Female Size and Nest Depth in Coho Salmon (*Oncorhynchus kisutch*)

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Nest depth was strongly correlated with female size in coho salmon (*Oncorhynchus kisutch*). Since nests of different-sized females are at different depths, they are differentially vulnerable to destruction by floods and to other females competing for the same nest sites.

La profondeur du nid était en étroite corrélation avec la taille de la femelle du saumon coho (*Oncorhynchus kisutch*). Parce que les nids de femelles de tailles différentes se trouvent à des profondeurs variables, leur vulnérabilité varie face à la destruction par les inondations ou à la compétition des autres femelles pour les mêmes sites de reproduction.

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Female salmonids spawn into nests they construct in stream beds. Nests are excavated using a series of lateral body flexures, which produce a vortex, lifting gravel to be carried downstream by the current. After egg deposition, the female moves upstream and with the same digging motion, covers the nest (Foerster 1968; McCart 1967; Tautz and Groot 1975). The function of egg burial is to increase brood survivorship by decreasing predation (Reed 1967; Stuart 1953, cited in Jones 1959), mechanical damage, and agitation, which is lethal during critical periods of brood development (Smirnov 1955). The relationship between substrate quality and brood survivorship has been well studied (Coble 1961; Dill and Northcote 1970; and others). However, an important but less well studied factor for brood survivorship is nest depth. Increased depth will afford greater protection from mechanical damage and exposure when gravel is shifted by floods and when nests are superimposed by competing females. Superimposition, or reuse of a nest site by later-spawning females, is a common phenomenon in salmonids and is responsible for considerable brood loss (McNeil 1962; Schroder 1973; and others).

Studies reporting nest depth give depths at which investigators encountered eggs in the course of excavating redds (e.g. Burner 1951; Hawke 1978). Such data may be relatively inaccurate due to the frequent and often extensive gravel shifts associated with fluctuating water levels. McNeil (1962), for instance, showed gravel shifts in one season to exceed 25 cm at one third of his sites. Shifts of such magnitude would destroy many of the shallower nests, removing them from the sample. A further important shortcoming of existing nest depth data is the lack of information on female size. Larger females make deeper nests in brown trout (*Salmo trutta*) (Ottaway et al. 1981) and possibly in salmon (Jones 1959; Major and Craddock 1962; Ricker 1972). If so, the destructive effect of nest reuse and flooding will differentially affect females of different size; this would have important management implications for salmonid populations. Therefore, we measured nest depths when coho salmon (*Oncorhynchus kisutch*) of known body size spawned.

Methods

We collected data on a small wild population of spawning coho salmon native to a tributary of Deer Creek, 1.8 km west of Index, Snohomish Cty, WA. During November–January of 1981–82 and 1982–83, all fish were caught at a weir near the mouth of the stream. The fish were measured to the nearest half centimetre (fork length), sexed, and tagged using color-coded Petersen disk tags (Floy Tag Co., Seattle, WA). Tagging permitted subsequent recognition of individual fish. All fish were released above the weir to spawn naturally.

Substrate samples, each consisting of about 4 kg of material, were collected with a shovel at 2-m intervals in midstream along the entire spawning ground. This provided samples to a depth of 25 cm, which we considered to be representative of that affected by the fishes' digging. Examination of the stream substrate showed no significant layering to that depth (analysis of six samples taken at 0–5, 10–15, and 20–25 cm, MANOVA (Nie et al. 1975) P = 0.699, 0.908, 0.821, and 0.560 for comparisons between depths). All gravel in the stream was of a smooth, rounded texture. Samples were analyzed in the laboratory and fredle indices were calculated (Lotspeich and Everest 1981). Nest sites were characterized by superimposing the fredle scores on a grid map locating the nests. To minimize the effects of spacial heterogeneity in gravel, only those nests with centers within 50 cm of a gravel sampling locality were used.

Nest depth was defined as the maximum depth that a female excavated her nest. This 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 top of undisturbed substrate around the nest. A series of nest measurements were taken preceding and following the spawning. The

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greatest depth is used here as the final nest depth. Measurements were made from shore using a meterstick attached at right angles to a pole; this minimized spawning disturbance. Records were kept, until death, on 83 of 160 females that spawned in the stream. Of these, measurements were obtained during daylight hours for nests of 42 females. Because of the often unpredictable moment of egg release, observation periods on individual fish were of variable duration. Although the females could not be observed at night, the locations of their nests and the identity of the females were rarely in doubt, since digging was often initiated during the daytime and covering frequently continued long after sunrise. Disturbance of gravel for new nests also contrasted strongly with algae-covered substrate in the surrounding areas, and females rarely abandoned a completed nest prior to dying. It was therefore possible to obtain reliable data on the number of nests they constructed.

Results

Females studied ranged in length from 40.5 to 76 cm, which is representative of the size range in the stream. They constructed an average of 2.07 ± 0.84 nests with 20 (28.6%), 27 (38.6%), 21 (30.0%), and 2 (2.8%) fish making 1, 2, 3, and 4 nests, respectively. Larger females dug significantly more nests than did smaller ones (comparing female size categories >70, 61–70, 51–60, and <50 cm, $N = 70$, $X = 20.4$, df = 3, $P < 0.01$). Depths of first nests for individual females did not differ significantly from nests they excavated last (paired *t*-test, $t = 0.695$, $P = 0.5$) (Table 1). Females spawned into each nest they dug. Nests were relatively cone shaped, with the smallest diameter at the bottom where the eggs were laid.

Nest depth averaged 13.7 ± 4.0 cm ($N = 42$); however, nest depth was strongly correlated with female size ($r = 0.778$, $P < 0.01$) (Fig. 1). Large females buried their eggs as much as 2.5-fold deeper than small females. This could result from (1) larger females selecting nest sites that are easier to excavate, (2) larger females having greater strength or a mechanical advantage for lifting gravel, or (3) the greater fecundity of large females necessitating deeper nests. The third alternative is ruled out because the greater egg volume of large females is divided among more nests (see also Hawke 1978). To examine the first two alternatives, we regressed nest depth on both female size and gravel size. The multiple regression (Nie et al. 1975) revealed that 71% of the variance in nest depth is explained by female body size alone ($P < 0.01$) and only 5% is explained by gravel size ($P = 0.57$). Therefore, the second explanation appears to be the most plausible.

TABLE 1. Nest depths of the first and last nests made by 13 female coho salmon. Last row of data is X ± SE.

Female size (cm)	First nest (cm)	Last nest (cm)
46.5	8.9	11.4
50	14.0	15.2
53	11.4	14.0
53.5	12.7	14.0
56	12.7	11.4
56	9.0	11.4
58	10.5	12.5
61.5	14.0	17.8
65.5	22.8	23.4
67	15.2	15.2
68	17.8	16.5
69	20.3	17.8
74	26.7	21.6
59.8 ± 8.3	15.1 ± 5.2	15.5 ± 3.7

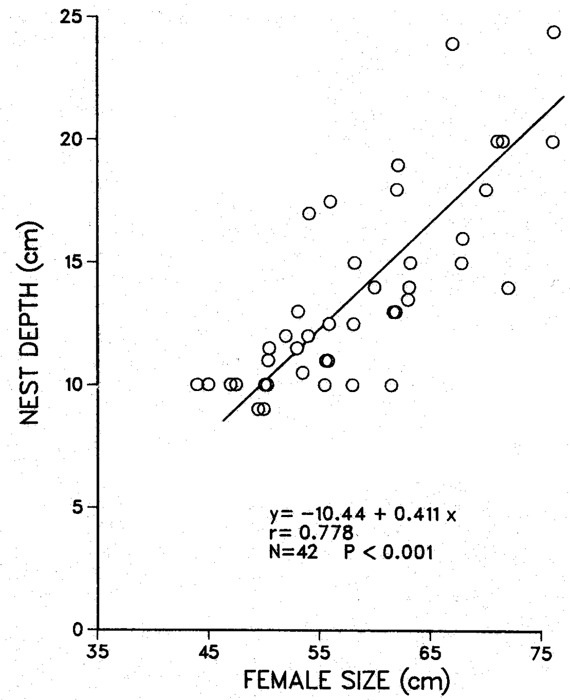

FIG. 1. Nest depth as a function of female size in coho salmon.

Discussion

We have shown that larger females dig deeper nests. Our analysis suggests that the difference in depth is due to a mechanical or energetic advantage from larger body size. Approximately one quarter of the variance in nest depth among females is not explained by body size; however, female energy reserves probably varied considerably. Oceanic ectoparasites were still attached to some of the fish, suggesting that these came directly from the sea. By contrast, some coho were observed in the main river near the mouth of the stream in early September, 2 mo prior to spawning activity. Such disparity in river residence time probably causes considerable variation of energy reserves. Current velocity may account for some variance in nest depth; however, if currents had a major influence, gravel size would have been more strongly correlated with depth, since gravel size is closely linked with current velocity (Novak 1973).

Female salmonids compete aggressively among themselves for nest sites, and eggs are often dug up by later arriving females (Hanson and Smith 1967; McNeil 1962; Schroder 1973; and others). Since larger females bury their eggs as much as 2.5-fold deeper, their broods will be less susceptible to damage from superimposition because there are fewer potential competitors that can dig as deep. Furthermore, due to the cone-shaped nature of nests, the area disturbed by digging decreases with increasing depth. Shallow nests are thus vulnerable to females excavating off center, whereas deep nests are vulnerable only if subsequent nests are precisely centered. Shallower nests are also subject to a higher probability of destruction by gravel movement during heavy runoff. By contrast, mortality costs of deeper burial are probably negligible over the range of nest depths found in nature. Hatching success and alevin mortality have not been found to differ over a range of gravel depth to 30.5 cm (Dill and Northcote 1970). Managers of salmon populations should recognize that there is a selective advantage to larger bodied females resulting from their ability to dig nests deeper.

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