Trophic Interactions of Nonnative Lake Trout and Lake Whitefish in the Flathead Lake Food Web

David A. Beauchamp
US Geological Survey-Biological Resources Division, Washington Cooperative Fisheries and Wildlife Research Unit[1], School of Aquatic and Fisheries Sciences, University of Washington,
Box 355020, Seattle, WA 98195-5020
(206) 221-5791 davebea@u.washington.edu

Mark W. Kershner
Department of Biological Sciences, Kent State University, Kent, OH 44242-0001.
(330) 672-2738, mkershne@kent.edu

Nathanael C. Overman, James Rhydderch, Jocelyn Lin, Lorenz Hauser
School of Aquatic and Fisheries Sciences, University of Washington, Box 355020, Seattle, WA 98195-5020

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Abstract---Nonnative lake trout, lake whitefish, and *Mysis relicta* became the predominant species in the Flathead Lake food web during the mid-1980s. This change in food web structure complicated predator-prey interactions, causing the kokanee population to crash, and was implicated in significant declines of sensitive, threatened and endangered native fishes (e.g., bull trout, westslope cutthroat trout, pygmy whitefish). We quantified the trophic interactions of the lake trout and lake whitefish by using population abundance, annual growth, and seasonal diet, depth distribution, temperature data for lake trout and lake whitefish during June 1998-August 2001 in bioenergetics model simulations of size-structured, seasonal consumption rates on key prey species. These simulations identified forage species that contributed most to the annual energy budget of lake trout and lake whitefish, and quantified seasonal predation patterns on native fishes (pygmy whitefish, bull trout, westslope cutthroat trout) and key non-native species (lake trout, lake whitefish, yellow perch, and mysids).

Lake trout fed heavily on mysids, fish, and other benthic invertebrates. Mysids were the most important component of the energy budget for lake trout ≤ 625 mm total length (TL). Piscivory was measurable in lake trout > 200 mm TL, and increased progressively with predator size until fish became the predominant prey for lake trout > 625 mm TL. The primary prey fishes were lake whitefish and yellow perch, followed by pygmy whitefish, lake trout, and other salmonine fishes. Predation on lake whitefish began with lake trout >375 mm TL remained high during all seasons. Predation on yellow perch also began with lake trout > 375 mm TL, but was heaviest during fall-winter and peaked with 501-750 mm TL lake trout. Predation on pygmy whitefish was exhibited by 200-500 mm lake trout and was greatest during spring-fall. Predation on westslope cutthroat trout occurred during summer-fall by lake trout >375 mm TL, whereas predation on bull trout was concentrated primarily in October by lake trout ≥ 626 mm TL. Cannibalism was exhibited by lake trout > 200 mm TL and was heaviest by 501-625 mm TL lake trout.

Lake whitefish fed almost exclusively on invertebrates. Juvenile lake whitefish (age 0-1; TL < 200 mm) relied heavily on *Daphnia,* primarily during summer-fall. Older lake whitefish (age 2-7; 200-650mm) fed particularly heavily on chironomids, followed by mysids, *Daphnia*, and other invertebrates.

Bioenergetics model simulations indicated that the lake trout population consumed a greater biomass of mysids (1,216 $\mathrm{MT{\cdot}yr^{-1}}$) than did lake whitefish (985 $\mathrm{MT{\cdot}yr^{-1}}$). Consumption by a size-structured unit population of 1,000 lake trout (ages 1-30) consumed 760 kg of mysids per year compared to 210 $\mathrm{kg{\cdot}yr^{-1}}$ by 1,000 age 0-7 lake whitefish. However, since lake trout also consumed lake whitefish, the net effect of removing 1,000 lake trout (with a size structure mirroring the population) would be an increase in mysid biomass of 659 kg, or an increase in areal density of approximately 0.13 $\mathrm{mysids{\cdot}m^{-2}}$.

The combined predation by the lake trout and lake whitefish populations consumed an estimated 55% (2,186 MT) of the estimated annual mysid production; however, the remaining surplus production (1,815 MT) represented 2.74 times the estimated standing stock biomass of mysids. Therefore, unless other significant sources of mortality exist (e.g., predation by yellow perch, etc.), the mysid population would be expected to increase dramatically. Because considerable uncertainty was associated with the estimates for mysid production, any inferences drawn from the production-based calculations should be considered cautiously.

Introduction

Introductions of non-native lake trout *Salvelinus namaycush*, lake whitefish *Coregonus clupeaformis*, and the invasion of opossum shrimp *Mysis relicta* have drastically altered the fish and invertebrate community in Flathead Lake, Montana. Although lake trout were introduced in the early 1900s, populations remained low until 1980, when *Mysis relicta* were discovered in the lake. Between the early 1980s and mid-1990s, catch rates of lake trout in gill net surveys increased 14-fold, while catch rates of native bull trout *Salvelinus confluentus*, westslope cutthroat trout *Oncorhynchus clarki lewisi*, and pigmy whitefish *Prosopium coulteri* declined by factors of 5-10 (Deleray et al. 1999). *Daphnia* density declined as mysid populations increased during the early-mid 1980s (Beattie and Clancey 1991; Spencer et al. 1991, 1999), and the kokanee population declined precipitously from an annual average of 1 million harvested plus spawning adults, to a few thousand adults detected annually thereafter (Beattie and Clancy 1991; Deleray et al. 1999). Although the kokanee decline was originally attributed to competition from mysids, subsequent analysis concluded that predation by the rapidly expanding lake trout population was responsible (Beauchamp 1996). Mysids may have triggered the rapid expansion in the lake trout population by enhancing survival of juvenile lake trout. Beauchamp (1996) speculated that the diel vertical migration behavior of mysids provided a consistent food source, replenished daily, enabling juvenile lake trout to feed in relatively safe, localized foraging areas, with reduced risk of cannibalism. Improved juvenile survival likely increased lake trout recruitment significantly, thus expanding the population of this non-native apex predator. Co-managers of the Flathead Lake fishery considered a program to reduce lake trout abundance or size structure, but were concerned about direct and indirect effects of a lake trout reduction on the native fishes and their zooplankton food base.

The Flathead Lake food web has undergone a dramatic shift from a pelagic energy pathway dominated by kokanee, to an assemblage dominated by more benthically-oriented, nonnative consumers (e.g., lake trout, lake whitefish). This change in food web structure has significant implications for predator-prey interactions among non-native and native species. For example, given the historical importance of kokanee in the diets of lake trout and bull trout (Leathe and Graham 1982; Beauchamp 1996), the loss of this highly abundant prey resource could intensify lake trout predation on sensitive native fishes (e.g., bull trout, westslope cutthroat trout, pygmy whitefish) and on the *Mysis* population. This shift in predation pressure presents an interesting management dilemma given that increased predation on native fishes is undesirable, whereas a reduced *Mysis* population would be desirable.

We quantified the trophic interactions of lake trout, lake whitefish in Flathead Lake during 1998-2001. The objectives of this study were to: 1) describe the size-structured, seasonal diet patterns of lake trout and lake whitefish; 2) estimate population-level predation rates by lake trout on native and non-native fishes and mysids; 3) estimated population-level predation rates by lake whitefish on mysids and other key prey; 4) identify the strong interactors in the Flathead Lake food web and evaluate the possibility that shifts in predatory demand have or may result in higher predation levels on native salmonines and introduced mysids. We used seasonal diet and distribution data for all fish species collected from Flathead Lake, Montana during 1998-2001, to assess seasonal patterns of predation, particularly with respect to predation on native fishes (e.g., bull trout, westslope cutthroat trout), and *Mysis*. A series of bioenergetic modeling simulations were designed to assess the potential impact of lakewide predatory demand (scaled up to the population level) on prey fishes and mysids. The simulations allowed us to integrate information regarding the size structure of the various predator populations, species-specific seasonal diet shifts, temporal changes in thermal experience by the predators, such that we were able to estimate predation rates on key prey species and growth efficiency of the predators during this period. By combining estimates of species-specific prey consumption (as opposed to focusing on a single predator species), we gained a much better understanding of system-wide predator-prey dynamics and food web structure, allowing us to make focused management recommendations.

Study Area

Flathead Lake is a large oligo-mesotrophic lake (chl a < 2.0μ/L; Ellis et al. 2001) in northwestern Montana with surface area of 510 km^2, mean depth of 50 m and maximum depth of 113 m (Zackheim 1983). Kerr Dam, built in 1938 and located 7 km downstream of the natural outlet, regulates the top 3 m of lake elevation to provide hydroelectric power, flood control, and recreational opportunities: the lake surface is annually dropped to a prescribed low pool elevation of 879.3 m by 15 April, increased to 881.5 m by 30 May, then raised to full pool elevation by 15 June and maintained through the first week in September (Deleray et al. 1999). The fisheries resources of the lake are co-managed by the Confederated Salish and Kootenai Tribe in the southern half of the lake and Montana Fish, Wildlife and Parks in the northern half.

A diverse range of native and introduced fishes and invertebrates inhabit the lake. The non-native species that have become abundant and play a potentially ecologically significant role in the lake include lake trout, lake whitefish, yellow perch *Perca flavescens*, and *Mysis relicta*. The major piscivores include the native bull trout, northern pikeminnow *Ptychocheilus oregonensis*, and non-native lake trout. Species at intermediate trophic levels in the lake include non-native lake whitefish, mysids, yellow perch, and rainbow trout *Oncorhynchus mykiss*, and native westslope cutthroat trout, mountain whitefish *Prosopium williamsoni*, pygmy whitefish *Prosopium coulteri*, largescale sucker *Catastomus macrocheilus*, longnose sucker *C. catostomus*, peamouth *Mylocheilus caurinus*, redside shiner *Richardsonius balteatus*, and slimy sculpin *Cottus cognatus*. The primary crustacean zooplankton include mysids, the copepods *Leptodiaptomus ashlandi*, *Epischura nevadensis*, and *Diacyclops thomasi*, and cladocerans *Daphnia thorata*, *D. pulicaria*, *Bosmina longirostrus*. Less information was available for the benthic invertebrate community; however, chironomids were common.

Methods

Fish sampling and diet processing

Fish samples were collected from both annual spring monitoring and seasonal gill net sampling surveys conducted from May 1998 through August 2001 by Montana Fish Wildlife and Parks in the northern region and the Confederated Salish and Kootenai Tribe southern regions of Flathead Lake. During the spring monitoring program, a standard set of floating and sinking gill nets were fished at fixed sites in each of five areas during late April and early May while the lake was still isothermal (Deleray et al. 1999). Horizontal sinking gill nets were fished overnight, from afternoon to mid-morning hours, in five areas with a combination of fixed and random sites in each area. At each site, standard sinking multi-strand nylon nets were 38.1 m long and 1.8 m deep and consisted of five panels of bar mesh sizes 19, 25, 32, 38, and 51 mm. All nets were set perpendicular to shore in gangs of two nets at depths of 10-35 m.

For the seasonal sampling program, sinking gill net sets were randomly stratified among five geographic areas and five depth strata with netting effort allocated in proportion to the relative availability of area within each strata: littoral zone (8 sets), bottom depth < 30 m (10 sets), 30-60 m depths (14 sets), 60-90 m depths (13 sets), and depths > 90 m (3 sets). Each net consisted of 10 randomly arranged mesh sizes, ranging from 19-76 mm (3/4" to 3") bar measure 6-mm (1/4") increments. The summer and winter sets, and the additional spring sets were also done randomly and with the 10 mesh nets.

Nets were retrieved during the morning and fish were kept on ice until they could be processed. For all species, total length, and weight were recorded. For game fishes and northern pikeminnow, depth of capture and maturity were recorded; stomach contents and scales or otoliths were taken for age and growth analysis. Stomach samples were also collected from a representative subsample of the non-game species.

Diet Analysis

Stomach contents were examined using a dissecting microscope and separated into fish and invertebrate components. Prey fishes were generally identified to species (often based upon vertebrae and other diagnostic bones). When identification to species was not possible, fish were typically identified to family, but some remained in an unidentified fish category. Of the 78 unidentifiable fish prey, 37 could be identified to salmonines (whitefishes, char, or trout), 7 to trout or char; 30 of the 78 unidentifiable samples were available for genetic examination, and 26 of these 30 were identified (see section below). We measured standard, total, or vertebral lengths of prey fish when possible (based upon the condition of the partially digested fish). Fish eggs were also counted and weighed. Invertebrate prey were also identified to the functional taxonomic groups including *Mysis*, *Daphnia*, copepods, bivalves, chironomids, other insects, and a broad range of rarer taxa that were pooled into an “other invertebrates” category. For each stomach sample, the mass of each prey category was blotted dry and weighed to the nearest 0.01 g. The proportional wet-weight contribution of each prey category was computed for each non-empty stomach, and these proportions were averaged within each season-by-size class cell for each species of consumer.

Diet composition was summarized by season and size class of consumer. We examined scattergrams of predator length versus the diet proportions of major prey categories to stratify the diet analyses by size classes. For lake trout, only two invertebrate prey groups were categorized: mysids and a general invertebrate category in which all other invertebrates were combined. The weight of each prey category was converted to a proportion of the total weight of food within each stomach, and the proportions from each non-empty stomach were averaged for each season for each size class of consumer.

Genetic Identification of Prey Fishes

Diet analysis revealed several cases of predation by lake trout on native bull trout (4 out of 497 non-empty lake trout stomachs contained identifiable bull trout). Initial bioenergetics modeling simulations indicated that even these seemingly low predation rates could translate into severe mortality for bull trout in the lake. Meanwhile, stomach samples from 96 lake trout contained unidentifiable prey fish; many were identified as salmonine prey from bones (whitefish, trout, or char species), but no further taxonomic resolution was possible. Because estimates of predation on bull trout were based on very few identifiable samples of bull trout in stomach samples, identification of as many of the remaining samples as possible would significantly reduce uncertainty associated with potential for extrapolation errors in current estimates of predation on bull trout by lake trout.

Baseline samples--In order to genetically identify unknown prey items, representatives of the most common fish species inhabiting Flathead were collected to create a reference baseline (**Table 1**). In most cases, several individuals from each species were assayed to characterize the intra-specific genetic variation.

DNA extraction--DNA was isolated for both baseline and prey samples using DNeasy Tissue Kit (Qiagen) following the manufacturer's protocol for mouse tails. As the DNA extracted from the prey tissues are likely degraded, a smaller elution volume (100 µl x 2 elutions) was used to concentrate the yield.

PCR--Two mitochondrial DNA markers were employed to identify species (i) a 368 base pair portion of NADH3/COIII (Domanico and Phillips, 1995) (hereafter ND3) and/or (ii) 270 base pair section of the 16S ribosomal gene (Parker and Kornfield, 1996). The ND3 locus was designed for Pacific salmon (*Oncorhynchus*) and does not amplify non-salmonid and whitefish species (Schwenke et al unpublished). However, it is more polymorphic among members of *Oncorhynchus* and *Salvelinus* and thus better discriminates these species (Purcell et al. 2004).

ND3 and 16S were amplified separately in 50 µl reactions each with the same reagent conditions of 1X *Taq* buffer (Promega), 2.5 mM $MgCl_2$, 0.2 mM of each dNTP (Promega), 0.1 µM of each primer, 1X bovine serum albumin (NE BioLabs), 1.25 U *Taq polymerase* (Promega) and approximately 1 to 30 ng DNA template. Both markers utilized the following thermal profile: an initial denature step of 94°C for 3 min, 35 amplification cycles of 94°C 40 sec, 55°C for 40 sec, 72°C for 40 sec, and a final extension of 72°C for 10 min. The PCR product quality and yield was checked by visualization on a SYBER Gold (Molecular Probes) stained 2% agarose gel. The remaining PCR product was washed and filtered using Montage PCR_{96} Cleanup Plates (Millipore) following the manufacturer's protocol. A 5 µl PCR sequencing reaction was performed on the cleaned product using 1µl BigDye v.3.1 (Applied Biosystems), 3.2 pmol primer, 0.5X sequencing buffer (Applied Biosystems) and approximately 10 ng PCR template, for both forward and reverse primers. The sequencing PCR consisted of 30 cycles of 96°C for 30 sec, 50°C for 5 sec, and 60°C for 4 min. The sequencing PCR products were purified using CleanSEQ Dye Terminator Removal System (Agencourt Bioscience). Sequence data was collected on an ABI 3100 Sequencer following standard procedures. Finally, sequences were aligned and analyzed in Sequencher 4.5 (Gene Codes Corp).

Bioenergetic modeling simulations

Bioenergetic modeling simulations were applied to lake trout and lake whitefish to estimate seasonal consumption patterns by the two predominant non-native fishes.
We used the bioenergetics model (Hanson et al. 1997) parameterized for lake trout (Stewart et al. 1983) and for lake whitefish (Rudstam et al. 1994, modified by Madenjian et al. 2006) in conjunction with species-specific seasonal diet data, size distributions, annual growth rates, and thermal history data for lake trout and lake whitefish in Flathead Lake. Simulations began in spring with 1 April representing day 1 of the 365-d simulations.

Annual Growth

The gillnet data from this study provided seasonal size and age distributions of lake trout and lake whitefish for all size class-by-season cells. These size/age distributions were combined with annual simulations for each age class to generate size-structured, population-level consumption estimates for lake trout and lake whitefish. Unfortunately, few fish smaller than 200 mm were sampled. These smaller size classes can be important because they are more abundant than older, larger fish, and typically exhibit very different diet compositions than older, larger individuals.

We modeled lake trout growth for ages 1-21 using annual growth increments **(Table 2)**, based on length-at-age data from otoliths (Deleray et al. 1999; Stafford et al. 2002) and a length-weight regression for lake trout in Flathead Lake ($r^2 = 0.978$; $P < 0.001$; $N = 426$).

$$Wt(g) = 0.0000055 * TL^{3.054}$$

To account for the potential influence of spawning on growth and consumption, we assumed spawning weight losses for lake trout of 5% of the body mass for ages 5-7 and 8% for age 8 and older (averaged over both sexes for lake trout) based on size and age at maturity data for lake trout in Lake Tahoe after mysids became established (D. Beauchamp, unpublished data). Spawning losses were subtracted from the body weight of mature lake trout on day 198 (15 October) of the bioenergetic simulations for lake trout > 375 mm (ages 5 and older).

For lake whitefish, growth increments **(Table 3)** were identified by tracking length frequency modes in the spring gill net samples for ages 2-6, and total lengths were converted to weights using a length-weight regression generated from fish sampled during this study ($r^2 = 0.982$; $P < 0.001$; $N = 308$).

$$Wt(g) = 0.0000029 * TL^{3.167}$$

Adult lake whitefish were assumed to lose an average 5.2% body mass for ages ≥5 years spawning on simulation day 129 (15 November), based on data from lake whitefish in Lake Michigan (Madenjian et al. 2006).

Thermal Experience

To generate the thermal history for input into the model, the seasonal depth distribution for each size class of lake trout and lake whitefish was coupled with vertical temperature profiles to produce depth-averaged monthly temperature patterns for each species and size class. The proportion of the seasonal catch per unit effort in each depth stratum was multiplied by the mean monthly temperature within each depth stratum, and these products were summed over all depths to produce a weighted monthly temperature experienced by that size class. However, we were unable to obtain temperature data for the period of June 1998 – June 1999. Thus, thermal histories used in this study for lake trout and lake whitefish **(Table 4)** were computed by coupling observed depth distributions from this sampling effort with the depth-specific temperature data used by Beauchamp (1996) to estimate the thermal experience for lake trout. Seasonal depth distributions used in this study represented combined data from fish capture in the northern and southern regions.

Diet and Prey Energy Density Inputs

Seasonal changes in proportional diet composition (see Results) for different size classes of lake trout (**Table 5**) and lake whitefish (**Table 6**) were used in bioenergetics model simulations. With the exception of the 100-200 mm size class for lake trout, the diet composition for each size class of lake trout or lake whitefish was applied to multiple ages. The diet proportions were allowed to shift daily during simulations by linear interpolation from the proportions entered on a specified simulation day to the next specified date in the diet input file.

For lake trout prey, seasonal energy densities (J/g) were held constant throughout the year except for lake whitefish which varied seasonally using a size-specific, seasonal relationship (Rudstam et al. 1994): 6,280 J/g in January-March, 10,695 J/g in April-June, and 8,456 J/g July-December. For all other prey, constant energy densities were assigned as follows: 5,834 J/g for cutthroat trout and all unidentified trout; 5,890 J/g for bull trout and lake trout; 4,186 J/g for yellow perch, cyprinids, sculpin, and other nongame forage fish; 2,800 J/g for *Daphnia*; 3,474 J/g for mysids; and a composite value of 3,430 J/g for other invertebrates (**Table 7**).

For lake whitefish, energy densities of all prey groups were held constant throughout the year: fish eggs 4186 J/g, mysids 3474 J/g, *Daphnia* 3800 J/g, copepods 2260 J/g, chironomid pupae and other insects 3400 J/g, bivalves 2200 J/g, other invertebrates and miscellaneous prey were both 3430 J/g.

Estimates of population-level predatory demand

Lake trout abundance was estimated by expanding the estimated annual sport harvest of 12,800 age 6 lake trout to ages 1-30, based on an annual survival rate of S=75% for ages 4-30, and S=50% for ages 1-3. We assumed that harvest accounted for all mortality in ages 4-30 lake trout. Age-specific catch rates from gill nets were adjusted for size-selectivity (Rudstam et al. 1985). After this adjustment, age-6 lake trout were the youngest age that was fully recruited to the gill nets used. We regressed the $\log_e$-transformed standardized gill net catch rate against age for ages 6-15 ($r^2 = 0.98$; $P < 0.00001$; **Figure 1**); the slope = -0.288 represented the instantaneous annual mortality of $Z = 0.288$; therefore, $S = e^{-0.288} = 75\%$ annual survival and annual mortality = 25%. By assuming that harvest accounted for all mortality, the age-6 harvest of 12,800 = 25% of the age-6 population, so 12,800/0.25 = 51,200 age-6 lake trout in Flathead lake at the beginning of each year. Age-6 abundance was expanded to ages 4-30 by applying an annual survival rate of 75%. An assumed survival rate of 50% for ages 1-3 was used to expand the abundance of age-4 lake trout to abundance for ages 1-3. This estimation procedure yielded an estimate of 273,000 age 5-30 lake trout (TL > 400 mm; **Table 2)**. A comparable abundance estimate by Deleray et al. (1999) was 235,024 (95% CI = 151,415 to 467,149) age-5 and older lake trout (total length > 400 mm). This estimate was based on the average of Schnabel mark-recapture estimates which alternatively included or omitted an assumed 20% annual mortality of marked fish and 0-30% annual tag loss (Deleray et al. 1999).

Lake whitefish abundance was estimated from a hydroacoustic and pelagic gill net survey in August 2003. A BioSonics echosounder with 200 kHz, 6.8° full-angle splitbeam transducer was operated at 3 $\text{pings}\cdot\text{s}^{-1}$ with a minimum target strength threshold of -60 dB (approximately representing post-larval fish ≥ 20 mm TL; Love 1977). The transducer was towed an average 5.2 knots at a depth of 0.5 m. We conducted 10 transects at night during August 11-12, 2003: 6 perpendicular to shore and 3 zig-zag transects in the main basin, plus a zig-zag transect in Big Arm Bay (**Figure 2**). These transects were confined to regions of the lake where bottom depth ≥ 10 m. An exploratory transect was also run through Polson Bay, but was omitted from analysis because of the shallowness of the bay and depth constraints of the hydroacoustic gear. A full moon and clear skies were present during the survey, and these conditions might have caused the coldwater pelagic fishes to move deeper or form schools (Luecke and Wurtsbaugh 1993), thus potentially affecting the accuracy of the abundance estimates. Water transparency was high (Secchi depth = 14 m), and the lake was strongly stratified with epilimnetic temperatures of 18-

21°C in depths of 0-9 m followed by a sharp thermocline with $3^{\circ}\ m^{-1}$ decline in temperature through the 10-15 m metalimnion, and 5-6°C hypolimnion over 15-100 m depths (B. Ellis, Flathead Lake Biological Station, University of Montana, Polson, Montana, personal communication).

Acoustic target densities were estimated for each 5-m depth interval within each transect and averaged among transects (**Figure 3**). The abundance of fish ≥ 20 mm TL was estimated within each 5-m depth interval by expanding depth-specific density estimates by the volume of water within the area of each depth interval where the bottom depth was deeper than 10 m, based on a hypsographic curve for the lake (Deleray et al. 1999). We were unable to stratify fish densities by size, because a wiring problem in the transducer prevented reliable estimates of target strength, so the hydroacoustic data were analyzed using an echo-counting method pooled over all sizes of fish. The whitefish species complex was assumed to be numerically dominated by lake whitefish, and the whitefish fraction of the catch in pelagic gill nets (**Figure 3**) was multiplied by the total pelagic fish abundance in the epilimnion (17% of 7.2 million fish), metalimnion (59% of 2.8 million), and hypolimnion (45% of 3.9 million), thus producing an estimated abundance of 4.6 million pelagic whitefish (ages 0-8; TL ≥ 20 mm), or 1.7 million age 2-8 pelagic whitefish (TL > 150 mm). This estimate compared favorably to an estimate of 1.2 million pelagic whitefish from a hydroacoustic-gillnetting survey during August 1995.

Size structure of lake whitefish was estimated by regressing the $\log_e$ number of each age class (age 2-8) from samples during 1986-1989 reported in Tohtz (1993). These years were selected because they followed the rapid increase in abundance of piscivorous-sized lake trout, as indicated by the abrupt crash in kokanee during 1985-1986 (Beattie and Clancy 1991; Beauchamp 1996). Thus, we assumed that any restructuring of the lake whitefish size and age pattern from predation would be reflected by samples from these years. The regression yielded an estimated annual survival rate of S = 60% ($r^2 = 0.75$; $P = 0.007$; **Figure 1**). The size-structured abundance, when fitted to an abundance of 4.6 million age 0-8 lake whitefish and assuming a constant annual survival of 60% for all ages, resulted in an abundance of 1.9 million age-0 and 32,000 age-8 lake whitefish (**Table 3**).

Estimating Biomass and Production of Lake Trout, Lake Whitefish, and Mysids

The biomass and production of lake trout, lake whitefish, and mysids were estimated for comparison to predation losses. The mean standing stock biomass was computed as the sum of the products of the geometric means for the initial and final abundances (N_t and N_{t+1}) and body masses (W_t and W_{t+1}) for each age class of lake trout (Table 2) and lake whitefish (Table 3). Annual production rates for each age of fish P_t were estimated as:

$$P_t = G_t \cdot B_t$$

where $G_t = \log_e(W_{t+1}/W_t)$ and Bt = average biomass of age t fish during the year. Annual production for the population was calculated by summing P_t over ages t = 1 to 30 for lake trout and ages 0-7 for lake whitefish.

More assumptions were required to estimate production and biomass of mysids, so more uncertainty was associated with these estimates and subsequent calculations using these estimates. The mean mysid density in the lake was 44 $\text{mysids}\cdot m^{-2}$ during summer surveys in 1998-2000 (Ellis et al. 2001). We confined this density to the area of the lake where the bottom depth exceeded 20 m (337 km^2), based on reported maximum thermal tolerances of ≤13-14°C for *Mysis relicta* (DeGraeve and Reynolds 1975; Martinez and Bergersen 1991). The monthly average dry energy content of mysids during May-December 1992 and 1993 (from Figure 7 in

Chess and Stanford 1998) were converted to wet body mass by assuming a constant energy density of 3747 J·g-1 wet body mass. From December through May, we assumed that the body mass and energy density of mysids did not change: $W_t = 0.00027$ g in April and 0.06939 g during December-March.. The resulting April-March (11-month) growth rate was converted into an annual growth rate $G = \log_e(0.06939/0.00027)\cdot 12/11 = 6.066$. A simplifying assumption of a constant density of 44 mysids·m^{-2} through the year was combined with the annual growth trajectory (as described for lake trout and lake whitefish above) to calculate an estimated mean standing stock biomass of 662 metric tons (MT). The annual growth rate was combined with standing stock biomass to calculate an annual production rate for mysids of 4,016 MT·yr^{-1}.

Because the numerical density and energy density of mysids could change both ontogenetically and seasonally, the true biomass and production of mysids could vary considerably from the dynamics assumed here. Nonetheless, in the absence of more information these calculations provide a reference level of biomass and production for comparison to the annual consumption rates estimated for their primary predators. These comparisons could be systematically adjusted as improved information regarding seasonal density, growth and production of mysids becomes available.

Results

Genetic Identification of Prey Fishes

All baseline samples amplified at 16S and the number of intraspecific polymorphisms were detected (**Table 1**). All the species surveyed could be unambiguously discriminated with 16S; however, it exhibited low levels of divergence among salmonid taxa. For example, only a single base pair discriminated between bull trout and lake trout. For this reason, a ND3 baseline for members of the genera *Oncorhynchus* and *Salvelinus* inhabiting Flathead Lake were screened, and additional ND3 data from a broader geographic scale were incorporated (Schwenke et al. unpublished; **Table 1**). The ND3 baseline increased the number of parsimoniously informative bases greatly. To continue the bull trout and lake trout example comparison, ND3 showed 6 polymorphisms that were diagnostic between these two species.

Prey samples

Of the 30 prey samples, 4 failed to amplify at either locus, 26 amplified at 16S, and 7 amplified at ND3 in addition to 16S. Twenty of the samples were unambiguously identified to one of the reference species using 16S or both 16S and ND3: 10 lake white fish, 6 lake trout, 3 yellow perch (*Perca flavescens*), 1 kokanee (*Oncorhynchus nerka*) and 1 peamouth (*Mylocheilus caurinus*). In addition, 4 samples were concordant with the largescale sucker (*Catostomus macrocheilus*) 16S reference samples, but some ambiguities due to marginal sequence quality were observed. These samples were discordant with all other reference taxa making their classification as *Catostomus macrocheilus* reasonably certain. Finally, one prey was not unequivocally identifiable as it was 2.67% divergent from its most homologous reference sample, the prickly sculpin (*Cottus asper*). This prey item likely represents one of the sculpin species inhabiting Flathead Lake, but for which tissue was not readily available for genetic analysis.

Size-structured Seasonal Diet Composition

Mysids and other invertebrates dominated the diets of 100-500 mm TL lake trout, but lake trout became progressively more piscivorous with increasing size (**Table 5**). No identifiable prey fish species represented more than 9% of the diet during any season for lake trout < 500 mm

TL. Pygmy whitefish and lake trout entered the diet of lake trout > 200 mm TL, followed by lake whitefish, yellow perch, and westslope cutthroat trout for predators > 375 mm TL. Lake whitefish became the single most important prey species for lake trout >625 mm TL (8-67% of the diet by weight) followed by a mix of salmoniform fishes, other fishes, and invertebrates (**Table 5**). Sensitive native fishes like pygmy whitefish appeared in the diets of lake trout > 200 mm TL during summer or fall; westslope cutthroat trout represented 4% of the diet for 376-500 mm lake trout during fall, but increased to 24-33% during fall for lake trout >625 mm TL; bull trout composed 12% of the diet for 626-750 mm lake trout during fall and 4% of the diet for lake trout >750 mm TL during spring.

Lake whitefish primarily ate *Daphnia*, chironomid pupae, mysids, and other benthic invertebrates; fish eggs represented only 1% of the diet, and only during winter or spring (**Table 6)**. For smaller lake whitefish, *Daphnia* were especially important during summer-fall, whereas chironomids, mysids, and other benthic invertebrates became progressively more important in the diet of larger consumers.

Bioenergetic modeling simulations of consumption

Consumption by the Lake Trout Population

Seasonal consumption on different prey varied among size classes in response to the combined effects of size-specific dynamics in growth, diet, per capita consumption rate, and abundance of lake trout. Despite the numerical superiority of small lake trout (**Table 2**), model simulations indicated that total consumption by 100-200 mm lake trout was considerably lower than by the 201-375 mm size class (due to higher per capita consumption by larger fish), but was comparable to consumption by the 376-500 mm and 501-625 mm size classes; consumption was lowest for lake trout >625 mm, because the effect of declining abundance was stronger than the increasing per capita consumption rates (**Table 7).** Mysids contributed most to the seasonal and annual energy budgets of lake trout up to 625 mm, but represented a minor fraction of the prey biomass eaten by lake trout 625-1000 mm **(Figure 4**). Piscivory began modestly with 200-375 mm lake trout and peaked with the 500-750 mm size classes, but predation on different prey fish species differed among size classes of predators (**Figure 5**). Most predation on pygmy whitefish was imposed by 201-500 mm lake trout (spring-fall). All size classes of lake trout >375 mm consumed significant biomass of lake whitefish throughout the year; with peak predation exerted by the 626-750 mm size class. Predation on yellow perch was particularly heavy by 500-750 mm lake trout and was primarily concentrated during fall-winter. Cannibalism began with 201-375 lake trout and was particularly high during spring-summer with 501-625 mm predators. Lake trout >375 mm consumed significant biomass of westslope cutthroat trout, primarily during summer and fall. Predation on bull trout was confined to the 626-750 mm size class of lake trout during October-November and to lake trout > 750 mm during April. The size of prey fishes consumed by lake trout increased with increasing body size of the predator; the length of most prey fishes were ≤ 40% the body length of lake trout, but some lake whitefish were slightly over 50% of the length of the lake trout that had eaten them (**Figure 6**).

The size-structured population-level consumption of lake trout > 100 mm TL (ages 1-30) annually removed over 1200 metric tonnes (MT) of mysids and 308 MT of other invertebrates, and 328 MT of fish prey **(Table 8)**. Population-level predation rates by lake trout on sensitive prey species included 2,260 kg of bull trout, 32,227 kg of pygmy whitefish, and 12,596 kg of westslope cutthroat trout. Lake trout predation annually removed an estimated biomass (descending order) of 77 MT of lake whitefish, 68 MT of yellow perch, 32 MT of pygmy whitefish, 25 MT of lake trout, 19 MT of cyprinids, 13 MT of catastomids, 13 MT of westslope cutthroat trout, 7 MT of cottids, and 2 MT of bull trout. In addition, 3 MT of unidentified trout or char, 27 MT of unidentified salmonines (trout, char, or whitefishes), and 41 MT of other unidentifiable nonsalmonine fishes were consumed annually by lake trout.

Consumption by the Lake Whitefish Population

Simulated consumption rates were highest during summer and lowest during winter for all size classes of lake whitefish, and the larger size classes collectively ate more prey biomass, despite being much less abundant (**Figure 7**). For lake whitefish <200 mm TL, *Daphnia* contributed the most to the annual energy budget and were primarily consumed during summer-fall; for the 201-370 mm size class, chironomids, *Daphnia*, and mysids were most important; and for lake whitefish >370 mm, chironomids, mysids, and other prey consumed during all seasons contributed most to the annual energy budget. Consumption demand by lake whitefish increased with fish size, demonstrating the importance of accurate estimates of the size and age structure of the consumer population.

When simulated consumption was summed across all size classes and seasons, the lake whitefish population annually consumed 985 MT of mysids, 780 MT of *Daphnia*, 36 MT of copepods, 2,1843 MT of chironomids, 200 MT of other insects, 427 MT bivalves, 114 MT of other benthic invertebrates, 530 MT of other prey, and 12 MT of fish eggs **(Table 9)**.

Lake Trout – Lake Whitefish – Mysid Interactions

Lake trout predation was a strong enough interaction to potentially regulate its own population (through cannibalism) as well as recruitment of lake whitefish, but the combined effect of predation by lake trout and lake whitefish on mysid dynamics was less clear. Lake trout > 375 mm TL became significant predators on lake whitefish (**Figure 5**), but no strong relationship was evident between the size of lake trout and the size of lake whitefish eaten (**Figure 6**). Lake trout consumed 14% of the biomass and 19% of the estimated annual production of lake whitefish population. When applied to specific age classes of prey, annual predation rates by lake trout exceeded the combined standing stock biomass for ages 0-1 lake trout and for ages 0-1 lake whitefish (**Figure 8**). When extended to older prey, lake trout predation represented 60% of the biomass of age 0-2 lake whitefish and 45% of age 0-2 lake trout. Predation impacts declined as progressively older ages were included as prey. However, since the body mass of these prey changed significantly during the predation period, predation rates were also compared to the production rates of single and combined age classes of prey. Predation by lake trout could be entirely absorbed by the annual production of single age classes for ages 0-2 lake whitefish (C/P_t = 65-85%) and ages 0-1 lake trout (C/P_t = 50-60%), whereas older age classes required that some of the predation demand be absorbed by production from younger conspecifics (**Figure 9**).

Lake trout and lake whitefish both fed heavily on mysids, but lake trout also fed heavily on lake whitefish, creating a complex combination of direct and indirect trophic interactions among these three introduced species and other species in the food web. Nearly all of the mysids consumed annually by lake trout were eaten by fish ≤625 mm TL, whereas nearly all of the mysids consumed by lake whitefish were eaten by fish ≥200 mm TL (**Figure 10**). Lake trout ate more mysids than did lake whitefish on a per capita basis. Consumption by a size-structured unit population of 1,000 lake trout (ages 1-30) consumed 760 kg of mysids per year compared to 210 kg of mysids consumed annually by 1,000 age 0-7 lake whitefish. However, since 1,000 lake trout also consumed 48.4 kg of lake whitefish per year at a mean size of 100 g each, 484 more lake whitefish would survive to consume an additional 101.4 kg mysids per year, thus partially counteracting the reduction in direct mysid predation by lake trout. Overall, the net effect of removing 1,000 lake trout from the population would result in an estimated net increase in mysid biomass of 659 kg, or an increase of 0.13 mysids$\cdot$m^{-2}.

The combined annual predation on mysids by lake trout (1,216 MT) and lake whitefish (985 MT) consumed over three times the estimated average standing stock biomass of mysids (662 MT), but this predation rate only represented a fraction of the estimated annual production rate of 4,016 MT$\cdot$yr^{-1} for mysids. Lake trout consumed an estimated 30% of the annual mysid production compared to 25% consumed by lake whitefish. The combined predation by the lake trout and lake whitefish populations consumed an estimated 55% (2,186 MT) of the estimated annual mysid production; however, the remaining surplus production (1,815 MT) represented 2.74 times the estimated standing stock biomass of mysids. Therefore, unless additional, significant sources of mortality exist (e.g., predation by yellow perch, etc.), the mysid population would be expected to increase dramatically. Because considerable uncertainty was associated with the estimates for mysid production, any inferences drawn from the production-based calculations should be considered cautiously.

Discussion

Non-native lake trout and lake whitefish were both major consumers in the Flathead Lake food web. Lake trout were an important top predator, whereas both lake trout and lake whitefish relied heavily on mysids and benthic invertebrates. Lake trout were heavily dependent on mysids which contributed 71% of the total energy budget for consumers <625 mm TL. Larger lake trout > 625 mm TL shifted to piscivory, and mysids contributed only 6% of the prey biomass. Predation by lake trout potentially regulated populations of key native and non-native fishes in Flathead Lake, but their direct and indirect impact on mysids was less clear. Lake trout predation accounted for significant percentages of the biomass and annual production rates of lake whitefish and mysids, suggesting that lake trout predation was a significant source of mortality. Cannibalism also appeared to be an important self-regulating mechanism for lake trout. Lake trout consumed considerable biomass of native pygmy whitefish, westslope cutthroat trout, and bull trout, but more information about the abundance, biomass, and production of these prey was needed to interpret the significance of predation losses in terms of mortality rates for these species. Despite reasonable sample sizes for seasonal diets among size classes of lake trout, the low frequency of occurrence of westslope cutthroat trout and bull trout in the diet of lake trout lead to volatile predation estimates in model simulations, due to stochastic variability in the proportion of these relatively rare prey in the diet. Genetic identification of the most important unidentifiable prey fish samples substantially reduced the uncertainty regarding the potential volatility of the predation estimates on native fishes.

The seasonal, size-structured feeding diet patterns of lake trout provide opportunities for potentially managing their impacts on native fishes, non-native fishes, and mysids by manipulating the size structure of the lake trout population. For instance, bull trout predation was only evident for lake trout > 625 mm TL. These larger lake trout also exhibited heavy predation on lake whitefish and relatively high predation on westslope cutthroat trout, whereas mysid predation was minimal and cannibalism rates were much lower than by smaller lake trout.

Therefore, differentially reducing the abundance of lake trout > 625 mm TL could simultaneously relieve predation mortality on bull trout, westslope cutthroat trout, and lake whitefish while minimizing reductions in cannibalism, and perhaps increasing mysid mortality by increasing the survival of the larger size classes of lake whitefish which eat the greatest biomass of mysids. A substantive decline in mysids could enable recovery of depressed cladoceran populations and potentially enhance recruitment of native fishes.

The combined predation by lake trout and lake whitefish exceeded the standing stock biomass of mysids in the lake, but only removed an estimated 55% of annual production. Because of the high production to biomass ratio for mysids, the remaining surplus production would lead to a nearly 3-fold increase in the current biomass of mysids in the lake. This suggests that, in addition to predation by lake trout and lake whitefish, other significant sources of mortality (e.g., predation by yellow perch) likely contribute to regulating the dynamics of mysid population. However, because considerable uncertainty was associated with estimates for mysid production, any inferences drawn from the production-based calculations should be considered cautiously.

The change in food web structure also altered predator-prey interactions in this system. Since the 1980s, the emerging dominance of lake trout, lake whitefish, and mysids, and the concurrent crash of the kokanee population have dramatically shifted the energy flow to higher trophic levels from the previous pelagic pathways (zooplankton-kokanee-piscivores) to a more benthic pathway (chironomids-lake whitefish-lake trout) or bentho-pelagic pathway (benthos and zooplankton-mysids-lake whitefish and smaller lake trout-lake trout). The effect of higher non-native fish consumption on benthos, especially lake whitefish feeding on chironomids, on native fishes like westslope cutthroat trout, juvenile bull trout, and cyprinids, is currently unknown, but increased competition for these food resources could reduce feeding, growth, and potentially survival or reproduction.

Yellow perch were the second most important prey fish species in the energy budget of lake trout. This suggests that their current abundance in the lake is high; therefore, it will be important to understand their ecological role in the food web. In similar lakes, age 0-1 yellow perch are highly planktivorous, whereas older life stages feed predominantly on benthic invertebrates (including chironomids and mysids) and small fish, especially larval or juvenile sculpins and yellow perch (McIntyre et al. in press). Given this trophic ontogeny, yellow perch could potentially serve as an important mysid predator or as a competitor with mysids and other planktivorous fishes.

Future sampling efforts would also benefit from using a broader array of sampling gear to capture representative size classes for each major species, including age 0-1 lake trout, lake whitefish, pygmy whitefish, and yellow perch. Smaller-mesh gill nets, beach seines, fyke nets, midwater trawls, and/or minnow traps may be required to effectively sample species and size classes in appropriate seasonal habitats. Given the potentially large cohorts associated with younger age classes, characterization of their seasonal distribution and feeding patterns will be important, particularly with respect to regulating mysids and potential competition with native planktivorous and invertebrate-feeding fishes. Any future research should also focus on carefully documenting seasonal and spatial patterns of predation on pygmy whitefish, westslope cutthroat trout and bull trout, especially regarding seasonal migrations into or out of the lake by juveniles or adults.

Acknowledgments

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References

Beattie, W.D. and P.T. Clancey. 1991. Effects of *Mysis relicta* on the zooplankton community and kokanee population in Flathead Lake. American Fisheries Society Symposium 9:39-48.

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.

Chess, D.W. and J.A. Stanford 1998. Comparative energetics and life cycle of the oppossum shrimp (Mysis relicta) in native and non-native environments. Freshwater Biology 40:783-794.

DeGraeve, G.M., and J. B. Reynolds. 1975. Feeding behavior and temperature and light tolerance of Mysis relicta in the laboratory. Transactions of the American Fisheries Society 104:394-397.

Deleray, M.A., T.M. Weaver, and W.L. Knotek. 1997. Fisheries monitoring surveys for Flathead Lake-River system. Report for Montana Department of Fish, Wildlife, and Parks.

Deleray, M., L. Knotek, S. Rumsey, and T. M. Weaver. 1999. Flathead Lake and River system fisheries status report. Montana Department of Fish, Wildlife and Parks. Dingell-Johnson Report Number F-78-R-1 through 5. 229 pages.

Domanico, M. J., and R. B. Phillips. 1995. Phylogenetic analysis of Pacific salmon (genus *Oncorhynchus*) based on mitochondrial DNA sequence data. Mol. Phylogenet. Evol. 4:366−371.

Ellis, B. K., J. A. Craft, and J. A. Stanford. 2001. Monitoring water quality in Flathead lake, Montana: 2001 Progress Report. Open File Report 166-01. Flathead Lake Biological Station, University of Montana, Polson, Montana. 34 pages.

Hanson, P.C., T.B. Johnson, D.E. Schindler, and J.F. Kitchell. 1997. Fish bioenergetics model 3.0. Center for Limnology, University of Wisconsin Sea Grant Institute.

Leathe, S. A., and P. J. Graham. 1981. Flathead Lake fish food habits study. Environmental Protection Agency, Region VIII, Water Division. Denver, Colorado.

Madenjian, C. P., and D. V. O'Connor. 1999. Laboratory evaluation of a lake trout bioenergetics model. Transactions of the American Fisheries Society 128:802-814.

Madenjian, C. P., and eight co-authors. 2006. Evaluation of a lake whitefish bioenergetics model. Transactions of the American Fisheries Society 135:61-75.

Martinez, P. J., and E. P. Bergersen. 1991. Interactions of zooplankton, *Mysis relicta*, and kokanees in Lake Granby, Colorado. American Fisheries Society Symposium 9:49-64.

McIntyre, J.K., D.A. Beauchamp, M.M. Mazur, and N.C. Overman. (in press). Ontogenetic trophic interactions and bentho-pelagic coupling in Lake Washington: evidence from stable isotopes and diet analysis. Transactions of the American Fisheries Society

Montana Fish, Wildlife and Parks, and Confederated Salish and Kootenai Tribes. 1993. Fisheries mitigation plan for losses attributable to the construction and operation of Hungry Horse Dam. Kalispell, Montana.

Parker, A. and I. Kornfield. 1996. An improved amplification and sequencing strategy for phylogenetic studies using the mitochondrial large sub-unit rRNA gene. Genome 39:793-797.

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

Rudstam, L.G., F.P. Binkowski, and M.A. Miller. 1994. A bioenergetics model for analysis of food-consumption patterns of bloater in Lake Michigan. Transactions of the American Fisheries Society 123: 344-357.

Schwenke, P., Baker, J., and L. Park. unpublished. Identification of Pacific Salmonids Using COIII/NADH-3 Consensus Sequence Baseline for Forensic Applications.

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

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 131:994-1003.

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.

Tohtz, J. 1993. Lake whitefish diet and growth after the introduction of *Mysis relicta* to Flathead Lake, Montana. Transactions of the American Fisheries Society 122:629-635.

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 122:1058-1069.

Zollweg, E. C. 1998. Piscine predation on bull trout in the Flathead River, Montana. Master of Science Thesis. Montana State University. Bozeman. 97 pages.

Table 1. Number of individuals for each species genetically screened at 16S and ND3 (brackets indicated the number of intraspecific polymorphisms).

Species	16S	ND3	*Sample locations*
kokanee	2 (0)	30 (4)	Flathead Lake +
cutthroat trout	3 (1)	62 (8)	Flathead Lake +
rainbow trout	2 (0)	64 (3)	Flathead Lake +
lake trout	4 (0)	6 (1)	Flathead Lake +
bull trout	8 (2)	14 (2)	Flathead Lake +
northern pikeminnow	6 (0)	n/a	Flathead Lake
peamouth	6 (0)	n/a	Flathead Lake
pygmy whitefish	5 (0)	n/a	Flathead Lake
lake whitefish	6 (0)	n/a	Flathead Lake
mountain whitefish	4 (1)	n/a	Flathead Lake, Lake Washington
largescale sucker	6 (1)	n/a	Flathead Lake, Lake Chelan
longnose sucker	6 (0)	n/a	Flathead Lake
yellow perch	6 (0)	n/a	Flathead Lake
prickly sculpin	1	n/a	Lake Washington

n/a – does not amplify with Domanico and Phillips (1995) ND3 primers

+ ND3 data combines Flathead Lake samples with sequence data from broader geographic survey by Schwenke et al. unpublished

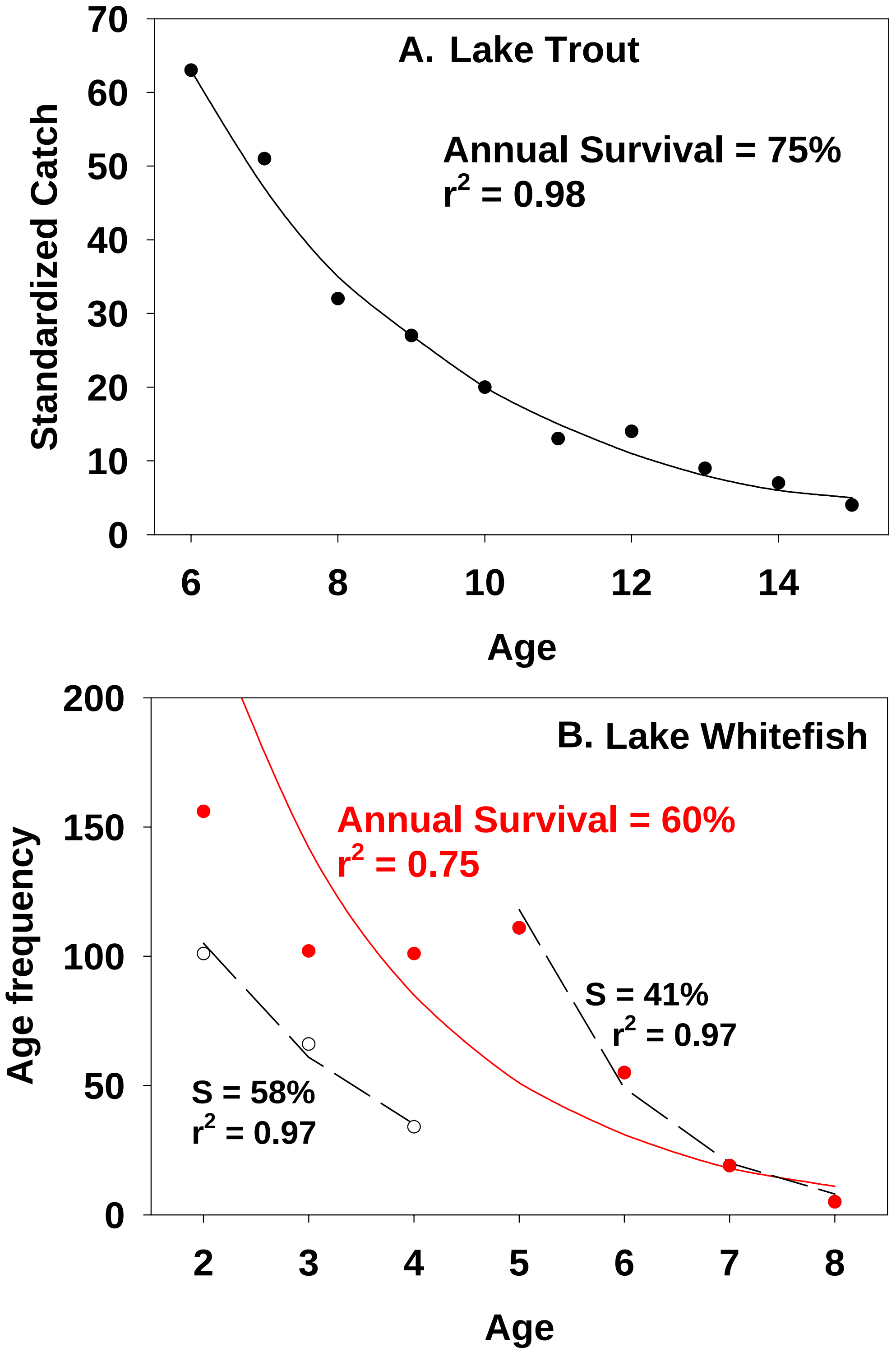

Figure 1. Survival estimates for A. lake trout and B. lake whitefish in Flathead Lake. Regression lines were fitted to standardized catch of lake trout after adjusting for size-selectivity of gill nets, and to age frequency data for lake whitefish from Tohtz (1993) after mysids became established.

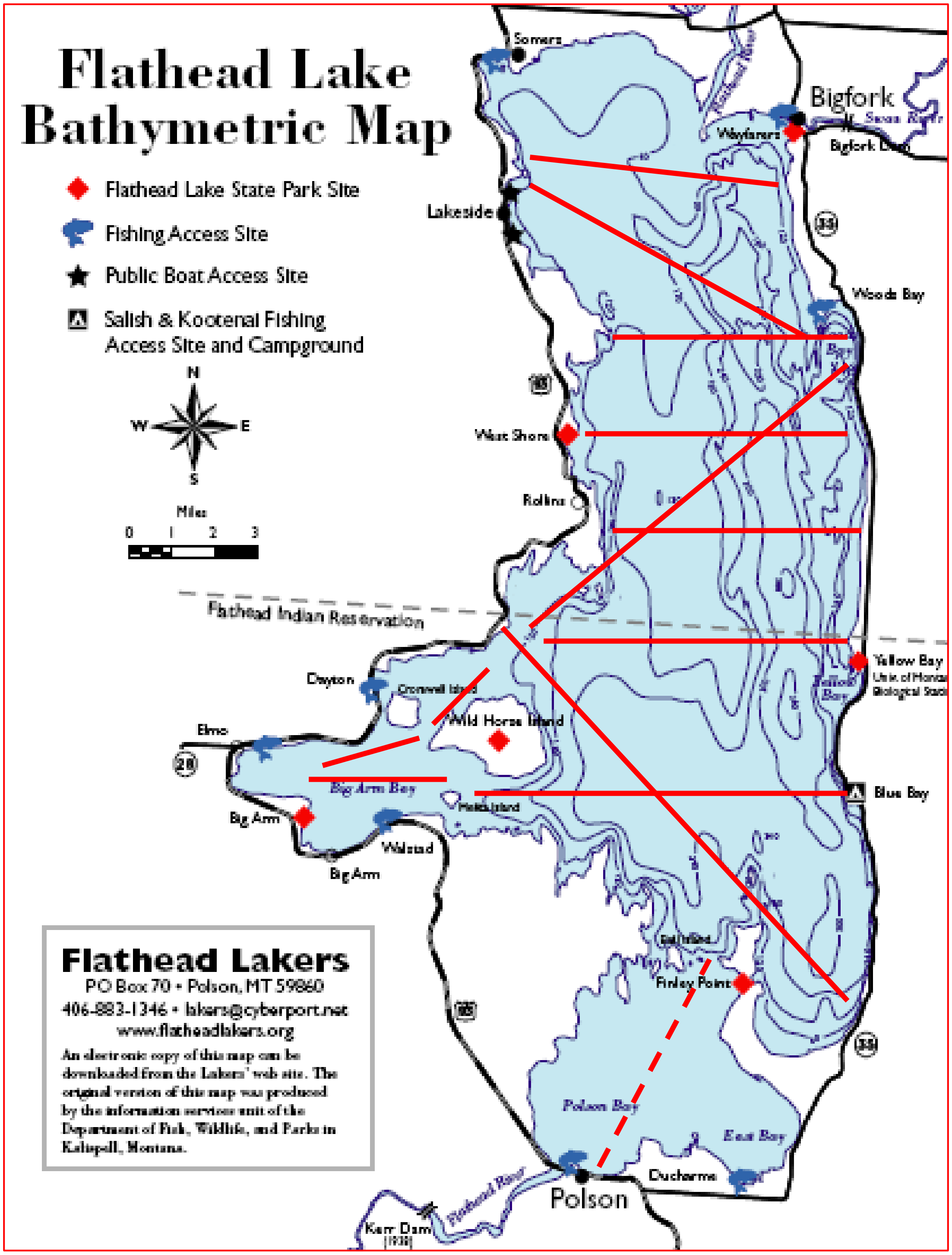

Figure 2. Transects used during a night hydroacoustic survey during August 11-12, 2003 are indicated as solid lines. The dashed in Polson Bay represents an exploratory transect that was omitted from the analysis because of depth limitations.

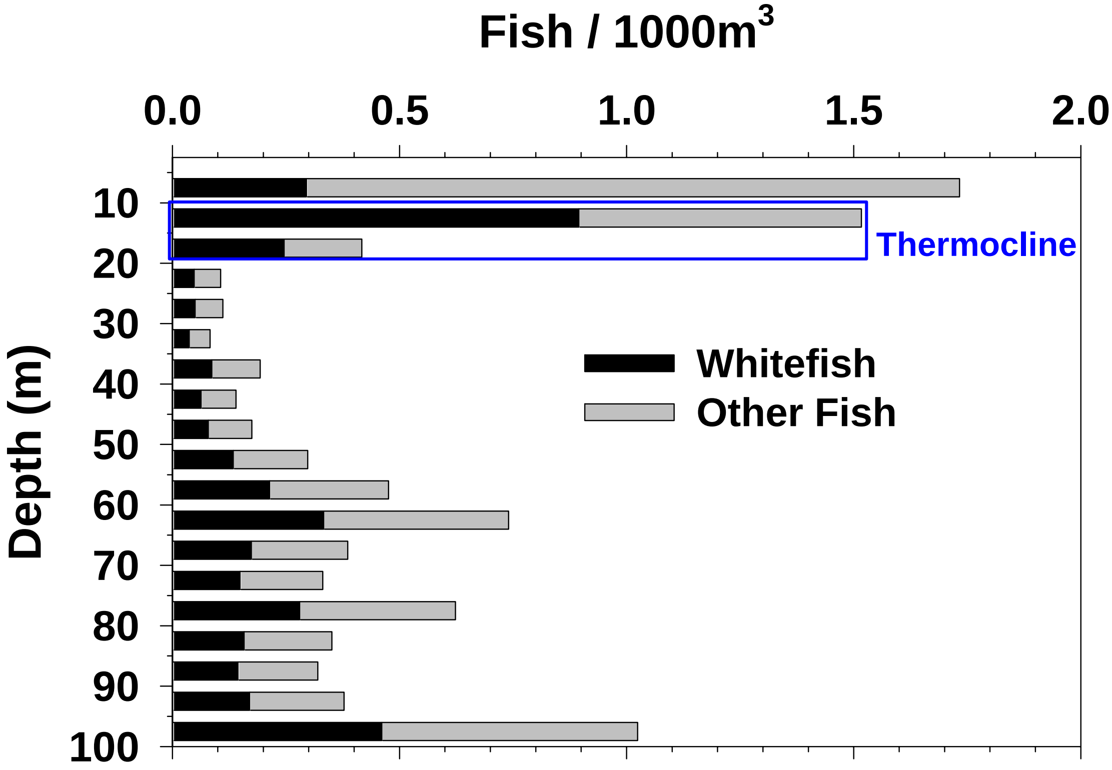

Figure 3. Depth-specific densities of coregonids (lake and pygmy whitefishes) and other fishes, estimated from a hydroacoustic survey and depth-specific gill net sampling in limnetic and slope zones of Flathead Lake during August 2003. The thermocline at 10-20 m is indicated.

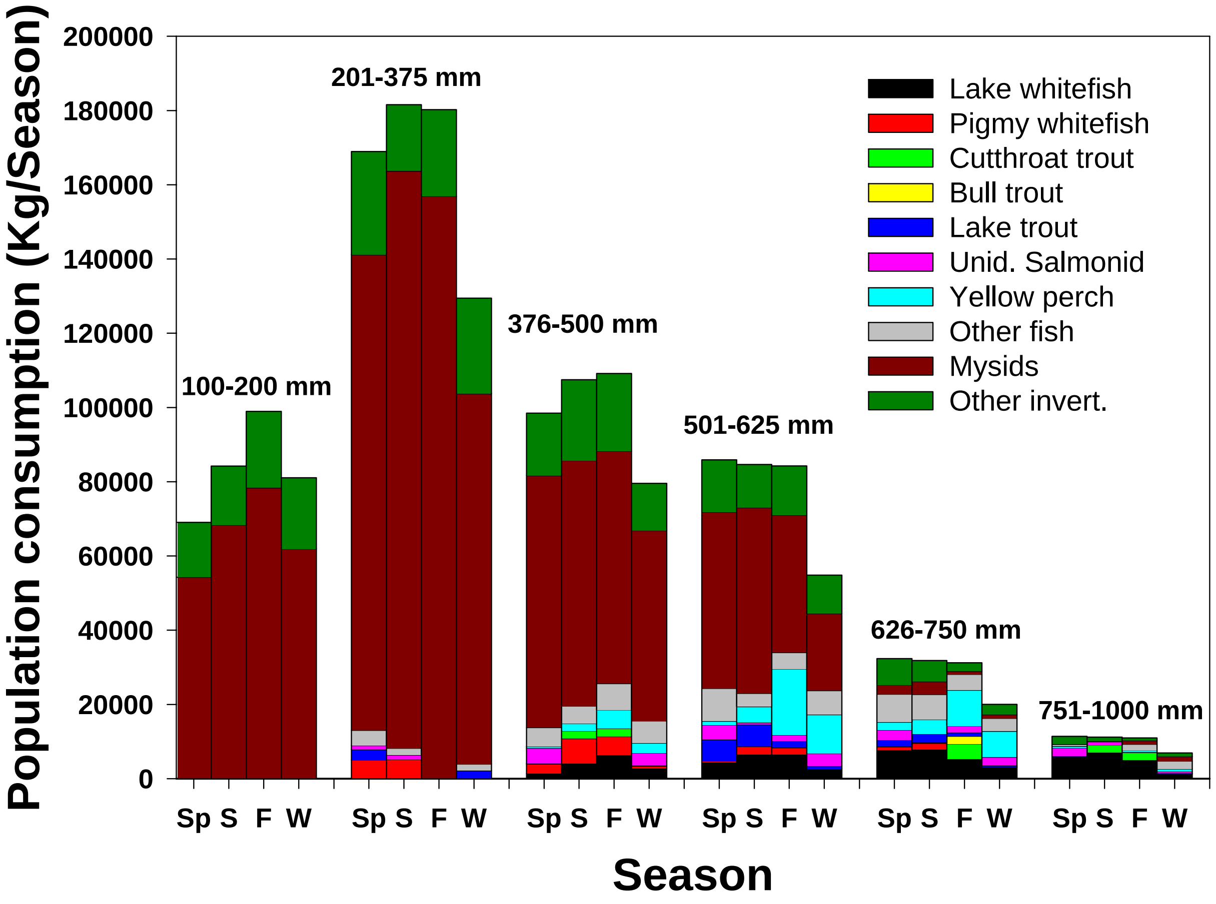

Figure 4. Seasonal, population-level consumption of all major prey categories by different size classes of lake trout in Flathead Lake during 1998-2001.

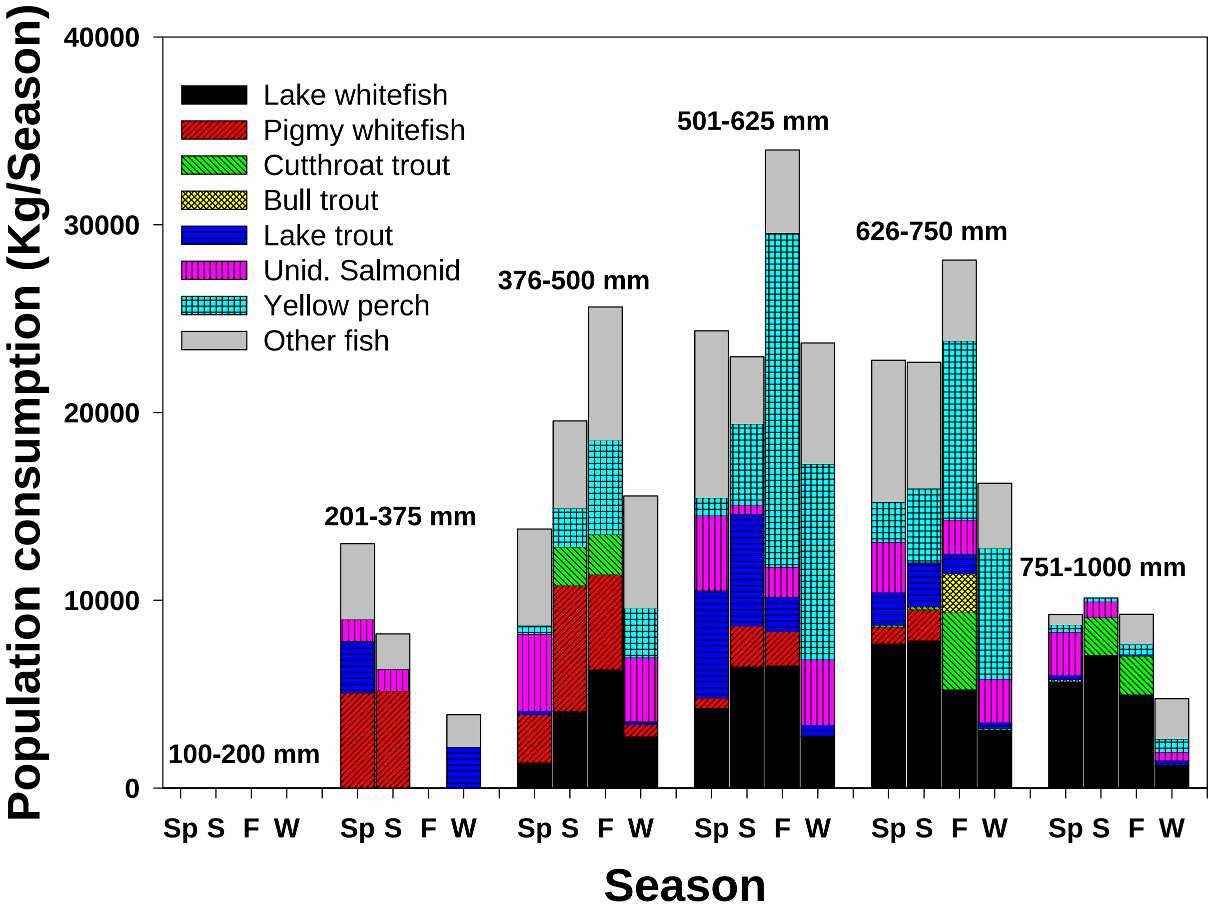

Figure 5. Seasonal, population-level consumption of prey fishes by different size classes of lake trout in Flathead Lake during 1998-2001. Invertebrate prey from the previous figure have been removed to highlight predation patterns on prey fishes.

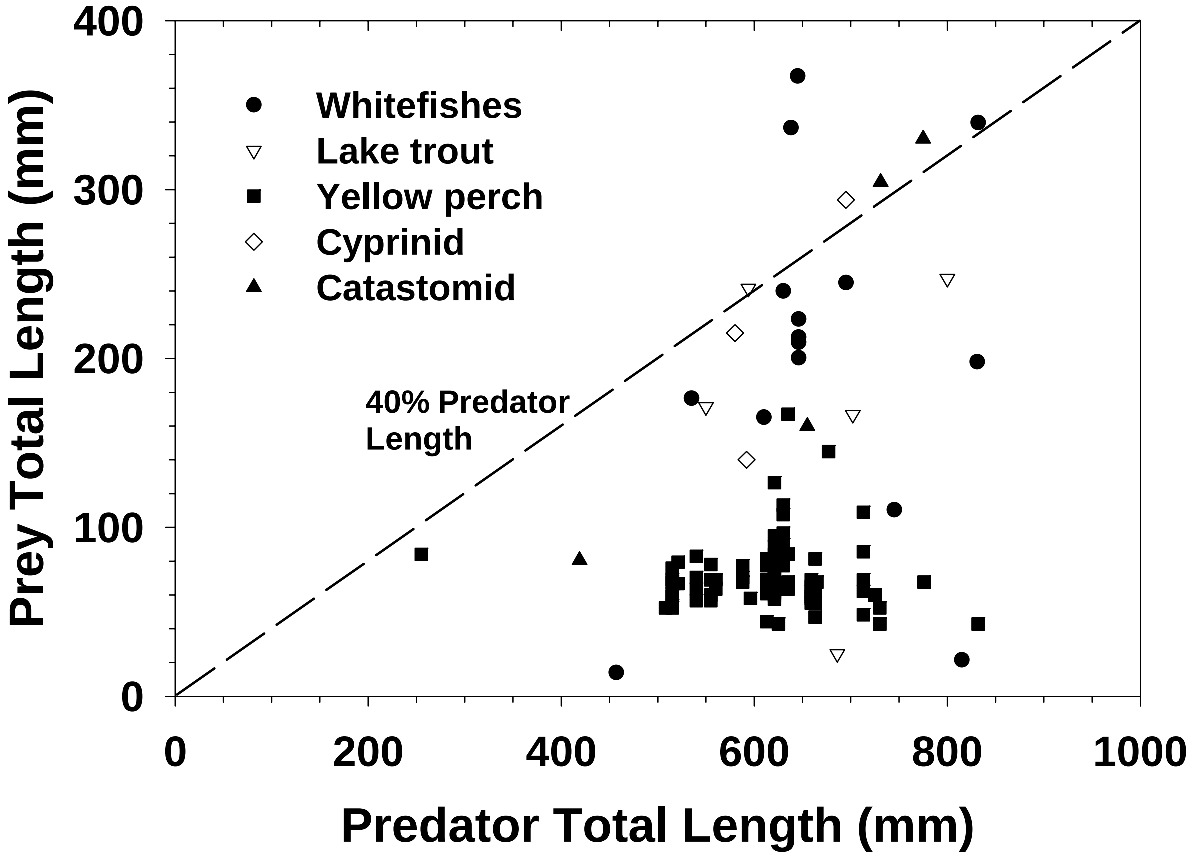

Figure 6. Total length of prey fishes eaten by different sizes of lake trout during 1998-2001.

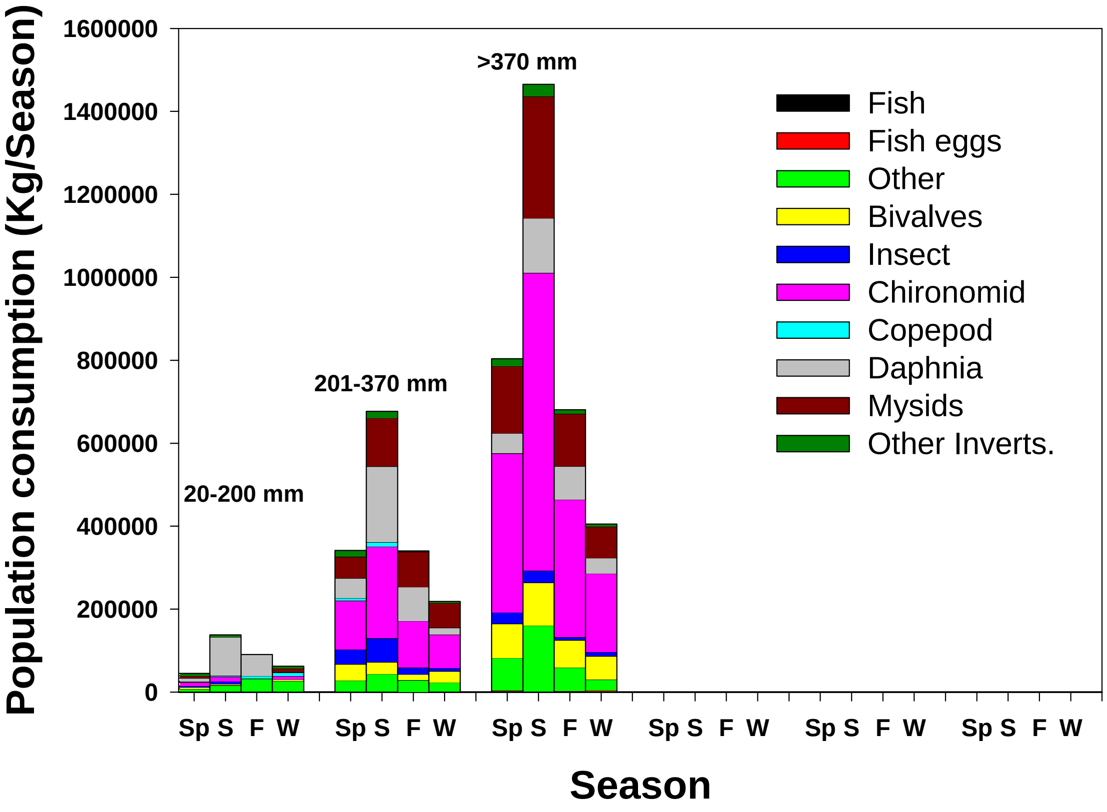

Figure 7. Seasonal, population-level consumption of all major prey categories by different size classes of lake whitefish in Flathead Lake during 1998-2001.

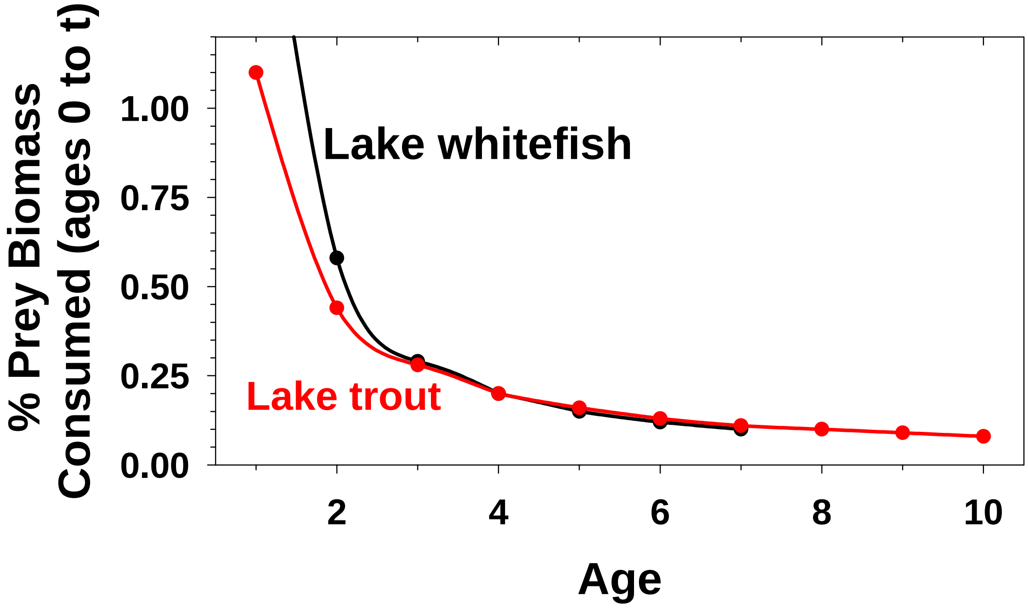

Figure 8. The effects of lake trout predation on lake whitefish and lake trout: the annual predation by lake trout is graphed as a percentage of the standing stock biomass of age t and younger lake whitefish and lake trout. The graph suggests that lake trout predation could consume the entire biomass of ages 0-1 lake trout and lake whitefish, but only 60% of the biomass of age 0-2 lake whitefish and 45% of age 0-2 lake trout. These curves do not account for the annual production generated by the different age classes of prey (see next figure).

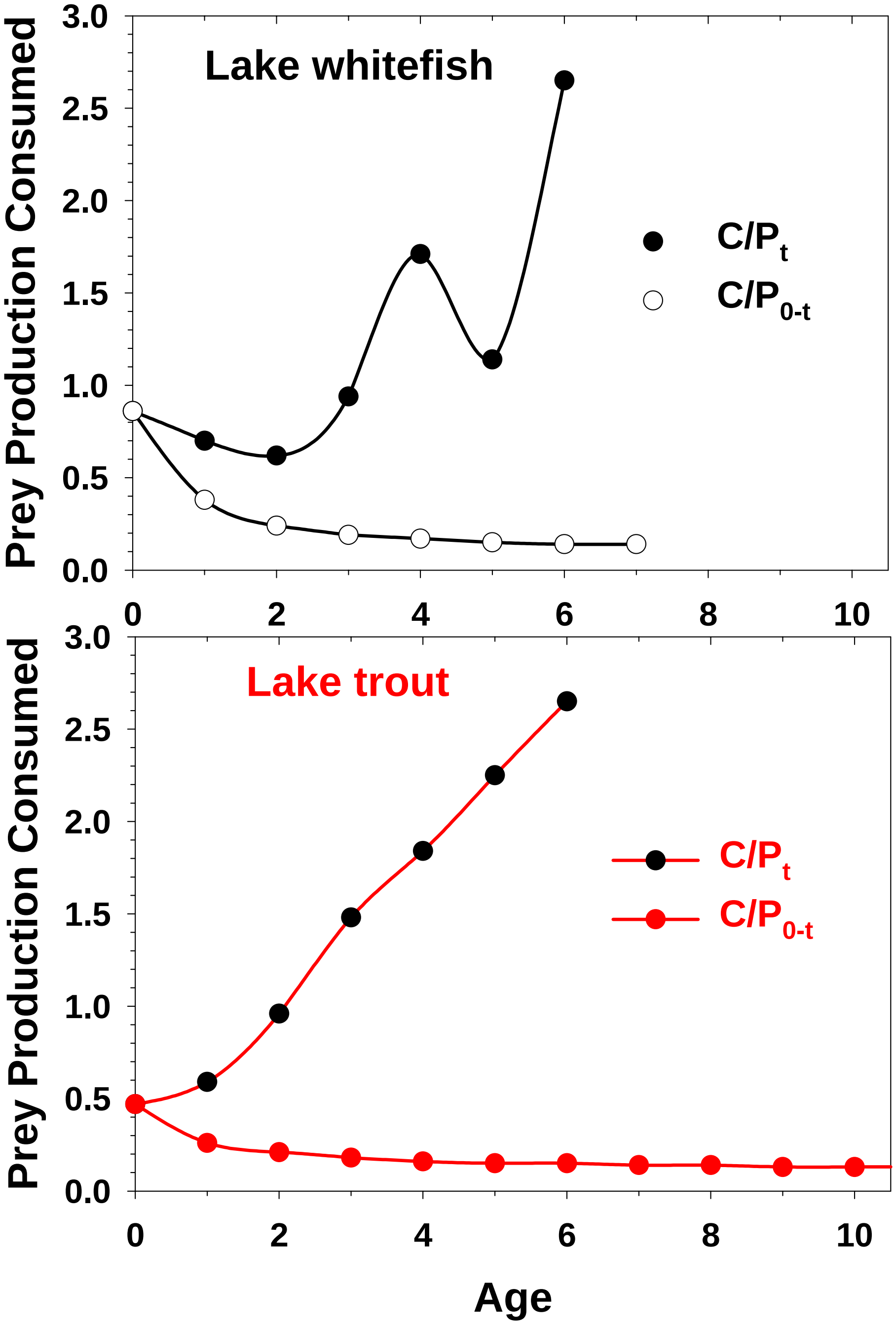

Figure 9. The effects of lake trout predation on lake whitefish (upper panel) and cannibalism (lower panel): annual prey-specific predation by lake trout is graphed both as a percentage of the annual production by each age class of lake whitefish and lake trout (C/P_t) and for age t and younger prey ($C/P_{0\text{-}t}$). The graph suggests that annual production by individual age classes 0-2 lake whitefish and 0-1 lake trout can entirely absorb predation by lake trout, whereas older age classes of prey would need to rely on production by younger conspecifics to absorb some of the predation demand.

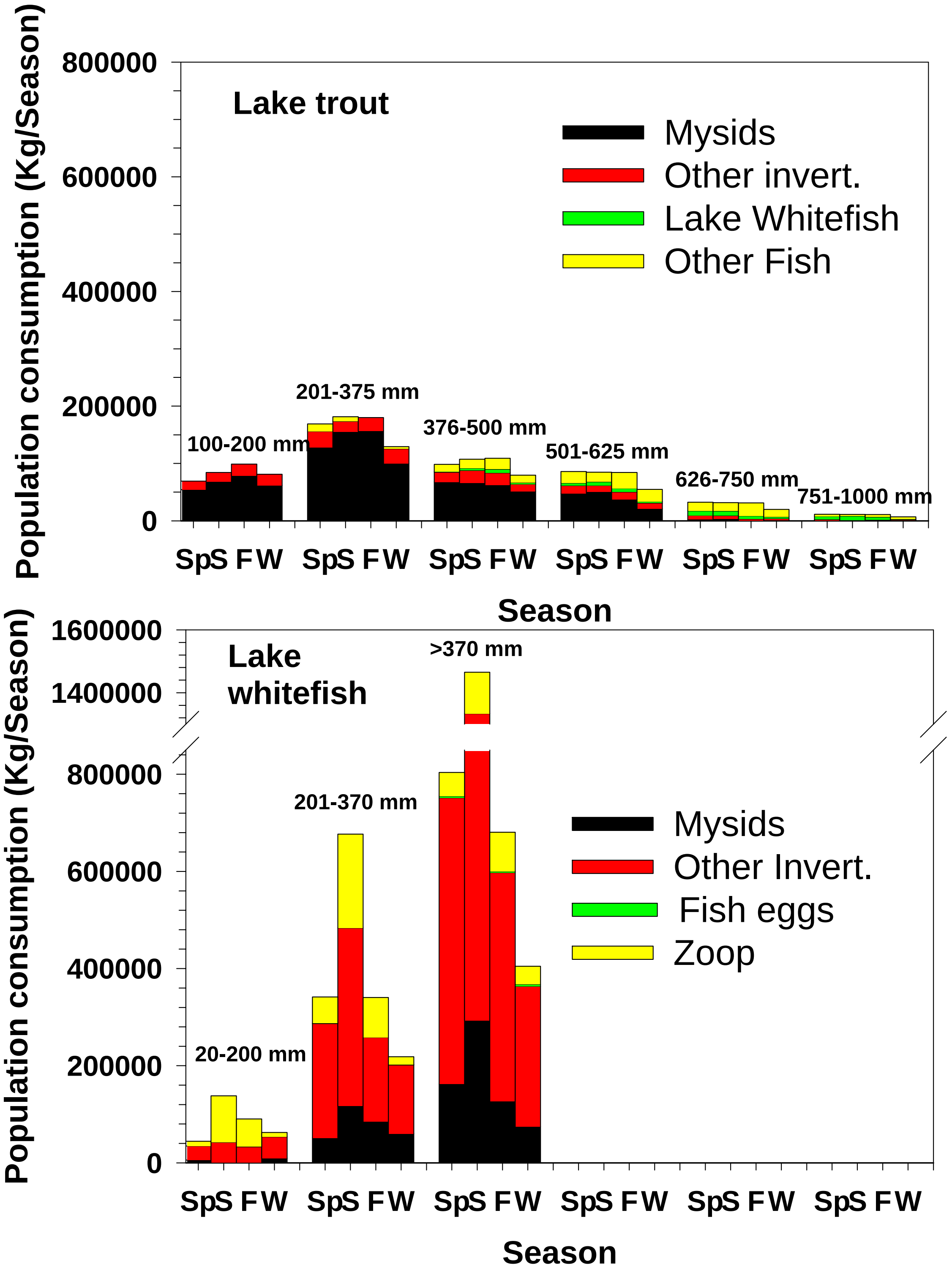

Figure 10. Comparative seasonal, population-level consumption of common prey types by different size classes of lake trout and lake whitefish.

APPENDIX

Flathead Lake hydroacoustic survey (August 11-14, 2003).

August 11, 2003 (2200-0430)-Conducted hydroacoustic survey of Flathead Lake: 4 long zig zag transects from Skidoo Bay in the SE to the point north of Big Arm Bay to Woods Bay (in NE near the Raven Brew Pub) to the point north of Lakeside (is this the right name?) in the NW. A nearly full moon rose in mostly clear skies during the first quarter of the first transect. Lake transparency (Secchi depth =14 m) was remarkably clear for August, and *Daphnia* were relatively abundant (B. Ellis, personal communication) The lake was strongly stratified with surface temperatures of 21^{o}C, epilimnetic temperatures at 19-21^{o}C. A very sharp thermocline began at 9 m with up to a 3^{o} drop/m. A BioSonics 200 kHz splitbeam (6.8^{o} beam angle) transducer was deployed 0.5 m deep and towed at 5.2 knots.

Fish target densities were light to moderate for most transects. A consistent moderate density of targets (mostly -44 to –38 dB) occurred at 60-70 m depths and were suspended 1-10 m above the bottom. When depths became shallower, these targets were located closer to the bottom and then disappeared at bottom depths < 55-60 m.

A second layer of targets was suspended at 10$\pm$2 m and occurred sporadically in the southern 2 transects, but became very consistent in the last transect from Woods Bay to Lakeside.

Fish were sparse in intermediate depths with low densities appearing sporadically in 20-50 m, but were generally centered around 30 m.

Several factors may have affected distributions of pelagic fish during this survey and should be considered when gillnetting to obtain species identification of the acoustic targets. Nocturnal fish distributions were likely influenced by the full moon. A common response by planktivorous fishes is to move deeper or perhaps re-aggregate into schools. A *Hexagenia* hatch was underway, and anglers reported that the lake whitefish were feeding heavily on them. This episodic feeding behavior might aslo have induced a shift in spatial distribution of fishes.

YOY yellow perch, ~30-70 mm, were numerous in nearshore regions in the upper 2 m of the water column and were also reported near the surface more than a km offshore (B. Ellis, pers. comm.). Just offshore of the Blue Bay Marina, before and during early dusk, whole schools of this sized fish were observed jumping in a manner suggesting avoidance response to predatory fish.

Summary of Data Needs and Uncertainties

The frequency of occurrence of bull trout in the diet of piscivorous lake trout can be a useful metric. If 36,500 age 3 bull trout enter the lake, there are also 36,300 lake trout > 625 mm TL available to eat them, so about one for each predator over the year. At a 2-day digestion time and 6 months of potential predation (fall and winter) we would see about 1 bull trout in every 90 gut samples. 4 out of 136 lake trout > 625 mm TL contained bull trout over all seasons. Seasonally, 2 out of 77 lake trout > 625 mm TL in spring and 2 out of 20 lake trout > 625 mm TL in fall contained bull trout. If lake trout generally eat prey fish 50% of their own total length, then a 290-300 mm TL age 3 bull trout can't be eaten by lake trout much smaller than 625 mm anyway. Fraley and Shepard (1989) reported that 49% of the bull trout migrants were age 2 and 32% were age 3, so the age 2 bull trout (about 234 mm TL) would certainly be susceptible to more of the smaller predators (e.g.,153,500 piscivorous lake trout >468 mm TL in the population and large enough to eat a 234 mm TL age 2 bull trout).

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Food Habits of Flathead Lake Fishes

Other fishes-- For some fishes, diet data were pooled across size classes or seasons when sample sizes were inadequate to permit seasonal or size-specific stratification (**Table A1**). Bull trout (N = 13) were highly piscivorous and consumed lake whitefish, unidentified salmonine fishes, yellow perch, suckers, and cyprinids. Rainbow trout (N = 5 during winter-spring) ate sculpins, unidentified fish, and aquatic insects; westslope cutthroat trout (N = 9 during spring) and hybrid rainbow x cutthroat trout (N = 3 during spring) ate aquatic insects and other invertebrates. Northern pikeminnow stomachs (N = 29) contained primarily unidentified salmonids, unidentified fish, and other invertebrates. Yellow perch (N = 11 during spring) ate predominantly smaller yellow perch (54%) and benthic invertebrates (45.5%), but very few mysids (0.5%). Longnose and largescale suckers, mountain and pygmy whitefish, and peamouth fed exclusively on invertebrates.