Size-Biased Survival in Steelhead Trout (*Oncorhynchus mykiss*): Back-Calculated Lengths from Adults' Scales Compared to Migrating Smolts at the Keogh River, British Columbia

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Lengths of wild, winter-run steelhead smolts, estimated by back-calculation procedures from adults' scales, were compared with observed lengths of migrating smolts sampled near the mouth of the Keogh River, Vancouver Island. Size-biased smolt-to-adult survival rates were estimated for several length categories by utilizing length frequencies from observed smolts, smolt length frequencies which were back calculated from adults' scales, smolt yield, and adult returns. Back-calculated smolt length (BSL) of adults returning from smolts of 1977 to 1982 averaged 193 mm compared to 176 mm for observed smolt length (OSL). Mean BSL was larger than OSL in every year. Adults from odd-numbered smolt years had larger BSL than adults from even-numbered smolt years similar to the pattern in OSL. BSL increased with increased years spent in salt water, based on ageing adults' scales. Males and females had different BSL based on number of years spent in fresh water and salt water, although they exhibited the same mean BSL overall. The smolt-to-adult survival estimates were in close agreement with previous estimates derived from the mean OSL. Predictability of survival in the ocean based on the length of smolts was extended over a broad range of the length distribution of wild steelhead smolts.

Les longueurs de smolts de truite arc-en-ciel en descente hivernale estimées par rétrocalcul à partir d'écailles d'adultes ont été comparées aux longueurs mesurées de smolts en migration recueillis près de l'embouchure de la rivière Keogh sur l'île Vancouver. Nous avons calculé les taux de survie en fonction de la taille, du stade de smolt au stade adulte, pour plusieurs classes de longueur à partir de la fréquence des différentes longueurs de smolts échantillonnés, de la fréquence des longueurs obtenues par rétrocalcul à partir d'écailles d'adultes, du rendement de la production de smolts et de la quantité d'adultes au moment de la montaison. Les longueurs des smolts obtenues par rétrocalcul ("back-calculated smolt length", ou BSL) à partir des écailles d'adultes en montaison qui étaient au stade de smolt de 1977 à 1982 étaient en moyenne de 193 mm, comparé à une longueur moyenne mesurée ("observed smolt length", ou OSL) de 176 mm. La BSL était supérieure à l'OSL à chaque année. Les adultes qui étaient smolts durant les années impaires ont donné des BSL supérieures à celles des adultes qui étaient smolts durant les années paires. Les résultats sont similaires dans le cas des OSL. Nous avons trouvé, en nous basant sur les renseignements fournis par les écailles des adultes, que la valeur des BSL varie en raison directe du nombre d'années passées en eau douce et en raison inverse du nombre d'années passées en eau salée. Suivant le nombre d'années passées en eau douce et en eau salée, les mâles et les femelles ont des BSL différentes, mais, globalement, leurs BSL moyennes étaient identiques. Les estimations du taux de survie du stade de smolt au stade adulte correspondaient étroitement avec les estimations réalisées antérieurement à partir des OSL moyennes. Les prévisions relatives à la survie dans l'océan, prévisions fondées sur la longueur des smolts, ont été étendues pour couvrir un large spectre de la distribution suivant la longueur des smolts de truite arc-en-ciel sauvage.

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Recently, Carlander (1986) summarized the use of fish scales in age and growth studies, and it was evident that there have been few attempts to use scale back-calculation procedures (Ricker 1975) to estimate survival rates of fish. Maher and Larkin (1954) estimated smolt length of steelhead *Oncorhynchus mykiss* (formerly *Salmo gairdneri*) from the Chilliwack River, B. C., using scale samples collected from anglers' catch for the back-calculation exercise, but they did not compare their results with wild smolt data. West and Larkin (1987) used otolith–body length relations and back-calculation procedures to demonstrate that mortality of juvenile sockeye (*Oncorhynchus nerka*) salmon in Babine Lake was size-selective. However, no attempt has been made to employ back-calculation procedures to estimate the smolt-to-adult survival of salmonids as far as we are aware from the scientific literature, nor have scales been used with back-calculation procedures to estimate survivals during the various life stages of wild steelhead.

In an earlier paper, we demonstrated that smolt-to-adult survival for steelhead was positively correlated with smolt size (Ward and Slaney 1988). Our understanding of the relationships between smolt size and smolt-to-adult survival was based on mean smolt size and was thus limited to the range in mean smolt length (160–187 mm). Since a large proportion of migrants occur outside this range, it was desireable for predictive purposes to expand the range of the steelhead smolt length and survival studies to encompass all smolt sizes evident in the annual seaward migration. In addition, the relationship between smolt size and age-at-return in the previous paper was confounded by smolt age and size interactions since it was not possible to separate the influence of freshwater age from smolt size in that study. We assumed that because fish ages in freshwater years and ocean years were inversely related, and smolt length increased with the number of years spent in fresh water, smolt size at migration was also inversely related to the number of years spent in the ocean. We also suggested that the backcalculated smolt length of males and females be compared from scales of 2- and 3-yr-ocean fish, to provide further evidence of an inverse relationship between smolt length and return age.

Accordingly, the objectives of the current study were: (1) to estimate the size-biased smolt-to-adult survival of steelhead smolts over their range in length, and, (2) to compare observed smolt lengths (OSL) to backcalculated smolt length (BSL) from adult scales of male and female steelhead which had spent 2–4 yr in fresh water, and 1–3 yr in the ocean. We thus required knowledge of the smolt yield of the Keogh River as well as the OSL frequency distributions, the number of returning adults, the age of the returning adults, and the frequency distributions of the BSL, determined from adult scales as the time of ocean entry. The composition of smolts in length intervals was calculated from the length-frequency distribution of smolts and the numerical smolt yield. That composition was compared to the composition of adults in length intervals, which was based on the BSL frequency distribution and adult returns. From these two sources we estimated size-biased survival, utilizing data from 6 yr of smolt yield (1977–82) and subsequent adult returns (1978–85).

Methods

The Keogh River, on northern Vancouver Island, has been described elsewhere (Perrin et al. 1987; Johnston et al. 1986; Slaney et al. 1986; Slaney and Harrower 1981; Ward and Slaney 1981; Smith and Slaney 1980), as have most of the sampling details concerned with this investigation (Ward and Slaney 1988). A fish enumeration fence, 300 m upstream from the mouth of the 33 km river, has been utilized to capture steelhead trout adults, kelts and smolts since 1976.

Calculation of survival rates for the marine phase of steelhead life history required enumeration of both smolts and adults. The number of the adults returning each year was estimated using a Peterson mark–recapture method (Ricker 1975). Detailed methods are provided in Ward and Slaney (1988). Briefly, adults passing upstream through the fish fence had a 6 mm hole punched in their operculum, and kelts passing downstream were examined for this mark. On average, 62% of the population was enumerated as upstream migrant adults or unmarked downstream migrant kelts, 39% of the population was marked while passing upstream, and 23% of the marked males were recaptured while 43% of the marked females were recaptured (Ward and Slaney 1988). Steelhead smolts were enumerated from early April to mid-June at the counting fence using the method described in Ward and Slaney (1988). Briefly, smolts were removed from collection boxes and counted daily, and samples of lengths and scales randomly obtained. Trap efficiency of capture was about 90%, which was determined by marking and releasing large coho salmon smolts (>120 mm) 50 m above the fence (Irvine and Ward 1989).

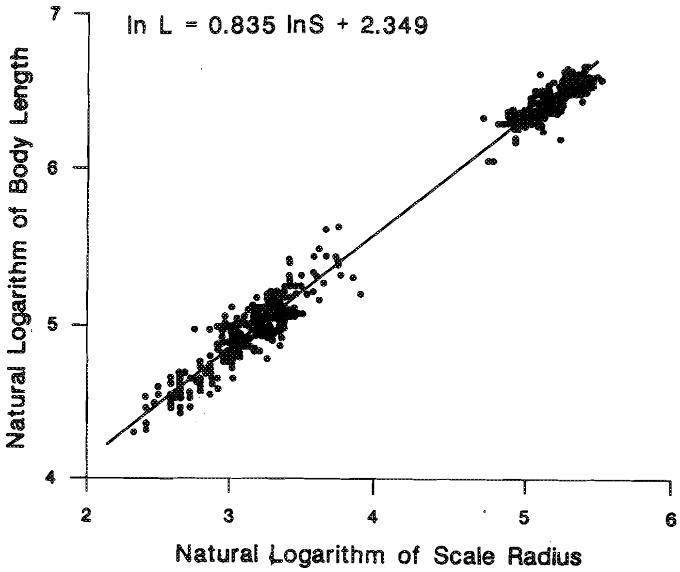

FIG. 1. The relationship between the natural logarithm of fork length (ln L) and the natural logarithm of scale radius (ln S) for steelhead trout of the Keogh River.

Adults were identified by sex, measured for length, and a scale sample was removed from the preferred zone for ageing (Maher and Larkin 1954). Plastic impressions of scales were prepared for analysis (Hooton et al. 1987) and then interpreted with the aid of photomicrographs. The number of years fish spent in the ocean was validated by comparison with marked hatchery fish (Slaney and Harrower 1981). Interpretation of the number of years spent in fresh water was aided by sampling of steelhead parr throughout the river, which assisted us in recognizing annuli formed during their freshwater phase. Estimates of the returns were tabulated based on the year fish were smolts (i.e., the smolt year) and were calculated from the adult population estimates and the age composition of the adult population. Thus, returns after 1, 2, and 3 yr in salt water comprised the total survivors from a smolt year. Fish in their second or greater spawning migration, which on average comprised 10% of the population (Ward and Slaney 1988), were excluded from the analysis.

The back calculation of fish size from scales was dependent on the relationship between fish scale radii and fish length. We obtained a large sample of fish of several life stages from several years, without weighting. Parr, smolt, and adult samples of scales and lengths were obtained from 1977 to 1982 (n = 345) to define this relationship. The Fraser–Lee method of back calculation was used (Ricker 1975; Bartlett et al. 1984; Hooton et al. 1987). Fish > 45 mm only were used in this relationship since many of the fish sampled below this size were within the period of formation of the initial scale placode.

Smolt length was back calculated from 896 adult scales, representing returns from smolts which migrated from the Keogh River between 1977 and 1982. Actual number of adults sampled was higher but some scales (about 20%) were not useful for back calculation due to regeneration in the section of the scale representing freshwater residence. Recognition of the transfer from fresh water to salt water was consistently apparent in adult scales, as described by Maher and Larkin (1954). Reabsorption of the edge (ocean residence) of the adults' scales was not apparent in fish captured moving upstream at the river mouth although this was apparent in kelts migrating to sea. Mean BSL

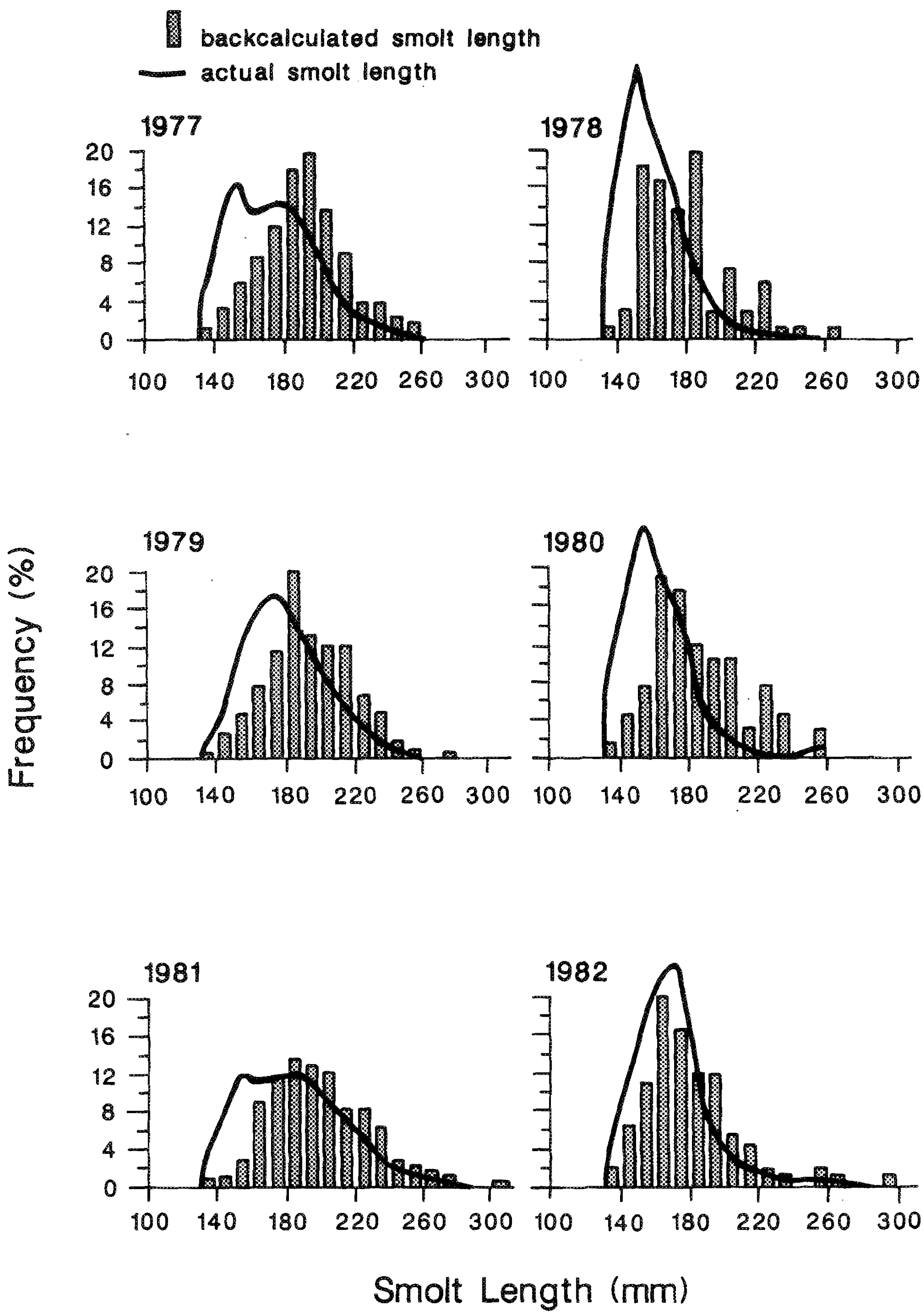

FIG. 2. Frequency distributions of observed (OSL) and back-calculated smolt lengths (BSL) from steelhead trout of the Keogh River for smolt years 1977–82.

from adult fish that were smolts in a given year was compared to the mean size of smolt migrants from that year. With data for all years combined (unweighted), the mean BSL of adults that spent 2 yr in fresh water (age 2.) before becoming smolts (n = 256), 3 yr in fresh water (age 3., n = 561), and 4 yr in fresh water (age 4., n = 77) were calculated and compared to the mean OSL reported for smolts of the same ages in Ward and Slaney (1988). We compared the BSL of males (n = 371) and females (n = 524), and of males and females from different ocean ages (sample size for .1 = 13, for .2 = 623, for .3 = 259).

Estimates of survival of smolts from 1977 to 1982 in six different length groups were based on the mean BSL of each length group. The numerical composition of smolts in their OSL frequency distributions was determined by multiplying the proportion in each length interval by the total number of smolt migrants each year. Similarly, the composition of adult returns within each BSL interval was determined by multiplying the proportion/interval by the number of survivors. The latter was documented by Ward and Slaney (1988) and was estimated by ageing adults to determine composition by age based on years spent in the ocean, and the mark–recapture population esti-

TABLE 1. Observed (OSL) (from Ward and Slaney 1988) and back-calculated lengths (BSL) of Keogh River steelhead smolts in relation to the number of years in freshwater, the number of years in saltwater, the sex of the adult fish, and the year of smolting from the 1977 to 1982 smolt years. SD = standard deviation, n = sample size.

	Mean OSL (mm)	Mean BSL (mm)	BSL SD	BSL n
Years in fresh water				
2	153	177	22.8	256
3	177	196	25.6	561
4	218	220	26.5	77
Years in salt water				
1 males		218	41.5	13
females		—	—	—
2 males		192	25.4	265
females		193	28.5	358
3 males		195	29.5	93
females		188	25.5	166
Sex of adults				
males		192	27.7	524
females		194	27.5	371
Smolt year				
1977	174	193	23.7	185
1978	160	181	26.0	65
1979	180	193	24.2	165
1980	161	186	26.8	68
1981	187	201	28.9	303
1982	170	178	27.8	110

mates. For example, the adult returns from 1977 smolts were comprised of a proportion of the 1978 adults, the 1979 adults and the 1980 adults. Estimates of the number of smolts that migrated within a given size range and of the number of adults they produced permitted calculations of smolt-to-adult survival values for each of the six smolt length intervals. It was necessary to lump data for some intervals, particularly in the larger size categories in some years, to provide adequate sample sizes (>10 estimated survivors). Weighted least squares regression was performed on the survival and smolt length data with all smolt years combined.

Results

A linear relationship was found between the natural logarithms of fork length and scale radius (r^2 = .98, Fig. 1). The relationship was described by the line

$$\ln L = 0.835 \ln S + 2.349$$

where

L = fork length (mm)
S = total scale radius (mm)

Residuals were stabilized and normally distributed after logarithmic transformations.

Because the logarithm of fish length was proportional to the log of the scale radius, with a correction factor (the intercept), we used the modified form of the Fraser–Lee equation for the back calculation of length at age (Bartlett et al. 1984; Hooton et al. 1987):

$$\ln L_a = (\ln L - c) \ln S_a / \ln S) + c$$

where

c = intercept from the regression of ln (fork length) and ln (scale radius)
S_a = scale radius at a given annulus
L_a = fork length of fish at a given annulus

For all smolt years (1977 to 1982), the mean BSL was 192.5 mm, whereas the overall mean OSL was 16.3 less at 176.2 mm (P <0.05). BSL was unimodally distributed and skewed to the right up to 300 mm (Fig. 2). The trend for BSL to be greater than OSL was apparent in every year (Fig. 2).

The mean differences of BSL and OSL ranged from a low of 9 mm in 1982 to a high of 24.5 mm in 1980 (Table 1). Despite this range, the pattern of the mean length over the 6 yr was similar for both BSL and OSL. BSL was normally distributed whereas OSL frequencies were truncated at 130 mm (Fig. 2). Fish smaller than 130 mm were purposely excluded from OSL and considered to be parr, although a few appeared silver. Differences between the shape of the distributions appeared mainly in the lower length intervals. An exception was in 1982, where the BSL frequency distribution was similar to the OSL frequency distribution. Evidently there was relatively less mortality among small smolts in 1982 (Fig. 2).

Mean BSLs were significantly different (P <0.05) among smolt years 1977 to 1982 (Table 1). Adults that had been smolts in 1977, 1979, and 1981 had been consistently larger as smolts than adults that had been smolts in 1978, 1980, and 1982. Similarly, OSLs in the even-numbered years were also smaller (P <0.05; Scheffe's multiple range test) than those in the odd-numbered years.

BSL increased with older age in freshwater years (P <0.05, Table 1), similar to OSL. The BSL of adults that had spent 4 yr in fresh water was >40 mm longer than that of adults that as smolts had spent 2 yr in fresh water. The difference between BSL and OSL of Keogh smolts decreased with increasing number of years spent in fresh water. Adults that had spent 2, 3,

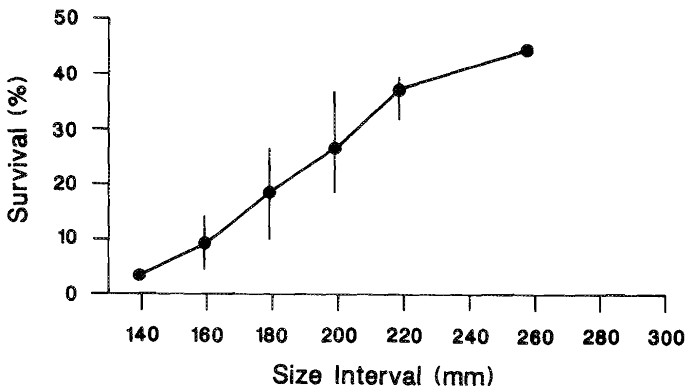

FIG. 3. The weighted least squares regression of steelhead smolt length and smolt-to-adult survival based on the back-calculation of smolt length from adults' scales, for the 1977 to 1982 smolts and subsequent returns. The data points are for all years combined, weighted by sample size; the vertical bars represent the range in survival estimates where sample/interval exceeded 10 fish.

and 4 yr in fresh water had, on average, a BSL that was 24, 16, and 2 mm longer, respectively, than OSL at age. As younger smolts were smaller (Table 1), greatest differences between BSL and OSL were in the smaller size classes, which is consistent with a positive size-survival relationship.

As years spent in the salt water increased, BSL decreased (P <0.05, Table 1) although the difference between age .2 and .3 fish was insignificant when both sexes were considered together. There were differences in the BSL of males and females based on years spent in salt water. Jacks (age .1) were derived from large male smolts but females age .1 were not found. Age .2 males and females had similar BSL, and age .3 females were slightly smaller smolts than males. Males had a significantly larger BSL if they were age .1 rather than ages .2 and .3 (P <0.05), but there was no difference between BSL from .2 and .3 males. However, females aged .3 exhibited significantly smaller (by 5.6 mm) BSL than females aged .2 (P<0.05).

The weighted least squares regression of smolt length and survival was non-significant ($r^2 = .29, P>0.05$) when all smolt years were included in the analysis (n = 820 adult scales). With the exclusion of the 1982 smolts (cf Ward and Slaney 1988), the r^2 improved to .74, and the relationship was positive (P <0.05) but non-linear (residuals were not normally distributed). The slope of the line appeared to decrease at both ends of the line similar to a logistic curve, particularly at the largest length interval of 200–260 mm (Fig. 3). Differences in survival appeared large: smolts of 200 mm in length had >8 times the survival of smolts 140 mm in length. The average-sized smolt (176 mm) was predicted to survive at about 17% from the weighted least squares regression equation.

Discussion

The results presented here on smolt length, survival and age-at-return are in agreement with relationships between mean smolt length and survival and age-at-return in Ward and Slaney (1988). The smolt-to-adult survival of steelhead trout was positively related to smolt length, but the range in smolt length examined was greatly extended through the use of back calculation of smolt length from adult scales. At the limits of the curve established by Ward and Slaney (1988) we found similar survivals (differences of less than 2% at 160 and 187 mm) based on the back-calculation method, and the slope and intercepts did not differ. However, we have not identified the mechanisms that result in poorer survival of smaller smolts. Perhaps larger smolts with their greater swimming speed have advantages in both capture of prey (hence more rapid growth than their smaller cohorts) and escape from predators (cf. Taylor and MacPhail 1985). However, the shape of the relationship between survival and smolt length suggests an asymptote is reached at about 250 mm.

There were no differences in the BSL of males and females. Ward and Slaney (1988) did not detect a difference in the sex ratio of male and female smolts within and between 4 size intervals, but their sample size was small. Keogh River steelhead smolts apparently do not display the size-related sex ratio differences found in smolts of some Atlantic salmon populations (Ritter et al. 1986). For modelling of steelhead adult returns based on smolt length, sex ratio differences between length intervals may not be a significant factor. This also implies that there are few, if any, mature male parr in steelhead populations at this latitude.

On average, BSL was lowest for fish that spent more years in salt water. Since years spent in fresh water and years spent in salt water were inversely related (Ward and Slaney 1988) and BSL also was inversely related to years in salt water, it appears larger smolts are the first to mature. However, the maturation rate differs for males and females. Ritter et al. (1986) and Chadwick et al. (1986) provided evidence that there was a parental influence on smolt age and size in Atlantic salmon. If this also applies to steelhead, then adults of older age-at-maturity (based mainly on ocean years) can be expected to yield smaller smolts. Larger adults tend towards larger egg size and subsequent fry size (Gall 1974) and fingerling size (Fowler 1972) which, for steelhead, may result in faster growth in general and earlier smoltification. However, this may also be further affected by the rearing environment; for example, a fish rearing in the cold headwaters or in relatively cold years may smolt at a later age (and possibly a larger smolt size) than under other conditions, despite the parental influence. This may explain why Hooton et al. (1987) found no correlation between adult size and BSL of angler-caught steelhead from Vancouver Island — the highly variable coastal stream environment and plasticity in life history traits could mask any genetic effect. Several other studies of salmonid life history have demonstrated a relationship between smolt size and age-at-return (Hyatt and Stockner 1985).

Hyatt and Stockner (1985) also noted that the timing of the smolt migration may play a significant role in both the age-at-return and survival in the ocean. It was not possible for us to separate smolt timing effects in the back-calculation exercise. However, we noted that smolts occurring early in the smolt migration were consistently larger (by an average of 10 mm, P <0.05, data on file) than smolts occurring at the peak migration time, a trend also observed with Keogh coho smolts (Irvine and Ward 1989). To provide a more definitive examination, the interactions of size with timing of smolt migrations should be examined in wild steelhead, along with the relationship between survival and age-at-return. We are unsure if the differences in smolt size between odd- and even-numbered smolt years is related to smolt-timing effects or a function of other ecological relationships during the freshwater rearing stage (e.g., variation in odd- and even-year pink salmon (*Oncorhynchus gorbuscha*) abundance — Johnston et al. 1986).

A variety of back-calculation techniques to estimate smolt size of steelhead trout have been reported (Maher and Larkin 1954; Chapman 1958; Narver and Withler 1971; Narver and

Anderson 1974; Whately 1977; Horncastle 1981). Hooton et al. (1987) established a back-calculation procedure mathematically similar to Bartlett et al. (1984) yet separately and almost simultaneously derived. However, Hooton et al. (1987) dealt almost entirely with angler-caught fish, sample sizes were low in many cases, and there was no test of the back-calculation model against empirical data. The similarity between survival rates based on mean smolt length (Ward and Slaney 1988) and rates based on BSL provided evidence that the back-calculation method of this paper was valid.

Variation in the difference between BSL and OSL further suggested that conditions for survival in the ocean can change. This was particularly evident for the 1982 smolts which experienced higher survival of the smaller size classes compared to other years. Changes associated with the 1982–83 El Niño event may possibly be correlated with increased survival of steelhead post-smolts at this latitude (Ward and Slaney 1988; Wooster and Fluharty 1985). Despite this variation, the descriptive model of Ward and Slaney (1988) should incorporate the new evidence of this paper to perhaps assist in the forecasting of returns of adult steelhead trout based on smolt length. Given longer term data on climatic change (e.g., sea-surface temperature) and smolt survival, the former might be included with variables in the prediction of adult returns. To gain an understanding of the role of the marine environment in size-biased smolt survival and age-at-return will require greater research into the early sea-life of steelhead trout.

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