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Streaking Behaviour of Mature Male Parrs of the Miyabe Charr, *Salvelinus malma miyabei*, during Spawning

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Abstract Twenty-two examples of spawning of mature stream resident males vs. lake run males of the Miyabe charr, *Salvelinus malma miyabei*, were observed under natural conditions in an inlet stream of Shikaribetsu Lake, Hokkaido, Japan. During spawnings of pairs of lake run type charrs, two types of behaviour were observed in the stream resident males; (1) they rushed in quickly to release sperm simultaneously with the spawning pair, and (2) they dashed in to eat eggs. From the behavioural point of view, the former represents streaking behaviour.

As judged from ecological and morphological aspects, most of the genera *Salvelinus* and *Salmo* of anadromous salmonid fishes include mature males of two types, sea-run and river or stream resident types as derived from the same progeny. Comparing the characteristics of these two types at their maturation in *Salvelinus*, the most striking difference is that the stream resident type is more precocious and several times smaller in body weight and size than that of the sea run type (Blackett, 1973; Maekawa, 1978; Armstrong and Morrow, 1980; Johnson, 1980; Power, 1980).

Many detailed observations have been made on the spawning behaviour of *Salvelinus* under artificial and natural conditions (Fabricius, 1953; Fabricius and Gustafson, 1953; Needham and Vaughan, 1952; Blackett, 1968; Kimura, 1972; Leggett, 1980; Maruyama, 1981). It is well-known that usually one male of the charr like salmon fish assumes dominance according to its body size in aggressive interactions with other males. If this is true, how does a stream resident male, usually subordinate, take part in the spawning in order to reproduce his own offspring? Gross (1982) predicted alternative strategies, probably such as sneakers and satellites, for precocial males (mature parr male) in salmonids in his report about North American sunfishes.

As far as we know, the behaviour of the stream resident charr male vs. sea-run male has not been examined due to the difficulty of conducting observations under natural conditions. At present, no such detailed report is available, except the reports on *Salmo salar* by Jones (1949, 1959) and Jones and King (1952), and *Oncorhynchus nerka* by Hanson and Smith (1967). I describe, in the present paper, some behavioural aspects of the stream resident type of the Hokkaido Miyabe charr, *Salvelinus malma miyabei* which is known as a lucustrine type of the Dolly Varden, during spawning.

Study area and methods

Shikaribetsu Lake is situated in a mountainous area at an elevation of about 800 m above sea level and nearly 43°N in central Hokkaido. The lake has four small inlet streams. Observations of spawning Miyabe charr were made under natural conditions at Yamada creek, approximately one kilometer upstream from its confluence with the Yambetsu River, an inlet stream. The spawning site observed was about 600 m in length. Having a steep gradient and gentle slopes, the creek is of the so-called "Bb" type in the stream classification according to Kani (1944) and Mizuno and Kawanabe (1981), and its water is very clear.

Twenty-two spawnings were observed and/or recorded on cassette tapes by Video camera from a bank of the creek from the 14th of September to the 18th of October, 1982. Thirty-three stream resident males and 11 immature fish of 12 spawning groups were collected along with a pair of lake run fish or without the pair by a casting net about 10 minutes after oviposition in order to examine the developmental degree of the testis and stomach contents. Of these groups, one group included only one immature fish. Collections included fish from 4 spawning

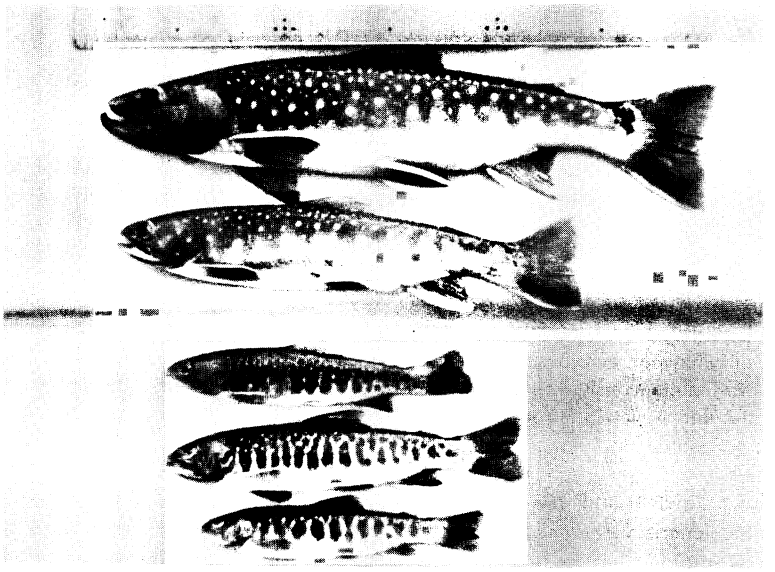

Fig. 1. Photograph of lake run female and male and stream resident males of Miyabe charr caught during postspawning acts. Lower three fishes are stream resident males.

groups recorded by Video camera and the others were during undulating behaviour of adult females as observed visually; most of these fish were thought to have taken part in spawning. Fish collected were preserved in about 10% formalin.

Observations

Life cycle of the Miyabe charr. Like the anadromous Dolly Varden, *Salvelinus malma malma*, which ascends to coastal rivers from the sea for spawning, the Miyabe charr returns for spawning to small inlet streams from the lake from August to November. The Miyabe charr included both lake run and stream resident types like the anadromous Dolly Varden with its sea-run and stream resident types, respectively (Maekawa, 1977, in press). Lake run type females mature from 3^+ years of age at about 180 mm in fork length (F.L.), the male is larger in body size (probably >200 mm F.L.) and older in age than the female. The stream resident type male matures from 1^+ year of age at about 90 mm F. L. (Maekawa, 1978). Most of the stream resident types are mature males. Therefore, stream resident individuals can be distinguished from lake-run individuals by body size, body colour and sexual dimorphism; the male of the lake run type develops a pronounced type and its abdomen changes to red in colour.

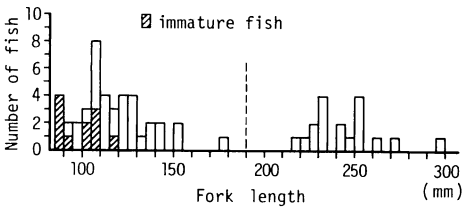

Fig. 2. Size frequency of lake run males and stream resident males of Miyabe charr during spawning season.

Stream resident individuals, on the other hand, show a small dorsal projection at the tip of the lower jaw and light-brown body colour with some blackish patterns (Fig. 1). The most striking characteristic of the former is that it is two or three times larger in body size than the latter (Fig. 2). In the present study, the body sizes of stream resident males captured during the spawning season were 87～178 mm F.L. (121 mm in average), and lake run males were 220.0～298.0 mm F.L. (243.7 mm in average). Traps set in the Yambetsu river in 1982 revealed that the ratio of lake run females and males was about 2.0: 1 from a total of about ten thousand fishes caught from September to October; consequently, the ratio of lake run males and stream resident mature males was considered to be 1:

Fig. 3. Photograph of stream resident males concentrated around a pair. F, lake run female; M, lake run male; R, stream resident males.

$\geqq$2, since the latter are more precocious than the former.

Behaviour of stream resident males during spawning. Of 22 pairs observed from the prespawning act to oviposition, all pairs were composed of lake run males and females. Males in pairs were usually larger in body size than females. However, when a lake run male or female was absent, stream resident males were frequently observed to court lake run females, or at times even lake run males, respectively. No oviposition was observed in interactions between stream resident males and lake run females. During spawning activities, several stream resident individuals concentrated around a pair (Fig. 3). Based on direct visual observations, most of these were mature river resident males with a few immature fishes. The mean number of males was 3.0 fishes ranging from 0 to 5 fishes. These fishes intruded frequently into the territory of a pair. Both the male and female of the pair were interrupted in their courtship and both interacted aggressively with the intruders. If the intruder happened to be a lake run male, the female paid little attention to him, but if when females or stream resident males approached, she assumed a threat posture with fins fully erected or attacked with open jaws. The male of the pair was more aggressive than the female. He attacked both lake run males and stream resident males. However, if the intruder happened to be a larger lake run male than the male of a pair, the latter was driven away from a territory by the former. As compared to the behaviour toward other lake run male intruders, a pair drove away stream resident intruders more aggressively by chasing or biting them. For example, the number of aggressive activities of the pair during 180 minutes just before beginning a oviposition on the 22nd of September (Table 1) was 339 for the stream resident male with the largest body size, 105 for smaller ones, 13 for immature fish and 36 for other lake run males.

A hierarchy was recognized in the stream resident males concentrated around the pair, according to body size. The most dominant individual, the largest in body size, occupied a regular position just behind the pair. Although he was attacked by both the male and female of the pair, he also attacked other subordinate individuals, smaller ones in body size, and defended his position against them. Except for such activities, stream resident males were usually inactive and lay in the gravel at the bottom of the creek, or hid under shelters constructed from plants or the roots of a tree, as if attempting to avoid attack by the pair.

Behaviour of the stream resident male during the spawning act of a pair. Females of a pair assumed a crouched posture just before beginning oviposition. The posture brought on courtship by the attending male; if the male of the pair was absent, subordinate males of the lake run type, or even stream resident males, conducted

courtship with the female. In most cases, the resident males rushed into the spawning redd during courtship of a pair but were counter-attacked and driven away by one member of the pair.

Oviposition was accomplished always by a pair of lake run type fish. The climax of the pair spawning with mouth wide open continued for three or four seconds, and it occurred successively from one to four times in an egg pit. If the resident male was absent around the pair, two subsequent ovipositions were usually observed in the same depression at intervals of about 5 seconds immediately after the first one. A distinct cloud of sperm could be observed but not the release of eggs during each spawning. The number of intrusions by resident males and other behaviour are shown at the climax of spawning of the pair in Table 1. If several resident males took part in the spawning, the female covered the fine sand on the redd by a single and quick digging upstream of the depression before the next oviposition; if more than two males participated in the first spawning, there was a tendency that the female of the pair discontinued the second spawning act (6 of 7 spawning acts observed as shown in Table 1).

The behaviour of stream resident males can be divided into two actions; (1) they rushed between a pair or beside the female or male during the spawning and then opened their mouths wide near the nest of the redd. The rushing success of stream resident males into the territory of a pair was 13 of 38 spawnings (about 34%) observed, except 8 spawnings at which behaviour of the resident males were unknown (Table 1). Other behaviour included (2) pecking within the egg pit. Such pecking actions were never observed in the lake run type male of a pair nor in other lake run types. Both the female and male of the pair counterattacked and drove away the stream resident males which intruded into the redd directly before the undulating of the female. Thereafter, during the undulating of the female,

Table 1. Number of stream resident males concentrated around each pair and the behaviour during spawning. Mark (→) shows the exchange of lake run male just before the oviposition. e, eating; op, opening mouth wide; L, lake run individual

Date	Total length of the pairs		No. of resident type	Behaviour of resident type during pair spawning			
	♀	♂		1st	2nd	3rd	4th
Sep. 14	21	23	4	3 (unknown)			
17	20	18→unknown	5	—	—	—	—
18	20	27	5	—	—	—	—
19	22	25	1	0	1 (op)	0	
20	unknown	unknown	5	3 (unknown)			
22	20	30	3	1 (unknown)			
24	23	27	5	3 (unknown)			
25	20	27	4	1 (e)	0	2 (unknown)	1 (op)
29	22	27	5	2 (op)	2 (op)	1 (op), 1 (e)	
30	20	23	1	0	0	0	
Oct. 1	23	30	0	0	0	0	
4	25	35	1	0	1 (e)		
6	20	25→40	2	1 (unknown)	0		
6	25	30	4	1 (op)	unknown		
9	22	24	0	0	0	0	
10	27	35	4+L♂	1 (op)	0	1 (op)	2 (e)
11	20	25	2	0	0	1 (op)	
12	23	37	2	2 (e)			
16	23	23	5	unknown	1 (op), 1 (e)		
17	24	28	4>	2 (op), 2 (e)			
18	22	24	3	1 (op)	2 (op)	3 (e)	
18	24	28	3	3 (e)	1 (e)	0	

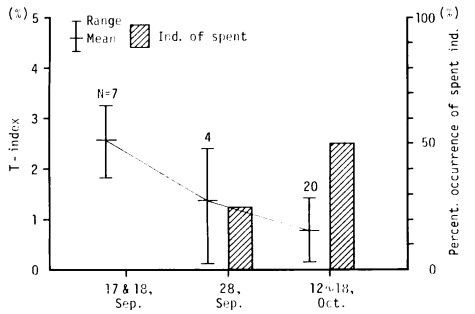

Fig. 4. Relationships of the T-index and percentage frequency of spent individuals of stream resident male during reproductive season.

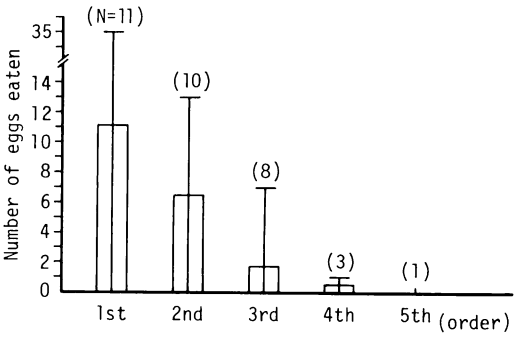

Fig. 5. Mean number of eggs eaten by stream resident male according to the order in each spawning group.

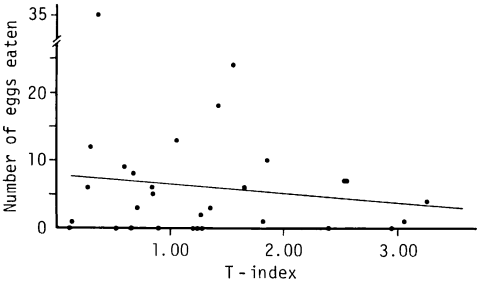

Fig. 6. Relationships of the T-index and number of eggs eaten.

only the male engaged in chasing away intruders.

We could not observe visually the release of sperm and the actual results of pecking of the resident males, because these activities took place within a nest constructed by stones or within a cloud of sperm from the lake run male. Fig. 4 shows the ratio of the testis weight to the body weight (T-index) and the percentage frequency of spent individuals (T-index <0.84) during the reproductive season in order to estimate whether or not they released the sperm during spawning. The ratio of T-index and spent individuals decreased and increased respectively as days went by. Therefore, it is possible that the mouth-opening behaviour cited above might be related to sperm release, as is found in the case of lake run individuals. Sperm-release success by stream resident males was about 1%, determined by caliculation of total number of stream resident males who released sperm $\times 100$/total number of stream resident males $\times$ total number of pair spawnings observed, except for 8 unknown examples, showing extremely low success (Table 1).

The stomach contents were examined from resident males and juvenile fish collected from each spawning group immediately after spawning. Several eggs were recognized in the stomachs of individuals, ranging in number from 0 to 35 eggs (6.0 on the average). The mean number eaten by each group was 17.0 eggs. In the resident males of each spawning group, as mentioned earlier, a hierarchy was recognized according to their body size. The mean number of eggs eaten by resident male individuals of each group increased according to dominance rank (Fig. 5). Food items besides eggs were larvae of insects and juvenile charr, but only one individual ate both eggs and a juvenile fish. Out of 33 males collected, the stomachs of six individuals were nearly empty. Three males were observed to eat only insects. When the resident male group was caught with a casting net, eleven immature fish were caught together with the resident males. Only one of these had eaten eggs (N=6); the others ate only the larvae of insects.

No significant correlations were recognized between the T-index and the number of eggs consumed (Fig. 6, $p>0.25$). However, there was a tendency that the number of eggs eaten was not more numerous at higher values of the T-index.

Discussion

The present observations showed that stream resident males were unable to form pairs with lake run females because of their usual smaller

body size as compared to lake run individuals. Female usually choose a larger male in body size than her own. On the contrary, stream resident males rushed quickly into the redd or territory of a pair of the lake run type, released sperm simultaneously with the spawning pair without showing any aggressive activities and left quickly. This behaviour may be looked upon as a successful compensatory spawning act. The body colouration of the stream resident male parr should be noted here. The light-brown body colouration with blackish patterns was very similar to the colour of the gravel at the bottom of the creek around the spawning site; it appears to be protective colouration defence against large males. This type of behaviour of stream resident males is similar to "streaking" behaviour observed in labroid fishes (cf. Warner et al., 1975; Warner and Robertson, 1978; Alcock, 1979; Krebs and Davies, 1981). This behaviour was seen also in *Oncorhynchus masou* by Komiyama (unpublished). Therefore, it is reasonable to assume that streaking behaviour may be found during spawning of other anadromous salmonid fishes.

At present, it is very important to note again a pioneer observation of the behaviour in Atlantic salmon by Jones and King (1950, 1952) and Jones (1949, 1959). Jones (1949) observed that mature male parr of the Atlantic salmon were in constant attendance of the female, and that during each act of spawning they pushed excitedly under her vent. They failed at this time to observe, however, that the male salmon parr extruded sperm. Following their first report, Jones and King (1952) asserted that the parr took part in the normal spawning of adult fish (sea run type) and that the presence of the salmon parr was in effect a safety factor. Jones reported that the sperm of the salmon parr were released in very close proximity to the eggs and thus always had a good chance of reaching the eggs.

It remains unresolved in salmon fishes with sea run and stream resident males whether the frequency of occurence of each is due to environmental factors or to differences in genetics (e.g., Jones, 1959; Utoh, 1981; Maekawa and Goto, 1982). However, it is reasonable to suggest that male dimorphism of salmonid species has been influenced, more or less, genetically. It may be important for the stream resident male to take part in the spawning as a streaker in order to transmit its own genes. If this is true, spawning by the female and lake run male (and also the sea run type) offers a chance to guarantee the propogation of the streaker's own offspring.

From the fact that eggs were present in the stomach of the spent parr of *Salmo salar* but at no time during any of the spawnings were parr seen to eat eggs, Jones and King (1952) suggested that the eggs consumed by the parr were stray ones. Most of the resident males of the Miyabe charr, however, preyed on eggs by pecking within the egg pit, and the more dominant males ate larger numbers of eggs, which suggest a purposeful behaviour. These phenomena were observed also in *Oncorhynchus masou* by Komiyama (unpublished). Maekawa (unpublished) counted 30 to 43 eggs (36.5 in average) from five redds in a spawning site of the Miyabe charr observed in 1974. If these values can be applied here, then predation takes 17 eggs on the average from each redd, about 30%, though it is possibile to overestimate the value, as some of the present specimens of resident males may have eaten eggs in two redds or more. We cannot discuss the significance of egg predation from the present data. However, Jones (1959) never saw a parr took any eggs from the bed of the female with whom he had just spawned. If such a phenomenon was applicable to the present case, it might be suggested that rather than the "safety factor" hypothesis, stream resident males mature rapidly to a small size, and being unable to form a pair with a female, improve their reproductive success by streaking and/or by removing the lake run rival's genetic input by eating eggs. Conversely, sea (lake) run type fish may grow slowly to a large size, court a female, be territorial and consequently improve their reproductive success. Considering extremely low success of sperm-release by stream resident males in the present study, however, it is clear that more detailed work of charr behaviour, including fertilized ratio by lake run (sea run) and stream resident males, is necessary before broad theories on the evolution of charr mating systems can be adequately formulated.

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然別湖産オショロコマの産卵中における河川残留型の streaking 行動

前川光司

多くのサケ科魚類の雄には，降海型と河川残留型の二型がみられる．然別湖に生息する陸封型オショロコマ（ミヤベイワナ）も同様に，雄の二型が知られている．1982年9月から10月にかけて，放精・産卵に至る23例の産卵行動を観察した．pair は体の大きな降湖型で形成され，体の小さな河川残留型数尾がその回りに集中した．残留型は pair を形成する降湖型雌雄にはげしく追い払われた．pair の放精放卵中，残留型には二つの行動が認められた．一つはすばやく産卵床に突入して放精し，他は卵を食べる，という行動であった．こうした行動は，他の動物にみられる streaking とよく似ていた．これは pair を形成できない残留型が，自らの仔を残すための繁殖戦略であるかもしれない．

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