Fishery Data Series No. 10-46

Stock Assessment of Lake Trout in Paxson Lake, 2002-2004

by

Klaus Wuttig

July 2010

Alaska Department of Fish and Game

Divisions of Sport Fish and Commercial Fisheries

Symbols and Abbreviations

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Weights and measures (metric)	
centimeter	cm
deciliter	dL
gram	g
hectare	ha
kilogram	kg
kilometer	km
liter	L
meter	m
milliliter	mL
millimeter	mm
Weights and measures (English)	
cubic feet per second	ft^3/s
foot	ft
gallon	gal
inch	in
mile	mi
nautical mile	nmi
ounce	oz
pound	lb
quart	qt
yard	yd
Time and temperature	
day	d
degrees Celsius	°C
degrees Fahrenheit	°F
degrees kelvin	K
hour	h
minute	min
second	s
Physics and chemistry	
all atomic symbols	
alternating current	AC
ampere	A
calorie	cal
direct current	DC
hertz	Hz
horsepower	hp
hydrogen ion activity (negative log of)	pH
parts per million	ppm
parts per thousand	ppt, ‰
volts	V
watts	W

General	
Alaska Administrative Code	AAC
all commonly accepted abbreviations	e.g., Mr., Mrs., AM, PM, etc.
all commonly accepted professional titles	e.g., Dr., Ph.D., R.N., etc.
at	@
compass directions:	
east	E
north	N
south	S
west	W
copyright	©
corporate suffixes:	
Company	Co.
Corporation	Corp.
Incorporated	Inc.
Limited	Ltd.
District of Columbia	D.C.
et alii (and others)	et al.
et cetera (and so forth)	etc.
exempli gratia (for example)	e.g.
Federal Information Code	FIC
id est (that is)	i.e.
latitude or longitude	lat. or long.
monetary symbols (U.S.)	$, ¢
months (tables and figures): first three letters	Jan,...,Dec
registered trademark	®
trademark	™
United States (adjective)	U.S.
United States of America (noun)	USA
U.S.C.	United States Code
U.S. state	use two-letter abbreviations (e.g., AK, WA)

Measures (fisheries)	
fork length	FL
mideye-to-fork	MEF
mideye-to-tail-fork	METF
standard length	SL
total length	TL
Mathematics, statistics	
all standard mathematical signs, symbols and abbreviations	
alternate hypothesis	H_A
base of natural logarithm	*e*
catch per unit effort	CPUE
coefficient of variation	CV
common test statistics	(F, t, χ^2, etc.)
confidence interval	CI
correlation coefficient (multiple)	R
correlation coefficient (simple)	r
covariance	cov
degree (angular)	°
degrees of freedom	df
expected value	*E*
greater than	>
greater than or equal to	≥
harvest per unit effort	HPUE
less than	<
less than or equal to	≤
logarithm (natural)	ln
logarithm (base 10)	log
logarithm (specify base)	log_2, etc.
minute (angular)	'
not significant	NS
null hypothesis	H_O
percent	%
probability	P
probability of a type I error (rejection of the null hypothesis when true)	α
probability of a type II error (acceptance of the null hypothesis when false)	β
second (angular)	"
standard deviation	SD
standard error	SE
variance	
population	Var
sample	var

FISHERY DATA SERIES NO. 10-46

STOCK ASSESSMENT OF LAKE TROUT IN PAXSON LAKE, 2002-2004

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ABSTRACT

The abundance of lake trout *Salvelinus namaycush* was estimated in Paxson Lake during 2002–2004. A series of five sampling events (fall 2002, spring 2003, fall 2003, spring 2004, and fall 2004) were fielded and produced five different two-sample mark-recapture estimates of abundance. Two of the estimates (fall 02–fall 03, and fall 03–fall 04) came from designs that used beach seines to capture spawning aggregations during fall. These designs provided estimates of the abundance of mature male lake trout ≥450 mm FL. Another estimate (spring 03–spring 04) of the total abundance of fish ≥400 mm FL was calculated with data collected using a combination of gear: boat electrofishing gear, gill nets, fyke nets, jug lines, and hook-and-line. The series of events permitted additional analyses (e.g., fall 02–spring 03, fall 03–spring 04) to evaluate alternative designs. A spring 2002–spring 2003 estimate was not possible because model assumptions were violated. The estimated abundance of male lake trout ≥450 mm FL was 1,991 (SE=128) in 2002, and 1,906 (SE=161) in 2003. These estimates were statistically similar to those calculated under the alternative designs (e.g., fall 02–spring 03, fall 03-spring 04). The abundance of male lake trout has been used by managers as an index to monitor total population sizes relative to harvests, and estimates of abundance of male lake trout during 2002–2004 were similar to past experiments from 1988 to 1994, which suggested intervening harvest levels were sustainable.

Key words: Lake trout, Salvelinus namaycush, population, abundance, stock assessment, yield, harvest, mark-recapture, Paxson Lake

INTRODUCTION

Paxson Lake, which is located in the Copper River drainage (Figure 1), holds one of the most intensively managed and monitored populations of lake trout *Salvelinus namaycush* within Alaska. The population of lake trout in Paxson Lake supports an important recreational fishery that has periodically ranked as the largest single lake trout fishery in terms of angler days, catch, and harvest within Region III (the Upper-Copper Upper Susitna Management Area and the Arctic-Yukon-Kuskokwim region).

In 1986, a population monitoring program was initiated for the major lake trout fisheries within Region III to formulate a basis for evaluating sustained yields. This work, combined with knowledge that lake trout are easily overexploited (Olver 1991) and observed trends in harvests, has resulted in a series of more restrictive regulations for all lake trout fisheries with concomitant changes in catch and harvests (Figure 2).

Population monitoring in Paxson Lake was conducted from 1988 to 1994 using a combination of mark-recapture experiments. The primary experiment consisted of annual (1988–1995) sampling events during which male lake trout were captured from their spawning beds and marked. The abundance of these fish was then estimated using a Jolly-Seber model (Seber 1982). Secondary attempts were made to estimate the abundance of fish ≥400 mm FL using two-sample mark-recapture techniques by marking lake trout in the fall on the spawning grounds during the first event and subsequently capturing and examining fish for marks in a second event during summer by sport anglers or from hook-and-line sampling conducted by the department. Total abundance was estimated using this approach from 1990 to 1993 and estimates ranged from 6,845 (SE = 1,112) to 45,601 (SE = 22,233) fish. These estimates, however, were considered too imprecise for management applications (Szarzi and Bernard 1997). Szarzi and Bernard (1995) also concluded that these estimates of total population size were potentially biased and recommended summer sampling efforts be terminated. Instead, they recommended using the male spawning population as an index of abundance to monitor population sizes (Szarzi and Bernard 1997).

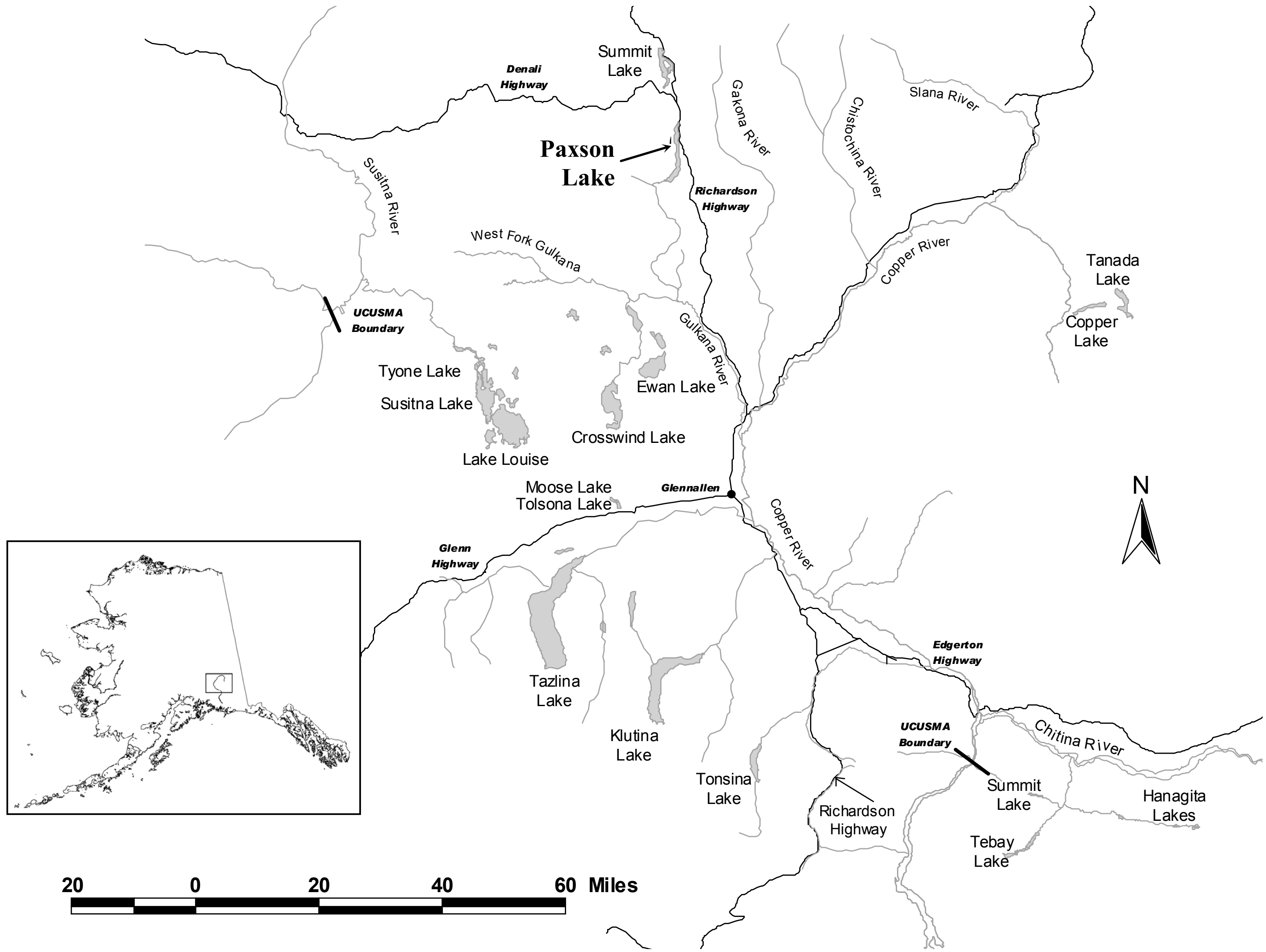

Figure 1.–Map depicting the location of Paxson Lake in the Upper Copper/Upper Susitna Management Area.

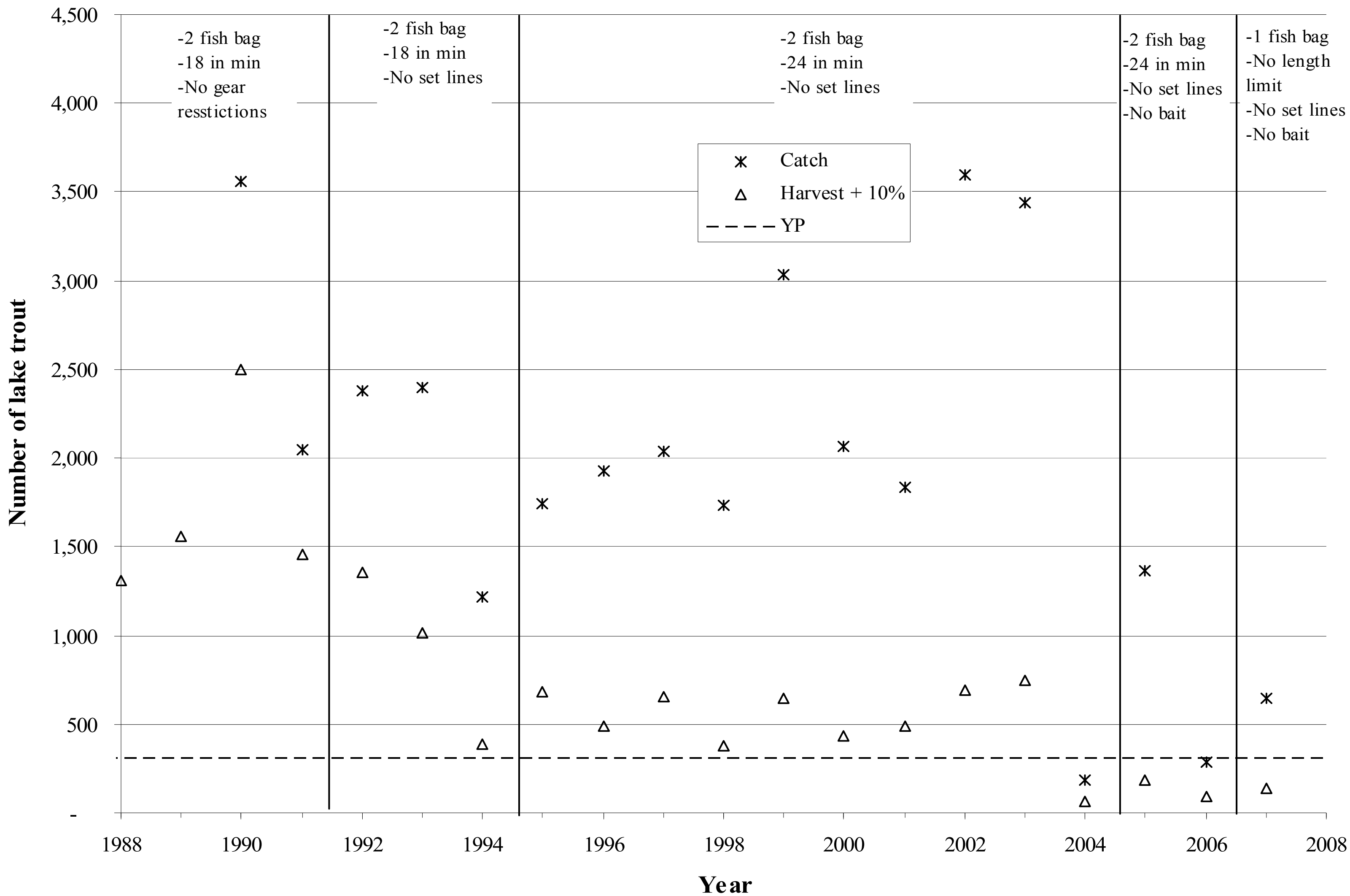

Figure 2.–Estimated number of lake trout harvested (assuming a 10% hooking mortality of caught and released fish) and caught compared to the estimated yield potential (YP) of 306 fish which was calculated under a 24 in length limit. Catch and harvests are reported by Somerville (2008). Vertical lines delineate major changes in regulation.

In 2002, development of the *Lake Trout Management Plan* (Burr 2006) was initiated. This plan ultimately established the current management approach for managing wild lake trout populations within Region III by using a lake area (LA) model. This model developed by Evans et al. (1991) estimates yield potential (YP), or rather the sustainable amount of biomass that can be harvested annually, based on the surface area of a lake. The estimated yield potential, expressed as biomass (kg lake trout/year), is converted to numbers of fish using a predicted average weight of harvested fish. If there is a regulation for a minimum size limit (e.g. 22 inches), then the average weight for all fish ≥22 in is used. In 2005 the regulation was a one fish bag limit with a minimum size limit of 24 in, which provided a YP of 306 fish. In 2006, the regulation was changed to a one fish bag limit and with no length limit, which resulted in a YP of 585 fish assuming all fish harvested by anglers are ≥18 in.

The yield potential estimated by the LA model is treated as a guideline because of the recognized imprecision of the model and lake specific estimates of harvest from the Statewide Harvest Survey (Burr 2006). In lakes where harvests approach or periodically exceed its YP, abundance-based management and research (e.g. monitoring male spawning populations) is preferred to determine appropriateness of the yield potential. During development of the *Lake Trout Management Plan*, Paxson Lake was identified as being potentially more productive than most lakes in Region III. Its yield potential was considered too conservative based on its limnology, and the work conducted by Szarzi and Benard (1997) that indicated a potentially much larger total population size compared to other lakes in the region.

The purpose of this study was two-fold. First, after an eight-year hiatus, a reassessment of the spawning population was needed to support potential short-term management actions because fishing mortality had consistently exceeded guideline levels. For example, a 50% reduction in the spawning population would lead to an immediate reduction in fishing mortality through changes in regulations. Secondly, this study was part of a broader effort to evaluate if the LA model estimate of yield potential for Paxson Lake is too conservative (i.e., underestimates true YP) and if current regulations could be relaxed to allow for a greater annual harvest of lake trout.

OBJECTIVES

The objectives of this study were addressed using a series of five sampling events: sampling male lake trout on known spawning grounds in Paxson Lake during the fall of 2002, 2003 and 2004, and sampling the total population following ice-out in the spring of 2003 and 2004. These five sampling events also permitted a subsequent set of objectives to estimate abundances of lake trout that were of secondary importance, but were deemed useful for evaluating alternative designs for mark-recapture studies.

The primary objectives of this study were to:

1. estimate the abundance of male lake trout ≥450 mm FL spawning on the known spawning areas in Paxson Lake in September 2002 (first event in September 2002, second event in September 2003) such that the estimate is within 25 percent of the true abundance 95% of the time;
2. estimate the abundance of male lake trout ≥350 mm FL spawning on the known spawning areas in Paxson Lake in September 2003 (first event in September 2003, second event in September 2004) such that the estimate is within 15 percent of the true abundance 95% of the time;

3. estimate the abundance of lake trout ≥300 mm FL in all of Paxson Lake in June 2003 (first event in June 2003, second event in June 2004) such that the estimate is within 25 percent of the true abundance 95% of the time;
4. estimate the ratio of spawning of the total abundance of male lake trout ≥300 mm FL in Paxson Lake in June 2003 to the abundance of male lake trout ≥450 mm FL on known spawning areas in September 2002 such that the estimate is within 35 percentage points of the true value 95% of the time;
5. estimate the ratio of spawning male lake trout to the total abundance of all lake trout ≥ 300 mm FL in Paxson Lake in June 2004 and to the abundance of male lake trout ≥450 mm FL on known spawning areas in September 2003 such that the estimate is within 35 percent of the true value 95% of the time;
6. estimate the length composition of the lake trout ≥450 mm FL on the known spawning grounds in Paxson Lake in September 2002 such that the proportion estimates are within 5 percentage points of their actual values 95% of the time for males and within 10 percentage points of their actual values 95% of the time for females;
7. estimate the length composition of the lake trout ≥350 mm FL on the known spawning grounds in Paxson Lake in September 2002 such that the proportion estimates are within 5 percentage points of their actual values 95% of the time for males and within 10 percentage points of their actual values 95% of the time for females; and,
8. estimate the length composition of the lake trout ≥300 mm FL in Paxson Lake in June 2003 such that the proportion estimates are within 5 percentage points of their actual values 95% of the time.

The secondary objectives were to:

9. estimate the abundance of male lake trout ≥450 mm FL in all of Paxson Lake in June 2003 (first event in September 2002, second event in June 2003), such that the estimate is within 35 percent of the true abundance 95% of the time;
10. estimate the abundance of male lake trout ≥450 mm FL in all of Paxson Lake in June 2003 (first event in June 2003, second event in September 2003) such that the estimate is within 25 percent of the true abundance 95% of the time;
11. estimate the abundance of male lake trout ≥450 mm FL in all of Paxson Lake in June 2004 (first event in September 2003, second event in June 2004) such that the estimate is within 25 percent of the true abundance 95% of the time;
12. estimate the abundance of male lake trout ≥300 mm FL in all of Paxson Lake in June 2004 (first event in June 2004, second event in September 2004) such that the estimate is within 25 percent of the true abundance 95% of the time;
13. using a Jolly Seber Model, estimate the abundance of male lake trout ≥350 mm FL spawning on the known spawning areas in Paxson Lake in September 2003 (first event in September 2002, second event in September 2003, third event September of 2004) such that the estimate is within 15 percent of the true abundance 95% of the time; and,
14. estimate survival between September 2002 and 2003 and recruitment to the September 2003 population such that these estimates are within 12 percentage points of the actual value 95% of the time and within 25 percent of the true value 95% of the time, respectively.

METHODS

DESCRIPTION OF STUDY AREA

Paxson Lake (62˚50' N, 145˚35' W), located in the upper Copper River drainage, makes up part of the Gulkana River system (Figure 1). The Gulkana River parallels the Richardson Highway 8 km south of the community of Paxson and flows downstream from Summit Lake into Paxson Lake. The river resumes its flow at the south end of Paxson Lake forming the lake's outlet. Paxson Lake is 1,575 ha in surface area, has a maximum depth of 29 m and an elevation of 625 m (Szarzi 1992). A campground, two boat launches, and several cabins are at the lake. In addition to lake trout, other species found in Paxson Lake include sockeye salmon *Oncorhynchus nerka*, Arctic grayling *Thymallus arcticus*, lake whitefish *Coregonus clupeaformis*, Alaska whitefish *Coregonus nelsonii*, and burbot *lota lota.*

STUDY DESIGN, SAMPLING PROTOCOLS, AND DESIGN CONSIDERATIONS

With the exception of Objective 13, abundance was estimated using two-sample mark-recapture techniques for a closed population (Seber 1982). For each of the experiments, the assumptions necessary for accurate estimation of abundance were that:

1) the population was closed (no change in the number or composition of lake trout during the experiment);
2) all lake trout had the same probability of capture in the marking sample or in the recapture sample, or marked and unmarked trout mixed completely between marking and recapture events;
3) marking of lake trout did not affect their probability of capture in the recapture event;
4) lake trout did not lose their mark between events; and,
5) all marked lake trout were reported when recovered in the recapture event.

The sampling design and data collected allowed the validity of these assumptions to be ensured or tested. The specific form of the estimator used was determined from the experimental design and the results of the diagnostic tests performed to evaluate if the assumptions were met (Appendices A1-A3).

A total of five sampling events were conducted during either fall spawning or immediately following ice-out in spring. Different sampling protocols were used during the two periods in order to optimize catches of lake trout (Table 1).

During fall sampling, the study area was partitioned at threes scales, by individual spawning areas, by grouping of spawning areas into four quadrants (NW, NE, SW and SE), and by grouping spawning areas into northern and southern clusters: Northern cluster included spawning beds 9, 10, 14, 15, 19; Southern cluster included the remaining spawning areas (Figure 3). The spawning areas within Paxson Lake are well documented from previous sampling (1988–1994), and it is believed that all significant spawning areas had been identified.

Table 1.–Sampling dates, crew sizes, and gear used to capture lake trout at Paxson Lake (2002–2004).

Event	Dates	Crew Size	Gear
Fall 2002	9/11–9/16	Two 3-person crews	Beach seine
Spring 2003	6/4–6/16	Five 2-person crews	Hook-and-line, Jug lines, Gillnets, and Fyke nets
Fall 2003	9/11–9/16	Two 3-person crews	Beach seine
Spring 2004	6/4–6/16	Five 2-person crews	Electrofishing boat in outlet stream, Hook-and-line gear, Jug lines, 1.0-in bar mesh gillnets.
Fall 2004	9/11–9/16	Two 3-person crews	Beach seine

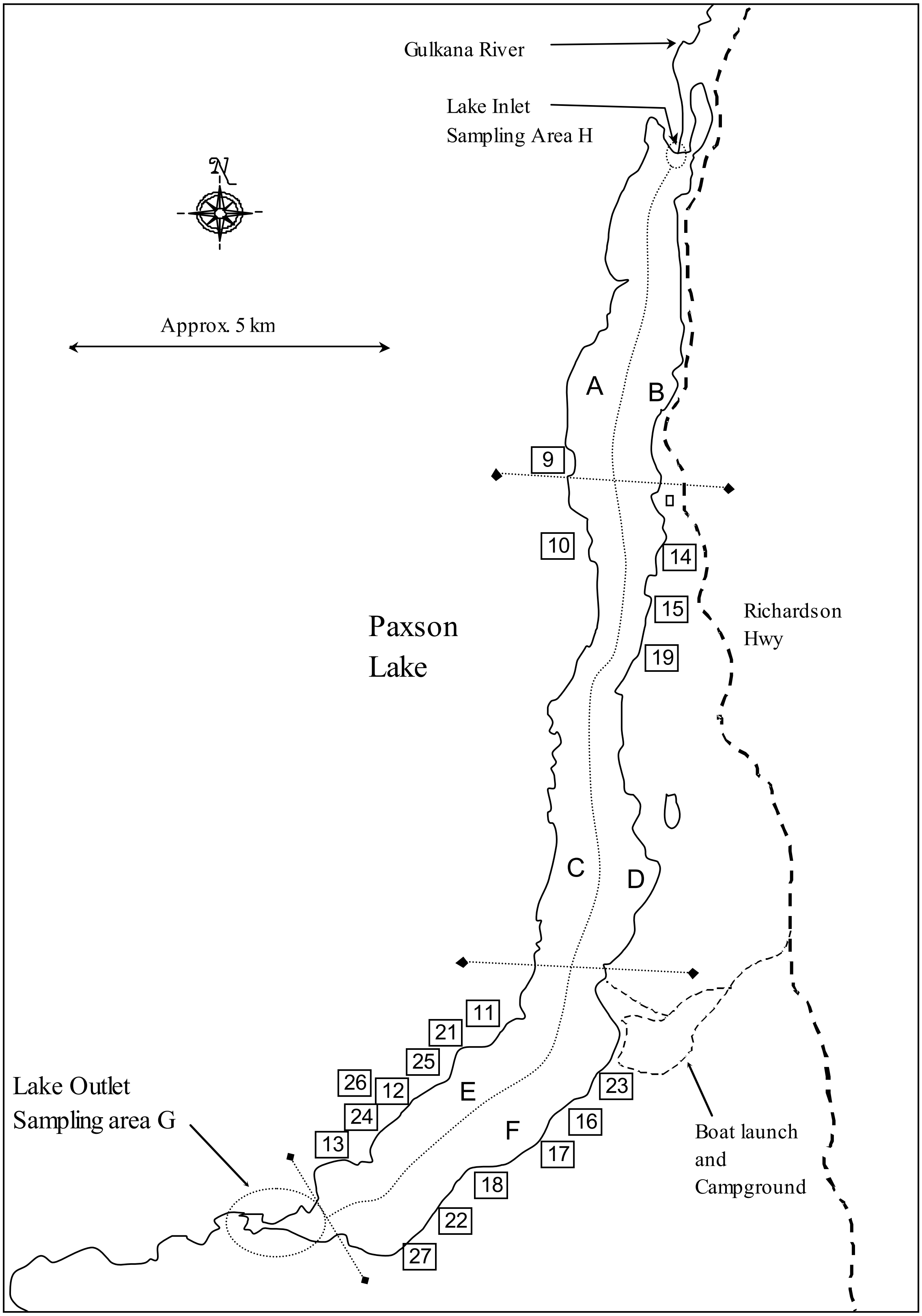

Figure 3.–Paxson Lake with shoreline stretches of spawning areas (#1–#26) and sampling areas (A–G) demarcated, 2002–2004.

Because the northern and southern spawning clusters are separated by a large distance (approximately 5 km), clusters were alternately sampled each night by one or both crews. Within each cluster on any given night, sampling began at a spawning bed identified by a random number and preceded in a clockwise fashion for the duration of the night. Seining, using a 400-ft beach seine, was conducted during peak spawning from approximately 2000 to 0300 hours, and a particular spawning location was fished provided sufficient numbers of fish could be spotted on the spawning location (i.e. usually one or two seine hauls). In cases where inclement weather precluded sampling in either cluster, sampling was proportionally increased later to compensate. This general rotational seining strategy was done in an attempt to distribute fishing effort equally among known spawning locations.

During spring events, sampling was conducted immediately after ice-out when catch rates are generally better than those typical in mid-summer. Paxson Lake was partitioned into eight sampling areas (Areas A–H), which also corresponded to the four spawning quadrants: NW = areas A, B and H, NE = Areas B and D, SW = Area E, and SE = Area F. Areas G and H contained no spawning areas. Three crews fished gillnets (100 x 8 ft multifilament nets with 1-in bar mesh) and each crew was assigned to a third of the lake: upper (Areas A, B and H), middle (Areas C and D) or lower (Areas E and F). Each crew set three gillnets in their assigned area and soaked them for approximately 15 to 20 minutes. Crews systematically set gillnets along the shoreline and set near features such as points where fish could be concentrated and were soaked for 15-20 min. at a time.

A fourth crew was assigned to set and retrieve approximately 30 jug lines. Jug lines were distributed equally among all areas on the leeward half of the lake with baited lines descending to depths from 10 to 30 ft. The jug lines were allowed to drift throughout the lake. Lines were checked and rebaited in the late morning and early evening. Jug lines were baited by tying cut whitefish to the line (without hooks), which could be removed from the stomachs of captured fish by gently pulling on the line.

A fifth crew was assigned to fish the lake's outlet area with hook-and-line gear, where it was presumed that lake trout would be concentrated to feed on out-migrating sockeye smolt. In 2004, an electrofishing boat was used to capture fish concentrated in the narrow outlet channel. In 2003, four fykes nets were used in the lower third of the lake (sections A and B), but were discontinued in 2004 because of their low capture rates (e.g., one or two fish per night for all fykes). In both years, hook-and-line sampling was conducted opportunistically by crews assigned to gillnetting and fishing jug line (e.g., between gillnet sets or after deploying jug lines). At the lake's outlet, unsuccessful attempts were made using a cast net thrown at lake trout feeding at the water surface.

DESIGN CONSIDERATIONS

Paxson Lake was considered a closed system relative to lake trout migrating into and out of the lake. Lake trout have never been seen or captured in the Gulkana River either upstream or downstream of Paxson Lake. Summit Lake, located at the headwaters of the Gulkana River, supports a lake trout population but the distance between the lakes (approximately 15 km), steep gradient (i.e., ~0.4 m/km), and low discharge of the Gulkana River precludes any significant exchange of fish.

Biases in abundance estimates due to combined immigration and mortality could not be completely eliminated, but were judged to be insignificant relative to total population size. Bias associated with immigration via growth recruitment was also judged to be insignificant based on prior observations of very slow annual growth for mature-sized fish (i.e., < 10 mm). Some emigration due to natural and fishing mortality occurred, but was judged to be minimal because harvest estimates are small, and lake trout are relatively long-lived. For the fall-to-fall experiments, bias attributed to immigration or emigration from undocumented spawning areas (i.e., a fraction of the population not subject to capture) was unlikely because Paxson Lake has been extensively surveyed.

The fall-to-spring and spring-to-fall abundance estimates (i.e., for mature males) relied on the assumption that the population of lake trout in Paxson Lake had an equal number of males and females. Because fish could not be sexed during spring sampling events, the number of fish either marked (n_1) or examined for marks (n_2) in the spring was reduced by half to provide the number of males marked or examined for marks. For example, in calculating the spring-to-fall abundance n_1 was calculated by halving the number of fish marked, and n_2 was all males sampled from the spawning grounds, and m_2 was recaptured males. Relative to the fall-to-fall estimates, only positively identified males were included in the estimation of spawning abundance because males generally spawn every year and tend to spend a longer period of time on the spawning beds than females. This difference in behavior in prior experiments has resulted in large differences in capture probabilities (e.g., 1%–2% for females and 15%–25% for males).

Relative to Objective 13, the assumptions necessary for satisfying the Petersen estimator also satisfy those for the Jolly-Seber model. One exception to the Jolly-Seber model is that immigration and emigration can occur, but they must be permanent.

DATA COLLECTION

During each sampling event, all captured fish were measured for length (mm FL), carefully examined for the presence of primary marks (individually-numbered Floy FD-94 internal anchor tag) and secondary marks (fin clips). All fish not bearing a primary mark received one and all fish received an event-specific fin clip to eliminate duplicate sampling and identify tag loss. Fish captured in the first event that exhibited signs of injury, excessive stress, or imminent death were not marked and censored from the experiment. During fall all captured fish were sexed: males were identified by expulsion of milt and females were determined by expulsion of eggs or observing the ovipositor.

DATA ANALYSIS

Movement/Spawning Site Fidelity

Tagging and recovery data from this study and previous studies (1988–1995) were used to construct matrices of annual movement between sampling areas. These matrices were visually examined to assess geographic spawning fidelity at three scales: specific spawning location, spawning quadrant, and spawning cluster.

Abundance Estimates (Two-event)

Violations of Assumption 2 relative to size selective sampling were tested using two Kolmogorov-Smirnov (K-S) tests. There were four possible outcomes of these two tests relative to evaluating size selective sampling (either one of the two samples, both, or neither of the samples were biased) and two possible actions for abundance estimation (length stratify or not). The tests and possible actions for data analysis are outlined in Appendix A1.

The tests for consistency of the Petersen estimator (Seber 1982; Appendix A2) were used to determine if length strata needed to be further stratified by location. The results of these tests were used to select the most appropriate abundance estimator: the pooled Chapman-modified Petersen estimator, the completely stratified Chapman-modified Petersen estimator, or a partially stratified estimator (Darroch 1961). Documentation of capture location for each fish permitted the examination of multiple geographic stratification schemes for purposes of assumption testing and were performed at the scale of a quadrant.

Abundance Estimates (Jolly Seber)

Abundance, survival rate and recruitment statistics were generated for spawning male lake trout in Paxson Lake using the Jolly-Seber model (Seber 1982) and the computer program JOLLY (Model A) developed by Brownie et al. (1986; see Pollock et al. 1990 for a description of JOLLY). Model A is the most general form of the Jolly-Seber model and assumes capture probabilities and survival rates vary over time. The model requires three temporally separated sampling events to estimate abundance and the resulting estimate is lagged one event from the most recent sampling event. Two estimates of survival are generated and are lagged one and two events from the most recent sampling event. One estimate of surviving recruitment is generated and is lagged two events from the most recent sampling event.

Length Composition

Length compositions were estimated for each population abundance estimate using the procedures outlined in Appendix A. Length composition was estimated as proportions within 25-mm length categories.

RESULTS

SPAWNING SITE FIDELITY

Spawning location data collected from previous studies conducted from 1987 to 1995 were incomplete. However, successive spawning location observations were available for 2,028 lake trout. This historical data combined with locations from the fall-to-fall experiments from this study (i.e., F02–F03 and F03–F04) showed there was a spawning fidelity related to distance with more fidelity exhibited at a larger scale, such as a cluster (Table 2, Appendices B1–B3). Inter-annual mixing was not complete (p-values < 0.01) for all geographic scales examined. The observed movement within a quadrant was substantial and deemed sufficient to satisfy concerns that no significant segment of the male spawning population was isolated from the experiment in the event a specific sampling location(s) had not been sampled.

Table 2.–Numbers and proportions of recaptured male lake trout captured during fall moving between spawning quadrants from archived data (1988–1995) and from this study (2002–2004) in Paxson Lake.

1988–1995

Quadrant — Area Recaptured

Area marked		NW	NE	SW	SE	Total
(numbers)	NW	11	3	3	0	17
	NE	6	117	31	11	165
	SW	9	61	942	133	1,145
	SE	3	24	181	493	701
(proportion)	NW	0.65	0.18	0.18	0.00	1.0
	NE	0.04	0.71	0.19	0.07	1.0
	SW	0.01	0.05	0.82	0.12	1.0
	SE	0.00	0.03	0.26	0.70	1.0

Cluster — Area recaptured

	Upper	Lower	Total
Upper	137	45	182
Lower	97	1,749	1,846
Upper	0.75	0.25	1.0
Lower	0.53	0.94	1.0

2002–2003

Quadrant

Area marked		NW	NE	SW	SE	Total
(numbers)	NW	4	0	0	0	4
	NE	3	42	3	1	49
	SW	1	3	55	11	70
	SE	0	0	10	56	66
(proportion)	NW	1.00	0.00	0.00	0.00	1.0
	NE	0.06	0.86	0.06	0.02	1.0
	SW	0.01	0.04	0.79	0.16	1.0
	SE	0.00	0.00	0.15	0.85	1.0

Cluster

	Upper	Lower	Total
Upper	49	4	53
Lower	4	132	136
Upper	0.92	0.08	1.0
Lower	0.03	0.97	1.0

2003–2004

Quadrant

Area marked		NW	NE	SW	SE	Total
(numbers)	NW	13	1	0	0	14
	NE	8	70	2	0	80
	SW	0	3	107	3	113
	SE	1	1	8	20	30
(proportion)	NW	0.93	0.07	0.00	0.00	1.00
	NE	0.10	0.88	0.03	0.00	1.00
	SW	0.00	0.03	0.95	0.03	1.00
	SE	0.03	0.03	0.27	0.67	1.00

Cluster

	Upper	Lower	Total
Upper	92	2	94
Lower	5	138	143
Upper	0.98	0.02	1.0
Lower	0.03	0.97	1.0

ABUNDANCE ESTIMATES

Based on measured growth of recaptured fish, growth recruitment between events was judged to be inconsequential for all two-sample mark-recapture experiments. The extent of observed average growth between the two events ranged from 1.50 mm (S03–F04) to 10.9 mm (F03–F04).

For the fall-to-spring experiments, abundance estimates were considered germane to the spring event because immature males, immature females, and potentially skip-spawning females may have immigrated into the sampled population. The fall-to-fall and spring-to-fall experiments were considered germane to the second event because some mortality, although minor, likely occurred between events.

Abundance estimates were generated for a number of size strata. For estimates that included a fall sampling event, 450 mm FL was chosen as an appropriate lower size limit because fish this size and larger were almost entirely mature based on length-at-maturity assessments conducted by Burr (1997). However, fish below this criterion were also marked and examined to provide the opportunity to estimate abundance for a larger proportion of the population (i.e., fish ≥400 mm FL or the total male spawning population). A criterion of 400 mm FL corresponded to minimum the size at which recaptured fish were consistently sampled for all five sampling events (F02–F03=385 mm FL, F02–S03=370 mm FL, S03–F03=395 mm FL, F03–F04=385, F03–S04= 408 mm FL, S04–F04= 400 mm FL). Szarzi and Bernard (1997) applied the Jolly-Seber model to all mature males (i.e., those that extruded milt) sampled annually from the spawning grounds and their approach was repeated to facilitate comparisons.

Abundance estimates were attained for all objectives, except for the spring 03 to spring 04 experiment (Table 3). For all two-sample experiments, stratification by length was not required based on K-S test results (Table 4). Results of consistency tests necessitated the use of the partially stratified estimator (Darroch 1961) for three of the experiments: F02–F03 ≥400 mm; F03–F04 ≥400; and F03–F04 ≥450 mm (Table 5). Chapman's modification of the Petersen estimator was used for the remaining two experiments (Chapman 1951, Appendix A3). A summary of supporting diagnostic test results and catch statistics are presented for all two-event experiments for fish ≥450 mm FL (Tables 4 and 5). For fish ≥400 mm FL, test results were not presented because they were nearly identical to fish ≥450 mm FL.

The estimated abundance for the male spawning population ≥450 mm FL in fall 2003 using the Jolly Seber estimator was 1,796 (SE = 205). Estimated survival between 2002 and 2003 was 0.84 (SE = 0.079). The estimated abundance of all mature male fish in fall 2003 was 2,420 (SE = 211) and the estimated annual survival rate between 2002 and 2003 was 0.74 (SE= 0.36).

Relative to Objectives 3-5 (S03–S04), total abundance of lake trout in Paxson Lake could not be estimated due to the fact that no fish marked in a large segment of the lake (Areas A, B, C, and D) were ever recaptured **(**Table 6).

Table 3.–Estimated abundance of male lake trout in Paxson Lake, 2002–2004.

Population of Inference	Experiment	Abundance (SE)	95% CI
Fall 02			
≥ 400 mm FL	F02–F03	2,573 (178)	2,290–2,856
≥450 mm FL	F02–F03	1,991 (128)	1,740–2,243
Spring 03			
≥ 400 mm FL	F02–S03	2,649 (432)	1,801–3,497
≥ 400 mm FL	S03–F03	3,273 (453)	2,384–4,161
≥450 mm FL	F02–S03	1,692 (301)	1,102–2,282
≥450 mm FL	S03–F03	2,516 (416)	1,701–3,332
Fall 03			
All males	F02–F03–F04[a]	2,420 (211)	2,006–2,833
≥ 400 mm FL	F03–F04	2,729 (168)	2,401–3,058
≥450 mm FL	F03–F04	1,906 (161)	1,590–2,222
Spring 04			
≥ 400 mm FL	F03–S04	3,133 (312)	2,521–3,746
≥ 400 mm FL	S04–F04	3,414 (447)	2,539–4,290
≥450 mm FL	F03–S04	2,185 (223)	1,748–2,622
≥450 mm FL	S04–F04	2,638 (336)	1,922–3,355

[a]Estimated using Jolly-Seber model.

Table 4.–Results of diagnostic tests used to detect and correct for size selective sampling (Appendix A1) for estimating abundance and length composition of lake trout ≥450 mm FL in Paxson Lake.

Experiment	Test Results		Conclusion
	M vs. R	C vs. R.	
F02–F03	D = 0.05 *P*-value = 0.96 Fail to reject H_0	D = 0.08 *P*-value = 0.56 Fail to reject H_0	Case I, do not stratify, use lengths from both events for composition analysis
F02–S03	D = 0.14 *P*-value = 0.82 Fail to reject H_0	D = 0.13 *P*-value = 0.87 Fail to reject H_0	Case I, do not stratify, use lengths from both events for composition analysis
S03–F03	D = 0.28 *P*-value = 0.09 Fail to reject H_0	D = 0.18 *P*-value = 0.40 Fail to reject H_0	Case I, do not stratify, use lengths from both events for composition analysis
F03–F04	D = 0.06 *P*-value = 0.64 Fail to reject H_0	D = 0.04 *P*-value = 0.94 Fail to reject H_0	Case I, do not stratify, use lengths from both events for composition analysis
F03–S04	D = 0.17 *P*-value = 0.06 Reject H_0	D = 0.10 *P*-value = 0.59 Fail to reject H_0	M vs. R test suspect, Case II, do not stratify, use lengths from first event for composition analysis
S04–F04	D = 0.12 *P*-value = 0.71 Fail to reject H_0	D = 0.36 *P*-value = 0.00 Reject H_0	Case III, do not stratify, use lengths from second event for composition analysis

Table 5.–Results of tests of consistency for the Petersen estimator by location (quadrant; Appendix A2) and supporting catch statistics for lake trout ≥450 mm FL in Paxson Lake.

Experiment	Test	χ^2	*P*-value	Catch statistics							
F02–F03					Area recaptured						
					NW	NE	SW	SE	m_2	n_1	m_2/n_1
	Mixing	292	0.00	Area marked NW	2	0	0	0	2	3	0.67
				Area marked NE	2	26	2	1	31	87	0.36
	m_2/n_2[a]	25.5	0.00	Area marked SW	0	2	40	6	48	134	0.36
				Area marked SE	0	0	8	39	47	165	0.28
	m_2/n_1[b]	3.81	0.28	m_2	4	28	50	46			
				n_2	58	185	277	138			
				m_2/n_2	0.07	0.15	0.18	0.33			
F02–S03					Area recaptured						
					NW	NE	SW	SE	m_2	n_1	m_2/n_1
	Mixing	9.2	0.69	Area marked NW	0	0	0	0	0	4	0.00
				Area marked NE	0	2	2	0	4	121	0.03
	m_2/n_2[a]	0.75	0.86	Area marked SW	1	1	2	1	5	156	0.03
				Area marked SE	3	0	8	1	12	210	0.06
	m_2/n_1[b]	1.95	0.58	m_2	4	3	12	2			
				n_2	49	27	93	20			
				m_2/n_2	0.08	0.11	0.13	0.10			
S03–F03					Area recaptured						
					NW	NE	SW	SE	m_2	n_1	m_2/n_1
	Mixing[a]	3.20	0.78	Area marked NW	0	4	2	4	10	67	0.15
				Area marked NE	0	2	1	1	4	37	0.11
	m_2/n_2[b]	6.78	0.08	Area marked SW	0	6	7	7	20	123	0.16
				Area marked SE	0	1	2	0	3	23	0.13
	m_2/n_1[c]	0.72	0.87	m_2	0	13	12	12			
				n_2	82	267	387	203			
				m_2/n_2	0.00	0.05	0.03	0.06			
F03–F04					Area recaptured						
					NW	NE	SW	SE	m_2	n_1	m_2/n_1
	Mixing[a]	343	0.00	Area marked NW	10	1	0	0	11	58	0.19
				Area marked NE	7	59	1	0	67	185	0.36
	m_2/n_2[b]	11.9	0.01	Area marked SW	0	3	89	2	94	277	0.34
				Area marked SE	1	0	7	12	20	138	0.14
	m_2/n_1[c]	24.8	0.00	m_2	18	63	97	14			
				n_2	42	172	222	67			
				m_2/n_2	0.43	0.37	0.44	0.21			
F03–S04					Area recaptured						
					NW	NE	SW	SE	m_2	n_1	m_2/n_1
	Mixing[a]	6.24	0.98	Area marked NW	0	0	2	1	3	58	0.05
				Area marked NE	2	1	6	6	15	185	0.08
	m_2/n_2[b]	2.45	0.48	Area marked SW	5	1	16	8	30	328	0.09
				Area marked SE	2	1	6	1	10	87	0.11
	m_2/n_1[c]	1.89	0.59	m_2	9	3	30	16			
				n_2	48	41	197	104			
				m_2/n_2	0.19	0.07	0.15	0.15			

-continued-

Table 5.–Page 2 of 2.

Experiment	Test	χ^2	*P*-value			Catch statistics					
						Area recaptured					
						NW	NE	SW	SE	m_2	n_1	m_2/n_1
S04–F04												
	Mixing[a]	13.3	0.34	Area marked	NW	1	1	1	0	3	48	0.06
					NE	0	1	1	0	2	41	0.05
	m_2/n_2[b]	0.4	0.93		SW	2	4	13	4	23	197	0.12
					SE	0	6	3	0	9	104	0.09
	m_2/n_1[c]	0.4	0.43		m_2	3	3	18	4			
					n_2	42	172	222	67			
					m_2/n_2	0.07	0.02	0.08	0.06			

[a]Test for complete mixing
[b] Test for equal probability of capture (m_2/n_2) during first event.
[c] Test for equal probability of capture (m_2/n_1) during second event.

Table 6.–Number of lake trout marked (n_1), examined (n_2), and recaptured (m_2) during sampling spring 2003 and spring 2004 sampling events in Paxson Lake.

		Area where recaptured										
		A	**B**	**C**	**D**	**E**	**F**	**G**	**H**	m_2	n_1	m_2/n_1
Area where marked	**A**	0	0	0	0	0	0	0	0	0	32	0.00
	B	0	0	0	0	0	0	0	0	0	19	0.00
	C	0	0	0	0	0	0	0	0	0	23	0.00
	D	0	0	0	0	0	0	0	0	0	24	0.00
	E	0	0	0	0	0	2	0	0	2	31	0.06
	F	0	0	0	0	1	2	1	0	4	24	0.17
	G	0	0	1	1	1	6	20	0	29	93	0.31
	H	0	0	0	0	0	1	0	0	1	17	0.06
	m_2	0	0	1	1	2	10	21	0			
	n_2	24	7	35	41	30	117	189	0			
	m_2/n_2	0.00	0.00	0.03	0.02	0.07	0.09	0.11	0.00			

LENGTH COMPOSITION

The length frequency distribution of fish captured during all five sampling events combined showed male lake trout between 425 mm and 500 mm FL to be most frequent (Figure 4, Appendix C). No significant differences were observed in the length composition of male fish sampled between fall 2002 and 2003 or between fall 2003 and 2004 (Figure 4, Appendix C). The differences between fall samples and spring samples are attributed to the spring samples including the typically larger female fish (Figure 5).

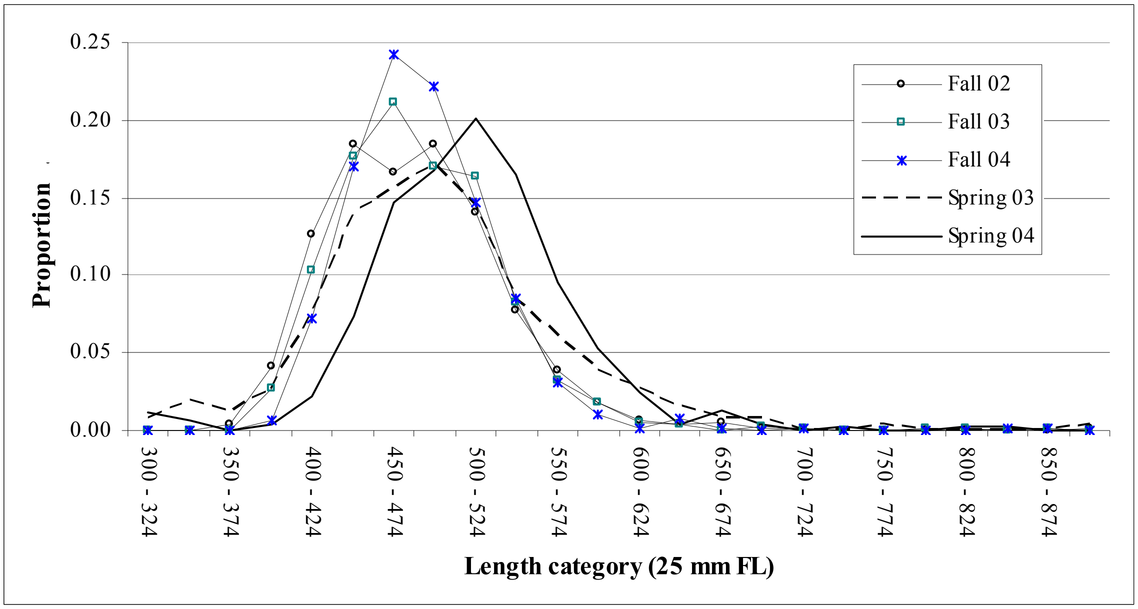

Figure 4.–Length composition of all male lake trout sampled during fall and all lake trout (sex undetermined) during spring from Paxson Lake, 2002–2004.

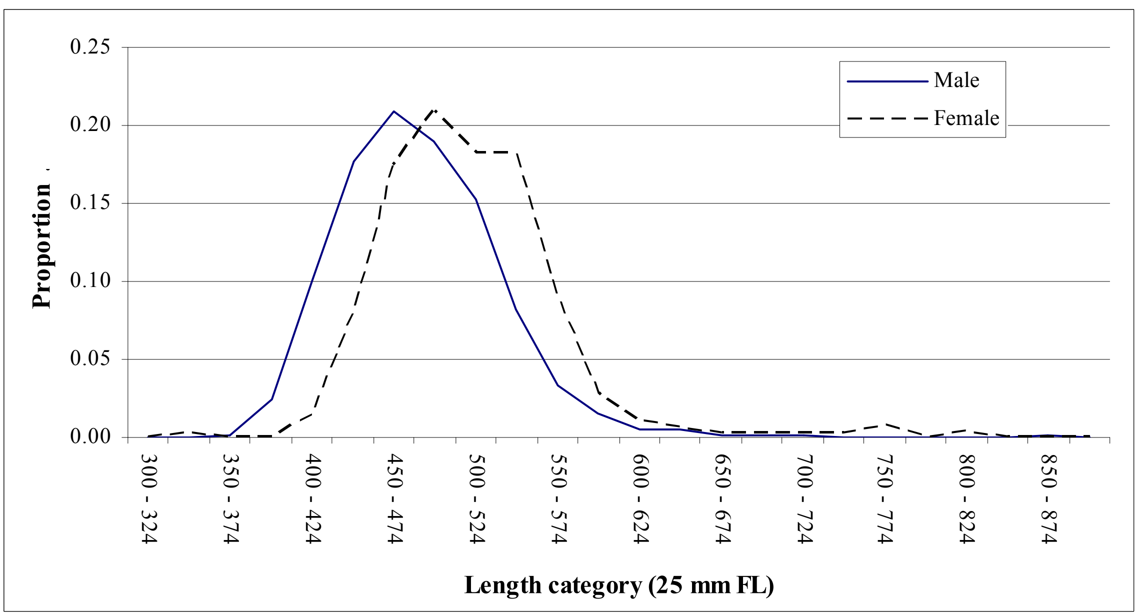

Figure 5.–Length composition of all male and female lake trout sampled during fall from spawning areas in Paxson Lake, 2002–2004.

DISCUSSION

This study helped to address questions related to our ability to representatively sample the male spawning population in Paxson Lake and the reliability of using estimates of male lake trout as an index to monitor total population sizes. Our ability to representatively sample all male lake trout has been a concern because it was believed that lake trout may have been isolated from sampling due to spawning site fidelity or spawning at undocumented spawning areas and our inability to sample all spawning areas in a given sample event. For example, despite years of study on this lake, from 2002 to 2004, two new minor spawning aggregations (#25 and #26) were found near (~200 m) previously documented spawning areas (Figure 3). Prior to this study, a comprehensive examination of spawning site fidelity had not been conducted. The results of this study demonstrated that spawning fidelity at the scale of a quadrant does exist (Appendix B1 and B2), but that relatively large proportions of fish tended to move between spawning areas within a quadrant (Appendix B1and B2). This behavior was somewhat counter to our preconceived notion that lake trout exhibit strong fidelity to a specific spawning location. However, the data also demonstrated the importance of accounting for most spawning areas and distributing sampling effort accordingly.

The results of this study when compared with historical harvest levels provided evidence that the LA model was too conservative for Paxson Lake. Prior to 2004, fishing mortality consistently exceeded the estimated yield potential (Figure 2) and yet the estimated abundances using the Jolly-Seber models were similar for all years including 2004. Unsustainable harvest levels should be reflected in a declining population size, which was not observed (Figure 6). Therefore, more restrictive regulations are not warranted if harvests consistently exceed the estimated YP by a small margin (e.g., 25%) or periodically exceed by a large margin (e.g., 100%).

The approach for estimating abundance of mature males (i.e., ≥450 mm FL) using a fall-to-fall experiment has proven to be a reliable and cost effective method that provide a good index of total population abundance. This assertion is supported by the similarity of the estimates between the fall-to-fall experiments and the fall-to-spring and spring-to-fall experiments (Figure 7). Large differences would have suggested that a substantial portion of the population was not being sampled or that sex ratios were vastly different than 1:1.

Conducting consecutive sampling events (e.g., fall-to-spring) at Paxson Lake has identified alternative methods for assessing abundance in Paxson Lake as well as in other lakes. When complete mixing is realized during either a fall-to-spring or spring-to-fall experiment, which was observed in this study, abundance can be reliably estimated not only within a shorter time frame, but also by sampling a subset of the spawning areas within a given lake. These conditions could also provide abundance estimates at a reduced cost compared to methods used in the past.

In Paxson Lake, for example, an alternative approach may be to mark male lake trout (e.g., fall 2003) on the spawning grounds in the fall and then to use electrofishing gear at the lake's outlet (Area G) where lake trout are concentrated following ice out (spring 2004). In spring 2004, approximately half of all fish sampled were captured in Area G using a shocker boat for approximately 30 minutes over two evenings. This approach resulted in the recapture of 23 fish, an experiment that passed all diagnostic tests for equal probability of capture (*p*-values ≥0.59), and generated an abundance estimate for male fish ≥450 mm FL (1,931, SE = 280), that was nearly identical to the fall03–fall 04 estimate ($\hat{N}$ = 1,906).

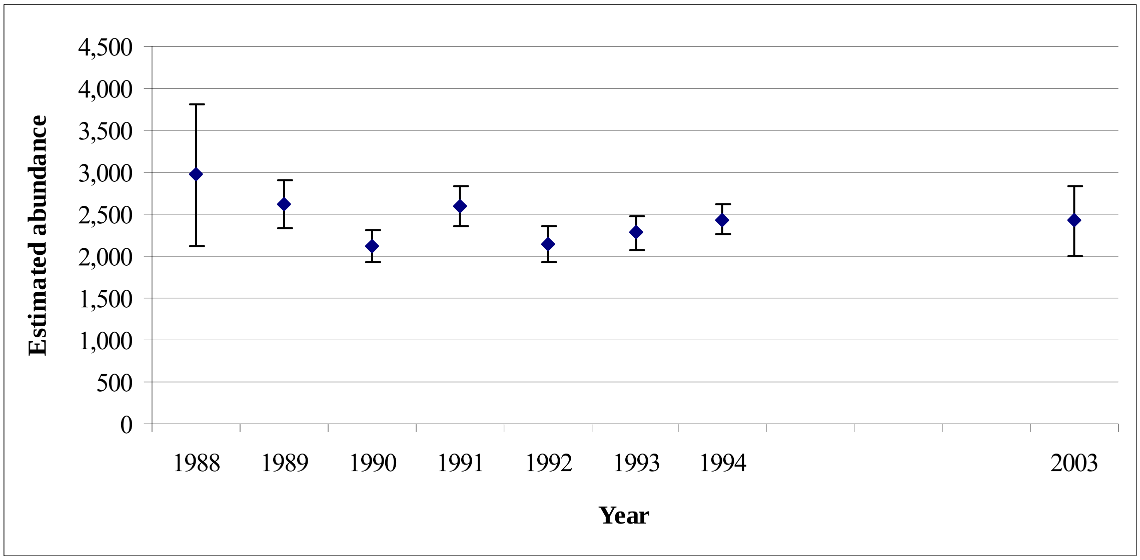

Figure 6.–Estimated abundance (±95% CI) of spawning male lake trout using the Jolly Seber model in Paxson Lake. Estimates from 1988 to 1994 were taken from Szarzi and Bernard (1997).

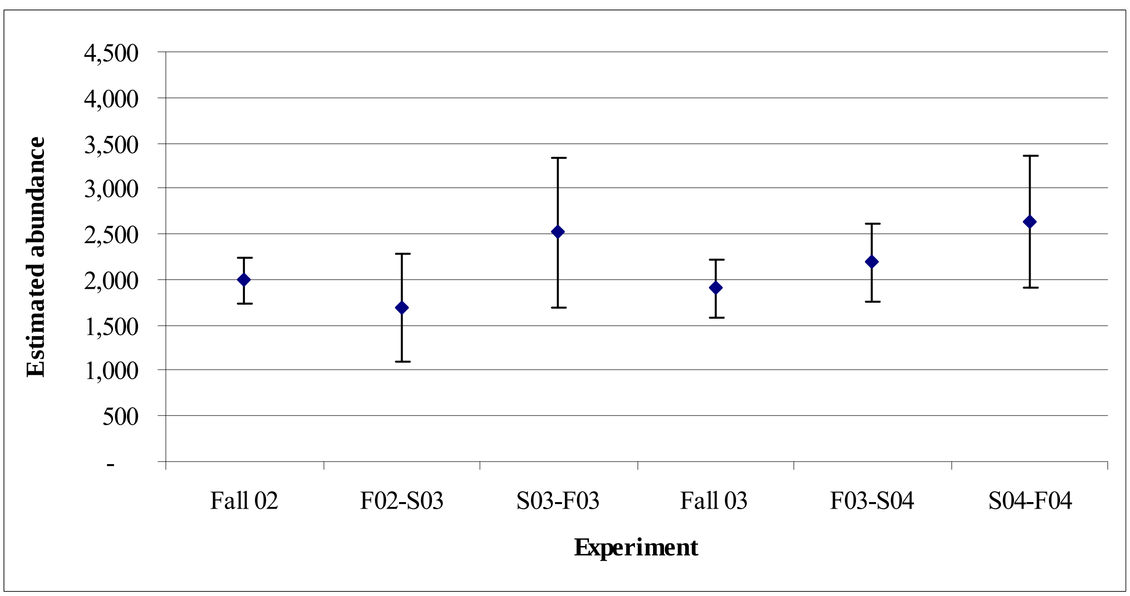

Figure 7.–Estimated abundance (±SE) of male lake trout ≥450 mm FL by experiment in Paxson Lake, 2002–2004.

The approach of seining fish in the fall and sampling fish in the spring may be warranted for lakes where a large proportion of the known spawning beds are difficult or impossible to sample or if it is likely there are undocumented spawning areas, such as with Lake Louise and Susitna Lake in the Upper Susitna River basin. During 1991 to 1993, a similar approach was attempted in Lake Louise. Annual fall sampling events were conducted from 1991–1995 on two spawning clusters to estimate abundance of a sub-population of male spawners (i.e., those assumed to be fidel to the two clusters). In the summer of 1992 and 1993, the anglers' creel was periodically sampled in an attempt to estimate total population size. Although details from the experiment are lacking in the attendant reports, Szarzi (1993) did report sampling 17 tagged fish from the creel for Lake Louise, eight of which were marked in Lake Louise (Fall 1992) and nine from fish that were tagged in the connecting Susitna Lake in 1991 and 1992. Unfortunately, the sample size of fish examined in the creel was too small for rigorous testing or estimating abundance and the creel data lacked good geographic information, although significant mixing was concluded (Szarzi 1993). The experiment also identified the presence of a mixed stock of both Susitna Lake and Lake Louise male spawners in summer and the potential for estimating total population sizes using more rigorous spring sampling. The use of an electrofishing boat would not be feasible in these systems, and therefore spring sampling would still require the use of gillnetting, which can be labor intensive due to low catch rates. However, spring sampling efforts could be made more efficient by targeting areas of higher catch rates as opposed to distributing effort in all waters. The sample sizes required in the spring would be relatively smaller because this experiment would rely on the high catch rates of lake trout that can be attained during fall.

Lastly, attempts at estimating total population sizes in Paxson Lake (and likely other lakes as well) using a spring-to-spring experiment are not recommended. This sampling was labor intensive and catch rates were very low.

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APPENDIX A

Appendix A1.–Procedures for detecting and adjusting for size or sex selective sampling during a 2-sample mark recapture experiment.

Overview

Size and sex selective sampling may result in the need to stratify by size and/or sex in order to obtain unbiased estimates of abundance and composition. In addition, the nature of the selectivity determines whether the first, second or both event samples are used for estimating composition. The Kolmogorov-Smirnov two sample (K-S) test (Conover 1980) is used to detect significant evidence that size selective sampling occurred during the first or second sampling events and contingency table analysis (Chi-square test) is generally used to detect significant evidence that sex selective sampling occurred during the first or second sampling events.

K-S tests are used to evaluate the second sampling event by comparing the length frequency distribution of all fish marked during the first event (M) with that of marked fish recaptured during the second event (R), using the null test hypothesis (H_o) of no difference. The first sampling event is evaluated by comparing the length frequency distribution of all fish inspected for marks during the second event (C) with that of R. Chi-square tests are used to compare the counts of observed males to females between M&R and C&R according to the null hypothesis that the probability that a sampled fish is male or female is independent of the sample. When the proportions by gender are estimated for a subsample (usually from C), rather than observed for all fish in the sample, contingency table analysis is not appropriate and the proportions of females (or males) are compared using a two sample test (e.g. Student's t-test).

Mark-recapture experiments are designed to obtain sample sizes sufficient to 1) achieve precision objectives for abundance and composition estimates; and, 2) ensure that the diagnostic tests (i.e., tests for selectivity) have power adequate for identifying selectivity that could result in significantly biased estimates. Despite careful design, experiments may result in inadequate sample sizes leading to unreliable diagnostic test results due to low power. As a result, detection and adjusting for size and sex selectivity involves evaluating the power of the diagnostic tests.

The protocols that follow are used to classify the experiment into one of four cases. For each case the following are specified: 1) whether stratification is necessary; 2) which sample event's data should be used when estimating composition; and, 3) the estimators to be used for composition estimates when stratifying. The first protocols assume adequate power. These are followed by supplemental protocols to be used when power is suspect and guidelines for evaluating power.

Protocols given Adequate Power

Case I:

M vs. R	**C vs. R**
Fail to reject H_o	Fail to reject H_o

There is no size/sex selectivity detected during either sampling event. Abundance is calculated using a Petersen-type model from the entire data set without stratification. Composition parameters may be estimated after pooling length, sex, and age data from both sampling events.

Case II:

M vs. R	**C vs. R**
Reject H_o	Fail to reject H_o

There is no size/sex selectivity detected during the first event but there is during the second event sampling. Abundance is calculated using a Petersen-type model from the entire data set without stratification. Composition parameters may be estimated using length, sex, and age data from the first sampling event without stratification. If composition is estimated from second event data or after pooling both sampling events, data must first be stratified to eliminate variability in capture probability (detected by the M vs. R test) within strata. Composition parameters are estimated within strata, and abundance for each stratum

-continuedneeds to be estimated using a Petersen-type formula. Overall composition parameters are estimated by combining stratum estimates weighted by estimated stratum abundance according to the formulae below.

Case III:

M vs. R	**C vs. R**
Fail to reject H_o	Reject H_o

There is no size/sex selectivity detected during the second event but there is during the first event sampling. Abundance is calculated using a Petersen-type model from the entire data set without stratification. Composition parameters may be estimated using length, sex, and age data from the second sampling event without stratification. If composition is estimated from first event data or after pooling both sampling events, data must first be stratified to eliminate variability in capture probability (detected by the C vs. R test) within strata. Composition parameters are estimated within strata, and abundance for each stratum needs to be estimated using a Petersen-type formula. Overall composition parameters are estimated by combining stratum estimates weighted by estimated stratum abundance according to the formulae below.

Case IV:

M vs. R	**C vs. R**
Reject H_o	Reject H_o

There is size/sex selectivity detected during both the first and second sampling events. The ratio of the probability of captures for size of sex categories can either be the same or different between events. Data must be stratified to eliminate variability in capture probability within strata for at least one or both sampling events. Abundance is calculated using a Petersen-type model for each stratum, and estimates are summed across strata to estimate overall abundance. Composition parameters may be estimated within the strata as determined above, but only using data from sampling events where stratification has eliminated variability in capture probabilities within strata. If data from both sampling events are to be used, further stratification may be necessary to meet the condition of capture homogeneity within strata for both events. Overall composition parameters are estimated by combining stratum estimates weighted by estimated stratum abundance.

When stratification by sex or length is necessary prior to estimating composition parameters, an overall composition parameters (p_k) is estimating by combining within stratum composition estimates using:

$$\hat{p}_k = \sum_{i=1}^{j} \frac{\hat{N}_i}{\hat{N}_\Sigma} \hat{p}_{ik} \text{ , and} \quad \text{(B1-1)}$$

$$\hat{V}[\hat{p}_k] \approx \frac{1}{\hat{N}_\Sigma^2} \left(\sum_{i=1}^{j} \hat{N}_i^2 \hat{V}[\hat{p}_{ik}] + \left(\hat{p}_{ik} - \hat{p}_k \right)^2 \hat{V}[\hat{N}_i] \right) \quad \text{(B1-2)}$$

where:
- j = the number of sex/size strata;
- $\hat{p}_{ik}$ = the estimated proportion of fish that were age or size k among fish in stratum i;
- $\hat{N}_i$ = the estimated abundance in stratum i;
- $\hat{N}_\Sigma$ = sum of the $\hat{N}_i$ across strata.

Protocols when Power Suspect (re-classifying the experiment)

When sample sizes are small (guidelines provided in next section) power needs to be evaluated when diagnostic tests fail to reject the null hypothesis. If this failure to identify selectivity is due to low power (that is, if selectivity is actually present) data will be pooled when stratifying is necessary for unbiased estimates. For example, if the both the M vs. R and C vs. R tests failed to identify selectivity due to low power, Case I may be selected when Case IV is true. In this scenario, the need to stratify could have been overlooked leading to biased estimates. The following protocols should be followed when sample sizes are small.

Appendix A2.–Tests of consistency for the Petersen estimator (from Seber 1982, page 438).

TESTS OF CONSISTENCY FOR PETERSEN ESTIMATOR

Of the following conditions, at least one must be fulfilled to meet assumptions of a Petersen estimator:

1. Marked fish mix completely with unmarked fish between events;
2. Every fish has an equal probability of being captured and marked during event 1; or,
3. Every fish has an equal probability of being captured and examined during event 2.

To evaluate these three assumptions, the chi-square statistic will be used to examine the following contingency tables as recommended by Seber (1982). At least one null hypothesis needs to be accepted for assumptions of the Petersen model (Bailey 1951, 1952; Chapman 1951) to be valid. If all three tests are rejected, a geographically stratified estimator (Darroch 1961) should be used to estimate abundance.

I.-Test For Complete Mixing[a]

Section	Section Where Recaptured				Not Recaptured
Where Marked	**A**	**B**	**…**	**F**	(n_1-m_2)
A					
B					
...					
F					

II.-Test For Equal Probability of capture during the first event[b]

	Section Where Examined			
	A	**B**	**…**	**F**
Marked (m_2)				
Unmarked (n_2-m_2)				

III.-Test for equal probability of capture during the second event[c]

	Section Where Marked			
	A	**B**	**…**	**F**
Recaptured (m_2)				
Not Recaptured (n_1-m_2)				

[a] This tests the hypothesis that movement probabilities (θ) from section i (i = 1, 2, ...s) to section j (j = 1, 2, ...t) are the same among sections: H_0: $\theta_{ij} = \theta_j$.

[b] This tests the hypothesis of homogeneity on the columns of the 2-by-t contingency table with respect to the marked to unmarked ratio among sections: H_0: $\Sigma_i a_i \theta_{ij} = kU_j$, where k = total marks released/total unmarked in the population, U_j = total unmarked fish in stratum j at the time of sampling, and a_i = number of marked fish released in stratum i.

[c] This tests the hypothesis of homogeneity on the columns of this 2-by-s contingency table with respect to recapture probabilities among sections: H_0: $\Sigma_j \theta_{ij} p_j = d$, where p_j is the probability of capturing a fish in section j during the second event, and d is a constant.

Appendix A3.–Equations for calculating estimates of abundance and its variance using the Chapman-modified Petersen estimator.

Abundance was estimated using Chapman's modification of the Petersen two-sample model (Seber 1982). This estimate was calculated using:

$$\hat{N} = \frac{(n_2+1)(n_1+1)}{m_2+1} - 1 \qquad (1)$$

where:

$\hat{N}$ = the abundance of lake trout in the Paxson Lake study area;
n_1 = the number of lake trout marked and released during the first event;
n_2 = the number of lake trout examined for marks during the second event; and,
m_2 = the number of lake trout recaptured in the second event.

Variance of this estimator was calculated as:

$$V\hat{a}r\left[\hat{N}\right] = \frac{(n_1+1)(n_2+1)(n_1-m_2)(n_2-m_2)}{(m_2+1)^2(m_2+2)} \qquad (2)$$

APPENDIX B

Appendix B1.–Number of recaptured male lake trout moving between individual spawning areas and quadrants summarized from archived data (1988–1995) in Paxson Lake. Bordered cells indicate fish that were marked and recovered in the same spawning area, shaded cells indicate fish that were marked and recovered in the same quadrant, and unshaded cells indicate movement out of a spawning quadrant.

Spawning area where marked		Spawning area where recaptured																
		NW	NW	NE	NE	NE	SW	SW	SW	SW	SW	SW	SE	SE	SE	SE	SE	
		9	10	14	15	19	11	21	12	24	13	20	23	16	17	18	22	Total
NW	9	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	2
NW	10	3	7	2	0	0	1	2	0	0	0	0	0	0	0	0	0	15
NE	14	0	2	29	12	6	9	0	4	0	1	0	1	1	2	0	0	67
NE	15	2	1	20	13	3	0	0	2	1	1	0	0	2	3	1	0	49
NE	19	0	1	2	9	23	8	1	3	1	0	0	0	0	0	1	0	49
SW	11	1	3	18	16	13	400	29	123	17	36	1	2	22	36	20	2	739
SW	21	0	0	0	1	0	8	1	6	2	1	0	0	0	0	1	0	20
SW	12	0	2	3	0	3	33	8	76	15	25	1	0	3	9	6	4	188
SW	24	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SW	13	2	1	2	2	3	33	5	72	9	39	0	0	4	10	10	4	196
SW	20	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	2
SE	23	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1
SE	16	1	0	2	4	0	21	2	27	2	3	0	4	41	42	24	6	179
SE	17	0	1	4	3	5	30	3	29	6	28	0	2	55	148	63	14	391
SE	18	0	0	1	2	2	4	2	13	5	6	0	0	18	39	26	7	125
SE	22	0	1	0	0	0	0	0	0	0	0	0	0	0	1	2	1	5
	Total	5	20	85	62	58	547	53	357	58	140	2	9	146	290	154	38	2,028

Appendix B2.–Number of male lake trout marked during fall 2002 and recaptured during fall 2003 by individual spawning areas and quadrants in Paxson Lake.

		Spawning area where recaptured																			
		NW	NW	NE	NE	NE	SW	SW	SW	SW	SW	SW	SW	SW	SE	SE	SE	SE	SE	SE	
		9	10	14	15	19	11	21	12	24	13	20	25	26	27	23	16	17	18	22	Total
Spawning area where marked	NW 9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	NW 10	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4
	NE 14	0	2	28	1	3	1	0	0	0	1	0	0	0	0	1	0	0	0	0	37
	NE 15	0	1	5	3	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	10
	NE 19	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SW 11	0	0	0	1	1	9	0	3	1	1	0	0	2	1	0	1	0	0	0	20
	SW 21	0	0	0	0	0	7	5	4	3	2	0	0	1	3	0	0	1	0	0	26
	SW 12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SW 24	0	0	0	0	1	1	1	4	0	1	0	0	0	2	0	0	1	0	0	11
	SW 13	0	0	0	0	0	1	1	3	1	0	0	0	1	0	0	0	0	0	0	7
	SW 20	0	1	0	0	0	1	1	0	0	1	0	0	0	1	0	0	0	1	0	6
	SW 25	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SW 26	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SE 27	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SE 23	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SE 16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SE 17	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	8	2	0	12
	SE 18	0	0	0	0	0	1	0	1	0	1	0	0	0	3	1	5	12	2	0	26
	SE 22	0	0	0	0	0	1	0	3	1	0	0	0	0	2	1	2	12	5	0	27
	Total	0	8	33	5	5	24	8	19	6	7	0	0	4	12	3	8	34	10	0	186

Appendix B3.–Number of male lake trout marked during fall 2003 and recaptured during fall 2004 by individual spawning areas and quadrants in Paxson Lake.

Spawning area where marked		Spawning area where recaptured																			
		NW 9	NW 10	NE 14	NE 15	NE 19	SW 11	SW 21	SW 12	SW 24	SW 13	SW 20	SW 25	SW 26	SE 27	SE 23	SE 16	SE 17	SE 18	SE 22	Total
NW	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NW	10	0	13	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	14
NE	14	0	6	36	13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	55
NE	15	0	2	6	4	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	14
NE	19	0	0	1	0	8	1	0	1	0	0	0	0	0	0	0	0	0	0	0	11
SW	11	0	0	1	0	0	16	0	6	0	12	0	0	0	0	0	0	0	0	0	35
SW	21	0	0	0	0	0	2	0	8	0	3	1	0	0	0	0	1	0	0	0	15
SW	12	0	0	1	0	0	1	0	10	0	14	0	0	0	0	0	0	1	0	0	27
SW	24	0	0	1	0	0	1	0	3	0	8	0	0	0	0	0	0	0	0	0	13
SW	13	0	0	0	0	0	1	0	5	0	6	1	0	0	0	0	0	1	0	0	14
SW	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SW	25	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SW	26	0	0	0	0	0	0	0	3	0	6	0	0	0	0	0	0	0	0	0	9
SE	27	0	1	0	0	0	2	0	0	0	4	0	0	0	0	0	0	1	0	0	8
SE	23	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
SE	16	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	3
SE	17	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	2	11	0	0	14
SE	18	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	2	1	0	0	4
SE	22	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Total		0	22	46	18	11	24	0	37	0	54	2	0	0	0	0	7	16	0	0	237

APPENDIX C

Appendix C1.–Length composition of male lake trout sampled from the spawning ground in Paxson Lake, 2002–2004.

	All males lake trout						Male lake trout ≥450 mm FL[a]					
Category	Fall 2002		Fall 2003		Fall 2004		Fall 2002		Fall 2003		Fall 2004	
(mm FL)	n	P	n	P	n	P	P	n	P	n	P	n
350–359	2	0.003	0	0.000	0	0.000		0.000		0.000		0.000
375–384	25	0.041	26	0.027	4	0.006		0.000		0.000		0.000
400–409	76	0.126	98	0.103	48	0.072		0.000		0.000		0.000
425–434	111	0.184	167	0.176	114	0.170		0.000		0.000		0.000
450–459	100	0.166	201	0.212	162	0.242	100	0.257	201	0.305	162	0.322
475–484	111	0.184	162	0.171	148	0.221	111	0.285	162	0.246	148	0.294
500–509	85	0.141	155	0.163	98	0.146	85	0.219	155	0.236	98	0.195
525–534	47	0.078	78	0.082	57	0.085	47	0.121	78	0.119	57	0.113
550–559	23	0.038	30	0.032	21	0.031	23	0.059	30	0.046	21	0.042
575–584	11	0.018	17	0.018	7	0.010	11	0.028	17	0.026	7	0.014
600–609	4	0.007	5	0.005	1	0.001	4	0.010	5	0.008	1	0.002
625–634	2	0.003	4	0.004	5	0.007	2	0.005	4	0.006	5	0.010
650–659	3	0.005	0	0.000	1	0.001	3	0.008	0	0.000	1	0.002
675–684	1	0.002	2	0.002	0	0.000	1	0.003	2	0.003	0	0.000
700–709	1	0.002	1	0.001	1	0.001	1	0.003	1	0.002	1	0.002
725–734	0	0.000	0	0.000	0	0.000	0	0.000	0	0.000	0	0.000
750–759	0	0.000	0	0.000	0	0.000	0	0.000	0	0.000	0	0.000
775–784	0	0.000	1	0.001	0	0.000	0	0.000	1	0.002	0	0.000
800–809	0	0.000	1	0.001	0	0.000	0	0.000	1	0.002	0	0.000
825–834	0	0.000	0	0.000	1	0.001	0	0.000	0	0.000	1	0.002
850– 859	0	0.000	1	0.001	1	0.001	0	0.000	1	0.002	1	0.002
875–884	1	0.002	0	0.000	0	0.000	1	0.003	0	0.000	0	0.000
900–909	0	0.000	0	0.000	0	0.000	0	0.000	0	0.000	0	0.000
	603		949		669		389		658		503	

[a]Length composition for fish ≥450 mm FL for all years are representative of the population based on K-S testing (i.e. Case I).

Appendix C2.–Length composition of lake trout sampled from Paxson Lake during spring 2003 and 2004.

Category	2003		2004	
(mm FL)	n	P	n	P
300–324	2	0.01	5	0.01
325–349	5	0.02	3	0.01
350–374	3	0.01	0	0.00
375–399	7	0.03	2	0.00
400–424	20	0.08	10	0.02
425–449	37	0.14	33	0.07
450–474	41	0.16	66	0.15
475–499	45	0.17	75	0.17
500–524	38	0.14	90	0.20
525–549	22	0.08	74	0.16
550–574	16	0.06	43	0.10
575–599	10	0.04	24	0.05
600–624	7	0.03	11	0.02
625–649	4	0.02	2	0.00
650–674	2	0.01	6	0.01
675–699	2	0.01	2	0.00
700–724	0	0.00	0	0.00
725–749	0	0.00	1	0.00
750–774	1	0.00	0	0.00
775–799	0	0.00	0	0.00
800–824	0	0.00	1	0.00
825–849	0	0.00	1	0.00
850–874	0	0.00	0	0.00
875–899	1	0.00	0	0.00
Total	263	1.00	449	1.00

APPENDIX D

Appendix D1.–Number of lake trout ≥450 mm FL marked (n_1), examined (n_2), and recaptured by sampling area during the fall 02–spring 03 events in Paxson Lake.

		Area where recaptured										
		H	A	B	C	D	E	F	G	m_2	n_1	m_2/n_1
Area Marked	NW	0	0	0	0	0	0	0	0	0	4	4
	NE	0	0	1	0	1	0	0	2	4	117	121
	SW	1	0	1	0	0	1	1	1	5	151	156
	SE	1	1	0	1	0	3	1	5	12	198	210
	m_2	2	1	2	1	1	4	2	8			
	n_2	15	21	15	13	12	20	20	73			
	m_2/n_2	0.27	0.10	0.27	0.15	0.17	0.40	0.20	0.11			

Appendix D2.–Number of lake trout ≥450 mm FL marked (n_1), examined (n_2), and recaptured by sampling area during the fall 03–spring 04 events in Paxson Lake.

		Area where recaptured										
		H	A	B	C	D	E	F	G	m_2	n_1	m_2/n_1
Area Marked	NW	0	0	0	0	0	0	1	2	3	58	0.05
	NE	0	0	0	2	1	0	6	6	15	185	0.08
	SW	0	3	1	2	0	2	8	14	30	328	0.09
	SE	0	0	0	2	1	0	1	6	10	87	0.11
	m_2	0	3	1	6	2	2	16	28			
	n_2	0	19	7	29	34	29	104	168			
	m_2/n_2	0	0.16	0.14	0.21	0.06	0.07	0.15	0.17			

Appendix D3.–Number of male lake trout marked during spring 2003 and recaptured during fall 2003 by sampling area in Paxson Lake.

		Area recaptured																					
		NW	NW	NE	NE	NE	SW	SW	SW	SW	SW	SW	SW	SW	SE	SE	SE	SE	SE	SE			
		9	10	14	15	19	11	21	12	24	13	20	25	26	27	23	16	17	18	22	m_2	n_1	m_2/n_1
Area marked NW	H	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	2	15	0.13
NW	A	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	3	21	0.14
NW	C	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	13	0.00
NE	B	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	2	15	0.13
NE	D	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	12	0.08
SW	E	0	0	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	3	20	0.15
SW	G	0	0	1	0	1	3	1	0	0	0	0	0	1	1	1	1	0	0	0	10	73	0.14
SE	F	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	3	20	0.15
	m_2	0	0	3	1	3	7	1	0	0	0	0	0	2	3	1	2	1	0	0	24		
	n_1	8	50	93	35	57	111	29	70	17	28	0	0	22	38	11	13	62	14	0			
	m_2/n_1	0.00	0.00	0.03	0.03	0.05	0.06	0.03	0.00	0.00	0.00	0.00	0.00	0.09	0.08	0.09	0.15	0.02	0.00	0.00			

Appendix D4.–Number of male lake trout marked during spring 2004 and recaptured during fall 2004 by sampling area in Paxson Lake.

		Area recaptured																				
		NW	NW	NE	NE	NE	SW	SW	SW	SW	SW	SW	SW	SW	SE	SE	SE	SE	SE	SE			
Area marked		9	10	14	15	19	11	21	12	24	13	20	25	26	27	23	16	17	18	22	m_2	n_1	m_2/n_1
NW	H	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.00
NW	A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	19	0.00
NW	C	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	3	29	0.10
NE	B	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	0.00
NE	D	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	2	34	0.06
SW	E	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	29	0.03
SW	G	0	2	3	0	1	2	0	4	0	6	0	0	0	0	0	0	4	0	0	22	168	0.13
SE	F	0	0	3	1	2	1	0	1	0	1	0	0	0	0	0	0	0	0	0	9	104	0.09
	m_2	0	3	6	2	4	3	0	7	0	8	0	0	0	0	0	0	4	0	0			
	n_1	0	42	100	37	35	62	0	67	0	86	7	0	0	0	0	20	43	0	4			
	m_2/n_1	0.00	0.07	0.06	0.05	0.11	0.05	0.00	0.10	0.00	0.09	0.00	0.00	0.00	0.00	0.00	0.00	0.09	0.00	0.00			