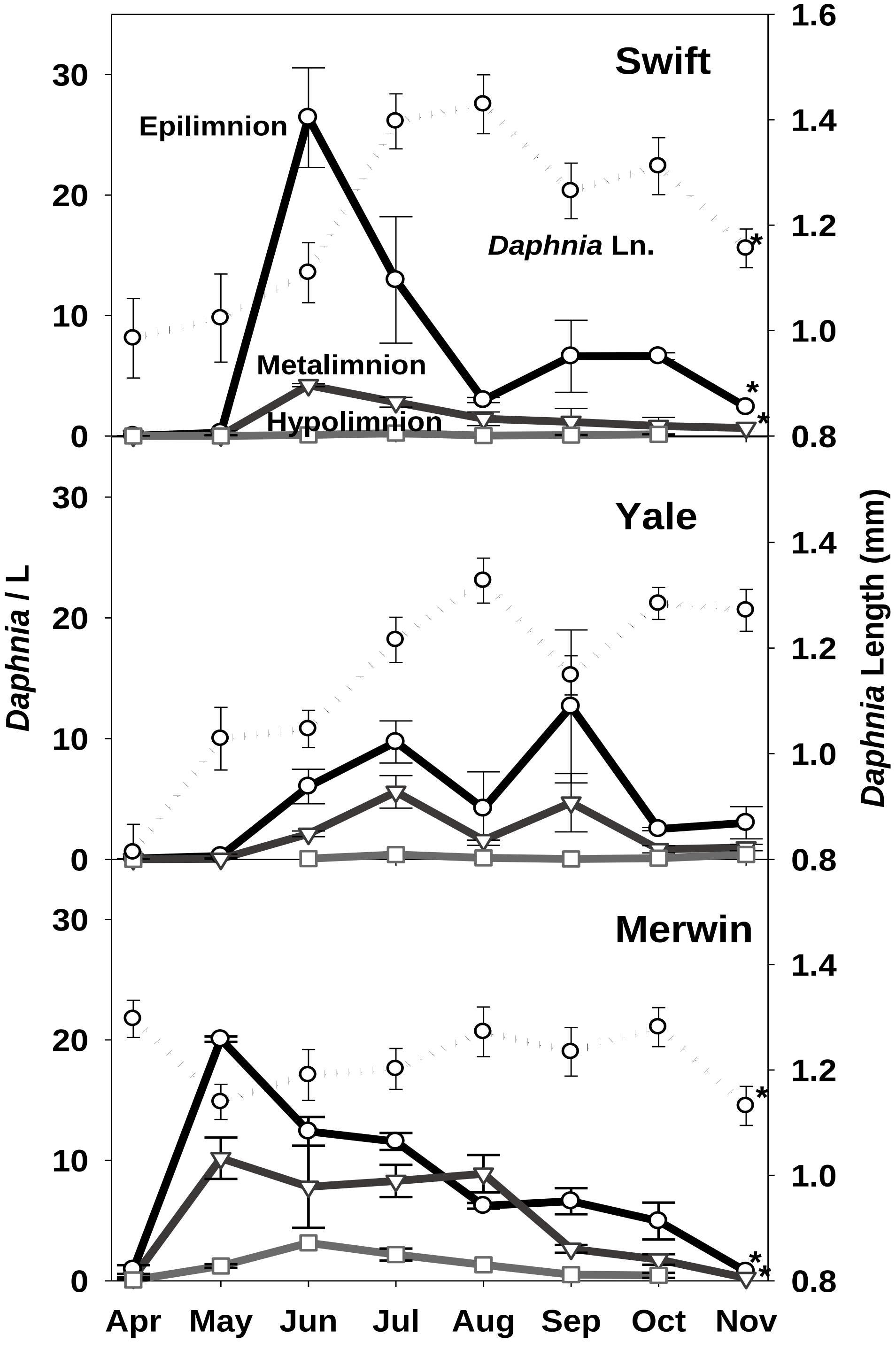

Figure 9. The average monthly densities of *Daphnia* (±1 SE) in Swift, Yale, and Merwin Reservoirs and the average length of *Daphnia* (±1 SE). *Data from the lower sampling site in Swift and Merwin Reservoirs collected in November 2013 were used to complete the growing season, as samples could not be collected in these reservoirs in November 2014.

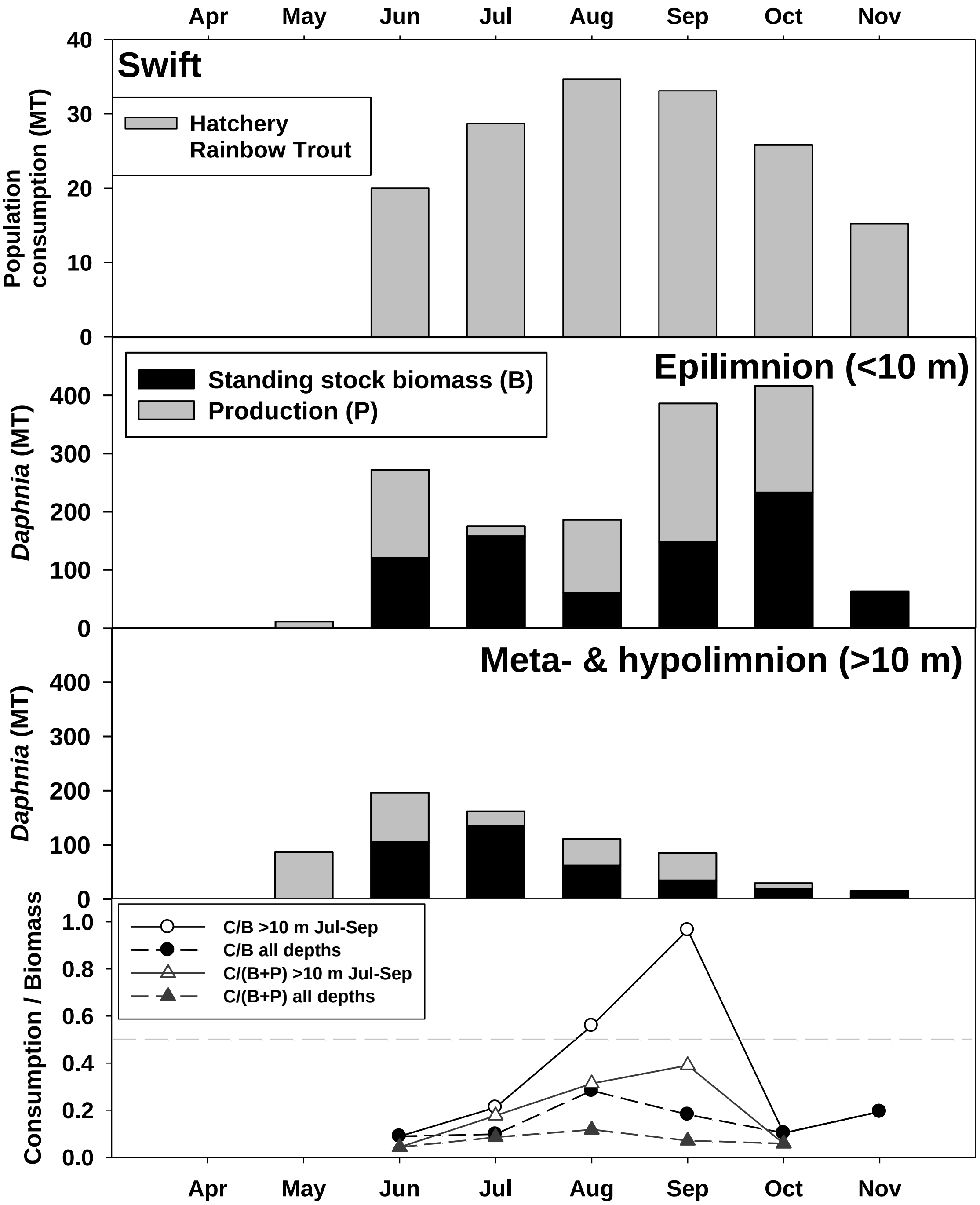

Figure 10. Top three panels: Monthly consumption demand of *Daphnia* by a cohort of hatchery reared Rainbow Trout and depth stratified *Daphnia* supply from April through November in Swift Reservoir. Bottom Panel: Ratio of consumption demand to prey supply for a range of prey supply scenarios. Dotted line represents 50% consumption over biomass ratio at which carrying capacity is reached.

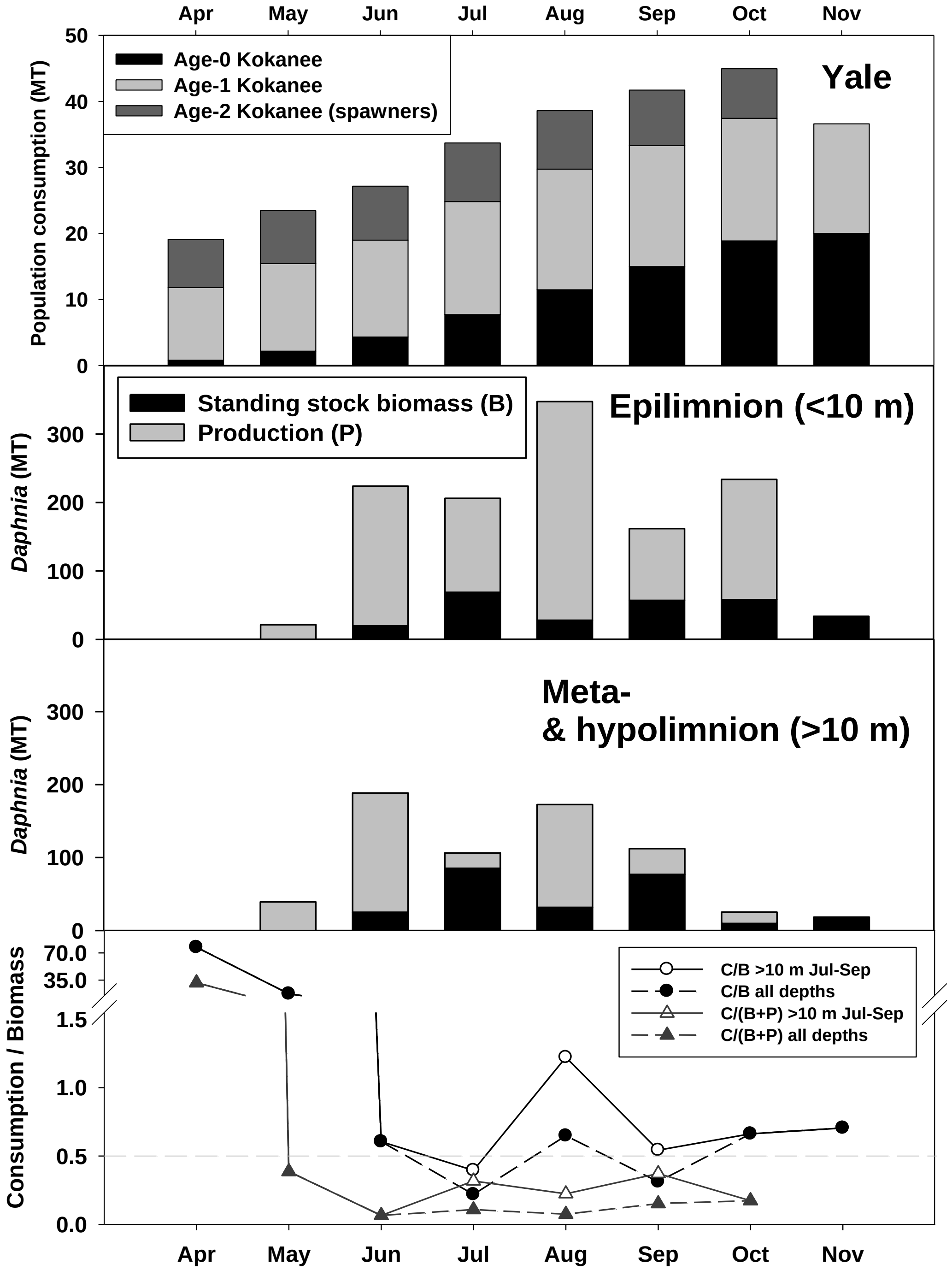

Figure 11. Top three panels: Monthly consumption demand of *Daphnia* by three age classes of Kokanee and depth stratified *Daphnia* supply from April through November in Yale Reservoir. Bottom Panel: Ratio of consumption demand to prey supply for a range of prey supply scenarios. Dotted line represents 50% consumption over biomass ratio at which carrying capacity is reached.

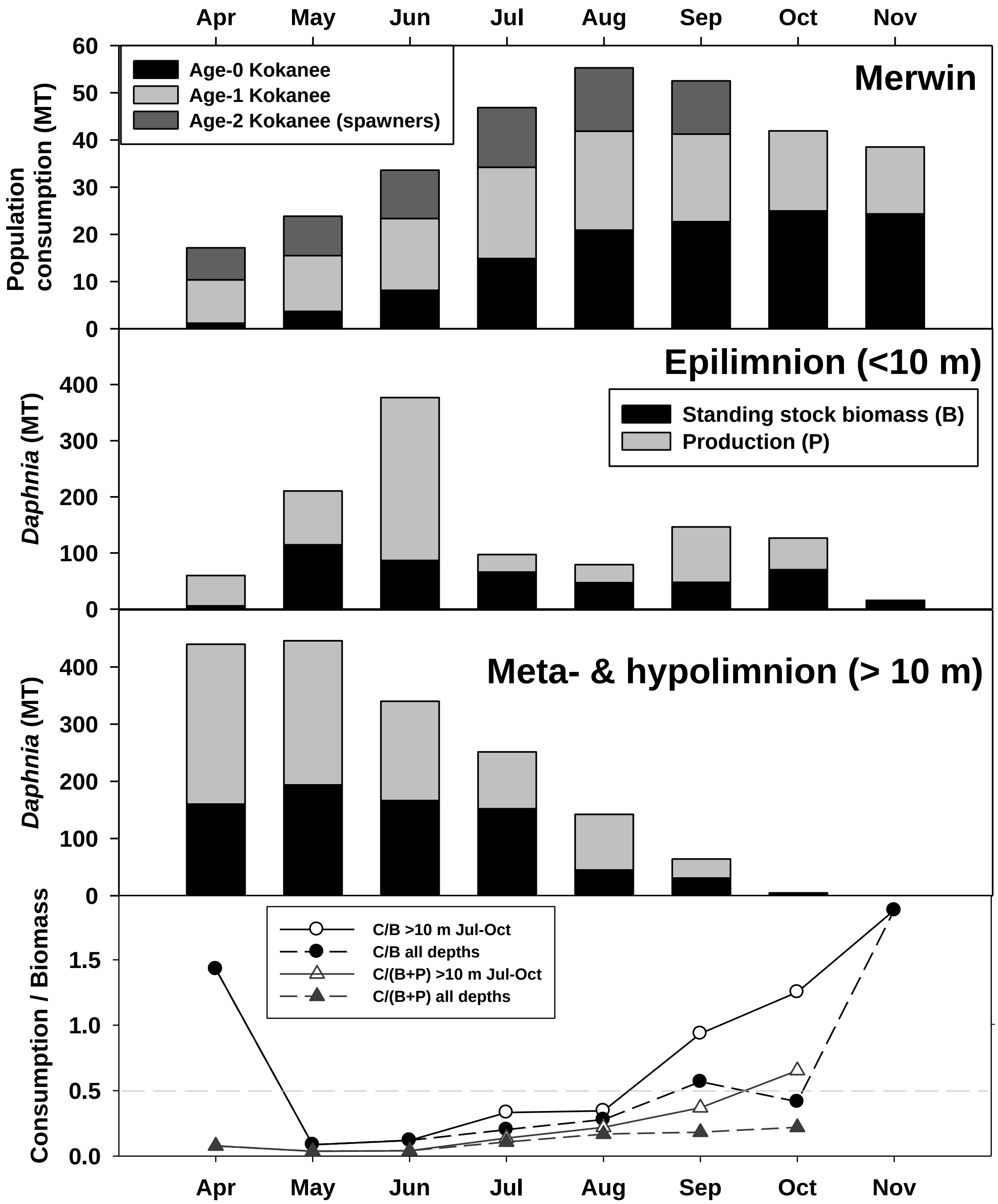

Figure 13. Top three panels: Monthly consumption demand of *Daphnia* by three age classes of Kokanee and depth stratified *Daphnia* supply from April through November in Merwin Reservoir. Bottom Panel: Ratio of consumption demand to prey supply for a range of prey supply scenarios. Dotted line represents 50% consumption over biomass ratio at which carrying capacity is reached.

Appendix

Table A1. Mean δ^{15}N and δ^{13}C stable isotope values for fish and invertebrates by location and size class. Abbreviations PS = Pumpkinseed Sunfish, CCT = Coastal Cutthroat Trout, RBT = Rainbow Trout, LMB = Largemouth Bass, LSS = Largescale Sucker, NPM = Northern Pikeminnow, SB = Three-spine Stickleback, and MWF = Mountain Whitefish.

	Spp.	Size Class (mm)	N	Mean δ ^{15}N	Minimum δ ^{15}N	Maximum δ ^{15}N	Mean δ ^{13}C	Minimum δ ^{13}C	Maximum δ ^{13}C
Merwin	PS	100–199	3	5.860	5.637	6.201	–25.895	–26.350	–25.592
	Clam	–	4	3.231	2.607	3.848	–28.656	–30.751	–25.627
	Coho	200–299	4	6.288	5.888	6.723	–26.236	–27.546	–24.334
	Copepods	–	1	3.160	3.160	3.160	–28.711	–28.711	–28.711
	Sculpin	<100	9	6.112	5.307	6.685	–25.386	–27.959	–21.971
		100–199	3	8.068	6.839	8.946	–23.354	–24.257	–22.855
	Crayfish	–	2	4.054	2.801	5.306	–21.718	–24.198	–19.238
	CCT	100–299	3	7.318	7.037	7.844	–26.639	–29.092	–23.817
	Daphnia	0	1	–0.758	–0.758	–0.758	–31.270	–31.270	–31.270
	Diptera	0	1	1.726	1.726	1.726	–26.537	–26.537	–26.537
	Hemiptera	0	1	1.194	1.194	1.194	–27.648	–27.648	–27.648
	Holopedium	0	1	0.695	0.695	0.695	–30.916	–30.916	–30.916
	RBT	<299	7	5.605	4.992	6.489	–24.342	–26.121	–22.133
		300–399	7	9.186	6.544	10.757	–20.956	–26.262	–17.692
		500–699	6	13.081	12.329	13.656	–17.658	–18.230	–17.177
	Kokanee	<399	9	6.423	5.232	7.573	–26.713	–28.186	–25.062
	LMB	300–499	2	9.084	8.585	9.582	–22.085	–22.768	–21.402
	LSS	<200	4	5.841	5.415	6.286	–24.051	–24.763	–23.791
		300–499	5	6.182	5.849	6.380	–27.943	–29.670	–25.710
	NPM	<200	9	5.451	4.639	6.963	–27.315	–29.245	–26.005
		200–299	6	6.519	6.179	7.626	–25.242	–25.543	–24.708
		300–399	5	8.640	7.353	9.627	–24.584	–26.729	–23.479
		400–599	9	9.348	8.278	10.048	–23.714	–24.899	–21.826
	Juga snail	–	4	2.576	1.993	3.135	–20.409	–22.691	–16.770
	Tiger Muskie	400–799	11	8.333	7.546	9.275	–24.513	–25.396	–23.345
		800–1099	9	9.608	8.902	10.236	–24.048	–25.041	–22.930
Yale	Bull Trout	300–399	2	7.923	7.913	7.933	–24.729	–26.582	–22.876
		400–799	11	9.385	8.844	10.164	–24.682	–27.557	–22.203
	Copepods	–	1	3.684	3.684	3.684	–31.088	–31.088	–31.088
	Sculpin	<100	5	6.189	5.285	7.603	–25.036	–28.558	–21.887
		100–199	1	7.057	7.057	7.057	–22.094	–22.094	–22.094

	Crayfish	–	2	3.037	2.568	3.507	–23.325	–26.952	–19.697
	CCT	200–399	7	7.499	5.706	8.549	–24.756	–27.164	–22.960
	Daphnia	–	2	0.463	–0.126	1.053	–31.221	–31.654	–30.789
	Holopedium	–	1	0.872	0.872	0.872	–31.094	–31.094	–31.094
	Plankton	–	1	1.034	1.034	1.034	–26.575	–26.575	–26.575
	Kokanee	<299	13	6.266	5.460	6.897	–30.441	–33.570	–27.435
	LSS	200	4	4.664	4.148	5.021	–21.376	–24.634	–19.008
		300	5	6.128	5.707	6.956	–26.099	–27.727	–24.416
	NPM	<200	8	4.753	4.207	5.263	–26.657	–29.247	–25.138
		200–299	6	6.304	5.640	6.988	–25.143	–25.543	–24.682
		300–399	6	8.083	7.431	9.427	–23.124	–26.712	–21.698
		400–599	4	8.564	7.962	9.356	–24.831	–26.950	–21.637
	RBT	200	4	6.095	5.182	7.708	–24.074	–26.922	–19.334
	SB	<100	5	6.334	4.580	7.355	–28.276	–30.050	–26.715
Swift	Bull Trout	100–299	4	8.618	7.146	11.898	–23.433	–24.877	–22.047
		300–699	16	10.417	8.664	11.846	–24.100	–27.718	–21.579
	caddisfly	–	1	–0.297	–0.297	–0.297	–24.516	–24.516	–24.516
	Chinook	100–299	7	5.504	4.817	7.126	–26.201	–27.380	
	Coho	<200	8	5.405	4.398	6.721	–25.534	–27.146	–23.786
		200–299	5	6.454	5.441	7.224	–26.336	–26.931	–25.486
	Copepods	–	1	3.675	3.675	3.675	–29.048	–29.048	–29.048
	Sculpin	<100	5	4.856	3.796	7.048	–25.573	–29.037	–22.757
		100–199	3	6.243	4.360	8.016	–25.588	–27.891	–23.361
	Crayfish	–	4	3.911	3.118	5.608	–23.728	–25.457	–22.432
	CTT	200–399	11	7.045	5.832	8.201	–24.368	–25.813	–22.616
	Daphnia	–	1	0.708	0.708	0.708	–28.709	–28.709	–28.709
	RBT	100–199	5	4.924	2.845	6.378	–24.982	–25.904	–23.550
		200–299	9	6.236	5.120	8.003	–25.191	–27.289	–23.040
		300–399	11	7.595	5.245	11.187	–23.379	–27.230	–19.048
		500–599	3	11.410	10.194	12.211	–18.278	–20.058	–17.073
	LSS	<500	8	4.584	3.563	6.652	–24.382	–25.928	–22.315
	Snails	–	1	2.415	2.415	2.415	–23.750	–23.750	–23.750
	MWF	200–399	4	5.387	4.921	5.844	–21.953	–22.420	–20.770
	SB	400	1	7.498	7.498	7.498	–20.548	–20.548	–20.548

Chapter 2 — Potential for predation on reintroduced anadromous salmonids in Merwin Reservoir on the North Fork Lewis River, Washington

Abstract

The suitability of reservoir habitat for rearing anadromous salmonids and potential interactions with resident fish should be evaluated explicitly when considering the feasibility of reintroductions above high–head dams. We evaluated the potential for predation on reintroduced anadromous salmonids in Merwin Reservoir on the Lewis River in Washington State under different scenarios of reservoir rearing or smolt migration. We characterized the role of the primary predator Northern Pikeminnow *Ptychocheilus oregonensis* in the reservoir food web using stable isotopes and stomach content analysis, quantified seasonal and size–dependent per capita predation using bioenergetics modeling, estimated their abundance using mark–recapture techniques, and combined these inputs to estimate size–structured, population–level predation rates on salmonids and other key prey. We used the resident age 0–1 Kokanee Salmon *Oncorhynchus nerka* as imperfect surrogates for reintroduced anadromous salmonids, because limnetic life stages of juvenile Chinook Salmon *O. tshawytscha* were expected to behave similar to Kokanee in reservoirs. We used the modeled predation impact on resident salmonids to infer likely predation on reintroduced anadromous salmonids under different reservoir use scenarios. Northern Pikeminnow ≥ 300 mm fork length were most piscivorous, but were disproportionately much less abundant than expected: 11,000 compared to an estimated 550,000 smaller (200–299 mm) much less piscivorous conspecifics. The estimated annual predation on Kokanee (in biomass) by a size structured unit of 1,000 Northern Pikeminnow ≥300 mm FL would be analogous to 16,000–40,000 age 0–1 spring Chinook Salmon rearing in Merwin Reservoir year–round, or 400–1,000 age–1 smolts migrating during April–June. Per–capita consumption of

salmonids by Northern Pikeminnow ≥200mm was very low, due in large part to spatial segregation during the summer and the skewed size distribution of the predator population.

Introduction

The construction of high–head dams on tributaries of the Columbia River in the 20th century blocked access by anadromous salmonids from parts of their historic range, contributing to significant declines in many populations. While some dams have been razed because adverse impacts on fish outweigh other societal contributions (Loomis 1996), other dams continue to provide valuable services such as renewable energy, irrigation, and flood control. A proposed solution to the dilemma between the benefits of high–head dams and harm to anadromous fish has been to reintroduce these species above the dams by providing active transport (trap–and–haul) around them. Reintroductions of anadromous salmonids above high–head dams using trap–and–haul are being proposed with increasing frequency as part of relicensing agreements with the Federal Energy Regulatory Commission and other regulatory agencies. Local extirpations of Pacific Salmon *Oncorhynchus spp.* due to dams are common, and reintroductions above these barriers can help conservation and enhancement efforts by making reservoir and tributary habitats available to anadromous salmonids in the upper portions of watersheds.

Habitats and food webs have been altered upstream of dams by creation of storage reservoirs with new hybrid communities of resident fishes and altered thermal and flow regimes. The quality and availability of food and habitat and interactions with resident fish could either undermine or support a successful reintroduction by influencing the survival, growth, behavior, and distribution of reintroduced anadromous fish (Pess et al. 2011; Carey et al 2012). Therefore, understanding these factors is crucial for determining the feasibility of reintroductions (Anderson et al. 2014).

At a minimum, reservoir habitat will act as a migration corridor for smolts, but juvenile anadromous fish produced in tributaries may also use the reservoirs extensively for rearing. Sockeye Salmon *O. nerka* typically require lentic habitat for rearing, whereas other species of Pacific salmon utilize lentic habitats to varying degrees. Of these, juvenile Chinook Salmon *O. tshawytscha* most consistently rear in lentic habitats, as in North Fork Reservoir on the Clackamas River, reservoirs on the upper Willamette River, Snake River, Columbia River, Lake Washington, and other lakes and reservoirs (Connor et al. 2005; Koehler et al. 2006; Lowery and Beauchamp 2010; Naiman et al. 2012; Monzyk et al. 2013). Juvenile Coho Salmon *O. kisutch* sometimes rear in lentic habitats such as in Cultus Lake, 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 Trout primarily use lotic habitat for feeding and rearing (e.g. Everest and Chapman 1972; Bisson et al. 1988; Lowery and Beauchamp 2010), whereas adfluvial Rainbow Trout *O. mykiss* commonly rear in lakes. It is reasonable to assume that juveniles from one or more species of anadromous salmonids would use reservoir habitat for rearing. Thus, determining whether the reservoir is favorable for growth and survival, and evaluating factors (e.g. thermal structure and predation) that could limit these processes is an important step when planning new reintroductions above dams.

Merwin Reservoir, on the North Fork Lewis River in Washington State, is one such reservoir being evaluated for potential reintroduction. The operating utility, PacifiCorp Energy, proposed the reintroduction of Steelhead Trout, Coho Salmon, and spring Chinook Salmon, which were extirpated from the upper watershed by the construction of Merwin Dam in 1931. Beginning in 2010, a reintroduction of the same suite of species, using trap–and–haul to pass adults above the dams, was implemented in Swift Reservoir, located upstream of Merwin

Reservoir on the North Fork Lewis River (Figure 1). A floating surface collector above Swift Dam went into operation in spring 2012 to trap outmigrating smolts for transport and release below Merwin Dam, and a similar strategy is being considered for Merwin Reservoir if reintroductions seem feasible after evaluating the production potential and ecological constraints on tributary and reservoir rearing. Successful reintroductions of salmon in these reservoirs and their tributaries would be important for broader conservation efforts of anadromous fish in the Lewis River basin and Columbia River basin as a whole.

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 identified as the most abundant predator of juvenile salmon in Merwin Reservoir during that study with a mark–recapture estimate of 350,000 ≥ 200 mm fork length (FL) in 1961, but the population has not been assessed since. Additionally, the Washington Department of Fish and Wildlife began stocking approximately 1,300 Tiger Muskellunge *Esox lucius x 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 formally evaluated. The duration and magnitude of predation on salmonids by Northern Pikeminnow in Merwin Reservoir is also currently unknown. The primary objective of this study was to estimate the magnitude of predation mortality on current resident salmonids and project potential predation impacts on reintroduced juvenile anadromous salmonids in the future. A secondary objective was to evaluate the impact of Tiger Muskellunge on the Northern Pikeminnow and salmonid populations. This information will ultimately be integrated with a concurrent study evaluating the potential production in tributary habitat to develop a more complete evaluation of the feasibility of the proposed reintroduction and to calibrate expectations for reintroduction success.

Methods

Site description — Merwin Reservoir is located in southwest Washington on the North Fork Lewis River, a tributary of the lower Columbia River at river km 140 (Figure 1). It was created by the construction of Merwin Dam in 1931 for hydroelectric power generation. The oligotrophic reservoir is approximately 23.3 km long (PacifiCorp, 2004), with a maximum depth of 73 m and a mean depth of 31 m (PacifiCorp, unpublished data), a mean Secchi depth of roughly 5 m and < 0.02 mg/l total phosphorus (PacifiCorp and Cowlitz 2004a; Table 1). 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. Surveys suggest that a total of 6 km of stream habitat is accessible to anadromous fish in tributaries connected to Merwin Reservoir (Al–Chokhachy et al. 2014).

Catches in nets and other sampling gears set in Merwin Reservoir were dominated by Northern Pikeminnow, Largescale Suckers *Catostomus macrocheilus*, Sculpins *Cottus spp*., and Pumpkinseed Sunfish *Lepomis gibbosus*, but Kokanee *O. nerka,* Cutthroat Trout *O. clarki clarki,* Rainbow Trout *O. mykiss*, Coho Salmon, Tiger Muskellunge, Three-spine Stickleback *Gasterosteus acouleatus*, and Largemouth Bass *Micropterus salmoides* were present at moderate to low levels (Table 2). The Kokanee population is supplemented annually with approximately 45,000 hatchery fingerlings stocked in October and 48,000 yearlings stocked in spring (PacifiCorp and Cowlitz 2014). Natural production of Kokanee from Merwin Reservoir tributaries is considered minimal, and entrainment from upstream Yale Reservoir is considered the primary source of recruitment of naturally produced Kokanee (PacifiCorp and Cowlitz 2004b).

Approach — We characterized the temporal–spatial dimensions of the thermal environment, and the abundance, distribution, size– and age–structure, and diet of Northern Pikeminnow and Tiger Muskellunge in Merwin Reservoir. We examined the food web structure of Merwin Reservoir through stable isotope analysis and higher–resolution data on seasonal and size–specific diet composition by these piscivores to identify potential prey of piscivorous fishes and examine their ontogenetic shifts in predatory behavior. These data informed bioenergetics model simulations constructed to estimate the seasonal and size–specific consumption rates and predation impact of Northern Pikeminnow on resident salmonids and alternative prey fish species, and of Tiger Muskellunge on Northern Pikeminnow and salmonids. We used the results from the bioenergetics simulations to infer the likely predation impact by Northern Pikeminnow on reintroduced anadromous salmonids under different scenarios regarding rearing in versus migrating through the reservoir by sub-yearling and yearling fish. We also used the results of the bioenergetics simulations to evaluate the cannibalism of smaller Northern Pikeminnow and predation of Northern Pikeminnow by Tiger Muskellunge.

Fish sampling — Fish were sampled in June, late July, and November of 2013 to obtain biological samples, and characterize seasonal depth distribution and size structure. Paired small mesh (2.5, 3.2, 3.8, 5.1, 6.4, and 7.6 cm stretched mesh) and large mesh (8.9, 10.2, 11.4, 12.7, and 15.2 cm stretched mesh) sinking gill nets of monofilament construction 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. Additional samples were gathered opportunistically during the mark–recapture study and other targeted sampling in 2013 and 2014.

We identified, sexed, and counted fish by species and recorded fork lengths (FL; mm) and wet weights (W; g) in the field. Whole dissected stomachs or stomach contents, scales from the preferred 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 and analysis in the laboratory. Fish were handled and released or euthanized according to UW–IACUC protocol #3286–21.

Northern Pikeminnow mark–recapture — Northern Pikeminnow ≥ 200 mm were tagged with 2.54–cm individually numbered Floy© tags. In 2013, we captured and tagged 1,123 fish using short–duration (30 – 120 min) gill net sets (5.1, 6.4, and 7.6 cm stretched mesh) near shore. Catch rates were greatest at dusk, so we preferentially netted at these times. Our initial goal was to tag and release 2,000–5,000 fish during late spring and early summer; however, difficulty in capturing sufficient numbers necessitated an extended tagging period over two years: June–August 2013 and May–July 2014. In 2014, we exclusively used Merwin traps (Hamilton et al. 1970; Lynch 1993) to capture fish, and tagged an additional 956 individuals. Merwin traps were most effective during the peak of the Northern Pikeminnow spawning migration in June. Specifically, the trap set at Cresap Creek (Figure 1) captured approximately 95% of all fish tagged in 2014. A total of 98 tagged Northern Pikeminnow were held in net pens for 48 h to evaluate short–term tagging mortality and tag retention on Jul 30–Aug 3, 2013 (Epilimnion = 22 °C). All fish survived for 48 h, supporting the assumption that tagging mortality was negligible.

After tagged fish were allowed time to redistribute in the reservoir, a total of 2,470 Northern Pikeminnow were captured, measured, and examined for tags in August and September 2014 with small mesh (5.1, 6.4, 7.6 cm stretched mesh) and large mesh (8.9, 10.2, 11.4, 12.7, and 15.2 cm stretched mesh) gill nets set for 24 h methodically around the perimeter of the reservoir.

An additional 185 individuals were captured by a separate investigator from Meridian Environmental Inc. using an electrofishing boat in the inlet to the reservoir in late July–November 2014. Thirteen fish were recaptured, four from the 2013 tagging period, and nine from 2014. We hoped that fish captured and tagged during their spawning migration in June would have redistributed throughout the reservoir by August; however, most recaptured individuals were caught within the same quadrant of the reservoir where they were tagged. This suggested that either there was not a major spawning migration to the upper part of the reservoir, or the fish had not redistributed by August.

Mark–recapture analysis — We explored multiple models and ad–hoc approaches to estimate the abundance of Northern Pikeminnow ≥ 200 mm, given potential biases that emerged during the recapture phase of the study. First, the sizes of recaptured fish were biased toward ≥300 mm individuals, which was likely the result of greater natural mortality and gill net selectivity against 200–299 mm fish (Beamesderfer and Rieman 1988). Therefore, we estimated the abundance of the 200–299 mm population of Northern Pikeminnow and the population ≥ 300 mm separately. Second, the majority of tags were recovered within the upper quadrant of the reservoir, where most were initially released, suggesting that tagged fish were not randomly mixed with the rest of the population. Consequently, we estimated abundance in the upper quadrant of the reservoir alone, in addition to our analysis of the entire reservoir as a whole. We divided the reservoir into quadrants based on geographic features such as points and bends (Figure 1), then proportionally expanded estimates from the upper quadrant (# 1 on map) to the remaining quadrants based on relative catch per unit effort (CPUE) in gill nets and the shoreline length of each quadrant.

Ultimately, the least biased and most precise abundance estimate used the Chapman estimator (Chapman 1948, Seber 1982) for Northern Pikeminnow ≥ 300 mm in the upper quadrant of the reservoir, expanded based on length and CPUE in the other quadrants of the reservoir. We used just the upper quadrant of the reservoir for our estimate because four of six recovered tags were captured in this quadrant. All six recovered tags occurred within the same quadrant where they were released, suggesting considerable site fidelity for this size class. The Chapman estimator was used because mortality was expected to be negligible for these large individuals during the 13 month study.

We estimated the abundance of the smaller 200–299 mm Northern Pikeminnow using the POPAN formulation of the Jolly–Seber model in the program MARK (White and Burnham 1999), based on encounters from the entire reservoir. We used the POPAN estimator because we expected significant mortality for these smaller fish over the 13–month study. We used a fixed annual survival rate (39.7%) based on a catch–curve analysis (Miranda and Bettoli 2007) which had an AICc of 138.4; however, the model that fit survival (12.9%) to the mark–recapture data had an AICc of 143.2 (Table A1). Data from the entire reservoir was used because one of the seven recovered tags was recovered on the other side of the reservoir from where it was released. This suggested that tagged fish of this size class had mixed between regions.

Northern Pikeminnow size distribution — The length frequency distribution of Northern Pikeminnow captured in gill nets was adjusted for effort by mesh size, size–dependent encounter probability (Spangler and Collins 1991), and gill–net size–selectivity (Hansen et al. 1997) to estimate an unbiased size distribution. Only catches from mesh sizes 5.1 cm (2–inch stretch mesh) and above were used, as these meshes contributed the majority of the effort and catch of fish ≥ 200 mm. We only adjusted catches from Merwin traps for the probability of encounter, as these large nets allow for equal retention of fish across a wide range of sizes. The adjusted length distribution from the Merwin traps were averaged with those from gill nets, and separate size distributions were created for male and female Northern Pikeminnow to account for sex–specific differences in growth and survival. Chi–square (χ^2) tests were used to compare the adjusted and unadjusted length distributions to examine the degree of size selection by each gear. We also compared length distributions between this study and the 1958–1963 study (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, and thus changed predation risk to juvenile salmonids. Length frequency data from both study periods were adjusted for gear selectivity.

Tiger Muskellunge survival and abundance — Using stocking records and a catch–curve analysis, we constructed an age–structured population estimate. Records of the number, size, and release dates of Tiger Muskellunge in Lake Merwin from 1995 to 2013 were provided by WDFW. Since 2004, fish have been reared at Ringold Springs Hatchery at a constant water temperature of approximately 16°C (Richard French, WDFW, *personal communication*), and an average of 1,340 fish (range = 500–2,220) have been stocked at age–1 in April–June. The large size at which Tiger Muskellunge are stocked (range: 140 – 348 mm, mean = 302 mm, SE = 12.1 mm), and the cool surface water temperatures and seemingly abundant forage base of small northern pikeminnow in spring suggest that stocking mortality is negligible.

Annual survival for age 1–10 Tiger Muskellunge (the range of ages observed) was estimated with a catch–curve analysis and is likely a function of natural and overwinter mortality. To estimate annual survival, we used cleithra–based ages and the observed size distribution to estimate a population age structure. We then used a catch–curve analysis (Miranda and Bettoli 2007) to estimate an annual survival rate based on the estimated age–structure of the population. Annual survival was estimate to be 71% for aged 1–10 fish in Lake Merwin. The minimum size for legal retention of Tiger Muskellunge in Merwin Reservoir was above the maximum size observed, therefore the majority of angling was catch–and–release. Post release survival approached 100% in Canadian rivers using a variety of handling procedures (Landsman et al. 2011). Thus, fishing pressure does not significantly reduce survival rates.

Bioenergetics model inputs — Bioenergetics models are energy balance equations that operate on a daily time–step and estimate the feeding rate (% of maximum theoretical consumption; % C_{max}) and the consumption rate (g of prey/d) needed to achieve the growth observed by different age classes of consumers over the time interval of the simulations. 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). We collected field data on growth, seasonal diet composition, and thermal experience (daily temperature experienced by the consumer) to construct a set of model inputs specific to Northern Pikeminnow and Tiger Muskellunge in Merwin Reservoir.

Thermal experience and depth distribution — Seasonal thermal experience 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 (Table 3; Beauchamp et al. 2007). Temperature profiles were recorded monthly from April to November at 1–meter intervals from the surface to 30 m and every 2 m thereafter down to 60 m at two limnology stations located at 1/3 and 2/3 of the length of the reservoir (Figure 1). Depth–specific measurements were averaged between stations in each month. Temperature profiles recorded by PacifiCorp in November 1999, January 2000, and March 2000 in the lower half of the reservoir were used to fill data gaps and complete the characterization of the seasonal thermal regime (PacifiCorp and Cowlitz 2004a). Relative catch at different depths in different seasons was then used to calculate the average daily thermal experience for each species and size class of consumer.

Stable isotope analysis — Stable isotopes provide an integrative signal of diet over several months to a year, 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 and thermal experience. We examined $\delta^{13}C$ and $\delta^{15}N$ for a range of sizes of Northern Pikeminnow and Tiger Muskellunge and representative samples of benthic invertebrates, terrestrial insects, zooplankton, zooplanktivores, pelagic– and benthic–feeding fishes, and piscivores (Table A2; Vander Zanden and Rasmussen 1999; McIntyre et al. 2006). Fin tissue from fish, muscle tissue from clams and crayfish, and whole bodies of insects were placed on ice in the field and then frozen within 12 h for storage. Samples were dried at 60 °C for 48 h, homogenized with mortar and pestle, and 0.4–0.6 mg of material was weighed in aluminum capsules for analysis. Isotope samples were analyzed by the University of Washington IsoLab using a Costech Elemental Analyzer, Conflo III, MAT253 for continuous flow based measurement of solid organic material. 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 (Table 4) and Tiger Muskellunge (Table 5) as inputs for the bioenergetics model. Stomach contents were identified under a dissecting microscope to species for prey fish and to order for invertebrates. Lengths of prey fish were measured or reconstructed from diagnostic bones (Hansel et al. 1988). We calculated diet proportions by blotted wet weight (Chipps and Garvey 2007) for two size classes of Northern Pikeminnow (200–299 mm and ≥ 300 mm), the breakpoint reflecting a transition to piscivory based on $\delta^{15}N$ signatures. 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 non–empty stomachs obtained. The energy densities of prey items were taken from literature values (Table 6).

Age and growth of Northern Pikeminnow — We measured the age and growth of Northern Pikeminnow from scales to obtain annual growth increments for different age–classes in the bioenergetics model (Table 7). Opercles were also analyzed for a subset of individuals to corroborate the scale–based ages. Scales were measured along a transect 20° off the scale's anterior–posterior axis from the center of the focus out to the edge of each annulus and additionally to the margin of the scale using a dissecting microscope with a digital camera and Image Pro© analysis software. 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 (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 ($\chi^2 = 12.88$, DF = 3, $P < 0.005$). The greatest scale–based age observed was 14 years (431 mm male and 542 mm female). While scales often underestimate ages of Northern Pikeminnow > 350 mm (Takata et al. 2007), our analysis of opercles helped reduce this bias by identifying older annuli on >350 mm fish. The von Bertalanffy growth parameters fit for females were $L_\infty = 786.64$ mm, K = 0.0665, and $t_0 = –2.0139$ (N = 34). 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 weight–at–age using length–weight relationships developed for Northern Pikeminnow in Merwin Reservoir. Separate relationships were developed for individuals < 300 mm and ≥ 300 mm due to the inability of a single power function to fit length and weight measurements over the entire range of FL’s observed. The FL to W relationship for Northern Pikeminnow < 300 mm was (N = 2,941, range: 34–299 mm; $R^2 =$ 0.972, $P < 0.001$):

$$W = 0.000012 * FL^{2.979}$$

The relationship for individuals ≥ 300 mm was (N = 354, range: 300–574 mm; $R^2 =$ 0.974, $P < 0.001$):

$$W = 0.0000015 * FL^{3.348}$$

Spawning losses were calculated separately for each sex by subtracting the average gonadosomatic index (100 * gonad mass/body mass) of spent from ripe fish in the spring. Spawning losses were then 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 males age 3–14, 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 consumption were determined with age–to–length and weight–length relationships (Table 8). Age was determined using standard cleithra aging procedures for a parent species, Northern Pike *Esox luscious*, of Tiger Muskellunge (Euchner, 1988). Fish are routinely implanted with blank wire tags in various locations on their bodies that indicated their brood year, and a number of individuals were aged based on the location of these tags to corroborate cleithra–based ages. We used the proportional linear relationship

$$TLi = (TL - 1.41)(CLi/CL) + 1.41$$

derived for the other parent species, Muskellunge *Esox masquinongy* (Harrison and Hadley 1979), where total length at age i (TLi) is back calculated based on measurements from the origin of the cleithra to each annuli i (CLi), the origin to edge of the cleithra (CL), and total length at capture (TL). A von Bertalanffy growth curve was fit to total length at age ($K = 0.389$, $L_\infty = 1023.9$, $t_0 = 0.00$). Total Length (TL, mm) 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 weight at–age with the equation ($N = 62$, range: 324–975 mm, $R^2 = 0.988$, $P < 0.001$)

$$W = 0.00000037 * FL^{3.479}$$

Bioenergetics modeling simulations of seasonal predation — The Wisconsin bioenergetics model (Hanson et al. 1997) parameterized for Northern Pikeminnow (Petersen and Ward 1999) was used to estimate seasonal consumption demand. The bioenergetics model fit the daily per–capita consumption, starting April 1st, needed to satisfy the observed growth of an average Northern Pikeminnow from each age class and sex over an annual cycle. Age–frequency distributions within each size class were developed from the unbiased size distribution estimated above and an age–length key (Isely and Grabowski 2007). Per–capita consumption demand was expanded to separate age–structured populations of 1,000 Northern Pikeminnow of the 200–299 mm and ≥300 mm size classes, assuming an even sex ratio. We then used estimates of consumption of resident salmonids to gauge potential predation on reintroduced anadromous salmonids under different reservoir use scenarios (i.e., rearing in versus migrating through the reservoir).

Estimating predation on reintroduced salmon — In order to estimate maximum potential predation on reintroduced anadromous salmonids, we assumed that all observed predation on resident Kokanee would switch to anadromous fish once they were reintroduced. Thus the monthly biomass of Kokanee that was consumed from 1 April to 30 March based on bioenergetics simulations was divided by the estimated monthly weight of an age–0 Chinook Salmon that adopted a year–round reservoir rearing strategy to estimate how many individuals could be lost to predation. We divided Northern Pikeminnow's monthly consumption of salmonid biomass by the monthly mass of individual age–0 stream–type Chinook Salmon estimated using a bioenergetics simulation. For the bioenergetics simulation of age–0 Chinook Salmon growth in the reservoir, we assumed that Kokanee and sub-yearling stream–type Chinook Salmon used similar depth distributions during thermally–stratified periods and would therefore share similar thermal experiences in reservoirs. This assumption, based on observations of Chinook Salmon in North Fork Reservoir on the Clackamas River (Lowery and Beauchamp 2010), also suggests similar overlap with predatory Northern Pikeminnow, supporting our use of Kokanee as a surrogate to estimate predation on juvenile anadromous salmonids. For the bioenergetics simulation of age–0 Chinook in the reservoir, we assumed a diet of zooplankton and insects, and a feeding rate of 93% C_{max}, as informed by observations of age–1 Chinook Salmon smolts that residualized in Swift Reservoir (also on the North Fork Lewis River) following releases in 2013. Information on the diet and feeding rate of age–0 Chinook salmon in Swift Reservoir was not available. Fish in this simulation grew from 0.36 g (35 mm) on 1 April to 45 g (155 mm) on 15 November, after which their mass was held constant through 30 March to simulate reduced prey supply and growth during winter. The mass that smolts achieved in this simulation was similar to the upper end of the length distribution of smolts outmigrating from the

Columbia River that survived at least 30 d in the marine environment (Tomaro et al 2012). We also simulated the magnitude of predation on reservoir–rearing Chinook Salmon that achieved a mass of only 18 g (~120 mm), at the lower end of the length distribution of 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 age–1 smolts migrating through Merwin Reservoir.

Some juvenile stream–type Chinook Salmon smolts might only use the reservoir as a migration corridor after rearing in tributaries. Therefore, we estimated potential predation on smolts traversing the reservoir to evaluate the impact of Northern Pikeminnow on their survival during the spring outmigration period. As before, our estimate of population–level consumption demand of Kokanee Salmon by Northern Pikeminnow was divided by the mass of individual stream–type Chinook Salmon. However, to estimate predation on smolts, we restricted the simulation to April through June, spanning the months for peak outmigration (PacifiCorp and Cowlitz 2004b). We used the same potential average smolt sizes (18 and 45 g), which were held constant for the three month simulations. Unlike in the reservoirs on the mainstem Columbia River, there is no tailrace area in Merwin Reservoir where disoriented salmon smolts would concentrate and provide easy access for Northern Pikeminnow (e.g. Rieman et al. 1991), so we did not simulate Northern Pikeminnow feeding at an elevated rate in response to a smolt outmigration.

These estimates of predation on age–0 or age–1 Chinook Salmon represent the maximum potential predation on either age class, because the same population–level consumption by Northern Pikeminnow was used to estimate losses in both scenarios. However, we expect that this overall consumption rate of salmonids by Northern Pikeminnow 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.

We calculated predation rates for size–structured population units of 1,000 predators for each of the two size classes of Northern Pikeminnow rather than for the entire populations, given the uncertainty surrounding our population abundance estimates. These estimates contain all the major variability related to seasonal and size–specific diet, consumption rates, and relative abundance of each size/age class. These estimates of predation by size–structured units of 1,000 predators can be multiplied by however many thousands of predators of that size range 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 used as inputs in a bioenergetics model (Bevelhimer et. al. 1985) coded in Microsoft Excel to determine annual consumption rates for each age class of Tiger Muskellunge. Individual consumption demands were then expanded by the respective abundance estimates of each age–class to determine the total consumption by the population.

We used the biomass of Northern Pikeminnow consumed by Tiger Muskellunge estimated with bioenergetics combined with the lengths of Northern Pikeminnow found in stomachs to estimate the number and size distribution of prey consumed by the predator population. For age–1 and age 2–10 predator size classes, we converted the lengths of Northern Pikeminnow found in Tiger Muskellunge diets to masses with a weight–length regression. We then used the masses of individual prey fish and the estimates of consumption demand to calculate how many of each size class of Northern Pikeminnow were consumed by each size class of Tiger Muskellunge.

Results

Seasonal Distribution and Thermal Experience of Northern Pikeminnow — The epilimnion was approximately 8 m deep, the metalimnion ranged from roughly 8–18 m, and the hypolimnion was 18 m and deeper (Figure 2). Epilimnetic temperatures began at 14–16°C in May and peaked at 22–24°C in July and August. The hypolimnion warmed from 5–6°C in April to 15–18°C in October.

The depth–distribution of Northern Pikeminnow varied by season. Most Northern Pikeminnow and especially those ≥ 300 mm occupied warmer surface waters nearshore in 0–15 m depths during thermally stratified periods in June–September, but were deeper during isothermal conditions in November (Figures 2 and 3). The CPUE of the larger fish was significantly higher in 0–15 m depths (4.8 fish/net) than deeper (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 (1.5 fish/net), although this difference was not significant (two–sided t–test: t = 1.89, DF = 3, $P = 0.155$). The CPUE of Northern Pikeminnow 200–299 mm was also significantly higher at 0–15 m depths (24.3 fish/net), but a sizeable number also occupied 15–30 m (13.4 fish/net) during stratification (two–sided t–test: DF = 14, $t = 3.42$, $P = 0.004$). Northern Pikeminnow 200–299 mm exhibited the same distribution pattern as fish ≥ 300 mm in November, and their CPUE in 16–30 m depths (15 fish/net) was also not significantly higher than in 0–15 m (10.4 fish/net) (two–sided t–test: DF = 3, $t = 0.65$, $P = 0.561$). Tiger muskellunge remained in the epilimnion in spring–fall similarly to large Northern Pikeminnow.

The density of Northern Pikeminnow was greater in the lower half of the reservoir (quadrants 3–4) in summer based on CPUE. Although not significant, the CPUE of Northern Pikeminnow ≥300 mm in gill nets was greater in the lower half (6 fish/net) than the upper half of the reservoir (3.1 fish/net) during the recapture phase of the mark–recapture study in August–September 2014 (two–sided t–test; DF = 6, $t = 2.08$, $P = 0.083$). The CPUE of 200–299 mm Northern Pikeminnow during this recapture effort was also significantly higher in the lower half of the reservoir (27.1 fish/net) than the upper half (17.8 fish/net; two–sided t–test; DF = 58, $t = 2.79$, $P = 0.007$). This pattern suggests that Northern Pikeminnow redistributed to the lower half of the reservoir by August after spawning in Canyon Creek (at the top of the reservoir; Figure 1), or a segment also spawned near tributaries in the lower reservoir as also observed by Hamilton et al. (1970).

Stable isotopes — Northern Pikeminnow became increasingly piscivorous and reliant on benthically derived energy with increasing 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 ≥ 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 bentho–littorally derived carbon, and increased in trophic level steadily throughout their lives (Figure 5). Tiger Muskellunge increased by nearly one trophic level (typically represented by a ~3.4‰ increase in δ^{15}N [Minagawa and Wada 1984, Hussey et al. 2014]) over the range of 450–1,050 mm FL (Figure 4). Thus stable isotopes suggest 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, with an increasing reliance on prey fish at larger sizes, 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 4). Diets of the ≥300 mm Northern Pikeminnow 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 increasing during fall, 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 by Northern Pikeminnow 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. Six 200–325 mm Kokanee were observed in ≥ 400 mm Northern Pikeminnow. As prey, the average FL of Northern Pikeminnow eaten by 300–399 mm cannibals 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 Sunfish, Signal Crayfish, and aquatic insects represented smaller proportions (Table 5). Only one salmonid (FL = 451 mm) was found in a Tiger Muskellunge's stomach, a 920 mm fish captured in September when Kokanee Salmon were using the littoral zone as a spawning–migration corridor. Tiger Muskellunge consumed a wide size range of Northern Pikeminnow (57–394 mm) (Figure 6). The majority of prey fish were approximately 40% of their consumers' fork lengths, but a significant number of Northern Pikeminnow were also <20% of the predators' lengths. Age–1 Tiger Muskellunge (FL > 300 mm) began feeding on Northern Pikeminnow ≥ 200 mm. The mean fork length of Northern Pikeminnow consumed was not significantly different between age–1 (152 ± 49 mm [mean ± SD]) and ages 2–10 Tiger Muskellunge (195 ± 97 mm) (t–test: DF = 19, $T = -1.354$, $P = 0.192$). The mean fork length 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: $F = 0.087$, $P = 0.917$, DF = 21).

Size distribution — The length frequency distributions of male and female Northern Pikeminnow were skewed toward smaller (200–299 mm) individuals, and exhibited a decrease in modal FL from 1958–1963 to 2013–2014 (Figure 7). Fish 200–299 mm made up 83% of the population of ≥200 mm Northern Pikeminnow in the present study. The adjusted length distribution was significantly different than the unadjusted distribution for fish captured in gill nets ($\chi^2 = 336$, DF = 224 $P = 0.003$), but not in Merwin traps ($\chi^2 = 456$, DF = 418 $P = 0.097$), suggesting that the degree of selectivity was greater for gill nets (Figure A1). Males in the present study were significantly smaller on average than in the historic study ($\chi^2 = 192$, DF = 80 $P < 0.001$) as were females ($\chi^2 = 336$, DF = 224, $P < 0.001$), whereas the current female size structure was significantly larger than males.

Mark recapture — Estimates of Northern Pikeminnow abundance (Appendix Table A1) were imprecise due to the relatively few recaptures (<1%). It was difficult to estimate the abundance of fish because they were only vulnerable to capture in certain locations and exhibited considerable site fidelity, eliminating much of the mixing of marked and unmarked fish necessary for accurate estimation in this type of study design. The estimate of the fully piscivorous ≥ 300 mm Northern Pikeminnow was 11,240 fish (95% CI: 3,730–39,880), and 544,259 (95% CI: 190,609–1,554,062) 200–299 mm Northern Pikeminnow. This abundance estimate of smaller Northern Pikeminnow was roughly 50 times greater than the abundance of ≥ 300 mm fish whereas the observed size distribution of the population suggests that this ratio should be only approximately six times greater. This disagreement suggests some bias in the estimates of the population size distribution or abundance.

Tiger Muskellunge Abundance — The population abundance of Tiger Muskellunge based on the 71% annual survival rate was 5,488 fish. We expanded individual consumption demands by the population abundance estimate as well as calculating predation by a size–structured population of 1,000 Tiger Muskellunge for comparison with Northern Pikeminnow.

Population–level consumption demand of Northern Pikeminnow — Total monthly consumption demand by Northern Pikeminnow on salmonids and other fish was highly influenced by the size structure and abundance of the population, as well as the thermal regime, which influenced metabolic rates and seasonal diet compositions. Overall consumption started low in spring and increased as the water warmed. The greatest consumption of fish biomass was estimated in October, when relatively warm water allowed a high metabolic rate, and predators ate a higher proportion of fish (Figure 8). Consumption demand was very low in winter, when water temperature limited metabolic rates. The feeding rate of the 200–299 mm Northern Pikeminnow was 55–65% C_{max} , but declined to 22–25% C_{max} for the ≥300 mm size class (Table 7). Consumption by a size structured population of 1,000 Northern Pikeminnow 200–299 mm over the entire year totaled 1,069 kg of Zooplankton (peak = August), 382 kg of plant matter (peak = August), and 159 kg of Sculpins (peak = October) (Figure 8). Consumption by 1,000 ≥ 300 mm fish over the entire year totaled 1,118 kg of Crayfish (peak = August), 557 kg of Northern Pikeminnow (peak = June), and 384 kg of salmonids (peak = October).

Dividing monthly consumption demand of salmonids by the mass of an age–0 stream–type Chinook Salmon in the corresponding month and summing across months provided an estimate of 39,250 Chinook Salmon consumed from 1 April to 31 March (peak = September) by a size–structured population of 1,000 Northern Pikeminnow ≥300 mm, if the salmon reached 18 g by November, and 16,022 fish if they reached a mass of 45 g by November (Figure 9). Our estimates of potential predation on age–1 Chinook Salmon smolts was considerably less than on age–0's.

Consumption of salmonids by a size–structured population of 1,000 large Northern Pikeminnow during peak months of smolt outmigration in April–June was only 17 kg (Figure 8). This biomass was equivalent to 969 salmon smolts weighing 18 g each, or 388 smolts weighing 45 g each. 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 the spring months.

Cannibalism on smaller Northern Pikeminnow by 1,000 predators ≥ 300 mm was 557 kg (Figure 8). Using the length distribution of cannibalized individuals and a length–weight regression, we estimated that this was equivalent to 1,862 fish of 200–299 mm and 9,311 Northern Pikeminnow <200 mm.

Population–level consumption demand of Tiger Muskellunge — We estimated that 29,069 Northern Pikeminnow ≥ 300 mm, 142,508 of 200–299 mm, and 247,736 of <200 mm were consumed by the population of Tiger Muskellunge (ranged 316–970 mm) over the course of a year (Figure 10).The equivalent consumption by a size–structured population unit of 1,000 Tiger Muskellunge was 5,296 Northern Pikeminnow ≥ 300 mm, 25,967 of 200–299 mm, and 45,141 of <200 mm. The numerical estimate of Northern Pikeminnow ≥ 300 mm consumed was based on a single observation of a 394 mm Northern Pikeminnow in one Tiger Muskellunge's stomach, which could have been an anomaly that skewed our data due to our relatively small sample size of prey fish examined.

Discussion

Predation by Large Northern Pikeminnow and Tiger Muskellunge on smaller Northern Pikeminnow resulted in an attenuated size structure that reduced their predation pressure on salmonids. Our simulations indicate that a unit 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. These estimates could be expanded to the population level when more robust abundance estimates are available. A parallel study of the potential production of Chinook Salmon fry in tributaries will enable a comparison of potential production and predation for lake rearing juvenile Chinook Salmon. The likely magnitude of predation mortality during a hypothetical age–1 smolt outmigration in spring was 400–1,000 smolts per 1,000 large Northern Pikeminnow, suggesting that Merwin Reservoir might be a functional migration corridor. Preliminary estimates of smolt production in the Merwin Reservoir basin are 18,927 Coho Salmon and 2,794 winter Steelhead (while no spawning habitat has been identified for spring Chinook Salmon [Mobrand Biometrics 2004]). Our collaborators are currently updating these estimates of smolt production based on new empirical and experimental data; however, there could be significant additional smolt production if fry choose to adopt a reservoir–rearing life history and conditions in the reservoir are conducive for their growth and survival. This is the case in reservoirs in the Willamette and Clackamas basins where age–0 stream–type Chinook Salmon consistently rear in reservoirs year–round (Lowery and Beauchamp 2010, Monzyk 2013). Test releases of stream–type Chinook Salmon fry in tributaries of Merwin Reservoir are needed to examine their timing and extent of dispersal into the reservoir, as well as their behavior, growth performance, and survival in the reservoir. The response of the Northern Pikeminnow populations to the addition of Chinook Salmon could also be examined more directly by replicating aspects of our study following the release. Our findings suggest that predation should not preclude the feasibility of reintroducing anadromous salmonids and such experiments would be worthwhile, largely because of two factors that significantly reduce predation on Kokanee by Northern Pikeminnow —a partial thermal refuge from predation and the truncated size structure of the predator population.

Thermal stratification segregated Northern Pikeminnow from salmonids during the peak growing season, which created a partial predation refuge. Additionally, cold water in destratified periods metabolically reduced overall consumption and therefore predation in early spring, fall, and winter. Consumption of salmonids increased in summer relative to spring, suggesting that thermal stratification only partially mitigated conditions that still enabled Northern Pikeminnow some access to Kokanee. The crucial assumption that Chinook Salmon would exhibit a similar depth distribution and diel vertical migration to Kokanee 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 (Plumb and Moffitt 2015) and Northern Pikeminnow (Ward and Petersen 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 and fed predominantly on invertebrates, Sculpins, and plant matter, with seemingly no consumption of salmonids.

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 accounts for a portion of this mortality based on our bioenergetics simulations and the length distribution of cannibalized fish observed in diets; however, only two cannibalized fish >200 mm were observed. The lengths of Northern Pikeminnow consumed were highly variable even for similar–sized consumers, which is likely the result of seasonal availability of different prey sizes due to prey growth and shifts in spatial–temporal overlap. Examining additional stomach contents would provide a more precise characterization of the seasonal size distribution of cannibalized Northern Pikeminnow.

Predation by Tiger Muskellunge also contributed significantly to the high mortality rates observed for 200–299 mm Northern Pikeminnow, and in combination with cannibalism, may explain the decrease in modal fork length of the Northern Pikeminnow population between the 1960s and the present. Tiger Muskellunge fed heavily on Northern Pikeminnow, as intended. Furthermore, the Tiger Muskellunge appear to be surviving and growing well in Merwin Reservoir. Predation is clearly driving a significant portion of the mortality of 200–299 mm Northern Pikeminnow, which in turn potentially reduces predation rates on salmonids in this system. The size structure of Northern Pikeminnow consumed by Tiger Muskellunge was also based on a small sample size, and we may have overestimated the number of >300 mm fish consume as a result. If fewer fish of this large size were consumed, then more fish of 200–299 mm would have been eaten.

The bioenergetics simulations indicated that a size–structured unit of 1,000 Tiger Muskellunge consumed 4,108 kg of Northern Pikeminnow annually, and a unit of Northern Pikeminnow consumed 557 kg of conspecifics per year. The proportion of that biomass that was composed of 200–299 mm fish was roughly 56% for Tiger Muskellunge and 44% for Northern Pikeminnow; however, inaccuracy in these proportions, which were based on relatively small sample sizes, could have large effects on the estimated number and size of prey consumed. An average Northern Pikeminnow ≥ 300 mm consumed roughly 11 smaller conspecifics per year, and an average Tiger Muskellunge consumed 86 smaller Northern Pikeminnow per year. Therefore the per–capita consumption of Northern Pikeminnow is 8 times greater for Tiger Muskellunge than cannibals.

The Tiger Muskellunge stocking program in Merwin Reservoir appears to be effective at reducing the survival and modal size of Northern Pikeminnow, which benefits the survival of resident salmonids which are vulnerable to ≥300 mm Northern Pikeminnow. This would also benefit juvenile anadromous salmonids if they were reintroduced. Managers could consider using Tiger Muskellunge as a biological control in other reservoirs where Northern Pikeminnow present a threat to valuable salmonid populations. However, we warn that Merwin Reservoir might be a unique case because of the abundant smaller size class of Northern Pikeminnow that are highly susceptible to predation, just as they are also becoming piscivorous. Furthermore, additional factors such as cannibalism are contributing to the size distribution of the Northern Pikeminnow population as well. We strongly caution against assumptions that Tiger Muskellunge would play a similar role in other systems. Without a thorough mechanistic understanding of the abiotic and biotic factors that affect distribution, behavior, growth and feeding of species, the unique characteristics of different aquatic system could produce dramatically different predator–prey interactions despite similar species assemblages.

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 issues of 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 around this uncertainty by estimating size–structured predation rate per 1,000 predators separately for >300 mm Northern Pikeminnow, thus insulating this analysis from some of the uncertainty in relative abundance of small versus large Northern Pikeminnow.

Our abundance estimates of Northern Pikeminnow suffered due to the difficulty in marking a significant proportion of the population in a relatively short period and the lack of mixing of marked and unmarked fish; however, it appears that the population has maintained a similar magnitude of abundance since the 1960s. The size structure appears to have decreased in modal length over this interval, which has resulted in a somewhat lower predation impact on salmonids. If more accurate information about the abundance of predators is needed, then our study could be used as a pilot for a larger–scale experiment.

The small percentage of recovered tags was the greatest source of uncertainty surrounding our population abundance estimates. The skew in the spatial distribution of marking effort and tag recoveries was accounted for by restricting our estimate of the population of ≥ 300 mm individuals to the upper quadrant of the reservoir and then expanding that estimate by the area and CPUE of the other parts of the reservoir. For estimation of the abundance of the 200–299 mm size class, we controlled for the skew in marking effort and tag recoveries toward the upper end of the reservoir by distributing sampling effort around the entire reservoir during the recapture phase; however, the disparity in the ratios of 200–299 mm to ≥ 300 mm individuals based on mark–recapture techniques versus the observed size distribution indicates a bias in these estimates of abundances and size distribution.

Another source of uncertainty in our study was the use of Kokanee as a surrogate for evaluating potential predator–prey interaction 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 (Monzyk et al. 2013; Lowery and Beauchamp 2010; Koehler et al. 2006). This occupancy of the littoral zone in spring would increase the fry's spatial–temporal overlap with Northern Pikeminnow at a size when they would be highly vulnerable to predation. The predators might therefore respond differently to this size and distribution of salmonid prey than the contemporary population of salmonids in the reservoir, which could have a large effect on mortality. A shift toward consumption of salmonids by the abundant <300 mm size class of Northern Pikeminnow could lead to numerical predation rates higher than those estimated in this study; although, Northern Pikeminnow's consumption rates are metabolically depressed by cold water in spring. Furthermore, the relatively low % C_{max} of Northern Pikeminnow indicated that they may increase their consumption if presented with additional prey resources. Peterson and ward (1991) found that salmonid consumption by Northern Pikeminnow was greater in the forebay of John Day Dam than in the main reservoir, suggesting that predation might occur at a higher rate in Merwin Dam forebay in response to a smolt outmigration as well. 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 outmigration) and behavior (schooling and diel vertical migration) of juvenile salmon and the response by predators in this watershed.

Despite the uncertainty, this study suggests that significant predation losses of juvenile Chinook Salmon are likely to occur, but should not preclude the feasibility of reintroducing anadromous salmonids in the Merwin Reservoir basin. Further evaluation of the capacity of the habitat in Merwin Reservoir and its tributaries to produce juvenile salmonids, as well as the salmonids' use of the habitat and the predators' response to their addition, are needed to inform the decision whether to implement a reintroduction. Continued monitoring of the abundance, size distribution, vertical and horizontal distribution, and diet of the predator population will be highly beneficial for guiding management decisions. We hope that our approach of examining and integrating aspects of the physical environment as well as physiological and behavioral characteristics of fish populations to examine predator–prey interactions is useful for evaluating other questions of feasibility of and limitations on salmonid reintroductions.

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Tables

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

Characteristic	Value
Surface area (km^2)	15.7
Length (km)	23.3
Mean depth (m)	31
Max depth (m)	73
Mean Secchi depth transparency (m)	~5
Water residence time (days)	118.4
Total phosphorus (mg/L)	<.02
Trophic status	Oligotrophic
Months stratified	May–Sept.
Top of thermocline (m)	~8
Ice cover	no
Range of surface temps (°C)	23–5
Maximum surface elevation (m msl)	73

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

Species	Abundance	Habitat
Kokanee	High*	Limnetic
Rainbow/Steelhead Trout	Moderate*	Littoral / limnetic
Cutthroat Trout	Rare	Littoral / limnetic
Juvenile Coho Salmon	Rare*	Littoral / limnetic
Juvenile Chinook Salmon	Rare*	Littoral / limnetic
Northern Pikeminnow	High	Bentho–limnetic
Largescale Suckers	High	Benthic
Sculpins	Moderate	Benthic (limnetic as fry)
Three-spine Stickleback	Rare	Littoral / limnetic
Tiger Muskellunge	Moderate*	Littoral
Pumpkinseed Sunfish	High	Littoral
Largemouth Bass	Rare	Littoral

* hatchery–supplemented population

Table 3. Thermal experiences of by Northern Pikeminnow and Tiger Muskellunge in Merwin Reservoir.

		Thermal experience (°C)		
Date	Simulation day	200–299 mm	≥300 mm	Tiger Muskellunge
1–Apr	1	7.7	8.3	8.3
15–May	45	11.5	12.3	12.3
30–Jun	89	15.6	16.7	16.7
19–Jul	109	17.8	19.1	19.1
15–Aug	135	18.8	20.1	20.1
18–Sep	168	18.6	19.3	19.3
10–Oct	190	17.5	17.6	17.6
18–Nov	228	12.5	12.7	12.7
15–Dec	255	5.8	5.8	5.8
1–Jan	270	5.5	5.5	5.5
1–Mar	330	6	6.3	6.3
31–Mar	365	7.7	8.3	8.3

Table 4. Diet proportions of two size classes of Northern Pikeminnow. ZOOP-zooplankton, KOK-Kokanee, COT- Sculpin, NPM-Northern Pikeminnow, CRAY- Signal Crayfish

Day	Season	n	ZOOP	Terrestrial insects	Aquatic insect	KOK	COT	NPM	CRAY	Plant
200–299 mm										
45	spring	23	0.72	0.05	0.10	0.00	0.03	0.00	0.09	0.03
135	summer	9	0.88	0.00	0.11	0.00	0.00	0.00	0.00	0.01
225	fall	12	0.12	0.00	0.00	0.00	0.26	0.00	0.00	0.63
300+ mm										
45	spring	11	0.01	0.00	0.09	0.00	0.00	0.43	0.45	0.02
135	summer	29	0.00	0.00	0.07	0.14	0.09	0.19	0.51	0.00
225	fall	26	0.08	0.04	0.00	0.28	0.14	0.10	0.29	0.08

Table 5. Diet proportions of Tiger Muskellunge.

			Diet proportions				
Season	n	FL range (mm)	N. Pikeminnow	L. Suckers	Pumpkinseeds	Kokanee	Inverts.
spring	10	300–975	0.80	0.10	0.10	0.00	0.00
summer	15	375–1025	0.65	0.20	0.00	0.07	0.08
fall	4	525–850	0.75	0.25	0.00	0.00	0.00

Table 6. Energy density (Joules/gram) of prey items of Northern Pikeminnow and Tiger Muskellunge. ZOOP-zooplankton, TERR INS – Terrestrial insects, COT-Sculpin, NPM-Northern Pikeminnow, L SUC- Largescale Sucker, PUM- Pumpkinseed Sunfish, CRAY- Signal Crayfish

Day	ZOOP	TERR INS	Aquatic insect	Salmonids	COT	NPM	L SUC	PUM	CRAY	Plant
1	1950[a]	5000	3400[b]	5200	4305[c]	6703[d]	3641	4186	3318[c]	1435
365	1950	5000	3400	5200	4305	6703	3641	4186	3318	1435

a. D.A. Beauchamp, *unpublished data*
b. Hansen et al. 1997
c. Mazur 2004
d. Peterson and Ward 1999

Table 7. Bioenergetics inputs of growth and spawning losses, and output of % maximum consumption (% C_{max}), and total, Kokanee, Northern Pikeminnow, Sculpins, and Signal Crayfish annual consumption by individual male and female Northern Pikeminnow age 3–14. Spawning losses were 3.9% of body mass for males age 3–14, 6% for age 3 females and 8.9% for age 4–14 females.

					Annual Consumption (g)				
Age	Initial fork length (mm)	Initial weight (g)	Final weight (g)	% C_{max}	Total	Kokanee	N. Pike–minnow	Sculpins	Signal Crayfish
males									
3	208	94	137	60%	1290	0	0	90	21
4	236	137	188	57%	1622	0	0	116	26
5	263	188	258	57%	2060	0	0	144	34
6	288	258	335	55%	2480	0	0	182	42
7	311	335	421	25%	1481	0	0	215	640
8	333	421	515	24%	1708	223	316	126	739
9	354	515	617	23%	1939	256	366	144	839
10	373	617	724	23%	2170	289	417	163	940
11	392	724	837	23%	2401	323	468	182	1041
12	409	837	954	22%	2630	356	519	201	1140
13	425	954	1075	22%	2856	389	570	219	1239
14	440	1075	1197	22%	3078	421	620	238	1336
females									
3	223	115	180	62%	1602	0	0	107	25
4	259	180	259	60%	2107	0	0	146	34
5	293	259	387	28%	1456	0	0	189	625
6	325	387	518	26%	1784	224	305	126	768
7	354	518	667	25%	2139	271	379	152	923
8	382	667	831	25%	2504	322	457	181	1082
9	408	831	1009	24%	2873	375	537	211	1243
10	432	1009	1198	23%	3244	428	619	241	1404
11	455	1198	1396	23%	3614	482	701	272	1565
12	476	1396	1601	23%	3978	535	783	302	1724
13	496	1601	1811	22%	4337	587	864	331	1880
14	515	1811	2025	22%	4687	639	944	360	2033

Table 8. Bioenergetics inputs of growth–at –age and outputs of % maximum consumption (% C_{max}), total consumption, and growth efficiency by individual Tiger Muskellunge aged 1–10.

Age	Initial fork length (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%

Figures

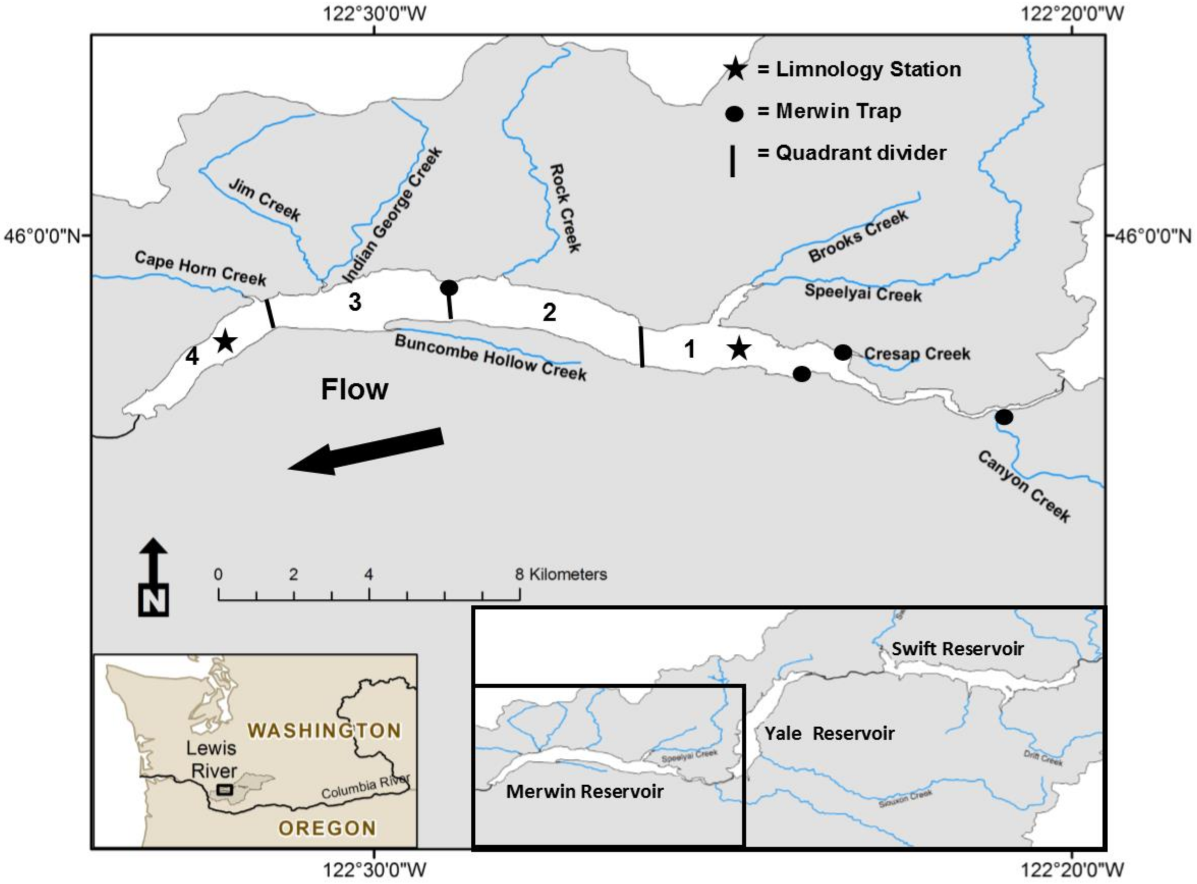

Figure 1. Map of Merwin Reservoir and select tributaries. Locations where vertical temperature profiles were measured, Merwin trap locations, and quadrant delineations are also included.

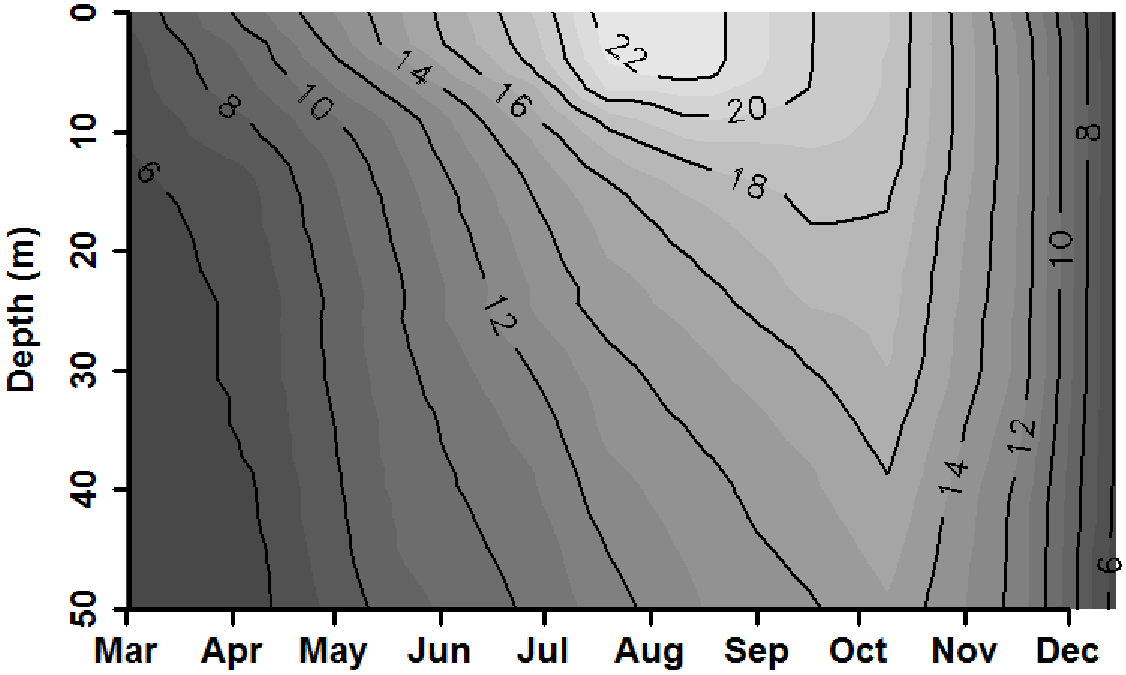

Figure 2. Isoclines of average water temperature (°C).

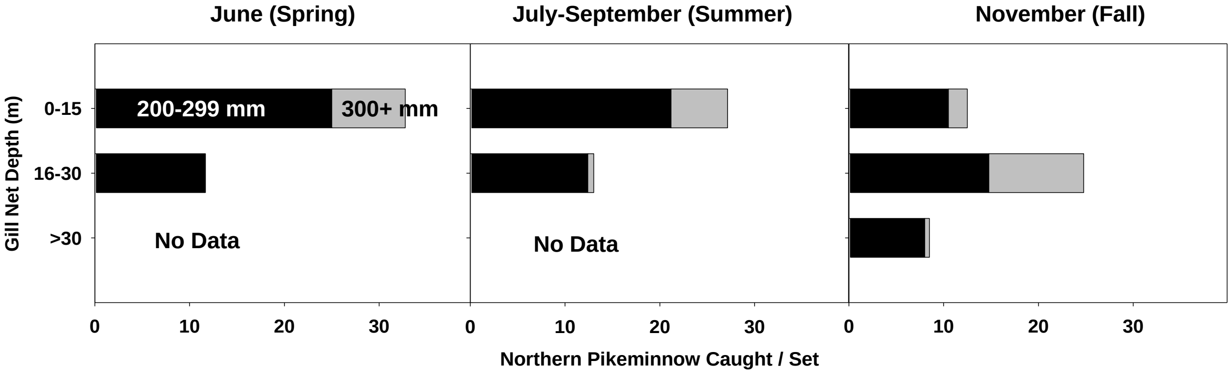

Figure 3. Catch per unit of effort for Northern Pikeminnow ≥200 mm by depth and season.

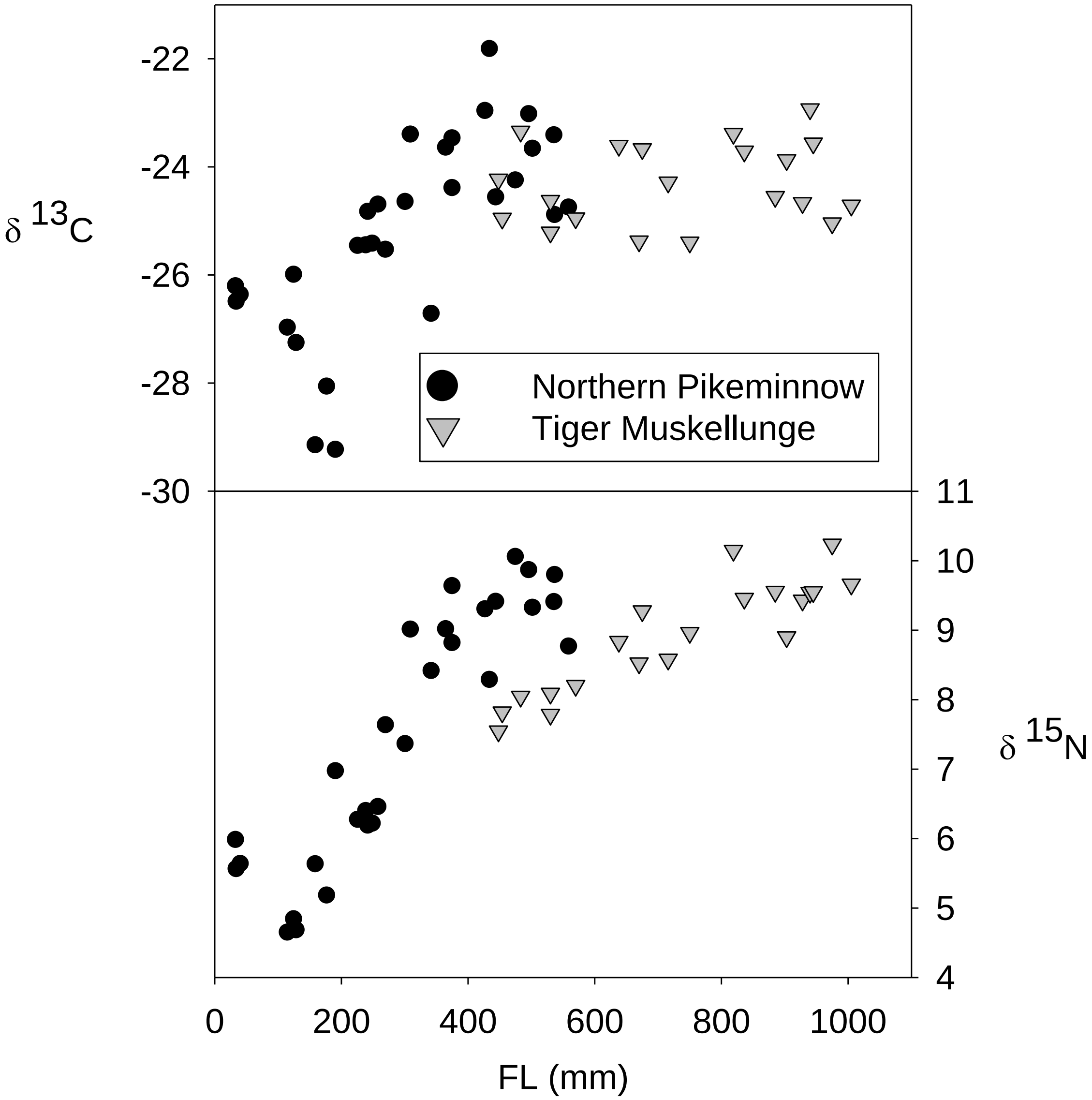

Figure 4. Stable isotope values of individual Northern Pikeminnow and Tiger Muskellunge as a function of fork length.

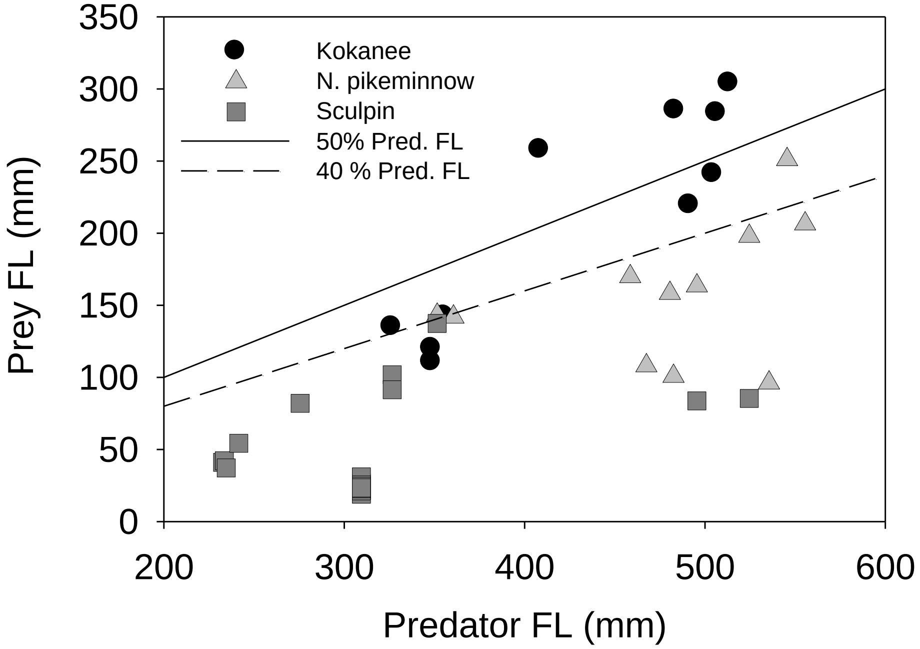

Figure 5. The relationship between Northern Pikeminnow's fork length and prey fish's fork length.

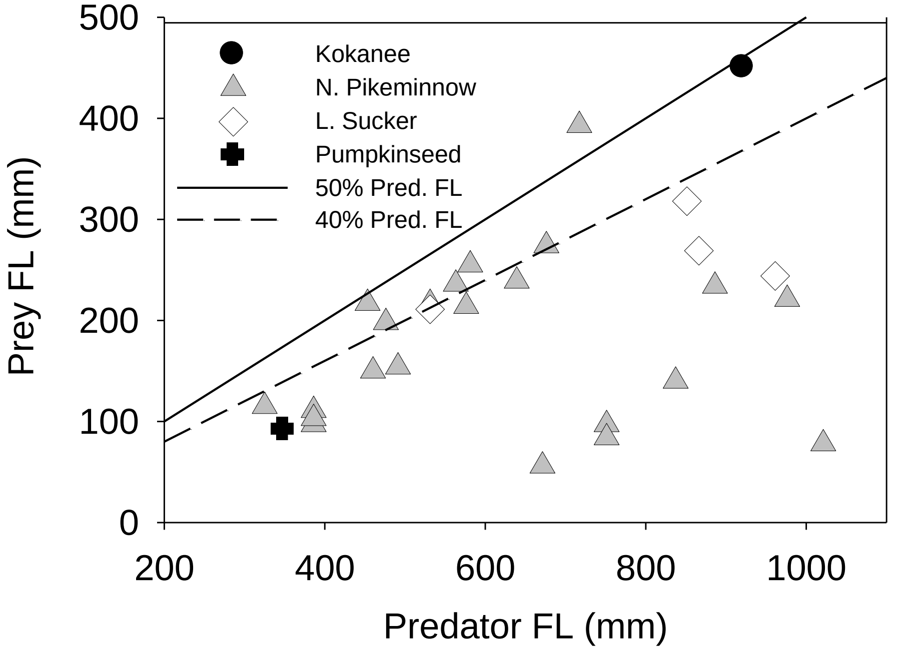

Figure 6. The relationship between Tiger Muskellunge's fork length and prey fish's fork length.

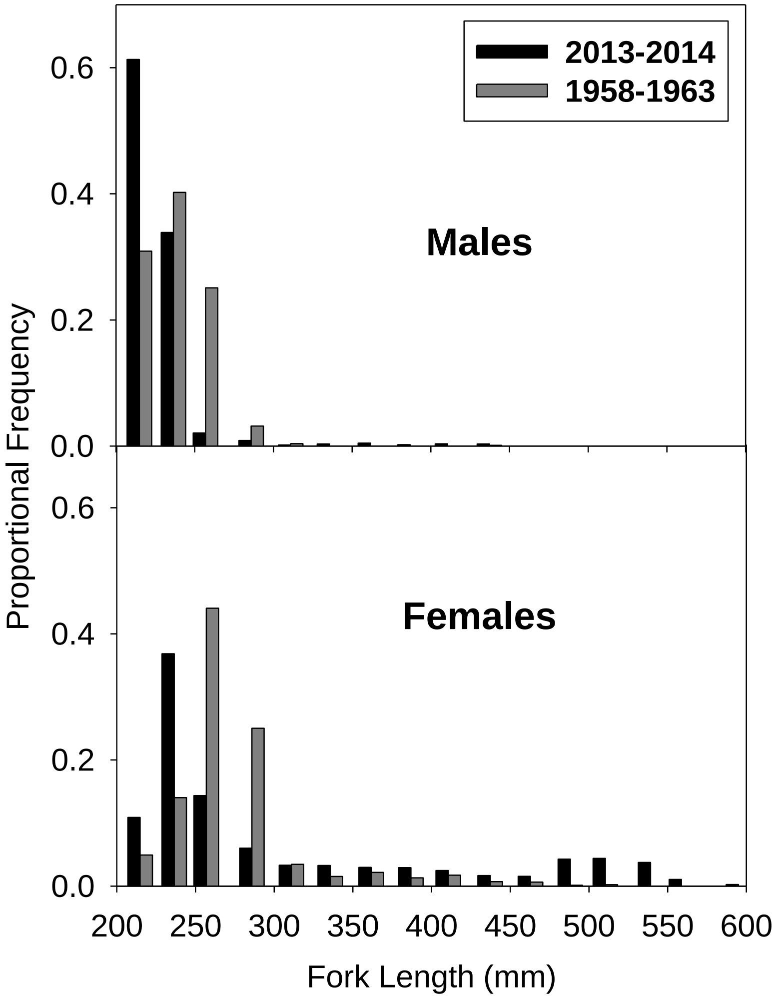

Figure 7. Length frequency distributions of male and female Northern Pikeminnow in 2013–2014 and 1958–1963 (Hamilton et al. 1970). The contemporary gill netting included larger mesh sizes than the historical, which were included in the 2013–2014 distribution shown here to best characterize the current size distribution of the population. Efforts were made to standardize the length frequencies by including only fish captured in similar areas.

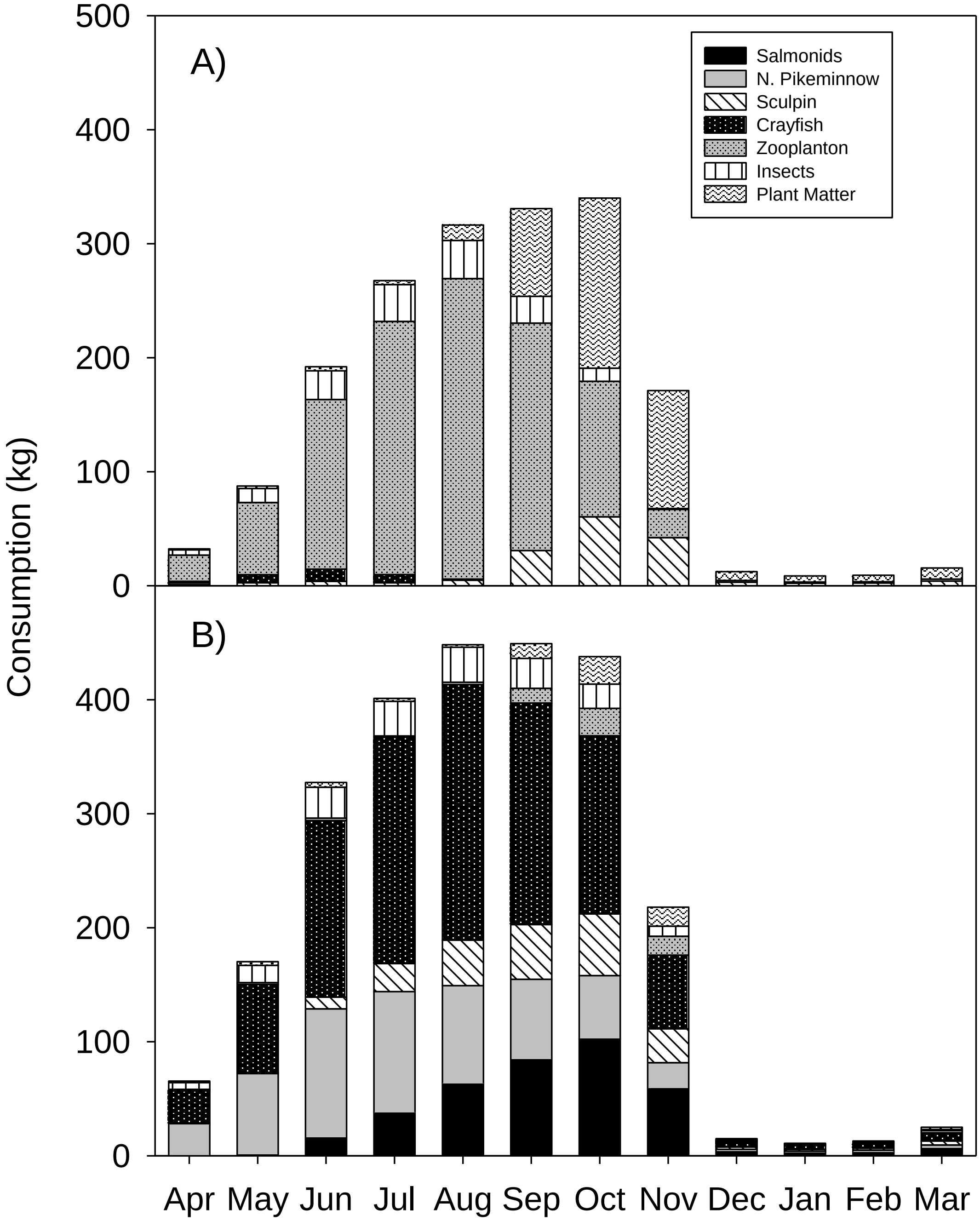

Figure 8. Modeled monthly biomass of prey consumed by a size–structured populations of 1,000 Northern Pikeminnow 200–299 mm (A), and ≥ 300 mm (B).

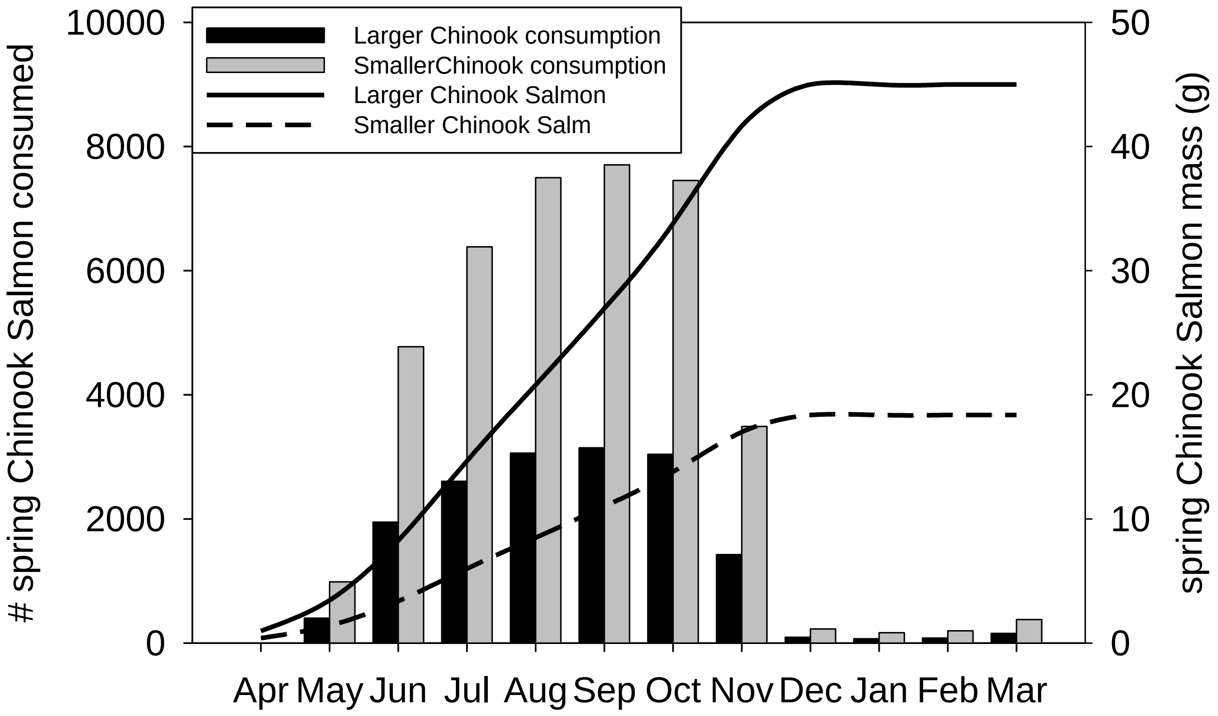

Figure 9. Estimate of potential number of sub-yearling spring Chinook Salmon that could be consumed monthly by a size–structured population unit of 1,000 large Northern Pikeminnow, and the expected monthly masses of reservoir–rearing sub-yearling Chinook Salmon (shown as lines and secondary y–axis).

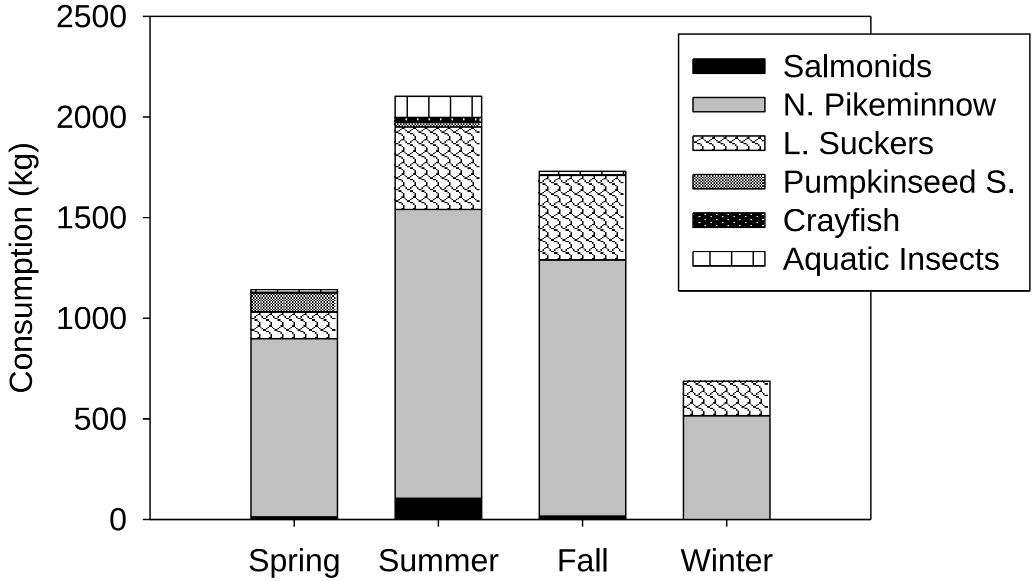

Figure 10. Seasonal biomass of prey consumed by an age–structured population of 5,488 Tiger Muskellunge.

Appendix

Table A1. Abundance estimates of different size classes of Northern Pikeminnow. Abbreviations: PJS = POPAN formulation of the Jolly–Seber model, LP = Chapman estimator for the Lincoln–Peterson model.

Region	Model	Size class	Fixed survival	Survival	AIC_c	N–hat	Expansion	**Expanded N–hat**	Lower 95%	Upper 95%
whole	PJS	≥200	N	34.4%	225.5	311,754	1.0	311,754	92,582	1,049,770
whole	PJS	≥200	Y	73.2%	225.0	400,090	1.0	400,090	218,667	732,039
whole	LP	≥200	Y			367,119	1.0	367,119	205,405	682,972
upper 1/4	PJS	≥200	N	13.6%	180.1	101,082	5.5	559,003	109,973	2,841,476
upper 1/4	PJS	≥200	Y	73.2%	181.5	179,574	5.5	993,077	567,608	1,737,469
upper 1/4	LP	≥200	Y			147,548	5.5	815,966	419,394	1,684,744
Average		≥200						**574,502**	**268,938**	**1,454,745**
whole	PJS	200–299	N	12.5%	143.2	322,748	1.0	322,748	50,872	2,047,624
whole	PJS	200–299	Y	39.7%	138.4	544,259	1.0	544,259[a]	190,609	1,554,062
whole	LP	200–299	Y			518,795	1.0	518,795	232,607	1,061,451
upper 1/4	PJS	200–299	N	–	110.2	10,458	6.3	66,381	55,742	79,050
upper 1/4	PJS	200–299	Y	39.7%	126.7	250,101	6.3	1,587,446	746,217	3,377,012
upper 1/4	LP	200–299	Y			178,794	6.3	1,134,846	475,760	3,076,582
Average		200–299						**695,746**	**291,968**	**1,865,964**
whole	PJS	≥300	N	20.3%	85.7	1,499	1.0	1,499	639	3,517
whole	PJS	≥300	Y	85.1%	86.3	2,590	1.0	2,590	945	7,102
whole	LP	≥300	Y			5,894	1.0	5,894	2,448	15,828
upper 1/4	PJS	≥300	N	8.7%	66.7	713	3.5	2,530	1,304	4,909
upper 1/4	PJS	≥300	Y	85.1%	72.6	1,482	3.5	5,261	1,850	14,962
upper 1/4	LP	≥300	Y			3,100	3.5	11,002[a]	3,728	39,878
Average		≥300						**4,796**	**1,819**	**14,366**

[a] Best estimate

A2. Stable isotope values for fish and invertebrates by size class. Abbreviations: PS = Pumpkinseed Sunfish, CCT = Coastal Cutthroat Trout, RBT = Rainbow Trout, LMB = Largemouth Bass, LSS = Largescale Sucker, NPM = Northern Pikeminnow.

	Spp.	Size Class (mm)	N	Mean δ ^{15}N	Minimum δ ^{15}N	Maximum δ ^{15}N	Mean δ ^{13}C	Minimum δ ^{13}C	Maximum δ ^{13}C
Merwin	PS	100–199	3	5.860	5.637	6.201	–25.895	–26.350	–25.592
	Clam	–	4	3.231	2.607	3.848	–28.656	–30.751	–25.627
	Coho	200–299	4	6.288	5.888	6.723	–26.236	–27.546	–24.334
	Copepods	–	1	3.160	3.160	3.160	–28.711	–28.711	–28.711
	Sculpin	<100	9	6.112	5.307	6.685	–25.386	–27.959	–21.971
		100–199	3	8.068	6.839	8.946	–23.354	–24.257	–22.855
	Crayfish	–	2	4.054	2.801	5.306	–21.718	–24.198	–19.238
	CCT	100–299	3	7.318	7.037	7.844	–26.639	–29.092	–23.817
	Daphnia	–	1	–0.758	–0.758	–0.758	–31.270	–31.270	–31.270
	Diptera	–	1	1.726	1.726	1.726	–26.537	–26.537	–26.537
	Hemiptera	–	1	1.194	1.194	1.194	–27.648	–27.648	–27.648
	Holopedium	–	1	0.695	0.695	0.695	–30.916	–30.916	–30.916
	RBT	<299	7	5.605	4.992	6.489	–24.342	–26.121	–22.133
		300–399	7	9.186	6.544	10.757	–20.956	–26.262	–17.692
		500–699	6	13.081	12.329	13.656	–17.658	–18.230	–17.177
	Kokanee	<399	9	6.423	5.232	7.573	–26.713	–28.186	–25.062
	LMB	300–499	2	9.084	8.585	9.582	–22.085	–22.768	–21.402
	LSS	<200	4	5.841	5.415	6.286	–24.051	–24.763	–23.791
		300–499	5	6.182	5.849	6.380	–27.943	–29.670	–25.710
	NPM	<200	9	5.451	4.639	6.963	–27.315	–29.245	–26.005
		200–299	6	6.519	6.179	7.626	–25.242	–25.543	–24.708
		300–399	5	8.640	7.353	9.627	–24.584	–26.729	–23.479
		400–599	9	9.348	8.278	10.048	–23.714	–24.899	–21.826

Juga snail	–	4	2.576	1.993	3.135	–20.409	–22.691	–16.770
Tiger Muske.	400–799	11	8.333	7.546	9.275	–24.513	–25.396	–23.345
	800–1099	9	9.608	8.902	10.236	–24.048	–25.041	–22.930

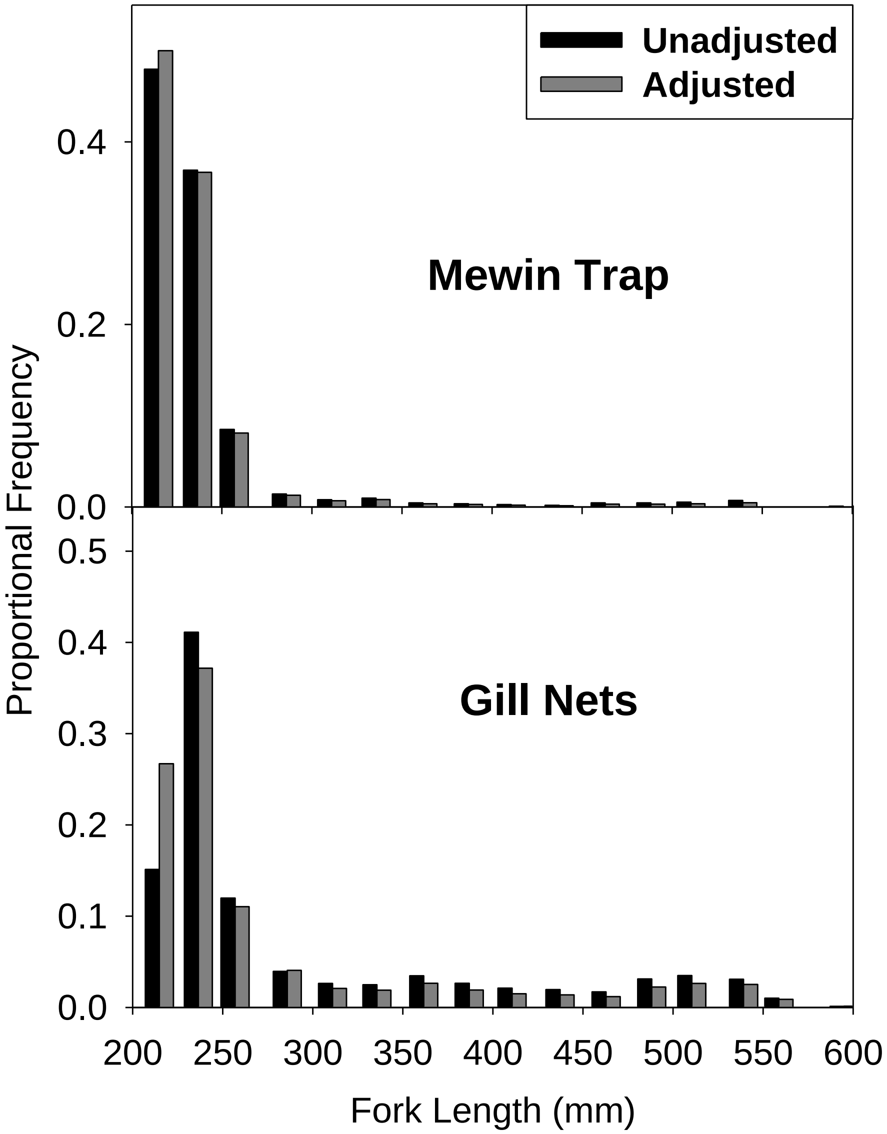

Figure A1. Length frequency histograms from raw–catch data and data adjusted for size selectivity. The top panel shows Merwin trap data, and the bottom panel shows gill net data.

Conclusions

- All three reservoirs, Swift, Yale and Merwin, are stratified from May–October. The hypolimnion warms during summer in Merwin but not in the other two reservoirs.
- The primary pelagic planktivores, which share prey resources with anadromous salmonids, are hatchery–reared rainbow trout in Swift Reservoir and Kokanee in Yale and Merwin Reservoirs.
- Salmonids had limited access to prey resources in the epilimnion from July through September in Yale and Swift Reservoirs, and July through October in Merwin Reservoir, due to water temperatures above their thermal preferences and evidenced by hydroacoustics results.
- All planktivores exhibited some diel vertical migration, although Kokanee migrated more than rainbow trout. Kokanee were densely distributed at the thermocline in Yale Reservoir at night during the summer. Kokanee were more loosely distributed in Merwin Reservoir, which had a less defined thermocline due to the warming of the hypolimnion.
- *Daphnia* were the most important prey for Kokanee and Rainbow Trout, although the contribution of insects to the energy budget of Rainbow Trout was unclear based on a discrepancy between stable isotope and stomach content analysis results.
- *Daphnia* bloomed once in spring with a smaller secondary bloom in early fall in all three reservoirs. Epilimnetic *Daphnia* densities were generally approximately two times that of the metalimnion, and hypolimnetic densities were < 1/liter with the exception of May-August in Merwin Reservoir.

- Monthly production of *Daphnia* was highly variable between months. Production was greater than standing stock biomass in months preceding or during blooms, and lower as the bloom declined.
- Kokanee in Merwin Reservoir fed at a higher rate (92–123% C_{max}) than Kokanee in Yale or Rainbow Trout in Swift Reservoir. Age–2 Kokanee (Spawners) in Yale Reservoir fed at the lowest rate (59% C_{max}) of any age class of planktivore examined.
- Consumption demand did not exceed 50% of accessible standing stock plus production of *Daphnia* biomass in any month during the growing season.
- September was the month with the highest consumption demand to prey supply ratio in all three reservoirs. In this month, warm water drove fast metabolism when prey was less available in the metalimnion, and the epilimnion was too warm for salmonids.
- The surplus prey resources available for additional consumption without exceeding our estimate of the maximum–sustainable consumption rate could support approximately 130,000–330,000 more age–0 Chinook Salmon during the most limiting month(s) of the growing season (late summer) in each reservoir, and for the remainder of their reservoir rearing.
- A logical next step would be to release large numbers of fry in tributaries and examine if and when they distribute into the reservoirs, how they behave and survive in the reservoirs, and when they outmigrate.
- Northern Pikeminnow were the most abundant species sampled in the littoral and slope zone of Merwin Reservoir, followed by largescale suckers.
- Northern Pikeminnow ≥200 mm were most densely distributed in the upper 15 m of the water column in spring and summer, and from 15 to 30 m in fall. This vertical

distribution decreased their spatial overlap with salmonids, which were more deeply distributed below the thermocline during summer. Much of the disparity in the vertical distributions of Northern Pikeminnow and salmonids can be explained by physiological differences in their temperature–dependent specific growth potentials.

- Thermal stratification is an important process that influences seasonal carrying capacity of salmonids and partially segregates salmonids from predatory Northern Pikeminnow.
- The density of Northern Pikeminnow >200 mm was greater in the lower half of the reservoir during August.
- Stable isotope analysis suggested that between 200 and 300 mm, Northern Pikeminnow transition from invertivory (and a heavier reliance on pelagically derived nutrients) to piscivory (and heavier reliance on bentho–littorally derived nutrients).
- Stomach content analysis revealed that 200–299 mm Northern Pikeminnow derive most of their energy from zooplankton, insects, sculpin, and plant material. Approximately ½ of the diet of ≥ 300 mm Northern Pikeminnow was composed of Crayfish with cannibalism, Kokanee, and Sculpins making up the remainder. Cannibalized individuals were mostly < 200 mm, but a small proportion were >200 mm.
- Based on stable isotopes and diet analysis, Northern Pikeminnow in Merwin Reservoir become effective piscivores at 300mm.
- The Northern Pikeminnow population consisted of approximately 550,000 fish of 200–299 mm and 11,000 fish ≥ 300 mm based on mark–recapture techniques; however, there is significant uncertainty surrounding these estimates.
- The size distribution of >200 mm Northern Pikeminnow population consisted of 83% 200–299 mm, and 17% ≥ 300 mm fish. Therefore, the abundance of >200 mm

individuals is not a good indicator of the magnitude of predation on salmonids, because the majority are not effective piscivores on salmonids.

- Annual consumption of Kokanee by a size–structured populations of 1,000 Northern Pikeminnow ≥ 300 mm was analogous to 16,022–39,250 age–0 stream–type Chinook Salmon rearing in the reservoir year round.
- Consumption of Kokanee by a size–structured populations of 1,000 Northern Pikeminnow ≥ 300 mm during the peak months of stream–type Chinook Salmon smolt outmigration (April–June) was equivalent to 388–969 smolt–sized fish. These estimates are relatively low due to cold water temperatures driving slow metabolic rates for predators and a low proportion of salmonids in Northern Pikeminnow diets over the entire spring season.
- We estimated that 1,862 Northern Pikeminnow >200 mm and 9,311 fish <200 mm were cannibalized by a size–structured unit population of 1,000 conspecifics over an entire year. An additional 5,296 Northern Pikeminnow >300 mm, 25,967 fish 200–299 mm, and 45,141 fish <200 mm were consumed by a size–structured unit population of 1,000 Tiger Muskellunge per year as well.
- Tiger Muskellunge consumed mostly Northern Pikeminnow, and ate larger sized fish as they grew. A large proportion of their consumption of Northern Pikeminnow consisted of >200 mm prey.
- The estimated population of Tiger Muskellunge was approximately 5,500 individuals.
- Predation on juvenile anadromous salmonids rearing in the reservoir or migrating through it could be significant; however, predation potential is much reduced as a result of the attenuated size distribution of Northern Pikeminnow resulting from cannibalism and

predation by Tiger Muskellunge, as well as the differing depth distributions of Northern Pikeminnow and salmonids during much of the growing season.

- Test releases of fry in tributaries of Merwin Reservoir would enable examination of the predatory response to their increase in abundance, in addition to providing insight on their timing and usage of reservoir habitat.