Patterns of Growth of the Pink Salmon *Oncorhynchus gorbuscha* in Year-Classes with Different Survival Rates during the Marine Life-history Phase

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Catches of pink salmon *Oncorhynchus gorbuscha* off the eastern Sakhalin Island decreased almost threefold, from 93,181 metric tonnes (on average for 2001–2014) to 33,328 metric tonnes (on average for 2015–2019). This decrease became particularly pronounced in the dominant line of odd-numbered years: from 134,971 to 19,911 metric tonnes. A poor harvest did not meet the pre-season forecast and left fishermen disappointed. The search for the causes of a sharp pink salmon stock decline have become an urgent issue. First, it was found that pink salmon abundance decline could be caused by typhoons which led to spawning area destruction by floods and to high mortality of juvenile salmon entering the sea during storms (Kaev 2018). Then it was shown that the early temporal form of pink salmon abundance declined first, and this can serve as a precursor to the general reduction in pink salmon stocks (Kaev 2019). In this study, we analyze the growth patterns of pink salmon as one of the most important indicators of species' response to changes in habitat conditions. It was previously believed that a study of growth helps to predict fish abundance variations (Dementyeva 1976).

Despite their high importance, the number of fish growth studies decreased (Reshetnikov et al. 2013), although scale measurement technique improvements allowed expanding the range of method applications for constructing fish scale patterns (Dgebuadze and Chernova 2009). This is particularly true for Pacific salmon: there have only been a few articles in which growth was considered as an attribute of stock dynamics. In recent years, the interest in growth pattern studies in Pacific salmon has increased in light of the critical size hypothesis suggesting that juvenile salmon must reach some minimum critical size to survive their first winter at sea (Beamish and Mahnken 2001; Howard et al. 2016). The problem of size-selective mortality has become widely discussed (Beacham et al. 2018).

The objective of this article is to evaluate the significance of pink salmon growth in its stock dynamics based on a retrospective assessment of growth patterns in year-classes with different survival rates at sea. Pink salmon return to the southeastern coast of Sakhalin Island from 2005–2020 is studied. This stock is the most abundant in the Sakhalin and has the longest data series on inter-circuli distances on scales. The survival rate of each year class is estimated as a percentage of the adult fish that returned to spawn from the number of juveniles that migrated from rivers (return rate, RR). The run size is calculated as a sum of the number of salmon in commercial fishing (the catch biomass divided by mean salmon weight) and escaped to spawn (from visual counts in several control rivers). The abundance of downstream migrants is estimated from the number of spawners in all rivers on the coast multiplied by the downstream migration index obtained annually in two or three control rivers (Kaev and Klovach 2014; Kaev and Irvine 2016).

Inter-circuli distances on scales were measured along the greater radius, starting from the 2nd circulus. The 1st circulus (central plate in the scale focus) was not measured due to errors that may arise from different degrees of scale focus deformation, being typical to all salmon at the final stages of spawning migration. The fish body length by the time of first circulus formation was assumed to be 0.133 of adult fork length (Kaev 2015b). The growth rate analysis was carried out starting from the second circulus. Body length of juveniles with the specified number of circuli is assumed to be the sum of the length that increases during their formation, except for the central plate in the scale focus.

The growth study was carried out for pink salmon females only. Furthermore, we used samples collected only during the mass migration of the late-run pink salmon (on average, 85% of catches) to exclude any impact of morphological and biological differences between seasonal forms. The growth patterns of 1,556 females (from 44 to 240 annually) from 45 samples (from two to six annually) were studied. The distance to the median of five adjacent circuli inclusive with the smallest sum of inter-circuli distances was assumed to be the first year of scale growth; then the number of circuli in the first annual zone was normalized to 23 circuli (Kaev 2015a). The number of circuli of the second year of growth was not normalized, since only the first five circuli measurements were used.

The data were tested for normality of distribution (by the χ^2 test) using the Statistical software package. The analysis showed that 361 of 405 empirical size-frequency distributions did not differ significantly from the normal distribution (χ^2 values varied in the range of 0.46–18.88 at p —from 0.997 to 0.052). In 35 distributions, a difference from the normal distribution exceeded the first statistical level of significance (χ^2 from 6.19 to 19.19, p —from 0.011 to 0.049). In nine cases, it proved to be higher than the second statistical level of significance (χ^2 from 11.66 to 26.02, p —from 0.002 to 0.009), which is acceptable for biological studies (Plokhinsky 1970). Statistical analysis was carried out using the MS Office Excel package.

Table 1. Survival rate of pink salmon during the marine phase with the year-classes divided into groups with low, medium, and high return rate (RR) values

Low RR		Medium RR		High RR	
Year of return	RR, %	Year of return	RR, %	Year of return	RR, %
2015	0.87	2005	7.65	2009	10.32
2017	1.49	2007	6.53	2011	10.40
2019	1.81	2012	8.77	2013	15.09
2008	4.20	—	—	2006	18.02
2016	4.49	—	—	2010	12.99
2018	2.84	—	—	—	—
2020	1.78	—	—	—	—

Pink salmon year-classes were arranged into three groups: with low, medium, and high survival rates during the marine phase (Table 1). The range of RR variations did not differ much between odd- and even-numbered year-classes which made it possible to consider them together in a relatively short observation series. The year-class returned in 2014 (RR 13.99%) was removed from the analysis since its unexpectedly high abundance was partly caused by straying of salmon of Kuril Islands origin (Kaev and Zhivotovsky 2017).

Fig. 1. Body length increase during the formation of respective circuli on scales of female pink salmon from the year-classes with high (1), medium (2), and low (3) survival rates during the marine phase.

Comparing pink salmon survival rate with its growth rate (Fig. 1), we pay attention first to the period of inshore residence (before the formation of the 5th–6th circuli), which is a decisive time for the strength of year-class formation (Kaev and Irvine 2016). This agrees quite well with a study of the marine growth of juvenile pink salmon and their survival rate in the northern Gulf of Alaska, which indicates a decrease in predation mortality after juveniles' migration offshore (Malick et al. 2011). In the southeastern Sakhalin, the pink salmon year-class returned in 2013 with the fastest growth in coastal waters were referred to the group with high survival rates, and the year-class returned in 2016 with the slowest growth were referred to the group with low survival rates. However, the

survival rate of the former year-class was not record-breaking high, while that of the latter was the highest in its group with a low survival rate.

The variance (CV) and configuration (A_s) of the obtained length-frequency distributions were analyzed at the time of 2 (conditional onset of marine growth in the coastal area), 7 (after its completion), and 23 circuli (overwintering) formation (Table 2). First, there is a reduction in variability with growth that becomes especially pronounced for the period of first circuli formation. CV value averaged for all year classes reduced from 13.7 to 11.2% during salmon growth between the 2nd and 7th circuli formation. This reduction further occurred during salmon growth to the 23rd circulus, down to 7.5%, but its rate per circulus slowed down twofold. For juveniles' body length, there is a larger variance within the group of year-classes with a high survival rate at the 2nd circulus; the differences in the variance within groups decrease until it levels out completely.

Table 2. Body length (FL), variability (CV), and skewness (A_s) of size-frequency distribution for pink salmon females with 2, 7, and 23 circuli on scales from year-classes with high, medium, and low survival rates during the marine phase

Year of return	FL , cm			CV , %			A_s		
	2	7	23	2	7	23	2	7	23
High survival rate									
2009	1.24	6.67	26.4	11.5	8.1	6.4	0.20	0.01	0.02
2011	1.07	6.26	23.3	12.8	11.1	8.3	0.11	-0.06	-0.22
2013	1.31	7.22	26.8	11.1	9.9	7.2	0.36	0.14	0.29
2006	1.13	6.32	24.3	12.0	8.8	7.3	-0.03	0.52	0.25
2010	1.15	6.25	24.3	13.1	10.6	6.9	0.81	0.32	0.17
Mean	1.18	6.54	25.0	12.1	9.7	7.2	0.29	0.19	0.10
Medium survival rate									
2005	1.09	6.12	23.7	12.9	12.2	8.7	-0.15	0.01	-0.35
2007	1.09	6.03	24.1	12.5	11.7	7.6	0.38	0.60	-0.10
2012	1.06	5.82	21.9	15.0	11.3	7.2	-0.15	-0.56	-0.16
Mean	1.08	5.99	23.2	13.5	11.7	7.8	0.03	0.01	-0.20
Low survival rate									
2015	1.07	6.35	24.3	15.0	13.8	9.8	0.35	-0.17	-0.18
2017	1.11	6.58	26.2	15.3	11.7	7.4	0.23	0.45	0.08
2019	1.20	6.90	19.0	11.8	10.1	6.3	0.42	0.11	-0.07
2008	1.10	6.13	24.2	16.6	13.9	7.8	-0.08	-0.42	-0.02
2016	0.97	6.04	23.8	15.7	11.6	6.4	0.42	0.11	-0.01
2018	1.06	6.39	24.6	14.6	11.5	7.3	0.12	-0.43	0.15
2020	1.06	5.62	24.4	15.1	11.6	7.3	0.73	0.45	0.67
Mean	1.08	6.29	23.8	14.8	11.7	7.1	0.31	0.04	0.13

A comparison of skewness A_s of the length-frequency distributions between groups with different survival rates does not provide such a well-defined trend as obtained with CV . However, it is worth noting that a large difference appears between A_s values within the groups at the time of comparison. The greatest difference is observed within the group with a low survival rate.

Below we consider how the size-frequency distribution of juveniles in different groups changed between the time of formation of circuli 2 and 7, i.e., during their inshore residence. Due to the significant difference in salmon body size, data on their body lengths is presented as percentage proportions of the mean values in samples for each year-class, which were then arranged into groups with low, medium, and high survival rates (Fig. 2). During the inshore residence, the proportion of modal size groups increased while proportions of small- and large-sized fish

decreased. A decrease in the proportion of small-sized fish prevailed, especially in the group with low survival rates. In length classes of 60–80% from average, the percentage decreased by 6.4%. In the groups with medium and high survival rates, the percentage decrease was 3.3 and 2.5%, respectively. The percentage of large-sized fish also decreased, but not as significantly.

Fig. 2. Size structure (in % relative to mean size) of pink salmon with two (1) and seven (2) circuli on scales, averaged for the year-classes with low (a), medium (b), and high (c) survival rates during the marine life-history phase.

Fig. 3. Body length increase in pink salmon underyearlings during the formation of respective circuli and variations in skewness of size-frequency distribution, averaged for the year-classes with high (1), medium (2), and low (3) survival rates during the marine phase.

In all three groups of year-classes with different survival rates, the positive skewness in the length-frequency distribution decreased during inshore residence (Fig. 3). In groups with high and medium survival rates, this process was relatively short, especially in the first group, while in the low survival rate group it was the most profound and

prolonged. Patterns of skewness variations in length-frequency distribution of groups with high and medium survival rates were similar, but different in the group with a low survival rate.

At first glance, the data on the growth rate of pink salmon in the early marine phase is consistent with the opinion that fast-growing juveniles typically manifest a higher survival rate (Cross et al. 2008). From the other side, there is a non-significant correlation between the growth increase during the formation of the first four circuli (from 2nd to 5th) and the survival rate of the respective year classes ($r = 0.32$; $p > 0.05$). In our opinion, a direct strong relationship of survival rate with growth rate is unlikely. This relationship is determined not only by fish feeding success but also by many other factors, such as predators. The mentioned relationship was mostly strengthened by the contribution of three year-classes (two with the fastest and one with the slowest growth) while growth graphs for the rest of the year-class are located quite compactly for the time of inshore residence (see Fig. 1) and interspersed among three groups with different survival rates. Thus, in our case, the growth rate of juveniles does not certainly increase the survival rate of pink salmon year classes under consideration.

After downstream migration, juvenile pink and chum salmon show a sharp increase in size variability, which is determined by rapid growth due to the transition to external feeding and by the timing of their sea entry. New smaller migrants continuously join the already grown-up juveniles in inshore waters (Kaev and Romasenko 2002). Chum salmon year-classes in inshore bays that are initially characterized by a strongly pronounced positive skewness in the size structure manifest a low survival rate. For pink salmon, such a pattern could not be identified clearly, apparently due to earlier seaward migrations. Some pink salmon, mainly the largest individuals, might leave the survey area before observations (Kaev 2003). There is an opinion that reduction of size variability as juveniles grow in marine waters is a common phenomenon associated with a higher mortality of smaller fish (Beacham et al. 2018). It could be agreed upon, but a similar size variability reduction is observed among survivors considered separately (Table 2).

In general, survived adult fish had a larger size at the beginning of the marine phase compared to the body length distribution in the entire juvenile population previously observed inshore (Moss et al. 2005; Cross et al. 2009; Claiborne et al. 2011). Nevertheless, it is rather possible that captured juveniles did not characterize the entire population. The proportion of larger juvenile individuals that could leave the sampling area was underestimated, and as a result, the impact of size-selective mortality was overestimated (Beacham et al. 2018). Growth patterns identified in survived fish may cause additional uncertainty on this issue. A predominant reduction in smaller fish numbers, which is especially pronounced in year-classes with a low survival rate (see Fig. 2), fully meet the criteria for size-selective mortality. This is also consistent with variations in the skewness of length-frequency distributions towards negative asymmetry during inshore residence that mean a reduction in smaller fish proportion and are also pronounced in year-classes with a low survival rate (Fig. 3). This effect was observed in juvenile chum salmon when they were caught in the coastal zone off Iturup Island before and after the storm. In latter samples, the proportion of smaller juveniles reduced, probably due to their increased mortality in extreme weather conditions. Grown-up juveniles have a higher swimming ability which is very important for surviving at early life stages. Salmon fry that recently migrate from rivers also become slow-moving under storm conditions, aggregating in dense schools (Kaev 1992).

In offshore waters, trends in skewness of length–frequency distributions remained similar between the pink salmon year-classes with high and medium survival rates (Fig. 3). Pink salmon underyearlings spend summer–autumn feeding season mainly in the deep-water Sea of Okhotsk (Shuntov and Temnykh 2008), where the highest amount of macrozooplankton per unit of nekton biomass is recorded (Shuntov 2001; Dulepova 2002). Despite an almost three-fold fluctuation in macrozooplankton biomass there in different years (Volkov 2008), no food deficiency for young salmon have been reported. If a certain food shortage sometimes occurred in semi-enclosed inshore bays, it could affect the growth rate of salmon and their distribution, but there is no reliable evidence of any strict limitation of their abundance by the food factor obtained to date (Volkov 2016; Shuntov et al. 2010a, b, 2017, 2019). Variations in the growth of pink salmon during the offshore period are likely not significant for survival. This is evidenced by two year-classes with an abnormally low growth rate in open waters of the Sea of Okhotsk (see Fig. 1): one of them which returned in 2011 is in the group with a high survival rate, and the other returned in 2012 is in the group with average survival rate.

Excess mortality among slow-growing pink salmon during the winter-spring period in the ocean was shown by a comparison of inter-circuli distances within groups of circuli in underyearlings that completed their feeding season in the Sea of Okhotsk and in two-year-old salmon that migrated towards the Sea of Okhotsk in the following year (Zavolokin and Strezhneva 2013). These results should be considered with great caution since the proportions of fish of different origin in samples taken are unknown. In fact, circuli diagrams significantly differ between fish from different parts of the Sakhalin–Kuril region (Kaev 2015a), and even more on the interregional level (Temnykh

1998). It should also be considered that the growth rate is influenced by a multitude of factors, e.g., water temperature, which accelerates or slows down the metabolic processes in poikilothermic organisms.

The anomalous decline in growth rates in the year-classes 2011 and 2012 was associated with temperature conditions, rather than with the transition to feeding on secondary forage organisms (Kaev 2015b), which is fully consistent with the opinion of V.P. Shuntov considering the lack of density-dependent factors' effect on salmon in offshore waters. The emergence of such year-classes suggests that mortality rates during overwintering, related to fish size, are not decisive in the formation of pink salmon year-class strength. No reliable evidence has been obtained to date to confirm the hypothesis of a "critical size" for juvenile salmon that, if not reached by the end of the summer-autumn feeding season, substantially decreases chances to survive the wintertime (Beacham et al. 2017, 2018).

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