Ecological Functioning of Lake Kuril Relative to Sockeye Salmon Production

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Lake Kuril is the hatchery and nursery area for the largest Asian stock of sockeye salmon (*Oncorhynchus nerka*) within the Ozernaya River watershed. The average annual return for the last decade was 6.3 million sockeye and the range was 3.7 to 10.4 million. Trophic data for Lake Kuril such as water temperature, phosphorus input, phytoplankton and zooplankton densities, size and abundance of smolts, and the number of returning sockeye are available for 30-50 years and were examined relative to sockeye production. Ecosystem dynamics of Lake Kuril indicated the presence of a density-dependent regulating system for sockeye salmon. Smolt size was dependent on zooplankton biomass, and smolt weight was strongly correlated ($R^2 = 0.73$) with adult survival. The estimate of optimum escapement based on stock-recruitment analysis and size of spawning area is 1.5 million; however, when the zooplankton forage base is considered the estimate of optimum escapement can drastically vary. Our work demonstrates the need to consider the current limnological conditions in a lake to assess escapement goals and emphasizes the need to collect limnological and freshwater fisheries data to effectively manage sockeye stocks.

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INTRODUCTION

Lake Kuril serves as the major hatchery and rearing area for the largest sockeye salmon population within the Ozernaya River watershed. This sockeye stock is currently managed for an optimum escapement (1.5 million) based on stock-recruitment analyses and the spawning area (Selifonov 1988). However, it is well known that the freshwater rearing environment effects juvenile sockeye growth and can even limit sockeye production (Koenings and Burkett 1987; Kyle et al. 1988). Thus, a density-dependent regulating function can occur in sockeye lakes whereby the biomass of juvenile sockeye is dependent on zooplankton biomass (Brocksen et al. 1970; Kyle et al. 1988; Koenings and Kyle 1997).

A long-term collection of fisheries and limnological data is available to evaluate the ecosystem of Lake Kuril respective to sockeye production and in particular to assess if a density regulating mechanism is evident. This type of controlling function in lakes has been thoroughly documented and is quite characteristic for sockeye nursery lakes (Krogius 1961; Burgner 1964; Mathisen and Kerns 1964; Mathisen 1969; Goodlad et al. 1974; Bugaev 1983; Kyle et al. 1988; Eggers and Rogers 1987). Based on controlling freshwater conditions the rearing capacity of lakes can be over- or under-estimated when using only spawning area or stock-recruitment analyses. The objective of this paper is to show the influence of Lake Kuril's ecosystem in controlling sockeye production, and to incorporate the rearing capacity (forage base) in the assessment of the optimum escapement in order to maximize return and harvest.

METHODS

Study Site Description

Lake Kuril is located in southern Kamchatka and drains into the Ozernaya River. The lake has a watershed area of 392 km^2, a surface area of 77.1 km^2, and a volume of 14.6 km^3 (Resursy..., 1966). The maximum and mean depths are 316 and 180 m, respectively, and the water residence time is 17.4 years. Lake Kuril is basically an oligotrophic lake (Table 1) but demonstrates mesotrophic features in some years. Phytoplankton in Lake Kuril is dominated by diatoms (mainly *Melosira*, *Stephanodiscus*, *Cyclotella*, and *Synedra* (E. V. Lepskaya, personal communication). *Melosira italica* is the major phytoplankton species and the main food source for zooplankton. The average density of *M. italica*, depending on phosphorus levels, is 0.25 to 11753 million cells m^{-3}. Zooplankton in Lake Kuril comprises of two

Table 1. Limnological features of Lake Kurilskoye

Variable	Range	Average
Euphotic Zone depth (May-October), m	13..8 - 18.3	15.5
Average annual precipitation, mm	471 - 1220	776
Average annual water temperature in the outlet, °C	2.3 - 4.9	3.6
Average annual water temperature in the lake at depth 0 - 100 m (dwelling zone of sockeye salmon fry), °C	2.4 - 4.2	3.5
Degree days with average water temberature at a depth of 0 - 100 m that is 4°C or greater (Period of active sockeye fry growth), °C - day	259 - 1190	712
Average annual contribution of phosphorus released from sockeye carcasses, tons	0.91 - 22.39	4.8
Chlorophyll, mg/m^3	0.2 - 6.8	1

copepods (*Cyclops scutifer* and *Acanthocyclops gigas*), two cladocerans (*Daphnia longiremis* and *Bosmina longirostris*), and nine Rotifer species. *Cyclops scutifer* and *Daphnia longiremis* are main prey of sockeye salmon fry in Lake Kuril The average density of *Cyclops* ranged from 0.6 to 21.9 thousand m^{-3}, that for *Daphnia* ranged from 0.1 to 0.7 thousand m^{-3}, and Rotifers ranged in density from 3.6 to 49.8 thousand m^{-3}. Average annual biomass of all zooplankton ranged from 15.5 to 242.0 mg m^{-3}. The abundance of sockeye salmon in Lake Kuril has ranged from 0.26 million during depressed years to 6 million in peak years. The average spawner abundance is 1.6 million (Selifonov 1988). Spawning area of this lake comprises just over 1 million m^2 (Ostroumov 1970), and the substrate consists of massive layers of pumice sand lying above bedrock (Brajtseva et al. 1965). The mild climate in southern Kamchatka and the thick snow cover during the winter prevents the spawning area from freezing. The lake was fertilized in 1981, 1982, 1985, 1987, and 1989 in an attempt to increase the zooplankton forage base, and ultimately to benefit rearing sockeye fry.

Physical Features and Phosphorus

Annual water and air temperatures (at the outlet of Lake Kuril), as well as precipitation and water levels are available since 1942 (data of KamchatNIRO). Average annual input of phosphorus was calculated after Dillon (1975), and the phosphorus retention coefficient was calculated after Ostrofsky (1978). The contribution of phosphorus from salmon carcasses was based on Kizzevetter (1942) estimate of 0.28% P_2O_5 per sockeye salmon, and expressed as total phosphorus. In this paper we consider the major sources of phosphorus input to Kuril Lake are salmon carcasses and fertilizers.

Plankton

Phytoplankton (*Melosira*) density and biomass data were available since 1972. This time period was sufficient to track the influence exerted by phosphorus input on *Melosira* biomass, as this period encompassed a period of minimum and maximum phosphorus input to the lake. Zooplankton data (density and biomass) were available since 1950. Net samples (collected from the entire water column) were taken at established stations once or twice per month depending on season, and analyzed for species composition, density, fecundity, and age/life stage.

Juvenile and Adult Sockeye

Sockeye egg to emergent fry survival was determined by standardized digging of the spawning redds in the lake, tributaries, and lake outlet. Egg to emergent fry survival data were available since 1941. Smolt weight data (available since 1942) were collected with the use of a trap placed in the face of the weir at the lake's outlet. The abundance of smolts was estimated from the number of spawners expressed by the relationship:

1) $SN = 28.48 + 0.0188E$ ($r = 0.66$; $p<0.001$)

where SN = the number of smolts (millions) and E = the escapement (thousands). Sockeye spawner data (size, weight, sex, age, and fecundity) were collected by use of a weir in the lake's outlet, and were available since 1940.

RESULTS AND DISCUSSION

An excess in Kuril Lake sockeye escapement occurred in 1943, 1947, 1949, 1951, 1952, 1959, and 1961 before the very large escapements starting in the 1980s (Fig. 1). During 1962-1977, sockeye escapements were below the optimum of 1.5 million. The highest spawner deficiency occured from 1969 through 1976. Beginning in the early 1980s, the sockeye escapement reached historical high levels. Correspondingly, the annual input of phosphorus (from fish carcasses and fertilizers) was also the highest in the 1980s (Fig. 1). The amount of total phosphorus contribution from fertilizers was 7.38 tons in 1981, 19.10 tons in 1982, 8.48 tons in 1985, 3.1 tons in 1987, and 4.63 tons in 1989.

The annual biomass of *Melosira* corresponded with the increase in phosphorus as in the early 1970s the biomass was at minimum levels and during the 1980-1990s the biomass reached maximum levels. The first major peak of *Melosira* occurred in 1986, and in 1990 *Melosira* biomass was the highest. In 1986, 1990 and 1991 *Melosira* biomass in Lake Kuril passed the lower limit defined for mesotrophic lakes (100-300 mg C m^{-3}). Between the major peaks of *Melosira*, there were 2- and 3-year long periods of depressed levels. Apparently, following periods of high biomass, *Melosira* settles to the bottom depositions, and in subsequent years, under low water temperature conditions the release of phosphorus sets the stage for another peak in *Melosira*. As phosphorus declines, *Melosira* again decreases in biomass. In the late 1980s and early 1990s energy transformation in Lake Kuril followed this cycle as the ecosystem was a detrital type; a very small amount of phytoplankton was consumed by zooplankton.

Temperature, precipitation, and sockeye egg survival for Lake Kuril are plotted in (Fig. 2). There was no dependency between egg survival, substrate type, freezing of substrate, presence or absence of ice, and water temperature (Selifonov 1975). Egg survival depends to a high degree on precipitation, and to a lower degree on spawner abundance. The relationship of survival to precipitation and spawner abundance is expressed by:

Fig. 1 **Summary of sockeye escapement, annual phosphorus input and *Melosira* concentration in Lake Kuril.**

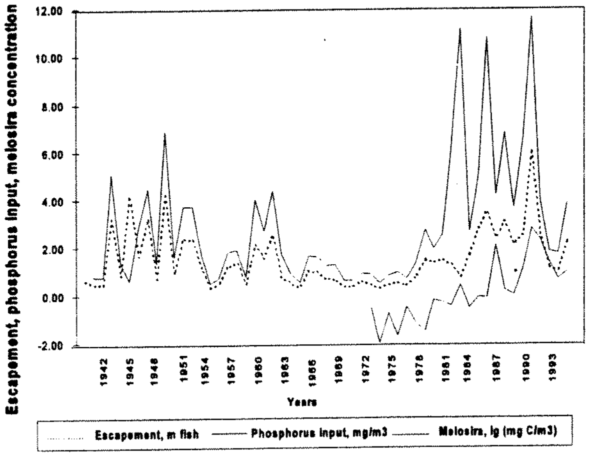
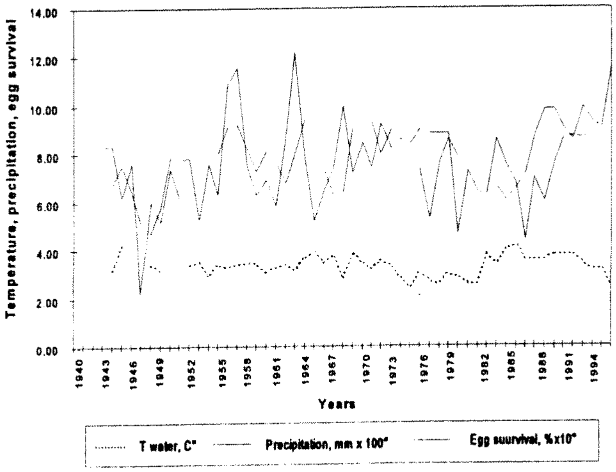


Fig. 2 **Summary of annual water temperature (0-100m), precipitation, and sockeye egg survival in Lake Kuril.**



2) $ES = 39.175 + 0.05817P - 0.00643SA$ ($R^2 = 0.70$; $p < 0.05$)
where ES = egg survival (%), P = average annual precipitation (mm), and SA = spawner abundance (thousands).

The historical trend in zooplankton biomass shows a steady increase from the 1950s to the mid 1970s, followed by a decline from the mid 1970s to 1980 (Fig. 3). During the 1980s zooplankton biomass was at high levels, peaked in 1986, and was followed by another decline through the early 1990s to the lowest recorded levels.

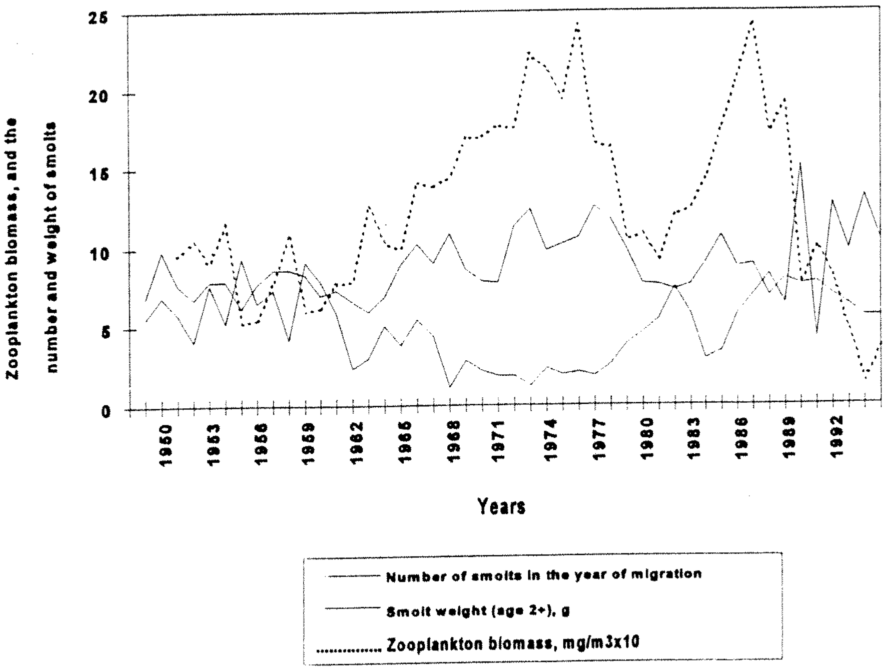
From the mid 1950s through the mid 1970s the sockeye escapement and phosphorus input decreased (Fig. 1), and most assuredly the number of rearing juveniles decreased. In contrast, during this period the zooplankton biomass increased (Fig. 3). In addition, the highest zooplankton biomass (since the early 1970s) was observed in the years with the lowest biomass of *Melosira* (Fig.1). The influence of *Melosira* biomass on zooplankton biomass was insignificant (r was ~ 0). This suggests that *Melosira* biomass provided for a near maximum feeding ration for zooplankton. Therefore, a minimum content of *Melosira* was sufficient for meeting the nutritional needs of zooplankton, such that the *Melosira* biomass could increase. The rapid decline of zooplankton biomass in the late 1970s cannot be explained by the low *Melosira* biomass, but rather by the growing abundance of rearing sockeye juveniles.

The increase of zooplankton biomass in the 1980s is influenced by the increase in average water temperature (Fig. 2) along with a sufficient abundance of *Melosira*. The zooplankton biomass increase occurred initially despite an increase in the abundance and biomass of rearing sockeye juveniles; however, consecutive years of high escapements appeared to over-crop the zooplankton forage base as the lowest zooplankton biomass was observed in the early 1990s.

The dramatic decline in zooplankton biomass also occurred when the annual water temperature dropped (from 3.0° C in 1990 to 2.4° C in 1994). Zooplankton biomass was found to be associated with the biomass of rearing juvenile sockeye (as indexed by escapements) and average annual water temperature (at 0-100 m), and is represented by a multiple regressive equation:

3) $ZB = 1276.87 - 0.986JB - 577.66T + 0.000039JB^2 + 72.64T^2 + 0.259JB*T$ ($R^2=0.55$; $p<0.01$)
where ZB = zooplankton biomass ($mg\ m^{-3}$), JB = juvenile sockeye biomass (tons), T = water temperature at 0-100 m (°C).

Fig. 3 Dynamics of zooplankton biomass, number of 2+ smolt and weight in Lake Kuril.



When sockeye escapement into Lake Kuril is low (up to 1 million), the smolt number fluctuates primarily between 20 and 50 million (Fig. 4). At an average escapement (1.6 million), the smolt number ranges from 30 to 80 million, and with larger escapements the smolt number increases with a higher dispersion of points.

In our assessment of rearing capacity we considered a zooplankton biomass level of 100 mg m^{-3} and a smolt production of 60 million (<300 tons in biomass) as low, a zooplankton range of 100-150 mg m^{-3} and a smolt production of 40-60 million (300-500 tons) as medium, and a zooplankton biomass over 150 mg m^{-3} and a smolt production >60 million (>500 tons) as high. During the 1970s, when the smolt number and biomass were lowest and water temperatures were cooler a high zooplankton biomass was observed. During the 1980s, when the smolt number and biomass were high and water temperatures were warmer a high zooplankton biomass was also observed. In the early 1990s, when the water temperature decreased but the smolt number and biomass was high the zooplankton biomass was low. Thus, a high zooplankton biomass in Lake Kuril is possible under conditions of cooler water temperatures (2.4°-3.3° C) providing that the biomass of juvenile sockeye remains in the medium range. However, if smolt number and biomass are high, a high level of zooplankton biomass is possible only for a short period of time (initial years) and only if the average annual temperature is warmer (3.6°-4.2° C) and *Melosira* biomass remains adequate. These conditions are necessary to ensure zooplankton regeneration.

An additional assessment of the rearing capacity was the weight of the major (87% by composition) age class (2+) of smolts in Kuril Lake. During the 42-year observation period, age 2+ smolts ranged from 5.6 to 12.6 g, and averaged 8.4 g. The weight of smolts, even during periods of high juvenile abundance, was far greater than the threshold value of 2 g (Koenings and Burkett 1987). The largest smolts were observed during the period of low juvenile abundance and high zooplankton biomass (1970s and mid 1980s). In contrast, the smallest smolts were observed in the early 1990s when juvenile abundance was high and the zooplankton biomass was at record lows. Smolt weight was dependent upon the preceding year's zooplankton biomass as well as smolt number, and is represented by a multiple regression equation:

4) $SW = 5.95809 - 0.01812SN + 0.04063ZB + 0.00014SN^2 - 0.00006ZB^2 - 0.00018SN*ZB$ ($R^2 = 0.53$; $p<0.001$)

where SW = smolt weight of age 2+ (g), SN = number of smolts (millions), and ZB = zooplankton biomass.

From this relationship, an average smolt weight (8.4 g) is produced if zooplankton biomass is over 125 mg m^{-3} and smolt production is 50 million. A larger smolt (>10.4 g) is possible if zooplankton biomass is over 150 mg m^{-3} and the number of smolts does not exceed 40 million. Thus, smolt weight is equally dependent on smolt number (fry rearing abundance) and zooplankton biomass during the first and second year of rearing (Fig. 5). Also, from (Fig. 5) one can conclude that at low and medium zooplankton biomass, this dependency is expressed more distinctly.

Fig. 4 Relationship between adult sockeye spawners and number of 2+ smolts in Lake Kuril.

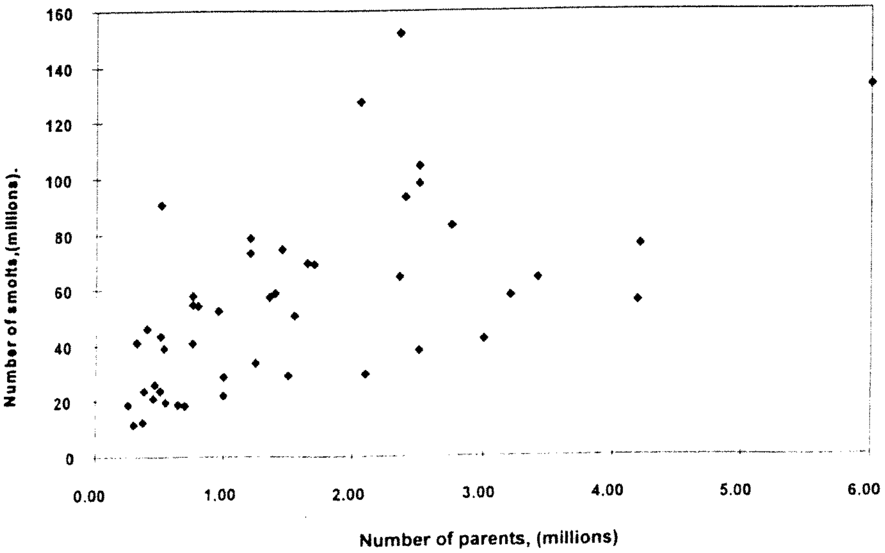
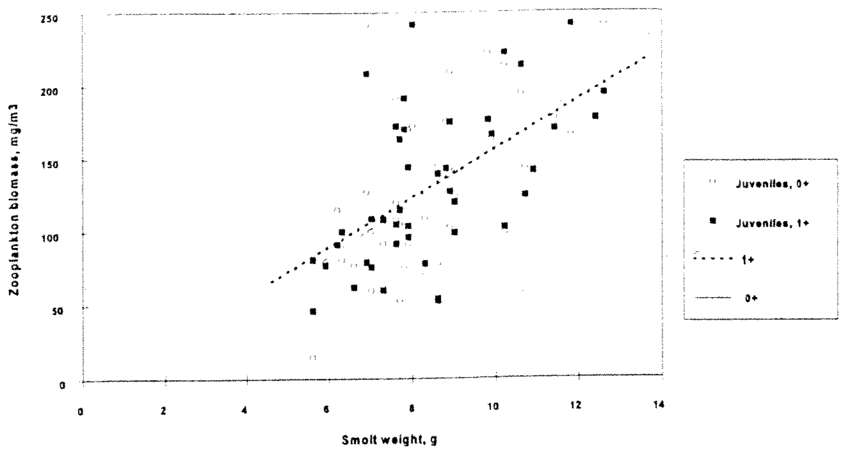


Fig. 5 Dependence of smolt 2+ weight on zooplankton biomass during the first and second rearing year, Kuril Lake.



Chronology of Trophic Level Changes in Lake Kuril

The ecosystem of Lake Kuril relative to sockeye salmon production from 1940 through 1994 has undergone some major changes that need to be considered in order to assess the escapement goal and rearing capacity. Since 1950s, sockeye escapements gradually declined and reached a low from 1970 to 1974. At the same time, the smolt number decreased, smolt weight increased, and zooplankton biomass increased to a maximum in the mid 1970s. The increase in zooplankton biomass resulted from a low forage pressure by juvenile sockeye and excellent trophic conditions in the lake - mainly due to a period of high precipitation that increased allochthonous nutrient input. Thus, the years 1970 to 1974 were a critical point of change in the ecosystem of Lake Kuril relative to sockeye production, and were characterized by low sockeye escapements, a high level of precipitation (watershed nutrient input), low smolt numbers of large size, and a high forage base (zooplankton biomass). The sockeye of Lake Kuril began to restore in the early 1980s as larger escapements were achieved and lake fertilization was implemented. However, a gradual increase in smolt number (rearing juveniles) had a negative effect on the forage base and resulted in smaller smolts. The decline in the average smolt weight was presumably due to intraspecific competition and as such the increase in forage pressure had more of a negative effect on the zooplankton community than fertilization exerted as a positive effect on the zooplankton community. The latest period (1990-1994) was a crucial change in the lake's ecosystem as the number of spawners was very high, and the precipitation level, egg survival, and smolt number were at their maximum for the 55-year period. The record number of rearing juveniles (as indexed from the escapements) had a severe effect on the zooplankton community as zooplankton biomass was at unprecedented low levels.

Management Implications

If only the spawning ground area and stock-recruitment analysis are used to assess the optimum escapement for Lake Kuril the estimate is 1.5 million sockeye. However, these analyses are limited and based on the premise that freshwater conditions do not change. As the above chronology portrayed, Lake Kuril has undergone some dynamic changes in trophic level production, and in order to better manage this system trophic interactions need to be considered:

1) Lake Kuril spawning grounds possess unique ambient characteristics and provide for a consistently high egg survival; thus, a close relationship exists between the number of spawners and smolts ($r = 0.66$), which allows modeling of abundance;

2) Smolt number influences zooplankton biomass and at low water temperatures zooplankton development is further hindered. Zooplankton biomass affects smolt weight (see Fig. 3 and Fig. 5). The dependence between zooplankton biomass, smolt biomass, and temperature is related (see equation 3). By knowing the temperature, zooplankton biomass, and taking into account responses on juvenile sockeye, it is possible to evaluate rearing conditions in the lake. This can be used to evaluate current rearing capacity and to forecast responses to existing limnological conditions in the lake.

3) There is a strong dependence (R^2 = 0.73; p = 0.01) between smolt weight and survival (Fig. 6 & 7). These figures show data since 1964 when such data were available. Consequently, future survival can be predicted, and this relationship serves as a decision-making basis for management of future runs.

Using the empirical data from Lake Kuril to define relationships dealing with trophic level responses to various limnological conditions and escapements, a table can be formulated to assess sockeye production (Table 2). This table can assist in assessing escapement goals and in making management decisions using data pertinent to the current state of the rearing environment. For example, this can be demonstrated in reference to a situation for Lake Kuril in 1996. Let us assume that a decision was made to allow 2 million sockeye to escape into the lake in 1995. However, in 1996 the zooplankton biomass was extremely low (~35 mg m^{-3}), and as such the rearing juveniles reared under an impoverished forage base and were relatively small. If the smolt weight of these fry is less than 6.6 g, their survival factor would be 1.5 for a total return of 3 million sockeye salmon (Table 2). Now, lets assume it was decided to allow only 1 million spawners instead of 2 million under the same condition of low zooplankton biomass.

According to (Table 2), a higher survival factor would result (1.7) because their would be less intraspecific competition for food. In this case, the forecast return will amount to about 1.7 million sockeye. The escapement of 2 million spawners resulted in a return of 1.3 million more sockeye than the escapement of 1 million; however, to accomplish this 1 million more fish had to be taken from the catch and the consequences of putting more fish into a depressed rearing environment need to be considered. That is, the recovery time for the zooplankton community and the low adult returns during the restorative years would most likely be more costly than the short-term benefits of a higher catch in one year.

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Fig. 6 **Smolt 2+ weight dynamics and survival measure for sockeye generations, corresponding to smolt brood years, Kuril Lake.**

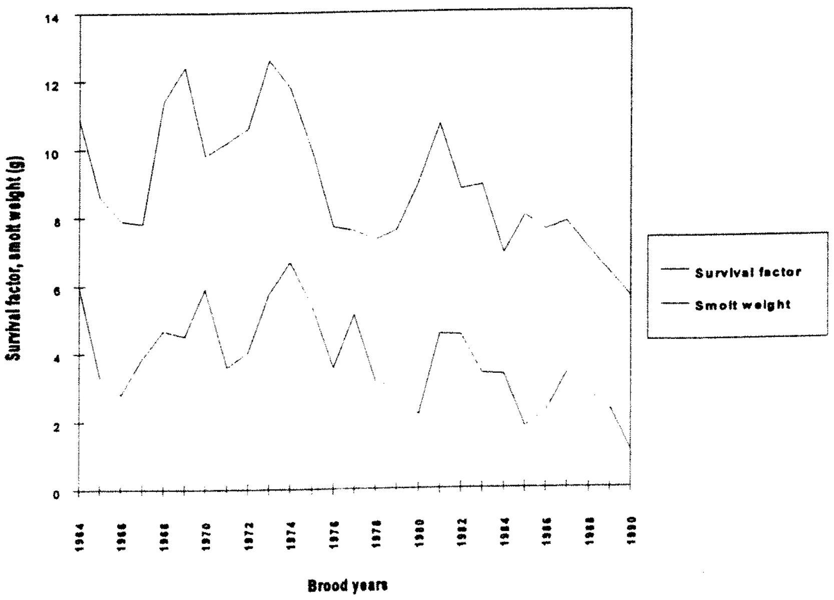

Fig. 7 Relation between suvival factor and smolt 2+ weight for Lake Kuril sockeye salmon.

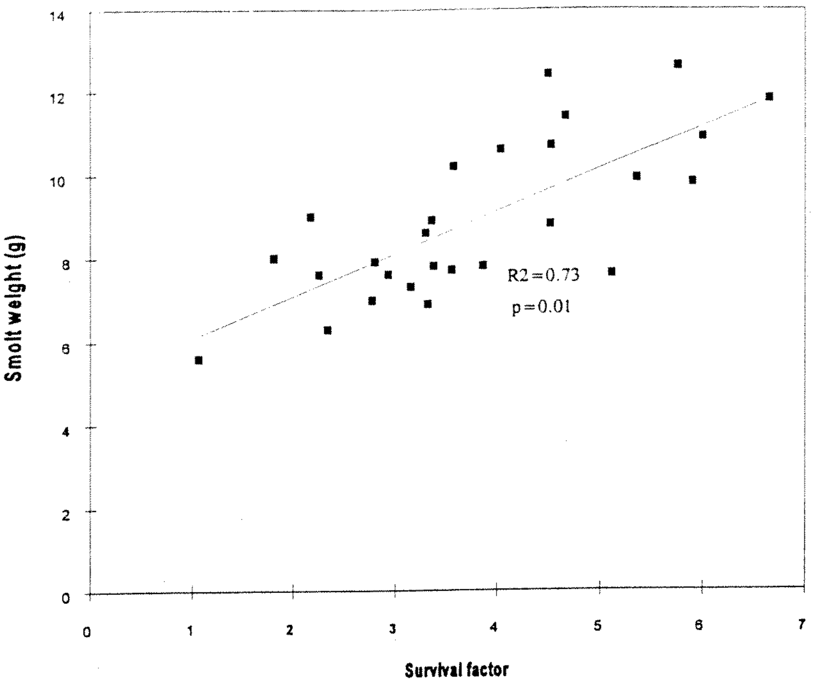

Table 2. Approximate weight of smolts and survival factors of Lake Kuril sockeye at various spawner and zooplankton concentrations.

Relative Conditions	Zooplankton concentration, mg/m³	Forecast range of smolt weight, (g)	Forecast survival factor
		Escapement of 1 M spawners (47 M smolts)	
Below medium	under 50	=< 6.9	=< 1.7
Below medium	50-100	6.8-8.0 (7.4)	2.5
Medium	100-150	8-9 (8.5)	3.2
High	150-200	9-9.5 (9.2)	4.0
High	over 200	over 9.5	>= 4.5
		Escapement of 2 M spawners (66 M smolts)	
Below medium	under 50	under 6.6	under 1.5
Below medium	50-100	6.6-7.5 (7.0)	2.0
Medium	100-150	7.5-8.2 (7.8)	2.6
High	150-200	8.2-8.7 (8.4)	3.2
High	over 200	8.5-8.9 (8.7)	3.5
		Escapement of 3 M spawners (85 M smolts)	
Below medium	under 50	under 6.4	under 1.4
Below medium	50-100	6.4-7.2 (6.8)	1.6
Medium	100-150	7.2-7.8 (7.5)	2.4
High	150-200	7.8	2.6
High	over 200	7.9-8.1 (8.0)	2.8

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