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Variation in Body Size, Fecundity, and Egg Size of Sockeye and Kokanee Salmon, *Oncorhynchus nerka*, Released from Hatchery

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Abstract. — Adult sockeye salmon (*Oncorhynchus nerka*) returning to the Bibi River, which were originally derived from Lake Shikotsu kokanee salmon,and adult kokanee salmon in Lake Shikotsu were examined for variation in body size, fecundity, and egg size. Both groups of adults originated from hatchery-released juveniles. Larger adult females had higher fecundity. Fecundity and fork length fitted allometric formula within each population. There was no relationship between fork length and egg size in Lake Shikotsu kokanee salmon or in age-1.1 sockeye salmon from the Bibi River although the sockeye salmon were approximately 65% larger in fork length than the kokanee salmon. Age-1.2 sockeye salmon, however, had eggs about 12% larger than did kokanee and age-1.1 sockeye salmon. We suggest fecundity in hatchery-released sockeye salmon vary with body size influenced by environmental components, and that their egg size would be affected by both environmental and genetic components such as polygene model within a cohort or population because of exclusion from the breeding competition and parental care.

Introduction

An anadromous form of sockeye salmon (*Oncorhynchus nerka*) is not naturally found in Japan, although the lacustrine form (kokanee salmon) released from hatcheries are observed in several oligotrophic lakes. Lake Shikotsu kokanee salmon were derived from kokanee eggs from Lake Akan on Hokkaido in 1893 and sockeye eggs from Lake Urumobetsu on Iturup Island during 1925-1940. The population in Lake Shikotsu has been geographically landlocked in this lake for more than 15 generations. Anadromous sockeye salmon have been produced from Lake Shikotsu kokanee salmon by smolt release technology in the Bibi River of the Abira River system, central Hokkaido (Kaeriyama, 1989, 1991, 1992; Urawa, 1991; Kaeriyama et al., 1992).

Among Pacific salmon, female sockeye salmon have the highest fecundity and the smallest egg size per given size of fish (Burgner, 1991). For sockeye salmon, mean fecundities range from about 2,000 to 5,000 eggs female^{-1}. Fecundity in kokanee salmon is much lower and may range from about 300 to less than 2,000 eggs female^{-1} (Foerster, 1968; Burgner, 1991). Several studies have presented evidence that body size contributed to adult female fitness such as biomass of egg production (Holtby and Healey, 1986; van den Berghe and Gross, 1989; Beacham and Murray, 1993), and a significant positive relationship between body size and egg production (fecundity and egg size) has been observed among Pacific salmon populations (Watanabe, 1955; Beacham and Murray, 1986, 1988; Beacham et al., 1988; Fleming and Gross, 1990; Tallman and Healey, 1991).

Relative distance of freshwater migration to spawning grounds generally has a marked effect on both fecundity and egg size, and populations spawning in the upper portions in drainages of large rivers have reduced fecundity and egg size compared with coastal spawning populations (Beacham and Murray, 1993). Generally, fecundity is higher, and egg size is lower in more northern populations of Pacific salmon (Fleming and Gross, 1990; Beacham and Murray, 1993). Timing of spawning in Pacific salmon can have a genetic component (Bams, 1976; Taylor, 1980). Within an area, early-spawning populations have higher proportions of older and larger individuals than late-spawning ones (Beacham and Murray, 1987). The seasonal decrease in egg size coincides with a seasonal decrease in the body size of spawners, and then progressively smaller fish lays progressively smaller eggs in Pacific salmon populations (Beacham

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and Murray, 1987; Beacham et al., 1988).

We examine factors affecting fecundity and egg size in Lake Shikotsu kokanee salmon and Bibi River sockeye salmon.

Materials and Methods

Beginning with 1983-brood year eggs, Lake Shikotsu kokanee salmon were reared at Chitose Hatchery and then released as yearling smolts (age-1.0) in the spring of 1985 in the Bibi River of the Abira River system (Fig. 1). Anadromous sockeye salmon have returned to the Bibi River as the first (F-1) and second (F-2) filials at age 1.1 or 1.2 since 1986 (Kaeriyama, 1992; Kaeriyama et al., 1992).

To study variation in female body size, fecundity, and egg size, we examined age-3.0 adult of kokanee salmon in Lake Shikotsu during 1988-1994 and adult sockeye salmon in the Bibi River during 1990-1993 (Fig. 1). Fork length (mm) and wet body weight (g) of females were measured and scales were collected to determine age. In addition, eggs were stripped from each female, weighed to calculate a gonad somatic index (GSI), and fertilized by sperm. The following equation was used to determine GSI: $GSI = GSW/BW \times 100$, where *GSW* is gonad somatic weight (g), and *BW* is wet body weight. Eggs, isolated from each female, were subsequently reared in Atkin's incubator trays. At eyed egg stage, the total number of eggs per female was counted, and egg size was determined from volume (ml) of live water-hardened eggs with excess surface moisture removed as follows: $D_e = 20\ (4V_e/(3\pi N_e))^{1/3}$, where D_e is egg diameter (mm), V_e and N_e are volume and number of total alive water-hardened eggs, respectively (Watanabe, 1955).

Relationships between body size and breeding characters were analyzed using the following allometric regression (log-transformed linear regression): $B_c = aL^b$, where B_c is fecundity (eggs female^{-1}) or egg diameter (mm), L is fork length (mm), a is initial growth constant, and b is a relative growth coefficient.

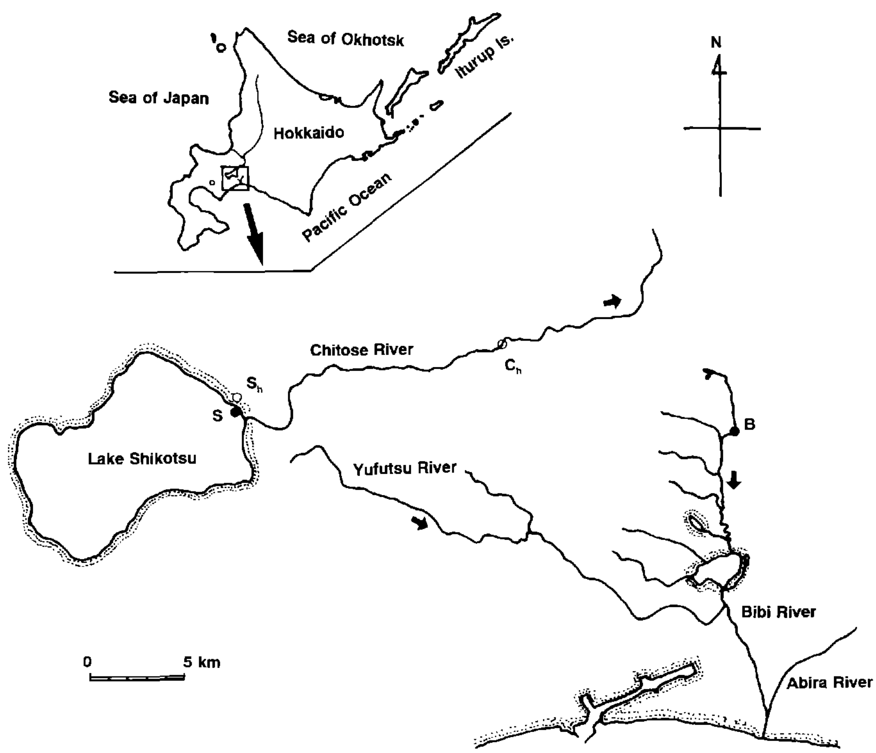

Fig. 1. Locations where kokanee and sockeye salmon were sampled. B, the Bibi River of the Abira River system; S, Lake Shikotsu of the Ishikari River system; S_h, Shikotsu Hatchery where kokanee salmon eggs were reared; C_h, Chitose Hatchery where sockeye salmon eggs were reared.

To analyze differences in body size, GSI, fecundity, and egg size among kokanee salmon, age-1.1 and age-1.2 sockeye salmon populations, the Bartlet method was first used to determine whether variances were equal. The analysis of variance (ANOVA) and the nonparametric Kruskal-Wallis test were used to compare populations. To determine differences in egg size between populations, the least significant difference (LSD) method was also used.

Results

Annual changes in body size, fecundity, and egg size of kokanee salmon

Fork length of adult female kokanee salmon in Lake Shikotsu averaged 215 mm during 1984-1988 (Kaeriyama, 1991), showed increasing trend since 1989, and attained to 288 mm (SD = 8) in 1994 with 32% larger than in 1988 (Table 1). Fecundity also increased with body size since 1989. Mean fecundity (666 eggs female^{-1}) of 1994 age-3.0 adult females was twice than that (316 eggs female^{-1}) of 1988 females (Table 1). Fork length and fecundity were significantly related ($n = 70$, $r^2 = 0.6463$, $P < 0.001$); $F = 0.00059\ L^{2.4399}$, where L and F are the fork length (mm) and the fecundity (eggs female^{-1}) respectively in the 1988-1994 adult female kokanee salmon (Fig. 2A).

However, both GSI and egg size (egg diameter) did not show annual changes, and remained stable at about 17% and 5 mm respectively during 1988-1994 (Table 1). There was no relationship between the fork length and the egg size of Lake Shikotsu kokanee salmon during 1988-1994 ($n = 67$, $r^2 < 0.001$, $P > 0.5$; Fig. 2B).

Variations in body size, fecundity, and egg size of anadromous sockeye salmon

Table 2 shows fork length, GSI, fecundity and egg size of Lake Shikotsu kokanee salmon in 1988-1994 and of Bibi River sockeye salmon in 1990-1993. There are significant differences between kokanee salmon, age-1.1 and age-1.2 sockeye salmon concerning the body size and fecundity (Kruskal-Wallis test, $P < 0.001$). However, there was no difference between any groups in GSI which remained at about 17% (Kruskal-Wallis test, $P > 0.05$). Significant difference (ANOVA, $P < 0.001$) in egg size was observed among populations. Although there was not any difference of egg size between kokanee salmon and age-1.1 sockeye salmon (LSD test, $P = 0.708$), age-1.2 sockeye salmon

Table 1. Annual changes in breeding characters of adult female kokanee salmon in Lake Shikotsu during 1988-1994. Average, standard error, and number of individuals are presented by Ave, Se, and n, respectively.

Year		1988	1989	1990	1991	1992	1993	1994
Fork length	Ave	219	244	264	252	248	249	288
(mm)	Se	0.8	0.4	0.8	0.6	0.7	0.5	0.5
	n	156	940	200	250	190	90	141
Body weight	Ave	111	168	202	174	159	176	280
(g)	Se	1.4	0.8	1.8	1.1	1.3	1	1.9
	n	156	940	200	250	190	190	141
GSI (%)	Ave	16.9	17.7	18.9	17.5	18.7	17.8	17.1
	Se	0.44	0.82	0.54	0.7	1.52	0.54	0.54
	n	10	10	10	10	10	10	10
Fecundity	Ave	316	330	401	454	412	435	666
(eggs female^{-1})	Se	9.5	15.8	11.4	18.3	27.8	28.1	31
	n	10	10	10	10	10	10	10
Egg diameter	Ave	4.8	5.2	5.1	5	5	5.1	4.8
(mm)	Se	0.06	0.06	0.03	0.03	0.03	0.09	0.06
	n	10	10	10	10	10	10	10

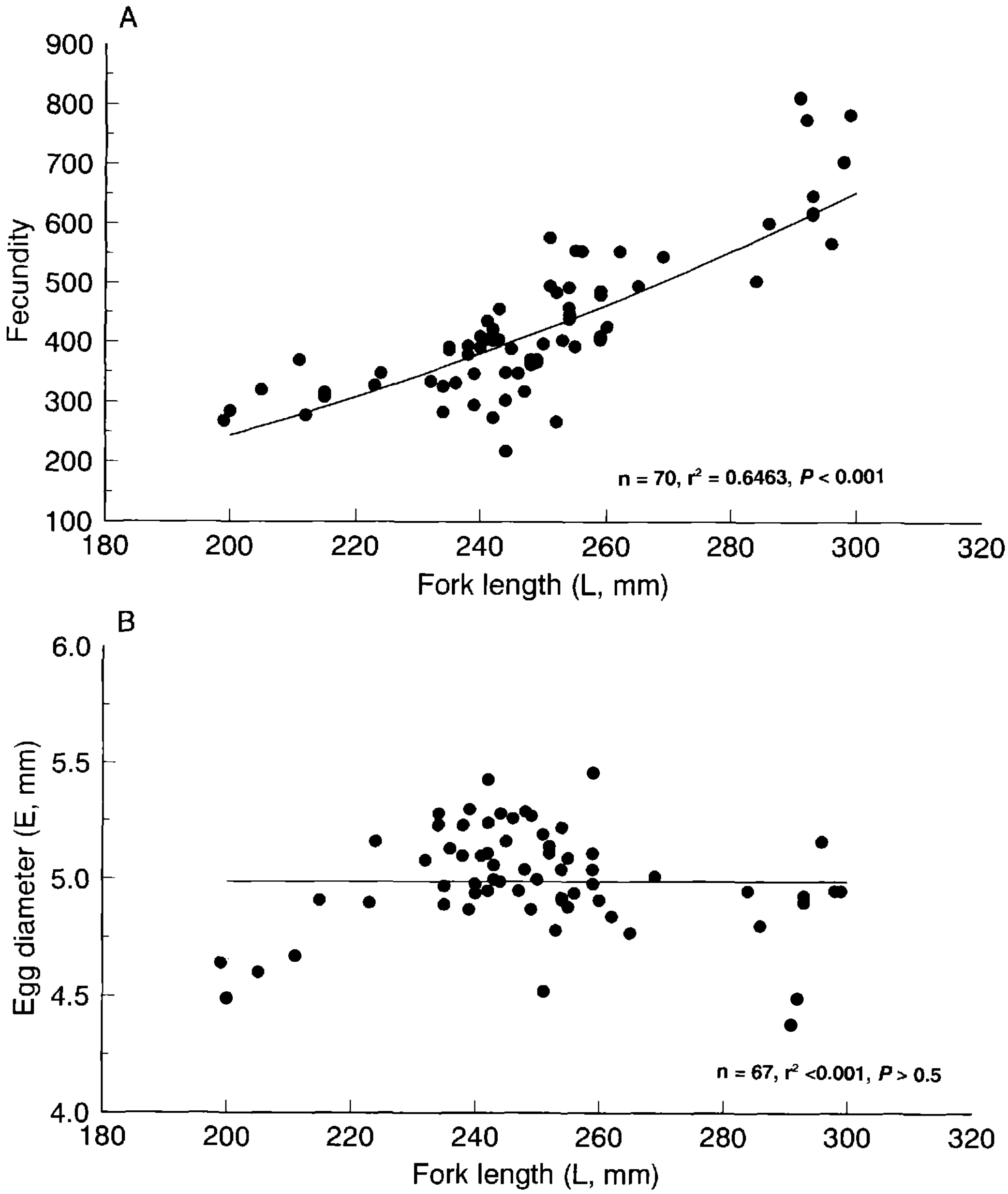

Fig. 2. Allometric relationships between fork length and fecundity (A), or egg diameter (B) of kokanee salmon in Lake Shikotsu during the 1988-1994 spawning seasons.

had eggs approximately 12% larger than did kokanee and age-1.1 sockeye salmon (LSD test, $P < 0.001$).

Relationships between fork length and fecundity ($n = 37$, $r^2 = 0.5520$, $P < 0.001$), and between fork length and egg size ($n = 37$, $r^2 = 0.6935$, $P < 0.001$) for sockeye salmon are described by; $F = 0.2280\ L^{1.4951}$ and $E = 0.2289\ L^{0.5126}$, where L, F, and E are fork length (mm), fecundity (eggs female^{-1}), and egg diameter (mm) respectively in the 1990-1993 adult female sockeye salmon (Fig. 3).

Allometric formula relationships between body size and breeding characters

The fecundity and egg size on body size regres-

Table 2. Fork length, gonad somatic index (GSI), fecundity, and egg size of Lake Shikotsu kokanee and Bibi River sockeye salmon. Average, standard errors, and number of individuals are presented as Ave, Se, and n, respectively. Probability level of significance between populations is represented by *P*.

		Kokanee salmon	Sockeye salmon		*P*
			age-1.1	age-1.2	
Fork length (mm)	Ave	249	410	498	< 0.001
	Se	2.7	2.8	5	
	n	70	16	21	
GSI (%)	Ave	16.8	17.4	17.6	> 0.05
	Se	0.32	0.93	0.68	
	n	70	9	21	
Fecundity (eggs female^{-1})	Ave	430	1875	2477	< 0.001
	Se	15.2	57.8	103	
	n	70	16	21	
Egg size (mm)	Ave	5.0	5.0	5.6	< 0.001
	Se	0.02	0.05	0.04	
	n	70	16	21	

sions are frequently calculated as allometric formula (Holtby and Healey, 1986; Beacham et al., 1988). The allometric regressions by each population (kokanee salmon, age-1.1, and age-1.2 sockeye salmon) were observed in relationship between fork length and fecundity ($r^2 > 0.18$, $P < 0.05$), but were not observed in relationships between fork length and egg size ($r^2 <$ 0.06, $P > 0.05$), and between fecundity and egg size (r^2 <0.003, $P > 0.05$; Table 3). Allometric regressions for all populations combined were observed in relationships between fork length and fecundity ($r^2 = 0.947$, $P < 0.001$), between fork length and egg size ($r^2 = 0.315$, $P < 0.001$), and between fecundity and egg size ($r^2 =$ 0.508, $P < 0.001$; Table 3).

Discussion

There appears to be a trade-off between fecundity and egg size in fish (Fleming and Gross, 1990; Beacham and Murray, 1993). Since Pacific salmon are semelparous, gametic effort should only reflect trade-offs with present reproductive demands. These include competition for breeding sites, parental care, and migration costs (Fleming and Gross, 1990). Van den Berghe and Gross (1989) found that body size contributed to adult female fitness in three ways; 1) an increased initial biomass of egg production, 2) the ability to acquire a high-quality territory for egg development, and 3) success in nest defense. Fleming and Gross (1990) reported that egg size of coho salmon was larger in hatchery populations than in wild ones because hatchery-released salmon has no breeding competition in the spawning site. Hatchery-released Pacific salmon would be useful to evaluate their gametic effort affected by migration costs because of exclusion from the breeding competition and parental care.

In our analysis for hatchery-released salmon in Lake Shikotsu and the Bibi River, larger adult female had higher fecundity, although the GSI showed a constant value (about 17%) in all females from both populations. The fecundity of Lake Shikotsu kokanee salmon annually fluctuated with change in body size, although their egg size did not show annual changes. Fecundity-length relationships for these salmon were observed to fit allometry formula. Salmon populations that allocate a greater proportion of their energy reserves to migration accomplish their life history by reducing the energy allocated to gonadal development (Beacham and Murray, 1993). A relative growth coefficient (2.4399) of allometry between fork length and fecundity in Lake Shikotsu kokanee salmon was distinctly higher than that (1.4951) in Bibi River sockeye salmon. In sockeye salmon, generally, age-.2 females consistently had a higher fecundity per a given body

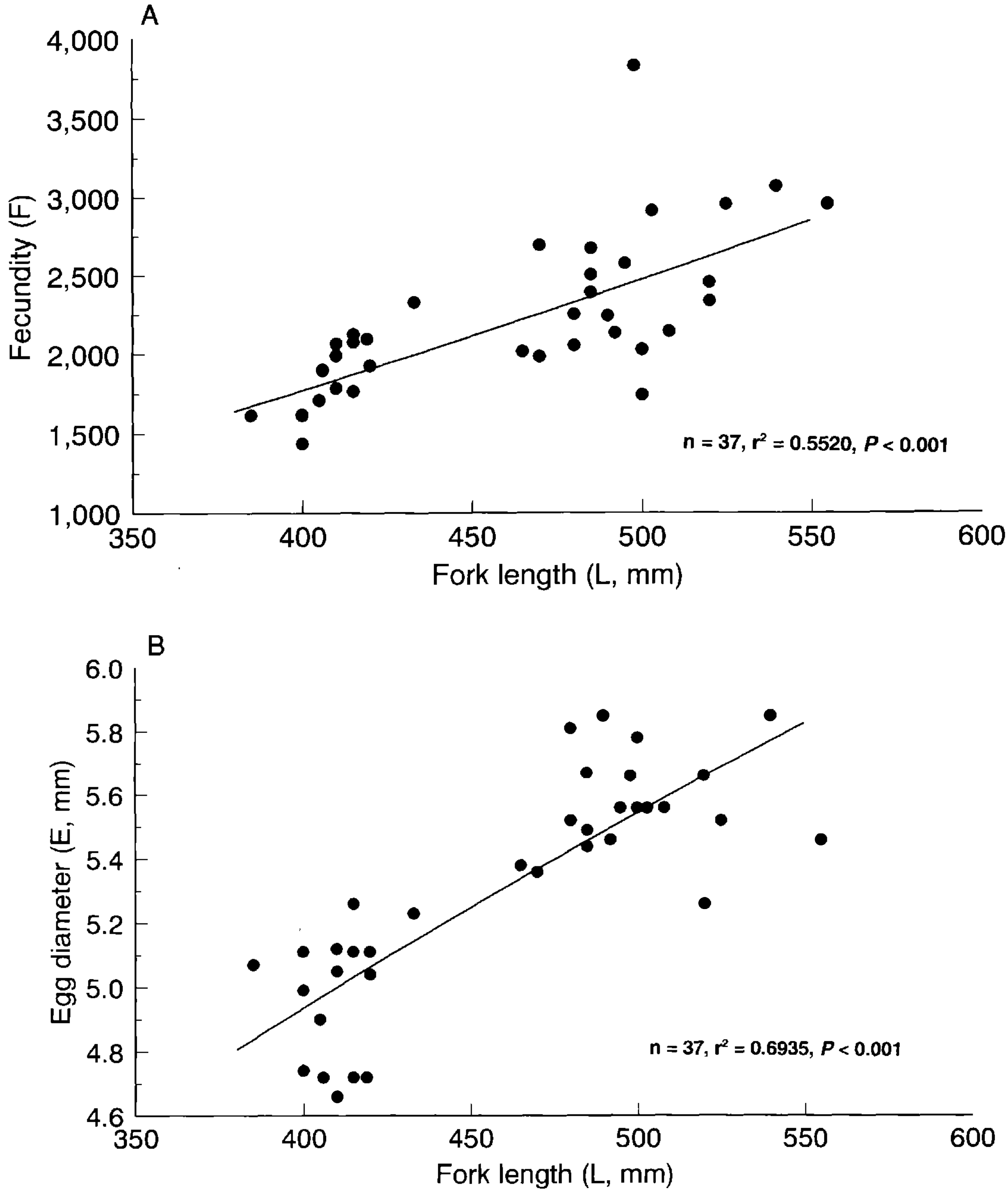

Fig. 3. Allometric relationships between fork length and fecundity (A), and between fork length and egg diameter (B) of age-1.1 and age-1.2 sockeye salmon in the Bibi River during the 1990-1993 spawning seasons.

weight than age-.3 fish (Burgner, 1991). Burgner (1991) reported the primary criteria determining fecundity within populations are size of females and the number of years spent in the ocean. For hatchery-released sockeye salmon having a constant gametic effort (GSI) without breeding competition and parental care, therefore, fecundity differences within a population may be largely attributable to variation in female body size caused by environmental variations and perhaps by intraspecific competition such as density

Table 3. Allometric formulas ($Y = a X^b$) concerning breeding characters of Lake Shikotsu kokanee and Bibi River sockeye salmon. Initial growth constant and relative growth coefficient are presented by a and b in allometry, respectively. Coefficient of determination is showed by r^2. Probability that $b=0$ is represented by P (NS: $P > 0.05$, *: $P < 0.05$, **: $P < 0.01$, ***: $P < 0.001$).

Population	Kokanee	Sockeye		All populations
Age	3.0	1.1	1.2	combined
Number of individuals	70	16	21	107
Fork length - Fecundity				
a	0.00059	2×10^{-7}	0.04416	0.00017
b	2.43995	3.78223	1.75804	2.66433
r^2	0.64627	0.63216	0.18825	0.94719
P	**	***	*	***
Fork length - Egg size				
a	4.93803	1.02468	2.31919	2.75617
b	0.00188	0.26242	0.14039	0.10712
r^2	0.00002	0.03096	0.05408	0.31537
P	NS	NS	NS	***
Fecundity - Egg size				
a	5.01134	4.35479	4.70905	4.02616
b	-0.00073	0.01752	0.02098	0.03565
r^2	0.00002	0.00312	0.01983	0.50849
P	NS	NS	NS	***

effects on growth.

Our results show no relationship between fork length and egg size in Lake Shikotsu kokanee salmon. Although age-1.1 sockeye salmon had mean fork lengths approximately 65% larger than did kokanee salmon, there was no significant difference in egg size between these two populations. Age-1.1 female sockeye salmon returning after one year in the ocean are scarce with small body as termed "jacks" (Burgner, 1991). Thus, the age-1.1 females may not abapt to ocean life history. In this study, body size influenced fecundity but not egg size within kokanee salmon and age-1.1 sockeye salmon populations.

Age-1.2 sockeye salmon had eggs about 12% larger than did kokanee salmon and age-1.1 sockeye salmon. In salmonids, generally, larger females produce more eggs, and also produce larger eggs (Sargent et al., 1987). Interaction between fecundity and egg size has been considered as a trade-off for maximizing a female's fitness returns per unit of ovarian resource (Fleming and Gross, 1990; Beacham and Murray, 1993). However, McGinley et al. (1987) reported that this trade-off model (Smith and Fretwell, 1974) was not always related with the effect of environmental variation on offspring investment, and that the variability in offspring size was viewed as an adaptation to variable environments. Thus, we think that a range of optimal egg sizes varies with the habitat and life history pattern of sockeye salmon. The egg size may be affected by drastic changes in habitable environment and life history pattern such as regime shift of environment or ocean migration patterns in anadromous form of the species.

In our conclusion, for sockeye salmon, although fecundity varies with body size according to environmental factor, egg size may be affected by both environmental and genetic components such as polygene model within a cohort or population. For hatchery-released sockeye salmon, especially, egg size may strongly relate to genetic component.

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ふ化場産ベニザケの体サイズ，孕卵数および卵サイズに関する変異性

帰山雅秀・浦和茂彦・福若雅章

ふ化場から放流された支笏湖産ヒメマスとそれを起源とする美々川放流ベニザケの親魚の体サイズ，孕卵数および卵サイズに関する変異性が調べられた．各々の個体群において，孕卵数と体サイズは連動して変化し，両者の間にはallometry式が適合した．ヒメマスとベニザケ1.1歳魚は，体サイズの変化に関わらず，一定の卵サイズ（卵径約5.0 mm）を示した．一方，ベニザケ1.2歳魚の卵サイズのみがヒメマスやベニザケ1.1歳魚に比べて大型（卵径約5.6 mm）であった．ふ化場産ベニザケについては，産卵場における繁殖競争とparental careが排除されていることから，孕卵数は生育環境の変化に伴う体サイズの関数で表されるが，卵サイズの変異は量的遺伝モデルのように生育環境要因と遺伝的要因の両構成要素により支配されている可能性の大きいことが示唆された．