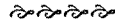


Recent Reduction in Chum Salmon (*Oncorhynchus keta*) Growth and its Consequences for Reproduction

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Abstract: A statistically significant decrease in body length and fecundity of the Iturup Island chum salmon (*Oncorhynchus keta*) after 1985 coincided with an increase in mean age and decline in adult returns. These changes were accompanied by an increase in ocean mortality, but conditions of fry growth in the coastal zone appeared to be the determining factor in changes in overall chum salmon survival in the sea. The rate of sexual maturation was positively related to age at maturity of parents. Increased age of chum salmon spawners, associated with low spawning numbers, partially compensated for decreasing fecundity. This is an example of reproductive homeostasis.

INTRODUCTION

Since the middle 1980s uncommonly strong anomalies in ice formation were recorded in the northwestern part of the Pacific Ocean as a consequence of climate changes (Khen 1997). Early in the 1990s water circulation and structure of zooplankton and nekton communities altered in response to global climate change (Shuntov et al. 1996; Radchenko et al. 1997). A decrease in Pacific salmon catches in the second half of the 1990s may be connected with these changes (Klyashtorin and Sidorenkov 1996; Beamish et al. 1997).

If this climate change seriously affects chum salmon (*Oncorhynchus keta*) feeding and growth in the ocean, the consequences should become apparent in various biological indices. An investigation of these indices is the objective of the present study. Long-term changes in growth, fecundity and age at maturation of chum salmon are considered in an attempt to explain changes in population abundance.

MATERIALS AND METHODS

Chum salmon reproduction has been studied at Iturup Island (Kuril Islands) since 1974. These salmon were from a comparatively isolated group from Kuril Bay and the rivers Kurilka, Rybatskaya and Kitovaya flowing into the Okhotsk Sea. Adults were sampled from commercial catches during chum salmon mass migration every 7–10 days. Fork length (FL), body weight, sex, and female fecundity were

determined. Scales were collected from 2–4 rows above a lateral line behind the dorsal fin. Fish age is denoted by the number of years of life completed (e.g. 0.3: 0 years in freshwater, 3 full sea years and part of the following year). Annual growth was determined by back calculation from scale ring increments. Scales were measured along the longest radius. The numbers of adult fish were determined from commercial catch data in the bay and river mouths, and from visual counting in rivers by foot-survey. The small size and shallow depth of these rivers facilitated this task. Annually in the first half of November, while chum salmon were spawning, the number of live and dead fish were counted in 70–90% of the total area of chum salmon distribution from river mouths to upper reaches. Then the number of chum salmon, calculated per total area, was increased 20% in expectation of later returns (Kaev 1989).

The number of fry migrating down the Rybatskaya River was determined from net traps set at night. A standard method for such studies (Hunter 1959; Volovik 1967) modified for small rivers of the Kuril Islands was used (Kaev 1989). A coefficient of downstream migration was determined from a ratio of number of fry migrants to the total female fecundity (nos. of females x average individual fecundity) in the Rybatskaya River. This coefficient from the Rybatskaya River (4,200 m² of spawning grounds) was used to estimate numbers of fry migrants in the rivers Kurilka (15,200 m²) and Kitovaya (2,300 m²). On the basis of estimated numbers of fry migrants, chum

salmon abundance in rivers, and commercial catch data, a return coefficient was calculated as the ratio of returning adult fish to the number of fry migrants. As for the Rybatskaya River, a coefficient of fry downstream migration was determined for the Ilyushin River at Kunashir Island (Kuril Islands), where the author has conducted regular investigations since 1994.

Fry migrants were sampled for body length since 1974, but only since 1977 were fry sampled in numbers proportional to catches throughout the period of downstream migration. In addition, fry were caught every 10 days from Kuril Bay during May, June and July to determine their length, weight, feeding indices, and scale structure. Fry growth could not be determined directly from their body length because of continuous arrival and departure of fish into or out of the bay. Some fry had left the rivers recently and were without scales. Others had been in the bay for some time and had scales with several rings. Sampled fry were divided into groups with equal numbers of scale rings. For each group a bar chart of body length composition was made. Then all bar charts were combined and a coefficient of asymmetry (A_s) was determined. This index has been suggested as representing fry condition during early sea life (Kacv 1979).

Between 100 and 400 adult fish were collected in most years for determination of their age, length and fecundity (Table 1). Fry were also sampled both as migrants in the river, and as fry with scales from the bay (Table 1). The author participated in collecting and processing these samples from 1974 to 1988, and from 1989 to 1995 determined age and annual scale increments from samples collected by A.I. Ardavičius.

Significance of the difference between means was assessed using the formula from Plochinsky (1970, p. 296):

$$F_d = [(M_1 - M_2)^2 \sigma_z^{-2}] [n_1 n_2 (n_1 + n_2)^{-1}] \geq F_{st}$$

where F_d is Fisher's criterion for significant difference;

$M_1 - M_2$ is the difference between means;

n_1, n_2 is the number of fish in first and second samples;

$$\sigma_z^2 = [(n_1 - 1) \sigma_1^2 + (n_2 - 1) \sigma_2^2] (n_1 + n_2 - 2)^{-1}; \sigma$$

means standard deviation;

F_{st} – standard values of Fisher criterion at 95 %, 99 % and 99.9 % significance levels.

Table 1. Numbers of adult chum salmon sampled annually for age, length and female fecundity from commercial catches near mouths of rivers in the Kuril Bay area (Iturup Island) 1974–1995, numbers of downstream migrating fry in the Rybatskaya River sampled for length, and numbers of fry sampled in the bay for length, and number of sclerites on their scales.

Year	Numbers of adult chum salmon		Numbers of fry	
	Age and Length	Fecundity	River	Bay
1974	300	130	263	287
1975	300	121	93	106
1976	400	202	-	143
1977	200	102	112	188
1978	200	103	158	274
1979	300	140	176	276
1980	300	156	256	323
1981	271	162	319	163
1982	100	44	254	144
1983	300	95	322	274
1984	200	120	396	461
1985	300	168	403	323
1986	380	183	321	260
1987	300	134	631	329
1988	200	99	536	225
1989	200	79	-	-
1990	188	90	-	-
1991	193	36	-	-
1992	207	-	-	-
1993	149	29	-	-
1994	193	-	-	-
1995	197	19	-	-

RESULTS

Chum salmon return to spawn in the rivers of Iturup Island at the age of 0.2–0.6. Fish of the most abundant age groups (0.3 and 0.4) were used to follow long-term changes in body length and fecundity. First, anomalies in chum salmon growth were noticed in the second half of the 1980s (Kaev 1994), and therefore data were grouped by year of return before and after 1985. Mean fish length from 1974–1984 was significantly greater ($p < 0.05$ Fisher test) than from 1985–1995 (Table 2). Annual growth did not decline uniformly at all ages. The growth of age 0.3 fish decreased in the third year of life, and growth of age 0.4 fish decreased in the third and fourth years of life. There were no significant differences in length in both age groups when aged 0.1.

Together with reduced growth, variability in length increased in recent years. This is illustrated by age 0.4 fish, which have growth marks at both age 0.3 and 0.4, that is at both ages at which anomalously low annual growth appears. In the most recent 10 years, annual growth increment for age 0.4 fish has increased compared to 0.3, and the coefficient of variation has also increased (Fig. 1). A significant decrease in female fecundity in this period was also noted (Table 2).

In recent years the proportion of older chum salmon in returns has increased. The proportion of age 0.2 fish declined by half, the proportion of 0.3 also declined, and the proportions of older fish increased respectively (Table 3). The proportions of

age 0.2, 0.5 and 0.6 fish among returns were very small, and therefore to characterize chum salmon age trends, the percentage relationship of age 0.4 fish in the total of age 0.3 and 0.4 fish was used. Not only did the proportion of older fish increase, but also the fluctuation of ages in returns in contiguous years increased (Fig. 2). The increased variability occurred despite a reduction in average abundance of chum salmon. For instance, the returns of chum salmon in 1971–1981 averaged 315,000 individuals, and the difference in numbers between contiguous generations averaged 2.2 times, while returns of 1982–1991 averaged only 48,000 individuals, with contiguous generations differing by a factor of 3.6 times.

Estimated survival from egg to downstream migrant (downstream migration coefficient, Fig. 3), and mean length of fry migrants (Fig. 4) tended to increase as the proportion of parents aged 0.4 increased over the proportion aged 0.3. Fry length in different years was associated with the average age of their parents ($R^2 = 0.37$; $n = 12$; $p < 0.05$) rather than their parents' body length ($R^2 = 0.04$; $n = 12$; $p > 0.05$).

In recent years chum salmon survival at sea declined. Marine survival of brood year classes from 1973–1981 ranged from 0.57 to 1.90%. In later years survival at sea declined, ranging from 0.12 to 0.84% (Fig. 5). Because of the dependence of marine survival on the asymmetry of fry growth, representing condition, in the coastal zone before 1982 and after 1982, one can say that condition appeared to be a factor determining chum salmon survival in the sea.

Table 2. Absolute fecundity (AF, eggs), fork length (FL, cm) and annual mean length increment (FL_i, cm) of chum salmon at Iturup Island at the age of 0.3 and 0.4 during two periods.

Age	Indices	1974–1984			Fisher criterion	1985–1995		
		Mean	S.D.	<i>n</i>		Mean	S.D.	<i>n</i>
0.3	AF	2550	232	11	12.01**	2261	101	9
	FL	71.22	1.16	11	21.50***	68.22	1.77	10
	FL ₁	27.67	0.73	11	0.01	27.71	1.27	10
	FL ₂	16.75	0.57	11	0.55	16.53	0.78	10
	FL ₃	12.31	0.83	11	14.73**	10.75	1.03	10
	FL ₄	14.48	0.73	11	4.53*	13.25	1.76	10
0.4	AF	2613	179	11	15.12**	2294	173	8
	FL	76.80	1.78	11	24.95***	72.67	2.01	10
	FL ₁	26.85	0.69	11	0.75	27.25	1.35	10
	FL ₂	16.37	0.81	11	2.39	15.82	0.82	10
	FL ₃	11.65	1.30	11	21.70***	9.24	1.04	10
	FL ₄	10.81	0.94	11	14.86**	9.17	1.01	10
	FL ₅	11.07	0.79	11	0.66	11.18	1.07	10

Note: *symbols, values of Fisher's criterion exceeding the critical values at 95% (*), 99% (**) and 99.9% (***) significance levels comparing means in the two periods; SD, standard deviation; *n*, number of observation years; F₁, F₂..., annual mean length increments in 1, 2... and last not full year of life.

Table 3. Proportion of different age chum salmon from Kuril Bay (Iturup Island) in 1974–1984 and in 1985–1995.

Years	Percentage of chum salmon at age				
	0.2	0.3	0.4	0.5	0.6
1974–1984	6.1	69.2	24.3	0.4	0
1985–1995	2.8	55.5	40.8	0.8	0.1

Fig. 1. Average growth in length during the third and fourth year (A), as a percentage of growth during the first year of life, and coefficient of variation (CV) of growth (B) during the third and fourth year of Iturup Island age 0.4 chum salmon maturing in 1974–1996.

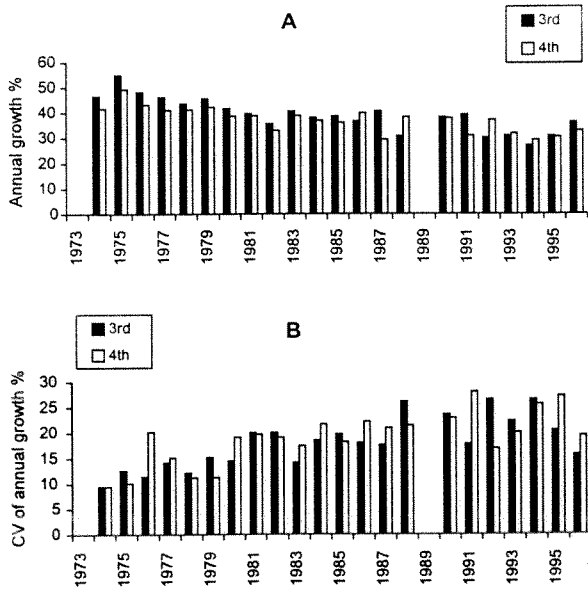


Fig. 2. Proportion of returning age 0.4 chum salmon and the corresponding proportion of age 0.4 fish of their parents (A), and the growth rate in the third year of life of age 0.3 and age 0.4 fish (B).

A: $R^2 = 0.59$; $p < 0.001$; $n = 17$.

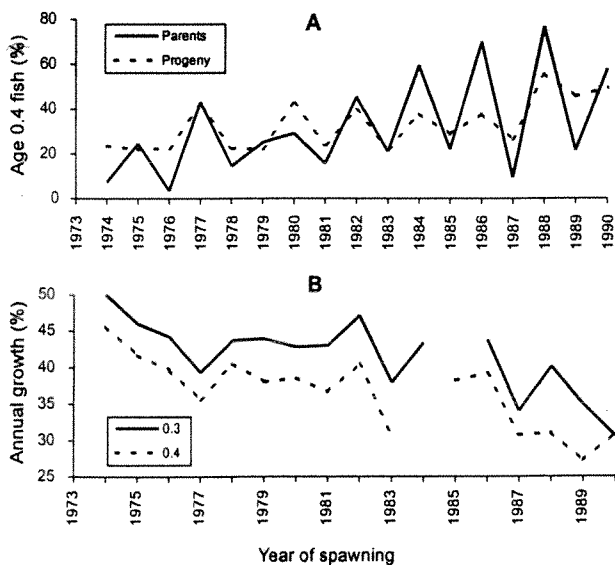


Fig. 3. Relationship between the coefficient of downstream migration (estimated survival egg to fry) of chum salmon and proportion of older (age 0.4) parents in rivers of Iturup Island (1975–1987) and Kunashir Island (1990–1991, 1994–1998). For Iturup chum salmon: $R^2 = 0.18$; $p > 0.05$; $n = 13$.

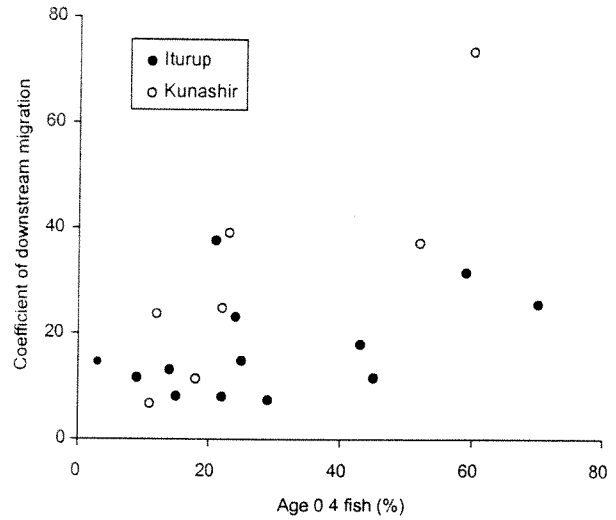


Fig. 4. Relationship between fork length of downstream migrating chum salmon fry in the Iturup Island rivers in 1977–1988 and the proportion of age 0.4 fish among their parents.

$R^2 = 0.37$; $p < 0.05$; $n = 12$.

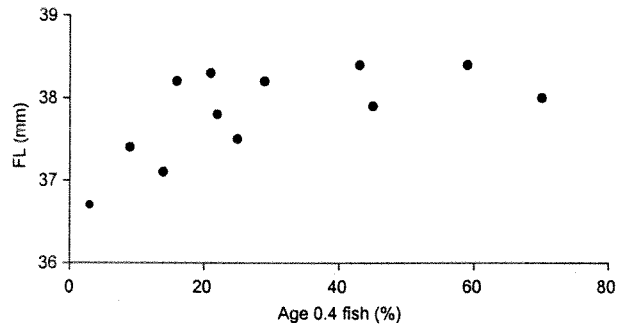
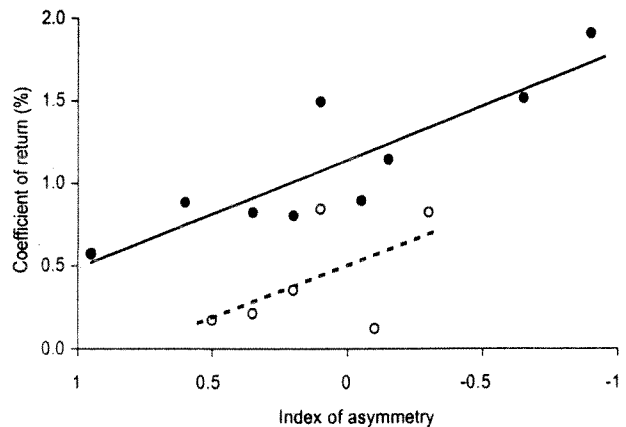


Fig. 5. Relation between coefficient of return of chum salmon and index of asymmetry (condition) of fry in the coastal shallows of Iturup Island for broods from 1973–1981 (dark circles, full line) and from 1982–1987 (light circles, dotted line).

1973–1981: $Y = 1.14 - 0.65x$; $R^2 = 0.76$; $p < 0.01$; $n = 9$.
 1982–1987: $Y = 0.50 - 0.63x$; $R^2 = 0.29$; $p > 0.05$; $n = 6$.



DISCUSSION

The results of the Iturup Island chum salmon monitoring indicate considerable change in reproductive success in recent years. The reduction in chum salmon length and fecundity, and increasing age of spawners coincided with an increase in survival of fry prior to entering the sea, and a decrease thereafter. The reduction in annual growth at sea has been recorded for different chum salmon populations on Asian coasts (Kaev 1994; Kaeriyama 1996) and American coasts (Helle and Hoffman 1995) of the Northern Pacific Ocean. Moreover the "disruption" of chum salmon growth appeared to be not only in reduction of annual growth, especially after the second year of life in the ocean, during the period 1985–1992 compared to 1976–1980 (Kaeriyama 1996), but in the increased variability of annual growth in the latter period (Kaev 1994).

The reduction in size of returning adults may be caused by a density-dependent factor arising from the doubling of Pacific salmon abundance since the early 1980s (Bigler et al. 1996). But other factors must be taken into account: (a) a documented re-establishment of zooplankton communities in the early 1990s (Shuntov et al. 1996), (b) strong differences in annual growth increments for contiguous years (Fig. 1), (c) no significant changes in chum salmon growth in Sakhalin, Kuril and Hokkaido populations during the first and second year of life, when living in the Okhotsk Sea and adjacent waters of the Pacific Ocean.

Increasing age of chum salmon spawners could be expected as a result of reduced growth in recent years (Gritsenko and Kovtun 1986; Nikolaeva 1987). Older age with slower growth has also been described in chum salmon of American and Asiatic origins (Helle and Hoffman 1995; Kaeriyama 1996). As noted above, the Iturup Island chum salmon have also become older and smaller. However, analyses do not confirm a deceleration in maturity with slow growth.

The increased age of chum salmon spawners in recent years was apparently caused by the interaction of two factors: the rate of sexual maturation and appearance of contiguous generations greatly differing from each other in abundance. That is, at return of age 0.3 chum salmon of a less abundant brood the proportion of age 0.4 fish appears greater in that year because of the return of age 0.4 adults of the preceding much more abundant cohort. As a result not only is the number of spawning fish increased, but also the age and proportion of females is increased (females accounted for 65.7% of age 0.4 fish). Thus, in most cases, the slower growing cohorts of chum salmon matured younger. A strong relationship (Fig. 2) between the age of parents and their progeny was revealed, which speaks in favor of genetic control of chum salmon age at sexual maturation.

The increased proportion of older fish on spawning grounds is also important. Earlier a significant reduction in fecundity and increase in egg weight with age in equally sized females was observed for chum salmon (Kaev and Kaeva 1986). As in single-age populations of pink salmon (*O. gorbuscha*), not only does the number of eggs produced increase with size within an age group of chum salmon, but egg size is also weakly correlated with body length (Kaev and Kaeva 1986). Therefore, fecundity within age groups is subject to both quantitative and qualitative changes with increase in age. In some years older females can be less fecund than young ones, but their average egg size is larger. In this respect the increased age of chum salmon spawning in recent years means not so much a proportional increase in larger and more fecund older females, as an increase in females with larger eggs.

A tendency of migrant fry body length to increase with parental age was shown (Fig. 4). Although fry of smaller length resulted from parents with a wide range of ages, nevertheless the largest fry originated from older parents with potentially large eggs, and the smallest fry from younger parents with potentially small eggs.

Large-sized progeny from large eggs is well known. High survival of progeny from older parents or from larger eggs has also been reported (Wallace and Aasjord 1984; Hislop 1988; Helle 1989; Markevich et al. 1993). Differential survival of progeny may be due to better protection of deeper-buried eggs during embryogenesis (Van den Berghe and Gross 1989), or the selective mortality of different-sized juveniles (West and Larkin 1987; Kaev 1992). Therefore it would be expected that greater survival from the egg to the downstream migrant would be associated with older parents (Fig. 3). Because of many incidental factors (river floods, changes in flow of ground water and so on) the relationship was not significant. However, in all the years with higher proportions of age 0.4 spawners, the ratios of fry migrant numbers to egg numbers were higher than the average long-term ratio. Analogous data for chum salmon from the Ilyushin River (Kunashir Island) show a similar trend (Fig. 3).

CONCLUSIONS

A reduction of chum salmon length and fecundity in 1985–1995 compared to 1974–1984 was observed in Iturup Island chum salmon. These changes were accompanied by an increase of chum salmon growth variability and an increase in their mortality in the ocean. Fry growth in the coastal zone was positively associated with survival for individual cohorts. In most cases the slower growing cohorts of chum salmon may have matured younger. A strong positive

relationship between the age of parents and their progeny was found, which suggests a genetic influence on chum salmon age of sexual maturation. A mixed chum salmon age composition is an important component in maintaining a stable reproductive potential in a population, not only because interannual fluctuations in numbers of spawners are smoothed over succeeding generations, but also because qualitative differences in spawning fish increase reproductive efficiency. This should be considered as an example of reproductive homeostasis.

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