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Heritability of Age at Maturity in Steelhead

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Abstract.—Brood stock of winter steelhead *Oncorhynchus mykiss* were selected on the basis of age at maturity. Progeny were sampled as returning adults to determine if age at maturity was heritable. Although overlap was observed, progeny of fish that matured after 2 years at sea (2s) tended to return after 2 years, and progeny of fish that matured after 3 years (3s) tended to return after 3 years. The 3s progeny were significantly longer than 2s progeny in 2 years of return for both sexes. No difference was observed in return rates between groups, possibly suggesting that most steelhead mortality occurs before the second summer in salt water, or there is differential mortality associated with ocean distribution.

Winter steelhead *Oncorhynchus mykiss* are an important, intensely managed sport fish in the Pacific Northwest. Juvenile steelhead generally reside from 1 to 4 years in fresh water before smolting; ocean residence also ranges from 1 to 4 years, although most fish return to natal streams to spawn as mature adults after 2–3 years at sea (Larson and Ward 1955; Withler 1966; Narver and Withler 1971; Leider et al. 1986). As expected, large adult fish are generally older than smaller fish (Narver and Withler 1971; Leider et al. 1986). Length (Tipping 1984) and weight (Narver and Withler 1971) of fish returning after 3 years at sea (3s) average about 79–86 cm and 5.5 kg versus 65–71 cm and 3.0 kg for fish spending only 2 years at sea (2s). Steelhead are generally managed as two races, winter and summer, distinguished by their relative sexual maturity and time of freshwater migration (Withler 1966; Leider et al. 1986).

Size of hatchery smolts is important to adult return rates; research has shown that large smolts (>45 g) generally outperform small smolts (≤45 g), and therefore have a higher adult return rate (Larson and Ward 1955; Wagner 1967; Royal 1972). In Washington, most juvenile hatchery steelhead are reared to smolts in about 1 year, with a target size of about 76 g and a corresponding length (Piper et al. 1975) of about 20.0 cm. Royal (1972) noted that 3s fish constituted 25.6% of wild stocks versus 5.5% of hatchery stocks. He suggested that the relatively large smolt size of hatchery fish had reduced the occurrence of 3s fish in hatchery stocks. This inverse relationship of steelhead smolt size and age at maturity was substantiated by Wagner (1967) for hatchery fish and Ward et al. (1989) for wild fish. However, large smolts are needed for optimum adult return rates.

Selective manipulation of brood stocks is not uncommon. Return timing has been advanced in Washington's Chambers Creek Hatchery winter steelhead and Skamania Hatchery summer steelhead stocks (Royal 1972). Stocks of rainbow trout *Oncorhynchus mykiss* in Washington have been altered with regard to spawning time and age at maturity (Crawford 1979). Gall et al. (1988) found that age at spawning in rainbow trout was moderately to highly heritable.

Increasing the proportion of 3s steelhead in some hatchery stocks could be desirable in several ways: (1) adult returns would be distributed over two years, so a fishery would not be dependent on a single production year; (2) increased environmental adaptiveness might be realized by mimicking age at maturity of wild stocks; (3) larger body size would result in increased fecundity and possibly more fry (Buckley 1967; Randolph 1986; Schuck et al. 1989); and (4) anglers generally prize large steelhead over smaller fish. However, increasing the proportion of 3s fish could decrease total steelhead returns due to an additional year of ocean mortality.

To determine if the percent of 3s fish could be increased in a hatchery stock, an experiment was conducted to compare returns and lengths of adult progeny from 2s and 3s brood stock.

This experiment was conducted on the Cowlitz River, which enters the lower Columbia River in southwest Washington. Two large dams, Mayfield and Mossyrock, were constructed across the Cowlitz River in 1962 and 1968, respectively, and subsequently, runs of winter steelhead have been maintained through production at the Cowlitz Trout Hatchery, completed in 1967. A barrier dam and fish-sorting facility were also constructed on the Cowlitz River about 11 km upstream from the Cowlitz Trout Hatchery.

TABLE 1.—Size and age at maturity of parents and size of progeny at release for steelhead spawnings at Cowlitz Trout Hatchery, Washington.

Spawning date	Age of parents at maturity[a]	Mean fork length of parents (cm)		Mean weight of progeny at release (g)
		Males	Females	
28 Dec 1983	3s	>80 (N = 29)	78–88 (N = 31)	76 (N = 50,903)
1 Feb 1984	2s	57–69 (N = 59)	60–69 (N = 66)	70 (N = 54,554)

[a] Age: 2s and 3s = fish maturing after 2 and 3 years at sea, respectively; ages determined by scale analysis.

In December 1983, a group of large male winter steelhead was spawned with a group of large females at the Cowlitz Trout Hatchery (Table 1). In February 1984, a group of small males was crossed with small females. Sperm from several males was pooled and then applied to eggs of individual females. Scale analysis indicated that all of the small males were first-spawning 2s fish, except one that had previously spawned as a 2s fish. All of the small females were 2s except one 3s fish. All except three of the large males were 3s fish; the exceptions were 4s fish. All large females were 3s, although two were repeat-spawning 3s fish.

Progeny were reared similarly in raceways and released at the same Cowlitz River locations in April 1985. Before release, the 3s smolts received a left-ventral fin clip, whereas the 2s smolts received a right-ventral fin clip. Smolt size was assumed biologically similar: with a condition factor (K) of 0.94, (K = 100 [weight, g]/[length, cm]^3; Piper et al. 1975), the 3s smolts would have been 20.0 cm and the 2s smolts 19.5 cm.

Adults entering the barrier-dam separator were sampled to compare returns and lengths of 2s and 3s progeny. Adults were recovered between November 1986 and June 1987, and from November 1987 through 5 February 1988. The separator was closed in February 1988 for maintenance. However, 91.1% of the 1986–1987 total had returned by February 5, and 3s fish typically decline in relative abundance from about 25% in February to less than 5% in May (Tipping 1984).

Returning steelhead jumped over a false weir at the separator and passed down a flume into a tank of anesthesia. All steelhead were then examined for marks, fork length, and sex, and transported by truck back to the river for release. In 1986–1987 and 1987–1988, 10,659 and 7,537 steelhead were examined for marks, respectively. A portion of the adipose fin was removed so that individual fish were not measured more than once. Chi-square was used to test differences in return rates between groups, and Student t-tests were used to test differences in length between groups.

Crosses with 2s parents produced significantly (P < 0.01) more 2s progeny than 3s progeny, whereas crosses with 3s parents produced significantly ($P \ll 0.005$) more 3s progeny than 2s progeny (Table 2). A total of 57.0% of the 2s progeny returned as 2s adults, whereas only 20.6% of the 3s progeny returned as 2s adults. However, females in both groups appeared predisposed to return as 3s fish, whereas males were not; significantly more females from the 2s cross returned as 3s fish (χ^2 = 32.23, P = 0.05) than as 2s fish. A total of 73.0% of females from 2s parents and 96.4% of females from 3s parents returned as 3s fish, whereas 22.7% of males from 2s parents and 60% of males from 3s parents returned as 3s fish.

There was no significant difference in total returns between groups, 0.69% versus 0.72% for 2s and 3s progeny, respectively (χ^2 = 0.21, P = 0.05). Returning males and female progeny from 3s parents were significantly longer than males and females from 2s parents in both years of return (Table 3).

Steelhead age at maturity appears to be at least partially heritable and, in addition to smolt size, is a parameter determining age at return. Saltwater environmental factors affect population survival, fish growth, and possibly, age at maturity. Environmental factors might explain why many 2s progeny returned as 3s fish in this study. Ward and Slaney (1988) suggested that age at maturity of male steelhead was influenced by environmental conditions, whereas female age at maturity was under greater genetic control. Returns in this study suggest the reverse. Several profiles of the Cowlitz River winter steelhead population have shown that males dominate 2s returns, whereas females often dominate 3s returns (Tipping 1984). However, for Atlantic salmon *Salmo salar*, Randall et al. (1986) and Dempson et al. (1986) felt that the saltwater environment was not a major influence on age at maturity.

Female steelhead smolts in this study may have been smaller than male smolts and returned a year later, which would be consistent with the inverse relationship between smolt size and age at return. Male smolts of coho salmon *Oncorhynchus kisutch* (Hager and Noble 1976; Washington 1982) and sea-run cutthroat trout *Oncorhynchus clarki* (Tipping 1986) tend to be larger than females. If male steelhead smolts are larger than female smolts, the

TABLE 2.—Returns of Cowlitz River winter steelhead from parents with different ages at maturity; 2s and 3s = fish maturing after 2 and 3 years at sea, respectively. The critical value of χ^2 at $P = 0.05$ is 3.84.

Age of parents at maturity	Number of smolts released	Number of adult returns					χ^2
		At 2s		At 3s			
		Male	Female	Male	Female	Total	
2s	54,554	174	41	51	111	377	7.49
3s	50,903	68	7	102	187	364	126.27

hatchery practice of removing smaller juveniles during rearing could influence sex ratios in some populations.

Genetically influenced age at maturity could explain the apparent size increase of Cowlitz River adult steelhead after a 1970s selective breeding program, even though smolt size remained similar. Mean length of adults increased from 69.0 cm in 1970–1972 (Young 1971, 1974) to 74.2 cm for six years sampled between 1977 and 1987 (Tipping et al. 1979; Tipping 1984).

In this study, the increased length of 3s fish in both years of return suggests that steelhead might have a genetically influenced ocean distribution that affects growth. Light et al. (1989) noted that some steelhead ocean distribution was influenced by age and stock. The Snake River (Idaho) stock of "B-run" summer steelhead averages about 80 cm at an age of 2s (Thurow 1987), whereas most other stocks of similar age average 70 cm (Howell et al. 1984).

The similar return rate of both groups might indicate that most steelhead mortality occurs before the fish have spent 2 years at sea, with relatively little mortality thereafter. Peterman (1982) suggested that mortality of sockeye salmon *O. nerka* was most severe within the first 15 months after smolting. Mathews and Buckley (1976) found that the mortality rate of coho salmon decreased as fish grew. Healy (1982) indicated that mortality of chum salmon *O. keta* was high during early ocean residence. Also, if steelhead ocean distribution is genetically influenced, perhaps differential mortality is associated with geographical areas.

There is no evidence that selective harvest by in-river sport anglers is responsible for the similar return rate: mean length of fish in the sport catch sampled in mid-December 1983 was 74.8 cm (SD = 8.1, N = 146), whereas steelhead sampled in early January 1984 at the barrier dam averaged 75.3 cm (SD = 8.4, N = 285).

Additional research is needed to determine the relative influence of smolt size, parentage, and environmental factors on steelhead age at maturity. Also, the potential of similar survival for 2s and 3s fish should be fully explored; if there is little difference, selection for 3s fish may be desirable. However, researchers should avoid using only length frequency as an indicator of age at return in heritability studies.

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TABLE 3.—Mean fork lengths of returning Cowlitz River steelhead from parents with different ages at maturity; 2s and 3s = fish maturing after 2 and 3 years at sea, respectively. Values in parentheses represent SD. Sample sizes are shown in Table 2.

Age of parents at maturity or statistic	Lengths (cm) of returning adults			
	At 2s		At 3s	
	Male	Female	Male	Female
2s	64.5 (3.30)	63.2 (2.67)	79.5 (4.55)	75.5 (2.78)
3s	66.9 (3.40)	66.4 (2.97)	82.9 (4.19)	76.7 (3.18)
Calculated t	5.04	2.89	4.67	3.29
Tabled t ($P = 0.05$)	1.98	2.01	1.98	1.98

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