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Growth of Lake Trout captured during Spring, Summer, and Fall Index Gill Netting in 10 northeastern Minnesota lakes

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Abstract.--Growth curves fitted to weight-at-age data of lake trout *Salvelinus namaycush* sampled from 10 lake trout lakes in spring, summer, and fall were compared and evaluated. Data from the three sampling periods were combined to increase sample size and to derive a single pooled curve to describe lake trout growth for each lake. For most lakes, pooling data from the three sampling periods resulted in sample sizes large enough to obtain useable growth models to make comparisons among lakes. Differences in weight-at-age curves among lakes relate to differences in fish communities and forage base. Lake trout that are not piscivorous or cannibalistic probably cannot attain large size. In lakes having a relatively large-sized forage fish, such as cisco *Coregonus artedi*, lake trout attain larger sizes than in lakes having smaller forage fish, such as rainbow smelt *Osmerus mordax*, or in lakes with few fish forage species, where lake trout are predominantly planktivorous or insectivorous. Weight and age data, however, are biased estimators of population characteristics due to aging and sampling biases. Therefore, growth models for individual lakes are biased and comparisons among lakes were made cautiously, especially when age estimates were less certain. Larger sample sizes and more certain age estimates are needed to increase precision.

Introduction

Lake trout *Salvelinus namaycush* growth depends on quantity, quality, and availability of prey (Martin and Olver (1980). Martin (1966) reported that planktivorous lake trout grew more slowly than piscivorous lake trout. Donald and Alger (1986) reported that lake trout feeding primarily on aquatic insects and zooplankton, having no fish or amphipod forage, grew very slowly. Cisco *Coregonus artedi* abundance and mean size explained 81 % of the variation in asymptotic lake trout size in 10 northwestern Ontario lakes (Trippel and Beamish 1989). Carl et al. (1990), citing various investigators, discussed lake trout growth efficiency and maximum size as it relates to forage base and prey size. The

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maximum size of planktivorous lake trout, in lakes without suitably-sized fish forage, will be small due to bioenergetic constraints of this feeding mode. Lake trout grow to larger sizes in lakes where yellow perch *Perca flavescens*, rainbow smelt *Osmerus mordax*, and especially coregonines are the prey base. These and other species, however, may eat potential lake trout prey species and limit their availability to lake trout at various life stages. Juvenile lake trout in southern Lake Ontario were opportunistic feeders, their diet varying with season, year, and prey abundance, preying on slimy sculpin *Cottus cognatus*, rainbow smelt, alewive *Alosa pseudoharengus*, and Johnny darter *Etheostoma nigrum* (Elrod and O'Gorman 1991). In Minnesota, lake trout growth varied greatly among four small lakes, was related to forage base, and was size dependent (Siesennop 1992). In that study, modeled growth curves suggested juvenile lake trout have a competitive relationship with rainbow smelt and cisco, effective plankton feeders, and perhaps with smallmouth bass, that feed on zooplankton, macroinvertebrates and small forage fish. Larger lake trout, however, have a predatory relationship with rainbow smelt and cisco.

The purposes of this study were to analyze size-at-age data obtained from lake trout captured during relative abundance index gill netting in 10 lakes during spring, summer, and fall, to compare growth among the collections within lakes, to characterize overall lake trout growth for individual lakes, and to relate growth trajectories to forage and predator communities.

Study Lakes

Physical and chemical characteristics and fish communities of the 10 lakes were described by Siesennop (1992, 1997). Kemo, Trout, West Bearskin, Loon, Greenwood, Mayhew, Clearwater, and Gunflint lakes are in Cook County in northeastern Minnesota. Ojibway and Snowbank lakes are in adjacent Lake County. Lake size ranged from 74 to 1,704 hectares, with maximum depths ranging from 19 to 62 m.

Most of the 10 study lakes have similar lists of major fish species (Table 1), with some exceptions. Disregarding cyprinids and other small forage species, Ojibway Lake and the six other lakes have more diverse ($N \geq 8$) fish populations than Kemo, Mayhew, or Trout lakes ($N \leq 6$). Chemical reclamation of Kemo Lake in 1962 and Mayhew Lake in 1969 accounts, in part, for the lower species diversity in these two lakes. Past introductions of several species, including smallmouth bass *Micropterus dolomieu*, largemouth bass *M. salmoides*, bluegill *Lepomis macrochirus*, rainbow smelt, cisco, walleye *Stizostedion vitreum*, and others account for higher species diversity in some of the lakes. Rainbow smelt were illegally introduced into West Bearskin, Gunflint, and Trout lakes from 5 to nearly 30 years ago. All the lakes, except Trout Lake, have a long history of lake trout stocking (MNDNR lake files). Minnows (Cyprinidae) and other small, known or potential, forage species (Table 2) compose the remainder of the species lists.

Methods

Lake Trout Capture -- In 10 northeastern Minnesota lakes, lake trout were captured by three index netting methods: short duration gill netting in near-shore waters during daylight hours in spring (Lester et al. 1991) and fall in water less than 14°C (57°F), and overnight gill netting in relatively deep water less than 12.8°C (55°F) during in summer. Five lakes were sampled 1993 and another five in 1994. Details of gill net construction, index netting methods, and other field and laboratory procedures were described *IN* Siesennop (1997).

Lake Trout Aging -- Precise ages were assigned to known-age lake trout (i.e. stocked fish with cohort-specific fin clips). Stocked lake trout with non-cohort-specific fin clips or unknown-age trout were assigned an age after interpreting growth indicated on thin-sections of pectoral fin rays, acetate impressions of scales, and when available, thin-sections of

Table 1. Major fish species known to be present (P) in 10 northeastern Minnesota lake trout lakes, excluding cyprinids and small forage species. Note: (p) denotes species believed to be of minor importance; **L** indicates the species has been recovered from lake trout stomachs; (x) denotes a species present prior to chemical reclamation: (Mayhew Lake in 1969 and Kemo Lake in 1964).

Common Name	Species code	Species Name	Lake name abbreviation[a]									
			KE	MH	TR	WB	LN	GW	CW	GF	OJ	SB
Longnose sucker	LNS	*Catostomus catostomus*	-	-	-	-	-	-	P	-	-	-
White sucker	WTS	*Catostomus commersoni*	P	P	-	P	P	P	P	p	p	p
Northern pike	NOP	*Esox lucius*	-	(x)	-	(p)	P	-	(p)	P	P	P
Rainbow smelt	RBS	*Osmerus mordax*	-	-	**L**	**L**	-	-	-	**L**	-	-
Cisco	TLC	*Coregonus artedi*	-	-	**L**	-	**L**	**L**	**L**	**L**	**L**	**L**
Lake whitefish	LKW	*Coregonus clupeaformis*	-	-	-	-	-	p	-	-	-	-
Shortnose cisco	SNC	*Coregonus reighardi*	-	-	-	-	-	-	-	P	-	-
Shortjaw cisco	SJC	*Coregonus zenithicus*	-	-	-	-	-	-	-	P	-	-
Rainbow trout	RBT	*Oncorhynchus mykiss*	-	-	P	-	-	-	-	-	-	-
Round whitefish	RDW	*Prosopium cylindraceum*	-	-	-	-	-	P	P	-	-	-
Brook trout	BKT	*Salvelinus fontinalis*	(p)	-	(p)	-	(p)	P	-	-	-	P
Lake trout	LAT	*Salvelinus namaycush*	P	P	P	P	P	P	P	P	P	-
Splake	SPT	*S. fontinalis x S. namaycush*	p	-	-	-	(p)	-	-	-	P	-
Burbot	BUB	*Lota lota*	-	-	-	-	-	-	**L**	**L**	**L**	P
Rock bass	RKB	*Ambloplites rupestris*	-	-	-	-	P	-	-	P	P	-
Green sunfish	GSF	*Lepomis cyanellus*	-	**L**	-	**L**	P	P	P	-	P	-
Pumpkinseed	PMK	*Lepomis gibbosus*	-	-	-	-	-	-	-	(p)	p	-
Bluegill	BLG	*Lepomis macrochirus*	-	-	-	(p)	(p)	-	(p)	-	p	-
Smallmouth bass	SMB	*Micropterus dolomieu*	-	-	-	**L**	**L**	P	P	P	P	P
Largemouth bass	LMB	*Micropterus salmoides*	-	-	-	-	-	-	-	-	P	-
Yellow perch	YEP	*Perca flavescens*	(x)	P	P	P	(p)	**L**	**L**	**L**	P	P
Walleye	WAE	*Stizostedion vitreum*	-	-	-	(p)	P	(p)	(p)	P	P	P
Number of major species:			3	4	5	6	8	9	9	12	14	8

[a] Lake name abbreviations: KE = Kemo, MH = Mayhew, TR = Trout, WB = West Bearskin, LN = Loon, GW = Greenwood, CW = Clearwater, GF = Gunflint, OJ = Ojibway, SB = Snowbank.

Table 2. Minnows (cyprinids) and other small species that are known or potential lake trout prey species, present in 10 northeastern Minnesota lake trout lakes. Note:L indicates species that have been recovered from lake trout stomachs; (x) denotes a species present in Mayhew Lake prior to lake reclamation with a fish toxicant in 1969. Rainbow smelt occurrence: see Table 1.

Common Name	Species code	Species Name	Lake name abbreviation[a]									
			KE	MH	TR	WB	LN	GW	CW	GF	OJ	SB
Lake chub	LKC	*Couesius plumbeus*	-	-	-	-	-		-	p	-	--
Common shiner	CSH	*Luxilus cornutus*	L	-	p	-	-		-	-	p	p-
Pearl dace	PRD	*Margariscus margarita*	-	p	p	-	-		-	-	-	--
Golden shiner	GOS	*Notemigonus crysoleucas*	-	(x)	p	p	-		p	-	-	-p
Blacknose shiner	BNS	*Notropis heterolepis*	p	(x)	-	-	-		-	-	p	pp
Spottail shiner	SPO	*Notropis hudsonius*	-	(x)	-	-	-		-	p	p	-p
Mimic shiner	MMS	*Notropis volucellus*	-	-	-	-	-		-	-	-	-p
Finescale dace	FND	*Phoxinus neogaeus*	p	-	-	-	-		-	-	-	--
Bluntnose minnow	BNM	*Pimephales notatus*	-	-	-	-	-		-	p	p	pp
Fathead minnow	FHM	*Pimephales promelas*	p	L	-	-	-		-	p	-	p-
Blacknose dace	BND	*Rhinichthys atratulus*	-	(x)	-	-	-		-	P	-	--
Longnose dace	LND	*Rhinichthys cataractae*	-	-	-	-	-		p	-	p	--
Creek chub	CRC	*Semotilus atromaculatus*	p	p	p	-	-		p	-	p	--
Tadpole madtom	TPM	*Noturus gyrinus*	-	-	-	-	-		-	-	-	-p
Trout-perch	TRP	*Percopsis omiscomayus*	-	-	-	-	-		-	-	p	-L
Brook stickleback	BST	*Culaea inconstans*	L	p	-	-	-		-	-	-	--
Mottled sculpin	MTS	*Cottus bairdi*	-	-	p	-	-		-	p	p	--
Sculpins	SCU	*Cottus spp.*	L	-	L	-	L		p	-	-	L-
Iowa darter	IOD	*Etheostoma exile*	-	L	-	-	-		-	-	p	--
Johnny darter	JND	*Etheostoma nigrum*	-	-	-	-	-		-	-	p	--
Darters	DAR	*Etheostoma spp.*	L	-	-	-	-		-	-	-	p-
Logperch	LGP	*Percina caprodes*	-	-	-	-	-		-	-	-	-p
Opossum shrimp	MYS	*Mysis oculata relicta*	-	-	L	-	-		-	L	L	L-
Scuds	AMP	*Amphipoda*	-	L	-	-	L		L	-	-	--
Number of known or potential forage fish:			8	5	6	1	1		4	6	10	69

[a] Lake name abbreviations: KE = Kemo, MH = Mayhew, TR = Trout, WB = West Bearskin, LN = Loon, GW = Greenwood, CW = Clearwater, GF = Gunflint, OJ = Ojibway, SB = Snowbank.

otoliths. Otoliths were collected from all dead lake trout during spring and fall index gill netting and from West Bearskin Lake in summer 1993 and from Mayhew, Clearwater, Gunflint, and Snowbank lakes in summer 1994. Non-lethal sampling, however, precluded collecting otoliths from most lake trout during spring and fall index netting. The number of lake trout assigned to each cohort were summarized for four 5-year age categories for each lake. The Chi-square test for heterogeneity (Snedecor and Cochran 1980) was used to compare the numbers of lake trout by age category.

Growth Modeling -- Schnute's (1981) generalized growth model was used to fit growth curves to the weight-at-age data for all 30 lake trout data sets (10 lakes and 3 abundance index gill netting methods per lake). All lake trout for which weight was measured and age was estimated were included in the growth analyses, including newly stocked yearling lake trout (17-18 months old). For purposes of this study, 1 January was assumed to be the hatch date for lake trout. Thus, 0.4, 0.6, or 0.8 year, respectively, was added to the known or assigned age of lake trout captured during spring (May-early June), summer (July-August), or fall (October) netting periods. For example, a 3 year old trout captured during its fourth spring would be assigned an age of 3.4 years. If captured in fall of the same year, however, it would be assigned an age of 3.8 years.

Weight-at-age data were fitted to several growth submodels (generalized von Bertalanffy, Gompertz, Richards, and *t*th-power) to describe lake trout growth by lake and collection season. The Likelihood-Ratio-Test (Weisberg 1985), comparing residual sums of squares of the various submodels, was used to select the growth submodel that adequately described the weight-age relationship or growth trajectory for each lake and season. The 4-parameter generalized von Bertalanffy model was used when it provided a significantly better fit than simpler models, otherwise a simpler 2 or 3-parameter growth model was fitted to weight-at-age data.

Growth curves from the three collections for each lake were compared graphically. Data from the three collections was pooled to increase sample size and an overall growth model was estimated for pooled data from each lake. Again, the Likelihood-Ratio-Test (Weisberg 1985) was used to decide which submodel was adequate for the data. A different submodel than indicated by the statistical test was selected, however, if it made more biological sense. Residual plots were examined for heteroscedasticity, serial correlation, skewness, and autocorrelation (Wilkinson 1990). The selected growth model for each lake was used to estimate weight-at-age 1.0, 2.0, ..., n years within the range of ages modeled for each lake. Single cohort growth curves for lake trout captured from 1983 to 1990 for West Bearskin and Mayhew lakes in a previous study (Siesennop 1992) were compared with multiple cohort growth curves for West Bearskin Lake in 1993 and Mayhew Lake in 1994.

Maximum lake trout size -- An estimate of the maximum size lake trout may attain in each lake was obtained by searching existing MN DNR lake files and by contacting anglers or resort owners. The largest lake trout reported may approach a theoretical maximum size for that species for a given lake.

Lake trout forage and species lists -- No lake trout food habits information was obtained from lake trout captured during this study because most lake trout were captured live and released. Preliminary species and lake trout forage lists, however, were compiled from MN DNR lake files, reports, and anecdotal information. Species lists for some lakes are preliminary because sampling gear, methods, and effort varied over time and among lakes. For most lake surveys and population assessments only gill nets and 19 mm mesh-size trap nets were used, and in some cases only gill nets were used and relatively few species were captured. Infrequently, sampling gear included small mesh (13 mm or 6.4 mm) trap nets and seines. Species named in qualitative or quantitative descriptions (MN DNR lake files or Fisheries Investigational Reports) of lake trout stomach contents were added to species and potential forage lists. For some Minnesota lake trout lakes, unsummarized qualitative or anecdotal forage information exists on archived data sheets and on fish scale envelops (S. Persons, personal communication, 1997). These potential information sources, however, were not examined for this study.

Results

Lake trout sample size

Lake trout sample size was small for most of the study lakes, with fewer than 40 lake trout captured in 73% (22 of 30) of the collections (Table 3). Total sample size was greater in fall (N=461) than in summer (N=332) or spring (N=222). Sample size was greater than 40 for one-half of the lakes in fall and for only 30% of the lakes in summer. For individual lakes, sample size ranged from 6 to 38 fish in spring, from 12 to 69 in summer, and from 16 to 98 in fall. Pooled sample sizes for a given lake (total catch of spring, summer, and fall) used for growth modeling ranged from 51 to 151 lake trout.

Aging lake trout

The proportion of known-age lake trout varied among the 10 study lakes, and ranged from 0 to 77% (Table 4). In Kemo, Trout, Clearwater, Gunflint, and Snowbank lakes, fewer than 5% of lake trout captured were known-age fish. Greater proportions of known-age lake trout were captured in Mayhew (22.6%), Greenwood (23.2%), Loon (41%), Ojibway (73.1%), and West Bearskin (76.5%) lakes. Lake trout yearlings, stocked in spring 1993 or 1994, composed a larger proportion of the summer catch than the spring and fall catch in West Bearskin, Loon, and Greenwood lakes in 1993 and in Ojibway Lake in 1994 (Table 4).

Known and assigned lake trout ages ranged from 1 to 26 years among the 10 study lakes, but only 8.8% were older than 10 years and less than 1% were older than 15 years. Lake trout less than 5 years old and those 6 to 10 years old each composed about 46% of the total catch (Table 5). Proportions of lake trout in the four age categories, however, were heterogeneous among lakes (χ=248.85, P<0.001, 27 df).

Table 3. Number of lake trout aged that were sampled in spring, summer, and fall in ten northeastern Minnesota lake trout lakes, 1993 or 1994.

Lake name	Year	Number of Lake Trout Aged			
		Spring	Summer	Fall	Total
Kemo	1993	25	17	88	130
Trout	1993	28	20	57	105
West Bearskin	1993	17	34	98	149
Loon	1993	33	45	27	105
Greenwood	1993	38	69	44	151
Mayhew	1994	22	17	45	84
Clearwater	1994	26	36	37	98
Gunflint	1994	18	26	19	52
Ojibway	1994	6	56	16	78
Snowbank	1994	9	12	30	51
Summary statistics:					
minimum		6	12	16	51
maximum		38	69	98	151
mean		22.2	33.2	46.1	100.3
median		23.5	30.0	40.5	101.5
sum		222	332	461	1003
number of lakes		10	10	10	10

Table 4. Numbers and percentages of unknown age and known or partially known-age lake trout captured during spring, fall, and summer relative abundance index gill netting in 10 Minnesota lakes, 1993 or 1994. Unmarked fish are either wild or those stocked without a cohort-identifying fin clip. Age 1 denotes fin clipped fish stocked as yearlings in spring 1993 or 1994. Age 2 fish are those fin clipped and stocked in spring in years prior to 1993 or 1994.

			Unknown age (unmarked)		Known age (fin clipped)			
					Age ≥2		Age 1	
Lake	Year	Season	*N*	%	*N*	%	*N*	%
Kemo	1993	Spring	28	100	0	0	0	0
		Fall	96	100	0	0	0	0
		Summer	18	100	0	0	0	0
Trout	1993	Spring	28	100	0	0	0	0
		Fall	57	100	0	0	0	0
		Summer	26	100	0	0	0	0
Snowbank	1994	Spring	9	100	0	0	0	0
		Fall	31	97	1	3	0	0
		Summer	13	100	0	0	0	0
Gunflint	1994	Spring	18	100	0	0	0	0
		Fall	18	95	1	5	0	0
		Summer	20	95	1	5	0	0
Clearwater	1994	Spring	23	88	3	12	0	0
		Fall	37	95	2	5	0	0
		Summer	36	97	1	3	0	0
Mayhew	1994	Spring	20	83	4	17	0	0
		Fall	40	85	7	15	0	0
		Summer	6	43	8	57	0	0
Greenwood	1993	Spring	27	69	10	26	2	5
		Fall	39	91	2	5	1	2
		Summer	46	64	2	3	24	33
Ojibway	1994	Spring	6	100	0	0	0	0
		Fall	11	65	4	24	2	12
		Summer	6	10	19	33	33	57
Loon	1993	Spring	23	70	10	30	0	0
		Fall	14	52	13	48	0	0
		Summer	22	51	10	23	11	26
W. Bearskin	1993	Spring	5	29	12	71	0	0
		Fall	20	22	70	78	0	0
		Summer	8	25	18	56	6	19

Table 5. Number of lake trout in 5-year age categories sampled in 10 northeastern Minnesota lake trout lakes, 1993 or 1994. Spring, summer, and fall data are pooled.

		Number of lake trout by age category			
Lake name	Year	1-5 years	6-10 years	11-15 years	≥16 years
Kemo	1993	53	60	17	0
Trout	1993	56	45	4	0
West Bearskin	1993	106	38	5	0
Loon	1993	29	72	4	0
Greenwood	1993	58	89	4	0
Mayhew	1994	52	26	6	0
Clearwater	1994	17	58	19	4
Gunflint	1994	11	33	5	3
Ojibway	1994	63	14	1	0
Snowbank	1994	12	23	15	1
sum		457	458	80	8
percentage		45.6	45.7	8	0.8

Growth modeling

The number of age-classes for which growth was modeled varied among lakes and collection periods, ranging from 5 to 14 (median=8; mean=8.3) for unpooled data sets (Tables A1 and A2). The median age at which growth modeling began was age 3 (range: 1-7 years) for all 30 data sets. The median age at which modeling ended was age 13 (range: 8-26 years).

Shapes and relative positions of the growth curves varied among the lakes and among seasons within lakes (Figure 1a - 1j) and parameters determining the shapes of the lake trout growth curves are listed in Table A3. For some lakes, growth trajectories for spring, summer, and fall differed among seasons. For six lakes, weight-at-age was greater for lake trout collected in spring than for those collected in fall. This was particularly noticeable for Kemo and Trout lakes, but also occurred in data sets for West Bearskin, Loon, Clearwater, and Ojibway lakes. This contrast was not evident for Greenwood, Mayhew, Gunflint, or Snowbank lake data sets.

Growth models derived from the pooled spring, summer, and fall data estimate lake trout growth trajectories for each lake (Figures 2a, 2b; and 3a, 3b); Table 6. Although residuals were not serially correlated with age and error distributions were not skewed, not all the criteria needed for hypothesis testing were met. Variation in weight increased with age for all pooled data sets, except those for Kemo, Trout, and Snowbank lakes. Also, residuals from data sets from Kemo, Trout, West Bearskin, Greenwood, and Clearwater lakes showed autocorrelation. Thus, some growth curves did not fit the data well in all portions of the range of modeled ages.

In Kemo Lake, lake trout grew slowly until age 2. Growth then accelerated and slowed abruptly at approximately age 7, with the trout weighing approximately 2.5 kg at age 10 to 15 (Figure 2b). In Mayhew Lake, lake trout also appeared to grow slowly, but may attain a larger size than lake trout in Kemo Lake, perhaps 4 kg at age 15. Growth curves for Kemo and Mayhew lakes (Figure 2b) are not as steep as those for Trout and West Bearskin lakes (Figure 2a). Lake trout growth trajectories in Trout and West Bearskin lakes are similar, and lake trout may attain 4.5 kg in 10 to 13 years. Lake trout growth patterns for Ojibway, Loon, and Greenwood (Figures 3a, 3b) lakes are similar, having relatively slow growth to about age 9 to 11, followed by a period of accelerated growth, with some trout exceeding 4 kg. Growth models indicate lake trout in Gunflint, Snowbank (Figure 3a), and Clearwater lakes (Figures 3a, 3b) did not attain 4 kg by age 13 or 14. Lake trout growth curves for these three lakes indicate slow growth may be more prolonged than in Loon, Greenwood, and Ojibway lakes. Lake trout size-at-age varied among lakes, increasing with age, but it also varied within lakes. This was particularly noticeable for Clearwater Lake, where growth of some individuals accelerated at age 8 to 10 years, while others continued to grow slowly beyond age 15 (Figure 3b).

Growth trajectories for lake trout sampled from West Bearskin Lake in 1993 (Figure 4a) did not differ greatly from those of the 1981 cohorts of the Gillis Lake and Isle Royale lake trout strains (Table 7), for which growth was modeled in a previous study (Siesennop 1992), perhaps indicating that prey-predator relationships may not have changed measurably in recent years. Growth curves of the Isle Royale and Marquette 1981 cohorts in Mayhew Lake, estimated for the same study, however, may indicate that these cohorts (Table 7), sampled 1983 - 1990, may have grown faster as subadults and adults than lake trout captured in 1994 (Figure 4b).

The growth models enable comparison of estimated lake trout weights at specified ages, among the 10 lakes, within the range of ages modeled (Table 8). Juvenile lake trout captured in lakes such as, West Bearskin, Mayhew, Loon, Greenwood, and Ojibway lakes that had been stocked with yearling lake trout, tended to be larger than lake trout of the same age in lakes that were not stocked (e.g., Trout Lake) or were stocked with smaller fall fingerlings (e.g., Kemo Lake). Modeled

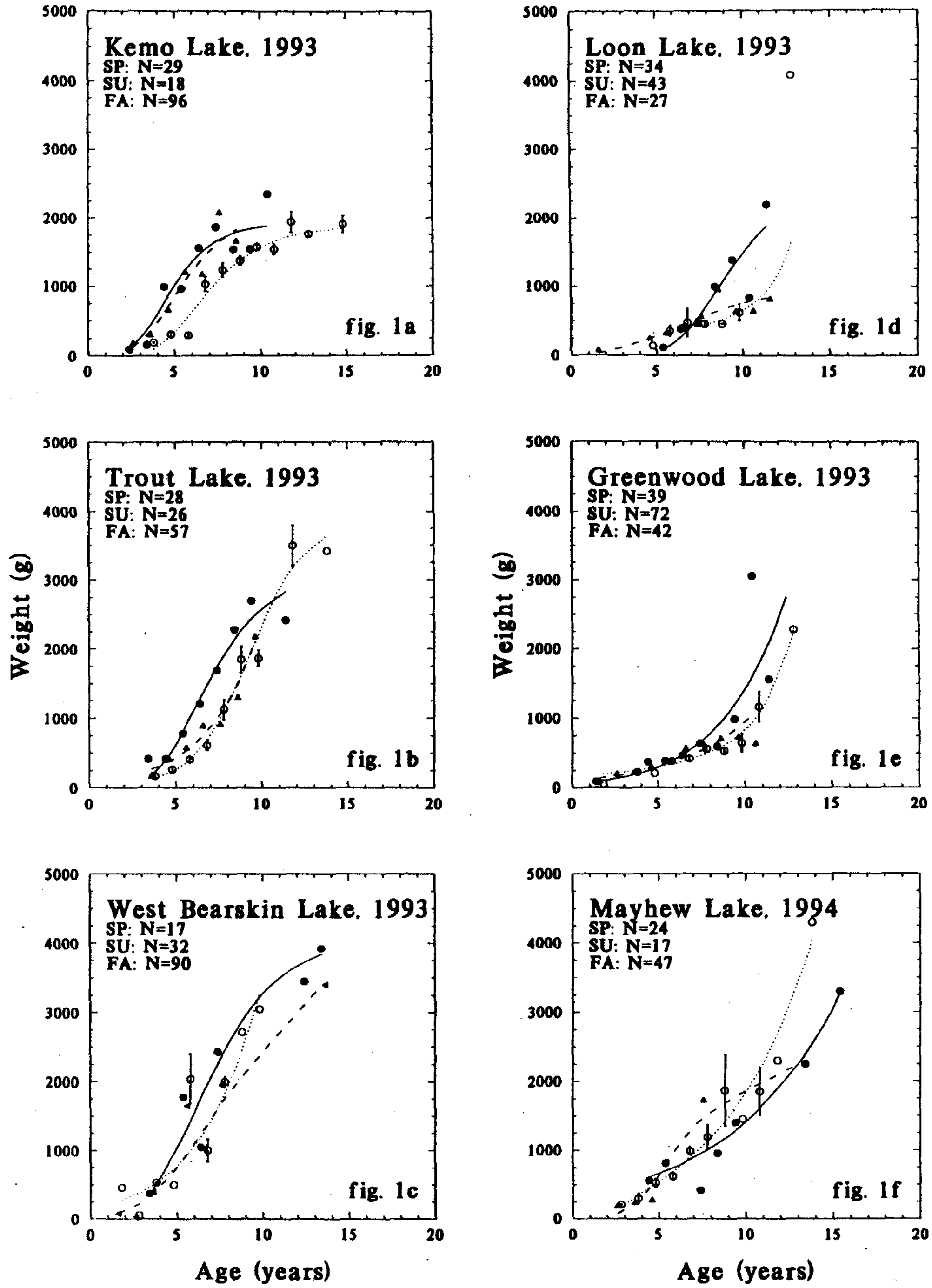

FIGURE 1. Lake trout growth (mean weight vs. estimated age) in 10 northeastern Minnesota lakes, as indicated by measurements made in spring (filled circles), summer (filled triangles), and fall (open circles), 1993 or 1994. Growth of fish captured in spring (solid lines), summer (dashed lines), and fall (dotted lines) was modeled using Schnute's (1981) generalized growth model. Error bars = SE.

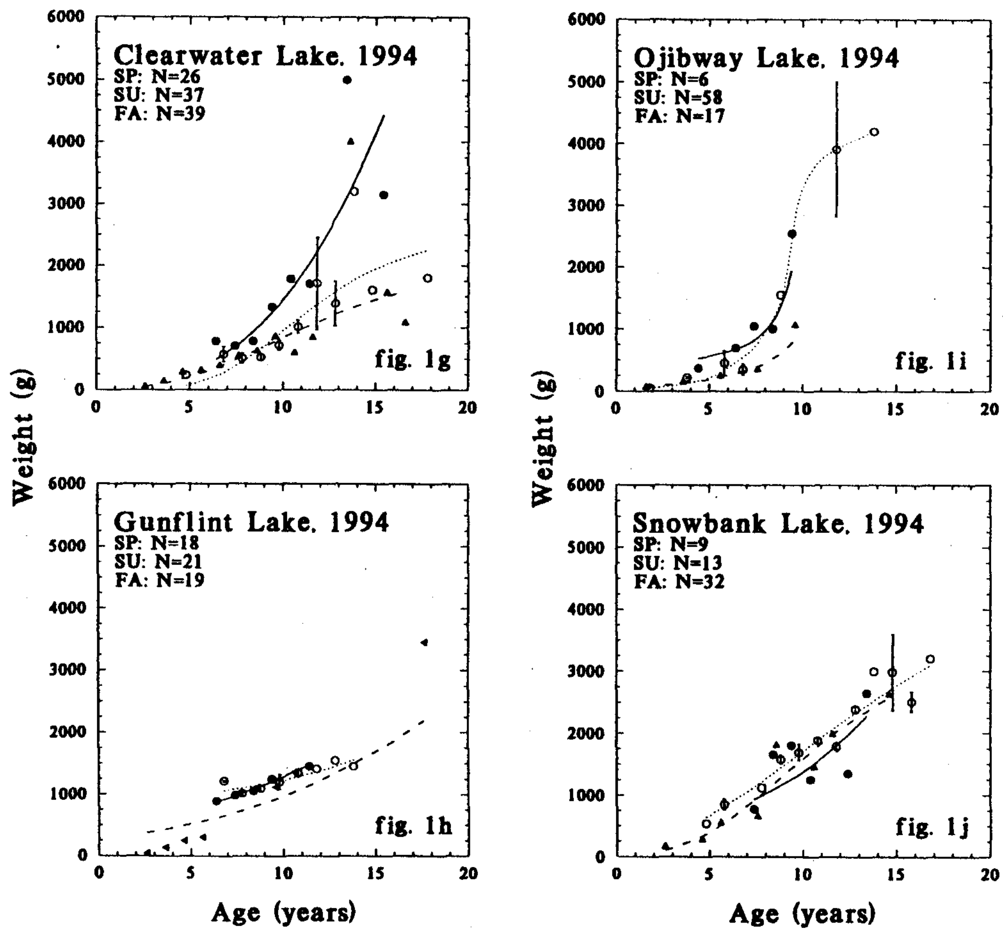

FIGURE 1. Continued.

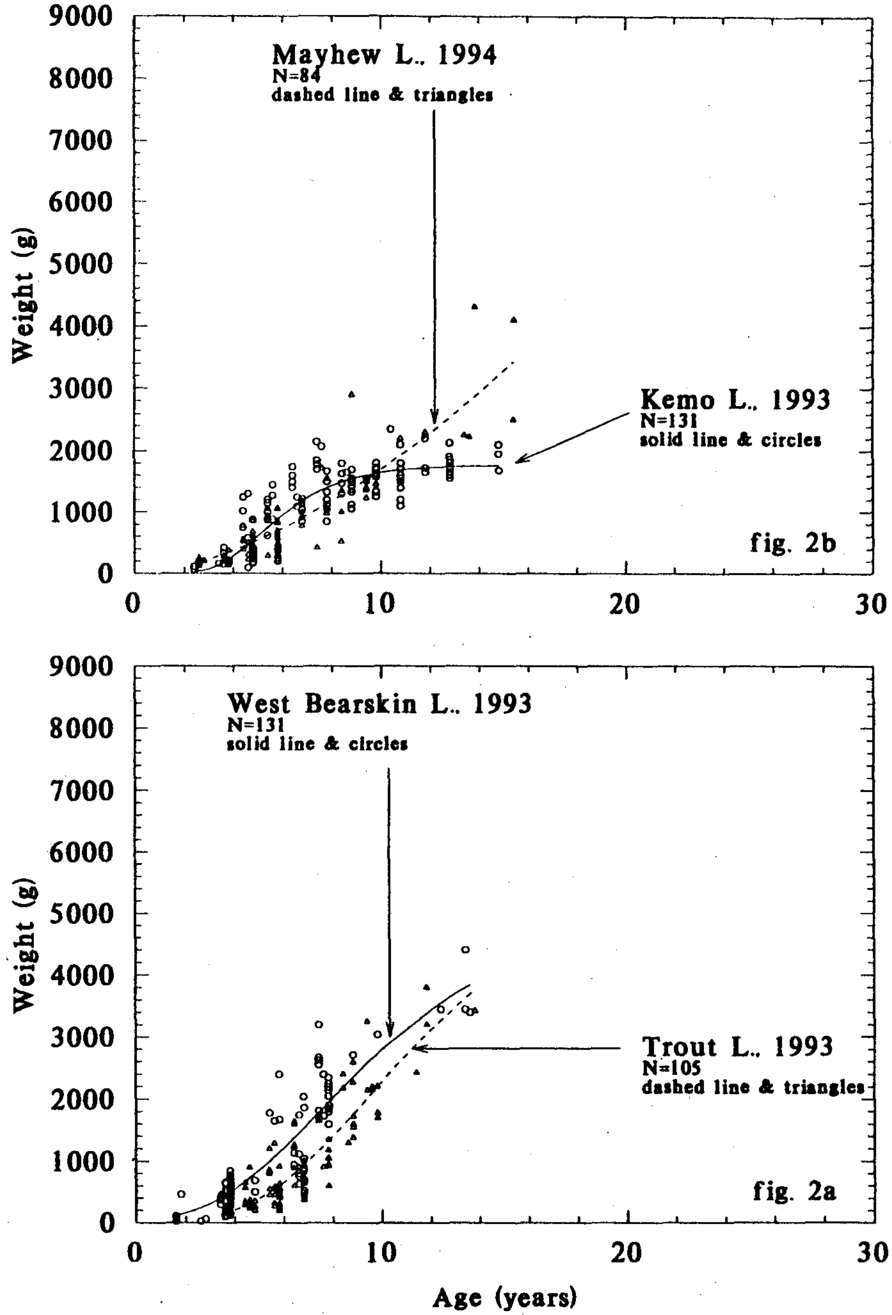

FIGURE 2. Lake trout growth (weight at estimated age) in 4 northeastern Minnesota lakes, as indicated by pooled data from various cohorts sampled in spring, summer, and fall, 1993 or 1994. Growth trajectories were estimated with Schnute's (1981) generalized growth model.

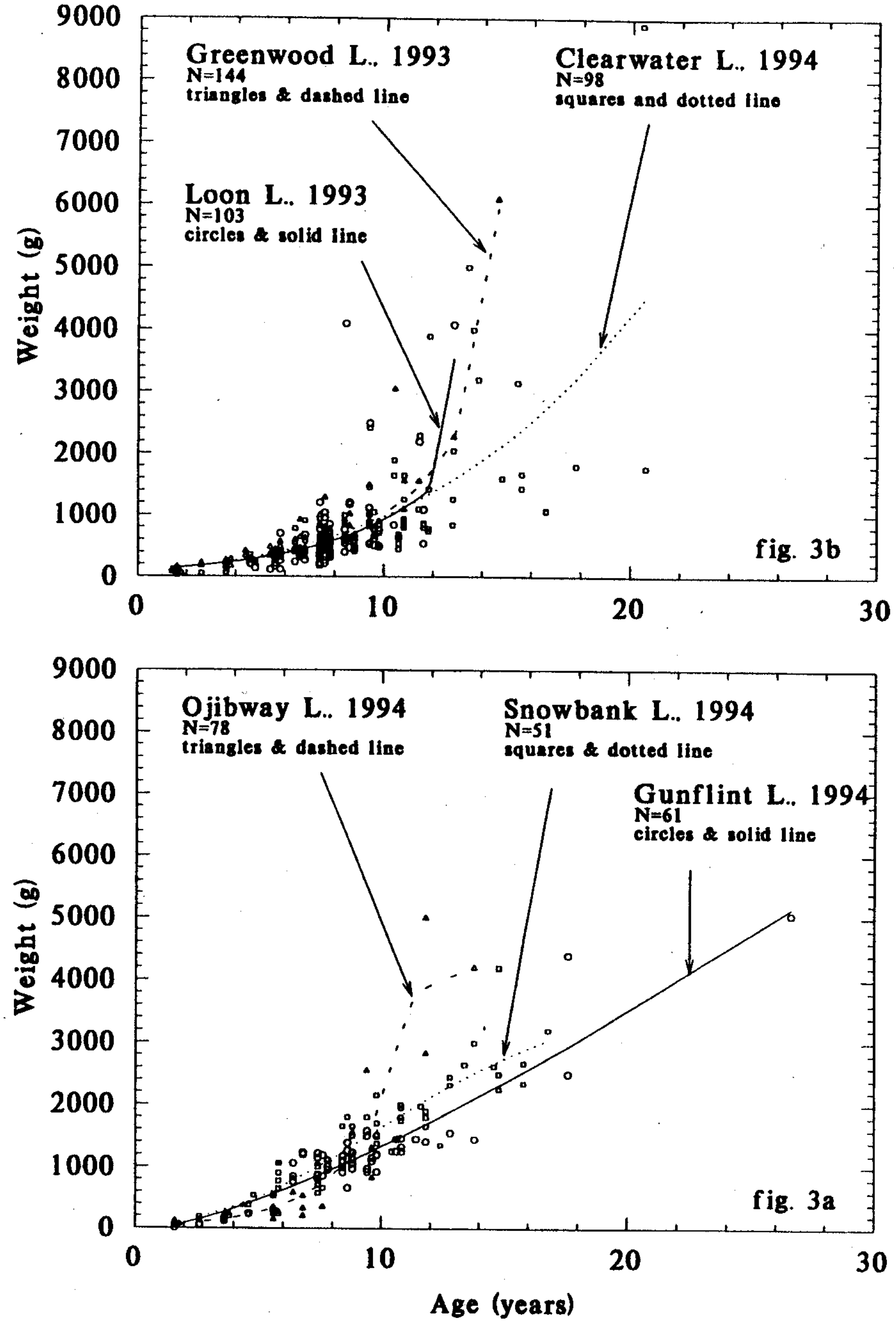

FIGURE 3. Lake trout growth (weight at estimated age) in 6 northeastern Minnesota lakes, as indicated by pooled data from various cohorts sampled in spring, summer, and fall, 1993 or 1994. Growth trajectories were estimated with Schnute's (1981) generalized growth model.

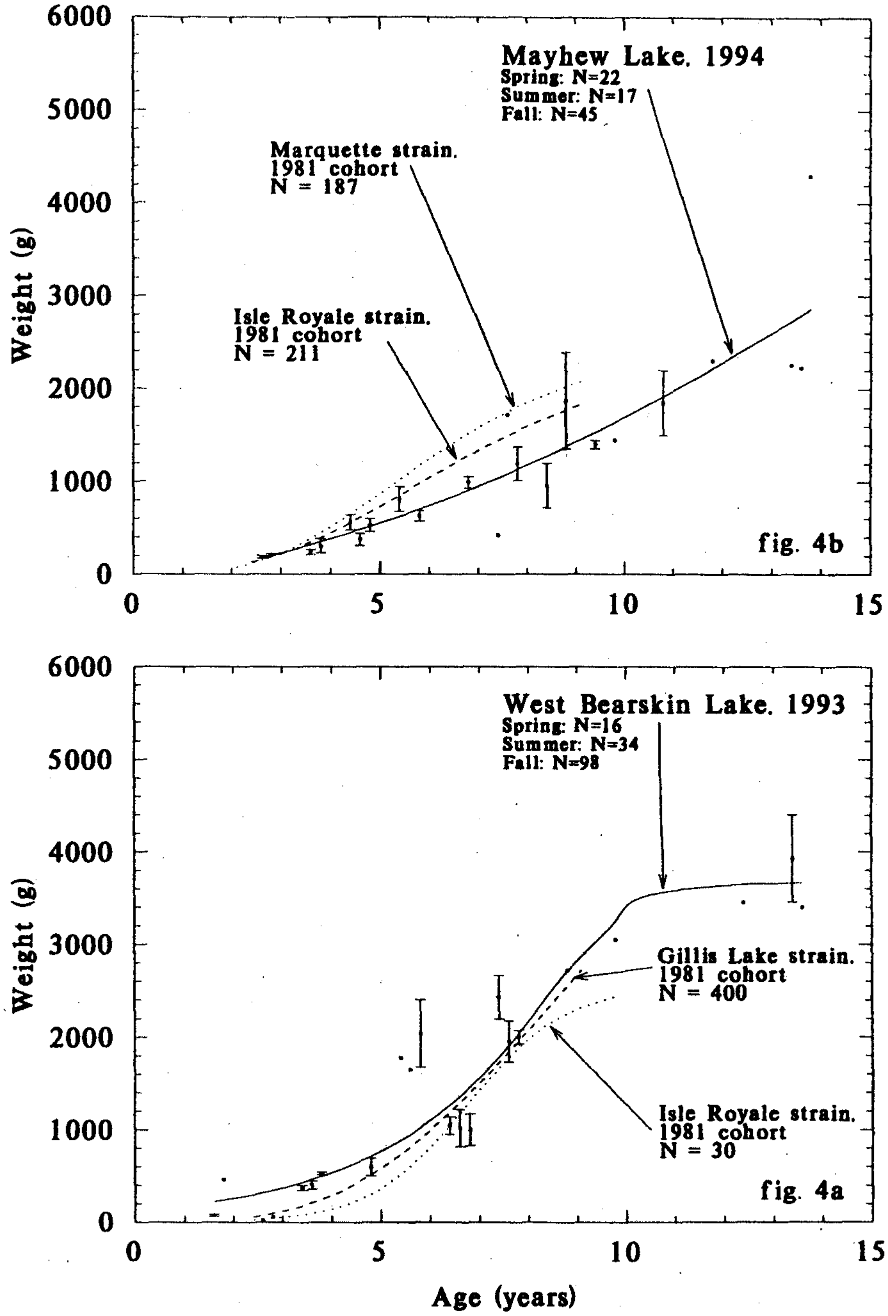

FIGURE 4. Lake trout growth (weight at estimated age) in 2 northeastern Minnesota lakes, as indicated by pooled data from various cohorts sampled in spring, summer, and fall, 1993 or 1994 (solid line), and compared with growth of 1981 cohorts (dashed or dotted lines) stocked as age 1+ yearlings in 1982 and recaptured from 1982 through 1990 (Siesennop 1992). Growth trajectories were estimated with Schnute's (1981) generalized growth model. Error bars (SE) pertain to the Mayhew L. 1994 and W. Bearskin 1993 data sets.

Table 6. Selected weight-at-age growth submodels and associated parameters for lake trout captured in gill nets fished in spring, summer, and fall in 10 Minnesota lakes in 1993 or 1994. Data from three seasons were pooled to increase sample size. Growth submodels: VB=generalized von Bertalanffy; GP=Gompertz; and RC=Richards are those plotted in Figures 2 and 3. Note: na = not applicable.

Variable[a]		Lake Name									
and units		Kemo	Trout	Bearskin	Loon	Greenwood	Mayhew	Clearwater	Gunflint	Ojibway	Snowbank
Sample year		1993	1993	1993	1993	1993	1994	1994	1994	1994	1994
Sample size		131	105	148	103	144	84	98	61	78	51
Growth model		GP	GP	VB	VB	VB	RC	RC	RC	GP	GP
τ_1	years	2.4	3.4	1.6	1.6	1.4	2.6	2.6	2.6	1.6	2.6
τ_2	years	14.8	13.8	13.6	12.8	12.8	15.4	20.6	26.6	13.8	16.8
y_1	grams	23.30	134.33	224.94	141.24	137.65	185.73	173.09	146.06	8.91	185.26
b	none	na	na	-3.60	-10.84	-2.08	0.62	0.30	0.77	na	na
y_2	grams	1762.63	3768.16	3662.98	4066.03	2273.98	3424.42	4537.87	5150.91	4698.75	3044.04
a	$year^{-1}$	0.54	0.22	1.30	2.44	0.48	na	na	na	0.17	0.16

[a] Parameters associated with the growth submodels: τ_1 = first age specified; τ_2 = second age specified; a = constant relative rate of relative growth rate; b = incremental relative rate of relative growth rate; y_1 = size at age τ_1; y_2 = size at age τ_2

Table 7. Selected weight-at-age growth submodels and associated parameters for three strains of the 1981 lake trout year-class captured in gill nets or trap nets fished in spring or and fall, or by winter angling in Mayhew and West Bearskin lakes, 1982-1990 (Siesennop, 1992). Data from three seasons was pooled to increase sample size and growth curves were plotted (see (Figure 4). Abbreviated names of growth submodels: VB = generalized von Bertalanffy, GP = Gompertz, and RC = Richards. Note: na = not applicable.

Variable[a] and units	Known age cohorts			
Lake	Mayhew		West Bearskin	
Year-class	1981	1981	1981	1981
Strain	Marquette	Isle Royale	Isle Royale	Gillis Lake
Sample size (*N*)	187	211	30	400
Growth model	GP	GP	VB	GP
τ_1 (year)	2.1	2.4	2.4	2.4
τ_2 (year)	9.1	9.1	9.8	9.1
y_1 (g)	76.894	125.022	28.246	62.883
b none	na	na	-0.920	na
y_2 (g)	2072.841	1827.987	2436.279	2718.496
a (year^{-1})	0.409	0.346	0.255	0.254

[a] Parameters associated with the growth submodels: τ_1 = first age specified; τ_2 = second age specified; a = constant relative rate of relative growth rate; b = incremental relative rate of relative growth rate; y_1 = size at age τ_1; y_2 = size at age τ_2.

Table 8. Lake trout weight-at-age, calculated from selected nonlinear growth models; vB = generalized von Bertalanffy, G = Gompertz, R = Richards (Schnute 1981). Pooled data fitted to growth models were measured weights and estimated ages of lake trout sampled in spring, summer, and fall 1993 or 1994 from 10 northeastern Minnesota lakes (See Figures 2 and 3). Numbers in **bold** type denote approximate age limits of growth modeling. Lake name abbreviations: KE = Kemo, TR = Trout, WB = West Bearskin, LN = Loon, GW = Greenwood, MH = Mayhew, CW = Clearwater, GF = Gunflint, OJ = Ojibway, SB = Snowbank.

	Selected growth model									
	G	G	vB	vB	vB	R	R	R	vB	G
	Calculated weight (g) by Lake									
AGE	KE	TR	WB	LN	GW	MH	CW	GF	OJ	SB
1.0	-	10	-	123	126	37	101	-	52	73
2.0	8	36	**260**	**155**	**158**	120	143	81	**78**	135
3.0	**77**	96	373	194	199	**235**	**195**	**194**	116	225
4.0	283	**212**	535	242	249	379	259	324	174	349
5.0	608	401	767	304	314	546	337	469	261	506
6.0	949	671	1098	380	396	737	429	624	390	695
7.0	1231	1015	1561	476	499	948	538	789	585	908
8.0	1432	1415	2169	596	632	1179	665	963	875	1141
9.0	1565	1849	2833	747	802	1428	812	1144	1311	1385
10.0	1648	2292	3329	935	1026	1696	980	1331	1962	1633
11.0	1699	2724	3559	1172	1329	1981	1171	1526	2923	1878
12.0	1729	3131	3636	**1487**	**1760**	2282	1387	1726	4012	2115
13.0	1747	**3501**	**3658**	-	2442	2600	1630	1931	**4206**	2339
14.0	**1757**	3831	3665	-	3827	2933	1901	2142	4206	2549
15.0	1764	4117	3666	-	18,219	**3281**	2203	2357	-	2742
16.0	1767	4364	3667	-	-	3644	2536	2577	-	**2917**
17.0	1769	4573	3667	-	-	4021	2904	2802	-	3074
18.0	1770	4748	-	-	-	4412	3307	3031	-	3215
19.0	1771	4893	-	-	-	4817	3748	3264	-	3339
20.0	1772	5014	-	-	-	5236	**4229**	3500	-	3448
21.0	1772	5113	-	-	-	5667	4752	3741	-	3544
22.0	-	5194	-	-	-	6112	5319	3984	-	-3628
23.0	-	5260	-	-	-	6569	5932	4232	-	3700
240	-	5313	-	-	-	7039	6592	4483	-	3763
25.0	-	5357	-	-	-	7521	7303	4738	-	3817
26.0	1772	5392	3667	-	-	8015	8066	**4995**	4206	3864

weight-at-age varied considerably among lakes, ranging from approximately 0.3 to 0.8 kg at age 5, from 0.9 to 3.3 kg at age 10, and from 1.4 to 4.0 kg at age 12. These growth models should not be used to predict size-at-age beyond age 12 because of sample sizes of older fish are small and size-at-age is increasingly variable.

Estimates of Lake Trout Maximum Size

For all lakes, except Mayhew, the heaviest fish captured in this study was less than the maximum lake trout weight reported for the same lakes (Table 9) by anglers, resorts, or captured in previous MN DNR fish sampling efforts. This indicates the latter sources may provide better estimates of theoretical maximum size for the study lakes. The heaviest lake trout captured during this study ranged from 2.4 kg for Kemo Lake to 9.6 kg for Gunflint Lake, while the largest reported by other sources ranged from approximately 3 to nearly 16 kg, showing that lake trout eventually may attain large sizes, if they are not harvested. The age of these large fish, however, generally are not estimated because large fish often are released alive by managers and biologist. Also, anglers typically have not donated otoliths or fin rays from harvested lake trout.

The 10 study lakes may be categorized as having one of several types of growth patterns for juvenile, sub-adult, and adult fish based on the shape and position of the growth curves relative to age (Table 10). Juvenile lake trout growth is slow in most lakes, sub-adult growth generally accelerates, and adult growth rates vary from slow to fast. Lake trout growth rates for specific lakes apparently depend on forage type, size, and abundance.

Species Lists and Lake Trout Forage

Lake trout feed on a variety of invertebrate and fish taxa. Lake trout food habits for the 10 study lakes are generally similar to those discussed in Scott and Crossman (1973). Known and potential forage varied among the 10 study lakes (Tables 1 and 2) changing with life history stage, season, and prey availability (MacLean et al. 1990). Coregonines occurred in 7 of 10 lakes, and lake trout are known to prey on them (MN DNR lake files; Micklus 1959; Eiler and Sak 1993). Rainbow smelt are present in 3 of the 10 lakes and lake trout are known to prey on them (Hassinger and Close 1984). Kemo and Mayhew lakes have neither rainbow smelt nor coregonines, but have several smaller forage species (Table 2). In Mayhew Lake, lake trout prey on young-of-year (yoy) green sunfish during winter (Siesennop, personal observation). In West Bearskin and Mayhew lakes, diets of yearling lake trout (age 1+ stocked in May) included *Daphnia* spp., Amphipoda, Diptera (larvae and pupae), and Ephemeroptera (Siesennop 1988). In West Bearskin Lake, lake trout ate many yoy smallmouth bass and yoy green sunfish during winter (Siesennop, personal observation). The presence of sculpin in 4 study lakes is known from qualitative reports of lake trout stomach contents and in 3 other lakes from incidental catches in gill nets or small-mesh trap nets (MN DNR lake files). Burbot, documented in lake trout stomachs in 3 study lakes, are present in 4 lakes. Lake trout in some situations may be cannibalistic, adults preying on juveniles (Martin 1970) or juveniles feeding on newly-spawned lake trout eggs (Siesennop, unpublished data).

Many of the smaller species present in the lakes (Table 2) have not been verified as lake trout forage because stomach contents of lake trout captured during fisheries assessments and lake surveys have not been routinely examined or summarized and few detailed lake trout food habits studies have been done for Minnesota lakes. Eight study lakes have a variety of small fish, including 4 to 11 cyprinids or other fish species, that are known or potential lake trout forage. Very few small forage species, however, have been reported for West Bearskin and Loon lakes. Only rainbow smelt and golden shiner are listed for West Bearskin Lake, and only *Cottus* spp. for Loon Lake.

Table 9. Size of the largest lake trout captured in 10 Minnesota lake trout lakes during this study (1993 or 1994) and large lake trout captured prior during MNDNR fisheries sampling or reported by anglers or resorts.

	This Study		Other Sources			
Lake Name	Length (mm)	Weight (kg)	Length (mm)	Weight (kg)	Year	Information Sources
Kemo	653	2.35	---	≈3	≈1990	Steinle, S. (1997, personal comm.)
			---	≈3.6	1995	Sopoci, R. (1997, personal comm.)
Mayhew	765	4.30	767	4.20	1985	Siesennop (1992)
Snowbank	735	4.45	≈770	-----	1986	MN DNR lake files (1986)
			---	5.4	var.	J. Geis (1997, personal comm.)
West Bearskin	819	4.40	844	6.05	1984	Siesennop (1992)
			---	7.26	≈1988	Schliep, D. (1997), personal comm.)
Ojibway	950	5.00	950	≈9.1	1994	MN DNR lake files
Trout	790	3.80	---	11.11	≈1993	Trout Lake Resort (1997)
			940	≈9.07	1996	MN DNR lake files
Loon	723	4.10	---	11.11	≈1985	Loon Lake Lodge (1997)
Gunflint	819	5.05	---	14.51	1936	Gunflint Lodge (1997)
			---	12.70	≈1982	Walsh, K.
Greenwood	900	9.60	---	14.97	≈1983	Brazell, R.D.
Clearwater	963	8.90	---	15.88	≈1990	unidentified angler
			---	16.33	≈1958	Schliep, D. (1997, personal comm.)
			---	12.25	1995	Johnson, T. (1995, personal comm.)

Table 10. Relative growth rate and estimated maximum size of juvenile, subadult, and adult lake trout, based on weight-at-age models estimated for 10 northeastern Minnesota lake trout lakes, and probable prey base of adult lake trout. Abbreviations for growth rate descriptors: S = slow; M = Moderate; F = Fast.

Lake name	Relative growth rate, by age group			Estimated maximum lake trout size (kg)	Prey base of adult lake trout in addition to invertebrates
	Juvenile	Subadult	Adult		
Kemo	S	M-F	S	small; 4.0	cyprinids, sculpins, darters, sticklebacks, other small fish
Mayhew	S	M-F	M-S	medium; 4.5	cyprinids, darters, yellow perch, yoy centrarchids, amphipods.
West Bearskin	M	M-F	M	mediium; 6.5	**rainbow smelt**, yoy centrarchids.
Snowbank	S	S	S-M	medium; 6.0	**coregonids**, trout-perch, other?
Ojibway	S	S	M-F	medium; 9.5	**coregonids**, sculpins, burbot, *Mysis relicta*, other?
Trout	S	M	M	medium-large; 11.5	cyprinids, sculpins, **rainbow smelt, coregonids**, Mysis relicta
Loon	S	S	M-F	medium-large; 16.0	**coregonids**, sculpins, centrarchids, amphipods, other?
Greenwood	S	S	M-F	medium-large; 16.0	**coregonids**, yellow perch, amphipods, other?
Clearwater	S	S	S-M-F	large; 16.0	**coregonids**, yellow perch, burbot, *Mysis relicta*, other?
Gunflint	S	S	S-M	large; 14.5	**coregonids, rainbow smelt**, burbot, yellow perch, ***Mysis relicta***, other?

Discussion

Ages assigned to unknown age lake trout are biased because interpretation of the growth records of fin rays, scales, and otoliths may be positively or negatively biased. Ages assigned to older lake trout from scales, however, are more likely to be negatively biased because scale age tends to underestimate age of older lake trout. Various investigators cited by Lester et al. (1991) showed that ages estimated from scales differ from those assigned from aging other structures, including otoliths, branchiostegal rays, fin rays, cleithra, vertebrae, and opercular bones. Lester et al. (1991) recommended that seven years be regarded as the oldest age reliably determined from scales and indicated otoliths are the most reliable structure for aging lake trout.

Growth curves fitted to the lake trout weight-at-age data in this study are imprecise due to aging bias and because sample size for each age-class usually was small. Precision of the growth curves is less for lake trout collections having smaller proportions of known-age or partially known-age fish. For most data sets, catches of large, old lake trout were rare and are difficult to age reliably from scales and fin rays. Therefore, bias is greater for older lake trout and upper portions of the growth curves are less reliable than the lower and middle portions that describe growth of younger fish. The middle portions of some curves may be more reliable than the lower portions because young fish, not fully vulnerable to the gill nets, were uncommon or under-represented in Trout, Clearwater, and Snowbank lake collections. The lake trout growth model for West Bearskin Lake probably is the most precise among the 10 lakes because a high proportion of the catch was known-age fish and they were represented several age-classes from age 1 to 13. Growth models for Clearwater, Gunflint, and Snowbank lakes may be less precise than those for the remaining lakes because few known-age fish were sampled and a high proportion of the unknown age fish were assigned ages greater than seven years.

Growth trajectories were generally similar among the three collections for a given lake. Among season differences in growth trajectories for some lakes may have resulted from small sample sizes for some collections, may indicate incorrect age assignments, or may reflect large variation in lake trout size-at-age. Therefore, growth comparisons among lakes are tentative because of the uncertainties.

Despite data limitations, several types of lake trout feeding and growth scenarios may explain the observed growth curves. Lake trout in Kemo and Trout lakes showed relatively fast juvenile growth, perhaps because their food, presumably zooplankton, insects, and various small forage fish, may be more abundant in the absence of centrarchids and walleye. There are, however, no cisco or other larger prey species in Kemo Lake, so lake trout feeding efficiency may decline at approximately 1.5 - 2 kg and few fish exceed 3 kg. This situation may be an example of rapidly declining growth efficiency and small maximum size for lake trout in lakes without a coregonine prey base (Carl et al. 1990). In contrast, Trout Lake has larger prey items, rainbow smelt and larger cisco. In this lake, feeding efficiency may remain relatively high for a longer time and lake trout have greater potential for more rapid and prolonged growth. Fish exceeding 4 kg were collected.

In Mayhew Lake, where few adult lake trout exceed 4 kg, their growth pattern was similar to that in Kemo Lake. Because larger forage species, such as rainbow smelt and cisco are not present in Mayhew Lake, a greater proportion of the invertebrate and small fish forage may be available to juvenile lake trout and their growth may be faster than in lakes having competitors for zooplankton. Some lake trout in Mayhew Lake, however, attain a larger size than in Kemo Lake because they can prey on y-o-y green sunfish, other small forage fish, and perhaps white sucker. Slower growth of the juvenile lake trout sampled in 1994 in Mayhew Lake relative to that of 1981 cohorts, however, may indicate changing community trophic relationships, results of the introduction or immigration of yellow perch (*circa* 1988) and their increasing abundance in the 1990s. Lake trout growth rates in Mayhew Lake may stabilize, increase, or decrease, depending on life history stage, and how yellow perch interact with green sunfish and other elements of the forage community.

In West Bearskin Lake, juvenile lake trout growth began slowly, but it accelerated at ages 3 to 5 (Siesennop 1992), as lake trout begin to prey on rainbow smelt (Hassinger and Close 1984). Juveniles, and also adults, at times feed heavily on y-o-y smallmouth bass and green sunfish, as well as, rainbow smelt in West Bearskin Lake (Siesennop, personal observation), although Scott and Crossman (1973) and MacLean et al. (1990) made no mention of centrarchids as lake trout forage. Adult growth may slow, perhaps because prey larger than smelt are not abundant and attaining weights larger than 5 kg may require 15 or more years in West Bearskin Lake. In lakes with few large predator species, lake trout foraging efficiency probably is greater and may be influenced more by intraspecific competition, including cannibalism and other lake specific factors, than in lakes with several potential competitors. Cannibalism may be most common in winter (Martin 1970; Ball 1988), may be a major cause of juvenile mortality in some lakes (Evans et al. 1990), and may be important energy source for adult lake trout.

When food (energy) is shared among more species, a smaller proportion of total energy in a lake is available for lake trout. In Loon, Clearwater, Greenwood, Gunflint, Ojibway, and Snowbank lakes, relatively slow growth of juvenile lake trout may be a result of competition with introduced coregonids, centrarchids, and percids for zooplankton, other invertebrates, or small forage fish. Each of these six lakes also have one or more additional large predator species (northern pike, burbot, walleye, or smallmouth bass) that may eat species that are potential lake trout prey at some life stage. These predators may contribute to reduced lake trout feeding efficiency, prolonging the period of slow lake trout growth in some of these lakes. Eventually some lake trout attain greater size when they become more piscivorous, feeding efficiency improves and growth rates accelerate by feeding on coregonines. Lake trout exceeding 5 kg, probably more than 10 years old and perhaps more than 15 years old, occasionally are captured in these lakes by anglers or in gill nets. Some of the large variation in size-at-age in lakes such as Clearwater, may be explained by some lake trout becoming more piscivorous with increasing size and age. Other lake trout in the same lake, however, may continue to grow slowly if they do not switch from a predominantly plankton, insect, or small fish diet to largely piscivorous food habits.

Trophic relationships in the seven study lakes with coregonines may parallel that of Lake Opeongo, Ontario where juvenile lake trout growth was slowed by cisco feeding more efficiently on plankton, but growth rate and fecundity of subadult and adult lake trout increased because they could prey on cisco (Colby et al. 1987). Matuszek et al. (1990) described changes in growth and mortality rates of non-piscivorous 1 and 2 year old lake trout and piscivorous sub-adult and adults over time and related them to the introduction of cisco into Lake Opeongo and the accompanying changes in feeding relationships.

Competition between lake trout and another species, such as smallmouth bass or walleye, is difficult to demonstrate because among lakes differences preclude controls or replicated experimental designs. Shuter et al. (1987) indicated that direct competition between lake trout and smallmouth bass would not occur during summer in Lake Opeongo if lake trout remained in the hypolimnion and smallmouth the epilimnion. Some evidence indicates interaction, if not competition, exists. Juvenile lake trout growth was greater in Birch and Mayhew, on lakes without smallmouth bass, than in West Bearskin and Duncan, lakes with smallmouth bass (Siesennop 1992). Although these observations may suggest competition, differences in forage fish may also explain the differences in juvenile growth rates (Eiler and Sak 1993). They also noted that smallmouth bass may have faster growth rates in lakes without lake trout. In northeastern Minnesota, however, lakes managed for lake trout, especially those where lake trout are indigenous, the introduction or spread of non-native smallmouth bass, or another species, may reduce lake trout growth or survival and be undesirable.

In summary, the lake trout growth curves for the study lakes provide more evidence indicating size dependent growth in northeastern Minnesota lakes and that predator-prey relationships are complex. The limited forage data available from this study and more detailed information from other investigators show that lake trout feed on a variety of prey items. Juvenile, subadult, and adult lake trout prey on cisco, rainbow smelt, sculpin, juvenile centrarchids, other minnows or small fish, various invertebrates (insects, crustaceans, and zooplankton). Lake trout growth rates vary with life stage and depend on prey size, abundance, and availability.

Management Implications

Examining lake trout growth patterns and making comparisons among lakes can give clues to understanding lake trout feeding relationships. Monitoring growth and food habits can help managers and biologists understand how changes in community structure affect lake trout populations. This knowledge can help managers and biologists make better fisheries management decisions. Growth models must be used with caution, however, recognizing limitations of aging lake trout from bony structures, particularly scales. Lake trout otoliths should be obtained from dead trout and should be used to more precisely estimate lake trout age and describe growth.

When sample sizes are small it is acceptable to pool data from different seasons and sampling methods to estimate indices of lake trout growth, mortality, and condition according to Lester et al. (1991). It is also useful to pool data from various seasons to improve growth modeling, although variation in weight of mature fish may increase due to seasonal differences in gonadal development and spawning condition. Lake trout weights measured in spring probably being the least variable at a given age for mature fish. Growth curves from lake trout collected only in fall, with differing states of gonadal development and spawning condition, would be more biased than models derived from fish collected in spring or summer. It may also be acceptable to pool data sets from different years to model and characterize lake trout growth, provided fish community structure has been relatively stable in a given lake. Extrapolation of growth to ages beyond those modeled is not appropriate.

Fisheries managers should not introduce new species to natural lake trout lakes or other lakes now managed for lake trout. It will be a challenge to prevent the almost inevitable expansion of smallmouth bass, walleye, and other species into watersheds and specific lakes where lake trout are native. Changes in lake trout growth, survival, abundance, and the sport fishery that may result from these species range expansion will be difficult to monitor. Potential adverse effects of introductions may be more drastic in small lakes that have less varied habitats and fewer feeding alternatives for lake trout.

Failure to sample large lake trout in some lakes may indicate insufficient sampling effort, that forage constraints may prevent lake trout from attaining large size, or it may be a symptom of over-exploitation in lakes where most lake trout are caught before they can grow to large size.

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Table A1. Number of lake trout sampled by age class during spring, summer, and fall gill netting in 10 Minnesota lake trout lakes in 1993 and subsequently used in growth modeling. Total catch for spring, summer, and fall is shown in **bold** type. Asterisks (*) denote stocked lake trout year-classes (cohorts). Numbers of known-age fish (fin-clipped) are underlined.

Year-class	92	91	90	89	88	87	86	85	84	83	82	81	80	79	78	77	76	75	74	73	72	71	70	69	68	67
Season / Age-class (years)	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
Kemo Lake																										
Spring	.	3	1	3	5	4	4	4	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Summer	.	4	3	3	3	2	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Fall	.	.	5	18	5	3	7	10	11	12	4	10	.	3	.	.	.	.	.	.	.	.	.	.	.	.
Total	.	**7**	**9**	**24**	**13**	**9**	**12**	**15**	**12**	**12**	**4**	**10**	.	**3**	.	.	.	.	.	.	.	.	.	.	.	.
		*		*				*	*	*		*		*	*	*	*	*	*	*	*	*		*		
Trout Lake																										
Spring	.	.	2	5	7	6	2	2	3	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Summer	.	.	4	5	6	1	1	1	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Fall	.	.	7	3	17	10	7	6	4	.	2	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.
Total	.	.	**13**	**13**	**30**	**17**	**10**	**9**	**9**	.	**3**	.	**1**	.	.	.	.	.	.	.	.	.	.	.	.	.
									*																	
West Bearskin Lake																										
Spring	.	.	4	.	1	2	6	.	.	.	.	1	3	.	.	.	.	.	.	.	.	.	.	.	.	.
Summer	7	1	16	.	1	5	3	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.
Fall	1	1	70	2	2	10	10	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Total	**8**	**2**	**90**	**2**	**4**	**17**	**19**	**1**	**1**	.	.	**1**	**4**	.	.	.	.	.	.	.	.	.	.	.	.	.
	*		*			*	*				*	*	*											*		
Known	7	.	79	.	.	15	9	.	.	.	.	1	3	.	.	.	.	.	.	.	.	.	.	.	.	.
Loon Lake																										
Spring	.	.	.	.	1	4	15	8	3	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Summer	11	.	.	2	7	4	12	3	3	1	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Fall	.	.	.	1	7	2	12	2	2	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Total	**11**	.	.	**3**	**15**	**10**	**39**	**13**	**8**	**2**	**3**	**1**	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	*		*		*		*				*		*			*	*	*	*		*	*	*			
*Known	11	.	.	.	8	.	24	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

Table A1. Continued.

	Year-class																									
	92	91	90	89	88	87	86	85	84	83	82	81	80	79	78	77	76	75	74	73	72	71	70	69	68	67
	Age-class (years)																									
Season	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
													Greenwood Lake													
Spring	2	.	.	2	3	8	15	1	4	1	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Summer	24	2	8	1	6	6	12	6	2	1	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.
Fall	1	.	3	1	5	11	10	6	3	3	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Total	**27**	**2**	**11**	**4**	**14**	**25**	**37**	**13**	**9**	**5**	**1**	**2**	.	**1**	.	.	.	.	.	.	.	.	.	.	.	.
	*		*				*		*		*		*			*	*	*	*							
Known	<u>22</u>	.	0	.	.	0	<u>11</u>	.	<u>2</u>	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	

Table A2. Number of lake trout sampled by age-class during spring, summer, and fall gill netting in 10 Minnesota lake trout lakes in 1994 and subsequently used in growth modeling. Total catch for spring, summer, and fall is shown in **bold** type. Asterisks (*) denote stocked lake trout year-classes (cohorts). Numbers of known-age fish (fin-clipped are underlined.

	Year-class																									
	93	92	91	90	89	88	87	86	85	84	83	82	81	80	79	78	77	76	75	74	73	72	71	70	69	68
	Age-class (years)																									
Season	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
													Mayhew Lake													
Spring	.	.	.	4	5	.	1	3	6	.	.	.	1	.	2	.	.	.	.	.	.	.	.	.	.	
Summer	.	8	3	4	.	.	1	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.
Fall	.	2	2	8	16	6	3	3	1	2	1	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.
Total	.	**10**	**5**	**14**	**21**	**6**	**5**	**6**	**7**	**2**	**1**	.	**3**	.	**2**	.	.	.	.	.	.	.	.	.	.	.
		*		*			*	*				*	*				*	*	*		*			*		
Known	.	<u>10</u>	.	<u>2</u>	.	.	<u>3</u>	<u>2</u>	.	.	.	.	<u>2</u>	.		.	.	.	.							
													Clearwater Lake													
Spring	.	.	.	.	.	1	3	10	5	2	2	.	1	.	1	.	.	.	.	1	.	.	.	.	.	.
Summer	.	1	6	3	2	2	5	1	2	5	3	.	1	.	2	2	.	.	.	1	.	.	.	.	.	.
Fall	.	.	.	1	4	4	.	6	4	8	4	3	1	1	.	.	1	.	.	-	.	.	.	.	.	.
Total	.	**1**	**6**	**4**	**6**	**7**	**8**	**17**	**11**	**15**	**9**	**3**	**3**	**1**	**3**	**2**	**1**	.	.	**2**	.	.	.	.	.	
		*	*			*				*			*	*			*	*	*	*	*			*		*
Known	.	.	.	.	.	<u>1</u>	.	.	.	<u>2</u>	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
													Gunflint Lake													
Spring	.	.	.	.	.	3	5	5	4	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Summer	4	2	2	1	2	.	2	4	2	2	.	.	.	.	1	1	2	.	.	.	.	.	.	.	.	1
Fall	.	.	.	.	.	2	3	4	4	3	1	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.
Total	**4**	**2**	**2**	**1**	**2**	**5**	**10**	**13**	**10**	**5**	**2**	**1**	**1**	.	**1**	**1**	**2**	.	.	.	.	.	.	.	.	**1**
			*		*		*		*		*		*		*		*	*	*		*	*	*	*		*
Known	.	.	.	.	<u>1</u>	.	.	.	<u>1</u>	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
													Ojibway Lake													
Spring	.	.	.	1	.	2	1	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Summer	33	.	15	.	5	.	1	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Fall	2	.	3	.	4	3	.	1	.	2	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Total	**35**	.	**18**	**1**	**9**	**5**	**2**	**2**	**3**	**2**	.	**1**	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	*		*		*					*					*											
Known	<u>35</u>	.	<u>18</u>	.	<u>4</u>	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

Table A2. Continued

	Year-class																									
	93	92	91	90	89	88	87	86	85	84	83	82	81	80	79	78	77	76	75	74	73	72	71	70	69	68
	Age-class (years)																									
Season	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
												Snowbank Lake														
Spring	.	.	.	.	.	.	4	1	1	1	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.
Summer	.	2	.	3	2	.	1	1	.	1	1	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.
Fall	.	.	.	1	4	.	1	2	5	5	3	2	1	3	2	1	.	.	.	.	.	.	.	.	.	.
Total	.	**2**	.	**4**	**6**	.	**6**	**4**	**6**	**7**	**4**	**3**	**2**	**4**	**2**	**1**	.	.	.	.	.	.	.	.	.	.
		*		*		*		*		*		*	*	*	*		.	.	.	.	.	.	.	.	.	.
Known	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.		.	.	.	.

Table A3. Selected weight-at-age grown submodels and associated parameters for lake trout in 10 Minnesota lakes sampled in spring, summer, and fall. Growth submodel titles: VB=generalized von Bertalanffy; GP=Gompertz; RC=Richards; and tP=*t*th power.

Variable[a] and units		Sampling Season, lake, and year					
		Spring	Fall	Summer	Spring	Fall	Summer
		Kemo Lake: 1993			**Trout Lake: 1993**		
Growth	model	GP	GP	GP	GP	GP	GP
(N)	number	29	96	18	28	57	26
τ_1	years	2.4	3.8	2.6	3.4	3.8	3.6
τ_2	years	10.4	14.8	8.6	11.4	13.8	9.6
y_1	grams	102.1	104.3	121.0	142.4	59.3	273.7
b	none	0	0	0	0	0	-0.001
y_2	grams	1888.4	1851.1	1831.1	2835.7	3786.0	2122.8
a	$year^{-1}$	0.587	0.443	0.474	0.410	0.277	0.0
		West Bearskin: 1993			**Loon Lake: 1993**		
Growth	model	GP	GP	GP	GP	RC	GP
(N)	number	17	90	96	28	26	57
τ_1	years	3.4	2.8	1.6	5.4	4.8	1.6
τ_2	years	13.4	9.8	13.6	11.4	12.8	11.6
y_1	grams	357.0	387.0	86.4	86.0	328.0	31.7
b	none	0	0	0	0	-1.438	0
y_2	grams	3842.0	3300.6	3430.0	1889.4	4079.9	843.8
a	$year^{-1}$	0.351	0.015	0.239	0.385	0	0.295
		Greenwood Lake: 1993			**Mayhew Lake: 1994**		
Growth	model	GP	RC	VB	RC	VB	GP
(N)	number	39	42	72	24	47	17
τ_1	years	1.4	1.8	1.6	4.4	2.8	2.6
τ_2	years	12.4	12.8	10.6	15.4	13.8	13.6
y_1	grams	82.3	197.5	142.5	609.1	170.7	78.5
b	none	0	-0.579	-3.308	-0.059	1.938	0
y_2	grams	2745.9	2289.6	1088.9	3281.1	4030.7	2301.1
a	$year^{-1}$	0.032	0	0.742	0	-0.390	0.388

Table A3. Continued.

Variable[a] and units		Spring	Fall	Summer	Spring	Fall	Summer
		Sampling Season, lake, and year					
		Clearwater Lake: 1994			**Gunflint Lake: 1994**		
Growth	model	GP	GP	GP	GP	GP	RC
(N)	number	26	39	37	18	19	21
τ_1	years	6.4	4.8	2.6	6.4	6.8	2.6
τ_2	years	20.4	17.8	20.6	11.4	13.8	17.6
y_1	grams	493.7	63.3	57.8	879.4	1056.6	34.7
b	none	0	0	0	0	0	0.711
y_2	grams	8769.2	2254.3	1830.6	1474.0	1557.0	3428.9
a	year-1	0.081	0.250	0.185	0.018	-0.086	0
		Ojibway Lake: 1994			**Snowbank Lake: 1994**		
Growth	model	RC	VB	VB	*t*P	GP	GP
(N)	number	6	17	58	9	32	13
τ_1	years	4.4	1.8	1.6	7.4	4.8	2.6
τ_2	years	9.4	13.8	9.6	13.4	16.8	14.6
y_1	grams	524.8	49.0	75.0	936.7	641.8	104.7
b	none	-1.864	-3.351	-12.389	0	0	0
y_2	grams	2546.2	4194.1	1060.1	2282.4	3089.6	2577.8
a	year-1	0	1.623	3.463	0	0.131	0.200

[a] Parameters associated with the growth submodels: τ_1 = the first age specified; τ_2 = the second age specified; *a* = constant relative rate of relative growth rate; *b* = incremental relative rate of relative growth rate; y_1 = size at age τ_1; y_2 = size at age τ_2.

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