FISHERY RESEARCH

MARK-RECAPTURE STUDY OF LAKE TROUT USING LARGE TRAP NETS IN LAKE PEND OREILLE

INTERIM PROGRESS REPORT
July 1, 2006 — November 30, 2006

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ABSTRACT

Trap nets were fished from September 10 through December 15, 2005 and gill nets were fished from February 12 to April 6, 2006 to quantify movement and abundance of lake trout *Salvelinus namaycush* in Lake Pend Oreille. Size structure of the lake trout population in Lake Pend Oreille in 2005 was skewed toward fish 50–80 cm long based on trap-netting and 40–80 cm long based on gillnetting. Catch rates of trap nets were generally higher in the central and northern parts of the lake than the southern part of the lake and decreased steadily from the first lift date to the last lift date. Recapture rates of previously tagged lake trout ranged 0–23% at all trap-net locations, except at Sheepherder Point, where the recapture rate was 65%. Recapture rates of previously tagged lake trout were much lower in the northern (16%) and southern (27%) areas of the lake than in the central area of the lake (65%). Abundance of lake trout was about 11,000 adult fish and 36,000 total fish in Lake Pend Oreille on December 15, 2005. Abundance of lake trout estimated by mark-recapture in 1999, 2003, and 2005 in Lake Pend Oreille was nearly perfectly described by a simple exponential growth model, for which the instantaneous rate of growth was $r = 0.428$ and the annual rate of increase was $\lambda = 1.535$. Based on these population growth rates, the adult lake trout population in Lake Pend Oreille would double every 1.6 years and reach 131,000 adult fish by 2010, if the population did not reach carrying capacity sooner. The cause of the recent increase in lake trout abundance is unclear, but population modeling should be used to evaluate sustainability of the population in the face of increased exploitation.

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INTRODUCTION

The Idaho Department of Fish and Game (IDFG) undertook a mark-recapture study to quantify changes in abundance of lake trout *Salvelinus namaycush* in response to a predator removal program in Lake Pend Oreille (Peterson and Maiolie 2005). The motivation to remove lake trout (and rainbow trout *Oncorhynchus mykiss*) from Lake Pend Oreille was based on a goal to sustain kokanee salmon *Oncorhynchus nerka* at levels that would support a recreational fishery. In addition, predation by lake trout (and rainbow trout) was thought to be suppressing the kokanee salmon population to levels that were too low to support a fishery (Maiolie et al. 2002). Last, lake trout were thought to be suppressing the bull trout *Salvelinus confluentus* population, a federally-listed species, through direct competition for prey resources (Donald and Alger 1993; Fredenberg 2002).

The lake trout population appears to have grown rapidly in Lake Pend Oreille in the last decade, so any predator removal program will require accurate targets for removal. Population growth was evident from three recent estimates of lake trout abundance and harvest. First, in 1999, a tag-recapture study estimated the lake trout population at 1,792 fish (95% CI = 1,054–5,982 fish ≥406 mm fork length; Vidergar 2000). Second, in 2000, a creel survey on Lake Pend Oreille quantified angler harvest at ~4,700 lake trout (Peterson and Maiolie 2005). Third, in 2003, a tag-recapture study estimated the lake trout population at 6,376 fish (95% CI = 5,247–8,124 fish ≥520 mm total length; Peterson and Maiolie 2005). Last, given estimated numbers of lake trout in 1999 and 2003 and the annual population growth rate over the 4-year period (λ = $(6376/1792)^{0.25}$ = 1.373), lake trout would number 12,027 fish by 2005 if the population did not reach carrying capacity sooner.

Our objective was to determine if the lake trout population increased exponentially as expected from abundance estimates in 1999 and 2005 in Lake Pend Oreille, Idaho. To achieve our objective, we summarized the results of a mark-recapture study of lake trout using large trap nets that was undertaken during 2005–2006. The study mimicked a study in 2003 by the same contractor, Harbor Fisheries Inc. (Bailey's Harbor, Wisconsin), so we compared results of the two studies, where possible, to shed light on changes in the lake trout population over the period of the two studies (Peterson and Maiolie 2005). We also sought to identify peak times and areas of spawning movement for use in future control efforts of the lake trout population.

STUDY AREA

Lake Pend Oreille is located in the northern panhandle of Idaho. Lake Pend Oreille is Idaho's largest lake and has 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 salmonids (Figure 1). Albeni Falls Dam, completed in 1955 downstream on the Pend Oreille River, regulates the top 3.5 m of the lake (Figure 1). Summer pool elevation (July–September) is about 628.7 m, and winter pool level is typically between 625.1 to 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; Bowles et al. 1987, 1988, 1989). Surface temperatures are as high as 24°C in hot summers. Thermal stratification occurs from late June to September, and the thermocline typically lies between 10 and 24 m.

Steep, rocky slopes characterize most of the shoreline, which is largely undeveloped. Littoral areas are limited and mostly characterized by having a very steep bottom, although some littoral areas are characterized by gradual or moderately sloping bottoms (found mostly in the northern end of the lake and in bays). Most fish habitat occurs in the pelagic area of the lake.
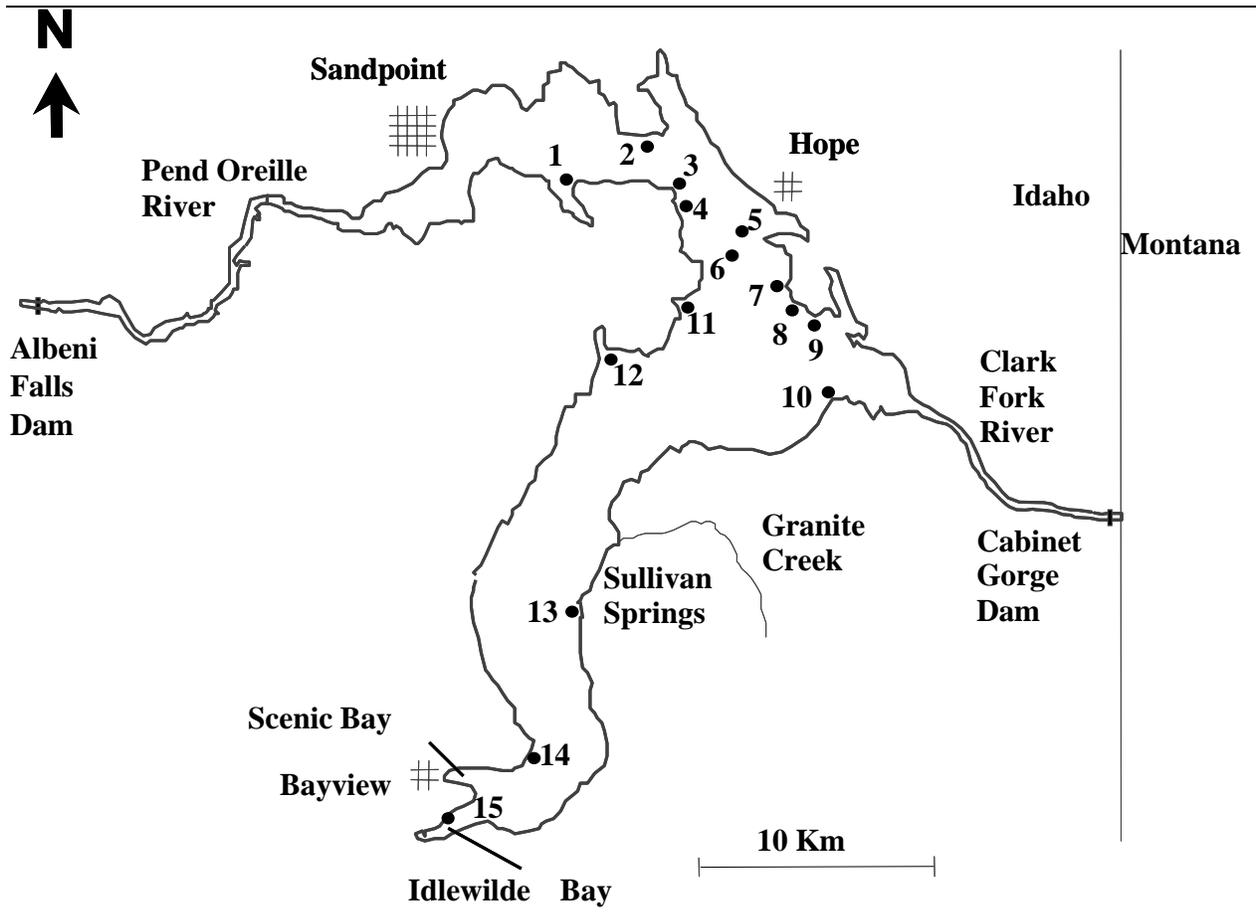
Figure 1.   Trap-net locations on Lake Pend Oreille, Idaho, during mark-recapture sampling in 2003 and 2005. Numbers correspond to names shown in Table 1.

Historically, bull trout and northern pikeminnow *Ptychocheilus oregonensis* were the top two native predatory fish in Lake Pend Oreille (Hoelscher 1992). The historic native prey population was probably made up of mountain whitefish *Prosopium williamsoni*, pygmy whitefish Prosopium *coulterii*, slimy sculpin *Cottus cognatus*, suckers *Catostomus spp.*, peamouth *Mylocheilus caurinus*, redside shiner *Richardsonius balteatus*, and juvenile salmonids (bull trout and westslope cutthroat trout *Oncorhynchus clarkii lewisi*). In 1925, lake trout were introduced, and in 1941, Gerrard strain rainbow trout from Kootenay Lake, British Columbia, were introduced. Presently, the top four predator fish are rainbow trout, bull trout, lake trout, and northern pikeminnow. Other fish that make up the remainder of the predator community occur in low numbers, including northern pike *Esox lucius*, brown trout *Salmo trutta*, cutthroat trout, smallmouth bass *Micropterus dolomieu*, largemouth bass *Micropterus salmoides*, and walleye

Sander vitreus (Hoelscher 1992). Introduced kokanee, which migrated down from Flathead Lake, Montana via the Clark Fork River in the 1930s (Maiolie et al. 2002), are well established and are the principal prey for rainbow trout, lake trout, and bull trout >415 mm (Vidergar 2000). Northern pikeminnow >305 mm use kokanee for about half of their total consumed food items (Vidergar 2000).

PROJECT GOALS

Project goals were to 1) estimate numbers of lake trout in Lake Pend Oreille and 2) remove lake trout in support of predator control goals related to kokanee management in Lake Pend Oreille. Herein, we report on the first project objective stated below.

PROJECT OBJECTIVES

Objective 1.   Complete a mark-recapture study to estimate numbers of lake trout.

Objective 2.   Evaluate by-catch mortality on nontarget species, especially bull trout.

Objective 3.   Evaluate the effectiveness of deep-water trap nets for exploiting lake trout.

Objective 4.   Quantify population attributes of the lake whitefish population.

METHODS

Trap nets used in 2005 were similar to those used in 2003 (Peterson and Maiolie 2005), and locations fished were generally the same in the two years of study (Figure 1; Table 1). Sampling was initiated one month earlier in 2005 (September 8, 2005 through December 15, 2005) but continued for three months later in 2003 (September 30, 2003 through March 31, 2004). In 2005, most trap nets were soaked between lifts for three or seven nights, with some nets soaked for up to 16 nights (Figure 2); whereas in 2003, trap nets were soaked for two nights in October–November and three to four nights in December–March (Peterson and Maiolie 2005).

Table 1.   Areas, locations, latitude, and longitude of large trap-net locations used in Lake Pend Oreille, Idaho, in 2003 and 2005.

| Area	Location	Latitude	Longitude	2003	2005
Northern	1. Bottle Bay	48°15.345	116°26.932	No	Yes
	2. Sunnyside Bay	48°16.362	116°23.611	Yes	Yes
	3. Anderson Point	48°15.173	116°22.332	Yes	No
	4. Sunrise Bay	48°14.723	116°22.691	Yes	Yes
Central	5. Warren Island	48°13.965	116°20.042	Yes	Yes
	6. Pearl Island	48°13.072	116°19.945	No	Yes
	7. Memaloose Island	48°12.723	116°17.891	Yes	No
	8. Thompson Point	48°11.659	116°17.619	Yes	Yes
	9. Sheepherder Point	48°11.298	116°16.886	Yes	Yes
	10. Lee Point	48°09.024	116°15.368	Yes	No
	11. Camp Bay	48°12.899	116°18.798	Yes	No
Southern	12. Garfield Bay	48°10.531	116°25.984	Yes	Yes
	13. Whiskey Bay	48°03.317	116°27.473	Yes	Yes
	14. Cape Horn	47°58.840	116°30.629	Yes	Yes
	15. Idlewilde Bay	47°57.178	116°33.913	Yes	Yes
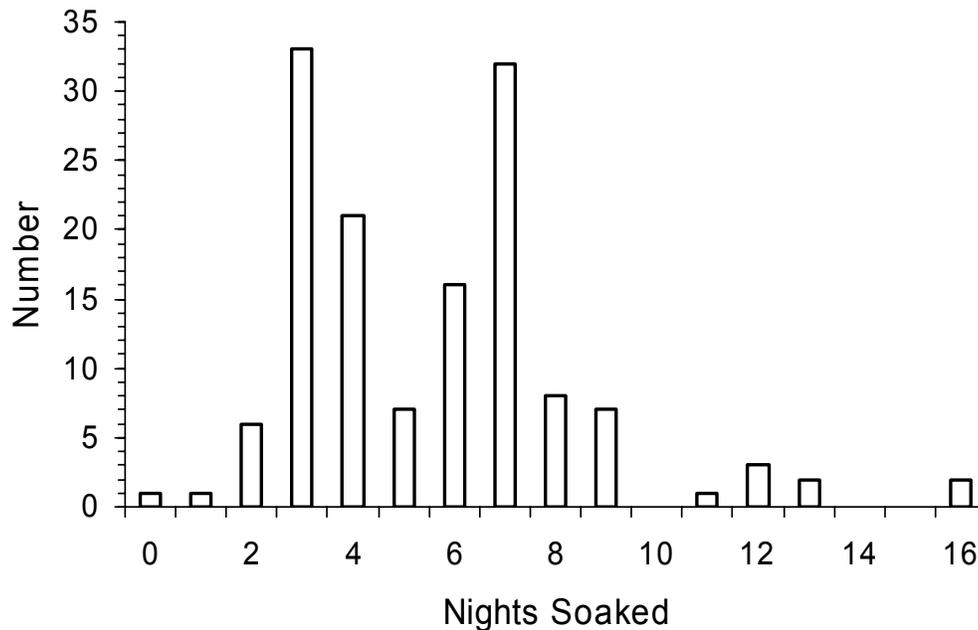
Figure 2.   Number of nights soaked by large trap nets in Lake Pend Oreille from September 10, 2005 through December 15, 2005.

Gill nets were used in 2005 to provide a random sample of the fraction of marked fish in the population to overcome the potential weakness of trap nets that were fished in a limited and nonrandomly selected set of locations. Gill net sampling locations were randomly selected from a 0.5 km grid in the (shallow) northern section of the lake and 0.5 km distances along shore in (deep) central and southern sections of the lake. Gill nets were fished beginning on February 12, 2006 and continuing to April 6, 2006. Each net was soaked for one night. Nets were of graded meshes from 6.35 cm (2.5 in) to 15.24 cm (6.0 in) stretch measure, in 1.27 cm (0.5 in) increments.

Lake trout were measured in length (0.1 cm; 0.04 in), tagged with uniquely-numbered spaghetti tags (if no tag was present), and released. Data on length was used to quantify population size structure for fish caught by gillnetting and trap-netting, under the assumption that gill nets provided a more representative sample of the population size structure than trap nets. Population size structure was indexed as relative stock density (RSD; Anderson and Neumann 1996), where stock length = 30 cm (12 in); quality length = 50 cm (20 in); preferred length = 65 cm (26 in); memorable length = 80 cm (31 in); and trophy length = 100 cm (39 in; Hubert et al. 1994). The RSD index expresses the ratio of the number of fish of a given length category (e.g., preferred, memorable, or trophy) to the number of fish of stock size or larger. A population is thought to be in balance with its prey supply if the RSD index for fish of quality length (RSD-Q) falls near 50 (i.e. half of the fish in the sample longer than stock length are also of quality length).

Data on locations and dates of capture were used to quantify movement of recaptured fish from their location of tagging to their location of recapture in Lake Pend Oreille in 2005. For

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each recaptured lake trout, the location and area (upper, middle, or lower; Table 1) of tagging in trap nets was cross-tabulated with the location and area of recapture in trap nets to quantify rates of movement from marking to recapture during the autumn spawning period. Movement was then quantified as the percentage of all recaptures at a tagging location or area that originated in a different tagging location or area.

Data on numbers examined (C_t), numbers recaptured (R_t), numbers marked (M_t), and numbers removed (Z_t) on each date were used to estimate abundance. Schnabel and Schumacher-Eschmeyer multiple-census models were used to estimate abundance of sexually mature (adult) fish that were vulnerable to capture in trap nets during autumn (marking and recapture samples). Chapman's modification of the Petersen single-census model was used to estimate abundance of all lake trout in the population from a combination of trap net catches in autumn (marking sample) and gill net catches in spring (recapture sample; Ricker 1975).

Abundance estimates were apportioned into 2 cm (0.8 in) length classes using the length frequency from trap-netting for multiple-census estimates of the sexually mature adult fraction of the population and the length frequency from gillnetting for the single-census estimate of total abundance. Size selectivity of trap nets was estimated as the ratio of number of fish captured in trap nets to the number of fish estimated to be present in the population, based on recaptures of marked fish in gill nets fished from February 12, 2006 to April 6, 2006.

An exponential growth model was fit to estimates of lake trout abundance in 1999 (Vidergar 2000), 2003 (Peterson and Maiolie 2005), and 2005 (this study) to test the hypothesis that the lake trout population in Lake Pend Oreille grew exponentially during 1999–2005. Before fitting the exponential growth model, estimates for 1999 and 2005 were adjusted to include only fish longer than 52 cm, so all three estimates included the same sizes of fish (the estimate for 2003 included only fish 52 cm, 20 inches, or longer). For the 1999 abundance estimate, we multiplied the estimate and its 95% CI by the fraction of fish that were 52 cm or longer (using data shown in Figure 1.2 in Vidergar 2000). For the 2005 abundance estimate, we estimated the number of lake trout in the population that were 52 cm or longer by including only fish of those lengths in the numbers of marked fish at large during trap-netting, numbers of fish examined for marks during gillnetting, and numbers of fish recaptured during gillnetting (modified Chapman estimator).

RESULTS

Catch rates of lake trout in trap nets varied greatly among sampling locations in Lake Pend Oreille in autumn 2005 (Table 2). Within the lake, catch rates of trap nets were generally higher in the central and upper parts of the lake than the lower part of the lake. Catch rates were much higher at Sheepherder Point than at any other locations, next highest at Thompson Point, lower at Bottle Bay and Warren Island, and very low elsewhere. Catch rate decreased steadily from the first lift date to the last lift date (Figure 3).

Size structure of the lake trout population in Lake Pend Oreille in 2005 was skewed toward fish 50–80 cm long based on trap-netting and 40–80 cm long based on gillnetting (Figure 4). Relative stock density (RSD) indices for gill-net caught fish were balanced for fish of quality length (RSD-Q = 54), preferred length (RSD-P = 24), and memorable length (RSD-M = 9), but low for fish of trophy length (RSD-T <1). In contrast to gill nets, RSD indices for trap-net caught fish were skewed toward fish of quality length (RSD-Q = 94) and preferred length (RSD-P = 51), but similar for fish of memorable length (RSD-M = 10) and trophy length (RSD-T <1).

Table 2.   Areas, locations, number of lake trout captured (catch), number of net-nights fished (effort), and catch/effort (CPE = fish per net-night) in large trap nets in Lake Pend Oreille, Idaho during 2003 and 2005.

| Area	Location	2003			2005		
		Catch	Effort	CPE	Catch	Effort	CPE
Northern	Bottle Bay				84	30	2.80
	Sunnyside Bay	3	22	0.14	20	23	0.87
	Anderson Point	63	41	1.55			
	Sunrise Bay	71	33	2.13	43	49	0.88
Central	Warren Island	76	133	0.57	223	96	2.32
	Pearl Island				18	44	0.41
	Memaloose Island	2	26	0.08			
	Thompson Point	450	181	2.49	398	98	4.06
	Sheepherder Point	209	120	1.74	710	96	7.40
	Lee Point	23	111	0.21			
	Camp Bay	11	77	0.14			
Southern	Garfield Bay	172	157	1.10	75	79	0.95
	Whiskey Bay	51	112	0.45	85	86	0.99
	Cape Horn	33	127	0.26	48	91	0.53
	Idlewilde Bay	22	153	0.14	94	91	1.03
Total		1,186	1,293	0.92	1,798	783	2.30
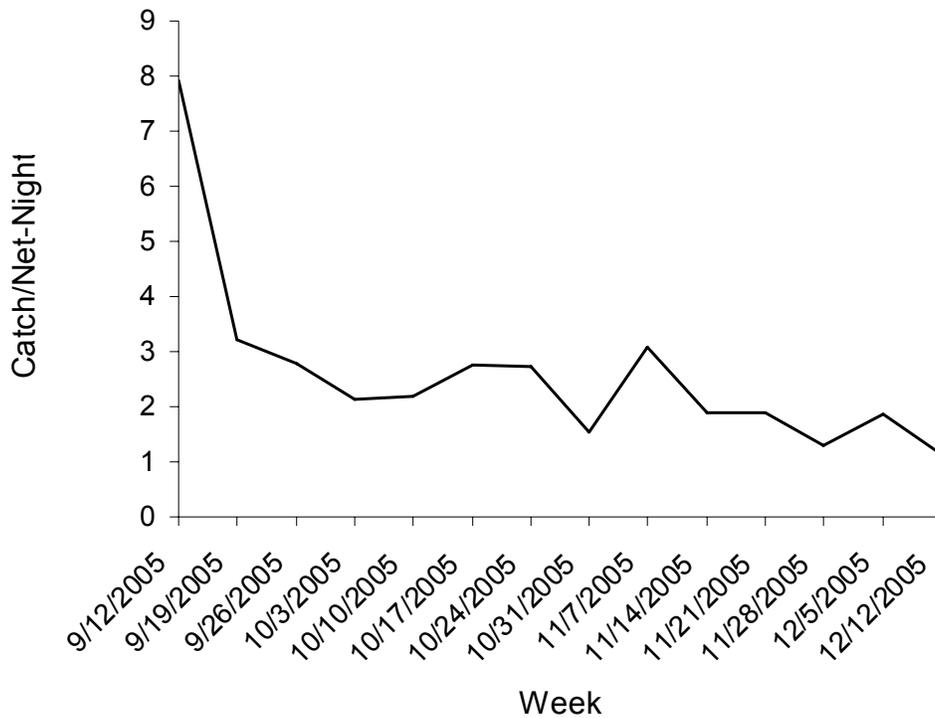
Figure 3.   Catch of lake trout per night soaked over 14 weeks of sampling by large trap nets in Lake Pend Oreille, Idaho from September 10, 2005 through December 15, 2005.
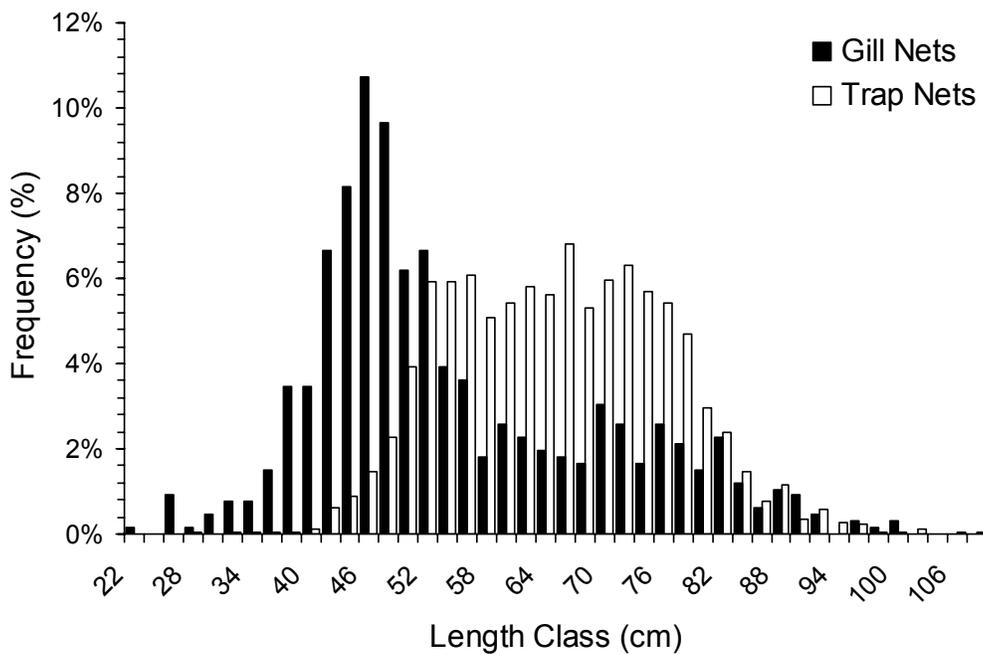

Figure 4.   Frequency (%) of lake trout in each 2 cm length class caught in Lake Pend Oreille in trap nets from September 10, 2005 through December 15, 2005 and in gill nets from February 12, 2006 to April 6, 2006.

Few lake trout were recaptured in the same locations or areas where they were tagged and released during trap-net sampling in Lake Pend Oreille in fall 2005. Recapture rates of previously tagged lake trout ranged 0–23% at all trap-net locations except Sheepherder Point, where the recapture rate was 65% (Table 3). Similarly, recapture rates of previously tagged lake trout were much lower in the northern (16%) and southern (27%) areas of the lake than in the central area of the lake (65%; Table 4).

Abundance of lake trout was estimated to be about 11,000 adult fish (based on trap netting only) and 36,000 total fish (based on spring gill-netting recaptures) in Lake Pend Oreille on December 15, 2005 (when marking was concluded). Based on trap-netting in fall 2005, the Schnabel model estimate of 10,741 adult lake trout (9,008–12,798, Figure 5) was nearly identical to the Schumacher-Eschmeyer model estimate of 10,906 adult lake trout (9,285–13,212, Figure 6). The average of these two estimates was within 10% of the estimate (see Introduction above) based on the increase in mark-recapture estimates from 1999 (Vidergar 2000) to 2003 (Peterson and Maiolie 2005). Based on gillnetting recaptures in spring 2006, the Chapman-model estimate was 35,801 total lake trout (25,270–52,634).

Abundance of lake trout in 2 cm length classes showed that trap nets did not effectively sample fish shorter than 58 cm (Figure 7). Trap-net estimates of lake trout abundance were lower than gill-net estimates for nearly all 2 cm length classes, but were especially lower for length classes below 58 cm. Relative selectivity of trap nets in autumn was quite low for fish shorter than 50 cm, increased sharply from 50 cm to 66 cm, the length where lake trout were fully vulnerable to capture in trap nets, and then declined more gradually as length increased above 66 cm (Figure 8).

Table 3. Recaptures of previously tagged lake trout at 11 sampling locations in Lake Pend Oreille from September 10, 2005 through December 15, 2005. Names of tagging locations are abbreviated as defined in parentheses for recapture locations.

| Recapture Location | Tagging Location | | | | | | | | | | | |
	BB	SYB	SRB	WI	PI	TP	SP	GB	WB	CH	IB	Total
Bottle Bay (BB)	2	0	0	0	0	2	8	0	0	0	0	12
Sunnyside Bay (SYB)	0	0	0	0	0	0	1	0	0	0	1	2
Sunrise Bay (SRB)	1	0	0	1	0	1	2	0	0	0	0	5
Warren Island (WI)	0	0	0	3	1	3	9	0	0	1	0	17
Pearl Island (PI)	0	0	0	0	0	0	0	0	0	0	0	0
Thompson Point (TP)	1	0	1	3	0	7	15	1	1	1	0	30
Sheepherder Point (SP)	0	0	1	1	0	6	17	0	1	0	0	26
Garfield Bay (GB)	0	0	0	0	0	1	5	0	1	0	0	7
Whiskey Bay (WB)	0	0	0	2	0	0	4	0	0	0	0	6
Cape Horn (CH)	0	0	0	0	0	0	2	0	2	0	2	6
Idlewilde Bay (IB)	0	0	0	0	1	0	4	0	1	0	1	7
Total	4	0	2	10	2	20	67	1	6	2	4	118

Table 4.   Recaptures of previously tagged lake trout in upper, middle, and lower parts of Lake Pend Oreille from September 10, 2005 through December 15, 2005.

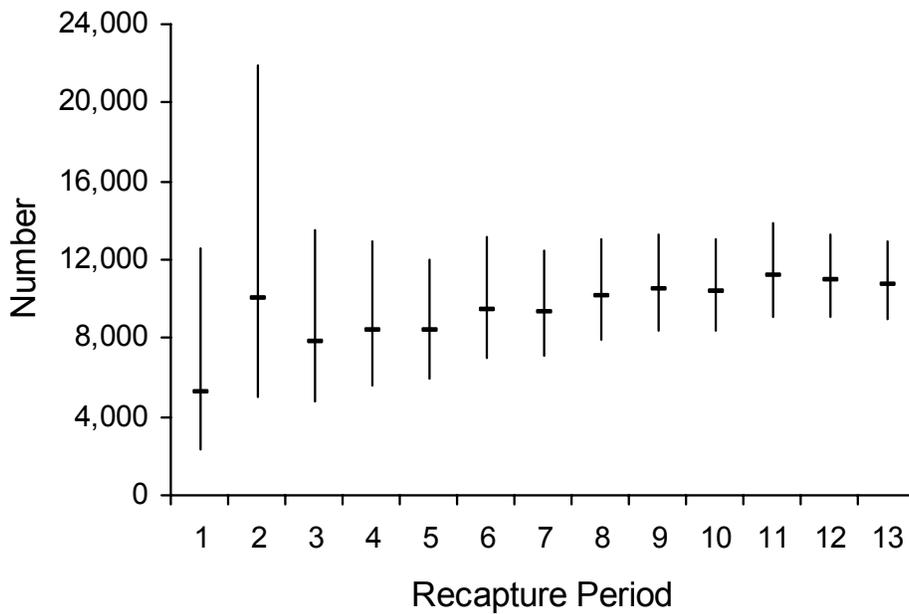| Recapture Area	Marking Area			
	Northern	**Central**	**Southern**	**Total**
Northern	3	15	1	19
Central	3	65	5	73
Southern	0	19	7	26
Total	6	99	13	118

Figure 5.   Multiple-census mark-recapture estimate (Schnabel model) of lake trout abundance (number) over 13 weekly recapture periods in Lake Pend Oreille, Idaho from September 10, 2005 through December 15, 2005.
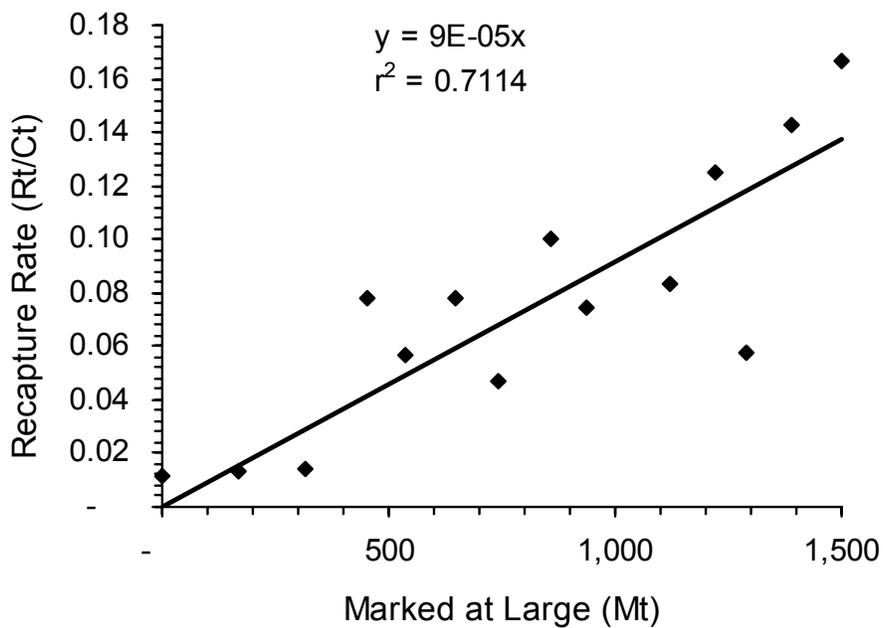

Figure 6.   Schumacher-Eschmeyer multiple-census mark-recapture model of the recapture rate of previously marked lake trout (Rt/Ct) versus the number of marked lake trout at large (Mt) over 14 weekly sampling periods in Lake Pend Oreille, Idaho from September 10, 2005 through December 15, 2005.
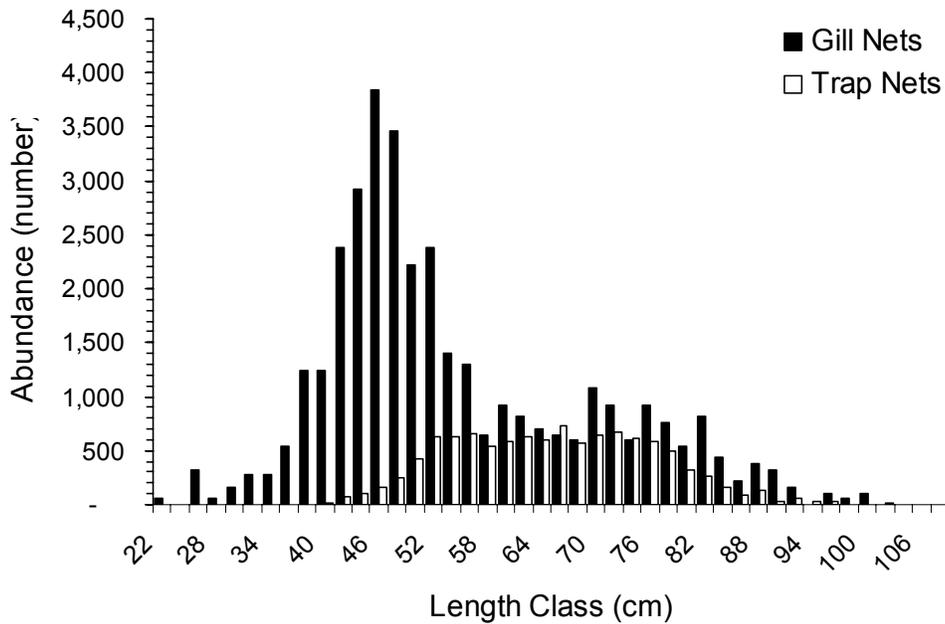
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Figure 7. Abundance of lake trout in 2-cm length classes in Lake Pend Oreille based on fish marked and recaptured in trap nets from September 10, 2005 through December 15, 2005 (Schnabel multiple-census model) and recaptured in gill nets from February 12, 2006 to April 6, 2006 (Chapman single-census model).
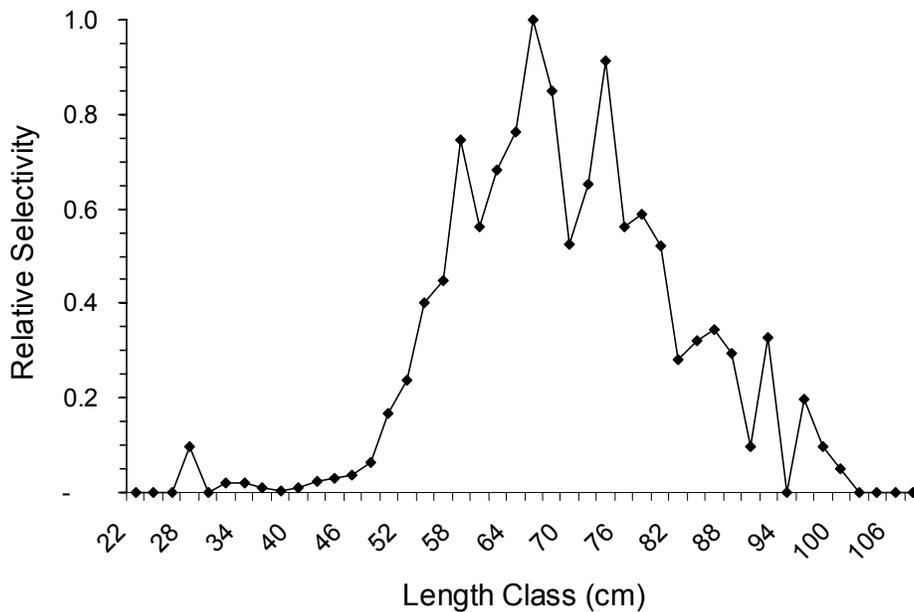

Figure 8. Vulnerability to capture of lake trout in large trap nets set in Lake Pend Oreille from September 10, 2005 through December 15, 2005. Relative selectivity was estimated as the ratio of number of fish captured in trap nets to number of fish estimated to be present in the population (based on recaptures of marked fish in gill nets fished from February 12, 2006 to April 6, 2006.

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Abundance of lake trout in 1999 (Vidergar 2000), 2003 (Peterson and Maiolie 2005), and 2005 (this study) in Lake Pend Oreille was nearly perfectly described by a simple exponential growth model (r^2 = 0.99974; Figure 9). The instantaneous rate of growth of the lake trout population in Lake Pend Oreille during 2000–2005 was r = 0.428, and the annual rate of increase was λ = 1.535. Based on these population growth rates, the adult lake trout population in Lake Pend Oreille would double every 1.6 years and reach 131,000 adult fish by 2010, if the population did not reach carrying capacity sooner.
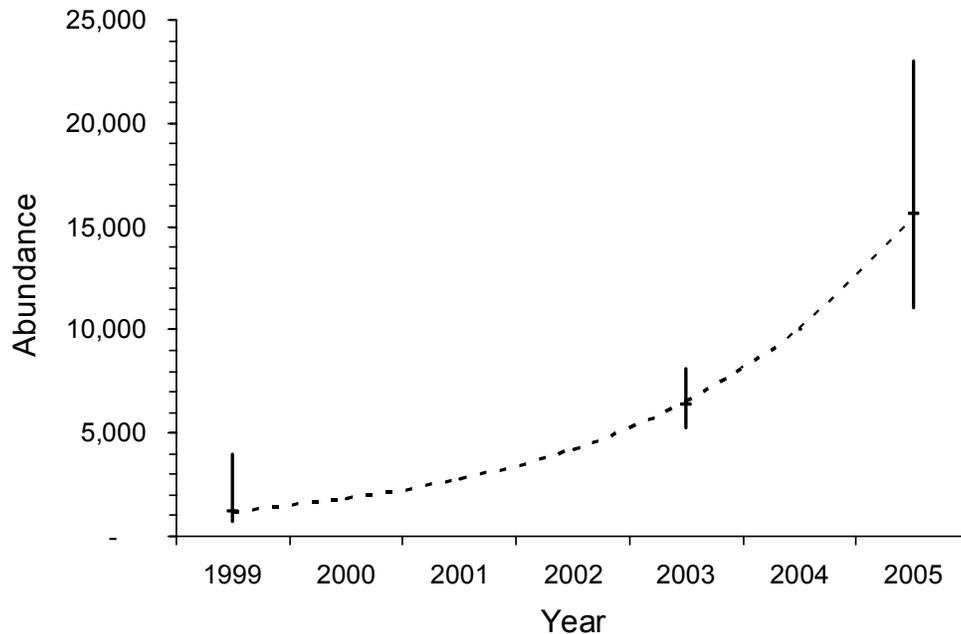

Figure 9.   Abundance of lake trout (≥52 cm) in Lake Pend Oreille, Idaho estimated by mark-recapture in 1999, 2003, and 2005 (error bars) and by an exponential growth model fit to the three annual mark-recapture estimates (dashed line; r^2 = 0.99974).

DISCUSSION

Catch rates of lake trout in trap nets in Lake Pend Oreille varied greatly among sampling locations, but were highest at Sheepherder Point, Thompson Point, Bottle Bay, and Warren Island in 2005 and Thompson Point, Sunrise Bay, Sheepherder Point, and Anderson Point in 2003. High catch rates in both years at Sheepherder Point and Thompson Point suggest that these locations were associated with either lake trout movement or spawning aggregation in both years. In Lake Superior, lake trout also tend to spawn repeatedly in the same locations year after year (Hansen et al. 1995).

In both 2003 and 2005, catch rate decreased steadily from the first lift date to the last lift date, so the onset of lake trout spawning movement was likely before the first sample date in both years of trap-netting. Examination of gonads or egg deposition would be needed to confirm

peak periods and sites of egg deposition in Lake Pend Oreille, but catch rates suggest that spawning movement (perhaps not egg deposition) likely began in September or even earlier. In Lake Superior, peak spawning movement is likely similar because egg deposition occurs from the middle of October through early November (Hansen et al. 1995).

Few fish shorter than 50 cm were caught in trap nets in either 2003 or 2005, likely because sampling was during the lake trout spawning season in areas where juvenile fish of stock length were not present. Juvenile lake trout are rarely encountered in areas where adult lake trout gather for spawning, so are not vulnerable to capture in any gear set in spawning areas during spawning periods. The increasing limb of the relative selectivity curve of trap nets for lake trout mimicked a logistic maturity curve, which suggests that vulnerability to capture in trap nets in autumn was driven by changes in maturity with length.

Recapture rates of previously marked lake trout showed that few fish were marked and recaptured in the same sampling locations except at Sheepherder Point, which suggests that most marked fish were recaptured while moving rather than spawning, and that most areas sampled were not primary spawning areas. Mature male lake trout, in particular, aggregate on spawning grounds while they wait for females to appear, so males should be vulnerable to capture and recapture during the entire spawning period if handling does not alter their behavior. Therefore, based on data from Lake Pend Oreille, none of the areas sampled except for Sheepherder Point were likely areas of lake trout spawning. In Lake Superior, 90% of tagged lake trout were recaptured within 41.79 km of their tagging location during the spawning period and 82.88 km during the rest of the year (Kapuscinski et al. 2005). Similar movement distances for lake trout in Lake Pend Oreille would include the entire lake.

Density of the lake trout population in Lake Pend Oreille was much lower than the restored lake trout stock in eastern Wisconsin waters of Lake Superior, which suggests that the lake trout population in Lake Pend Oreille has room to grow (if both lakes are of similar productivity). Density of lake trout in Lake Pend Oreille (0.93 adults/ha; 3.09 total/ha; where area = depths shallower than 70 m) was much lower (27% as many adults and 41% as many fish) than the density of lake trout in eastern Wisconsin waters of Lake Superior (3.43 age-8-and-older adults/ha; 7.46 age-4-and-older fish/ha; where area = depths shallower than 80 m; Nieland 2006). In Lake Superior, lean lake trout, the same form that occurs in Lake Pend Oreille, reside predominantly at depths shallower than 73 m (40 fathoms; Hansen et al. 1995).

Growth of the lake trout population from 1999 to 2005 in Lake Pend Oreille suggests that the population would double every 1.6 years and reach 131,000 adult fish by 2010, if the population does not reach carrying capacity sooner. The population growth rate of lake trout in Lake Pend Oreille during 1999–2005 ($\lambda = 1.535$) was greater than the population growth rate of lean lake trout in Michigan waters of Lake Superior during 1970–1981 ($\lambda = 1.279$), when the catch/net-night of lean lake trout increased 15-fold (based on data from Wilberg et al. 2003). If lake trout population density in Lake Pend Oreille reaches a level similar to that in eastern Wisconsin waters of Lake Superior, then adult lake trout numbers could increase up to four times (40,000 fish), and total lake trout numbers could increase up to six times (86,000 fish). Therefore, the lake trout population in Lake Pend Oreille would reach carrying capacity at the same density as in eastern Lake Superior by the year 2007 when the current rate of exponential growth would first exceed 40,000 adult fish.

Causes of the recent increase in the lake trout population in Lake Pend Oreille are unclear, because lake trout were first introduced in 1925 and *Mysis relicta* were introduced in 1966–1970, established by 1972, and abundant by 1976 (Bowles et al. 1991). In nearby Priest

Lake, lake trout increased greatly in abundance shortly after *Mysis relicta* were established, presumably because *Mysis relicta* provided an ideal prey for juvenile lake trout, which were previously prey limited (Bowles et al. 1991). If juvenile lake trout in Lake Pend Oreille were prey limited, as in Priest Lake, then lake trout abundance should have increased greatly in the 1970s and 1980s after *Mysis relicta* reached high abundance. Differences in timelines for lake trout population growth in the two lakes may stem from differences in bathymetry and fish assemblages in the two lakes. First, Lake Pend Oreille is much deeper (maximum depth = 351 m) and steeper-sided (mean depth = 164 m) than Priest Lake (maximum depth = 112 m; mean depth = 38 m; Bowles et al. 1991), so habitat for spawning by adults or rearing of juveniles may have limited population growth in Lake Pend Oreille longer than in Priest Lake. Second, Lake Pend Oreille supports abundant populations of Gerard-strain rainbow trout and bull trout that are absent from Priest Lake (Bowles et al. 1991), which may have delayed population growth of lake trout through interspecific competition in Lake Pend Oreille.

To suppress lake trout abundance in Lake Pend Oreille, fishing mortality will need to increase enough to cause recruitment overfishing. Trap-netting in autumn 2005 captured 1,798 lake trout (113 killed), gillnetting in spring 2006 captured 662 lake trout (471 killed), angling from spring through autumn 2006 killed 10,130 lake trout, and gill- and trap-netting in fall 2006 killed 2,948 lake trout. Collectively, these catches and removals represent a hypothetical exploitation rate of 43.4% and an actual exploitation rate of 38.2% of all lake trout in Lake Pend Oreille. If natural mortality is similar to the level in Lake Superior (M = 0.1649; Nieland 2006), then total annual mortality would have exceeded 50% during 2005, the threshold beyond which lake trout populations in North America decline in abundance (Healey 1978). The effect of these and future removals should be modeled to determine the level of exploitation and the number of years of sustained overexploitation at which recruitment overfishing causes the lake trout population in Lake Pend Oreille to collapse. The next phase of research will address this problem using an age-structured stochastic simulation modeling approach (Schueller 2005; Nieland 2006).

CONCLUSIONS

The mark-recapture study in 2005 improved upon and added to the mark-recapture study in 2003 for several reasons. First, the 2005 estimate relied on randomized gill-net sampling, rather than fixed-location trap-net sampling, to estimate the proportion of marked fish in the population. Randomized recapture sampling in 2005 more likely ensured that marked and unmarked fish in the population were equally vulnerable to sampling, a critical assumption of mark-recapture studies. Second, the study design used in 2005 enabled estimation of the entire lake trout population, rather than just the fraction of the population that was vulnerable to trap-netting. Therefore, the abundance estimate in 2005 was directly comparable to numbers of lake trout removed by anglers, because anglers target lake trout of all sizes and ages, not just sexually mature lake trout that are vulnerable to capture in trap nets in autumn. Third, the abundance estimate in 2005 enabled estimation of population growth over time. Future mark-recapture studies would enable evaluation of the effect of population reduction programs for reducing the rate at which the lake trout population (both adults and subadults) is growing.

RECOMMENDATIONS

1. Maintain incentives for angler harvest of lake trout from Lake Pend Oreille until the lake trout population shows signs of population stress (e.g., reduced population density, increased growth rate, and reduced age of maturation).

2. Maintain removals of lake trout by trap-netting and gillnetting from Lake Pend Oreille until the lake trout population shows signs of population stress (e.g., reduced population density, increased growth rate, and reduced age of maturation).

3. Repeat a mark-recapture study using trap-netting and gillnetting to estimate abundance of lake trout at periodic intervals (e.g., 2–5 year intervals) and to monitor future progress of lake trout suppression in Lake Pend Oreille.

4. Model the effect of population removals on sustainability of the lake trout population in Lake Pend Oreille and quantify the most likely level of fishery exploitation that will drive the population to low density or extinction.

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