Dynamics of Chum Salmon, *Oncorhynchus keta*, Populations Released from Hokkaido, Japan

Masahide Kaeriyama
Research Division, National Salmon Resources Center, Fisheries Agency of Japan
2-2 Nakanoshima, Toyohira-ku, Sapporo 062, Japan

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Kaeriyama, M. 1998. Dynamics of chum salmon, *Oncorhynchus keta*, populations released from Hokkaido, Japan. N. Pac. Anadr. Fish Comm. Bull. No. 1: 90-102

Body size of Hokkaido chum salmon (*Oncorhynchus keta*) at maturity showed a significant decreasing trend from the late 1970s to the early 1980s and has remained relatively constant since the late 1980s. A significant negative relationship between population abundance and fork length was observed. In Hokkaido chum salmon population, average age at maturity in cohorts increased from 3.7 years in the 1972 cohort to over 4 years in cohorts after 1980. A significant positive relationship between population abundance and average age at maturity of cohorts was observed in the Hokkaido chum salmon population. Growth analysis back-calculated from scales showed that a growth reduction occurred after the second year, especially in the third year of oceanic life of Hokkaido chum salmon. The synchronous decreasing body size and increasing age at maturity of Hokkaido chum salmon occurred in face of rising marine survival rates and ocean conditions favorable for growth. This suggested that reduced growth and increasing age at maturity was due to density dependent intraspecific competition and high abundance of chum salmon on the North Pacific Ocean.

INTRODUCTION

In the last two decades, the population size of chum salmon (*O. keta*) released from Japan has increased significantly (Kaeriyama 1989). Since the 1980s, the biomass of Pacific salmon has been increasing throughout the North Pacific Ocean. According to FAO fisheries statistics the annual catch of Pacific salmons in the area averaged 0.72 million tons during 1981-1993, and in 1995 exceeded 0.95 million tons, which surpassed the previous historical high. Biomass of chum, sockeye (*O. nerka*), and pink salmon (*O. gorbuscha*) is increasing in the North Pacific Ocean (Fig. 1). This increase is thought to have coincided with favorable oceanic conditions and successful artificial enhancement programs (Beamish and Bouillon 1993; Brodeur and Ware 1992; Kaeriyama 1996; Pearcy 1992).

However, with this increase in population abundance, individual growth reduction has been observed for many Pacific salmon populations, such as Bristol Bay sockeye (Rogers and Ruggerone 1993), Japanese chum (Kaeriyama 1989, 1996; Ishida et al. 1993), and North American pink salmon (Bigler et al. 1996). These findings suggest that salmon research from a view point of population ecology is very important in order to carry out the stock management and effective artificial enhancement program of Pacific salmon.

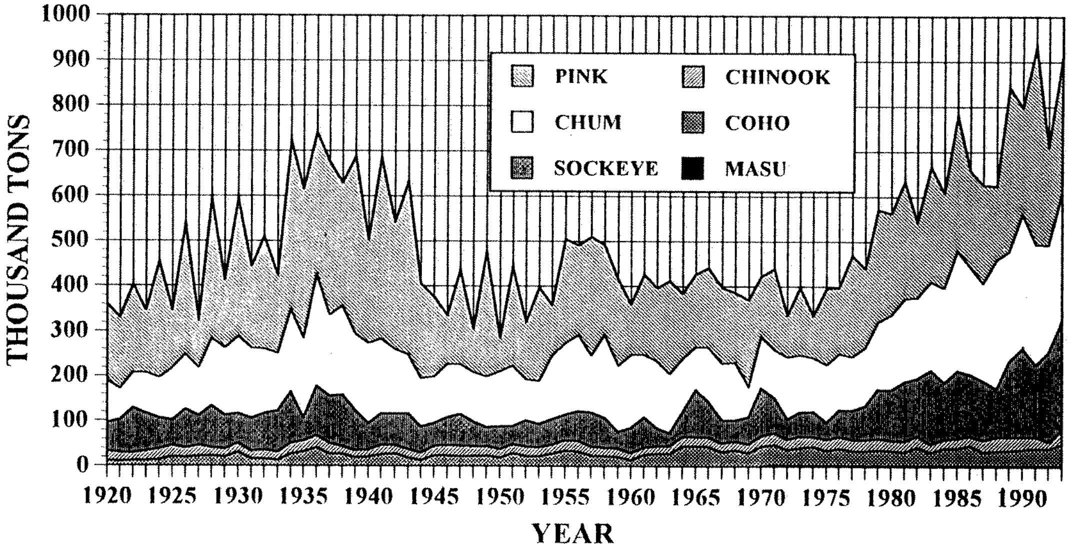
The purpose of this paper is to examine changes in body size, age at maturity, and growth pattern, and to clarify population-density-dependent effects as intraspecific competition on Hokkaido chum salmon for the elucidation of factors affecting the biological characteristics of Pacific salmon populations.

MATERIALS AND METHODS

Fork length data of female adults returning to 11 rivers in Hokkaido from 1953 to 1995 were used to quantify change in body size at maturity of chum salmon. Condition factors (CF) were calculated from fork length (L, cm) and body weight (W, g) of male adult chum salmon returning to Ishikari River; $CF = W/L^3 \times 1000$. These sample sizes per age were more than 10 individuals by sex in each river population. Especially, the sample size for age 4 was more than 60 individuals. The following data were excepted from analysis: (1) cohorts which sample size was less than 10 individuals, and (2) cohorts indicating more than 10 % in coefficient of variations of fork length and body weight.

Scales of chum salmon collected in Ishikari River during 1976-1995 were measured with a scale image processor (Ratoc System Engineering Co.) to provide an index of growth during each year at sea. Distances

Fig. 1 Change in annual catch of Pacific salmon in the North Pacific Ocean during 1920-1993 (from FAO Fisheries Statistics). Statistics for mariculture and aquaculture production are excepted.



and number of circuli from the focus to the inner edges of individual annuli of approximately 100 scales from each age group by year were measured to the nearest one micrometer along the longest axis.

Fecundity and egg size of age-4 female chum salmon (78 individuals) were examined in the Ishikari River from 1986 to 1995. Fecundity was counted as total number of eggs per female, and egg size was determined from volume of water-hardened eggs with excess surface moisture removed as follows: $D=20(4V/(3\pi N))^{1/3}$, where D is egg diameter (mm), V and N are volume (ml) and number of total alive water-hardened eggs, respectively (Watanabe 1955).

Data on sea surface temperature (SST) were provided as the monthly mean global sea surface temperature data of two by two degree grid by marine division of Japan Meteorological Agency. SSTs were examined in western (48-50°N, 164-166°E), central (48-50°N, 179°E-179°W), and eastern (Gulf of Alaska; 48-50°N, 144-146°W) areas of the Subarctic North Pacific Ocean during salmon growth period (from May to October).

Exponential smoothing analysis (SPSS Inc.) was used to estimate the trend of annual change in fork length of Ishikari River adult chum salmon. Alpha values were 0.4 in age-3, 0.5 in age-4, and 0.4 in age-5. Analysis of variance (ANOVA) and nonparametric Mann-Whitney test were used to compare slopes in regression lines between population size and fork length among age groups and breeding characters of age-4 female between 1940-1943 and 1986-1995 in Ishikari River adult chum salmon respectively.

RESULTS

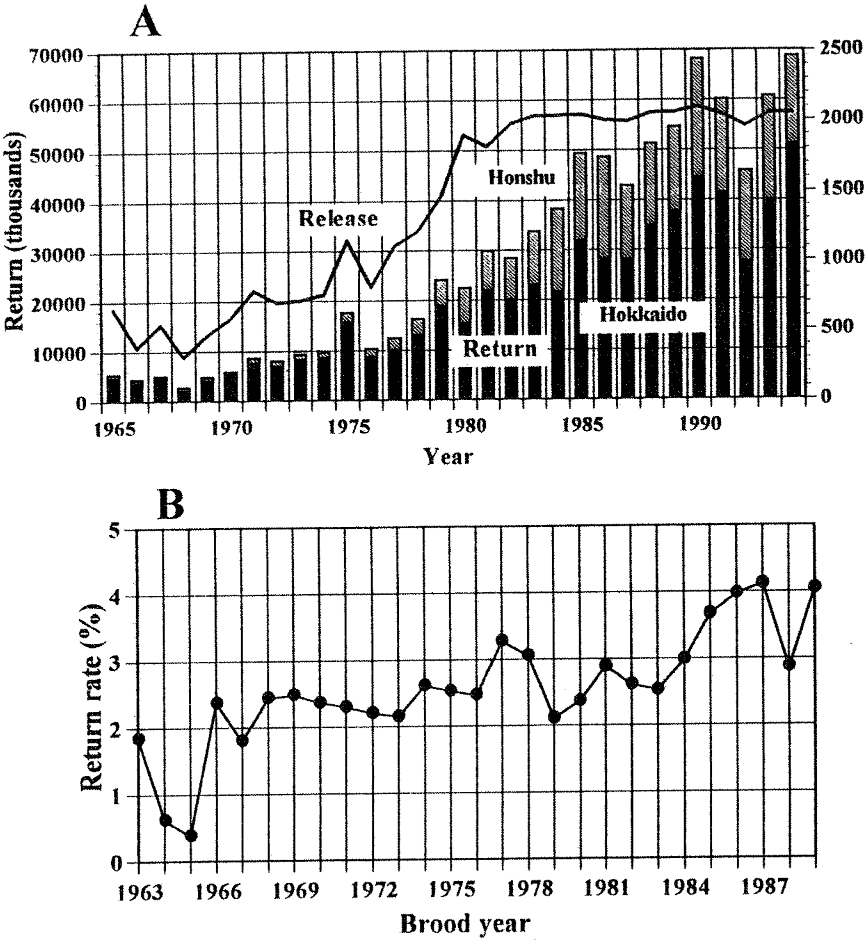
1. Changes in production trends and return rate of chum salmon in Japan

The number of adult chum salmon returning to Japan from 1900 through 1970 averaged about 3 million individuals, ranging from 1 to 5 million individuals. Since the late 1970s, adult returns have increased to more than 50 million individuals until the late 1980s, and reached 77 million individuals (57 million individuals in Hokkaido and 20 million individuals in Honshu) in 1995 (Fig. 2A). This population size accounted for 70-80% to all chum salmon catch in the North Pacific Ocean. The number of juveniles released increased from 800 million individuals in the early 1970s to 2 billion individuals in 1982, and has been limited to about 2 billion individuals since the early 1980s (Fig. 2A).

In the Hokkaido chum salmon population, return rate (adult returns as a percentage of juveniles released) for a brood-year population had fluctuated around 1% until 1965. The return rate has increased to above 2% after 1966, attained more than 3% after 1984, and has tended to increase (Fig. 2B). Therefore, the considerable increase in adult return since the 1980s was due to increase in survival of released juveniles.

The rise in the return rate was the effect of successful artificial enhancement programs such as the technology of release after feeding (Kobayashi 1980; Mayama 1985; Kaeriyama 1989) as well as influence of favorable oceanic conditions in the North Pacific Ocean. For instance, significant positive relationship between the proportion of reared fish to

Fig. 2 Annual changes in numbers of adult returns, juvenile releases (A), and return rate (B) of chum salmon in Japan during 1965-1995.



total juvenile released and the return rate was observed in the Hokkaido salmon population ($r=0.799$, $P<0.001$; Fig. 3A). Change in return rate was similar to that in average body weight of juvenile released ($r=0.665$, $P<0.05$; Fig. 3B).

2. Body size and average age at maturity of Hokkaido chum salmon

Figure 4 illustrates annual changes in mean fork length at maturity of age-3, 4, and 5 female chum salmon returning to the Ishikari River in 1953-1995. A decrease in body size of age 3-5 chum salmon occured after the late 1970s coincident with increases in abundance. The mean fork length of age 3-5 female chum salmon decreased from 1979 to 1984. For instance, the average fork length of age-4 female declined by about 9 % from the late 1970s (687 mm) to the early 1980s (638 mm). Exponential smoothing analysis demonstrates that fork length has remained stable and small size since the late 1980s (Fig. 4).

A significant negative relationship between population size of Hokkaido chum salmon and mean fork length of adult chum salmon returning to Ishikari River was observed ($r<-0.6$, $P<0.001$; Fig. 5). Negative linear relationships between population size and fork length were observed in all river populations examined in Hokkaido (Table 1). Averages and standard deviations of slopes (b) in regression lines indicated -1.08 ± 0.28 mm / age-3 million fish, -1.53 ± 0.25 mm / age-4 million fish, and -1.54 ± 0.28 mm / age-5 million fish. Slopes for age-4 and -5 were significantly more negative than that of age-3 fish (t-test; $P<0.001$).

Condition factor of male adult chum salmon returning to the Ishikari River did not change annually after the 1970s, although it fluctuated in the 1950s and the 1960s (Fig. 6). If condition factor is used as indicator of fatness, health or well-being of a population (Cone 1989), then the stable condition factor observed for Hokkaido chum salmon since the 1980s indicates healthiness of the population.

The age composition of a brood-year population

Fig. 3 Relationships between rearing rate (A) or body size (B) of juvenile released and return rate in Hokkaido chum salmon population. Rearing rate indicates percentage of reared fish to total juvenile released. Return rate is the percentage of adult returns to juveniles released.

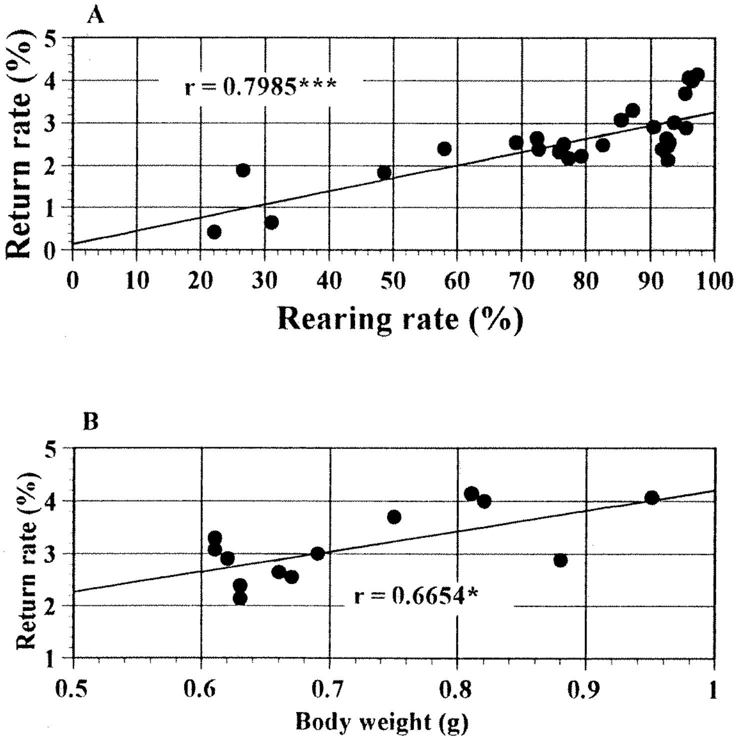


Fig. 4 Annual change in average fork length of female adult chum salmon returning to the Ishikari River in 1953-1995. Lines indicate result of exponential smoothing analysis. Alpha values were 0.4 in age -3, 0.5 in age -4, and 0.4 in age -5.

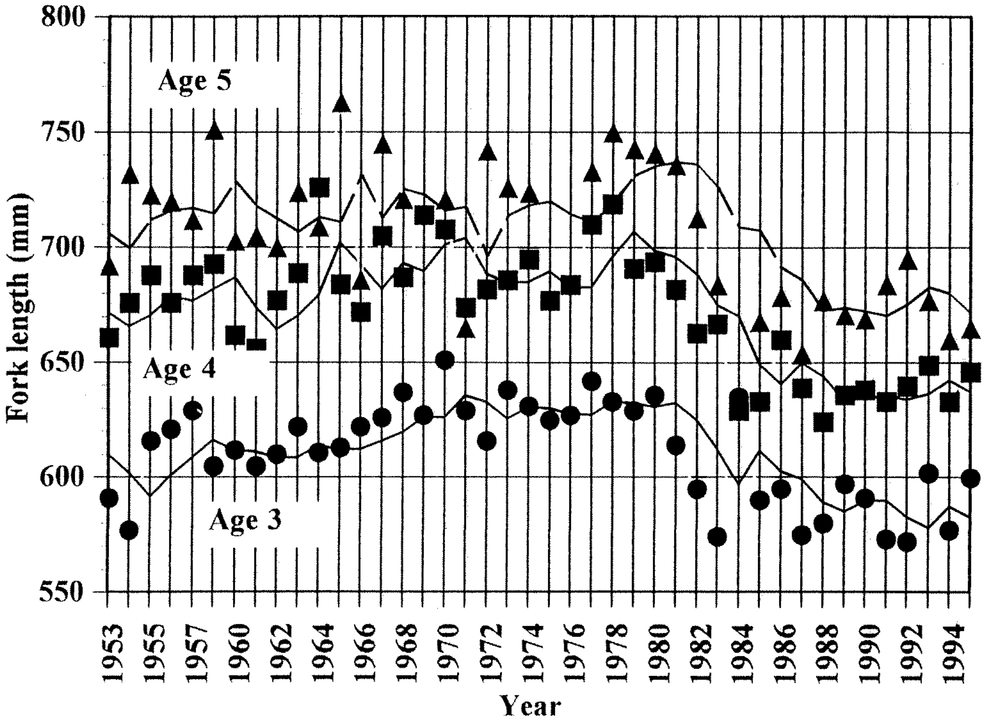


Fig. 5 Relationship between population size of Hokkaido chum salmon and average fork length of female adult chum salmon returning to the Ishikari River in 1953-1995. Age -3: r= -0.5700(P<0.001), Age -4: r= -0.7145 (P<0.001), Age -5: r= -0.6682 (P<0.001).

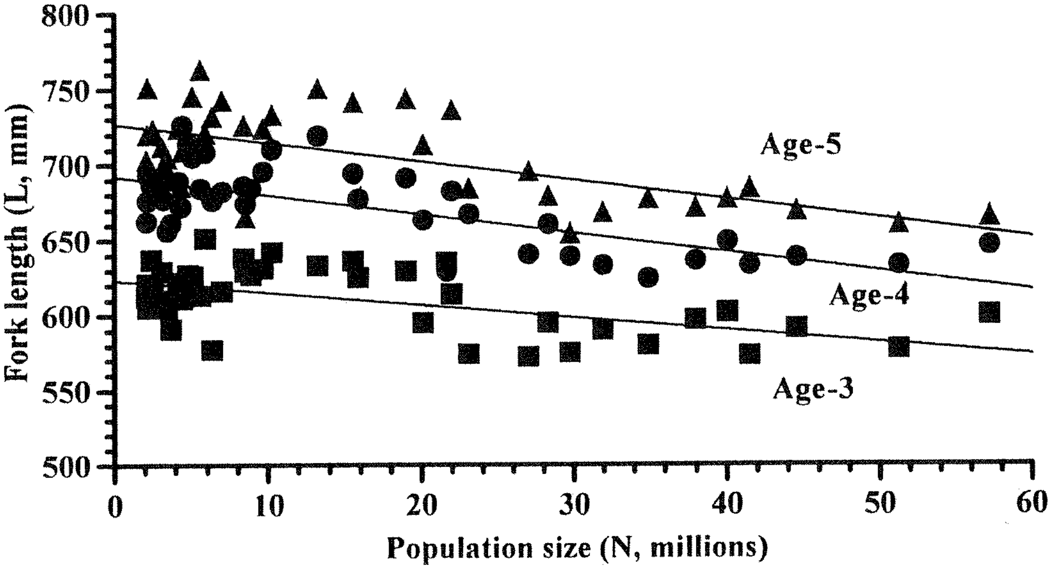
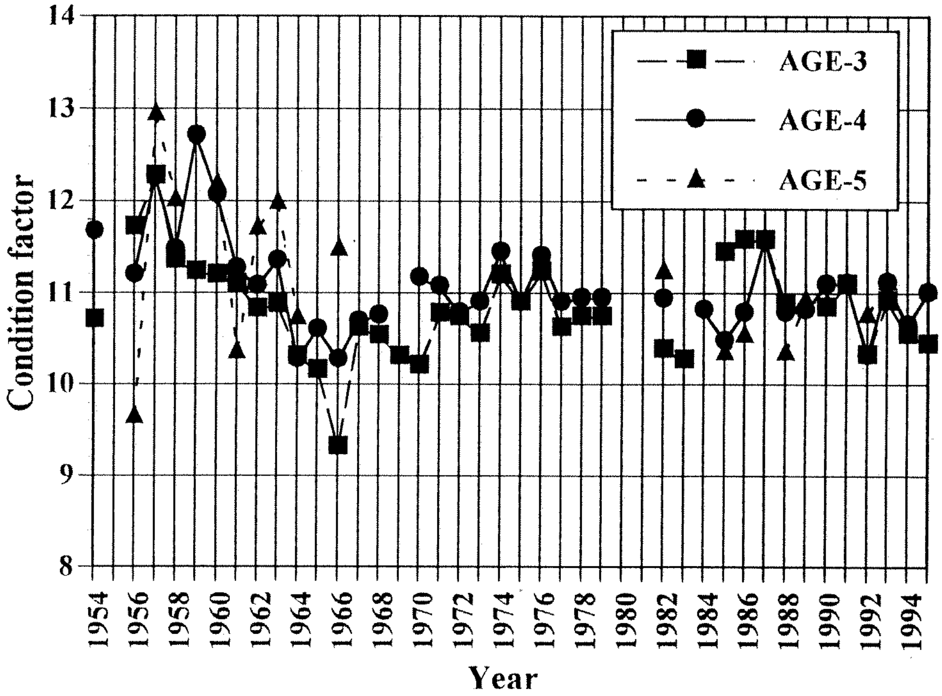


Table 1. Relationships between population size and average fork length of Hokkaido chum salmon populations. n = number of years of data, a =constant, b = slope, r = the correlation coefficient, and P = the probability that b=0 (*: P<0.05, **: P<0.01, ***: P<0.001).

Area*	River	Age	n	a	b	r	P
OKS	Abashiri	3	32	620	-0.755	-0.4194	*
		4	32	689	-1.406	-0.7133	***
		5	31	715	-0.970	-0.4132	***
	Shari	3	21	632	-1.369	-0.6693	***
		4	21	707	-1.829	-0.8234	***
		5	19	744	-1.798	-0.7730	***
NMS	Shibetsu	3	25	643	-1.524	-0.6911	***
		4	25	703	-1.922	-0.8811	***
		5	23	741	-1.996	-0.8811	***
	Nishibetsu	3	30	644	-1.459	-0.7771	***
		4	36	706	-1.617	-0.8131	***
		5	36	743	-1.626	-0.7376	***
NEP	Tokachi	3	37	636	-0.755	-0.4157	*
		4	37	711	-1.204	-0.5504	***
		5	35	770	-1.740	-0.8359	***
	Kushiro	3	32	635	-1.006	-0.5506	***
		4	34	709	-1.475	-0.7583	***
		5	34	755	-1.649	-0.7456	***
NWP	Shizunai	3	30	629	-0.829	-0.4829	**
		4	34	709	-1.168	-0.6538	***
		5	32	752	-1.380	-0.6344	***
	Yurappu	3	31	653	-0.982	-0.4854	**
		4	31	736	-1.488	-0.7702	***
		5	30	773	-1.287	-0.6051	***
	Shiriuchi	3	31	659	-1.018	-0.6732	***
		4	31	733	-1.723	-0.8011	***
		5	31	772	-1.763	-0.8081	***
NJS	Ishikari	3	40	623	-0.822	-0.570	***
		4	42	693	-1.257	-0.7145	***
		5	40	728	-1.289	-0.6682	***
	Teshio	3	32	636	-1.313	-0.6097	***
		4	34	699	-1.761	-0.8022	***
		5	32	727	-1.471	-0.6242	***

*OKS: Okhotsk Sea area, NMS: Nemuro Strate area, NEP: Northeastern Pacific Ocean area, NWP: Northwestern Pacific Ocean area, NJS: North Japan Sea area.

Fig 6. Annual change in condition factor of male adult chum salmon returning to Ishikari River in 1954-1995.



has changed with recent large returns of Hokkaido chum salmon. The average age at maturity of a brood-year population was about 3.7 years until 1972, then increased gradually and exceeded 4 years since 1980 (Fig. 7A). A significant positive relationship between population size and average age of a population at maturity was observed ($r=0.909$, $P<0.001$; Fig. 7B). The increase in age at maturity was synchronous with the decrease in body size until the 1980 brood year. The Hokkaido chum salmon population continues to increase in age at return after 1980 although the fork length has remained stable at small size.

3. Changes in growth of body and scale

Figure 8 demonstrates normal and narrow types of scales from age-4 chum salmon returning to Hokkaido in 1993. Scale width in the third-year zone of narrow type is evidently smaller than those in other zones. Recently, narrow-type scales have been frequently observed in adult chum salmon returning to Japan. Changes in mean scale width by each year zone of age-4 adult female chum salmon returning to the Ishikari River (Fig. 9) indicated that 1) scale width of first-year zone remained stable (about 1.3 mm), 2) scale widths of second- and third-year zones were decreasing, 3) scale width of fourth-year zone was increasing rather than stable since 1993.

Annual growth in fork length of Ishikari River adult chum salmon from 1976 to 1995 was estimated by back-calculation, estimating fork length as scale radius (S, μm) and fork length (L, mm): $L=0.0358(S-114)^{1.2406}+40$ (Fig. 10; $r^2=0.990$, $P<0.001$), where values "114" and "40" estimate focus radius (Fukuwaka and Kaeriyama, 1994) and fork length at squamation (Kaeriyama and Bunya, 1982). Growth differences between 1976-1980 (large-size period) and 1985-1995 (small-size period) adults showed (Table 2);

1) growth reduction in the third year was considerably higher than those in the other years,
2) growth reduction in the first year increased with increasing age, and
3) growth in the second year of age 4 fish and in the fourth year of age 5 fish was reduced 14.7 % and 18.2 % respectively.

These findings suggest that the growth reduction of Hokkaido chum salmon occurs after the second year of oceanic life, especially in the third year when they extend their migration to the eastern North Pacific Ocean and the Bering Sea (Ogura and Ito 1994).

Fig 7. Annual changes in population size and average age (A), and relationship between population size and average age (B) at maturity of Hokkaido chum salmon population during the brood years of 1963-1989

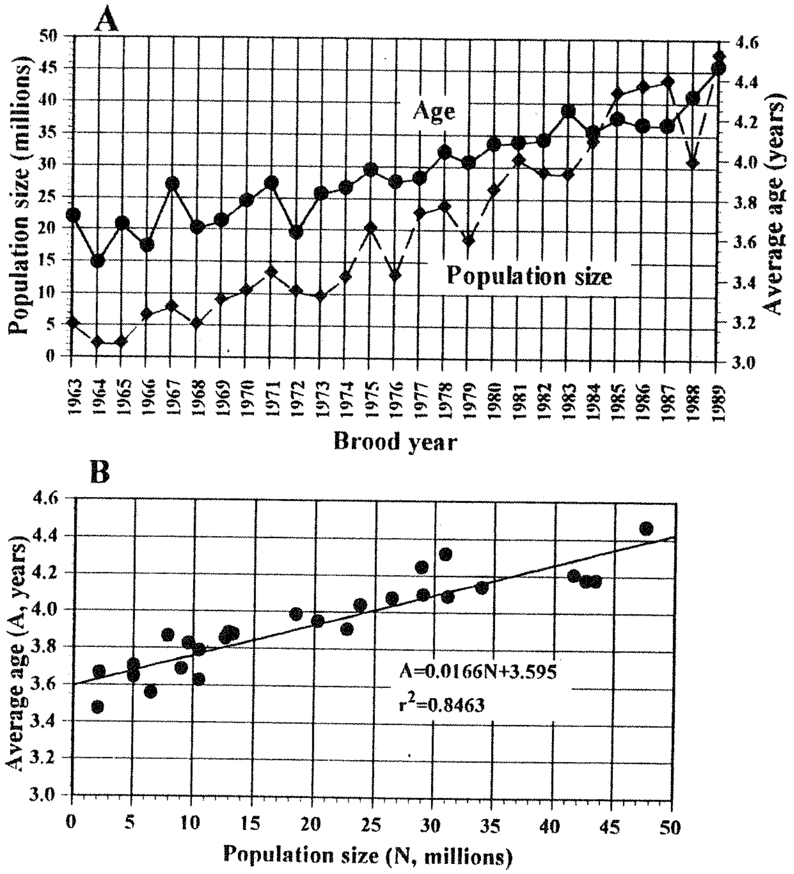


Fig 8. Photographs of normal (A) and narrow (B) types of scale from age-4 chum salmon returning to Hokkaido in 1993.

Fig. 9 Annual changes in mean scale width by each year zone of age-4 female adult chum salmon returning to Ishikari River in 1979-1995. W1: width of first year zone, W2: width of second year zone, W3: width of third year zone, W4: width of fourth year zone.

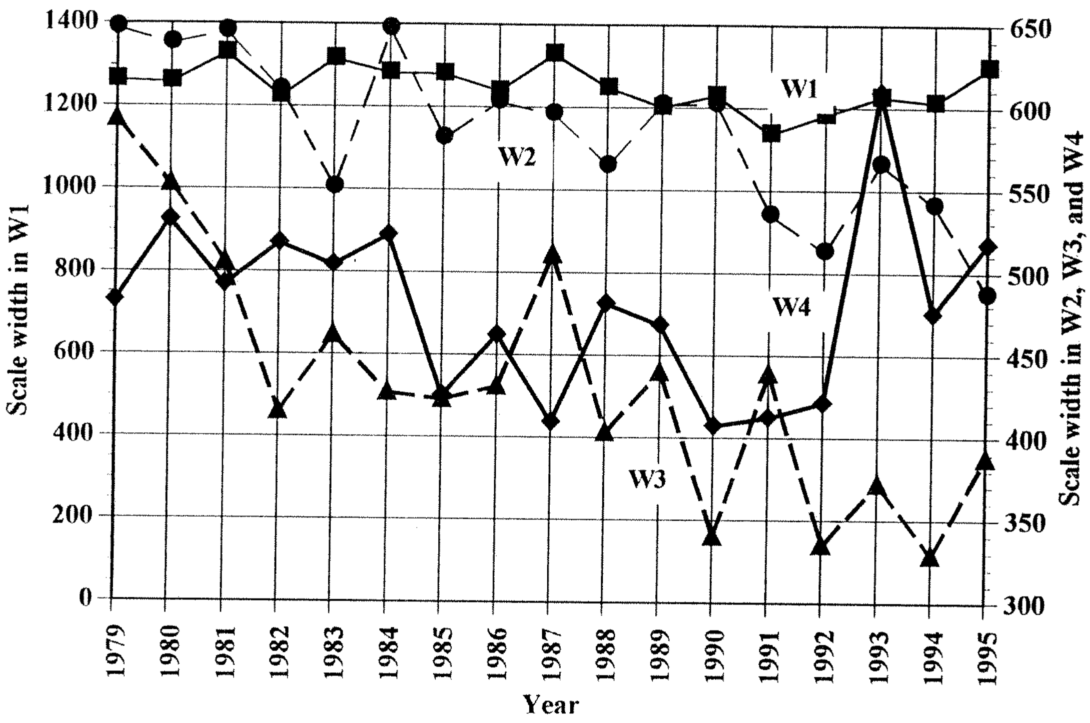
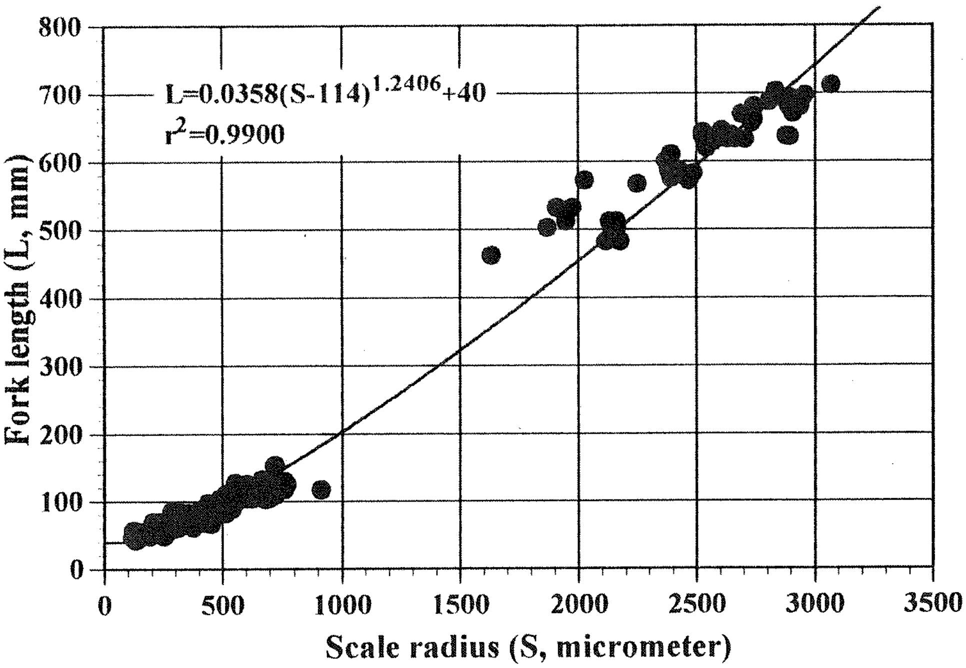


Table 2. **Calculative growth reduction of adult chum salmon returning to the Ishikari River from 1976 to 1995. Annual growth is estimated from the back calculation in allometry formula between the scale radius (S, μm) and fork length (L, mm): $L = 0.0358\ (S - 114)^{1.2406} + 40$.**

Age class	Ocean life period	Annual mean growth (mm)		Growth reduction	
		1976-1980	1985-1995	mm	(%)
3	1st year	267	264	3	(1.2)
	2nd year	171	158	14	(8.0)
	3rd year	168	146	22	(13.0)
	Total	606	568	39	(6.3)
4	1st year	268	256	12	(4.3)
	2nd year	165	141	24	(14.7)
	3rd year	147	108	39	(26.4)
	4th year	152	132	20	(13.3)
	Total	732	637	95	(13.0)
5	1st year	276	249	26	(9.6)
	2nd year	140	135	5	(3.7)
	3rd year	131	92	39	(29.9)
	4th year	128	105	23	(18.2)
	5th year	106	116	-10	(9.5)
	Total	781	697	83	(10.6)

Fig. 10 Relationship between scale length and fork length of chum salmon.



4. Changes in reproduction characters of adult chum salmon

Fecundity of Pacific salmon varies with body size, and is influenced by environmental factors. Although their egg size is affected by both environmental and genetic factors, it remains constant within a cohort (Kaeriyama et al. 1995).

Figure 11 illustrates comparison of body size (body weight), fecundity, and egg size of Ishikari River age-4 female chum salmon between 1940-1943 (from Watanabe 1955) and 1986-1995. Body weight in 1986-1995 was significantly smaller than that in 1940-1943 (U-test, $P<0.01$), and no differences were observed in fecundity and egg size (U-test, $P>0.05$). This result indicates that recent growth reduction had no significant effect on fecundity and egg size of Hokkaido chum salmon.

5. Relation between SST anomaly and change in growth

Climate of the Subarctic North Pacific Ocean changed during the late 1970s. Temperature anomalies in the Gulf of Alaska and Bering Sea illustrate a relative warm period in the late 1950s, followed by cooling especially in the early 1970s and a rapid temperature increase in the latter part of that decade (U. S. GLOBEC 1995). Beginning in the 1980s, sea surface temperature (SST) during the growth period of salmon (May to October) in the western and eastern Gulf of Alaska was generally higher than normal, although in the eastern and central areas of the Subarctic North Pacific Ocean SST fluctuated normaly (Fig. 12).

A significant positive relationship between mean SST anomaly during the ocean life period and the population size of Hokkaido chum salmon was observed in the Gulf of Alaska ($r^2=0.318$, $P<0.001$). Body size of adult chum salmon in Ishikari River was negatively related to the mean SST anomaly in Gulf of Alaska ($r^2>0.239$, $P<0.01$). However, there was no significant correlation between SST anomaly and population size or body size in other areas of Subarctic North Pacific Ocean (Tables 3, 4).

DISCUSSION

The Aleutian Low intensified after the late 1970s (Trenberth and Hurrell 1994). SST rose rapidly by several degrees in Gulf of Alaska (Rogers and Ruggerone 1993). Zooplankton biomass and catches of epipelagic nekton increased after the mid 1970s in the Northeast Pacific Ocean (Brodeur and Ware 1992, 1995). Salmon catches from the North Pacific increased sharply in the late 1970s, and exceeded historical levels in the early 1990s (Fig. 1).

Three factors have been suggested for decrease in size at maturity: 1) effect of changes in the ocean environment (Killick and Clements 1963; Rogers

Fig. 11 Comparison of body weight (BW), fecundity (Fec), and egg sizes (ES) of age-4 adult chum salmon returning to Ishikari River between 1940-1943 and 1986-1995. Bars represent standard deviation.

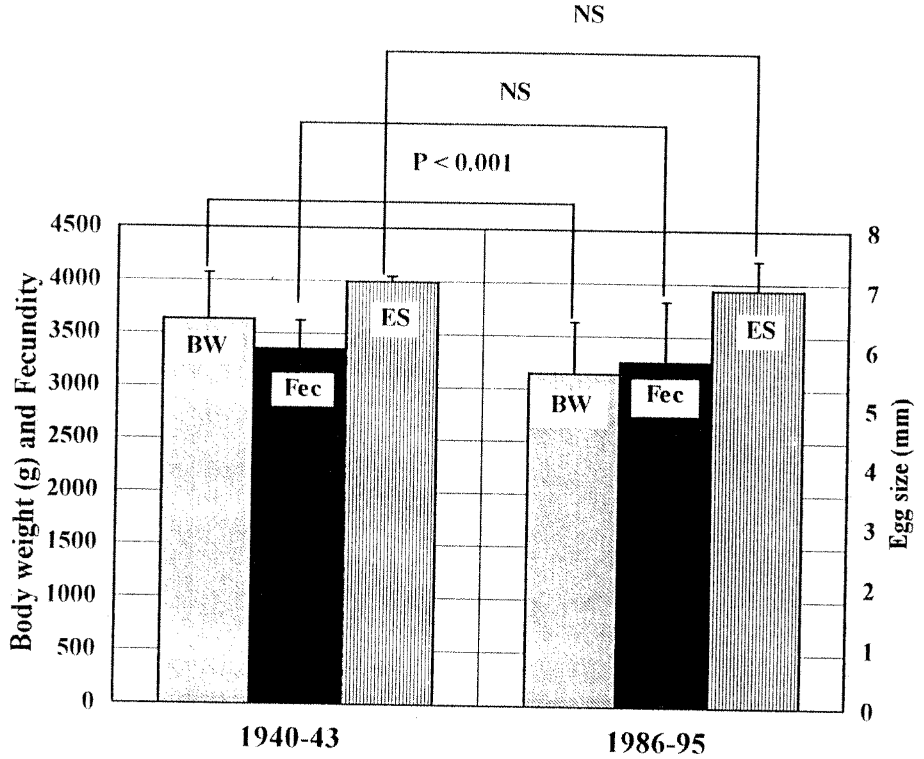


Fig. 12 Annual changes in sea surface temperature (SST) anomalies in western (48-50°N, 164-166°E), central (48-50°N, 179°E-179°W), and eastern (Gulf of Alaska; 48-50°N, 144-146°W) areas of Subarctic North Pacific Ocean during 1946-1995.

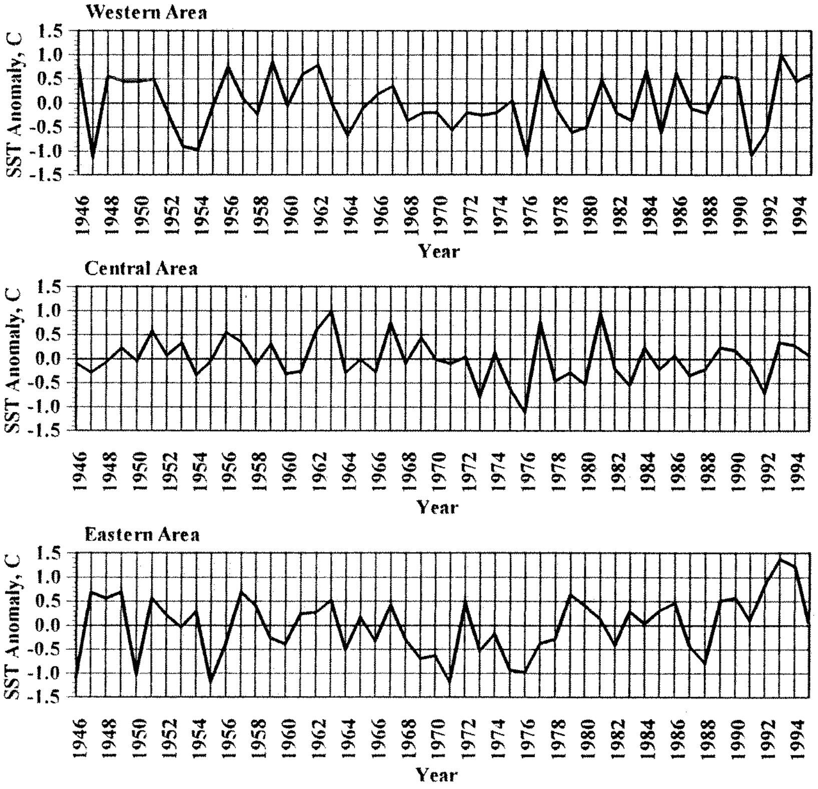


Table 3. Relationship between SST anomaly in the North pacific Ocean and population size of Hokkaido chum salmon. n = number of years of data, a =constant, b = slope, r^2 = the coefficient of determination, and P = the probability that b=0 (NS: P>0.05, ***: P<0.001).

Location	Western Area 48-50N164-166E	Central Area 48-50N179E-179W	Eastern Area 48-50N144-146W
n	42	42	42
a	17,029	14,961	17,979
b	11,409	-24,936	23,638
r^2	0.1761	0.3153	0.5639
P	NS	Ns	***

Table 4. Relationship between SST anomaly in the Subarctic North Pacific Ocean and fork length of Ishikari River adult chum salmon. n = number of years of data, a =constant, b = slope, r^2 = the coefficient of determination, and P = the probability that b=0 (NS: P>0.05, **: P<0.01, ***: P<0.001).

Location	Western Area 48-50N164-166E			Central Area 48-50N179E-179W			Eastern Area 48-50N144-146W		
Age	3	4	5	3	4	5	3	4	5
n	42	42	38	42	42	38	42	42	38
a	609	670	704	609	673	706	608	669	701
b	-8.92	-23.90	-48.20	-4.73	18.11	-4.88	-30.30	-36.10	-60.90
r^2	0.1127	0.2083	0.3300	0.0500	0.1300	0.0030	0.5595	0.4887	0.5966
P	NS	NS	NS	NS	NS	NS	***	**	***

and Ruggerone 1993; Ishida et al. 1995), 2) selection and cumulative genetic effect by fishing gear (Ricker 1981), and 3) population-density effects such as those shown for sockeye (Rogers 1980; Peterman 1984; Kaeriyama 1991; Rogers and Ruggerone 1993) and chum salmon (Kaeriyama 1989, 1992, 1996; Ishida et al. 1993).

The results of the present study show that significant negative relationships between population size and body size was observed for Hokkaido chum salmon population (Fig. 5, Table 1), and that the body size of Ishikari River adult chum salmon was negatively related to the mean SST anomaly during salmon growth period in Gulf of Alaska while those relationships were not observed in other areas of the Subarctic North Pacific Ocean (Table 3, 4). Rogers and Ruggerone (1993) noted that the size of adult sockeye salmon in Bristol Bay was inversely related to the Bristol Bay sockeye population size and positively related to SST during winter and spring. Ishida et al. (1995) reported that growth of salmon was positively correlated with spring SST in the central North Pacific, and stated that growth reduction caused by decreasing SST and increasing population-density. For the Hokkaido chum salmon population, however, the present result of a negative relationship between SST anomaly during the growth period in the ocean and body size at maturity suggests that growth reduction may be affected by their population size rather than change in the SST.

Response of body size to selection by fisheries and hatchery practices may not be the main factor affecting the recent growth reduction because there has been a synchronous increase in age at maturity (Fig. 7). Therefore, population-density effect appears to have a great potential for explaining the cause of the individual growth reduction and the increase in age of Hokkaido chum salmon population.

For the Hokkaido chum salmon population, the recent individual growth reduction has not brought about detectable changes in fecundity and egg size (Fig. 11). Condition factor has been stable since the 1970s (Fig. 6). These results indicate that adult chum salmon returning to Hokkaido are reproductively fit. Return rate, which is survival rate from release to return, continues to rise (Fig. 2B). Several tests of population-density-dependent effects such as Morris and Varley-Gradwell methods shows that density-dependent mortality has not occurred in Hokkaido chum salmon population (Kaeriyama 1992).

On the other hand, body size has remained stable at small size despite the increases in population size and age since the late 1980s (Fig. 4, 7A). Scale analyses show that growth reduction of Hokkaido chum salmon occurs after the second year of ocean life, especially in the third year (Table 2). The possible causes responsible for these are; 1) Japanese adult chum salmon has already attained a biological minimum size at maturity. In age-4, only individuals which grow extremely rapidly at 4 year will be able to mature and to return; 2) profitable ocean environment may restrain the population-density effect. However, aging is now in progress; and 3) carrying capacity of Hokkaido chum salmon population has increased in the North Pacific Ocean.

If adults have attained the biological minimum size at maturity, the population-density effect may progress to the next step from the individual growth reduction in Japanese chum salmon population.

In conclusion, the synchronous decreasing body size and increasing age at maturity of Hokkaido chum salmon was caused due to intraspecific competition and high abundance of chum salmon on the North Pacific Ocean. In future, therefore, it is extremely important issue for the salmon enhancement program to establish an optimum population system by clarifying the mechanism of population regulation such as population-density-dependent effect, and by monitoring biological characters of population such as migration pattern, body size, age composition, fecundity, and egg size.

ACKNOWLEDGEMENTS

I thank Yukimasa Ishida and Makoto Okazaki, National Research Institute of Far Seas Fisheries, and the marine division of Japan Meteorological Agency for providing information about SST data. This work was supported in a part by a Grant-in-Aid (Bio Cosmos Program) from the Ministry of Agriculture, Forestry and Fisheries.

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