

Salmonid predator–prey dynamics in Lake Pend Oreille, Idaho, USA

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Abstract Our objective was to evaluate the 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, Idaho, USA, while providing for bull trout *Salvelinus confluentus* and kokanee *Oncorhynchus nerka* recovery. In order to achieve our objective, we developed a density-dependent stochastic predator–prey simulation model for the three major predators (lake trout, rainbow trout, and bull trout) 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 by 38%. Abundance of adult bull trout increased by 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 would increase by 20% if fishing mortality on lake trout and rainbow trout declined by 30% from 1996 levels, and would decrease by 14% if fishing mortality on lake trout and rainbow trout increased by 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. Therefore, fishing mortality would need to be at least 6% higher on both lake trout and rainbow trout to reduce the likelihood of kokanee collapse to 50%. We conclude that kokanee biomass is presently out of balance with predation in Lake Pend Oreille, because kokanee production cannot compensate for all predation loss. Our findings suggest that a combination of unusually high kokanee production and unusually low predation are 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, and so is generally thought to be susceptible to over-fishing (Healey, 1978; Martin & Olver, 1980). For example, the largest populations of lake trout in the world, those residing in the Laurentian Great Lakes, declined in abundance from over-fishing 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 & Alger, 1993). A crucial precursor for lake trouts to achieve dominance in many western lakes was the 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 & 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, 2008). In 1999, lake trout exerted insignificant predation on kokanee (2% of kokanee production), compared to rainbow trout (53%) and bull trout (10%) predation on kokanee production (Vidergar, 2000). However, after 1999, 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., 2006). Lake trouts were also thought to present a threat to the bull trout population through competition for prey (Donald & Alger, 1993; Fredenberg, 2002). In response to the increase in the lake trout population, 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 on Lake Pend Oreille (Hansen et al., 2007, 2008). 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%; Hansen et al., 2007, 2008) mostly exceeded the 50% threshold beyond which the species generally declines in abundance (Healey, 1978).

Our objective was to evaluate the long-term sustainability of lake trout and rainbow trout under varying levels of fishing mortality in Lake Pend Oreille, while providing for bull trout and kokanee recovery. In order to achieve our objective, we 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.

Study area

Lake Pend Oreille, located in north Idaho, is the largest lake of Idaho, 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 (Fig. 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).

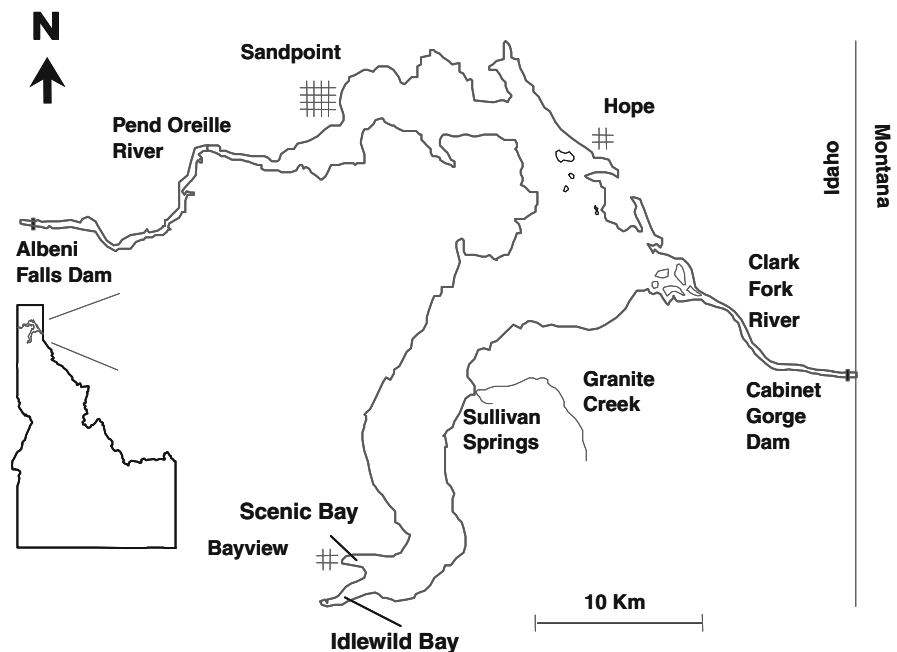
Lake Pend Oreille is a temperate, oligotrophic lake. Summer water temperature (May–October) averages about 9°C in the upper 45 m of water (Rieman, 1977). Surface temperatures are as high as 24°C in hot summers. Thermal stratification occurs from late June to September, and the thermocline is usually at depths of 10–24 m. Steep, rocky slopes occur along most of the largely undeveloped shoreline, so that 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. At present, 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*, redbreast 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., 2008). 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 (77%), lake trout (87%), and bull trout (66%), whereas only large northern pikeminnow (≥ 305 mm) prey mostly on kokanee (Vidergar, 2000).

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



Methods

Overall model structure

The predator–prey model included sub-models for populations of the three major predator species (lake trout, rainbow trout, and bull trout) and the single prey species (kokanee). Sub-models for the three predators produced estimates of predation by each predator that added up to total predation on kokanee (part of total kokanee yield). In order to enable modeling of age-specific fishing mortality on lake trout and rainbow trout, sub-models for these two species were age-structured density-dependent stochastic simulation models, based on biological attributes of and fisheries for both species in Lake Pend Oreille. Fishing for bull trout was prohibited, and so age-specific mortality was not required for modeling population dynamics of this species and the sub-model for bull trout was treated as a logistic population growth model, based on annual redd counts in spawning streams of Lake Pend Oreille. In order to enable modeling predation (yield) on kokanee, the sub-model for kokanee was a production–biomass model, based on estimated production, biomass, and yield (sum of predation and non-predation mortality) 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 sub-model

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 & Deriso, 1999; Haddon, 2001):

$$N_{i+1, j+1} = N_{ij}e^{-Z_{ij}} \quad (1)$$

Numbers present in each age class j for the first year of the simulation $i = 0$ were specified as model inputs (Table 1), from the total number estimated by mark-recapture at the end of 2005 (Hansen et al., 2007, 2008), the length frequency of a gillnet sample

in spring 2006 (Hansen et al., 2007, 2008), and the age–length key described below. We assumed that the length frequency of fish caught in gillnets in spring 2006 represented the population of all the lake trouts (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).

The population age structure for the simulation model was estimated from a subsample of lake trouts collected during trap netting, gillnetting, and angling on Lake Pend Oreille between October 12, 2003 and June 1, 2004 (Hansen, 2007). Lake trouts 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 sanded 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 40–100 \times 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-cm length classes (rows) for sub-sampled 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.

The total instantaneous mortality rate Z_{ijk} for each age j in each gear k 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_{ijk}) for each age j in each gear k and year i :

$$Z_{ijk} = F_{ijk} + M \quad (2)$$

Total instantaneous natural mortality (M ; Table 2) was estimated from Pauly's equation using parameters

Table 1 Age-specific abundance, relative selectivity, maturity, and kokanee consumption for lake trout and rainbow trout in Lake Pend Oreille, Idaho

Species	Age (<i>j</i>)	Number ($N_{i=2005, j}$)	Relative selectivity (S_{jk})			Maturity (M_j)	Kokanee (kg/fish)
			Trap Net	Gill Net	Angling		
Lake trout	0	36,910	0.0000	0.0000	0.0000	–	0.0
	1	27,255	0.0000	0.0000	0.0000	–	0.0
	2	20,126	0.0000	0.0000	0.0000	–	0.0
	3	14,861	0.0002	0.0183	0.0008	–	0.0
	4	10,974	0.0059	0.2522	0.0850	–	1.4
	5	9,410	0.0655	1.0000	0.5693	–	2.3
	6	8,652	0.2146	1.0000	0.8518	–	3.0
	7	3,952	0.5794	1.0000	1.0000	–	3.7
	8	2,267	0.9327	1.0000	0.7095	–	4.4
	9	1,889	1.0000	1.0000	0.4699	–	5.0
	10	1,711	0.9205	1.0000	0.3682	–	5.5
	11	1,443	0.8191	1.0000	0.3313	–	5.8
	12	1,118	0.6795	1.0000	0.3093	–	6.1
	13	819	0.5387	1.0000	0.3062	–	6.3
	14	566	0.4253	1.0000	0.3068	–	6.4
	15	383	0.3429	1.0000	0.2879	–	6.5
	16	248	0.2866	1.0000	0.2498	–	6.7
	17	144	0.2461	1.0000	0.2202	–	6.9
	18	70	0.2204	1.0000	0.1784	–	7.1
	19	27	0.1954	1.0000	0.1522	–	7.4
20	10	0.1911	1.0000	0.1409	–	8.1	
Rainbow trout	0	28,960	–	–	0.0000	0.0000	0.0
	1	21,139	–	–	0.0000	0.0000	0.0
	2	15,430	–	–	0.0000	0.0000	0.0
	3	11,263	–	–	0.3434	0.0256	0.0
	4	8,221	–	–	1.0000	0.1282	4.8
	5	4,180	–	–	1.0000	0.4701	5.5
	6	2,429	–	–	1.0000	1.0000	7.5
	7	407	–	–	1.0000	1.0000	13.1
	8	56	–	–	1.0000	1.0000	17.0

of the Von Bertalanffy length–age model (L_∞ , K ; Hansen, 2007) 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).

Growth parameters for estimating the instantaneous natural mortality rate were estimated for the Von Bertalanffy length–age model (Hansen, 2007):

$$L_j = L_\infty \left(1 - e^{-K(j-j_0)}\right) e^{\varepsilon_j} \quad (3)$$

In the length–age model, L_∞ = asymptotic length for an average fish in the population (953 mm), K = the instantaneous rate at which an average fish of age j grows from L_j to L_∞ (0.164/year), 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.

Table 2 Parameters of a predator–prey simulation model for Lake Pend Oreille, Idaho

Sub-model	Parameter	Estimate
Lake trout	Trap-net fishing mortality ($F_{i=2005, k=gill}$)	0.5006
	Gill-net fishing mortality ($F_{i=2005, k=trap}$)	0.0199
	Angling fishing mortality ($F_{i=2005, k=angling}$)	0.7463
	Instantaneous natural mortality (M)	0.2084
	Recruitment alpha (α)	5.698
	Recruitment beta (β)	0.00007851
	Recruitment error (ε)	0.1974
Rainbow trout	Angling fishing mortality ($F_{i=2005, k=angling}$)	0.2949
	Instantaneous natural mortality (M)	0.3170
	Recruitment alpha (α)	7.488
	Recruitment beta (β)	0.00013473
	Recruitment error (ε)	0.1900
Bull trout	Starting abundance ($N_{i=2005}$)	4,019
	Population growth Rate (r)	0.05642
	Carrying capacity (K)	5,306
	Model error (ε)	0.1180
	Kokanee consumption (kg/fish)	1.856
Kokanee production	Starting biomass ($B_{i=2005}$)	100,200
	Production/consumption (α)	2.973
	Density dependence (β)	0.004480
	Model error (ε)	0.1313
Kokanee non-predation mortality	Maximum non-predation mortality (α)	1.156
	Exponential rate of decline (β)	-5.167

The fishing mortality rates for lake trout and rainbow trout baseline rates, around which a range of simulated rates were evaluated (lake trout, $F = 0.0$ – 1.0 ; rainbow trout, $F = 0.0$ – 0.3)

Total instantaneous fishing mortality F_{ijk} for each age j in each gear k and year i was simulated from the relative selectivity S_{jk} of the gear k for lake trout of age j and the fully selected fishing mortality rate F_{ik} of the gear k for each year i (Hansen, 2007):

$$F_{ijk} = S_{jk}F_{ik} \quad (4)$$

Fully selected fishing mortality F_{ik} 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 ($k =$ 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 (Table 2). Age-specific selectivity, $s_{jk} = C_{jk}/N_j$, was estimated for gill nets, trap nets, and angling from age-specific catches C_{jk} at age j in each gear k (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, 2007). Relative selectivity, $S_{jk} = s_{jk}/\max(s_{jk})$, for each capture method k was then estimated as age-specific selectivity divided by the maximum age-specific selectivity (Table 1).

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):

$$N_{i+1, j=0} = \alpha(N_{i, j=8+}) (e^{-\beta N_{i, j=8+}}) e^\varepsilon \quad (5)$$

In the stock–recruit model, $\alpha =$ recruits per adult at low adult density, $\beta =$ the instantaneous rate at which recruits/adult declines with adult density, and $\varepsilon =$ multiplicative process error. Adults were the total number of lake trout vulnerable to trap netting (sum product of the number present N_{ij} at age j in year i and the relative selectivity S_j of trap netting for age j). 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, we assumed that the reproductive rate (α) and recruitment variability (ε) were constant within species (Myers et al., 1999; Myers, 2002). Therefore, we used the same reproductive rate (α) and recruitment variation (ε) for the lake trout population in Lake Pend Oreille estimated for the lake trout population in eastern Lake Superior (Table 2; Nieland, 2006). Next, Lake Superior and Lake Pend Oreille have similar bathymetry and habitat features (Hansen et al., 2007, 2008). Therefore, we scaled the instantaneous rate of density dependence in Lake Pend Oreille (β) based on the amount of surface area (11,568 ha) that lies over depths (<70 m; Hansen et al., 1995) that are suitable for lake trout (Table 2; Lake Superior = 280,772 ha; $\beta = 3.235 \times 10^{-6}$; Nieland, 2006).

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 consumed an insignificant fraction of the kokanee population (Vidregar, 2000). 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 sub-model

The rainbow trout sub-model was identical in form to the lake trout sub-model, 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 (Table 1). Second, instantaneous natural mortality (M) was estimated from catch curves and exploitation rates in 1999 and 2006 (Table 2). 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 (Table 1), 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 (Table 2).

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, Idaho Department of Fish and Game [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 40–100 \times 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 sub-sampled 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 ($u = R/M$, where u = exploitation rate, R = number of previously tagged rainbow trout that were recaptured, and M = number of rainbow trout previously tagged) and instantaneous total mortality ($F = uZ/A$, where $A = 1 - e^{-Z}$; Ricker, 1975). Last, instantaneous natural mortality in each year was estimated from instantaneous total and fishing mortality (Table 2; $M = Z - F$).

Age-specific selectivity, $s_j = C_j/N_j$, was estimated for 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. In order 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 (Table 1). Relative selectivity, $S_j = s_j/\max(s_j)$, was then estimated as the age-specific selectivity divided by the maximum age-specific selectivity (Table 1).

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 sampled in Lake Pend Oreille. We estimated the proportion of mature fish M_j in each age class j as the total number of mature rainbow trouts in each age class, divided by the total number of mature fish sampled, scaled to the maximum proportion mature in any single age class (Table 1; data from studies in 1972–1976, 1983–1984, and 1997–1998, summarized by Vidergar, 2000). 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 (Maiolie et al., 2008), the length frequency of angler-caught fish caught during 2006 (Maiolie et al., 2008), and the age-length key described above (Table 1). We 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 trouts that was recruited to the population in each year was predicted from the number of adult rainbow trouts that spawned in the previous year using a Ricker stock–recruit model, as for lake trout (Ricker, 1975). For the stock–recruit model, model parameters (α , β , and ε) were derived from estimates for rainbow trout abundance in Lake Pend Oreille in 1999 and 2006 (Table 2; Vidergar, 2000; Maiolie et al., 2008). First, we estimated the number of age-0 rainbow trout that was 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). These catch-curve-based estimates were plausible, based on comparisons to mark-recapture estimates of rainbow trout (Maiolie et al., 2008). Next, we 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, we estimated the peak of the stock–recruit curve ($X = 1/\beta$, $Y = \alpha/\beta e$; Ricker) from the average number of adults ($\beta = 1/7422$) and recruits ($\alpha = 20466/7422e$) in 1999 and 2006. Last, we 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.

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 (Vidregar, 2000). 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 sub-model

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 & Jakubowski, 2006). The number 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 the number of 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 (Vidregar, 2000) to the estimated number of adult bull in Lake Pend Oreille during 1999 (as described above).

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

$$N_{t+1} = N_t e^{r(1-\frac{N_t}{K})+\varepsilon} \quad (6)$$

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 (Table 2). 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:

$$N_{t+1} = N_t e^{r+\varepsilon} \quad (7)$$

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, we 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 (Table 2).

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. Recovery plan criteria 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 sub-model

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., 2008). Total consumption of kokanee by lake trout, rainbow trout, and bull trout was estimated from per capita consumption rates of kokanee by each predator species (Table 1; Vidergar, 2000). Non-predation natural mortality of kokanee was modeled from differences between estimated yield of kokanee during 1995–2006 (Maiolie et al., 2008) and estimated total predation on kokanee in the same years (described above).

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 :

$$B_t = B_{t-1} + P_t - Y_t \quad (8)$$

Starting biomass of kokanee B_{t-1} was assumed to be the estimated biomass in 2006 (Table 2; Maiolie et al., 2008).

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:

$$P_t = \alpha B_{t-1} (e^{-\beta B_{t-1}}) e^\varepsilon \quad (9)$$

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 (Table 2). Parameters of the model were estimated with linear regression from biomass and production during 1995–2006 (Maiolie et al., 2008) on the \log_e -transformed version of the model:

$$\log_e(P_t/B_{t-1}) = \log_e(\alpha) - \beta B_{t-1} + \varepsilon \quad (10)$$

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 (Table 1; Vidergar, 2000). Non-predation mortality was estimated in future years from the relationship between kokanee consumption (described above) and total yield of kokanee (Maiolie et al., 2008) during 1999–2006:

$$(Y_t - C_t) = \alpha e^{-\beta C_t + \varepsilon} \quad (11)$$

In the mortality model, α = non-predation mortality (%) in the absence of predation, β = the instantaneous rate at which non-predation mortality declines with predation mortality, ε = multiplicative process error, and variables were as defined above (Table 2). Parameters of the model were estimated with linear regression from non-predation and predation mortality rates during 1999–2006 (Maiolie et al., 2008) on the \log_e -transformed version of the model:

$$\log_e(Y_t - C_t) = \log_e(\alpha) - \beta C_t + \varepsilon \quad (12)$$

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/h 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

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 (Fig. 2, 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 (Fig. 2, 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 (Fig. 2, 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 (Fig. 3). 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 the methods combined reduced the population 34% by 2010 and 67% by 2015. Time to suppression was 24 years (20–29 years) for all the 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 the methods combined and angling alone and 0% for gillnetting and trap netting alone.

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 (Fig. 4, upper panel). Time to suppression declined rapidly as F increased from 0.10 to 0.14 (Fig. 4, middle panel). The likelihood of population suppression within 200 years increased sharply as F increased from 0.06 to 0.13 (Fig. 4, lower panel).

Bull trout redd counts and estimated numbers of adults declined during 1983–1995 and increased during 1996–2006 (Fig. 5). During 1983–1995, prior

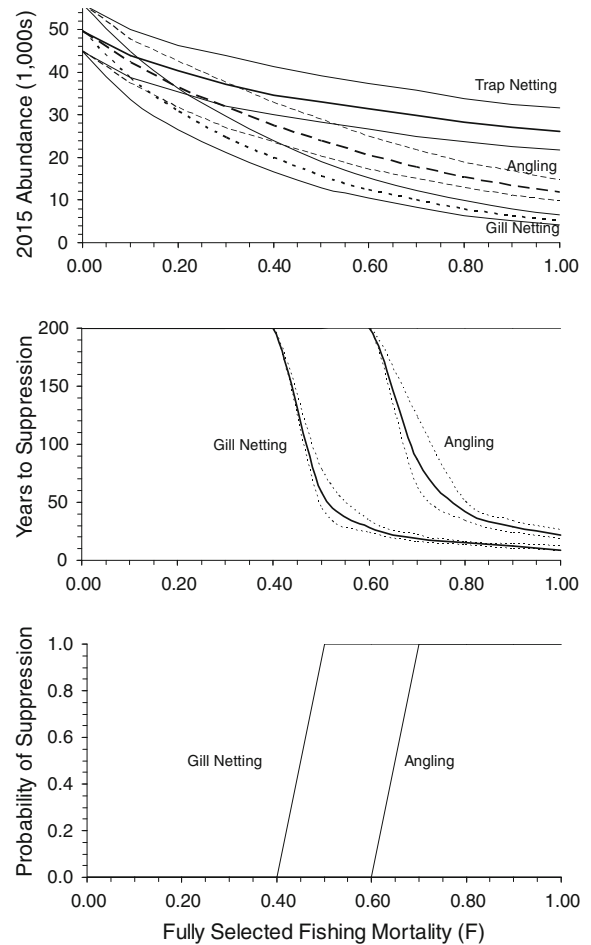


Fig. 2 Average abundance in 2015 ($\pm 95\%$ confidence limits; upper panel), years to population collapse ($\pm 95\%$ confidence limits; middle panel), and probability of population collapse (lower panel) for lake trout subjected to a range of fishing mortality rates by three capture methods in Lake Pend Oreille, Idaho

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 \times 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

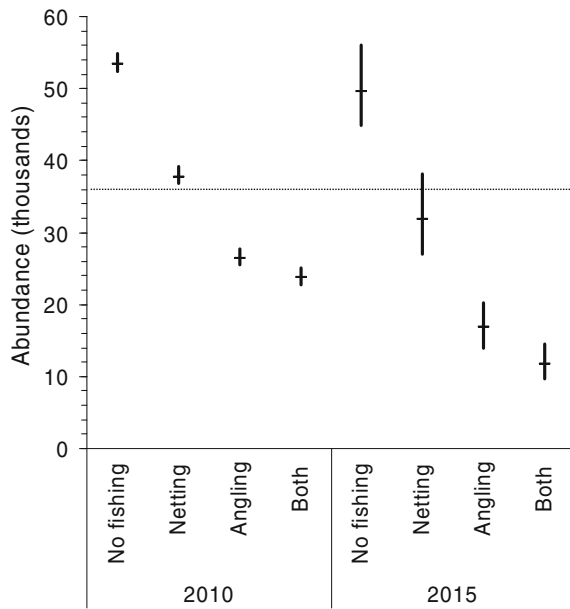


Fig. 3 Average abundance of lake trout in Lake Pend Oreille, Idaho in 2010 and 2015 at fishing mortality rates observed in 2006 for netting, angling, and all methods combined. The horizontal line depicts abundance in 2006

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.

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 the three predators increased from 167 tonnes (146–198 tonnes) to 201 tonnes (181–235 tonnes) if fishing mortality was reduced by 30% from the rate exerted in 2006 and declined to 143 tonnes (123–174 tonnes) if fishing mortality was increased by 30% from the rate exerted in 2006 (Fig. 6). 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

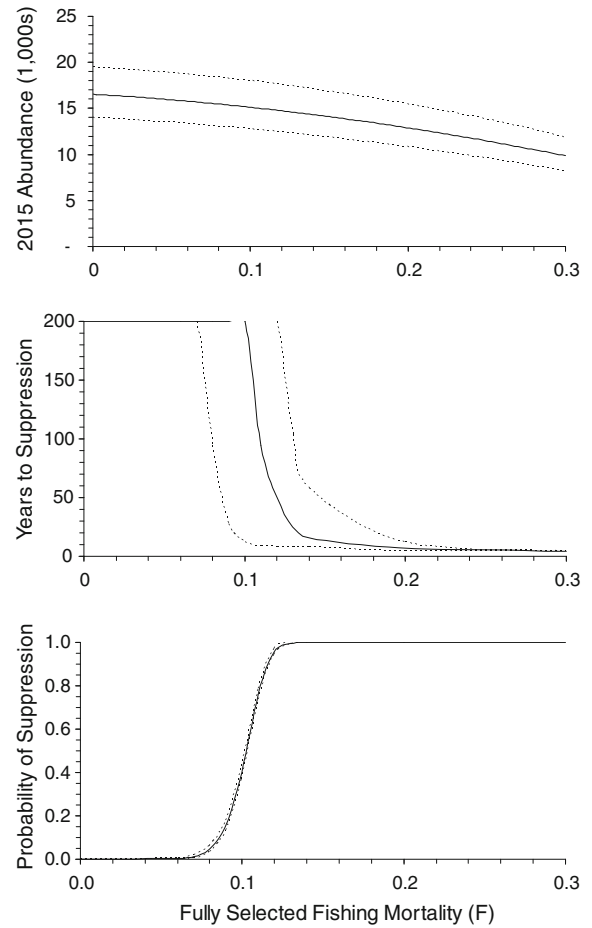


Fig. 4 Average abundance in 2015 ($\pm 95\%$ confidence limits; upper panel), years to population suppression ($\pm 95\%$ confidence limits; middle panel), and probability of population suppression (lower panel) for rainbow trout subjected to a range of fishing mortality rates by angling in Lake Pend Oreille, Idaho

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 (Fig. 6). 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 (Fig. 7). At rates of fishing mortality exerted on lake trout and rainbow trout in 2006 (0% change), the

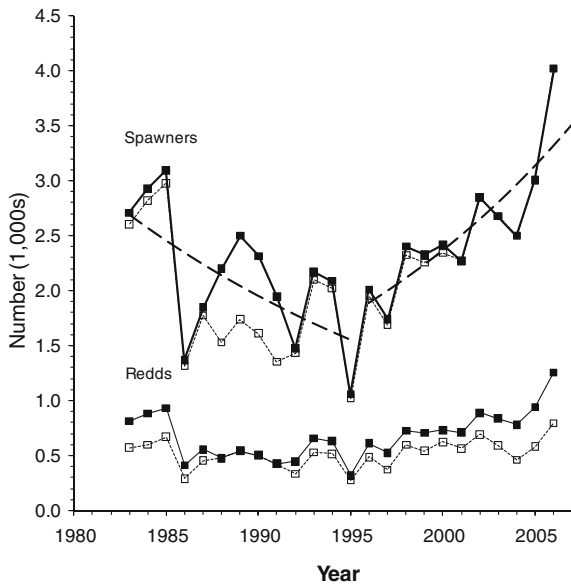


Fig. 5 Numbers of redds counted and number of adults spawning in tributary streams of Lake Pend Oreille, Idaho, during 1983–2006. For redds, *open boxes* show redds counted in six index streams, and *closed boxes* show redds counted in all streams. For spawners, *open boxes* show spawners estimated by expanding redds by 3.2 spawners/redd, and *closed boxes* show spawners estimated by expanding surveyed streams to all streams

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).

Discussion

Our modeling suggests that the predator suppression program in Lake Pend Oreille will greatly reduce the lake trout population, while not greatly affecting the rainbow trout population and elevating the bull trout to become the predominant predator. The net effect of the predator suppression program is a shift in the predominant predator without likely preventing the collapse of kokanee. Nonetheless, a combination of

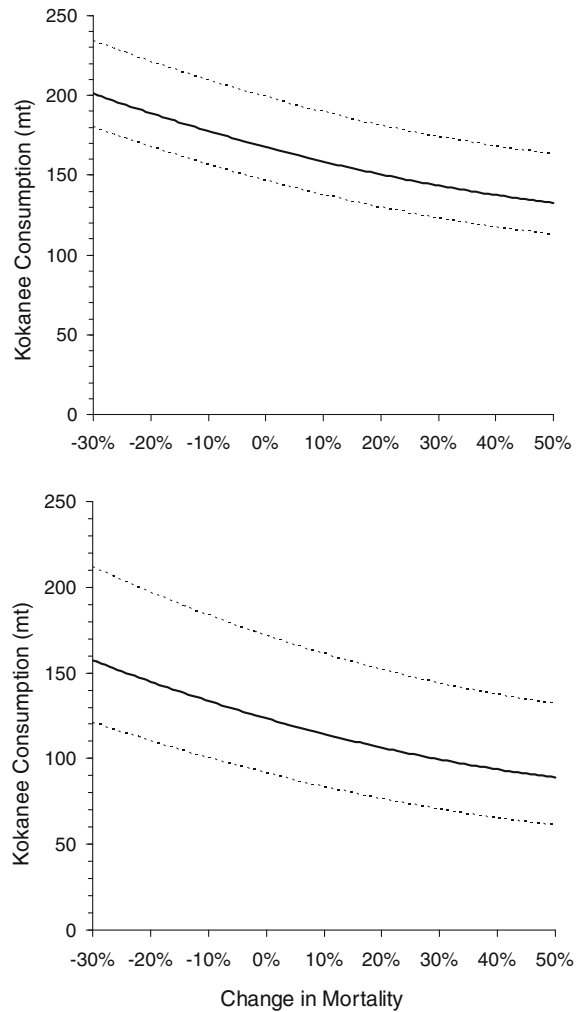


Fig. 6 Total consumption of kokanee by lake trout, rainbow trout, and bull trout (tonnes) in relation to relative changes in the fishing mortality rate (%) exerted on lake trout and rainbow trout in 2006 in Lake Pend Oreille, Idaho in 2010 (*top panel*) and 2015 (*bottom panel*)

lower than average predation and higher than average kokanee production could permit the kokanee population to persist into the future.

Fishing mortality rates exerted on the lake trout population in Lake Pend Oreille in 2006 will likely 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 (Hansen, 2007). Our modeling suggests that

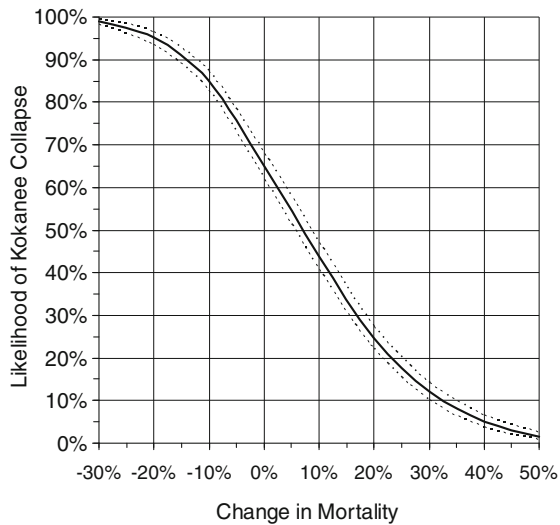


Fig. 7 Likelihood of collapse for kokanee in Lake Pend Oreille in relation to relative changes in the fishing mortality rate (%) exerted on lake trout and rainbow trout in 2006 in Lake Pend Oreille, Idaho

fishing mortality rates exerted in 2006 will suppress the lake trout population 34% by 2010 and 67% by 2015. Achievement of the management objective will require 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. Long-term suppression of the lake trout population will require sustained fishing mortality by gillnetting and angling, which should each be more effective than trap netting for suppressing the lake trout population in Lake Pend Oreille. Our 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). Our results also suggest that angling will be less effective than gillnetting for suppressing the lake trout population because the fully selected fishing mortality rate will need to be higher ($F = 0.6$ –0.7; $A = 0.55$ –0.59), likely because angling removes a smaller fraction of

sub-adult fish from the population for any level of fully selected fishing mortality. Last, our results suggest that trap netting will not be 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).

The fishing mortality rate exerted on the rainbow trout population in Lake Pend Oreille in 2006 will likely 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 (Hansen, 2007). The fishing mortality rate exerted on rainbow trout in 2006 was likely too low to reduce rainbow trout abundance enough to increase kokanee survival. Survival of age 1–2 kokanee in 2006 was only 13%, which continues a steady decline since 2003 (Maiolie et al., 2008) 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. Our modeling suggests that abundance of rainbow trout would decline by 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, and 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.

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, including ≥ 6 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 (Hansen, 2007). 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 the 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.

Fishing mortality rates exerted on lake trout and rainbow trout populations in Lake Pend Oreille in 2006 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; Hansen, 2007). However, our modeling suggests that the kokanee population will likely collapse (65% likelihood) even if fishing mortality rates exerted in 2006 continue in the future. In order 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 our 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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