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Abstract. - Adult anadromous sockeye salmon (*Oncorhynchus nerka*) returning to the Bibi River, which were originally derived from Lake Shikotsu resident sockeye salmon, and adult resident sockeye 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 was observed to fit allometric formula within each population. There was no relationship between fork length and egg size in Lake Shikotsu resident sockeye salmon or in age-1.1 anadromous sockeye salmon from Bibi River although the anadromous sockeye salmon were approximately 65% larger in fork length than the resident sockeye salmon. Age-1.2 anadromous sockeye salmon, however, had eggs about 12% larger than did resident sockeye and age-1.1 anadromous sockeye salmon. In hatchery-released sockeye salmon having a constant gametic effort without breeding comptition and parental care, egg size may be stable within a cohort or a population regardless of body-size variation, although fecundity is expressed by the function of body size affected by environmental factors. Therefore, analyses of fecundity and egg size in hatchery-released sockeye salmon population may be useful to assessument of stock status and biological monitoring, respectively, for anadromous stocks in the North Pacific Ocean.

Introduction

The objective of the North Pacific Anadromous Fish Commission (NPAFC) is to promote the conservation of anadromous stocks in the Convention Area (Article VIII-2). A goal of scientific research for the Committee on Scientific Research and Statistics (CSRS) are, therefore, to establish the conservation methods for each anadromous stocks, which may be defined as local population (deme) or Mendelian population . The CSRS research should be extensively done in the Convention Area and adjacent waters, where necessary, from various aspects such as ecology, gentics and oceanography (Fisheries Agency of Japan, 1993). Fisheries Agency of Japan proposes that stock assessment of salmon in the North Pacific

Ocean should be recognized as a most important issue of the CSRS (Fisheries Agency of Japan, 1994). In the CSRS research, methods for stock identification and biological monitoring should be basic and important issues to conserve anadromous stock.

An anadromous sockeye salmon (*Oncorhynchus nerka*) is not naturally found in Japan, although the lake-resident sockeye salmon released from hatcheries are observed in several oligotrophic lakes. Lake Shikotsu resident sockeye salmon were derived from resident sockeye eggs from Lake Akan on Hokkaido in 1893 and anadromous 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 resident sockeye salmon by smolt release technology in Bibi River of 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, with populations spawning in the upper portions in drainages of large rivers having 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, so progressively smaller fish lays progressively smaller eggs in Pacific salmon populations (Beacham and Murray, 1987; Beacham *et al.*, 1988).

We examine whether there are annual changes or influences between fecundity and egg size relation to body size of adult females for Lake Shikotsu resident sockeye salmon and Bibi River anadromous sockeye salmon.

Materials and Methods

To study variation in female body size, fecundity, and egg size, we examined age-3.0 adult of lake-resident sockeye salmon in Lake Shikotsu during 1988–1994 and adult anadromous sockeye salmon in Bibi River during 1990–1993 (Fig. 1). Fork length (millimeters) and wet body weight (grams) of females were measured and scales were collected to assess age. In addition, eggs were stripped from each female, measured to calculate a gonad somatic index (GSI), and fertilized by sperm. The following equation was used to determine GSI: GSI = GSW/BW × 100, where *GSW* is gonad somatic weight (grams), *BW* is wet body weight. Eggs, isolated by female, were subsequently reared in Atkin's incubator trays. At eyed egg stage, the total number of eggs per female was counted, egg size determined from volume (milliliter) 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 (millimeters), 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 breeding character (fecundity, eggs female^{-1}; egg size, millimeters), L is fork length (millimeters), a is initial growth constant, and b is a relative growth coefficient.

To determine 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 for 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 resident sockeye salmon in Lake Shikotsu

Fork length of adult female resident sockeye salmon in Lake Shikotsu averaged 215 mm during 1984–1988 (Kaeriyama, 1991), showed increasing trend since 1989, and attained 288 mm (SD = 8) in 1994 with 32% larger than in 1988. Fecundity also increased with body size since 1989. That is, mean fecundity (666 eggs $female^{-1}$) of 1994 age–3.0 adult females was twice that (316 eggs $female^{-1}$) of 1988 females (Fig. 2). 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. 3A).

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 (Fig. 2). There was no relationship between the fork length and the egg size of Lake Shikotsu resident sockeye salmon during 1988–1994 (n = 67, $r^2 < 0.001$, $P > 0.5$; Fig. 3B).

Variations in body size, fecundity, and egg size of anadromous sockeye salmon derived from Lake Shikotsu resident sockeye salmon

Beginning with 1983–brood year eggs, Lake Shikotsu resident sockeye salmon were reared at Chitose Hatchery and then released as yearling smolts (age–1.0) in the spring of 1985 in Bibi River of Abira River System. 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).

Figure 4 shows fork length, GSI, fecundity and egg size of Lake Shikotsu resident sockeye salmon in 1988–1994 and Bibi River anadromous sockeye salmon in 1990–1993. There are significant differences between resident 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 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. 5).

Allometric formulas relationships between body size and breeding characters in given populations of sockeye salmon

The fecundity and egg size on body size regressions are frequently calculated as allometric formula (Holtby and Healey, 1986; Beacham *et al.*, 1988). The allometric regressions by each population (lake-resident sockeye salmon, age−1.1, and age−1.2 anadromous sockeye salmon) were observed in the 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 1). Allometric regressions for all populations combined were observed in the 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 1).

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, though 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 than wild population because hatchery−released salmon has no breeding competition in spawning site. Hatchery−released Pacific salmon would be useful to evaluate their gametic effort affected by the only migration costs because of exclusion from the breeding competition and parental care.

In our analysis for hatchery−released sockeye salmon in Lake Shikotsu and Bibi River, larger adult female had higher fecundity than the others, although the GSI showed a constant value (about 17%) in all females from both populations. The fecundity of Lake Shikotsu resident sockeye 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 this 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 for Lake Shikotsu resident salmon was distinctly higher than that (1.4951) for Bibi River sockeye salmon. In sockeye salmon, generally, age−.2 females consistently had a higher fecundity per a given body weight (kg) 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 probably are largely attributable to variation in female body size caused by environmental variations and perhaps intraspecific competition such as density effects on growth.

Our results show no relationship between fork length and egg size in Lake Shikotsu salmon. Although age−1.1 sockeye salmon had mean fork lengths approximately 65% larger than did resident salmon, there was no significant difference in egg size between these two populations. Age−1.1 sockeye salmon returning after one year in the ocean are much smaller, are scarcely female, and as such are termed "jacks" (Burgner, 1991). Thus, the age−1.1 females may not be more enough to spend ocean life than age−1.2 females. In this study, change in body size had influence on egg size than on fecundity within resident sockeye salmon and age−1.1 anadromous sockeye salmon populations.

Age−1.2 anadromous sockeye salmon had eggs about 12% larger than did resident and age−1.1 anadromous sockeye salmon. In salmonids, generally, not only do larger females produce more eggs, but they 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 by Smith and Fretwell (1974) did not necessarily consider 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 there is not one optimal egg size but a range of optimal egg sizes that varies with the habitat and the life history for 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 a population. In hatchery−released sockeye salmon having a constant gametic effort without breeding competition and parental care, egg size may be stable within a cohort or a population regardless of body−size variation, although fecundity is expressed by the function of body size affected by environmental factors. Therefore, Analyses of fecundity and egg size in hatchery−released sockeye salmon populations may be useful to assessment of stock status and biological monitoring, respectively, for anadromous stocks in the North Pacific Ocean.

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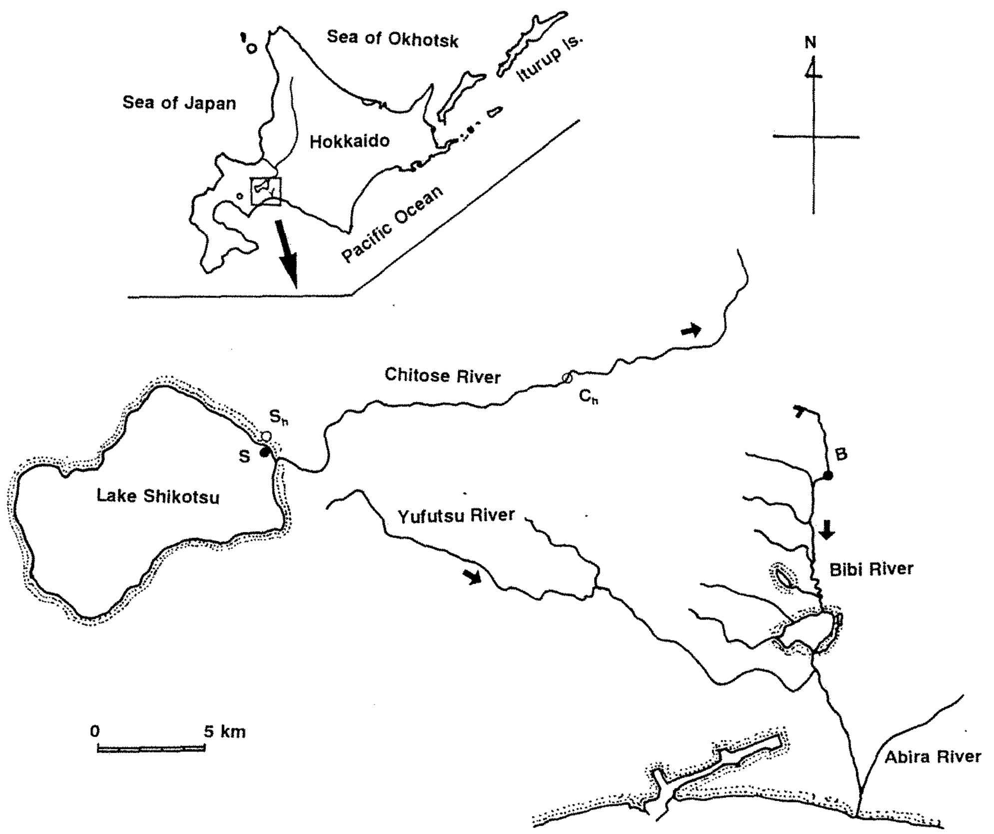

Fig. 1. Locations where kokanee and sockeye salmon were sampled. B: Bibi River of Abira River System, S: Lake Shikotsu of Ishikari River System, S_h: Shikotsu Hatchery where kokanee salmon eggs were reared, C_h: Chitose Hatchery where sockeye salmon eggs were reared.

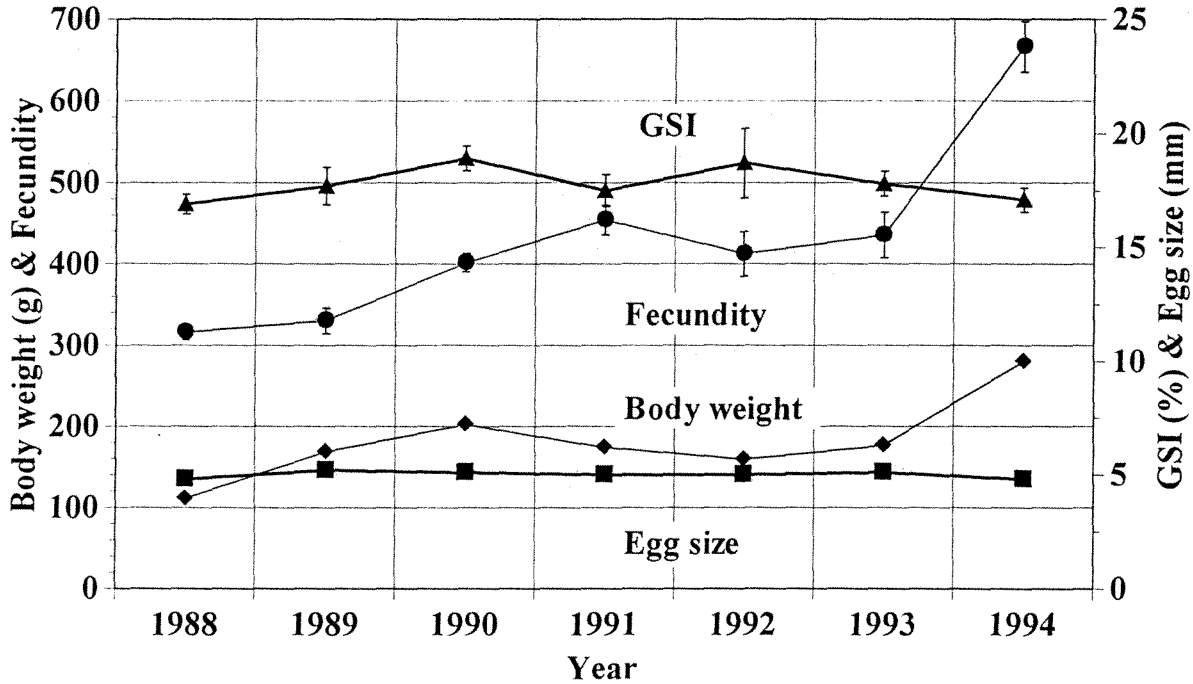

Fig. 2. Annual changes in average and standard errors of reproductive characters for adult female resident sockeye salmon in Lake Shikotsu during the 1988–1994 spawning seasons.

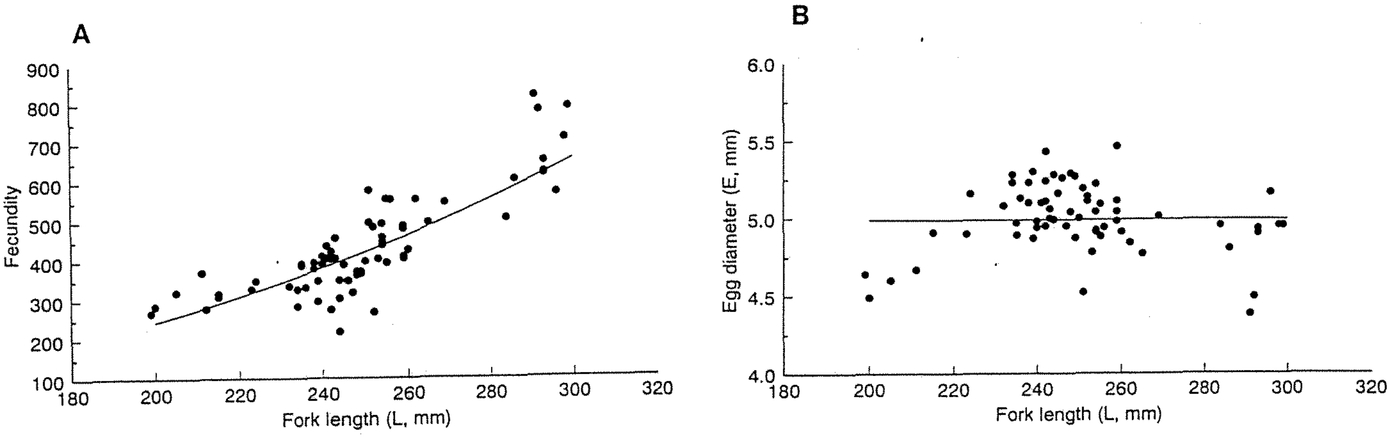

Fig. 3. Allometric relationships between frok length and fecundity (A), and between fork length and egg diameter (B) of kokanee salmon in Lake Shikotsu during the 1988–1994 spawning seasons. (A) $n = 70$, $r^2 = 0.6463$, $P < 0.001$, (B) $n = 67$, $r^2 < 0.001$, $P > 0.5$.

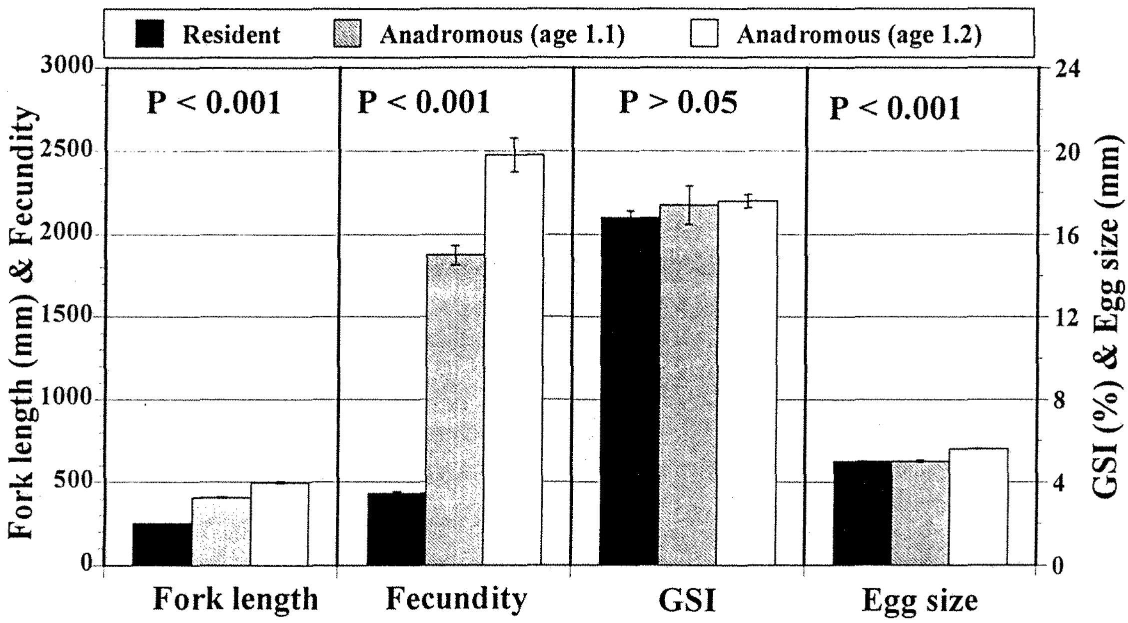

Fig. 4. Average and standard errors of reproductive characters for resident and anadromous sockeye salmons released from hatchery. Probability level of significance between populations is represented by *P*.

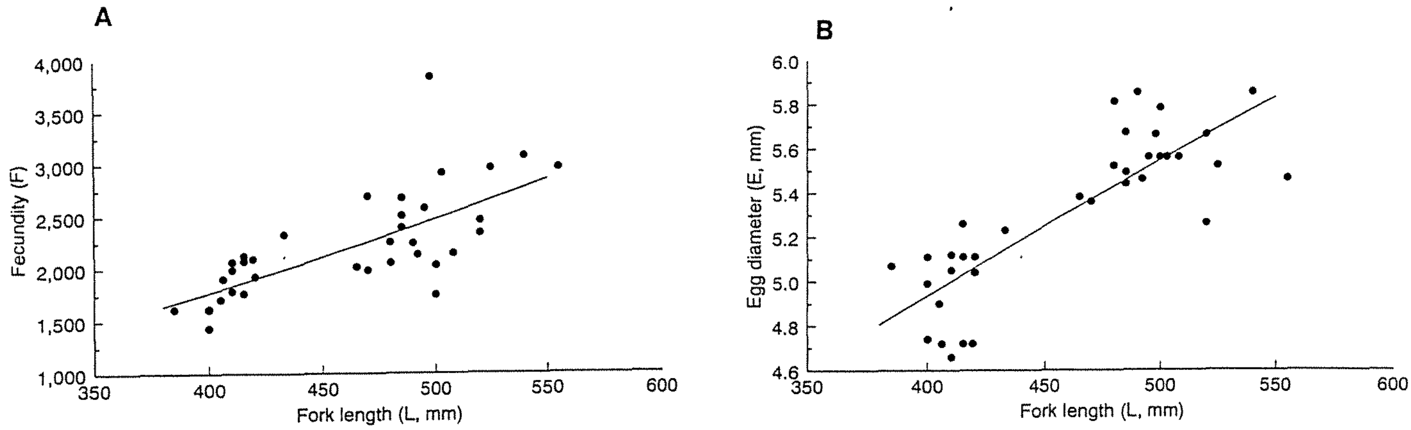

Fig. 5. Allometric relationships between fork length and fecundity (A), and between fork length and egg diameter (B) of age–1.1 and age–1.2 sockeye salmon in Bibi River during the 1990–1993 spawning seasons. (A) n = 37, $r^2 = 0.5520$, $P < 0.001$, (B) n = 37, $r^2 = 0.6935$, $P < 0.001$.

Table 1. 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	***