Predation impacts of lake trout and Chinook salmon in Lake Chelan, Washington: Implications for prey species and fisheries management

Erik R. Schoen
David A. Beauchamp

Washington Cooperative Fish and Wildlife Research Unit
US Geological Survey
University of Washington
Box 355020
Seattle, WA 98195

Table of Contents

Executive Summary

The 2007 Lake Chelan Fishery Plan charges fishery managers to prioritize the conservation and restoration of native species, while maintaining healthy recreational fisheries. Achieving these goals requires an accurate understanding of the relationships between the major predators and their prey in the lake. The aim of this study was to provide guidance to managers by identifying the major predators of salmonids in the lake, quantifying spatial, seasonal, and size-structured patterns of predation, and describing trends in lake trout harvest and population dynamics. We quantified lake trout and Chinook salmon predation during the 2004-06 sampling period, and used population models to forecast lake trout population dynamics.

Lake trout were the most important predator on kokanee and other salmonids, consuming substantial numbers of salmonids in both basins of Lake Chelan. Burbot, northern pikeminnow were less important predators of salmonids. No salmonid prey were detected in smallmouth bass diets. No westslope cutthroat trout were detected in diets of any fish species.

Lake trout predation patterns differed markedly between lake basins. Lake trout grew larger on average in Lucerne Basin than in Wapato Basin, but lake trout density was nearly 8-fold greater in Wapato Basin. Lake trout in Lucerne Basin consumed mostly fish, including large proportions of kokanee. In the Wapato Basin, lake trout consumed primarily *Mysis* during most of the year, but switched to kokanee when seasonally available during spring. The largest size class of lake trout (> 550 mm fork length, age ≥ 10 yr) was responsible for 63% of kokanee consumption in Lucerne Basin and 97% of kokanee consumption in Wapato Basin. We estimated annual consumption rates for size-structured "unit populations" of 1,000 lake trout (> 180 mm FL, age 2-16 yr). In Lucerne Basin, annual consumption was approximately 4,764 kokanee and 138 Chinook salmon annually per 1,000 lake trout. In Wapato Basin, annual consumption was approximately 1,198 kokanee and 1,057 lake trout per 1,000 lake trout. However, taking into account the 8-fold higher density of lake trout in the Wapato Basin, lake trout predation on kokanee was actually 1.8 times higher per unit area in Wapato Basin than in Lucerne Basin.

We also estimated predation by Chinook salmon based on limited data from Lake Chelan and information from other lakes. The diet of Chinook salmon was mostly composed of *Mysis* (~62%), and contained only roughly 5% kokanee. Bioenergetic simulations estimated that Chinook salmon consumed approximately 741.2 kg of kokanee annually, per 1,000 predators (ages 1-4). This corresponded to approximately 7,910 age-1 kokanee per 1,000 Chinook salmon, or 7.6% of the age 1 population in August 2005. If management goals include rebuilding the Chinook population, these estimates can serve as a guideline for keeping predation rates in balance with kokanee abundance.

Recent predation patterns have been driven by the large cohorts of lake trout stocked during the 1990s. As these fish aged and grew in the 2000s, the total abundance of lake trout declined, but the numbers of large fish increased substantially. In 2000, only one cohort had reached the largest, most piscivorous size class. By 2008, nine cohorts had achieved this size. As the biomass of predators steadily increased, kokanee escapement declined by 80% between 2003 and 2008. Predation pressure is likely near its peak and will decline slightly between 2010 and 2013, due to mortality of the large, stocked fish. The younger, naturally spawned cohorts of lake trout appear to be smaller, but how much smaller is a critical unknown. We present limited data showing a reduction in recruitment and total abundance, and we recommend further monitoring to track this trend. The lake trout population is a valuable resource, and quantifying

the rate of natural reproduction carries important benefits for the lake trout fishery as well as for the conservation of prey species. Implementing a monitoring program will enable managers to determine the population trajectory of lake trout after the expected temporary decline in lake trout numbers, and avoid a destabilizing rapid expansion of the lake trout population, similar to the recent occurrences in Lake Pend Oreille ID, Flathead Lake MT, and Yellowstone Lake WY.

We recommend the following steps to achieve the management goals for Lake Chelan fisheries. First, begin monitoring trends in lake trout density, distribution, and size structure. Second, assess the recruitment and abundance of kokanee in the lake, ideally with an annual hydroacoustics survey during summer stratification. Third, develop a plan to control lake trout population growth, in case this becomes necessary. Fourth, if rebuilding the Chinook salmon fishery is a management goal, consider waiting until the kokanee population rebounds, and then start slowly.

List of Tables

List of Figures

Introduction

In many western North American lakes, balancing non-native predators with prey populations presents a classic fishery management dilemma. While introduced apex predators such as lake trout (*Salvelinus namaycush*) support popular fisheries, they often also prey heavily on native and sport fishes (Eby et al. 2006; Martinez et al. 2009; Ruzycki et al. 2003). The introduced opossum shrimp *Mysis relicta* compounds these effects in many systems by competing with planktivorous fish and boosting predator populations (Lasenby et al. 1986; Nesler and Bergersen 1991). The effects of introduced species on lake ecosystems can be difficult to predict. Lake trout and *Mysis* have coexisted with prey species such as kokanee (*Oncorhynchus nerka*) for decades in some lakes, often with support from hatchery stocking (Johnson and Martinez 2000; Richards et al. 1991). In other systems, the food web impacts of these introduced species have been severe, leading to the extirpation of kokanee (Bowles et al. 1991; Spencer et al. 1991) and bull trout (Donald and Alger 1993), and inhibiting the recovery of native cutthroat trout (*O. clarki*) (Al-Chokhachy et al. 2009; Vander Zanden et al. 2003). Aggressive lake trout removal programs have recently been instituted in some lakes to reduce predation rates (Bigelow et al. 2003; Hansen et al. 2008; Martinez et al. 2009).

Quantifying piscivore consumption rates can be a valuable tool for assessing impacts on prey populations (Stewart et al. 1981), limiting environmental factors (Beauchamp and Van Tassell 2001), and the effectiveness of management strategies (Johnson and Martinez 2000; Luecke et al. 1994; Ruzycki et al. 2003). The trajectory of predator population growth is another important factor affecting prey populations. For example, while some introduced lake trout populations achieve rapid growth (Hansen et al. 2008), others become self-sustaining and relatively stable, and still others exhibit little natural reproduction and remain reliant on stocking (Hassler et al. 1986; Ruzycki et al. 2001). Quantifying the consumption rates and population trends of piscivores is an important step towards successful management of these systems (Beauchamp et al. 2007).

Lake Chelan is the largest natural lake in Washington, and represents an important fisheries and recreation resource for the state. The lake contains a remnant population of native westslope cutthroat trout (*Oncorhynchus clarki lewisi*) and introduced populations of kokanee, lake trout, and landlocked Chinook salmon (*O. tshawytscha*), all of which are targeted by anglers (DES 2000; Hagen 1997). Many of these species are also influenced by the introduced population of *Mysis relicta* (Schoen 2007). Fisheries managers face a complex task in meeting the management goals for Lake Chelan, which prioritize the conservation and restoration of native species, while maintaining healthy recreational fisheries (Chelan PUD 2007). Achieving these potentially competing priorities depends on a detailed and accurate understanding of the interactions between piscivores and prey species in the lake. Previous research suggested that kokanee were not predominately food limited in Lake Chelan when their abundance was relatively high (Schoen 2007). Thus, recent declines in kokanee escapement (Keesee et al. 2009) prompted further study on the impacts of predation.

In this study, we characterize piscivory by lake trout and other species in Lake Chelan. Our specific goals were 1) to identify the major predators of salmonids in the lake, with a focus on predators of kokanee and westslope cutthroat trout, 2) to quantify the spatial, seasonal, and size-structured patterns of predation, and 3) to describe trends in lake trout abundance and

harvest and provide a baseline for future comparison. Based on our findings, we provide recommendations for policy actions and further research.

Study Area

Lake Chelan is a deep (maximum depth 453 m), glacially-formed lake located in the Cascade Range in north-central Washington (48° N, 120° W; Figure 1). The lake is long and narrow (length 81 km, maximum width < 3 km), and is composed of two basins joined by a narrow channel. Lucerne Basin in the northwest is extremely deep and steep-sided (mean depth 190 m), while Wapato Basin in the southeast is relatively broad and moderately deep (mean depth 45 m; Figure 2; Kendra and Singleton 1987). The two lake basins also differ slightly in thermal regime, as expected given the difference in depth and volume (Wetzel 1983); the deeper Lucerne Basin begins to stratify approximately one month later and has cooler surface water during peak stratification (approx. 17º vs. 19º C) than the shallower Wapato Basin (Pelletier et al. 1989). Both lake basins are ultraoligotrophic (total phosphorus averages 3.2 µg/L), and Wapato Basin is slightly more productive than the Lucerne Basin. Lake Chelan is slightly less transparent than other lakes of similarly low productivity due to small amounts of glacial flour in the water (annual mean Secchi depth 13 m; Pelletier et al. 1989).

Native fish species in Lake Chelan include bridgelip sucker (*Catostomus columbianus*), burbot (*Lota lota*), largescale sucker (*Catostomus macrocheilus*), northern pikeminnow (*Ptychocheilus oregonensis*), peamouth (*Mylocheilus caurinus*), slimy sculpin (*Cottus cognatus*), threespine stickleback (*Gasterosteus aculeatus*), and westslope cutthroat trout. Bull trout (*Salvelinus confluentus*) were native to Lake Chelan but became extirpated c. 1950. Westslope cutthroat trout were once the dominant sport fish in the lake, but populations collapsed during the mid-20th century due to excessive egg takes, overfishing, the introduction of rainbow trout (*Oncorhynchus mykiss*), and loss of spawning habitat due to flooding and dam operations (Brown 1984). Many nonnative fish and invertebrate species have been introduced to the lake, primarily to enhance sport fisheries, including landlocked Chinook salmon, kokanee, lake trout, *Mysis relicta*, rainbow trout, smallmouth bass (*Micropterus dolomeiu*), and tench (*Tinca tinca*) (Brown 1984; Wydoski and Whitney 2003). Anglers currently target kokanee, lake trout, cutthroat trout, rainbow trout, landlocked Chinook salmon

Kokanee were introduced to Lake Chelan in 1917 and have supported a popular fishery for decades (Brown 1984; Hagen 1997; DES 2000). Most Lake Chelan kokanee exhibit a 4-year life cycle, spawning at age 3, with smaller numbers of spawners at ages 2 and 4 (Peven 1990). Over 90% of kokanee spawning takes place in the Stehekin River and its tributaries at the north end of the lake, during September and October (Keesee et al. 2009; Peven 1990). Kokanee escapement has fluctuated over 20-fold during recent decades. Kokanee were very numerous but small in size during the 1960s. The kokanee population declined substantially during the late 1970s following the introductions of *Mysis relicta* and landlocked Chinook salmon (Brown 1984). Annual spawner surveys beginning in 1981 indicate that the kokanee population recovered during the following two decades and reached a peak escapement index of 101,309 in 2003. Kokanee escapement has declined in each subsequent year since 2003, to an index value of 21,607 in 2008 (Figure 3; data from Keesee et al. 2009). These surveys are considered to accurately indicate the kokanee escapement trend, but not the complete number of spawners because the proportion of the population spawning in the Stehekin River mainstem and side-channels is unknown (PUD 2007).

Landlocked Chinook salmon were introduced to Lake Chelan in 1974 and supported a very popular sport fishery during the 1980s and 1990s before crashing in 1999 (Viola and Foster 2002). During years of peak abundance, the Chinook salmon trophy fishery was very popular, and many community members would like the fishery to be rebuilt (PUD 2007). Lake trout were introduced to Lake Chelan in 1980 and stocked heavily from 1990-2000. Natural lake trout reproduction was documented in the lake by 2000 (DES 2000). Two Washington state record lake trout were caught in 2001 (33 lb. 6.5 oz, and 35 lb. 7 oz.), as the trophy fishery grew in popularity. Sport harvest trends suggested that the lake trout population expanded rapidly during the early 2000s (PUD 2007), leading managers to remove harvest limits in 2004 (Martinez et al. 2009). The lake trout fishery remains popular and supports several charter guides. Other species targeted by anglers include burbot, rainbow trout, smallmouth bass, and westslope cutthroat trout (DES 2000; Hagen 1997; PUD 2007). Chinook salmon, kokanee, rainbow trout, and westslope cutthroat trout are currently stocked in Lake Chelan annually.

Methods

We collected field data to identify important trophic interactions in Lake Chelan. We quantified the predation impacts of lake trout and Chinook salmon on key species using stable isotope analysis and bioenergetics models. We identified spatial, seasonal, and size-based patterns in these predation impacts. Comparing consumption rates to a hydroacoustics estimate of kokanee abundance, we quantified predation losses of kokanee, and examined potential impacts of changes in predator abundance on predation mortality for kokanee.

Field sampling

We collected limnological and fisheries data from Lake Chelan between August 2004 and September 2008. Standardized sampling was conducted every three months from August 2004 through May 2006 to quantify the seasonal diet, distribution, and growth patterns of key fish and invertebrates in the food web. Additional targeted sampling was conducted in June, July, and August 2006, and in September 2008. Fish were captured with horizontal sinking gill nets at five fixed sites in the lake, two in Wapato Basin and three in Lucerne Basin (Figure 1). At each sampling site, each of four depth strata were sampled with one small-mesh net (2.5, 3.2, 3.8, 5.1, 6.4, and 7.6 cm stretched mesh) and one large-mesh net (8.9, 10.2, 11.4, 12.7, and 15.2 cm stretched mesh). The four sampling depth strata (0-15, 15-30, 30-50, and 50-70 m) corresponded with the epilimnion, metalimnion, and two depths in the hypolimnion during late summer. Within each depth stratum, the small- and large-mesh nets were separated laterally by at least 100 m. Additional horizontal sinking gill nets were deployed opportunistically in other areas to supplement the sample sizes for diet and growth of species and size classes that were underrepresented in standardized gill net catches. Gill nets were set during daylight hours, left to soak overnight, and retrieved during daylight the next day; kokanee were sampled opportunistically by angling and using horizontal midwater gill nets and large "curtain" gill nets (Beauchamp et al. 2009). Small littoral fishes were sampled using minnow traps deployed with a subset of the sinking gill nets. Additional littoral fishes were contributed by the Washington Department of Fish and Wildlife. These samples were collected by gill netting and electrofishing in the Wapato Basin during August 2004. Additional whole fish, fish stomachs, and diet samples collected by gastric lavage were contributed by local anglers and the Washington Department of Fish and Wildlife throughout the study. Kokanee fry were collected

from the Lake Chelan Fish Hatchery during May 2005 to determine their stable isotope signature at the time of stocking.

Fork length (mm), body weight (g), and sex of captured fish were recorded in the field. Fish that required additional processing in the laboratory were placed immediately on dry ice in ice chests to arrest degradation of the samples. Stomachs, gonads, and dorsal muscle samples for stable isotope analysis were collected and frozen immediately. For age and growth analysis, opercles and otoliths were collected from lake trout, and scales were collected from kokanee. Vertical thermal profiles were collected with a Hydrolab Datasonde (Hach Environmental Inc.) at each sampling site concurrently with gill netting.

Key invertebrates were also collected for stable isotope analysis. *Mysis relicta* were sampled in deep water adjacent to each standardized sampling site at night. *Mysis* were collected with vertical hauls from 80 m depth to the surface at night, using a conical 1-m-diameter, 1-mm-mesh net. Other invertebrate species were collected using terrestrial pitfall traps, snorkeling, and surface tows with a neuston net. Chironomid pupae and crayfish were sampled from fish stomachs and rinsed liberally with distilled water to remove any contaminating tissue or digestive fluids from the predator. The isotopic signatures of samples extracted from stomachs were used only for general illustrative purposes and were not included in quantitative analyses.

Hydroacoustic surveys

To quantify the abundance of kokanee, a hydroacoustics survey was conducted during moonless nights on 30-31 August 2005, during late-summer thermal stratification when schooling behavior was minimized (Luecke and Wurtsbaugh 1993). Night surveys were conducted during February, May, and November 2005 as well to characterize seasonal kokanee migration patterns and horizontal-vertical distribution. Each survey consisted of 21 transects in a zig-zag pattern across the full length of the lake (Figure 1). Hydroacoustic sampling was conducted from a 7-m aluminum boat with a Biosonics DE 6000 200-kHz system. A split-beam transducer with a 6.7° full beam angle was mounted on a 1.8-m aluminum tow body facing downwards. The tow body was lowered approximately 1 m below the surface and towed beside the boat at between 8 and 10 km/h. For kokanee surveys, the data acquisition software settings included a minimum target strength detection threshold of -55 dB (approximately equivalent to a 20 mm FL fish), a 0.4 ms pulse width, and a ping rate of 1 ping / s.

Kokanee density was estimated by echo counting single targets, and density was expanded to estimate total kokanee abundance using bathymetric data. Hydroacoustic data were analyzed using Echoview version 4.2 software (Myriax Pty Ltd). Target density was determined by echo counting; the depth-specific sample volume across each transect was calculated, and the sum of all targets within each depth stratum and target-strength size class was divided into that volume. The density of pelagic targets was generally low (mean = 37 targets / ha), and no schools were detected during the surveys, justifying this method. Initial analyses indicated that target densities measured in the top 4 m of the water column were highly variable and biased due to low sample volumes. Subsequently, target densities from 0-4 m were assumed to be equal to densities from 4-8 m depth. We assumed that all small (< 330 mm fork length), pelagic targets were kokanee, because: 1) kokanee were the dominant pelagic fish in Lake Chelan; 2) kokanee comprised 95% of our mid-water gill net catch; and 3) modal sizes of acoustic targets corresponded with the size distribution of kokanee. We converted target strength values to fork lengths using Love's (1971) equation and a length-length relationship for kokanee (FL = 0.923 TL). We used size modes coupled with biological samples of kokanee to apportion targets into

age classes (age 0, -54.3 to -44.3 dB, 30-100 mm FL; age 1, -44.3 to -38.6 dB, 100-200 mm FL; ages 2-4, -38.6 to -34.4 dB, 200-330 mm FL). Mean depth- and age-specific target densities (targets / 1000 m^3) were calculated for each transect. Densities were expanded to estimates of kokanee abundance by multiplying the depth-specific density by the volume of water in the lake within that depth stratum (Kendra and Singleton 1987), and adding these values across all depth strata. This yielded 21 separate estimates of total age-specific kokanee abundance, with each transect representing a sampling unit. We characterized the estimated age-specific kokanee abundance as the mean ± SE of these abundance estimates.

Diet estimation by stomach and genetic analyses

Fish stomach contents were identified to species for prey fishes and to family and life stage for invertebrates when possible. The blotted wet weight of each prey type was recorded. Only roughly half of salmonid prey specimens were identifiable to the species level based on bone morphology (all were kokanee); the remaining specimens could not be identified to the species level based on the available bones (Parrish et al. 2006). When lake trout stomachs were analyzed, the gonads were weighed to determine the proportion of body mass lost annually to spawning.

The lengths of intact fish prey specimens were recorded and the lengths of partially digested fish prey were estimated when possible. We measured the standard length, vertebral column length, or lengths of diagnostic bones (cleithrum, dentary, and opercle) of partially digested fish prey with digital calipers (± 0.1 mm precision). We used published relationships to estimate prey lengths based on these measurements (Hansel et al. 1988; Yule and Luecke 1993). To convert fork length estimates (*L*, mm) to weight (*W*, g) we used length-weight relationships developed from Lake Chelan specimens captured in our gill nets. For Chinook salmon (r^2 = 0.97, N = 5, P < 0.002):

$$W = 0.000000817 \cdot L^{3.41} \tag{1}$$

for kokanee (r^2 = 0.99, N = 93, P < 0.0001):

$$W = 0.00000402 \cdot L^{3.20} \tag{2}$$

and for lake trout (r^2 = 0.93, N = 390, P < 0.0001):

$$W = 0.0000118 \cdot L^{3.01} \tag{3}$$

To improve the resolution of diet data, the species identification of unidentified salmonid specimens was analyzed using genetic techniques. DNA was analyzed from 23 prey specimens that were classified as salmonids based on bone morphology, but could not be identified to the species level based on morphological traits alone. Five positively identified reference samples were also analyzed, including one specimen of each salmonid species known to occur in Lake Chelan (Chinook salmon, kokanee, lake trout, rainbow trout, and westslope cutthroat trout). Reference samples were composed of dorsal muscle tissue from fish captured in Lake Chelan, except for Chinook salmon, for which we used an archived DNA sample from another population.

Genetic analysis was performed by the Marine Molecular Biology Laboratory at the University of Washington. Unidentified prey specimens were briefly soaked in a bleach solution to destroy any contaminating DNA from the predator or from other prey items in the stomach. Then DNA was extracted from the center of the prey item, which was not affected by the bleach. Three prey specimens were judged as too small and too highly degraded to treat with bleach without destroying all target DNA and were analyzed without this step. Reference samples were also analyzed without the bleach treatment because these fish were not removed from predator

stomachs, and unlikely to be contaminated. DNA was extracted with a Qiagen DNeasy® micro-extraction kit following the manufacturer's protocol (Qiagen Inc. Valencia, CA). DNA samples were amplified by polymerase chain reaction (PCR) with two primers, 16S and ND3, the latter of which is designed to amplify only salmonine DNA (Purcell et al. 2004; Schwenke et al. unpublished). The PCR products were sequenced and the sequences from unidentified prey were grouped by phylogeny with the sequences from reference samples. Species assignments were accepted for specimens with a high degree of certainty based on genetic data (>90% bootstrap values), and these assignments were included in the diet analysis.

We calculated seasonal diet proportions separately for four size classes of lake trout in each of the lake basins, yielding eight size-basin groups for each of four seasons. Because the main goal of this analysis was estimating consumption of salmonid prey, we chose size classes to best characterize the ontogeny of salmonid consumption. Diet data indicated that the smallest size class consumed no salmonids, and larger size classes consumed progressively more salmonid prey. We reported diet proportions by weight for each group (W_i; Chipps and Garvey 2007).

Diet estimation by stable isotope analysis

We used stable isotope analysis and a mixing model to describe the trophic linkages among key species within the food web, to estimate the diet composition of Chinook salmon, and to corroborate estimates of lake trout diets. Stable isotope values are conventionally reported in δ ("del") units, which indicate the ratio of heavy to light atoms in a sample, relative to a standard (Peterson and Fry 1987). Carbon isotopic values (δ^{13}C) are commonly used to indicate diet sources within a food web. In lakes, lower, "depleted" δ^{13}C values indicate a diet primarily based on carbon fixed by phytoplankton in the pelagic zone, while higher, "enriched" δ^{13}C values indicate a diet primarily based on carbon fixed in the littoral zone by epiphyton (Hecky and Hesslein 1995; Post 2002). Nitrogen isotopic values (δ^{15}N) are commonly used to indicate trophic position of consumers within a food web because consumers typically have enriched δ^{15}N values relative to their food, with each higher trophic level represented by an average increase in δ^{15}N of ~3.4‰ (Minagawa and Wada 1984; Post 2002; Vander Zanden et al. 1997). Stable isotope data can be interpreted qualitatively to characterize general patterns of energy flow through food webs. Mixing models offer a quantitative approach to estimating consumer diets by comparing the isotopic ratios of consumers to those of their potential diet sources.

We estimated diet composition using the MixSIR stable isotope mixing model, version 1.04 (Moore and Semmens 2008; Semmens et al. 2009). MixSIR is an improvement over previous mixing models (e.g., Lubetkin and Simenstad 2004; Phillips and Gregg 2003) because it incorporates the variability in isotopic signatures to estimate probability distributions of diet proportions, rather than using only the mean values to estimate nominal diet proportions (Moore and Semmens 2008). This approach is especially well suited to management questions because it allows the estimation of best- and worst-case scenarios rather than simply a single "best guess" diet. The MixSIR model is based on Bayesian inference, the benefits and limitations of which are discussed in detail elsewhere (e.g., Cressie et al. 2009; Hilborn and Mangel 1997; Lele and Dennis 2009). Inputs to the mixing model included: 1) the mean and standard deviation (SD) of the isotopic signatures for each prey type (Table 1), 2) the mean and SD of the fractionation rate for each prey type (Table 1), and 3) the stable isotope signatures of individual consumers (Table 2). The fractionation rate is the difference between the stable isotope ratios of a consumer's aggregate diet and those of its own tissue. We used our own samples for consumer and prey

isotopic signatures, and used fractionation rates reported in the literature (Minagawa and Wada 1984; Post 2002; Vander Zanden et al. 1997). Details of model inputs are described below. The MixSIR model also allows the inclusion of "prior knowledge" about diet composition, to be considered in addition to isotopic input data. We wished to produce an independent estimate of diet composition, so we used an uninformative prior distribution. We note that mixing model results were not fully independent of stomach data because we used stomach data to select the potential diet sources; however, the mixing model provided valuable independent information on the relative importance of diet sources. All model runs used 10,000,000 iterations and produced acceptable diagnostics (Moore and Semmens 2008).

Stable isotope samples were rinsed under distilled water, oven dried for ≥48 h at 60° C, ground to a fine powder with a stainless steel mortar and pestle, and weighed to 1.00 ± 0.2 mg in a tin capsule. Samples were shipped to the Colorado Plateau Stable Isotope Laboratory at Northern Arizona University for analysis. Stable carbon and nitrogen isotopes were measured via continuous flow using a Carlo Erba 2100 elemental analyzer interfaced with a Thermo-Finnagan Delta^{plus} isotope ratio mass spectrometer. Every 10th sample was analyzed in duplicate to quantify the variation between replicates.

We corrected the δ^{13}C values of consumers and prey to account for differences in lipid content among samples. Variation in lipid content can affect δ^{13}C values (Deniro and Epstein 1977; McConnaughey and McRoy 1979) and substantially alter conclusions about consumer diets. Lipid correction equations allow researchers to take these lipid effects into account and more accurately characterize the transfer of C among organisms (Kiljunen et al. 2006; Post et al. 2007; Sweeting et al. 2006). These equations estimate the lipid content of each sample based on its atomic C:N ratio and adjust its δ^{13}C signature accordingly. Several alternative correction models have recently been proposed, and evidence suggests that separate models should be used for different taxa and tissue types (Logan et al. 2008; Post et al. 2007). We used four separate, well-supported methods to correct δ^{13}C values of fishes, *Mysis*, and other invertebrates. We corrected the δ^{13}C values of fish samples with equation 1*a* of Logan et al. (2008) for fish muscle tissue because this model was developed with data from more freshwater fishes across a wider range of C:N values than alternative models (Kiljunen et al. 2006; Post et al. 2007). We corrected *Daphnia* signatures with the equation of Smyntek et al. (2007) for copepod and cladoceran zooplankton because this was the only model developed for these taxa. We corrected *Mysis* signatures with the equation of Leggett (1998; p. 234) because this was the only model developed for *Mysis*. We corrected the signatures of other invertebrates with equation 2 of Logan et al. (2008) for aquatic invertebrates because this was the only general invertebrate model that was fit to a large dataset. *Mysis* was the only invertebrate included in mixing model analyses so lipid corrections for *Daphnia* and other invertebrates affected only a bivariate stable isotope plot used for qualitative characterization of the food web.

The two basins of Lake Chelan differ ecologically and morphometrically (Brown 1984; Schoen 2007); this prompted us to compare stable isotope values between basins and predator size classes to determine whether to estimate the diets of these groups separately. We used two-way ANOVA models to determine whether to pool lake trout predator signatures among lake basins or size classes. Separate two-way ANOVA models were run using δ^{13}C and δ^{15}N as response variables, and tested for fixed effects of basin, size class, and basin $\times$ size class. Results indicated that δ^{13}C values differed between basins ($p < 0.001$), and δ^{15}N values differed among size classes ($p < 0.01$). Thus, we estimated the diet separately for each lake trout size class $\times$ lake basin combination. We estimated a single overall diet for Chinook salmon because

the sample size was too low (n = 6) to subdivide by size class or lake basin. When regressed on fork length, neither δ^{13}C (r^2 = 0.00) nor δ^{15}N (r^2 = 0.04) showed a trend with body size over the range of our Chinook salmon samples (411-785 mm FL). This limited evidence suggested that Chinook salmon diets did not change markedly across the size range that we sampled, and supported the utility of a single diet estimate.

We tested whether prey isotope signatures differed between lake basins using separate t-tests for δ^{13}C and δ^{15}N for each prey type. We found no basin differences in isotope signatures for any fish prey type (all p > 0.13), so we pooled samples from both basins for the mixing model analysis. The sample size of threespine stickleback (n = 5) was too small to make this comparison, so we pooled samples from both basins for this species as well. *Mysis* δ^{13}C signatures differed between lake basins (t-test; p < 0.005), so we analyzed data from each basin separately. We pooled *Mysis* prey signatures from both basins for the Chinook salmon analysis because this analysis did not distinguish between basins.

We used diet data from the stomach analysis to choose the potential diet sources to include in the lake trout mixing models. For each lake trout size class × lake basin group, we included all diet items that contributed ≥ 2.5% of the annual diet, as indicated by stomach analysis. This resulted in 2-6 diet items per size class × lake basin group (Table 1). For example, burbot, threespine stickleback, and *Mysis* each comprised ≥ 2.5% of the annual diet of lake trout 180-400 mm FL in Lucerne Basin, and these potential prey items were included in the mixing model for that predator group. One lake trout group (551-910 mm FL, Lucerne Basin) was assigned only two potential diet items (kokanee and peamouth) by this criterion. A preliminary mixing model run did not converge, suggesting that the isotopic signatures of this lake trout group could not be explained by these two diet sources alone. We included two additional potential diet sources (northern pikeminnow and threespine stickleback) in the model for this group, both of which were present in stomach samples, but comprised < 2.5% of the annual diet. Because we collected only a single non-empty Chinook salmon stomach, we did not have enough stomach data to select the diet items to include in the Chinook salmon mixing model. Instead, we included every diet item that comprised >5% of the annual diet of any lake trout size class × lake basin group. This yielded 10 potential diet items.

Some prey fish species included individuals that were too large to be vulnerable to lake trout or Chinook salmon predation. These larger individuals generally exhibited different isotopic signatures than smaller conspecifics (e.g., because of ontogenetic diet shifts), so they were excluded when characterizing the isotopic signatures of prey species. We considered individuals invulnerable to predation when they were > 50% of the length of the largest lake trout sampled in the study (Beauchamp et al. 2007; largest lake trout FL = 902 mm, "invulnerable prey" FL >= 451 mm). We included invulnerable individuals when characterizing the signature of Chinook salmon because only one isotopic sample was available from a "vulnerable" individual, making it impossible to calculate a SD without including the additional samples. We considered this exception justified because we did not detect an ontogenetic diet shift among the Chinook salmon that we sampled, as noted above.

We assumed fractionation rates of 0.4 ± 1.3 ‰ (mean ± SD) for δ^{13}C and 3.4 ± 1.0 ‰ for δ^{15}N for all diet sources (Post 2002). We considered alternative fractionation rate estimates by McCutchan et al. (2003) and Caut et al. (2009), and found that the choice of values often influenced our results. However, we considered Post's values most appropriate for our analysis because they best matched fractionation rates reported specifically for lake trout (Harvey et al. 2002; Vander Zanden and Rasmussen 2001) and were most likely to cause our mixing models to

converge on a solution, which suggested better agreement with our empirical data. We encourage additional study in the field of fractionation rates, as our findings were consistent with recent reports that fractionation rates can be influential inputs to mixing models (Caut et al. 2008; Caut et al. 2009).

Lake trout growth and survival

We used field data to characterize the growth and survival rates of lake trout in both basins of Lake Chelan. We attempted to age lake trout with two techniques: break-and-burn using saggittal otoliths and surface examination using opercles. We were unable to determine reliable ages from the otoliths, so we sent them to an outside laboratory with extensive lake trout aging experience (Northern Bioscience, Thunder Bay, Ontario). This lab confirmed that the otoliths had a crystalline structure, which is characteristic of certain lake trout populations and causes the otoliths to be very difficult to age reliably (J. Tost, *pers. comm.*, 5/20/2009). We successfully aged the lake trout using opercles, following the methods of Sharp and Bernard (1988), who showed that ages from opercles were similar in precision to ages from otoliths, and more precise than ages from scales for long-lived lake trout.

Lake trout growth was characterized by fitting a von Bertalanffy growth model to empirical length and age data from the subset of fish that were aged (n = 188), and converting length to wet weight with a linear model fit to data from all fish captured (n = 506). We used the von Bertalanffy model parameterization of Gallucci and Quinn (1979) to estimate length at age:

$$L_t = L_\infty \cdot (1 - e^{-(\omega/L_\infty) \cdot t}) \tag{4}$$

where L_t is fork length (mm) at age t (yr), L_∞ is the asymptotic maximum length (mm), and ω indicates the growth rate in length of young fish (mm/yr). We tested whether von Bertalanffy parameters differed between lake basins by fitting a full model with separate L_∞ and ω values for each basin, and three simpler models with basin-specific values for L_∞ only, ω only, and identical parameters for the both basins. We used AIC_c to select the best growth model, assuming lognormal process error (Burnham and Anderson 2002).

We used the following model to estimate weight at length:

$$W = a \cdot L^b \tag{5}$$

where W is wet weight (g), L is fork length (mm), and *a* and *b* are fitted parameters. We tested whether the natural log of the weight-length relationship differed between lake basins by fitting a linear model using backward model selection, beginning with a fully parameterized model and iteratively dropping the least significant predictor based on t-tests of significance, given all other predictors in the model, until all predictors met a significance criterion of $p < 0.05$ (Kutner et al. 2005). The full model predicted $\log_{10}(W)$ and included season and lake basin as fixed factors, $\log_{10}(L)$ as a covariate, and all possible interaction factors. We back transformed this result into the form of equation 2.

The age frequency distribution of captured lake trout was corrected for gill net size selectivity (Hansen et al. 1997) and for inequalities in effort among mesh sizes (Ruzycki et al. 2003). All subsequent analyses used these adjusted catch rates. A comparison of the length frequency histograms of all lake trout captured versus the subset selected for aging indicated differences in the proportions of aged fish, with respect to length (i.e., the smallest and largest fish were overrepresented in the aged subsample). We corrected for this bias by dividing the lake trout samples into 50 mm length classes and calculating an aging selectivity for each length class, equal to the proportion of fish in that length class that were aged. We corrected the age-

frequency distribution by constructing an age-length key, dividing the frequency of lake trout in each age-length cell by the aging selectivity for the corresponding length class, and adding the quotients among length classes within each age. The instantaneous annual mortality rate (Z) was estimated by fitting a linear regression model to the descending limb of the natural log of corrected catch frequency plotted against age; Z was estimated as the inverse of the regression slope (Miranda and Bettoli 2007). We used fish 7-12 years of age to estimate Z, because the corrected age-frequency plots indicated that age-7 lake trout were the youngest age class that was fully recruited to the gill nets. The annual survival rate (S) and stable age distribution were determined for the lake trout population using this estimate of the mortality rate. Mortality and survival rates were estimated separately for lake trout in each lake basin.

Consumption by lake trout

Lake trout per capita consumption rates were estimated with a bioenergetics model (Fish Bioenergetics 3.0; Hanson et al. 1997) using lake trout physiological parameters from Stewart et al. (1983), as modified by Luecke et al. (1999) for the temperature dependence of maximum consumption. Simulations were run separately for each age (2-16 yr) within each lake basin using a daily time step, with model day 1 representing 1 May. Model inputs included annual growth (weight at age), seasonal diet composition, the water temperature experienced by the consumer ("thermal experience"), the energy densities of prey organisms, and energy losses due to spawning.

Lake trout growth inputs were generated from the length-age and weight-length relationships derived above (Table 3). Seasonal diet composition was estimated for each size class – lake basin group using stomach content data. For simplicity, prey were grouped into 10 categories for the analysis (Table 4). No diet data were available for the 551-910 mm lake trout size class in Lucerne Basin during summer. Diet composition for this season was set equal to the mean annual diet for that predator group. The resulting diet proportion for kokanee was similar to the corresponding diet proportion for the adjacent size class (501-550 mm), suggesting that this value was realistic. Seasonal thermal experience for each lake trout size class – basin group was estimated from gill net CPUE and thermal profiles (Beauchamp et al. 2007). For each basin, we calculated the mean water temperature in four depth intervals (spanning 0-70 m depth) during each season. For each lake trout size class – basin group, we multiplied the proportion of total CPUE in each depth interval by the mean temperature of that depth interval, and summed the products across depths to estimate the mean temperature experienced by that consumer group (Table 5). Prey energy density estimates were taken from the literature (Table 6). Prey indigestibility was assumed to be 3% for fishes and 17% for invertebrates (Beauchamp et al. 2007). For salmonid prey species, we converted annual consumption estimates from biomass into numbers of fish consumed by dividing by the mean wet weight of prey specimens consumed. Prey weight was estimated from the mean reconstructed length of prey specimens and length-weight relationships developed from samples captured in Lake Chelan.

We incorporated energy losses to reproduction into model simulations by reducing lake trout body mass annually according to observed patterns of gonadal development. The gonadosomatic index (GSI) was calculated for each fish as the ratio of gonadal mass to total body mass. We plotted GSI against fork length to determine the length at the onset of reproductive maturity (~400 mm). The greatest GSI values for female lake trout occurred during November and were bimodally distributed, suggesting that some sampled fish had completed spawning, while others had not yet spawned. This pattern could also be explained if female lake

trout spawned only every other year, as has been reported in some other populations (e.g., Ruzycki et al. 2003). We considered this unlikely because the distribution of GSI for female lake trout was unimodal during August and September, before the spawning season began, suggesting that all lake trout were preparing to spawn. However, if some mature females did not spawn, our simulations would slightly overestimate consumption rates. We simulated spawning by reducing lake trout body mass by 6.8% (the mean of female GSI values in the large mode and unimodal male GSI values) on 15 November of each year after they exceeded 400 mm fork length.

To present estimates of lake trout consumption in a metric relevant to management, we expanded daily estimates of the prey biomass consumed by individual lake trout to aggregate seasonal and annual consumption estimates for a size-structured "unit population" of 1,000 lake trout ≥ 2 years old. A unit population was characterized separately for each lake basin as a group of 1,000 fish from 2-16 yr old, with the proportion of individuals at each age determined by the annual survival rate. This method accounted for the increasing proportions of fish in the diet and increasing per capita consumption due to the growth of individuals, as well as the decreasing numbers of predators at each age due to mortality. These size-structured population consumption estimates were intended to be scaled upwards to allow estimation of the impact of management strategies that would add or remove thousands of lake trout from the system. This type of extrapolation assumes that per capita consumption rates remain constant as predator abundance changes; this is most justifiable for modest changes in abundance.

The size-structured consumption estimates per 1,000 lake trout provided a useful measure of the predation impact of lake trout, but to compare these impacts between lake basins, we also took differences in the relative density of lake trout into account. To make this comparison, we scaled the unit population consumption estimates for each basin by the relative density of lake trout. We estimated relative lake trout density by assuming that density was proportional to catch per unit effort (CPUE) in sinking gill nets. This comparison assumed that our gill nets sampled lake trout with similar efficiency in both basins. However, if the steeper bathymetry of the Lucerne Basin reduced the efficiency of the nets, this would lead to an underestimate of lake trout density in that basin. Although we could not test this assumption directly, we used the relative CPUE of two other common, large-bodied piscivores, burbot and northern pikeminnow, to validate the performance of the gill nets. If gill nets performed poorly in Lucerne Basin, we expected CPUE of all three piscivore species to be lower in that basin, relative to the Wapato Basin. Alternatively, if CPUE of these piscivores was not generally lower in the Lucerne Basin, this would suggest that gill nets performed adequately.

Consumption by Chinook salmon

We estimated per capita consumption rates for Chinook salmon using a bioenergetics model (Fish Bioenergetics 3.0; Hanson et al. 1997) with physiological parameters developed by Stewart et al. (1981) and modified by Stewart and Ibarra (1991). Model inputs included annual growth (weight at age), diet composition, seasonal thermal experience, and the energy densities of prey. The Chinook salmon population was small during the study period, and the sample size (n = 6, but only 1 nonempty stomach) was inadequate to estimate diet composition, except by stable isotope analysis. We assembled model inputs from these stable isotope data, previous unpublished data from Lake Chelan, and published data from other lake-resident Chinook salmon populations. Due to a lack of separate growth and survival estimates for each Chinook salmon life history (e.g., age 1, 2, and 3 spawners; Stewart et al. 1981), we followed the method

of previous bioenergetics studies of lake-resident Chinook salmon, which modeled a single, generalized life history (Murry et al. 2010; Negus et al. 2008; Rand and Stewart 1998). Simulations used a daily time step beginning on 15 May, and were run for 365 d for ages 1-3 and for 154 d for age 4. The endpoint of the age 4 simulation represented 15 October, the approximate date that Chinook salmon would stop feeding in Lake Chelan and begin staging to spawn (Brown 1984). To encompass the range of potential predation rates on kokanee, we modeled consumption using five estimates of diet composition and three estimates of growth, for a total of 15 consumption scenarios. This approach produced our best estimate of consumption, plus scenarios representing the lower and upper bounds of consumption.

We compiled growth inputs from previous Lake Chelan studies and the literature. Weights of angler-caught Chinook salmon were recorded at Lake Chelan fishing derbies held during spring (27 April – 8 June) from 1990-2000 (Washington Department of Fish and Wildlife, *unpubl. data*). Sample sizes were small for age 3 (n = 54) and age 4 (n = 14) fish, and interannual variability in weight at age overwhelmed much of the increase in mean weight with increasing age. To generate reasonable growth inputs from this limited dataset, we tracked the annual growth of individual cohorts when > 5 samples were available for consecutive years. We simulated growth starting with the mean weight at age 2 (3515 g, n = 199 samples), and added the mean growth increments from ages 2-3 (776 g; n = 3 cohorts) and ages 3-4 (1845 g; n = 1 cohort). We considered these generous estimates of true weights because samples came from fishing derbies, when anglers likely targeted the largest individuals. We also used growth curves from published studies of other lake-resident Chinook salmon populations. Weight during spring (1 May or 1 June) was reported for Chinook salmon ages 1-4 yr in Lake Michigan (Wesley 1996), Lake Ontario (Rand and Stewart 1998), and the west arm of Lake Superior (Negus et al. 2008). Eleven growth curves were reported for Lake Michigan, and one was reported for each of the other lakes. These 13 curves spanned a wide range of growth rates, with over a two-fold difference between the high and low weights at each age from 1-4 yr. For the nominal consumption scenario, we used the Lake Chelan data to define weight at ages 2-4 yr. Insufficient data were available from Lake Chelan to estimate weight at age 1, so we used the mean literature value for the nominal scenario (Table 7). We used the literature data to define growth for the lower and upper consumption scenarios, using the least and greatest weights at each age, respectively (Table 7). We assumed that age 4 fish achieved 7% growth during this period (Table 7; Negus et al. 2008).

We used the stable isotope mixing model analysis to define diet composition inputs to the Chinook salmon bioenergetics model. The mixing model generated a distribution of potential diet compositions fitting the stable isotope data. Because our goal was to quantify predation on kokanee, we selected five diet compositions that represented a wide range of possible kokanee diet proportions. We used the diet compositions that contained the estimated 5th, 25th, 50th, 75th, and 95th percentile probabilities for the proportions of kokanee in the diet. We used seasonal thermal profiles from five sampling sites in Lake Chelan to define thermal experience inputs. Thermal experience was defined as the mean metalimnetic temperature across these sampling sites or the mean temperature of the top 80 m of the water column during nonstratified seasons (Table 9). We assumed that Chinook salmon generally avoided the warm epilimnion in Lake Chelan because their diet was dominated by coldwater prey such as *Mysis relicta*; this contrasted with the epilimnetic distribution reported for Chinook salmon in Lake Ontario, where the dominant prey is alewife (Wurster et al. 2005). Prey energy density and indigestibility inputs were the same as used for the lake trout simulations (Table 6).

Daily estimates of individual-level consumption were expanded to estimate the aggregate annual consumption demand of an age-structured "unit population" of 1,000 Chinook salmon 1-4 yr old, with the numbers in each age class determined using age-specific mortality rates reported for the Chinook salmon population in the west arm of Lake Superior (Table 7; Negus et al. 2008).

Lake trout harvest trends

We analyzed harvest records from the lake trout fishery to characterize harvest trends and estimate the total harvest of lake trout. Three of the four primary charter guides on Lake Chelan reported their total number of charters each year from 2005-2008, and provided harvest records for a subset of trips during 2004-2006. Harvest records consisted of standardized questionnaire forms completed by guided anglers indicating the duration of the charter (full day or half day) and the numbers of each fish species harvested. We excluded data from questionnaires that indicated the number of fish harvested, but not the species. Harvest records with usable data were collected on 87 trips in 2004, 74 trips in 2005, and 136 trips in 2006. These represented 37% of all trips by the participating guides during 2005 and 66% of trips during 2006, the two years for which the total number of trips were available. Records from 2004 and 2006 were well distributed across all seasons, whereas records from 2005 were only available from February through August. Examination of 2004 and 2006 data showed that harvest patterns during February through August were very similar to overall annual patterns. We calculated the annual reported harvest and catch per unit effort (CPUE), with effort defined as the number of full day equivalent charters per year. Mean harvest on half day trips was 57.3% of mean harvest on full day trips, so we considered half day trips equivalent to 0.573 days of effort. For 2005 and 2006, we estimated the total annual effort by participating guides from the total number of charters and the proportions of half day and full day trips in the reported subsample. We estimated total annual harvest by these guides as the annual mean CPUE multiplied by the annual effort. Lake trout were also harvested by a fourth charter guide and by unguided anglers, for whom data were unavailable. We assumed that this additional harvest was roughly equivalent to 50% of the harvest of the participating guides (i.e., 33% of the total harvest), and was very likely between 20% and 100% of the harvest of participating guides (i.e., 17-50% of the total harvest). We generated nominal, minimum, and maximum estimates of total harvest by expanding the harvest of the participating guides by these factors.

Lake trout population dynamics

We simulated lake trout population dynamics with a deterministic, age-structured population model. Model inputs included stocking records and empirical data from Lake Chelan and literature values from other lakes. The numbers of lake trout N_{ij} at age j in year i were projected forward to indicate the numbers $N_{i+1,j+1}$ at the next age $j + 1$, in the next year $i + 1$, according to the instantaneous annual mortality rate Z (Hilborn and Walters 1992):

$$N_{t+1} = N_t e^{-Z} \tag{6}$$

We used the overall mortality rate for both lake basins combined for these calculations. Numbers at age 0 in each year were specified as the sum of stocked fish (Art Viola, WDFW, *unpubl. data*) and naturally reproduced fish. Reproductive rates of lake trout in Lake Chelan were unknown; thus, we simulated population dynamics under three scenarios: no reproduction; moderate, density-dependent reproduction; and rapid, density-independent reproduction. For the

latter two scenarios, reproduction was estimated with a Ricker stock-recruit model (Ricker 1975):

$$N_{i+1,\,j=0} = \alpha \, S_i \, e^{-\beta \, S_i} \tag{7}$$

where $N_{i+1,\,j=0}$ was the number of recruits in year $i+1$, S_i was the number of mature adults (spawners) in the population in year i, α was the maximum number of recruits per spawner at low population density, β was the instantaneous rate at which the number of recruits per spawner declines with increasing population density. Following the methods of Hansen (2007), who modeled the lake trout population in Lake Pend Oreille, we adapted estimates of α and β reported for eastern Lake Superior (Nieland 2006), which has similar deep bathymetry to Lake Chelan. We assumed that the maximum recruitment rate α was equal to the value reported for eastern Lake Superior (5.698 recruits / adult). For the moderate-reproduction scenario, we adjusted the density-dependence parameter β to account for the smaller habitable area of Lake Chelan. We divided the surface area that lies over depths habitable for lake trout (< 70 m; Hansen et al. 1995) of Lake Superior (280,772 ha; Nieland 2006) by that of Lake Chelan (8,597 ha; Kendra and Singleton 1987, E.S. *unpubl. data*). We multiplied the estimate of β for Lake Superior (3.235 x 10^{-5}) by this ratio, yielding an estimate of 1.057 x 10^{-4} for β in Lake Chelan. For the rapid-reproduction scenario, we set β to zero. This caused spawners to reproduce at the maximum rate, simulating the dynamics of a rapidly expanding population well below carrying capacity. We also simulated lake trout population dynamics using a modeling framework developed for Ontario lakes (Shuter et al. 1998). This alternative model incorporated more life-history complexity to estimate lake trout recruitment and produced similar results; thus, we report only the results of the simpler model here.

We simulated the numbers of lake trout at each age for ages 0-30, in each year from 1980-2020, under each scenario. We estimated spawning biomass in each year by multiplying the numbers at age by mean weight-at-age values determined previously, and adding across all ages ≥ 7 yr. We estimated the biomass of the largest lake trout size class (>550 mm FL) using the same method for ages ≥ 10 yr.

Statistical analyses were performed using R version 2.10.0 (Ihaka and Gentleman 1996).

Results

Piscivore distribution and catch patterns

Lake trout catch per unit of gill net effort (CPUE) was much less in Lucerne Basin than in Wapato Basin, but this pattern did not hold for northern pikeminnow or burbot. Lake trout CPUE was 7.8 times greater overall in the shallower Wapato Basin than in the deeper Lucerne Basin and was consistently greater in the Wapato Basin than the Lucerne Basin across all four size classes (Figure 4). Northern pikeminnow CPUE was similar between basins overall (2% greater in Lucerne Basin than Wapato Basin), but patterns varied among size classes (Figure 4). Burbot CPUE was 60% greater in Lucerne Basin than in Wapato Basin, and this difference was driven largely by small (<450 mm total length) burbot (Figure 4). Smallmouth bass were captured only in Wapato Basin. Chinook salmon, rainbow trout, and wild-origin westslope cutthroat trout were captured only in Lucerne Basin, in small numbers. Hatchery-origin westslope cutthroat trout were captured in both basins.

Kokanee abundance and distribution

Lake Chelan supported a population of approximately 742,000 kokanee (ages 0-4) during August 2005, based on a quantitative hydroacoustic survey of the lake. Age-0 kokanee accounted for over half of this number (421,431 ± 222,125; mean estimate ± 1 SE). The abundance of age-1 kokanee was 104,263 ± 19,546 (mean ± 1 SE). The abundance of kokanee age 2 and older was 216,463 ± 129,039 (mean ± 1 SE). Large numbers of kokanee were aggregated near Stehekin, with lower densities distributed throughout the rest of the lake (Figure 5). The length distribution of acoustic targets included a distinct mode at 70 mm FL corresponding to age-0 kokanee, a smaller mode at roughly 120 mm FL corresponding to age-1 kokanee, and larger targets corresponding to age 2-4 kokanee (Figure 6). Targets larger than 330 mm FL likely represented piscivorous species (Figure 7). These largest targets were most common in the Stehekin area. Kokanee were primarily distributed in the metalimnion and hypolimnion in both lake basins during August, although some age-0 and age-1 kokanee were distributed in warm epilimnetic waters (Figure 8).

Diet estimation by stomach and genetic analyses

We analyzed 1296 stomachs, 896 of which contained prey (Tables A1 and A2). Fourteen of the 23 salmonid prey specimens that were not identifiable to the species level, based on bone morphology, were assigned to a species with genetic techniques. Of the 23 prey specimens that were analyzed genetically, 7 were too digested for their DNA to be amplified. DNA from the remaining 16 specimens amplified with the ND3 primer, confirming that these were salmonines. Of these samples, 11 were identified as kokanee, two as lake trout, and one as Chinook salmon. The two remaining salmonine samples clustered most closely with kokanee and Chinook salmon, but were not assigned a positive species identification. No samples were identified as rainbow trout or westslope cutthroat trout. All of the species assignments indicated a high level of genetic support (bootstrap values > 90%) and we accepted these assignments for our diet analysis. In total, 9 prey specimens were not assigned a species ID based on the genetic results. We characterized these specimens as "unidentified salmonids".

Lake trout diet composition differed markedly between lake basins, with *Mysis relicta* comprising most of the diet in the Wapato Basin and kokanee comprising a large proportion of the diet in the Lucerne Basin (Figure 9; Table 4). *Mysis relicta* comprised > 50% of the diet of the smallest lake trout (180-450 mm fork length) in both lake basins. In the Lucerne Basin, lake trout began consuming kokanee and other salmonids when they reached the 451-500 mm size class, and kokanee comprised 91% of the diet of the largest (551-910 mm FL) lake trout. The ontogenetic transition to piscivory occurred more gradually in the Wapato Basin, where *Mysis* remained the primary prey of lake trout until they reached the largest size class. Lake trout consumed kokanee and unidentified salmonids during winter, summer, and fall in the Lucerne Basin, but only during winter and spring in the Wapato Basin (Table 4). Most kokanee in lake trout diets (6 of 7 prey specimens with reconstructed body sizes) were age 1 or older (FL: 158-217 mm; wet weight: 83.0 g mean, 26.8 g SD). Four additional kokanee prey specimens were clearly age 1 or older (approximately 200 mm FL), although their body sizes could not be precisely reconstructed. Only a single age-0 kokanee was found in a lake trout diet (77 mm FL, 4.3 g, captured during November). We detected no obvious differences in kokanee prey size among seasons, although the sample size was very small. Lake trout stomachs contained three cannibalized lake trout, all from the Wapato Basin (reconstructed body size of one specimen: 200.0 mm FL, 99.5 g). Lake trout stomachs contained one Chinook salmon eaten in the Lucerne

Basin (reconstructed body size: 237.0 mm FL, 103.4 g). Lake trout consumed substantial proportions of cyprinid prey in both lake basins, and most of this consumption occurred during spring (Table 4). The lengths of ingested prey fishes were < 40% of lake trout lengths (n = 54; Figure 10).

Only four Chinook salmon stomachs were collected and only one contained prey (Table A1). *Mysis* was the only prey item found in this stomach.

Northern pikeminnow consumed large proportions of invertebrate prey as well as fish in both lake basins (Figure 11; Table A2). Kokanee represented 26% and unidentified salmonids 40% of the diet of large (401-610 mm FL) northern pikeminnow in the Wapato Basin. Northern pikeminnow consumed kokanee in the Wapato Basin only during spring, but ate unidentified salmonids during spring, summer, and fall (Table A2). In the Lucerne Basin, kokanee were absent from the diet of northern pikeminnow and unidentified salmonids contributed < 1% of the diet (Table A2). The lengths of ingested prey fishes were < 45% of northern pikeminnow lengths (n = 25; Figure 12).

The diet of burbot was composed primarily of *Mysis*, crayfish, and fish (Figure 13; Table A2). Many burbot inverted their stomachs upon capture, and relatively few non-empty stomachs were collected (n = 60). Burbot stomachs contained only a single salmonid prey specimen, which was unidentifiable to species. Because of the large size of this specimen, unidentified salmonid prey represented 40% of the diet of large (451-700 mm TL) burbot in Wapato Basin. The lengths of ingested prey fishes were < 30% of burbot lengths (n = 2; Figure 12).

Smallmouth bass diets contained large proportions of non-salmonid fishes, including northern pikeminnow (20%), suckers (17%), and peamouth (15%), as well as crayfish (16%; Figure 14). No salmonid prey were found in smallmouth bass stomachs (Table A2), although most samples were collected during summer when kokanee densities were low in the Wapato Basin. The lengths of ingested prey fishes were < 47% of smallmouth bass lengths (n = 5; Figure 12).

Diet estimation by stable isotope analysis

Stable isotope signatures indicated the general structure of the Lake Chelan aquatic food web (Figure 15). Invertebrates were depleted in δ^{15}N, indicating low trophic positions, and their δ^{13}C values grouped into two distinct clusters. The pelagic and profundal invertebrates *Daphnia*, *Mysis relicta*, chironomid larvae, and Asiatic clams (*Corbicula fluminea*) were depleted in δ^{13}C, indicating a reliance on carbon fixed by phytoplankton. The littoral invertebrates crayfish and Chinese mystery snails (*Cipangopaludina chinensis*) were enriched in δ^{13}C, indicating a reliance on carbon fixed by periphyton. Terrestrial insects were also relatively depleted in δ^{13}C. Fishes were relatively enriched in δ^{15}N, indicating higher trophic positions than invertebrates, and exhibited a wide range of δ^{13}C signatures. The low δ^{15}N values for kokanee, peamouth, suckers, and wild cutthroat trout reflected an almost exclusively invertebrate diet. Depleted δ^{13}C values for kokanee indicated a diet of pelagic or profundal invertebrates. This was consistent with stomach data, which included zooplankton and chironomid pupae and larvae. Enriched δ^{13}C values for suckers were consistent with stomach data indicating a littoral diet. Intermediate δ^{13}C values for peamouth were consistent with the observed diet, which included littoral invertebrates, terrestrial invertebrates, and zooplankton. The intermediate δ^{13}C values of wild cutthroat trout were consistent with the observed diet of terrestrial and profundal invertebrates (mostly adult Hymenoptera, Ephemeroptera larvae, and chironomid pupae; Table A1). Piscivorous species had enriched δ^{15}N signatures, reflecting high trophic positions. A comparison of δ^{13}C values

among piscivores suggested that Chinook salmon consumed mostly pelagic prey, smallmouth bass and northern pikeminnow consumed mostly littoral prey, and lake trout and burbot were apex predators, consuming a mixture of prey types. Kokanee fry sampled directly from the Lake Chelan Fish Hatchery and hatchery-origin cutthroat trout sampled from the lake had the most enriched δ^{15}N values in the system, likely reflecting enriched δ^{15}N in hatchery feed (i.e., fish meal from marine sources). The isotopic signatures of these hatchery fish contrasted sharply with their wild counterparts.

The mixing model analysis indicated that the diet of Chinook salmon was composed largely of *Mysis relicta* (Figure 16). The median estimate of the *Mysis* diet proportion in the annual diet was 62% (49-72%; 5th and 95th percentile estimates, respectively). Kokanee and peamouth were the most important fish prey. Kokanee comprised a median value of 5% of the diet (0.4-20%; 5th and 95th percentiles). Peamouth comprised a median value of 5% of the diet (0.4-22%; 5th and 95th percentiles). The median diet proportion estimates for all other potential prey species were less than 4%, and 95th percentile estimates were less than 15%.

Lake trout diet composition as estimated by the mixing model was broadly similar to the diet composition estimated using stomach contents. The mixing model analysis indicated that fish prey dominated the lake trout diet in the Lucerne Basin, with kokanee becoming more important with greater lake trout size. The estimated diet of 180-400 mm lake trout was composed predominantly of threespine stickleback and *Mysis*. Kokanee entered the diet of the 401-450 mm size class, comprising 13% of the diet (median estimate; 1-40%, 5th and 95th percentile estimates). Kokanee became slightly more important for the 451-500 mm size class, comprising 16% of the diet (median estimate; 1-42%; 5th and 95th percentiles). The largest lake trout size class (551-910 mm) consumed the most kokanee, an estimated 40% (median estimate; 17-59%, 5th and 95th percentiles). Non-salmonid fishes represented most of the remainder of the diet for the three largest lake trout size classes. Detailed results are included in the appendix (Figures A1-A4).

Mysis and non-salmonid fishes comprised the bulk of the diet for all size classes of lake trout in the Wapato Basin, and diets of the largest lake trout likely contained a substantial proportion of kokanee, according to mixing model estimates. The two smallest lake trout size classes (180-400 and 401-450 mm FL) ate mostly *Mysis* and threespine stickleback, plus small amounts of peamouth. *Mysis* dominated the diet of 451-500 mm lake trout, comprising 73% of the diet (median estimate; 54-86%, 5th and 95th percentile estimates). Model results were relatively uninformative for the largest lake trout size class (551-910 mm), with broad probability distributions indicating that many combinations of prey types had similar probabilities. Diets of this size class likely contained a substantial proportion of kokanee (32%, median estimate), although 5th and 95th percentile estimates encompassed a large range of values (3 and 62%, respectively). The largest lake trout also likely consumed a substantial proportion of *Mysis* (21%, median estimate; 3-49%, 5th and 95th percentiles). Cannibalism of small lake trout contributed approximately 13% of the diet (median estimate; 2-26%, 5th and 95th percentiles). Detailed results are included in the appendix (Figures A5-A8).

Lake trout growth and survival

Lake trout growth patterns differed between lake basins (Figure 17). The von Bertalanffy growth parameter L_∞ was greater in Lucerne Basin (707 mm FL) than in Wapato Basin (657 mm FL), indicating that lake trout achieved a larger maximum length in Lucerne Basin. The

parameter ω did not differ between basins (125 mm • year^{-1}), indicating that young lake trout grew in length at a similar rate in both basins.

Lake trout weighed less at small lengths but gained weight faster with increasing length in Lucerne Basin than in Wapato Basin, and these differences were significant (ANCOVA; main effect of basin, $F_{1, 493} = 46.2$, $p < 0.0001$; basin $\times$ $\log_{10}$(FL) interaction, $F_{1, 493} = 4.47$, $p < 0.05$). The ANCOVA model yielded the following length-weight relationships for Lucerne Basin ($r^2 = 0.93$, N = 105, P < 0.0001):

$$W = 0.00000360 \cdot L^{3.18} \tag{8}$$

and for Wapato Basin ($r^2 = 0.93$, N = 390, P < 0.0001):

$$W = 0.0000118 \cdot L^{3.01} \tag{9}$$

where W is wet weight (g) and L is fork length (mm).

Lake trout mortality was estimated from catch-at-age curves (Figure 18). The instantaneous annual mortality rate (Z) for lake trout was 0.4413 for Lucerne Basin (n = 37 fish ages 7-12 y, $r^2 = 0.55$) and 0.3072 for Wapato Basin (n = 86 fish ages 7-12 y, $r^2 = 0.84$). Corresponding annual survival rates (S) were 64% for Lucerne Basin and 74% for Wapato Basin. When data were pooled for the entire lake, Z was estimated at 0.3396 (n = 123, $r^2 = 0.80$), resulting in a value of 71% for S. We did not consider the Lucerne Basin rate reliable because of the poor model fit (low r^2), small sample size, and because we considered it unlikely that mortality of mature lake trout was substantially greater in the Lucerne Basin than in the Wapato Basin, where the vast majority of lake trout harvest occurs. Thus, we used the survival rate estimated from the pooled data for subsequent Lucerne Basin analyses.

Consumption by lake trout

Annual consumption rates were estimated for size-structured unit populations of 1,000 lake trout ages 2-16 in each lake basin (Figure 19). Lake trout in Lucerne Basin consumed 2,527 kg of prey annually per unit population, including 1,549 kg of fish prey and 965 kg of *Mysis*. Wapato Basin lake trout consumed 3,277 kg of prey annually per unit population, including 1,011 kg of fish prey and 2,180 kg of *Mysis*. Therefore, mysids contributed 38% of the annual prey biomass consumed in Lucerne Basin, but 67% in Wapato Basin. In both basins, salmonids comprised less than one third of fish prey consumed by the lake trout population (Figure 20). A unit population of lake trout consumed 477 kg of salmonids in Lucerne Basin, including 446 kg of kokanee, 14 kg of Chinook salmon, and 16 kg of unidentified salmonids. Wapato Basin lake trout consumed 217 kg of salmonids, including 112 kg of kokanee and 105 kg of lake trout per unit population. The mean estimated wet weights of prey specimens consumed by lake trout were 83.0 g (SD = 26.8 g) for kokanee age 1 and older (n = 6 prey specimens with reconstructed lengths); 103.6 g for Chinook salmon (n = 1), and 99.5 g for lake trout (n = 1). Dividing the biomass of consumed prey by these prey sizes yielded estimated annual consumption of 5,378 kokanee and 138 Chinook salmon per 1,000 lake trout in Lucerne Basin and 1,352 kokanee and 1,057 lake trout per 1,000 lake trout in Wapato Basin. The largest lake trout size class (551-910 mm FL) was responsible for 63% of salmonid consumption in Lucerne Basin and 97% of salmonid consumption in Wapato Basin.

Prey consumption by lake trout showed strong seasonal patterns in both lake basins (Figure 21). Total prey consumption was generally greatest during July-December, when lake trout experienced higher water temperatures (Table 5). Seasonal changes in prey consumption generally mirrored diet composition input data (Figure 22). Lake trout consumed most kokanee prey between July and March in the Lucerne Basin, with little kokanee consumption during

April-June. In Wapato Basin, lake trout consumed most kokanee during January-March and April-June, and cannibalized other lake trout most heavily during July-September. Lake trout consumed most cyprinid prey during April-June in both lake basins.

To allow comparison of the relative impact of lake trout predation between lake basins on a per area basis, we scaled annual lake trout consumption estimates by catch per unit effort. Thus, we compared the prey consumption of 1,000 lake trout in Wapato Basin with the consumption of 140 lake trout in Lucerne Basin, where CPUE was lower. Lake trout consumed 10.9 times more total prey, 4.89 times more fish prey, and 1.79 times more kokanee per unit area in Wapato Basin than in Lucerne Basin.

Consumption by Chinook salmon

Model simulations indicated that for every 1,000 age 1-4 Chinook salmon, approximately 14,850 kg of total prey (nominal estimate) were consumed per year. In the nominal simulation, age-1 cohort consumed the most total prey (6,032 kg) with consumption declining for the older cohorts (age 2: 4,089 kg; age 3: 3,779 kg; age 4: 949 kg). Chinook salmon consumed roughly 741.2 kg of kokanee annually per unit population (Table 10; 50th percentile diet and nominal growth scenario). Substantial uncertainty was associated with this estimate: the extreme low estimate (5th percentile diet and low growth) was 42.4 kg, and the extreme high estimate (95th percentile diet and high growth) was 4,393 kg (Table 10). If Chinook salmon consumed primarily kokanee age 1 and older, of the same size as consumed by lake trout (mean 83.0 g), the nominal estimate of kokanee biomass consumed would correspond to 8,927 individual kokanee consumed per 1,000 Chinook salmon, per year. This represented approximately 2.8 % of the number of kokanee age 1 and older in the lake during August 2005.

Lake trout harvest

Lake trout catch per unit effort (CPUE) declined from 12.6 fish per full day charter in 2004 to 8.7 fish per day in 2005 and 8.8 fish per day in 2006. Estimated total annual harvest was 1968 lake trout in 2005 (nominal estimate; 1575 minimum to 2624 maximum) and 2076 lake trout in 2006 (nominal estimate; 1660 minimum to 2767 maximum).

Lake trout population dynamics

The simulated lake trout population grew substantially with heavy stocking during 1990-2000 (Figure 23). After stocking ceased, the total abundance of lake trout age $\geq$ 2 yr began to decline under all three reproduction scenarios. Under the no-reproduction scenario, abundance continued to decline. Under the moderate reproduction scenario, abundance declined to a minimum by 2011, then increased slightly to a stable population. Under the rapid reproduction scenario, abundance increased substantially beginning in 2005.

The dynamics of lake trout spawning biomass followed the total abundance trends, after a roughly five-year lag as successive cohorts grew to maturity. Under both scenarios that allowed reproduction, spawning biomass increased rapidly during 1995-2007, and then declined briefly until 2010. Under the moderate reproduction scenario, spawning biomass continued to decline before stabilizing during the late 2010s. Under the rapid reproduction scenario, spawning biomass increased rapidly after 2010.

The dynamics of the largest lake trout size class (> 550 mm FL; $\geq$ 10 yr) mirrored the trend of total abundance, after a roughly eight-year lag. The biomass of large lake trout increased substantially during the 2000s as the cohorts stocked during the 1990s reached this size

class. Large lake trout biomass declined from 2010-2013 under all scenarios. After 2013, the biomass of large lake trout continued to decline in the no-reproduction scenario, declined to a stable biomass in the moderate-reproduction scenario, and increased sharply in the rapid-reproduction scenario. This largest lake trout size class was responsible for most kokanee consumption, meaning that the trend of kokanee predation mortality was closely tied to the biomass of lake trout in this group.

Discussion

Major predators on salmonids

Lake trout were the only abundant piscivores that fed extensively on kokanee and other salmonids in both lake basins. Northern pikeminnow and burbot fed on salmonids in Wapato Basin, but not in Lucerne Basin. Smallmouth bass were only captured in Wapato Basin, and no salmonids were detected in bass diets. Because kokanee and wild cutthroat trout densities were generally greater in Lucerne Basin, and because that basin encompassed most of the lake, we considered lake trout the most important predator of salmonids in the lake. Chinook salmon abundance was extremely low during our sampling period, but we included them in our piscivory analysis to allow managers to weigh the tradeoffs associated with the potential rebuilding of the population.

Lake trout predation

Lake trout consumed substantial amounts of kokanee and other fish prey throughout Lake Chelan, but predation pressure differed between lake basins in several important respects. Lake trout in the deeper Lucerne Basin ate predominantly fish, with the largest predators eating mostly kokanee, but the density of predators was relatively low. Conversely, in the shallower Wapato Basin, lake trout density was seven-fold greater, and lake trout consumed less kokanee on an individual basis. The contrast in diet composition between basins was reflected clearly both in stomach contents and the mixing model results for stable isotope data. On a per area basis, lake trout consumed more kokanee in the Wapato Basin than in the Lucerne Basin, reflecting their much greater density.

Although they represented only about 10% of the population, the largest size class of lake trout was responsible for most predation on salmonids in both basins. Lake trout greater than 550 mm in fork length (approximately 2 kg or 10 yr) accounted for 63% of lake trout predation on salmonids in the Lucerne Basin and 97% in the Wapato Basin. Lake trout less than 450 mm in fork length (approximately 800 g or 5 yr) consumed mostly *Mysis relicta* and no salmonid prey. The greater maximum body size (L_∞ and weight at length) achieved by lake trout in Lucerne Basin may be due to the heavy utilization on kokanee and other fish prey in that basin, and less *Mysis* in the diet (Martinez et al. 2009). Our results were consistent with findings from the native lake trout range that populations in larger, lower productivity lakes tended to exhibit slower initial growth but ultimately achieve a greater body size, while populations in smaller, higher productivity systems achieve greater juvenile growth and recruitment and greater densities (Shuter et al. 1998).

Consumption patterns varied seasonally, with Lucerne Basin lake trout consuming most kokanee between July and March, and Wapato Basin lake trout consuming most kokanee between January and June. Not surprisingly, this pattern generally matched the kokanee

migration between lake basins (Brown 1984; Schoen 2007). Although lake trout in Wapato Basin primarily consumed *Mysis* through most of the year, they switched to feed heavily on kokanee when available during winter-spring. Lake trout also consumed substantial numbers of cyprinids between April and June both basins, before thermal stratification forced lake trout into deep water and spatially segregated them from these prey.

Lake trout also consumed other salmonid species, including cannibalized lake trout, Chinook salmon, and unidentified salmonids. We detected no predation on westslope cutthroat trout, indicating that they were not important prey for lake trout. However, the wild cutthroat trout population is very small, and we cannot rule out that even a low level of undetected predation could limit its recovery. Non-native lake trout are important predators on native cutthroat trout in Bear Lake (Ruzycki et al. 2001), Fallen Leaf Lake (Al-Chokhachy et al. 2009), and Yellowstone Lake (Ruzycki et al. 2003), and have been implicated as the cause of extirpation or precipitous declines in other western lakes (Deleray et al. 1999). Cutthroat trout might be especially vulnerable to predation during fry outmigration and pre-spawning aggregations near tributaries. We avoided targeted gill net sampling near cutthroat trout pre-spawning aggregations because we judged the potential benefits of identifying a predation event not to be worth the risk of inflicting gill net mortality on the cutthroat trout. Future sampling might be more successful at detecting predation events if it targeted large piscivores without risking cutthroat trout mortality (by using non-lethal gear or gill nets with very large mesh, e.g., >10 cm stretch mesh, to allow the largest cutthroat to pass) during these potentially sensitive periods in the cutthroat trout life history.

Lake trout population trajectory

The lake trout population growth rate is a critical factor influencing Lake Chelan fisheries. Because the rate of natural reproduction was unknown, we modeled the population under three very different scenarios, assuming that natural reproduction was nonexistent, moderate and stable, or rapid and unchecked. Lake trout were observed spawning in the lake as early as 2000 (DES 2000), and we captured many fish too young to have been stocked, so the no-reproduction scenario represented an extreme lower bound, rather than a likely outcome. While none of these models was expected to predict the true lake trout population trend with precision, they represent the range of possibilities. The model results are also informative in the areas where they agree. All three scenarios predicted that the total abundance of lake trout was stable or declining during the 2004-2006 sampling period, and that the biomass of large (> 550 mm FL) lake trout increased substantially during the 2000s and declined somewhat from 2010-2013. These results indicated that regardless of the success of natural reproduction, lake trout predation on kokanee is currently greater than at any time since lake trout were introduced to the lake. After a likely slight decline in predation on kokanee during the next three years, predation could continue to decline, stabilize, or increase, depending on the reproductive rate. This makes determining the lake trout reproductive rate a critical research priority.

Aside from reproductive rates, the results of the lake trout population model depended on other important assumptions. First, we assumed that the lake trout per-capita consumption rates that we estimated for the 2004-2006 sampling period would not change in the future. Lake trout are opportunistic predators and may have switched to target other prey as the kokanee population declined from high escapements during that period. Lake trout in Lake Tahoe show great interannual variability in the proportion of fish in the diet (Richards et al. 1991), and consume more kokanee when kokanee densities are greater (Thiede 1997). However, lake trout in the

Great Lakes sustain similar consumption rates across a 100-fold range of prey fish densities, suggesting the capability to severely reduce fish populations (Eby et al. 1995). Thus, although prey switching behavior may have moderated an increase in predation, it is unlikely to have compensated for the substantial increase in large lake trout biomass. Second, we applied the mortality rates we observed for age 7-12 lake trout during 2004-2006 to all ages of lake trout during all simulation years. While this simplifying assumption influenced the absolute results of the simulations, it was unlikely to affect the simulation trends or the study conclusions.

Two lines of evidence support the population modeling results suggesting that the total abundance of lake trout was in decline during the mid-2000s. First, catch rates of the lake trout charter fishery reportedly declined during the study period. Catch per unit effort of participating anglers declined by 30% from 2004 to 2005, and remained stable during 2006. This CPUE trend should be interpreted cautiously, because the time series included only three years, and not all anglers participated. Further, CPUE of lake trout fisheries does not always accurately reflect abundance trends, as angler expertise often improves over time (Shuter et al. 1998). However, the trend is consistent with the observations of an experienced charter guide, who characterized 2002-2005 as the best years of the fishery, 2007-2008 as being the most difficult years since the late 1990s, and 2009 as being slightly improved (A. Jones, *pers. comm.,* 9/18/2009).

Second, a comparison of gill net catch curves suggests that lake trout < 400 mm FL were underrepresented by roughly 50% in the Lake Chelan population relative to the established, self-sustaining population sampled with similar methods in Lake Tahoe (Thiede 1997). This pattern suggests that the Lake Chelan population experienced a drop in recruitment around the time that stocking ceased in 2000 (Viola and Foster 2002), and that natural reproduction may not produce as many recruits as were stocked annually during the 1990s. Again, we interpret this result with caution because gill nets are not an effective means of sampling small lake trout, and other factors such as differences in depth distribution could have caused the pattern. In combination with the population modeling results and insights from the charter fishery, these limited empirical results suggest that the lake trout population was stable or declining during the mid 2000s.

Indirect benefits of lake trout?

One question facing managers is whether lake trout provide an indirect benefit to kokanee by reducing the density of *Mysis* and thereby enhancing the density of zooplankton (Brown 1984; Viola and Foster 2002). Based on evidence from Lake Chelan and other lakes, we conclude that this potential indirect benefit appears negligible compared to the direct, negative effect of lake trout predation on kokanee.

First, it is unclear whether lake trout predation significantly reduces *Mysis* density. *Mysis* densities in Lake Chelan were lowest at a sampling site with a high density of small lake trout (midlake near Minneapolis Beach; Schoen 2007), and this may have been due to lake trout predation. Alternatively, mysids may have actively avoided this relatively shallow area (Johannsson 1995) or been entrained through the hydropower system (Martin and Northcote 1991). Theide (1997) found that lake trout in Lake Tahoe consumed only 2-17% of *Mysis* standing stock biomass annually, but consumed 21-58% of potential kokanee spawners. Although mysids comprised a large proportion of the lake trout diet, they were too numerous to be limited by this level of predation.

Second, while *Mysis* can clearly reduce kokanee growth, there is little evidence that they can reduce zooplankton densities enough to cause kokanee to starve. *Mysis* predation reduces

the density and seasonal availability of cladoceran zooplankton (Morgan et al. 1978; Rieman and Falter 1981; Spencer et al. 1999), and this likely reduces kokanee growth (Chipps and Bennett 2000; Clarke and Bennett 2002; Martinez and Wiltzius 1995). However, considerable research on resource competition between *Mysis* and kokanee has failed to find evidence that *Mysis* reduces zooplankton densities to low enough levels to cause kokanee to starve (e.g., Clarke et al. 2004). Kokanee occur in systems with extremely low zooplankton density, such as Crater Lake, OR (Buktenica et al. 2007). Because kokanee survival is strongly size-dependent (McGurk 1999), reduced growth due to competition with *Mysis* likely makes kokanee more vulnerable to predation. But increasing the abundance of predators seems unlikely to solve that problem.

Third, distribution patterns show that given the choice between a safer, food-poor habitat or a riskier, food-rich habitat, kokanee in Lake Chelan generally choose the former (Schoen 2007). Zooplankton densities were consistently less and consumption rates by *Mysis* were greater in Lucerne Basin than in Wapato Basin. The net result was less available food for kokanee in Lucerne Basin. However, density of all kokanee age classes was generally greater in Lucerne Basin. Age-2 and older kokanee migrated into Wapato Basin seasonally, likely to take advantage of the earlier availability of *Daphnia* and the emergence of chironomids. Fewer age-0 and age-1 kokanee migrated to Wapato Basin. Water temperature did not explain the preference for Lucerne Basin, as kokanee were mostly distributed in the metalimnion and thermal experience was similar in both basins. In contrast, lake trout density was 7-fold greater in Wapato Basin, which likely explained the pattern of generally higher kokanee densities in the Lucerne Basin. These results suggest that for kokanee, access to enhanced food resources is not worth sustaining an increased risk of predation, at least in this case.

Chinook salmon predation

Stable isotope analysis provided strong evidence that the Chinook salmon diet was dominated by *Mysis relicta*. These results were surprisingly informative, given the small sample of six Chinook salmon, and the wide range of potential diet items included in the mixing model. Historical stomach contents data and recent reports from anglers also supported the heavy use of *Mysis*, lending credibility to this finding. This diet heavy in *Mysis* was unusual for lake-resident Chinook salmon, which feed primarily on fish prey in other lakes, even when *Mysis* are present (Murry et al. 2010; Negus et al. 2008; Stewart and Ibarra 1991). The low densities of kokanee and other fishes in Lake Chelan may explain this difference. We were forced to sacrifice realism in this analysis by not incorporating seasonal or ontogenetic diet changes. If the Chinook salmon population continues to increase, new diet data could readily improve these estimates.

Chinook salmon consumed over four times more total prey than lake trout on a per capita basis. Chinook salmon also consumed more kokanee per capita in most scenarios than did lake trout. Based on nominal estimates, Chinook salmon consumed 66% more kokanee than lake trout in the Lucerne Basin, and nearly 7 times more kokanee than lake trout in the Wapato Basin, on a per capita basis. These results mirrored findings from other lakes, showing much greater per capita consumption by Chinook salmon than by lake trout (Negus et al. 2008; Rand and Stewart 1998; Stewart and Ibarra 1991). Chinook fed at a relatively high proportion of their maximum consumption rates (0.49 – 1.28) under all consumption scenarios (Table 11). This suggested that total per-capita consumption was unlikely to increase substantially in the future, although the proportion of prey fish in the diet could certainly increase. We considered the high growth simulations to represent very generous estimates of consumption because Chinook salmon fed at greater than their theoretical maximum consumption rate in many of these

simulations (Table 11). These results suggested that it was unlikely that Chinook salmon could achieve such rapid growth given the water temperature and prey composition in Lake Chelan, and that true consumption rates were less than predicted by the high-growth simulations.

The recent advance incorporating uncertainty into stable isotope mixing models (Moore and Semmens 2008; Semmens et al. 2009) was critical to producing relevant results in this study. Although the stable isotope analysis indicated that kokanee comprised only approximately 5% of the Chinook salmon diet, there was considerable uncertainty around this value (0.4 – 20%; 5th – 95th percentile estimates) and we were able to include the relevant range of diet compositions in our bioenergetics simulations. Using a single nominal estimate from a traditional mixing model would have made our results much less useful for managers concerned not only with the most likely result, but also with the best- and worst-case scenarios. We encourage the development of analogous probability-based methods to allow uncertainty in all model inputs to be propagated through bioenergetics analyses.

The consumption estimates reported here provide interim guidelines on the tradeoff between Chinook salmon recovery and increased predation on prey populations. While we intend for these results to be useful to decision-makers in the short term, we stress that they are provisional and should be interpreted with caution and revised as new data become available.

Conclusions

Recent declines in kokanee escapement likely reflect increased predation from the increase in larger-sized lake trout as the population matures. The kokanee population grew steadily during the 1980s and 1990s, reaching peak abundances from 1999-2005. This may have been a window of low predation, after the Chinook salmon population crashed in 1999, and while most lake trout were still too small to pose a significant threat. Although small numbers of lake trout were stocked in the early 1980s, most stocking occurred from 1990-2000 (Viola and Foster 2002; WDFW unpubl. data). Our results showed that lake trout roughly ≥ 10 yr old (FL > 550 mm) were responsible for most kokanee consumption. In 2000, only one cohort had reached this more piscivorous size. By 2008, nine cohorts had achieved this size. Kokanee escapement declined by 80% between 2003 and 2008 (Keesee et al. 2009). Because kokanee abundance is volatile, it is difficult to attribute this decline conclusively to predation, but managers should treat this as the leading hypothesis. Total lake trout abundance was likely steady or in decline during the mid 2000s; however, this trend could quickly be reversed when the offspring of the stocked cohorts begin recruiting to the population.

Targeted improvements in monitoring could reduce the uncertainty associated with future lake trout and kokanee trends, and allow managers to react more quickly to signs of trouble. Currently, the status of each kokanee cohort is unknown until it becomes vulnerable to the fishery at age 2-3, and the population trend is not fully quantified until after spawning. This means that a serious event such as recruitment failure of age-0 kokanee would not be detected for 2-3 years. Without a plan in place, any necessary management actions to reduce lake trout predation and rebuild a depleted kokanee population would likely take several more years to successfully implement, as in Lakes Pend Oreille and Yellowstone (Hansen et al. 2008; Ruzycki et al. 2003), or might simply be prohibitively expensive, as in Flathead Lake (Beauchamp 1996; Beauchamp et al. 2007).

The lake trout population is an important resource that supports a popular trophy fishery. If managers plan to sustain this fishery, improved monitoring would help to avoid either of two unsatisfactory outcomes. First, rapid lake trout population growth would clearly be undesirable, due to negative impacts on kokanee and other prey fish, and also because without kokanee prey the growth rates of lake trout and Chinook salmon would likely decline dramatically. While lake trout populations can persist after kokanee become extirpated from a system, the switch to a *Mysis*-dominated diet has reduced the body size of lake trout in several fisheries, including Priest Lake and Flathead Lake (Martinez et al. 2009; Stafford et al. 2002). Second, if natural reproduction is insufficient to sustain the lake trout population as the stocked cohorts dwindle, then lake trout catches will decline. Monitoring the recruitment of juveniles could detect this trend years before it significantly affects catch rates.

Recommendations for management and monitoring
- Begin monitoring trends in lake trout density, distribution, and size structure. The rate of recruitment from natural reproduction is a key unknown. This could be accomplished with annual gill net sampling or detailed creel surveys. A standardized gill net sampling regime should ideally use the mesh sizes, depths, and locations used in this study, so that the catch rates and size structure reported here can serve as a baseline for comparison. Sampling during late summer would reduce the variability in catch rates and provide the most useful time series (Beauchamp et al. 2009). Periodic creel surveys could collect data on catch, effort, and harvest (i.e., whether fish were released or killed) and length measurements for a representative subset of fish. One method for monitoring changes in size structure is to ask the primary charter guides to record the length of the first 30 lake trout caught each month.
- Assess the recruitment and abundance of kokanee in the lake, ideally with an annual hydroacoustics survey during summer stratification. This would indicate population trends several years earlier than is currently possible with spawner surveys. The combination of abundance estimates from multiple age classes in the lake with escapement trends from spawner surveys would also provide insight into which life stages limit kokanee population growth, and management actions could be focused appropriately.
- Develop a plan to control lake trout population growth, in case this becomes necessary. In particular, locating the lake trout spawning aggregations in advance would allow a control program to be implemented swiftly. The lake trout control effort in Lake Pend Oreille became much more successful after researchers located spawning aggregations by using sonic telemetry to track mature lake trout back to previously unknown spawning areas (Martinez et al. 2009).
- If rebuilding the Chinook salmon fishery is a management goal, consider waiting until the kokanee population rebounds, and then start slowly. The consumption estimates reported here can provide preliminary guidelines on expected predation losses given different levels of Chinook salmon stocking. These estimates should be improved when new diet and growth rate data become available.

Literature Cited

Adare, K. I., and D. C. Lasenby. 1994. Seasonal changes in the total lipid content of the opossum shrimp, *Mysis relicta* (Malacostraca, Mysidacea). Canadian Journal of Fisheries and Aquatic Sciences 51(9):1935-1941.

Al-Chokhachy, R., M. Peacock, L. Heki, and G. Thiede. 2009. Evaluating the reintroduction potential of Lahontan cutthroat trout in Fallen Leaf Lake, California. North American Journal of Fisheries Management 29(5):1296-1313.

Beauchamp, D. A. 1996. Estimating predation losses under different lake trout population sizes and kokanee stocking scenarios in Flathead Lake. Final Report for Montana Department of Fish, Wildlife, and Parks.

Beauchamp, D. A., D. Parrish, and R. A. Whaley. 2009. Salmonids/coldwater species in large standing waters. Pages 97-117 *in* S. Bonar, D. W. Willis, and W. A. Hubert, editors. Standard Sampling Methods for North American Freshwater Fishes. American Fisheries Society, Bethesda, MD.

Beauchamp, D. A., D. J. Stewart, and G. L. Thomas. 1989. Corroboration of a bioenergetics model for sockeye salmon. Transactions of the American Fisheries Society 118(6):597-607.

Beauchamp, D. A., and J. J. Van Tassell. 2001. Modeling seasonal trophic interactions of adfluvial bull trout in Lake Billy Chinook, Oregon. Transactions of the American Fisheries Society 130(2):204-216.

Beauchamp, D. A., D. Wahl, and B. M. Johnson. 2007. Predator-Prey Interactions. Pages 765-842 *in* C. S. Guy, and M. L. Brown, editors. Analysis and Interpretation of Freshwater Fisheries Data. American Fisheries Society, Bethesda, MD.

Bigelow, P., and coauthors. 2003. Protection of native Yellowstone cutthroat trout in Yellowstone Lake, Yellowstone National Park, Wyoming. Technical report NPS/NRWRD/NRTR-2003/314. National Park Service, Water Resources Division, Fort Collins, CO.

Bowles, E. C., B. E. Rieman, G. R. Mauser, and D. H. Bennett. 1991. Effects of introductions of *Mysis relicta* on fisheries in northern Idaho. American Fisheries Society Symposium 9:65-74.

Brown, L. G. 1984. Lake Chelan Fishery Investigations. Chelan County Public Utility District No. 1 and Washington Dept. of Game.

Buktenica, M. W., S. F. Girdner, G. L. Larson, and C. D. McIntire. 2007. Variability of kokanee and rainbow trout food habits, distribution, and population dynamics, in an ultraoligotrophic lake with no manipulative management. Hydrobiologia 574:235-264.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York.

Caut, S., E. Angulo, and F. Courchamp. 2008. Caution on isotopic model use for analyses of consumer diet. Canadian Journal of Zoology 86(5):438-445.

Caut, S., E. Angulo, and F. Courchamp. 2009. Variation in discrimination factors (Delta N-15 and Delta C-13): the effect of diet isotopic values and applications for diet reconstruction. Journal of Applied Ecology 46(2):443-453.

Chipps, S. R., and D. H. Bennett. 2000. Zooplanktivory and nutrient regeneration by invertebrate (*Mysis relicta*) and vertebrate (*Oncorhynchus nerka*) planktivores: Implications for

trophic interactions in oligotrophic lakes. Transactions of the American Fisheries Society 129(2):569-583.

Chipps, S. R., and J. E. Garvey. 2007. Quantitative assessment of food habits and feeding patterns. Pages 473-514 *in* C. S. Guy, and M. L. Brown, editors. Analysis and Interpretation of Freshwater Fisheries Data. American Fisheries Society, Bethesda, MD.

Clarke, L. R., and D. H. Bennett. 2002. A net-pen experiment to evaluate kokanee growth rates in autumn in an oligotrophic lake with *Mysis relicta*. Transactions of the American Fisheries Society 131(6):1061-1069.

Clarke, L. R., P. S. Letizia, and D. H. Bennett. 2004. Autumn-to-spring energetic and diet changes among kokanee from North Idaho Lakes with and without *Mysis relicta*. North American Journal of Fisheries Management 24(2):597-608.

Cressie, N., C. A. Calder, J. S. Clark, J. M. V. Hoef, and C. K. Wikle. 2009. Accounting for uncertainty in ecological analysis: the strengths and limitations of hierarchical statistical modeling. Ecological Applications 19(3):553-570.

Deleray, M., L. Knotek, S. Rumsey, and T. Weaver. 1999. Flathead Lake and River system fisheries status report. Montana Fish, Wildlife and Parks, Kalispell, MT.

Deniro, M. J., and S. Epstein. 1977. Mechanism of carbon isotope fractionation associated with lipid synthesis. Science 197(4300):261-263.

DES. 2000. Lake Chelan Fisheries Investigation, Lake Chelan Hydroelectric Project No. 637. Prepared for Public Utility District No. 1 of Chelan County. Duke Engineering and Services, Bellingham, WA.

Donald, D. B., and D. J. Alger. 1993. Geographic distribution, species displacement, and niche overlap for lake trout and bull trout in mountain lakes. Canadian Journal of Zoology 71(2):238-247.

Eby, L. A., L. G. Rudstam, and J. F. Kitchell. 1995. Predator responses to prey population dynamics: An empirical analysis based on lake trout growth rates. Canadian Journal of Fisheries and Aquatic Sciences 52(7):1564-1571.

Gallucci, V. F., and T. J. Quinn. 1979. Reparameterizing, fitting, and testing a simple growth model. Transactions of the American Fisheries Society 108(1):14-25.

Hagen, J. E. 1997. An Evaluation of a Trout Fishery Enhancement Program in Lake Chelan. Master's thesis. University of Washington, Seattle.

Hansel, H. C., S. D. Duke, P. T. Lofy, and G. A. Gray. 1988. Use of diagnostic bones to identify and estimate original lengths of ingested prey fishes. Transactions of the American Fisheries Society 117(1):55-62.

Hansen, M. J. 2007. Predator-prey dynamics in Lake Pend Oreille. Idaho Department of Fish and Game, Boise.

Hansen, M. J., N. J. Horner, M. Liter, M. P. Peterson, and M. A. Maiolie. 2008. Dynamics of an increasing lake trout population in Lake Pend Oreille, Idaho. North American Journal of Fisheries Management 28(4):1160-1171.

Hansen, M. J., C. P. Madenjian, J. H. Selgeby, and T. E. Helser. 1997. Gillnet selectivity for lake trout (*Salvelinus namaycush*) in Lake Superior. Canadian Journal of Fisheries and Aquatic Sciences 54(11):2483-2490.

Hansen, M. J., and coauthors. 1995. Lake trout (*Salvelinus namaycush*) populations in Lake Superior and their restoration in 1959–1993. Journal of Great Lakes Research 21:152-175.

Hanson, P. C., T. B. Johnson, D. E. Schindler, and J. F. Kitchell. 1997. Fish Bioenergetics 3.0. University of Wisconsin Sea Grant Inst., Madison, WI.

Harvey, C. J., P. C. Hanson, T. E. Essington, P. B. Brown, and J. F. Kitchell. 2002. Using bioenergetics models to predict stable isotope ratios in fishes. Canadian Journal of Fisheries and Aquatic Sciences 59(1):115-124.

Hassler, T. J., M. E. Coleman, and B. R. Nielson. 1986. Hatcheries and wild trout management. American Fisheries Society.

Hecky, R. E., and R. H. Hesslein. 1995. Contributions of benthic algae to lake food webs as revealed by stable isotope analysis. Journal of the North American Benthological Society 14:631-653.

Hilborn, R., and M. Mangel. 1997. The Ecological Detective: Confronting Models with Data. Princeton University Press, Princeton, NJ.

Hilborn, R., and C. Walters. 1992. Quantitative Fisheries Stock Assessment: Choice, Dynamics, and Uncertainty. Kluwer Academic Publishers, Norwell, MA.

Ihaka, R., and R. Gentleman. 1996. R: A language for data analysis and graphics. Journal of Computational and Graphical Statistics 5(3):299-314.

Johannsson, O. E. 1995. Response of *Mysis relicta* population dynamics and productivity to spatial and seasonal gradients in Lake Ontario. Canadian Journal of Fisheries and Aquatic Sciences 52(7):1509-1522.

Johnson, B. M., and P. J. Martinez. 2000. Trophic economics of lake trout management in reservoirs of differing productivity. North American Journal of Fisheries Management 20:127-143.

Johnson, T. B., D. M. Mason, S. T. Schram, and J. F. Kitchell. 1999. Ontogenetic and seasonal patterns in the energy content of piscivorous fishes in Lake Superior. Journal of Great Lakes Research 25(2):275-281.

Keesee, B. G., S. L. Hemstrom, and L. M. Keller. 2009. Lake Chelan Kokanee Spawning Ground Surveys 2008. Final Report. Chelan County Public Utility District, Wenatchee, WA.

Kendra, W., and L. R. Singleton. 1987. Morphometry of Lake Chelan. Water Quality Investigations Section, Washington State Department of Ecology, Olympia.

Kiljunen, M., and coauthors. 2006. A revised model for lipid-normalizing delta C-13 values from aquatic organisms, with implications for isotope mixing models. Journal of Applied Ecology 43(6):1213-1222.

Kutner, M. H., C. J. Nachtschiem, J. Neter, and W. Li. 2005. Applied Linear Statistical Models, 5th edition edition. McGraw-Hill Irwin, Boston.

Lasenby, D. C. 1971. The ecology of *Mysis relicta* in an arctic and a temperate lake. Doctoral dissertation. University of Toronto, Toronto.

Lasenby, D. C., T. G. Northcote, and M. Furst. 1986. Theory, practice, and effects of *Mysis relicta* introductions to North American and Scandinavian lakes. Canadian Journal of Fisheries and Aquatic Sciences 43(6):1277-1284.

Leggett, M. F. 1998. Food-web dynamics of Lake Ontario as determined by carbon and nitrogen stable isotope analysis. Ph.D. dissertation. University of Waterloo.

Lele, S. R., and B. Dennis. 2009. Bayesian methods for hierarchical models: Are ecologists making a Faustian bargain. Ecological Applications 19(3):581-584.

Logan, J. M., and coauthors. 2008. Lipid corrections in carbon and nitrogen stable isotope analyses: comparison of chemical extraction and modelling methods. Journal of Animal Ecology 77(4):838-846.

Love, R. 1971. Dorsal aspect target strength of an individual fish. The Journal of the Acoustical Society of America 49:816.

Lubetkin, S. C., and C. A. Simenstad. 2004. Multi-source mixing models to quantify food web sources and pathways. Journal of Applied Ecology 41(5):996-1008.

Luecke, C., T. Edwards, M. Wengert, S. Brayton, and R. Schneidervin. 1994. Simulated changes in lake trout yield, trophies, and forage consumption under various slot limits. North American Journal of Fisheries Management 14(1):14-21.

Luecke, C., M. W. Wengert, and R. W. Schneidervin. 1999. Comparing results of a spatially explicit growth model with changes in the length-weight relationship of lake trout (*Salvelinus namaycush*) in Flaming Gorge Reservoir. Canadian Journal of Fisheries and Aquatic Sciences 56:162-169.

Luecke, C., and W. A. Wurtsbaugh. 1993. Effects of moonlight and daylight on hydroacoustic estimates of pelagic fish abundance. Transactions of the American Fisheries Society 122(1):112-120.

Martin, A. D., and T. G. Northcote. 1991. Kootenay Lake: An inappropriate model for *Mysis relicta* introduction in north temperate lakes. American Fisheries Society Symposium 9:23-29.

Martinez, P., B. Hansen, N. Horner, and S. Lehr. 2009. Western lake trout woes. Fisheries 34(9):424-442.

Martinez, P. J., and W. J. Wiltzius. 1995. Some factors affecting a hatchery-sustained kokanee population in a fluctuating Colorado reservoir. North American Journal of Fisheries Management 15(1):220-228.

Mazur, M. M. 2004. Linking Visual Foraging with Temporal Prey Distributions to Model Trophic Interactions in Lake Washington. Doctoral dissertation. University of Washington, Seattle.

McConnaughey, T., and C. P. McRoy. 1979. Food web structure and the fractionation of carbon isotopes in the Bering Sea. Marine Biology 53(3):257-262.

McCutchan, J. H., W. M. Lewis, C. Kendall, and C. C. McGrath. 2003. Variation in trophic shift for stable isotope ratios of carbon, nitrogen, and sulfur. Oikos 102(2):378-390.

McGurk, M. D. 1999. Size dependence of natural mortality rate of sockeye salmon and kokanee in freshwater. North American Journal of Fisheries Management 19(2):376-396.

Minagawa, M., and E. Wada. 1984. Stepwise enrichment of N-15 along food chains: Further evidence and the relation between delta N-15 and animal age. Geochimica Et Cosmochimica Acta 48(5):1135-1140.

Miranda, L. E., and P. W. Bettoli. 2007. Mortality. Pages 229-277 *in* C. S. Guy, and M. L. Brown, editors. Analysis and Interpretation of Freshwater Fisheries Data. American Fisheries Society, Bethesda, MD.

Moore, J. W., and B. X. Semmens. 2008. Incorporating uncertainty and prior information into stable isotope mixing models. Ecology Letters 11(5):470-480.

Morgan, M. D., S. T. Threlkeld, and C. R. Goldman. 1978. Impact of the introduction of kokanee (*Oncorhynchus nerka*) and opossum shrimp (*Mysis relicta*) on a subalpine lake. Journal of the Fisheries Research Board of Canada 35(12):1572-1579.

Murry, B. A., M. J. Connerton, R. O'Gorman, D. J. Stewart, and N. H. Ringler. 2010. Lakewide estimates of alewife biomass and Chinook salmon abundance and consumption in Lake Ontario, 1989–2005: Implications for prey fish sustainability. Transactions of the American Fisheries Society 139(1):223-240.

Negus, M. T., and coauthors. 2008. Bioenergetics evaluation of the fish community in the western arm of Lake Superior in 2004. North American Journal of Fisheries Management 28(6):1649-1667.

Nesler, T. P., and E. P. Bergersen, editors. 1991. Mysids in fisheries: hard lessons from headlong introductions, volume 9. American Fisheries Society Symposium.

Nieland, J. L. 2006. Modeling the sustainability of lake trout fisheries in eastern Wisconsin waters of Lake Superior. University of Wisconsin - Stevens Point.

Parrish, J. K., and coauthors. 2006. Small-bodied and Juvenile Fishes of the Mid-Columbia Region Including Keys to Diagnostic Otoliths and Cranial Bones. Draft Version, March 2006. University of Washington, Seattle.

Pelletier, G., C. R. Patmont, E. B. Welch, D. Bandon, and C. C. Ebbesmeyer. 1989. Lake Chelan Water Quality Assessment. Washington Department of Ecology, Olympia.

Peterson, B. J., and B. Fry. 1987. Stable isotopes in ecosystem studies. Annual Review of Ecology And Systematics 18:293-320.

Peven, C. M. 1990. Lake Chelan Spawning Ground Surveys. Chelan County Public Utility District, Wenatchee, WA.

Phillips, D. L., and J. W. Gregg. 2003. Source partitioning using stable isotopes: coping with too many sources. Oecologia 136(2):261-269.

Post, D. M. 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology 83(3):703-718.

Post, D. M., and coauthors. 2007. Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotope analyses. Oecologia 152(1):179-189.

PUD, 2007. Lake Chelan Fishery Plan. Chelan County Public Utility District, Wenatchee, WA.

Purcell, M., G. Mackey, E. LaHood, H. Huber, and L. Park. 2004. Molecular methods for the genetic identification of salmonid prey from Pacific harbor seal (*Phoca vitulina richardsi*) scat. Fishery Bulletin 102(1):213-220.

Rand, P. S., and D. J. Stewart. 1998. Prey fish exploitation, salmonine production, and pelagic food web efficiency in Lake Ontario. Canadian Journal of Fisheries and Aquatic Sciences 55(2):318-327.

Richards, R., C. Goldman, E. Byron, and C. Levitan. 1991. The mysids and lake trout of Lake Tahoe: A 25-year history of changes in the fertility, plankton, and fishery of an alpine lake. American Fisheries Society Symposium 9:30-38.

Ricker, W. 1975. Computation and interpretation of biological statistics of fish populations, Ottawa, Canada.

Rieman, B. E., and C. M. Falter. 1981. Effects of the establishment of *Mysis relicta* on the macrozooplankton of a large lake. Transactions of the American Fisheries Society 110(5):613-620.

Ruzycki, J. R., D. A. Beauchamp, and D. L. Yule. 2003. Effects of introduced lake trout on native cutthroat trout in Yellowstone Lake. Ecological Applications 13(1):23-37.

Ruzycki, J. R., W. A. Wurtsbaugh, and C. Luecke. 2001. Salmonine consumption and competition for endemic prey fishes in Bear Lake, Utah-Idaho. Transactions of the American Fisheries Society 130(6):1175-1189.

Schoen, E. R. 2007. Pelagic Trophic Interactions in Contrasting Basins of Lake Chelan. Master's Thesis. University of Washington, Seattle.

Semmens, B. X., J. W. Moore, and E. J. Ward. 2009. Improving Bayesian isotope mixing models: a response to Jackson et al. (2009). Ecology Letters 12(3):E6-E8.

Sharp, D., and D. R. Bernard. 1988. Precision of estimated ages of lake trout from five calcified structures. North American Journal of Fisheries Management 8:367-372.

Shuter, B. J., M. L. Jones, R. M. Korver, and N. P. Lester. 1998. A general, life history based model for regional management of fish stocks: the inland lake trout (*Salvelinus namaycush*) fisheries of Ontario. Canadian Journal of Fisheries and Aquatic Sciences 55(9):2161-2177.

Smyntek, P. M., M. A. Teece, K. L. Schulz, and S. J. Thackeray. 2007. A standard protocol for stable isotope analysis of zooplankton in aquatic food web research using mass balance correction models. Limnology and Oceanography 52(5):2135-2146.

Spencer, C. N., B. R. McClelland, and J. A. Stanford. 1991. Shrimp stocking, salmon collapse, and eagle displacement. Bioscience 41(1):14-21.

Spencer, C. N., D. S. Potter, R. T. Bukantis, and J. A. Stanford. 1999. Impact of predation by *Mysis relicta* on zooplankton in Flathead Lake, Montana, USA. Journal of Plankton Research 21(1):51-64.

Stafford, C. P., J. A. Stanford, F. R. Hauer, and E. B. Brothers. 2002. Changes in lake trout growth associated with *Mysis relicta* establishment: A retrospective analysis using otoliths. Transactions of the American Fisheries Society 131(5):994-1003.

Stewart, D. J., and M. Ibarra. 1991. Predation and production by salmonine fishes in Lake Michigan, 1978-88. Canadian Journal of Fisheries and Aquatic Sciences 48(5):909-922.

Stewart, D. J., J. F. Kitchell, and L. B. Crowder. 1981. Forage fishes and their salmonid predators in Lake Michigan. Transactions of the American Fisheries Society 110(6):751-763.

Stewart, D. J., D. Weininger, D. V. Rottiers, and T. A. Edsall. 1983. An energetics model for lake trout (*Salvelinus namaycush*): application to the Lake Michigan population. Canadian Journal of Fisheries and Aquatic Sciences 40:681-698.

Sweeting, C. J., N. V. C. Polunin, and S. Jennings. 2006. Effects of chemical lipid extraction and arithmetic lipid correction on stable isotope ratios of fish tissues. Rapid Communications In Mass Spectrometry 20(4):595-601.

Thiede, G. P. 1997. Impact of lake trout predation on prey populations in Lake Tahoe: a bioenergetics assessment. Masters Thesis. Utah State University, Logan.

Vander Zanden, M. J., G. Cabana, and J. B. Rasmussen. 1997. Comparing trophic position of freshwater fish calculated using stable nitrogen isotope ratios (delta N-15) and literature dietary data. Canadian Journal of Fisheries and Aquatic Sciences 54(5):1142-1158.

Vander Zanden, M. J., S. Chandra, B. C. Allen, J. E. Reuter, and C. R. Goldman. 2003. Historical food web structure and restoration of native aquatic communities in the Lake Tahoe (California-Nevada) Basin. Ecosystems 6(3):274-288.

Vander Zanden, M. J., and J. B. Rasmussen. 2001. Variation in delta N-15 and delta C-13 trophic fractionation: Implications for aquatic food web studies. Limnology and Oceanography 46(8):2061-2066.

Viola, A. E., and J. H. Foster. 2002. Lake Chelan Comprehensive Fishery Management Plan. Final Draft. Washington Department of Fish and Wildlife, Olympia.

Wesley, J. K. 1996. Age and growth of Chinook salmon in Lake Michigan: Verification, current analysis, and past trends. Masters Thesis. University of Michigan, Ann Arbor.

Wetzel, R. G. 1983. Limnology. Saunders, Toronto, ON.

Wurster, C. M., W. P. Patterson, D. J. Stewart, J. N. Bowlby, and T. J. Stewart. 2005. Thermal histories, stress, and metabolic rates of Chinook salmon (*Oncorhynchus tshawytscha*) in Lake Ontario: evidence from intra-otolith stable isotope analyses. Canadian Journal of Fisheries and Aquatic Sciences 62(3):700-713.

Wydoski, R. S., and R. R. Whitney. 2003. Inland Fishes of Washington, 2nd edition. University of Washington Press, Seattle.

Yule, D. L., and C. Luecke. 1993. Lake trout consumption and recent changes in the fish assemblage of Flaming Gorge Reservoir. Transactions of the American Fisheries Society 122(6):1058-1069.

Table 1. Prey isotopic signatures, fractionation rates, and potential prey inputs to MixSIR stable isotope mixing model.

			δ^{15}N		δ^{13}C		Potential prey types for each predator group								
							Chinook salmon	Lake trout							
								Lucerne Basin				Wapato Basin			
Input type	Species	Lake basin	Mean	SD	Mean	SD		180-450	451-500	501-550	551-910	180-450	451-500	501-550	551-910
Prey	Burbot	Both	10.61	1.07	-23.05	2.16	X	X							
Prey	Chinook salmon	Both	9.22	0.71	-24.27	1.33	X		X						
Prey	Kokanee	Both	7.02	0.72	-25.01	1.17	X		X	X	X				X
Prey	Lake trout	Both	10.46	0.69	-23.80	1.47	X								X
Prey	Northern pikeminnow	Both	8.72	1.14	-18.59	2.55	X		X	X	X				X
Prey	Peamouth	Both	6.39	0.89	-21.58	2.74	X		X	X	X	X	X	X	X
Prey	Sculpin	Both	8.03	0.85	-20.48	3.10	X		X	X					
Prey	Smallmouth bass	Both	9.88	0.86	-16.89	0.92	X							X	
Prey	Threespine stickleback	Both	8.31	0.76	-22.26	1.52	X	X	X			X	X	X	
Prey	*Mysis relicta*	Both	5.11	0.78	-26.15	0.75	X								
Prey	*Mysis relicta*	Lucerne	4.97	0.71	-26.37	0.48		X	X	X					
Prey	*Mysis relicta*	Wapato	5.51	0.85	-25.51	1.03						X	X	X	X
Fractionation			3.4	1	0.4	1.3									

Note: Potential prey types for lake trout were identified using stomach content data. Potential prey types were identified separately for each lake trout size class (FL, mm) in each lake basin. Within these size-basin groups, only those prey types that contributed ≥ 2.5% of the annual diet, based on stomach contents, were included in the mixing model (see Methods for exceptions). Stomach content data for Chinook salmon were insufficient to identify potential prey; all lake trout prey types were included in the Chinook salmon mixing model.

Table 2. Predator isotopic signature inputs to stable isotope mixing model.

Predator species	Lake basin	Size class (FL, mm)	$\delta^{15}N$	$\delta^{13}C$	Predator species	Lake basin	Size class (FL, mm)	$\delta^{15}N$	$\delta^{13}C$
Chinook			9.22	-25.26	Lake trout	Lucerne	551-910	11.39	-21.72
Chinook			9.69	-21.75	Lake trout	Lucerne	551-910	11.84	-20.80
Chinook			9.95	-24.51	Lake trout	Lucerne	551-910	11.80	-21.62
Chinook			8.00	-25.49	Lake trout	Lucerne	551-910	10.73	-22.99
Chinook			8.88	-24.38	Lake trout	Wapato	180-450	10.67	-25.00
Chinook			9.61	-24.26	Lake trout	Wapato	180-450	10.95	-23.31
Lake trout	Lucerne	180-450	9.09	-25.83	Lake trout	Wapato	180-450	11.25	-24.89
Lake trout	Lucerne	180-450	9.51	-24.14	Lake trout	Wapato	180-450	10.34	-23.68
Lake trout	Lucerne	180-450	11.11	-21.87	Lake trout	Wapato	180-450	10.51	-24.33
Lake trout	Lucerne	180-450	11.71	-22.99	Lake trout	Wapato	180-450	10.23	-23.69
Lake trout	Lucerne	180-450	9.72	-26.17	Lake trout	Wapato	180-450	10.55	-24.91
Lake trout	Lucerne	180-450	10.25	-24.39	Lake trout	Wapato	180-450	10.31	-24.70
Lake trout	Lucerne	180-450	9.81	-20.10	Lake trout	Wapato	180-450	10.36	-24.87
Lake trout	Lucerne	180-450	10.39	-24.37	Lake trout	Wapato	180-450	10.60	-24.81
Lake trout	Lucerne	180-450	9.39	-23.70	Lake trout	Wapato	180-450	10.22	-22.71
Lake trout	Lucerne	180-450	10.65	-23.27	Lake trout	Wapato	451-500	10.12	-25.06
Lake trout	Lucerne	180-450	11.82	-22.75	Lake trout	Wapato	451-500	10.52	-25.92
Lake trout	Lucerne	180-450	11.19	-20.82	Lake trout	Wapato	451-500	11.04	-24.41
Lake trout	Lucerne	451-500	11.91	-17.94	Lake trout	Wapato	451-500	11.10	-21.43
Lake trout	Lucerne	451-500	11.08	-23.20	Lake trout	Wapato	501-550	10.37	-24.68
Lake trout	Lucerne	451-500	10.69	-20.52	Lake trout	Wapato	501-550	10.07	-23.68
Lake trout	Lucerne	451-500	12.00	-23.32	Lake trout	Wapato	501-550	10.55	-25.05
Lake trout	Lucerne	451-500	10.62	-22.77	Lake trout	Wapato	501-550	6.97	-20.80
Lake trout	Lucerne	451-500	9.63	-23.90	Lake trout	Wapato	501-550	8.89	-25.19
Lake trout	Lucerne	451-500	10.84	-22.25	Lake trout	Wapato	501-550	10.66	-23.76
Lake trout	Lucerne	451-500	10.86	-21.41	Lake trout	Wapato	501-550	10.11	-24.56
Lake trout	Lucerne	451-500	12.14	-22.44	Lake trout	Wapato	551-910	10.30	-24.85
Lake trout	Lucerne	501-550	10.25	-22.68	Lake trout	Wapato	551-910	10.90	-22.75
Lake trout	Lucerne	501-550	10.45	-23.80	Lake trout	Wapato	551-910	10.52	-24.01
Lake trout	Lucerne	501-550	10.85	-22.11	Lake trout	Wapato	551-910	9.93	-24.60
Lake trout	Lucerne	501-550	9.94	-22.70	Lake trout	Wapato	551-910	9.61	-23.94
Lake trout	Lucerne	501-550	10.17	-22.84	Lake trout	Wapato	551-910	10.58	-23.50
Lake trout	Lucerne	501-550	11.25	-21.84	Lake trout	Wapato	551-910	10.52	-23.49
Lake trout	Lucerne	501-550	10.08	-21.66	Lake trout	Wapato	551-910	12.24	-19.14
Lake trout	Lucerne	501-550	10.84	-21.60	Lake trout	Wapato	551-910	10.00	-23.87
Lake trout	Lucerne	501-550	9.82	-25.15	Lake trout	Wapato	551-910	10.17	-23.56
Lake trout	Lucerne	501-550	9.04	-22.24	Lake trout	Wapato	551-910	10.83	-22.15
Lake trout	Lucerne	551-910	9.71	-24.58	Lake trout	Wapato	551-910	9.84	-24.48
Lake trout	Lucerne	551-910	10.39	-23.14	Lake trout	Wapato	551-910	11.36	-23.56
Lake trout	Lucerne	551-910	10.68	-21.80	Lake trout	Wapato	551-910	11.33	-22.99
Lake trout	Lucerne	551-910	10.57	-23.11	Lake trout	Wapato	551-910	10.35	-22.48
Lake trout	Lucerne	551-910	10.85	-22.08	Lake trout	Wapato	551-910	10.79	-23.58

Table 3. Growth, size class, age structure, and proportion of maximum consumption rate (C_{max}) values used for bioenergetics simulations of lake trout in Lucerne and Wapato Basins of Lake Chelan

Age (yr)	Wet weight (g)		Size class (FL, mm)		Numbers per 1,000 fish		Proportion of C_{max}	
	Lucerne	Wapato	Lucerne	Wapato	Lucerne	Wapato	Lucerne	Wapato
2	88	112	180-450	180-450	289.5	266.4	0.62	0.69
3	247	292	180-450	180-450	206.0	196.0	0.62	0.68
4	479	538	180-450	180-450	146.7	144.1	0.62	0.67
5	762	823	180-450	180-450	104.4	106.0	0.56	0.71
6	1075	1124	451-500	180-450	74.3	78.0	0.35	0.69
7	1396	1422	501-550	451-500	52.9	57.4	0.44	0.67
8	1712	1705	501-550	501-550	37.6	42.2	0.38	0.64
9	2011	1966	551-910	501-550	26.8	31.0	0.37	0.53
10	2288	2200	551-910	551-910	19.1	22.8	0.36	0.44
11	2540	2408	551-910	551-910	13.6	16.8	0.36	0.44
12	2765	2589	551-910	551-910	9.7	12.3	0.35	0.43
13	2963	2745	551-910	551-910	6.9	9.1	0.35	0.43
14	3137	2879	551-910	551-910	4.9	6.7	0.35	0.42
15	3288	2993	551-910	551-910	3.5	4.9	0.34	0.42
16	3418	3090	551-910	551-910	2.5	3.6	0.34	0.42
17	3530	3171	551-910	551-910	1.8	2.7		

Notes: Size classes were used to assign diet and thermal experience inputs to lake trout in the model. Numbers per 1,000 fish indicate the expected numbers of lake trout at each age, in a unit population of 1,000 fish of age ≥ 2 yr with the observed age structure. Size class and numbers inputs were adjusted on a daily time step in simulations but are represented here on an annual basis for simplicity. Values indicate the size class and numbers per 1,000 recruits on model day 1 of each year of age. Lake trout shifted between size classes on the model day that they exceeded the transitional length, as estimated with a von Bertalanffy growth model. Lake trout consumption was modeled for ages 2-16; inputs for age 17 were used only as the endpoints for the age 16 simulation.

Table 4. Diet composition inputs for bioenergetics simulations of four size classes of lake trout in Lucerne and Wapato Basins of Lake Chelan.

Lake basin	Size class (FL; mm)	Simulation day	Diet proportions by weight									
			Burbot	Chinook salmon	Cyprinids	Kokanee	Lake trout	Threespine stickleback	Unidentified salmonids	Other fish	*Mysis relicta*	Other invertebrates
Lucerne	180-450	1	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	1.000	0.000
		92	0.796	0.000	0.000	0.000	0.000	0.174	0.000	0.000	0.000	0.030
		183	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.085	0.915	0.000
		274	0.000	0.000	0.000	0.000	0.000	0.398	0.000	0.000	0.602	0.000
		365	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	1.000	0.000
	451-500	1	0.000	0.000	0.999	0.000	0.000	0.000	0.000	0.000	0.000	0.001
		92	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.999	0.001	0.001
		183	0.000	0.000	0.000	0.291	0.000	0.625	0.000	0.085	0.000	0.000
		274	0.000	0.000	0.119	0.322	0.000	0.137	0.000	0.000	0.417	0.004
		365	0.000	0.000	0.999	0.000	0.000	0.000	0.000	0.000	0.000	0.001
	501-550	1	0.000	0.000	0.992	0.000	0.000	0.001	0.000	0.007	0.000	0.000
		92	0.000	0.146	0.000	0.664	0.000	0.000	0.164	0.027	0.000	0.000
		183	0.000	0.000	0.425	0.363	0.000	0.000	0.000	0.212	0.000	0.000
		274	0.000	0.000	0.000	0.217	0.000	0.010	0.000	0.007	0.760	0.005
		365	0.000	0.000	0.992	0.000	0.000	0.001	0.000	0.007	0.000	0.000
	551-910	1	0.000	0.000	0.983	0.000	0.000	0.000	0.000	0.017	0.000	0.000
		92	0.000	0.000	0.334	0.650	0.000	0.003	0.000	0.013	0.000	0.000
		183	0.000	0.000	0.000	1.000	0.000	0.000	0.000	0.000	0.000	0.000
		274	0.000	0.000	0.020	0.950	0.000	0.009	0.000	0.022	0.000	0.000
		365	0.000	0.000	0.983	0.000	0.000	0.000	0.000	0.017	0.000	0.000
Wapato	180-450	1	0.000	0.000	0.526	0.000	0.000	0.071	0.000	0.000	0.398	0.005
		92	0.000	0.000	0.000	0.000	0.000	0.025	0.000	0.040	0.826	0.108
		183	0.000	0.000	0.000	0.000	0.000	0.200	0.000	0.045	0.748	0.007
		274	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	1.000	0.000
		365	0.000	0.000	0.526	0.000	0.000	0.071	0.000	0.000	0.398	0.005
	451-500	1	0.000	0.000	0.690	0.000	0.016	0.000	0.000	0.000	0.291	0.004
		92	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.024	0.974	0.003
		183	0.000	0.000	0.000	0.000	0.000	0.215	0.000	0.005	0.750	0.030
		274	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.969	0.031
		365	0.000	0.000	0.690	0.000	0.016	0.000	0.000	0.000	0.291	0.004
	501-550	1	0.000	0.000	0.433	0.000	0.000	0.002	0.000	0.367	0.170	0.029
		92	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.960	0.040
		183	0.000	0.000	0.000	0.036	0.000	0.428	0.000	0.019	0.506	0.010
		274	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.999	0.001
		365	0.000	0.000	0.433	0.000	0.000	0.002	0.000	0.367	0.170	0.029
	551-910	1	0.000	0.000	0.785	0.156	0.000	0.000	0.000	0.018	0.035	0.006
		92	0.084	0.000	0.000	0.000	0.840	0.000	0.000	0.000	0.075	0.000
		183	0.000	0.000	0.000	0.000	0.007	0.259	0.000	0.003	0.732	0.000
		274	0.000	0.000	0.000	0.906	0.000	0.008	0.000	0.000	0.078	0.008
		365	0.000	0.000	0.785	0.156	0.000	0.000	0.000	0.018	0.035	0.006

Note: Simulation day 1 represents 1 May.

Table 5. Thermal experience inputs for bioenergetics simulations of four size classes of lake trout in Lucerne and Wapato Basins of Lake Chelan.

Size class (FL; mm)	Simulation day	Thermal experience (˚C)	
		Lucerne	Wapato
180-450	1	8.2	6.7
	91	9.8	11.2
	182	10.9	8.5
	273	6.3	5.2
	365	8.2	6.7
451-500	1	8.8	6.8
	91	13.2	10.7
	182	10.7	9.3
	273	6.3	5.1
	365	8.8	6.8
501-550	1	7.9	6.9
	91	9.4	10.7
	182	10.5	9.7
	273	6.3	5.2
	365	7.9	6.9
551-910	1	9.0	7.0
	91	9.4	9.8
	182	10.7	9.9
	273	6.3	5.3
	365	9.0	7.0

Table 6. Energy density estimates (J/g wet weight) of prey items used for bioenergetics simulations of lake trout and Chinook salmon.

Prey item	Surrogate	Energy density (J/g)	Reference
Burbot		5125	Johnson et al. (1999)
Chinook salmon		5863	Stewart and Ibarra (1991)
Cyprinids	Peamouth	7093	Mazur (2004)
Kokanee	Sockeye salmon	6008	Beauchamp et al. (1989)
Lake trout		6009	Stewart et al. (1983)
Threespine stickleback		6949	Mazur (2004)
Unidentified salmonids	Sockeye salmon	6008	Mazur (2004)
Other fish	Sculpin	4178-4514	Mazur (2004)
Mysis relicta		2976-3720	Lasenby (1971), Adare and Lasenby (1994)
Other invertebrates	Crayfish	3318	Mazur (2004)

Notes: Energy densities for Chinook salmon, kokanee, and lake trout were estimated for a prey weight of 100 g. Energy densities of "other fish" and *Mysis relicta* varied seasonally within the specified range.

Table 7. Growth, age structure, and proportion of maximum consumption (C_{max}) values experience inputs used for bioenergetics simulations of Chinook salmon.

Age (yr)	Simulation day	Wet weight (g)			Numbers per 1000 fish	Proportion of C_{max}		
		Lower	Nominal	Upper		Lower	Nominal	Upper
1	1	290.0	539.1	725.6	438.7	0.81	0.97	0.79
2	1	1,240	3,515	3,301	272.0	0.78	0.54	0.83
3	1	2,550	4,291	7,381	190.4	0.79	0.67	0.89
4	1	4,100	6,135	12,641	99.0	0.65	0.58	0.67
4	154	4,400	6,584	13,566				

Notes: Numbers per 1,000 fish indicate the expected numbers of Chinook salmon at each age, in a unit population of 1,000 fish of ages 1-4 yr. Numbers inputs were adjusted on a daily time step in simulations but are represented here on an annual basis for simplicity. Values indicate the numbers per 1,000 fish on model day 1 of each year of age. The simulation for age 4 Chinook salmon ended on day 154, corresponding to 15 October, the approximate date that Chinook salmon stage to spawn in Lake Chelan.

Table 8. Diet composition inputs used for bioenergetics simulations of Chinook salmon.

Kokanee diet percentile	Diet composition by weight							
	Burbot	Chinook salmon	Cyprinids	Kokanee	Lake trout	Threespine stickleback	Other fish	*Mysis relicta*
5	0.000	0.002	0.052	0.004	0.011	0.012	0.263	0.656
25	0.045	0.048	0.085	0.021	0.013	0.094	0.048	0.646
50	0.001	0.031	0.244	0.050	0.045	0.026	0.023	0.579
75	0.008	0.053	0.066	0.095	0.016	0.046	0.085	0.632
95	0.016	0.022	0.247	0.195	0.004	0.021	0.062	0.432

Notes. Diet was estimated using a mixing model that generated a distribution of potential diet compositions that fit stable isotope data from Lake Chelan. The diet compositions that included the 5th, 25th, 50th, 75th, and 95th percentile estimates of the proportion of kokanee in the diet were used to estimate consumption.

Table 9. Thermal experience inputs used experience inputs for bioenergetics simulations of Chinook salmon.

Simulation day	Thermal experience (°C)
1	8.5
31	8.4
61	10.4
92	12.8
122	12.4
183	8.8
274	5.9
365	8.5

Table 10. Annual kokanee consumption (kg) per 1,000 Chinook salmon ages 1-4.

Growth	Proportion kokanee in diet (by weight)				
	0.004	0.021	0.050	0.095	0.195
Low	42.4	186	400	852	1,424
Nominal	79.6	346	741	1,587	2,628
High	135	582	1,243	2,676	4,393

Notes. Consumption was estimated with bioenergetics model simulations using five potential diet compositions and three potential growth rates. Proportions of kokanee in the Chinook salmon diet were estimated from stable isotope data with a mixing model, and represent the 5th, 25th, 50th, 75th, and 95th percentile estimates, respectively. Growth inputs were compiled from Lake Chelan data and the literature, and represented low, moderate, and high growth of lake-resident Chinook salmon populations.

Table 11. Proportion of theoretical maximum consumption rates (C_{max}) achieved by Chinook salmon in bioenergetics simulations.

Growth	Age (yr)	Proportion kokanee in diet (by weight)				
		0.004	0.021	0.050	0.095	0.195
Low	1	0.81	0.72	0.65	0.73	0.59
Low	2	0.78	0.69	0.62	0.70	0.57
Low	3	0.79	0.70	0.64	0.71	0.58
Low	4	0.65	0.58	0.53	0.58	0.49
Nominal	1	1.26	1.09	0.97	1.10	0.88
Nominal	2	0.68	0.60	0.54	0.61	0.50
Nominal	3	0.83	0.74	0.67	0.75	0.61
Nominal	4	0.72	0.64	0.58	0.65	0.54
High	1	1.11	0.97	0.87	0.98	0.79
High	2	1.17	1.01	0.91	1.03	0.83
High	3	1.28	1.11	0.99	1.12	0.89
High	4	0.90	0.80	0.72	0.81	0.67

Notes. Proportion of C_{max} was estimated for each age class (1-4 yr) with bioenergetics model simulations using five potential diet compositions and three potential growth rates. Proportions of kokanee in the Chinook salmon diet were estimated from stable isotope data with a mixing model, and represent the 5th, 25th, 50th, 75th, and 95th percentile estimates, respectively. Growth inputs were compiled from Lake Chelan data and the literature, and represented low, moderate, and high growth of lake-resident Chinook salmon populations.
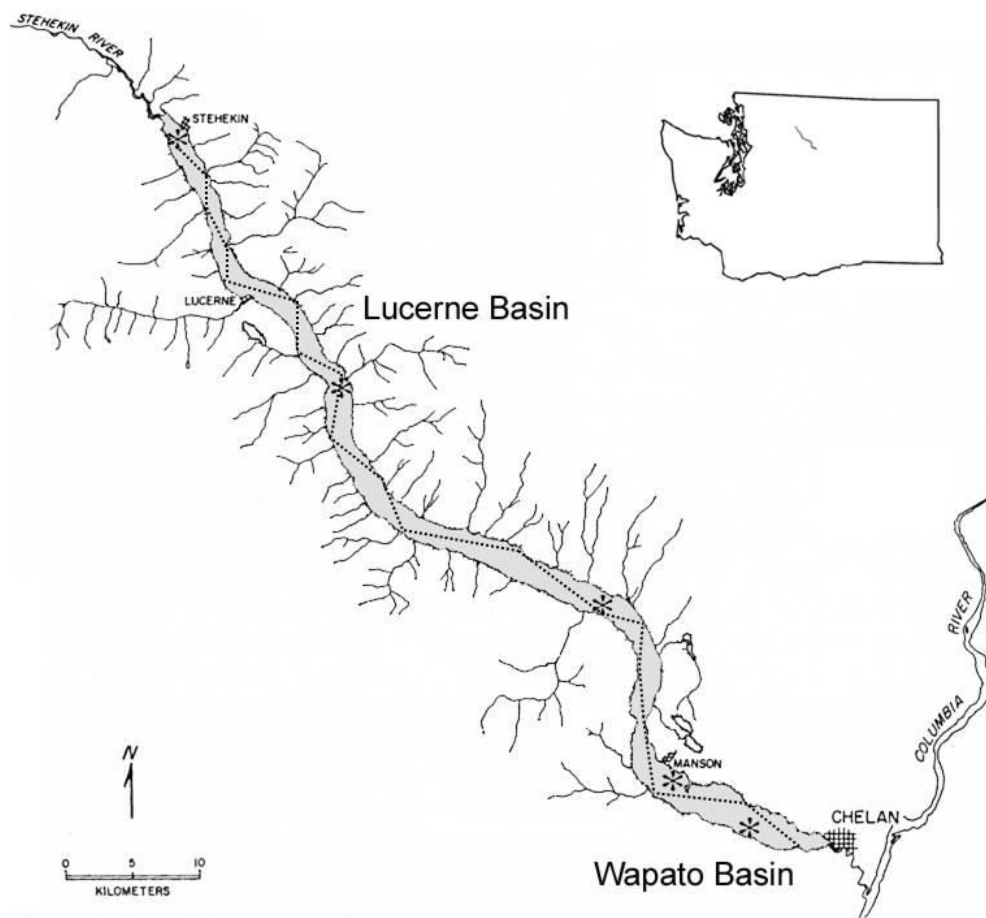
Figure 1. Map of Lake Chelan, showing the two lake basins, principal sampling sites (stars), and hydroacoustic transects (dotted lines). The inset shows the location of the lake in north-central Washington, USA.
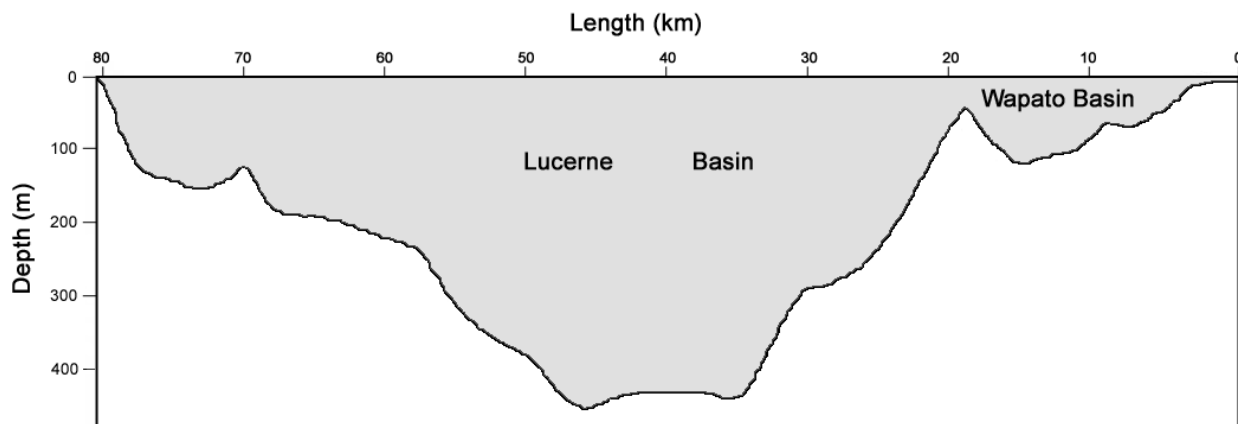
Figure 2. Longitudinal depth profile of Lake Chelan, showing pronounced depth difference between lake basins. Horizontal axis represents distance from lake outlet along the primary axis of the lake (adapted from Kendra and Singleton 1987).
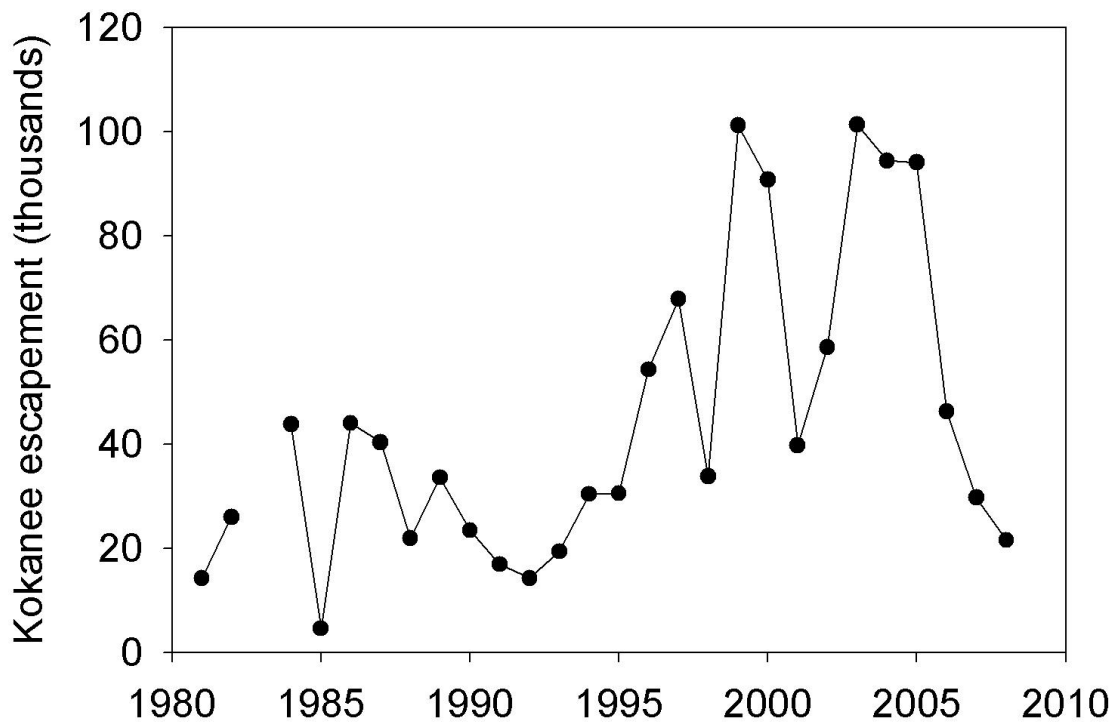
Figure 3. Index of kokanee escapement in the Lake Chelan drainage (data from Keesee et al. 2009).
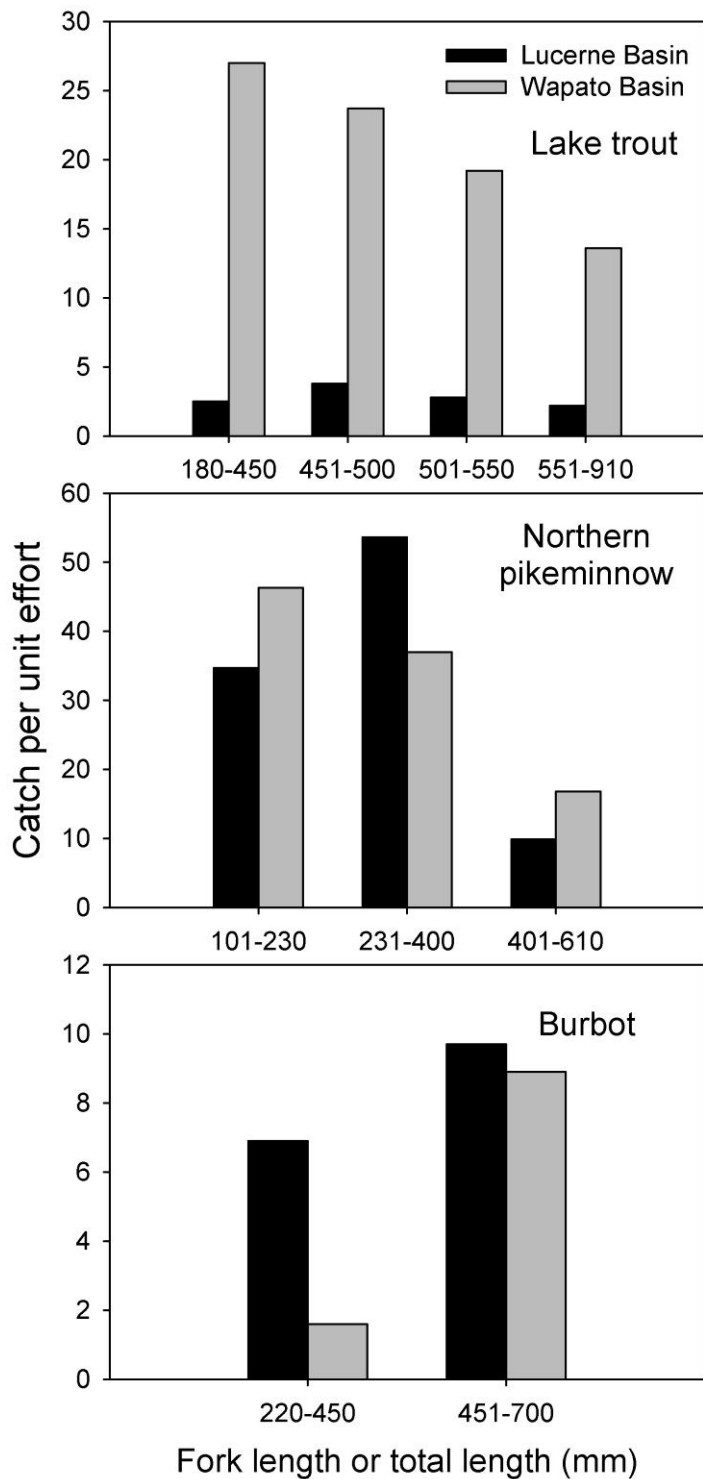
Figure 4. Catch per unit effort of lake trout, northern pikeminnow, and burbot in Lucerne and Wapato Basins of Lake Chelan. One unit of effort was defined as a "gang" of eight sinking gill nets deployed overnight at four depth strata. Size classes were defined by fork length (lake trout and northern pikeminnow) or by total length (burbot).
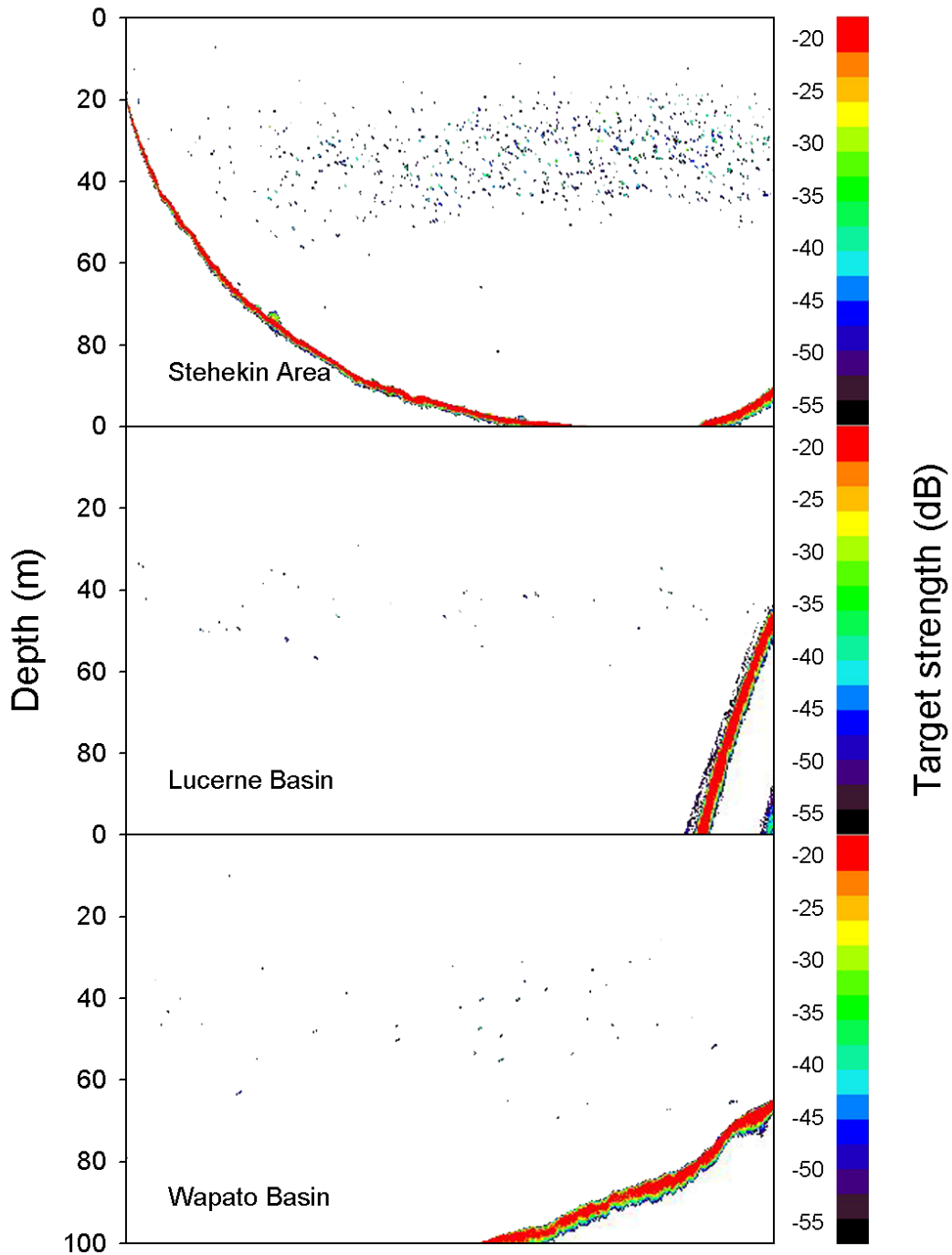
Figure 5. Echograms showing density and distribution of targets encountered during representative segments of a mobile hydroacoustic survey on 30-31 August, 2005. Target density was much greater in the Stehekin area than in the remainder of Lucerne Basin or in Wapato Basin. The vertical dimension represents depth, the horizontal dimension represents time (horizontal distance), and color represents target strength.
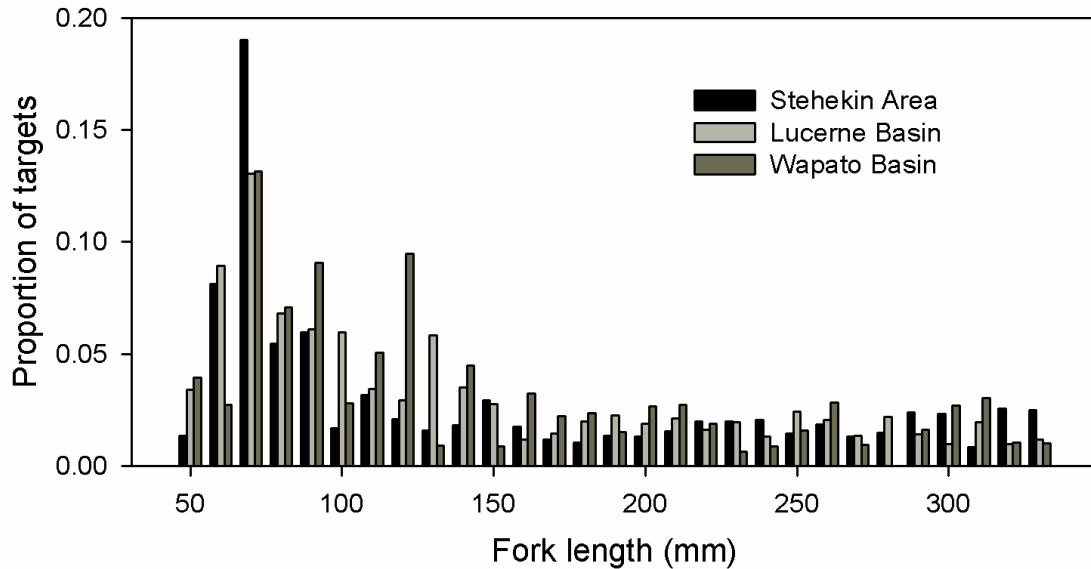
Figure 6. Length-frequency histograms of kokanee-sized (40-330 mm FL) hydroacoustic targets encountered during a mobile hydroacoustic survey on 30-31 August, 2005. Length distributions were determined separately for the Stehekin area, the remainder of Lucerne Basin, and Wapato Basin. Bar heights indicate proportions of all hydroacoustic targets (> -55 dB) in the respective size bins, after correcting for increased sampling volume (beam spreading) with increased depth.
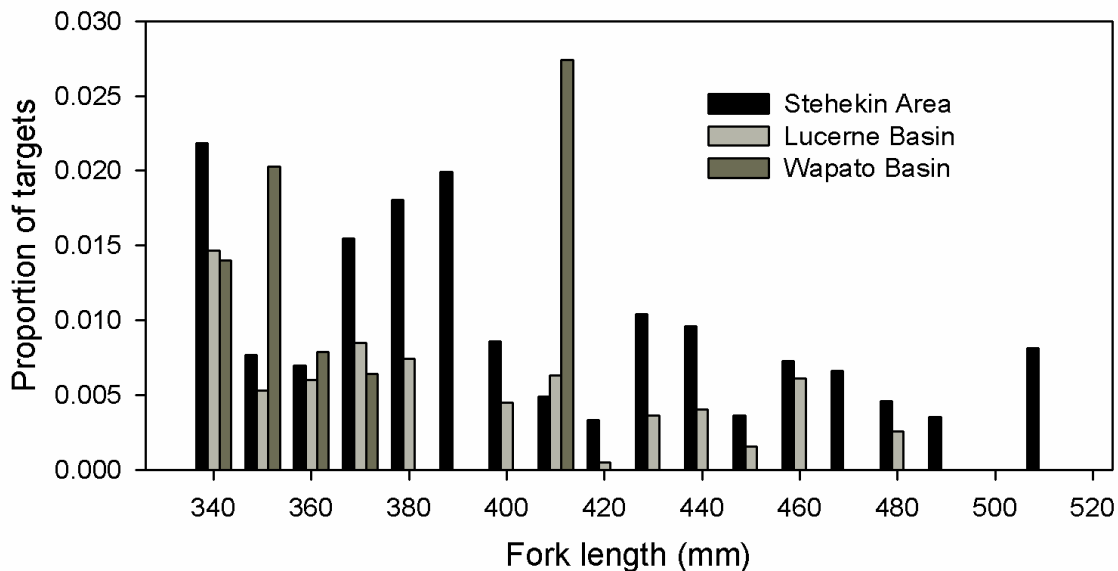
Figure 7. Length-frequency histograms of large hydroacoustic targets encountered during a mobile hydroacoustic survey on 30-31 August, 2005. Length distributions were determined separately for the Stehekin area, the remainder of Lucerne Basin, and Wapato Basin. Bar heights indicate proportions of all hydroacoustic targets (> -55 dB) in the respective size bins, after correcting for increased sampling volume (beam spreading) with increased depth.
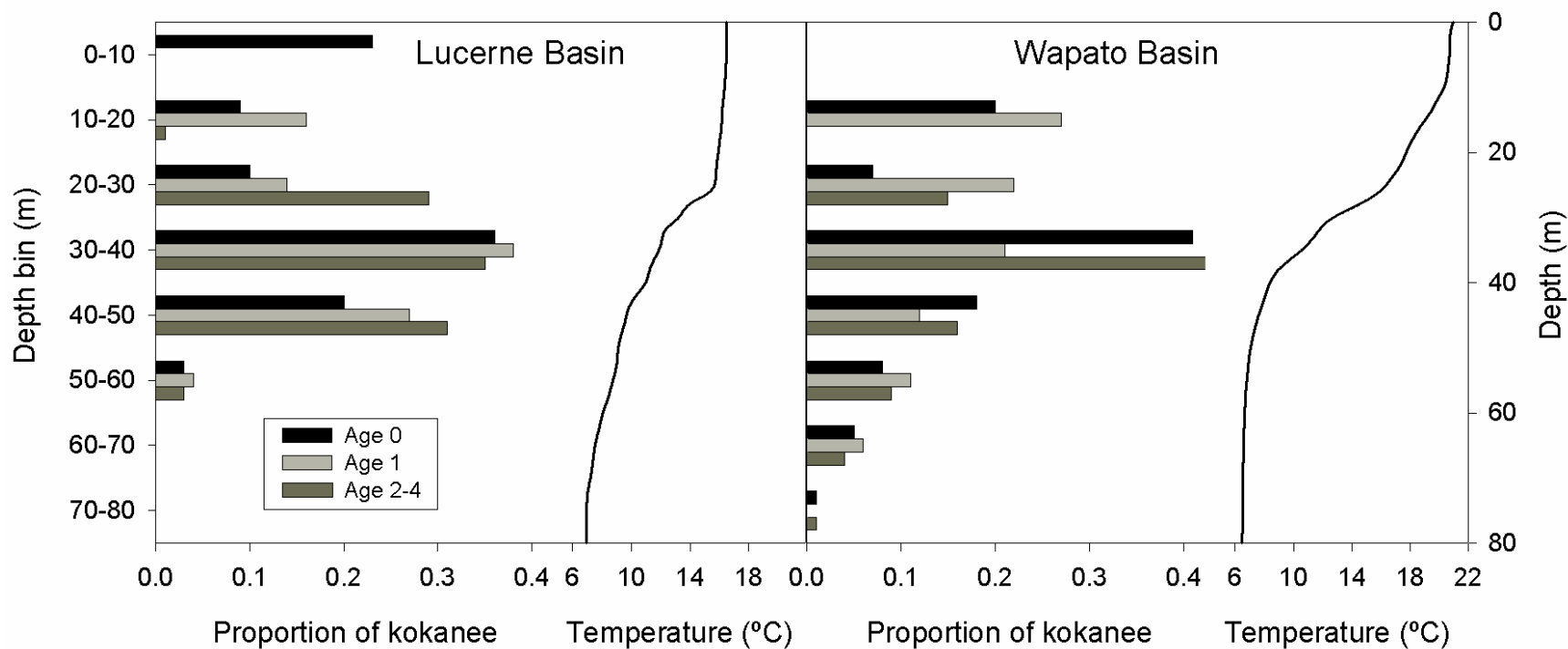
Figure 8. Vertical distribution of kokanee at night in Lucerne and Wapato Basins during 30-31 August 2005. Kokanee distributions were determined with a hydroacoustic survey. Solid lines represent thermal profiles near Prince Creek (Lucerne Basin) and First Creek (Wapato Basin).
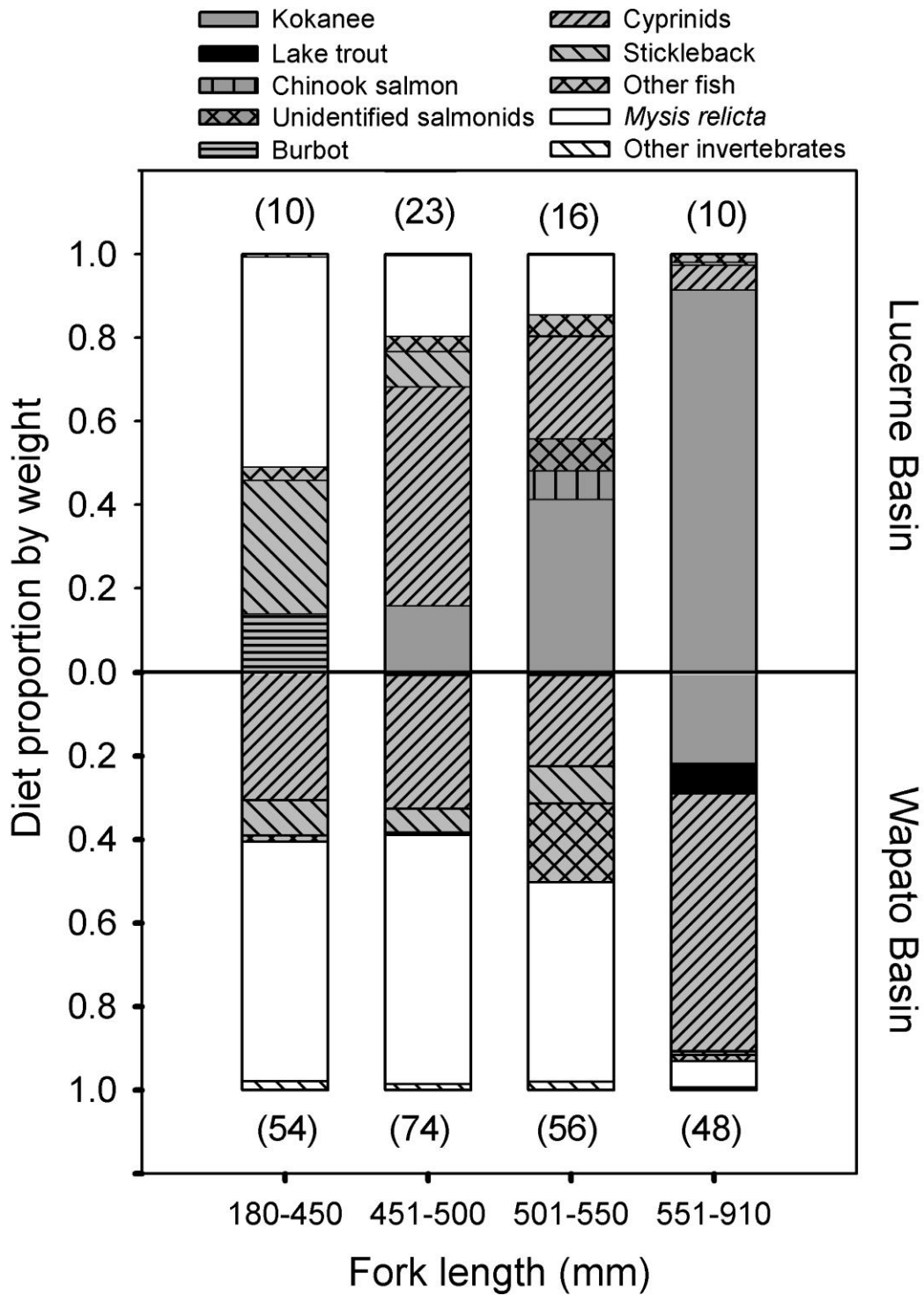
Figure 9. Lake trout annual diet composition, shown for four size classes in the Lucerne and Wapato Basins. Sample sizes (non-empty stomachs) are indicated in parentheses.
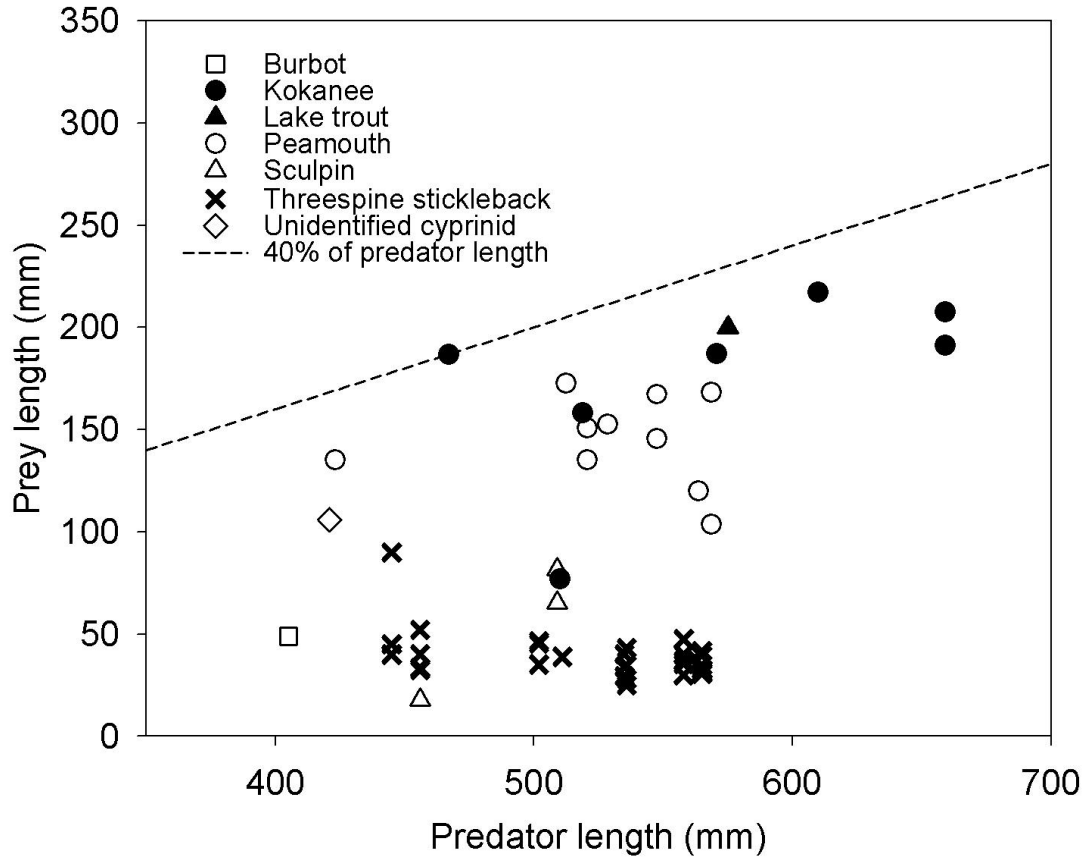
Figure 10. Relationship between lengths of piscivorous lake trout and lengths of ingested prey fishes. Symbols indicate prey species. Prey length indicates total length for burbot and threespine stickleback, and fork length for all other species. All prey lengths were < 40% of predator lengths (n = 54).
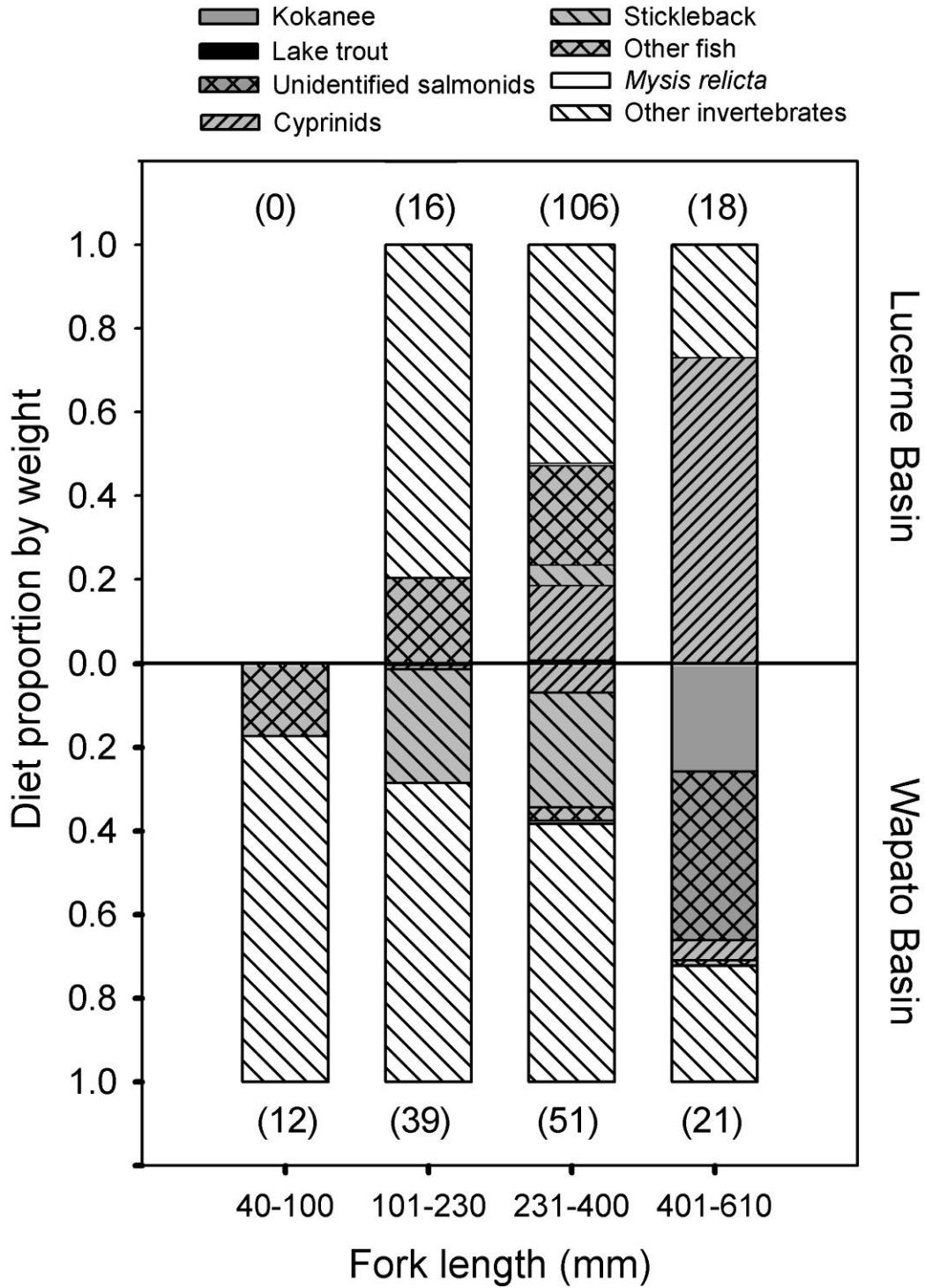
Figure 11. Northern pikeminnow annual diet composition, shown for four size classes in the Lucerne and Wapato Basins. Sample sizes (non-empty stomachs) are indicated in parentheses.
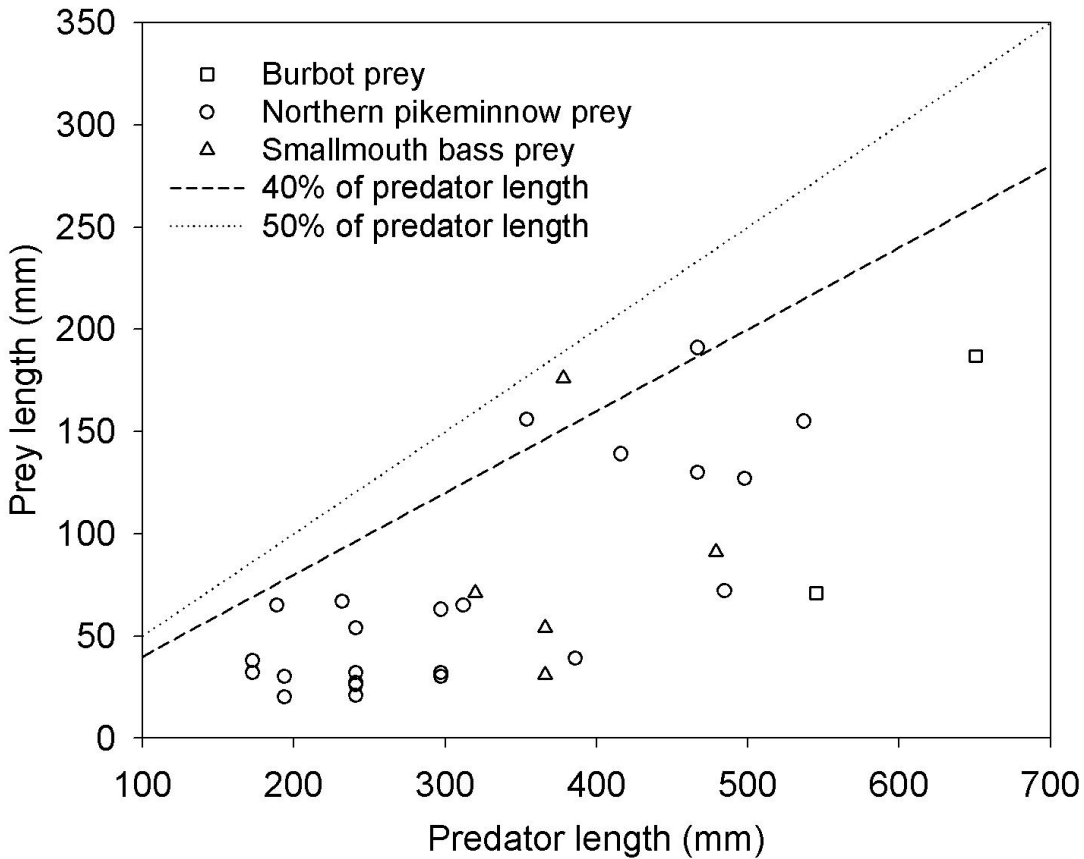
Figure 12. Relationship between lengths of piscivorous burbot, northern pikeminnow, and smallmouth bass and lengths of prey fishes ingested by these species. Symbols indicate predator species. Length indicates total length for burbot and threespine stickleback, and fork length for all other species. All prey lengths were < 30% of predator lengths for burbot (n = 2), < 45% for northern pikeminnow (n = 25), and < 47% for smallmouth bass (n = 5).
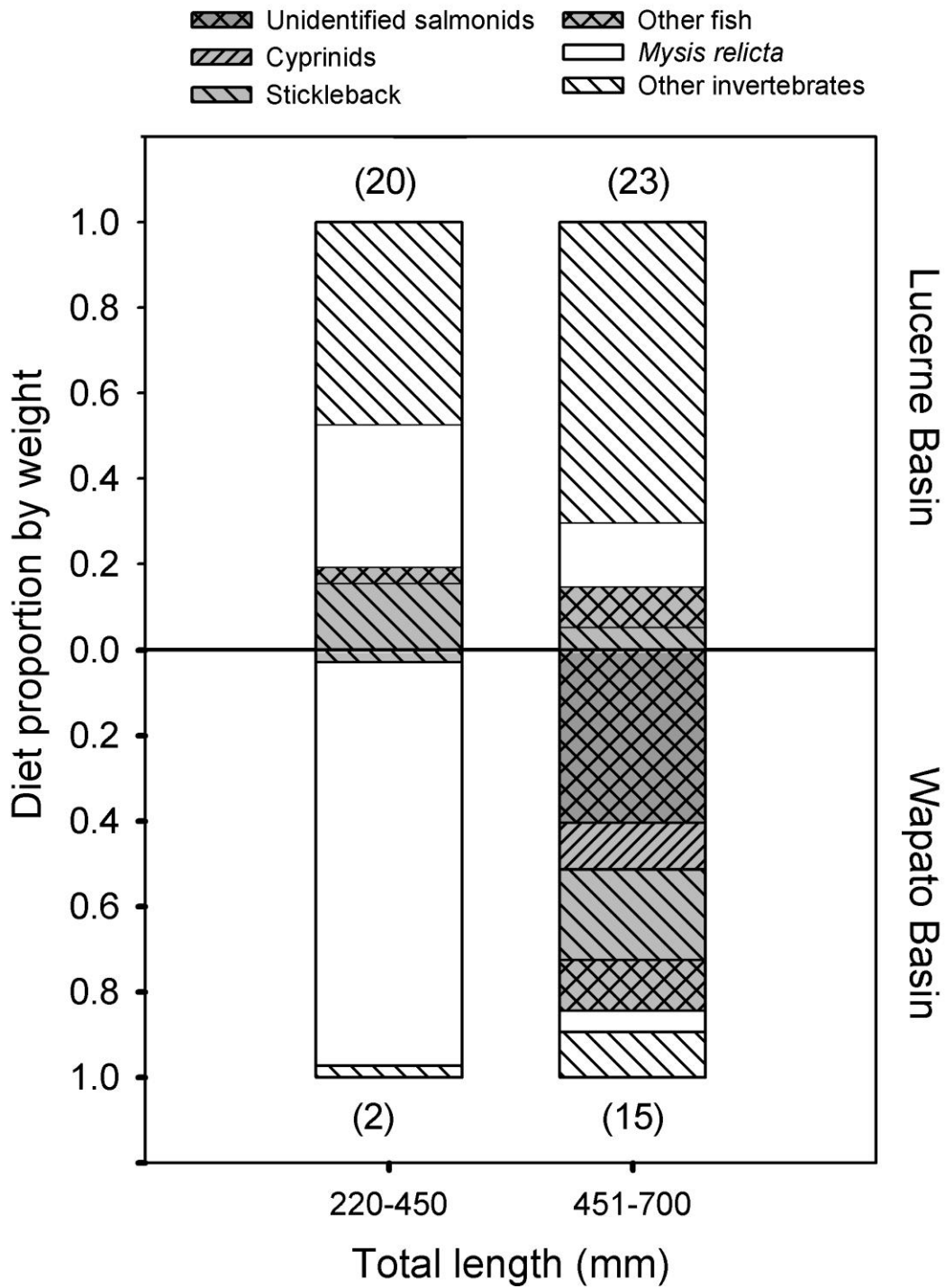
Figure 13. Burbot annual diet composition, shown for two size classes in the Lucerne and Wapato Basins. Sample sizes (non-empty stomachs) are indicated in parentheses.
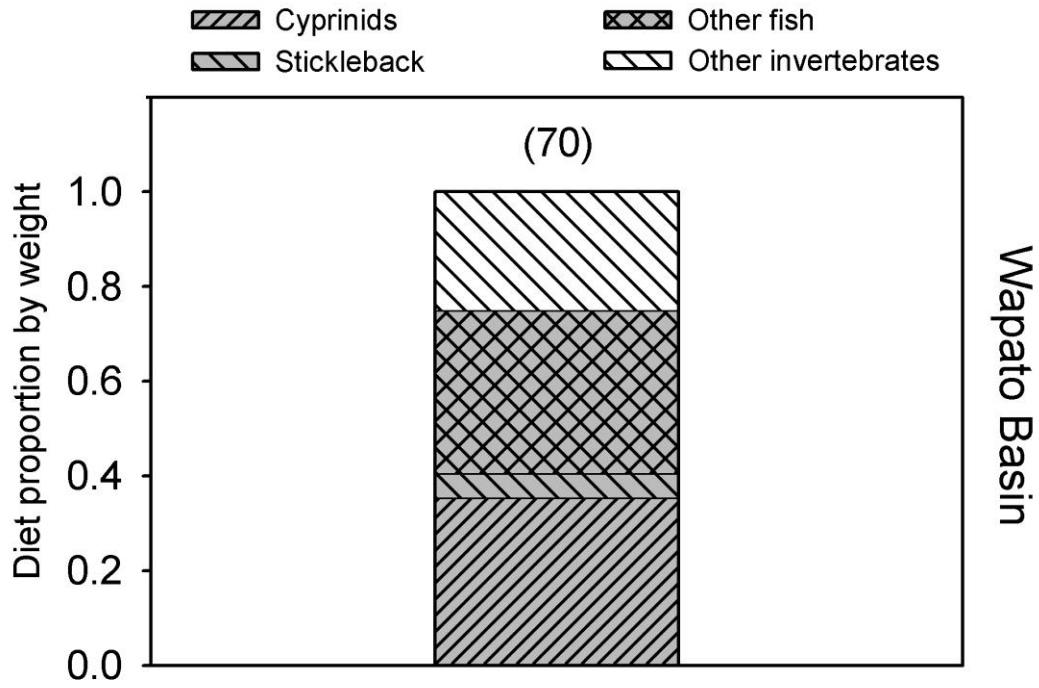
Figure 14. Smallmouth bass annual diet composition in Wapato Basin. No smallmouth bass were captured in Lucerne Basin. Sample size (non-empty stomachs) is indicated in parentheses.
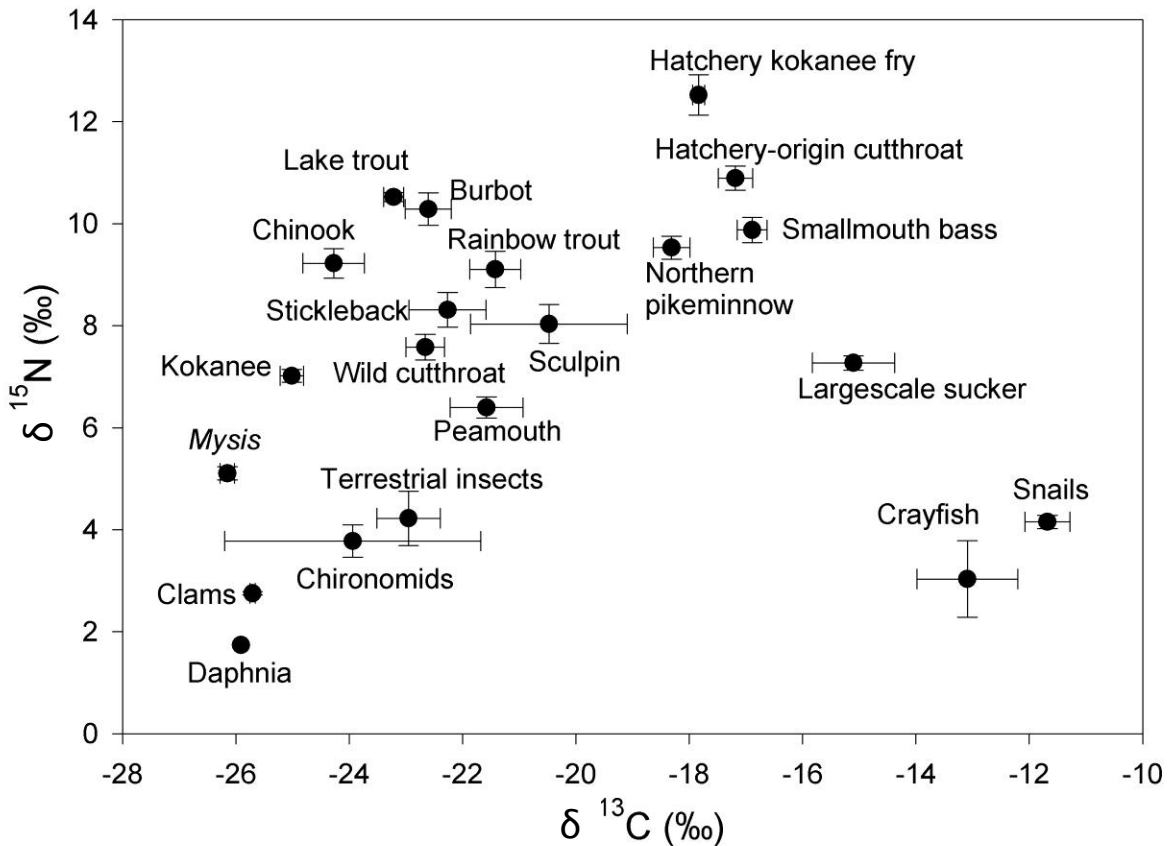
Figure 15. Stable isotope signatures of Lake Chelan organisms (means ± 1 SE; *Daphnia* symbol represents a single sample). $\delta^{13}C$ values are corrected to account for variable lipid content among samples. More negative, "depleted" $\delta^{13}C$ values indicate a diet primarily based on carbon fixed in the pelagic zone by phytoplankton, while less negative, "enriched" $\delta^{13}C$ values indicate a diet primarily based on carbon fixed in the littoral zone by epiphyton. Nitrogen isotopic values ($\delta^{15}N$) indicate trophic position of consumers within the food web. The position of a consumer on the plot is expected to be near the mean of its aggregate diet on the x-axis and roughly 3.4‰ greater than the mean of its diet on the y-axis.
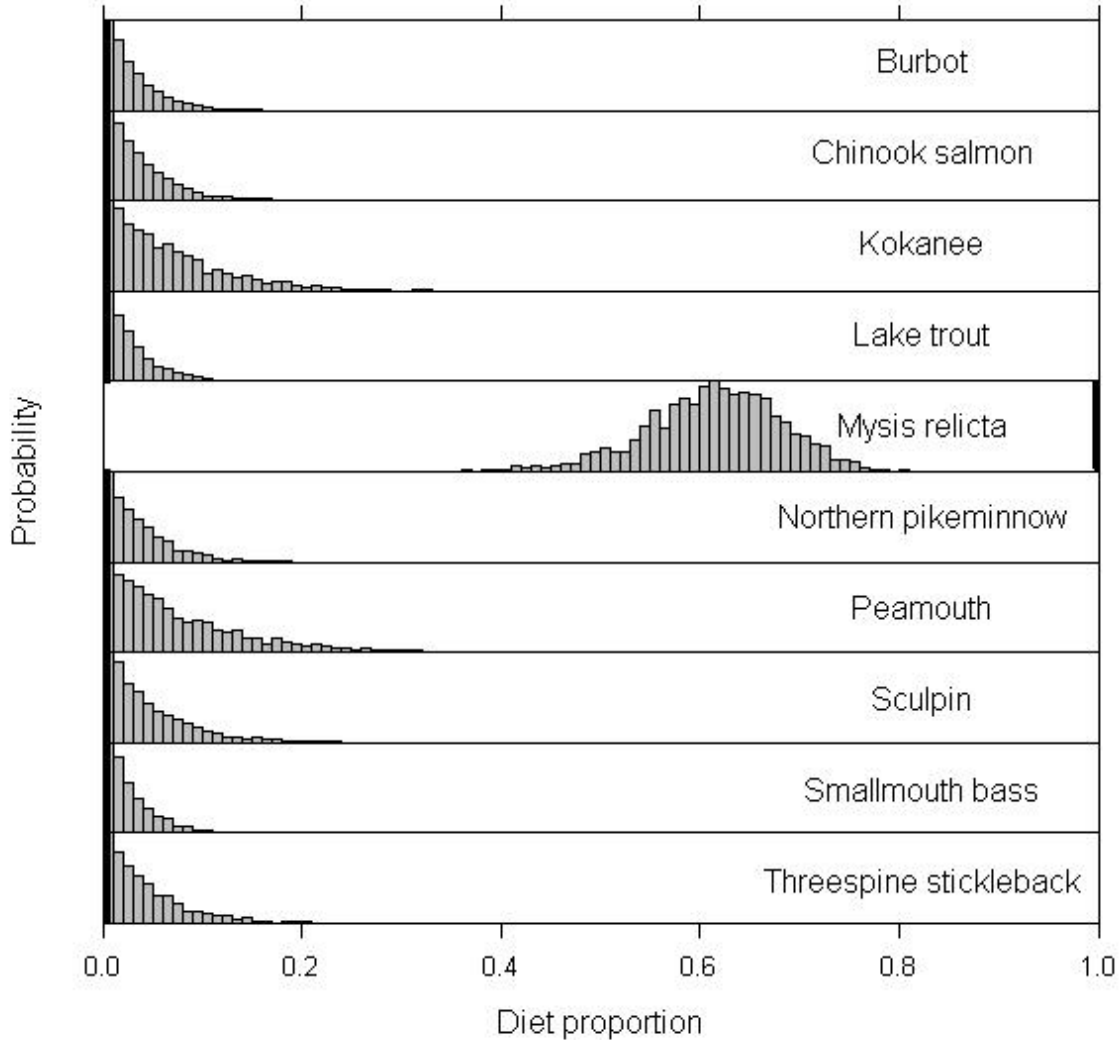
Figure 16. Diet composition of Chinook salmon in Lake Chelan, as estimated by a stable isotope mixing model. Each horizontal panel is a histogram representing the probability distribution of diet proportions for one prey type. The mixing model indicated that *Mysis relicta* was the most important prey for Chinook salmon, comprising 49-72% of the annual diet (5th and 95th percentile estimates, respectively). Kokanee represented 0.4-20% of the diet (5th and 95th percentile estimates). Black vertical bars indicate the diet composition as estimated by stomach content analysis. Note that *Mysis* comprised 100% of the diet from the single non-empty Chinook salmon stomach sample collected.
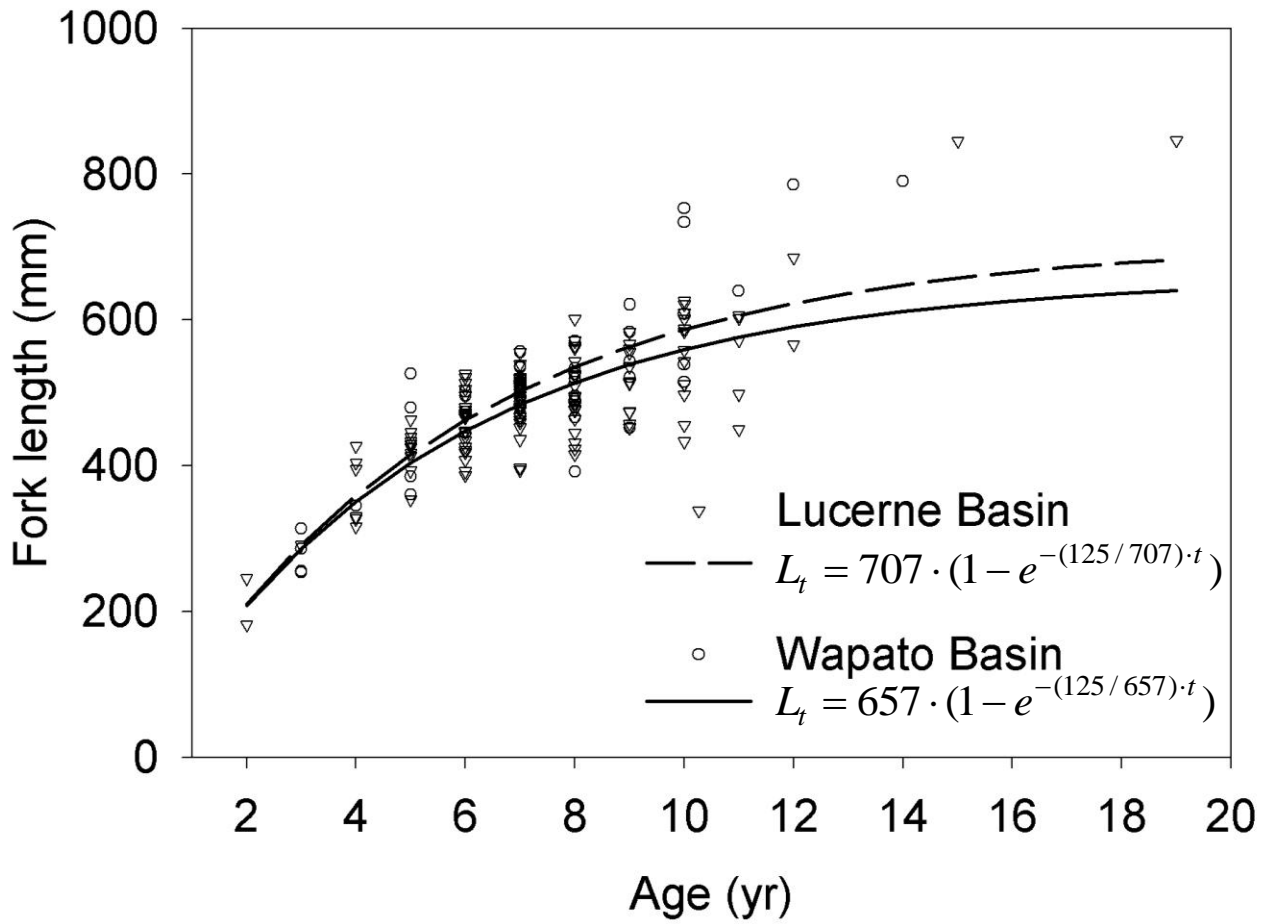
Figure 17. Lake trout length at age in Lucerne and Wapato Basins of Lake Chelan. Curves represent best fit von Bertalanffy growth relationships for each basin.
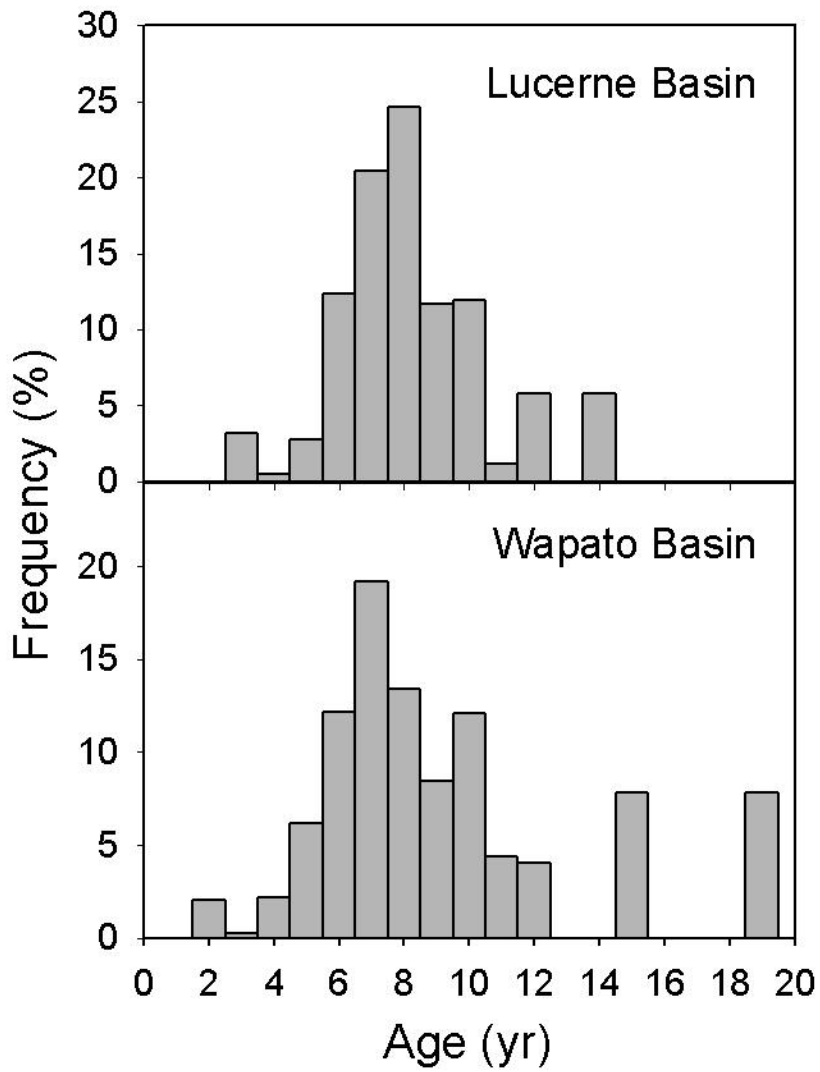
Figure 18. Age-frequency distributions for lake trout captured in gill nets in the two basins of Lake Chelan. Values are corrected for bias as indicated in the text.
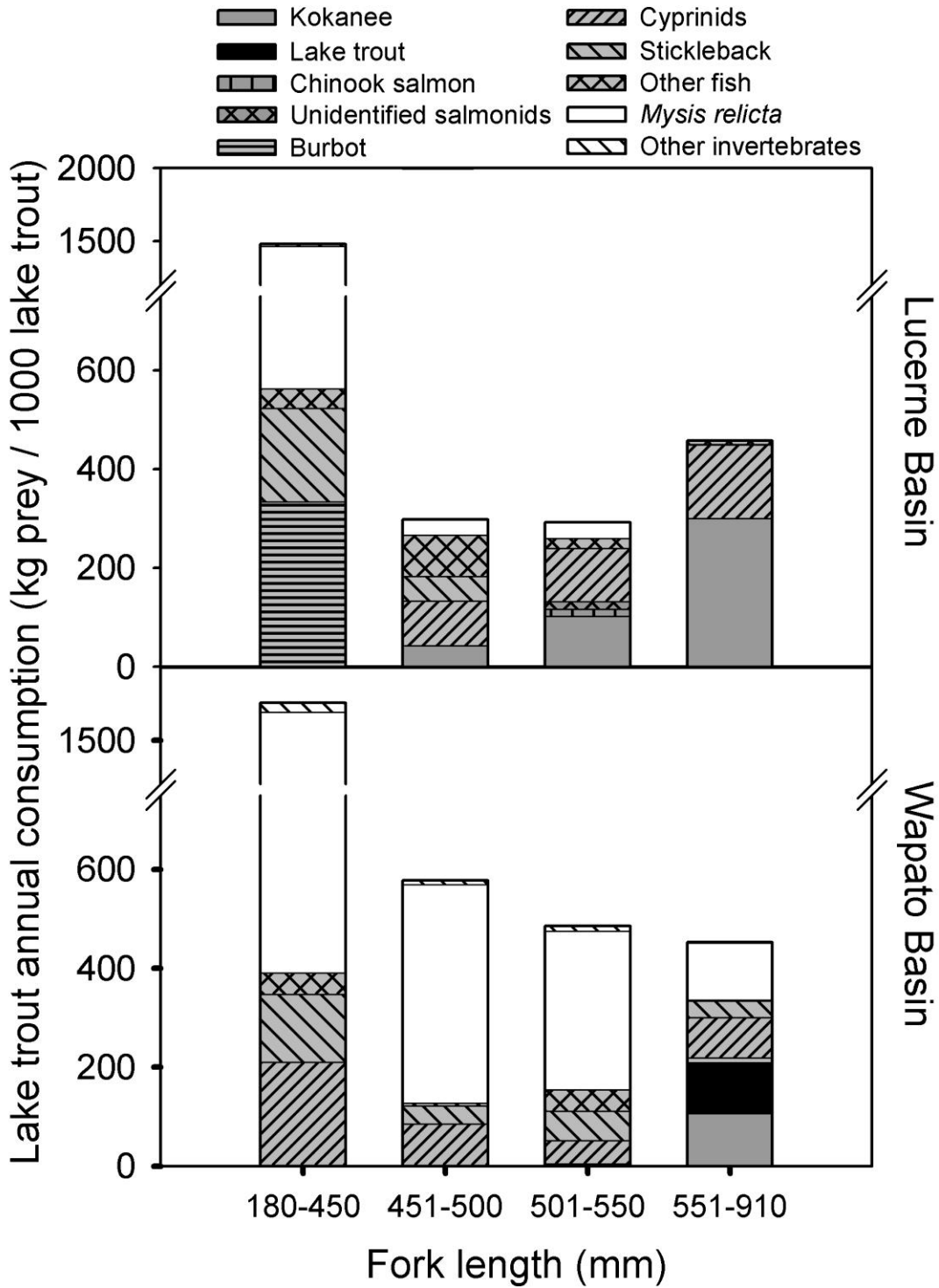
Figure 19. Annual prey consumption by size structured "unit populations" of 1,000 lake trout in Lucerne and Wapato Basins of Lake Chelan. Consumption was estimated using a bioenergetics model and summarized for four size classes of lake trout.
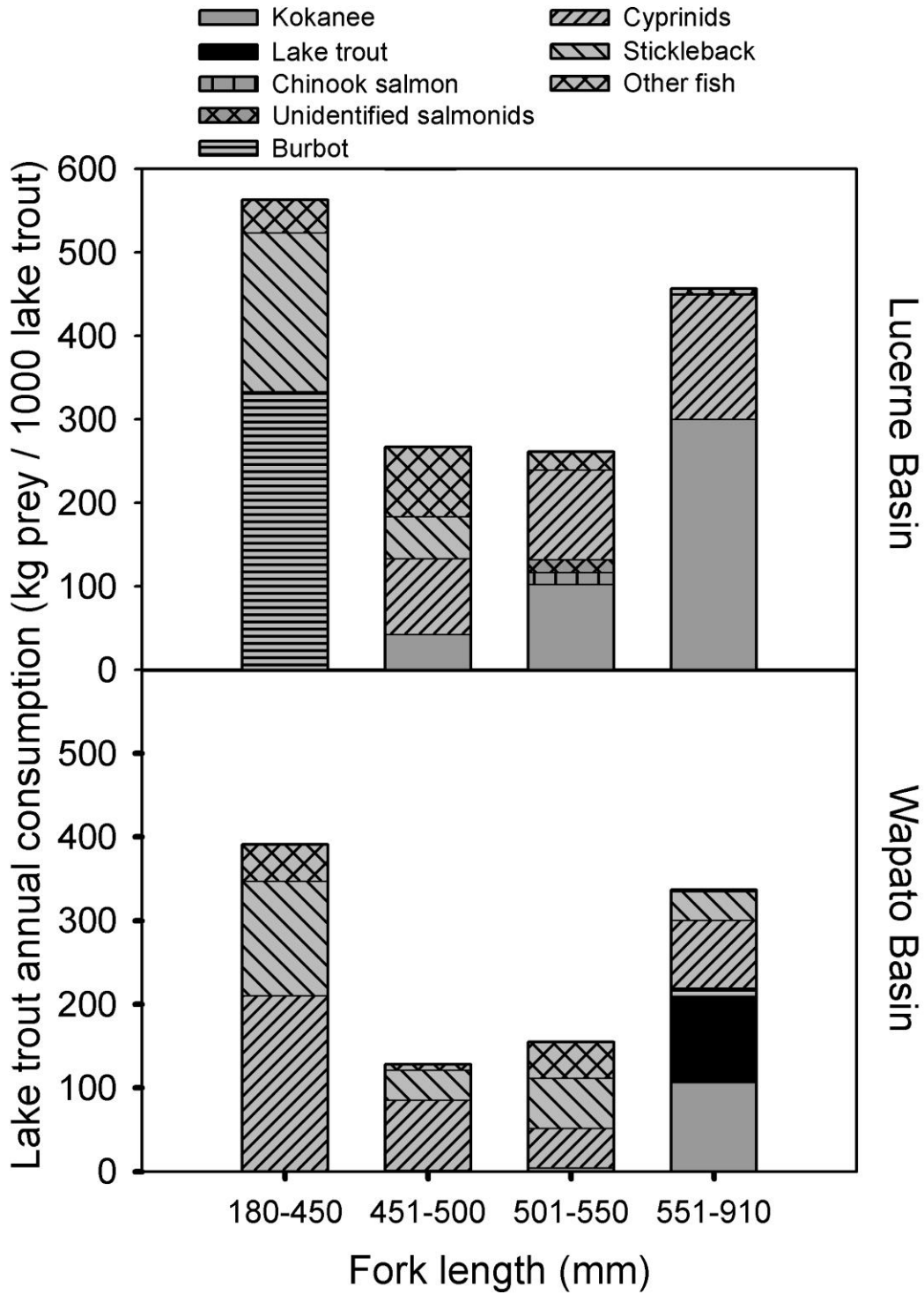
Figure 20. Annual fish consumption by size structured "unit populations" of 1,000 lake trout in Lucerne and Wapato Basins of Lake Chelan. Consumption was estimated using a bioenergetics model and summarized for four size classes of lake trout. Invertebrate prey are excluded for clarity.
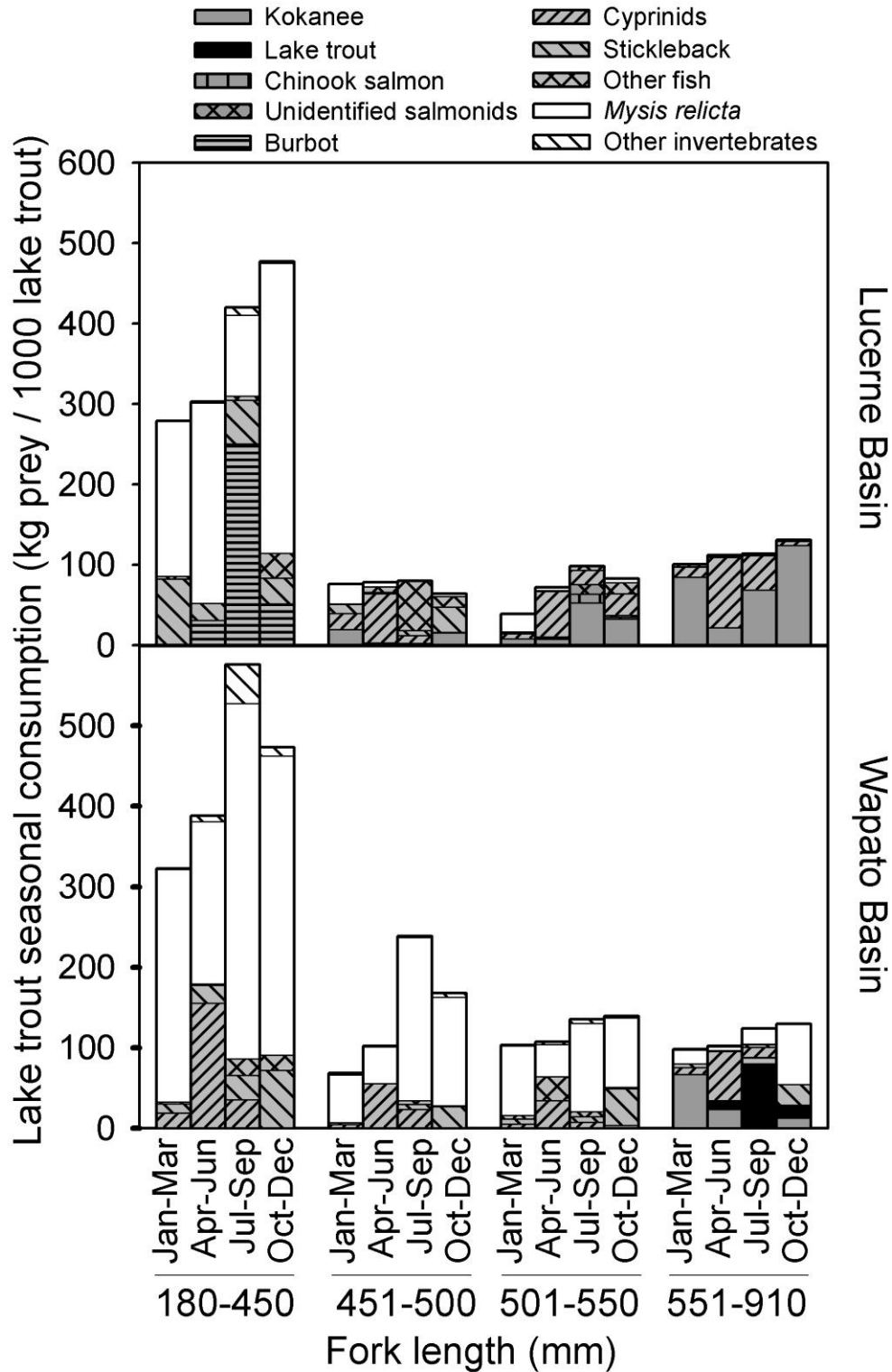
Figure 21. Seasonal prey consumption by size structured "unit populations" of 1,000 lake trout in Lucerne and Wapato Basins of Lake Chelan. Consumption was estimated using a bioenergetics model and summarized for four size classes of lake trout.
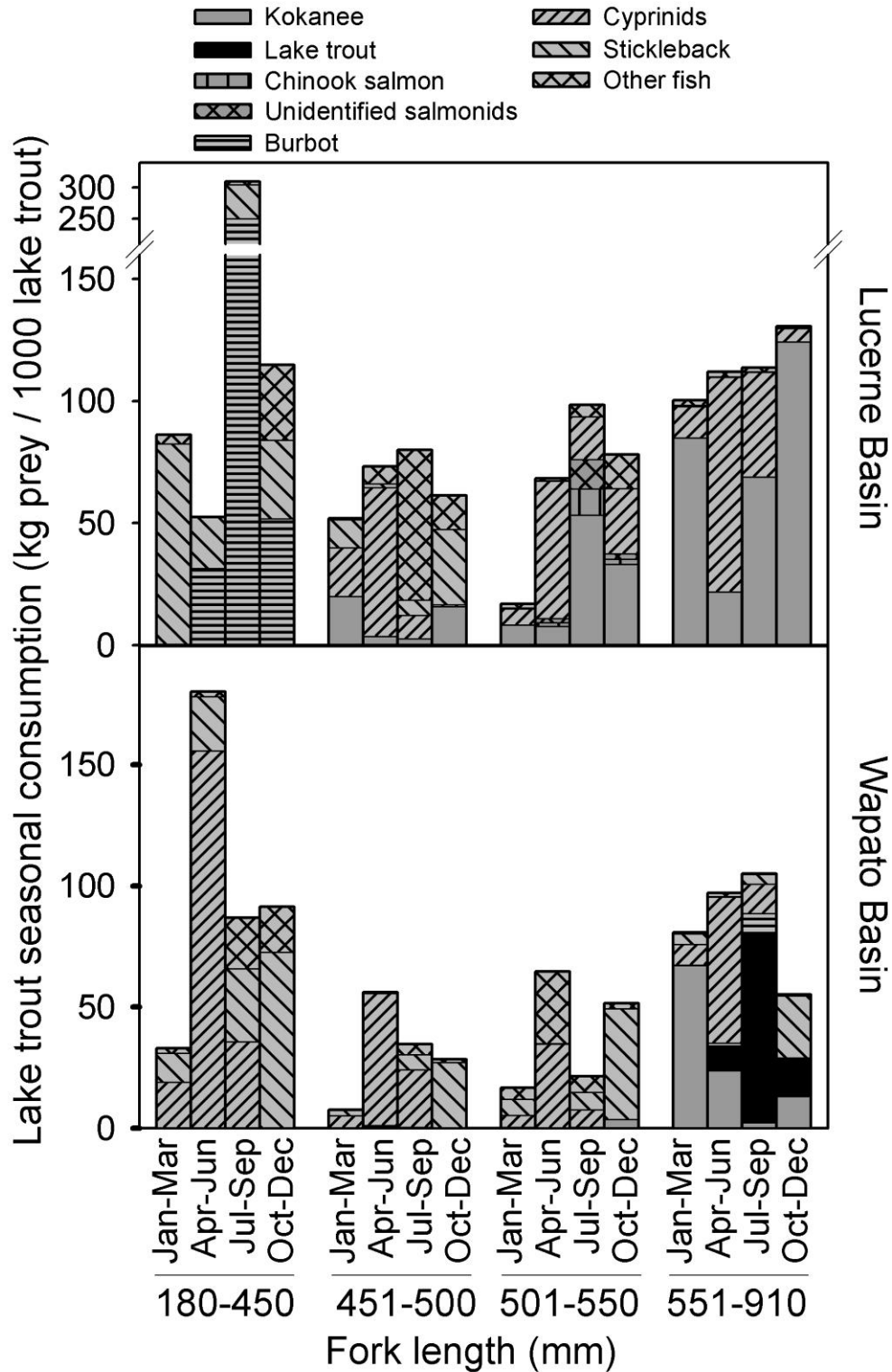
Figure 22. Seasonal fish consumption by size structured "unit populations" of 1,000 lake trout in Lucerne and Wapato Basins of Lake Chelan. Consumption was estimated using a bioenergetics model and summarized for four size classes of lake trout. Invertebrate prey are excluded for clarity.
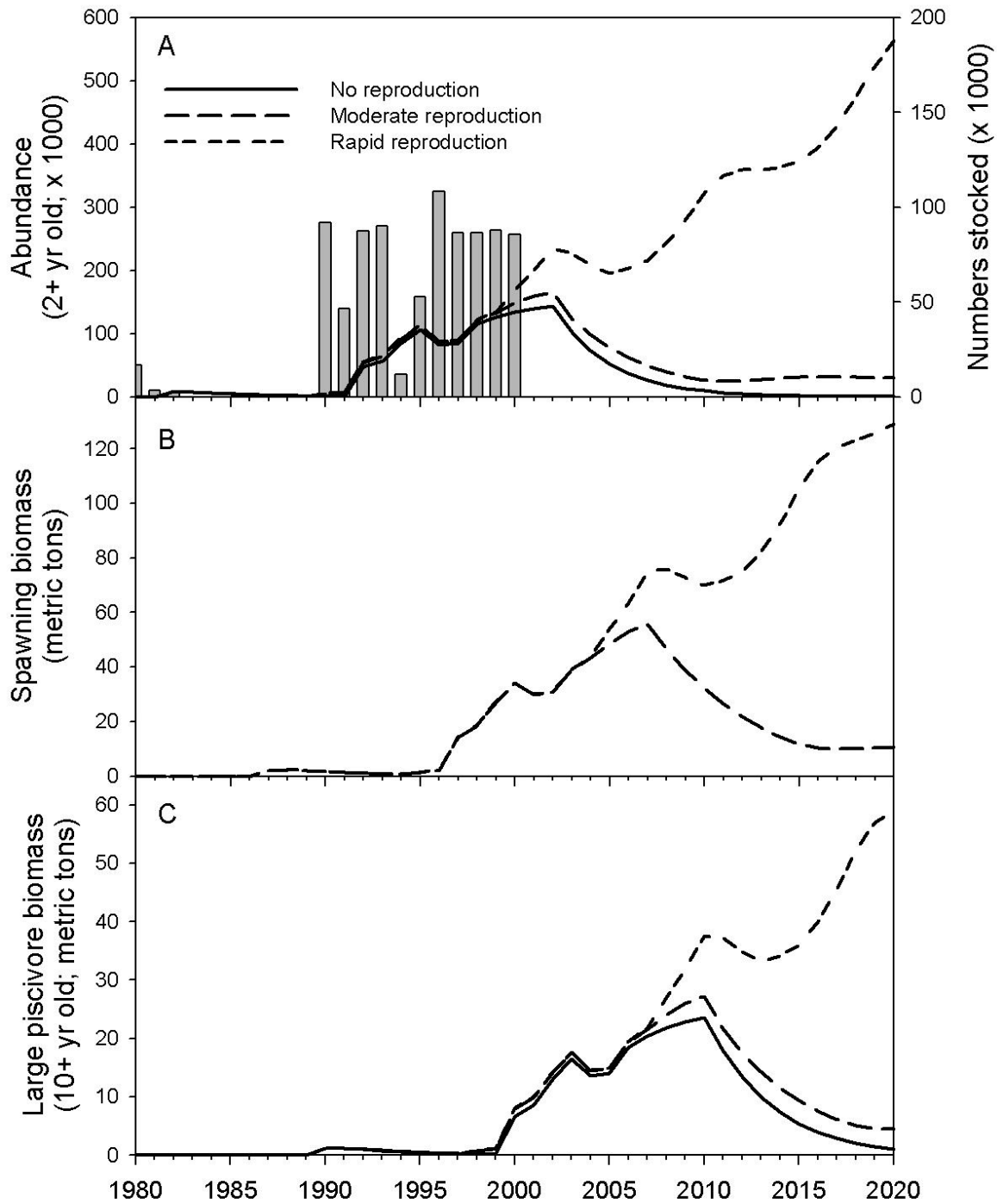
Figure 23. Simulated population dynamics of lake trout under three scenarios: no natural reproduction; moderate, density-dependent reproduction; and rapid, density-independent reproduction. A: Numbers of lake trout stocked (bars) and abundance of lake trout age ≥ 2 yr (lines). B: Biomass of reproductively mature lake trout (age ≥ 7 yr). C: Biomass of the largest lake trout size class (> 550 mm FL; age ≥ 10 yr), which preyed heavily on salmonids.

Appendix

Table A1. Annual diet composition of Lake Chelan fishes

Predator species	Basin	Size class (FL; mm)	n (Total)	n (Non-empty)	Diet proportions by weight								
					Burbot	Chinook salmon	Kokanee	Lake trout	Northern pikeminnow	Peamouth	Sculpins	Smallmouth bass	Threespine stickleback
Burbot	Lucerne	220-450	26	20	0.000	0.000	0.000	0.000	0.000	0.000	0.036	0.000	0.156
Burbot	Lucerne	451-700	46	23	0.000	0.000	0.000	0.000	0.000	0.000	0.094	0.000	0.053
Burbot	Wapato	220-450	2	2	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.029
Burbot	Wapato	451-700	26	15	0.000	0.000	0.000	0.000	0.000	0.000	0.015	0.000	0.212
Chinook	Lucerne	ALL	4	1	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Cutthroat trout (hatchery)	Lucerne	ALL	32	27	0.000	0.000	0.000	0.000	0.000	0.083	0.000	0.000	0.000
Cutthroat trout (hatchery)	Wapato	ALL	8	5	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Cutthroat trout (wild)	Lucerne	ALL	4	3	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Kokanee	Lucerne	ALL	18	13	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Kokanee	Wapato	ALL	53	38	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Lake trout	Lucerne	180-450	15	10	0.140	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.320
Lake trout	Lucerne	451-500	30	23	0.000	0.000	0.159	0.000	0.462	0.055	0.032	0.000	0.084
Lake trout	Lucerne	501-550	23	16	0.000	0.068	0.414	0.000	0.028	0.203	0.045	0.000	0.002
Lake trout	Lucerne	551-910	13	10	0.000	0.000	0.915	0.000	0.015	0.046	0.000	0.000	0.007
Lake trout	Wapato	180-450	67	54	0.000	0.000	0.000	0.000	0.000	0.093	0.000	0.000	0.084
Lake trout	Wapato	451-500	102	74	0.000	0.000	0.000	0.007	0.000	0.254	0.000	0.000	0.057
Lake trout	Wapato	501-550	76	56	0.000	0.000	0.007	0.000	0.000	0.201	0.005	0.167	0.089
Lake trout	Wapato	551-910	62	48	0.007	0.000	0.219	0.065	0.081	0.533	0.000	0.000	0.008
Northern pikeminnow	Lucerne	101-230	30	16	0.000	0.000	0.000	0.000	0.000	0.000	0.204	0.000	0.000
Northern pikeminnow	Lucerne	231-400	171	106	0.000	0.000	0.000	0.004	0.023	0.137	0.029	0.000	0.048
Northern pikeminnow	Lucerne	401-610	48	18	0.000	0.000	0.000	0.000	0.000	0.528	0.000	0.000	0.000
Northern pikeminnow	Wapato	40-100	15	12	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Northern pikeminnow	Wapato	101-230	55	39	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.273
Northern pikeminnow	Wapato	231-400	90	51	0.000	0.000	0.000	0.000	0.000	0.071	0.019	0.000	0.274
Northern pikeminnow	Wapato	401-610	53	21	0.000	0.000	0.259	0.000	0.000	0.000	0.009	0.000	0.000
Peamouth	Lucerne	ALL	28	12	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Peamouth	Wapato	ALL	47	23	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Rainbow trout	Lucerne	ALL	11	11	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Rainbow trout	Wapato	ALL	28	24	0.000	0.000	0.000	0.000	0.026	0.000	0.000	0.000	0.011
Smallmouth bass	Wapato	ALL	94	70	0.000	0.000	0.000	0.000	0.202	0.152	0.000	0.029	0.052
Suckers	Lucerne	ALL	6	1	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Suckers	Wapato	ALL	12	10	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Tench	Lucerne	ALL	1	0									

Table A1 concluded. Annual diet composition of Lake Chelan fishes

Predator species	Basin	Size class (FL; mm)	Suckers	Fish eggs and larvae	Unidentified cyprinids	Unidentified salmonids	Unidentified other fish	Benthos	Crayfish	*Mysis relicta*	Terrestrial invertebrates	Zooplankton
						Diet proportions by weight						
Burbot	Lucerne	220-450	0.000	0.000	0.000	0.000	0.000	0.004	0.466	0.334	0.003	0.000
Burbot	Lucerne	451-700	0.000	0.000	0.000	0.000	0.000	0.001	0.701	0.150	0.000	0.000
Burbot	Wapato	220-450	0.000	0.000	0.000	0.000	0.000	0.026	0.000	0.945	0.000	0.000
Burbot	Wapato	451-700	0.000	0.000	0.109	0.405	0.105	0.018	0.088	0.049	0.000	0.000
Chinook	Lucerne	ALL	0.000	0.000	0.000	0.000	0.000	0.000	0.000	1.000	0.000	0.000
Cutthroat trout (hatchery)	Lucerne	ALL	0.000	0.000	0.000	0.000	0.000	0.221	0.012	0.000	0.684	0.000
Cutthroat trout (hatchery)	Wapato	ALL	0.000	0.000	0.000	0.000	0.000	0.877	0.000	0.003	0.119	0.000
Cutthroat trout (wild)	Lucerne	ALL	0.000	0.000	0.000	0.000	0.000	0.139	0.000	0.006	0.854	0.000
Kokanee	Lucerne	ALL	0.000	0.000	0.000	0.000	0.000	0.001	0.000	0.000	0.008	0.990
Kokanee	Wapato	ALL	0.000	0.000	0.000	0.000	0.000	0.421	0.000	0.000	0.001	0.577
Lake trout	Lucerne	180-450	0.000	0.031	0.000	0.000	0.001	0.001	0.000	0.503	0.003	0.001
Lake trout	Lucerne	451-500	0.005	0.000	0.008	0.000	0.000	0.003	0.000	0.193	0.000	0.000
Lake trout	Lucerne	501-550	0.000	0.001	0.013	0.077	0.006	0.001	0.000	0.142	0.000	0.000
Lake trout	Lucerne	551-910	0.000	0.000	0.000	0.000	0.018	0.000	0.000	0.000	0.000	0.000
Lake trout	Wapato	180-450	0.000	0.009	0.214	0.000	0.006	0.010	0.000	0.573	0.001	0.009
Lake trout	Wapato	451-500	0.000	0.001	0.067	0.000	0.004	0.010	0.003	0.597	0.000	0.000
Lake trout	Wapato	501-550	0.000	0.004	0.016	0.000	0.012	0.019	0.000	0.478	0.000	0.000
Lake trout	Wapato	551-910	0.000	0.007	0.004	0.000	0.007	0.006	0.000	0.063	0.000	0.000
Northern pikeminnow	Lucerne	101-230	0.000	0.000	0.000	0.000	0.000	0.655	0.094	0.002	0.046	0.000
Northern pikeminnow	Lucerne	231-400	0.000	0.117	0.019	0.004	0.092	0.104	0.365	0.006	0.052	0.000
Northern pikeminnow	Lucerne	401-610	0.000	0.000	0.203	0.000	0.000	0.006	0.262	0.000	0.000	0.000
Northern pikeminnow	Wapato	40-100	0.000	0.000	0.000	0.000	0.174	0.439	0.000	0.000	0.386	0.000
Northern pikeminnow	Wapato	101-230	0.000	0.000	0.010	0.004	0.000	0.137	0.000	0.000	0.516	0.061
Northern pikeminnow	Wapato	231-400	0.000	0.000	0.000	0.000	0.013	0.296	0.291	0.007	0.029	0.000
Northern pikeminnow	Wapato	401-610	0.000	0.003	0.047	0.403	0.001	0.087	0.175	0.000	0.015	0.000
Peamouth	Lucerne	ALL	0.002	0.001	0.000	0.000	0.000	0.321	0.000	0.025	0.406	0.246
Peamouth	Wapato	ALL	0.000	0.000	0.000	0.000	0.000	1.000	0.000	0.000	0.000	0.000
Rainbow trout	Lucerne	ALL	0.000	0.004	0.000	0.000	0.000	0.314	0.021	0.000	0.660	0.000
Rainbow trout	Wapato	ALL	0.000	0.000	0.000	0.000	0.000	0.125	0.000	0.000	0.839	0.000
Smallmouth bass	Wapato	ALL	0.170	0.000	0.000	0.000	0.144	0.033	0.160	0.000	0.056	0.000
Suckers	Lucerne	ALL	0.000	0.000	0.000	0.000	0.189	0.000	0.810	0.000	0.001	0.000
Suckers	Wapato	ALL	0.000	0.000	0.000	0.000	0.000	0.892	0.000	0.000	0.108	0.000
Tench	Lucerne	ALL										

Table A2. Seasonal diet composition of Lake Chelan fishes

Predator species	Lake basin	Size class (FL; mm)	Season	n (Total)	n (Non-empty)	Burbot	Chinook salmon	Kokanee	Lake trout	Northern pikeminnow	Peamouth	Sculpins
						Diet proportions by weight						
Burbot	Lucerne	220-450	Winter	5	3	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Burbot	Lucerne	220-450	Spring	11	9	0.000	0.000	0.000	0.000	0.000	0.000	0.023
Burbot	Lucerne	220-450	Summer	3	2	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Burbot	Lucerne	220-450	Fall	7	6	0.000	0.000	0.000	0.000	0.000	0.000	0.057
Burbot	Lucerne	451-700	Winter	13	6	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Burbot	Lucerne	451-700	Spring	16	12	0.000	0.000	0.000	0.000	0.000	0.000	0.015
Burbot	Lucerne	451-700	Summer	8	2	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Burbot	Lucerne	451-700	Fall	9	3	0.000	0.000	0.000	0.000	0.000	0.000	0.225
Burbot	Wapato	220-450	Fall	2	2	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Burbot	Wapato	451-700	Winter	4	1	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Burbot	Wapato	451-700	Spring	5	2	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Burbot	Wapato	451-700	Summer	11	6	0.000	0.000	0.000	0.000	0.000	0.000	0.026
Burbot	Wapato	451-700	Fall	6	6	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Chinook	Lucerne	ALL	Winter	1	1	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Chinook	Lucerne	ALL	Spring	1	0							
Chinook	Lucerne	ALL	Summer	1	0							
Chinook	Lucerne	ALL	Fall	1	0							
Cutthroat trout (hatchery)	Lucerne	ALL	Summer	25	21	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Cutthroat trout (hatchery)	Lucerne	ALL	Fall	7	6	0.000	0.000	0.000	0.000	0.000	0.526	0.000
Cutthroat trout (hatchery)	Wapato	ALL	Summer	3	2	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Cutthroat trout (hatchery)	Wapato	ALL	Fall	5	3	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Cutthroat trout (wild)	Lucerne	ALL	Winter	2	1	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Cutthroat trout (wild)	Lucerne	ALL	Spring	2	2	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Kokanee	Lucerne	ALL	Spring	1	1	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Kokanee	Lucerne	ALL	Summer	17	12	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Kokanee	Wapato	ALL	Spring	53	38	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Lake trout	Lucerne	180-450	Winter	6	4	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Lake trout	Lucerne	180-450	Spring	4	1	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Lake trout	Lucerne	180-450	Summer	3	3	0.796	0.000	0.000	0.000	0.000	0.000	0.000
Lake trout	Lucerne	180-450	Fall	2	2	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Lake trout	Lucerne	451-500	Winter	12	12	0.000	0.000	0.322	0.000	0.000	0.119	0.000
Lake trout	Lucerne	451-500	Spring	6	3	0.000	0.000	0.000	0.000	0.983	0.000	0.000
Lake trout	Lucerne	451-500	Summer	5	4	0.000	0.000	0.000	0.000	0.000	0.000	0.853
Lake trout	Lucerne	451-500	Fall	7	4	0.000	0.000	0.291	0.000	0.000	0.000	0.085
Lake trout	Lucerne	501-550	Winter	6	5	0.000	0.000	0.217	0.000	0.000	0.000	0.007
Lake trout	Lucerne	501-550	Spring	7	5	0.000	0.000	0.000	0.000	0.160	0.757	0.007
Lake trout	Lucerne	501-550	Summer	4	4	0.000	0.146	0.664	0.000	0.000	0.000	0.013
Lake trout	Lucerne	501-550	Fall	6	2	0.000	0.000	0.363	0.000	0.000	0.425	0.212
Lake trout	Lucerne	551-910	Winter	8	7	0.000	0.000	0.950	0.000	0.020	0.000	0.000
Lake trout	Lucerne	551-910	Spring	3	2	0.000	0.000	0.000	0.000	0.000	0.983	0.000
Lake trout	Lucerne	551-910	Fall	2	1	0.000	0.000	1.000	0.000	0.000	0.000	0.000
Lake trout	Wapato	180-450	Winter	6	6	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Lake trout	Wapato	180-450	Spring	19	15	0.000	0.000	0.000	0.000	0.000	0.160	0.000
Lake trout	Wapato	180-450	Summer	7	6	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Lake trout	Wapato	180-450	Fall	35	27	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Lake trout	Wapato	451-500	Winter	10	10	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Lake trout	Wapato	451-500	Spring	45	30	0.000	0.000	0.000	0.016	0.000	0.546	0.000
Lake trout	Wapato	451-500	Summer	13	11	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Lake trout	Wapato	451-500	Fall	34	23	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Lake trout	Wapato	501-550	Winter	8	7	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Lake trout	Wapato	501-550	Spring	33	22	0.000	0.000	0.000	0.000	0.000	0.400	0.010
Lake trout	Wapato	501-550	Summer	8	6	0.000	0.000	0.000	0.000	0.000	0.000	0.000

Table A2 continued. Seasonal diet composition of Lake Chelan fishes

Predator species	Lake basin	Size class (FL; mm)	Season	Smallmouth bass	Threespine stickleback	Suckers	Fish eggs and larvae	Unidentified cyprinids	Unidentified salmonids
							Diet proportions by weight		
Burbot	Lucerne	220-450	Winter	0.000	0.000	0.000	0.000	0.000	0.000
Burbot	Lucerne	220-450	Spring	0.000	0.312	0.000	0.000	0.000	0.000
Burbot	Lucerne	220-450	Summer	0.000	0.000	0.000	0.000	0.000	0.000
Burbot	Lucerne	220-450	Fall	0.000	0.002	0.000	0.000	0.000	0.000
Burbot	Lucerne	451-700	Winter	0.000	0.000	0.000	0.000	0.000	0.000
Burbot	Lucerne	451-700	Spring	0.000	0.094	0.000	0.000	0.000	0.000
Burbot	Lucerne	451-700	Summer	0.000	0.000	0.000	0.000	0.000	0.000
Burbot	Lucerne	451-700	Fall	0.000	0.000	0.000	0.000	0.000	0.000
Burbot	Wapato	220-450	Fall	0.000	0.029	0.000	0.000	0.000	0.000
Burbot	Wapato	451-700	Winter	0.000	1.000	0.000	0.000	0.000	0.000
Burbot	Wapato	451-700	Spring	0.000	0.000	0.000	0.000	0.949	0.000
Burbot	Wapato	451-700	Summer	0.000	0.000	0.000	0.000	0.000	0.714
Burbot	Wapato	451-700	Fall	0.000	0.660	0.000	0.000	0.000	0.000
Chinook	Lucerne	ALL	Winter	0.000	0.000	0.000	0.000	0.000	0.000
Chinook	Lucerne	ALL	Spring						
Chinook	Lucerne	ALL	Summer						
Chinook	Lucerne	ALL	Fall						
Cutthroat trout (hatchery)	Lucerne	ALL	Summer	0.000	0.000	0.000	0.000	0.000	0.000
Cutthroat trout (hatchery)	Lucerne	ALL	Fall	0.000	0.000	0.000	0.000	0.000	0.000
Cutthroat trout (hatchery)	Wapato	ALL	Summer	0.000	0.000	0.000	0.000	0.000	0.000
Cutthroat trout (hatchery)	Wapato	ALL	Fall	0.000	0.000	0.000	0.000	0.000	0.000
Cutthroat trout (wild)	Lucerne	ALL	Winter	0.000	0.000	0.000	0.000	0.000	0.000
Cutthroat trout (wild)	Lucerne	ALL	Spring	0.000	0.000	0.000	0.000	0.000	0.000
Kokanee	Lucerne	ALL	Spring	0.000	0.000	0.000	0.000	0.000	0.000
Kokanee	Lucerne	ALL	Summer	0.000	0.000	0.000	0.000	0.000	0.000
Kokanee	Wapato	ALL	Spring	0.000	0.000	0.000	0.000	0.000	0.000
Lake trout	Lucerne	180-450	Winter	0.000	0.398	0.000	0.000	0.000	0.000
Lake trout	Lucerne	180-450	Spring	0.000	0.000	0.000	0.000	0.000	0.000
Lake trout	Lucerne	180-450	Summer	0.000	0.000	0.000	0.174	0.000	0.000
Lake trout	Lucerne	180-450	Fall	0.000	0.000	0.000	0.000	0.000	0.000
Lake trout	Lucerne	451-500	Winter	0.000	0.137	0.000	0.000	0.000	0.000
Lake trout	Lucerne	451-500	Spring	0.000	0.000	0.000	0.000	0.016	0.000
Lake trout	Lucerne	451-500	Summer	0.000	0.000	0.145	0.000	0.000	0.000
Lake trout	Lucerne	451-500	Fall	0.000	0.625	0.000	0.000	0.000	0.000
Lake trout	Lucerne	501-550	Winter	0.000	0.010	0.000	0.000	0.000	0.000
Lake trout	Lucerne	501-550	Spring	0.000	0.001	0.000	0.000	0.075	0.000
Lake trout	Lucerne	501-550	Summer	0.000	0.000	0.000	0.002	0.000	0.164
Lake trout	Lucerne	501-550	Fall	0.000	0.000	0.000	0.000	0.000	0.000
Lake trout	Lucerne	551-910	Winter	0.000	0.009	0.000	0.000	0.000	0.000
Lake trout	Lucerne	551-910	Spring	0.000	0.000	0.000	0.000	0.000	0.000
Lake trout	Lucerne	551-910	Fall	0.000	0.000	0.000	0.000	0.000	0.000
Lake trout	Wapato	180-450	Winter	0.000	0.000	0.000	0.000	0.000	0.000
Lake trout	Wapato	180-450	Spring	0.000	0.071	0.000	0.000	0.366	0.000
Lake trout	Wapato	180-450	Summer	0.000	0.025	0.000	0.000	0.000	0.000
Lake trout	Wapato	180-450	Fall	0.000	0.200	0.000	0.045	0.000	0.000
Lake trout	Wapato	451-500	Winter	0.000	0.000	0.000	0.000	0.000	0.000
Lake trout	Wapato	451-500	Spring	0.000	0.000	0.000	0.000	0.143	0.000
Lake trout	Wapato	451-500	Summer	0.000	0.000	0.000	0.000	0.000	0.000
Lake trout	Wapato	451-500	Fall	0.000	0.215	0.000	0.005	0.000	0.000
Lake trout	Wapato	501-550	Winter	0.000	0.000	0.000	0.000	0.000	0.000
Lake trout	Wapato	501-550	Spring	0.332	0.002	0.000	0.000	0.033	0.000
Lake trout	Wapato	501-550	Summer	0.000	0.000	0.000	0.000	0.000	0.000

Table A2 continued. Seasonal diet composition of Lake Chelan fishes

Predator species	Lake basin	Size class (FL; mm)	Season	Diet proportions by weight					
				Unidentified other fish	Benthos	Crayfish	Mysis relicta	Terrestrial invertebrates	Zooplankton
Burbot	Lucerne	220-450	Winter	0.000	0.000	0.834	0.166	0.000	0.000
Burbot	Lucerne	220-450	Spring	0.000	0.000	0.537	0.122	0.006	0.000
Burbot	Lucerne	220-450	Summer	0.000	0.909	0.000	0.000	0.091	0.000
Burbot	Lucerne	220-450	Fall	0.000	0.010	0.329	0.602	0.000	0.000
Burbot	Lucerne	451-700	Winter	0.000	0.000	0.012	0.988	0.000	0.000
Burbot	Lucerne	451-700	Spring	0.000	0.000	0.857	0.033	0.000	0.000
Burbot	Lucerne	451-700	Summer	0.000	0.887	0.000	0.105	0.008	0.000
Burbot	Lucerne	451-700	Fall	0.000	0.000	0.573	0.202	0.000	0.000
Burbot	Wapato	220-450	Fall	0.000	0.026	0.000	0.945	0.000	0.000
Burbot	Wapato	451-700	Winter	0.000	0.000	0.000	0.000	0.000	0.000
Burbot	Wapato	451-700	Spring	0.000	0.015	0.000	0.035	0.000	0.000
Burbot	Wapato	451-700	Summer	0.184	0.028	0.001	0.047	0.000	0.000
Burbot	Wapato	451-700	Fall	0.000	0.001	0.279	0.060	0.001	0.000
Chinook	Lucerne	ALL	Winter	0.000	0.000	0.000	1.000	0.000	0.000
Chinook	Lucerne	ALL	Spring						
Chinook	Lucerne	ALL	Summer						
Chinook	Lucerne	ALL	Fall						
Cutthroat trout (hatchery)	Lucerne	ALL	Summer	0.000	0.257	0.013	0.000	0.729	0.000
Cutthroat trout (hatchery)	Lucerne	ALL	Fall	0.003	0.026	0.005	0.000	0.440	0.000
Cutthroat trout (hatchery)	Wapato	ALL	Summer	0.000	0.028	0.000	0.028	0.944	0.000
Cutthroat trout (hatchery)	Wapato	ALL	Fall	0.000	0.993	0.000	0.000	0.007	0.000
Cutthroat trout (wild)	Lucerne	ALL	Winter	0.000	0.839	0.000	0.161	0.000	0.000
Cutthroat trout (wild)	Lucerne	ALL	Spring	0.000	0.111	0.000	0.000	0.889	0.000
Kokanee	Lucerne	ALL	Spring	0.000	0.000	0.000	0.000	1.000	0.000
Kokanee	Lucerne	ALL	Summer	0.000	0.001	0.000	0.000	0.000	0.999
Kokanee	Wapato	ALL	Spring	0.000	0.421	0.000	0.000	0.001	0.577
Lake trout	Lucerne	180-450	Winter	0.000	0.000	0.000	0.602	0.000	0.000
Lake trout	Lucerne	180-450	Spring	0.000	0.000	0.000	1.000	0.000	0.000
Lake trout	Lucerne	180-450	Summer	0.000	0.007	0.000	0.000	0.017	0.007
Lake trout	Lucerne	180-450	Fall	0.085	0.000	0.000	0.915	0.000	0.000
Lake trout	Lucerne	451-500	Winter	0.000	0.004	0.000	0.417	0.000	0.000
Lake trout	Lucerne	451-500	Spring	0.000	0.001	0.000	0.000	0.000	0.000
Lake trout	Lucerne	451-500	Summer	0.000	0.001	0.000	0.001	0.000	0.000
Lake trout	Lucerne	451-500	Fall	0.000	0.000	0.000	0.000	0.000	0.000
Lake trout	Lucerne	501-550	Winter	0.000	0.005	0.000	0.760	0.000	0.000
Lake trout	Lucerne	501-550	Spring	0.000	0.000	0.000	0.000	0.000	0.000
Lake trout	Lucerne	501-550	Summer	0.012	0.000	0.000	0.000	0.000	0.000
Lake trout	Lucerne	501-550	Fall	0.000	0.000	0.000	0.000	0.000	0.000
Lake trout	Lucerne	551-910	Winter	0.022	0.000	0.000	0.000	0.000	0.000
Lake trout	Lucerne	551-910	Spring	0.017	0.000	0.000	0.000	0.000	0.000
Lake trout	Lucerne	551-910	Fall	0.000	0.000	0.000	0.000	0.000	0.000
Lake trout	Wapato	180-450	Winter	0.000	0.000	0.000	1.000	0.000	0.000
Lake trout	Wapato	180-450	Spring	0.000	0.005	0.000	0.398	0.000	0.000
Lake trout	Wapato	180-450	Summer	0.040	0.046	0.000	0.826	0.000	0.062
Lake trout	Wapato	180-450	Fall	0.000	0.001	0.000	0.748	0.005	0.000
Lake trout	Wapato	451-500	Winter	0.000	0.003	0.027	0.969	0.000	0.000
Lake trout	Wapato	451-500	Spring	0.000	0.004	0.000	0.291	0.000	0.000
Lake trout	Wapato	451-500	Summer	0.024	0.003	0.000	0.974	0.000	0.000
Lake trout	Wapato	451-500	Fall	0.000	0.030	0.000	0.750	0.000	0.000
Lake trout	Wapato	501-550	Winter	0.000	0.001	0.000	0.999	0.000	0.000
Lake trout	Wapato	501-550	Spring	0.025	0.029	0.000	0.170	0.000	0.000
Lake trout	Wapato	501-550	Summer	0.000	0.040	0.000	0.960	0.000	0.000

Table A2 continued. Seasonal diet composition of Lake Chelan fishes

Predator species	Lake basin	Size class (FL; mm)	Season	n (Total)	n (Non-empty)	Burbot	Chinook salmon	Kokanee	Lake trout	Northern pikeminnow	Peamouth	Sculpins
						Diet proportions by weight						
Lake trout	Wapato	501-550	Fall	27	21	0.000	0.000	0.036	0.000	0.000	0.000	0.000
Lake trout	Wapato	551-910	Winter	6	6	0.000	0.000	0.906	0.000	0.000	0.000	0.000
Lake trout	Wapato	551-910	Spring	34	28	0.000	0.000	0.156	0.000	0.103	0.677	0.000
Lake trout	Wapato	551-910	Summer	8	6	0.084	0.000	0.000	0.840	0.000	0.000	0.000
Lake trout	Wapato	551-910	Fall	14	8	0.000	0.000	0.000	0.007	0.000	0.000	0.000
Northern pikeminnow	Lucerne	101-230	Winter	14	7	0.000	0.000	0.000	0.000	0.000	0.000	0.734
Northern pikeminnow	Lucerne	101-230	Spring	7	3	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Northern pikeminnow	Lucerne	101-230	Summer	9	6	0.000	0.000	0.000	0.000	0.000	0.000	0.098
Northern pikeminnow	Lucerne	231-400	Winter	21	13	0.000	0.000	0.000	0.000	0.000	0.000	0.481
Northern pikeminnow	Lucerne	231-400	Spring	27	18	0.000	0.000	0.000	0.000	0.000	0.001	0.079
Northern pikeminnow	Lucerne	231-400	Summer	66	42	0.000	0.000	0.000	0.000	0.051	0.259	0.006
Northern pikeminnow	Lucerne	231-400	Fall	57	33	0.000	0.000	0.000	0.011	0.000	0.059	0.000
Northern pikeminnow	Lucerne	401-610	Winter	8	3	0.000	0.000	0.000	0.000	0.011	0.000	0.000
Northern pikeminnow	Lucerne	401-610	Spring	5	2	0.000	0.000	0.000	0.000	0.000	0.808	0.000
Northern pikeminnow	Lucerne	401-610	Summer	18	7	0.000	0.000	0.000	0.000	0.000	0.571	0.000
Northern pikeminnow	Lucerne	401-610	Fall	17	6	0.000	0.000	0.000	0.000	0.000	0.338	0.000
Northern pikeminnow	Wapato	40-100	Summer	15	12	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Northern pikeminnow	Wapato	101-230	Spring	12	4	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Northern pikeminnow	Wapato	101-230	Summer	39	31	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Northern pikeminnow	Wapato	101-230	Fall	4	4	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Northern pikeminnow	Wapato	231-400	Spring	38	20	0.000	0.000	0.000	0.000	0.000	0.147	0.040
Northern pikeminnow	Wapato	231-400	Summer	25	11	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Northern pikeminnow	Wapato	231-400	Fall	27	20	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Northern pikeminnow	Wapato	401-610	Winter	4	3	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Northern pikeminnow	Wapato	401-610	Spring	22	11	0.000	0.000	0.529	0.000	0.000	0.000	0.019
Northern pikeminnow	Wapato	401-610	Summer	15	4	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Northern pikeminnow	Wapato	401-610	Fall	12	3	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Peamouth	Lucerne	ALL	Winter	2	2	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Peamouth	Lucerne	ALL	Spring	11	5	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Peamouth	Lucerne	ALL	Summer	10	3	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Peamouth	Lucerne	ALL	Fall	5	2	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Peamouth	Wapato	ALL	Spring	46	23	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Peamouth	Wapato	ALL	Fall	1	0							
Rainbow trout	Lucerne	ALL	Unknown	9	9	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Rainbow trout	Lucerne	ALL	Fall	2	2	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Rainbow trout	Wapato	ALL	Summer	28	24	0.000	0.000	0.000	0.000	0.026	0.000	0.000
Smallmouth bass	Wapato	ALL	Spring	7	6	0.000	0.000	0.000	0.000	0.272	0.000	0.000
Smallmouth bass	Wapato	ALL	Summer	80	62	0.000	0.000	0.000	0.000	0.203	0.163	0.000
Smallmouth bass	Wapato	ALL	Fall	7	2	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Suckers	Lucerne	ALL	Spring	1	0	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Suckers	Lucerne	ALL	Summer	4	1							
Suckers	Lucerne	ALL	Fall	1	0							
Suckers	Wapato	ALL	Winter	1	1	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Suckers	Wapato	ALL	Spring	4	3	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Suckers	Wapato	ALL	Summer	3	3	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Suckers	Wapato	ALL	Fall	4	3	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Tench	Lucerne	ALL	Spring	1	0							

Table A2 continued. Seasonal diet composition of Lake Chelan fishes

Predator species	Lake basin	Size class (FL; mm)	Season	Diet proportions by weight					
				Smallmouth bass	Threespine stickleback	Suckers	Fish eggs and larvae	Unidentified cyprinids	Unidentified salmonids
Lake trout	Wapato	501-550	Fall	0.000	0.428	0.000	0.019	0.000	0.000
Lake trout	Wapato	551-910	Winter	0.000	0.008	0.000	0.000	0.000	0.000
Lake trout	Wapato	551-910	Spring	0.000	0.000	0.000	0.009	0.005	0.000
Lake trout	Wapato	551-910	Summer	0.000	0.000	0.000	0.000	0.000	0.000
Lake trout	Wapato	551-910	Fall	0.000	0.259	0.000	0.002	0.000	0.000
Northern pikeminnow	Lucerne	101-230	Winter	0.000	0.000	0.000	0.000	0.000	0.000
Northern pikeminnow	Lucerne	101-230	Spring	0.000	0.000	0.000	0.000	0.000	0.000
Northern pikeminnow	Lucerne	101-230	Summer	0.000	0.000	0.000	0.000	0.000	0.000
Northern pikeminnow	Lucerne	231-400	Winter	0.000	0.289	0.000	0.000	0.000	0.000
Northern pikeminnow	Lucerne	231-400	Spring	0.000	0.050	0.000	0.000	0.132	0.000
Northern pikeminnow	Lucerne	231-400	Summer	0.000	0.005	0.000	0.266	0.000	0.000
Northern pikeminnow	Lucerne	231-400	Fall	0.000	0.078	0.000	0.000	0.000	0.011
Northern pikeminnow	Lucerne	401-610	Winter	0.000	0.000	0.000	0.000	0.000	0.000
Northern pikeminnow	Lucerne	401-610	Spring	0.000	0.000	0.000	0.000	0.000	0.000
Northern pikeminnow	Lucerne	401-610	Summer	0.000	0.000	0.000	0.000	0.428	0.000
Northern pikeminnow	Lucerne	401-610	Fall	0.000	0.000	0.000	0.000	0.000	0.000
Northern pikeminnow	Wapato	40-100	Summer	0.000	0.000	0.000	0.000	0.000	0.000
Northern pikeminnow	Wapato	101-230	Spring	0.000	0.000	0.000	0.000	0.000	0.368
Northern pikeminnow	Wapato	101-230	Summer	0.000	0.000	0.000	0.000	0.016	0.003
Northern pikeminnow	Wapato	101-230	Fall	0.000	0.758	0.000	0.000	0.000	0.000
Northern pikeminnow	Wapato	231-400	Spring	0.000	0.049	0.000	0.000	0.000	0.000
Northern pikeminnow	Wapato	231-400	Summer	0.000	0.310	0.000	0.000	0.000	0.000
Northern pikeminnow	Wapato	231-400	Fall	0.000	0.516	0.000	0.000	0.000	0.000
Northern pikeminnow	Wapato	401-610	Winter	0.000	0.000	0.000	0.000	0.000	0.000
Northern pikeminnow	Wapato	401-610	Spring	0.000	0.000	0.000	0.005	0.097	0.122
Northern pikeminnow	Wapato	401-610	Summer	0.000	0.000	0.000	0.000	0.000	0.642
Northern pikeminnow	Wapato	401-610	Fall	0.000	0.000	0.000	0.000	0.000	0.855
Peamouth	Lucerne	ALL	Winter	0.000	0.000	0.064	0.043	0.000	0.000
Peamouth	Lucerne	ALL	Spring	0.000	0.000	0.000	0.000	0.000	0.000
Peamouth	Lucerne	ALL	Summer	0.000	0.000	0.000	0.000	0.000	0.000
Peamouth	Lucerne	ALL	Fall	0.000	0.000	0.000	0.000	0.000	0.000
Peamouth	Wapato	ALL	Spring	0.000	0.000	0.000	0.000	0.000	0.000
Peamouth	Wapato	ALL	Fall						
Rainbow trout	Lucerne	ALL	Unknown	0.000	0.000	0.000	0.005	0.000	0.000
Rainbow trout	Lucerne	ALL	Fall	0.000	0.000	0.000	0.000	0.000	0.000
Rainbow trout	Wapato	ALL	Summer	0.000	0.011	0.000	0.000	0.000	0.000
Smallmouth bass	Wapato	ALL	Spring	0.000	0.086	0.000	0.000	0.000	0.000
Smallmouth bass	Wapato	ALL	Summer	0.031	0.052	0.183	0.000	0.000	0.000
Smallmouth bass	Wapato	ALL	Fall	0.000	0.000	0.000	0.008	0.000	0.000
Suckers	Lucerne	ALL	Spring	0.000	0.000	0.000	0.000	0.000	0.000
Suckers	Lucerne	ALL	Summer						
Suckers	Lucerne	ALL	Fall						
Suckers	Wapato	ALL	Winter	0.000	0.000	0.000	0.000	0.000	0.000
Suckers	Wapato	ALL	Spring	0.000	0.000	0.000	0.000	0.000	0.000
Suckers	Wapato	ALL	Summer	0.000	0.000	0.000	0.000	0.000	0.000
Suckers	Wapato	ALL	Fall	0.000	0.000	0.000	0.000	0.000	0.000
Tench	Lucerne	ALL	Spring						

75

Table A2 concluded. Seasonal diet composition of Lake Chelan fishes

| Predator species	Lake basin	Size class (FL; mm)	Season	Unidentified other fish	Benthos	Crayfish	*Mysis relicta*	Terrestrial invertebrates	Zooplankton
				Diet proportions by weight					
Lake trout	Wapato	501-550	Fall	0.000	0.010	0.000	0.506	0.000	0.000
Lake trout	Wapato	551-910	Winter	0.000	0.008	0.000	0.078	0.000	0.000
Lake trout	Wapato	551-910	Spring	0.009	0.006	0.000	0.035	0.000	0.000
Lake trout	Wapato	551-910	Summer	0.000	0.000	0.000	0.075	0.000	0.000
Lake trout	Wapato	551-910	Fall	0.001	0.000	0.000	0.732	0.000	0.000
Northern pikeminnow	Lucerne	101-230	Winter	0.000	0.045	0.211	0.009	0.000	0.000
Northern pikeminnow	Lucerne	101-230	Spring	0.000	0.642	0.000	0.000	0.358	0.000
Northern pikeminnow	Lucerne	101-230	Summer	0.000	0.794	0.074	0.000	0.034	0.000
Northern pikeminnow	Lucerne	231-400	Winter	0.034	0.005	0.189	0.000	0.002	0.000
Northern pikeminnow	Lucerne	231-400	Spring	0.003	0.633	0.048	0.000	0.054	0.000
Northern pikeminnow	Lucerne	231-400	Summer	0.037	0.028	0.236	0.013	0.098	0.000
Northern pikeminnow	Lucerne	231-400	Fall	0.193	0.000	0.646	0.001	0.002	0.000
Northern pikeminnow	Lucerne	401-610	Winter	0.000	0.000	0.989	0.000	0.000	0.000
Northern pikeminnow	Lucerne	401-610	Spring	0.000	0.000	0.192	0.000	0.000	0.000
Northern pikeminnow	Lucerne	401-610	Summer	0.000	0.001	0.000	0.000	0.000	0.000
Northern pikeminnow	Lucerne	401-610	Fall	0.000	0.020	0.641	0.000	0.000	0.000
Northern pikeminnow	Wapato	40-100	Summer	0.174	0.439	0.000	0.000	0.386	0.000
Northern pikeminnow	Wapato	101-230	Spring	0.000	0.632	0.000	0.000	0.000	0.000
Northern pikeminnow	Wapato	101-230	Summer	0.000	0.074	0.000	0.000	0.811	0.096
Northern pikeminnow	Wapato	101-230	Fall	0.000	0.242	0.000	0.000	0.000	0.000
Northern pikeminnow	Wapato	231-400	Spring	0.001	0.533	0.198	0.000	0.032	0.000
Northern pikeminnow	Wapato	231-400	Summer	0.000	0.408	0.116	0.000	0.165	0.000
Northern pikeminnow	Wapato	231-400	Fall	0.028	0.013	0.427	0.016	0.000	0.000
Northern pikeminnow	Wapato	401-610	Winter	0.000	0.997	0.000	0.003	0.000	0.000
Northern pikeminnow	Wapato	401-610	Spring	0.002	0.063	0.131	0.000	0.031	0.000
Northern pikeminnow	Wapato	401-610	Summer	0.000	0.005	0.353	0.000	0.000	0.000
Northern pikeminnow	Wapato	401-610	Fall	0.000	0.000	0.145	0.000	0.000	0.000
Peamouth	Lucerne	ALL	Winter	0.000	0.021	0.000	0.872	0.000	0.000
Peamouth	Lucerne	ALL	Spring	0.000	0.136	0.000	0.000	0.864	0.000
Peamouth	Lucerne	ALL	Summer	0.000	0.144	0.000	0.000	0.046	0.811
Peamouth	Lucerne	ALL	Fall	0.000	1.000	0.000	0.000	0.000	0.000
Peamouth	Wapato	ALL	Spring	0.000	1.000	0.000	0.000	0.000	0.000
Peamouth	Wapato	ALL	Fall						
Rainbow trout	Lucerne	ALL	Unknown	0.000	0.313	0.022	0.000	0.661	0.000
Rainbow trout	Lucerne	ALL	Fall	0.000	0.365	0.000	0.000	0.635	0.000
Rainbow trout	Wapato	ALL	Summer	0.000	0.125	0.000	0.000	0.839	0.000
Smallmouth bass	Wapato	ALL	Spring	0.041	0.196	0.405	0.000	0.000	0.000
Smallmouth bass	Wapato	ALL	Summer	0.153	0.026	0.152	0.000	0.036	0.000
Smallmouth bass	Wapato	ALL	Fall	0.000	0.000	0.000	0.000	0.992	0.000
Suckers	Lucerne	ALL	Spring	0.000	0.000	0.000	0.000	0.000	0.000
Suckers	Lucerne	ALL	Summer						
Suckers	Lucerne	ALL	Fall						
Suckers	Wapato	ALL	Winter	0.000	1.000	0.000	0.000	0.000	0.000
Suckers	Wapato	ALL	Spring	0.000	1.000	0.000	0.000	0.000	0.000
Suckers	Wapato	ALL	Summer	0.000	0.778	0.000	0.000	0.222	0.000
Suckers	Wapato	ALL	Fall	0.000	1.000	0.000	0.000	0.000	0.000
Tench	Lucerne	ALL	Spring						
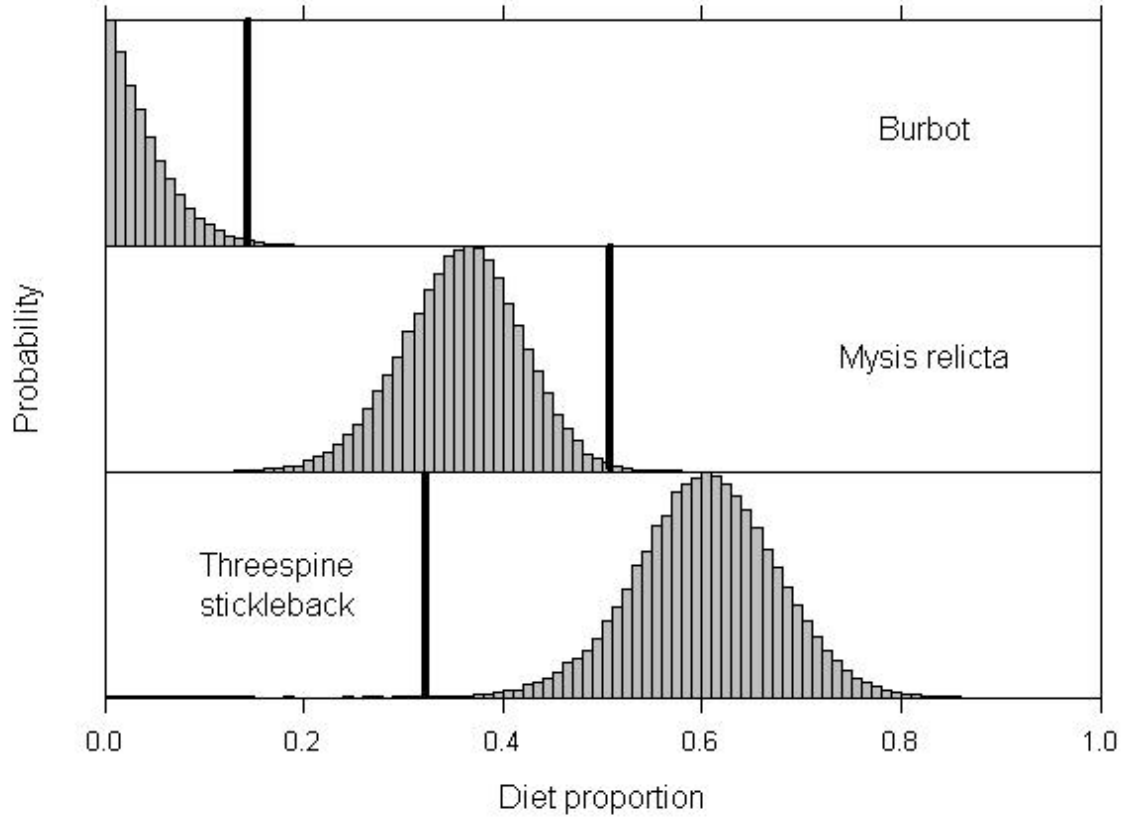
Figure A1. Diet composition of lake trout 180-400 mm (FL), in the Lucerne Basin, estimated by a stable isotope mixing model. Each horizontal panel is a histogram representing the probability distribution of diet proportions for one prey type. Black vertical bars indicate the diet composition as estimated by stomach content analysis. The mixing model indicated that threespine stickleback and *Mysis relicta* were the most important prey. Burbot was a minor prey item.
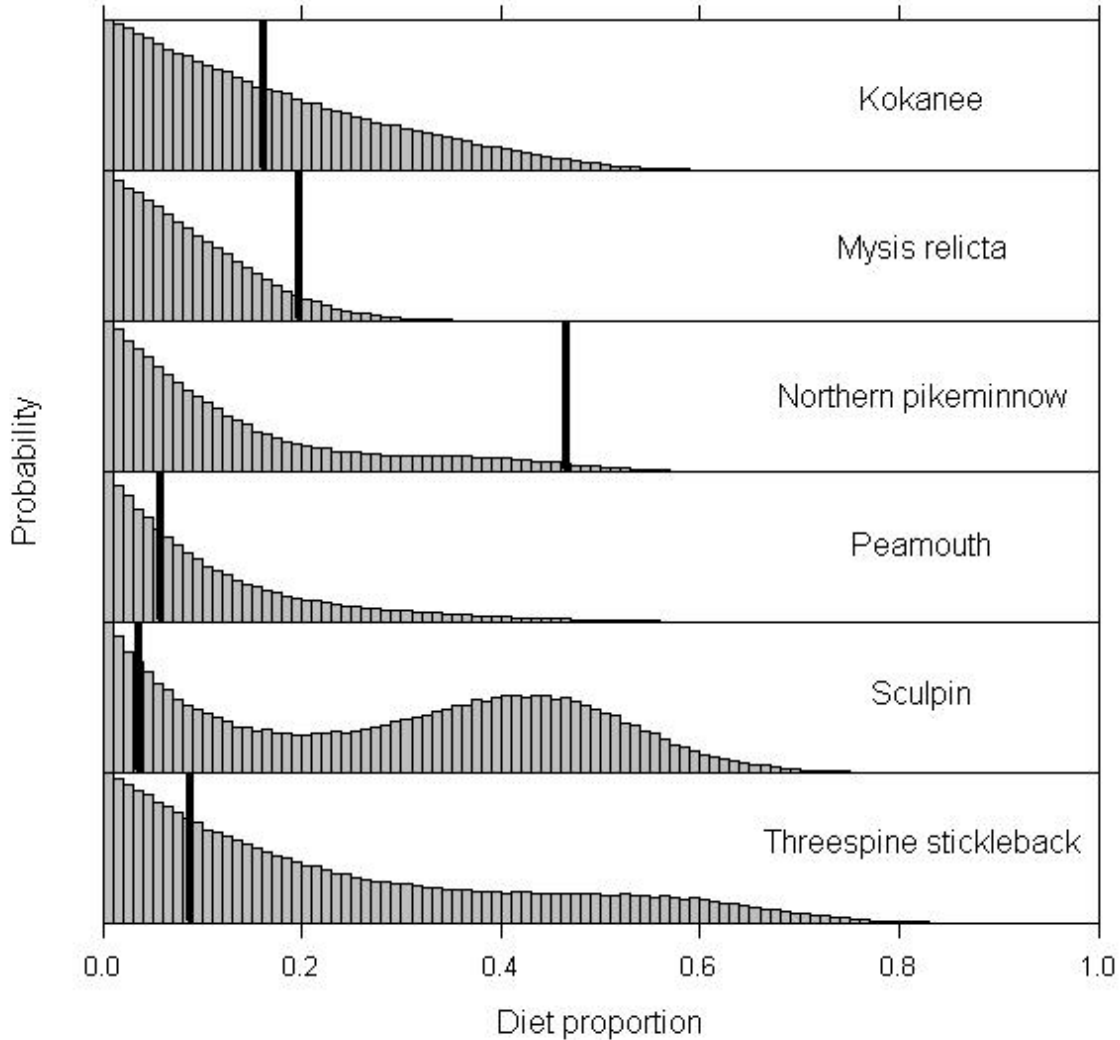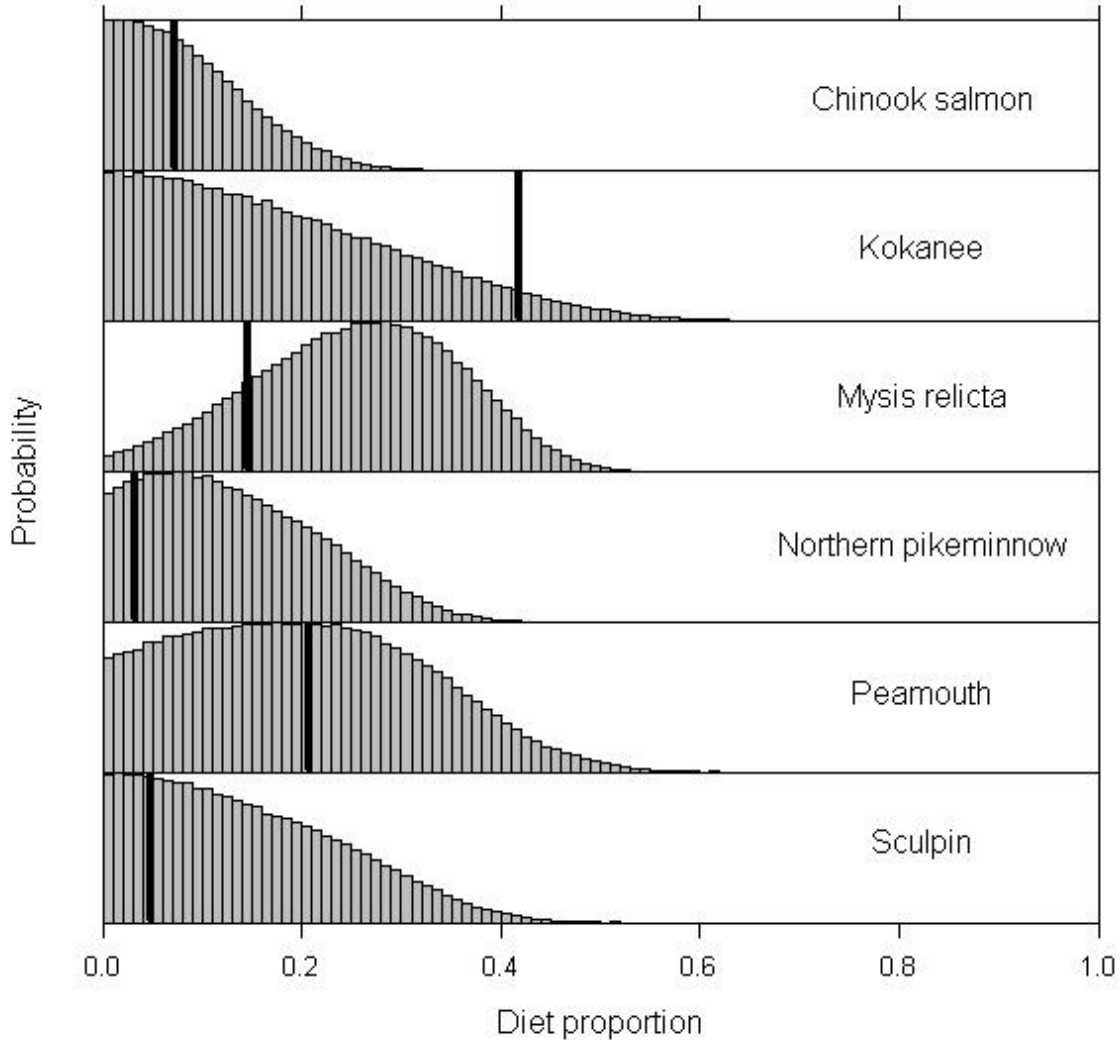
Figure A2. Diet composition of lake trout 401-450 mm (FL), in the Lucerne Basin, estimated by a stable isotope mixing model. Each horizontal panel is a histogram representing the probability distribution of diet proportions for one prey type. Black vertical bars indicate the diet composition as estimated by stomach content analysis. Mixing model results were not very informative for this combination of stable isotope signatures of predators and potential prey. Mixing model results suggested that kokanee comprised 1-40% of the diet (5th and 95th percentile estimates). The kokanee diet proportion estimated by stomach content analysis (16%) fell in this interval.
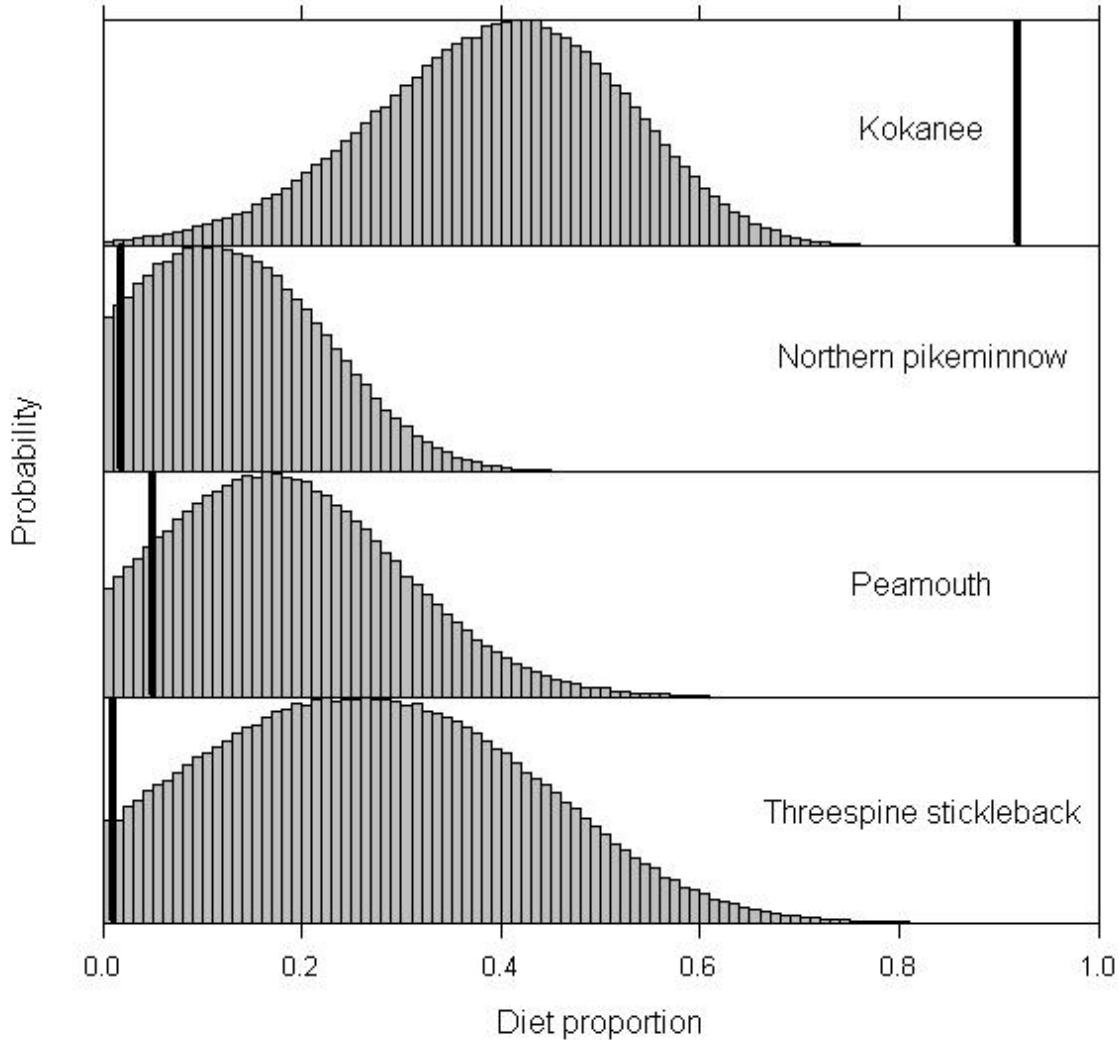
Figure A3. Diet composition of lake trout 451-500 mm (FL), in the Lucerne Basin, estimated by a stable isotope mixing model. Each horizontal panel is a histogram representing the probability distribution of diet proportions for one prey type. Black vertical bars indicate the diet composition as estimated by stomach content analysis. Mixing model results were not very informative for this combination of stable isotope signatures of predators and potential prey. Mixing model results suggested that kokanee comprised 1-42% of the diet (5th and 95th percentile estimates). The kokanee diet proportion estimated by stomach content analysis (41%) fell near the upper limit of this interval.
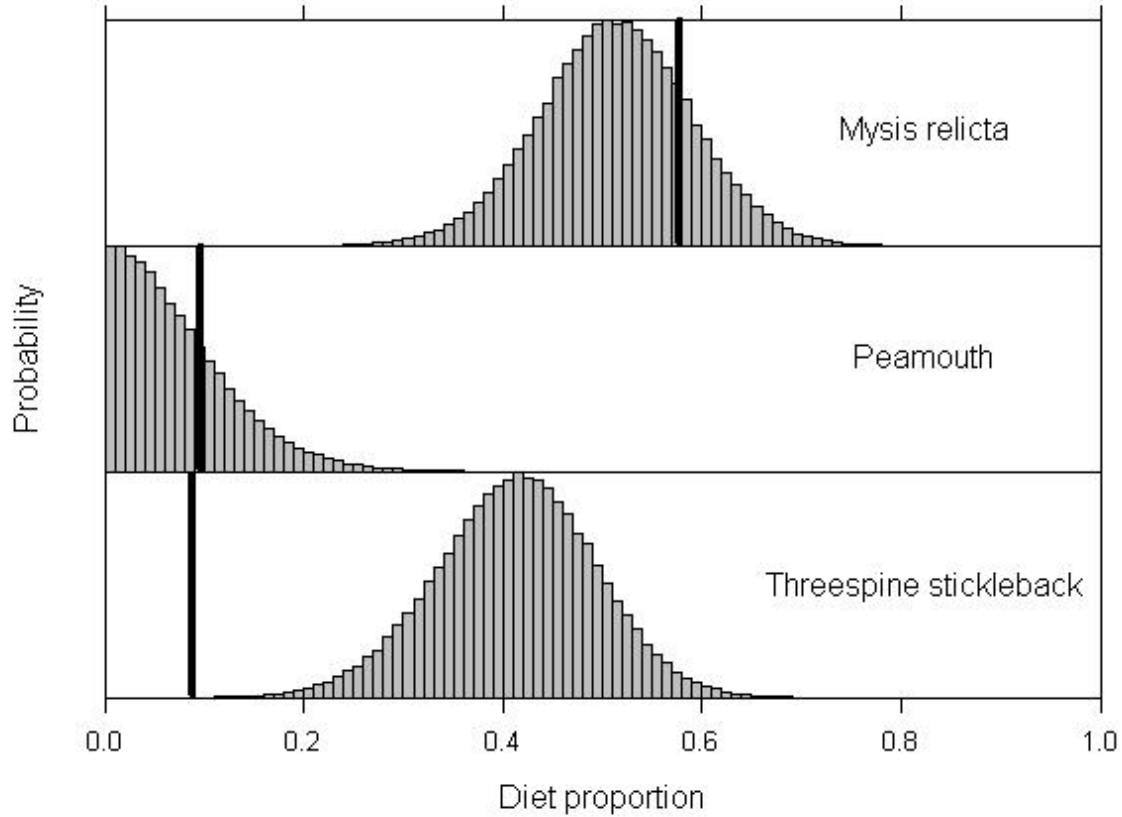
Figure A4. Diet composition of lake trout 501-910 mm (FL), in the Lucerne Basin, estimated by a stable isotope mixing model. Each horizontal panel is a histogram representing the probability distribution of diet proportions for one prey type. Black vertical bars indicate the diet composition as estimated by stomach content analysis. Mixing model results suggested that kokanee comprised a substantial proportion of the diet (17-59%, 5th and 95th percentile estimates), but less than the 92% indicated by stomach contents.
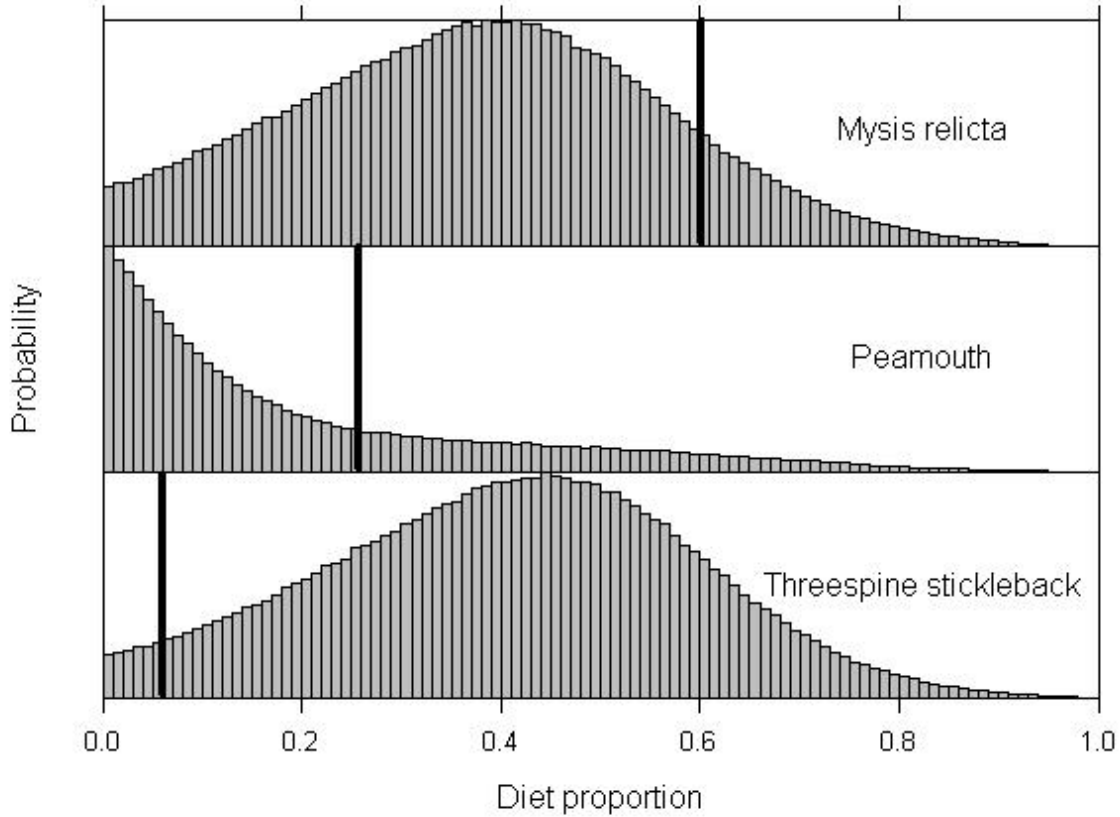
Figure A5. Diet composition of lake trout 180-400 mm (FL), in the Wapato Basin, estimated by a stable isotope mixing model. Each horizontal panel is a histogram representing the probability distribution of diet proportions for one prey type. Black vertical bars indicate the diet composition as estimated by stomach content analysis. Mixing model results indicated that *Mysis relicta* was likely the most important diet item, in agreement with stomach analysis. Mixing model results suggested that threespine stickleback was a more important diet item than indicated by stomach analysis.

Figure A6. Diet composition of lake trout 401-450 mm (FL), in the Wapato Basin, estimated by a stable isotope mixing model. Each horizontal panel is a histogram representing the probability distribution of diet proportions for one prey type. Black vertical bars indicate the diet composition as estimated by stomach content analysis. Broad probability distributions suggested that the diet was composed largely of *Mysis relicta*, threespine stickleback, or both prey. Peamouth was a minor diet item.
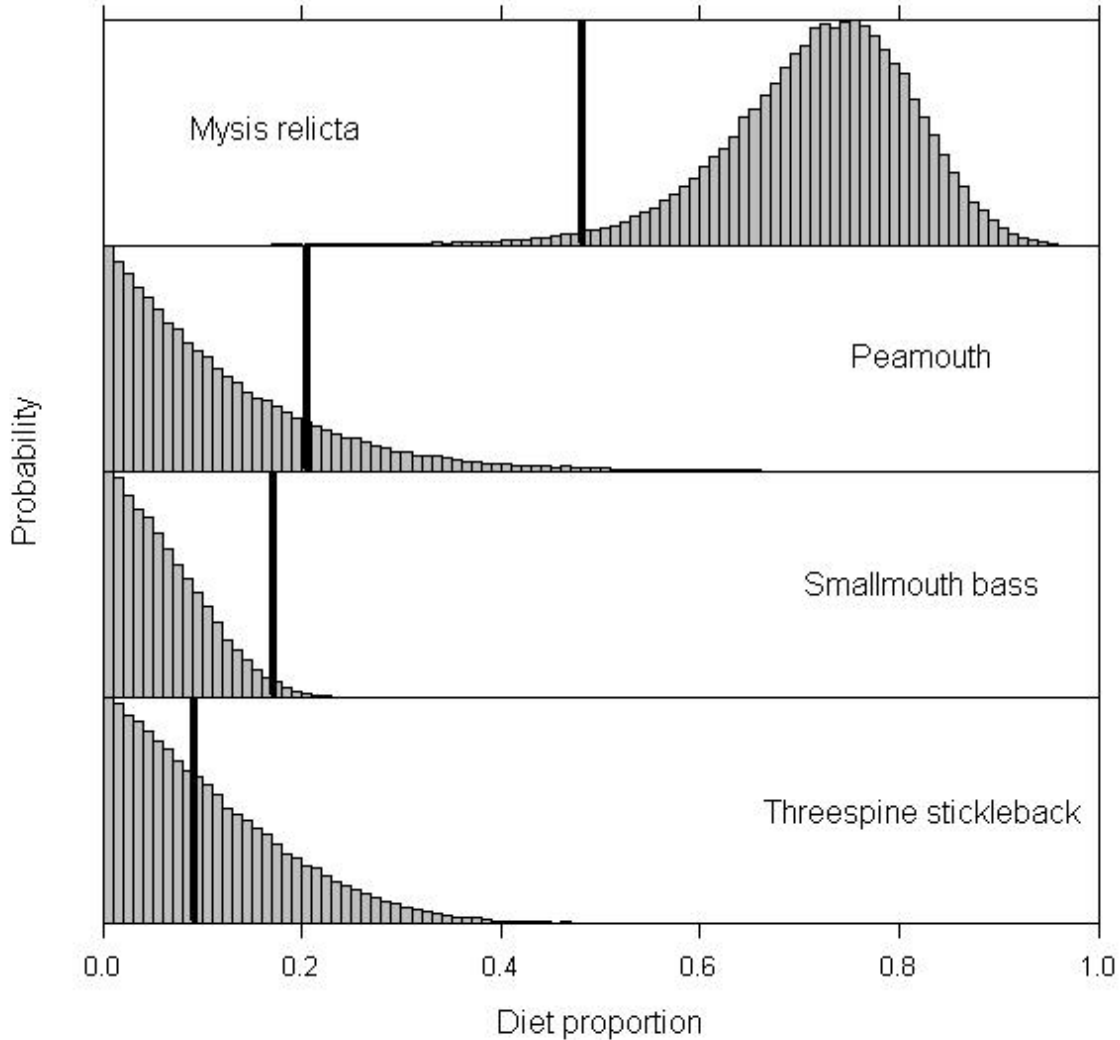
Figure A7. Diet composition of lake trout 451-500 mm (FL), in the Wapato Basin, estimated by a stable isotope mixing model. Each horizontal panel is a histogram representing the probability distribution of diet proportions for one prey type. Black vertical bars indicate the diet composition as estimated by stomach content analysis. The mixing model indicated that *Mysis relicta* was the most important prey item, comprising 54-86% of the diet (5th and 95th percentile estimates). The mixing model suggested that *Mysis* comprised more of the diet than indicated by stomach contents (48%).
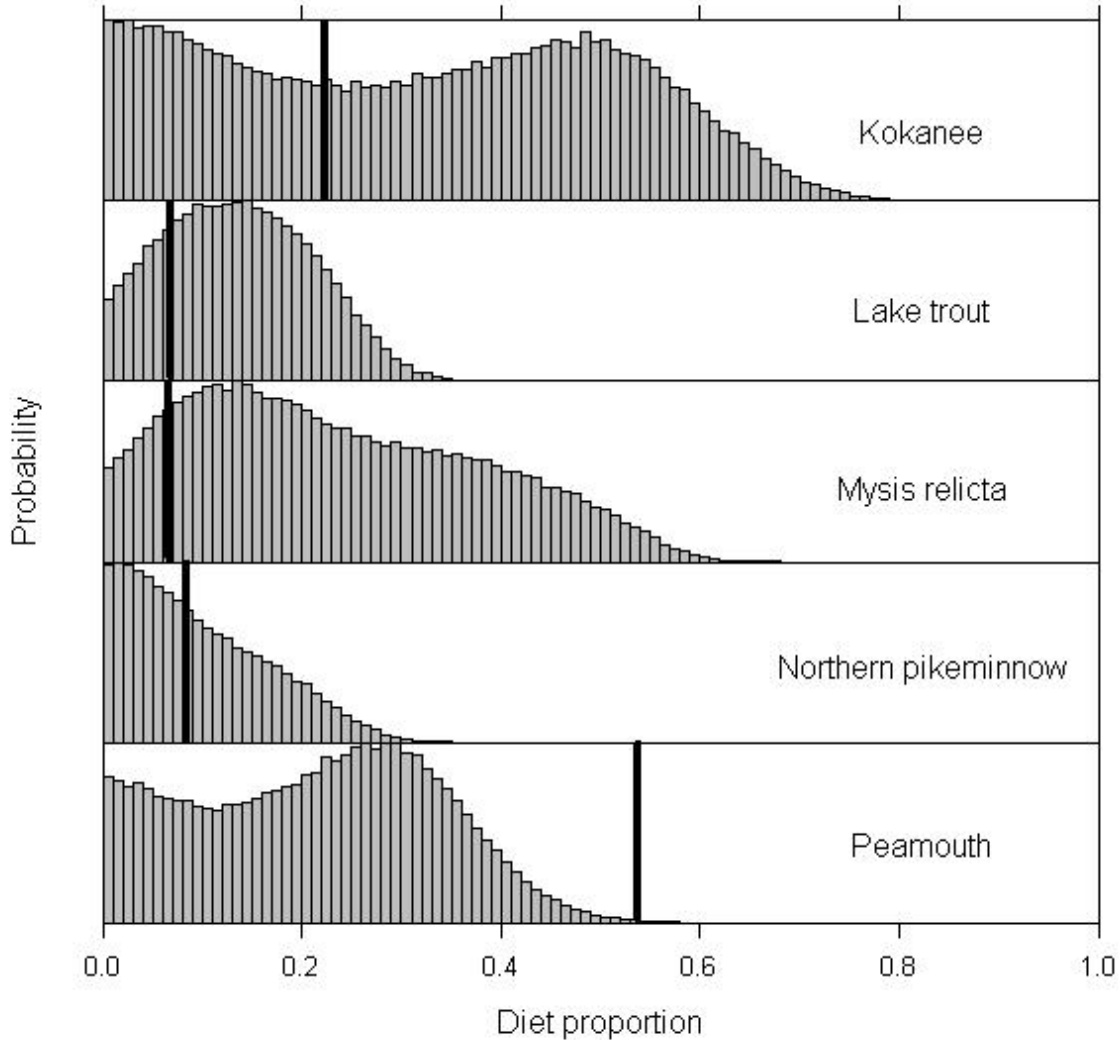
Figure A8. Diet composition of lake trout 501-910 mm (FL), in the Wapato Basin, estimated by a stable isotope mixing model. Each horizontal panel is a histogram representing the probability distribution of diet proportions for one prey type. Black vertical bars indicate the diet composition as estimated by stomach content analysis. Mixing model results were relatively uninformative for this combination of isotopic signatures from predator and potential prey. Mixing model results suggested that kokanee comprised 3-62% of the diet (5th and 95th percentile estimates). The kokanee diet proportion estimated by stomach content analysis (22%) fell inside this interval.