The influence of habitat complexity and fish size on over-winter survival and growth of individually marked juvenile coho salmon (*Oncorhynchus kisutch*) in Big Beef Creek, Washington

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Abstract: Wild juvenile coho salmon (*Oncorhynchus kisutch*) were individually marked in October 1990 and 1991 to evaluate the effects of habitat complexity and fish size on over-winter survival in Big Beef Creek, Washington. Habitat complexity was quantified for the habitat unit where the fish were collected and, in 1991, also for the 500-m reach downstream from the collection site. Survival, estimated from recovery of marked smolts at the stream's mouth, differed between years (25.4 and 46.2%) and also varied among habitat units and reaches within years. Survival was at most weakly correlated with complexity of the habitat units but was strongly correlated with the quantity of woody debris and density of habitat units in the 500-m reach, and distance from the estuary. Because distance covaried with habitat complexity, we could not ascertain which factor had the primary influence on survival. In addition, larger fish generally survived at a higher rate than smaller individuals. However, fish tagged above William Symington Lake were smaller in the fall but larger as smolts and had higher survival rates than those tagged below the lake. Taken together, these results reveal complex relationships between size, habitat, and growth that may affect over-winter survival and subsequent life-history events.

Résumé : Nous avons marqué individuellement des juvéniles de saumon coho (*Oncorhynchus kisutch*) sauvage, en octobre 1990 et 1991, pour évaluer les effets de la complexité de l'habitat et de la taille des poissons sur la survie hivernale dans le Big Beef Creek (Washington). Nous avons quantifié la complexité de l'habitat dans l'unité d'habitat où les poissons ont été prélevés et, en 1991, nous l'avons fait également dans le tronçon de 500 m situé en aval du lieu de prélèvement. La survie, estimée d'après la récupération de smolts marqués à l'embouchure du cours d'eau, différait d'une année à l'autre (25,4 et 46,2%) et variait aussi selon les unités d'habitat et les tronçons une même année. Le taux de survie était au moins faiblement corrélé à la complexité des unités d'habitat, et était fortement corrélé à la quantité de débris de bois et à la densité des unités d'habitat dans le tronçon de 500 m, et avec la distance par rapport à l'estuaire. Étant donné que la distance variait avec la complexité de l'habitat, nous n'avons pas pu établir quel facteur avait l'influence la plus forte sur la survie. De plus, les poissons de grande taille survivaient généralement en plus grande proportion que les individus de petite taille. Toutefois, les poissons marqués au-dessus du lac William Symington étaient plus petits à l'automne mais plus grands au stade du smolt, et présentaient des taux de survie plus élevés, que ceux marqués au-dessous du lac. Considérés ensemble, ces résultats révèlent des relations complexes entre la taille, l'habitat et la croissance, relations qui peuvent affecter la survie hivernale et les événements subséquents du cycle biologique.
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Introduction

Studies of the ecology of juvenile salmonid fishes in freshwater often attempt to identify factors affecting growth, distribution, and survival of individuals and dynamics of the population. Such studies reveal interactions between egg production by the parental generation, density-dependent processes, and climatic factors resulting in variation in size and abundance of parr and smolts (e.g., Atlantic salmon, *Salmo salar*: Symons 1979; Baglinière et al. 1993; brown trout, *Salmo trutta*: Elliott 1993; steelhead trout, *Oncorhynchus mykiss*: Ward and Slaney 1993). Most juvenile coho salmon (*Oncorhynchus kisutch*) spend 1 or 2 years in freshwater prior to seaward migration and populations seem to be limited by the amount of freshwater rearing habitat available (e.g., Marshall and Britton 1990). This limitation results in part from their territorial behavior (Chapman 1962, 1966) and the stream's carrying capacity may be set during the summer low-flow period (Smoker 1955; Lestelle et al. 1993) by the amount of pool space (Nickelson et al. 1979). As a result of limited freshwater rearing space, the production of seaward migrating smolts is typically asymptotically related to the number of adults in the parent population. That is, once the stream's carrying capacity for juveniles is reached, an increase in the number of spawning adults will not increase the abundance of

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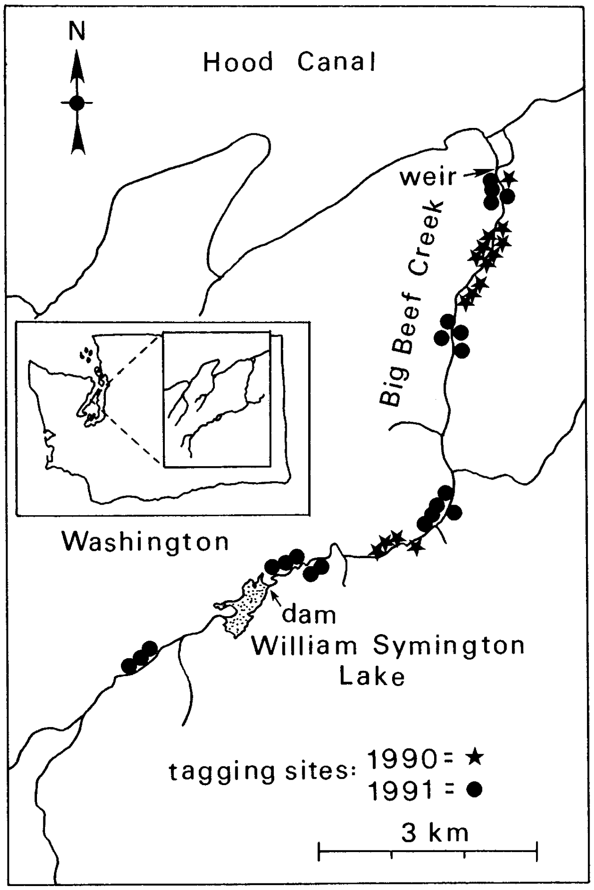
Fig. 1. Map of Big Beef Creek, showing approximate locations where juvenile coho salmon were tagged and released in October 1990 (stars) and 1991 (circles). The inset shows the study site's location on the Kitsap Peninsula, Washington.



smolts. Some of the variability around the asymptote may be related to interannual variation in summer flow conditions, but winter mortality can be severe and highly variable (Hartman et al. 1987) and may chiefly be a function of habitat rather than density-dependent factors (Murphy et al. 1984).

In coastal streams, winter freshets frequently cause stream bank erosion, streambed scour and fill, and rearrangements of accumulations of large woody debris (LWD). Juvenile coho salmon often move from summer nursery areas in streams to off-channel and floodplain habitats in winter (Cederholm and Scarlett 1982; Peterson 1982) but also overwinter in stream habitats (Scarlett and Cederholm 1984; Brown and Hartman 1988). During the winter, juvenile coho selectively inhabit deep pools with substantial accumulations of LWD (Bustard and Narver 1975; Murphy et al. 1986). Experiments by McMahon and Hartman (1989) and Shirvell (1990) indicated that coho salmon were attracted to the low velocities in the lee of woody obstructions. Thus, while off-channel habitat improves over-winter survival and growth for a segment of the population, the instream LWD that is a dominant feature of streams in forested watersheds (Bilby and Ward 1989, 1991) creates habitat conditions for most of the population. However, the association of coho salmon with LWD is not direct evidence that the debris reduces winter mortality.

Over broad expanses of the Pacific Northwest, removal of mature streamside forests during the initial logging and subsequent stream clean-out programs altered the amount and character of in-channel woody debris, resulting in simplified stream habitat (Bisson et al. 1987, 1992; Fausch and Northcote 1992). While loss of LWD from streams has been associated with reduced abundance of juvenile salmonids (Elliott 1986; Dolloff 1986), growth and production, particularly in summer, may also be strongly influenced by temperature (Holtby 1988), prey populations (Murphy et al. 1986; Bilby and Bisson 1987, 1992), fry density and freshets, and interactions among these factors (e.g., Scrivener and Andersen 1984). Holtby (1988) indicated that over-winter survival of underyearling coho salmon in Carnation Creek, British Columbia, could be explained in large part by the average fish size at the end of the summer. Estimating population-level changes that might result from habitat alteration may be difficult, in part because a small population may be composed of relatively large individuals at the end of summer that might experience above-average over-winter survival. Finally, marine survival of coho salmon may be related to both the smolt size and date of seaward migration (hatchery-produced salmon: Bilton et al. 1982; Morley et al. 1988; wild salmon: Thedinga and Koski 1984). Emigration date often varies with body size; larger and (or) older smolts often leave freshwater before smaller smolts (e.g., coho salmon: Seiler et al. 1981, 1984; Irvine and Ward 1989; Atlantic salmon: Jonsson et al. 1990; brown trout: Bohlin et al. 1993; sockeye salmon (*Oncorhynchus nerka*): Crawford and Cross 1992).

Woody material and the habitat complexity associated with it are thus interrelated with fish size in the ecology of juvenile stream-dwelling salmonids in complex ways (Bisson et al. 1987; Hartman et al. 1987). Studies of size, habitat, and survival have been largely limited to interannual comparisons (e.g., Hartman et al. 1987); data on individual fish are scarce and not always consistent with the predicted association between large size and survival (e.g., Brown 1985). However, as research on marine survival (e.g., Holtby et al. 1990; Henderson and Cass 1991) has revealed, the benefits of size may be more apparent within than among years. To better understand the interaction between summer growth and physical habitat as influences on over-winter survival, we measured and individually marked coho salmon from various habitats within a stream at the end of the summer and monitored their size and survival when they emigrated as smolts. Our specific hypotheses were (*i*) over-winter survival and size as smolts would be positively correlated with their size as underyearlings, (*ii*) the complexity of the habitat unit and stream reach where the fish were collected at the end of the summer would be positively correlated with survival, and (*iii*) larger smolts would leave earlier than smaller ones.

Methods

Study area

Big Beef Creek flows into Hood Canal from the Kitsap Peninsula, Washington (Fig. 1). It has a basin area of approximately 38 km^2 and contains 18 km of main stream channel, 8 km upstream and 10 km downstream of William Symington Lake, a 198-ha artificial impoundment constructed in 1965 (Williams 1970; Seiler et al. 1981). Fish pass over the 10-m dam and into the lake and streams above it via a pool and weir fishway. Big Beef Creek's watershed is lower than 400 m elevation and the stream's dominant storm flows are from rains between November and March. A maximum flow of 21 m^3/s was recorded in 1971 and summer low flows near the mouth average 0.08 m^3/s. Above the lake the main stream channel is very flat (0.2% gradient) and in places is connected to extensive riparian wetlands. Below the lake the stream gradient lessens gradually from 1.5% in reaches below the dam to 0.5% near the mouth. Several small, relatively steep, intermittent tributaries enter Big Beef Creek in the 10 km below William Symington Lake.

In some of the lower stream reaches, coarse sediment generated during the basin's initial logging (as early as the late 1800s) has accumulated in the stream channel and is gradually being transported through the system (Madej 1975). Numerous old cedar stumps on the stream banks reflect the original conifer riparian forest that has regrown to red alder (*Alnus rubra*), vine maple (*Acer circinatum*), and bigleaf maple (*Acer macrophyllum*). Second-growth western hemlock (*Tsuga heterophylla*), western red cedar (*Thuja plicata*), and Douglas-fir (*Pseudotsuga menziesii*) are also present.

Fish tagging and recovery

Juvenile coho salmon were captured in the 1st week of October 1990 and 1991 to represent the end of the summer growing period, prior to winter redistribution. Collections were made by stick seine from 15 habitat units in three stream reaches (all below the lake) in 1990 and 21 pools in five reaches in 1991, including sites above and below the lake. The fish were anesthetized with MS–222; fork length, weight, and home pool were recorded; and either a sequential coded wire (s-CW) or a passive integrated transponder (PIT) tag was implanted. They were allowed 30–60 min to recover and then returned to the pool where they had been collected. A 12-gauge hand-held hypodermic needle and syringe were used to implant the PIT tag into the body cavity (Peterson et al. 1994), and a 24-gauge needle and syringe were used to implant the s-CW tag into the fish's cranial cartilage. The adipose fin of each s-CW tagged fish was excised. A total of 717 and 954 fish were tagged in 1990 and 1991, respectively, evenly divided between s-CW and PIT tags.

Marked fish were recovered the following spring at a permanent weir at the mouth of the stream, operated from April 7 to June 14, 1991, and to June 15, 1992. All individuals were electronically scanned for the presence of PIT tags. The codes from individuals carrying PIT tags were recorded and the fish were weighed, measured, and released. All adipose-clipped fish were weighed, measured, and then sacrificed for subsequent s-CW tag extraction and reading. Survival was calculated as the proportion of fish tagged in the fall that were recovered in the spring. Individuals migrating downstream before or after the smolt sampling period would be classified as mortalities. The weir was operated during the period when almost all smolts emigrate (Seiler et al. 1984), but the survival estimates should be regarded as minima. We recovered seven age–2 smolts that had been marked in 1990 (three s-CW and four PIT tagged). Of the fish marked in 1991, no s-CW tagged individuals were recovered as age–2 smolts (they were not examined for PIT tags). Age–2 smolts were omitted from analysis because of their scarcity and because their longer residence period in the stream prevented comparison with age–1 smolts.

Habitat surveys

For purposes of comparing fish survival, we defined habitat complexity at two spatial scales: habitat unit and reach. A variety of features commonly used to describe streams in monitoring programs were measured for each habitat unit where the fish were collected. Habitat units were classified according to Bisson et al. (1982); most coho were taken from scour pools of various configurations, a plunge pool, and several glides. Bank-full channel width, low flow pool dimensions, and residual pool depth (Lisle 1987) were measured for each unit. An inventory of all the LWD in the study reaches was conducted and the volume of each piece of wood within the bank-full channel and below the bank-full depth (corresponding to influence zones 1 and 2 of Robison and Bestcha 1990) was measured using large calipers. LWD count and volume were related to reach length. In addition, LWD loading was computed as the number of pieces per square metre of bank-full channel.

In 1991, in addition to measurements of the habitat units, the 500-m reach of stream immediately downstream from each habitat unit was also surveyed for correlation with unit-specific survival rates. This definition of reach was based on the finding that most juvenile coho salmon in two small Olympic Peninsula streams spent the winter within 500 m downstream of their location at the onset of winter (Scarlett and Cederholm 1984). However, some of the lowermost reaches were less than 500 m above the estuary and were only measured to the counting fence at the upper edge of the estuary. Owing to this variation in reach length, we standardized our reporting of habitat reach characteristics to 100 m length of stream (e.g., LWD volume per 100 m). Some habitat units were less than 500 m apart, thus the 500-m reaches below habitat units sometimes overlapped. In addition to reporting habitat complexity as units per length of stream, we also used pool spacing, a more common metric used by fluvial geomorphologists to assess channel characteristics (e.g., Keller and Melhorn 1978; Montgomery et al. 1995). Pool spacing was calculated by dividing the length of the reach by the average channel width and the number of pools. We also evaluated the role of LWD in controlling habitat complexity (i.e., units per lineal distance and pool spacing). Over 3 km of stream was inventoried in reach-level surveys in 1991. No habitat surveys were done for the units above the lake because we assumed that the fish would overwinter in the lake or the numerous riverine wetlands that could not be clearly associated with one habitat unit or another.

Results

Overall estimated survival differed between years (25.4% in 1990–1991 and 46.2% in 1991–1992, $\chi^2 = 76.06$, $p < 0.01$; Table 1), but no differences in growth or survival could be attributed to effects of tag type in either year (Peterson et al. 1994). As a result of these findings and because the mean length and weight of fish differed between years at the time of marking (length: $t = 8.49$, $p < 0.01$; weight: $t = 14.82$, $p < 0.01$) and at the time of smolting (length: $t = 11.58$, $p < 0.01$; weight: $t = 9.80$, $p < 0.01$), we pooled data by tag type but analyzed size and habitat effects within each year separately. More of the fish tagged above the lake in 1991 survived than did those tagged below it (56.7 vs. 44.1%). However, the difference in survival between years was significant, even when the data from fish above the lake were removed and only lower reaches were compared (25.4% in 1990–1991 versus 42.1% in 1991–1992, $\chi^2 = 43.77$, $p < 0.001$).

Fish in larger size-classes showed a higher survival rate than smaller fish in 1990–1991 ($\chi^2 = 15.40$, $p < 0.01$) but not in 1991–1992 ($\chi^2 = 0.98$, $p = 0.91$; Fig. 2). Similarly, the average size at tagging between nonsurvivors and survivors differed in 1990–1991 but not in 1991–1992 (Table 1). Fish from a given area of the stream maintained their relative size ranking within the population; smaller fish at the end of the summer period were generally smaller smolts (Fig. 3). However, the fish tagged upstream from William Symington Lake were smaller in the fall than fish tagged below the lake but grew considerably more than their downstream-dwelling counterparts over the winter and were significantly larger as smolts (Table 2, Fig. 3).

Survival of fish from discrete habitat units varied in both

Table 1. Relationship between size in early October and over-winter survival of juvenile coho salmon in Big Beef Creek, Washington.

	Survivors			Nonsurvivors		
Season	*n*	Length (mm)	Weight (g)	*n*	Length (mm)	Weight (g)
1990–1991	182	75.7±7.8**	4.50±1.54**	535	73.6±7.4	4.05±1.40
1991–1992	441	76.5±8.1	5.12±1.64	513	76.0±7.8	5.03±1.50

Note: Values are given as the mean ± standard deviation. **, $p < 0.01$ (unpaired *t* test).

Table 2. Size of juvenile coho salmon captured above William Symington Lake (lake fish) and below the lake in Big Beef Creek (creek fish) in the fall when they were tagged and in the spring when the survivors were recovered as smolts.

	Lake fish			Creek fish		
Season	*n*	Length (mm)	Weight (g)	*n*	Length (mm)	Weight (g)
Fall	134	69.8±9.3	4.00±1.80	820	77.3±7.2	5.25±1.45
Spring	76	129.3±9.8	20.89±4.78	362	107.0±9.1	11.85±3.24

Note: Values are given as the mean ± standard deviation. All differences were significant at $p < 0.001$ on the basis of unpaired *t* tests.

Fig. 2. Over-winter survival of juvenile coho salmon of different sizes tagged at the end of summer in Big Beef Creek below William Symington Lake in 1990 (solid bars) and 1991 (hatched bars).

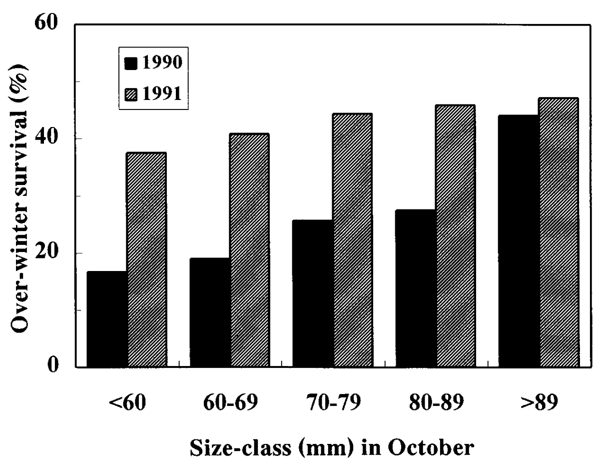
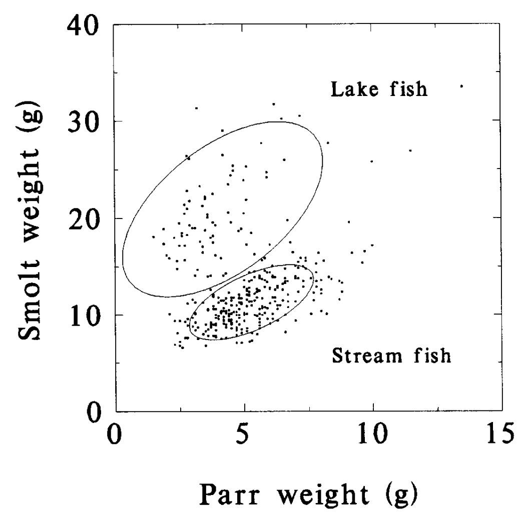


Fig. 3. Relationship between the weight of juvenile coho salmon in October 1991 and their weight as smolts in 1992. Individuals tagged above and below William Symington Lake are designated lake and stream fish, respectively. Ellipses are centered around the sample means and oriented along each axis of covariance.



years (1990–1991: $\chi^2 = 52.19$, df = 14, $p < 0.001$; 1991–1992: $\chi^2 = 51.55$, df = 20, $p < 0.001$). Habitat complexity, measured by variables in the individual habitat units, was poorly correlated with survival. No correlations were found with any of the variables tested in 1990–1991: depth and volume of the pool and volume and count of LWD. In 1991–1992 the volume and count of LWD in the unit showed weak positive correlations with survival (Table 3), but the other features of the units were not correlated with survival. However, survival was positively correlated with the number of habitat units below the tagging site, negatively correlated with pool spacing (Fig. 4), positively correlated with gradient and LWD volume and count, and negatively correlated with residual pool mean depth in the reach (Table 3). In both years, survival was positively correlated with distance from the estuary (Fig. 5). This relationship was calculated without the fish from the three habitat units above the lake that experienced relatively high survival rates (56.7% overall).

Stepwise multiple regression with number of habitat units per lineal distance, LWD frequency, and distance from the estuary as the independent variables indicated that survival was primarily controlled by distance ($r^2 = 0.77$). The addition of habitat unit frequency significantly increased explanatory power (multiple $r^2 = 0.84$), but LWD frequency made no additional statistical contribution to the model. Similar results were obtained when pool spacing was substituted for habitat units per lineal distance in the multiple regression (multiple $r^2 = 0.82$). Comparisons between habitat variables revealed significant ($p < 0.005$) correlations between habitat unit frequency and LWD frequency, volume, and loading, and distance from the estuary . Pool spacing was also significantly correlated ($p < 0.001$) with all measures of LWD abundance (e.g., Fig. 6) but not with distance from the estuary.

The median emigration dates were the 127th and 120th days of the year in 1991 and 1992 (i.e., 7 May and 30 April), respectively (Fig. 7). There was no clear relationship between smolt length and emigration date. However, the fish that had been tagged above the lake in 1991 were captured at the weir

Table 3. Significant relationships between habitat features, measured at the scale of habitat unit or reach, and the over-winter survival of juvenile coho salmon tagged in Big Beef Creek in October 1990 (15 units) and 1991 (18 units).

Habitat feature	Scale	Year	r^2	p	Intercept	Slope
LWD count	Unit	1991	0.23	0.04	44.16	0.11
LWD volume	Unit	1991	0.23	0.04	44.00	0.23
LWD count	Reach	1991	0.61	0.001	30.50	0.34
LWD volume	Reach	1991	0.45	0.002	35.36	0.47
Residual depth	Reach	1991	0.34	0.01	70.62	–36.74
Gradient	Reach	1991	0.76	0.001	20.03	24.27
Pool spacing	Reach	1991	0.27	0.03	69.89	–9.21
No. of habitat units	Reach	1991	0.77	0.001	16.26	5.06
Distance from weir		1990	0.57	0.001	13.68	0.0035
		1991	0.77	0.001	32.87	0.0029

Note: Only units below William Symington Lake are included. LWD, large woody debris.

Fig. 4. Relationship between over-winter survival of juvenile coho salmon in Big Beef Creek and pool spacing in the 500-m reach below the unit where they were captured. Habitat units above William Symington Lake were not included in the analysis. Different symbols indicate distance from estuary (see Figs. 5 and 1).

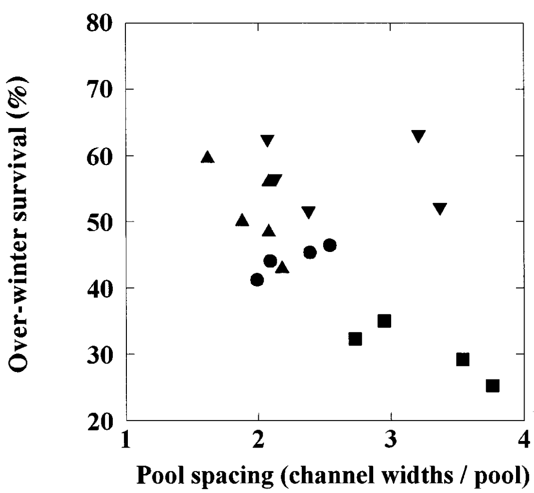
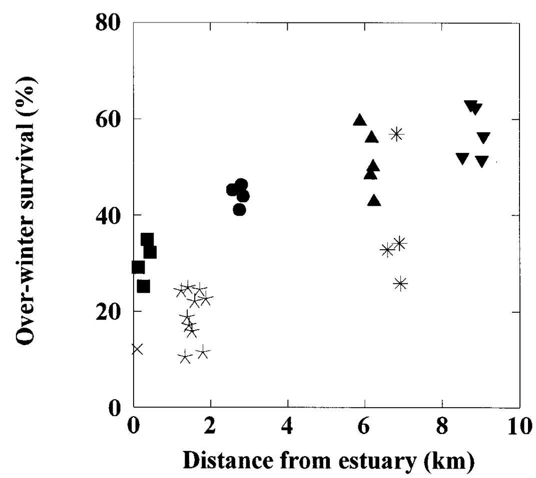


Fig. 5. Relationship between over-winter survival of juvenile coho salmon and the distance from the estuary (i.e., the smolt counting weir) of the unit in which they were caught at the end of the summer. Units from the three reaches sampled in 1990 are indicated with a cross and five- and eight-pointed stars; the four reaches sampled in 1991 are indicated with solid symbols. Different symbols refer to groups of fish tagged at various distances form the estuary (see Fig. 1). Habitat units above William Symington Lake were not included in the analysis.



later than those tagged in the stream (day of the year 124.8 ± 6.4 (mean ± SD) vs. 120.8 ± 8.0, $t = 3.74$, $p < 0.01$).

Discussion

The salient findings of this study were the positive correlations between survival and body size, distance from the estuary, and reach-scale habitat complexity, and the difference in survival between years. Hartman et al. (1987) reported that the interannual variation in average survival of coho in Carnation Creek, British Columbia, was related to body size, but limited data on individual fish from an ephemeral swamp did not support this pattern (Brown 1985). Recent data on PIT-tagged chinook salmon in the Snake River indicated that the larger fish at the time of tagging in the summer were more likely to be detected as downstream migrating smolts the following spring (Walters et al. 1994; Achord et al. 1995*a*, 1995*b*). Our results indicated that the fish that were large in October maintained their size advantage to the smolt stage and had a higher probability of survival. The exceptions to this pattern were the fish tagged above William Symington Lake. They were relatively small at the end of the summer (perhaps because water temperatures tend to be cooler than those below the lake; Williams et al. 1968) but were larger than average as smolts, indicating a higher growth rate than that of fish tagged below the lake, and they also had high survival rates. We cannot be certain where any of the fish actually spent the winter, but such rapid growth would be consistent with pond or lake residence (Peterson 1982; Swales et al. 1988; Irvine and Ward 1989). However, they might also have overwintered in wetlands above the lake. Our results are consistent with those of Williams et al. (1968), who reported that coho sampled in the stream above the lake in September were smaller (mean length 54 mm) than those caught in the lake (91 mm) or in the stream below the lake (60–78 mm) but that by spring the fish in the upper stream had equaled the size of fish in the lower stream.

The causal link between fish size and survival is unclear.

Fig. 6. Relationship between pool spacing and large woody debris (LWD) frequency in study reaches of Big Beef Creek surveyed in 1991.

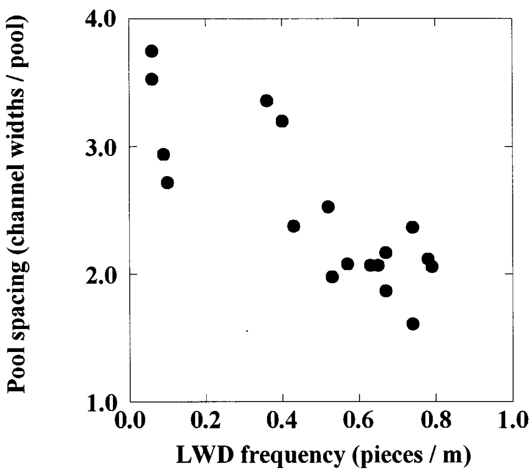
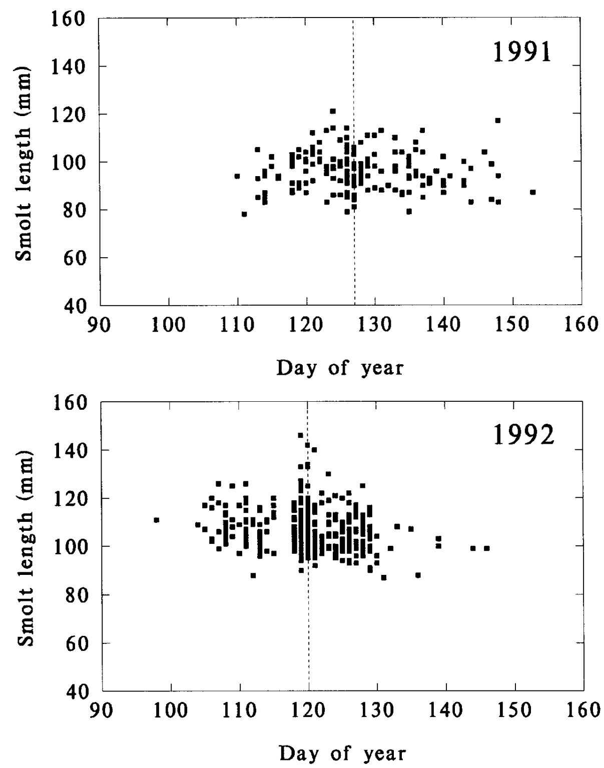


Fig. 7. Smolt length and date of migration of coho salmon tagged as underyearlings in Big Beef Creek. Broken lines indicate median migration dates. The 2-day gap in migration in 1992 resulted from retention of all fish without counting when tagging equipment malfunctioned.



Hunt (1969) attributed the positive relationship observed between brook trout (*Salvelinus fontinalis*) size and survival to energetic efficiency at low temperatures rather than size-selective predation. Experiments in semicontrolled settings with rainbow trout (*O. mykiss*) also related the higher survival of larger fish to relatively warm temperatures and the presence of rocky cover (which tended to elevate temperatures; Smith and Griffith 1994). We do not know the causes of mortality in Big Beef Creek, but the mild temperature regime (rarely below 4°C: Williams 1970) makes it unlikely that thermal stress was a major factor. Avian predation was observed in an experimental channel adjacent to the creek in the summer (Spalding et al. 1995), and the river otters present likely prey on salmonids as well (Dolloff 1993). Size-selective predation by birds, mammals, or fishes (e.g., sculpins, *Cottus* spp., or cutthroat trout, *Oncorhynchus clarki*) may have been responsible for the higher survival rate of larger salmon.

The size advantage of juvenile coho at the end of the summer may have ramifications for their entire lives. It initially affected their likelihood of over-winter survival and size as smolts. Marine survival is positively correlated with size within year-classes of coho salmon (Mathews and Ishida 1989; Holtby et al. 1990) and other salmonids such as chum salmon (*Oncorhynchus keta*; Healey 1982), sockeye salmon (Henderson and Cass 1991; Koenings et al. 1993), cutthroat trout (Tipping and Blankenship 1993), and steelhead trout (Ward and Slaney 1988; Ward et al. 1989). We did not observe a relationship between smolt length and date of capture at the weir. However, there is evidence from other years that large size is associated with early emigration from Big Beef Creek (Seiler et al. 1981, 1984), consistent with other studies of coho salmon (Irvine and Ward 1989) and anadromous brown trout (Bohlin et al. 1993). Marine survival is also strongly related to the time of seawater entry (e.g., coho, Bilton et al. 1982; Thedinga and Koski 1984; Morley et al. 1988), hence indirectly to smolt size.

Several factors may have affected the difference in survival between years. In 1991 we tagged fish above the lake, and they experienced particularly high survival rates. Even without these fish, however, the survival rate of fish from reaches below the lake was higher in 1991. The fish tagged were larger in 1991 than 1990, which might have improved their survival rate. However, for a given size-class, survival differed between years (Fig. 2), indicating that factors other than habitat conditions and fish size affected mortality. Environmental conditions varied between the years. Most notably, the maximum daily flow during the winter rearing period of the 1990 group was almost twice that experienced by the 1991 group (Lestelle et al. 1993). High flow could have resulted in either mortality within the river or displacement from it. In contrast to coastal systems such as Big Beef Creek, low winter flows have been indirectly linked to poor survival of Atlantic salmon in rivers experiencing very cold winters and low flow rates (Gibson and Myers 1988; Hvidsen 1993). We do not know which year's survival rate (if either) was typical of this stream, and the specific causes of mortality are not known. However, the survival rates (25 and 46%) were comparable with values from the literature reviewed by Murphy et al. (1984): Southeast Alaska, 26 and 35%; British Columbia, 35%; Washington, 31 and 80%; Oregon, 40, 51, 54, and 86%.

The second major finding was the relationship between habitat complexity (abundance of LWD and number of discrete habitat units per length of stream reach or pool spacing) at the end of the summer and over-winter survival. The affinity of coho salmon for woody debris increases in winter (Bustard and Narver 1975; Heifetz et al. 1986; Murphy et al. 1986;

Taylor 1988), but we did not assume that the salmon spent the winter in the habitat units where they were captured and released in October. Indeed, the strongest correlations with survival were not with the complexity of the fish's immediate environment (i.e., habitat unit) but rather with the 500 m below the capture point. Movement during winter is known in other salmonids (e.g., Atlantic salmon: Cunjak and Randall 1993) and coho salmon tend to move downstream in fall to overwinter in side channels, ponds, and sloughs (Carnation Creek: Brown and Hartman 1988; interior British Columbia: Swales et al. 1986; coastal Washington: Peterson 1982; coastal Oregon: Nickelson et al. 1992), though upstream movement from stream–estuary ecotones has also been documented (Murphy et al. 1984). Off-channel and side-channel habitat is limited in Big Beef Creek, and we assumed that the coho salmon survived the winter and smolted from main-channel habitat. The superior survival and growth of coho salmon marked above the lake is consistent with studies (e.g., Cederholm et al. 1988; Cederholm and Scarlett 1991) documenting excellent coho salmon over-winter growth and survival in small constructed ponds. However, the wetlands above the lake may also have provided suitable rearing locations. We assumed that the fish captured and released below the lake would not ascend the fishway into the lake because the fishway is designed to pass adults, not juveniles. However, 13 fish from the habitat unit closest to the lake displayed the high growth rate of "lake" fish, and we consider it possible that they moved upstream and overwintered in the lake or its associated wetlands.

One important factor that confounded our interpretation of the role of habitat complexity in over-winter survival was the tendency for simpler reaches (i.e., those with lower volumes of large wood and fewer habitat units per length of stream below them) to be situated near the mouth of the stream. Channelization in 1969 simplified the habitat in the lowermost 800 m of Big Beef Creek. Even though the stream soon began to reconfigure itself into the former channel pattern (Cederholm 1972), the lack of LWD may be a persistent effect. Fish moving downstream in fall from the lower reaches may have left the stream before they were able to find suitable habitat whereas fish starting farther upstream had a better chance of finding habitat before they reached the mouth of the stream. This would imply that the correlation of survival and habitat complexity resulted only from the location of the simple habitats in the lower part of the stream. However, Tschaplinski and Hartman (1983) reported that structurally complex reaches of Carnation Creek retained more juvenile coho salmon during the winter than simpler reaches, so our reaches in the lower portion of the stream might have produced higher survival rates had they been more complex.

We used linear regression to test for relationships of habitat features with salmon survival, but the underlying patterns are unlikely to be linear. Beyond some threshold, increasing habitat complexity and distance upriver would presumably not be associated with increased survival. The strong correlations between LWD abundance and habitat complexity are consistent with the established role of LWD in structuring stream channels (Bilby and Ward 1991; Montgomery et al. 1995). However, the multiple regression results indicated that survival was controlled more by habitat complexity than the LWD per se, consistent with observations by Shirvell (1990) and McMahon and Hartman (1989) that the behavior of coho salmon was keyed to the velocity regimes created by the LWD rather than the LWD itself.

In addition, there were two habitat features at the reach level whose significant correlations with survival were almost certainly spurious, artifacts of the covariation among features within Big Beef Creek. Gradient was positively correlated with survival and the mean depth of habitat units below the study unit was negatively correlated with survival, probably because the deeper, low-gradient lower portion of the stream was structurally simple and near the mouth. All other things being equal, we would expect low-gradient channels with deep pools to favor over-winter survival. The existence of these paradoxical relationships highlights the question of which stream habitat features best reveal the health of a stream and the effects of land management. We conclude that assessment and monitoring protocols should be organized to produce information at a spatial scale appropriate to the life-history traits of the animals and the covariation of physical features unique to each stream.

Emigration in winter from a stream the size of Big Beef Creek would normally lead fry into the main stem of a large river, whereas in Big Beef Creek they would enter directly into Hood Canal. Such fry might not survive but in any case would not be captured at the fence in spring and so would have been classified as mortalities. The ambiguity between premature emigration and mortality in our study highlights the overall uncertainty about the causes of winter mortality. Some combination of size-biased predation and resistance to displacement by floods may explain the superior survival of larger fish. It would require a study in a stream with a different configuration of habitat units or a detailed study of the movements of individual fish to disentangle the relationships between size, proximity to the stream's mouth, habitat complexity, and survival. However, in the absence of such information it seems prudent to assume that some aspect of habitat complexity enhanced the over-winter survival of coho salmon and that management practices should encourage continued functioning and succession of riparian forests (Beschta 1991) to maintain and enhance this complexity.

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