Quantifying the impact of two native predators on juvenile sockeye salmon survival in Lake Washington

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Abstract

Understanding the mechanisms regulating population fluctuations, such as births, reproduction, and deaths, remains a persistent question in ecology. Mortality can be incurred at any point during the lifecycle, but mortality rates can be high for juvenile animals in particular. One source of this early life history mortality is via predation. Accurately measuring predation rates requires intensive studies, and is further complicated by variability in habitats and changes in the extent of spatial and temporal overlap between predators and prey. In this study, we examined abundance, spatial distributions and diets of two piscivorous fishes and their predation impact on juvenile salmonids in a well-studied large western lake, Lake Washington. We addressed the following questions: (i) What is the abundance of cutthroat trout and northern pikeminnow in Lake Washington? (ii) At what rates do these predators consume juvenile salmon throughout the year, and how many total juvenile salmon are consumed given the predator population size? Understanding which factors influence predation and the extent of this predatory impact requires temporally and spatially explicit data on the interaction between predators and prey, including both juvenile sockeye salmon and the main alternative prey fish species. To observe these interactions, we used several overlapping sampling types across trophic levels. We used a Chapman-modified population estimation procedure to estimate a cutthroat trout population size of 22,791 ≥300 mm FL and the same procedure to estimate a northern pikeminnow population size of 13,582 ≥300 mm FL. We also used a relative catch method to estimate a northern pikeminnow population size of 112,816 ≥300 mm FL. The magnitude of predation on juvenile salmon and other prey fishes varied considerably among months and between cutthroat trout and northern pikeminnow, between small and large size classes of each predator species, and between years. In 2015, predation mortality of lake entry

2015 (sub-yearling) sockeye salmon was 20% of fry production in that year, and predation losses of lake entry 2014 (yearling) sockeye were 56% of pre-smolt production. In 2016, mortality of lake entry 2016 (sub-yearling) sockeye was 44% of fry production, and predation losses of lake entry 2014 sockeye were 473% of pre-smolt production of that year. Our work shows that the current predation rate is high enough and these predator populations are of sufficient size that predation is a significant source of mortality for juvenile sockeye and Chinook salmon in this system. This work highlights a scenario of combined physical and biological factors that influence mortality in juvenile fish, and can potentially inform the potential for predation mortality in other lake systems.

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List of Tables

List of Figures

Quantifying the impact of two native predators on juvenile sockeye survival

Introduction

Understanding the mechanisms regulating population fluctuations remains a persistent question in ecology. Population fluctuations are driven by changes in rates of births, reproduction, and mortality (Meats 1971). Mortality can be incurred at any point during the lifecycle, and deaths that occur before reproduction generally have highest impacts on population abundance (Giesel 1976). Commonly, a source of early life history mortality is through predation.

Accurately measuring predation rates requires intensive studies, and is further complicated by variability in habitats and changes in the extent of spatial and temporal overlap between predators and prey (Murdoch and Oaten 1975). From foraging theory, we know that heterogeneous habitats produce unequal foraging opportunities and therefore unequal distributions of animals across landscapes (Levins 1962, Brown 2000). This dynamic is further complicated by the diversity of behavioral responses by predators and prey to one another (Sih 1984). These challenges of assessing predation can be especially pronounced in large, heterogeneous habitats, and where species may occupy multiple habitats during its life history (e.g. anadromous fishes).

Large western lakes are heterogeneous habitats primarily structured by vertical gradients of temperature, thermal-chemical, and light, and by an onshore-offshore axis of habitat complexity. These features are typically combined with pronounced seasonal variation in the extent of this vertical structuring. Additionally, these lakes are often occupied by planktivorous and piscivorous fishes, one or more species of which are anadromous. Planktivorous fishes inhabit different habitats based on tradeoffs between food availability, thermal tolerance, and susceptibility to predation (Narver 1970, Brett 1971, Eggers 1978, Clark and Levy 1988). Different species, life stages and life history strategies respond to habitat heterogeneity in different ways, and these varied responses are an essential part of species interactions, including predation.

Lake Washington is a large, seasonally-varying lake occupied by multiple planktivorous and piscivorous fishes, including anadromous sockeye salmon *Oncorhynchus nerka*. The distribution of prey fishes in the lake varies seasonally depending on which habitat is most suitable for growth and predator avoidance. Planktivorous longfin smelt *Spirinchus thaleichthys* use benthic habitats extensively during winter but inhabit pelagic zones during the remainder of the year. Threespine stickleback *Gasterosteus aculeatus* and juvenile sockeye salmon remain primarily in the pelagic zone, except during periods of spawning or migration (Traynor 1973, Eggers 1978, Beauchamp 1994, Chigbu et al. 1998, Quinn et al 2012).

In nearshore zones, defined here as littoral and slope zones within and below the thermocline, prey fishes overlap with piscivorous predators including Cutthroat trout *Oncorhynchus clarki*. Cutthroat trout exhibit ontogenetic and seasonal shifts in distribution by foraging in littoral zones during late fall, winter, and early spring, but shift to improved foraging opportunities and beneficial thermal conditions in pelagic and slope zones within the thermocline (Nowak and Quinn 2002, Nowak et al. 2004). Another common predatory species found in Lake Washington is Northern Pikeminnow *Ptychocheilus oregonensis*, which are a generalized predator, preying on invertebrates and fish that overlap seasonally (Eggers et al. 1978, Brocksmith 1999, Sorel et al. 2016). The period and extent of thermal stratification and the seasonal supply of zooplankton control the duration of overlap between prey fish and northern pikeminnow in and above the thermocline. In addition, water temperatures govern when northern pikeminnow are effective predators. In winter, water temperatures are homogeneously cold, which reduces metabolic rate as well activity level. In spring, surface water temperatures warm and northern pikeminnow begin to forage at a higher rate. The duration of spatial overlap between active northern pikeminnow and prey fish in nearshore zones can vary widely depending on the intensity of warming in the spring, but this overlap could control the strength of the interaction between northern pikeminnow and prey fishes.

In this study, we examined spatial distributions and diets of two piscivores, cutthroat trout and northern pikeminnow, to address the following questions: (i) What is the abundance of cutthroat trout and northern pikeminnow in Lake Washington? (ii) At what rates (number per capita) do these predators consume juvenile salmon throughout the year? (iii) How many juvenile salmon do these predators consume each year? Understanding which factors influence predation and the extent of this predatory impact requires temporally and spatially explicit data on the interaction between predators and prey, including both juvenile sockeye salmon and the main alternative prey fish species. To observe these interactions, we used several overlapping sampling types across trophic levels in a well-studied model system, Lake Washington. Understanding these interactions is an important tool for assessing risk for species of conservation concern and developing effective restoration measures (Ward et al. 2012).

To determine the timing and magnitude of predation by cutthroat trout and pikeminnow on prey species, we completed the following objectives: (i) performed a minimally biased predator abundance estimate, (ii) quantified predation rate by sampling to determine the size structure of cutthroat trout and northern pikeminnow, their monthly diet and distribution, then applied these data as inputs for bioenergetics model simulations to estimate annual feeding rates of predators, and (iii) estimated the predation mortality for each brood year of sockeye and Chinook salmon that overlapped with the study.

Methods

Study system – Lake Washington is a large lowland glacially-carved lake located alongside Seattle, Washington, USA (Figure 1). The lake has maximum depth of 65 meters, an average depth of 33 meters, is 35 km long, and has a surface area of 88 km^2. Lake Washington is a dynamic, heterogeneous system that experiences a phytoplankton bloom in spring, is thermally stratified from May to October, and remains destratified and ice free in winter (Edmondson 1994, Arhonditsis et al. 2003, 2004, Figure 2). The lake serves as a rearing habitat and migration corridor for Sockeye *Oncorhynchus nerka*, Chinook *O. tshawytscha* and Coho Salmon *O. kisutch* and hosts approximately 43 other species, of which less than half are native. Species were determined to be relevant to this study based on abundance, distribution, or trophic niche (McIntyre et al. 2006). The dominant pelagic planktivores are longfin smelt *Spirinchus thaleichthys* and threespine stickleback *Gasterosteus aculeatus*, followed by juvenile sockeye salmon. Prickly sculpin *Cottus asper* and coast range sculpin *Cottus aleuticus* are found in littoral and benthic habitats, and small post-larval sculpin are commonly observed in modest densities in limnetic habitats at night (Hansen et al. 2016, Clark et al. 2017). Yellow perch *Perca flavescens* are abundant and reside predominantly in littoral habitats, but ages 0-1 commonly feed on zooplankton while suspended around the periphery of the limnetic zone during summer. Coastal cutthroat trout are the dominant pelagic piscivore in the lake throughout the year, but also forage in littoral and deeper slope zones during winter, spring, and fall (Beauchamp et al. 1992, Nowak and Quinn 2002, Nowak et al. 2004, Hansen and Beauchamp 2014a). The dominant cool-water piscivore is northern pikeminnow (Eggers et al. 1978, Beauchamp 1990, Brocksmith 1999).

Lake Washington is well suited for study of predator-prey relationships because it has been the focus of decades of limnology (Edmondson 1993, 1994) and fish ecology research (Eggers et al. 1978, Beauchamp 1990, Beauchamp et al. 1995, Koehler et al. 2006, Mazur and Beauchamp 2006, McIntyre et al. 2012). Intensive sampling efforts have documented relatively recent shifts in primary productivity, with implications for the planktivore community (Winder and Schindler 2004). Historical sampling efforts include: physical features of the lake (temperature, dissolved oxygen, light, turbidity); phytoplankton and zooplankton (abundance, distribution, and species composition) collected at intervals of every two weeks to monthly for over 50 years; and planktivorous fish estimates for many of the years since the early 1970s (Edmondson 1994, Hansen et al. 2016, Clark et al 2017).

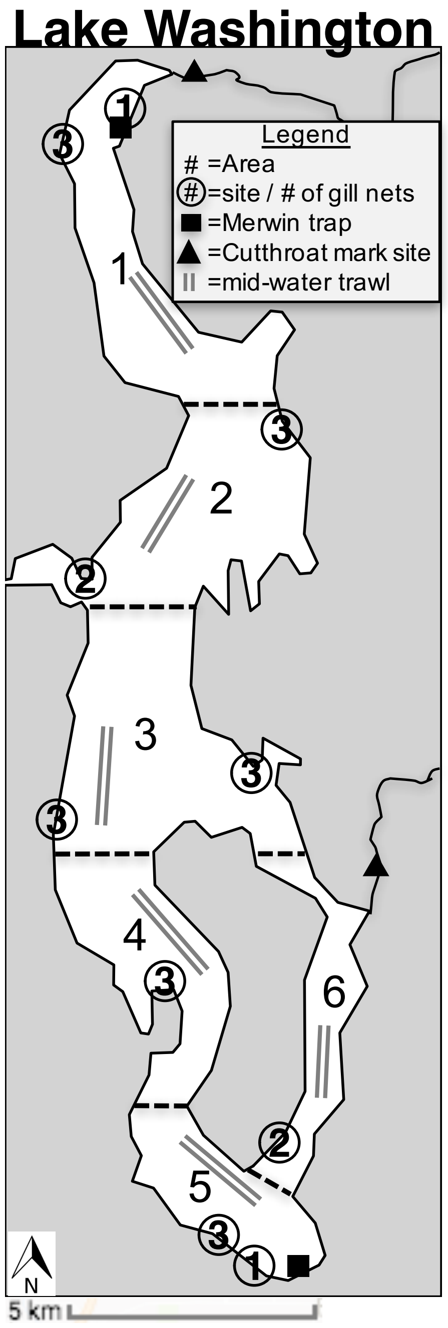

Figure 1: Lake Washington, Washington State, USA showing sampling areas of lake, site and number of gill nets, Merwin trap locations, cutthroat trout marking locations in tributaries, and mid-water trawl tracks.

Approach – We used a variety of methods to assess the predatory impacts of coastal cutthroat trout and northern pikeminnow by assessing their abundance, size distribution, and food habits. To do so it was important to capture representative samples and avoid spatial- and size-selective biases. We used electrofishing and trapping during spawning migrations to capture, mark and release adult cutthroat trout and northern pikeminnow, then after allowing marked fish to redistribute in the lake, we relied on captures in gill nets and purse seines during the capture-recapture phase of abundance estimation. In the lake, we conducted seasonal gill netting, purse seining, and midwater trawling to collect representative samples of the predator populations, diet and distribution of predators and predator-prey overlap, which complemented ongoing sampling of the planktivore community in Lake Washington.

Predator Abundance Estimate

Cutthroat trout- To estimate the abundance of predatory cutthroat trout (FL ≥ 300 mm) in Lake Washington, we used a mark/recapture approach with phases that were distinct in time, location, and gear types. Based on diet and stable isotope analyses, McIntyre et al. (2006) reported that Cutthroat trout became maximally piscivorous at FL ≥ 300 mm and predominantly fed upon pelagic prey fishes. To mark cutthroat trout, we intercepted mature fish in or near spawning tributaries as they migrated upstream to spawn during January through April 2015 and 2016 (Trotter 1989). We initially used Merwin traps and other traps to capture adult Cutthroat trout in or near spawning tributaries, but were forced to abandon this method, because of frequent depredations by river otters *Lutra canadensis*. As a result, electrofishing was the primary method of capture for the marking phase for cutthroat trout and, to avoid spatial and size-selective bias, sampling effort occurred in two of the primary tributaries to the lake (Figure 1). We surveyed the two primary tributaries, Sammamish River and Kelsey Creek, walked or boated 1-2 times per week during the marking period in both years. We also sampled many other tributaries, but most yielded few fish. We measured, weighed, sexed, marked adults with individual Floy anchor tags, took a fin clip from the lower caudal lobe as a secondary mark, and allowed all fish to recover before release. From a subsample of fish, we removed scales from the preferred area posterior and below the dorsal fin for age and growth analysis and froze the fin clip for isotope analysis. We marked and released an additional 64 cutthroat trout in May 2015 captured by purse seine in the northern area of Lake Washington. Cutthroat trout tagged following purse seine capture were an exception to our sampling design in that these fish were captured and recaptured with the same gear type, though the two phases were still distinct in time.

We allowed cutthroat trout to disperse into the lake before initiating the capture phase (April 26, 2016 to October 27, 2016). Fish were sampled without replacement during the capture phase, with purse seines in the offshore habitat and sinking variable-mesh gill nets in nearshore and slope zone habitats (Beauchamp et al. 2007, Beauchamp et al. 2009).

Northern Pikeminnow - We used a mark-recapture approach to estimate the abundance of northern pikeminnow (FL ≥ 300 mm) in Lake Washington. Like Cutthroat trout, northern pikeminnow become maximally piscivorous at FL ≥ 300 mm (Jeppson and Platts 1959, Brocksmith 1999, McIntyre et al. 2006, Clarke et al. 2005). To capture live northern pikeminnow for marking, we used a diversity of sampling gear in an attempt to intercept mature fish as they migrated to spawning locations, but this proved difficult as spawning locations were both still largely unknown. In addition to netting, snorkel surveys in streams and bays were also performed throughout the spring and during June, the presumed spawning period (Gadomski et al. 2011), but we were unsuccessful in locating spawning aggregations. We caught the majority of northern pikeminnow for marking in 2015 in two Merwin traps, one located at the north end of the lake near the outlet of the Sammamish River and one located at the south end of the lake near the outlet of the Cedar River (Figure 1). We also used gill nets, which were set for 30 minutes or less, to capture and mark northern pikeminnow in July 2015 and April-May 2016. In addition, we caught and marked northern pikeminnow in the Sammamish River while electrofishing for cutthroat trout in January-March 2015 and 2016 (2015 N=2; 2016 N=26). All fish were measured, weighed, sexed, marked with individually-numbered Floy anchor tags, a fin clip from the lower caudal lobe was taken as a secondary mark, and they were allowed to recover before release at the site of capture. For a subset of fish, we froze the fin clip for isotope analysis.

Northern pikeminnow were allowed to disperse in the lake before we initiated the capture phase (May 23, 2016 to October 27, 2016). Fish were sampled without replacement during the capture phase using sinking variable-mesh gill nets in nearshore and slope zone habitats (Beauchamp 2009).

Estimation Procedure - Abundance estimates for freshwater predators are challenging and relatively rare, especially in large deep lakes with highly mobile bentho-pelagic species. Top predators are much less abundant than their prey and are challenging to catch in sufficient quantity to generate abundance estimates. Given these limitations, our sampling design met the minimum assumptions required for a Chapman-modified population estimation procedure (Ricker 1975) by consolidating marks over 2 years. The number of 1st year marks at large was discounted by the survival rate computed for these populations and we initiating the capture/recapture phase only after marking was completed in the 2nd year.

Relative catch - Despite deploying a diversity of capture gear and numerous visual surveys, large aggregations of pikeminnow were not located in either year; therefore, they were not marked in numbers similar to those of cutthroat trout. As a secondary indicator of abundance, we compared gill net catch during months when peak catch for both cutthroat trout and northern pikeminnow coincided; June, July, and August 2015-2016. The ratio of northern pikeminnow to cutthroat trout caught in gill nets during this target period was considered a reasonable indicator of the relative abundance of each species.

<u>Predation Rate</u>

Predator sampling – Depth-stratified gill net sampling was conducted monthly from February or March through October in 2015 and 2016 across 6 areas of the lake to examine depth distributions of nearshore predators and associated species, and to obtain stomach samples for both predators (Figure 1). Sinking monofilament gill nets with variable mesh panels were deployed perpendicular to shore for approximately 24 h in nearshore and slope zone regions of the lake 1-2 times monthly from March to October in 2015 and February to October in 2016. Two sizes of gill nets were deployed; small nets (46 meters x 2 meters with 6 mesh panels; 63.5, 76.2, 88.9, 101.6, 114.3, 127 mm) and large nets (61 meters x 3 meters with 5 mesh panels; 88.9, 101.6, 114.3, 127, 152.4 mm). Gill nets were deployed at the same sites each month and, where depths allowed, gill nets were deployed at three different depth intervals (0-10 m, 10-20 m, and 20-35 m) at each site to sample specific thermal layers during the stratified period (i.e. epilimnion, metalimnion, and hypolimnion) and similar depths during the de-stratified seasons in the lake. All fish were removed from the net on site and we recorded mesh size of capture, fork length, and species. All predators and an occasional subsample of non-target species were immediately placed on ice and returned to the lab for subsequent processing.

As thermal stratification intensified and temperatures became stressful to salmonids above the thermocline, cutthroat trout move into deeper areas of the littoral zone, slope habitat, along with larger cutthroat that also move to pelagic habitats (Nowak et al. 2004, Beauchamp 2009). Consequently, the catches of cutthroat trout in shallower gill nets decreased during the stratified period, while catches persisted in deeper slope habitats during the stratified period. A pilot feasibility study in 2005-2006 exhibited relatively high catches of piscivores and prey fish in the top 25 m of the water column using a purse seine (Beauchamp et al. 2006). To capture pelagic cutthroat trout during the stratified season, we contracted a purse seine for two nights each in May, June, and October and one night in July in 2015 and repeated the sampling in 2016. The purse seine was primarily set after dark, supplemented by pre-dusk, dusk sets, and dawn sets. Timing of purse seine sets was determined based on timing of pelagic planktivore distributions in the water column and the diel feeding chronology reported for pelagic piscivores in the system (Beauchamp et al. 1992, Mazur and Beauchamp 2006). Most pelagic planktivores in Lake Washington either consolidate into hard-to-find schools or descend to deeper low-light refuges during daylight as predator avoidance behaviors. The planktivores begin to disperse from schools or ascend into the water column at dusk, become maximally dispersed and shallower at night, then reverse this pattern at dawn (Mazur and Beauchamp 2006, Quinn et al. 2012, Hansen and Beauchamp 2014b).

In May 2015 all predators were measured, weighed, subjected to gastric lavage, marked with a Floy tag, and released to increase the number of marked fish for the predator abundance estimate. During all other purse seining periods, all predators were euthanized before stomach, scale, and fin tissue for isotopes samples were taken and fork length and weight were recorded. In each set, pelagic planktivores were identified to species, enumerated either by counting or sub-sampling, and a subsample of planktivores were measured and kept. All diets and other samples were immediately placed on dry-ice to preserve quality.

Thermal experience and depth distribution – Monthly thermal experiences of cutthroat trout and northern pikeminnow were estimated using thermal profiles and depth distribution patterns. Thermal profiles, in 1 m increments from the surface to 60 m, are recorded multiple times daily by a solar-powered buoy operated by King County (King County, May 1, 2017). Depth distributions for cutthroat trout were estimated from the mean depth of acoustically-tagged trout (Clark et al. 2017, in prep). Depth distribution patterns for northern pikeminnow were inferred from catches in the monthly depth-stratified gill nets.

Isotope analysis – Isotope analysis was used to indicate the trophic position and energy pathway of predator and prey fishes and the size at which predators exhibit ontogenetic shifts in piscivory and reliance on benthic or pelagic prey. Fin clips from a range of sizes of each predator were submitted to the University of Washington Isolab for $\delta^{13}C$ and $\delta^{15}N$ analysis (for each species we sampled 10 fish from 200-300 mm and another 13 fish ≥300 mm covering the range of lengths evenly). A sample of sizes of the major prey species were also submitted for $\delta^{13}C$ and $\delta^{15}N$ analysis (*Table 1)*.

Diet analysis – We analyzed diets to determine the proportion of major prey categories present in each non-empty stomach sample and compiled average proportions for each year, month, and size class of cutthroat trout (*Table 2)* and northern pikeminnow *(Table 3*). Diets were preserved in a freezer until they were analyzed in the laboratory. All insects and aquatic invertebrates were identified at least to order and all fish were identified to species. Blotted, wet weight was measured for each prey category. For prey fishes, the number of fish in the diet was recorded and fork length of each intact fish was measured. Species-specific regressions of fish lengths to diagnostic bone lengths were compiled during diet analysis to reconstruct fish lengths for partially-digested fish or fish identified only from diagnostic bones. The presence of parasitic nematodes and all non-organic items was noted, but were not weighed or enumerated. For any month where low sample sizes or no diet was available, we used a linear interpolation from the preceding month to the succeeding month to estimate prey proportions.

Growth and size structure – We aged scales from 73 cutthroat trout and opercles from 101 northern pikeminnow as the first step in determining annual growth increments for each age class of fish ≥ 200 mm FL for inputs in the bioenergetics model simulations. Once a representative sample of each species was aged, we fit a von Bertalanffy growth curve to the length-at-age data with the "FSA" package in R (Ogle 2016) and used the fit parameters (cutthroat trout: L_∞ = 87.9702, K = 0.1483, and t_0 = -0.7654; northern pikeminnow: L_∞ =56.272, K = 0.167, and t_0 = -1.332) to calculate annual growth increments (Figure 3). These annual growth increments were then converted from fork length to wet-weight based on species-specific regressions empirically derived for cutthroat trout (r^2 = 0.96; N = 497):

$$W(g) = 0.000007 \cdot FL(mm)^{3.07}$$

and northern pikeminnow ($r^2 = 0.90$; N = 1193):

$$W(g) = 0.000009 \cdot FL(mm)^{3.05}$$

Population size structure was based on an annual survival rate estimated from a catch-curve analysis for cutthroat trout (S=33.2%, N=5 ages) and northern pikeminnow (S=69.0%, N=16 ages) (Figure 4). Purse seine catch, while limited to sampling in open water, is a non-size selective capture method of that habitat and thus was the source of length frequency of catch for the cutthroat trout catch-curve analysis (Figure 5). For northern pikeminnow, we corrected gill net catch for size and selective biases in net encounter and retention (Rudstam et al. 1984, Spangler and Collins 1992, Sorel et al. 2016) and used the resulting proportional length frequency in the catch-curve analysis (Figure 6).

Bioenergetics model – We used a bioenergetics model to link empirical diet, distribution, and growth data from predator samples to species-specific predation rates. Bioenergetics models use an energy balance equation where consumption is equal to the sum of growth, metabolism, and waste over a specified simulation period, while accounting for mass- and temperature-dependent physiological effects on metabolism, consumption, and temporal variability in diet composition. Estimated consumption rates can be fit to observed growth over a defined simulation period for each age class of predator using daily time steps to track changes in body mass, diet composition, and thermal experience. In this study, we targeted sampling to collect information on observed annual growth of each age class, monthly diet proportions and associated energy densities for each prey category (Mazur and Beauchamp 2006, McIntyre et al. 2006, Hovel et al. 2015), and thermal experience for both cutthroat trout (Table 2) and pikeminnow (Table 3). We used species-specific physiological parameters for cutthroat trout (Hewitt and Johnson 1987, Beauchamp et al. 1995, Mazur and Beauchamp 2006) and northern pikeminnow (Petersen and Ward 1999). Energy densities for the consumers were held constant at 6,268 J/g for cutthroat trout 200-299 mm, 6,819 J/g for cutthroat trout ≥300 mm, and 7,665 J/g for all northern pikeminnow. Energy densities for cutthroat trout and northern pikeminnow were calculated from bomb calorimetry measurements from a previous study of these population (J. McIntyre, unpublished data). We ran the model to fit consumption to annual growth increments for each age class of predator using January 1 as day 1 of the 365-d simulations. Simulations were performed for all age classes of predators that either grew into or started at sizes > 200 mm FL to cover the size ranges corresponding with individuals becoming increasingly piscivorous (200-299 mm FL) and predators that were maximally piscivorous (FL ≥ 300 mm; McIntyre et al. 2006). The output of the model provided estimates for feeding rate (% Cmax, the percentage of the theoretical maximum consumption rate for a consumer after accounting for the effects of temperature and body mass) and prey consumption (g of each prey eaten /day) for 7 age classes of cutthroat trout (Table 4) and 17 age classes of northern pikeminnow (Table 5).

To incorporate population size structure into the consumption estimate, a representative proportion of a unit population of 1,000 consumers was allocated to the age classes with a FL ≥300 mm, herein referred to as the unit population of ≥300 mm for each species. For cutthroat trout, the unit population included lake-ages 2-7 and for pikeminnow ages 3-18. Cutthroat trout exhibit some variability in age and size at recruitment to lake rearing, which adds variability to the initial size-at-age. Subsequent annual growth increments within the lake are more consistent and are the important inputs for fitting consumption estimates, which is why we chose to use lake-age for cutthroat trout for this analysis. The 200-299 mm age group for cutthroat trout was composed entirely of lake-age 1 fish. We back-calculated the proportional number of fish for lake-age 1 cutthroat trout by applying the annual mortality rate of 33.2% to the lake-age 2 cutthroat trout, assuming constant mortality across ages, which resulted in 2,014 cutthroat trout for the 200-299 mm group, herein referred to as the unit population of 200-299 mm cutthroat trout. Similarly, for 1,000 age 3-18 northern pikeminnow ≥ 300 mm FL, the corresponding abundance of 200-299 mm conspecifics was 1104, based on a back-calculated 69% annual survival to ages 1 and 2, herein referred to as the unit population of 200-299 mm northern pikeminnow.

Mortality Estimate

We scaled the unit population consumption estimate for each predator (consumption per 1,000 predators ≥ 300 mm FL for each species) up to match the corresponding absolute abundance estimates, and upper and lower confidence intervals for each predator, resulting in population consumption (biomass per year) for each predator (Cartwright et al. 1998). We partitioned the population consumption for each predator into numerical predation rates on key prey species by first identifying the mean size of prey consumed each month. The prey species, age class, and mean fork lengths were identified from diet analysis, and mean weights for relevant prey species and age classes were calculated from length-weight regressions generated from the catch of prey fishes in purse seine or mid-water trawl sampling.

Finally, we divided the monthly population-level consumption (kg/month) of a given prey species by the corresponding mean monthly weight of individual prey to compute a numerical monthly predation rate for each prey species and life stage. The monthly numerical predation rates for prey from each brood year were summed across each year. Because only one brood year of juvenile Chinook Salmon was ever present in Lake Washington, we assumed all Chinook Salmon consumed in a year were from the same brood year. Sockeye fry enter the lake primarily in February-April and leave the lake the following year in May, which leaves a period of several months when there are two brood years present in the lake (Kiyohara 2016, 2017). We calculated a mean monthly weight for each age class of sockeye when two distinct age classes were present. We allocated a proportion of consumption to each age class based on the ratio of sub-yearlings to yearlings present in diets.

Results

Predator Abundance Estimate

Mark-recapture abundance estimates- We marked 322 cutthroat trout from January 13, 2015 to May 17, 2015 and 327 cutthroat trout from January 18, 2016 to March 28, 2016. Marked cutthroat trout averaged 411 mm FL (range, 278-607 mm). Four were recaptured during sampling efforts from April 26, 2016 to October 27, 2016 and a total of 257 cutthroat trout were captured during the sampling period. Due to the time elapsed between the first marking period in 2015 and the capture/recapture period in 2016, we applied the annual survival rate of 33.2% to the cutthroat trout marked in 2015, which reduced the number of marked cutthroat trout from 2015 present in 2016 to 107. We used a Chapman-modified population estimation procedure to estimate a cutthroat trout population size of 22,791 $\geq$300 mm FL (95% CI; 16,791-40,038). Confidence intervals were calculated using a Poisson approximation (Ricker 1975).

We marked 163 northern pikeminnow from February 5, 2015 to July 24, 2015 and 80 pikeminnow from January 26, 2016 to May 17, 2016. Marked fish averaged 394 mm fork length (range, 275-545 mm). Four northern pikeminnow were recaptured during sampling efforts from May 23, 2016 to October 27, 2016 and a total of 350 northern pikeminnow were captured during the sampling period. Due to the amount time between the first marking period in 2015 and the capture/recapture period in 2016, we applied the annual survival rate of 69.0% to the marks in 2015, which reduced the number of marked fish from 2015 present in 2016 to 113. Again, we used a Chapman-modified population estimation procedure to estimate a northern pikeminnow population size of 13,582 ≥300 mm FL (95% CI; 9,743-24,106). Confidence intervals were calculated using a Poisson approximation (Ricker 1975).

Relative abundance and seasonal distribution of predators by depth and region- The relative abundance and seasonal distribution patterns of cutthroat trout and northern pikeminnow influence spatial-temporal overlap with prey fishes and the magnitude of their impact as predators. Catches of cutthroat trout in sinking gill nets were distributed across all depths during winter, but shifted to 10-20 m and 20-35 m depths during most of the thermally stratified period from May through October (Figure 7). Sinking gill net catches of northern pikeminnow were also distributed across all depths during winter, but shifted predominantly to 0-10 m during spring warming in April-June. During peak stratification, July-September, some northern pikeminnow remained in 0-10 m depth range but the majority shifted to 10-20 m depths before dispersing across all depths in October. The monthly longitudinal distribution of cutthroat was highly variable in both years compared to pikeminnow, which remained stable and more evenly spread across all areas (Figure 8). The variability in cutthroat could imply larger movements between areas, but could also be the result of variability associated with lower catches. The monthly longitudinal distribution of both predators does not suggest strong aggregative responses (e.g. smelt spawning in February-March at the mouth of the Cedar River in area 5; smolt emigration through areas 2-3 in May for sockeye or June-July for coho and Chinook Salmon).

The mean catch per unit effort (CPUE, catch per overnight gill net set) of northern pikeminnow decreased from 2015 to 2016 by 38%, yet it in both years CPUE of northern pikeminnow was significantly higher than for cutthroat trout. Mean CPUE for cutthroat was comparable in both years even though some months differed slightly. We calculated CPUE for cutthroat trout and pikeminnow by depth (Figure 7) and by area (Figure 8). The average ratio of CPUE was 6.4 northern pikeminnow to 1.0 cutthroat trout in 2015 and 4.5 to 1.0 in 2016. These CPUE ratios contradict the ratios between the mark-recapture abundance estimates of 1.0 cutthroat to 0.6 northern pikeminnow. During the target period, June-Aug, the average ratio of CPUE was 5.8 northern pikeminnow to 1.0 cutthroat trout in 2015 and 4.1 to 1.0 in 2016. The contrast between relative catch and abundance estimates suggests that the mark-recapture abundance estimate for northern pikeminnow was likely low. For this reason, we multiplied cutthroat the mark-recapture abundance estimate for cutthroat trout ≥300 mm FL by the average ratio of CPUEs for northern pikeminnow to cutthroat trout during target periods to produce an abundance estimate for pikeminnow. By this relative catch method, we estimated a population size of 112,816 northern pikeminnow ≥300mm in Lake Washington. We used both the point estimate of abundance from mark-recapture as well as this relative catch abundance estimate in our subsequent calculations for mortality.

Predation Rate

Isotope Analysis – Large cutthroat trout and northern pikeminnow were apex predators in the lake food web as indicated by δ^{15}N values that were 1.5-3.5‰ higher than the majority prey fishes and consumers at intermediate trophic levels, and both utilized benthic and pelagic energy pathways to varying degrees (Figure 9). For both cutthroat trout and northern pikeminnow, δ^{15}N values increased to an asymptote around 300-350 mm, indicating that both species became maximally piscivorous after attaining 300 mm FL (Figure 10). The wide variability in $\delta\ ^{13}$C across a broad range of fork lengths indicated that both predators initially relied on a mix of benthic and pelagic prey with larger cutthroat trout shifting to more pelagic prey fish, whereas larger northern pikeminnow shifted slightly to more benthic prey.

Consumption by size-structured unit populations of predators - The magnitude of predation on juvenile salmon and other prey fishes varied considerably among months and between cutthroat trout and northern pikeminnow, small and large size classes of each predator species, and between years (Figures 11, 12). The predicted consumption patterns were largely driven by temperature. Behavioral thermoregulation by cutthroat trout, a coldwater species, resulted in moderately depressed consumption rates during colder thermally-mixed periods compared to consumption during peak summer stratification and progressive destratification during the fall. In contrast, northern pikeminnow, a coolwater species, consumed very little during cold mixed periods, then consumption increased rapidly during April-May, remained at high levels during June-October, then declined rapidly during the latter stages of destratification in November, returning to low consumption rates from December through March (Figure 12).

Because the mark-recapture based abundance estimates targeted predators ≥300 mm FL, we computed predation rates based on a size-structured unit population 1,000 predators of each species ≥300 mm FL. However, because smaller individuals of both species started to become piscivorous within the 200-299 mm FL size range, we added the consumption by these more numerous smaller predators to account for the predation impact by the full range of sizes that potentially ate juvenile salmon. Consequently, we added the consumption associated with the abundance of 200-299 mm predators (2,015 younger cutthroat trout and 1,104 younger northern pikeminnow) to correspond with an assumed stable age and size structure of 1,000 predators ≥300 mm FL from each species.

Consumption by cutthroat trout– Consumption of sockeye by the unit population of cutthroat trout 200-299 mm in 2015 was relatively high compared to larger conspecifics, but there was no observed consumption of Chinook Salmon (Table 6). Consumption of sockeye in 2015 occurred in January and July-December with the peak in October (Figure 11). In 2016, consumption of sockeye was relatively low and was the only identified salmonid consumption by cutthroat trout 200-299 mm, though unidentified salmonids were also consumed. Consumption in 2016 of sockeye occurred in January and December, while consumption of unidentified salmonids occurred only during June. Consumption by the unit population of cutthroat trout 200-299 mm in 2015 was primarily composed of zooplankton, insects, longfin smelt, and threespine stickleback. Consumption by cutthroat trout 200-299 mm in 2016 was primarily composed of zooplankton, longfin smelt, insects, and other fish.

The consumption of sockeye by the unit population of cutthroat trout ≥300 mm occurred during most months of both years, but was notable during May-December 2015 with peaks in July and October (Figure 11). In 2015, Chinook Salmon consumption occurred in June. In 2016, sockeye consumption by cutthroat trout ≥300 mm occurred during January-March, June, and

September-December with the peak in September. Consumption of Chinook Salmon occurred in May and August 2015, and May, June, and September 2016. Consumption of Chinook Salmon peaked in May of both years, though it was much higher in 2016 than in 2015. In 2015, consumption by cutthroat trout ≥300 mm was primarily composed of longfin smelt, stickleback, other fish, insects. In 2016, consumption by cutthroat trout ≥300 mm was primarily composed of longfin smelt, sculpin, stickleback, mysids, and zooplankton. The other fish category for ≥300 mm cutthroat trout in March-April of both years was dominated by sunfish (e.g. bluegill *Lepomis macrochirus*, pumpkinseed *L. gibbosus*), while in May-July it was bolstered primarily by larval fish that were partly digested and difficult to identify. We assumed these larval fish were either longfin smelt or yellow perch, both of which were identified in other diets and caught in the purse seine during these same months.

Consumption by northern pikeminnow – No consumption of sockeye or Chinook Salmon occurred in 2015 by the unit population of northern pikeminnow 200-299 mm, though there was a small amount of consumption of unidentified salmonids in December 2015 (Table 6, Figure 12). In 2016, consumption of coho by northern pikeminnow 200-299 mm was very high, while sockeye consumption was relatively low, and there was a small amount of consumption of unidentified salmonids. Consumption in 2016 of coho occurred in June, consumption of sockeye occurred in April, and consumption of unidentified salmonids occurred in January, February, and December. Consumption by the unit population of northern pikeminnow 200-299 mm in 2015 was primarily composed of longfin smelt, insects, zooplankton, and other fish. Consumption by northern pikeminnow 200-299 mm in 2016 was primarily composed of longfin smelt, other fish, and coho. Results for 200-299mm northern pikeminnow, especially pertaining to salmonid consumption, were informed by low sample sizes and should be interpreted with caution.

The consumption of sockeye by the unit population of northern pikeminnow ≥300 mm occurred during January-March, May-August, and October-December 2015, with peaks in August and October (Figure 12). In 2015, Chinook Salmon consumption occurred in May, June, and December. In 2016, sockeye consumption by northern pikeminnow ≥300 mm occurred during most months but was notable May-December. Consumption of Chinook Salmon occurred in May-July and October-December 2015, and occurred in most months of 2016 but was notable in May-July. Consumption of Chinook Salmon peaked in June 2015 and July 2016, though it was much higher in 2016 than in 2015. In 2015, consumption by northern pikeminnow ≥300 mm was primarily composed of longfin smelt, insects, crayfish, sunfish, and other fish. In 2016, consumption by northern pikeminnow ≥300 mm was primarily composed of longfin smelt, crayfish, insects, threespine stickleback and sunfish. The other fish category for ≥300 mm northern pikeminnow in both years was primarily larval fish that were mostly digested and difficult to identify. We assumed these larval fish were either longfin smelt or yellow perch, both of which were identified in other diets and caught in the purse seine during these same months.

Mortality Estimate

In 2015, mortality of lake entry 2015 sockeye (sub-yearling) was 20% of fry production and predation losses of lake entry 2014 sockeye (yearling) were 56% of pre-smolt production (Table 7). In 2016 mortality of lake entry 2016 sockeye (sub-yearling) was 44% of fry production and predation losses of lake entry 2014 sockeye (yearling) were 473% of pre-smolt production which coincided with an extremely low estimate of 78,000 presmolts in March 2016 (Clark et al. 2017).

The number of sockeye consumed did decrease slightly between 2015 and 2016, but decreases in sockeye production resulted in the much higher percentages of mortality and predation losses. Note, only lake entry 2015 represents the full predation burden on sockeye across their sub-yearling and yearling life stages in the lake.

In 2015 mortality was 14% of Chinook Salmon production and 36% in 2016. The abundance of Chinook Salmon in 2015 was ca. 40% less than in 2016, but predation increased more dramatically than abundance resulting in a larger predation impact on Chinook Salmon in 2016. The estimated number of sockeye consumed was substantially higher than that of Chinook Salmon in 2015, and while the difference was less drastic in 2016, the number of sockeye consumed was still more than 2x that Chinook salmon (Table 7).

2015 and 2016 estimates of the number of sockeye and Chinook Salmon consumed by the total population of northern pikeminnow are higher than that of cutthroat trout regardless of which abundance estimate is used for pikeminnow. The order of magnitude of difference between the two abundance estimates for northern pikeminnow, wherein the mark-recapture abundance estimate is ca. 10% of relative catch abundance estimate, produce considerably different results, but the trends between the two are identical (Table 7).

In both years, Cutthroat trout and northern pikeminnow consumed the larger age class of sockeye in the lake during the months when more than one age class of sockeye was present. Cutthroat trout consumed yearling sockeye during March-April, a mix of both sub-yearlings and yearlings (2:1 smolts to fry) in May, and solely sub-yearlings after May (Figure 13). Northern pikeminnow consumed yearling sockeye March-June, a mix of both size classes (1:2 smolts to fry) July-August, and consumed solely sub-yearling sockeye after August.

Discussion

This study presents the current state of knowledge on the abundance of cutthroat trout and northern pikeminnow in Lake Washington. Additionally, this project used bioenergetics modeling to extend the population abundance and create an annual predation rate. Given the thermal environment and abundance of predators, the calculated predation rates account for significant mortality of the brood years of juvenile sockeye salmon and Chinook salmon present in Lake Washington during the years of our study.

The lake wide abundance of cutthroat trout was calculated to be 22,791, and northern pikeminnow was 13,582 using a mark-recapture approach and 112,816 using a relative catch approach. Northern pikeminnow were generally more abundant in the nearshore areas sampled. The CPUE of northern pikeminnow in gill nets was significantly greater than of cutthroat in every month of both years, despite substantial fluctuations between years. The disparity in CPUE of each species could be caused by differential susceptibility of each species to gill nets (Spangler and Collins 1992) or a difference in benthic versus pelagic habitat use (Nowak and Quinn 2002). Due to this uncertainty related to susceptibility of cutthroat and pikeminnow in gill nets, we believe the abundance estimate produced from our relative catch approach is likely to be high. We also believe that the mark-recapture abundance estimate for northern pikeminnow is low. Our CPUE analysis and previous research on Lake Washington (Eggers et al. 1978) provide a reason for scrutiny of our mark-recapture abundance estimates, but the reason why we question the pikeminnow mark-recapture estimate is due to the low number of northern pikeminnow marked during this study. Using the metrics outlined by Robson and Regier (1964), 300 marks are required to estimate a population of 10,000. For a population of 100,000, the required number of marks is 1,100. There is uncertainty surrounding both abundance estimation approaches for pikeminnow, but we believe that taking the relative catch approach as an upper bound and the mark-recapture approach as a lower bound, given the bias of each, brackets the range for the population abundance.

While our regular gill net sampling at established sites provided us with some consistency across sampling, it also limited the scope of our sampling. We sampled at a regular monthly interval and at established sites, which allowed us to compare catch and samples across months, whereas randomized sampling would have introduced variability in the habitats sampled and therefore variability in catch and samples. If episodic predation occurred outside of the time of our sampling or increased predation occurred in specific locations not overlapping with our sampling, we would miss those events. If there are episodic or specific locations of high predation, we are likely underrepresenting them in this work.

The current populations of cutthroat trout and northern pikeminnow impose substantial mortality on both juvenile sockeye and Chinook salmon during the time when these juveniles reside in Lake Washington. Cutthroat trout and northern pikeminnow are estimated to account for up to 44% mortality for juvenile sockeye salmon, and up to 36% mortality for juvenile Chinook salmon. Predation on both juvenile sockeye and Chinook salmon was considerably higher by northern pikeminnow than predation by cutthroat trout. However, predation impacts varied among years and this could be attributed to inter-annual differences in recruitment of juvenile salmon and availability of alternative prey. Because longfin smelt were a large proportion of consumption for both species, the large variation in smelt abundance likely affected predation of other prey species. There was a weak year class of age 0 smelt in 2015 (1.2 million) and a strong year class in 2016 (32 million) (Hansen et al. 2016, Clark et al. 2017). The significantly greater abundance of age 0 smelt in 2016 could have elicited a targeted feeding response resulting in predators feeding more heavily on the small, translucent age 0 smelt. Hansen and Beauchamp (2014) described this response in regards to cutthroat predation on longfin smelt in Lake Washington during 2005-2006. We saw greater total predation on juvenile sockeye salmon by both species of predators ≥300 mm in 2015, than in 2016, and we hypothesize that this difference could be a targeted feeding response triggered by the large abundance of age 0 smelt that diverted predation away from sockeye salmon in 2016.

The variability may also be attributed to varying spatial distributions, temperature-dependent consumption rates, and seasonal and size-dependent diets. Diet analysis indicated that predation by both cutthroat trout and northern pikeminnow focused on yearling sockeye during winter-spring and sub-yearlings during summer and fall. This is ecologically important because both predators were consuming older juvenile sockeye that had already survived other sources of natural mortality and were thus more valuable to the population due to the higher probability of surviving to adulthood. Between 93-99% of fry do not survive to the presmolt stage assessed in late March, two months before the smolt migration to sea (Clark et al. 2017). Predation on this later life stage is likely to have a large effect on the sockeye population by reducing the numbers of smolts that leave the system.

Previous work in this system indicated that cutthroat trout and northern pikeminnow predation could constitute a significant portion of juvenile sockeye salmon mortality if either predator population was sufficiently large. Eggers et al (1978) and Brocksmith (1999) both concluded that northern pikeminnow were a dominant predator in the Lake Washington and pose large potential impact on juvenile sockeye salmon. Nowak et al (2004) examined diets and size structure of cutthroat trout in Lake Washington 1995-2000, and found that 'cutthroat trout could account for significant losses of juvenile sockeye salmon in the Lake Washington system if their population size were sufficiently large.' Our work shows that the current predation rate is high enough and that these populations are of sufficient size to cause significant mortality of sockeye salmon.

Predation on juvenile sockeye salmon by northern pikeminnow and cutthroat trout have been observed elsewhere, such as Cultus Lake in British Columbia. Similar to our findings, Ricker (1941) found that cutthroat trout predate upon sockeye salmon in most months of the year. In addition, Ricker found that the large abundance of northern pikeminnow could impact juvenile sockeye survival, but the predation rate by northern pikeminnow was fairly low due to the majority of predation occurring during fall and winter when water temperatures were cold. This is similar in that we saw pikeminnow predation on sockeye in spring and fall, but very little in summer. We also saw a drastic decrease in consumption by northern pikeminnow in late winter in Lake Washington. However, temperatures in Lake Washington stay warm much later into the fall, which means that northern pikeminnow consumption remains relatively high during the fall and overlaps with the high rates of predation on sockeye.

Both bioenergetics modeling and abundance estimation are important tools in management of natural resources as they both further our understanding of the role of individual species in ecosystem functions. The suite of inputs for bioenergetics modeling build a framework for examining the interactions among species and trophic levels, which allows us to identify key interactions in the ecosystem. By combining population estimates and bioenergetics models, we were able to examine population-level predation within a framework that can identify and quantify factors that contribute to or limit predation impacts on prey populations. There are also limitations to both energetics modeling and abundance estimation. Bioenergetics modeling relies on extrapolating from defined inputs to determine consumption. Scaling up the unit population consumption from bioenergetics to match the abundance estimates for each predator will magnify any bias or errors in the inputs. In this study, we relied on diet samples, growth, size structure, and distribution to empirically define and model the role of the predator populations.

Despite uncertainty, this study suggests that significant predation losses of juvenile sockeye salmon occur, but the magnitude of that predation is highly variable from year to year. Further evaluation of the timing and location of predation would increase the precision of predation mortality estimates. In addition, work to identify if episodic or predation ‘hot spots’ exist would further understanding of the predatory role of cutthroat trout and northern pikeminnow and would also identify other potential predators in the system. We designed this project to be comparable to previous studies in Lake Washington, and we encourage future work with methodologies conducive to comparison with existing data sets, as we believe that looking at trends in abundance and distribution for many species will be beneficial for guiding management of the lake.

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Tables

Table 1: Average δ^{13}C and δ^{15}N values for predators and major prey species listed alphabetically by common name. Life stage, number of each species, mean and average fork length (mm) are also shown.

Common Name	Species	Life stage	N	Average FL (mm)	Range FL (mm)	Average δN15	Average δC13
Crayfish spp.	*Pacifastacus spp.*		4	64.0	60-67	11.35	-25.32
Coastal Cutthroat Trout	*Oncorhynchus clarkii clarkii*	Juvenile	10	247.3	197-294	13.67	-26.42
Coastal Cutthroat Trout	*Oncorhynchus clarkii clarkii*	Adult	13	442.4	348-555	16.04	-26.64
Longfin Smelt	*Spirinchus thaleichthys*	Juvenile	5	n/a	n/a	13.82	-28.98
Longfin Smelt	*Spirinchus thaleichthys*	Adult	5	n/a	n/a	14.16	-31.24
Northern Pikeminnow	*Ptychocheilus oregonensis*	Juvenile	10	255.9	202-299	13.41	-26.48
Northern Pikeminnow	*Ptychocheilus oregonensis*	Adult	13	433.4	305-540	15.54	-25.46
Rock Bass	*Ambloplites rupestris*		6	201.0	172-230	14.14	-24.35
Sculpin spp.	*Cottus spp.*		5	32.1	25.1-52.3	14.40	-28.35
American Shad	*Alosa sapidissima*		5	408.6	360-443	12.26	-25.87
Smallmouth Bass	*Micropterus dolomieu*		5	405.4	290-521	15.12	-24.25
Sockeye Salmon	*Oncorhynchus nerka*	presmolt	5	103.6	88-118	12.41	-30.69
Threespine Stickleback	*Gasterosteus aculeatus*	Juvenile	3	32.4	32.2-32.7	13.78	-25.60
Threespine Stickleback	*Gasterosteus aculeatus*	Adult	5	n/a	n/a	12.61	-30.64
Yellow Perch	*Perca flavescens*	Juvenile	3	34.9	32.1-36.8	13.40	-24.66
Yellow Perch	*Perca flavescens*	Adult	5	250.6	229-278	13.42	-27.07

Table 2: Diet proportions (blotted-wet-weight) of two size-classes of cutthroat trout. n = number of non-empty stomachs, SOC = sockeye, COH = coho, CHI= Chinook Salmon, LFS = longfin smelt, YP = yellow perch, COT= sculpin spp., STB = three-spine stickleback, FSH = Other fishes, ZOO = zooplankton, INS = insects, MYS = mysids. Prey energy densities are shown below row headings. Energy densities for the consumer (cutthroat trout) was held constant at 6,268 J/g for lake-ages 1-2 (200-299 mm FL) and 6,819 J/g for lake-ages 3-7 (≥300 mm FL). All "-" represent measured zeroes.

	Day	Temp (C)	n	SOC	COH	CHI	SAL	LFS	YP	COT	STB	FSH	ZOO	INS	MYS
				6068	6768	6768	6768	5438	5464	4453	6605	4495	2435	3571	4107
								2015 Cutthroat trout (200-299 mm)							
W	1	8.82	*	0.00	-	-	-	0.10	0.00	-	0.01	0.02	0.29	0.58	0.00
Spring	46	8.62	*	0.00	-	-	-	0.05	0.00	-	0.00	0.01	0.15	0.79	0.00
	74	9.31	*	-	-	-	-	-	-	-	-	-	-	1.00	-
	105	10.98	1	-	-	-	-	-	-	-	-	-	-	0.06	0.94
Summer	135	12.97	11	-	-	-	-	0.74	-	-	-	0.00	0.14	0.12	-
	166	11.04	28	-	0.02	-	0.02	0.18	0.10	-	0.21	0.10	0.23	0.14	-
	196	10.56	10	0.01	0.01	-	-	0.21	0.19	-	0.37	0.19	0.02	-	-
Fall	227	10.54	1	-	-	-	-	-	-	-	-	-	-	-	1.00
	258	10.28	1	0.90	-	-	-	-	-	0.10	-	-	-	-	0.00
	288	13.83	35	0.01	-	-	-	0.03	0.00	-	0.04	0.04	0.66	0.22	0.01
W	365	9.5	*	0.01	-	-	-	0.35	0.00	-	0.02	0.02	0.33	0.28	0.00
								2016 Cutthroat trout (200-299 mm)							
W	1	8.82	*	0.01	-	-	-	0.35	0.00	-	0.02	0.02	0.33	0.28	0.00
Spring	46	8.62	3	-	-	-	-	0.66	-	-	-	-	-	0.34	-
	74	8.28	*	-	-	-	-	0.34	-	-	-	0.02	0.38	0.26	-
	105	10.25	*	-	-	-	-	0.19	-	-	-	0.03	0.57	0.22	-
Summer	135	11.48	17	-	-	-	-	0.03	-	-	-	0.04	0.76	0.18	-
	166	9.79	50	-	-	-	0.04	0.40	-	-	0.03	0.00	0.52	0.01	-
	196	9.67	28	-	-	-	-	0.04	-	-	0.09	0.02	0.77	0.04	0.04
Fall	227	9.64	1	-	-	-	-	-	-	-	-	0.90	-	-	0.10
	258	9.48	*	0.00	-	-	-	0.19	-	-	-	0.46	0.25	0.04	0.05
	288	13.29	34	0.00	-	-	-	0.38	-	-	-	0.02	0.51	0.09	0.00
W	365	8.28	*	0.00	-	-	-	0.36	-	-	-	0.01	0.25	0.38	0.00
								2015 Cutthroat trout (300-600 mm)							
W	1	8.82	*	0.03	-	-	-	0.34	-	0.01	0.07	0.03	0.17	0.34	0.02
Spring	46	8.62	5	-	-	-	-	0.36	-	-	0.00	-	0.02	0.61	-
	74	9.31	8	-	-	-	-	0.23	-	-	0.11	0.21	-	0.45	-
	105	10.98	3	-	-	-	-	-	-	0.31	0.04	0.62	-	-	0.03
Summer	135	12.97	49	0.03	-	0.03	0.01	0.71	-	0.01	0.09	0.04	0.02	0.02	0.03
	166	11.04	33	0.02	0.07	-	0.01	0.18	0.03	0.16	0.24	0.13	0.07	0.05	0.03
	196	10.56	11	0.09	-	-	0.02	0.17	0.16	0.25	0.08	0.10	0.09	0.02	0.02
Fall	227	10.54	13	-	-	0.00	-	0.09	-	0.08	0.00	0.13	0.08	0.08	0.54
	258	10.28	3	-	-	-	-	0.33	-	0.00	0.33	0.30	-	0.04	-
	288	13.83	34	0.07	-	-	-	0.24	-	-	0.26	0.06	0.28	0.04	0.06
W	365	9.5	*	0.10	-	-	-	0.30	0.07	-	0.19	0.09	0.14	0.08	0.03

	Day	Temp	n	SOC	COH	CHI	SAL	LFS	YP	COT	STB	FSH	ZOO	INS	MYS
				2016 Cutthroat trout (300-600 mm)											
W	1	8.82	*	0.10	-	-	-	0.30	0.07	-	0.19	0.09	0.14	0.08	0.03
Spring	46	8.62	8	0.13	-	-	-	0.36	0.14	-	0.12	0.13	-	0.13	0.00
	74	8.28	10	0.00	-	-	-	0.14	0.10	0.11	0.30	0.11	0.04	0.20	0.00
	105	10.25	8	-	-	-	-	0.13	0.12	0.25	0.25	-	-	0.00	0.25
Summer	135	11.48	37	-	0.01	0.10	0.01	0.01	0.08	0.20	0.21	0.08	0.10	0.04	0.16
	166	9.79	29	0.01	-	0.04	0.00	0.07	0.01	0.29	0.46	0.05	0.03	0.00	0.04
	196	9.67	35	-	0.03	-	-	0.17	-	0.23	0.26	0.01	0.11	0.05	0.15
Fall	227	9.64	8	-	0.09	-	-	0.00	0.13	0.40	-	0.00	-	0.00	0.37
	258	9.48	7	0.14	-	0.03	-	-	-	0.40	-	0.14	-	-	0.29
	288	13.29	80	0.06	-	-	-	0.41	-	0.04	0.01	0.04	0.35	0.08	0.02
W	365	8.28	*	0.06	-	-	-	0.38	0.04	0.02	0.03	0.05	0.18	0.22	0.01

Table 3: Diet proportions of two size-classes of northern pikeminnow. n = number of nonempty stomachs, SOC = sockeye, COH = coho, CHI= Chinook Salmon, LFS = longfin smelt, YP = yellow perch, COT= sculpin spp., STB = three-spine stickleback, FSH = Other fishes, ZOO = zooplankton, INS = insects, CRA = crayfish. Prey energy densities are shown below row headings. Energy densities for the consumer (northern pikeminnow) was held constant at 7,665 J/g. All “-“ represent measured zeroes.

	Day	Temp	n	SOC	COH	CHI	SAL	LFS	YP	SUN	STB	FSH	ZOO	INS	CRA
		(C)		6068	6768	6768	6768	5438	5464	4186	6605	4495	2435	4445	3318
2015 Northern Pikeminnow (200-299 mm)															
W	1	8.82	*	-	-	-	-	0.66	-	-	-	0.25	0.09	0.00	-
Spring	46	8.74	*	-	-	-	-	0.67	-	-	-	0.29	0.04	0.00	-
	74	9.40	3	-	-	-	-	0.67	-	-	-	0.33	-	-	-
	105	11.05	*	-	-	-	-	0.69	-	-	0.00	0.17	0.00	0.07	0.07
Summer	135	14.45	7	-	-	-	-	0.71	-	-	0.00	0.00	0.00	0.14	0.14
	166	19.17	3	-	-	-	-	-	0.33	-	-	-	-	0.67	-
	196	22.17	5	-	-	-	-	0.79	0.00	-	-	0.00	0.00	0.20	0.00
Fall	227	21.99	7	-	-	-	-	0.49	-	-	0.14	-	-	0.36	-
	258	19.03	6	-	-	-	-	-	-	-	-	-	0.15	0.68	0.17
	288	16.47	3	-	-	-	-	0.32	-	-	-	0.33	0.34	-	-
W	365	9.00	*	-	-	-	0.02	0.42	0.13	-	-	0.26	0.17	0.00	-
2016 Northern Pikeminnow (200-299 mm)															
W	1	8.91	*	-	-	-	0.02	0.42	0.13	-	-	0.26	0.17	0.00	-
Spring	46	8.63	4	-	-	-	0.05	0.52	0.25	-	-	0.18	-	0.00	-
	74	8.36	*	0.10	-	-	0.02	0.38	0.23	-	-	0.17	-	0.10	-
	105	11.54	5	0.20	-	-	-	0.24	0.20	-	-	0.16	-	0.20	-
Summer	135	16.23	4	-	-	-	-	-	-	-	-	0.25	0.74	0.01	-
	166	16.92	1	-	0.97	-	-	-	-	-	-	-	-	0.03	-
	196	20.01	*	-	0.49	-	-	-	-	0.15	-	0.35	-	0.01	-
Fall	227	21.85	1	-	-	-	-	-	-	0.30	-	0.70	-	-	-
	258	19.70	*	-	-	-	-	0.50	-	0.15	-	0.35	-	0.00	-
	288	15.94	4	-	-	-	-	1.00	-	-	-	-	-	0.00	-
W	365	8.35	*	-	-	-	0.01	0.80	0.06	-	-	0.13	-	0.00	-
2015 Northern Pikeminnow (300-600 mm)															
W	1	8.82	*	0.06	-	-	-	0.29	0.02	0.17	0.11	0.14	0.01	0.13	0.07
Spring	46	8.74	*	0.04	-	-	-	0.21	0.03	0.22	0.14	0.16	0.01	0.13	0.06
	74	9.40	37	0.03	-	-	-	0.13	0.03	0.26	0.18	0.18	-	0.14	0.06
	105	11.05	40	-	-	-	-	0.10	0.07	0.42	0.22	0.05	-	0.08	0.06
Summer	135	14.45	49	0.04	0.00	0.00	0.00	0.17	0.06	0.15	0.09	0.19	-	0.11	0.18
	166	19.17	70	0.03	0.06	0.02	0.03	0.14	0.03	0.11	0.10	0.07	-	0.25	0.17
	196	22.17	37	0.03	0.00	-	0.00	0.23	0.03	0.09	0.05	0.03	0.05	0.28	0.21
Fall	227	21.99	26	0.12	0.04	-	0.12	0.22	-	0.04	0.04	0.07	-	0.14	0.22
	258	19.03	19	-	-	-	0.00	0.12	0.05	0.15	0.13	0.10	0.10	0.17	0.18
	288	16.47	15	0.07	-	-	-	0.45	-	0.10	0.07	0.12	-	0.13	0.07
W	365	9.00	*	0.06	-	0.03	-	0.45	0.04	0.16	0.06	0.09	-	0.07	0.03
2016 Northern Pikeminnow (300-600 mm)															
W	1	8.91	*	0.06	-	0.03	-	0.45	0.04	0.16	0.06	0.09	-	0.07	0.03

	Day	Temp	n	SOC	COH	CHI	SAL	LFS	YP	SUN	STB	FSH	ZOO	INS	CRA
Spring	46	8.63	17	0.06	0.00	0.06	-	0.46	0.08	0.22	0.06	0.07	-	-	-
	75	8.36	18	-	-	-	-	0.25	0.07	0.16	0.21	0.19	-	0.06	0.06
Summer	106	11.54	52	0.05	0.02	-	0.04	0.08	0.06	0.16	0.35	0.11	-	0.14	0.00
	136	16.23	63	0.06	0.07	0.03	0.07	-	0.07	0.10	0.32	0.05	-	0.15	0.08
	167	16.92	42	-	-	0.04	-	0.02	0.07	0.06	0.28	0.05	-	0.16	0.31
	197	20.01	20	0.05	-	0.05	-	0.02	0.05	0.15	0.25	0.10	-	0.14	0.20
Fall	228	21.85	25	0.02	-	-	-	0.16	0.04	0.22	0.04	0.04	-	0.25	0.22
	259	19.70	21	-	0.00	-	-	0.24	0.05	0.12	-	0.02	0.33	0.11	0.13
	289	15.94	23	0.13	-	-	-	0.47	0.04	0.06	-	0.07	0.04	0.10	0.09
W	365	8.35	*	0.08	-	0.01	-	0.38	0.05	0.15	0.06	0.10	0.02	0.08	0.06

Table 4: Bioenergetics inputs of initial and final length and weight, output of percent maximum consumption (%Cmax), and annual consumption of all prey (total), sockeye, Chinook Salmon, longfin smelt, and three-spine stickleback by individual cutthroat trout lake-ages 1-7. Energy densities for the consumers (cutthroat trout) were held constant at 6,268 J/g for lake-ages 1-2 and 6,819 J/g for lake-ages 3-7.

					Annual consumption (g)				
Lake-age (years)	Initial FL (mm)	Initial weight (g)	Final weight (g)	%C_{max}	Total	Sockeye	Chinook	Longfin Smelt	Stickle-back
2015 Cutthroat Trout									
1	203	87	278	43%	1,852	194	0	271	111
2	296	278	582	39%	3,021	120	8	794	460
3	376	582	979	41%	4,906	189	14	1,294	732
4	446	979	1,442	42%	7,016	265	20	1,855	1,034
5	506	1,442	1,944	44%	9,236	345	27	2,445	1,350
6	557	1,944	2,461	45%	11,473	425	33	3,041	1,666
7	602	2,461	2,979	46%	13,672	504	40	3,626	1,976
2016 Cutthroat Trout									
1	203	87	278	49%	2,016	1	0	568	21
2	296	278	582	39%	3,072	141	42	625	411
3	376	582	979	40%	4,934	226	69	996	678
4	446	979	1,442	42%	7,003	321	99	1,407	977
5	506	1,442	1,944	43%	9,167	420	129	1,837	1,293
6	557	1,944	2,461	44%	11,339	519	161	2,267	1,611
7	602	2,461	2,979	45%	13,467	616	191	2,689	1,924

Table 5: Bioenergetics inputs of initial and final length and weight, output of percent maximum consumption (%Cmax), and annual consumption of all prey (total), sockeye, Chinook Salmon, longfin smelt, and three-spine stickleback by individual northern pikeminnow ages 1-18. Energy densities for the consumers (northern pikeminnow) were held constant at 7,665 J/g.

					Annual consumption (g)				
Age (years)	Initial FL (mm)	Initial weight (g)	Final weight (g)	%C$_{max}$	Total	Sockeye	Chinook	Longfin Smelt	Stickle-back
2015 Northern Pikeminnow									
1	182	69	162	63%	1,463	0	0	549	31
2	240	162	286	58%	2,360	0	0	904	51
3	290	286	432	55%	3,110	148	14	777	263
4	332	432	588	52%	4,002	190	18	988	341
5	367	588	747	51%	4,844	229	22	1,187	414
6	397	747	902	49%	5,617	264	26	1,368	482
7	423	902	1,050	48%	6,315	297	29	1,531	543
8	444	1,050	1,186	47%	6,936	325	31	1,676	597
9	463	1,186	1,310	46%	7,483	351	34	1,803	645
10	478	1,310	1,422	46%	7,961	373	36	1,915	687
11	491	1,422	1,522	45%	8,377	392	38	2,011	723
12	502	1,522	1,609	45%	8,736	408	39	2,095	755
13	511	1,609	1,686	44%	9,046	422	41	2,167	782
14	519	1,686	1,753	44%	9,312	435	42	2,229	805
15	526	1,753	1,811	44%	9,540	445	43	2,281	825
16	532	1,811	1,861	44%	9,735	454	44	2,327	842
17	536	1,861	1,904	44%	9,901	462	45	2,365	857
18	540	1,904	1,941	43%	10,043	468	45	2,398	870
2016 Northern Pikeminnow									
1	182	69	162	58%	1,221	8	0	485	0
2	240	162	286	52%	1,997	16	0	741	0
3	290	286	432	53%	3,228	160	56	629	426
4	332	432	588	51%	4,119	202	72	789	556
5	367	588	747	49%	4,955	241	88	938	679
6	397	747	902	47%	5,721	277	102	1,074	792
7	423	902	1,050	46%	6,409	309	115	1,196	895
8	444	1,050	1,186	45%	7,021	338	126	1,303	986
9	463	1,186	1,310	45%	7,559	363	136	1,398	1,067
10	478	1,310	1,422	44%	8,029	385	145	1,480	1,137
11	491	1,422	1,522	44%	8,437	404	153	1,552	1,198
12	502	1,522	1,609	43%	8,789	420	159	1,613	1,251

					Annual consumption (g)				
Age (years)	Initial FL (mm)	Initial weight (g)	Final weight (g)	%C_{max}	Total	Sockeye	Chinook	Longfin Smelt	Stickle-back
13	511	1,609	1,686	43%	9,093	435	165	1,666	1,297
14	519	1,686	1,753	43%	9,353	447	170	1,712	1,336
15	526	1,753	1,811	42%	9,576	457	174	1,751	1,370
16	532	1,811	1,861	42%	9,767	466	178	1,784	1,399
17	536	1,861	1,904	42%	9,930	474	181	1,812	1,423
18	540	1,904	1,941	42%	10,068	480	183	1,836	1,444

Table 6: Annual consumption (kg) of prey species by unit population of cutthroat and pikeminnow in 2015 and 2016 in L. Washington. Each panel represents a size structured unit population of consumers.

Annual Consumption of prey species (kg)	**Cutthroat Trout**				**Northern Pikeminnow**			
	200-299 mm		**≧300 mm**		**200-299 mm**		**≧300 mm**	
	2015	**2016**	**2015**	**2016**	**2015**	**2016**	**2015**	**2016**
Sockeye	60	1	153	183	0	13	226	238
Chinook	0	0	11	56	0	0	22	87
Coho	14	0	23	46	0	293	64	38
Unid. Salmonids	5	11	15	3	3	3	99	40
Stickleback	408	40	591	542	43	0	410	672
Smelt	665	1098	1037	804	765	650	1172	926
Perch	180	0	103	204	98	30	130	260
Sculpin	4	0	263	688	0	0	0	0
Sunfish	0	0	0	0	0	156	602	616
Other fish	235	535	577	230	223	430	452	309
Zooplankton	1123	1525	392	461	236	97	104	277
mysid	239	68	291	463	0	0	0	0
Crayfish	0	0	0	0	79	0	699	744
Insects	930	620	477	300	567	24	809	689
Total	3,864	3,899	3,934	3,981	2,016	1,694	4,789	4,896
# of consumers in unit population	2,014	2,014	1,000	1,000	1,102	1,102	1,000	1,000

Table 7: 2015 and 2016 estimates of the number of juvenile sockeye and Chinook Salmon consumed by total population of cutthroat trout and northern pikeminnow FL ≥300 (mm) in L. Washington. Prey population and percent of prey population consumed are also shown. Predation on sockeye fry was defined as occurring between March of the year of lake entry and March of the following year. Predation that took place after this period was defined as sockeye pre-smolt predation. Of note, sockeye that entered Lake Washington in 2015 overlapped with this study for the full fry and presmolt periods in the lake, while sockeye that entered the lake in 2014 and 2016 only overlapped with this study for either the fry or presmolt period. *Northern Pikeminnow predation is based on catch ratio abundance estimate.

	Lake entry year for sockeye			**Lake entry year for Chinook**	
Prey abundance	2014	2015	2016	2015	2016
Fry	38,734,171	18,298,995	5,531,477	1,849,861	3,147,078
Presmolts	620,000	78,000	-		
Cutthroat Pred. 2015	12,924	442,262		30,558	
Pikeminnow Pred. 2015*	394,593	3,111,296		225,055	
Cutthroat Pred. 2016		72,782	340,596		125,129
Pikeminnow Pred. 2016*		313,742	2,068,313		1,007,846
Mortality as a % of fry production	0.16%	20%	44%	14%	36%
Predation loss as a % of presmolt production	56%	473%	-		
Pikeminnow predation based on Mark/Recapture abundance estimate					
2015	47,505	374,572		27,095	
2016		37,772	249,006		121,335

Figures

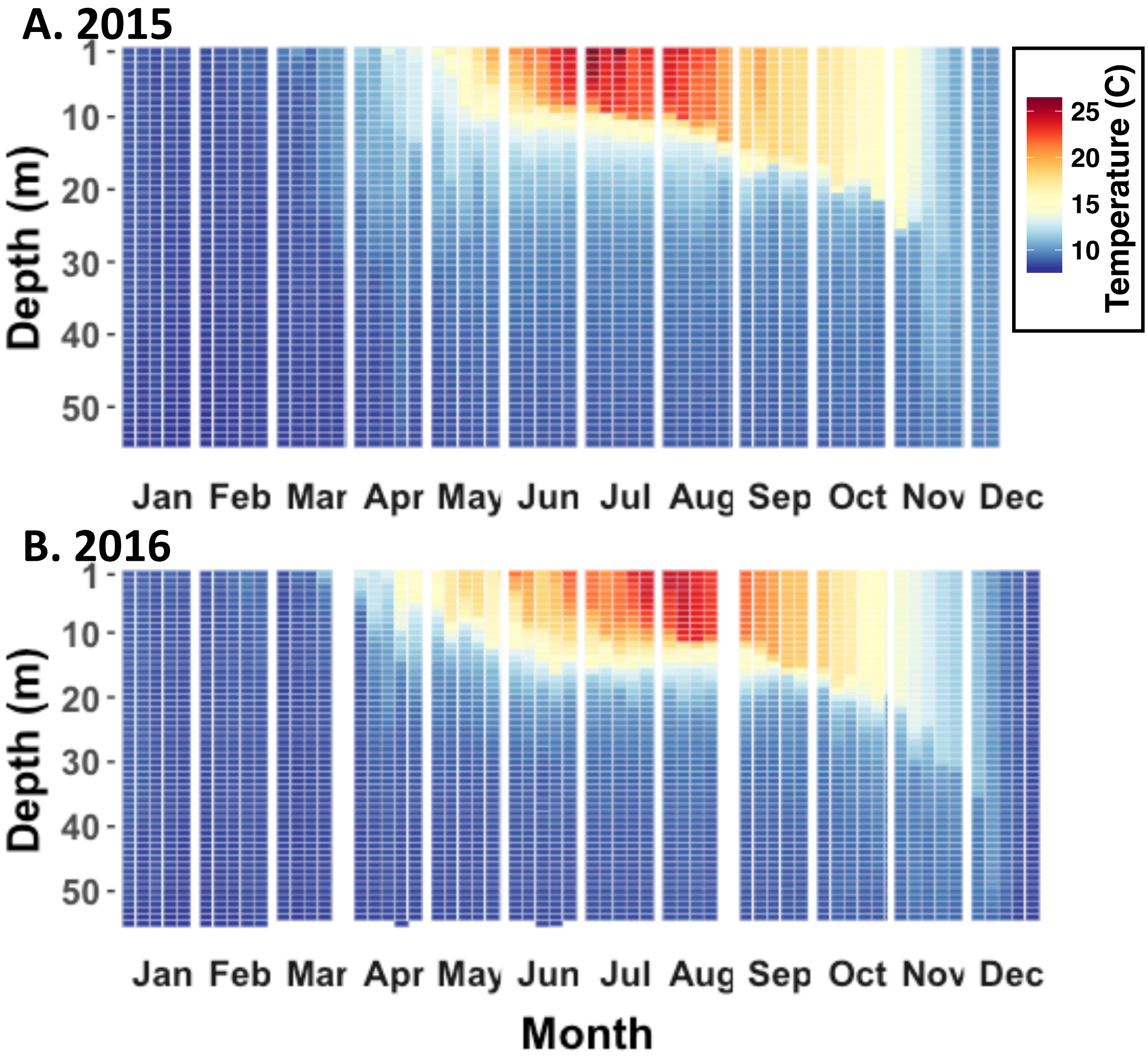

Figure 2: Mean temperature (Celsius) at depth (meters) per week for 2015 and 2016 in L. Lake Washington.

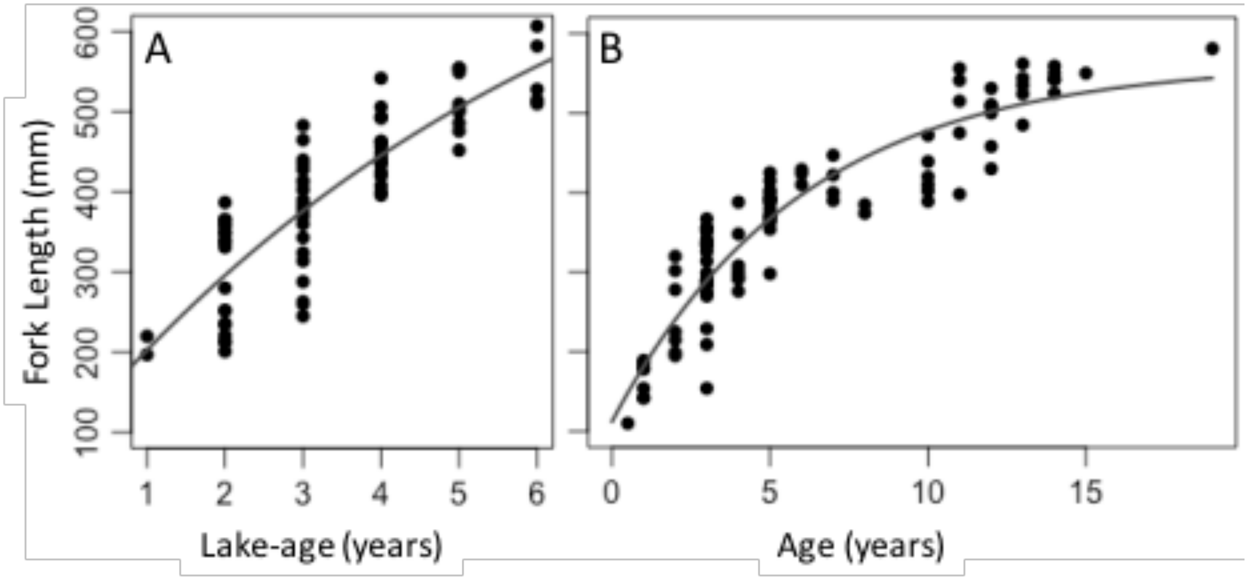

Figure 3: Fork length (mm) at age and Von Bertalanffy curves for cutthroat trout (A) aged from scales and northern pikeminnow (B) aged from opercle in L. Washington.

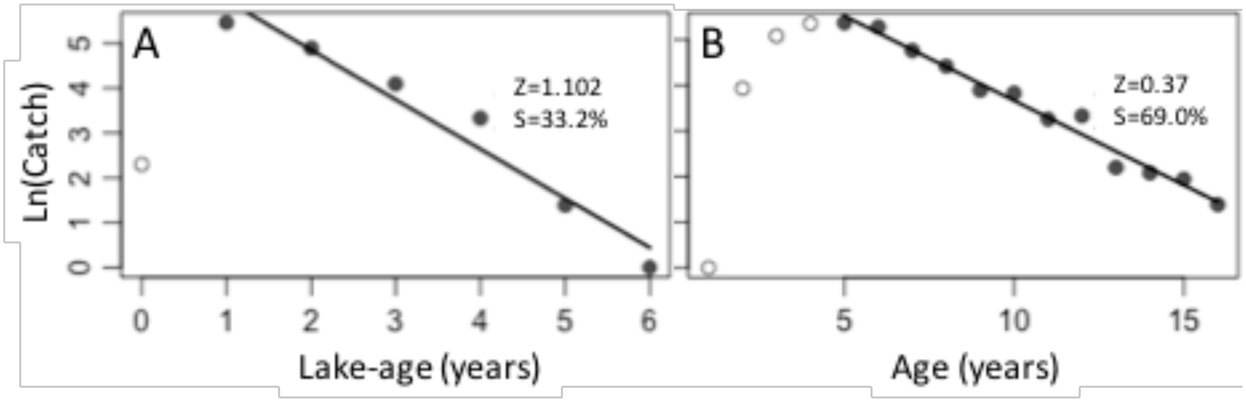

Figure 4: Catch curve analysis of cutthroat trout (A) and northern pikeminnow (B) with estimates of instantaneous mortality 'Z' and annual survival rate 'S' shown for each.

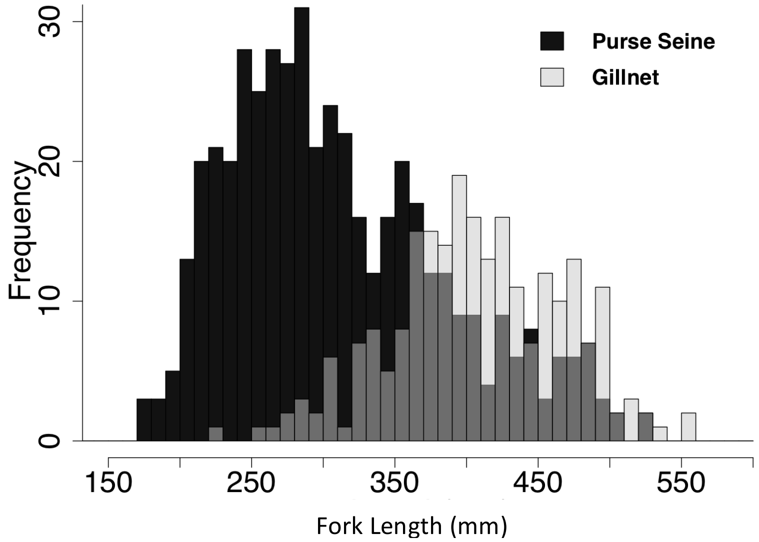

Figure 5: Cutthroat trout size distribution from purse seine and gill net catch in L. Washington. Dark gray bars represent overlapping, but independent frequencies for purse seine and gillnet samples. Note size selective bias of gill net catch. Cutthroat FL <250 (mm) were not susceptible to catch in gillnets.

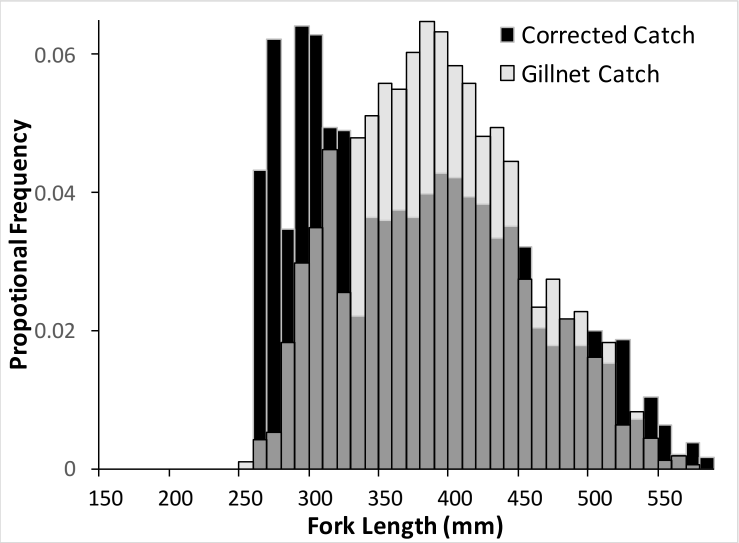

Figure 6: Northern pikeminnow size distribution from gill net catch in L. Washington and corrected catch for bias based on swimming speed and activity. Dark gray bars represent overlapping, but independent frequencies for catch and corrected catch of pikeminnow in gillnets. Pikeminnow FL <250 (mm) were not susceptible to catch in gillnets and therefore were not represented.

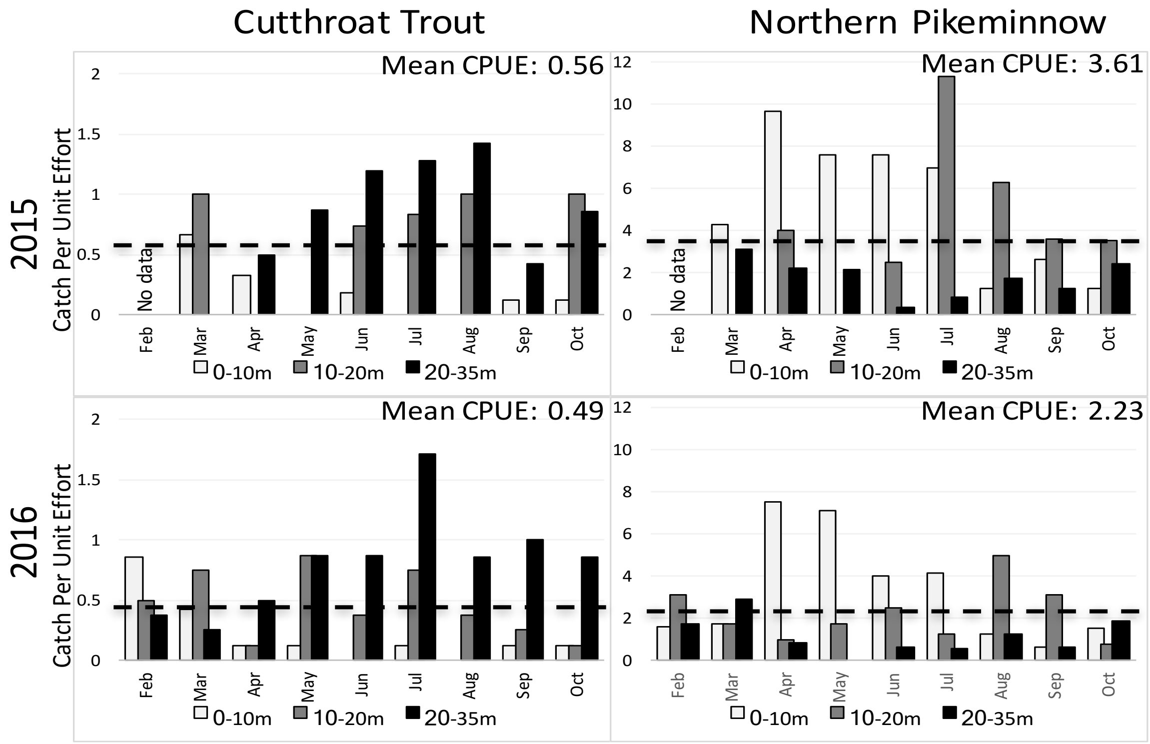

Figure 7: Catch per unit effort of cutthroat trout and northern pikeminnow in depth bins by month in 2015 and 2016 in L. Washington. Depth bins are defined as follows: 0-10 meters, 10-20 meters, and 20-35 meters.

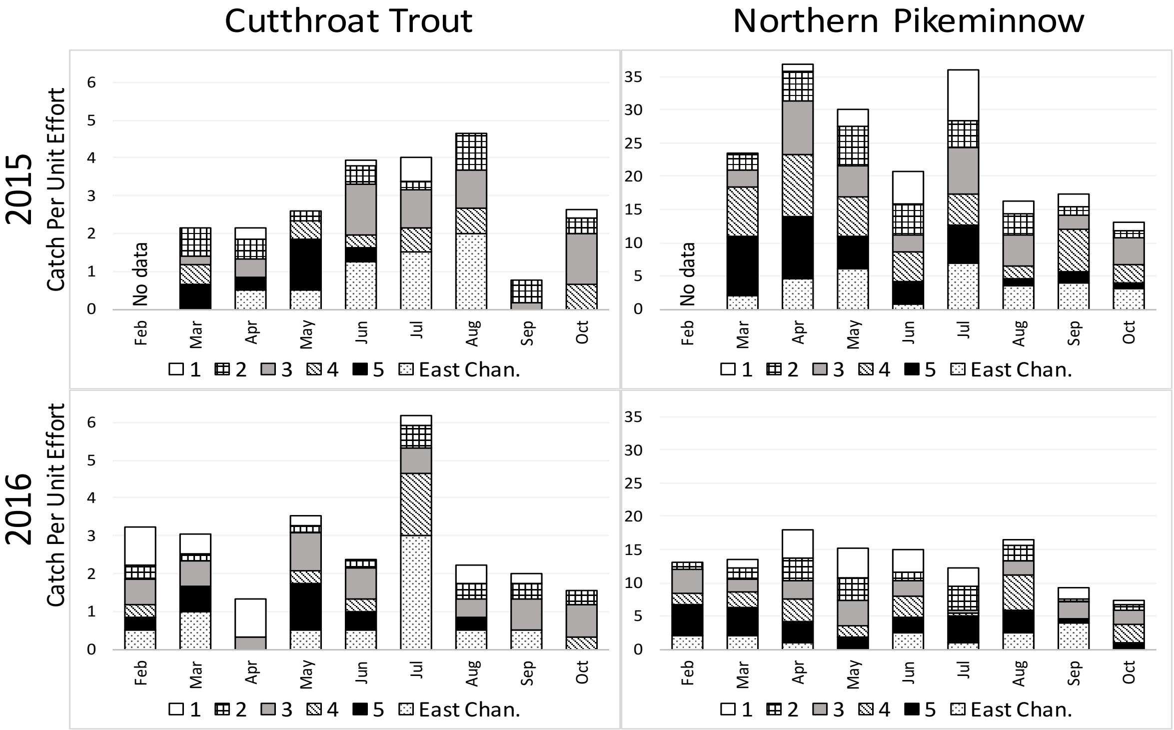

Figure 8: Catch per unit effort of cutthroat trout and northern pikeminnow by month in 2015 and 2016 in each of the 6 areas of L. Washington. Areas are defined as follows: 1-North end of lake to Sand Point; 2-Sand Point to 520 Bridge; 3-520 Bridge to I90 Bridge; 4- I90 Bride to south end of Mercer Island on west side of Mercer Island; 5- South

end of Mercer Island to south end of lake; East Channel- I90 Bride to south end of Mercer Island on east side of Mercer Island.

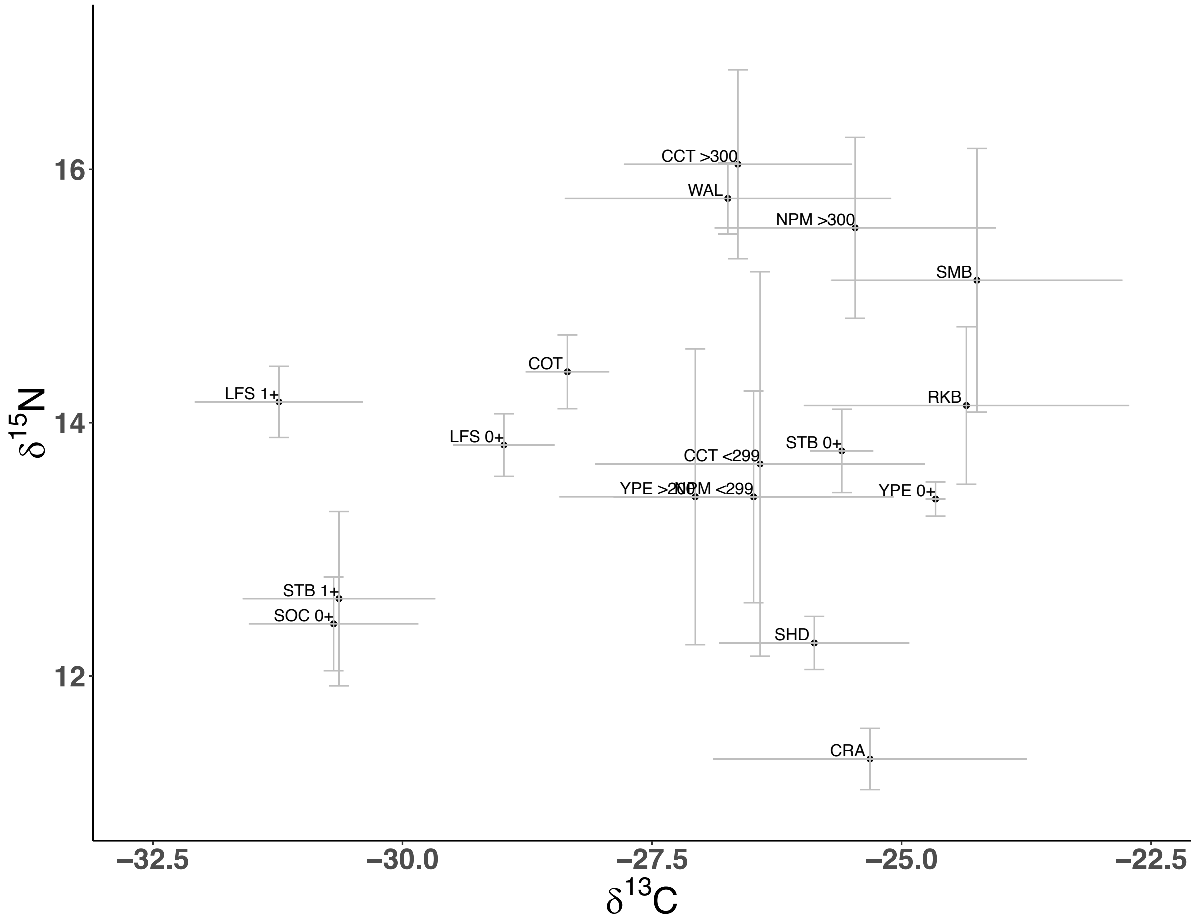

Figure 9: Stable isotope values for δ13C and δ15N of relevant species in L. Washington. Mean and standard of each species is shown. N=3-5 for each species with the exception of cutthroat trout and pikeminnow (N= 23 per species and size group). Species abbreviations are as follows: CCT- cutthroat trout; CRA- crayfish, COT- Cottidae spp.; LFS- longfin smelt (age zero or one); LMB-largemouth bass; NPM- northern pikeminnow; RKB- rock bass; SHD- American shad; SMB- smallmouth bass; SOC- sockeye salmon; STB- stickleback; WAL- Walleye; YLE- Yellow Perch.

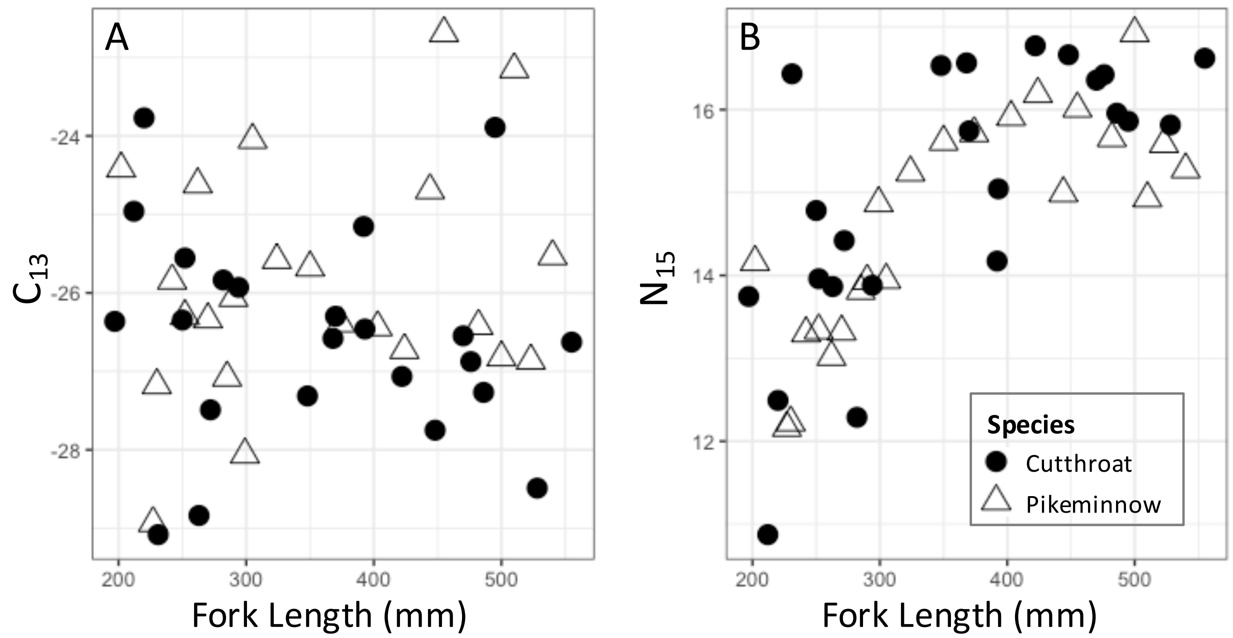

Figure 10: Stable isotope values for δ13C (A) and δ15N (B) of individual cutthroat trout (circles) and northern pikeminnow (triangles) as a function of fork length (mm).

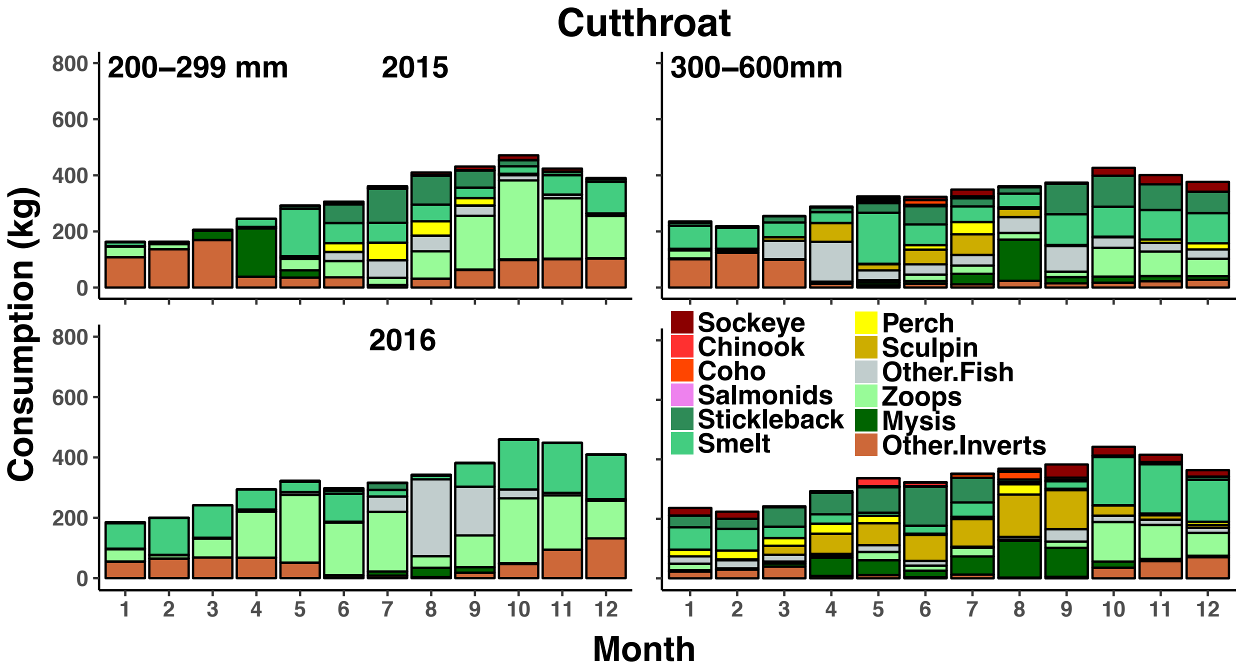

Figure 11: Consumption (kg per month) by cutthroat trout in 2015 and 2016 in L. Washington. Each panel represents a size structured unit population of 2,014 (200-299 mm) or 1,000 (300-600 mm) consumers.

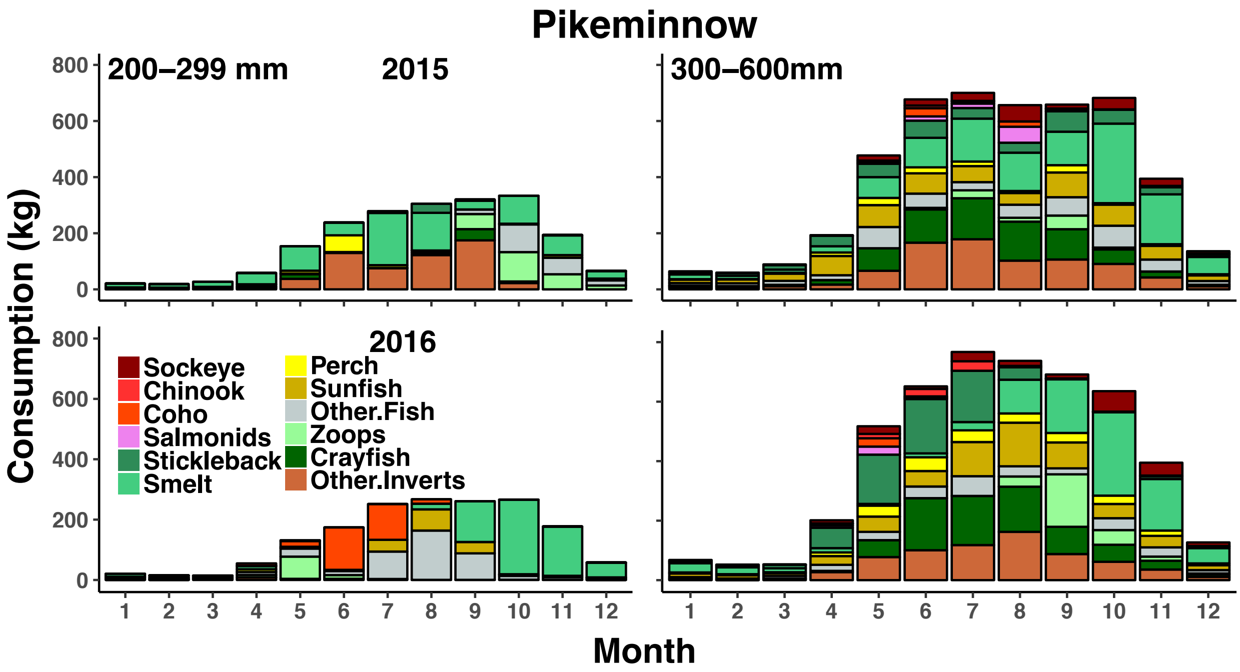

Figure 12: Consumption (kg per month) by northern pikeminnow in 2015 and 2016 in L. Washington. Each panel represents a size structured unit population of 1,102 (200-299 mm) or 1,000 (300-600 mm) consumers.

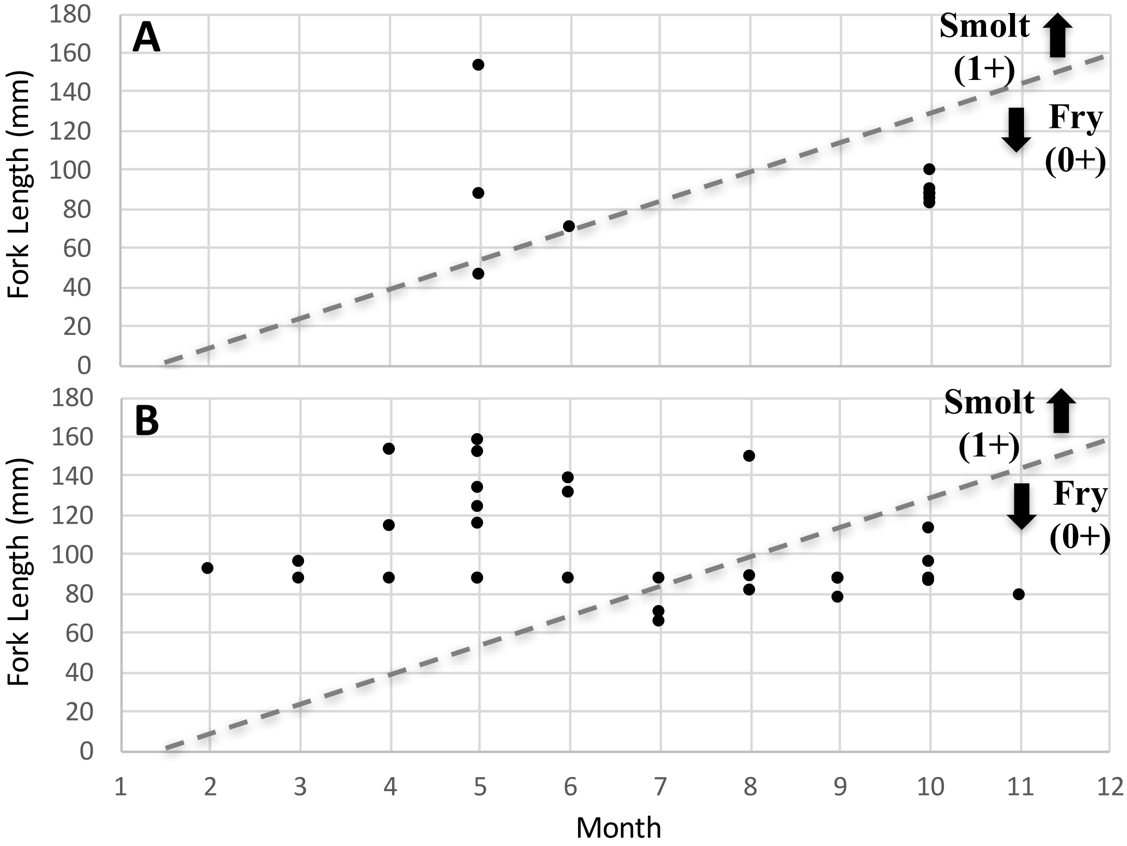

Figure 13: Fork length of sockeye by month from stomach samples of cutthroat trout (A) and northern pikeminnow (B). Dashed lines represent fry - smolt distinction, which was determined from catch in multiple gear types.