Spawning Habitat and Nest Depth of Female Dolly Varden *Salvelinus malma* of Different Body Size

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(Received January 20, 1995)

Spawning habitat and nest depth in relation to female body size were studied in a small population of Dolly Varden *Salvelinus malma*. Females selected areas where gravel was prevalent and currents were slow for spawning. Neither substrate score, water depth, nor current velocity was significantly correlated with the female body size. Nest depth, however, was strongly correlated with female size. These results suggest that nests made by smaller females are more vulnerable to destruction both from flooding and from nest site reuse by later-spawning females.

Key words: Dolly Varden, female, body size, spawning habitat, nest depth

Nest depth is an important factor determining brood mortality in salmonids. Increased depth may afford greater protection from mechanical damage and exposure when gravel is shifted by floods and when nests are superimposed by competing females. Superimposition through reuse of a nest site by later-spawning females is considered to be a major factor in progeny mortality,¹⁾ and thus is one of the important density-dependent processes regulating population density in salmonid fishes.^{2,3)}

Iteroparous charrs (genus *Salvelinus*) show little evidence of nest-guarding behavior, unlike semelparous salmonids (e.g. coho salmon *Oncorhynchus kisutch* guard their nests for an average of eight days before dying⁴⁾). Nest depth should, therefore, be critical for the seasonal reproductive success in female charrs. Nest depth may be influenced by female body size, as reported in other salmonids (brown trout *Salmo trutta*,⁵⁾ coho salmon⁶⁾). There are, however, few published quantitative works on the spawning habitat apart from Blakett,⁷⁾ or on the nest depth of Dolly Varden *Salvelinus malma*.

In the present study, we report some physical characteristics of the spawning habitat utilized by females, and also examine the relationship between female body size and nest depth in Dolly Varden.

Materials and Methods

Data was collected from a small wild population of Dolly Varden inhabiting the Tachinusu stream on the Shiretoko Peninsula, located in eastern Hokkaido, Japan, during two breeding seasons in 1992 and 1993 (Fig. 1). The stream ranges from 1–4 m in width and has a midchannel depth of 10–40 cm. The main study site was a 25-m-long section of the stream between an artificial weir and a fall, but an adjacent 35-m-long section was added in 1993. In 1992, data was collected on the spawning habitat of females, and in 1993, research concentrated on the nest depth. No apparent change in the channel morphology of the study site was evident during these two years. On 18 October 1992 and 20 October 1993, prior to the breeding of Dolly Varden, most of the examined fish were caught us-

ing a backpack electroshocker. The fish were measured for fork length, sexed, and tagged using colored ribbon-tags. Tagging permitted subsequent recognition of individual fish. All fish were then released in the same area of the stream to spawn naturally.

During both years, on the day before the fish were captured, water depth and surface substrate in the main study site were mapped. In 1992, current velocity was also measured. Mapping began by constructing a string grid over the wetted surface. The grid was marked at 1-m intervals and used to align a frame of polyvinyl chloride tubing that was placed on the stream bed. The dominant substrate in each grid was visually classified into five categories as either silt-sand (<0.5 cm diameter), gravel (0.5–2.0 cm), pebble (2.1–5.0 cm), pebble-cobble (5.1–10 cm), or cobble (≥10 cm) following Mark *et al.*,⁸⁾ and were scored from 1 (silt-sand) to 5 (cobble) for statistical analyses. We measured water depth and current velocity at the center of each grid. Current velocity was measured with a portable rotation meter (Yokogawa Hokushin Electric, 3631) at 0.6 times the water depth at each point.

Observations were made from the stream bank during 0600–1600 h each day from 19 October to 2 December 1992, and from 21 October to 31 November 1993. When identified Dolly Varden spawned, we located the nest on the map. The values of the grid were applied to physical variables of the spawning habitat. In 1993, when spawning by a female was witnessed, the nest was immediately approached and the depth was measured. Nest depth, defined as the maximum depth of the nest that a female excavated, was calculated as the distance from the top of the water column to the deepest place in the nest, minus the distance from the top of the water column to the undisturbed substrate around the nest. Females escaped from the nest site when an observer approached, but in most cases they returned to the original area within a few minutes after the person moved away, and continued post-spawning behavior, such as undulating or covering.⁹⁾

Female Dolly Varden are known to construct several nests in a season.¹⁰⁾ When the correlations between female body size and physical variables of the nests were exam-

Fig. 1. Location of the Tachiniusu stream and study site, showing the distributions of substrate (a) and the current velocity, deep area (deeper than 20 cm), and nest sites (b) in 1992.

ined, only the values of the nest observed first in the season were used.

Results

Fork lengths of mature females ranged from 13.6 cm to 23.1 cm (mean $\pm$ SD = 16.4 ± 2.5 cm, $N=16$) in 1992, and from 13.2 cm to 23.1 cm (mean $\pm$ SD = 17.2 ± 2.1 cm, $N=25$) in 1993. The difference in fork length between two

years was not statistically significant (Student's t -test, $t = -1.42$, $p > 0.05$).

We located 29 nests of 16 females in the study area in 1992 (see Fig. 1). The nests were constructed in an area where gravel was prevalent, water flow was slow, and depth was sufficient to allow spawning. The frequency distributions of substrate type, water depth, and current velocity where nests were constructed were significantly different from those of the overall study area (χ^2 -test; sub-

Fig. 2. Frequency distributions of (a) substrate score, (b) water depth, and (c) current velocity in 1992.

Open and closed bars represent the data in the overall study area ($N=99$) and at the nest sites ($N=29$), respectively.

Fig. 3. Relationships between female fork length and (a) substrate score, (b) water depth, (c) current velocity, and (d) nest depth. ***: $p < 0.001$, ns: $p > 0.05$.

strate: $\chi^2 = 36.7$, $p < 0.001$; water depth: $\chi^2 = 12.6$, $p < 0.01$; current velocity: $\chi^2 = 80.0$, $p < 0.001$; Fig. 2). Thus, the null hypothesis that females randomly constructed nests in the study area was rejected.

Data of the physical variables of nests relating to female size in 1992 and 1993 were combined for analyses. Habitat utilization by females for nest construction did not vary with body size. Fork length was not significantly correlated with either substrate score, water depth, or water velocity (substrate score: Kendall's $\tau = 0.19$, $z = 1.69$, $N = 38$, $p > 0.05$; water depth: $r = 0.30$, $N = 40$, $p > 0.05$; current velocity: $r = 0.10$, $N = 16$, $p > 0.05$; Fig. 3a–c). Nest depth, on the other hand, was strongly correlated with fork length ($r = 0.74$, $N = 28$, $p < 0.001$; Fig. 3d). The nest excavated by the largest female was three times the depth of the smallest female's nest.

Some females were observed to construct more than one nest in a breeding season (10/16 in 1992, 15/25 in 1993). The seasonal number of nests constructed by a female was not significantly different between large (FL ≥ 17 cm: mean $\pm$ SD = 2.0 ± 0.8 , $N = 20$) and small (FL < 17 cm:

mean $\pm$ SD = 1.7 ± 0.7 , $N = 21$) females (Mann-Whitney U -test; $z = -1.11$, $p > 0.05$). Among the 25 females observed to construct 2 or 3 nests, neither nest depth, substrate score, water depth, nor current velocity of the first nest differed from that of the last nest (Mann-Whitney U -test; nest depth: $z = -0.28$, $p > 0.05$; substrate score: $z = -1.36$, $p > 0.05$; water depth: $z = -0.50$, $p > 0.05$; current velocity: $z = -0.30$, $p > 0.05$).

Discussion

We have shown that: (1) female Dolly Varden constructed nests where gravel was prevalent, current was slow, and depth was sufficient for spawning, (2) this habitat utilization for spawning did not vary with the body size, and (3) larger females excavated deeper nests.

Habitat selection is responsible both for successful spawning of females and their brood survival in the nest in salmonids. An area with too coarse a substrate, too shallow a depth, or too fast a flow will be physically or energetically unsuitable for females to conduct spawning activities, although the threshold levels may vary with body size to some degree.¹¹ Several studies have shown that embryo mortality is correlated with the amount of fine sediment in the substrate, which increases mortality by impeding current flow through the gravel, restricting oxygen availability and sometimes precluding physical emergence of fry.^{12,13} In the present study, areas suitable for spawning were restricted to limited sites within the study area. Consequently, the limitation of spawning habitat could cause the overlapping or contagious distribution of nests by females.

A strong correlation between female size and nest depth could result from larger females having a mechanical or energetic advantage for lifting gravel, since there was no significant difference in the substrate type between large and small females. The area disturbed by digging increases with the nest depth, due to the mortar-shaped nature of nests. Thus, the nest of a small female could be superimposed by larger females, even when the nests of larger females do not exactly overlap the nests of smaller females.

The variation in fork length of fluvial Dolly Varden would be mainly due to their age, since older fish generally, attain a greater size. Kitano and Nakano¹⁴ reported mature female Dolly Varden measuring 12–20 cm FL corresponded to 2–5 years old, with the largest female (20 cm FL) having four times as many eggs as the smallest (12 cm FL: 50 eggs) in a population near the study stream.

In coho salmon, larger females construct more nests than smaller ones,⁶ and this may result in the higher probability of superimposition of nests made by small females. In contrast, no relationship between body size and the number of nests in a season has been observed for Dolly Varden. Female Miyabe charr (*S. malma miyabei*), which oviposit eggs from one to several times in one nest, discontinue the oviposition when satellite males attempt to eat the eggs.¹⁰ Female Dolly Varden in the study site might also adopt a similar spawning tactic, since egg-eating behavior by satellite males was observed (*S. Kitano*, unpublished data). Thus, the number of nests in a season may depend on the behavior of males during spawning, rather than on female body size.

In conclusion, the nests made by smaller females are more vulnerable to destruction from flooding or from superimposition by later-spawning females. It is suggested that such size-related differences may affect the seasonal reproductive success of female Dolly Varden.

Acknowledgments We are very grateful to Dr. H. Munehara and J. R. Bower for their critical comments and English correction on early drafts of the manuscript. We also thank M. Inoue for providing useful suggestions on the methodology, and M. Tazawa, M. Endo, H. Matsuo, Y. Takashima, A. Wada, T. Ueda, and E. Hayashi for their help during the field research.

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