Type-assortative Mating of Miyabe Charr

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In Shikaribetsu Lake and adjacent streams, Hokkaido, Japan, Miyabe charr, Salvelinus malma miyabei, comprises two types, a downstream type in which most or all females and some males migrate downstream to grow in the lake and then upstream to spawn (here termed lake-run or LR type), and stream resident males which remain in streams throughout their lives (here termed stream resident or SR type). In contrast to males, very few stream resident females occur (Maekawa, 1984, 1989). During an investigation of the charr spawning from 1971 to 1985, only two stream resident females were found paired with stream resident males (Maekawa, unpubl. data). These brief observations suggest type-

assortative mating as in other salmonid fishes (Foote, 1988; Foote and Larkin, 1988), but as yet there is no information on spawning behaviour of stream resident females, except for a few ecological aspects (Maekawa, 1984, 1989), because of their very rare occurrence.

Experiments were conducted to observe pair formation and spawning behaviour of stream-resident females of Miyabe charr under artificial conditions. This paper describes possible type-assortative mating of this charr.

Materials and Methods

According to Maekawa (1983, 1989), it is easy to distinguish between SR and LR type fish. The SR type is smaller (<18 cm in fork length) than the LR type (>20 cm) and has a distinct parr mark. A single SR female and several LR males and females, and 2 SR females and several SR males were collected by cast and chase nets from an inlet stream, Yambetsu Creek, from 25 September to 1 October 1990 and from 1 to 4 October 1991, respectively. On 1 October 1990, four mature SR females were collected during spawning in a branch of this creek upstream of a concrete dam which completely blocked the upstream migration of LR charrs. The fishes in this population had been transferred from a hatchery in 1987, and were of the SR type. Both LR and SR type fish collected included individuals that were in prespawning or postspawning condition. Each fish was

Table 1. Dominance relationships among males, based on number of attacks during observations in 1990. LR and SR in the individual code (IC) indicate lake run and stream resident males, respectively. Figures in parentheses following the fork length (FL) indicate dominance ranking

10	FL (cm)	Loser												
IC		LR1	LR2	LR3	SR1	SR2	SR3	SR4	SR5	SR6	SR7	SR8	SR9	SR10
Winner	_	_												
LR1	27.3 (1)		16	29	8	2	116	74		3	5	4	2	
LR2	27.8 (2)	3		18	34		34	20	2		45		4	1
LR3	21.2 (3)				2	1	5	2	1					
SR1	17.0 (4)			2		3	10		25	1	11	2	1	1
SR2	16.6 (4)						4							
SR3	16.3 (4)							18	2		19		5	7
SR4	16.2 (4)				2		1				2			
SR5	15.2 (4)						1				4			
SR6	15.0 (4)							1						
SR7	14.9 (4)						5	8				2	4	36
SR8	13.8 (11)													1
SR9	13.6 (12)													
SR10	13.3 (12)													

examined for ripeness or eggs by squeezing the belly. Those with eggs or sperm were used in the experiment. After the measurement of fork length (FL) and the attachment of coloured ribbon tags for individual identification, the fish were released into concrete tanks with flowing water and gravel beds (about $4 \,\mathrm{m} \times 2.5 \,\mathrm{m}$ in width and about 15 cm in water depth).

Behavioural interactions were examined between females and males all types (Experiment 1) and between a female and males in the absence of LR females (Experiment 2). From 29 September to 6 October 1990, five SR females, 10 SR males, two LR females (27.7 and 24.5 cm FL) and seven LR males were reared together in a tank (Exp. 1). However, four LR males and two SR females were eliminated from the analysis since they did not show any behavioural reactions. The FL of the remaining three SR females was 15.5, 15.5 and 14.3 cm, respectively; those of the remaining male fish are shown in Table 1. From 3 to 10 October 1991, one SR female (17.0 cm FL), one SR male (16.0 cm) and one LR male (28.4 cm) were kept in a tank (Exp. 2). Following release, courtship, agonistic behaviour and spawning were recorded by video camera and visual observation made. Total observation time was 3688 min. from 30 September to 6 October 1990 (Exp. 1) and 158 min on 5 October 1991 (Exp. 2). The method of determining dominance order among males followed Katano (1990).

Results

Experiment 1. Agonistic interactions among males showed a dominance hierarchy depending on their body size (Kendall's τ =0.817, n=13, p<0.01, Table 1). Just after release into the tank, the most dominant LR males and LR females formed pairs, whereas some SR males became satellites. LR males and LR females frequently attacked the satellite SR

Table 2. Number of courtship behaviour displays from stream resident (SR) and lake run (LR) males towards SR and LR females during observations in 1990. Figures in parentheses indicate number of actual spawnings

		Females				
		SR	LR			
Males	SR	176 (2)	19 (0)			
Maies	LR	0 (0)	179 (2)			

males. LR males also occasionally attacked SR females near the nest. SR males frequently courted SR females and attacked the stellite SR males around the nest, but no courtship interaction was observed between LR males and SR females, indicating nonrandom courtship ($\chi^2 = 750.57$, df = 3, p < 0.001, Table 2). Spawning occurred only between sexes of the same type, twice in both LR and SR pairs. In these spawnings, the dominant males spawned as paired males (LR1, LR2, SR1 and SR3 in Table 1), but at least one satellite SR male (individual code unknown) successfully sneaked at the LR pairs' spawnings. It is not known, however, if the satellites sneaked at the SR pairs' spawnings.

Experiment 2. Spawning occurred on 5 October. At first the SR male, being the paired male of the SR female, was observed to be quivering. The LR male displaced the SR male 30 min before spawning. Although the LR male sometimes attacked the SR male, no behavioural interactions were seen between the former and the SR female. Subsequently, the SR female spawned with the LR male, the SR male successfully sneaking at that time.

Discussion

The experimental results demonstrated that SR females formed pairs with SR males, whereas LR males always courted and mated with LR females when in the presence of both female types. This observation is consistent with our never having seen spawning interactions between SR females and LR males during field observations from 1971 to 1985 (Maekawa, unpubl.). However, LR males mated with SR females when LR females were absent. This suggests that male charr prefer the larger LR females available on the spawning grounds, as is the case with other salmonid fishes (e.g., Schroder, 1981; Foote, 1988). No size-assortative mating between LR females and LR males was recognized in Miyabe charr (Maekawa, unpubl. data). Therefore, typeassortative mating of this charr does not appear to result from size-assortative mating. In contrast, lacustrine and fluvial Japanese charr show clear sizeassortative mating, but since the LR and SR types have discrete body size differences, type-assortative mating can be recognized (Maekawa, Nakano and Yamamoto, unpubl. data). A possible consideration is that LR males of Miyabe charr distinguish between LR and SR females on the basis of both their body size and colour pattern. The difference in body

size of the respective females is discrete, with SR females having typical parr marks unlike LR females (Maekawa, 1989). In contrast to LR males, SR males either adopt sneaking tactics during spawning of LR pairs or pair with SR females. The choice of SR males appears to be conditional, depending on the situation. It is clear, therefore, that mating of Miyabe charr occurs assortatively by type.

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然別湖産ミヤベイワナの型による同類交配

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然別湖産ミヤベイワナには、河川残留型雌が極めて少数しか出現しないために、その産卵生態は解っていなかった。1990年に、残留型雌雄、1尾、残留型雌と降湖型雌雄各数尾を、また、1991年には残留型雌雄、降湖型雄各1尾を、それぞれコンクリート製水槽に入れ、産卵行動を観察した。各型が自由にペアを形成できる条件下では、残留型雌雄、降湖型雌雄がペアを形成し、降湖型雌がいない条件下では、降湖型雄と残留型雌がペアを形成した。自然条件下における型による同類交配形成の可能性について論じた。

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