

Spawning Behaviour of Dolly Varden in Southeastern Alaska, with Special Reference to the Mature Male Parr

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Many observations of the spawning behaviour of genus *Salvelinus* have been made under artificial and natural conditions (Fabricius, 1953; Fabricius and Gustafson, 1953; Kimura, 1972; Leggett, 1980). Most of them were limited to the behaviour of a pair spawning. Anadromous *Salvelinus* include mature males of two types, searun and stream resident type (mature male parr), and recently Maekawa (1983) and Maekawa and Onozato (in press) noticed that the mature male parr of the lacustrine Miyabe charr (land-locked form), *Salvelinus malma miyabei*, in Shikaribetsu Lake, Hokkaido, participated as a stalker in the spawning between a lake-run male and female, which is larger in body size and older in age at maturity than the male parr. However, little is known about the relationship between sea-run and stream resident mature males of anadromous dolly varden, *S. malma malma*, during breeding.

In this paper, we concentrate on the spawning behaviour of stream resident mature males during breeding of anadromous dolly varden in southeastern Alaska and present some new findings.

Study area and methods

The study was carried out in a tributary of Montana Creek in Juneau, southeastern Alaska, from the 1st to 14th of October, 1984. This tributary is located at approximately five kilometers upstream from its confluence with the Glacier River. The water is very clear, and the stream is about three meters in width and about 30 centimeters in depth in the observation area, and it belongs to Aa-Bb type according to the stream classification by Kani (1944). Spawning behaviour of dolly varden were recorded under natural conditions by video camera from the banks of the river. Several specimens of sea run and stream resident males were collected by cast and hand nets.

Observations

Characteristics and body size of mature male parr and sea run male. The two types of dolly varden males can be distinguished by certain morphological characters observed during breeding. The sea run type male develops a pronounced kype and its abdomen changes to red in colour without parr marks. The mature male parr shows a small dorsal projection at the tip of the lower jaw and parr marks on the abdomen, and in no individuals with relatively smaller size does the abdomen change to red. According to these characters, the size distributions of the two types of dolly varden were obtained (Fig. 1). All the mature male parrs were smaller in body size than

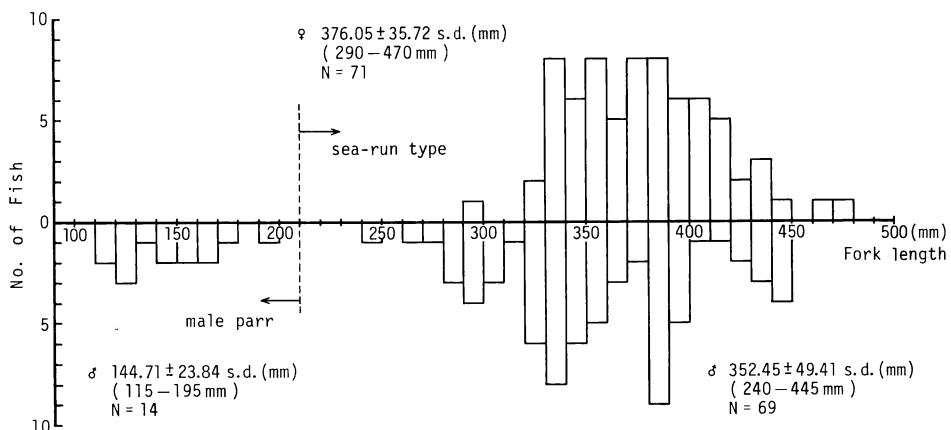


Fig. 1. Fork length distribution of dolly varden collected in Montana Creek.

the sea run males; therefore, the body size distributions of mature male parrs and sea run males do not overlap. The sea run type male is somewhat smaller than the female and smaller mature males in sea run males are probably precocial, as mentioned by Armstrong and Morrow (1980).

The mature male parr was younger in age (3⁺ and 4⁺, number examined=14) than the sea run male (over 5⁺, N=7), as determined by otolith rings.

Spawning behaviour. Sea run type fish migrated up from the main stream to the tributary, when the water had risen on the night of 3rd October, 1984. Most of the fish spawned only on the 4th and 5th of the month during the observation periods. Thereafter, most of the fish disappeared from the tributary.

Ten spawnings, from prespawning act to oviposition, were observed in this tributary. Most of the pairs, except for one spawning of which the pair was formed by a mature male parr and a sea run female as shown by an asterisk in Table 1, were composed of sea run males and females (Table 1). Males in pairs were usually larger in body size than females in spite of the difference of

body size among males and females, as mentioned in Fig. 1. Therefore, it was suggested that relatively smaller males of the sea run type become satellites or sneakers, although we could not observe a satellite individual of the sea run male around a pair in the present study, except for one fish as shown by (SR) in Table 1. In this case, the SR male was frequently driven away by an α male, but he successfully released sperm during a pair spawning.

During spawning activities a few mature male parrs concentrated around a pair. In addition to the 10 spawnings mentioned above, the number of mature male parrs around a pair was counted in 5 prespawning pairs. The mean number per pair was 0.93, ranging from 0 to 2 (N=15). These fish intruded frequently into the territory of a pair. Both the male and female of the sea run type interacted aggressively with the intruders by chasing or biting them. Most of the mature male parrs occupied a regular position, such as just behind the pair, or remained in shallow water.

Whenever females of a pair assumed a crouched posture just before beginning oviposition, the mature male parrs rushed into the spawning bed

Table 1. Number of mature male parrs per pair and behaviour of mature male parrs during pair spawning. Below the dotted line show only the number of mature male parrs during spawning acts.

| Pairs (Total length) | | Mature male parrs | | Behaviour of male parr during pair spawning | |
|----------------------|-------|-------------------|--------------|---|----------------|
| ♂ | ♀ | No. | Total length | O ₁ | O ₂ |
| 37 cm | 30 cm | 1+SR | 20 cm | S | |
| 37 | 27 | 2 | 18 | — | — |
| | | | 15 | — | S |
| 40 | 33 | 0 | — | — | |
| 40 | 30 | 1 | 18 | S | S |
| 40 | 37 | 2 | 15 | S | |
| | | | 15 | — | |
| 37 | 35 | 1 | 15 | — | — |
| 35 | 35 | 1 | 17 | S | |
| unrecorded | | 0 | — | — | — |
| 37 | 37 | 2 | 15 | S | |
| | | | 15 | S | |
| 15* | 37 | 1 | unrecorded | unknown | |
| 40 | 36 | 1 | | | |
| 40 | 37 | 1 | | | |
| 33 | 30 | 1 | | | |
| 30 | 27 | 0 | | | |
| 40 | 35 | 0 | | | |

S: spawning, *: mature male parr, SR: sea run male

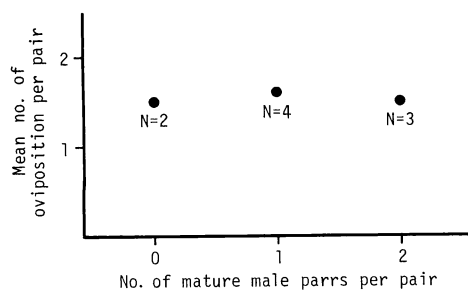


Fig. 2. Relation between the number of mature male parrs per pair and number of oviposition per pair.

but were driven away by the male or female of the pairs. Oviposition was accomplished by a pair of sea run type fish, except for one case in which a pair was formed by a female of the sea run type and a mature male parr. The climax of the pair spawning with mouth wide open continued for four or five seconds, and actual spawning occurred once (6/9) or twice (3/9). There is no relationship between the number of spawnings and the presence of potential streakers (Fig. 2).

During pair spawning, the stream resident males rushed between a pair or beside the female or male and then opened their mouths wide, suggesting the release of sperm. The rushing success of mature male parrs into the territory of a pair to one oviposition was about 61.5%, which was determined by total no. of mature male parrs which were successful to rush $\times 100$ / total no. of pair ovipositions ($= 100 \times 8/13$), except for one case of which a pair was formed by a sea run female and a mature male parr.

During a pair spawning and/or just after the spawning, mature male parrs never pecked within the egg pit or demonstrated egg-eating; that is they did not behave positively to eat the eggs. The stomach contents of 14 mature male parrs and about 10 juvenile fish of 0⁺ in age, which were collected on the 18th and 19th of October in this tributary, were examined. Several eggs were recognized in the stomachs of two of the mature male parrs and in all the juvenile fish, but we did not know about when or where they ate eggs.

Discussion

The spawning behaviour of a pair of dolly varden consists with that observed by Fabricius

(1953) and Leggett (1980); however, they did not describe the interaction between a pair and mature male parrs. Our present observations show that mature male parrs of the dolly varden take part in spawning as streakers, as suggested already in the Arctic charr (*S. alpinus*) by McCart (1980), while a pair of sea run type ovipose, like the mature male parr of other salmon (Jones and King, 1950, 1952; Jones, 1959; Hanson and Smith, 1967; Gross, 1985) and conspecific lacustrine Miyabe charr (Maekawa, 1983; Maekawa and Onozato, in press). The most important characteristics were that although the number of mature male parrs in southeastern Alaska was relatively few, their streaking success was high (about 0.62), and they almost never ate eggs during or after a pair spawning, although mature male parrs of Miyabe charr ate eggs positively.

Here, the spawning behaviour of a mature male parr should be compared with that of anadromous dolly varden and Miyabe charr, as already reported in detail. Maekawa and Onozato (in press) found that when one mature male parr participated in a pair spawning, his streaking success to one oviposition was about 0.6, and that any increases in the number of mature male parrs decreased their average success at streak spawning; conversely, any increase in that of mature males increased the average success for eating eggs. The small number and higher streaking success of dolly varden in southeastern Alaska might be similar to the case of the small number of mature male parrs per lake run males (equivalent to sea run) of the Miyabe charr. Therefore, the fact that the mature male parrs of dolly varden do not eat eggs probably depends on their high streaking success.

Up to now, we have not known whether or not the mature male parr becomes a smolt after its maturity in a stream. However, Maekawa and Onozato (in press) suggested that the mature male parr of Miyabe charr remained in the stream all year round. Armstrong (1970) reported that most dolly varden smolts in southeastern Alaska migrated down to the sea at ages 2⁺, 3⁺ and 4⁺, and that the fork length was from 100 to 180 mm. Since the ages of the mature male parrs of dolly varden in this district were 3⁺ and 4⁺, it is reasonable to consider that there is no difference in survival among smolt and parr individuals during their life in the stream. If this is true, we may be able to apply a mixed ESS model, according to Gross

and Charnov (1980), Maekawa and Onozato (in press) and Gross (1985), as an alternative reproductive strategy. If the fitness of both types is to be the same,

$$\frac{q}{1-q} = \frac{h}{1-h} \quad (1)$$

∴ $q=h$

q =proportion of mature male parr cohorts entering a precocious pathway

h =proportion of eggs fertilized by mature male parrs.

We conducted a preliminary examination of the above equation. The average proportion of eggs fertilized by one mature male parr in a successful rush of Miyabe charr was about 16.8% (Maekawa and Onozato, in press). The streaking success of the present dolly varden might be similar to that of one mature male parr of the Miyabe charr. Therefore, if the fertilization success of the Miyabe charr could be applied to the present case, the value of $\left(\frac{h}{1-h}\right)$ would become about 0.11 [$0.16 \times 0.62 / \{1 - (0.16 \times 0.62)\}$]. Armstrong (1970) reported that the male-female ratio of smolts was 47:53 under a large number of samples in southeastern Alaska. Estimating from the ratio, the present occurrence of mature male parrs must be made up of about 11% in cohorts $\left(\frac{q}{1-q} \doteq 0.12\right)$, assuming a 50:50 progeny sex ratio. This indicates that there is qualitative agreement between the proportion of sea run and mature male parrs and equation (1), suggesting that the life history of mature male parrs may exist in a mixed ESS with sea run males by negatively frequency dependent success as reported by Gross (1985). In future studies it is necessary to show whether or not the fitness of the two tactics is equal.

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アラスカ州南西部における降海型オショロコマと残留型の産卵行動

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1984 年 10 月, アラスカ州ジュノー近郊のモンタナ川において, 降海型オショロコマと河川残留型早熟雄の産卵行動を観察した. 降海型 1 ペアあたりの早熟雄の集中度率は約 0.9 (N=15) であったが, 降海型雌雄の産卵中における, 早熟雄の 1 産卵あたりの streaking 成功率は 0.6 と高かった. Streaking 行動のほとんどは放精行動であり, 顕著な卵食い行動はみられなかった.

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