Age Determination and Growth of Lacustrine Sockeye Salmon, *Oncorhynchus nerka*, in Lake Toya

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Sockeye salmon (*Oncorhynchus nerka*) inhabiting Lake Toya are considered to have a lacustrine (lake resident) type of life history. Although life history studies of anadromous sockeye salmon are numerous, there are few studies of lacustrine sockeye salmon. The present study was conducted to develop an age-determination method using scales and to determine factors responsible for growth variation of different year classes of lacustrine sockeye salmon in Lake Toya. In Lake Toya, annuli formation of scales of lacustrine sockeye salmon did not occur regularly. Age determination was conducted as follows; when the number of circuli between two checks was high, an annulus wasn't formed. When the number of circuli between two checks was low, a false annulus was formed. So age determination was done after discriminating false annuli and missing annuli from true annuli by the number of circuli between checks. Seasonal changes in growth rate calculated from growth curves showed that the growth difference from age 0^+ to 1^+ caused much of the growth variation between year classes. Makino and Ban (personal communication) observed annual changes of zooplankton biomass which corresponded to the growth rate of lacustrine sockeye salmon. In Lake Toya, the growth variation between year classes may be caused by zooplankton biomass fluctuations.

INTRODUCTION

Sockeye salmon (*Oncorhynchus nerka*) are classified into three types by the life history of this species; anadromous, lake resident, and kokanee (Ricker 1940). Anadromous sockeye migrate to sea after living in fresh water from 1 to 3 years. Kokanee live in fresh water habitat all of their life. The lake resident sockeye are a form that originates from the anadromous type and most of their individuals stay in lakes with migration of relatively few individuals. The hime masu of Japan was thought to be lacustrine sockeye salmon (Kaeriyama 1991).

Most studies of salmonids, including sockeye salmon, focused on population dynamics in the marine life stage and life history characters like return size and age. The growth of sockeye salmon in the marine life stage was thought to be affected by density-dependent factors (Rogers 1980; Peterman 1982), and the growth difference of sockeye salmon was thought to be because competition for prey was the result of not only intra-population but also inter-population competition between fish that originated from different rivers (Peterman 1984). In coho salmon (*O. kisutch*), the growth in early marine life stage was correlated with number of coho salmon (Mathews 1980), and the number of maturing fish was negatively correlated with weight (McGie 1984). Ricker (1981) suggested that increment of growth rate in sockeye salmon in British Columbia was affected by gradual cooling of the ocean.

A relationship between annulus formation and growth was observed for lacustrine sockeye salmon by analyzing growth patterns resulting from age determination using scales (Kurohagi and Sasaki 1964; Kurohagi 1965; Tokui 1988). A relationship between growth, age of maturity, and egg size was also reported (Kato 1978, 1980). In Lake Shikotsu, the number of returns of lacustrine sockeye salmon was negatively correlated with size, and a density-dependent mechanism was observed in Lake Shikotsu (Kaeriyama 1991). Rieman and Myers (1992) suggested that there was a negative correlation between age specific size and lake productivity, and also that density-dependent mechanism was higher in low-productivity lakes than in high-productivity lakes, for oligotrophic lakes where kokanee were found. Compared with anadromous sockeye salmon, few attempts have been made to study the basic and ecology of lacustrine sockeye salmon, and in particular to test the use of scales for age determination and growth variation. Furthermore, only fragmentary research was conducted on lacustrine sockeye salmon since they were stocked in Lake Toya in 1893. Over the past few decades no studies have been made on lacustrine sockeye salmon in Lake Toya since those of Oono and Ando (1932), Takayasu and Kondo (1934), Tanakadate (1940) and Watanabe (1960). Most lacustrine sockeye salmon die after spawning, however, individuals of each life history stage can be sampled throughout the year in Lake Toya. Therefore, we were able to investigate the effects of the limnological environment and prey abundance in the lake on stock abundance of lacustrine sockeye salmon, along with growth variations in each life history stage and age determination in different cohorts.

The purpose of this paper is to test the accuracy of scale characteristics for age determination by comparing scales of marked fish and to understand differences in growth patterns in different cohorts of lacustrine sockeye salmon in Lake Toya. From these data we establish an age determination method and discuss various mechanisms of growth for these fish in the lake.

MATERIALS AND METHODS

Study site

This study was carried out in Lake Toya, which is a large oligotrophic lake located in a caldera in the central area of Hokkaido, Northern Japan, at an elevation of 84 m. The lake has a surface area of 70.44 km^2, a maximum depth of 179 m, and an average depth of 116.3 m (Fig.1). Starting from 1939, the pH has gradually decreased due to the inflow of Osaru River which contains acid mine waste. The lowest level (pH 5.0) occurred in 1970. In 1972, neutralization was started and the pH rapidly increased. The pH is now about 7.0 (Imada et al., 1988). Mt. Usu, located near the lakeside, erupted in August 7, 1977. So much volcanic ash fell into the lake that the transparency decreased to about 1 m temporarily, but recovery began after October, 1977.

The most common commercial fish species in the lake were lacustrine sockeye salmon, Japanese pond smelt (*Hypomesus transpacificus nipponensis*), and masu salmon (*O. masou*). These species were introduced by fisherman. Lacustrine sockeye salmon were introduced from Lake Akan in 1893, and the catch (tonne) has been totaled from 1930 by the Toya Lake Fisherman's Association (Fig.2a). The catch of lacustrine sockeye salmon has fluctuated; it was about 25 tonnes in the 1930's, increased to about 100 tonnes in the 1950's, rapidly decreased following lake acidification, and showed no increase since the 1960's. Japanese pond smelt catches varied between 10 and 20 tonnes till 1966, when the catch increased to about 50 tonnes in 1986 (Fig. 2b). Masu salmon catch was low, although the Toya Lake Fisherman's Association did not record catch. However, in recent years, the number of returns of masu salmon has increased (Fig. 2c).

Surface water temperatures were as low as -0.3 ~ -0.9 °C during winter and as high as 20.0 ~ 23.3 °C during summer (Fig. 3). Average water temperature was high in 1990 and 1991, and was low in 1993.

Fish Sampling

Lacustrine sockeye salmon were sampled from May 1991 to October 1995. Sampling was conducted with gillnets and a beach seine in front of the Toya Lake Station for Environmental Biology. Additional samples were collected from June 1995 to August 1995 by the Toya Lake Fisherman's Association.

We used commercial gillnets with stretched mesh of 15, 24, 57, and 63 mm from May 1991 to September 1994, and two sets of research gillnets that have a stretched mesh of 19, 21, 24, 27, 33, 37, 42, 48, 54, 63, 72, and 82 mm from October 1994 to October 1995. It was thought that the research gillnets were non-selective (Takagi 1993). Gillnet sampling was conducted weekly each month, with nets set overnight and retrieved the next day. Spawners were collected by beach seine near the station. The number of lacustrine sockeye salmon caught by Toya Lake Station was around 3,059 and by Toya Lake Fisherman's Association was 196.

50,000 individuals of the 1991 brood were marked by cutting adipose fin and were released at about 1 g in Lake Toya.

Measurement of Fish

The samples from the station were measured to the nearest 1 mm for length and weight to the nearest 0.01 g fresh weight. Standard length was transformed to fork length by following formula,

Fig. 1 Map of sampling sites in Lake Toya.

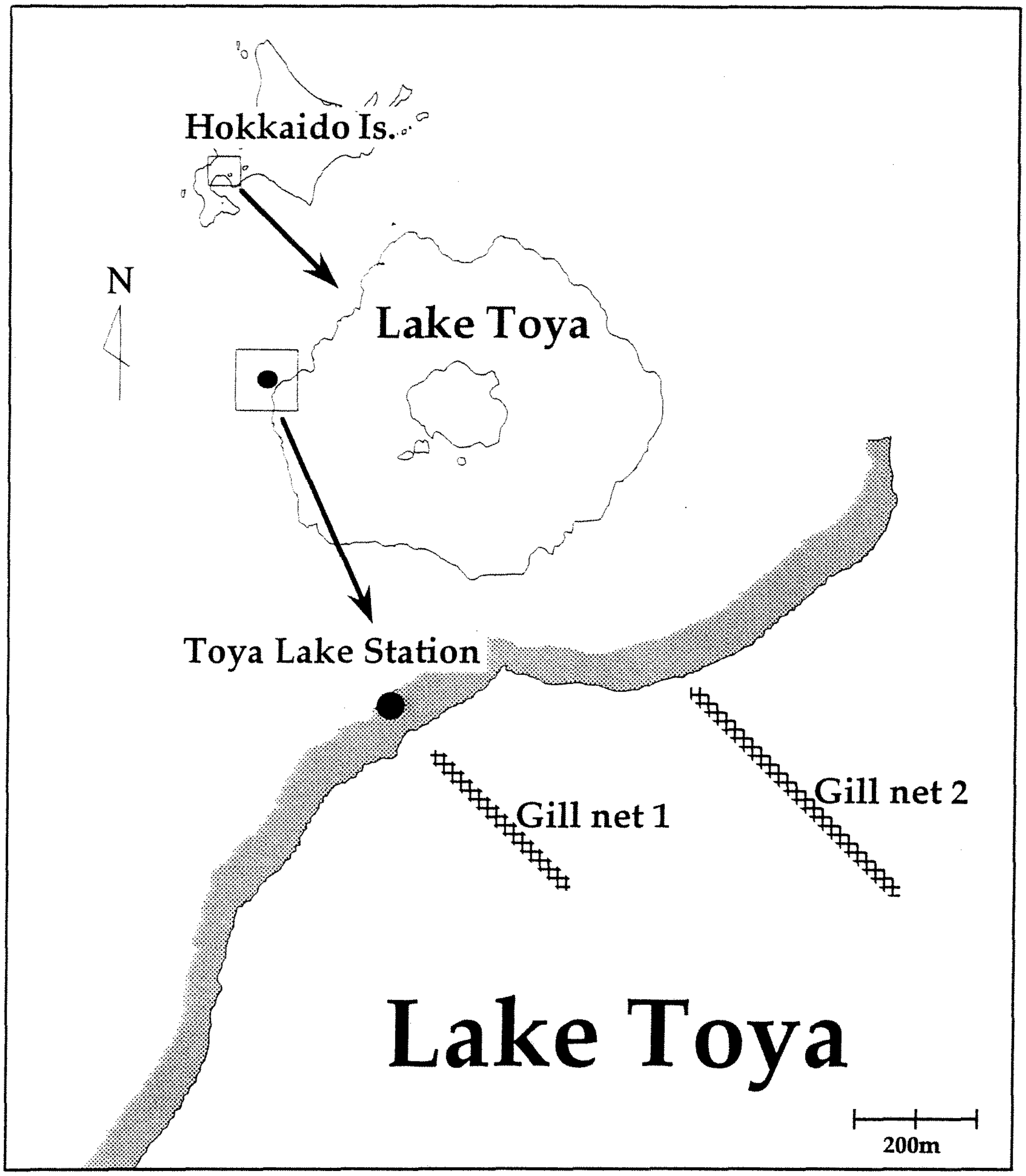


Fig. 2 **Annual changes in catch weight (tonnes) and number released (thousands) from 1930 to 1994. Solid bar and line indicate catch weight and number released for (Top) lacustrine sockeye salmon (thousands) and (Middle) pond smelt (millions), respectively. The sockeye salmon population collapsed in 1966. (Bottom) Annual changes in number of masu salmon returns from 1992 to 1995.**

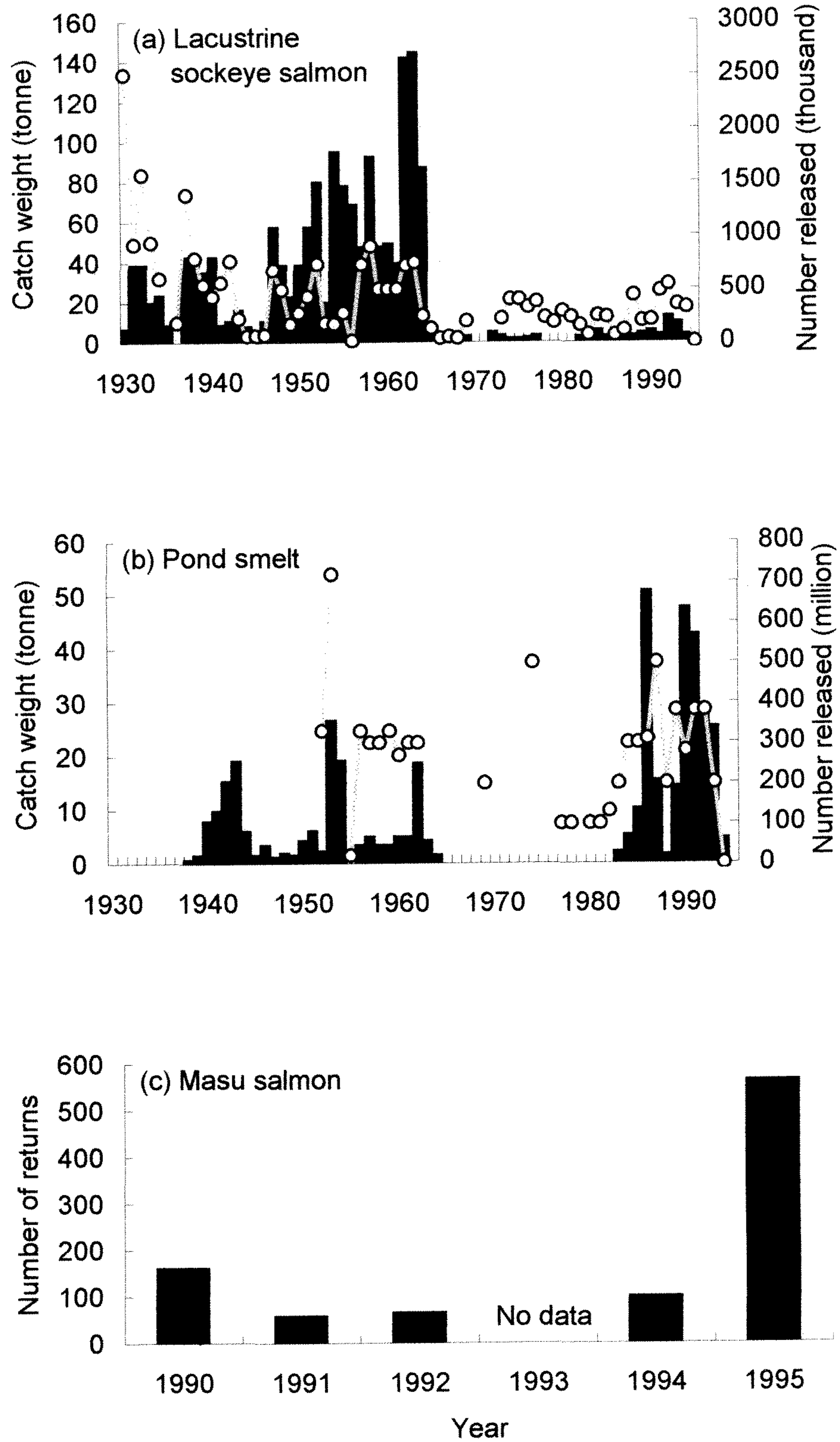
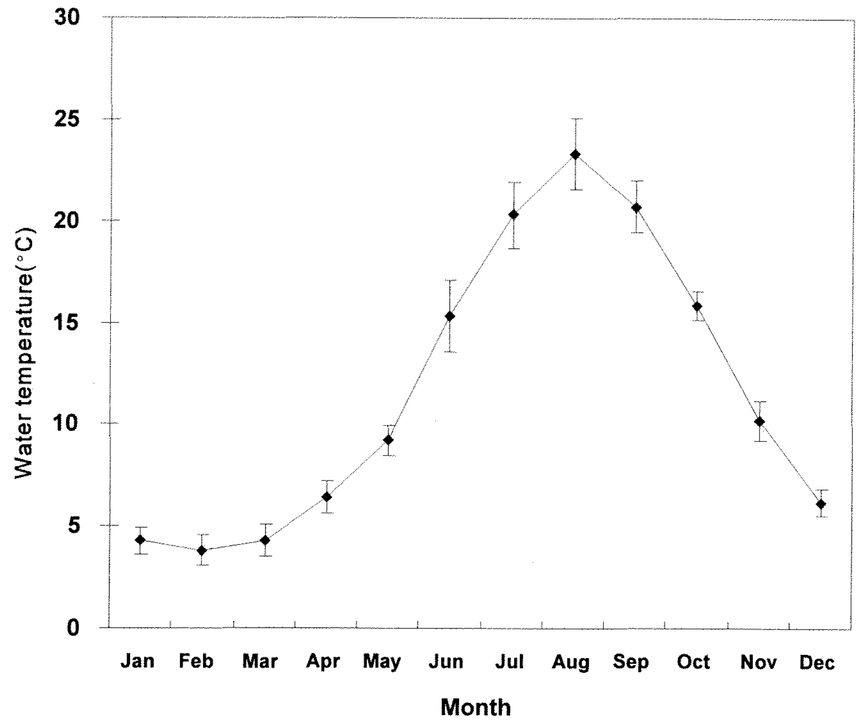


Fig. 3 Seasonal changes in average and standard deviation of surface water temperature in Lake Toya from 1988 to 1994.



Fork length = 1.081 × Standard length + 1.079 ($r = 0.97$, $p < 0.01$, $n = 71$).

Additional samples from the Toya Lake Fisherman's Association were measured to the nearest 1 mm and weight to the nearest 5g fresh weight.

Scales were taken for age determination ($n = 2{,}432$) from an area between the dorsal fin and the lateral line and were pressed in plastic plates following Koo (1955).

Scale Analysis and Age Determination

We used a projector to magnify each scale one hundred times, and measured the number of checks, circuli, and the lengths of the scale (Fig. 4). The lengths of 295 scales were measured along the long axis from the focus to each check on scale and to the edge of the scale. A check was identified in areas where the circuli interval was narrow or discontinuous. In marked fish, the annulus was a check which formed regularly, while false annuli were checks which formed irregularly. Annuli formation of the non-marked fish was identified by comparing the number of circuli in the last growth zone in the season that marked fish annuli was formed. Then we assumed that if the number of circuli was more, the scale had not formed an annulus, and if the number of circuli was fewer, the scale had formed a false annulus.

Finally, age determination was conducted by analyzing the number of annuli, the number of circuli between checks, and the fork length distribution. Age was designated by an Arabic numeral and a plus sign ($^+$): 0^+ young of the year; 1^+ in second year; 2^+ in third year; and so on.

Back Calculation

Fork length (cm) at earlier ages was back-calculated from the relationship between fork length and number of circuli. Fukuwaka and Kaeriyama (1994) suggested that back-calculation should be conducted from relationship between fork length and scale radius. However, since significant correlations exist between scale radius, number of circuli, and fork length, we calculated fork length from the relationship between fork length and number of circuli when the annuli were formed. Geometric mean regression (GMR; Ricker 1973) was used to calculate the relationship between fork length and number of circuli using the Fraser-Lee method as described by Ricker (1992). We assumed that the fork length was 4 cm when the scale was formed, following the result for sockeye salmon in Bristol Bay reported by Koo (1955) and for lacustrine sockeye in our experimental result (unpublished data).

Data Analysis

Correlation coefficients were used to analyze the

Fig. 4 Photograph of scale of marked lacustrine sockeye salmon (age 3^+) in Lake Toya. This fork length and scale radius was 29.9 cm and 1.650 mm, respectively.

relationships between fork length and number of circuli, and between scale radius and number of circuli. We used the Mann-Whitney U test to compare fork length between males and females. Estimation of the parameters of von Bertalanffy's growth curve was conducted by non-linear regression, using the simplex search method. AIC (Akaike's Information Criteria) was calculated from residual sum of squares.

RESULTS

Establishment of Age Determination Method

Checks were observed in 1,899 of 2,432 scale samples. Checks were not observed in 509 scales, and in 24 scales the check wasn't observed because of maturation or scale regeneration.

From the circuli distribution of the last growth zone (LGZ) on each check of marked fishes stocked in spring 1992, the relationship between checks and age was analyzed (Fig. 5). The mode of circuli in LGZ increased with month. In September 1992, only one scale had formed a check. From May to July 1993, a check formed on most scales, but scales with unformed checks were still found in May (1 of 17 fishes), June (3 of 34 fishes) and July (1 of 59 fishes).

To differentiate between irregular and regular formed check marks, the number and frequency distribution of circuli to the time of check formation was examined (Fig. 6). The number of circuli of the single fish with a check mark was 14 in September 1992, similar to the numbers observed of these fish with no checks. The number of circuli increased between September and the following May. Many fish with an unformed check in September increased

Fig. 5 Frequency distribution of number of circuli classified by presence of annuli for marked lacustrine sockeye salmon released in June, 1992 into Lake Toya. Open and solid bars indicate zero and one check on scale, respectively.

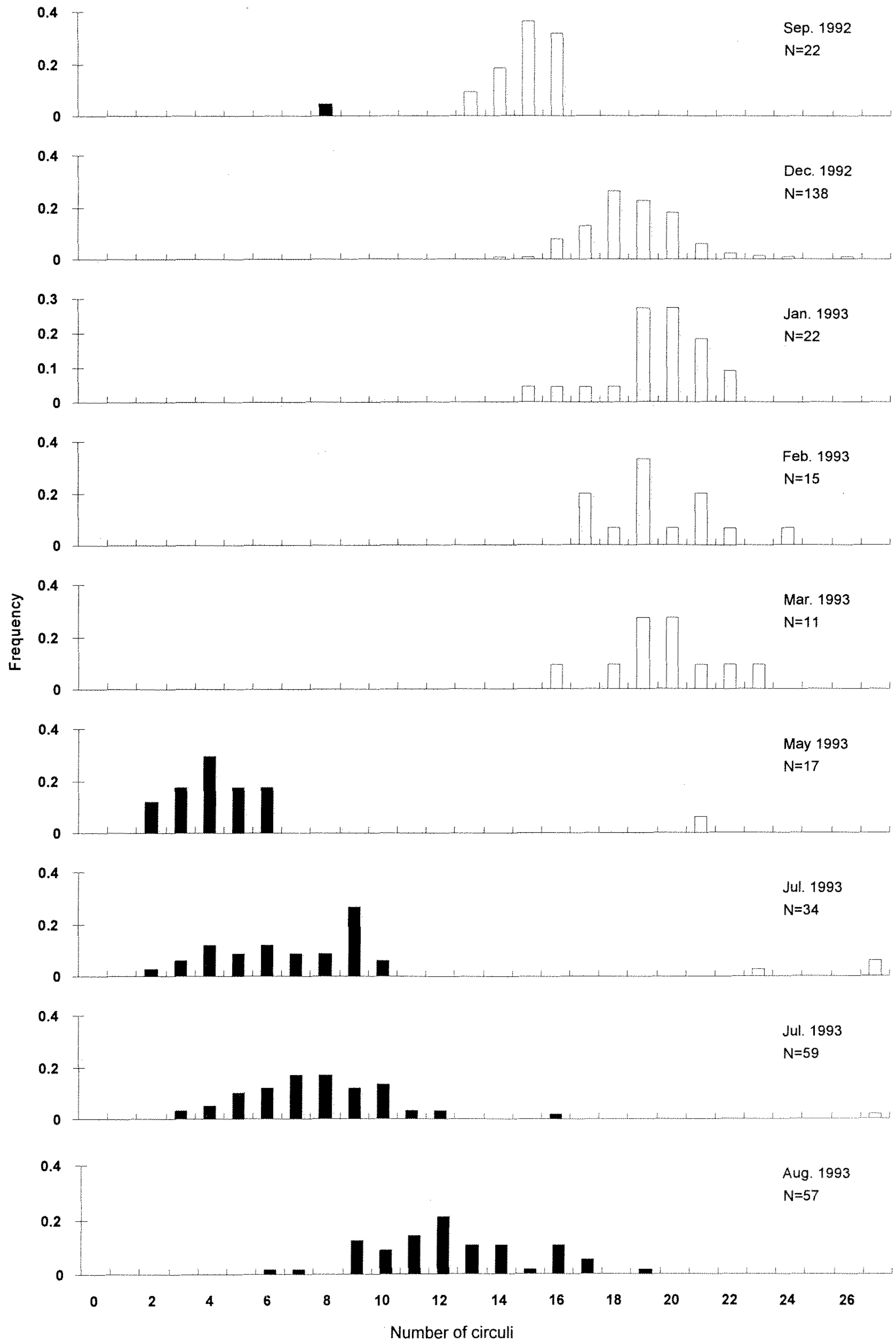
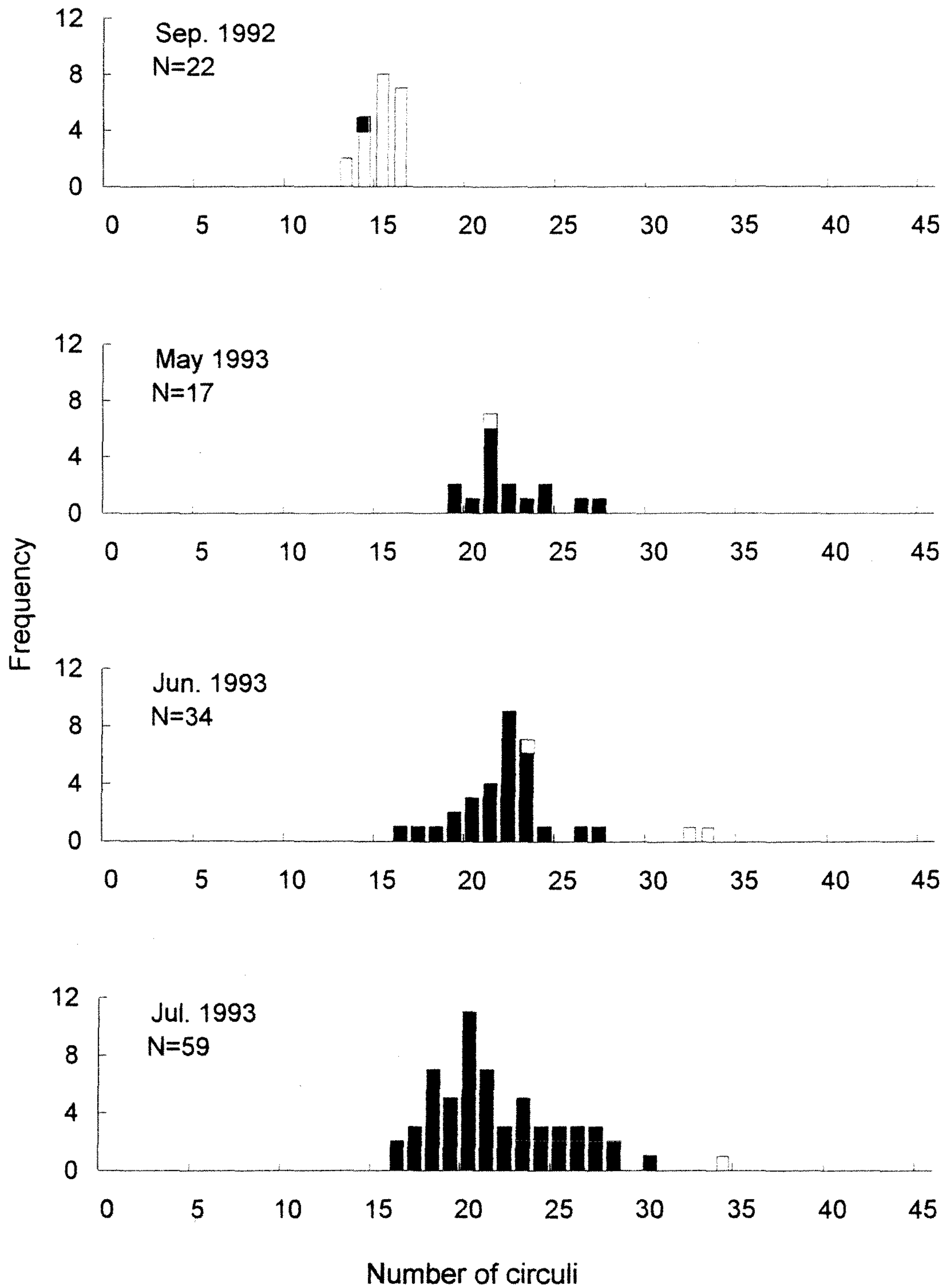


Fig. 6 **Frequency distribution of number of circuli to first check of marked lacustrine sockeye salmon in 1991 cohort captured in Lake Toya. Open and shaded bars indicate zero and one check on scale, respectively.**



the number of circuli to the first check and the first formed annulus in May 1993. Fish without checks in May, June, and July 1993 were of two types; the first type was fish with no difference in the number or distribution of circuli from fish with a check, and second type was fish that had more frequent numbers of circuli than those with a formed check (Fig. 6).

Fig. 7 shows the seasonal changes in number of circuli and clarifies when the circuli number increased and when the first check was formed. Most of the first check marks were formed during the period between May and June. In winter (from December to March), the number of circuli did not change and the check tended to be formed at the beginning of the period when the number of circuli began to increase again. Most marked fish formed a check around May which is defined as a true "annulus".

To estimate the period when checks formed on unmarked fish, seasonal changes in frequency distribution of number of circuli in last growth zone (LGZ) was examined (Table 1). Assuming that the month when the check was formed was the month when the number of circuli in the LGZ was low, the month when a check formed varied between years. For fish captured in 1991, it was thought that the second and third checks were formed about July. For fish captured in 1992, it was thought that each check was formed in May, while frequency distributions of number of circuli in LGZ indicated bimodality and variation for fish captured in 1993, 1994 and 1995. In June 1993, there was marked bimodality in frequency distribution of number of circuli in the second check, and many fish were judged to have formed a check from April to June.

For reasons mentioned above, age determination in lacustrine sockeye salmon in Lake Toya was conducted using the following procedure. From the number of circuli counted between two checks in scales of marked fish (mean and standard deviation: 21.0 and 2.8, max=30, min=14, n=198), we classified fish that had many circuli (>31) as fish that had not formed an annulus and those with few circuli (<14) as fish that had formed a false annulus. The true age was estimated by adding one to the age of fish without an annulus and by deducting one from the age of fish that had formed a false annulus. Furthermore, we excluded fishes that did not fit the expected age-specific fork length distribution.

Fig. 7 Seasonal changes in average and standard deviation (bars) of number of circuli of marked lacustrine sockeye salmon in 1991 cohort captured in Lake Toya. Arrows indicate times of annulus formation.

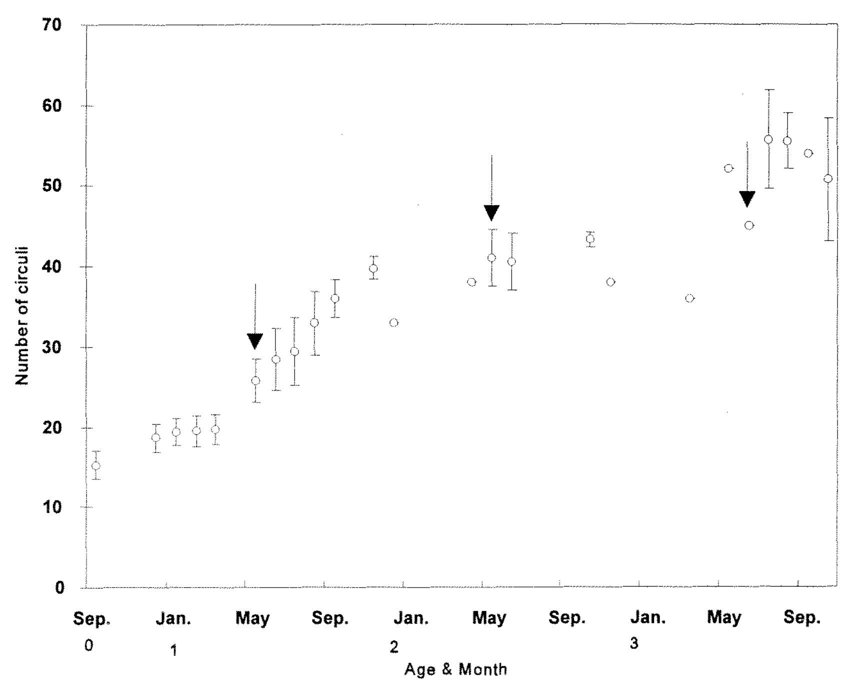


Table 1. Frequency distribution of number of circuli in last growth zone (LGZ) of scale from lacustrine sockeye salmon with one, two, and three checks in Lake Toya. These fish were captured in (1) 1991, (b) 1992, (c) 1993, (d) 1994, and (e) 1995.

(a) 1991

	Number of circuli																											
Month	0	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	+
Check number = 1																												
May																		1	1						1			
Jun.																					1							
Jul.																												
Check number =2																												
May	1			3		3	1	3	6	6	9	6	1	1														
Jun.		1		3			1	1	1		1	2																
Jul.	3	6	4	8	2	3	1	1	1	1																		
Check number =3																												
May	3																											
Jun.	3	2	1	1																								
Jul.	11	2	3		1																							

(b) 1992

	Number of circuli																											
Month	0	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	+
Check number=1																												
May		1																	1			1		4		1		
Jun.	1	1	2																									1
Jul.		1	1	10	22	15	5			1								1										
Check number=2																												
May			1	1	5	10	8	10	17	6	4																	
Jun.						1	1	7			1																	
Jul.							6	9	9	3	12	4	1	1	1													
Check number=3																												
May				2	2	7	5	9	6	3	1																	
Jun.							1	5		1	1																	
Jul.							1	5	6	2	9	4	4	3														

Table 1. (continued)

(c) 1993

Month	Number of circuli 0	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	+
Check number = 1																												
Apr.								1																				
May			2	3	5	3	3																					
Jun.	1		3	9	6	10	8	5	5	12	3								1	2	1	1	2	1				
Jul.			2	10	14	12	21	19	18	10	13	2	4		1		1											
Check number =2																												
Apr.	1	2		1	1																							
May		2	1	8	14	13	6																					
Jun.				1	1	3	1																					
Jul.					3	7		4	1	1	1	4	1															
Check number =3																												
Apr.	19	1			1	1		1																				
May	1	3	2	3	3	1			1			1																
Jun.							1																					

(d) 1994

Month	Number of circuli 0	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	+
Check number=1																												
Apr.																		1										
May																1	4	2	6	2								
Jun.		1												1		1	2	6	3		1							
Jul.			1																			1	1					
Check number=2																												
Apr.												1																
May	2									1	1	3	2	3	1													
Jun.	1	1		1																								
Jul.		4																										
Check number=3																												
May			1				1																					
Jun.		1																										

Table 1. (continued)

(e) 1995

	Number of circuli																											
Month	0	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	+
Check number = 1																												
Apr.									1		3				1		2	1			1							
May								1					1															
Jun.												1															1	
Jul.			2						1					2	2	1	1			1			1					
Check number =2																												
May		1								1				1	2	4	4	1			1							
Jun.		1		3											1		1										1	
Jul.			3	6	1	1	2	7	4	4	1			1	2	1		1		1			1					
Check number =3																												
Jun.			3	4	3																							
Jul.		6	10	14	9	8	9	3	4																			

Patterns of Scale Growth

To compare the number of circuli in each cohort, seasonal changes in the number of circuli in the 1990 and 1991 cohort were examined (Fig. 8). The number of circuli on scales of each cohort did not increase during the winter and increased only during summer, but the number of circuli was not stable. The increment of circuli in the 1990 cohort was large in age 1^+ and few in age 3^+, while the increment of circuli in 1991 cohort was low in age 1^+ and large in age 3^+.

Fig. 9 shows the number of circuli between annuli in two cohorts. The number of circuli in the 1990 cohort was largest at age 0^+ and 1^+, and decreased at age 2^+. Conversely, the number of circuli in the 1991 cohort changed very little with age.

These result show that the growth of the scale was minimal during winter and that the number of circuli differed over time and with age.

Growth Variation among Cohorts

Before turning to an examination of growth variation, we compared growth of males and females, by comparing fork lengths of males and females at ages 0^+, 1^+ and 2^+. No significant differences between males and females was found in except for age 0^+ fish captured in August 1993 (Mann Whitney U-test, $p<0.05$). As the difference in fork length between males and females in each age was small, the growth analysis described next was therefore conducted by pooling males and females.

The von Bertalanffy growth curves were fitted to 1990 and 1991 cohorts to compare growth patterns. The growth of the 1990 cohort was rapid at age 0^+, but the 1991 cohort was lower. Both the growth pattern and the parameter of the growth curve differed between cohorts (1990: $L_{max}=30.3$, $K=0.143$, $R^2=0.99$, $n=357$, AIC=2,699, 1991: $L_{max}=44.0$, $K=0.023$, $R^2=0.98$, $n=1,465$, AIC=13,334). The growth coefficient, K, of the 1990 cohort was larger than that of 1991, and L_{max} of the 1990 cohort was less than that of the 1991 cohort.

Changes in Growth Rate with Time

Fig. 10 shows the estimated changes in growth rate over time from the von Bertalanffy growth curves fitted to each cohort to clarify differences in growth pattern of each cohort. The growth rate of the 1991 cohort was initially lower than that of the 1990 cohort at young ages but declined more slowly, so that the growth rate of 1991 cohort was higher than that of 1990 cohort at ages>3 years. The major difference in growth pattern between the 1990 and 1991 cohorts was caused the difference in growth rates at age 0^+ and 1^+.

Fig. 8 Seasonal changes in average and standard deviation (bars) of number of circuli for 1990 and 1991 cohort of lacustrine sockeye salmon in Lake Toya. Solid horizontal bars indicate winter periods.

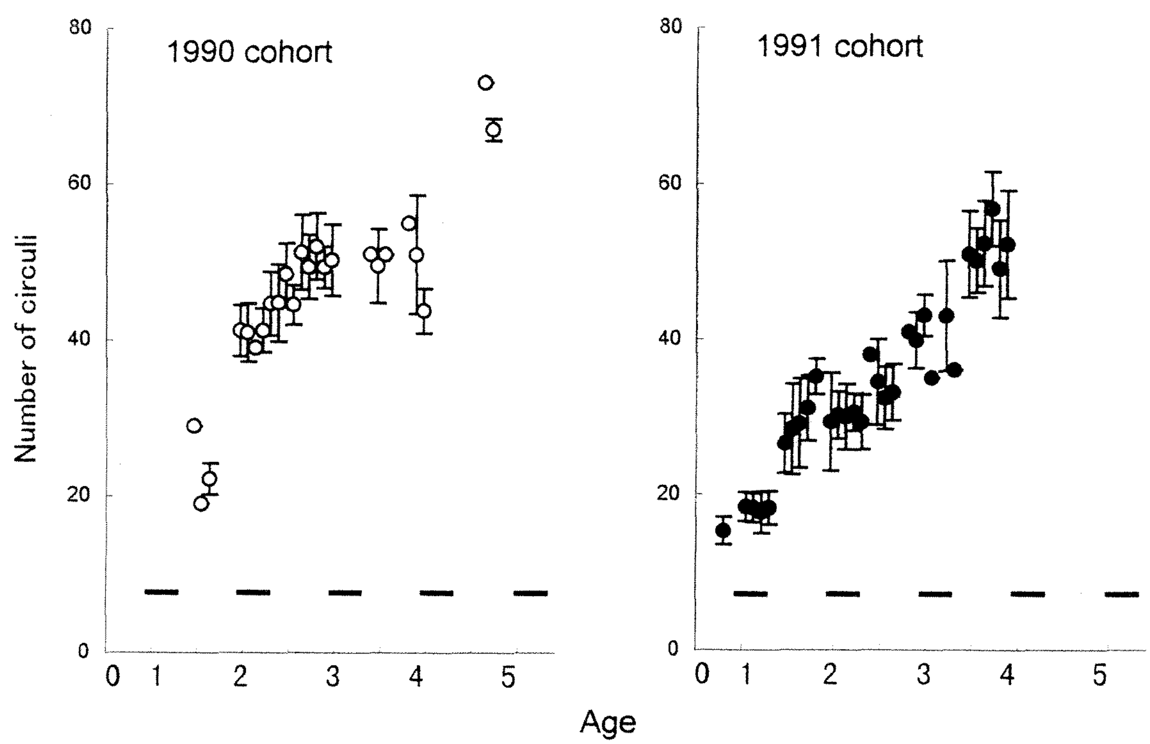


Fig. 9 Annual changes in average and standard deviation (bars) of circuli increments on scales of lacustrine sockeye salmon from 1990 and 1991 cohorts in Lake Toya. Parentheses show sample size.

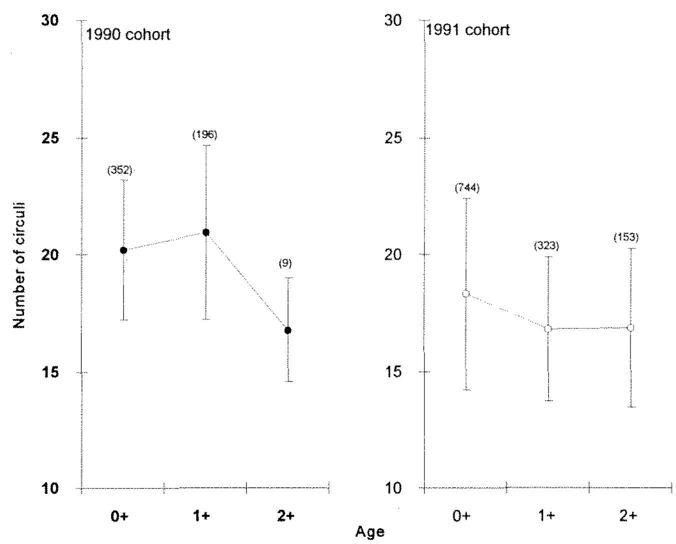
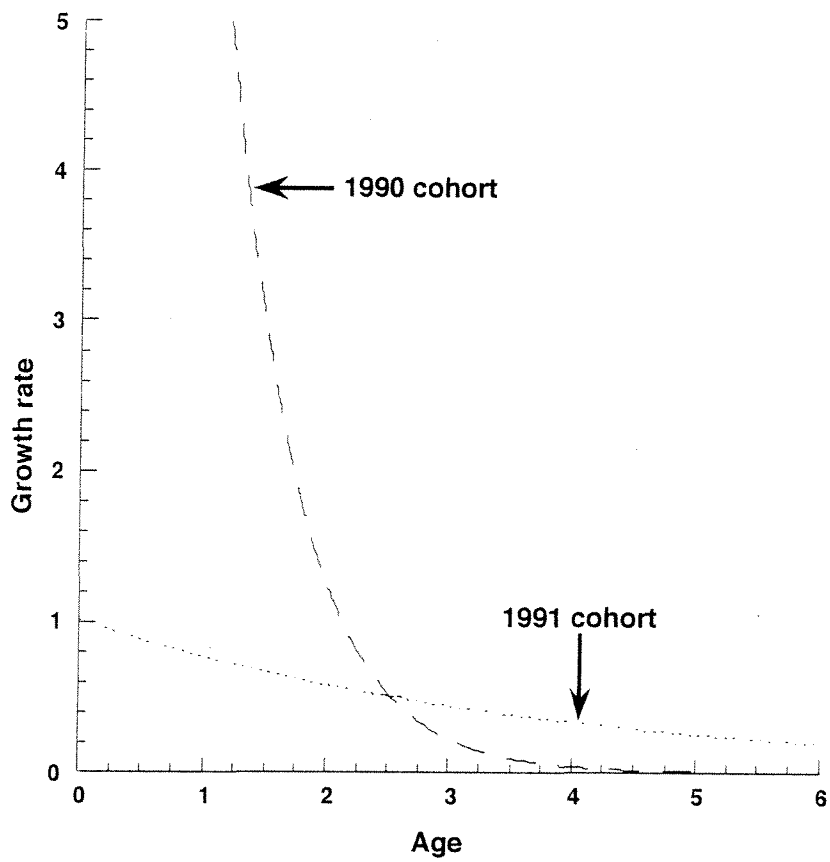


Fig. 10 Changes in growth rate of lacustrine sockeye salmon with time calculated from the fitted von Bertalanffy growth functions for the 1990 and 1991 cohorts.



We will expand this result for two cohorts to many, by comparing the growth coefficient back-calculated from fork length, to clarify at what ages most of the growth variation occur. We calculated the geometric mean regression equation by estimating relationship between fork length and number of circuli:

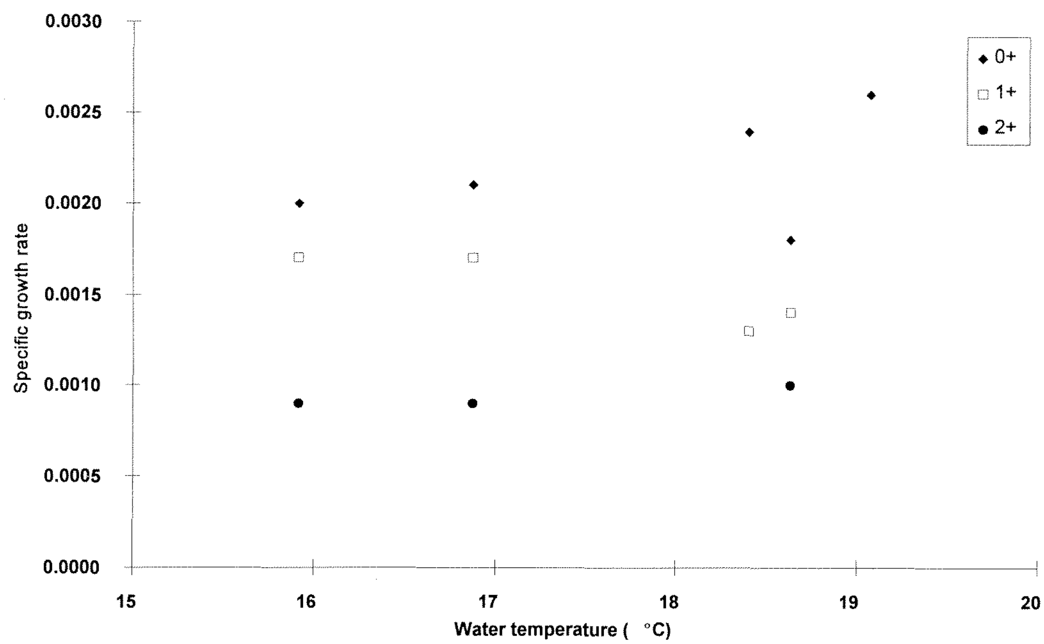
$$C = -3.89 + 1.97L \ (r^2=0.92)$$

where C is number of circuli and L is fork length (cm). The coordinates (Cs, Ls) of the standard point in the Fraser-Lee method is (4, 4.001), and back-calculated fork length at earlier sizes was calculated from the Fraser-Lee equation. The growth coefficient calculated from back-calculated fork length was compared between each cohorts (Fig. 11). The growth coefficient of the 1990 cohort is higher than that of the 1991 from age 0^+ to age 1^+, and lower than that of the 1991 for age 2^+ and 3^+, consistent with our previous analysis. The growth coefficients by age classes of all cohorts was highest in the age 0^+ period. The growth coefficients then decreased with age but varied by cohorts. These results showed that growth coefficients (or growth rates) might vary markedly between early life (e.g. age 0^+, and 1^+).

Fig. 12 shows the relationship between the growth coefficient and summer surface water temperature from 1990 to 1994. The growth coefficient does not relate to summer surface water temperature (Spearman's rank correlation, water temperature VS 0^+ growth rate; $p=0.40$, water temperature VS 1^+ growth rate; $p=0.30$, water temperature VS 2^+ growth rate; $p=0.16$).

Fig. 11 Comparison of specific growth rate (SGR) with (a) age 0^+, (b) 1^+ and (c) age 2^+ for 1989 to 1993 cohorts of lacustrine sockeye salmon captured in Lake Toya. Bars represente standard deviation.

Fig. 12 Relationships between summer surface water temperature and specific growth rate at age 0^+, 1^+ and 2^+.



DISCUSSION

From analysis of number of circuli in the last growth zone, it was clear that most of the marked fish in Lake Toya formed a check during the period of increasing circuli from April to June. We therefore defined a check formed in this period as the annulus. However, there were a few marked fish that formed a false annulus or failed to form an annulus during the growing season. The number of circuli to a false annulus was fewer than in fishes that formed a true annulus. Furthermore, the number of circuli in fish that failed to form an annulus was higher than in fish forming a true annulus. From observation of seasonal changes in the number of circuli, the annulus formation period for unmarked fish was from April to June, but the scale formation period differed each year.

Several articles have been reported on studies of age in lacustrine sockeye salmon, focusing on how and when annulus formation occurs. Kurohagi and Sasaki (1964) reported that the period of annulus formation in Lake Shikotsu lacustrine sockeye salmon was related to their body growth, and that the third annulus was formed between January to May. In contrast, Tokui (1985, 1988) reported that the annulus formed before the start of body growth, and that annuli were formed from May to August in Lake Shikotsu and about May in Lake Kuttara. These estimates of the time of annulus formation in lacustrine sockeye salmon differ between lakes and years. In this study, it was clear that the period of annulus formation occurred between April to June and that the annulus formed during periods of body growth. The period of annulus formation in unmarked fish was from April to June, but the possibility of variability in the time of annulus formation was noted by Kurohagi and Sasaki (1964) and was similar to results of previous studies. Bilton and Robins (1971) reported that change in even one factor was enough to affect check formation on scales of sockeye salmon (e.g., food). Based upon this study, Suzuki and Kaeriyama (1990) suggested that the width of circuli on scales of juvenile sockeye salmon was affected by the feeding level and that a check might be formed by increasing growth rate. The present results suggest that a false annulus was formed by increasing growth rate except in the period from April to June (i.e., just after release), and that fish showing no increased growth rate from April to June might not form an annulus. Therefore, in this paper, we distinguished fish with false annuli and without annuli from with true annuli by the number of circuli between checks.

The number of circuli on scales of juvenile sockeye salmon is related to scale increment and body growth (Fukuwaka 1995), and fish with a large number of circuli between two checks might indicate a large increment of body growth between the two checks. In marked fishes, it is clear that fish that had not formed an annulus had a large number of circuli between checks, while those which had formed a false annulus had fewer. Therefore, in unmarked fishes, it was thought that fish which had not formed an annulus likely had a greater number of circuli between two checks. Therefore, annulus discrimination should be conducted using the number of circuli between checks.

Generally, age determination using scale and otolith measurements requires corresponding data on fork length and number of rings, a stable time of ring formation, and known time interval of ring formation (Tanaka 1985). In lacustrine sockeye salmon in Lake Toya, regularity of annulus formation was not always observed, so it is important to distinguish fish that formed a false annulus and those without an annulus, and to consider the effect of the growing season on age determination. In this study, the errors of age determination were probably few, because only two fishes differed from the others in age specific fork length distribution.

The present results suggested that scale growth differ between cohorts. The von Bertalanffy growth curves of the 1990 and 1991 cohorts differed primary because of differences in growth rates at age 0^+ and 1^+. Furthermore, in cohorts without measured growth curves, differences in growth rates between annuli were also observed. Annual variation in the number of circuli was observed in sockeye salmon in Lake Azabach'e, Kamchatka River, and this phenomenon might be related to food supply, water temperature and population density (Bugaev et al. 1994). It should be concluded, from the previous reference and the present results, that the differences in growth pattern between 1990 and 1991 cohorts in lacustrine sockeye salmon in Lake Toya might be influenced by biotic factor in the lake. Makino and Ban (personal communication) observed annual changes of zooplankton biomass from 1992 to 1995. On the other hand, the growth rates of lacustrine sockeye salmon does not relate to summer surface water temperature. However, summer surface water temperature seems to relate to the growth rate of lacustrine sockeye salmon (Fig. 11). Brett et al. (1969) reported that water temperature also affected growth rate of fingerling sockeye salmon. Zooplankton biomass fluctuations and annual water temperature changes may affect the growth rate of lacustrine sockeye salmon in Lake Toya.

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