



**PREDATOR-PREY DYNAMICS
IN LAKE PEND OREILLE**

**FINAL REPORT
July 1, 2006 — June 30, 2007**



Photo courtesy of Lee T. Kern

Prepared by:

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Predator–Prey Dynamics in Lake Pend Oreille

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By

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ABSTRACT

My objective was to evaluate long-term sustainability of lake trout *Salvelinus namaycush* and rainbow trout *Oncorhynchus mykiss* populations subjected to a range of fishing mortality (F) in Lake Pend Oreille, while providing for kokanee *Oncorhynchus nerka* recovery. To achieve my objective, I developed a density-dependent stochastic predator-prey simulation model for three major predators (lake trout, rainbow trout, and bull trout *Salvelinus confluentus*) on kokanee in Lake Pend Oreille. As F increased from 0.0 to 1.0, lake trout numbers in 2015 declined 90% for gillnetting, 76% for angling, and 48% for trap netting. At fishing mortality rates observed in Lake Pend Oreille during 2006, all methods combined and angling alone suppressed the lake trout population, but not gillnetting or trap-netting alone. As F increased from 0.0 to 0.3, rainbow trout numbers in 2015 declined 38%. Abundance of adult bull trout increased 5.8% per year during 1996–2006, after implementation of no-kill regulations, which met the Federal Recovery Plan criterion of a stable or increasing trend in abundance. By 2010, total consumption of kokanee by lake trout, rainbow trout, and bull trout increased 20% as fishing mortality on lake trout and rainbow trout declined 30% from 1996 levels, and decreased 14% as fishing mortality on lake trout and rainbow trout increased 30% from 1996 levels. At rates of fishing mortality exerted on lake trout and rainbow trout in 2006, the likelihood of kokanee collapse was 65% within the next decade, so fishing mortality would need to increase by at least 6% on both lake trout and rainbow trout to reduce the likelihood of kokanee collapse to at most 50%. I conclude that kokanee biomass is presently out of balance with predation in Lake Pend Oreille, because kokanee production cannot compensate for all predation loss. My findings suggest that a combination of unusually high kokanee production and unusually low predation is likely needed for kokanee to survive the next decade in Lake Pend Oreille.

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INTRODUCTION

The lake trout *Salvelinus namaycush* is widely distributed across the northern half of North America (Crossman 1995), where the species co-dominates coldwater lakes with the lake whitefish *Coregonus clupeaformis* (Johnson 1976). The two species often make up 95% of total fish biomass and fishery yields, with lake trout predominating in deeper, colder lakes and lake whitefish predominating in shallower, slightly warmer lakes (Johnson 1976). The lake trout is relatively slow growing and late maturing, so is generally thought to be susceptible to over-fishing (Healey 1978; Martin and Olver 1980). For example, the largest populations of lake trout in the world, those residing in the Laurentian Great Lakes, were over-fished, so declined in abundance, before the appearance of sea lamprey (Hansen 1999). Similarly, the lake trout population in the western arm of Great Slave Lake, Northwest Territories, Canada, failed after only 10 years of fishing (Keleher 1972; Healey 1978). In an often-cited review, Healey (1978) concluded that lake trout populations could not withstand total annual mortality higher than 50% or annual yield higher than 0.50 kg/ha. Even today, exploitation is the single most critical stress affecting lake trout populations in Precambrian Shield lakes of eastern Canada and northeastern United States (Olver et al. 2004).

The lake trout was widely stocked in western North America during the late 1800s and early 1900s (Crossman 1995), where the species sometimes increased greatly in abundance and suppressed other species through competition or predation (Donald and Alger 1993). A crucial precursor for lake trout to achieve dominance in many western lakes was introduction of *Mysis relicta* (hereafter, *Mysis*), which were widely stocked after observing increased growth of kokanee *Oncorhynchus nerka* in Kootenay Lake, British Columbia shortly after *Mysis* became established (Martin and Northcote 1991). Lake trout recruitment is evidently limited in many western lakes, where population density remains low until *Mysis* provide an abundant prey supply for juvenile lake trout (Stafford et al. 2002). For example, shortly after *Mysis* reached high density, lake trout increased greatly in numbers and subsequently preyed heavily on kokanee and competed with bull trout *Salvelinus confluentus* (a federally listed species), both of which declined to very low abundance in Flathead Lake, Montana (Stafford et al. 2002) and Priest Lake, Idaho (Bowles et al. 1991).

In Lake Pend Oreille, Idaho, lake trout were introduced in 1925, remained at low density through the 1990s, but then grew exponentially during 1999–2005, despite largely unregulated harvest since 2000 (Hansen et al. 2007). Predation by the burgeoning population of lake trout, in combination with predation by the already robust population of rainbow trout *Oncorhynchus mykiss*, suppressed the kokanee population to levels that were too low to support a fishery or continued predation at such elevated levels (Maiolie et al. 2002). Lake trout were also thought to present a threat to the bull trout population through competition for prey (Donald and Alger 1993; Fredenberg 2002). In response to the increase in the lake trout population, a predator removal program was instituted in 2006 on Lake Pend Oreille (Hansen et al. 2007). In 2006, to suppress populations of lake trout and rainbow trout to levels that would not jeopardize sustainability of kokanee in Lake Pend Oreille, gillnetting and trap netting were used to remove lake trout and cash incentives were used to encourage harvest of lake trout and rainbow trout by anglers. In 2006, these suppression programs removed 44% of the lake trout and 22% of the rainbow trout present in Lake Pend Oreille at the start of the year. For lake trout, total annual mortality (58%) was well above the 50% threshold beyond which the species generally declines in abundance (Healey 1978).

My sabbatical objectives were to (1) evaluate the long-term sustainability of lake trout and rainbow trout under varying levels of fishing mortality in Lake Pend Oreille, while providing for kokanee recovery, (2) assist Idaho Department of Fish and Game (IDFG) personnel in educating interested publics about the proposed predator control program for lake trout and rainbow trout in Lake Pend Oreille, and (3) assist IDFG personnel with evaluations of the potential impacts of lake trout, lake whitefish, rainbow trout, and walleye on Lake Pend Oreille. To achieve my first objective, I developed a density-dependent stochastic predator-prey simulation model for three major predators (lake trout, rainbow trout, and bull trout) on kokanee in Lake Pend Oreille. To achieve my second objective, I participated in monthly meetings of the Lake Pend Oreille fishery recovery task force and sporadic meetings of other stakeholder and interest groups. To achieve my third objective, I provided IDFG personnel when requested with advice and evaluations about potential impacts of lake trout, lake whitefish, rainbow trout, and walleye *Sander vitreus* on the fish community of Lake Pend Oreille. Herein, I describe accomplishments in relation to my first objective.

METHODS

Study Area

Lake Pend Oreille, located in north Idaho, is Idaho's largest lake, with a surface area of 38,300 ha, a mean depth of 164 m, and a maximum depth of 351 m. The lake is natural, but two hydroelectric facilities influence the lake level and restrict upstream fish passage. Cabinet Gorge Dam, completed in 1952 upstream on the Clark Fork River, modifies water flow into the lake and blocks historical upstream spawning and rearing areas for adfluvial salmonids (Figure 1). Albeni Falls Dam, completed in 1955 downstream on the Pend Oreille River, regulates the top 3.5 m of the lake between high summer pool elevation (July–September = 628.7 m) and low winter pool elevation (October–June = 625.1–626.4 m).

Lake Pend Oreille is a temperate, oligotrophic lake. Summer water temperature (May–October) averages about 9°C in the upper 45 m of water (Rieman 1977; Maiolie et al. 2001, 2002, 2006). Surface temperatures are as high as 24°C in hot summers. Thermal stratification occurs from late June to September, and the thermocline is usually at depths of 10–24 m. Steep, rocky slopes occur along most of the largely undeveloped shoreline, so littoral areas are limited, although littoral areas in the northern end of the lake and in bays have more gradual or moderately sloping bottoms. Habitat for the coldwater fish species of interest to our study is mostly in the pelagic area of the lake.

Bull trout and northern pikeminnow *Ptychocheilus oregonensis* were the historic top native predatory fishes in Lake Pend Oreille (Hoelscher 1992). Lake trout were introduced from the Great Lakes in 1925, and Gerrard-strain rainbow trout were introduced from Kootenay Lake, British Columbia in 1941. Presently, the most abundant predator fishes are rainbow trout, bull trout, lake trout, and northern pikeminnow. Other less abundant predators include northern pike *Esox lucius*, brown trout *Salmo trutta*, smallmouth bass *Micropterus dolomieu*, largemouth bass *Micropterus salmoides*, and walleye.

The historic native prey assemblage included mountain whitefish *Prosopium williamsoni*, pygmy whitefish *Prosopium coulterii*, slimy sculpin *Cottus cognatus*, suckers *Catostomus* spp., peamouth *Mylocheilus caurinus*, redbelt shiner *Richardsonius balteatus*, and juvenile bull trout and westslope cutthroat trout *Oncorhynchus clarkii lewisi*. Kokanee migrated down from Flathead Lake, Montana via the Clark Fork River, became abundant in the 1930s, and

supported the largest recreational fishery in Idaho during the 1960s and 1970s (Maiolie et al. 2002). Closure of the Cabinet Gorge dam caused a long-term decline in kokanee abundance and angler harvest that was mitigated by construction of the Cabinet Gorge hatchery to annually supplement kokanee abundance through stocking. At present, kokanee are the principal prey for rainbow trout, lake trout, and bull trout, and are about half of all prey items eaten by northern pikeminnow (Vidergar 2000).

Overall Model Structure

The predator-prey model included submodels for populations of the three major predator species (lake trout, rainbow trout, and bull trout) and the single prey species (kokanee). Submodels for lake trout and rainbow trout were age-structured density-dependent stochastic simulation models, based on biological attributes of and fisheries for both species in Lake Pend Oreille. The submodel for bull trout was a logistic population growth model, based on annual redd counts in spawning streams of Lake Pend Oreille. The submodel for kokanee was a production-biomass model, based on estimated production, biomass, and yield of kokanee in Lake Pend Oreille. Simulated abundance of each predator in each year translated into kokanee consumption each year using previously estimated predation rates (Vidergar 2000). Total kokanee consumption by all predators in each year was subtracted from estimated kokanee production to derive kokanee biomass at the end of each annual time step.

Lake Trout Submodel

Submodel Structure

From a starting abundance N_{ij} at age j in year i , the number present $N_{i+1, j+1}$ at the next age $j+1$ in the next year $i+1$ was modeled as a function of the total instantaneous mortality rate Z_{ij} for each age class j in year i (Quinn and Deriso 1999; Haddon 2001):

$$N_j = N_0 e^{-Z_j} \tag{1}$$

Numbers present in each age class for the first year of the simulation $i = 0$ were specified as model inputs from the estimated numbers present in each age class at the end of 2005 (start of 2006; see below).

The total instantaneous mortality rate Z_{ij} for each age j and year i was the sum of total instantaneous natural mortality (M was assumed constant across all ages j and years i) and total instantaneous fishing mortality (F_{ij}) for each age j in year i :

$$Z_{ij} = F_{ij} + M \tag{2}$$

Total instantaneous natural mortality ($M = 0.208$) was estimated from Pauly's equation using parameters of the Von Bertalanffy length-age model ($L_\infty = 953$ mm, $K = 0.164$ /year; see below) and average annual water temperature occupied by sonic-tagged lake trout in Lake Pend Oreille from 19 March 2003 through 21 March 2004 ($T = 7^\circ\text{C}$; from original data summarized by Bassista et al. 2005). Total instantaneous fishing mortality F_{ij} for each age j in year i was simulated from the relative selectivity S_j of the gear for lake trout of age j (see below) and the fully selected fishing mortality rate F_i for each year i :

$$F_{ij} = S_j F_i \quad (3)$$

Fully selected fishing mortality F_i was specified as a model input for each simulation to cover a range of fishing mortality rates $F_i = 0.0$ – 1.0 . Each value of fully selected fishing mortality was simulated for each capture method (gillnetting, trap netting, and angling) in the absence of other capture methods, to evaluate the independent effect of each capture method on population sustainability metrics. In addition, sustainability of the specific allocation of fishing mortality observed during 2006 was simulated.

The number of age-0 lake trout $N_{i+1, j=0}$ that recruited to the population in each year $i+1$ was predicted from the number of adult lake trout $N_{i, j=8+}$ that spawned in the previous year i using a Ricker stock-recruit model (Ricker 1975):

$$N_{i+1, j=0} = \alpha (N_{i, j=8+}) e^{-\beta N_{i, j=8+}} e^{\varepsilon} \quad (4)$$

In the stock-recruit model, α = recruits per adult at low adult density, β = the instantaneous rate at which recruits/adult declines with adult density, and ε = multiplicative process error. For the stock-recruit model (Figure 2), adult lake trout were estimated from the maturity model (see below). Model parameters (α , β and ε) were derived from estimates for the lake trout population in eastern Lake Superior during 1980–2001 (Nieland 2006). First, I assumed that the maximum annual reproductive rate and recruitment variability were constant within species (Myers et al. 1999; Myers 2002). Therefore, I used the same base reproductive rate ($\alpha = 5.698$ recruits/adult) and recruitment variation ($\varepsilon = 0.197$) for the lake trout population in Lake Pend Oreille that was previously estimated for the lake trout population in eastern Lake Superior (Nieland 2006). Next, Lake Superior and Lake Pend Oreille have similar bathymetry and habitat features (Hansen et al. In review). Therefore, I scaled the instantaneous rate of density dependence in Lake Pend Oreille ($\beta = 7.851 \times 10^{-5}$) based on the amount of surface area (11,568 ha) that lies over depths (<70 meters; Hansen et al. 1995) that are suitable for lake trout (Lake Superior = 280,772 ha; $\beta = 3.235 \times 10^{-6}$; Nieland 2006).

Parameter Estimation

Parameters for the simulation model were estimated from length, weight, age, and maturity of a subsample of lake trout collected during trap netting, gillnetting, and angling on Lake Pend Oreille between October 12, 2003 and June 1, 2004 (Maiolie and Peterson, In press). Lake trout were measured in total length (0.1 mm) and weight (1.0 g), and otoliths were collected for age estimation. Gender (male or female) and maturity status (mature or immature) were classified from inspection of gonads after dissection. Otoliths were thermally glued, anterior edge up, to a glass slide and sanded with 600–2000 grit sandpaper down to the primordium. The otolith was then re-glued to the slide, sanded side down, and sanded down to a thin transverse section (300–500 μm). The top surface was polished using 1.0- μm Alpha alumina C micro-polish. Otoliths were examined under a light microscope at 40–100x by two researchers and discrepancies in estimated age were discussed to reach a consensus age. Ages were coded to coincide with the beginning of the calendar year.

An age-length key was used to convert subsample length-frequency data into sample age frequencies (Ricker 1975). The age-length key was created by cross tabulating age (columns) against 2.0 cm length classes (rows) for subsampled ages, and then calculating age frequencies (proportions of the total number sampled for age in each length class) within each

length class. The age-length key was then used to estimate the age frequency of fish sampled by each capture method (gillnets, trap nets, and angling) for which a length frequency of catches was obtained.

Age-specific selectivity, $s_j = C_j/N_j$, was estimated for gill nets, trap nets, and angling from age-specific catches C_j at age j (estimated from length frequencies for each gear and the age-length key described above) and abundances N_j at age j in Lake Pend Oreille (Hansen et al. 2007). Relative selectivity, $S_j = s_j/\max(s_j)$, for each capture method was then estimated as the age-specific selectivity divided by the maximum age-specific selectivity.

Growth parameters for estimating the instantaneous natural mortality rate were estimated for the Von Bertalanffy length-age model:

$$L_j = L_\infty \left(1 - e^{-K(j-j_0)}\right) e^{\varepsilon_j} \quad (6)$$

In the length-age model, L_∞ = asymptotic length for an average fish in the population, K = the instantaneous rate at which an average fish of age j grows from L_j to L_∞ , j_0 = the hypothetical age at which length is zero, and ε_j = multiplicative process error (Ricker 1975). Parameters of the length-age model were estimated with nonlinear least-squares methods.

Maturity of lake trout for determining ages to be included as adults in the stock-recruit relationship was modeled as a logistic function of age, where the proportion of mature fish in each age class M_j was related to each age class j using a logistic model:

$$M_j = \frac{1}{1 + e^{-r(j-j_m)}} + \varepsilon_j \quad (7)$$

In the maturity model, M_j = the proportion of mature fish in each age class j , r = the instantaneous rate at which the proportion of adult fish in each age class j approach maturity, j_m = the age at which 50% of the fish in each age class j were adult, and ε_j = additive process error (Quinn and Deriso 1999). Parameters of the maturity model were estimated with nonlinear least-squares methods.

Numbers present in each age class j in year $i = 0$ were estimated from the total number estimated by mark-recapture to be present at the end of 2005 (Hansen et al. 2007), the length frequency of the gillnet sample in spring 2006 (Hansen et al. 2007), and the age-length key described above. I assumed that the length frequency of fish caught in gillnets in spring 2006 represented the population of all lake trout (mature and immature) vulnerable to capture by any method in the lake (i.e. younger fish resided in the abyss, where they were not vulnerable to capture). Numbers at age for lake trout of pre-recruited ages (≤ 4 years) were estimated from the catch curve for numbers at age in the population for lake trout of fully recruited ages (≥ 5 years).

Simulation Metrics

The management objective for lake trout in Lake Pend Oreille is to reduce the population and ensure long-term population control by 2010 to a level where lake trout no longer threaten collapse of kokanee or priority native and sport fisheries. Therefore, simulation metrics included average abundance, probability of suppression, and time to suppression. The average density was the median of average densities for all simulations in 2010 and 2015, years specified for

evaluation of the predator suppression program in the Lake Pend Oreille fishery management plan. Confidence intervals (95%) for average density were approximated using the 2.5 and 97.5 percentiles of average density for all 1,000 simulations. The probability of suppression was the proportion of 1,000 simulations during the 200 year simulation period for which abundance fell to the 1999 level, an abundance level at which lake trout were not yet a problem. Time to suppression was the median number of years to suppression, where time to suppression for a simulation was set at 200 years if suppression did not occur. Confidence intervals (95%) for time to suppression were approximated using the 2.5 and 97.5 percentiles of time to suppression for all 1,000 simulations.

Rainbow Trout Submodel

Submodel Structure

The rainbow trout submodel was identical in form to the lake trout submodel, but with model parameters specified from attributes of the rainbow trout population and fishery in Lake Pend Oreille. First, numbers present in each age class for the first year of the simulation $i = 0$ were specified as model inputs from the estimated numbers present in each age class in spring 2006 (see below). Second, instantaneous natural mortality ($M = 0.317$) was estimated from catch curves and exploitation rates in 1999 and 2006 (see below). Third, fully selected fishing mortality F_i was specified as a model input for each simulation to cover a range of fishing mortality rates $F_i = 0.0$ – 0.3 , but was simulated only for angling (rainbow trout were not vulnerable to capture in gillnets or trap nets). Fourth, in the stock-recruit model, adult rainbow trout were defined using the maturity curve for rainbow trout in Lake Pend Oreille (see below), but model parameters (α , β and ϵ) were derived from mark-recapture estimates of the rainbow trout population in Lake Pend Oreille in 1999 and 2006.

Parameter Estimation

Parameters for the simulation model were estimated from length, weight, and age of a subsample of rainbow trout caught by anglers during a derby on Lake Pend Oreille between April 29 and May 7, 2006 (Bill Harryman, IDFG, unpublished data). Rainbow trout were measured in total length (0.1 mm) and weight (1.0 g), and scales were collected for age estimation. Scales were examined under a light microscope at 40–100x by two researchers and discrepancies in estimated age were discussed to reach a consensus age. Ages were coded to coincide with the beginning of the calendar year.

An age-length key was used to convert subsample length-frequency data into sample age frequencies (Ricker 1975). The age-length key was created by cross tabulating age (columns) against 5.0-cm length classes (rows) for subsampled ages, and then calculating age frequencies (proportions of the total number sampled for age in each length class) within each length class. The age-length key was then used to estimate the age frequency of fish sampled by angling for which a length frequency of catches was obtained.

Instantaneous natural mortality was estimated from population age frequencies and angling exploitation rates during 1999 and 2006. First, for each year, sample length frequencies were converted into age frequencies using the age-length key described above. Next, population age frequencies were derived as the product of sample age frequencies and mark-recapture estimates of total rainbow trout abundance in each year (Vidergar 2000; Greg Schoby, IDFG unpublished data). Next, instantaneous total mortality (Z) in each year was

estimated from the descending limb of the catch curve of population numbers at age. Next, instantaneous fishing mortality (F) in each year was estimated from tag recapture rates ($u = R/M$) and instantaneous total mortality ($F = uZ/A$, where $A = 1 - \exp(-Z)$; Ricker 1975). Last, instantaneous natural mortality in each year was estimated from instantaneous total and fishing mortality ($M = Z - F$).

Age-specific selectivity, $s_j = C_j/N_j$, was estimated from angling from age-specific catches C_j at age j and abundances N_j at age j in Lake Pend Oreille. Catch at age was estimated from the length frequency of angler-caught fish during 2006 (through the predator suppression program) and the age-length key described above. To receive rewards through the predator suppression program, anglers turn in only heads of fish caught, so head lengths were converted into total lengths using a relationship that was derived for rainbow trout in Lake Pend Oreille ($TL = 103.72 + 4.278HL$; Greg Schoby, IDFG, unpublished data). Abundance at age was estimated by apportioning the mark-recapture estimate of total rainbow trout abundance (Greg Schoby, IDFG, unpublished data) into age classes using the age frequency of angler-caught fish. Relative selectivity, $S_j = s_j/\max(s_j)$, was then estimated as the age-specific selectivity divided by the maximum age-specific selectivity.

Maturity of rainbow trout for estimating numbers of adults to be included in the stock-recruit relationship was estimated from age-specific maturity of rainbow trout previously estimated in Lake Pend Oreille. The proportion of mature fish M_j in each age class j was not estimated directly, so I estimated maturity at age as: the total number of mature rainbow trout in each age class sampled during previous studies, divided by the total number of mature fish sampled in all prior studies, scaled to the maximum proportion mature in any single age class (data from studies in 1972–1976, 1983–1984, and 1997–1998 summarized by Vidergar 2000; Appendix Table 1.5). This method assumes that all individuals were mature above the modal age and that the fraction of mature fish in younger age classes increased toward the modal age.

Numbers present in each age class j in year $i = 0$ were estimated from the total number estimated by mark-recapture to be present in spring 2006 (Greg Schoby, IDFG, unpublished data), the length frequency of angler-caught fish caught during 2006 (Greg Schoby, IDFG, unpublished data), and the age-length key described above. I assumed that the length frequency of fish caught by anglers during 2006 represented the population of all rainbow trout (mature and immature) in the lake (i.e. younger fish resided in streams, where they were not vulnerable to capture). Numbers at age for rainbow trout of pre-recruited ages (≤ 4 years) were estimated from the number at age 5 (the first fully recruited age) and the survival rate (assuming only natural mortality).

The number of age-0 rainbow trout that recruited to the population in each year was predicted from the number of adult rainbow trout that spawned in the previous year using a Ricker stock-recruit model, as for lake trout (Ricker 1975). For the stock-recruit model (Figure 3), adult rainbow trout were estimated from the maturity model (see below). Model parameters (α , β and ϵ) were derived from estimates for rainbow trout abundance in Lake Pend Oreille in 1999 and 2006 (Vidergar 2000; Greg Schoby, IDFG unpublished data). First, I estimated the number of age-0 rainbow trout that were associated with the population age frequency in each year (1999 = 14,434 age-0 fish; 2006 = 28,960 age-0 fish; back-transformed intercepts for catch curves in each year, see above). Next, I assumed that the geometric mean number of adults and recruits in 1999 and 2006 represented average adult (7,422 adult fish) and recruit (20,466 age-0 fish) abundance for the population at carrying capacity (i.e. the population was fished only lightly in both years, so was likely near carrying capacity). Next, I estimated the peak of the stock-recruit curve ($X = 1/\beta$, $Y = \alpha/\beta\epsilon$; Ricker) from the average number of adults ($\beta = 1/7422$)

and recruits ($\alpha = 20466/7422e$) in 1999 and 2006. Last, I estimated recruitment variation ε by trial and error until the stock-recruit curve reproduced the range of observed variation in recruitment in 1999 and 2006. Resulting parameters of the stock-recruit model were $\alpha = 7.488$ recruits/adult, $\beta = 1.347 \times 10^{-4}$, and $\varepsilon = 0.19$.

Simulation Metrics

The management objective for rainbow trout in Lake Pend Oreille is to reduce the population by 2010 such that age 1-2 kokanee survival is over 50%, and once kokanee are recovered, to manage for a long-term trophy rainbow trout fishery. Therefore, simulation metrics included average abundance, probability of suppression, and time to suppression. The average density was the median of average densities for all simulations in 2010 and 2015, years specified for evaluation of the predator suppression program in the Lake Pend Oreille fishery management plan. Confidence intervals (95%) for average density were approximated using the 2.5 and 97.5 percentiles of average density for all 1,000 simulations. The probability of suppression was the proportion of 1,000 simulations during the 200-year simulation period for which abundance fell to the 1999 level, an abundance level at which rainbow trout consumption was not out of balance with kokanee production. Time to suppression was the median number of years to suppression, where time to suppression for a simulation was set at 200 years if suppression did not occur. Confidence intervals (95%) for time to suppression were approximated using the 2.5 and 97.5 percentiles of time to suppression for all 1,000 simulations.

Bull Trout Submodel

Submodel Structure

Bull trout population dynamics were modeled using a logistic population growth model based on estimated numbers of bull trout present in Lake Pend Oreille during 1983–2006. Bull trout are federally protected and therefore not subject to fishing mortality, so an age-structured model was not needed to simulate future dynamics. First, numbers of adult bull trout in Lake Pend Oreille were estimated from numbers of redds counted in spawning streams during annual surveys (1983–2006) and the estimated ratio of adult bull trout per redd in Lake Pend Oreille (3.2 adults/redd; Downs and Jakubowski 2006). Next, numbers of streams in which redds were counted varied among years. Therefore, numbers of spawning adults in each year were estimated by multiplying the number of adults in each year by the weighted average ratio of adults during 2001–2006, the period when all streams were surveyed, to adults during periods when fewer streams were surveyed (1983–1987 = 1.039; 1988–1991 = 1.438; 1992–2000 = 1.034). Last, numbers of immature and mature bull trout in Lake Pend Oreille were estimated from the ratio of all bull trout living in Lake Pend Oreille during 1999 (Vidergar 2000) to the estimated number of adult bull in Lake Pend Oreille during 1999 (as described above).

Parameter Estimation

A logistic population growth model was used to simulate future abundance of bull trout in Lake Pend Oreille:

$$N_{t+1} = N_t e^{r \left(1 - \frac{N_t}{K} \right) + \varepsilon} \quad (8)$$

In the logistic model, N_{t+1} = number present in year $t+1$, N_t = number present in year t , r = instantaneous rate of population change, K = carrying capacity, and ε = multiplicative process error. Parameters of the logistic population growth model were estimated from growth of the bull trout population in Lake Pend Oreille during 1996–2006 and the assumed maximum number of spawning redds that can be supported by streams in Lake Pend Oreille. First, the population growth rate (r) was estimated from numbers of all bull trout in Lake Pend Oreille before (1983–1995) and after (1996–2006) imposition of no-kill regulations. During each period, the population growth rate was estimated from the exponential population growth model:

$$N_{t+1} = N_t e^{rt+\varepsilon} \quad (9)$$

In the exponential model, all terms are as defined for the logistic model, but the effect of density dependence is assumed to be negligible (i.e. N_t is far from carrying capacity K). The population growth rate for the logistic model was assumed to be equal to the population growth rate for the exponential model during 1996–2006 when fishing mortality was negligible. Second, carrying capacity of Lake Pend Oreille (K) was assumed to be limited by available spawning habitat. Therefore, I assumed that (1) the maximum number of redds ever observed in each stream represented the carrying capacity of each stream, and (2) the sum of all maximum redd counts for each stream represented the carrying capacity of Lake Pend Oreille for bull trout.

Simulation Metrics

The management objective for bull trout in Lake Pend Oreille is to restore a bull trout harvest fishery of at least 200 fish annually by 2008, while meeting Federal Recovery Plan criteria, which include a minimum of six local populations of more than 100 adult bull trout, at least 2,500 adult bull trout in the population, and stable or increasing trends in abundance. Based on redd counts in 2006, the population already includes seven local populations of more than 100 adults and more than 4,000 adults in the population. Therefore, the only simulation metric was to estimate the overall trend in abundance during 1996–2006. In addition, bull trout contributed to total predator consumption of kokanee, as part of metrics for evaluating kokanee management objectives (see below).

Kokanee Submodel

Submodel Structure

Kokanee population dynamics were simulated from a production-biomass model and estimated total consumption of kokanee by lake trout, rainbow trout, and bull trout. The production-biomass model was constructed from estimated production and biomass of kokanee during 1995–2006 (Maiolie et al. 2004; updated with unpublished data). Total consumption of kokanee by lake trout, rainbow trout, and bull trout were estimated from per capita consumption rates of kokanee by each predator species (Vidergar 2000). Non-predation natural mortality on kokanee was modeled from differences between estimated yield of kokanee during 1995–2006 (Maiolie et al. 2004; updated with unpublished data) and estimated total predation on kokanee in the same years (described above).

Parameter Estimation

Kokanee biomass in each year B_t was estimated from biomass in the prior year B_{t-1} , production in each year P_t , and yield in each year Y_t :

$$B_t = B_{t-1} + P_t - Y_t \quad (10)$$

Starting biomass of kokanee B_{t-1} was assumed to be the estimated biomass in 2006 (Maiolie et al. 2004; updated with unpublished data).

Kokanee production P_t in the first simulated year was estimated from the relationship between biomass in one year to production in the next year:

$$P_t = \alpha B_{t-1} (e^{-\beta B_{t-1}}) e^\varepsilon \quad (11)$$

In the production-biomass model, α = production/biomass at low biomass, β = the instantaneous rate at which production/biomass declines with biomass, ε = multiplicative process error, and variables were as defined above. Parameters of the model were estimated with linear regression from biomass and production during 1995–2006 (Maiolie et al. 2004; updated with unpublished data) on the \log_e -transformed version of the model:

$$\log_e(P_t / B_{t-1}) = \log_e(\alpha) - \beta B_{t-1} + \varepsilon \quad (12)$$

Total yield of kokanee (Y_t) included consumption of kokanee by all predators (C_t) and non-predation mortality ($Y_t - C_t$). Consumption of kokanee by lake trout, rainbow trout, and bull trout was extrapolated from simulated numbers of each predator species and estimated per capita consumption of kokanee by an average individual lake trout and rainbow trout of each age class or an average individual bull trout (Vidergar 2000; Maiolie and Peterson, In press). Non-predation mortality was estimated in future years from the relationship between kokanee consumption (described above) and total yield of kokanee (Maiolie et al. 2004; updated with unpublished data) during 1999–2006:

$$(Y_t - C_t) = \alpha e^{-\beta C_t + \varepsilon} \quad (13)$$

In the mortality model, α = non-predation mortality in the absence of predation, β = the instantaneous rate at which non-predation declines with predation mortality, ε = multiplicative process error, and variables were as defined above. Parameters of the model were estimated with linear regression from non-predation and predation mortality rates (%) during 1999–2006 (Maiolie et al. 2004; updated with unpublished data) on the \log_e -transformed version of the model:

$$\log_e(Y_t - C_t) = \log_e(\alpha) - \beta C_t + \varepsilon \quad (14)$$

Simulation Metrics

The management objective for kokanee in Lake Pend Oreille is to develop a kokanee fishery that provides an annual harvest of 300,000 fish with catch rates of 1.5 fish/hour by 2015 (2 kokanee generations). The fishery harvest objective is equivalent to an annual yield of

~27,216 kg, which must be balanced with predator consumption while sustaining kokanee production. Therefore, simulation metrics included total consumption by predators and the probability of collapse of the kokanee population. Total consumption by predators was the median of total consumption for all simulations in 2010 and 2015, years specified for evaluation of the predator suppression program in the Lake Pend Oreille fishery management plan. Confidence intervals (95%) for total consumption were approximated using the 2.5 and 97.5 percentiles of average density for all 1,000 simulations. The probability of collapse was the proportion of 1,000 simulations during the 200-year simulation period for which kokanee biomass fell to zero (extinction).

RESULTS

Lake Trout

Current Population Status

Selectivity of gillnetting, trap netting, and angling for lake trout varied greatly among capture methods in Lake Pend Oreille (Figure 4). Lake trout were first captured at age 3 in gill nets and angling, age 4 in trap nets, and were fully vulnerable to gillnetting at age 5, angling at age 6, and trap netting at age 8. Lake trout were fully vulnerable to capture from age 5 onward for gillnetting, whereas vulnerability to capture declined at similar rates beyond age 8 for trap netting and age 6 for angling.

Lake trout grew from a starting age of $t_0 = -0.135$ years toward their asymptotic length of $L_\infty = 953$ mm at an instantaneous rate of $K = 0.164$ /year in Lake Pend Oreille (Figure 5). Lake trout matured at a length of 632 mm and an age of 6.5 years for males and a length of 673 mm and an age of 7.3 years for females in Lake Pend Oreille (Figure 6). At the time of spawning in autumn, 50% of males were mature at age 7 and 50% of females were mature at age 8.

Abundance of lake trout vulnerable to capture in gillnets was 36,000 (estimated by mark-recapture) and abundance of all lake trout was 141,000 (estimated by mark-recapture and catch-curve) in Lake Pend Oreille at the end of 2005 (Figure 7). The population age structure reflected an instantaneous rate of total mortality of $Z = 0.304$, a total annual mortality rate of $A = 26\%$, an annual survival rate of $S = 74\%$, and an average annual recruitment of $N_0 = 36,910$ lake trout for fully recruited age classes (ages 5 and older). In 2006, gillnetting (471 lake trout), trap netting (4,431 lake trout), and angling (11,041 lake trout) increased Z to 0.861 and A to 58%, and reduced S to 42% (assuming $M = 0.20$).

Future Population Status

Gillnetting suppressed the lake trout population more effectively than either angling or trap netting at all levels of F . As F increased from 0.0 to 1.0, lake trout numbers fell from 50,000 fish (45,000–56,000 fish) to 5,000 fish (4,000–6,000 fish) for gillnetting, 12,000 fish (10,000–15,000 fish) for angling, and 26,000 fish (22,000–32,000 fish) for trap netting (Figure 8, upper panel). Time to suppression declined rapidly as F increased from 0.4 to 0.5 for gillnetting and from 0.6 to 0.8 for angling, whereas trap netting did not suppress the lake trout population within 200 years at any level of F from 0.0 to 1.0 (Figure 8, middle panel). The likelihood of lake trout population collapse within 200 years increased from 0.0 to 1.0 as F increased from 0.4 to 0.5 for gillnetting, 0.6 to 0.7 for angling, and beyond 1.0 for trap netting (Figure 8, lower panel).

At fishing mortality rates observed in Lake Pend Oreille during 2006, all methods combined and angling alone suppressed the lake trout population, but not gillnetting or trap-netting alone (Figure 9). Gillnetting and trap netting combined failed to suppress the lake trout population significantly below the 2006 level, whereas angling reduced the population 27% by 2010 and 53% by 2015 and all methods combined reduced the population 34% by 2010 and 67% by 2015. Time to suppression was 24 years (20–29 years) for all methods combined, 57 years (45–74 years) for angling alone, and longer than 200 years for gillnetting and trap netting alone. The likelihood of lake trout population collapse within 200 years was 100% for all methods combined and angling alone and 0% for gillnetting and trap netting alone.

Rainbow Trout

Current Population Status

The population age structure of rainbow trout in Lake Pend Oreille indicated that total mortality increased greatly from 1998 to 2006 (Table 1; Figure 10). Total mortality increased from $Z = 0.383$ ($A = 32\%$) in 1998 to $Z = 0.610$ ($A = 46\%$) in 2006. The increase in total mortality was largely explained by exploitation that increased from $u = 6\%$ in 1999 to $u = 22\%$ in 2006. Consequently, natural mortality was similar in 1999 ($M = 0.325$) and 2006 ($M = 0.315$). Vulnerability of rainbow trout to angling increased sharply from age 3 to age 4 (Figure 11). Maturity of rainbow trout increased gradually from age 3 to age 6 (Figure 12).

Future Population Status

Angling suppressed the rainbow trout population only gradually as fully selected fishing mortality F increased from 0.0 to 0.3. Rainbow trout numbers in 2015 fell from 16,000 fish (14,000–19,000 fish) to 10,000 fish (8,000–12,000 fish) as F increased from 0.0 to 0.3 (Figure 13, upper panel). Time to suppression declined rapidly as F increased from 0.10 to 0.14 (Figure 13, middle panel). The likelihood of population suppression within 200 years increased sharply as F increased from 0.06 to 0.13 (Figure 13, lower panel).

Bull Trout

Bull trout redd counts and estimated numbers of adults declined during 1983–1995 and increased during 1996–2006 (Figure 14). During 1983–1995, prior to implementation of no-kill regulations, abundance of adult bull trout declined 4.5% per year ($\lambda = 0.955$; 95% CI = 0.915–0.997). In contrast, during 1996–2006, after implementation of no-kill regulations, abundance of adult bull trout increased 5.8% per year ($\lambda = 1.058$; 95% CI = 1.031–1.085), which met the Federal Recovery Plan criterion of a stable or increasing trend in abundance. By 2006, seven tributary streams supported 100 or more adults (100 adults = 31 redds x 3.2 adults/redd), which exceeded the Federal Recovery Plan criterion of at least six local populations with at least 100 adults. The entire spawning population included more than 4,000 adult bull trout in 2006, which also exceeded the Federal Recovery Plan criterion of at least 2,500 adults. The sum of maximum redd counts in each stream suggested that carrying capacity of bull trout in Lake Pend Oreille was $K = 5,300$ adults, if spawning habitat limits total abundance.

Kokanee

Current Population Status

Kokanee production increased to a peak of 244.1 tonnes as biomass increased from zero to 223.2 tonnes, and then declined thereafter (Figure 15; upper panel). The production rate of kokanee biomass declined exponentially from 2.97 tonnes/tonne at low biomass to 1.09 tonnes/tonne at peak production and 0.32 tonnes/tonne at 500 tonnes of biomass (Figure 15; lower panel). Kokanee biomass explained 85% of the variation in logarithms of production/biomass. The standard error of the model was 0.13.

The rate of non-predation mortality on kokanee production declined from 50% to 5% as predation mortality on kokanee production increased from 20% to 60% (Figure 16). The rate of predation on kokanee explained 63% of the variation in logarithms of the rate of non-predation mortality. The standard error of the model was 0.69.

Future Population Status

Total consumption of kokanee by lake trout, rainbow trout, and bull trout increased gradually as fishing mortality on lake trout and rainbow trout declined from 1996 levels, and decreased gradually as fishing mortality on lake trout and rainbow trout increased from 1996 levels. By 2010, total consumption by all three predators increased from 167 tonnes (146–198 tonnes) to 201 tonnes (181–235 tonnes) if fishing mortality was reduced 30% from the rate exerted in 2006 and declined to 143 tonnes (123–174 tonnes) if fishing mortality was increased 30% from the rate exerted in 2006 (Figure 17). As fishing mortality changed from –30% to +60% of the base rate in 2006, lake trout consumption in 2010 remained constant at 36% of total kokanee consumption, rainbow trout consumption declined from 44% to 34%, and bull trout consumption increased from 20% to 30%. By 2015, total consumption by all three predators increased from 122 tonnes (92–173 tonnes) to 158 tonnes (121–210 tonnes) if fishing mortality was reduced 30% from the rate exerted in 2006 and declined to 100 tonnes (70–145 tonnes) if fishing mortality was increased 30% from the rate exerted in 2006 (Figure 17). As fishing mortality changed from –30% to +60% of the base rate in 2006, lake trout consumption in 2015 declined from 30% to 18% of total kokanee consumption, rainbow trout consumption declined from 43% to 34%, and bull trout consumption increased from 26% to 48%.

The likelihood of kokanee collapse declined from nearly 100% to nearly 0% as fishing mortality changed from –30% to +60% of the base rate in 2006 (Figure 18). At rates of fishing mortality exerted on lake trout and rainbow trout in 2006 (0% change), the likelihood of kokanee collapse was 65% (62–68%), so fishing mortality on lake trout and rainbow trout would need to be increased by at least 6% to reduce the likelihood of kokanee collapse to at most 50%. As fishing mortality on lake trout and rainbow trout changed from –30% to +60% of the base rate in 2006, the kokanee population collapsed in 1–200 years (lower 95% CI = 1–200 years; upper 95% CI = 4–200 years). If collapse occurred within 200 years, the kokanee population collapsed in 1–4 years (lower 95% CI = 1–2 years; upper 95% CI = 3–7 years), as fishing mortality on lake trout and rainbow trout changed from –30% to +60% of the base rate in 2006.

DISCUSSION

Lake Trout

My modeling suggests that fishing mortality rates exerted on the lake trout population in Lake Pend Oreille in 2006 will substantially reduce the population within 10–15 years. The management objective for lake trout in Lake Pend Oreille is to reduce the lake trout population and ensure long-term population control by 2010 to a level where lake trout no longer threaten collapse of kokanee or priority native and sport fisheries. My results suggest that fishing rates exerted in 2006 will suppress the lake trout population 34% by 2010 and 67% by 2015. Achievement of the management objective would require ensuring long-term population control by 2010, which seems assured if fishing mortality is sustained at 2006 levels. However, kokanee may still collapse, even if lake trout are held at low abundance, because lake trout are only one predator that currently threatens kokanee sustainability (see below).

Long-term suppression of the lake trout population will require sustained fishing mortality by gillnetting and angling, which were each more effective than trap netting for suppressing the lake trout population in Lake Pend Oreille. My results suggest that gillnetting would cause the lake trout population to collapse as F increased from 0.4 to 0.5, which is equivalent to annual mortality of $A = 0.45$ – 0.50 . Similarly, a review of lake trout in North America suggested that populations declined when annual mortality exceeded $A = 0.50$ (Healey 1978). Similarity of modeling and empirical results may stem from gillnetting being the primary fishing method used for the lake trout fisheries reviewed by Healey (1978). In contrast, my results also suggest that angling was less effective than gillnetting for suppressing the lake trout population because the fully selected fishing mortality rate needed to be higher ($F = 0.6$ – 0.7 ; $A = 0.55$ – 0.59), likely because angling removes a smaller fraction of subadult fish from the population for any level of fully selected fishing mortality. Last, my results suggest that trap netting was not effective for suppressing the lake trout population because no reasonable level of trap netting caused the lake trout population to collapse, likely because trap netting targets only adult fish in the population (e.g., fish can spawn before being removed).

Rainbow Trout

My modeling suggests that the fishing mortality rate exerted on the rainbow trout population in Lake Pend Oreille in 2006 will only gradually reduce the population within 15 years. The management objective for rainbow trout in Lake Pend Oreille is to reduce the population by 2010 such that age 1-2 kokanee survival is over 50%, and once kokanee are recovered, to manage for a long-term trophy rainbow trout fishery. The fishing mortality rate exerted on rainbow trout in 2006 was likely too low to reduce rainbow trout abundance enough to increase kokanee survival. For example, survival of age 1–2 kokanee in 2007 was only 10% (Melo Maiolie, IDFG, unpublished data), which continues a steady decline since 2003 and confirms that predator suppression (including lake trout) in 2006 was not drastic enough to increase kokanee survival to 50%. Longer-term objectives for rainbow trout trophy fishery management may be impossible if kokanee are lost from Lake Pend Oreille.

My results suggest that abundance of rainbow trout would decline 38% by 2015 (from 16,000 fish to 10,000 fish) as F is increased from 0.0 to 0.3, and that suppression to a 1999 abundance level could be achieved at $F = 0.10$ – 0.14 . Taken together, these results suggest that the fishing mortality rate exerted in 2006 ($u = 0.221$; $F = 0.296$) will likely drive the rainbow trout population down to levels last seen before 1999, when rainbow trout abundance was 14,607

fish ≥ 406 mm (Vidregar 2000). At that time, lake trout abundance was low enough that total predator consumption of kokanee was not out of balance with kokanee production. At present, rainbow trout are just one predator that jeopardizes kokanee sustainability, so their abundance may need to be driven well below levels that could support trophy fishery objectives, thereby postponing trophy fishery management well beyond 2015.

Bull Trout

My modeling suggests that the bull trout population in Lake Pend Oreille is increasing exponentially toward its natural carrying capacity. The management objective for bull trout in Lake Pend Oreille is to restore a bull trout harvest fishery of at least 200 fish annually by 2008, while meeting Federal Recovery Plan criteria (i.e., \geq six local populations of ≥ 100 adult bull trout, $\geq 2,500$ adult bull trout in the lake-wide population, and stable or increasing trends in abundance). As stated above, redd counts in 2006 show that the population already includes seven local populations of more than 100 adults and more than 4,000 adults in the population. Estimates of total adult abundance, expanded from redd counts and estimated numbers of adults per redd, are well described by an exponential growth model, which confirms that the population was growing exponentially during 1996–2006. If the bull trout population continues to grow exponentially toward a carrying capacity of 5,300 adults, bull trout will become a predominant predator on kokanee in Lake Pend Oreille by 2015. Consequently, management objectives for rainbow trout and lake trout must account for bull trout predation on kokanee.

Kokanee

My modeling suggests that fishing mortality rates exerted in 2006 on lake trout and rainbow trout populations in Lake Pend Oreille will not likely prevent the kokanee population from collapsing. The management objective for kokanee in Lake Pend Oreille is to develop a kokanee fishery that provides an annual harvest of 300,000 fish with catch rates of 1.5 fish/hour by 2015 (2 kokanee generations). However, my modeling suggests that the kokanee population will likely collapse (65% likelihood) even if fishing mortality rates exerted in 2006 continue in the future. To reduce the likelihood of kokanee collapse to less than 50%, fishing mortality will need to increase more than 6% on both lake trout and rainbow trout.

Kokanee biomass in Lake Pend Oreille is presently out of balance with predation, so kokanee production cannot compensate for all predation loss. A combination of unusually high kokanee production and unusually low predation is likely necessary for kokanee to survive the next 5–10 years in Lake Pend Oreille. Based on my modeling, the kokanee population either collapsed within a few years or were sustained through 200 years for all simulations. Therefore, kokanee are apparently now in a predator pit that will require good conditions for kokanee production and bad conditions for predator recruitment over the next 5–10 years if kokanee are to survive in Lake Pend Oreille. Continued stocking of kokanee during the next 5–10 years may help the population to survive collapse, but recovery then depends on reproduction by hatchery-origin rather than wild-origin fish.

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Table 1. Instantaneous total (Z), fishing (F), and natural (M) mortality rates, annual survival (S), mortality (A), and exploitation (u) rates, and conditional fishing (m) and natural (n) mortality rates of rainbow trout estimated from population age frequency (Z) and tag-recapture rates (u) in Lake Pend Oreille, Idaho in 1998 and 2006.

Rate	1998		2006	
	Ages 4+	Ages 0-3	Ages 4+	Ages 0-3
Z	0.383	0.325	0.610	0.315
$S = e^{-Z}$	0.682	0.723	0.543	0.730
$A = 1 - S$	0.318	0.277	0.456	0.270
$u = R/M$	0.048	0.000	0.221	0.000
$F = u(Z/A)$	0.058	0.000	0.295	0.000
$m = 1 - e^{-F}$	0.056	0.000	0.255	0.000
$M = Z - F$	0.325	0.325	0.315	0.315
$n = 1 - e^{-M}$	0.277	0.277	0.270	0.270

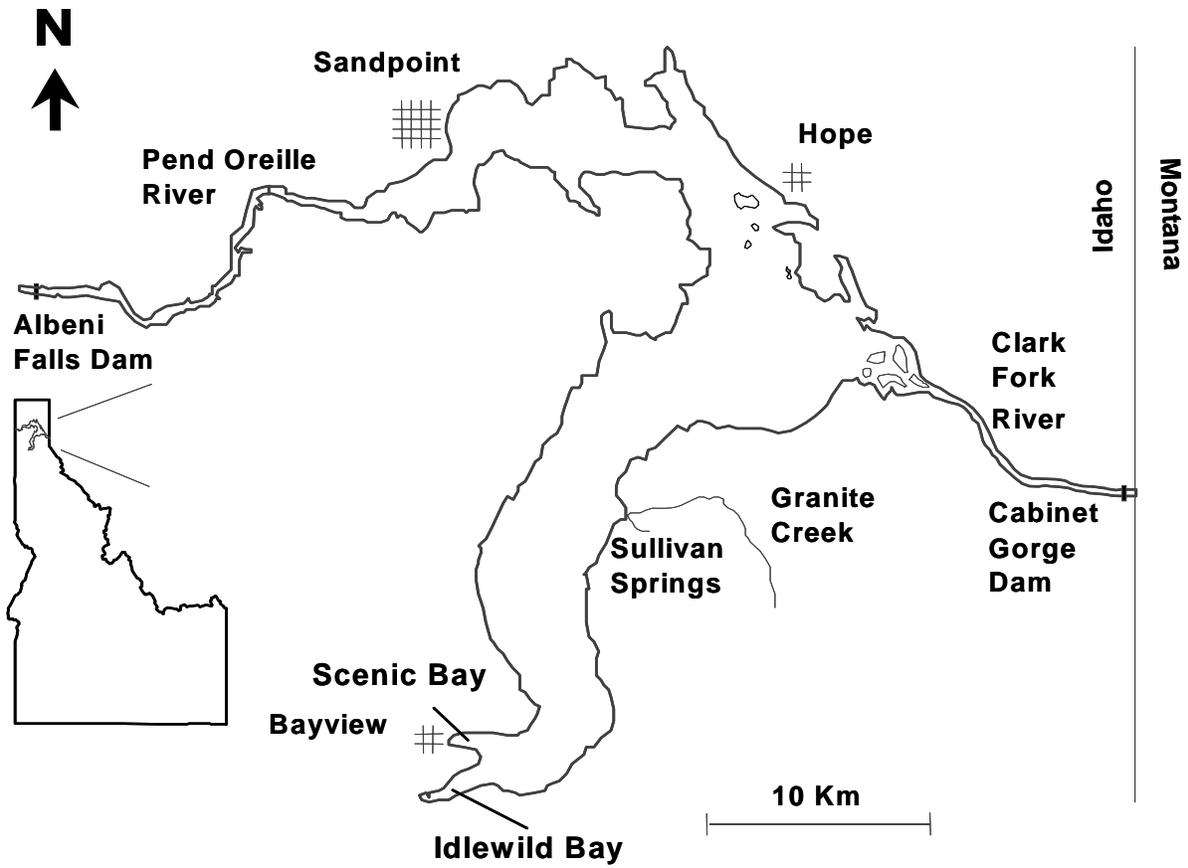


Figure 1. Lake Pend Oreille, Idaho, with major landmarks.

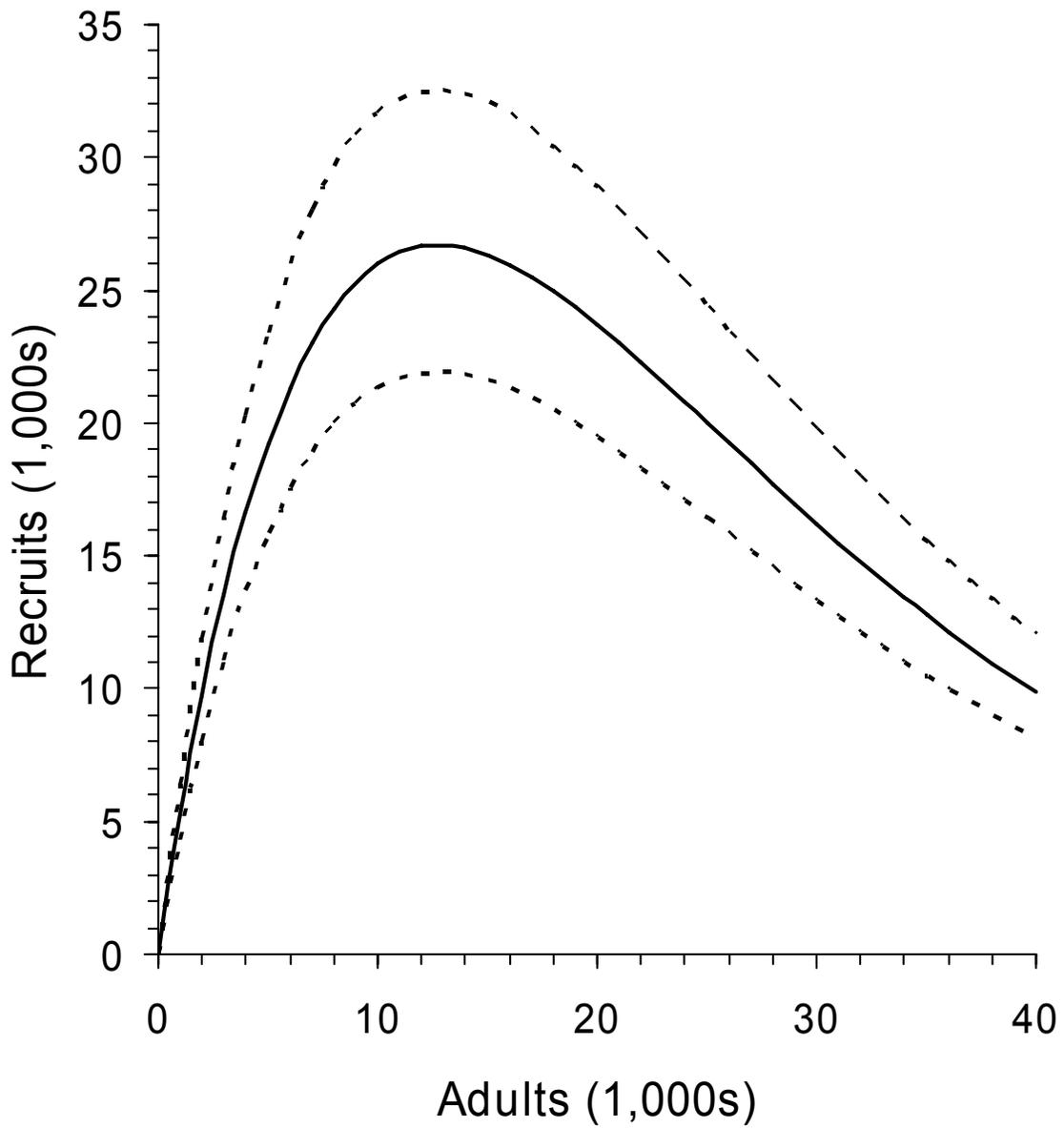


Figure 2. Numbers of age-0 lake trout (recruits) produced by adult lake trout (adults) in Lake Pend Oreille, Idaho. The model was developed from estimates for the lake trout population in eastern Lake Superior (Nieland 2006). Dotted lines depict one standard error above and below the mean number of recruits.

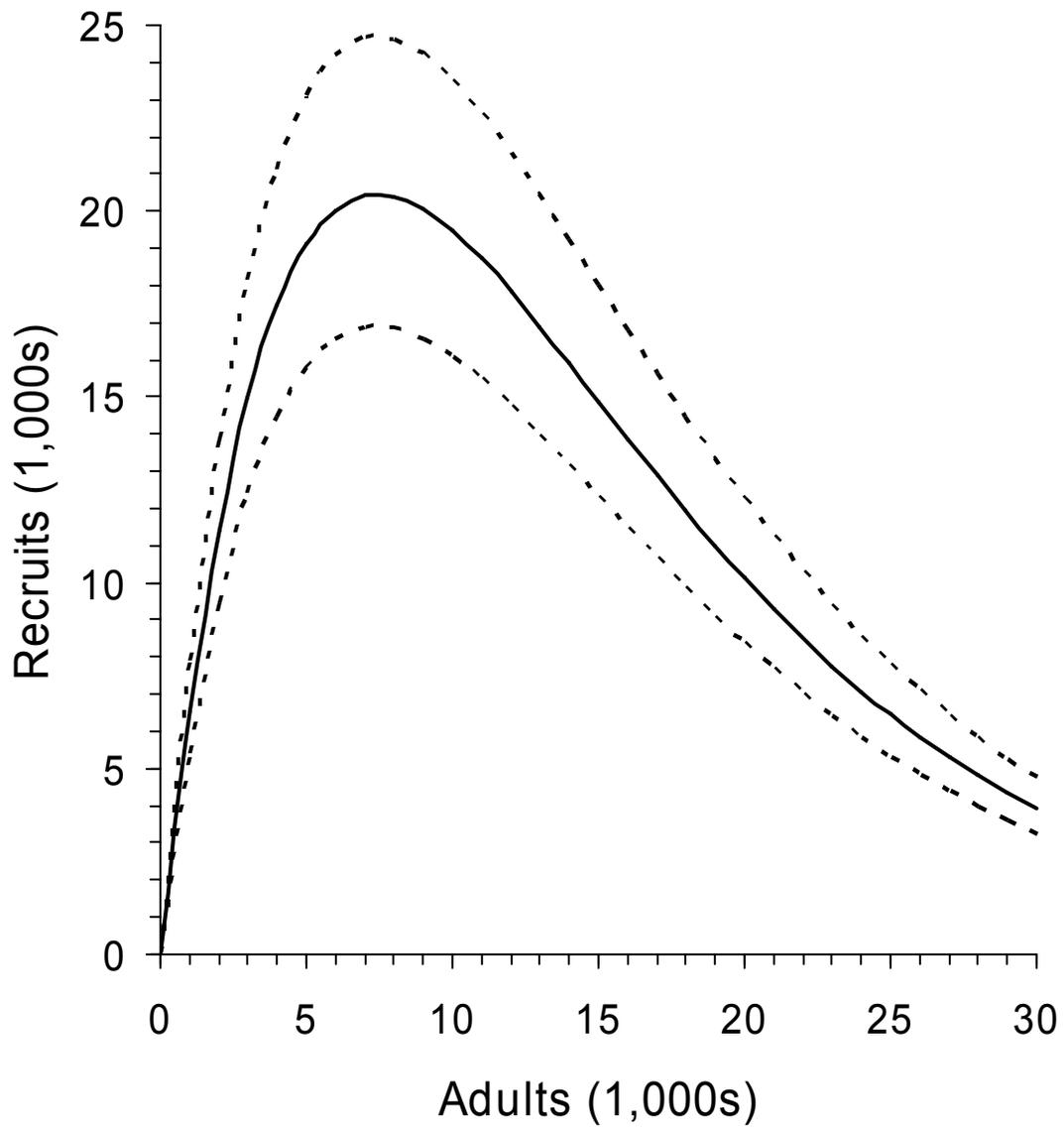


Figure 3. Numbers of age-0 rainbow trout (recruits) produced by adult rainbow trout (adults) in Lake Pend Oreille, Idaho. Dotted lines depict one standard error above and below the mean number of recruits.

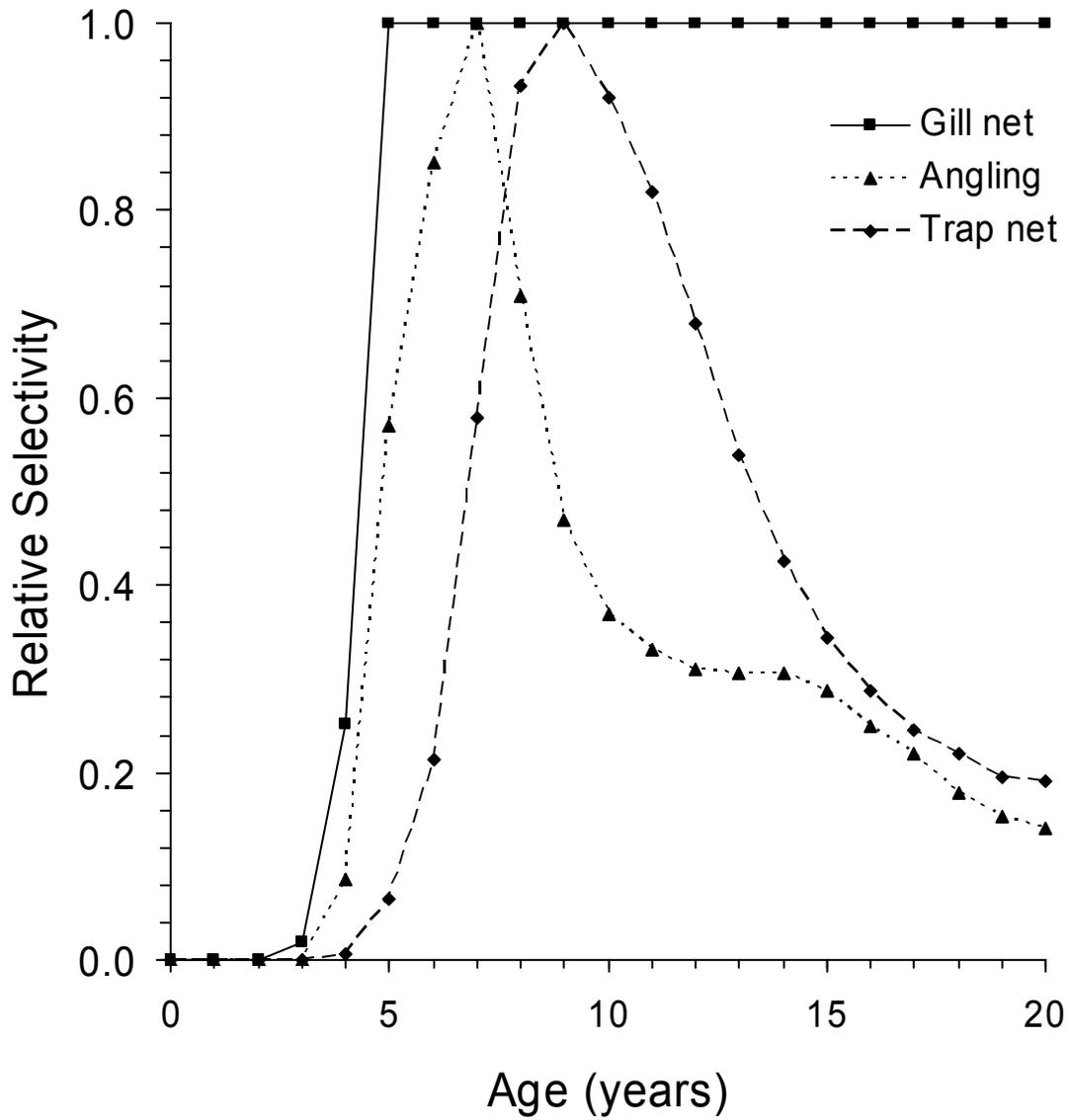


Figure 4. Relative selectivity of gillnets, trap nets, and angling for lake trout of ages 0–20 in Lake Pend Oreille, Idaho.

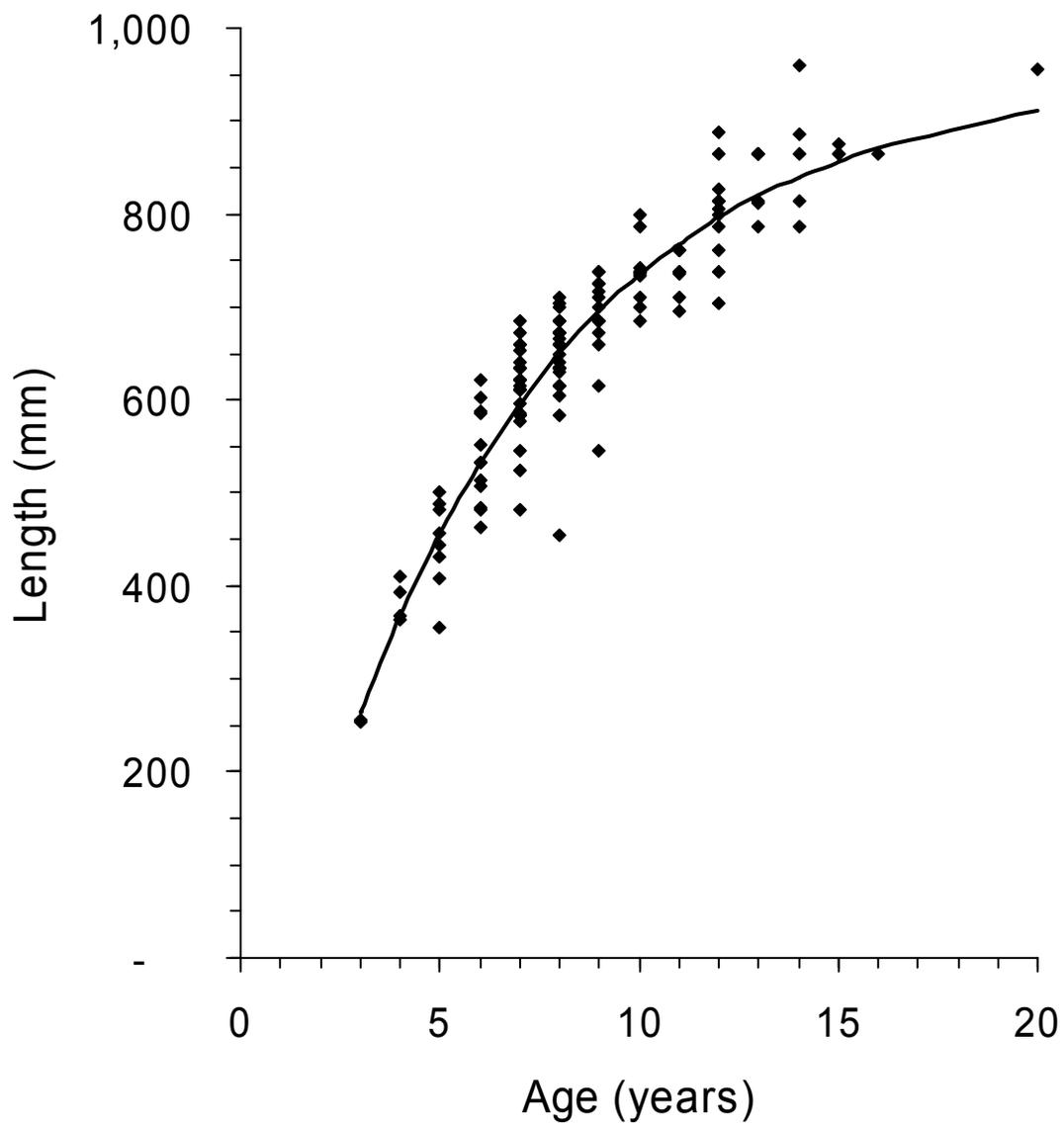


Figure 5. Length at age of lake trout collected during trap netting, gillnetting, and angling on Lake Pend Oreille, Idaho, between October 12, 2003 and June 1, 2004. The curve depicts the Von Bertalanffy model of length against age.

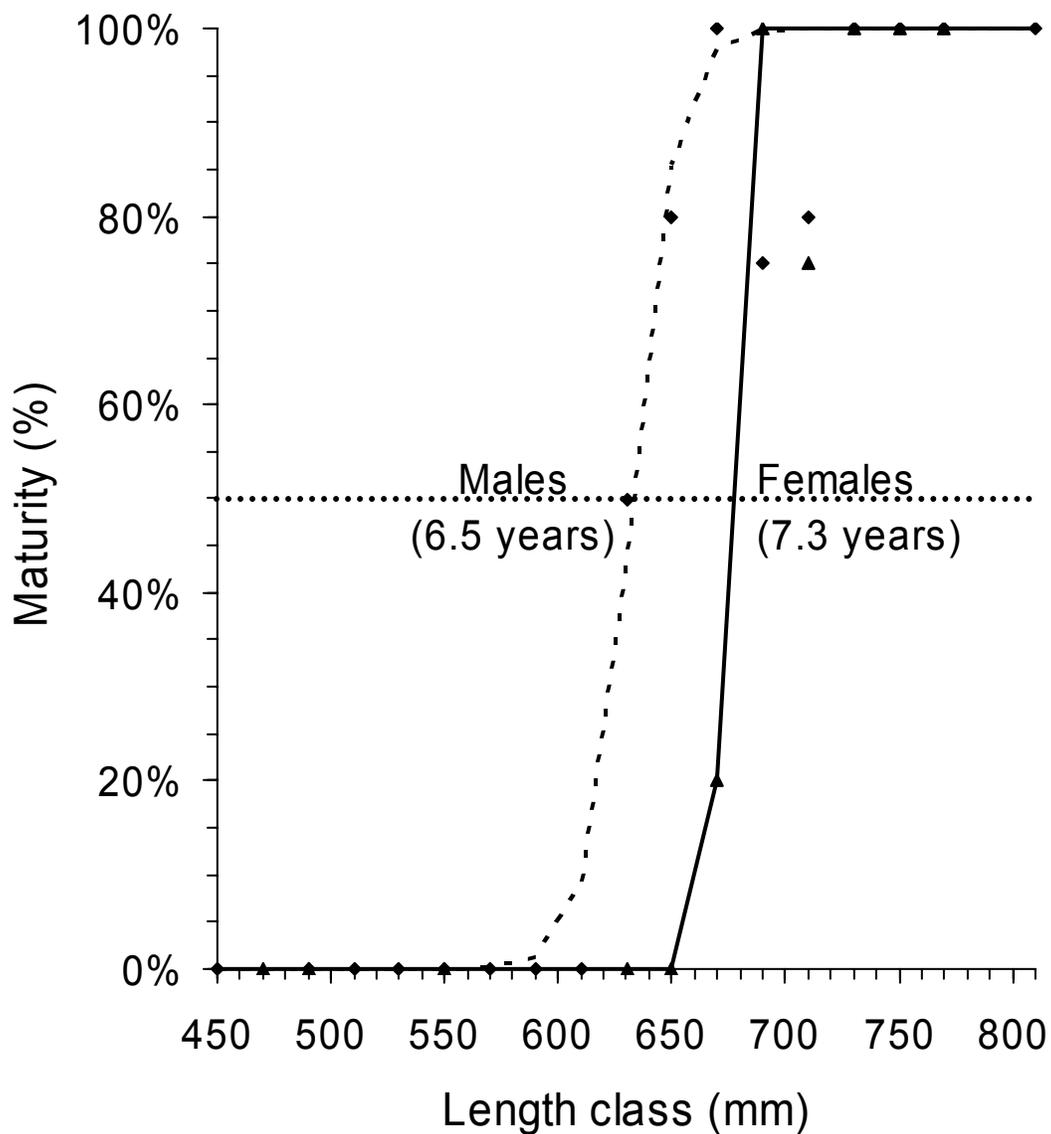


Figure 6. Percentage of mature male and female lake trout in 2 cm length classes collected during trap netting, gillnetting, and angling on Lake Pend Oreille, Idaho, between October 12, 2003 and June 1, 2004. Curves depict logistic models of percent maturity against length. Horizontal line depicts 50% maturity.

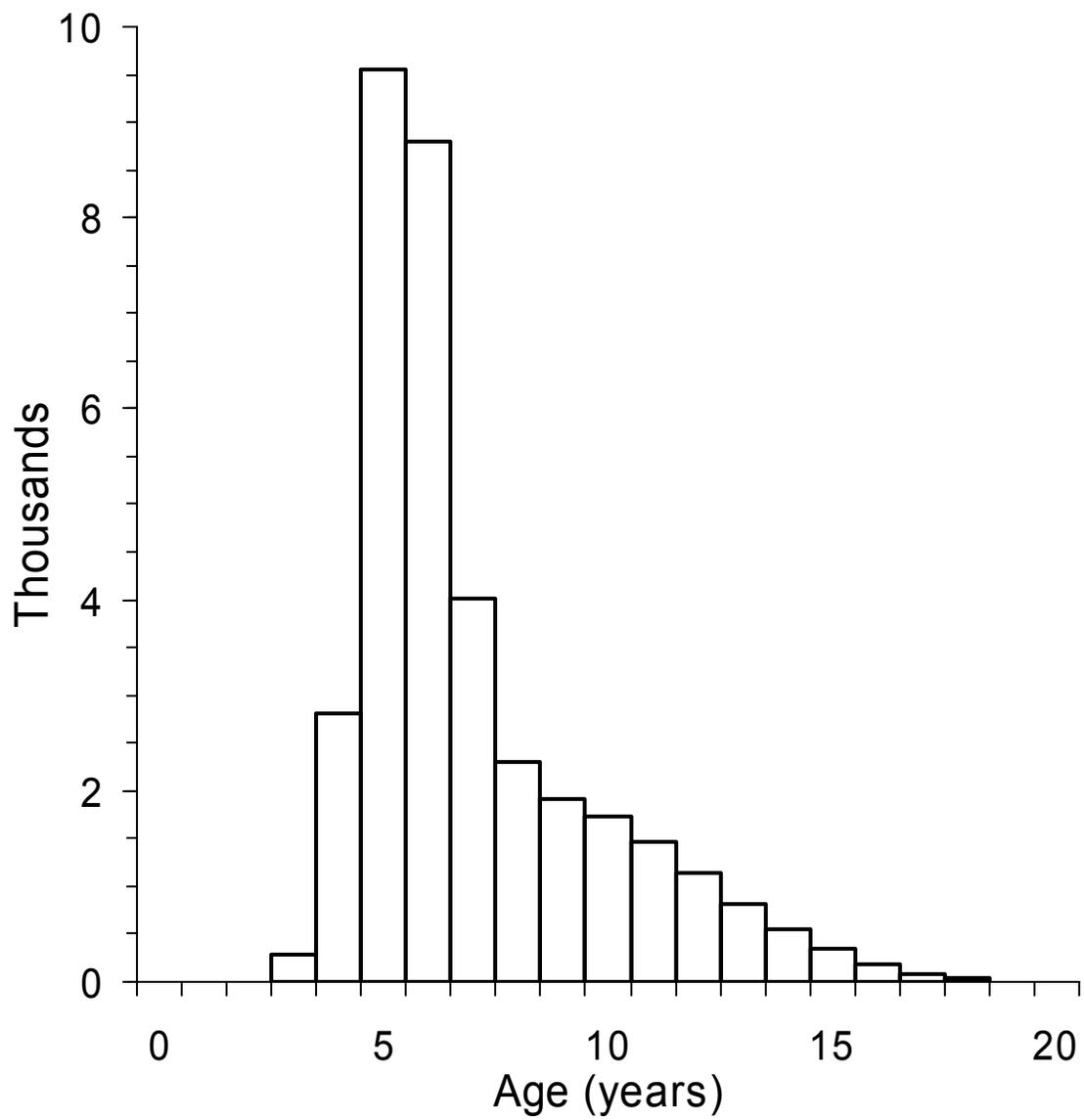


Figure 7. Numbers of lake trout estimated by mark-recapture to be present in each age class in Lake Pend Oreille, Idaho, on December 15, 2005.

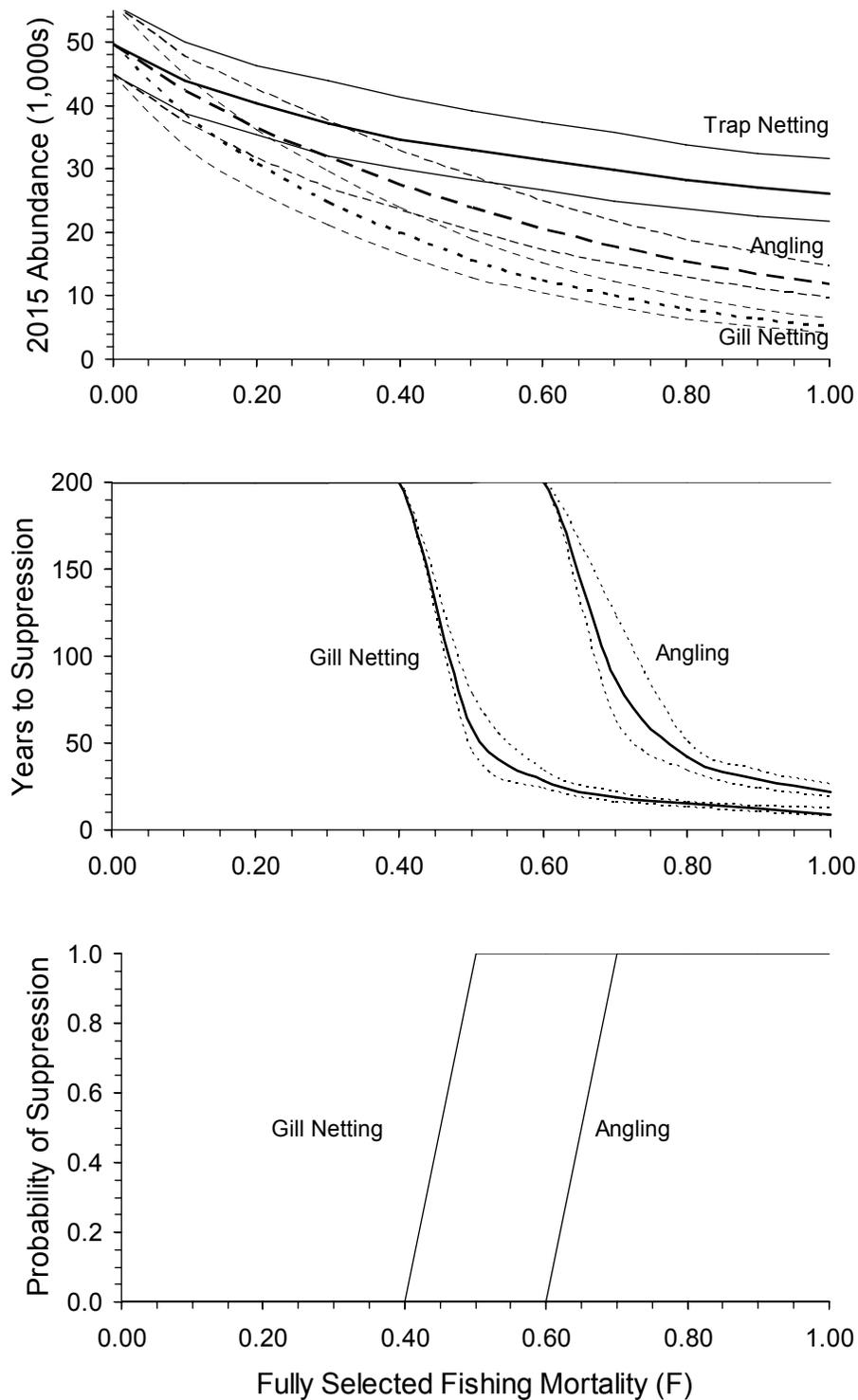


Figure 8. Average abundance in 2015 ($\pm 95\%$ confidence limits; upper panel), years to population collapse ($\pm 95\%$ confidence limits; middle panel), and probability of population collapse (lower panel) for lake trout subjected to a range of fishing mortality rates by three capture methods in Lake Pend Oreille, Idaho.

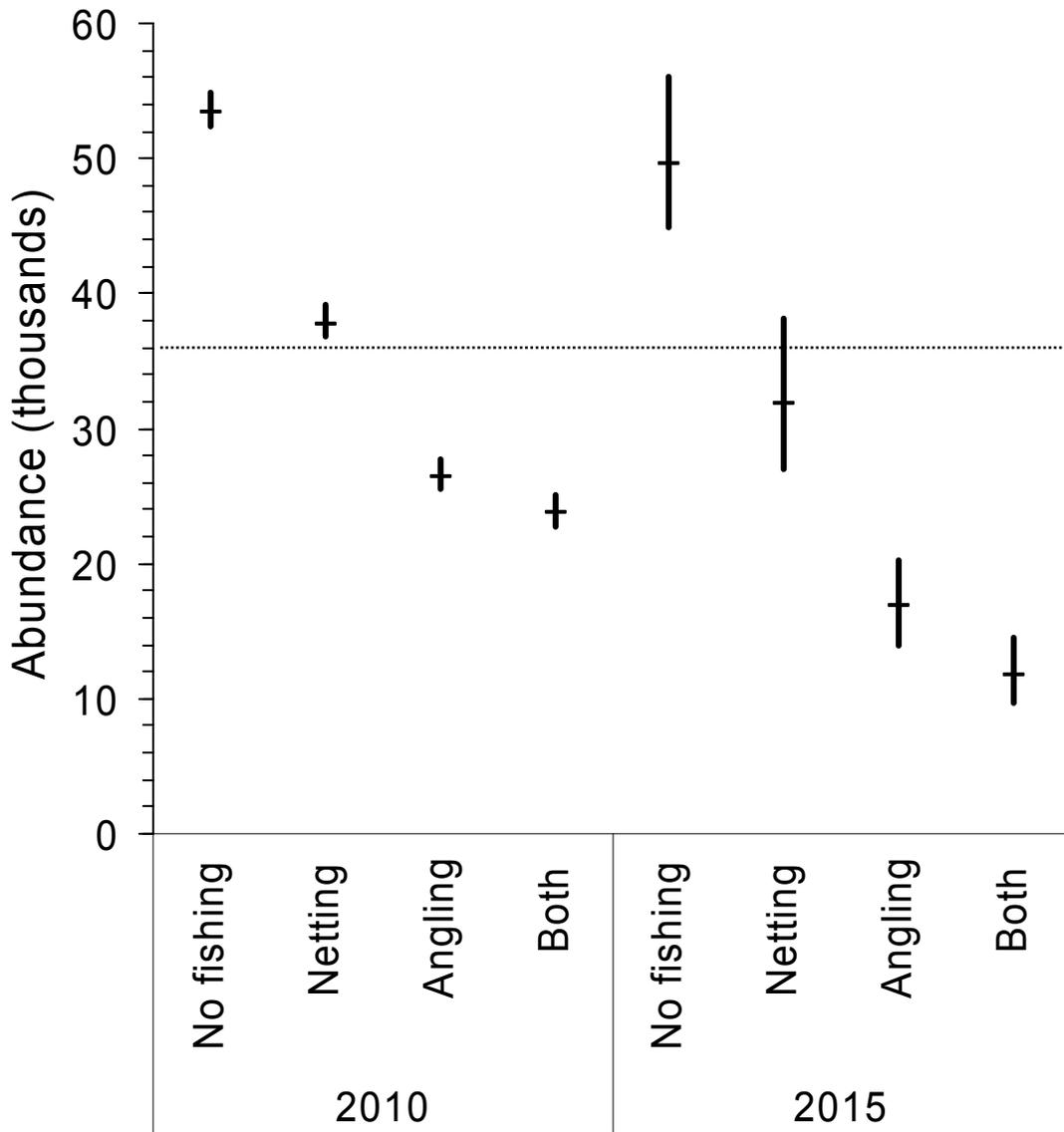


Figure 9. Average abundance of lake trout in Lake Pend Oreille, Idaho in 2010 and 2015 at fishing mortality rates observed in 2006 for netting, angling, and all methods combined. The horizontal line depicts abundance in 2006.

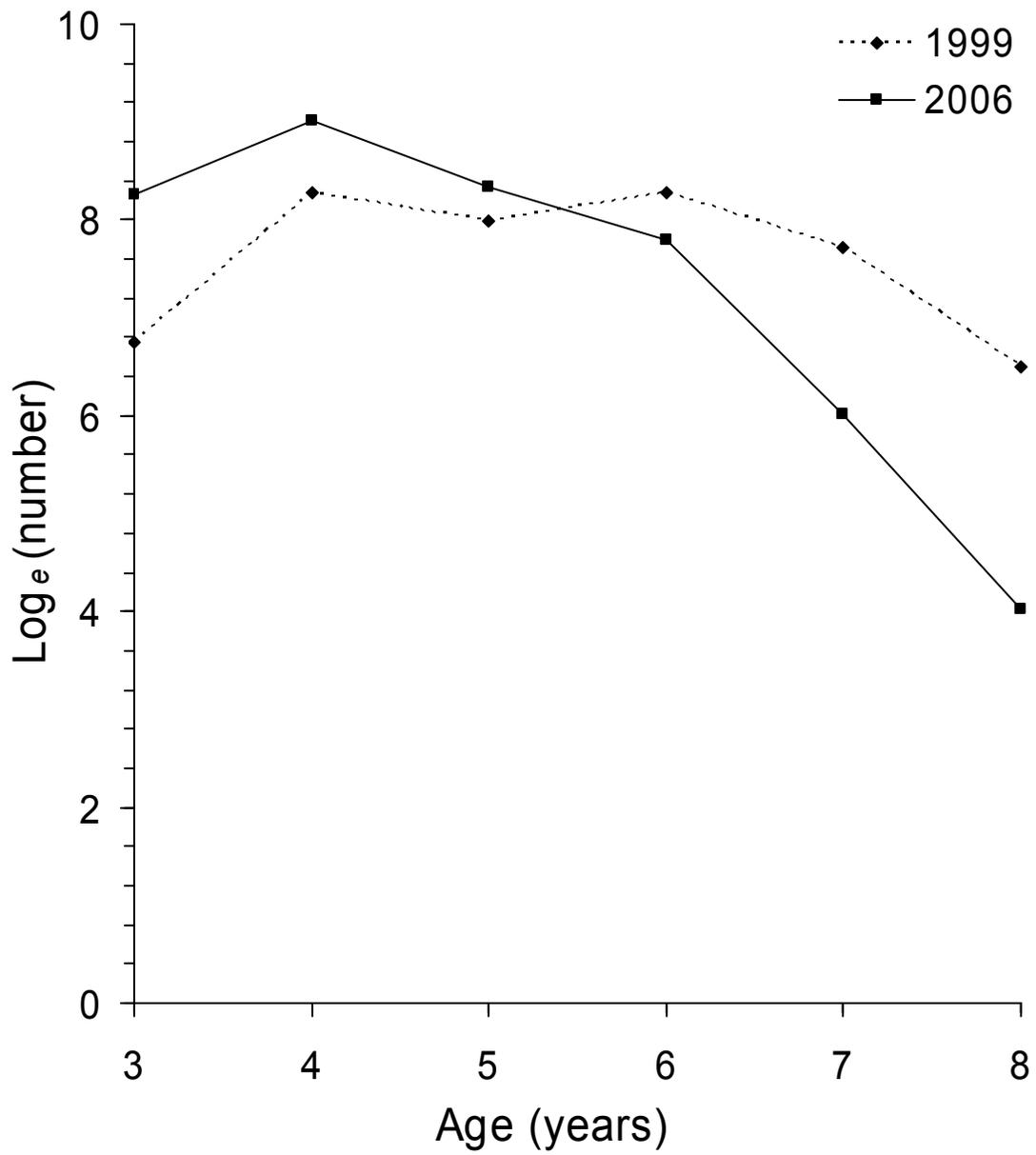


Figure 10. Logarithms of numbers of lake trout estimated by mark-recapture to be present in each age class in Lake Pend Oreille, Idaho, in spring 1999 and spring 2006.

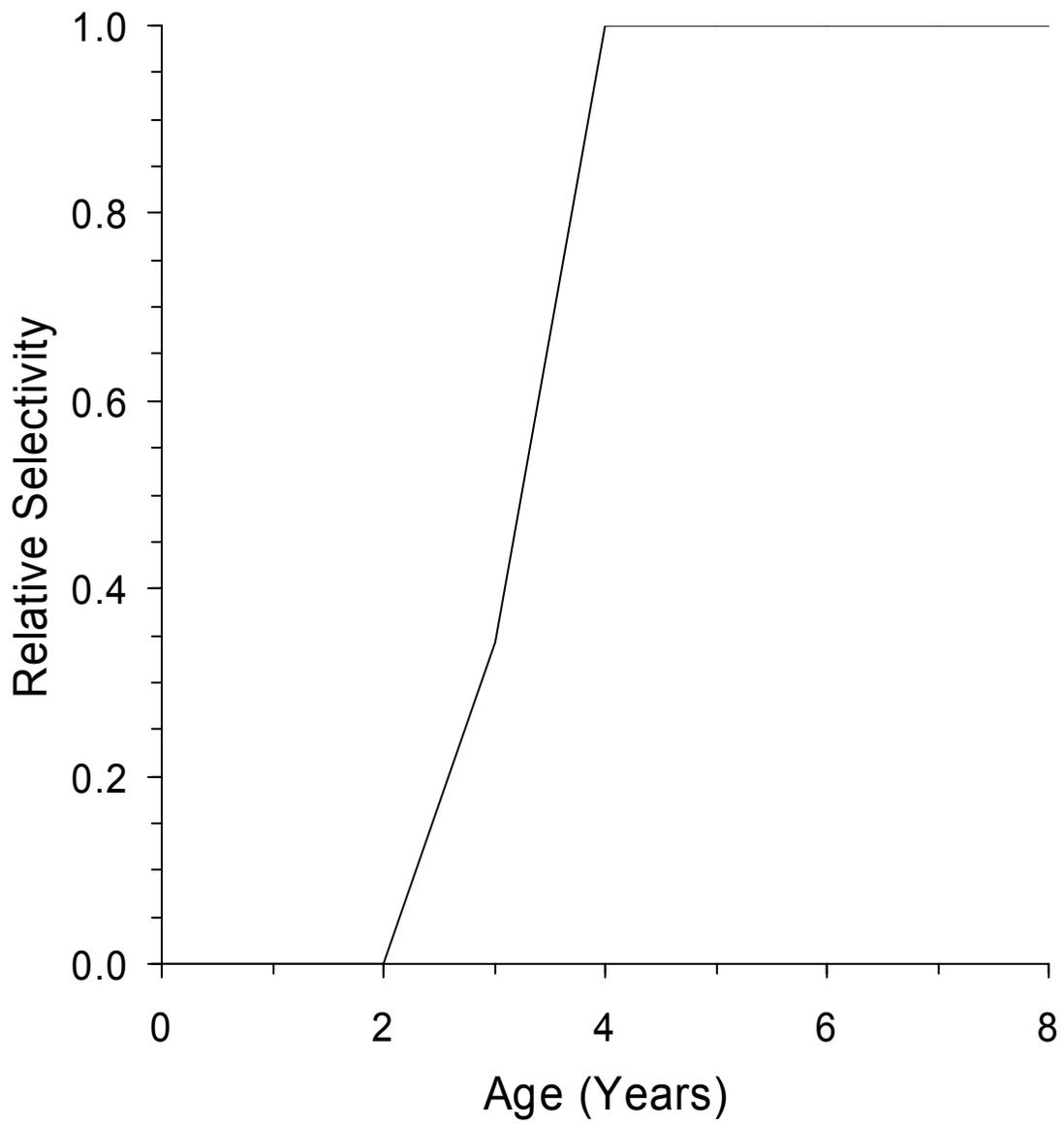


Figure 11. Relative selectivity of angling for age 0–8 rainbow trout in Lake Pend Oreille, Idaho.

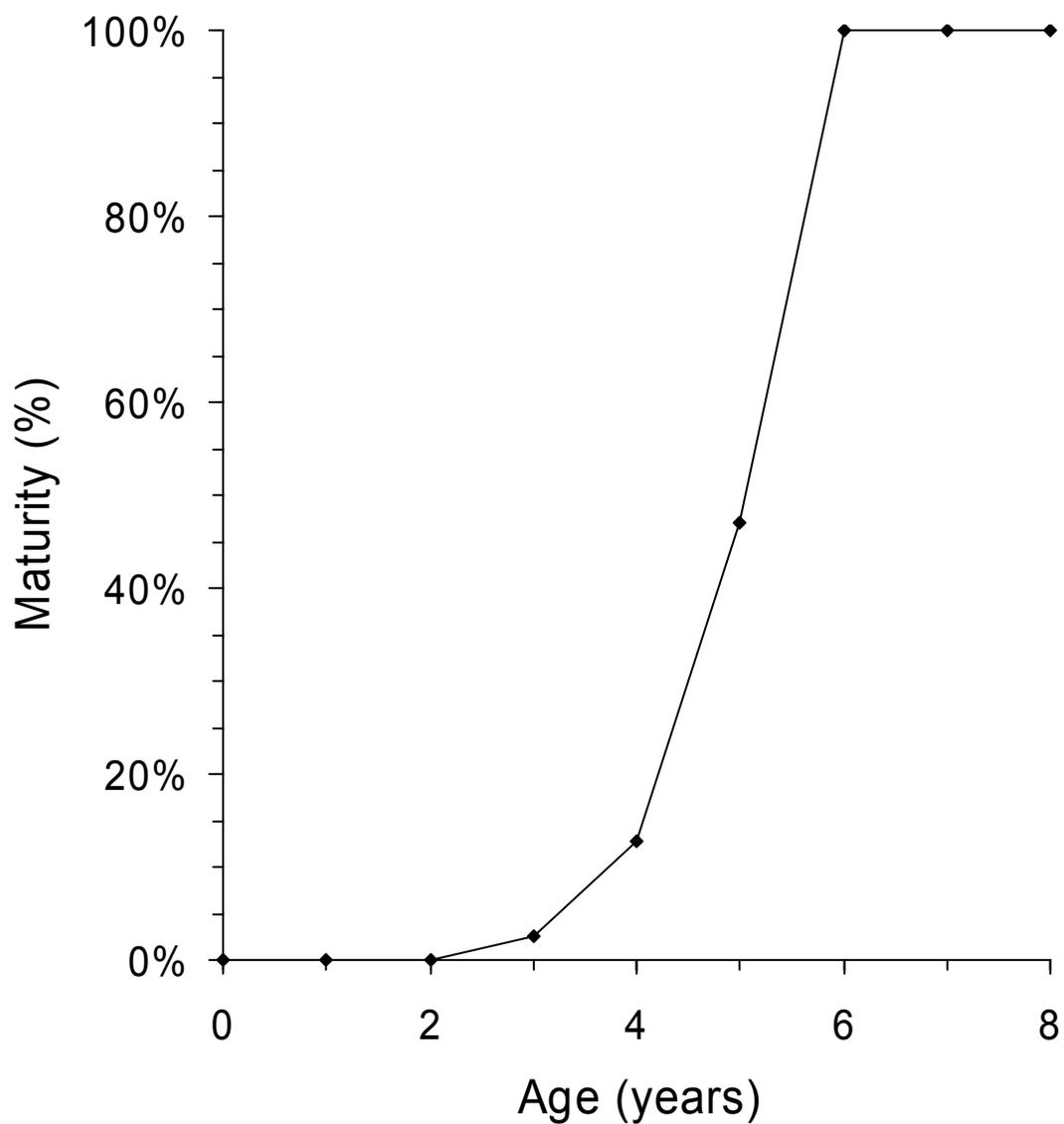


Figure 12. Percentage of mature rainbow trout at ages 0–8 caught by anglers in Lake Pend Oreille, Idaho, between April 29 and May 7, 2006.

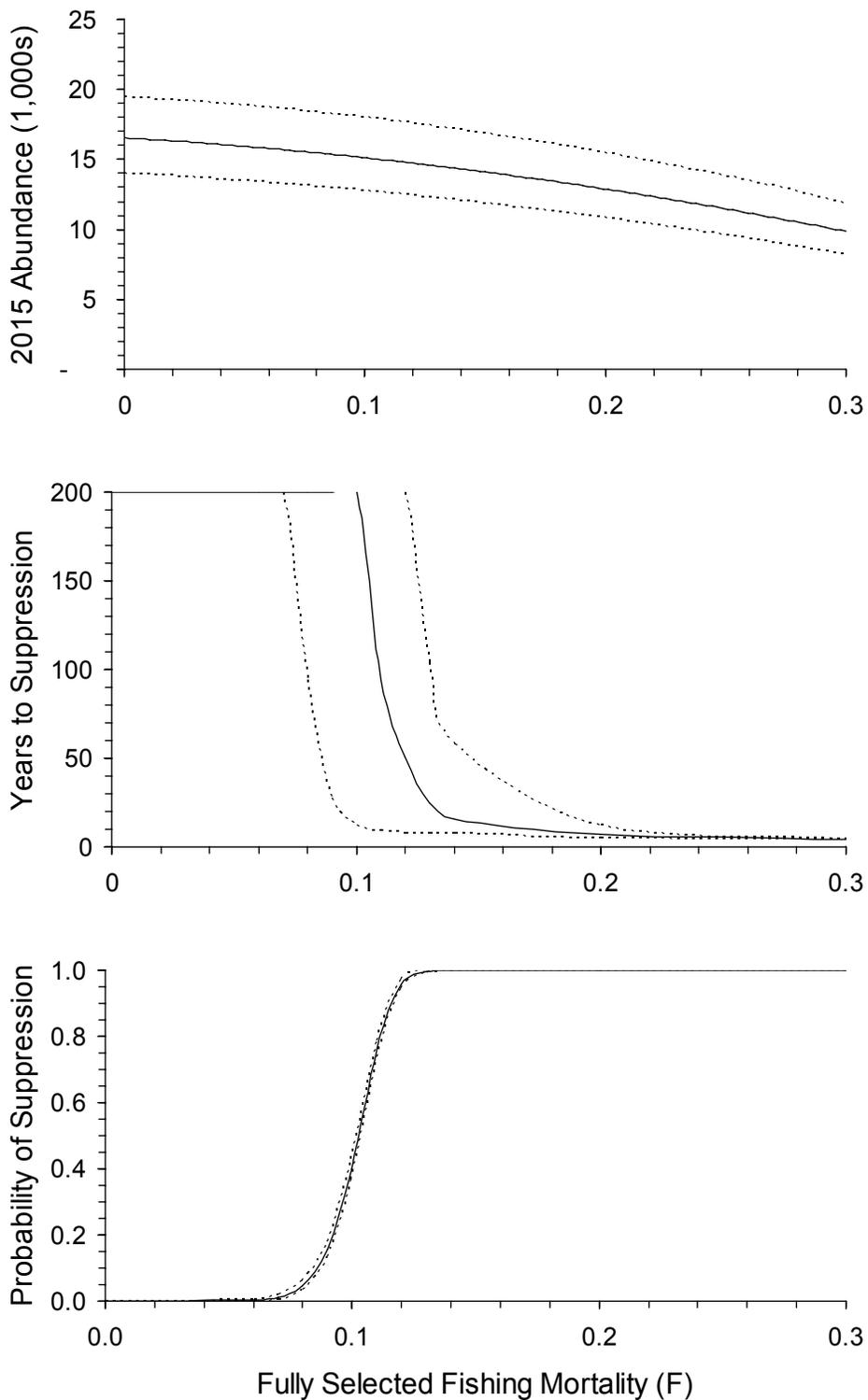


Figure 13. Average abundance in 2015 ($\pm 95\%$ confidence limits; upper panel), years to population suppression ($\pm 95\%$ confidence limits; middle panel), and probability of population suppression (lower panel) for rainbow trout subjected to a range of fishing mortality rates by angling in Lake Pend Oreille, Idaho.

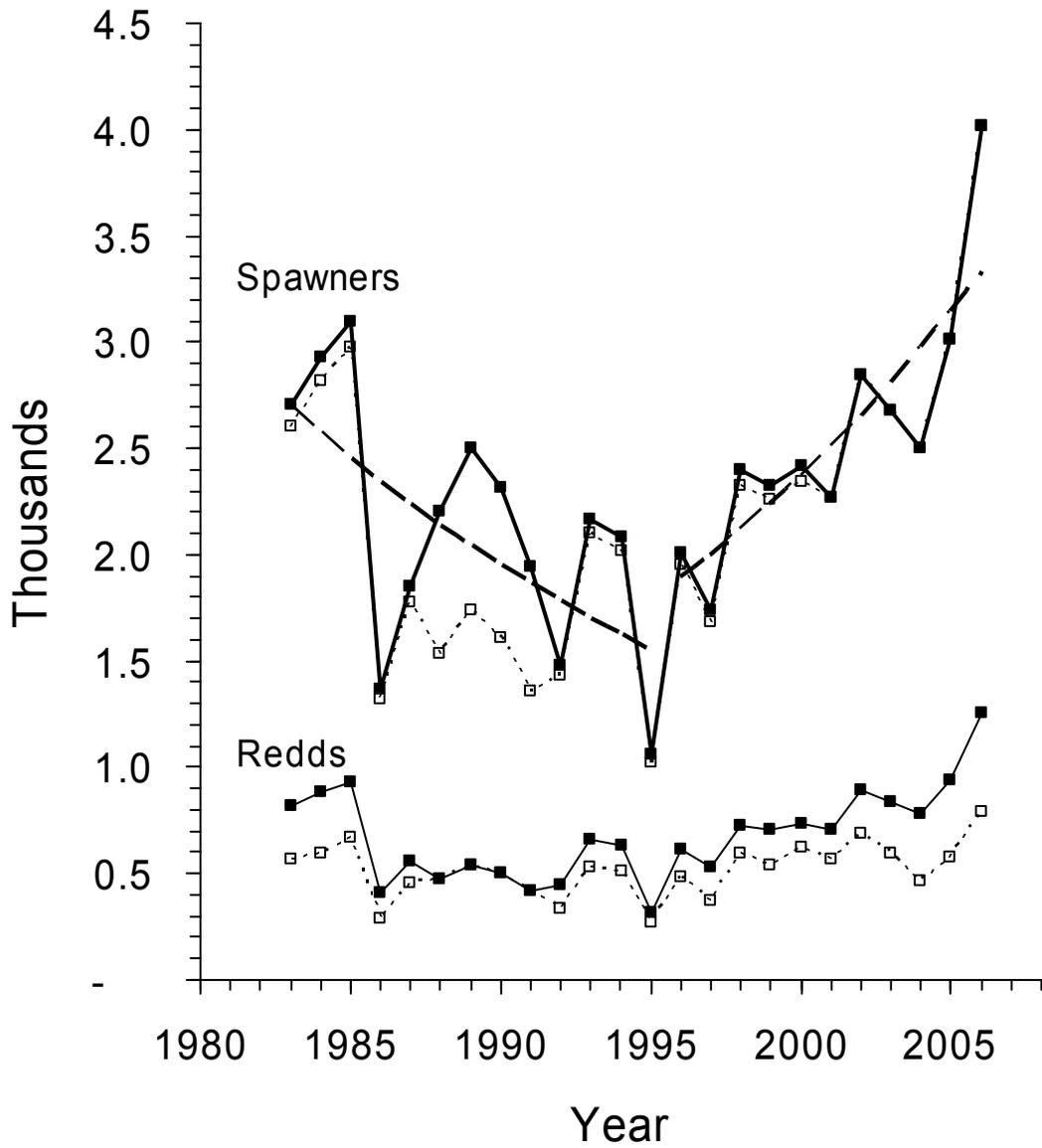


Figure 14. Numbers of redds counted and number of adults spawning in tributary streams of Lake Pend Oreille, Idaho, during 1983–2006. For redds, open boxes show redds counted in six index streams, and closed boxes show redds counted in all streams. For spawners, open boxes show spawners estimated by expanding redds by 3.2 spawners/redd, and closed boxes show spawners estimated by expanding surveyed streams to all streams.

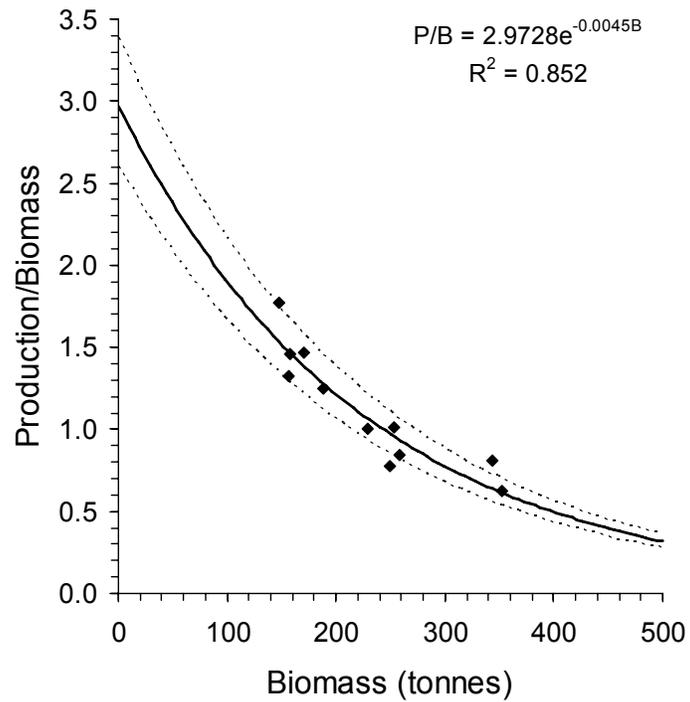
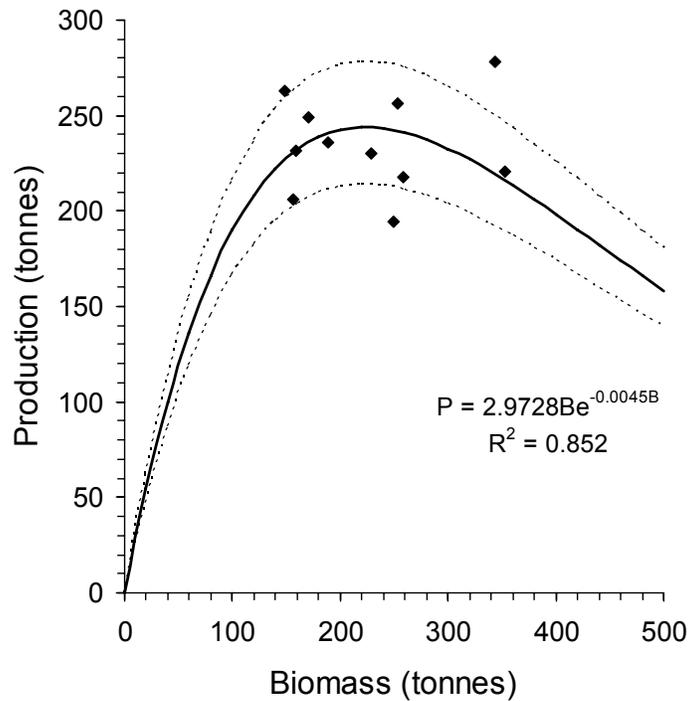


Figure 15. Production versus biomass (upper panel) and production/biomass versus biomass (lower panel) for kokanee in Lake Pend Oreille, Idaho, during 1995–2006. Black diamonds show estimates of annual production and biomass (Maiolie et al. 2004; updated through 2006 with unpublished data). Curves show production predicted from biomass (geometric mean production \pm one standard error).

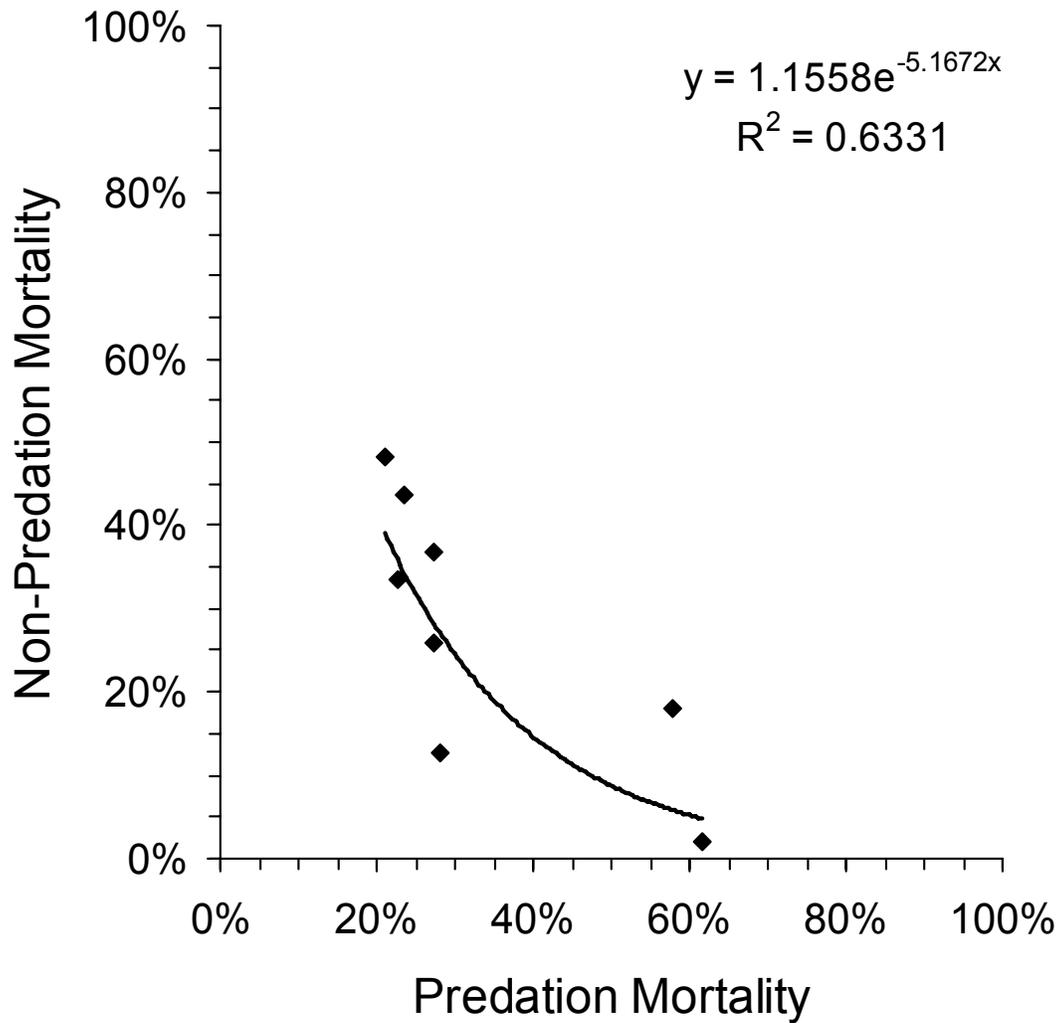


Figure 16. Non-predation mortality (%) versus predation mortality (%) for kokanee in Lake Pend Oreille, Idaho, during 1999–2006. Black diamonds show estimates of non-predation mortality rate derived from the difference between total yield (Maiolie et al. 2004; updated through 2006 with unpublished data) and consumption by lake trout, rainbow trout, and bull trout (this study). The curve shows non-predation mortality predicted from predation mortality.

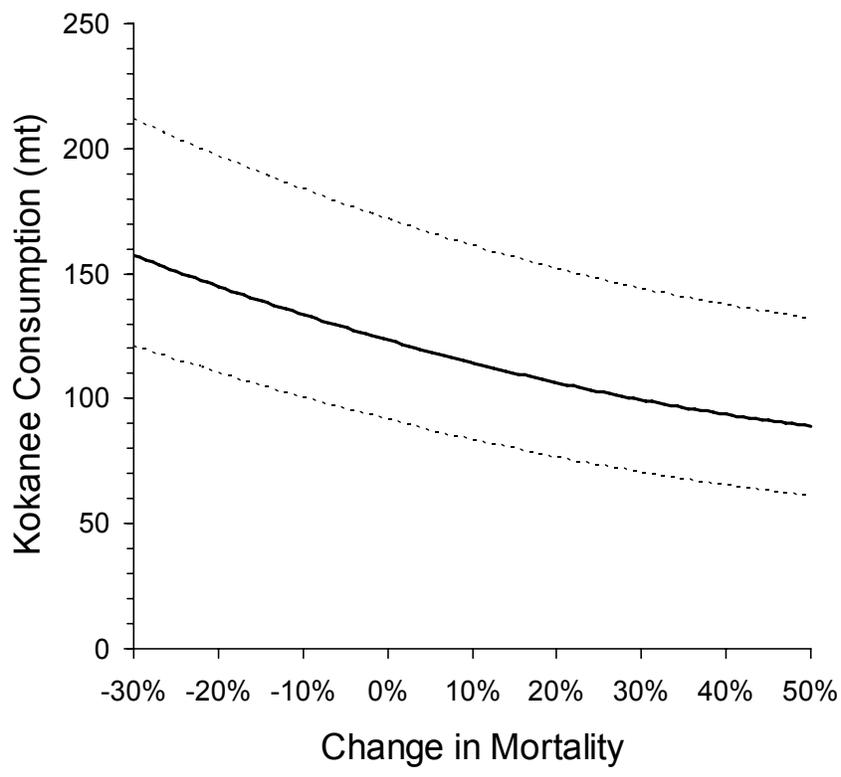
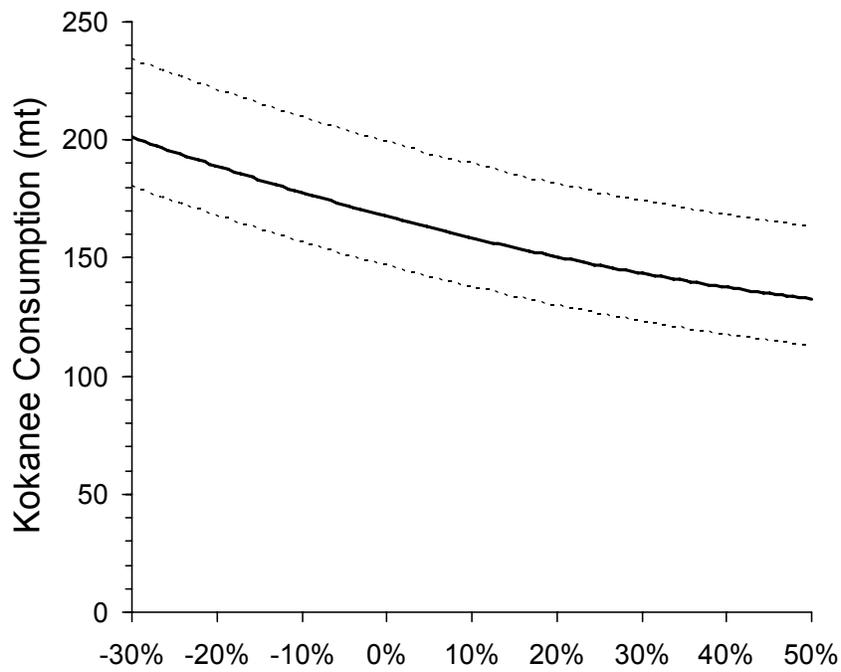


Figure 17. Total consumption of kokanee by lake trout, rainbow trout, and bull trout (tonnes) in relation to relative changes in the fishing mortality rate (%) exerted on lake trout and rainbow trout in 2006 in Lake Pend Oreille, Idaho in 2010 (top panel) and 2015 (bottom panel).

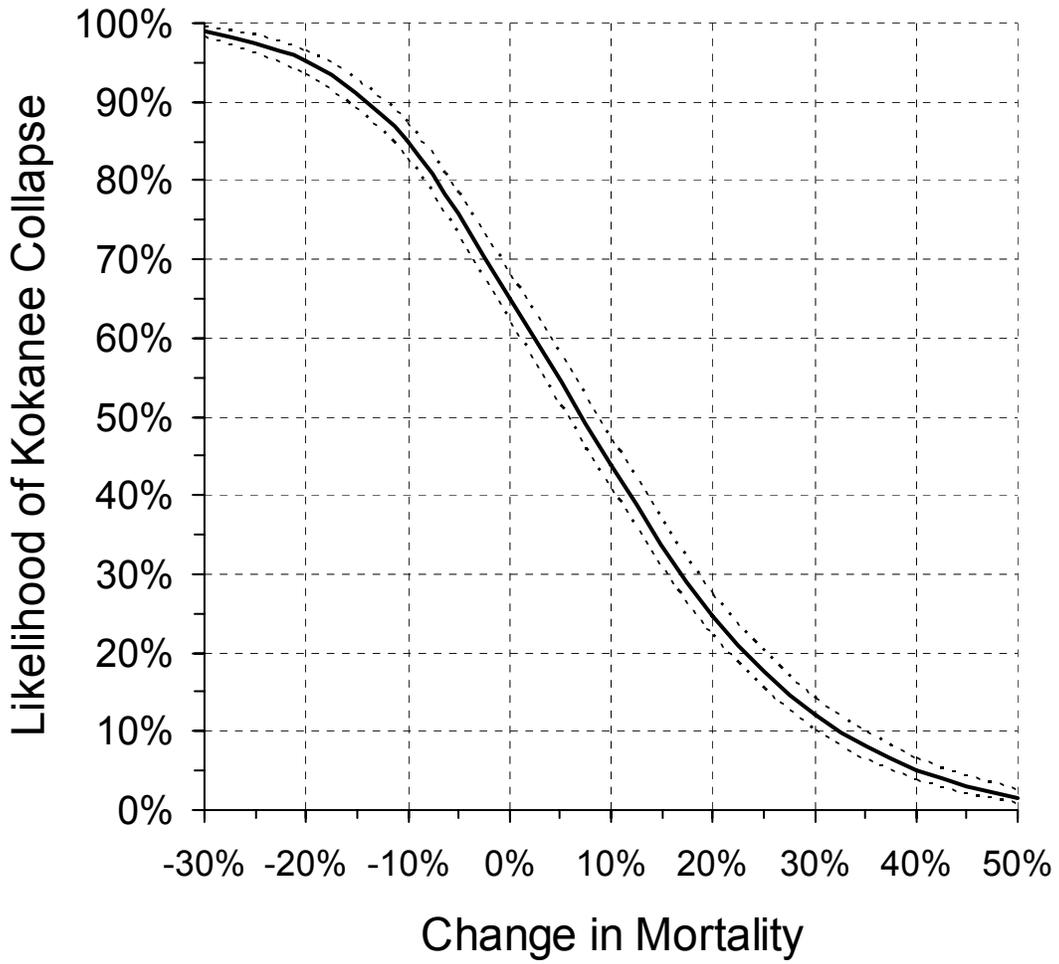


Figure 18. Likelihood of collapse for kokanee in Lake Pend Oreille in relation to relative changes in the fishing mortality rate (%) exerted on lake trout and rainbow trout in 2006 in Lake Pend Oreille, Idaho.

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