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Spatiotemporal change in growth of two populations of Asian chum salmon in relation to intraspecific interaction

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ABSTRACT: Spatiotemporal changes in growth patterns of chum salmon *Oncorhynchus keta* that returned to the Ishikari (Japan) and Namdae (Korea) rivers in 1984-1998 were investigated using scale analysis. Juvenile chum salmon from both populations left coastal marine areas after spring at a size of over 8 cm fork length (FL). In summer, juvenile salmon from the Namdae River entered the Okhotsk Sea at a larger FL than Ishikari River juveniles. There were no significant differences in annual growth between populations of one-, two-, and four-year-old fish. For three-year-old fish, however, Namdae River salmon had significantly higher synchronous and sympatric growth than Ishikari River salmon. Mean FL of adults was also larger in Namdae River salmon than in Ishikari River salmon. ANCOVA results showed (1) negative linear relations between FL and catch, (2) homogeneous slopes of those relations at regional and species levels, and (3) non-homogeneous slopes at the population level, indicating that density dependent effects on growth were most significant at this level. We concluded that growth of chum salmon was concurrently influenced by stronger effects of intrapopulation competition and weaker effects of inter- and intra-specific interactions in the Bering Sea.

KEY WORDS: “back-calculation”, “chum salmon”, “density-dependent effect”, “growth variability”, “intraspecific interaction”, “scale analysis”

INTRODUCTION

Pacific salmon *Oncorhynchus* spp. play an important role as a keystone species in North Pacific ecosystems [1]. The most abundant species caught is pink salmon *O. gorbuscha*, followed by chum *O. keta* and sockeye *O. nerka* salmon. Total catch of chum salmon has increased since the late 1970s in the North Pacific [2]. This increase has coincided with favorable oceanic conditions and successful artificial enhancement programs [3-8].

Concurrently with the dramatic increase in biomass, reduction in body size and increase age at maturity was observed in North Pacific chum salmon. Several hypotheses regarding the cause of these changes have been proposed, e.g., population density-dependent effects [6, 9-14], variation in ocean environment [15-17], and selection and cumulative genetic effects of fishing gear [18]. Density dependence is caused by intraspecific competition. The effect of competition on any individual is greater, as the number of competitors increases [19]. Chum salmon will return at smaller sizes and older ages when their ocean growth is reduced because of food limitation [20].

Tadokoro et al. [21] reported interspecific interactions (feeding competition) among chum, pink, and sockeye salmon for limited micronekton and crustacean prey resources in the subarctic North Pacific Ocean. Few studies, however, have investigated the effects of intrapopulation competition on the somatic growth of salmon in the ocean.

Chum salmon *O. keta* of Asian origin are distributed broadly through North Pacific Ocean [22]. There is very little information about the ocean distribution and migration of Korean chum salmon in the North Pacific Ocean [23]. In this study, we assumed that Korean chum salmon have a migration route similar to that of chum salmon released from Japanese hatcheries [24, 25]. Juvenile chum salmon of Japanese origin are distributed in the Okhotsk Sea from summer to late autumn, and overwinter in the western Subarctic Gyre. Thereafter, immature and maturing chum salmon of Japanese origin migrate between their summer feeding grounds in the Bering Sea and overwintering grounds in the Alaskan Gyre. After about four years, chum salmon return to their natal rivers for spawning [26, 27].

Chum salmon that migrate broadly can rear in spatiotemporally different environments in the North Pacific. Changes in the somatic growth of salmon affected by environmental change result in variation in the growth patterns of their hard tissues, i.e., scales and otoliths [28, 29]. Therefore, to clarify the

relations between intraspecific interactions and growth patterns of North Pacific chum salmon, we compared spatiotemporal changes in the growth patterns of two Asian (Japan and Korea) chum salmon populations using scale analysis and back-calculation from body size. To carry out this analysis, we made the reasonable assumption that after their first summer in the Okhotsk Sea most somatic growth of Japanese and Korean chum salmon occurs in summer in the Bering Sea [22, 25, 30].

MATERIALS AND METHODS

Salmon catch and measurement of biological data

Different aging systems have been developed to describe the age of salmon [31]. We used the “year-old” method, which refers to the year of life since egg deposition in the gravel. Because most age groups of adult chum salmon were collected too irregularly throughout sampling period, we used samples only from the most abundant age group, i.e., 4-year-old female salmon. We analyzed time-series of scale growth and fork length (FL) data from adult chum salmon catches in two locations: (1) the Ishikari River on the west coast of Hokkaido Island in Japan in 1984-1998, except 1985 [28]; and (2) the Namdae River on the east coast of Korea in 1984-1998, except 1995 [23].

Length estimation

A total of 1,513 and 1,112 scales were obtained from 4-year-old adult chum salmon in the Namdae and the Ishikari Rivers, respectively [23, 28]. The scales were measured from the focus to the check and to each annual rings (i.e., r_c , r_1 , r_2 , r_3 , R), and the data were used to estimate FL before (L_c) and after (L_o) the check and at the end of each year (i.e., L_1 , L_2 , L_3 , L_4) according to the back-calculation method (Fig. 1). R and r_i indicate total scale radius and scale radius at age i , respectively, and r_c indicates scale radius from the focus to the check formed when fish entered the Okhotsk Sea.

Although there was little information about check (r_c) formation, we assumed when the check formed from two different evidences. First, field research has shown that juvenile chum salmon of Japanese origin migrate offshore at approximately 8-12 cm FL [32, 33]. Especially, Mayama et al. [24, 33] reported

that Ishikari River chum salmon were 7.4-12.6 cm FL after they left the coastal area and before they migrated to the Okhotsk Sea. Second, our back-calculated estimate of mean size of Ishikari River salmon at check formation was 13.5 ± 1.8 cm FL, which is larger than the reported size of the Ishikari River salmon before they migrated to the Okhotsk Sea [24, 33]. Therefore, we presumed that the check on the scales of Ishikari River chum salmon was formed when fish entered the Okhotsk Sea. Later, we discuss check formation on the scales of Korean chum salmon.

The FL at a specific age i (L_i) was calculated using the following equation [34, 35]

$$L_i = L_t - (R - r_i) / (R - r_0) \times (L_t - L_0),$$

where L_i , L_t and L_c are the back-calculated fork length (FL, cm) at age i , FL of adult at capture, and FL at the check (r_c), respectively. L_0 and r_0 are FL and scale length at the time of scale formation (i.e., squamation). For chum salmon, $L_0 = 4.0$ cm and $r_0 = 0.0114$ cm [36].

Catch data collection

Data on catches of chum salmon in Asia (Japan, Russia, and Korea) and North America (U.S.A. and Canada) in 1950-2003 were taken from Eggers et al. [8] and Lee et al. [37]. Data on Japanese and Korean chum salmon consisted of coastal catches and escapements, while Russian data consisted of coastal catches by Russian and Japanese fisheries within the Russian EEZ. North American data included coastal catches. Total catch in the North Pacific included data on high-seas catches. The data on catches of Hokkaido chum salmon were reported by Kaeriyama and Edpalina [38].

Statistical analysis

We divided North Pacific catches into three levels: (1) population (total return including coastal catch and escapement in Hokkaido and Korea), (2) regional (total Asian catch), and (3) species (total North Pacific catch). To evaluate the effect of catch on body size (FL), slope coefficients in FL-catch linear relation among data sets ($n = 6$, FL of Ishikari River and Namdae River chum salmon at three catch levels) were compared using analysis of covariance (ANCOVA). The relationship between catch (C) and FL expressed as a natural logarithm equation ($FL = aC^b$) was analyzed with ANCOVA using SPSS 17.0J

(SPSS Japan Inc., Tokyo, Japan: license No. 6369952). The ANCOVA was of little use unless it was reasonably correlated with the dependent variable [36]. What the ANCOVA provided was a method by which we removed pretreatment variations, as measured by the control variable (or covariate, catch), from the post-treatment means (means of dependent variable, FL) prior to testing the significance of post-treatment differences among data sets [39]. Therefore, if we found significant linear relations between FL and catch and also a difference in FL among data sets, they were attributed to catch. To carry out this analysis, two assumptions (i.e., homogeneity of the regression slope coefficients and residual error variances) were required [40].

RESULTS

Changes in catch of chum salmon in the North Pacific

In the North Pacific, total catch of chum salmon has dramatically increased since the late 1970s (Fig. 2). The mean catch of Japanese chum salmon increased from 6 million fish in 1950-1975 to 43 million fish in 1976-2003. In North America, as above mentioned, Southeast Alaska has seen a large increase in chum salmon catches in the 1990s due to the establishment of large hatchery runs despite a decreasing trend in other regions. Catch of Russian chum salmon has gradually increased since the late 1970s, similar to Japan, in spite of low abundance during the 1950s and the early 1970s. Abundance of Korean chum salmon is now at a steady low level despite an increasing trend in the 1990s. The mean catch in recent years (2000-2003) of chum salmon was 94 million fish in the North Pacific (60 million fish in Japan, 22 million fish in North America, 12 million fish in Russia, and 0.4 million fish in Korea). The relation between year and catch of chum salmon since 1976 was well expressed as a natural logarithm equation (Table 1a). The slope of the equation showed no difference among populations (0.044 in Japan, 0.041 in Russia, and 0.032 in North America) except for the Korean population (0.218) (Table 1b).

Temporal change in body size of Korean and Japanese populations

Coincident with the broad increase in the catch of chum salmon in Asia (Japan and Korea), decreasing

trends in body size (i.e., FL) at maturity were observed in chum salmon returning to Japan and Korea since the end of 1970s (Fig. 3). Especially in 1984-1998, annual catches of chum salmon in Japan were extremely higher than catches in Korea (Fig. 2), whereas the FL at maturity of the Namdae River population was significantly larger than that of the Ishikari River population (ANOVA; $F = 12.75$, $P < 0.01$). The FL of the Ishikari River population showed a decreasing trend from the late 1970s to the mid 1980s, and has leveled off to a smaller size since then.

Relation between catch and body size of Korean and Japanese populations

The relation between catch and FL at maturity of chum salmon of the Namdae and the Ishikari Rivers was well expressed as a natural logarithm equation. The FL at maturity was negatively correlated with the catch at population, regional (total Asian catch), and species (total North Pacific catch) levels, respectively (Table 2). ANCOVA revealed that the slopes of regression lines were not identical within and without data sets (ANCOVA; $F = 2.52$, $P < 0.05$), indicating that the effects of catch on FL at maturity varied. Specially, slope coefficients (b in Table 2) were statistically heterogeneous at the population level (P in Table 2). The ANCOVA showed homogeneous slopes within and without two data sets except at the population level. These results indicated that FL at maturity was statistically homogeneous between the Namdae River and the Ishikari River chum salmon after accounting for catch at regional and species levels (regional level: $P = 0.63$; species level: $P = 0.69$).

Spatiotemporal variation in growth patterns of Korean and Japanese chum salmon populations

The results of back-calculation of annual growth showed that Namdae River chum salmon had more growth than Ishikari River chum salmon as three-year-olds, despite no differences in growth at other ages (Fig. 4). Concurrently, interannual variability in growth of Ishikari River chum salmon was significantly correlated with variability in growth of the Namdae River salmon except for one-year-old fish (Table 3). The Namdae River juvenile chum salmon had a larger body size before entering the Okhotsk Sea (L_c) and poorer growth in the Okhotsk Sea (L_o) than Ishikari River juveniles (Fig. 5). These results indicated that Ishikari River chum salmon migrated directly from Hokkaido coastal waters into the Okhotsk Sea at a

mean size of 10-12 cm FL, while the Nambae River population migrated from Korea coastal waters to the Japan Sea at a mean size of 8 cm FL (Fig. 6, Kang S, unpubl. data, 2008), and then migrated to the Okhotsk Sea at mean size of 20 cm FL (Fig. 5).

DISCUSSION

Carrying capacity and growth

There were major atmospheric, oceanographic, and ecological changes in 1976/77 in the North Pacific [41-43], which have been considered a regime shift. For example, the abrupt change in magnitude and sign of the Pacific Decadal Oscillation (PDO) Index, which broadly characterized decadal-scale (20-30 year) variation in Pacific climate and marine ecosystem productivity [43, 44], coincided with dramatic changes in population levels of numerous species in the Northeast Pacific [46]. The entire ecosystem of the region shifted from one steady state condition to another at this time [47]. The ocean carrying capacity of Pacific salmon is related not only to regime shifts, but also to density-dependent effects [1, 48]. The carrying capacity of sockeye, chum, and pink salmon after the 1976/77 regime shift was twice that of 1947-1975 [1]. However, there was a concurrent decrease in residual carrying capacity (*RCC*) [49], which was defined as $RCC = (carrying\ capacity - biomass) / carrying\ capacity^{-1}$. The decrease in *RCC* was demonstrated by a positive linear relation between decreased FL and increased age at maturity of Hokkaido chum salmon populations, indicating that a density-dependent effect reduced the somatic growth of individual fish [38]. This hypothesis that the biomass of Pacific salmon was approaching the total carrying capacity of the subarctic Pacific for Pacific salmon after 1976/77 regime shift, can be restated. For example, the relative abundance of the prey of Pacific salmon was below satiation level [47], and/or the shelter (habitat) that would support growth of Pacific salmon was severely restricted by thermal conditions and resulted in greater density of salmon [50].

The enhanced primary productivity caused by higher temperatures and shallow mixed layer depths in the Northeast Pacific following the 1977 regime shift might have worked its way up the food chain through increased zooplankton abundance [3] to produce the high abundance of Alaska salmon [5]. However, increases in salmon prey abundance in response to climate change are not well documented

because Pacific salmon opportunistically consume a variety of prey of unknown biomass [21, 51].

Although it is possible that greater prey biomass caused greater salmon biomass since the late 1970s, the declined FL of chum salmon suggest that food availability was limited [20, 52]. Pypers and Peterman [53] also reported that the mean sizes of individual salmon returning to their natal rivers to spawn has been declining since the late 1970s despite apparently more favorable feeding conditions in the central Gulf of Alaska in the 1980s. It appears that the positive effect of increased food supply on the growth of salmon was offset by increased abundances of salmon, resulting in greater competition and smaller individual body size [52, 53].

It is not easy to decouple the effects of food availability and seawater temperature on fish growth [23] because of the complexity of their relation to climatic-oceanic events. For example, Aydin et al. [54] showed that latitudinal variation in the July sea surface temperature (SST) minimum between 1994 and 1998 was related to changes in growth of salmon mediated by changes in prey distribution in the Gulf of Alaska. Brander [55] predicted that fish production may increase in some high-latitude regions because of global warming and decreased ice cover. Coincident with this prediction, Kaeriyama et al. [28] showed that first-year growth, determined by scale back-calculations, and survival of Ishikari River chum salmon in 1946-2004 was negatively correlated with sea ice concentration in winter. However, Kaeriyama [1] made two predictions about global warming effects on Hokkaido chum salmon based on optimal habitat conditions (SST) and the SRES-A1B greenhouse gas emission scenario of the Intergovernmental Panel on Climate Change (IPCC): (1) global warming will decrease their ocean carrying capacity by reducing distribution area, and (2) strong density-dependent effects will occur in populations in the future.¹ For Ishikari River chum salmon, this means that the positive effects of global warming suggested by Brander [55] have already occurred, and will turn to negative effects in the future. Welch et al. [56] and Ishida et al. [57] also suggested that global warming may cause a northward shift in the southern limit of salmon distribution in the ocean, leading to increased competition caused by stronger density-dependent effects because of habitat reduction [1].

Comparison between Korean and Japanese populations

Our results for three-year-old fish, showed that Namdae River chum salmon had sympatric-higher

growth than the Ishikari River salmon in the Bering Sea in 1984-1998. We suggest that this resulted from a stronger density-dependent effect at the population level caused by larger population size. Trends in catch since the late 1970s differed between Japanese and Korean chum salmon, which increased more rapidly in the 1990s, despite the common increasing trend in catch of chum salmon in all major salmon-producing nations of the North Pacific Rim. Between the mid 1980s and the late 1990s, the fluctuations in body size (FL) at maturity also differed between the Namdae River and Ishikari River populations. However, our results showed that long-term (1984-1998) spatiotemporal variation in growth patterns of these two populations was significantly similar during their second, third, and fourth years in the Bering Sea. This indicated (1) Namdae River and Ishikari River chum salmon experience similar open-ocean environments, e.g., physiological condition and prey community [52], though the migration route of Korean chum salmon remains uncertain [23]. And, it indicated (2) differences between populations in fluctuation in FL were caused by variation in growth of one-year-old fish. That is, juvenile chum salmon from the Namdae River grew more than those from the Ishikari River before entering the Okhotsk Sea, and vice versa after entering the Okhotsk Sea, where both populations spend their first summer and fall in the ocean.

In 1984-1998, the abundance of adult chum salmon returns in Japan was extremely higher than returns in Korea. On the other hand, the adult body size (FL) of the Namdae River population was larger than the Ishikari River population, which showed a decreasing trend in FL from the late 1970s to the mid 1980s and leveled off to a smaller size since then. The significant effect of catch on FL was more severe at the population level than at the regional and species levels. The slope coefficient of the FL-catch relation of the Ishikari River chum salmon at the population level was more than twice that of the Namdae River. This result suggested that (1) the density-dependent effect was also more severe at population level, and (2) smaller FL in the Ishikari River chum salmon was caused by larger population size. Because body size (FL) at maturity comprises past growth at younger ages, our research detected when and where this more severe density-dependent effect occurred in the Ishikari River chum salmon with more specificity than was previously known.

The comparative results of spatiotemporal change in growth of two populations in 1984-1998 showed that three-year old Namdae River chum salmon had sympatric-higher growth than three-year-old Ishikari River chum salmon. There were no between-population differences for other age groups. The key point

presented here is that interannual variation (1984-1998) in growth of three-year-old Namdae River and Ishikari River chum salmon was similar, despite the larger FL of Namdae River Chum salmon. These results suggest that individuals in each population can grow to a different size because of intraspecific interaction, including intrapopulation competition, even though it is a consequence of chum salmon growth being inhibited by either common biotic (food) or abiotic (temperature) factors. Namely, there is possibility that intraspecific interaction is inclusive not only of interpopulation but also intrapopulation competition, which will result in sympatric-lower or -higher growth of chum salmon of each population in the open ocean under circumstances such as decreased *RCC* (i.e., intensified competition for available food supply and shelter).

According to the early life history model of Japanese juvenile chum salmon [32], large individuals (12 cm FL) leave the coastal area during the optimum-temperature period (April-May) on a “foraging migration”. Small individuals (8 cm FL) migrate offshore during the late period (June-July) on an “escape migration” from the Pacific coast of the Tohoku Region. The Korean juvenile chum salmon grew up to 8 cm FL in the coastal area until early May (Fig. 6), and then migrated to the Japan Sea, where they grew up to 20 cm FL (L_c in Fig. 4). When the check (r_c in Fig. 1) was formed on the scale, the estimated mean length using the back-calculation method was 20.3 ± 1.4 cm FL (L_c in Fig. 4). These two results (L_c in Fig. 4 and Fig. 6) support the possibility that the check on Korean chum salmon scales was formed at entrance into the Okhotsk Sea. In addition, Korean chum salmon left the coastal area earlier than Japanese chum salmon. Mayama and Ishida [58] reported that Japanese chum salmon avoid warm water (14 °C) of the Tusima current. On the coast of Hokkaido, young salmon were distributed at seawater temperatures between 8 °C -13 °C, and disappeared at temperatures over 13°C. In 2006, warm water (15 °C) occurred in the coastal area near the Namdae River (38° 41' N) starting in mid May (Korean Oceanographic Data Center Web: <http://kodc.nfrdi.re.kr/home/kor/satellite/main.php> “Accessed 01 Nov 2008”), which might have caused early outmigration of juvenile chum salmon from the Korean coast.

Because of the lack of population-specific data, researchers frequently combine populations into regional- or species-level aggregates [59]. The finding that density-dependency appears to have a non-uniform effect on growth of chum salmon due to intrapopulation competition, demonstrates the importance of considering these effects when attempting to manage salmon populations.

Comparisons of spatiotemporal variation in growth of chum salmon of two Asian populations in 1984-

1998 using scale analysis showed synchronous- and sympatric-lower or -higher growth between populations of three-year-old chum salmon in the Bering Sea, despite showing no difference at other ages. Density-dependent processes had a stronger effect at the population level than at regional and species levels. The growth of chum salmon in the Bering Sea was controlled by inter- and intra-specific interactions such as carrying capacity and population density.

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Figure legends

Fig. 1 Measurement of the scale of a four-year-old adult chum salmon that returned to the Ishikari River, Japan. R indicates scale radius, and r_i is the radius at age i . L_i is back calculated fork length (FL) at age i . Radius r_c extends from the core to the check, which is formed at the entrance into the Okhotsk Sea. L_c is FL at the check on scale. L_o is FL after the check formation until r_l formation

Fig. 2 Annual changes in catch of chum salmon in the North Pacific. Data were from Eggers et al. [8] and Lee et al. [37]

Fig. 3 Annual changes in fork length (FL) of four-year-old adult chum salmon that returned to the Ishikari River in 1950-2003 (closed circle) and the Namdae River in 1984-1998 (open circle). Vertical bars indicate standard deviations. Data were from Kaeriyama et al. [28] and Seo et al. [23]

Fig. 4 Temporal changes in growth of four-year-old adult chum salmon that returned to the Namdai River (open circle) and the Ishikari River (closed circle) from the first (L_1) to the fourth year (L_4)

Fig. 5 Temporal changes in growth of four-year-old adult chum salmon that returned to the Namdae River (open circle) and the Ishikari River (closed circle) in the first year (L_c and L_o). The X-axis represents the year of growth (ocean entry year)

Fig. 6 Frequency distribution of fork length (FL) of Korean juvenile chum salmon collected in the Korean costal area on May 10 and 11 in 2006 (Kang S, unpubl. data, 2008)

Fig. 1

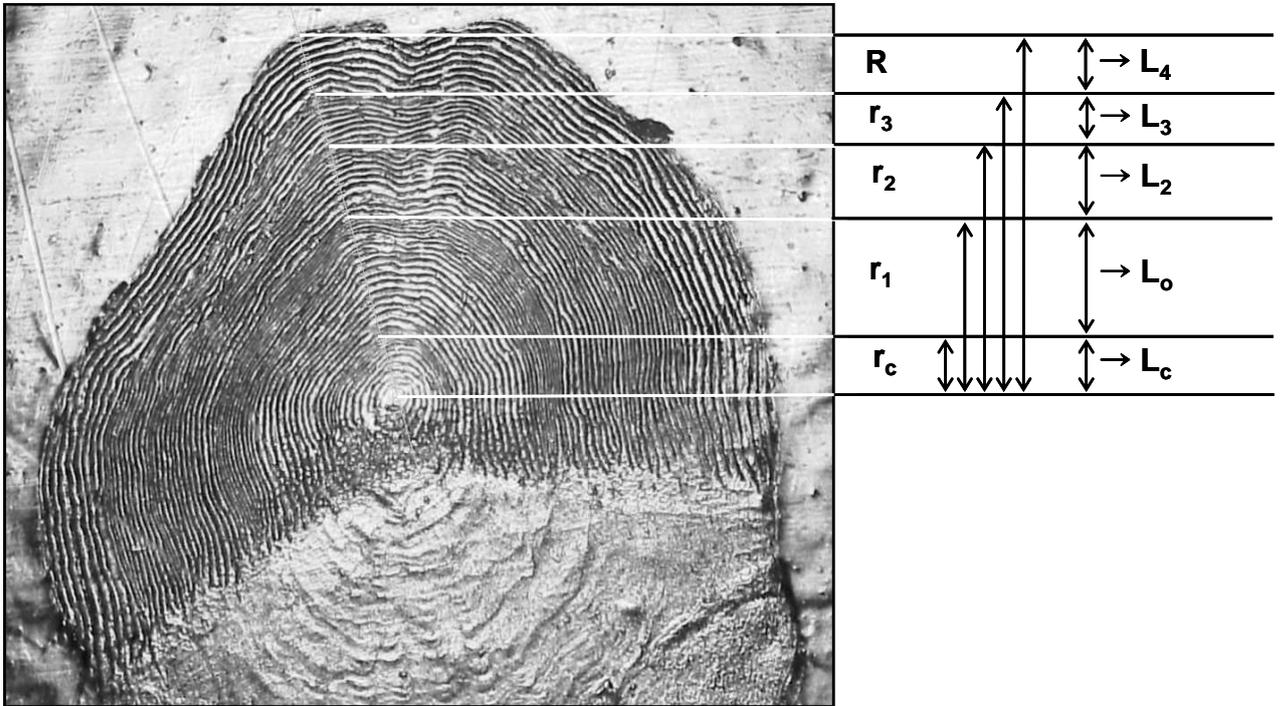


Fig. 2

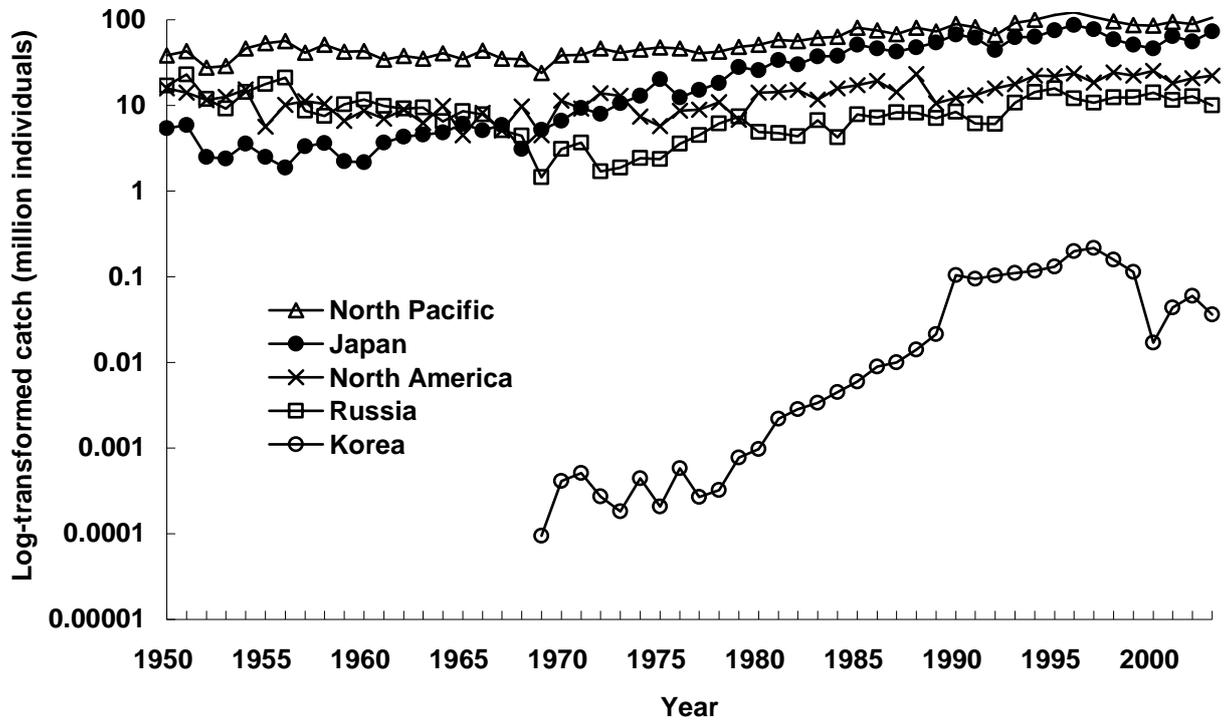


Fig. 3

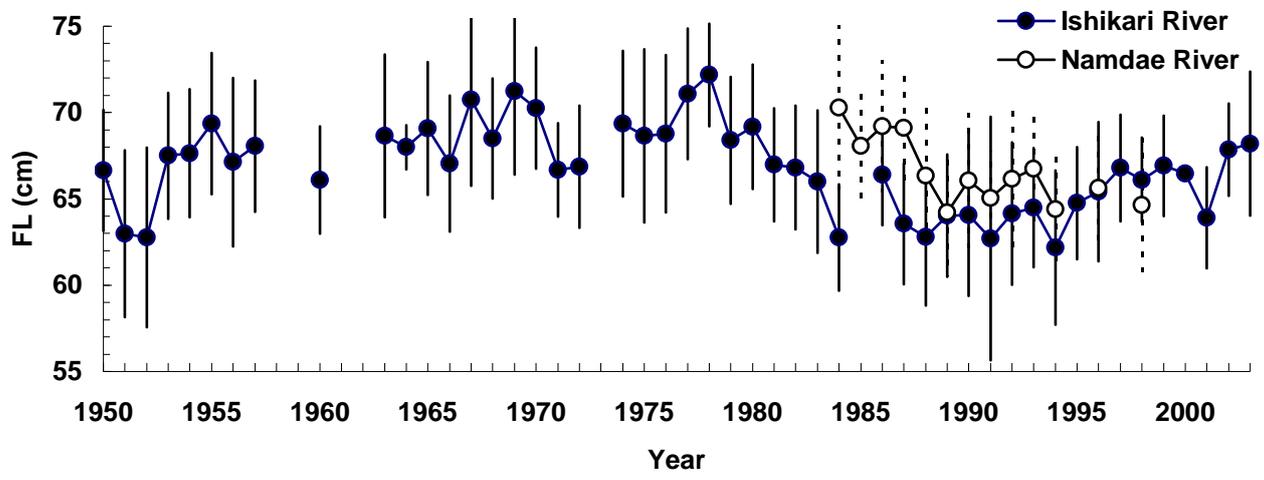


Fig. 4

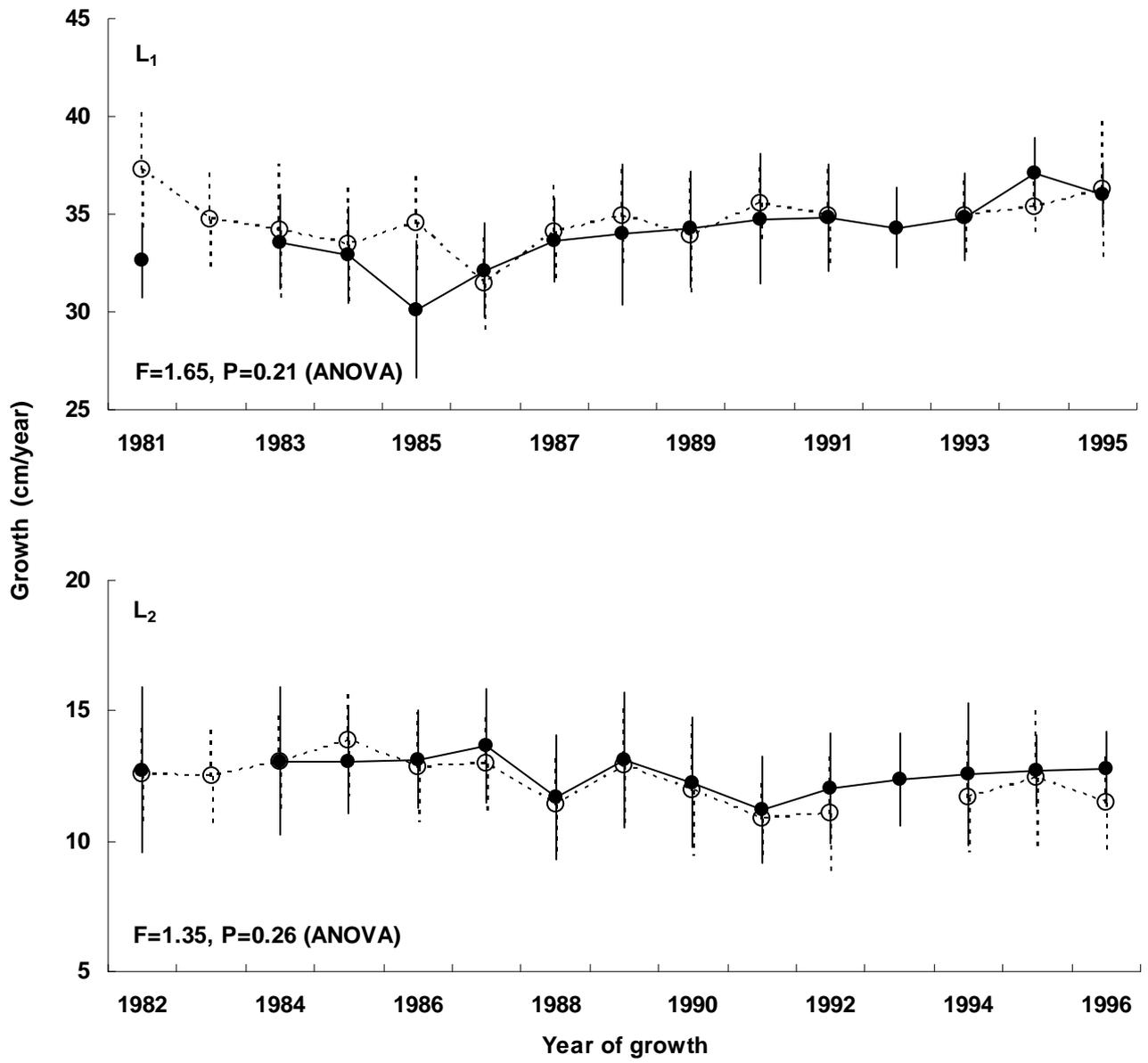


Fig. 4 (continued)

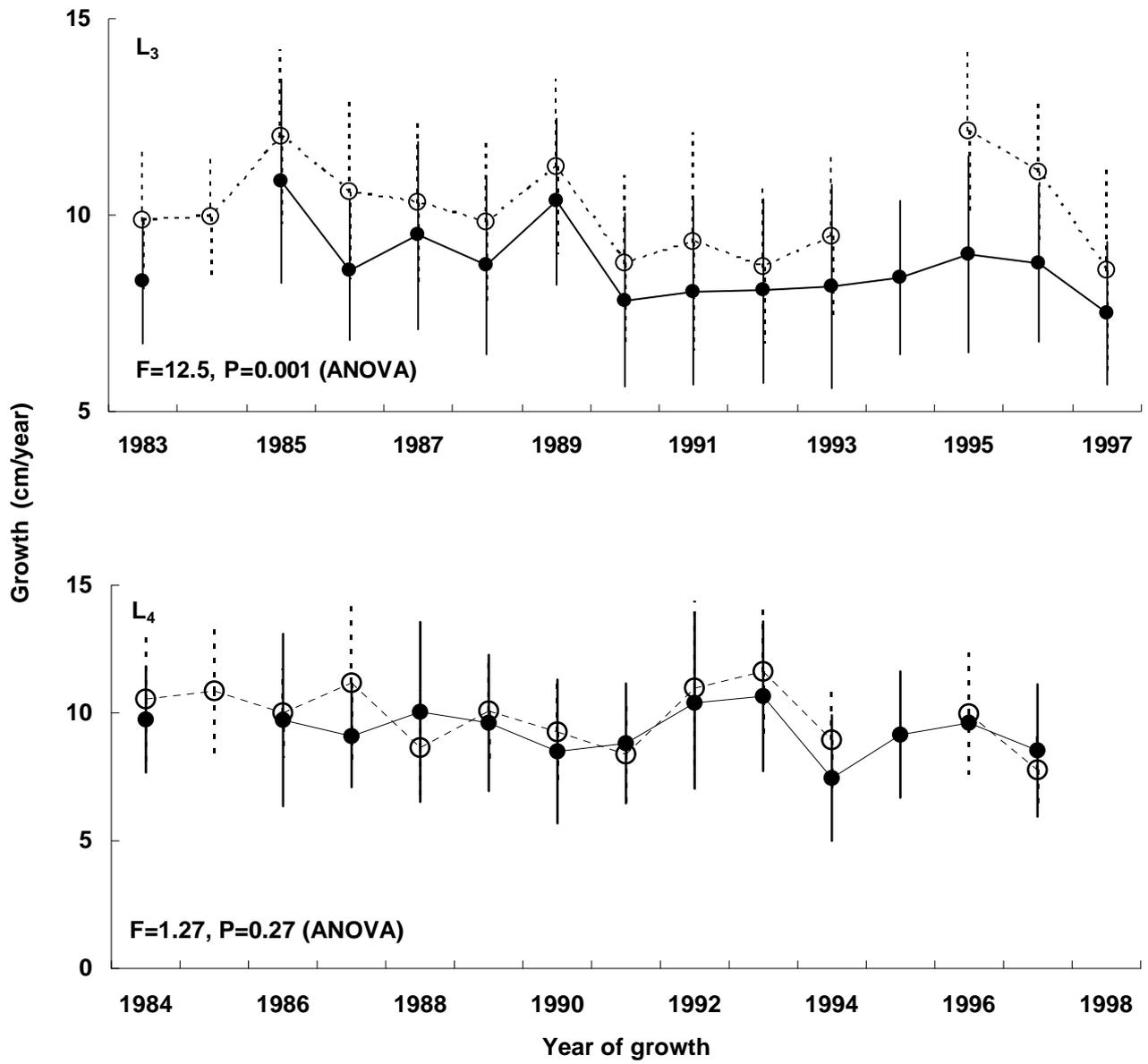


Fig. 5

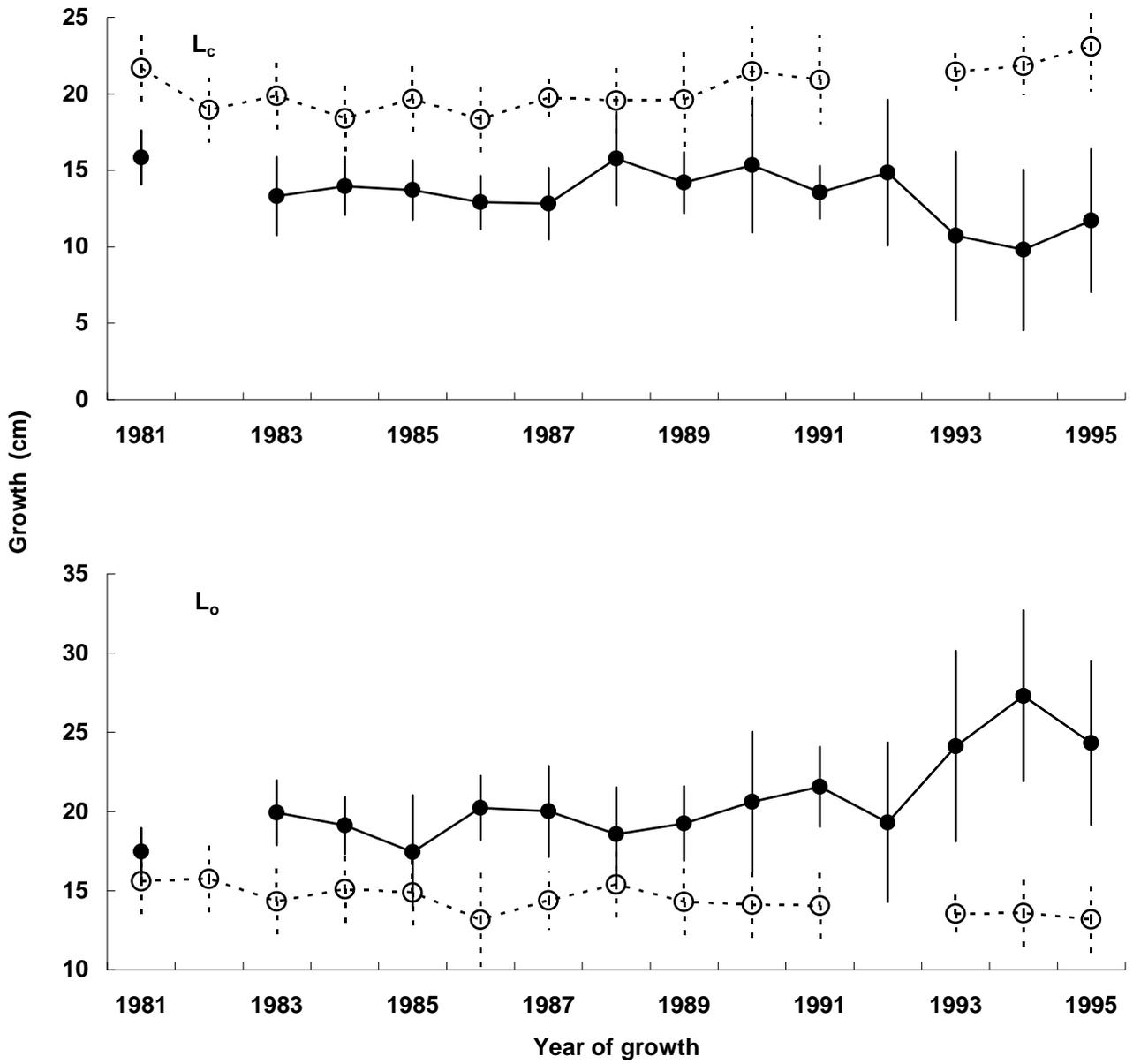


Fig. 6

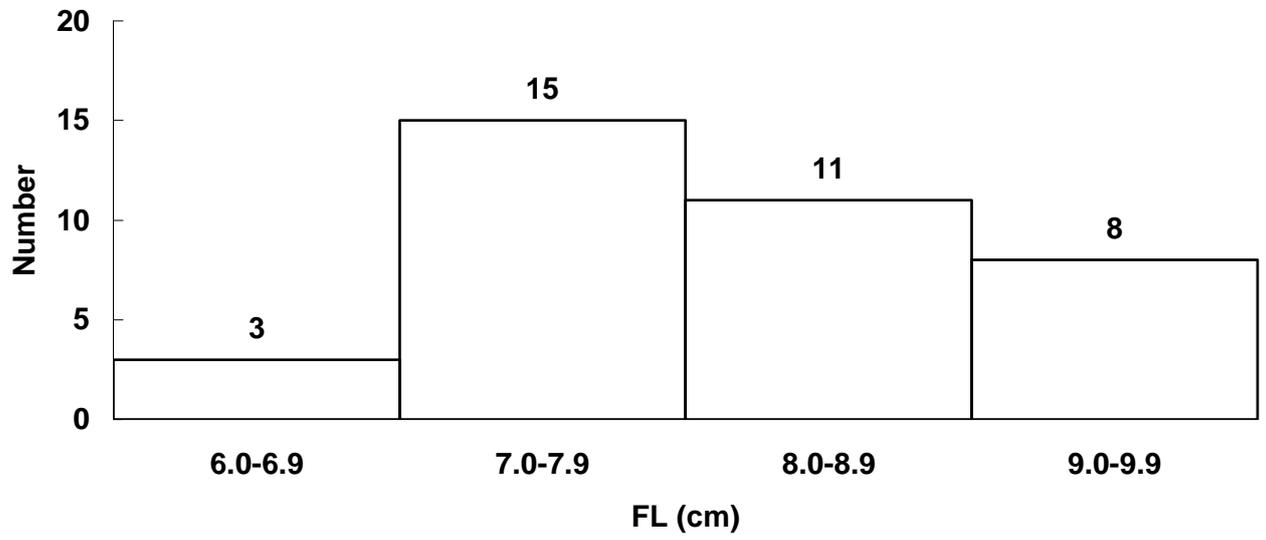


Table 1 (a) Relation between year and catch of chum salmon in Asia (Japan, Russia, and Korea) and North America, 1976 - 2003. The symbols are defined as follows: R^2 is coefficient of determination; b is slope coefficient; a is constant. (b) The difference in the slope (b) of the regression line (as shown in Table 1a) between populations using ANCOVA. P -values and t -values associated with each correlation are shown in the lower and upper triangle, respectively. Data on catches of chum salmon were taken from Eggers et al. [8] and Lee et al. [37]

(a)

$N=28$	North Pacific	North America	Japan	Russia	Korea
R^2	0.75	0.56	0.66	0.67	0.71
b	0.03	0.03	0.04	0.04	0.22
a	-60.19	-59.90	-84.62	-79.96	-438.56
F	75.53	32.25	49.34	51.89	62.18
P	<0.001	<0.001	<0.001	<0.001	<0.001

(b)

	North Pacific	North America	Japan	Russia	Korea
North Pacific	-	0.04	2.27	1.62	7.24
North America	0.97	-	1.99	1.36	7.15
Japan	0.03	0.05	-	0.76	6.44
Russia	0.11	0.18	0.45	-	6.75
Korea	<0.001	<0.001	<0.001	<0.001	-

Table 2 Regression coefficients for the slope of the linear relation of fork length (FL, cm) to biomass (1,000 individuals) for six data sets (FL of the Ishikari and the Namdae River populations with three levels of catch, e.g., population, regional, and species levels) in ANCOVA. All measurements were expressed as a natural logarithm equation. *P*- and *t*-values of comparisons of the slopes (*b*) of the FL-catch linear relation between data sets at the same level of catch are shown. Catch data for data sets of the Ishikari River chum salmon were reported by Eggers et al. [8] and Kaeriyama and Edpalina. [38] Catch data for data sets of the Namdae River salmon were reported by Lee et al. [37] and Eggers et al. [8]

Level of catch	River	R^2	<i>b</i>	<i>a</i>	<i>N</i>	Slope	
						<i>t</i>	<i>P</i>
Population	Namdae	0.577**	-0.016	4.26	13	2.11	0.04
	Ishikari	0.304**	-0.038	4.58	34		
Regional	Namdae	0.367*	-0.087	5.17	13	0.22	0.83
	Ishikari	0.313**	-0.066	4.91	32		
Species	Namdae	0.307*	-0.088	5.19	13	0.16	0.87
	Ishikari	0.304**	-0.068	4.59	32		

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Table 3 Results of correlation analysis (Pearson's correlation coefficients, r) on the growth of the Namdae River and the Ishikari River chum salmon at the same age (i.e., growth at the first-, second-, third, and fourth-year-olds is, L_1 , L_2 , L_3 , and L_4 , respectively) during period of 1984-1998

Growth	Pearson correlation		
	N	r	P
L_1	27	0.371	0.213
L_2	27	0.828	< 0.001
L_3	27	0.812	0.001
L_4	27	0.628	0.022

アジア系シロザケ 2 個体群の種内相互作用と成長パターンの時空間変動

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鱗分析と体サイズのバックカリキュレーション法に基づき, 1984-1998 年に北海道石狩川と韓国ナンダエ川へ回帰したシロザケの成長パターンの時空間変動を明らかにした。その結果, 石狩川系幼魚が沿岸から小型で直接オホーツク海へ移動するのに対して, ナンダエ川幼魚は日本海を回遊後オホーツク海へ大型で移動することが明らかとなった。シロザケ 4 歳魚の体サイズはベーリング海で 3 歳時に種内あるいは個体群間より個体群内で強い密度依存効果を受けることが示唆された。