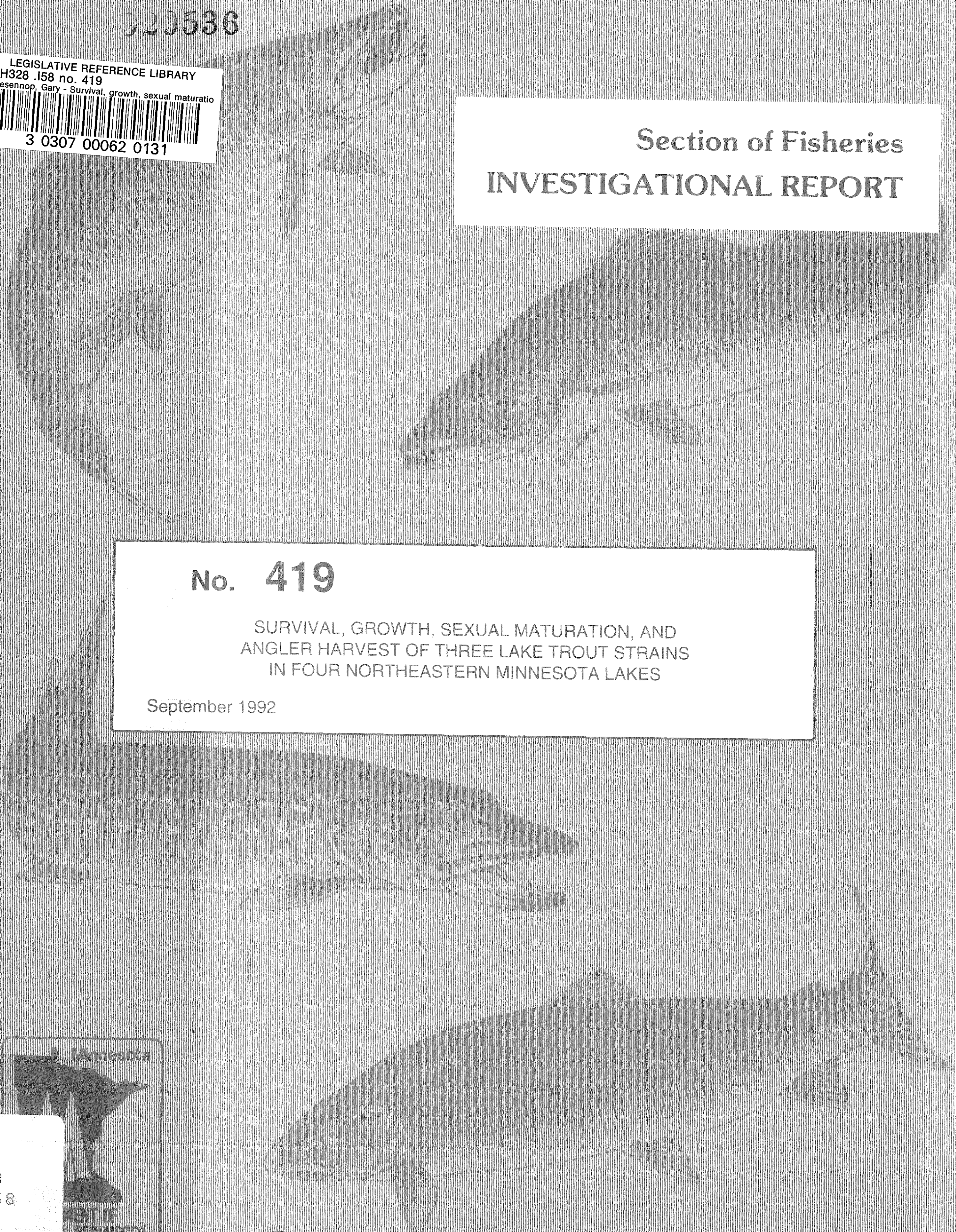

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SURVIVAL, GROWTH, SEXUAL MATURATION, AND ANGLER HARVEST OF THREE LAKE TROUT STRAINS IN FOUR NORTHEASTERN MINNESOTA LAKES

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Survival, Growth, Sexual Maturation, and Angler Harvest of Three Lake Trout Strains in Four Northeastern Minnesota Lakes[1]

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Abstract.-Performances of three strains of lake trout *Salvelinus namaycush* were evaluated in four lakes in northeastern Minnesota. Lake trout were stocked as spring yearlings and then monitored with trap nets, gill nets, and winter creel surveys for up to nine years. Trout of the native Gillis Lake strain survived better after stocking, and subsequently contributed more to the angler catch than the Isle Royale or the Marquette strains, when stocked with them. The differential survival by strain (and perhaps by year-class) may be determined within the first few months after stocking, as the ratios in which the strains were captured by various nets or anglers remained nearly constant. Predation by older lake trout or condition at stocking may have influenced survival of newly stocked yearlings.

Growth and age at sexual maturity were similar among strains within lakes, but lake-to-lake differences in growth and sexual maturation were large and dependent on the kinds of forage fish available. Juvenile lake trout grew and matured most rapidly in Birch Lake, and progressively slower in Mayhew, West Bearskin, and Duncan lakes. Growth curves suggest the maximum size reached in the four lakes is negatively related to juvenile growth rates. Growth in West Bearskin Lake accelerated three to four years after stocking, presumably when lake trout were able to consume rainbow smelt *Osmerus mordax*, a relatively large prey which was absent or rare in the other lakes. These results show lake trout stocks used for rehabilitating stressed lake trout fisheries, and for re-establishing populations in lakes where they have been extirpated should be from the local geographic area. Non-native or hatchery stocks may be less able to cope with potential predators or competitors, and may exhibit lower survival. The Schnute general growth model is recommended for describing growth and for comparing growth of fish stocks.

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Introduction

Minnesota fish managers have stocked several lake trout strains in inland lakes to augment or restore fishable stocks, but performance characteristics of the strains available in Minnesota have not been objectively evaluated. Genetic differences among lake trout strains affect behavior, physiology, survival, growth, and reproduction (Royce 1951; Haskell et al. 1952; Plosila 1977; MacLean et al. 1981). Ihssen (1976) warned that hatchery strains often lose heterozygosity due to inbreeding resulting in low survival. Krueger et al. (1981) suggested stocking to re-establish extirpated populations and to supplement depleted lake trout stocks should be done with lake trout from a similar environment, as these may be pre-adapted. Other workers have suggested that lake-to-lake differences in fish communities or the environment may be more important than strain in determining growth and survival of stocked lake trout. Predation (including cannibalism) and competition for food may influence the survival of young lake trout (Martin and Olver 1980; Matuszek et al. 1990; Elrod and Schneider 1992) and may mask genetic or strain effects.

Old Minnesota Department of Natural Resources (MN DNR) stocking records (often sketchy) indicate that lake trout spawn or fertilized eggs were obtained from hatcheries in Michigan, Isle Royale waters of lake Superior, many locations along Minnesota's Lake Superior shore, Ontario (Sault St. Marie), and accessible inland Minnesota lakes. In the 1970s and the first half of the 1980s, Minnesota depended on the semi-domesticated Marquette (Michigan) strain for its inland stocking program.

Plosila (1977) noted, however, that strain was more important than size in determining survival. Lake trout of various sizes and ages, described as newly hatched fry, swim-up fry, fall fingerlings, and spring yearlings were stocked in northeastern Minnesota lakes from the 1920s through the 1980s (MN DNR, unpublished data). After observing several apparent stocking failures, especially with fry, emphasis shifted toward fingerling and yearling stocking. In the 1970s and 1980s, a higher proportion of lake trout were stocked as fall fingerlings (age 0+) and spring yearlings (age 1+). The consensus among field managers and biologists was that the larger the lake trout were when stocked, the better the chance that they would survive. Plosila (1977) found that spring (12 g) and fall (27 g) yearling lake trout survived better than fall fingerlings (4.6 g). In the 1970s most lake trout stocked in inland Minnesota lakes were not marked. Attempts to differentiate between native and stocked lake trout subsequently captured with gill nets often were ineffective. Little effort was made to determine stocking success, or small sample sizes confounded efforts to evaluate effects of strain or size at stocking. Powell et al. (1986) found that lake trout in the 18 to 25 g range made a significant contribution to year class size in many lakes in the Ontario pre-Cambrian shield.

A test of the field performance of various lake trout strains was needed as part of a comprehensive lake trout management program. The primary objectives of this study were to determine if there were differences in survival, growth, age at sexual maturation, and winter angling harvest of two wild and one domestic lake trout strain when stocked in northeastern Minnesota lakes. Potential differences in performance were examined in lakes having different predator or competitor assemblages.

Methods

Lake Trout Strains

In 1980, lake trout from three geographically isolated sources were available (Table 1). The first was the domestic Marquette (MIC) strain lake trout, originating in Lake Superior and maintained at Michigan's Marquette State Fish Hatchery. This strain has been used for many years in Minnesota's inland lakes stocking program, and in the Lake Superior lake trout rehabilitation pro-

Table 1. Sources of three lake trout strains.

Strain (abbrev.)	Year-class	Parental status	Parent source and location
Gillis Lake (GIL)	1981	wild	Gillis Lake (NE Minnesota)
	1982	wild	
	1986	wild	
	1987	F_1, hatchery	
Isle Royale (IRY)	1981	wild	Isle Royale, Lake Superior (Michigan waters)
	1982	wild	
	1986	wild	
	1987	F_1, hatchery	
Marquette (MIC)	1981	hatchery	Marquette State Fish Hatchery (Marquette, Michigan)
	1982	hatchery	
(MIC)	1986	F_1, wild	North shore of Lake Superior (Minnesota waters)

gram. A second spawn source was the wild Isle Royale (IRY) stock obtained from near-shore waters off Isle Royale in northwestern Lake Superior. A third potential gamete source was the native, inland Minnesota lake trout stocks, most of which are found in relatively remote, small lakes in the Boundary Waters Canoe Area Wilderness (BWCAW). In July and August 1980, fish populations in some of the remote, native lake trout lakes (never stocked) in the BWCAW were sampled. Using the results of these surveys, Gillis Lake was selected (GIL) as the source of native lake trout spawn for this study. Thus, three lake trout strains were to be compared: Gillis, Isle Royale, and Marquette strains. Lake trout from these sources were reared and four year-classes were stocked as "spring yearlings" (approximately 17 months after hatching). The year-class denotes the year when the eggs hatched. Strain and year-class will be abbreviated as: GIL81 = Gillis Lake strain, 1981 year-class; MIC86 = Marquette strain, 1986 year-class; etc.

Selection and Background of Study Lakes

Birch, Mayhew, West Bearskin, and Duncan lakes are four relatively small, inland Minnesota lake trout lakes. Study lakes range in size from 89 hectares (Mayhew Lake) to 200 hectares (Duncan Lake). Watershed soils are glacial till vegetated by mixed hardwoods and conifers. Bedrock outcrops are a common feature of the terrain (Hassinger and Close 1984). Some physical, chemical, and biotic properties of the lakes are listed in Table 2. Theoretical lake trout yields, based on July thermal habitat volume (THV), range from 1.1 to 2.7 kg/hectare/year. Theoretical yields, based on the morphoedaphic index (MEI), range from 1.4 to 1.7 kg/hectare/year^{-1} (Table 2).

Birch, Mayhew, and West Bearskin lakes are accessible to small motorized boats via road or short carry during open water seasons and by snowmobile during winter. Motorized boats or snowmobiles are not allowed on Duncan Lake, which is just inside the BWCAW border, and reached via a 350 m portage.

All four lakes are ecologically classified as "lake trout" lakes. The lakes differ in stocking histories and fish species assemblages, with Birch and Mayhew lakes being more similar to each other than to either West Bearskin or Duncan lakes (Table 3). In fall 1969, Mayhew and Birch lakes were chemically rehabilitated (reclaimed with antimy-

Table 2. Study lakes characteristics.

	Mayhew	Birch	W. Bearskin	Duncan
Location:				
Latitude, N.	48°05′	48°04′	48°04′	48°05′
Longitude, W.	90°35′	90°31′	90°26′	90°28′
Abiotic variables:				
Lake surface area (hectares)	89	105	200	193
Littoral area (% <4.6 m)	16	29	19	27
Shoreline length (km)	7.9	10.5	12.1	11.9
Shoreline development index	2.4	3.0	2.4	2.4
Mean depth (m)	11.3	7.9	9.4	14.3
Maximum depth (m)	26	21	24	35
Volume (10^6 hm^3)	6.6	5.2	12.4	18.2
Secchi depth visibility (m)	6.4	5.2	7.0	4.6
Total alkalinity (mg/l)	12.6	12.4	13.5	14.9
Morphoedaphic index (MEI)[a]	1.11	1.57	1.44	1.04
Yield$_{MEI}$[a] (kg/hectare/year)	1.46	1.72	1.65	1.42
Yield$_{JTHV}$[b] (kg/hectare/year)	1.81	1.25	2.70	1.10
Biotic variables:				
Major species	1	2	4	4
Additional predators	0	0	3	4
Potential lake trout prey	12	11	10	13

[a] Morphoedaphic index (MEI) = total dissolved solids (TDS, mg/l) divided by mean depth (m); total alkalinity (mg/l) was substituted for total dissolved solids for these lakes because TDS measurements were not available (Ryder et al. 1974). Yield$_{MEI}$ is estimated in metric units, as $Y_{MEI} = 1.4\ (MEI)^{0.45}$.

[b] Thermal habitat volume (THV) (*i.e.* the volume of water considered to be suitable for lake trout) for each study lake. Yield$_{JTHV}$, was estimated from the predictive equation: $\log_{10}(\text{Harvest}) = 2.15 + 0.714 \log_{10}(\text{July thermal habitat volume})$ described by Payne et al. (1990).

cin). When this study began in 1980, fish communities in these two lakes were less diverse, especially at the piscivore level, than in West Bearskin and Duncan lakes, where non-native smallmouth bass *Micropterus dolomieui*, rainbow smelt *Osmerus mordax*, or cisco *Coregonus artedi* were also common or abundant. Various cyprinids and other potential lake trout forage species were re-introduced into Birch and Mayhew lakes via "bait-bucket" introductions or from small numbers that may have escaped the antimycin treatment.

After lake reclamation, Birch and Mayhew lakes were stocked annually or biennially to re-establish and maintain fishable lake trout populations. Fish management of these two lakes can be described as "put-grow-take" because relatively few lake trout escape to mature and the majority of harvested fish were stocked. Occasionally these two lakes were stocked with rainbow trout *Oncorhynchus mykiss* to add diversity to the angling experience and perhaps lessen angling pressure on lake trout. Splake *Salvelinus namaycush* x *S. fontinalis* stocked in Birch Lake in 1979 grew rapidly, became very popular with anglers, and were mostly removed within four years. Rainbow trout (Donaldson strain) stocked in Birch Lake in

Table 3. Fish species observed in the study lakes and their relative abundance. A=abundant; C=common; P=present; R=rare. A single asterisk (*) indicates potential lake trout prey species. Two asterisks (**) indicate known major lake trout prey species.

		Lake name			
Common name	Scientific name	Mayhew	Birch	W. Bearskin	Duncan
Cisco	*Coregonus artedi*	-	-	-	A**
Rainbow trout	*Oncorhynchus mykiss*	-	P	-	-
Lake trout	*Salvelinus namaycush*	C*	C*	C*	C*
Splake	*S. namaycush* X *S. fontinalis*	-	P	R	-
Rainbow smelt	*Osmerus mordax*	-	-	A**	R*
Central mudminnow	*Umbra limi*	P*	P*	P*	P*
Northern pike	*Esox lucius*	-	-	R	-
Lake chub	*Couesius plumbeus*	P*	P*	-	-
Golden shiner	*Notemigonus crysoleucas*	-	-	P*	P*
Fathead minnow	*Pimephales promelas*	P**	C**	-	P*
Finescale dace	*Phoxinus neogaeus*	-	P**	-	-
N. redbelly dace	*Phoxinus eos*	-	P**	-	-
Pearl dace	*Margariscus margarita*	P*	C*	-	-
Creek chub	*Semotilus atromaculatus*	P*	C*	-	-
White sucker	*Catostomus commersoni*	A*	C*	P*	P*
Brook stickleback	*Culaea inconstans*	P*	P*	P*	P*
Green sunfish	*Lepomis cyanellus*	A**	-	A**	A**
Bluegill sunfish	*Lepomis macrochirus*	P*	-	C*	-
Hybrid sunfish	*L. macrochirus* X *L. cyanellus*	-	-	P*	-
Smallmouth bass	*Micropterus dolomieui*	-	-	A*	A*
Black crappie	*Pomoxis nigromaculatus*	-	-	R	-
Yellow perch	*Perca flavescens*	P*	-	C*	C*
Walleye	*Stizostedion vitreum*	-	-	R*	R*
Iowa darter	*Etheostoma exile*	P**	C**	P*	P*
Mottled sculpin	*Cottus bairdi*	P*	P*	P*	P*
Number of species present:		13	14	17	14

1985 (during this study), also grew very rapidly, were very popular with some anglers, and most were harvested within two years. Managers felt that rainbow trout, thought to be less piscivorous than lake trout, would not strongly compete with them and would provide more potential for angling during the ice-free season.

Prior to 1970, lake trout stocking in West Bearskin Lake had been limited to fry and fingerlings. In 1970, at the start of a lake trout-rainbow smelt interaction study (Hassinger and Close 1984), West Bearskin Lake was stocked with 5,000 adipose-clipped, yearling lake trout (MIC69). Marquette yearlings (MIC80) were stocked in spring 1981 when few of the 1969 cohort remained.

Duncan Lake had been stocked with lake trout only once (1977, "fall fingerlings,". Its lake trout population at the start of this study consisted mainly of native or wild trout. Duncan Lake had a reputation for producing an occasional trophy (5-10+ kg), but mainly small lake trout and smallmouth bass.

Experimental Design

Initially, the three strains were to have been compared two at a time in each of six lakes, so each pairing would be replicated twice. Due to funding and labor limitations, and to shortages in the supply of the Gillis Lake strain, the number of study lakes was reduced to four. Each was stocked with two strains in 1982 and 1983. In spring 1987, all three strains were stocked in each of the four lakes. No MIC strain lake trout were available from Marquette after fall 1985 due to disease in the hatchery, but in spring 1987 I was able to substitute 1986 year-class lake trout spawned from fin-clipped MIC adults that were collected in fall 1985 along Minnesota's shore of Lake Superior (MIC-86). Each of the four study lakes was stocked with only the GIL and IRY 1987 cohorts in spring 1988, as no MIC lake trout yearlings were in Minnesota's hatchery system.

Stocking Density

The total stocking density for yearling lake trout ranged from 22 to 58 fish/hectare, varying by year-class. Stocking densities were equal for each strain and each lake stocked (Table 4). In spring 1983, stocking density for the 1982 year-class was reduced by approximately one-half in all lakes because the GIL82 yearlings were in short supply. No MIC87 lake trout were available because of disease problems, so in spring 1988 the stocking density of the GIL87 and IRY87 cohorts was increased by 50 percent.

Cohort Identification

Each cohort was marked with a different fin or maxillary bone clip one to two months prior to stocking so strain and year-class could be identified on recapture (Table 5). The 1982 year-class stocked in Birch Lake was given an additional mark with fluorescent pigment (Phinney et al. 1967). Red pigment was applied to the GIL82, and yellow-green pigment to the MIC82. The IRY82 and MIC82 cohorts were intraperitoneally injected with a 1% oxytetracycline (OTC) solution before being stocked into Mayhew Lake to put a time reference mark on the bony structures to aid in age validation studies (Holden and Vince 1973; Beamish and Chilton 1982). The nominal dosage was 0.1 mg OTC/g body weight. The 1986 and 1987 year-classes were marked with various combinations of pelvic and adipose fin clips (Table 5). A binary-coded wire tag in the cheek was used as an auxiliary mark. Detection and reading of coded-wire tags made it possible to separate strains and year-classes in some cases where fin-clip recognition was questionable due to regrowth, when slow growth (Duncan Lake) caused overlap in length distributions of the 1981-1987 year-classes, and when we were able to collect only lake trout heads from anglers.

Table 4. Total density of lake trout stocked in spring 1982, 1983, 1986, and 1987. Densities were equally divided among the strains stocked in each lake.

Lake name	Lake area (hectares)	Stocking density (number/hectare)			
		Year-class			
		1981	1982	1986	1987
Birch	105	50	22	54	52
Mayhew	89	46	22	54	56
W. Bearskin	200	50	24	57	56
Duncan	193	52	26	57	58

Table 5. Identifying marks assigned to lake trout yearlings stocked in spring 1982, 1983, 1986, and 1987. Abbreviations: R = right; L = left; P = pelvic fin; AD = adipose fin; M = maxillary bone. A dash indicates that no lake of the cohort were stocked.

Lake name	Year-class	Lake Trout Strain		
		Gillis	Isle Royale	Michigan
Mayhew	1981	–	RP	LP
	1982[a]	–	RM	LM
	1986[b]	RP-AD	AD	LP-AD
	1987[b]	LP	RP	–
Birch	1981	LP	–	RP
	1982[c]	LM	–	RM
	1986[b]	RP-AD	AD	LP-AD
	1987[b]	LP	RP	–
West Bearskin	1981	LP	RP	–
	1982	LM	RM	–
	1986[b]	RP-AD	AD	LP-AD
	1987[b]	LP	RP	–
Duncan	1981	–	RP-AD	LP-AD
	1982	–	RM	LM
	1986[b]	RP	AD	LP
	1987[b]	LP-AD	RP-AD	–

[a] Each fish was given an intraperitoneal oxytetracycline injection to add a time reference mark on fin rays and otoliths.

[b] Each fish was cheek-tagged with a coded-wire tag to indicate strain and year-class. Binary tag codes were: 16-47-05 = GIL86; 16-47-06 = IRY86; 16-47-07 = MIC86; 16-47-44 = GIL87; 16-47-42 = IRY87.

[c] Strains were spray-marked with fluorescent pigment as auxiliary identification marks: red = GIL82; green = MIC82.

Fish Transport and Stocking

Transport and receiving water conditions, including temperature and dissolved gases, were within acceptable ranges for lake trout stocking. All lake trout were transported from Lanesboro or Crystal Springs State Fish Hatchery. Trout were moved from the transport trucks directly to Birch, Mayhew, and West Bearskin lakes. Trout for Duncan Lake were carried approximately 3 km via floatplane, landed and dropped only 1 m to the lake surface. All lakes were stocked in late May or early June before thermal stratification (epilimnetic waters did not exceed 15°C). Avian predation was not observed during or immediately after the stocking procedure.

Size at Stocking

I used one-way analysis of variance (ANOVA) with Tukey's honest significant difference (HSD) test to compare mean lengths and weights. I used analysis of covariance (ANCOVA) to compare slopes and intercepts of linear regressions of $\log_{10}$weight on $\log_{10}$length, among strains within year-classes. The Kolmogorov-Smirnov two-sample (Smirnov) test was used to compare distributions of length and weight of strains within year-classes. I estimated mean weight per individual for the 1981 year-class from the hatchery "rates" (number of fish/kg just before transport and stocking). Individual weights were not available for the 1981 year-class, so ANOVA and ANCOVA could not be used to evaluate the perceived among cohort differences in size and condition at stocking. However, about 50 lake trout of each strain from each transport load were examined for fin-clip quality, and were measured to the nearest mm.

Fish Health at Stocking

A fish health examination was added to the stocking protocol for the 1982, 1986 and 1987 year-classes because the MIC81 cohort appeared to be heavier than either the GIL81 or the IRY81 cohorts when stocked. The method involved measurement of length and weight, and subjective observations related to fish health (gill, eye, fin condition, and amount of body fat; Goede 1990). Small numbers (25-50) of each cohort of the 1982, 1986, and 1987 year-classes were sacrificed at the time of stocking. Each fish sampled was rated from 0 - 4 to indicate the relative amount of the pyloric caeca that was obscured by fatty deposits, corresponding to fat coverage of 0%, 1-25%, 26-50%, 51-75%, and 76-100%. Chi-square tests were used to test for differences in body fat scores of the three strains (Sokal and Rolhf 1985). For these tests, the critical level of significance was $P=0.05$ for the 1987 year-classes (two strains) and was $P=0.017$ for the 1982 and 1986 year-classes (three-strains).

Post-stocking Mortality

To assess possible strain-related differences in post-transport and post-stocking mortality of the 1987 stockings, subsamples of lake trout of each strain of equal numbers were suspended in vertical cylindrical cages (measuring 0.9 m diameter and 2 m long) at approximately 10 m depth in West Bearskin Lake (21 May - 6 June 1987) and Birch Lake (27 May - 12 June 1987). In each of 12 cages (6 cages per lake), 26 lake trout were held at depth for 14 days. Scuba was used to assess mortality five times during the observation period.

In July 1987, undyed, graduated-mesh monofilament gill nets were fished to obtain a measure of relative abundance of the three 1986 cohorts to obtain better insight into when post-stocking mortality might take place. The mesh sizes were 13, 19, 25, and 32 mm, square measure. Nets were fished at depths ranging from approximately 8 to 21 m.

Sampling Methods

Netting and creel surveys were used to capture stocked lake trout to reduce potential sampling bias. Similar results, with respect to capture frequencies and relative survival, would suggest results reflect performance of different strains rather than gear bias.

Winter creel surveys.--The stratified random creel survey methods of Thompson (1981) were used to sample the lake trout catch of winter anglers from 1983 through 1990. The winter angling season for Mayhew, Birch, and West Bearskin lakes, which lie outside the BWCAW, extends from mid-January through mid-March (approximately 60 days). The winter angling season for Duncan Lake, which lies within the BWCAW, includes all of January, February, and March (approximately 90 days). Sampling was stratified by lake and day type (weekday/weekend). The length of the creel day was fixed at 10 hours. Roving creel clerks examined the anglers' catch, measuring length and weight of each kept lake trout and noting fin or maxillary bone clips. Angling effort was recorded to the nearest 15 minutes.

I compared observed total winter yield from each lake from 1983-1990 to the theoretical yield estimators described by Ryder et al. (1974) and Payne et al. (1990). Most of the angling harvest was believed to occur in winter (MN DNR unpublished data). Due to budget limitations, the ice-free angling season was not sampled, and estimates of annual yield could not be made.

Spring and fall netting.--Trap nets and gill nets were fished to sample stocked lake trout in spring (1983-1986) and fall (1983-1990). Trap nets were selected as the primary sampling gear to minimize mortality. These nets (13 and 19 mm, square measure, with 0.9 m x 6 to 18 m leads) were fished two nights along the shoreline of each lake in depths ranging from 1 to 4 m. Spring sampling began within 1-5 days after ice-out and continued for two weeks. Spring sampling was discontinued in 1987 since fall trap net catch per net lift (CPUE) generally was greater than spring CPUE. Fall sampling began when surface water temperature declined to approximately 13°C and ceased after 2 - 3 weeks when surface water temperatures declined to approximately 8°C. Gill nets were lethal to most fish when fished for more than a few hours and were used to a lesser extent to supplement the trap net catch on all lakes. Gill net gear, effort, and netting locations were not constant throughout the study. Lake trout were weighed (g) and measured (mm TL).

Sexual Maturation

Sexual maturity data were obtained from lake trout sampled in the fall, just prior to and during spawning. Sex, maturity, and condition (spawning state, or ripeness), if determined, were recorded. Sex was determined by observing eggs or milt when the sides of the fish anterior to the vent were stroked with slight pressure. Some more experienced workers were able to determine sex by closely examining the vent area and to detect fish that were mature but not "ripe". Sex was recorded as male, female, or unknown. Maturity was recorded as mature, immature, or unknown. Spawning condition was recorded as "green" (not ripe), ripe (eggs or milt running), or spent (all or nearly all eggs deposited). Some workers did not record all the information or could not determine the sex and maturity from each specimen.

Condition

To make within lake and among lakes comparisons of fall lake trout condition (plumpness), I compared linear regressions of log-transformed weight-length data using ANCOVA (Cone 1989). I did not do separate analyses of the weight-length data sets for males and females because of limited sample size for most cohorts.

Capture Frequencies and Relative Survival

To determine relative survival rates, the capture frequencies of the lake trout strains caught by anglers and nets were compared, by lake, considering each year-class separately. Trout captured more than once within a sampling period were counted only once in the appropriate cohort capture total for comparing frequencies between or among strains. Because each strain was stocked in equal numbers in a given lake, the expected probability of recovering each strain was 0.5 where two strains were compared and 0.333 where three strains were compared. When *N* was less than 26, observed frequencies were compared to the binomial or trinomial distributions for two- and three-strain comparisons (Sokal and Rohlf 1981). For all year-classes where sample size was 26 or greater, a G-test (Sokal and Rohlf 1981) was used to compare observed and expected strain frequencies captured by winter anglers (1983-1990), and by netting in spring (1983-1986) and fall (1983-1990). I used the chi-square test for heterogeneity (Snedecor and Cochran 1980) to evaluate strain capture patterns during the study. Capture frequencies for each combination of strain, year-class, lake, and sampling method were summed for the various sampling periods. The cumulative capture frequencies were compared as ratios among strains and within year-classes and lakes. I also calculated the relative survival index (RSI, Rybicki 1990a) for each cohort, by lake and capture method. Relative survival for netting or angling (percent return to the nets or to winter anglers) were the total number of each cohort captured (by netting or the estimated number harvested by winter anglers), summed over all sampling periods, and divided by the total number of each cohort originally stocked. Relative survival among strains was compared only within lakes, not among lakes, because netting or angling effort was not standardized on a lake area basis.

Growth

Because lake trout condition (plumpness) as measured by weight-length relationships, varied from lake to lake, growth was described as change in mean weight over the duration of the study. I used Schnute's (1981) non-linear general growth model, which encompasses the von Bertalanffy, Richards, Gompertz, logistic, and linear growth models as subsets, to obtain equations describing growth in weight from stocking through the last sampling period (fall 1990). Using Schnute's model, the growth curve is determined from the fish's weight at the start (Y_1) and end (Y_2) of the period (τ_1 and τ_2) or ages being modelled. The curve depends on four parameters Y_1, Y_2, A, and B. A and B are constants, specific to a data set, which determine acceleration of growth, measuring how sharply the left side and the right sides of the fitted curve bend.

First, the general four-parameter model was fitted using mean weights of lake trout recaptured in spring, fall, and winter sampling periods (weighted by sample size). If the B parameter was relatively small (close to zero), then a simpler three-parameter model was fitted to the data. I used a likelihood ratio test (LRT) (Weisberg 1985) to decide which model adequately described the growth trajectory of each cohort. In many cases, a relatively small likelihood ratio showed that B was zero, so the Gompertz model was adequate for the data. However, when neither B nor A was close to zero, the more complex four-parameter model better described the growth trajectory.

Schnute (1981) explained that when applying his growth model to a particular data set, "it may or may not define a curve which crosses the y-axis, has an inflection point, or exhibits asymptotic behavior." But, he provided formulae by which the age of theoretical zero size (τ_0), the asymptotic size (y^∞), the age of growth inflection (τ^*), the size at age of growth inflection (y^*), and the relative growth rate at an inflection point (z^*) can be calculated, if they exist for the data set, to facilitate comparison with traditional growth models.

I used Schnute's formulae and calculated the above parameters, when possible, so that growth of various strains in northeastern Minnesota lake trout lakes could be compared with historical and more recent lake trout growth data reported by other investigators. I applied the same analysis procedure to published mean weight at age data from Lake Cayuga, Lake Opeongo, Lac la Ronge, Great Slave Lake, Great Bear Lake, and Sassenach Lake (Carlander 1969; Scott and Crossman 1973; Donald and Alger 1986). Depending on the data set, four- or three-parameter models described growth of the various lake trout populations. Ages determined from these data sets (except for Sassenach Lake) probably were made from lake trout scales, not otoliths. The shape and elevation of these growth curves are approximations because ages determined from scales are believed to under-estimate age of older (>7 years) lake trout (Lester et al. 1991).

Desired sample sizes of larger or older lake trout often could not be obtained. Thus, the precise shape of the right-hand, or upper part, of the growth curves may be uncertain, but the general shape of the curves adequately describes the lake trout growth in the four lakes, particularly for ages 2 through 6.

Results

Size and Condition at Stocking

Length and weight at stocking varied among strains within year-classes, and also within strains among year-classes (Tables 6, 7). No strain was consistently longer (Figure 1), heavier, or in better condition than another. All strains in the 1982 cohort were smaller and in poorer condition than in the 1981, 1986, or 1987 year-classes. Inferences about length and weight distributions of the 1986 and 1987 year-classes are statistically sound because $N \approx 100$ fish/strain (S. Weisberg, Statistics Department, University of Minnesota, St. Paul, personal communication 1992). However, conclusions about size distributions of the 1981 and 1982 year-classes using the Smirnov test are somewhat tenuous because sample sizes are relatively low ($N \approx 50$ fish/strain).

1981 year-class.--The average MIC81 lake trout was larger than either the GIL81 or the IRY81 trout when stocked, based on the hatchery estimate of the number of lake trout/kg (Table 6). Mean lengths of the samples were significantly different (ANOVA, $P<0.001$), and Tukey's HSD multiple comparison test showed that mean length of the MIC81 cohort was larger than either the GIL81 ($P<0.001$) or the IRY81 ($P=0.004$) (Figure 1). The length distribution of the MIC81 cohort also was different from those of the GIL81 ($P=0.001$) and IRY81 ($P=0.020$) cohorts (Smirnov test). Mean lengths (Tukey's HSD, $P=0.979$) and length distributions (Smirnov test, $P=0.643$) of the GIL81 and IRY81 cohorts were similar.

1982 year-class.--The GIL82 lake trout were larger than either the IRY82 or the MIC82 at stocking (Table 6; Figure 1). Mean lengths (ANOVA, $P<0.001$) and weights (ANOVA, $P<0.001$) differed among strains. Tukey's HSD multiple comparison showed that the average GIL82 lake trout was longer ($P<0.001$) and heavier ($P<0.001$) than either the average IRY82 or the MIC82 lake trout. The length ($P<0.001$) and weight ($P<0.001$) distributions of the GIL82 cohort also were different from those of the IRY82 and MIC82 (Smirnov test). IRY82 lake trout were not significantly longer ($P=0.130$) or heavier ($P=0.174$) than MIC82 trout. Neither did length ($P=0.094$) or weight ($P=0.350$) distributions of the IRY82 and MIC82 differ. The slopes (ANCOVA, $P<0.001$) of the weight-length regression equations differed among strains within the 1982 year-class (Table 7). Beyond 125 mm and 16 g, the GIL82 cohort (111-175 mm) was more plump than either the IRY82 cohort (105-162 mm) or the MIC82 cohort (108-153 mm). Beyond 148 mm, total length, (23 g) the MIC82 cohort was more plump than the IRY82 cohort.

1986 year-class.--The MIC86 lake trout were longer and heavier than the other two strains at stocking, however the GIL86 were more plump than the other strains. Mean lengths (ANOVA, $P<0.001$) and weights (ANOVA, $P<0.001$) differed among samples of each strain collected just before the

Table 6. Size of stocked yearling lake trout.

Year-class	Size	Strain		
		Gillis Lake	Isle Royale	Marquette
1981	Number/kg	27.1	30.4	20.5
	Number/lb[a]	12.3	13.8	9.3
	Number measured	55	48	47
	Length (mm),			
	mean	149.5	150.5	168.2***[b]
	SE	3.9	3.4	3.9
	range	100-255	100-215	114-227
	Weight (g)[a]	37	33	49
1982	Number/kg	39.9	66.5	71.4
	Number/lb[a]	18.1	30.2	32.4
	Number measured	50	50	50
	Length (mm),			
	mean	148.7***	133.2	127.6
	SE	2.2	2.2	1.8
	range	111-175	105-162	108-153
	Weight (g),			
	mean	25.9***	17.7	15.3
	SE	1.2	0.8	0.8
	range	10-45	9-30	7-30
1986	Number measured	98	104	104
	Length (mm),			
	mean	153.3	160.9	175.1***
	SE	2.4	2.2	2.2
	range	93-202	107-233	126-251
	Weight (g),			
	mean	38.2	37.6	49.5***
	SD	18.2	16.0	19.7
	SE	1.8	1.6	1.9
	range	8-90	9-106	17-132
1987	Number/kg	27.5	27.1	
	Number/lb[a]	12.5	12.3	
	Number measured	116	104	
	Length (mm),			
	mean	149.5	162.8***	
	SE	2.5	2.1	
	range	88-225	109-207	
	Weight (g),			
	mean	35.6	39.0	
	SE	1.9	1.4	
	range	6-120	11-75	

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[a] MN DNR hatcheries normally provide a "rate" for each load transported, reported as the number of fish per pound. No samples of individual trout were weighed from the 1981 year-class. Hatchery rates were not available for the 1986 year-class.

[b] Asterisks denote differences between or among strains within year-classes. One * indicates a difference at $P \leq 0.05$; two ** indicates a difference at $P \leq 0.01$; and three *** indicates a difference at $P \leq 0.001$.

[c] No lake trout of the Marquette 1987 year-class (MIC87) were available in spring 1988.

Table 7. Weight-length relationships of the 1982, 1986, and 1987 year-classes of Gillis Lake (GIL), Isle Royale (IRY), and Marquette (MIC) lake trout strains when stocked in four northeastern Minnesota lakes, spring 1983, 1987, 1988. Significant differences in slopes or adjusted means (intercepts) are noted by an asterisk.

Year-class	Strain	N	Regression parameters Intercept	 Slope	r^2	(P)	Tests for equality of: Slope (P)	 Means (P)
1982[a]	GIL	50	-5.187	3.032	.949	<0.001	<0.001*	-
	IRY	50	-4.182	2.549	.898	<0.001		
	MIC	50	-5.954	3.367	.871	<0.001		
1986[b]	GIL	98	-5.341	3.152	.979	<0.001	0.185	<0.001*
	IRY	104	-5.088	3.008	.957	<0.001		
	MIC	104	-5.228	3.076	.958	<0.001		
1987[c]	GIL	116	-5.244	3.104	.968	<0.001	0.029*	-
	IRY	104	-4.876	2.914	.952	<0.001		

[a] Samples of hatchery trout were measured on 26 May 1983 at Crystal Springs Hatchery, before transport and stocking.

[b] At lake side, just prior to stocking in late May 1987, samples of fish were sacrificed for subsequent laboratory examination.

[c] At lake side, just prior to stocking on 25-26 May 1988, samples of fish were sacrificed for subsequent laboratory examination.

fish were stocked (Table 6; Figure 1). Mean lengths of all the strains differed from each other ($P<0.05$) and mean weight of MIC86 lake trout was significantly greater ($P<0.001$) than that of either GIL86 or IRY86 (Tukey's HSD). Mean weight of GIL86 and IRY86 did not differ significantly ($P=0.970$). The length ($P<0.001$) and weight ($P<0.001$) distributions of the GIL86 and IRY86 were significantly different from those of MIC86 (Smirnov tests). The length distributions of the IRY86 and MIC86 cohorts were different ($P=0.035$). The weight distributions of the IRY86 and MIC86 did not differ significantly ($P=0.545$). Slopes of the weight-length regression equations of the 1986 year-class did not differ among strains (ANCOVA, $P=0.185$)(Table 7), however, adjusted mean weights differed ($P<0.001$), with GIL86 being slightly heavier than either IRY86 or MIC86 at any given length.

Short-term survival of subsamples of all three 1986 cohorts held for two weeks in submerged cages in West Bearskin and Birch lakes was excellent. None died in the West Bearskin Lake cages and only 2% died in the Birch Lake cages.

1987 year-class.--Although hatchery estimates of the number of lake trout/kg suggested little difference between cohorts (Table 6; Figure 1), the IRY87 lake trout were longer (13 mm) than the GIL87 ($P<0.001$). Mean weights of these cohorts were not different ($P=0.168$), however, variances of length ($\chi^2=5.371$, $P=0.020$) and weight ($\chi^2=10.765$, $P=0.001$) data were not homogeneous. Length ($P<0.001$) and weight ($P=0.030$) distributions of the GIL87 and IRY87 were different (Smirnov test). The slope of the regression equation

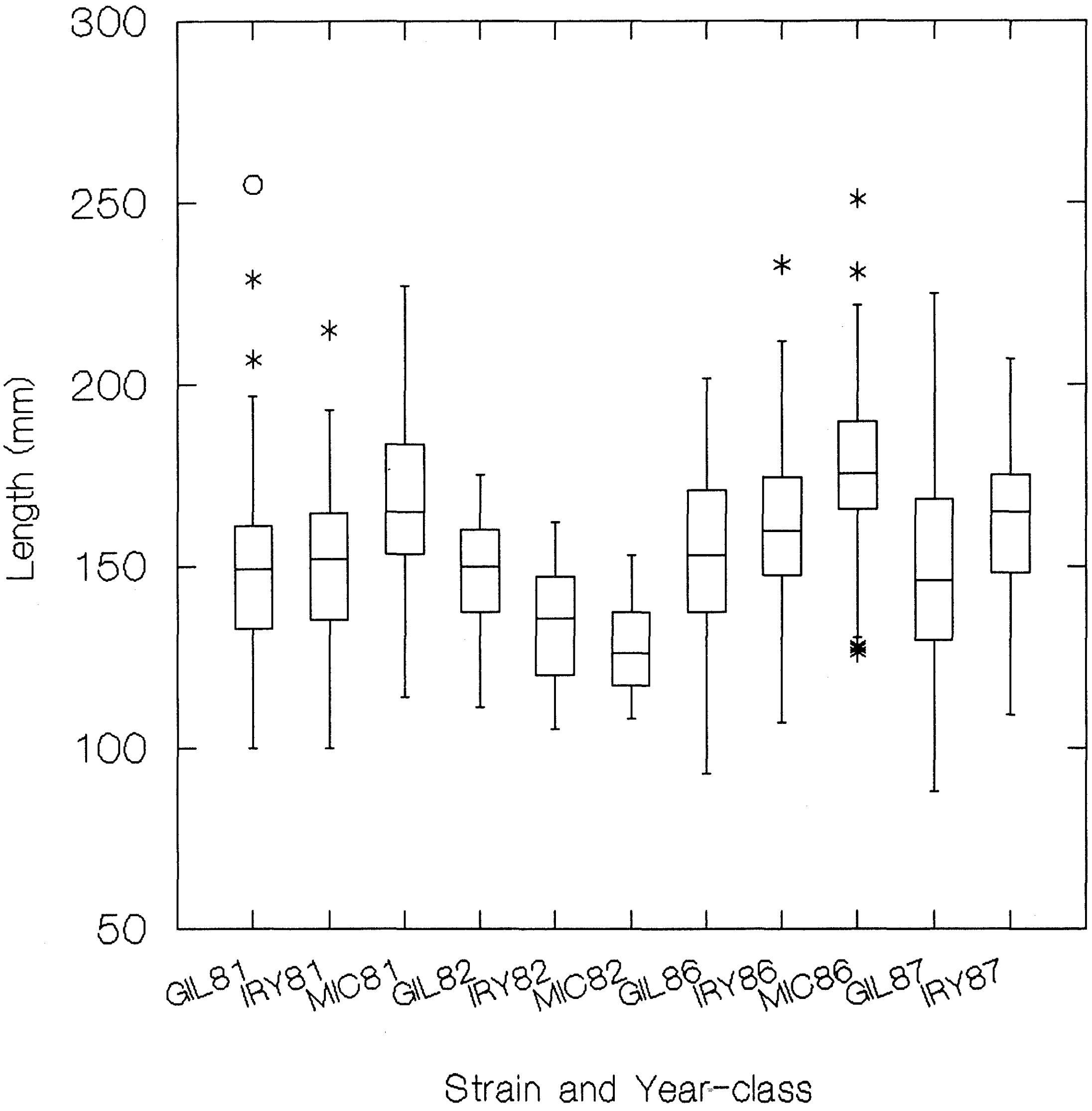

Figure 1. Box plots showing the length distributions at stocking of three strains and four year-classes of yearling lake trout. The number measured from each cohort ranged from 47 to 116. The "whiskers" show the range of values which fall within 1.5 H-spreads of the hinges. Astericks represent values outside the inner fences. Empty circles represent values outside the outer fences. GIL = Gillis Lake strain; IRY = Isle Royale strain; MIC = Marquette strain; 81 = 1981 year-class; 82 = 1982 year-class, etc.

for the GIL87 lake trout was significantly greater (ANCOVA, $P=0.029$) than the slope for the IRY87 lake trout (Table 7). GIL87 lake trout (88-225 mm, total length) beyond 109 mm tended to be more plump than the IRY87 cohort (109-207 mm).

Fat Reserves at Stocking

The amount of mesenteric body fat varied among strains of the 1982, 1986, and 1987 year-classes. Chi-square tests for heterogeneity indicated there were significant differences in the fat level among strains within year-classes at the time they were stocked. GIL82 lake trout had more mesenteric body fat than either IRY82 or MIC82 lake trout ($\chi^2_{6df}=24.08$, $P=0.0005$) (Table 8). The GIL86 and MIC86 cohorts tended to have more mesenteric body fat than the IRY86 cohort ($\chi^2_{8df}=57.06$, $P<0.0001$). Fat reserves of the GIL87 and IRY87 cohorts differed significantly ($\chi^2_{4df}=12.18$, $P=0.016$). The MIC81 trout appeared to be more plump than either the GIL81 or IRY81 trout at stocking, although fat reserves of the 1981 cohorts were not determined.

Fat reserves of each strain differed among year-classes (Table 8). The 1987 year-class tended to have greater fat reserves than the 1986 year-class, which in turn had greater fat reserves than the 1982 year-class. Chi-square statistics for the GIL, IRY, and MIC strains are 41.29, 8 df ($P<0.001$); 136.5, 8 df ($P<0.001$); and 72.93, 4 df ($P<0.001$). The 1982 year-class was smaller than the

Table 8. Frequency distribution of the relative amount of pyloric caeca obscured by fat in samples of three lake trout strains and three lake trout year-classes collected at the time of stocking, spring 1983, 1987, and 1988.

Year-class	Percentage of pyloric caeca obscured by fat	Strain: Gillis Lake No.	Gillis Lake %	Isle Royale No.	Isle Royale %	Marquette No.	Marquette %
1982	0	0	0.0	14	58.3	11	45.8
	1 - 25	11	45.8	8	33.3	8	33.3
	26 - 50	11	45.8	1	4.2	4	16.7
	51 - 75	2	8.4	1	4.2	1	4.2
	75 -100	0	0.0	0	0.0	0	0.0
	Number dissected	24	100.0	24	100.0	24	100.0
1986	0	4	4.1	5	4.8	0	0.0
	1 - 25	14	14.3	11	10.6	8	7.7
	26 - 50	22	22.4	59	56.7	23	22.1
	51 - 75	39	39.8	28	26.9	57	54.8
	75 - 100	19	19.4	1	1.0	16	15.4
	Number dissected	98	100.0	104	100.0	104	100.0
1987	0	12	10.3	2	1.9	"Cohort was not available for stocking."	
	1 - 25	14	12.1	9	8.7		
	26 - 50	18	15.5	28	26.9		
	51 - 75	39	33.6	43	41.3		
	75 - 100	33	28.5	22	21.2		
	Number dissected	116	100.0	104	100.0		

1981, 1986, and 1987 year-classes at stocking and probably had lesser fat reserves (Figure 3). The diet fed to the 1982 year-class had a greater percentage of soybean protein than that of the 1981 year-class whose diet had a greater percentage of fish protein. This diet problem did not recur for the 1986 and 1987 cohorts (John Huber, MN DNR, personal communication, 1988).

Short Term Survival, 1986 year-class

In three of the four study lakes, gill net catches (July 1987) of the recently-stocked 1986 year-class were skewed in favor of the GIL86 cohort. In West Bearskin, Duncan, and Mayhew lakes, GIL86 lake trout were the only representatives of the 1986 year-class captured, although samples sizes were small (*N*=10, 7, and 2). In Birch Lake, although more GIL86 strain trout (*N*=19) were captured than IRY86 (*N*=16) and MIC86 (*N*=10), a *G*-test indicated these initial capture frequencies were not different statistically ($G_{adj}=2.906 < X^2_{.05[2]} = 5.991$). Of the 64 lake trout sampled from all four lakes, 63 were larger than the estimated mean weight of their respective cohort at stocking just two months previously. This may indicate that growth had occurred, that larger trout from the size distribution had a survival advantage, or that larger fish were vulnerable to the gill nets used. All 1986 year-class lake trout were caught in 19-mm or larger mesh sizes, and ranged from 151 to 219 mm total length. No lake trout or other fish were caught in the 13-mm mesh, which appears underwater as a nearly solid wall.

Capture of Stocked Lake Trout in Nets

The timing of lake trout recruitment to the trap net gear varied among lakes, depending on growth of the stocked lake trout. The peak of lake trout catch per trap net lift (CPUE) occurred at age 2+ to age 3+ in Birch and Mayhew lakes where juvenile growth was rapid (Table 9). In West Bearskin and Duncan lakes, maximum or peak CPUE occurred at age 4+ or 5+, probably due to slower juvenile growth.

Within lakes, the pattern of the captures of stocked lake trout by strain generally was consistent (homogenous) among sampling periods, so captures were summed over time. If one strain dominated the net catches within two or three years after stocking, it continued to dominate the year-class in later sampling periods. When stocked with either the IRY or MIC strain, the GIL strain usually was captured in the nets in greater numbers.

Spring and fall netting, 1981 and 1982 year-classes.--The GIL81 and GIL82 cohorts comprised a much higher proportion of the lake trout net catches from Birch and West Bearskin lakes than the 1981 or 1982 MIC or IRY cohorts throughout the study. For Birch Lake, the cumulative capture ratio for GIL81:MIC81 was 7.4:1 ($P<0.001$) from spring 1983-fall 1990, and the GIL82:MIC82 ratio was 3.2:1 ($P<0.001$) from spring 1984-fall 1990 (Table 10). I was unable to determine if the red (GIL82) or green (MIC82) fluorescent pigments (visible without ultraviolet light at stocking) influenced post-stocking survival. In West Bearskin Lake, the cumulative capture ratio for GIL81:IRY81 was 13.5:1 ($P<0.001$) from spring 1983-fall 1990 and for GIL82:IRY82 the capture ratio was 27:1 ($P<0.001$) from spring 1984-fall 1990. As of fall 1990, the relative survival (percentage return to the netting gear) of the GIL81 and GIL82 cohorts was at least 3 times greater than the IRY81 and IRY82 cohorts in West Bearskin Lake or the MIC81 and MIC82 cohorts in Birch Lake (Table 11, Figure 2).

There were some large lake trout (MIC69), and juvenile lake trout (MIC80 year-class) in West Bearskin Lake when this study began. Seventeen of the MIC69 cohort were netted from spring 1983-fall 1990. During the winter creel surveys from 1983-1990, creel clerks noted only one MIC69 lake trout. From spring 1983 through fall 1990, 166 (3.3% of the 5,016 stocked) of the MIC80

Table 9. Age and length of stocked yearling lake trout at recruitment to trap nets (fall) and the winter sport fishery (1983-1990), and the number of years each cohort was captured after the maximum catch rate (CPUE) was observed, based on peaks in catch/trap net lift and catch/angling-hour.

Lake	Strain[a] and year-class	Age and mean length at maximum catch rate				Number of years the cohort was sampled after the maximum CPUE was observed for:	
		Netting		Angling			
		(Years)	(mm)	(Years)	(mm)	Netting	Angling
Birch	GIL81	2.75	403	3	407	8	2
	MIC81	4.75	590	3	414	2	3
	GIL82	3.75	500	3	409	1	1
	MIC82	-	-	3	386	0	2
	GIL86	3.75	492	3	428	1	1
	IRY86	3.75	536	3	433	0	1
	MIC86	3.75	517	3	442	0	1
Mayhew	IRY81	4.75	406	4	410	3	5
	MIC81	3.75	373	4	411	4	4
	IRY82	3.75	341	4	343	2	4
	MIC82	2.75	249	4	362	5	3
	GIL86	3.75	416	3	353	1	1
	IRY86	3.75	359	4	372	0	0
	MIC86	4.75	405	3	337	0	1
West Bearskin	GIL81	4.75	387	5	387	3	4
	IRY81	-	-	6	453	0	3
	GIL82	5.75	509	4	340	1	3
	IRY82	-	-	-	-	0	0
Duncan	IRY81	3.75	232	8	403	6	1
	MIC81	3.75	259	8	446	6	1
	IRY82	5.75	298	7	348	3	1
	MIC82	7.75	398	-	-	0	-

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[a] Strain and year-class abbreviations: GIL81 = Gillis Lake strain, 1981 year-class; IRY82 = Isle Royale strain, 1982 year-class; MIC86 = Marquette strain, 1986 year-class; etc.

Table 10. Cumulative number of captures and capture ratios by strain and year-class for lake trout sampled during spring and fall netting, and winter creel surveys, 1983-1990. Asterisks (*) denote significant among strain differences in capture ratios for data sets where ratios were homogeneous across years: *,$P\leq0.05$; **,$P\leq0.01$; ***,$P\leq0.001$.

		Cumulative strain capture totals (ratios in parentheses)			
Year-class	Strain[a] comparisons	Winter angling	Spring netting	Fall netting	Spring+Fall netting total
		BIRCH LAKE			
1981	GIL:MIC	86:28*** (3.1)	75:6*** (12.5)	96:17*** (5.7)	171:23*** (7.4)
1982	GIL:MIC	45:5 (9.0)	20:4** (5.0)	12:6 (2.0)	32:10 (3.2)
1986	GIL:IRY:MIC	61:16:27***	-	59:8:20***	-
	GIL:IRY	(3.8)		(7.4)	
	GIL:MIC	(2.3)		(3.0)	
	MIC:IRY	(1.7)		(2.5)	
1987	GIL:IRY	82:43 (1.9)	-	27:5*** (5.4)	-
		MAYHEW LAKE			
1981	IRY:MIC	92:91 (1.0)	55:42 (1.3)	78:58 (1.3)	133:100 (1.3)
1982	IRY:MIC	51:23** (2.2)	17:10 (1.7)	35:15** (2.3)	52:25** (2.2)
1986	GIL:IRY:MIC	104:27:56***	-	59:24:23***	-
	GIL:IRY	(3.9)		(2.5)	
	GIL:MIC	(1.9)		(2.6)	
	MIC:IRY	(2.1)		(1.0)	
1987	GIL:IRY	17:7 (2.4)	-	29:14* (2.1)	-

Table 10. Continued.

Year-class	Strain[a] comparisons	Cumulative strain capture totals (ratios in parentheses) Winter angling	Spring netting	Fall netting	Spring+Fall netting total
		WEST BEARSKIN LAKE			
1981	GIL:IRY	142:10*** (14.2)	106:4*** (26.5)	178:17*** (10.5)	284:21*** (13.5)
1982	GIL:IRY	26:6*** (4.3)	4:0 -	23:1*** (23.0)	27:1*** (27.0)
1986	GIL:IRY:MIC	49:2:15***	-	54:11:12***	-
	GIL:IRY	(24.5)		(4.9)	
	GIL:MIC	(3.3)		(4.5)	
	MIC:IRY	(7.5)		(1.1)	
1987	GIL:IRY	6:2 (3.0)	-	49:38 (1.3)	-
		DUNCAN LAKE			
1981	IRY:MIC	48:40 (1.2)	14:51*** (0.3)	158:134 (1.2)	172:185 (0.9)
1982	IRY:MIC	12:7 (1.7)	6:3 (2)	14:6 (2.3)	20:9 (2.2)
1986	GIL:IRY:MIC	14:10:6	-	45:17:48	-
	GIL:IRY	(1.4)		(2.7)	
	GIL:MIC	(2.3)		(0.9)	
	MIC:IRY	(0.6)		(2.8)	
1987	GIL:IRY	2:2 (1.0)	-	4:6 (0.7)	-

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[a] Abbreviations: GIL = Gillis Lake strain; IRY = Isle Royale strain; MIC = Marquette strain.

Table 11. Relative survival of stocked yearling lake trout measured as total captures and as percent (%) captured by netting and angling, 1983-1990. Angler harvests are estimates. Hyphens (-) indicate no fish were stocked.

		Lake trout strain					
Year-class	Measure	Gillis Lake No.	%	Isle Royale No.	%	Marquette No.	%
			Birch				
1981	stocked	2,614		-		2,637	
	netted	171	6.5			23	0.9
	angled	328	12.6			92	3.5
1982	stocked	1,198		-		1,166	
	netted	32	2.7			10	0.9
	angled	120	10.0			14	1.2
1986	stocked	1,840		1,840		1,840	
	netted	78	4.2	24	1.3	30	1.6
	angled	192	10.4	61	3.3	51	2.8
1987	stocked	2,751		2,761		-	
	netted	27	1.0	5	0.2		
	angled	161	5.9	109	4.0		
Birch subtotals: all	stocked	8,403		4,601		5,643	
	netted	308	3.7	29	0.6	63	1.1
	angled	801	9.5	170	3.7	157	2.8
			Mayhew				
1981	stocked	-		2,021		2,010	
	netted			134	6.6	101	5.0
	angled			293	14.5	293	14.6
1982	stocked	-		1,022		1,014	
	netted			52	5.1	26	2.6
	angled			117	11.5	35	3.5
1986	stocked	1,640		1,640		1,640	
	netted	61	3.7	24	1.5	23	1.4
	angled	298	18.2	73	4.5	130	7.9
1987	stocked	2,462		2,466		-	
	netted	29	1.2	14	0.6		
	angled	28	1.1	4	0.2		
Mayhew subtotals: all	stocked	4,102		7,149		4,664	
	netted	90	2.1	224	3.1	150	3.2
	angled	326	7.9	487	6.8	458	9.8

Table 11. Continued.

		Lake trout strain					
Year-class	Measure	Gillis Lake No.	%	Isle Royale No.	%	Marquette No.	%
		West Bearskin					
1981	stocked	5,022		5,020		-	
	netted	285	5.7	21	0.4		
	angled	568	11.4	31	0.6		
1982	stocked	2,317		2,303		-	
	netted	30	1.3	2	<0.1		
	angled	86	3.7	33	1.4		
1986	stocked	3,710		3,710		3,710	
	netted	64	1.7	11	0.3	12	0.3
	angled	74	2.0	4	0.1	15	0.4
1987	stocked	5,549		5,558		-	
	netted	49	0.9	38	0.7		
	angled	4	0.1	4	0.1		
West Bearskin subtotals:							
all	stocked	16,598		16,591		3,710	
	netted	428	2.6	72	0.4	12	0.3
	angled	732	4.4	72	0.4	15	0.4
		Duncan					
1981	stocked	-		5,011		4,999	
	netted			180	3.6	189	3.8
	angled			128	2.6	103	2.1
1982	stocked	-		2,552		2,567	
	netted			20	0.8	10	0.4
	angled			24	0.9	6	0.2
1986	stocked	3,600		3,600		3,600	
	netted	53	1.5	17	0.5	48	1.3
	angled	8	0.2	18	0.5	3	<0.1
1987	stocked	5,549		5,557		-	
	netted	4	<0.1	6	<0.1		
	angled	1	<0.1	0	0.0		
Duncan subtotals:							
all	stocked	9,149		16,720		11,166	
	netted	57	0.6	223	1.3	247	2.2
	angled	9	<0.1	170	1.0	127	1.1

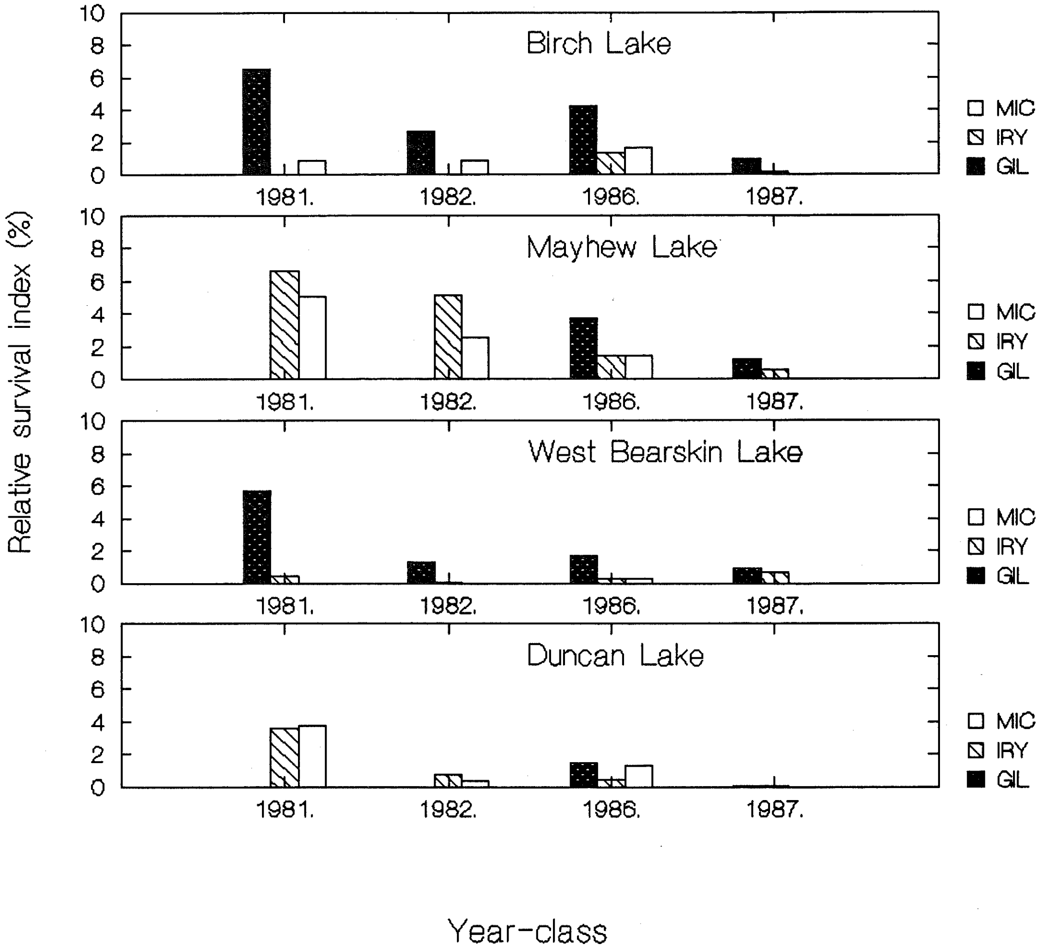

Figure 2. Relative survival (%) of three strains and four year-classes of lake trout stocked as yearlings into four northeastern Minnesota lakes, from trap netting and gill netting during spring 1983-1986 and fall 1983-1990.

cohort lake trout were caught in trap and gill nets. Creel clerks observed that at least 115 (2.3%) of the MIC80 cohort were caught by winter anglers (1983-1990).

The IRY81 and MIC81 cohorts in Mayhew and Duncan lakes had similar cumulative capture frequencies (Table 10) and relative survival indices, however, for the 1982 cohorts the indices differed, favoring the IRY82 cohort over the MIC82 cohort (Table 11). For Mayhew Lake, the IRY81:MIC81 cumulative capture ratio was 1.3:1 ($P=0.222$) and for Duncan Lake it was 1.2:1 ($P=0.677$) (Table 10). The IRY82:MIC82 cumulative capture ratios and relative survival indices for Mayhew and Duncan lakes were skewed in favor of the IRY82 cohort, although sample sizes were small (Figure 2). In both Mayhew ($P=0.004$) and Duncan ($P=0.099$) lakes the IRY82:MIC82 capture ratio was 2.2:1 (Table 10).

Fall netting, 1986 and 1987 year-classes.--As noted earlier, all three strains of the 1986 year-class were stocked in each lake in spring 1987, and both strains of the 1987 year-class (GIL and IRY) were stocked in each lake in spring 1988 (Table 5). In Birch, Mayhew, and West Bearskin lakes, survival of the GIL86 cohort was greater than that of the IRY86 or MIC86 cohorts, as measured by total netting captures during fall sampling, 1986-1990 (Figure 2). Cumulative capture ratios (GIL:IRY:MIC) of the 1986 year-class for this period were skewed in favor of the GIL86 cohort in Birch (7.1:1.0:2.4, $P < 0.001$), Mayhew (2.6:1.1:1.0, $P < 0.001$), and West Bearskin (5.0:1.0:1.1, $P < 0.001$) lakes (Table 10). Relative survival indices (percentage return to the netting gear) favored the GIL86 cohort over the IRY86 and MIC86 cohorts in three study lakes (Table 11). It is too early to speculate about the eventual relative survival or capture ratios of the three 1986 cohorts in Duncan Lake because the stocked lake trout grew more slowly and recruited to the gear more slowly than in the other three lakes.

Cumulative capture ratios of the 1987 year-class were skewed in favor of the GIL87 cohort in Birch (5.4:1, $P < 0.001$) and Mayhew (2.1:1, $P = 0.064$) lakes (Figure 2, Table 10). In West Bearskin and Duncan lakes neither the GIL87 or IRY87 cohort dominated the net catches. At least several more fall sampling periods would have been needed to make an assessment of relative survival of the 1986 and 1987 year-classes in West Bearskin and Duncan lakes.

Recruitment and Lake Trout Harvest in the Winter Fishery

The timing of recruitment and the proportion of harvest composed of stocked lake trout varied among the study lakes, depending on growth rate and the intensity of angling effort (angler-hours/hectare). Lake trout stocked for this study composed 79, 64, 54, and 74% of the harvest from Birch, Mayhew, West Bearskin, and Duncan lakes, respectively over 8 years. Because stocked lake trout grow rapidly in Birch Lake, exploitation began at age 2 during their first winter in the lake, with the peak harvest occurring at age 3 (Table 9). In Mayhew and West Bearskin lakes, peak harvest occurs at ages 4 and 5 (Table 9). In Duncan Lake, the peak harvest may occur at age 7 or 8 (Table 9). Angling CPUE generally did not peak until total length was at least 330 mm and weight reached 300 g (Table 9).

Winter angling intensity ranged from 0.5 hours/hectare (Duncan Lake) to 27 hours/hectare (Mayhew Lake). Mean angling intensity (1983-1990) was greater on Birch (16.3) and Mayhew (15.5) lakes than on West Bearskin (8.3) and Duncan (2.6) lakes, but it fluctuated with catch and harvest rates. Winter angling effort was directed almost exclusively at lake trout on Mayhew, West Bearskin, and Duncan lakes. Some of the angling effort on Birch Lake was directed at splake (1979 year-class) in the early years of the study and at rainbow trout (1985 year-class) in the latter years. A winter 1987 peak in angling intensity corresponded to the recruitment of the 1985 year-class of rainbow trout. Angling intensity may have been lower on Birch Lake, if splake and rainbow trout had not been stocked. Angling intensity peaked on Mayhew Lake, in winter 1986 when the 1981 and 1982 cohorts were harvested and may have peaked in winter 1990 with the recruitment of the 1986 cohort. Angling intensity peaked on West Bearskin Lake in winter 1987, when the 1980 and 1981 year-classes recruited to the fishery and may peak again in winter 1993 as the 1986 and 1987 cohorts recruit to the fishery.

The commonly estimated creel survey parameters, including angling effort, angling intensity, catch and harvest rates (number of lake trout/angler-hour), catch and harvest (number of lake trout), and yield (kg of lake trout harvested/hectare) fluctuated in the easily accessible Birch, Mayhew, and West Bearskin lakes. In Duncan Lake, all of the above measures tended to increase from 1983-1990. Peaks in catch, harvest, catch rate, and harvest rates correspond to the periods when the stocked lake trout became vulnerable to anglers (Figures 3-6). Birch Lake, having the fastest growth rate, shows a peak harvest (primarily the 1981 and 1982 year-classes) in 1984, several years earlier than the other three lakes. The second peak in lake trout harvest for Birch Lake occurred

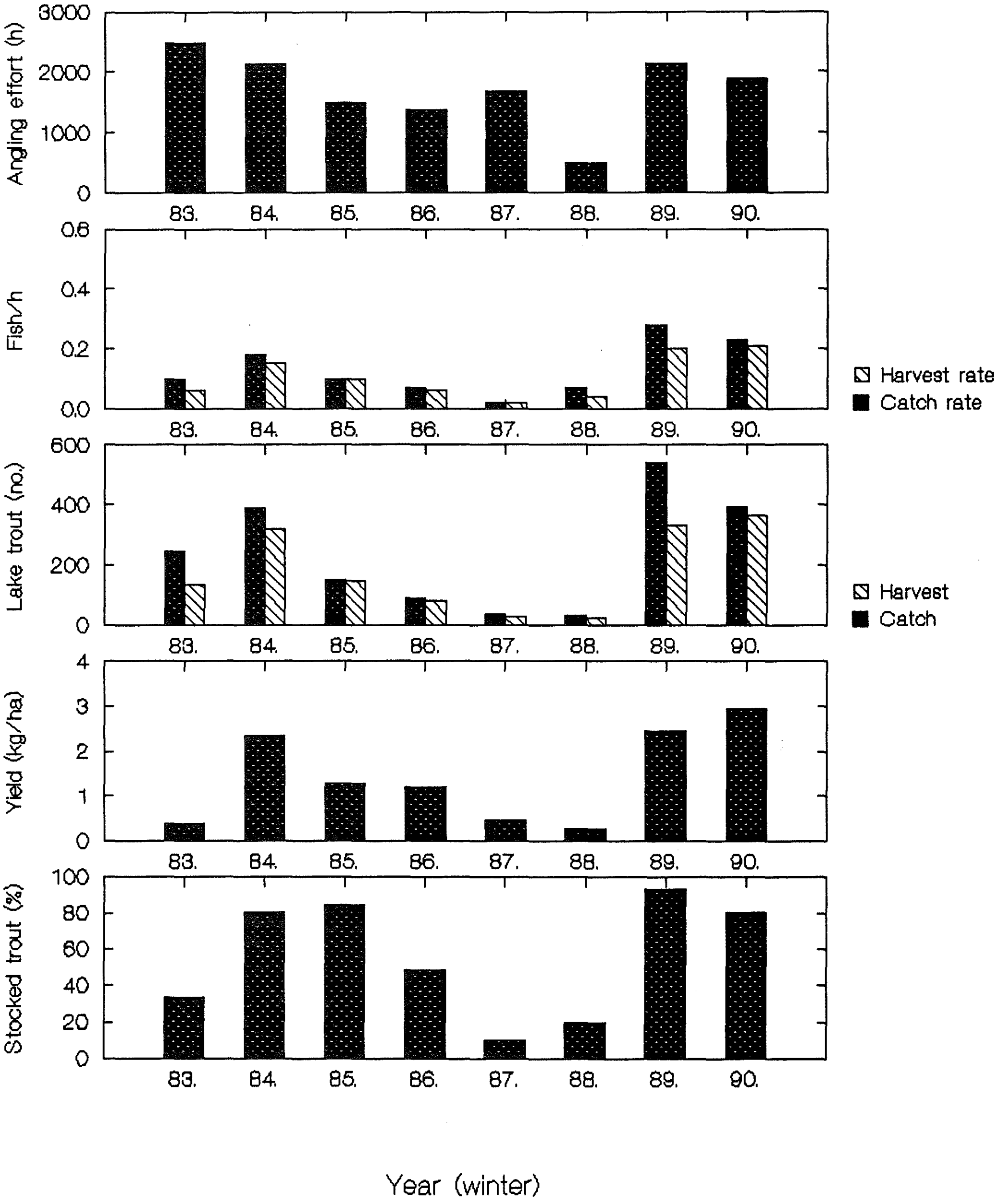

Figure 3. Angling effort, catch and harvest rate, catch, harvest, yield, and percentage of harvest that was composed of lake trout stocked as part of this study, Birch Lake, Minnesota, 1983-1990.

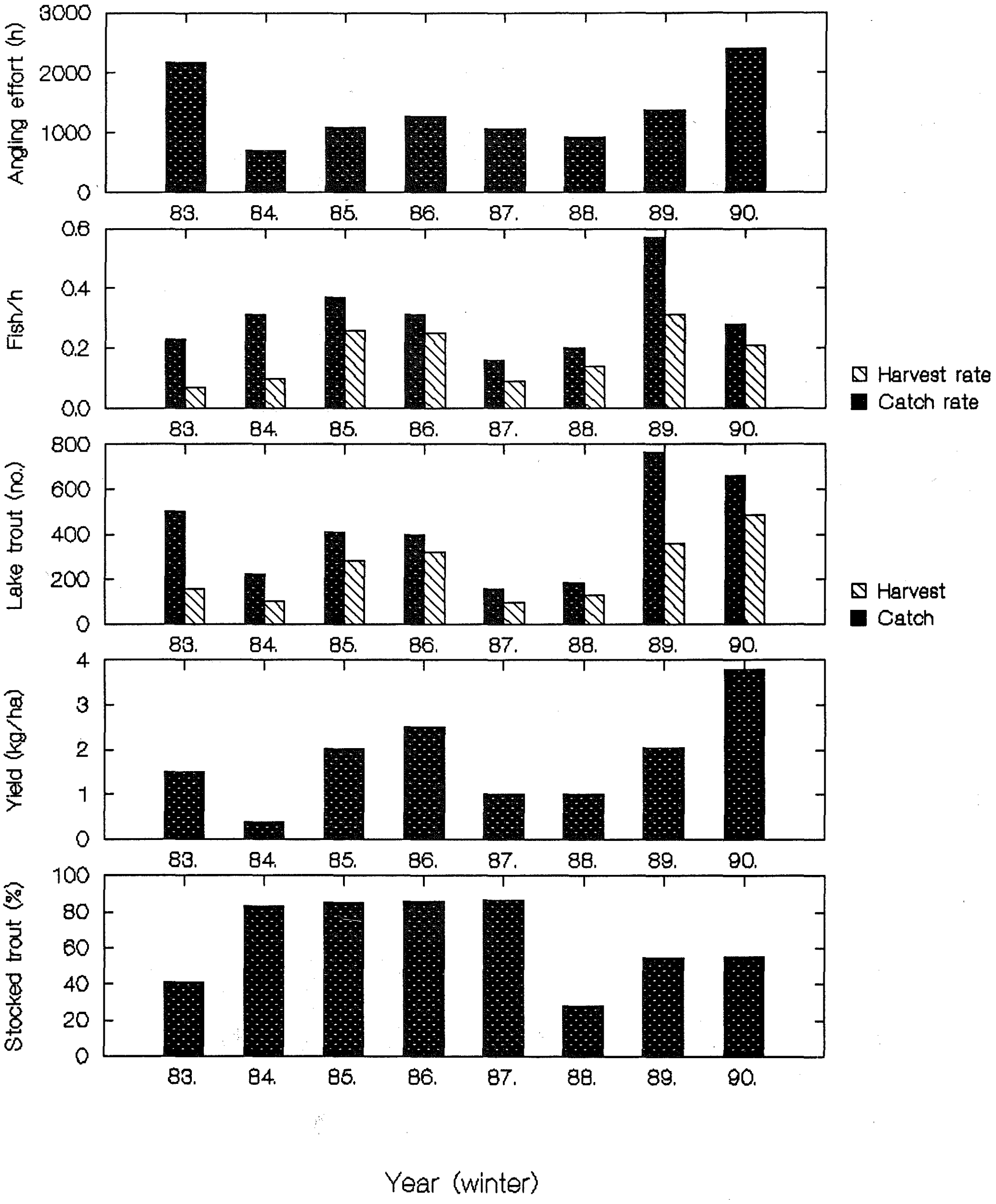

Figure 4. Angling effort, catch and harvest rate, catch, harvest, yield and percentage of harvest that was composed of lake trout stocked as part of this study, Mayhew Lake, Minnesota, 1983-1990.

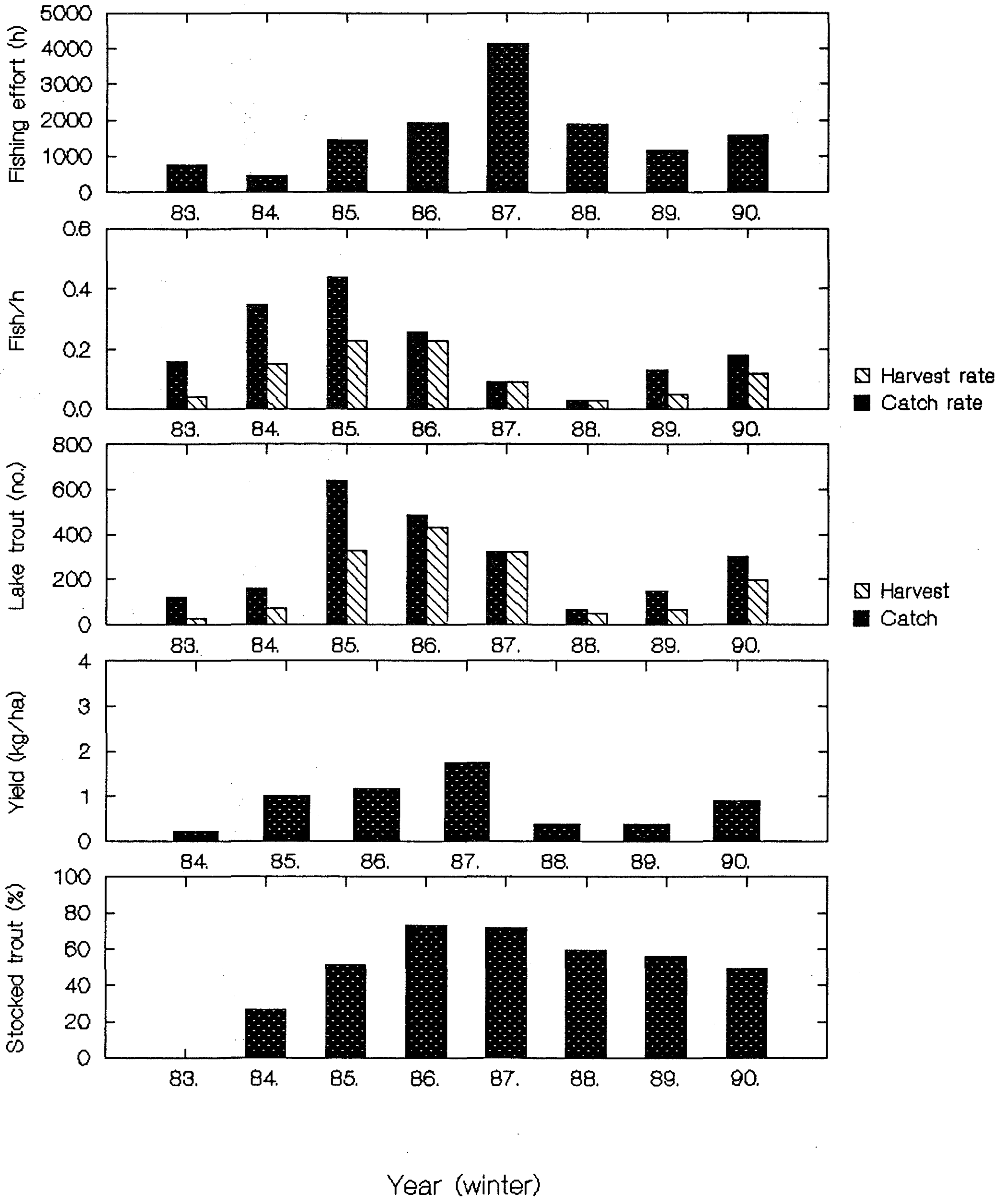

Figure 5. Angling effort, catch and harvest rate, catch, harvest, yield and percentage of harvest that was composed of lake trout stocked as part of this study, West Bearskin Lake, Minnesota, 1983-1990.

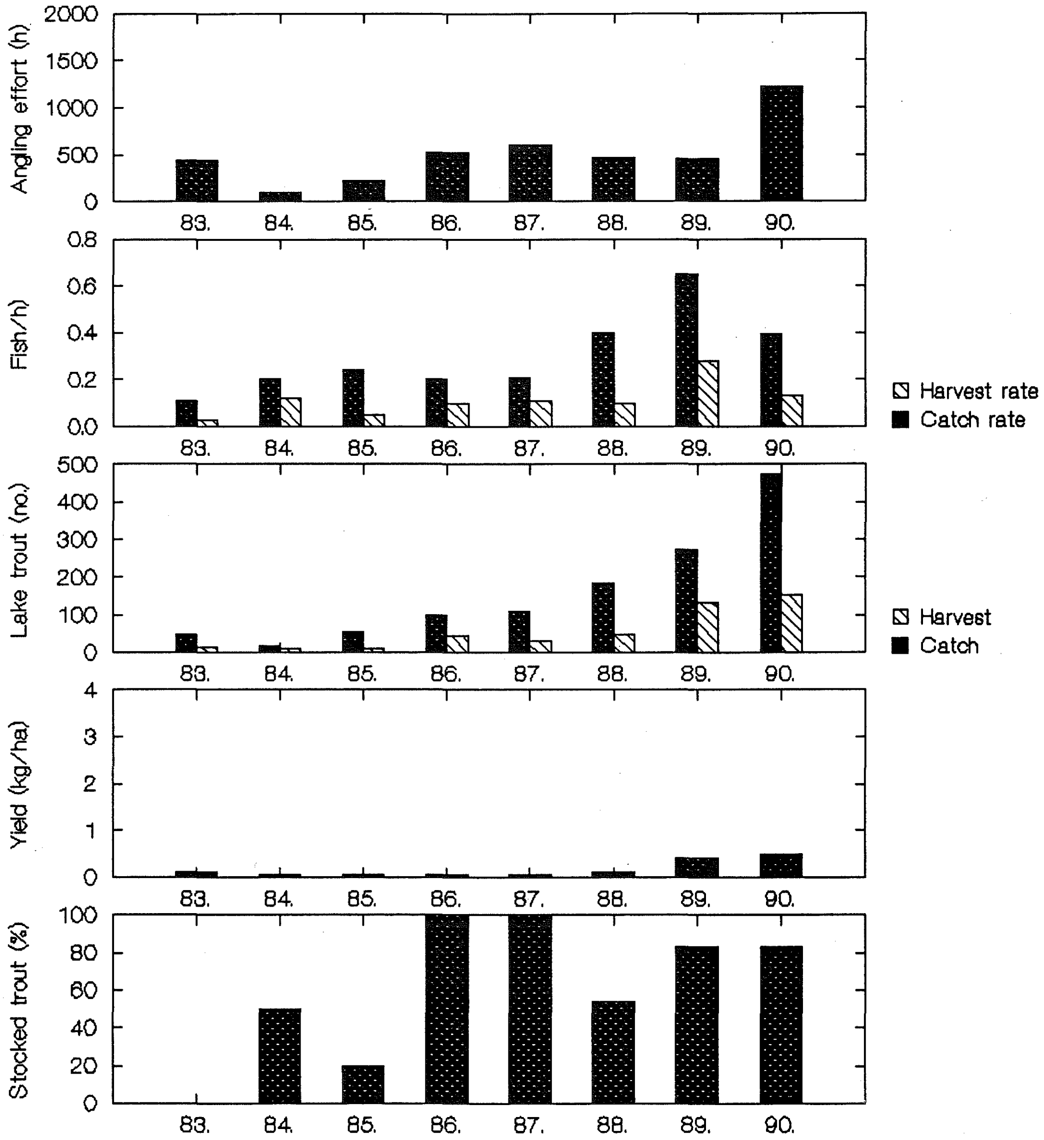

Figure 6. Angling effort, catch and harvest rate, catch, harvest, yield and percentage of harvest that was composed of lake trout stocked as part of this study, Duncan Lake, Minnesota, 1983-1990.

in 1990, when the 1986 and 1987 year-classes became vulnerable to anglers and increasing numbers of unclipped or "wild" lake trout were entering the sport fishery, presumably from successful natural reproduction. Peaks in harvest of the stocked 1981 and 1982 cohorts in Mayhew (winter 1986) and West Bearskin lakes (winter 1987) are delayed by two to three years due to the slower growth rates. The second upswing in yield for Mayhew Lake began in winter 1989 and may have peaked in winter 1990 or 1991. The increase in catch and harvest from Mayhew Lake is due, in part, to recruitment of the 1986 and 1987 year-classes, an increase in the number of wild lake trout, and an increase in angling effort. Peak harvest of the 1981 and 1982 year-classes in Duncan Lake may not yet have been attained by March 1990, presumably due to the extremely slow growth.

Angler catch rates of lake trout tended to be highest on Mayhew and Duncan lakes (0.3 fish/hr) and lowest on Birch Lake (0.1) (Figures 3-6). Harvest rates tended to be low, approximately 0.1 fish/hr on Birch, West Bearskin, and Duncan lakes, and were nearly double on Mayhew Lake (0.18). Reports of better than average catch rates tend to generate more angling interest and repeated trips by individuals. In Duncan Lake, rumors of high catch rates and harvest rates in winter 1989 seem to have generated more effort in winter 1990.

Winter anglers fishing Duncan Lake released a higher percentage of their catch (64%) than anglers fishing the other three lakes. Duncan Lake anglers often reported catching and releasing many small trout (<250 mm), especially from 1983-1988. Presumably most of these released trout belonged to the slow-growing 1981 or 1982 cohorts. In Birch Lake, which exhibits the fastest growth of juvenile trout, anglers released only 21% of their catch.

Lake trout yield to the fishery may be related to fish community composition and structure, as well as to, angling effort and stocking. Winter lake trout yield fluctuated about two estimates of potential yield (yield$_{THV}$ and yield$_{MEI}$) for Birch and Mayhew lakes, which held few potential competitors and predators. Winter lake trout yield from West Bearskin and Duncan lakes generally did not approach estimates of potential yield.

1981 and 1982 year-classes.--The winter harvest of the 1981 and 1982 lake trout cohorts from Birch and West Bearskin lakes showed the same patterns of cumulative capture frequency by strain as the netting data (Table 10). Harvest ratios did not change, so strain-specific differences in catchability were not evident. In Birch Lake, winter anglers caught 3.1 times as many GIL81 lake trout as MIC81 ($P<0.001$) and 9 times as many GIL82 trout as MIC82 trout ($P<0.001$) (Table 10). In West Bearskin Lake, 14.2 GIL81 lake trout were caught for every IRY81 trout ($P<0.001$) and 4.3 GIL82 lake trout were caught for every IRY82 trout ($P<0.001$).

Relative survival (percentage return to the creel) of the GIL81 and GIL82 cohorts was much greater than that of the corresponding MIC cohorts in Birch Lake or the IRY cohorts in West Bearskin Lake (Figure 7). During the winters of 1983-1990, 12.6% of the GIL81 cohort, but only 3.5% of the MIC81 cohort had been harvested from Birch Lake. During the same period, 11.4% of the GIL81 lake trout, but only 0.6% of the IRY81 cohort had been harvested from Birch and West Bearskin lakes by winter anglers (Table 11, Figure 7).

Cumulative capture frequencies determined from winter angling data from Mayhew and Duncan lakes were consistent with those from netting data. For the 1981 cohorts, the cumulative winter angling capture ratio (IRY:MIC) was 1:1 ($P=1.0$) for Mayhew Lake, and 1.2:1 ($P=0.456$) for Duncan Lake (Table 10). For the 1982 cohorts, the cumulative capture ratio (IRY82:MIC82) was 2.2:1 ($P=0.002$) in Mayhew Lake and 1.7:1 ($P=0.359$) in Duncan Lake.

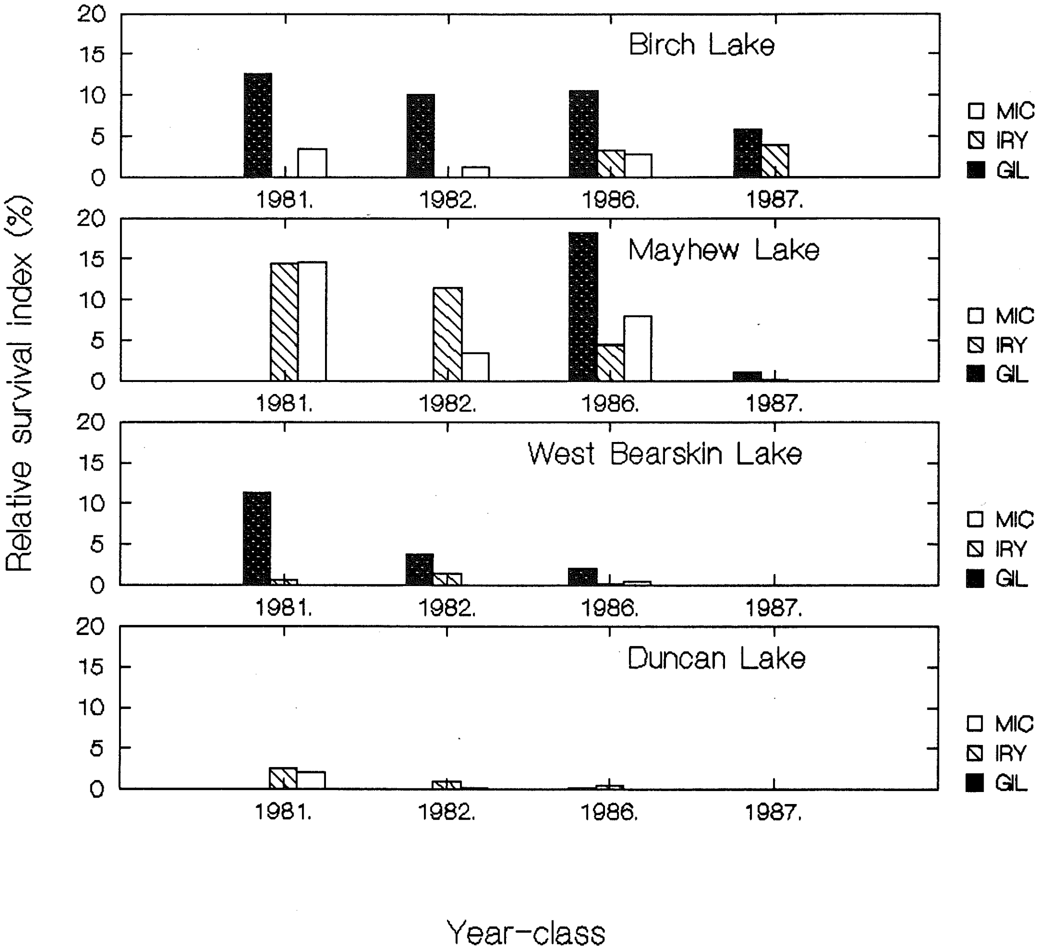

Figure 7. Relative survival (%) of three strains and four year-classes of lake trout stocked as yearlings into four northeastern Minnesota lakes, from anglers' catches during winter 1983-1990.

Relative survival of the IRY81 and MIC81 cohorts were 14.5% and 14.6% in Mayhew Lake (Table 11). In Duncan Lake, 3.6% of the IRY81 cohort and 3.8% of the MIC81 cohort had been harvested. In contrast, 11.5% of the IRY82 cohort was harvested from Mayhew Lake by the end of winter 1990, but only 3.5% of the MIC82 cohort. Harvest of the 1982 cohorts from Duncan Lake was similar in that 0.9% of the IRY82 and only 0.2% of the MIC82 cohorts were creeled by April 1990. Almost certainly, more of the 1981 and 1982 year-classes in Duncan Lake will be caught by anglers in future winters.

1986 and 1987 year-classes.--The Gillis Lake strain clearly dominated winter anglers' catches of the 1986 year-class in Birch, Mayhew, and West Bearskin lakes ($P < 0.001$) (Figure 7). The GIL86:IRY86:-MIC86 cumulative capture ratios were 3.8:1.0:1.7 in Birch Lake, 3.9:1.0:2.1 in Mayhew Lake, and 24.5:1.0:7.5 in West Bearskin Lake (Table 10). From winter 1988 through winter 1990, winter anglers were estimated to have harvested 10.4% of the GIL86, 3.3% of the IRY86, and 2.8% of the MIC86 from Birch Lake. During the same period, 18.2% of the GIL86, 4.5% of the IRY86, and 7.9% of the MIC86 were harvested from Mayhew Lake (Table 11). The 1986 year-class had not recruited to the winter fishery in Duncan Lake by winter 1990. The Gillis Lake strain also dominated winter anglers' catches of the 1987 year-class in those lakes where sample sizes allow comparison. In Birch and Mayhew lakes, the GIL87 cohort dominated by a factor of 1.9 in Birch Lake ($P<0.001$) and 2.4 in Mayhew Lake ($P=0.064$). The 1987 year-class had not recruited to either West Bearskin or Duncan lakes by winter 1990.

Condition of Captured Lake Trout

Comparisons among strains within lakes.--Weight-length relationships showed differences in condition among strains within some lakes. For most year-classes the slopes of the fall (1983-1990) regression lines were homogeneous, but the intercepts (adjusted mean weights) usually were different among strains. The GIL81 trout sampled from Birch and West Bearskin lakes were slightly heavier than the MIC81 or IRY81 trout, however, relatively few of the MIC81 or IRY81 trout were sampled, so this conclusion is not strong. Samples sizes of the 1981 cohort were larger in Mayhew and Duncan lakes. For Mayhew Lake, the regression parameters did not differ significantly between the IRY81 and MIC81 trout, nor between the IRY82 and MIC82 trout. But, in Duncan Lake, the IRY81 trout were slightly heavier at any given length than the MIC81 trout.

Often sample sizes of one or more of the strains of the 1986 year-class within a lake were small, making comparisons of condition tentative. For Mayhew and Duncan lakes, the MIC86 and IRY86 trout were heavier than the GIL86 trout at any given length. For these lakes, slopes of the regression lines were homogeneous, but intercepts were different (ANCOVA, $P<0.001$) . For Birch and West Bearskin lakes, slopes of the regression lines were different ($P=0.03$), but sample sizes of the MIC86 and IRY86 cohorts were small. In Birch, Mayhew, and Duncan lakes, sample sizes of the IRY87 or GIL87 cohorts were less than 20, not large enough to permit making inferences about weight-length relationships among strains and within lakes. In West Bearskin Lake, where larger samples of the 1987 cohorts were collected, juvenile GIL87 trout were slightly heavier than juvenile IRY87 trout (ANCOVA, $P<0.001$).

Comparisons among lakes within strains.--Weight-length regressions varied among the study lakes. Stocked lake trout captured in Birch and Mayhew lakes tended to be heavier at any given length than those in West Bearskin and Duncan lakes. The GIL81 cohort were heavier at length in Birch Lake than the GIL81 cohort in West Bearskin Lake ($P=0.011$). The IRY81 cohort captured in Mayhew Lake were heavier at length than the IRY81 cohort sampled from either West Bearskin or Duncan lakes ($P=0.005$). The MIC81 cohort sampled from Mayhew and Birch lakes were heavier at length than the MIC81 cohort from Duncan Lake ($P=0.001$). Adjusted mean weights differed among lakes ($P\leq0.001$) for the GIL82, IRY82, and MIC82 cohorts, but sample sizes from some of the lakes were not large. The 1986 year-class also indicates lake-to-lake differences in fish condition that are not related to strain. Juvenile lake trout of the 1986 year-class were in better condition (heavier at length) in Birch and Mayhew lakes than in West Bearskin and Duncan lakes. This may be due in part to faster growth and earlier maturation in Birch and Mayhew lakes.

Growth

Comparisons of strains within lakes.--There were few differences in growth rates between strains, and these were not consistent across lakes. In most cases, sample sizes for one or more strains of a given year-class were too low to permit rigorous testing. All strains of the 1981 and 1986 cohorts grew rapidly in Birch Lake (Figure 8). Similar observations were made regarding growth of the 1982 year-class in all four

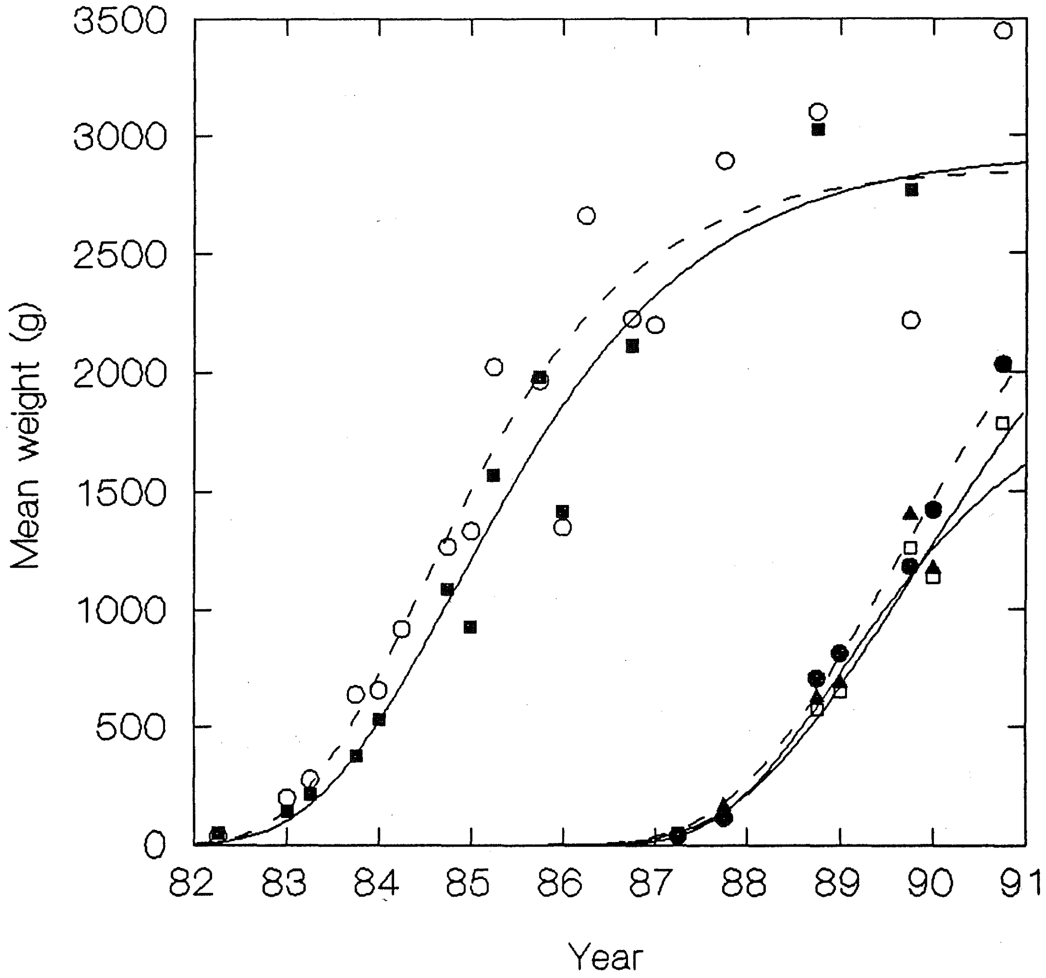

Figure 8. Growth curves of the 1981 and 1986 year-class lake trout, Birch Lake, spring 1982 - fall 1990. GIL81 = open circles (o); MIC81 = filled squares (■); GIL86 = filled circles (•); IRY86 = open triangles (▵); and MIC86 = open squares (□). In Figures 8 and 9, strains are abbreviated: GIL = Gillis Lake strain; IRY = Isle Royale strain; MIC = Marquette strain, and years and year-classes are abbreviated: 81 = 1981; 86 = 1986.

lakes. In Mayhew Lake, the IRY and MIC strains of the 1981 and 1986 year-classes show similar growth trajectories (Figure 9). Growth of the GIL86 cohort in Mayhew Lake was faster than that of the IRY86 and MIC86 cohorts, and their growth trajectories may diverge. The 1987 year-class was not monitored long enough to permit comparison of growth among strains.

Comparisons among lakes within strains.--Lake trout growth differed greatly among the four study lakes (Figures 10-12). Stocked trout grew fastest in Birch Lake and slowest in Duncan Lake. Lake trout in West Bearskin Lake grew more slowly than those in Mayhew Lake for the first two to four years (Figures 11, 12), then growth accelerated and they grew faster than the stocked trout in Mayhew Lake.

The Schnute growth curves describe the observed growth of the lake trout reasonably well, but I am not confident about the precise form and elevation of the growth trajectories for older fish. Because relatively few lake trout survived beyond age 6, due to fishing and natural mortality (except in Duncan Lake), sample sizes of older, mature

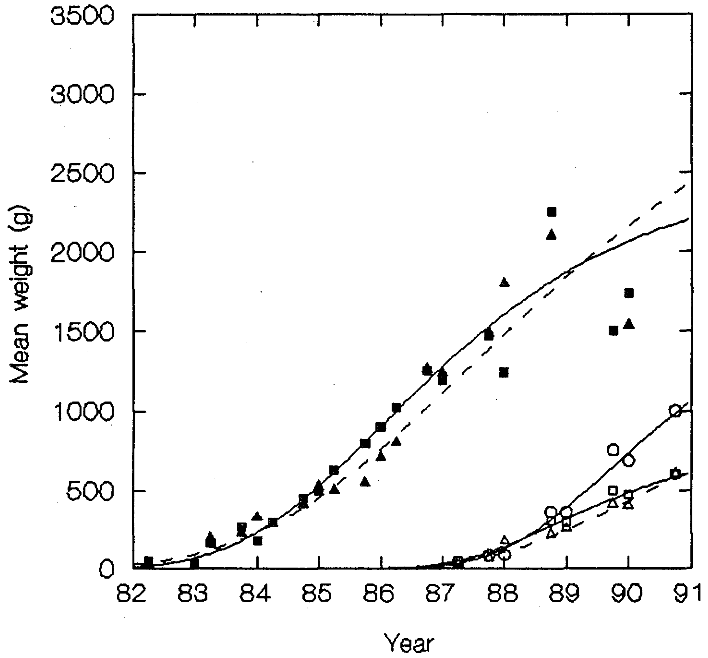

Figure 9. Growth curves of the 1981 and 1986 year-class lake trout, Mayhew Lake, spring 1982 - fall 1990. IRY81 = filled triangles (▲); MIC81 = filled squares (■); GIL86 = filled circles (•); IRY86 = open triangles (△); and MIC86 = open squares (□).

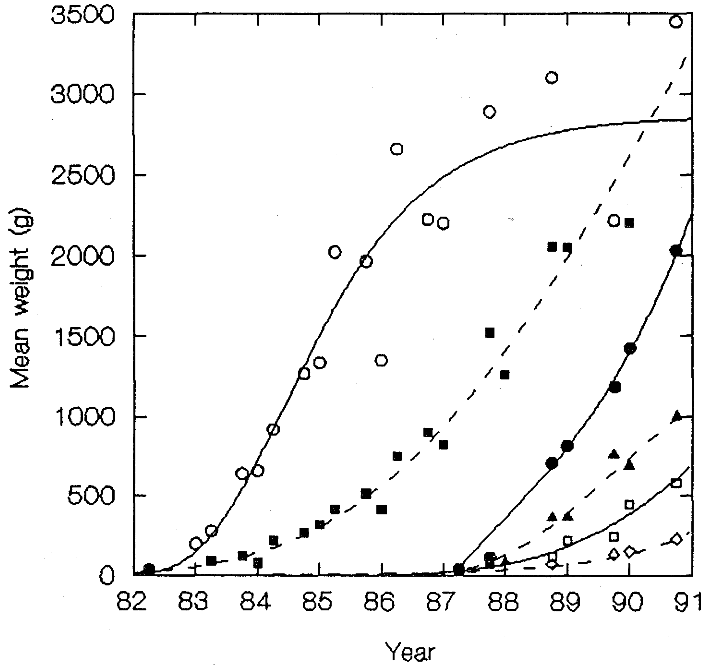

Figure 10. Growth curves of the Gillis Lake strain in different lakes. Growth of the 1981 cohort is shown for Birch (o) and West Bearskin (■) lakes, spring 1982 - fall 1990. Growth of the 1986 cohort is shown for Birch (•), Mayhew (▲), West Bearskin (□), and Duncan (◇) lakes, spring 1987 - fall 1990.

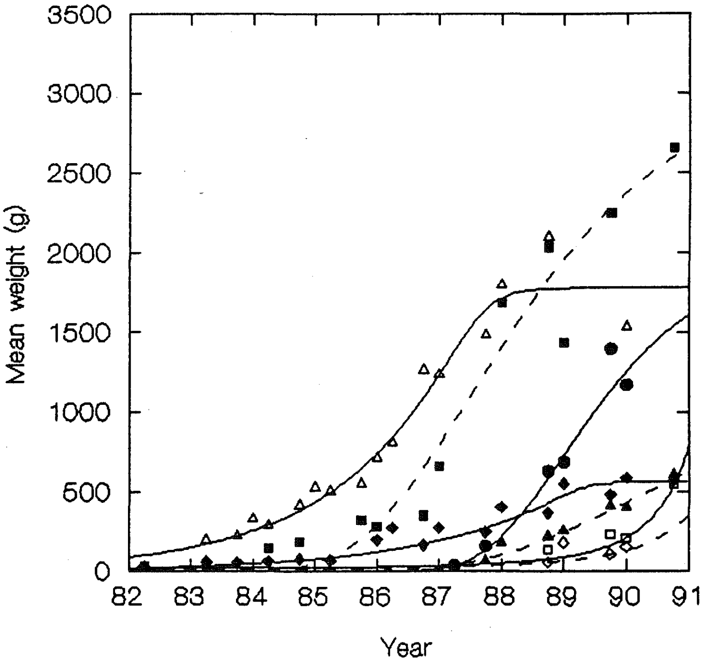

Figure 11. Growth curves of the Isle Royale strain in different lakes. Growth of the 1981 cohort is shown for Mayhew (△), West Bearskin (■), and Duncan (◆) lakes, spring 1982 - fall 1990. Growth of the 1986 cohort is shown for Birch (•), Mayhew (▲), West Bearskin (□), and Duncan (◇) lakes, spring 1987 - fall 1990.

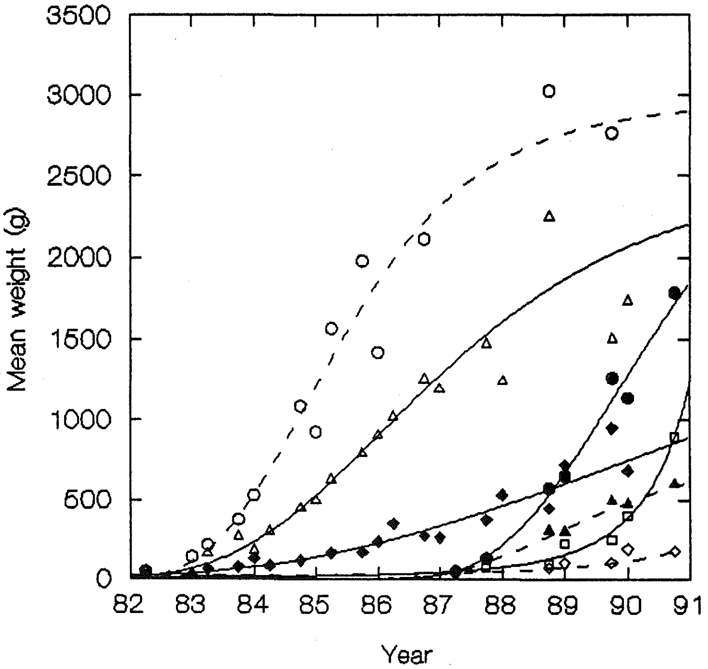

Figure 12. Growth curves of the Marquette strain in different lakes. Growth of the 1981 cohort is shown for Birch (o), Mayhew (△), and Duncan (◆) lakes, spring 1982 - fall 1990. Growth of the 1986 cohort is shown for Birch (•), Mayhew (▲), West Bearskin (□), and Duncan (◇) lakes, spring 1987 - fall 1990.

lake trout are not large. Lake trout length and weight at age are quite variable, thus a few old trout may strongly influence the right-hand portions of the growth curves.

Lake trout growth in weight was quite variable among the four Minnesota lakes, almost as variable as over the natural range of the species (Figure 13). From data developed by other investigators and compiled by Carlander (1969), Scott and Crossman (1973), and Donald and Alger (1986), Schnute growth model parameters and derived traditional parameters were computed for comparison with this study. Growth of juvenile lake trout in Birch Lake is among the fastest reported for the species while growth in Duncan Lake is among the slowest reported.

Sexual Maturity

I was not able to test for among strains differences in sexual maturation within lakes because sample sizes were inadequate. Age, size, and weight at sexual maturity varied greatly among lakes. Because sample sizes were small, a visual analysis of age and size at maturity was appropriate. Analyses such as those of Trippel and Harvey (1991) were not possible. Lake trout matured earliest in Birch Lake (age 3+ years) and latest in Duncan Lake (age 9+ years or more) (Table 12), with males tending to mature earlier than females.

In Birch Lake, the smallest and youngest (age 3+ years) mature male measured 425 mm TL and weighed nearly 800 g. The youngest mature female was age 3+ years, measured 542 mm, and weighed 1,400 g. Many male lake trout were mature at age 3+ years and most females matured at age 4+ years. All males and females were mature by age 4+ years in Birch Lake. Sexual maturation probably occurs earliest in Birch Lake because juvenile growth is very rapid.

Age at maturity in Mayhew and West Bearskin lakes was 1 - 2 years older and mean weight of mature fish was less than in Birch Lake, probably because growth was slower. In Mayhew Lake the smallest and youngest (age 3+) mature male measured 375 mm and weighed nearly 500 g. The youngest mature female (age 5+) was 487 mm long and weighed nearly 1,000 g. In West Bearskin Lake, the youngest (age 4+) mature male and female measured nearly 440 mm and weighed about 750 g. In Mayhew and West Bearskin lakes, 100% maturity of males and females was attained by age 7.

During this study, only one mature stocked lake trout (MIC81 cohort) was sampled in Duncan Lake. It was a gravid female, 724 mm total length and 4,000 g, atypical of other 1981 year-class lake trout captured in fall 1990. The second largest stocked lake trout collected from Duncan Lake in fall 1990 at age 9+, approximately 8.5 years after stocking was only 504 mm total length and weighed only 895 g. Sexual maturity appears to be delayed because of slow juvenile growth (Figures 11, 12).

Relative Abundance of Other Fish Species

During the study, there were few shifts in the abundance of major species in the four study lakes (Table 3), and few new species were introduced. In fall 1990, yellow perch *Perca flavescens* and bluegill *Lepomis macrochirus* were sampled in Mayhew Lake for the first time since the 1969 lake reclamation (Appendix Tables 18-21). These species were "bait-bucket" introductions by the public. In West Bearskin Lake, the relative abundance of bluegill increased gradually from 1983 to 1990, as measured by trap net CPUE, but they remain far less abundant than smallmouth bass and green sunfish *Lepomis cyanellus*.

In Birch Lake, there was a reduction in the abundance of cyprinids and a species shift away from finescale dace *Phoxinus neogaeus*, pearl dace *Margariscus margarita*, and creek chub *Semotilus atromaculatus* to a community more dominated by fathead minnows *Pimephales promelas*. I also observed a decrease in the numbers of crayfish *Orconectes virilis* in Birch and Mayhew

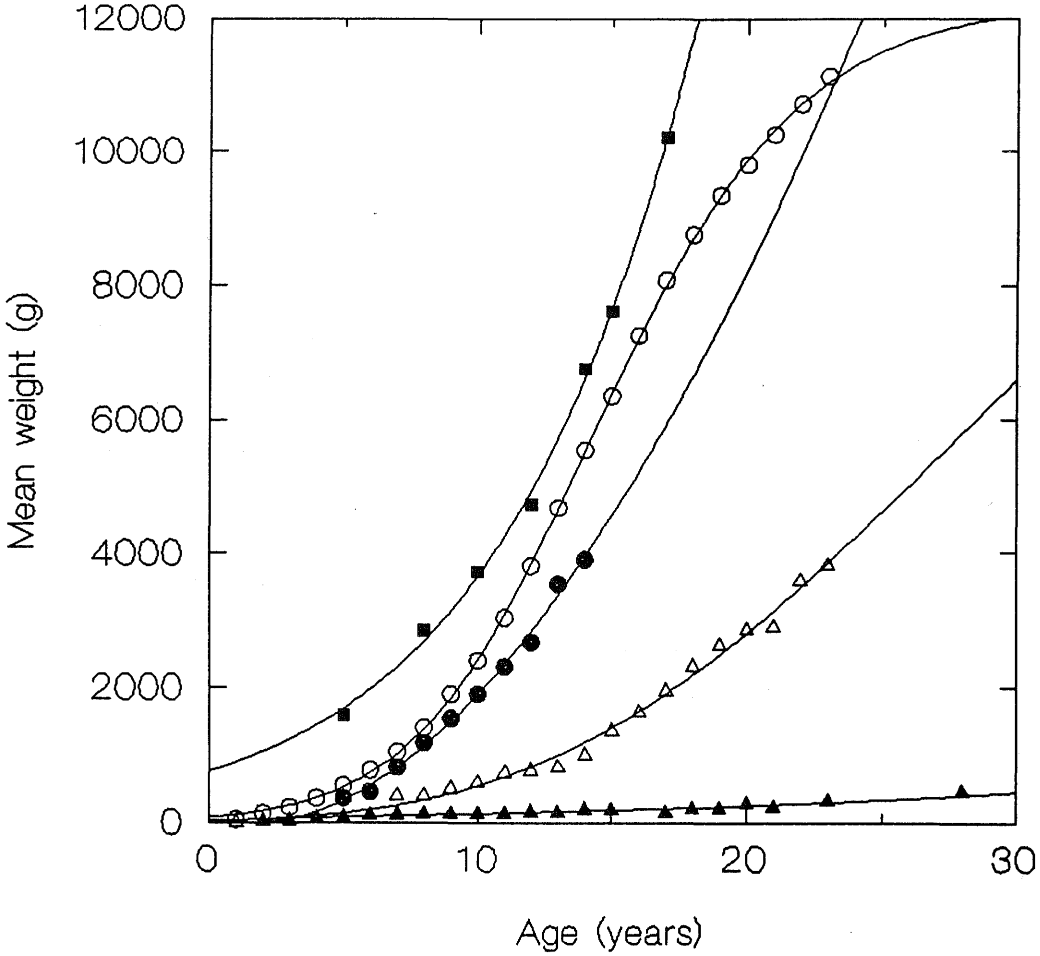

Figure 13. Variation in growth of lake trout. In order from largest to smallest weight at age, the populations are in Lac la Ronge (■), Saskatchewan; Great Slave Lake (o), Northwest Territories; Lake Opeongo (•), Ontario; Great Bear Lake (△) Northwest Territories; and Lake Sassanach (▲), Alberta. Data sources: Carlander (1969), Scott and Crossman (1973), and Donald and Alger (1986).

Table 12. Age and size at maturity for stocked lake trout (1981 year-class, strain ignored) based on trout captured in fall, 1983-1990. The ages of lake trout captured in the fall are marked with plus (+) signs to indicate that the age is greater than age t, but not yet age t+1; e.g., a 3 year-old lake trout captured in fall (end of September-early October) is considered to be approximately age 3.75 years.

Lake name	Variable	Youngest and smallest of the known mature		Oldest and largest of the known immature		Estimated age at 100% maturity	
		males	females	males	females	males	females
Birch[a]	age (years)	3+	3+	[b]	[b]	4+	4+
	length (mm)	425	542				
	weight (g)	790	1400				
Mayhew	age (years)	3+	5+	5+	4+	6+	6+
	length (mm)	385	487	531	528		
	weight (g)	675	980	1400	1160		
West Bearskin	age (years)	4+	4+	5+	5+	6+	6+
	length (mm)	437	435	570	575		
	weight (g)	730	750	1720	1760		
Duncan	age (years)	-	9+	9+	9+	[c]	[c]
	length (mm)	-	724	372	535		
	weight (g)	-	4000	325	1250		

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[a] Total number of 1981 year-class lake trout for which sex and sexual maturity was determined to be other than sex and maturity unknown: Birch Lake = 38; Mayhew Lake = 50; West Bearskin Lake = 46; and Duncan Lake = 20.

[b] All known males and females were mature at age 4+ in Birch Lake.

[c] Age at 100% attainment of sexual maturity in Duncan Lake cannot be estimated from these data.

lakes from 1983-1990. In contrast to Birch and Mayhew lakes, crayfish were rarely observed or absent in West Bearskin or Duncan lakes from 1983-1990. Also, cyprinids and other small forage species were rarely observed in either West Bearskin or Duncan lakes throughout the study.

Discussion

Survival

The most notable observation made in this study is that the GIL81 and GIL82 year-classes in Birch and West Bearskin lakes exhibited higher capture frequencies, as measured by netting and creel surveys, and higher relative survival (percentage harvested) than the IRY strain or the MIC strain. Returns from the 1986 cohorts in Mayhew, Birch, and West Bearskin lakes from fall 1987 through fall 1990 provided additional evidence that the Gillis strain survived better as indicated by greater numbers in the net catches and in the winter creel. The capture ratio of the 1987 year-class appears to favor the GIL87 cohort in Birch and Mayhew lakes.

The cause for the greater survival of the Gillis Lake strain, when stocked with the IRY or MIC strains, is not clear, but apparently occurred within the first months after stocking. By the early years of this study (1983-1986), both netting and winter creel data from Birch and West Bearskin lakes showed the Gillis Lake strain dominated the catch of the 1981 and 1982 year-classes. These catch ratios persisted throughout the study and in samples by various years, so they could not be attributed to behavioral differences among strains. Some unknown factor apparently caused substantial mortality within the first few months after stocking. This conclusion supports Pycha and King (1967), Plosila (1977), and Elrod and Schneider (1992) who indicated that the success of a lake trout stocking may be determined within the first few months or the first year after stocking. Short term survival tests of the 1986 cohorts in submerged cages in Birch and West Bearskin lakes indicated that there were no obvious among strain differences in response to transport and stocking, however, captures of the 1986 cohorts made with small-mesh gill nets about two months after stocking indicated that the GIL86 may have survived the immediate post-stocking period better in at least two of the four lakes (Duncan and West Bearskin).

Following the reasoning of Krueger et al. (1981), a native wild strain, such as the Gillis Lake strain, may be preadapted to environmental conditions in relatively small inland Minnesota lakes and survive better than hatchery or non-native strains. Rybicki (1990a) found no significant difference in relative survival rates among three strains of lake trout monitored through age 4 in northern Lake Michigan, however, all three strains (Marquette domestic, Apostle Islands out-cross, and Wyoming variety) had Lake Superior or northern Lake Michigan origins, and considerable potential for hatchery domesticity, so all may have been preadapted to northern Lake Michigan. Most recently, Elrod and Schneider (1992) suggested predation by salmonids in Lake Ontario had a larger impact than genetic strain on survival of stocked lake trout. Predation is the most likely agent causing differential survival in this study. The GIL strain juveniles may exhibit some behavioral difference, such as a depth or substrate preference, which allowed the newly stocked yearlings to escape cannibalism or predation by other species. In Birch, Mayhew, and West Bearskin lakes, previously stocked cohorts may have been able to prey upon (or compete with) newly stocked lake trout. There were no major predators other than lake trout in Birch Lake during most of this study. As noted earlier, West Bearskin Lake had a remnant population of stocked lake trout (1969 year-class), a recent stocking of the Marquette strain trout (MIC80), and well-established smallmouth bass and rainbow smelt populations when this study began. Alternatively, the GIL strain may be able to compete more effectively for food when stocked with equal numbers of the other strain(s), although competition seems unlikely in Birch Lake where growth was so rapid. When the GIL strain is not present, food or space for juvenile lake trout may be partitioned more evenly between the IRY and MIC strains, perhaps changing the time or location of exposure to predation.

Size and Condition at Stocking

In this study, size and condition at stocking are to some extent confounded with strains within each year-class, since the hatcheries did not produce identical size distributions. There were large size variations within hatchery-reared cohorts, so I could not directly determine the effect of size at stocking on relative survival rate or contribution to the angler's creel. Gunn et al. (1987), working with hatchery-reared lake trout older and often larger than those used in this study, found that large lake trout survived better than small or medium-sized trout. They indicated that large fish outcompete small fish and that the survivors of any group (cohort) may be the largest of the group when stocked. Rybicki (1990b) reported lake trout, stocked as spring yearlings (22 g) in Grand Traverse Bay, Lake Michigan, survived better than those stocked as fall fingerlings (17 g).

Although size and condition are to some extent confounding, the GIL strain survived better than the IRY or MIC strains, regardless of the initial size at stocking. Differences in average size and the amount of fat reserves among strains and among year-classes may have influenced relative rates of capture and survival. Because of their smaller average size and poorer condition (lower mesenteric body fat) at stocking, the 1982 year-class in general, and to greater extent the MIC82 cohort, may have been less able to escape predators and make the transition from hatchery feed to invertebrates and small forage fish. Fewer trout of the MIC82 cohort survived than either the GIL82 or IRY82 trout in Birch, Mayhew, and Duncan lakes, based on captures in nets and by winter anglers. Also, capture of the MIC82 and IRY82 cohorts did not occur in the same relative proportions as for the MIC81 and IRY81 cohorts in Mayhew and Duncan lakes.

Survival of all strains of the 1982 year-class may have been reduced by their maxillary bone clips, which may have decreased prey capture efficiency. The unclipped portion of the maxillary bone tended to remain inside the mouth, when the jaws were flexed open and closed, for 67 of 96 (69.8%) lake trout examined at stocking. Bonham (1968) concluded maxillary marks retarded growth of chinook salmon *Oncorhynchus tshawytscha*, and the length of jacks, marked as smolts, was shorter for those with more severe maxillary marks.

Genetic or strain-related factors (behavior and physiology) may account for the better survival of the native GIL strain in this study and may have influenced survival of stocked lake trout in previous studies. Haskell et al. (1952), sampling lake trout spawning beds in Raquette Lake, New York, found a capture ratio of 23.5:1, favoring the stocked, native Raquette Lake strain over the stocked, Seneca Lake strain. Plosila (1977), sampling Adirondack lakes in New York, reported a recovery ratio of 15.9:1, favoring the Upper Saranac Lake strain over the Seneca Lake strain. MacLean et al. (1981) also obtained results that support the hypothesis that genetic differences between lake trout stocks influence their survival. However, Rybicki (1990a) monitored three strains of lake trout through age 4 in northern Lake Michigan and found no significant differences in relative survival rate, instantaneous rate of growth in length, or straying. He recommended that the domestic, Marquette strain continue to be used to rebuild lake trout spawner biomass in Lake Michigan because of its many years of successful performance and availability. Working with hatchery-reared lake trout descended from three genetic strains stocked in Lake Ontario, Elrod and Schneider (1987) found that age-II Clearwater Lake (Manitoba) fish consistently were sampled at shallower depths and warmer temperatures than age-II Lake Superior (Marquette) lake trout. The distribution of Seneca Lake (New York) fish was similar to that of the Lake Superior strain. Among-strain differences in temperature and depth preference may tend to subject one strain to conditions which increase the likelihood of predation or cannibalism. Ihssen and Tait (1974) found two lake trout strains differed in ability to retain swim bladder gas. The ability to expel swim bladder gas quickly may confer a survival advantage when prey is pursued at various depths or where escape from predators requires rapid vertical movement.

In this study, the three strains of lake trout were stocked in lakes with varied community structure, supporting an extremely wide range of growth rates. Because of these environmental differences, one might expect considerable variation in which strains perform best. Elrod and Schneider (1992) noted that site-specific conditions (local concentrations of predators) had a greater influence on poststocking survival than genetic strain in Lake Ontario. Intra- or inter-specific competition have also been shown to influence survival or growth of stocked lake trout (Purych 1977; Powell et al. 1986; Gunn et al. 1987; Trippel and Beamish 1989). The consistent better survival of the Gillis strain indicates a genetic basis for survival. The similarity with which strains grew when in the same lake indicates a strong environmental influence in growth.

In some oligotrophic Minnesota lakes, survival and growth of juvenile lake trout may be limited by competition with non-native smallmouth bass, rainbow smelt, or perhaps cisco. Lake trout (Kettle and O'Brien 1978; Merrick et al. 1991) and smallmouth bass can influence the abundance and alter the species composition of prey species, though this was not monitored throughout this study. The potential for food competition with smallmouth bass probably is not limited to the spring season when spatial distribution of the species can overlap. Minnows and other small forage fish that prefer the shallow, relatively warmer water of the littoral zone may be eaten by smallmouth bass throughout the spring, summer, and early fall. These are potential prey which juvenile and adult lake trout could eat provided more of the prey species escaped smallmouth bass predation. Rainbow smelt and cisco, feeding on zooplankton, may compete more directly with age 0 and age 1 lake trout.

Lake trout populations may be more affected by other predators and competitors (particularly introduced species) in small lakes than in large lakes. Carl et al. (1990) found that fish community complexity is normally greater in large (>2,049 hectares) lake trout lakes than in small (<256 hectares) lakes, however, large lakes are likely to have more diverse habitats, and species such as lake trout and smallmouth bass may segregate by habitat type in large lakes. Martin and Fry (1973) reported that lake trout were not adversely affected by the introduction of smallmouth bass into the large Lake Opeongo (58.6 km^2). Introduced species may alter energy pathways (Evans and Loftus 1987), and adversely affect survival and growth of trout. In many oligotrophic northeastern Minnesota lakes, forage for top predators may be limited, so the introduction of non-native species may reduce survival and growth of native and stocked lake trout. All four lakes in this study are small (≤200 hectares), and juvenile lake trout grew faster in the two lakes without competing species. Throughout this study, it was my perception that potential forage (invertebrates and forage fish) for juvenile lake trout were more abundant in Birch and Mayhew lakes than in West Bearskin and Duncan lakes. After examining length at capture data and the results of linear growth modelling (Weisberg and Frie 1987), Eiler and Sak (1992) found that smallmouth bass appear to grow slower in lakes in which they are sympatric with lake trout than in allopatric situations.

In this study, the winter lake trout yield from Mayhew and Birch lakes fluctuated about the THV and MEI yields, while in West Bearskin and Duncan lakes winter lake trout yields were always less than the estimated THV and MEI yields. These differences may be due to greater fishing intensity (hours/hectare) for Birch and Mayhew lakes than for West Bearskin and Duncan lakes.

Size Dependent Growth Rates

Growth was similar among strains within lakes, but lake-to-lake differences in growth were large and dependent on the kinds of forage fish available. Juvenile lake trout grew and matured most rapidly in Birch Lake, and progressively slower in Mayhew, West Bearskin, and Duncan lakes, but both growth curves and the size of the largest fish observed suggest the maximum size reached in the four lakes is inversely related to juvenile growth rates. The size dependent growth pattern suggests small lake trout have a competitive relationship with cisco, rainbow smelt, and perhaps smallmouth bass, while larger lake trout have a predatory relationship. In Birch and Mayhew lakes, lake trout maximum size may be limited by the relatively small size of the available prey species, including green sunfish, darters *Etheostoma spp*, cyprinids, aquatic insects, and zooplankton. Although growth of juvenile trout is slow in both West Bearskin and Duncan lakes, adult lake trout can attain relatively large sizes by becoming more piscivorous and preying on larger fish. Growth in West Bearskin Lake accelerated three to four years after stocking, presumably when lake trout were able to consume rainbow smelt, a relatively large prey which was absent or rare in the other lakes.

In Ontario lakes without coregonine prey, lake trout up to about 1.3 kg showed a tendency to declining growth efficiency and small maximum size (Carl et al. 1990). Kerr (1971 a,b, and c) and Martin (1970) suggested that the metabolic demands of foraging for relatively small food items may limit lake trout growth. Konkle and Sprules (1986) studied stunted planktivorous lake trout and concluded lake trout must have increasingly larger prey if they are to attain large body size. Martin (1966) found that average size and growth rate of lake trout in lakes of Algonquin Park, Ontario, depended upon the amount of zooplankton or fish in the diet, with faster growth where fish were the dominant prey. Growth rates of age 6 to 12 lake trout from Lake Louisa (no ciscos) increased when they were transferred to Lake Opeongo where cisco had been introduced as forage (Martin 1966). Matuszek et al. (1990) found that growth of piscivorous lake trout (ages 3-8) in Lake Opeongo increased as cisco abundance increased, and then decreased as the abundance of piscivorous lake trout increased and the size of cisco eaten decreased. Trippel and Beamish (1989) found that cisco abundance and mean size explained 81% of the variation in asymptotic lake trout size in 10 northwestern Ontario lakes.

These size dependent interactions pose several challenges for managers. Most harvest is of small lake trout, so if bait-bucket introductions of other species reduce growth of small lake trout, then total lake trout yield to the fishery may be reduced. If they are to increase catch of trophy lake trout, managers may be required to reduce harvest of smaller lake trout. An abundance of large lake trout many control cisco numbers and allow faster growth of small lake trout, so harvest and trophy opportunities may be optimized under some size regulations, but the regulations may differ with community composition.

Sexual Maturity

MacLean et al. (1981) suggested that genetics may influence age of sexual maturation, because a Lake Superior stock matured one year later in Lake Simcoe, Ontario than Lake Simcoe and Manitoba stocks. In this study the strains examined showed similar growth and maturation within lakes.

Results of studies of lake trout size, growth, and age at sexual maturity have been inconsistent; the characters are highly variable and patterns observed in surveys across many populations may not be the same as patterns exhibited by one stock exposed to a changed environment (Alm 1959, cited in Carlander 1969; Martin 1966; Healey 1978; Martin and Olver 1980; Donald and Alger 1986; and Payne et al. 1990). Age at first maturity ranged from 4 to 19 years and weights from 30 to 2,500 g.

Lake trout sexual maturation has been linked more directly to food quantity and quality in transplant or stocking experiments. Matuszek et al. (1990) noted an increase in the age at maturity for lake trout in Lake Opeongo after cisco were introduced. They indicated juvenile lake trout, perhaps competing with cisco for invertebrate prey, had a slowed growth rate until ciscos became the major prey item in the diet at age 6-8. In this study, slow growth apparently has delayed sexual maturation to beyond age 8 in Duncan Lake, where abundant cisco and smallmouth bass may compete with juvenile lake trout, making them among the slower-growing and later-maturing lake trout reported. The fast-growing lake trout in Birch Lake are among the earliest maturing lake trout reported, with the most males and the first females maturing at age 3+ and virtually all trout being mature at age 4+.

Contribution of Stocked Lake Trout to the Breeding Population

I was not able to draw any conclusions about the relative contribution of the three strains to spawning stocks due to rapid exploitation. Increasing numbers of small, unmarked lake trout in Mayhew and Birch lakes, (both reclaimed lakes) and West Bearskin Lake shows at least one stocked cohort was able to successfully spawn. Powell et al. (1986) also were unable to draw any conclusions about the contribution of hatchery-reared lake trout to the future spawning stocks in eight Ontario lakes. Krueger et al. (1989) demonstrated the feasibility of using allozyme markers to identify the parental sources of naturally produced young. Genetic studies could indicate which strain(s) reproduce in stocked lakes in northeastern Minnesota.

Without significant recycling (catch-and-release) of angler-caught fish on the more readily accessible and heavily fished Minnesota lake trout waters, it is unlikely that many of the stocked lake trout will survive to spawn even once, much less grow to a relatively large size (10-12 kg) unless size and harvest limits are imposed. In Birch Lake, stocked lake trout are virtually fished out within 2 to 3 years.

Catching and releasing lake trout for sport was uncommon. Most of the lake trout released on these lakes are fish anglers consider too small to keep, though some anglers kept fairly small fish (<500 g) preferentially, believing they taste better or contain fewer contaminants than larger fish. Lake trout lakes with easy access, such as Birch and Mayhew, are managed similarly to "put-grow-take" stream trout fisheries in Minnesota. The easy access, angling vulnerability, lack of catch and release, and illegal harvest all contribute to the susceptibility of these lakes to over-exploitation (loss of large fish, possible yield over-fishing with reduction in weight harvested). Because lake trout are so vulnerable, lakes with more difficult access should be considered for management as sustainable wild trout fisheries. Greater escapement to spawning size, achieved by reducing harvest, may result in the re-establishment of successful breeding populations in at least some of the stocked lake trout lakes. In Duncan Lake, because access is somewhat more difficult, more stocked lake trout may survive to maturity. However, due to slow growth, sexual maturity is delayed and the period of vulnerability to predation is prolonged.

Summary

The findings of this study reinforce those of several fisheries biologists who suggested that native lake trout strains survive better than non-native strains in lakes similar to those from which the donor spawn was acquired (Haskell et al. 1952; Plosila 1977; MacLean et al. 1981; and Krueger et al. 1981). In spite of the confounding effect of size at stocking, it was clear that the GIL81 and GIL82 cohorts did contribute more to the winter sport catch and to the net catch in Birch and West Bearskin lakes than did either the IRY or MIC cohorts of the 1981 and 1982 year-classes. Also, the incomplete evaluation of the 1986 and 1987 year-classes, in all four lakes, supports the premise that GIL strain yearlings have a survival advantage, and provide a greater yield to winter anglers than either the IRY or the MIC strain.

Management Implications

Lake trout genetic strain must be considered by fisheries managers as they select among stocking strategies for management of individual lakes or groups of lakes in a watershed. In this study, whenever the Isle Royale and Marquette strain were stocked with equal numbers of the Gillis Lake strain, the IRY and MIC strains did not survive as well as the GIL strain, and therefore did not provide as great a return to the angler. If the goals of a lake management plan include maintaining or re-establishing a spawning population, then stocking a native strain will increase the chances of meeting the goal, as shown by greater survival here, and by successful reproduction in the source lakes. Native lake trout stocked into lakes having significant numbers of potential predators and competitors should be relatively large (at least 35-50 g). In the absence of substantial predator or competitor populations, younger and smaller lake trout may be suitable and more cost effective. Lakes with self-sustaining populations should not be stocked, but should be protected from overexploitation with carefully designed and enforced harvest or gear regulations. Lakes with native trout populations that have been stressed by angling may recover if angling pressure is reduced. One must be concerned with preserving genetic diversity of native stocks.

Lakes that are stocked frequently because of high exploitation rates and low potential for natural reproduction may be stocked with a non-native strain if there are few predators and competitors, if forage quantity and quality is good, and if the goals are to provide high catch rates without concern over establishing a self-sustaining spawning stock. It appears that native strains will yield the best returns.

Introductions or maintenance of species such as rainbow smelt (an exotic), cisco, smallmouth bass, and walleye in small lakes managed for lake trout should not be allowed because they may compete with lake trout for limited forage, and reduce growth and survival.

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Appendix tables with more specifics are available upon request.

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