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Age and Length of Steelhead Smolts from the Mid-Columbia River Basin, Washington

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Abstract.—Steelhead *Oncorhynchus mykiss* exhibit a wide range of life histories within and among stocks. Varying degrees of anadromy, length of freshwater life before emigration to the sea, and age at first maturity have been observed. Steelhead in the mid-Columbia River basin are at least partially descended from fish that were relocated to the major tributaries of the mid-Columbia River when Grand Coulee Dam was built. These fish do not spawn in the main-stem Columbia River and are strictly tributary spawners. Rearing conditions in these tributaries can be harsh. Researchers have observed a wide range of lengths and ages of juvenile *O. mykiss* (steelhead and nonanadromous rainbow trout) in these tributaries. This led to a need to document the age at migration of fish that were clearly smolts, as demonstrated by their downstream migration. Over 970 otoliths were collected from naturally produced steelhead smolts in 1988 and 1989 to determine the age at migration. Ages ranged from 1 to 7 years at Rock Island Dam and from 1 to 5 years at Rocky Reach Dam. These ages agreed with those estimated from adult otoliths. Age structure did not differ significantly between the two sampling sites, but length did, suggesting that fish emigrating from the Wenatchee River were shorter for a given age than fish produced above Rocky Reach Dam. Females made up 63.0% of the smolts collected at Rock Island Dam and were generally older than males, suggesting that males have a higher probability of remaining in freshwater. We attempt to explain the patterns observed in age and length of naturally produced steelhead smolts. We suggest that a more or less continuous downstream movement of juveniles occurs that takes them to areas with more adequate food supplies. Smoltification of individual fish appears to result as a threshold length is approached. Harsher growing conditions result in slower growth and older smolts, which may have implications for supplementation and introduction of steelhead where resident rainbow trout are present.

Steelhead *Oncorhynchus mykiss* exhibit a wide range of life histories within and among stocks (Withler 1966). Varying degrees of anadromy, length of freshwater life before emigration to the sea, and age at first maturity have been observed (Withler 1966; Randall et al. 1987; Ward and Slaney 1988). One of the most notable enigmas of the life history of *O. mykiss* is that the species appears in two forms: the resident rainbow trout and the anadromous steelhead. It is believed that progeny from rainbow trout have the potential to become anadromous and that progeny of steelhead have the potential to become resident (Rounsefell 1958; Chrisp and Bjornn 1978).

Steelhead do not spawn now, and never have spawned, in the main-stem Columbia River (Mullan et al. 1992). They are strictly tributary spawners. Mullan et al. (1992), who collected over 3,000 *O. mykiss* in the Methow River basin (Figure 1) over a 5-year period, found a wide range of length frequencies within age-classes in their samples (e.g., Figure 2). There was a need to extend this information by measuring ages and lengths of fish that were clearly smolts as demonstrated by their downstream migration. Length frequencies of steelhead smolts have been routinely determined along the Columbia River, but there has been no previous analysis of age structure of steelhead smolts.

The juvenile salmonid bypass sampler at Rock Island Dam (Figure 1) provided an opportunity to sample steelhead smolts. Testing of a prototype mechanical bypass system at Rocky Reach Dam, upstream of the Wenatchee River, offered the same

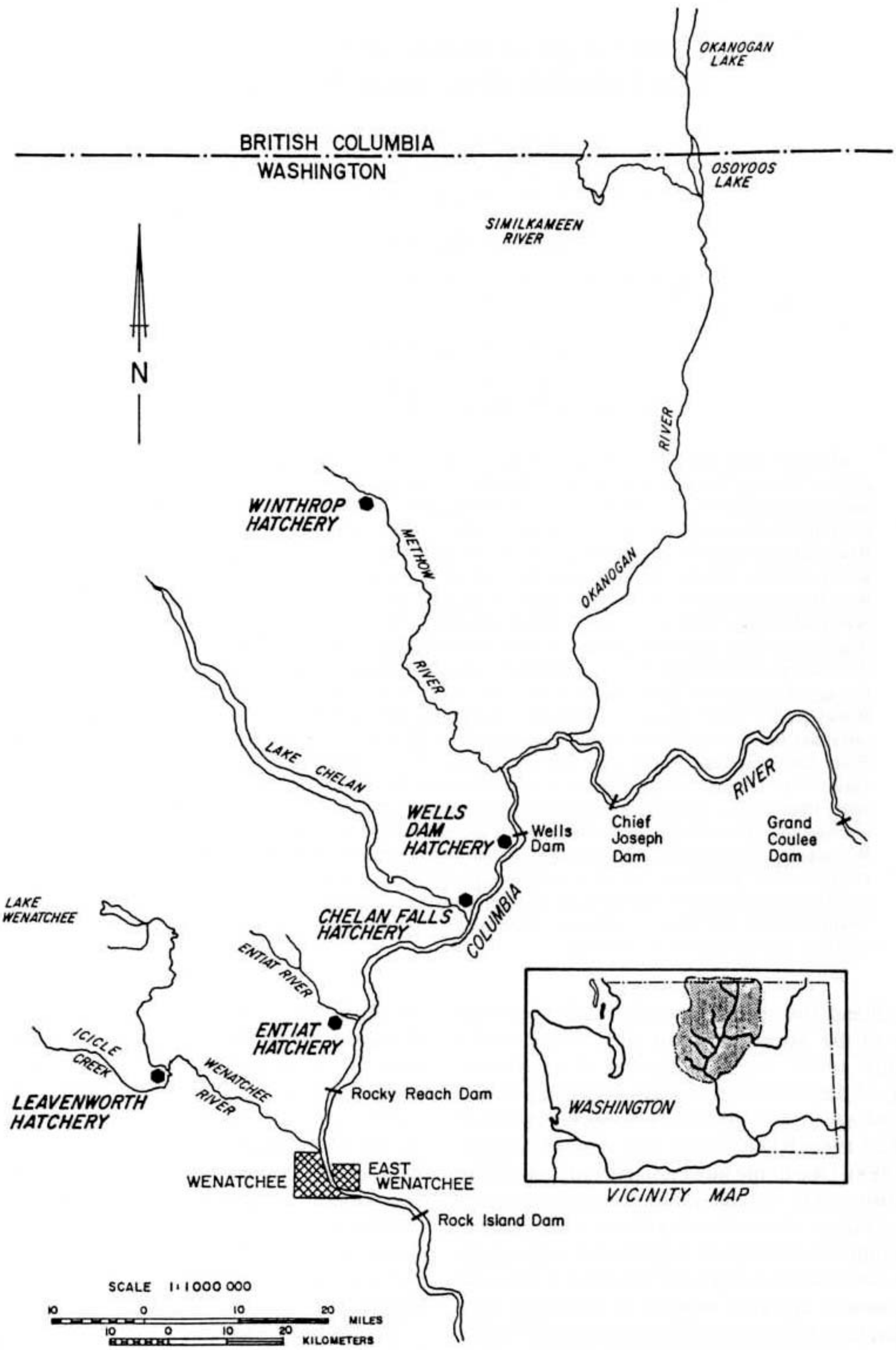

FIGURE 1.—The Columbia River basin from Rock Island to Grand Coulee dams, showing major tributaries, hatcheries, and dams.

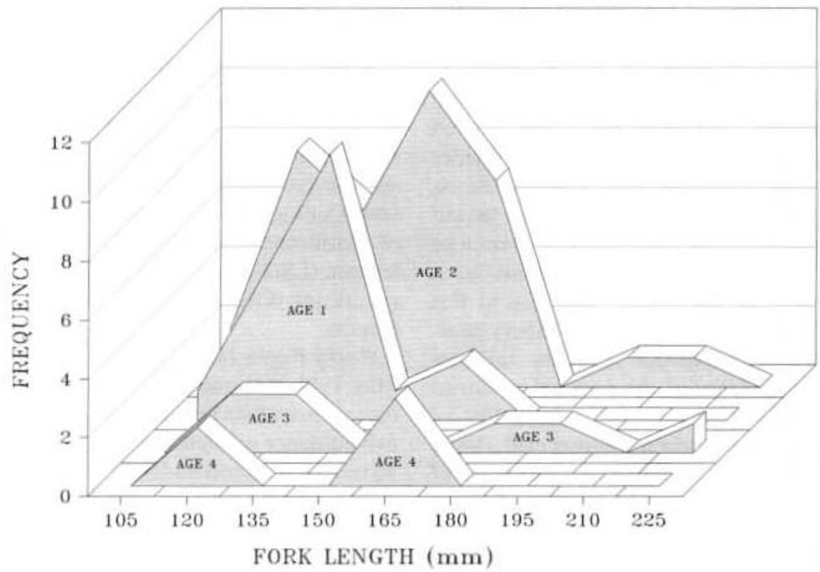

FIGURE 2.—Age–length comparisons of rainbow trout and steelhead sampled in the Wenatchee River system. (Data are from J. Mullan, U.S. Fish and Wildlife Service, personal communication.)

opportunity, and the opportunity to examine whether there might be a difference in age distribution or lengths of fish from different tributaries.

Current Stock Status

Today, four potential stocks (populations separated temporally or spatially during spawning) of summer-run steelhead spawn above Rock Island Dam (river kilometer [rkm] 729) in major tributaries of the mid-Columbia River (Figure 1): the Wenatchee, Entiat, Methow, and Okanogan river populations. These rivers also receive annual plants of steelhead smolts reared at hatcheries on the main stem of the Columbia River above Rock Island Dam (Figure 1). All of these stocks are at least partially descended from fish that were trapped at Rock Island Dam and relocated to these rivers from 1939 to 1943 after Grand Coulee Dam (rkm 961) prevented further upstream passage (Kendra 1985; Mullan 1987; R. L. Allen and T. K. Meekin, Washington Department of Fisheries, unpublished data, 1980).

Eggs for the hatchery plants were first collected from fish ascending the fish ladders at Wells Dam (rkm 547) in the 1960s. These fish, in turn, were at least partially descended from fish that had been planted into streams above Wells Dam from brood stock taken at Priest Rapids Dam (rkm 639; Kendra 1985). Between 1977 and 1989, the Skamania hatchery stock was also planted in the Wenatchee and Entiat rivers. The Skamania stock was derived at Skamania hatchery from brood stock from the Washougal and Klickitat rivers, tributaries of the lower Columbia River (below the confluence of the Snake River). The current source of the hatchery brood stock continues to be fish taken from the fish ladders at Wells Dam. The brood stock is made up of both naturally produced fish and hatchery-produced fish on their way to the tributaries where they had been released.

Study Area

The study area includes the Columbia River basin from Rock Island Dam (rkm 729) upstream to Chief Joseph Dam (rkm 877), and it thus embraces the Wenatchee, Entiat, Methow, and Okanogan rivers. The area drained is over 30,000 km^2, not including the Chelan River drainage, which has been blocked to anadromous fish near its mouth since glacial times (Figure 1). All of the major tributaries drain the east slopes of the North Cascade Mountain range, except part of the Okanogan River. Elevations in the study area range from 190 m to over 2,743 m; annual precipitation varies from 25 cm at the lower elevations to 254 cm at the crest of the Cascade Mountains.

Methods

Rock Island Dam bypass trap.—Otoliths of naturally produced downstream migrant steelhead were collected in 1988 at the Rock Island Dam juvenile salmonid bypass trap. About 3.4% of the steelhead smolts migrating down the river were collected at this facility (F. W. Olson, CH2M HILL, Inc., unpublished data, 1983). All salmonids were collected (7 d/week, 24 h/d), counted, and checked for fin clips and freeze brands (Peven and Fielder 1988). Captured steelhead were categorized as hatchery fish by the absence of an adipose fin (all steelhead smolts released since 1985 have been so marked), or if an adipose fin was present, by a worn appearance of the dorsal and ventral fins (Peven and Hays 1989). Routinely, fishery biologists identify catchable-size hatchery rainbow trout by the appearance of the pectoral or dorsal fins, characterized by the partial or total loss of fins from nipping and abrasion (Heimer et al. 1985). Scales were also collected from a subsample of smolts so annulus counts could be compared between scales and otoliths.

Only smolts were collected for aging. Smolts generally exhibit silvery body coloring, thin shape, blackened fin margins, and deciduous scales, whereas parr retain their freshwater coloration (visible parr marks) (Chrisp and Bjornn 1978; Loch et al. 1988). Only live fish were used in this differentiation. These indices are somewhat subjective.

The criterion used to determine the desired sample size was based on the estimated proportion of the oldest age-class that was thought to be present in the samples (Cochran 1977). The expected proportion of the oldest age-class in the sample was obtained from brood-stock otolith samples, with which ages at emigration to the sea could be back calculated, taken at Wells Dam Hatchery (K. R. Williams, unpublished data, 1988). Required sample sizes of 700–1,000 smolts at the Rock Island Dam bypass trap were estimated. Fish were placed in a lethal solution of MS-222 (tricaine) and then into individually marked plastic bags and frozen. Otoliths and scales were later removed and sex was identified.

A sampling schedule, based on the 1986 Rock Island Dam bypass trap catch of steelhead smolts (Peven and Hays 1989), was devised to obtain the desired sample of at least 700 fish. Basing the sampling schedule on the number of fish caught in 1986 was done to achieve a sample that was proportionate to run strength. All naturally produced steelhead caught every fifth day were sampled beginning 13 April. In May, every 10th naturally produced fish was sampled daily. On 12 May, because it appeared that sample sizes were lower than expected, every fifth fish was sampled daily. In June, all fish were sampled every fifth day, as in April.

A two-way analysis of variance (ANOVA; Zar 1984) was performed (sex and age as factors) to determine if there was a significant difference ($\alpha = 0.05$) among the length distributions for each age-class of males and females from the Rock Island Dam samples. We conducted a pairwise test of significance with Fisher's least-significant-difference (LSD) test (Sokal and Rohlf 1981) when significant differences were found among mean lengths.

Rocky Reach Dam sampling.—During April and May 1988, naturally produced steelhead were removed from fyke nets at Rocky Reach Dam during fish guidance efficiency (FGE) tests of a diversion screen (K. Truscott and S. G. Hays, Chelan County Public Utility District, unpublished data, 1989). Because of the nature of the FGE tests, it was difficult to obtain a sample that was representative of the run strength, but we believe the sample represents the run at large. The desired sample number at Rocky Reach Dam was similar to that at Rock Island Dam. However, it is likely that not all naturally produced steelhead caught in the nets were kept because damage to the fish made by the nets made it difficult to determine if the fish were of hatchery or natural origin. Weight and the qualitative degree of smoltification were not determined for the same reason. Samples were placed in individually marked plastic bags and frozen. Scales and otoliths were later removed, but no sex identification was made.

Seventy-nine steelhead were collected at Rocky Reach in 1988. Because the desired sample size of at least 700 was not met there in 1988, additional smolts were collected in April and May 1989 in another series of FGE tests (Hays and C. M. Peven, unpublished data, 1989). Toward the end of the study period in 1989, guided fish that were captured live were also placed in a lethal solution of MS-222 for sampling. The desired sample size was again not met.

Otolith sampling.—Otoliths were removed by making an incision with a small pocket knife on the medial dorsal surface of the head, from the area posterior of the eyes anteriorly through the snout, splitting the head in two equal parts. The sagittal otoliths were located below the cerebellum and removed with forceps. This method was preferred to that of Schneidervin and Hubert (1986) in that it did not require the removal of the gills and isthmus and the cutting of the parasphenoid, and it was thought to be more advantageous than the method described by Scarnecchia (1987) because the otoliths were visible after the cut was made.

Upon removal, otoliths were placed on a dark board under reflected light and examined with a binocular microscope. After observation, otoliths were placed in a premarked (date, sample number, and length) envelope. No deterioration was noted when otoliths were read again up to 1 year later.

Otoliths were first read dry, then wetted with tap water if clarification was needed. An otolith was read dry first to examine the "topography" of the different growth zones, which was sometimes easier to discern dry. The dark continuous hyaline zone was assumed to be an annulus; the white, opaque zone was considered summer growth (McKern et al. 1974; Bagenal and Tesch 1978; Chilton and Beamish 1982; Barber and McFarlane 1987). Caution was used not to read the "metamorphic" check (the hyaline zone that occurs around the nucleus of the otolith at hatching) as an annulus (McKern et al. 1974; Rybock et al. 1975; Martin 1978).

Scales.—Scales were removed from steelhead in an area between the most posterior ray of the dorsal fin and the most anterior ray of the anal fin, approximately three rows above the lateral line. Each scale was observed with a binocular compound microscope to ensure that it was not regenerated. At least two satisfactory scales were obtained from each fish. Scales were placed between two glass slides, taped together, and labeled.

Because scale reading may underestimate age (Beamish and McFarlane 1987), a subsample of 93 scales was used in age determination for comparisons with estimated ages from otoliths. Scale reading was aided by the Optical Pattern Recognition System (OPRS) of BioSonics, Inc., which digitizes the image of the scale with a video camera (mounted on a compound microscope) and a microcomputer (BioSonics 1987). A series of circuli with successively narrower spacing followed by wide circulus spacing, similar to that defined by Koo (1962), was the criterion used to identify an annulus.

Validation.—The lack of validation can be a serious problem in age determination studies (Van Oosten 1941; Dapson 1980; Chilton and Beamish 1982; Beamish and McFarlane 1983), and the ages of our samples have not been validated. However, it is widely held that the translucent hyaline zones seen in otoliths indeed represent winter growth, or annuli (e.g., Chugunova 1959; Irie 1960; McKern et al. 1974; Chilton and Beamish 1982; Heidinger and Clodfelter 1987). Practically all authors who have aged fish from otoliths agree that the hyaline zone is formed between late fall and late spring and can be safely assumed to account for the individual fish's winter growth (e.g., McKern et al. 1974; Bagenal and Tesch 1978; Chilton and Beamish 1982; Jearld 1983; Barber and McFarland 1987).

Age and length distributions.—The ages and length-frequency distributions of steelhead juveniles were compared between Rocky Reach and Rock Island Dams. An ANOVA was performed to test for significant differences ($\alpha = 0.05$) in length among age-classes at both dams (Sokal and Rohlf 1981). In testing fish between dams, we assumed that sex ratios were the same at both places.

Results

Rock Island Samples

In 1988, 753 juvenile steelhead were collected at the Rock Island Dam bypass trap. Of these, 722 (96%) were included in the analysis (Table 1). Of the 31 fish that were not included in the analysis, the otolith of 1 fish was lost, the otoliths of 8 fish were unreadable, and 22 fish were determined not to be smolts.

Scale and otolith ages agreed in 55% of comparisons; 1-year (36%) and 2-year (8%) differences resulted from other comparisons. Because scales tended to underestimate ages (i.e., scales indicated a younger age structure), we used the age estimates from otoliths in our analysis and conclusions.

The most common group of smolts (46.4%) collected at Rock Island Dam had spent three winters in freshwater (Table 1). Age-2 fish were the next most prominent cohort, making up 43.2% of the smolts sampled. Four-, 5-, 6-, and 7-year-olds made up 8.6, 0.8, 0.1, 0.1%, respectively of the smolts sampled at the bypass trap; only 0.7% of the fish sampled smolted at 1 year of age.

Females made up 63.0% of the fish sampled, and were predominantly 3-year-olds (Table 2). In general, female smolts sampled at Rock Island were older than males (which were predominantly age 2).

The two-way ANOVA showed significant interactions between age and sex ($F = 3.73$, $P = 0.025$), so we used pairwise comparisons to determine exactly where these interactions occurred. Age-2 females were significantly shorter ($F = 14.87$, $P < 0.001$) than age-3 or -4 female smolts, but not significantly different in size from age-5 female smolts (older fish were not included because of

TABLE 1.—Summary of age–length relationships for steelhead from Rock Island and Rocky Reach dams, 1988 and 1989. Lengths and weights are averages per age-class. Rocky Reach samples were not weighed. All ages are from otoliths.

Age (years) or statistic	Fork length (mm)		Weight (g)			Percent of each age-class
	Mean	SE	Mean	SE	N	
Rock Island Dam						
1	155.8	10.5	33.1	6.3	5	0.7
2	161.5	17.4	28.9	14.2	312	43.2
3	171.2	19.8	46.1	18.7	335	46.4
4	172.7	17.5	47.6	14.5	62	8.6
5	163.8	12.0	36.7	8.4	6	0.8
6	168.0		36.6		1	0.1
7	228.0		120.0		1	0.1
Total					722	100
Mean	166.8	19.2	43.0	16.9		
Minimum	127.0		16.0			
Maximum	270.0		185.0			
Rocky Reach Dam						
1	158.2	18.3			5	2.0
2	168.0	19.2			113	45.4
3	172.6	22.1			103	41.4
4	169.6	18.9			26	10.4
5	170.5	22.5			2	0.8
Total					249	100
Mean	169.9	20.6				
Minimum	119.0					
Maximum	270.0					

small sample sizes). Female age-5 smolts were not significantly different in length from age-3 or -4 females. Male length did not differ significantly among age-classes ($F = 2.28$, $P = 0.0795$). Age-4 female smolts were significantly longer than age-4 males (t-test, $P = 0.015$). Length differences between sexes at ages 2 and 3 were insignificant (ages 1 and 5 were not tested).

Rocky Reach Samples

Altogether, 267 juveniles were collected at Rocky Reach Dam in 1988 and 1989. Of these, 5% (13) were considered not to be smolts by external features, 1.5% (4) were of hatchery origin, and 1 had unreadable otoliths, leaving 249 for analysis (Table 1).

A chi-square analysis showed no significant difference between the age distributions at the two dams ($\chi^2 = 2.56$, $P = 0.265$). There was a significant difference in the average fish lengths at the two dams ($t = 1.98$, $P = 0.048$). The average length at Rocky Reach Dam (169.9 mm fork length, FL) was significantly longer than at Rock Island Dam (166.8 mm; Table 1). Within age-classes, age-2 smolts from Rocky Reach were significantly longer

TABLE 2.—Length–weight relationships of steelhead smolts collected at Rock Island Dam, 1988, separated by age-class and sex.

Age	Fork length (mm)		Weight (g)			Percent of each age-class
	Mean	SE	Mean	SE	N[a]	
Males						
1	155.3	11.7	32.2	6.8	4	1.7
2	163.8	19.8	40.4	16.5	114	47.1
3	169.5	15.5	43.5	13.3	101	41.7
4	166.2	17.6	42.9	15.8	23	9.5
Females						
1					0	0
2	161.2	15.7	38.8	12.9	181	39.8
3	172.2	21.2	46.7	20.6	228	50.1
4	177.2	15.9	52.6	12.8	38	8.4
5	163.8	12.0	36.7	8.4	6	1.3
6	168.0		36.6		1	0.2
7	228.0		120.0		1	0.2
Sex not determined						
1	158.0		36.5		1	4.0
2	148.6	11.0	28.5	5.5	17	68.0
3	165.0	23.8	40.2	14.8	6	24.0
4	150.0		28.4		1	4.0

[a] Total sample size = 722 fish: 242 males (33.5%), 455 females (63.0%), and 25 unsexed fish (3.5%).

than age-2 smolts from Rock Island ($F = 8.415$, $P < 0.001$). All other age-classes tested were not significantly different between sites.

Discussion

The oldest smolt ages observed at Rock Island Dam are higher than most of the observations in the literature. Steelhead smolts are known to migrate at ages 1–5, but most migrate at age 2 or 3 (Shapovalov and Taft 1954; Withler 1966; Hooton et al. 1987; Loch et al. 1988; Ward and Slaney 1988). Our observations ranged from 1 to 7 years; most of the fish smolted at ages 2 and 3 (Table 1). Williams (unpublished data, 1988, 1990), using otoliths for age determination, recorded returning adults that had had freshwater residencies ranging from 2 to 7 years.

The ages of steelhead smolts reported in the literature are predominantly estimates taken from scale readings (from smolts, or back-calculated from adult scales) and thus may have tended to be underestimates of true age. Jensen and Johnson (1982) and Lentsch and Griffith (1987) have shown that the first annulus may not appear on the scales of salmonids that inhabit cold waters in their first year of life. Laakso and Cope (1956) found three forms of cutthroat trout *Oncorhynchus clarki* in Yellowstone National Park: trout that did not form annuli in their first year; trout that had some scales with first-year annuli and some without; and trout that had fully formed first-year annuli on all their scales. Beamish and McFarlane (1987) reviewed many studies in which ages estimated from scales underestimated the true age of the fish.

Delayed spawning, extended incubation, and slow growth of steelhead originating in the Wenatchee, Entiat, Methow, and Okanogan river systems may preclude formation of the first-winter annulus on scales. Juveniles *O. mykiss* less than 40 mm FL have been found in cold headwater tributaries of the Methow River in October, when temperatures were between 2 and 5°C and dropping (Mullan et al. 1992).

Age at smoltification is determined by growth conditions in freshwater (Randall et al. 1987). The physiological factors that determine smoltification (Hoar 1976) and marine survival (Randall et al. 1987) of smolts are size dependent. The "physiological age" of parr in their presmolt year appeared to be a more important factor in parr–smolt transformation than chronological age for Atlantic salmon *Salmo salar* (Elson 1957). These factors suggest that unless a fish reaches a certain size within a certain time frame (window), the fish will remain in freshwater until the window next appears.

Most studies (e.g., Shapovalov and Taft 1954; Bjornn 1978; Chrisp and Bjornn 1978) have concluded that parr–smolt differentiation occurs at lengths around 140 mm, although some smolts are smaller than 140 mm FL (Wydoski and Whitney 1979; Loch et al. 1988; Ward and Slaney 1988). Lengths measured in our study (Table 2) agree with those observed by Loch et al. (1988) and Ward and Slaney (1988) in that some smolts appeared to be less than 140 mm FL. The temperature of the natal stream is probably the most important factor influencing growth of parr and subsequent smolt transformation (Symons 1979; Barnhart 1986; Loch et al. 1988).

Age and length were not directly related in our study (Table 1). Although lengths for the first three age-classes of both male and female smolts showed a positive relationship with age, lengths of older age-classes did not. Ward and Slaney (1988) reported that smolt length and age were directly related for fish from a Vancouver Island river, and that there was little variation in the average smolt length within freshwater ages. The difference between their results and ours from the mid-Columbia basin may be related to rearing conditions (temperatures). Because of a maritime climate and little variation in altitude, steelhead that rear on Vancouver Island probably experience a longer growing season than steelhead reared in north-central Washington.

Genetic influences on smoltification have also been proposed (Ricker 1972; Randall et al. 1987). Randall et al. (1987) concluded that "the age of migration must have a genetic component, but that it is also strongly influenced by environmental conditions." It appears that a fish has to retain in its genetic makeup the ability to vary according to what the environment dictates.

Symons (1979) concluded that the average smolt age for Atlantic salmon can be estimated by the number of days that the river temperature is above 7°C. Seven degrees was used because below that temperature, digestion of food was limited and growth negligible. He calculated that it would take approximately 500 d at or above 7°C to produce a 150-mm smolt, and he also associated this relationship with latitude. He felt it would take less than 2 years for fish to reach 150 mm in more southerly (warmer) rivers, and approximately 4 years in more northerly rivers.

We propose a conceptual model that would help explain why fish from colder areas take longer to achieve smolting size. The latitudinal relationships Symons spoke of could be analogous to elevational changes in temperature that are found in our study watersheds (Mullan et al. 1992). Figure 3 is a schematic representation of probable growth of parr in differing rearing habitats. Juveniles that rear in the colder, upstream habitats with shorter growing seasons take longer to achieve smolting size. Because these streams are smaller than the downstream areas in a given watershed or basin, density-dependent competition for food and space could also occur sooner than it would in downstream areas, requiring the growing parr to emigrate downstream to reach the smolting size threshold (Figure 3). Conversely, juveniles that rear in warmer downstream areas would reach the smolting size threshold at an earlier age.

We believe that our data suggest a relationship such as is shown in Figure 3. Williams (unpublished data, 1990) noted that 65% of the returning adults at Wells Dam (for years 1982–1990) were female. In our present study, 63.0% of the steelhead smolts sampled at Rock Island Dam were females, and female age composition was older than that of males, suggesting that males have a greater probability of remaining residents in freshwater than females. Ward and Slaney (1988) found that overall, females made up closer to half of the adult and smolt populations in the Keogh River

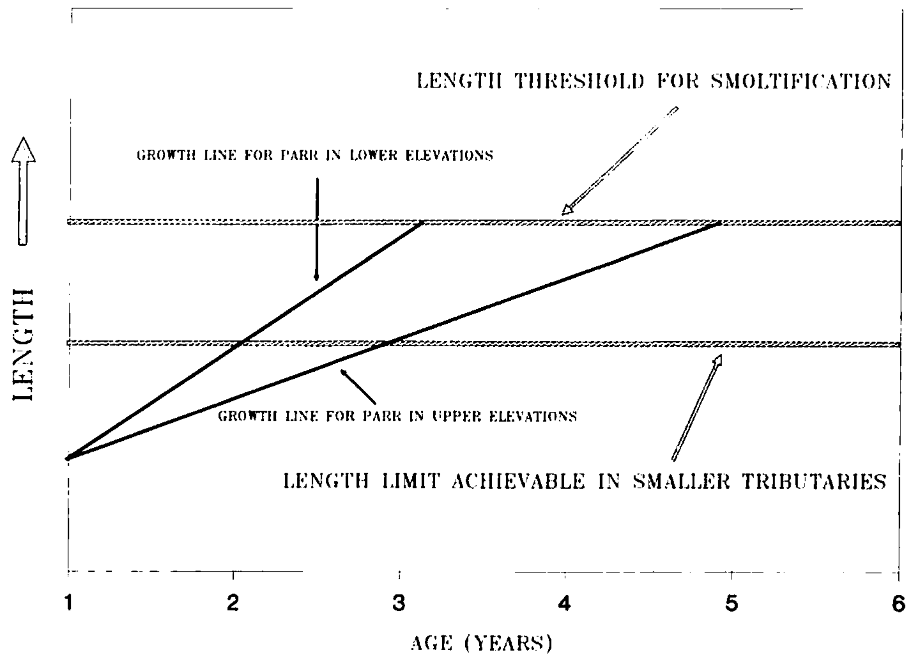

FIGURE 3.—A proposed conceptual model of steelhead emigration.

on Vancouver Island: 52.9% and 53.8%, respectively. Factors affecting the proportion of nonmigratory fish may differ between Vancouver Island and inland Washington, which could account for the differences noted.

Management Implications

Fisheries management agencies have proposed introducing steelhead and supplementing natural production with outplants of hatchery juveniles in areas of the Columbia basin that currently do not support steelhead. These proposals result from an effort to fulfill the Northwest Power Planning Council's interim goal of doubling the salmon and steelhead runs in the Columbia River Basin (NWPPC 1987). Many of these streams already have populations of resident rainbow trout. This raises the question about the effects of increased density on the resident populations. Perhaps in future studies, our conceptual model (Figure 3) could be developed into an empirical model describing the relationships of environmental variables to steelhead growth in the mid-Columbia River basin and the effects of such relationships on resident fish populations.

If parr move downstream out of colder areas in the small tributaries, they increase their chances of finding conditions that are more favorable for growth. Increased growth of parr before their outmigration to the sea makes them susceptible to sport fisheries that target resident rainbow trout. Although most smolts would be below the legal length limit, a substantial number of the fish that are caught and released do not survive, especially in "bait-allowed" areas (Hillman and Chapman 1989a). Resource managers may be able to protect the parr by restricting fishing in all main-stem areas where parr are known to rear in the late summer, when they might attain lengths that make them more susceptible to fishing. Further studies are needed to establish where these areas might be. Hillman and Chapman (1989a, 1989b) have identified some of these areas in the Wenatchee River.

Knowledge of the age distribution of smolts will make it possible to develop spawner–recruit curves for steelhead in the mid-Columbia. It will also be possible to develop an estimate of egg-to-smolt survival, a number that has been difficult for managers to obtain.

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