

## Factors Influencing Abundance of Sockeye Salmon (*Oncorhynchus nerka*) from the Ozernaya River, Southwest Kamchatka

V.F. Bugayev and V.A. Dubynin

Kamchatka Research Institute of Fisheries and Oceanography  
(KamchatNIRO), Naberezhnaya 18, Petropavlovsk-Kamchatsky, 683602, Russia



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**Abstract:** Numbers of sockeye salmon (*Oncorhynchus nerka*) returning to the Ozernaya River (including driftnet catches at sea) are greatly influenced by four factors. The first is the parent escapement of sockeye in Kuril Lake. The second factor is the length and weight of sockeye smolts migrating from Kuril Lake. The third is the inshore abundance of West and North-East Kamchatka juvenile pink salmon (*O. gorbuscha*) one year prior to ocean migration of sockeye smolts from Kuril Lake at age 2+ (representing competition between pink salmon underyearlings and migrating sockeye salmon smolts). Finally, the fourth factor is the inshore abundance of West and North-East Kamchatka mature pink salmon during the first, second and third years of sockeye salmon at sea.

### INTRODUCTION

In the basins of the rivers Ozernaya and Kamchatka in some years catch of sockeye salmon (*Oncorhynchus nerka*) made up 90–95% of the total sockeye catch in Asia (Anonymous 1989). Since 1985 through the present, catches of sockeye from the Ozernaya River rank first among catches of Asian sockeye surpassing catches of sockeye from the Kamchatka River (Bugayev 1995). At present, various mutually compatible explanations have been proposed for the increased sockeye abundance in the Ozernaya River spawning in Kuril Lake in the mid-late 1980s.

During the first years after natural fertilization of Kuril Lake in 1981 with ash from Alaid volcano, and with artificial mineral fertilizer in 1981, 1982, 1985, 1987 and 1989, and optimum levels of spawning, sockeye salmon abundance increased in the Ozernaya River (Kurenkov 1988; Dubynin and Bugayev 1988; Milovskaya 1991; Milovskaya and Selifonov 1993).

Ever since the very high abundance of pink salmon (*O. gorbuscha*) in West Kamchatka in 1983, the abundance of pink salmon in West and North-East Kamchatka began to fluctuate in counterphase from 1985 through the present, although before 1985 (1970–1984) the abundance of pink salmon in both areas fluctuated in phase (Bugayev 1995; Bugayev et al. 1996). Bugayev (1995) showed abundance of inshore runs of Kamchatka pink salmon were correlated with length and weight of mature sockeye salmon of the Ozernaya River. Bugayev (1995) as-

sumed that (in addition to fertilization and optimum levels on the spawning grounds in Kuril Lake), sockeye abundance increased as a result a sharp decrease in pink salmon abundance in the West Kamchatka, starting from 1985. When pink salmon increased in abundance in West Kamchatka in 1994, 1996 and 1998 the abundance of sockeye salmon in the Ozernaya River appeared to decrease.

Since the beginning of limitation of Japanese driftnet fishing and introduction of marine economic zones in 1977–1978 to the present, the pressure of the remaining Japanese driftnet fishing and of the Russian fishery, beginning in 1994, has fallen mostly on Asian sockeye stocks, mainly on sockeye from the Ozernaya and the Kamchatka rivers. As a result, we were able to assess the commercial harvest of sockeye from the Ozernaya and Kamchatka rivers in the Russian economic zone and to estimate numbers of these sockeye in the sea in the year of return to spawn (including driftnet catches). This paper is devoted to the analysis of fluctuations of sockeye abundance from the Ozernaya River.

### MATERIAL AND METHODS

Annual returns of sockeye salmon to the Ozernaya River from 1976–1998 (the 1971–1992 brood years) were used in the study.

Previously, Selifonov (1982, 1987, 1989) used catches by the Japanese driftnet fishery at sea from 1952–1975 to calculate the rate of harvesting of sockeye from the Ozernaya River. Later (up to 1996),

M.M. Selifonov (Naberezhnaya Street 18, KamchatNIRO, Petropavlovsk-Kamchatsky, 683602 Russia, personal communication) used only expert visual assessment of the rate of harvesting by driftnets to forecast abundance at sea of sockeye from the Ozernaya River.

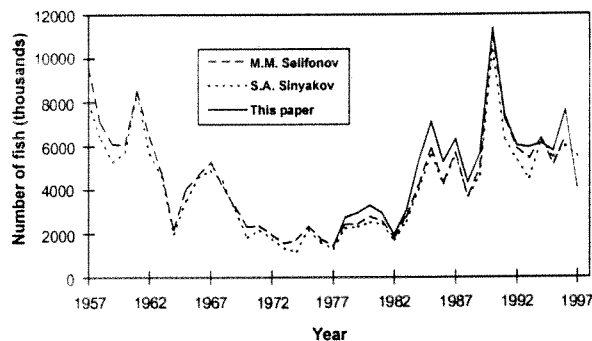
An expert visual assessment by Sinyakov of the rate of harvesting sockeye from the Ozernaya River by Japanese and Russian driftnet fishing is also available (S.A. Sinyakov, Naberezhnaya Street 18, KamchatNIRO, Petropavlovsk-Kamchatsky, 683602 Russia, personal communication, Milovskaya et al. 1998). It allowed investigators to assess the mature sockeye stock from 1940–1996, and to calculate the correlation between rate of return and smolt body weight. The results of the investigation showed that rate of return of adult sockeye to the Ozernaya River increased with their smolt body weight (Milovskaya et al. 1998). Unfortunately, the methods of assessment of the rate of harvesting sockeye from the Ozernaya River by Japanese and Russian driftnet fishing have not been published by Selifonov and Sinyakov (personal communication).

Differentiation between Japanese and Russian driftnet catches in Russia's economic zone, including the Ozernaya River, has only been performed on catches from 1995–1997 (A.V. Bugayev, KamchatNIRO, Petropavlovsk-Kamchatsky, 683602, Russia, personal communication). These investigations showed that sockeye salmon of Asian origin comprised the major portion of catches of Japanese and Russian driftnet fisheries in the Russian economic zone. This simplifies assessment of the rate of harvesting sockeye from the Ozernaya and Kamchatka rivers by driftnet starting from 1977 through the present. If salmon fishing in the Russian economic zone continues, assessment of sockeye salmon stock will be possible in the future as well. In general, sockeye salmon from the Ozernaya River comprise the majority of salmon caught in driftnets in the Russian economic zone.

For our estimates we have used the ratio (percent) of number of mature sockeye in inshore runs (escapement and total Russian domestic catches on the coast and in the rivers, omitting the Russian and Japanese highseas driftnet catches) between the Ozernaya and Kamchatka rivers from 1977–1998. We assumed that driftnet catches of sockeye from the Ozernaya and Kamchatka Rivers were correlated with the number of individuals returning to the Ozernaya and Kamchatka rivers. If the catches of sockeye from the Ozernaya River are excluded from the total, the remaining sockeye in the catches are from the Kamchatka River and other sources. We assumed also that of these remaining sockeye, 80% were from the Kamchatka River, and 20% were stocks from small Asian and other (American) rivers.

For example, in the 1996 inshore run of sockeye salmon, 4.844 million fish were from the Ozernaya River, and 2.885 million were from the Kamchatka River. Ozernaya River sockeye made up 62.67% of the total. The total Russian and Japanese driftnet catches of sockeye salmon was 10,940 tons in 1996. The catch of sockeye from the Ozernaya River was 6,860 tons, and from the Kamchatka River and other rivers was 4,080 tons (Kamchatka River – 3,260 tons, other stocks – 820 tons). The total number of mature sockeye salmon of Ozernaya River origin in the sea (before the beginning of the Russian and Japanese driftnet fisheries) was 7.588 million fish (Fig. 1), and from the Kamchatka River was 4.189 million fish. This standard approach can be easily reproduced. It can be used in the future to reveal any errors in the above assumptions.

Fig. 1. Number of mature sockeye salmon from the Ozernaya River at sea before the beginning of the drift net fishery, 1957–1997, in thousands of fish. Data from M.M. Selifonov and S.A. Sinyakov by personal communication.



The estimated abundance of sockeye from the Ozernaya River was compared with data provided by M.M. Selifonov and S.A. Sinyakov (personal communications) (Fig. 1). Our results on sockeye salmon from the Ozernaya River, in general, are similar to the earlier estimates from 1977–1997. In general, our evaluation of abundance of sockeye from the Ozernaya River was somewhat higher than the estimates of Selifonov and Sinyakov. However, in some years (1997, for example) the results are contradictory. In this paper we use our own estimates of abundance of sockeye salmon from the Ozernaya River (Fig. 1).

Bugayev (1995) showed that abundance of pink salmon off West and North-East Kamchatka influences the ocean growth-rate of sockeye from the Ozernaya River. Thus, in 1970–1984 with an increase in abundance of both West and North-East Kamchatka pink salmon, growth of mature sockeye from the Ozernaya River declined. In 1985–1991 a negative correlation remained only for West Kamchatka pink salmon; for North-East Kamchatka the pink salmon correlation changed from negative to positive (Bugayev 1995).

On the basis of the above, we separated our investigations on abundance of sockeye from the Ozernaya River from 1971–1992 into two periods (for addition and the more detailed picture): 1971–1981, and 1982–1992.

In this article we first used Spearman's regression method to calculate correlation coefficients of ranges ( $r_s$ ).

Second, by forward stepwise regression in program "STATISTICA" we calculated coefficients of multiple regression (R) (Borovikov and Borovikov 1998). Forward stepwise regression means that at every step some independent variable is included in the model. Thus, a lot of the most important variables can be defined. This allows us to reduce the number of variables described by the correlation. In using forward stepwise regression independent variables are included in the regression equation until it satisfactorily describes the dependent variable, RBS, which is the return by brood year class of mature sockeye salmon of the Ozernaya River while in the ocean (i.e., including driftnet catches at sea). Inclusion of variables is defined by the F-criterion (Borovikov and Borovikov 1998). The 15 independent variables tested are listed in Table 1.

## RESULTS

According to Selifonov (1975) and Bugayev (1995) there are 14 age patterns among sockeye salmon from the Ozernaya River, but most are rare. The major age patterns are the following: 2.2, 2.3, 3.2 and 3.3 (the first figure indicates years in freshwater and the second the years of marine life). These patterns from 1940–1975 comprised on average up to 98.4% of this sockeye stock. Patterns 2.2 (31.0%) and 2.3 (53.6%) on average comprised up to 84.6% of this stock (Selifonov 1982). As a result, success in forecasting return by brood year of sockeye salmon from the Ozernaya River depends, first, on accuracy of forecasting the proportion of individuals belonging to the two main age patterns, 2.2 and 2.3 (Selifonov 1975; Bugayev 1995).

Our investigations showed (Table 2) that there is a close correlation between the abundance of spawning adults in all 14 age patterns and the return by brood year in major age patterns 2.2, 2.3, 3.2, 3.3 from 1971–1992 ( $n = 22$ ),  $r_s = 0.876$ ,  $p < 0.001$  (Fig. 2). There is a positive correlation between body length or weight of smolts and rate of return as adults ( $r_s = 0.693$ ,  $p < 0.001$ , Fig. 3;  $r_s = 0.715$ ,  $p < 0.001$ , Fig. 4).

**Table 1.** Fifteen independent variables used in forward stepwise regression to define the dependent variable, RBS, return by brood year class of mature sockeye salmon in the Ozernaya River.

Independent Variable	Description
ES	the parent escapement of sockeye into Kuril Lake, in thousands of fish;
L2	length of sockeye smolts migrating from Kuril Lake at the age 2+, mm.
W2	weight of sockeye smolts migrating from Kuril Lake at the age 2+, g.
WP0	inshore run of mature West Kamchatka pink salmon (after driftnet harvesting) one year prior to ocean migration of sockeye smolts of the Ozernaya River (from Kuril Lake) at age 2+, millions of fish.
WP1	inshore run of mature West Kamchatka pink salmon (after driftnet harvesting) during the first year of marine life of sockeye salmon of the Ozernaya River, millions of fish.
WP2	inshore run of mature West Kamchatka pink salmon (after driftnet harvesting) during the second year of marine life of sockeye salmon of the Ozernaya River, millions of fish.
WP3	inshore run of mature West Kamchatka pink salmon (after driftnet harvesting) during the third year of marine life of sockeye salmon of the Ozernaya River, millions of fish.
EP0	inshore run of mature North-East Kamchatka pink salmon (after driftnet harvesting) one year prior to ocean migration of sockeye smolts from the Ozernaya River (from Kuril Lake) at the age 2+, millions of fish.
EP1	inshore run of mature North-East Kamchatka pink salmon (after driftnet harvesting) during the first year of marine life of sockeye salmon of the Ozernaya River, millions of fish.
EP2	inshore run of mature North-East Kamchatka pink salmon (after driftnet harvesting) during the second year of marine life of sockeye salmon of the Ozernaya River, millions of fish.
EP3	inshore run of mature North-East Kamchatka pink salmon (after driftnet harvesting) during the third year of marine life of sockeye salmon of the Ozernaya River, millions of fish.
WEP0	total inshore runs of mature West and North-East Kamchatka pink salmon (after driftnet harvesting) one year prior to ocean migration of sockeye smolts from the Ozernaya River (from Kuril Lake) at age 2+, millions of fish;
WEP1	total inshore runs of mature West and North-East Kamchatka pink salmon (after driftnet harvesting) during the first year of marine life of sockeye salmon of the Ozernaya River, millions of fish.
WEP2	total inshore runs of mature West and North-East Kamchatka pink salmon (after driftnet harvesting) during the second year of marine life of sockeye salmon of the Ozernaya River, millions of fish.
WEP3	total inshore runs of mature West and North-East Kamchatka pink salmon (after driftnet harvesting) during the third year of marine life of sockeye salmon of the Ozernaya River, millions of fish.

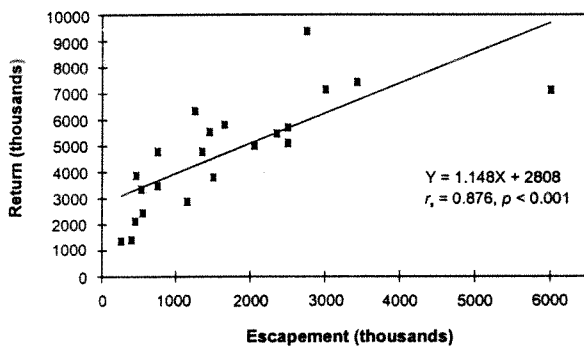
**Table 2.** Spearman correlation coefficients ( $r_s$ ) between return by brood year and length and weight of smolts, and between rate of return and length and weight of smolts for sockeye salmon in the Ozernaya River.

Parameters <sup>1</sup>	Return by brood year	Rate of return (RBS/ES)
1971–1992		
ES	0.876***	-
L2	-0.317	0.693***
W2	-0.45	0.715***
	n=22	n=22
1971–1981		
ES	0.764**	-
L2	-0.309	0.591
W2	-0.396	0.469
	n=11	n=11
1982–1992		
ES	0.802**	-
L2	0.218	0.591
W2	-0.009	0.633*
	n=11	n=11

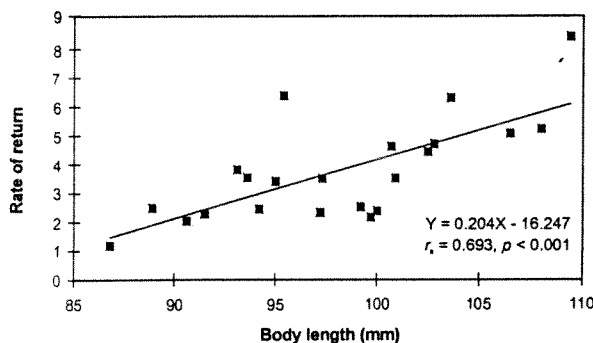
<sup>1</sup>\* -  $p < 0.05$ , \*\* -  $p < 0.01$ , \*\*\* -  $p < 0.001$ .

ES - parent escapement of sockeye salmon, thousands;  
 L2 - body length of sockeye salmon smolts at age 2+, mm;  
 W2 - body weight of sockeye salmon smolts at age 2+, g.

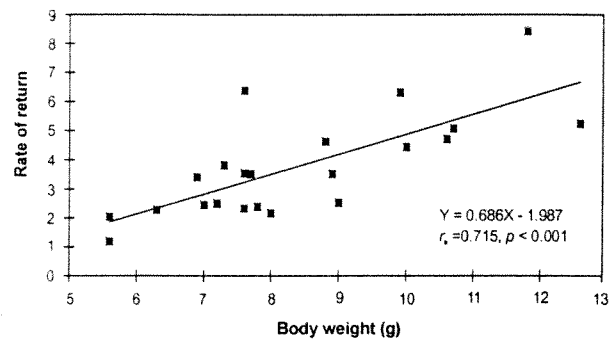
**Fig. 2.** Relation between return by brood year of sockeye salmon of the Ozernaya river and parent escapement, 1971–1992 brood years.



**Fig. 3.** Relation between rate of return of sockeye salmon from the Ozernaya River and their body length as age 2+ smolts, 1971–1992 brood years.



**Fig. 4.** Relation between rate of return of sockeye salmon from the Ozernaya River and their body weight as age 2+ smolts, 1971–1992 brood years.



During the period 1971–1981 ( $n = 11$ ) the correlation between abundance of spawners and return by brood year was  $r_s = 0.764$  ( $p < 0.01$ ) (Fig. 5). In the later period, 1982–1992 ( $n = 11$ ), the correlation between abundance of spawners and abundance of returning offspring was  $r_s = 0.802$  ( $p < 0.01$ ) (Fig. 6). The positive correlation between rate of return and smolt body weight in this period was  $r_s = 0.633$  ( $p < 0.05$ ) (Table 2).

Optimum escapement of pink salmon to West Kamchatka has been estimated by various investigators as 37–50 million fish (V.I. Karpenko and N.B. Markevich, Nabereznaya Street 18, KamchatNIRO, Petropavlovsk-Kamchatsky, 683602 Russia, personal communication). Only twice during the period 1983 to 1994 did abundance of West Kamchatka pink salmon spawners significantly exceed 50 million fish. For North-East Kamchatka the optimum escapement of pink salmon is estimated to be 13–25 million fish (V.I. Karpenko and N.B. Markevich, personal communication).

In the 1982–1992 period, there was no significant correlation between abundances of West and North-East Kamchatka pink salmon during the second sea-year of sockeye salmon and returns of sockeye salmon to the Ozernaya River ( $r_s = -0.600$ ,  $p > 0.05$ ,  $n = 11$ ). However, if the 1992 brood year of sockeye salmon which migrated to sea as 2+ smolts in 1995 is omitted, the negative correlation is significant ( $r_s = -0.745$ ,  $p < 0.05$ ,  $n = 10$ ) (Fig. 7). These sockeye would have competed with West Kamchatka pink salmon underyearlings from the 1994 brood year, in which year the pink salmon spawning grounds were seriously over-stocked, resulting in an unusually high abundance of pink salmon underyearlings, but anomalously low number of returning mature pink salmon. Correlation of sockeye salmon returns with abundance of returns in their brood year was not significant ( $r_s = 0.358$ ,  $p > 0.05$ ,  $n = 10$ ).

During the period 1982–1992, a significant negative correlation was found ( $r_s = -0.624$ ,  $p < 0.05$ ,  $n = 11$ ) between abundance of pink salmon inshore (after

Fig. 5. Relation between return of brood year of sockeye salmon to the Ozernaya River and parent escapement, 1971–1981 brood years.

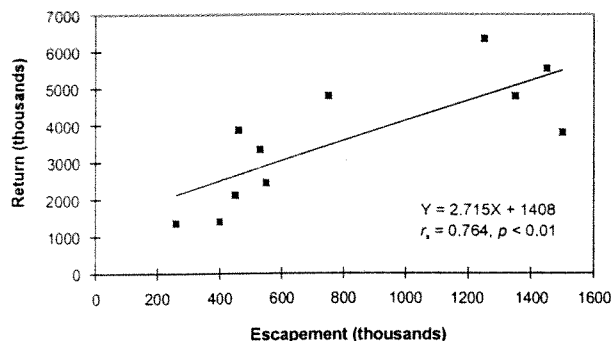


Fig. 6. Relation between return by brood year of sockeye salmon of the Ozernaya River and parent escapement, 1982–1992 brood years.

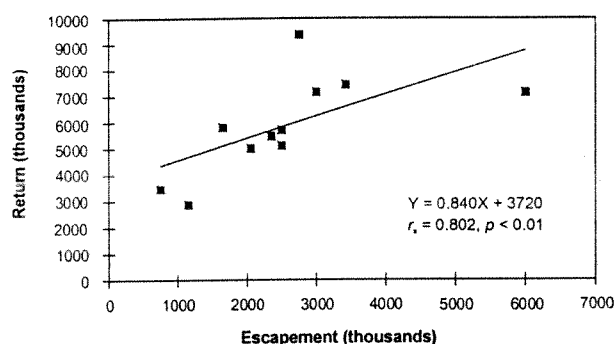
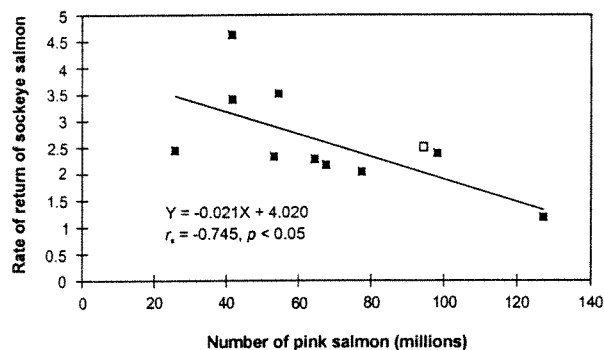


Fig. 7. Relation between rate of return of sockeye salmon (the 1982–1992 brood years) to the Ozernaya River and total inshore number of mature pink salmon off the coasts of West and North-East Kamchatka during the second year of marine life of sockeye salmon. The open square for 1992 data was omitted from the calculation of the significant correlation and regression.



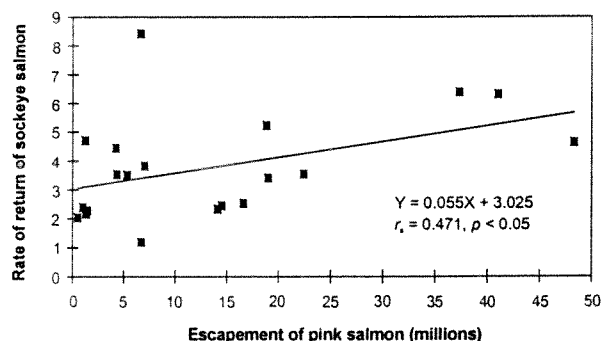
Russian and Japanese driftnet harvesting) in West Kamchatka (one year prior to ocean migration of sockeye smolts from Kuril Lake ad age 2+), and rate of return of sockeye salmon to Ozernaya River in the year following their contact at sea as age 2+ smolts with age 0+ pink salmon).

We assumed that this correlation resulted from the influence of West Kamchatka pink salmon under-yearling abundance on migrating sockeye salmon

smolts during their first year of marine life. When we replaced inshore run abundance of West Kamchatka pink salmon with abundance of pink salmon escapement in this area we also obtained a significant correlation ( $r_s = 0.627, p < 0.05, n = 11$ ) for sockeye salmon during the 1982–1992 brood years. Correlation with sockeye return by brood years was not significant,  $r_s = -0.436, p > 0.05 (n = 11)$ .

The abundance of pink salmon spawners in West Kamchatka one year prior to ocean migration of sockeye smolts was significantly and positively correlated with the rate of return of those sockeye salmon (over 1971–1992 brood years), when years with serious over spawning by pink salmon (1983, 1994), were excluded ( $r_s = 0.471, p < 0.05, n = 20$ ) (Fig. 8). Correlation with sockeye return by brood year was not significant ( $r_s = -0.254, p > 0.05, n = 20$ ).

Fig. 8. Relation between rate of return of sockeye salmon (the 1971–1992 brood years) to the Ozernaya River and the escapement of West Kamchatka pink salmon one year prior to the ocean migration of sockeye salmon smolts at age 2+ (the last freshwater year). Data from the 1983 return of sockeye (return, 5.07 million; pink escapement, 111.2 million) and the 1994 return of sockeye (return, 2.50 million; pink escapement, 81.1 million) were omitted from the figure and calculation of correlation and regression.



The 1974 brood year of sockeye salmon was unusual. The abundance of West Kamchatka pink salmon was low but the rate of return of sockeye salmon was equal to 8.42 times the average (which is extremely rare). Without brood year 1974, the correlation coefficient  $r_s$  is 0.551 ( $p < 0.05, n = 19$ ). The regression equation is:  $Y = 0.064X + 2.624$  (mean of X and Y as in Fig. 8); correlation with sockeye return by brood year was not significant, ( $r_s = -0.227, p > 0.05, n = 19$ ). The correlation coefficient between abundance of the parent escapement in West Kamchatka pink salmon (one year prior to smolts ocean migration) and returns by brood year in sockeye from the Ozernaya River was also not significant ( $r_s = 0.190, p > 0.05, n = 19$ ).

It is clear that no single factor (abundance of parent sockeye spawners, smolt length and weight, abundance of pink salmon at sea) influences brood year rate of return of sockeye salmon to the Ozernaya River alone. We therefore performed multiple re-

gression analysis ( $r$ ) of the cumulative effect of all the investigated factors.

For the period 1971–1992 the regression equation of brood year abundance for sockeye from the Ozernaya River is:

$$\text{LnRBS}(1971-1992) = -6.61 + 0.8006 \cdot \text{LnES} + 2.1465 \cdot \text{LnL2} + 0.1182 \cdot \text{LnWP0} + 0.0943 \cdot \text{LnWP3} - 0.1462 \cdot \text{LnWEP1} - 0.1371 \cdot \text{LnWEP2}; r = 0.952, p < 0.001, n = 22.$$

For the period 1971–1981 the regression equation of brood year abundance for sockeye from the Ozernaya River is:

$$\text{LnRBS}(1971-1981) = -30.79 + 0.9574 \cdot \text{LnES} - 0.6814 \cdot \text{LnWEP0} + 0.3378 \cdot \text{LnWP3} + 7.5250 \cdot \text{LnL2} - 0.6152 \cdot \text{LnEP1} + 0.3172 \cdot \text{LnWP0} + 0.0951 \cdot \text{LnWP1}; r = 0.998, p < 0.01, n = 11.$$

For the period 1982–1992 the regression equation of brood year abundance for sockeye salmon of the Ozernaya River is:

$$\text{LnRBS}(1982-1992) = -8.72 + 0.9529 \cdot \text{LnES} + 2.3267 \cdot \text{LnL2} - 0.2366 \cdot \text{LnEP0} - 0.1242 \cdot \text{LnWP2} - 0.1867 \cdot \text{LnEP2} + 0.3316 \cdot \text{LnWEP0} - 0.2029 \cdot \text{LnEP3} + 0.0713 \cdot \text{LnWP0} + 0.1221 \cdot \text{LnW2}; r = 1.000, p < 0.01, n = 11.$$

The two highest multiple correlation coefficients are for the 1971–1981 brood years,  $r = 0.998$ ,  $p < 0.01$  ( $n = 11$ ) and the 1982–1992  $r = 1.000$ ,  $p < 0.01$  ( $n = 11$ ). Note that the highest Spearman correlations for return by brood years are for the total 1971–1992 period (Table 2).

In this forward stepwise regression analysis, six of 15 independent variables were included in the first equation (the 1971–1992 period); seven variables were included in the second equation (the 1971–1981 period); and nine variables were included in the third equation (the 1982–1992 period). The multiple correlation coefficients for the entire 1971–1992 period was lower than for the two periods when separated. This again, justifies classifying the data according to the periods 1971–1981 and 1982–1992.

The difference between the initial (observed) values of the dependent variable and the predicted values is called the residual. To assess adequacy of the models it is necessary to perform an analysis of residuals (Borovikov and Borovikov 1998). Because we have only 11 (1971–1981 and 1982–1992) and 22 (1971–1992) data points, we have used graphical methods (Borovikov and Borovikov 1998). Graphical residual analysis of the three given models showed that residuals were randomly dispersed and there were no grounds to suggest that residuals were correlated among themselves. Neither were there any

distinguishing residuals. Therefore the above models adequately describe the data (Borovikov and Borovikov 1998).

During the period 1971–1992 sockeye returns by brood years were greatly influenced by the parent escapement of sockeye to Kuril Lake, and by the length of sockeye smolts migrating from Kuril Lake, positively influenced by the abundance of West Kamchatka pink salmon one year prior to ocean migration of sockeye smolts from Kuril Lake age 2+ (representing strength of competition between pink salmon underyearlings and migrating sockeye salmon smolts), by the abundance of West Kamchatka pink salmon during the third sea year of sockeye salmon, by the total abundance of West and North-East Kamchatka pink salmon during the first sea year of sockeye salmon, and by the total abundance of West and North-East Kamchatka pink salmon during the second sea year of sockeye salmon.

During the 1971–1981 period, sockeye returns by brood year were greatly influenced by the parent escapement of sockeye to Kuril Lake, the total abundance of West and North-East Kamchatka pink salmon one year prior to ocean migration of sockeye smolts from Kuril Lake at age 2+ (representing competition between pink salmon underyearlings and migrating sockeye salmon smolts), the abundance of West Kamchatka pink salmon during the third sea year of sockeye salmon, the length of sockeye smolts migrating from Kuril Lake, the abundance of North-East Kamchatka pink salmon during the first sea year of sockeye salmon, the abundance of West Kamchatka pink salmon one year prior to ocean migration of sockeye smolts from Kuril Lake at the age 2+, and the abundance of West Kamchatka pink salmon during the first sea year of sockeye salmon.

During the period 1982–1992 sockeye returns by brood years were greatly influenced by the parent escapement of sockeye to Kuril Lake, the length of sockeye smolts migrating from Kuril Lake, the abundance of North-East Kamchatka pink salmon one year prior to ocean migration of sockeye smolts from Kuril Lake at age 2+ (representing competition between pink salmon underyearlings and migrating sockeye salmon smolts), the abundance of West Kamchatka pink salmon during the second sea year of sockeye salmon, the abundance of North-East Kamchatka pink salmon during the second sea year of sockeye salmon, the total abundance of West and North-East Kamchatka pink salmon one year prior to ocean migration of sockeye smolts from Kuril Lake at age 2+, the abundance of North-East Kamchatka pink salmon during the third sea year of sockeye salmon, the abundance of West Kamchatka pink salmon one year prior to ocean migration of sockeye smolts from Kuril Lake at age 2+, and the weight of sockeye smolts migrating from Kuril Lake.

## DISCUSSION

As we have shown, the abundance of sockeye of the Ozernaya River is greatly influenced by three factors: 1 - the parent escapement of sockeye salmon to Kuril Lake; 2 - length and weight of sockeye smolts migrating from Kuril Lake; and 3 - abundance at sea of mature pink salmon off West and North-East Kamchatka. The first two factors belong to the period of spawning and freshwater life of sockeye. These factors have already been studied by various investigators (Selifonov 1975, 1988; Milovskaya et al. 1998). The possible influence of the third factor, abundance of pink salmon during the year of their maturation, has previously been only assumed (Krogius 1965; Birman 1985; Bugayev, 1995). Pink salmon dominate other salmonids in abundance, and greatly influence the ocean habitat and abundance of other Pacific salmon species (Birman 1985). However, this influence is indirect, taking place apparently through competition for the food resource.

The abundance of sockeye salmon of the Ozernaya River is also influenced by a fourth factor, the abundance of immature pink salmon (under-yearlings). However, we have no direct data on abundance of immature pink salmon at sea, and therefore must consider indirect data only.

After an exceptional escapement of pink salmon to the spawning grounds in West Kamchatka in 1983, the abundance of West and North-East Kamchatka pink salmon began to fluctuate in counterphase. This no doubt changed the food relationships among sockeye, chum (*O. keta*) and pink salmon at sea (Andriyevskaya 1975; Birman 1985; Welch and Parsons 1993; Karpenko 1998). We think it is necessary to analyse periods in the sea before 1985 (1984 and more early years) and begin from 1985 separately.

Birman (1985), Welch and Parsons (1993), Ricker (1995), Bigler et al. (1996) and Karpenko (1998) have all shown that abundance and growth rates of salmon at sea are interrelated. Birman (1985) suggested that in any area where abundance of pink salmon is high, reproductive capacity of local sockeye stocks is to a certain extent limited.

Krogius (1965) suggested that an increase in length and weight of sockeye from the Ozernaya River in the 1950s resulted mainly from a decline in pink salmon abundance. Later (Bugayev 1995) found that prior to 1984 the correlation between sockeye weight-length parameters and pink salmon abundance was different than that from 1985 through 1991. The mechanism whereby West and North-East Kamchatka pink salmon affect abundance and rate of return of sockeye salmon from the Ozernaya River should be sought among the competitive food relationships of these species during their marine life, and also in the specific distributions at sea of mature and immature individuals of these two species in

feeding areas during years of high and low abundance.

Abundance of Pacific salmon species during their downstream migration and early marine life is greatly influenced by predatory fish such as Arctic charrs (*Salvelinus malma* and *S. leucomaenis*), Asian smelt (*Osmerus mordax dentex*) and others.

Predation on salmon smolts depends mainly on density and intensity of downstream migration (Gorshkov et al. 1989) and on (overlap) of migration times of salmon smolts and predatory fish (Karpenko 1994). In coastal waters and in zones of estuaries smolts usually concentrate where there are high gradients of temperature and salinity; for migration through such zones smolts require a certain adaptation period (Karpenko 1994, 1998). Predatory fish affect Pacific salmon smolts in two ways: by consuming smaller fish they increase average smolt size and, in addition, by decreasing salmon abundance they optimize the food supply for the remaining smolts (Karpenko 1998).

According to a number of investigators (Konovalov 1971; Birman 1985) the marine habitat of sockeye salmon from the Ozernaya River is not limited to adjacent areas. According to Konovalov (1971) sockeye smolts of the Ozernaya River migrate along the Western coast of Kamchatka far to the north. Birman (1985) assumed that sockeye salmon smolts from the Ozernaya River concentrating in Kamchatkan coastal waters of the sea of Okhotsk interacted with abundant stocks of juvenile pink salmon from various rivers of West Kamchatka and probably from the Northern coast of the Sea of Okhotsk.

Most sockeye smolts from the Ozernaya River disperse during the year of downstream migration through coastal waters from 51° to 58°N (Erokhin 1998; Karpenko et al. 1998). During the last ten days of August and in early September sockeye salmon smolts feed in coastal waters up to 60 miles offshore. As a rule, pink and chum salmon under-yearlings by this time migrate to warm open waters, lowering food and habitat competition with sockeye salmon smolts.

As Karpenko et al. (1998) and Erokhin (1998) showed, in September and October feeding areas for smolts of pink salmon, chum and sockeye in the Sea of Okhotsk are separated. Pink salmon stay in offshore waters, sockeye salmon remain in coastal waters and chum concentrate in a so called "buffer zone" between these two populations. In years of high abundance, pink salmon apparently restrict chum to coastal waters. Chum then share feeding areas with sockeye salmon. The most productive feeding areas are always occupied by large gatherings of pink salmon (Erokhin 1998; Karpenko et al. 1998).

There are two ways for sockeye and chum salmon to avoid pink salmon. First, they may migrate to the north as they are tolerant of lower tem-

peratures than pink salmon (Erokhin 1998; Karpenko et al. 1998). Second, they may choose a different spectrum of food.

The factors influencing abundance of sockeye salmon and of their food competitors during marine life are multiple and various. Therefore, when abundance of pink salmon influences abundance of sockeye salmon of the Ozernaya River, the correlations may have several explanations. These explanations can supplement one another, but they do not provide complete answers to every question. Complex year-to-year investigations are required for this. We believe that our work will assist in planning investigations leading to an understanding of the mechanism underlying the correlations.

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