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# Sexual Difference in Masu Salmon: Female-Biased Sexual Size Dimorphism in a Lacustrine Population, Northern Hokkaido, Japan

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## ABSTRACT

To explore evolutionary processes of sex-specific traits, it is examined whether adult body size or growth during the migration phase (the lacustrine-phase after smolting) differ between the sexes in migratory (lake-run) masu salmon (*Oncorhynchus masou*) in a lacustrine population (Shumarinai Lake), northern Hokkaido, Japan. Although there was no difference in smolt length between the sexes, female adults were larger in body length than males of the same age, indicating female-biased sexual size dimorphism (SSD) occurs. It is supposed that breeding selection favouring a larger body size for females than for males in this population probably requires that females undertake more intensive foraging behaviour with faster growth rates during the migration phase. It therefore seems to be likely that the selection is the ultimate cause of the female-biased SSD.

**Keywords:** Body size, Sexual differences, Sexual size dimorphism (SSD)

## INTRODUCTION

Females and males often differ in some life history traits. For example, sexual size dimorphism (SSD) occurs in many taxa of animals, and several studies have suggested or demonstrated that SSD is attributable to sex-specific selection on body size [1–3].

In several salmonid populations, sexual differences in feeding behaviour [e.g., 3–4], mortality rate [e.g., 4–5] and body size at maturity [e.g., 2, 6] have been reported. For the same age at maturity, males often tend to be larger in mean body size than females in Pacific salmon (*Oncorhynchus* spp.) populations [6–7]. In some coho salmon (*O. kisutch*) populations, however, a female-biased SSD occurs [4–5]. Holtby and Healey [4] considered that the sexual difference would occur in coho salmon populations where breeding selection for larger adult size acts more strongly for females than for males be-

cause the sex-biased selection will lead females to an enhanced foraging behaviour with more rapid growth. Thus, these findings in coho salmon suggest that sex-specific ‘breeding’ selection causes sexual differences in feeding behaviour and body size.

Masu salmon (*O. masou*), a species of Pacific salmon, is distributed in Far East Asia. Like other salmonids, many populations of masu salmon consist of migratory (sea-run or lake-run forms) females and males and also some stream-resident males [8]. The life cycle of migratory masu salmon is as follows: parr (juvenile fish before smolting) usually spend 1 or 2 year (s) in rivers, then become ‘smolt’ (migratory juveniles just before transforming from the parr phase to the migration phase) in the spring (at one- or two year-old) and descend to the sea or lake. After 1 year of migration phase (marine- or lacustrine-phase after becoming smolt), they return to their natal streams and reproduce in the autumn (at two- or three-year-old). All adults die after repro-

duction [see 9]. For migratory adults, the fork length ranges from about 30 to 70 cm [9–11]. Unfortunately, the trend (male- or female-biased) of SSD in masu salmon has not been thoroughly investigated, except for a few populations [9, 12]. The aim of this study is to examine sexual differences in adult body size (or growth during the migration phase) in the migratory form (lake-run form) of a masu salmon population (Shumarinai Lake system) in Japan.

## MATERIALS AND METHODS

### Study Population

Shumarinai Lake (44°20'N, 142°05'E), which is located in northern Hokkaido, Japan (Fig. 1), was artificially constructed in 1943 by damming the upper reaches of the Uryu River (Ishikari River-System) for hydroelectric power generation. Masu salmon inhabiting the Shumarinai Lake system were originally land-locked [13] and now reproduce mainly in four inlet streams, Doro Creek (DR), Butokamabetsu Creek (BT), Bifukakoshizawa Creek (BF) and Moshiriunnai Creek (MS) (T. Tamate, unpubl. data). These streams are approximately 3–10 m in width. In all inlet streams of the lake, Hokkaido Government has prohibited capturing masu salmon since 1964. In masu salmon, all females become migratory (lake-run) fish while in males both migratory and stream-resident forms occur [11]. The life-cycle of the Shumarinai masu salmon is similar to that of anadromous populations in Japan [11].

### Fish Sampling

Smolts were captured in BF by electrofishing, cast netting and angling in spring (mid-May to early-July) from 1997 to 2001. Migratory adults were collected in four inlet streams (DR, BT, BF and MS) by electrofishing during the spawning season (late-August to mid-September) from 1997 to 2001. For all sampled fish, fork length (FL, mm) and body mass (g) of each fish were measured. Smolts were sexed by visual inspection of the gonads. Sex of migratory adults was judged by the sexual dimorphism of morphology [9]. Scales were used to determine age. Total sample sizes for the five years (1997–2001) were as follows: 1+ (one-year-old) smolts,  $n = 70$ ; 2+ smolts,  $n = 11$ ; 2+ migratory adults,  $n = 166$ ; 3+ migratory adults,  $n = 41$ .

### Statistical Analyses

The mean FL of 1+ female smolts did not vary among years (one-way analysis of variance (ANOVA),  $F_{3,53} = 1.239$ ,  $P = 0.305$ ). That of 1+ male smolts also did not ( $F_{3,9} = 0.398$ ,  $P = 0.758$ ). Annual FL data were therefore pooled for each sex of 1+ smolts. Annual sample sizes of each sex of 2+ smolts were too small to test statistically the variation in FL among years. In this study, it is assumed that the mean FL of each sex of 2+ smolts did not differ among years, like 1+ smolts: thus, yearly FL data were also combined for each sex of 2+ smolts. The mean FL of 2+ migratory female adults in a given year did not differ among the streams (one-

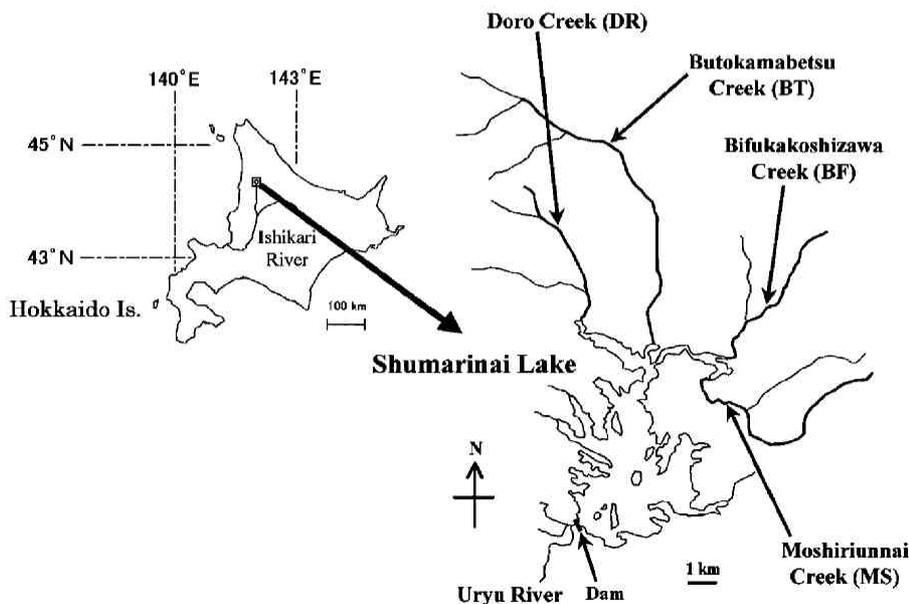


Fig. 1 Map of the Shumarinai Lake system with the locations of creeks studied and their abbreviations

way ANOVA,  $P > 0.109$  for all years examined). Likewise, the mean FL of 2+ migratory male adults in a given year were statistically indistinguishable (one-way ANOVA,  $P > 0.094$  for all years examined). Therefore, FL data among the streams in a given year were pooled for each sex of 2+ migratory adults. Most annual sample sizes of each sex of 3+ migratory adults were too few to perform the meaningful statistical test for examining the variation in FL among streams in a given year. It is assumed that, as established for each of sex of 2+ migratory adults, the mean FLs of each sex of 3+ migratory adults in a given year did not vary among streams. Thus, for each sex of 3+ migratory adults, FL data among the streams in a given year were also combined.

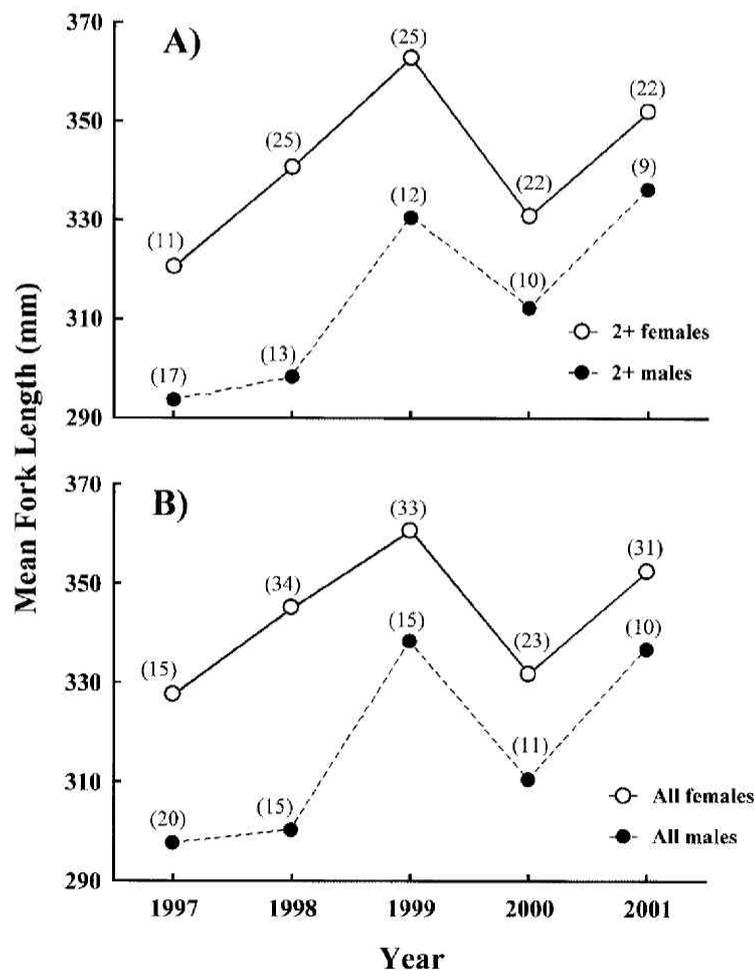
Two-way ANOVA (with replication) was used to examine if the mean FL of smolts differed between sexes. The factors of the ANOVA were 'age' and

'sex', both being considered as fixed factors. Three-way ANOVA (with replication) was performed to test if there were any sexual differences in the mean FL of migratory adults. The factors of the ANOVA were 'year' (random factor), 'sex' and 'age' (both fixed factors).

## RESULTS

### Size of Smolts and Returning Adults

The mean FL of smolts differed significantly between '1+' and '2+' (two-way ANOVA,  $F_{1,77} = 8.970$ ,  $P = 0.004$ ) but the effect of 'sex' was not significant ( $F_{1,77} = 1.246$ ,  $P = 0.268$ ). The interaction year  $\times$  sex was also not significant ( $F_{1,77} = 0.336$ ,  $P = 0.564$ ). The effects of 'year', 'sex' and 'age' influenced body length of migratory adults but the interactions among them did not (three-way ANOVA; 'year',  $F_{4,187} = 5.631$ ,  $P < 0.001$ ; 'sex',  $F_{1,4} = 11.085$ ,



**Fig. 2** Mean fork lengths (mm) of **A)** 2+ and **B)** all (2+ & 3+) migratory adults caught in the four inlet streams of Shumarinai Lake from 1997 to 2001. Numbers in parentheses indicate sample sizes.

$P = 0.029$ ; 'age',  $F_{1,4} = 8.022$ ,  $P = 0.047$ ; all interactions,  $P > 0.255$ ). Thus, for the same age, female adults were significantly larger in mean body length than male adults (Fig. 2).

## DISCUSSION

In masu salmon inhabiting the Shumarinai Lake system, smolt size did not differ between sexes but a female-biased SSD of migratory adults was observed. These observations indicate that the riverine growth did not differ between sexes while the mean growth rate during the migration phase was higher in females. The ultimate (evolutionary) factor of the sexual difference may be the breeding selection favouring larger adult size for females than for males, as supposed below.

For breeding success of females in salmonids, larger body sizes are absolutely advantageous, mainly because of the increased fecundity of larger females [14–15]. For breeding success of males in salmonids, although larger males usually seem to be more advantageous than smaller ones [e.g., 16], the difference in breeding success (fertilization success) between larger and smaller males varies with ecological factors affecting the male-male competition, e.g., the density of competitors [15]. Holtby and Healey [4] hypothesized for coho salmon populations with female-biased SSD that sexual selection on male body size (favouring larger males) is weak, i.e., small and large males have similar breeding success. In the breeding behaviour of male masu salmon, Yamamoto and Edo [17] observed that migratory males compete intensively among themselves but do not frequently interact with mature male parr. This suggests that the male-male competition among migratory males in masu salmon mainly shapes the pressure of sexual selection on adult size of migratory males: the more intensively the competition is, the larger males the selection favours. Sexual selection favouring larger migratory males will therefore be weaker in populations with lower competition among migratory males. In migratory populations of masu salmon where mature male parr frequently occur (as typically occurs in Japanese populations), breeding competition among migratory males is probably low because the sex ratio of migratory spawners is biased to females. It is also likely in the Shumarinai population, where mature male parr frequently occur [11], that the male-male competition is low because the sex ratio of migratory adults during 1997–2001 became more biased to females (T. Tamate, unpubl. data). These considerations sug-

gest that breeding selection for larger adult size acts more strongly in females than in males in the population studied. This breeding selection will make females undertake a more active feeding 'during the migration phase' because adult sizes in migratory salmonids mainly depend on growth in the sea or the lake. Therefore, the female-biased SSD or the higher growth rate of females found seems to be proximately attributable to the more active foraging of females. In future, further researches on breeding selection on adult size in salmonids will give us useful information on the evolution of SSD in salmonids.

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