$\frac{1}{\sqrt{2}}$ Ellis et al. 10.1073/pnas.1013006108

SI Materials and Methods

Monthly or more frequent measurements of limnological variables in Flathead Lake and the major tributaries and precipitation chemistry were made from 1977 to 2004 by the Flathead Lake Biological Station (FLBS) (1, 2; see ref. 2 for site locations). This very extensive data set is known as FlatDat and is archived electronically in spatially explicit format at FLBS. All raw data, standard curves, and quality control information have been entered into FlatDat for all chemical analyses ever performed at the FLBS since 1977. Analytical precision was quantified by replicating chemical analysis on every 10th sample. Analytical accuracy was quantified by analyzing quality control samples (unknown concentrations) from the Environmental Protection Agency (before 1998) or from Inorganic Ventures IV Laboratory (National Institute of Standards and Technology traceable; since 1998) during every analysis. Limits of quantitation and detection were calculated by analyzing three or more replicates of the lowest standard and multiplying the SD of the results by 10 and 3, respectively. All sample data, laboratory standard curves, and quality control information were electronically archived by the Biological Station Data Manager in the Biological Station's data storage and retrieval system (FlatDat).

Nitrogen (N) and phosphorus (P) concentrations (total N, total P, soluble reactive P, soluble P, nitrate + nitrite, ammonium) were determined using a Technicon autoanalyzer (3). Chlorophyll a concentrations were determined by acetone extraction and colorimetic analysis (4).

Nutrient Loading. Loading of N and P to Flathead Lake was determined from measurements of N and P forms from time-series collection on the major tributaries to the lake and the airshed. Grab samples were obtained from all tributary sites at midriver and middepth; a Van Dorn water sampler was deployed from bridges at large river sites. The major tributaries were sampled in relation to the hydrograph, with more intensive sampling during runoff events. Stream discharge data were obtained from the US Geological Survey (USGS) ([www.usgs.gov/;](www.usgs.gov/) accessed 2006), except on Ashley and Stoner Creeks, where flow was monitored by the Biological Station using USGS procedures (5, 6). Daily precipitation volume was determined from the National Weather Service Monitoring Station located at the Biological Station [\(www.noaa.gov/;](www.noaa.gov/) accessed 2005). A modification of the bulk precipitation collector described by Lewis and Grant (7) was used before 1984 and from 1986 to present. A composite sample was obtained from an Aerochem-Metrics atmospheric sampler (8) from 1984 to 1985 by combining wet and dry bucket contents; its use was discontinued owing to frequent contamination by bird droppings. Daily loading estimates were made by interpolating between known concentrations of nutrients in river and bulk precipitation. Measured daily river-flow and precipitation values were multiplied by N and P interpolations (concentrations) to estimate load.

Fishes. Data on species composition and abundance of fishes were obtained annually from standardized gill net sets since 1981 and were examined in light of the historical record of native and nonnative fishes. Netting occurred in spring (late April/early May) before spring runoff, when the lake temperatures were isothermal. In five different areas of the lake, three sets of floating and sinking multistrand nylon gill nets were deployed. Nets were 38.1 m long by 1.8 m deep and consisted of five panels of bar mesh sizes 19, 25, 32, 38, and 51 mm. Each set consisted of two ganged

nets, one sinking net tied end to end to another sinking net, and likewise for floating nets. Nets were set perpendicular to the shoreline. Floaters were set with one end close to shore in roughly 2 m of water, with the net stretched over deeper water. Sinking nets were set at depths greater than 10 m. Nets were deployed in late afternoon and retrieved in midmorning hours. To calculate catch-per-unit-effort (CPUE), number of each species captured in each sinking or floating set was divided by 2 to report catch per single standard net type. Percentage composition of catch by species was determined separately by net type. Total length, weight, age, sexual maturity, and food habit data were obtained from captured fish.

Bull trout abundance was determined annually since 1981 from standardized redd counts of adfluvial spawners in tributaries used by Flathead Lake fish. From the basin-wide survey, extensive index areas were identified for annual surveys. Preliminary surveys were conducted to determine appropriate timing for final counts. Surveys began after numerous redds, few adult fish and little evidence of active spawning were observed. Experienced field crews conducted the surveys by walking the stream channels of each index area and recording redds.

Earlier data pertaining to the fishes of Flathead Lake were found in the archives of the FLBS, the K. Ross Toole Archives at the University of Montana Mansfield Library, and along with various published papers produced before 1930 (9–12) provided reasonable documentation of the pristine limnology and native fisheries of the lake. Gill net sets made by M. Pace and M. Elrod in 1915–1916 were recorded on forms found in the archives, as were similar sets made by Royal Brunson in the 1950s. Elrod deployed 13 sinking gill nets around the lake from June 24, 1916 to August 28, 1916, whereas Pace set a similar series of gill nets during the summers of 1915 and 1916. Both Elrod and Pace generally set their nets near shore, the deepest depth reached being 27 m. These historical data have never been carefully studied and related to contemporary data until now. Mean CPUE was determined for both sinking and floating gill net sets.

Phytoplankton, Zooplankton, and Mysis. Monthly or more frequent phytoplankton samples were obtained at the midlake deep site from a 0- to 30-m tubular composite integrating sampler, preserved (1% Lugol's iodine), and enumerated using Utermohl chambers. Records of zooplankton species presence by period were as follows: 1891 (13), 1899–1903 (14), 1912–1919 (M. Elrod, FLBS archives), 1928–1930 (15, 16), 1956–1966 (17), 1965–1973 (D. Hanzel, FLBS archives), 1972–1973 (18), and 1985–2004 (FlatDat). Zooplankton data for 1972–73 as well as a retrospective analysis of prior data were from Potter (18); the sampling methods and sampling site used in 1972–1973 were similar to the post-Mysis monitoring of 1985–2004. Vertical net tows from 1972 to 1973 were standardized to the continuous record initiated in 1985; Potter used discrete 10-m tows, whereas data from 1985 on were tows made from 50 m to the surface. From 1985 to 2004, duplicate or triplicate 50 m to surface vertical hauls of zooplankton were made 15 times per year at the midlake deep site (see ref. 2) with a 29-cm-diameter, 64-μm-mesh Wisconsin style net and preserved $(4\%$ CaCO₃ neutralized formalin). A Hensen-Stempel pipette was used to transfer duplicate 1-mL aliquots from each sample to Sedgewick-Rafter cells for enumeration at $40\times$ for most cladocerans and larger copepods and $100\times$ for other taxon using a compound microscope. Discrete 10-m tows from 50 m to the surface and single tows from 50 to 0 m were collected on the same days throughout a year to determine net

efficiency. Zooplankton abundance by group from single tows (50–0 m) were corrected for reduced net efficiency due to backwelling (i.e., zooplankton abundance in single tows averaged 65–70% of summed discrete tows). Mysid numbers were standardized to sampling on moonless nights in September. Vertical hauls were made from near bottom to the surface at approximately 40 sites with a 1-m-diameter, 500-μm-mesh closing net. More detailed temporal sampling of Mysis revealed declining abundance through the fall; therefore, densities from three October sampling events were corrected for mortality.

Statistical Analyses. Deseasonalizing for statistical analysis was accomplished by fitting a cubic smoothing spline to an overlay of the limnological data for all of the years. The raw daily estimates were grouped into day-of-the-year pools, in the overlay for the spline, and wrapped around each end of the year for 365 d to encourage continuity at the year ends. The smoothing factor was constrained to the range displaying at least one mode but no more than two and then refined in an iterative search to minimize the cross-validation jackknife residuals when entire years were jackknifed out at a time. Seasonality in each of the variables was removed by subtracting the spline.

Because the time intervals for primary productivity (PP) measurement were irregular, and there was a tendency to make measurements on less cloudy days later in the record, PP values were light-corrected by a least squares regression. Photosynthetically active radiation (PAR) was estimated as 0.45 times the calculated solar radiation from the MT-CLIM model [\(http://www.](http://www.ntsg.umt.edu/bioclimatology/mtclim/) [ntsg.umt.edu/bioclimatology/mtclim/\)](http://www.ntsg.umt.edu/bioclimatology/mtclim/) using observed daily precipitation and maximum and minimum air temperatures at the Kalispell airport. These estimates of PAR showed a correlation of 0.92 (regression slope 0.99) with PAR measured by radiometer at Yellow Bay on those days when direct measurements were available. The PAR values were deseasonalized by spline smoothing in the same fashion as the PP. For the light-correction of the PP values, a least squares regression was done of deseasonalized PP on deseasonalized PAR ($R^2 = 0.073$; intercept = -8.54 , slope = 2.90), with PAR in units of Einsteins m⁻²^{d-1}. Residuals from this regression constituted the light-corrected deseasonalized PP.

Fitting a least squares linear regression to the deseasonalized, light-corrected, daily PP for the full span of years showed a modest but significant increasing trend [slope = 2.3 (mg C m^{-2}] $(d^{-1}) y^{-1}$; $R^2 = 0.04$; $P = 0.0008$; $n = 287$]. Owing in part to the large sample sizes several of the other limpological variables large sample sizes, several of the other limnological variables showed small long-term trends, which nevertheless were significant and therefore "correlated" over the same time span. In particular there was a slight but significant increasing trend in deseasonalized nitrate nitrogen loading (slope = 0.01 t nitrogen $d^{-1}y^{-1}$; $R^2 = 0.004$; $P = 3 \times 10^{-9}$; $n = 8,874$), and there was a substantial increasing trend in deseasonalized hypolimnetic a substantial increasing trend in deseasonalized hypolimnetic oxygen deficit (slope = −0.22% saturation y⁻¹; $R^2 = 0.09$; $P = 1 \times 10^{-6}$; $n = 253$) pointing possibly toward a trend in eutro- 1×10^{-6} ; $n = 253$), pointing possibly toward a trend in eutro-
phication driven by anthropogenic N loading. Although N limiphication driven by anthropogenic N loading. Although N limitation was observed in fall bioassays (when N declined to below detection limits in the epilimnion), colimitation by N and P dominated (19), and deseasonalized soluble reactive phosphorus (SRP) loading actually showed a slight but significant declining linear trend over the long-term (slope = -0.002 t SRP d⁻¹ y⁻¹ , $R^2 = 0.006; P < 0.0001, n = 7,826$, ruling out the hypothesis that increasing PP was due predominantly to cultural eutrophication.

Visual inspection of the graph of deseasonalized, lightcorrected PP against year (Fig. 5, main text) gives an impression that the trajectory shifted around 1987, more or less coincident with the *Mysis* explosion. Diagnosing the pattern by eye is hampered, however, by the considerable scatter and by the shift to more frequent measurements, also around 1987. To explore whether CTI might have been involved in the change in PP,

achieve much resolution of the slope magnitude [mean 1.42 (mg $\text{C m}^{-2} \text{d}^{-1}$) y⁻¹, SD 4.12]. Likewise, Bayesian linear regression just for the 1987–2004 segment ($n = 221$) was ambiguous regarding the sign of the trend (probability of nonpositive slope 0.602) and showed poor resolution of the slope $[\text{mean} -0.254 \ (\text{mg C m}^{-2} d^{-1})$ y^{-1} , SD 1.00]. Notwithstanding the large uncertainties about trend slopes for these two segments, their intersections with the enforced break point at 1987 were distinct: posterior probability that the postbreak line is higher than the prebreak line at this date is 98%, and the probability is 90% that the difference is greater than 22 mg C m^{-2} d⁻¹, and the probability is 80% that the difference is greater than 33 mg C m⁻² d⁻¹ (i.e., a step change

> greater than 12% of the long-term 1977–2004 mean). To resolve when this break occurred, the pattern of change over time in PP was further examined with a Bayesian change point model. The model was for two uncoupled linear regression lines, where the location of the change point (the vertical step from one line to the next), the two slopes, the two intercepts, and the common normal error SD (the parameter underlying the residual SD) were all unknown parameters (six in all). A joint set of values of the first five of these parameters define the pattern [as in the black line in Fig. 5 (main text) where the first slope and intercept define the line to the left of the change point (step), the second slope and intercept define the line to the right of the change point, and the two lines together along with the location of the change point define the step itself].

> separate regressions were tried, before and after Mysis. These failed to resolve significant slopes for PP in the two (before and after) segments but did indicate significant differences in the two means, prompting a closer Bayesian look at the time series, specifically investigating whether, and when, the time series might have shifted, Bayesian linear regression of deseasonalized light-corrected PP against date, for the full time series, using conventional vague priors for all three parameters (uniform for slope and intercept, and proportional to the reciprocal for error variance) showed almost no probability ($P = 0.0004$) of nonpositive slope; and resolved that slope with a posterior marginal

> Bayesian linear regression (with the same priors) just for the 1977–1986 segment ($n = 66$) was ambiguous regarding the sign of the trend (probability of nonpositive slope was 0.350) and did not

mean at 2.27 (mg C m⁻² d⁻¹) y⁻¹ and SD of 0.684.

The likelihood function, therefore, was a Gaussian distribution on the departures of the data points from this stepped line. The prior on the location (date) of the change point was uniform from 1 y in from the first and last data points (so any resulting left or right segment must span at least 1 y worth of data). The independent priors on the two intercepts were uniform and broad enough that their termini were not influential. The prior on the error SD was the conventional vague distribution whereby the probability is proportional to the reciprocal of the SD squared. The independent priors on the two slopes were uniform on the angle of the slope; this prior is not scale independent, but the usual alternative of an improper uniform prior on the slope regression coefficient favors steep slope angles, which were in fact picked up in the posterior distribution, but which, in this application, is not reasonable. With a uniform prior on the angle, and expressing time in years and PP in mg C m⁻² d⁻¹, slopes between + and -12.75 (mg C m⁻² d⁻¹) y⁻¹ made up approximately 90% of the prior probability, with long tails giving an SD of 573. This is generously broad in the context of the observed long-term least squares regression slope of 2.3 (mg C m⁻² d⁻¹) y⁻¹.

The numerical integration for the joint inference on the six parameters was carried out by MCMC (Metropolis-within-Gibbs, Gaussian random walk proposal). Convergence was unproblematic. For convenience in graphing, and interpretation, the joint posterior sample was transformed into alternative parameterizations to obtain posterior marginals for the height of the

step and the PP value at the bottom of the step, and the slopes in units of (mg C m⁻² d⁻¹) y⁻¹.

The posterior marginals for the two quantities of greatest interest (date of the change point and height of the step) are graphed in Fig. 5 in the main text. [Fig. S3](http://www.pnas.org/lookup/suppl/doi:10.1073/pnas.1013006108/-/DCSupplemental/pnas.201013006SI.pdf?targetid=nameddest=SF3) shows the posterior marginals of the remaining four parameters, in familiar units. The posterior marginals for the 2 slopes were broad, including 0 (consistent with the result from least squares analysis that the pre- and post-Mysis trends were not significant), but they did not simply recapitulate their uniform priors on the angle, and the steepest slope angles had much less posterior probability than in the priors (posterior marginal SDs on the before- and afterbreak slopes were 2.67 and 1.74, respectively).

SI Discussion

Fishes of Flathead Lake Before 1920. Early fish surveys of Flathead Lake were conducted by Morton Elrod and Maurice Pace in the summers of 1915 and 1916. These sinking gill nets deployed around the lake indicated that nine of the 10 native fish were present in the littoral zone of the lake; catches were numerically dominated by peamouth, followed by northern pike minnow, with a substantial number of bull trout, mountain whitefish, and suckers. The low catch of cutthroat likely reflects several factors, including the spawning migration of these fish into the river during the summer and the low catch of cutthroat in sinking nets relative to floating nets (as revealed by later surveys). However, cutthroat trout were very common in the lake and were avidly angled by locals who called them "flat trout" owing to the robust shape (9, 10).

An early account of the lake's native fishery (10) stated, "Mountain (cutthroat) trout are abundant, grow to a good size, and are readily caught: salmon trout or bull trout are also common and are caught at certain seasons in considerable numbers by trolling. The Columbia River (largescale) sucker also occurs in the lake, while the 2 large minnows, the Columbia chub (peamouth) and the squawfish (northern pikeminnow) are very abundant." Evermann also noted, "Whitefish (Rocky Mountain whitefish) are also found in the lake and, judging from the number of young that we saw, would seem to be common." Bull trout were commonly caught by local Indians.

Creel Surveys. The objectives of the 1962 creel survey on Flathead Lake by the US Bureau of Sport Fisheries and Wildlife were to determine utilization and harvest, activities of fishermen, and characteristics of the fish resources. There was no attempt to quantify species preference (i.e., target species). Angler pressure (angler days) was determined from on-site angler interviews and postal questionnaires.

The 1981 survey by Montana Department of Fish, Wildlife, and Parks was primarily designed to census boat fishermen during the spring, summer, and fall. Cars at fishing access points were tallied to generate an angler pressure estimate. Mail surveys and on-site interviews at access points and by roving boats were used to determine harvest. Target species information was collected for 80% of the surveyed period.

The Confederated Salish and Kootenai Tribes conducted the 1992 creel survey primarily to quantify Flathead Lake fishery status before Hungry Horse Dam mitigation efforts. Mail surveys, aerial boat counts, and on-site interviews at access sites and via a roving boat were used to generate angler pressure and fish harvest. Target species information was collected.

The most relevant and insightful information from the creel surveys was the comparison of harvest species composition before and after Mysis. Before Mysis (1981 survey) harvest was dominated by kokanee and yellow perch, which accounted for 77% and 17% of the angler harvest, respectively. After Mysis (1992 survey) lake trout, yellow perch, and lake whitefish represented 55%, 27%, and 17% of the harvest, respectively, whereas kokanee represented none of the harvest.

Acoustic Density Estimates of Kokanee in Flathead Lake. Kokanee population density data were collected using a modified hydroacoustic unit designed at the Applied Physics Laboratory at the University of Washington. Acoustic information was collected annually in early September from eight to nine lake transects in 1979–1982 and 11 transects in 1983, totaling 72 and 88 km. During September, salmon move into the midlake areas before their movements to spawning areas, making pelagic measures more reliable. Acoustic signals were recorded on magnetic tape while traveling 3.1 m s^{-1} . Fish numbers were enumerated using a direct count method by playing back acoustic signals viewed on a delayed-sweep oscilloscope. Small fish (20–30 cm) and large fish (30–41 cm) could be separated by signal strength differences. Counting thresholds for these sizes were established and used during target enumeration. A midwater trawl $(3.05 \times 3.05 \text{ m})$, 2.5% open area) and a purse seine $(18.3 \times 171 \text{ m}, 31.8\%$ open area) were used to verify both species and sizes of acoustic fish targets. Densities were calculated from number of fish targets within 3.6-m intervals from depths of 7–44 m. Densities for an entire transect were weighted averages of the sample densities, and in turn the average density of fish for the entire lake was a weighted average of the transect data. The highest lake salmon density estimates occurred in 1982, with 56.7 fish per hectare, and the lowest in 1981, with 38.8 fish per hectare.

Fish Diet Analysis for Bioenergetic Modeling. Fish samples were collected from both annual spring monitoring and seasonal gill net sampling surveys conducted from May 1998 through August 2001 by Montana Department of Fish, Wildlife, and Parks in the northern region and the Confederated Salish and Kootenai Tribe southern regions of Flathead Lake. Stomach contents were examined using a dissecting microscope and separated into fish and invertebrate components. Prey fishes were generally identified to species (often on the basis of 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), seven to trout or char; 30 of the 78 unidentifiable samples were available for genetic examination, and 26 of these 30 were identified. Standard, total, or vertebral lengths of prey fish were measured when possible (according to the condition of the partially digested fish). Fish eggs were counted and weighed. Invertebrate prey were 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 nonempty 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. Scattergrams of predator length vs. the diet proportions of major prey categories were examined 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 nonempty stomach were averaged for each season for each size class of consumer.

To genetically identify unknown prey items, representatives of the most common fish species inhabiting Flathead Lake were collected to create a reference baseline. In most cases several

individuals from each species were assayed to characterize the intraspecific genetic variation. DNA was isolated for both baseline and prey samples using DNeasy Tissue Kit (Qiagen) according to the manufacturer's protocol for mouse tails. Because the DNA extracted from the prey tissues are likely degraded, a smaller elution volume (100 μ L \times two elutions) was used to concentrate the yield. Two mitochondrial DNA markers were used to identify species: (i) a 368-bp portion of NADH3/ COIII (20) (hereafter ND3), and/or (ii) a 270-bp section of the 16S ribosomal gene (21). The ND3 locus was designed for Pacific salmon (Oncorhynchus) and does not amplify nonsalmonid and whitefish species. However, it is more polymorphic among members of *Oncorhynchus* and *Salvelinus* and thus better discriminates these species (22).

ND3 and 16S were amplified separately in 50-μL reactions, each with the same reagent conditions of $1 \times$ Taq buffer (Promega), 2.5 mM $MgCl₂$, 0.2 mM of each dNTP (Promega), 0.1 μ M of each primer, 1[×] BSA (NE BioLabs), 1.25 U Taq polymerase (Promega), and \approx 1–30 ng DNA template. Both markers used the following thermal profile: an initial denature step of 94 °C for 3 min, 35 amplification cycles of 94 °C 40 s, 55 °C for 40 s, 72 °C for 40 s, 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 PCR96 Cleanup Plates (Millipore) according to the manufacturer's protocol. A 5-μL PCR sequencing reaction was performed on the cleaned product using 1 μL BigDye v.3.1 (Applied Biosystems), 3.2 pmol primer, 0.5× sequencing buffer (Applied Biosystems), and ≈ 10 ng PCR template, for both forward and reverse primers. The sequencing PCR consisted of 30 cycles of 96 °C for 30 s, 50 °C for 5 s, and 60 °C for 4 min. The sequencing PCR products were purified using CleanSEQ Dye Terminator Removal System (Agencourt Bioscience). Sequence data were collected on an ABI 3100 Sequencer following standard procedures. Finally, sequences were aligned and analyzed in Sequencher 4.5 (Gene Codes).

Bioenergetics Modeling of Lake Trout Predation on Kokanee. To estimate how lake trout predation might have contributed to the crash of adult kokanee in 1986–1987, we reconstructed the abundance of lake trout and their size-specific diet, used bioenergetics model simulations to estimate lake trout predation on kokanee, then compared the biomass of kokanee eaten with the expected age-specific annual production rates of kokanee, based on comparable initial fry abundances, growth, and survival rates observed just before the kokanee crash. We first estimated the seasonal and annual predation losses that would have resulted from a standardized population of 1,000 age 5 y and older lake trout (plus additional predation by age 2–4 y lake trout), then expanded this size-structured predation estimate by multiples of 1,000 age 5–30 y predators, whereby the multiplication factors were generated from the reconstruction scenarios of the lake trout population and for the contemporary abundance of lake trout.

Lake Trout Abundance, Size Structure, and Growth. Population trends for lake trout were reconstructed using a time series of CPUE to back-calculate abundance during 1986–1987 from contemporary abundance estimates. The estimated abundance of lake trout during 1992–2005 was 235,000 (95% confidence interval, 152,000–467,000) on the basis of Schnabel estimates for age 5 y and older lake trout of total length $(TL) > 400$ mm. Because abundance estimates were derived for age 5 y and older lake trout, we used ages 5–30 y as the reference for reconstructing abundance and predation scenarios, then extrapolated the abundance of age 2–4 y lake trout, which were also predatory but fed on kokanee at a lower rate.

Lake trout CPUE increased from an average 0.10 fish net⁻¹ in 1983 to a relatively stable (mean \pm 2 SE) 1.73 \pm 0.26 fish net⁻¹ during 1992–2005. Comparable gill net sampling was not conducted during the intervening period, so we needed to reconstruct the trend in lake trout abundance between 1983 and 1992. To reconstruct lake trout abundance (N) , we assumed that (i) changes in CPUE were directly proportional to changes in abundance; and (ii) exponential population growth was constant over the 9 y between 1983 and 1992. Note that population growth could have increased more rapidly and leveled off earlier than 1992, so this reconstruction scenario represented a minimum rate of population increase by lake trout.

Assuming constant exponential population growth between 1983 and 1992, we calculated an instantaneous annual growth rate of $r = LN(1.73/0.10)/9 = 0.3167$. We reconstructed the abun-

- dance of lake trout during the kokanee crash (1986–1987) by:
 $N_{1986} = 235,000 \cdot e^{(-0.3167 \cdot 6)} = 35,142$ age 5–30 y lake trout in

1986 1986
	- N_{1987} = 235,000·e^(-0.3167·5) = 48,235 age 5–30 y lake trout in 1987

 $N_{1986-1987} = 235,000 \cdot e^{(-0.3167 \cdot 5.5)} = 41,171 \text{ age } 5-30 \text{ y lake}$ trout, geometric mean for 1986–1987

For comparison, a faster population increase (i.e., $r = 0.5700$) over 5 y) from 1983 to the contemporary abundance would result

in a population of lake trout during 1986–1987 of:
 $N_{1986-1987} = 235,000 \cdot e^{(-0.3167 \cdot 5.5)} = 56,523$ age 5–30 y lake

trout geometric mean for 1986–1987 trout, geometric mean for 1986–1987

According to age and size structure of the population during the 1990s through 2005, the annual survival rate for age 2 y and older lake trout was estimated at 75%. Age-specific catch rates from gill nets were adjusted for size-selectivity (23). After this adjustment, age 6 y 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 y ($r^2 = 0.98$; $P < 0.00001$); the slope = -0.288 represented
the instantaneous annual mortality of $Z = 0.288$; therefore the instantaneous annual mortality of $Z = 0.288$; therefore, $S = e^{-0.288} = 75\%$ annual survival. We assumed that age 2–5 y lake trout also experienced 75% annual survival to reconstruct the age and size structure of the predator population. To generate a standardized size-structured population of 1,000 age 5–30 y lake trout with 75% annual survival rate, we iteratively fit the abundance of age 5 y lake trout $N_5 = 250$ such that the total abundance of age 5–30 y $N_{5-30} = 1,000$ [\(Table S4](http://www.pnas.org/lookup/suppl/doi:10.1073/pnas.1013006108/-/DCSupplemental/pnas.201013006SI.pdf?targetid=nameddest=ST4)). The agespecific abundances of lake trout are presented for the reconstructed slow population increase (\approx 40,000 age 5–30 lake trout) and rapid increase (56,000) scenarios, and the contemporary abundance of 235,000 age 5–30 y lake trout [\(Table S4\)](http://www.pnas.org/lookup/suppl/doi:10.1073/pnas.1013006108/-/DCSupplemental/pnas.201013006SI.pdf?targetid=nameddest=ST4). Note that if survival was lower for the younger predators, then a higher abundance of younger lake trout would have been required to achieve the abundance estimates reported.

Bioenergetics Model Simulations. A bioenergetics model for lake trout (24) was used to estimate the consumption rate required to satisfy observed annual growth increments, and we simulated daily consumption of each prey category from May 1 through April 30 (May $1 = day 1$ of the simulation) during a year leading to the kokanee crash in the mid-1980s. Annual growth increments, diet, prey energy density, and thermal experience for lake trout were used as inputs to the bioenergetics model to estimate the seasonal and annual consumption rates by lake trout on kokanee and other key prey during the kokanee crash.

For the bioenergetics model simulations, we fit age-specific consumption rates to the estimated annual growth of age 2–21 y lake trout using annual growth increments ([Table S5](http://www.pnas.org/lookup/suppl/doi:10.1073/pnas.1013006108/-/DCSupplemental/pnas.201013006SI.pdf?targetid=nameddest=ST5)) according to length-at-age data from otoliths (25) and a length–weight regression for lake trout in Flathead Lake $(r^2 = 0.978; P < 0.001;$
 $n = 426$ $n = 426$).

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

Because low sample sizes precluded reliable growth estimates for older fish, the growth increment for age 21 y lake trout was also applied to ages 22–30 y in the bioenergetic simulations. 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 y and 8% for age 8 y and older (averaged over both sexes for lake trout) according to size and age at maturity data for lake trout in Lake Tahoe after mysids became established. Spawning losses were subtracted from the body weight of mature lake trout on simulation day 198 (October 15) of the bioenergetic simulations for lake trout >375 mm (ages 5 y and older).

Lake Trout Diet and Prey Energy Density. Kokanee represented 38% of the annual diet composition by weight for lake trout TL >400 mm during 1981–1982, but no data were reported for smaller lake trout. We examined size-specific diet composition data from the 1990s to provide a surrogate estimate for the contributions of kokanee and other fish to the diet of smaller lake trout. During the attempted kokanee reintroduction in the 1990s, yearling kokanee (TL >100 mm) represented 34–69% of the diet by weight for lake trout 200–375 mm TL during May and June but were absent in diet samples the remainder of the year. Lake trout were capable of consuming prey fishes up to 40–50% of their own body length, so age 0–1 y kokanee (28–240 mm TL; ref. 26) could progressively outgrow the gape limitation of increasingly larger lake trout in the age 2–4 y size class (200– 375 mm TL) through the year (27). Prey energy density ($J g^{-1}$ wet body weight) inputs in the bioenergetic simulations of lake trout predation were as follows: whitefish species day $1 = 6,280$, day 91 = 10,695, day 181 = 8,456, day 365 = 6,280; kokanee day $1 = 5,242$, remaining days = 5,370; yellow perch all days = 4,186; unidentified fish all days $=$ 4,186; invertebrates all days $=$ 3,474. May 1 represented day 1 of model simulations.

Thermal Experience of Lake Trout. A time- and depth-weighted average thermal experience was estimated for lake trout by combining monthly vertical temperature profiles and proportions of the lake trout catch from standardized, depth-stratified gill net catches. Thermal experience of lake trout used in bioenergetic model simulations ranged from 2.8 °C on day 307 to 6.7 °C on day 215; May 1 was day 1 of the simulation.

Kokanee Abundance, Growth, and Production. We compared annual production rates of kokanee during the pre-mysid period with the seasonal and annual predation rates by lake trout from bioenergetics model simulations during the kokanee crash to discern whether predation was a significant factor contributing to the kokanee crash. Beattie and Clancey (26) provided data on kokanee abundance, immigrant fry abundance (13–16 million per year), adult run size (sport harvest plus spawning escapement: 204,800–474,400 during 1981–1985; 99,200 during 1986; and 7,800 during 1987), fry-to-

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adult survival (2.9–3.0% during 1981 and 1985; 0.05–0.70% during 1986–1987), and size-at-age during 1981–1987. We computed seasonal and annual productivity for each age class of kokanee (ages $1-3$ y) as the sum of the seasonal production rates P_t , using:

$$
P_t = B t \ G_t, \quad
$$

where $B_t = W_t \cdot N_t$ was the mean biomass during season t, G_t was $Log_e(W_t/W_{t-1})$, and W_t and N_t were the estimated mean body weight and abundance of kokanee during season t. The expected production of kokanee was computed according to an initial abundance of 14,525,000 kokanee fry entering the lake and weighing 0.1 g on May 1, growing to 561.0 g over the next 3.5 y (42 mo) , with an assumed constant monthly survival rate of 92% (instantaneous monthly mortality rate $Z = 0.0840$), which was the average survival rate observed before the kokanee crash.

Modeled Lake Trout Predation on Kokanee. For every 1,000 age 5 y and older lake trout, an estimated 816 kg of kokanee were eaten each year, with the greatest consumption during spring (277 kg), followed by summer, fall, and winter [\(Table S6\)](http://www.pnas.org/lookup/suppl/doi:10.1073/pnas.1013006108/-/DCSupplemental/pnas.201013006SI.pdf?targetid=nameddest=ST6). The expected annual production of kokanee was estimated at 60 t (MT) for age 0 y, 315 MT for age 1 y, 167 MT for age 2 y, and 151 MT for age 3 y.

Under the slow population increase scenario, the abundance of age 5 y and older lake trout would have been ≥40,000 in 1986–1987. The corresponding annual predation on kokanee would have been 32,632 kg. If predation was focused on a single age class, then predation losses represented 54% of the expected production for age 0 y kokanee, 10% of the production for age 1 y, 19% for age 2 y, or 18% during the final 9 mo of life for age 3 y kokanee.

Under the rapid population increase scenario, the abundance of age 5 y and older lake trout would have been $\geq 56,000$ in 1986– 1987. The corresponding annual predation on kokanee would have been 45,684 kg. If predation was focused on a single age class, then these predation losses represented 76% of the expected annual production for age 0 y kokanee, 14% of the production for age 1 y, 27% for age 2 y, or 25% during the final 9 mo of life for age 3 y kokanee.

At contemporary population abundance of 235,000 age 5 y and older lake trout, the corresponding annual predation on kokanee would have been 191,711 kg. If predation was focused on a single age class, then these predation losses represented 320% of the expected annual production for age 0 y kokanee, 61% of the production for age 1 y, 114% for age 2 y, or 105% during the final 9 mo of life for age 3 y kokanee.

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Fig. S1. Seasonal, population-level consumption of prey by different size classes of (A) lake trout and (B) lake whitefish. (C) Seasonal consumption of prey fishes by different size classes of lake trout in Flathead Lake, 1998–2001 ([SI Discussion](http://www.pnas.org/lookup/suppl/doi:10.1073/pnas.1013006108/-/DCSupplemental/pnas.201013006SI.pdf?targetid=nameddest=STXT)).

Fig. S2. Percentage abundance of zooplankton in five size fractions, before Mysis (1972-1973) and after Mysis (1986-2003). Zooplankton were partitioned into size fractions depending on total length, including spines. Data are means from monthly or more frequent samples from April to October for each year. Primary taxa in size fractions: 0.0–0.2 mm = all small rotifers; 0.2–0.4 mm = all nauplii and Asplanchna priodonta; 0.4–0.7 mm = Bosmina longirostris, Kellicottia longispina, and Filinia terminalis; 0.7-1.1 mm = adult copepods, copepodites, and Daphnia longiremis; 1.1-2.4 mm = most cladocera and Epischura nevadensis.

Fig. S3. Posterior marginals for selected parameters of change point analysis. (A) Slope left of change point, (B) slope right of change point, (C) PP value at
bottom of step, and (D) "error" SD. Slopes are in units of (

 Δ

Table S1. Fishes of Flathead Lake, their preferred habitat, percent contribution in lakewide sunken gill nets, and current status

A, adfluvial; H, hypolimnetic; EL, epilimnetic but mostly littoral (larvae may occur in pelagic zone); E, epilimnetic; L, lacustrine.

*Although only largescale suckers were reported from the 1915–1916 gill netting, probably both species were present because longnose suckers were identified soon thereafter.

[†]Two sculpins have been collected and identified in the Flathead Basin upstream of Flathead Lake. Both of them could be in Flathead Lake, but no formal study of Flathead Lake sculpin has been done.

‡ Other nonnative fishes that were introduced (with date of introduction) but were never collected in the lake include white crappie (Pomoxis annularis, 1910), smallmouth bass (Micropterus dolomieui, 1910), Yellowstone cutthroat trout (Salmo clarkii bouvieri, 1913), arctic grayling (Thymallus arcticus, 1913), Chinook salmon (Oncorhynchus tschawytscha, 1916), golden trout (Oncorhynchus aguabonita, 1938), and coho salmon (Oncorhynchus kisutch, 1969).

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*Not present at the midlake deep site. † Only one specimen observed in 1985.

‡ Presence of these species assumed on basis of archival notes listing genus only.

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WCT, westslope cutthroat trout; BT, bull trout; MWF, mountain whitefish; NP, northern pikeminnow; PC, peamouth chub; LNS, longnose sucker; LSS, largescale sucker; RSS, redside shiners; NP/PC, northern pikeminnow-peamouth hybrids; LT, lake trout; LWF, lake whitefish; KOK, kokanee; YP, yellow perch; RT, rainbow trout; PI, northern pike.

Table S4. Age-specific abundance of lake trout used in predation estimates under different population scenarios

Abundance estimates were available for age 5–30 y lake trout, so all scenarios were referenced to this age group, but the abundance of ages 2–4 y were added because they also exhibited predation on kokanee.

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Table S5. Age-specific growth inputs (initial and final weights) and spawning losses, the resulting individual feeding rates (proportion of maximum daily rate and ration in percentage body weight day^{−1}), annual consumption, and growth efficiency from bioenergetic model simulations of lake trout in Flathead Lake during the kokanee crash

wt, weight; Bwt, body weight.

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Table S6. Seasonal, size-specific consumption of kokanee and other prey (kg of prey season⁻¹) by a size-structured population of 1,000 lake trout >400 mm TL, plus additional consumption by age 2–4 y (200–375 mm TL) cohorts

Size class (mm)	Season	Μt	Temp	Whitefishes	Kokanee	Perch	UnidFish	Inverts
200-375	Spring	441	4.6	12	93	$\mathbf 0$	147	273
	Summer	411	5.5	44	0	$\mathbf 0$	199	273
	Autumn	382	5.7	10	0	$\mathbf{0}$	298	273
	Winter	356	3.1	29	$\mathbf 0$	$\mathbf 0$	206	276
200-375 total		397	4.7	95	93	$\mathbf 0$	851	1,095
376-500	Spring	186	4.6	75	75	$\overline{2}$	45	0
	Summer	173	5.5	84	84	$\overline{2}$	51	0
	Autumn	161	5.7	84	84	$\overline{2}$	51	$\mathbf 0$
	Winter	150	3.1	59	59	$\overline{2}$	36	$\mathbf 0$
376-500 total		168	4.7	301	301	8	182	$\mathbf 0$
$501 - 625$	Spring	70	4.6	63	63	$\overline{2}$	38	$\mathbf 0$
	Summer	65	5.5	70	70	$\overline{2}$	42	$\mathbf 0$
	Autumn	60	5.7	67	67	$\overline{2}$	41	$\mathbf 0$
	Winter	56	3.1	46	46	1	28	0
501-625 total		63	4.7	246	246	6	149	$\mathbf 0$
626-750	Spring	18	4.6	36	36	1	22	$\mathbf 0$
	Summer	16	5.5	39	39	1	23	$\mathbf 0$
	Autumn	15	5.7	37	37	1	22	$\mathbf 0$
	Winter	14	3.1	25	25	1	15	$\mathbf 0$
626-750 total		16	4.7	137	137	4	83	$\mathbf 0$
751-1,000	Spring	6	4.6	10	10	$\mathbf 0$	6	$\mathbf 0$
	Summer	5	5.5	11	11	$\mathbf{0}$	$\overline{7}$	
	Autumn	5	5.7	10	10	$\mathbf 0$	6	0
	Winter	5	3.1	$\overline{7}$	$\overline{7}$	$\mathbf 0$	4	$\mathbf 0$
751-1,000 total		5	4.7	39	39	1	23	$\mathbf{0}$
Total for all sizes	Spring			196	277	5	259	273
	Summer			248	203	5	322	273
	Autumn			208	198	5	418	273
	Winter			167	138	4	290	276
Annual total				818	816	19	1,289	1,095

Nt, average abundance of lake trout present in each size class during each season. Temp, temperature in °C.