Importance of Smolt Size and Early Ocean Growth to Interannual Variability in Marine Survival of Coho Salmon (*Oncorhynchus kisutch*)[1]

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The importance of smolt size and early ocean growth to the marine survival of coho salmon was examined over a 17-yr period at Carnation Creek, British Columbia. Comparisons of overall marine survival were made both between-years, using two smolt age-groups of different mean sizes, and within-years using observed smolt size distributions and smolt size distributions back-calculated from the scales of returning adults. Large size did not confer a consistent survival advantage but large smolts did survive better in years when marine survival was relatively poor. Marine survivals were strongly correlated with early ocean growth as estimated by the spacing of the first five ocean circuli on the scales of returning adults. Marine survival and early ocean growth were positively correlated with ocean conditions indicative of strong upwelling along the northwest coast of Vancouver Island. Neither smolt survival nor early ocean growth were correlated with regional coho smolt production. Our observations suggest that interannual variability in smolt survival was being driven by ocean conditions that determined smolt growth rates which subsequently affected the susceptibility of smolts to a size-selective predator.

L'importance que revêtent pour la survie en mer du saumon coho la taille des saumoneaux de descente et leur croissance durant le début de leur séjour océanique a été étudiée sur une période de 17 ans à Carnation Creek, en Colombie-Britannique. Les comparaisons des taux de survie d'ensemble en milieu marin ont été effectuées à la fois entre les années en prenant deux groupes d'âge de saumoneaux de taille moyenne différente et à l'intérieur de chaque année sur la base des distributions de taille observées chez les saumoneaux de descente et calculées rétroactivement grâce aux écailles des adultes revenus. On a pu déterminer qu'une grande taille ne confère pas un avantage systématique du point de vue de la survie mais les grands saumoneaux ont néanmoins mieux survécu les années où le taux de survie en mer a été relativement faible. On a aussi pu constater une forte corrélation entre les taux de survie en mer et la phase initiale de croissance océanique telle qu'estimée en fonction de l'espacement des cinq premiers cercles océaniques sur les écailles des adultes revenus. Une corrélation positive a également été établie entre d'une part la survie en mer et les premiers stades de croissance dans l'océan et, d'autre part, des conditions océaniques révélant une forte résurgence d'eau froide de long de la côte nord-ouest de l'île de Vancouver. Ni la survie des saumoneaux de descente ni les premiers stades de la croissance océanique n'ont été mis en corrélation avec la production régionale de saumoneaux de descente coho. Nos observations donnent à penser que la variabilité inter-annuelle que l'on relève dans les taux de survie des saumoneaux de descente est surtout fonction de conditions océaniques ayant déterminé les taux de croissance des saumoneaux, ce qui s'est ensuite répercuté sur le degré auquel les saumoneaux ont été attaqués par un prédateur choisissant ses proies en fonction de leur taille.

Considerable mortality of Pacific salmon (*Oncorhynchus* sp) smolts occurs during a brief period after their entry into the ocean (Parker 1971; Mathews and Buckley 1976; Walters et al. 1978; Healey 1982). Several hypotheses have been proposed to explain variations in smolt survival. The "ocean–productivity" hypothesis links periodically unfavorable ocean conditions with slow fish growth and poor fish condition, and thus greater vulnerability to predation (Fisher and Pearcy 1988). Correlations between smolt survival and ocean upwelling in the first year of ocean residence are cited in support of this hypothesis (Scarnecchia 1981; Nickelson 1986). The "density–dependence" hypothesis relates the entry of large

numbers of smolts into the ocean with food limitation, slowed growth and increased predation or starvation (Foerster 1954; Peterman 1978; Walters et al. 1978). The "predation–intensity" hypothesis relates variations in smolt survival solely to levels of predation. Predation levels can vary because of a functional response by the predator to changes in the abundance of alternative prey species (Fisher and Pearcy 1988), because of changes in the distributions of predators or their prey (Ware and McFarlane 1988), or because of absolute changes in the abundance of predators.

Both the "ocean-productivity" hypothesis and the "density-dependence" hypothesis assume that a significant component of marine mortality of smolts is size-dependent. Consequently, a corollary of both hypotheses is that smolt mortality is inversely

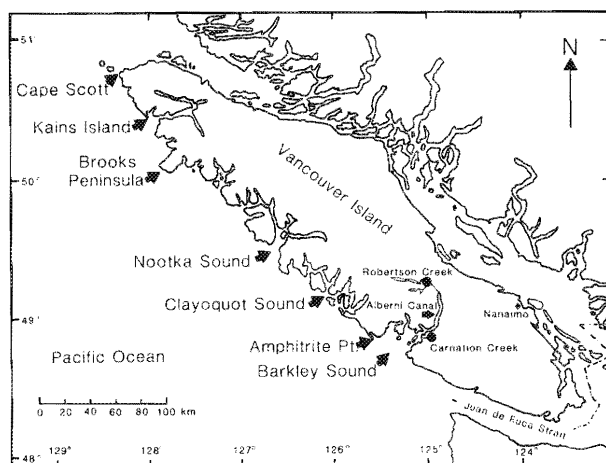*Can. J. Fish. Aquat. Sci., Vol. 47, 1990*

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FIG. 1. The west coast of Vancouver Island.

related to growth rate. In contrast, the "predation–intensity" hypothesis as presented by Fisher and Pearcy (1988) explicitly states that marine survival of smolts is independent of smolt size and growth and thus that smolt survival is independent of smolt densities and the direct effects of variable ocean productivity.

In this paper we describe relationships between smolt survival, smolt size, and early marine growth for a wild coho salmon (*Oncorhynchus kisutch*) population over the period 1971–1987 (smolt years). This examination will discriminate between the "predation–intensity" hypothesis on one hand and the "ocean–productivity" and "density–dependence hypotheses" on the other. To discriminate between the latter two hypotheses, we will test for density–dependent effects on survival and growth and describe relationships between smolt survival, early ocean growth, and oceanographic variables thought to be indicative of ocean conditions in the ocean rearing area.

Methods

Study Site

Carnation Creek is a small stream on the west coast of Vancouver Island that drains into Barkley Sound (Fig. 1). The stream supports a run of several hundred coho salmon and produces from 2500–4500 smolts·yr^{-1}. On average 75% (range 43–97%) of the smolts produced spend 1 yr in the stream (1^+ smolts), the remainder spend 2 yr (2^+ smolts). Beginning in 1970, Carnation Creek was the site of a long-term study of the effects of clear-cut logging on salmon production. Extensive descriptions of the study are available (Chamberlain 1987). Most of the fisheries data used here have been summarized by Andersen (1983, 1984, 1985, 1987; B.C. Andersen, unpubl. data). The effects of logging on the Pacific salmon populations of the stream have been summarized by Holtby (1988) and Holtby and Scrivener (1989).

Fish Enumeration and Aging

Adult coho salmon were captured at a fence located 75 m upstream of the mean high tide level from late September through early March from 1972 through 1988. In the fall of 1971, only a portion of the fish were captured at a fence and total escapement was estimated by mark-recapture. All fish,
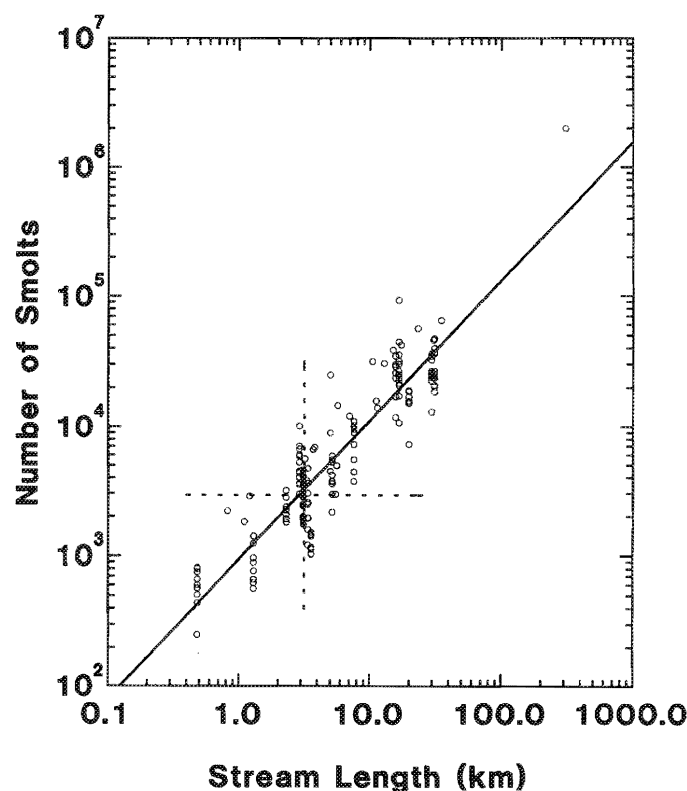

Stream Length (km)

FIG. 2. Coho salmon smolt production as a function of stream length for 36 streams on the west coast of North America. For most streams several years of data were available. The intersection of the dashed lines indicates the average smolt production at Carnation Creek before 1976.

including jacks (males that return after 6 mo in the ocean compared to the usual 18 mo), were measured to the nearest cm, sexed, and passed upstream of the fence. Between eight and 30 scales were taken from the preferred area (left side, just behind the dorsal fin and just above the lateral line; Clutter and Whitesel (1956). Because of the proximity of the counting fence to the ocean and immature condition of most adults, scale resorption was minimal. Two or three selected scales were mounted on gummed cards. Plastic impressions of the scales were made using standard procedures (Clutter and Whitesel 1956). Freshwater ages (either 1 or 2 yr, denoted by 1^+ or 2^+, respectively) and marine ages (either zero or one, respectively indicating 6 or 18 mo spent in the ocean) were determined by examining those impressions under $75 \times - 150 \times$ magnification. Fish that could not be aged, either because the freshwater zone of all scales taken were regenerated, or because the fish escaped during sampling, were apportioned between the two freshwater age-classes, according to the measured age composition by sex and marine age. In all years but 1971, at least 90% of the fish were aged.

Fish from Carnation Creek are caught in their second summer of ocean life in an intensive troll fishery off the west coast of Vancouver Island and the Queen Charlotte Islands (Argue et al. 1987). Jacks are not subject to the fishery and it is possible that more 2^+ than 1^+ smolts became jacks because of their larger size (Bilton et al. 1982). Consequently, an age composition at return calculated by summing jack and large adult returns may have been biased toward the older age-group. Since exploitation rates of Carnation Creek coho salmon were not measured, we assumed that they were the same as exploitation
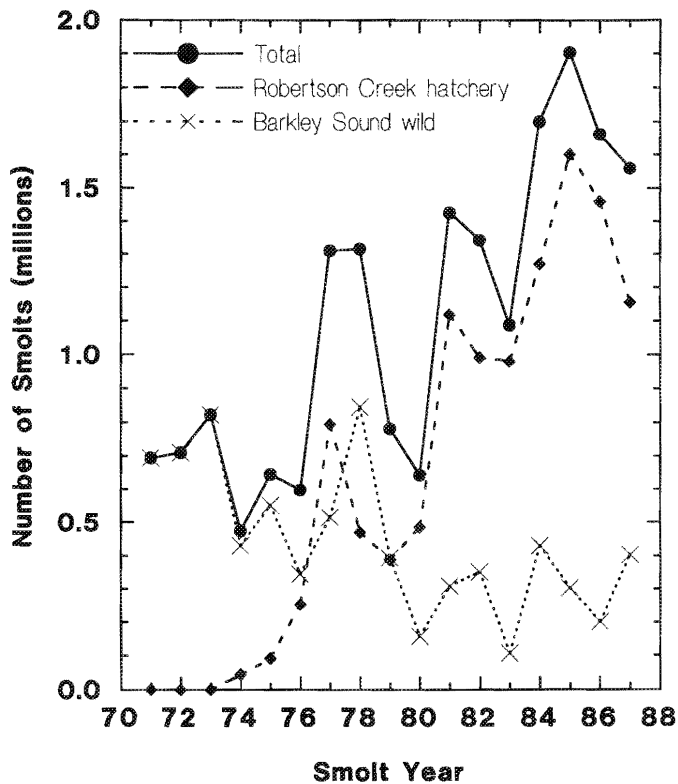
FIG. 3. Components of the estimated total coho salmon smolt production in Barkley Sound 1971–87.

FIG. 4. (A) Numbers of smolts and (B) smolt weights by freshwater age group vs. smolt year.

rates measured for coho salmon at the nearby Robertson Creek hatchery from (return year) 1975 to 1988. Exploitation rates were obtained from the Department of Fisheries and Ocean's mark-release database. Exploitation rates for the three return years prior to 1975 were set equal to the overall average exploitation rate of 65%. Female and non-jack male returns were expanded by the inverse of one minus the estimated exploitation rate before summing with the jack returns from the previous year. The age composition of all returning fish (adult females, jack, and adult males) was then calculated using the expanded numbers.

Outgoing smolts were captured in the spring at the same fence. In most years the forklengths (FL) of more than 95% of smolts were measured to the nearest mm. In 1971, 71 of the smolts were measured. At 7–10 d intervals sub-samples of smolts were weighed to the nearest 0.05 g and scales were taken from the preferred area, mounted between glass slides, and later examined under magnification to determine freshwater age. The age composition of the run was calculated by applying the proportion in the two age-classes to the total run in size-classes of approximately 5 mm. In many years, and particularly in later ones, scales from smaller fish (<70 mm) were under-sampled because their age was known with near certainty. At least 2%, and in most years 10%, of the smolts were aged.

Marine survivals of smolts by freshwater age-group and smolt year were calculated by dividing the expanded return by the smolt number. The arithmetic difference between the marine survivals of the 2^+ and 1^+ smolts of the same smolt year was termed the "2^+ survival differential," and was used to examine under what conditions survivals of the two age-groups differed. The age compositions of the smolts and adults were expressed as the proportions comprised of the younger freshwater age group (age 1^+).
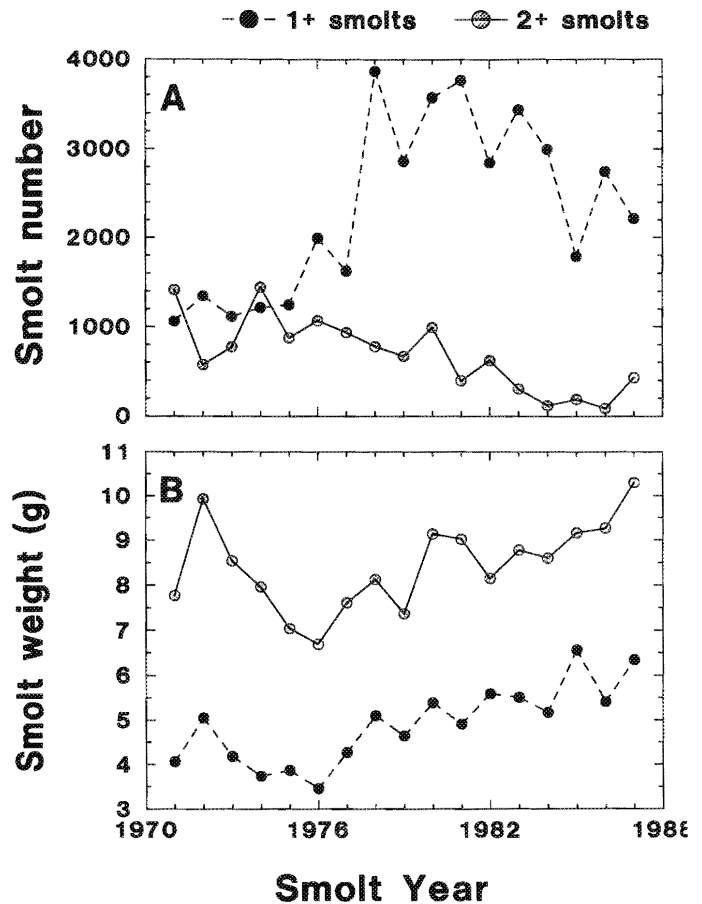
Back-Calculation of Smolt Size from Adult Scales

A demarcation between the freshwater and marine zones can usually be readily seen on scales of adult coho salmon. Circuli in the marine zone are further apart and more robust than those in the freshwater zone, and the two regions are usually separated by a "saltwater entry" check consisting of several fine and closely spaced or intertwined circuli. We used many simultaneous examinations of smolt scales and adult scales from the same cohort to learn how to properly identify the demarcation region. We then examined smolt scales magnified 75 ×, determined freshwater age, and measured the scale radius (the origin to the scale edge) to within 0.01 mm along an axis 30° to the anterior-posterior axis. At least two scales were measured per fish and the scale measurements were recored along with the age and FL (in mm). A total of 1210 scales was examined (44 to 146 per year for 14 yr). Forklength was regressed on scale radius by year and by freshwater age-class (1^+ or 2^+ yr old). A similar procedure was followed with the adult scales: two scales were examined per fish, the radius was measured along the same 30° axis, and the smolt FL was calculated from the average radius. All adult scales for which a freshwater age could be determined were processed. Adult scale radii were corrected upward by 2.0% to adjust for shrinkage occurring during scale preparation (Rankis 1987). Frequency distributions of smolt sizes based on back-calculation were corrected for the troll fishery harvest as described for the adult age composition. It uncorrected for the fishery harvest, then the back-calculated distribution of smolt sizes could have been biased toward larger
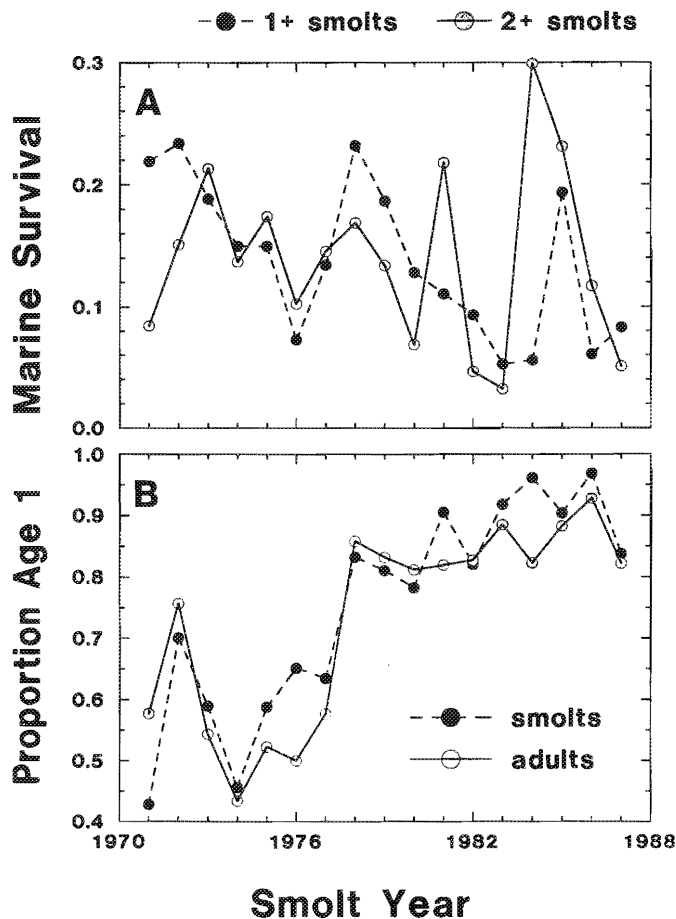
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FIG. 5. (A) Marine survival by freshwater age group and (B) proportion of freshwater age 1^+ fish in smolts and adults vs. smolt year.

smolts. Mean smolt sizes derived from the observed and back-calculated size distributions were compared with t-tests. Adult scales from smolt years 1974, 1977, and 1980 were not processed.

Determination of Effects of Smolt Size on Smolt Survival

The effect of smolt size on survival was first examined by comparing, within smolt years, the marine survivals of the age 1^+ and age 2^+ smolts. We used paired t-tests to compare the marine survivals of age 1^+ and age 2^+ smolts and the proportion of age 1^+ fish in the smolts and returning adults. We regressed survivals of both age-groups on smolt weight to test for an overall effect of size on survival. Although these tests assumed that the only difference between the two age-groups of smolts was size (i.e. there were no behavioural or physiological differences due to age), they required only that fish were correctly aged. The second approach consisted of back-calculating smolt size from measurements taken from adult scales and comparing, within smolt years, the observed size distribution with the expected distribution based on the smolt size-frequency distribution. The effects of smolt size on survival within-years were estimated by regressing smolt survivals on smolt FL within 5 mm length-classes. Length-classes were excluded when observed returns were less than five fish or where the smolt survival was undefined (observed return >0 when expected return = 0). The slope of the regression line ($\beta_{survival}$) indexed the effect of smolt length on survival. A positive slope indicated that survival increased with increasing
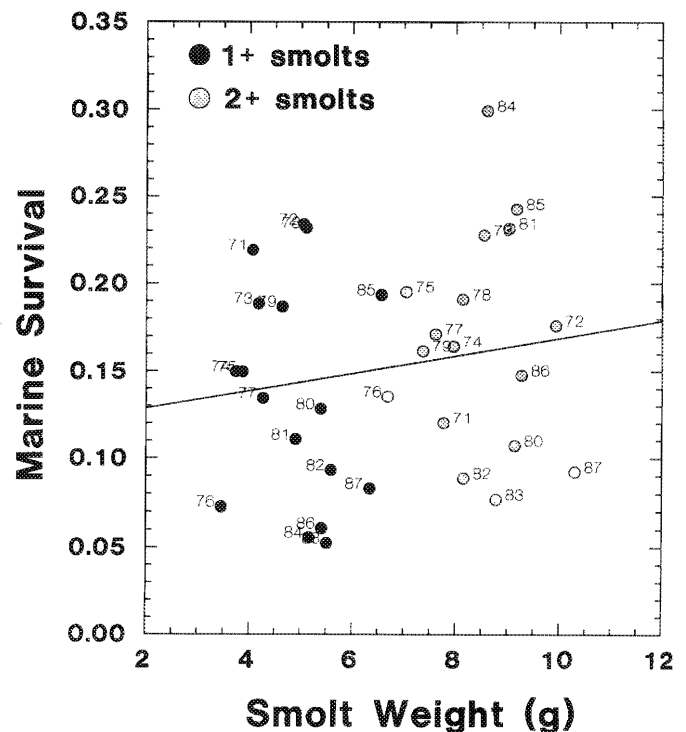

FIG. 6. Marine survival versus smolt weight for both freshwater age groups with fitted regression line.

smolt length and the steeper the slope, the greater was the survival advantage of larger size.

Marine Growth Rates

Estimates of early marine growth were made by measuring the average inter-circular distance over the first five ocean circuli. Inter-circular distances were measured at the same time other scale measurements were taken. Inter-circular distances averaged over the first 2–10 circuli were very similar. Inter-circular distance is correlated with growth rate over an approximately 60-d period after ocean entry (Fisher and Pearcy 1988).

Juvenile Coho Smolt Production in Barkley Sound

No direct estimates of coho smolt production for the Barkley Sound region were available. Average wild production of coho salmon from the region was estimated by first predicting average smolt production for each of the 62 streams in the region (Brown et al. 1987) with the relationship:

(1) $N_{smolts} = 941.4 \times$ stream length $(km)^{1.074}$ $(n = 168,$
$$r^2_{adjusted} = 0.84; \text{Fig. 2}).$$

The relationship was determined from data presented by Armstrong and Argue (1977), Argue et al. (1979), Holtby and Hartman (1982), and Baranski (1989). Inter-annual variability in that average was estimated by using the process-model of smolt production developed for the Carnation Creek population (Holtby 1988; Holtby and Scrivener 1989). The model predicted smolt production for Carnation Creek in the absence of logging for each smolt year between 1971 and 1987. Predicted smolt productions were divided by the overall mean predicted smolt production from Carnation Creek to give annual scaling factors. The estimated average smolt production from the region was then scaled to give an estimated wild smolt production by

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smolt year (Fig. 3). Beginning in 1974, a hatchery on Robertson Creek released up to 1.6 million coho smolts into the Alberni Canal at the head of the Sound. Hatchery production and estimated wild production were summed to give an estimated total smolt production (Fig. 3).

The reliability of our estimation procedure is uncertain, but we think that it should have revealed significant trends in wild smolt production for the following reasons. First, the relationship between stream length and average smolt production (Eq. 1) is strong and predicts average smolt production from Carnation Creek accurately. Carnation Creek is typical in size of streams in the Barkley Sound area. Second, the process models (Holtby 1988; Holtby and Scrivener 1989) have accurately predicted overall trends in coho catch off Vancouver Island over the period 1960–79 (Holtby and Scrivener 1989). Holtby and Scrivener (1989) concluded that the process model had captured the important components of interannual variability. Third, the abundances of juvenile coho salmon in four streams in the Barkley Sound region, including Carnation Creek, covaried over a 12-yr period (Holtby et al. 1984), suggesting that factors determining coho abundance in those Barkley Sound streams were operating on a regional scale.

Ocean Environment Data

Thomson et al. (1989) have characterized the physical oceanography off the west coast of Vancouver Island with four temporal domains. During the winter domain, from October through February, prevailing winds from the southeast and efflux of freshwater from the coastal inlets combine to produce a broad coastal current flowing poleward. Sometime during February through May, the spring transition domain, prevailing winds switch to the northwest and freshwater outflow from the inlets is reduced. Shelf-break currents along the continental margin are established flowing counter to the Vancouver Island Coastal Current. The coastal current continues to flow poleward over the continental shelf, driven by Fraser River outflows through the Juan de Fuca Strait (Thomson et al. 1989). Simultaneously, conditions favourable to upwelling are established along the continental margin. Early and abrupt transitions weaken the coastal current and may lead to increased transport of upwelled water onto the continental shelf north of Barkley Sound. Late or sporadic transitions prolong the flow of southerly surface waters poleward in the coastal current (Thomson et al. 1989). From May through September, the coastal current is driven by outflow from the Juan de Fuca Strait. To the north of Barkley Sound, the coastal current prevents onshore transport of water upwelling along the shelf-break. The summer domain is also characterized by strong upwelling off the northwest tip of Vancouver Island and transport of the upwelled water transported southward by a shelf-break current flowing between Cape Scott and the Brooks Peninsula. Interactions between this current and the poleward flowing coastal current are poorly understood (Thomson et al. 1989). During the fall transition domain from September through October, conditions of the winter domain are reestablished.

Peak smolt emigration from Carnation Creek occurs in late April and early May (Holtby et al. 1989), simultaneously, or as much as 12 wk after the spring transition. Coho smolts originating in Barkley Soud are thought to migrate northward along the coast of Vancouver Island reaching the northwest tip of the island within 3 mo of leaving Barkley Sound (K. Groot, Pacific Biological Station, Nanaimo, B.C., pers. comm.). Based on the oceanography of the coastal waters and the migration timing and pathways of Barkley Sound coho salmon, we examined correlations between marine survivals and growth rates and four time series of sea-surface salinity and temperature data from the Amphitrite Point and Kains Island lighthouses (Fig. 1; Giovando 1985; D. Blackbourn, Pacific Biological Station, Nanaimo, B.C., pers. comm.) and two time series of the coastal upwelling indices at points off the west coast of Vancouver Island. The timing and abruptness of the spring transition were indexed with salinities and temperatures at Amphitrite Point during May and by the magnitude of the coastal upwelling index at 48°N, 125°W during May (Bakun 1973; Mason and Bakun 1986; D. Mallicoate, Pacific Fisheries Environmental Group, N.M.F.S., P.O. Box 831, Monterey, CA 93942, pers. comm.). Relatively high salinities, low temperatures and large upwelling indices would indicate an early spring transition, a weak coastal current during the transition, and cross-shelf transport of water upwelled along the shelf margin. We hypothesized that those conditions should have resulted in favourable growth conditions for salmon smolts entering Barkley Sound and migrating north during May. Ocean conditions during the coho salmon's first summer were indexed by sea-surface salinities and temperatures at Kains Island (Fig. 1) and by the magnitude of

TABLE 1. Comparisons of observed mean smolt forklengths (FL in mm) with expected mean FL back-calculated from adult scales. H_0: no difference in mean sizes; *$P<0.05$; **$P<0.01$; ***$P<0.001$.

Smolt year	Age 1$^+$ FL (mm)			Age 2$^+$ FL (mm)			Overall FL (mm)		
	Observed		Expected	Observed		Expected	Observed		Expected
1971	74.3	>***	70.7	96.7	=	96.3	83.8	=	81.5
1972	79.9	<**	82.2	106.1	=	107.2	86.3	=	88.3
1973	75.5	=	75.1	94.4	<***	97.6	84.1	=	85.4
1975	80.6	>***	73.6	92.4	<**	94.7	86.2	>**	83.7
1976	80.5	>***	71.5	97.9	>***	88.0	89.2	>***	79.7
1978	84.0	=	83.5	98.7	=	100.1	86.1	=	85.9
1979	78.1	<***	80.6	97.4	=	96.3	81.3	<***	83.2
1981	87.3	>***	82.5	100.8	<*	104.2	89.7	>***	86.4
1982	86.8	=	86.9	105.8	>	100.1	90.0	=	89.1
1983	90.8	>***	88.1	98.0	<*	103.1	91.6	>***	88.1
1984	90.4	>***	84.2	102.3	=	102.5	92.5	>***	87.5
1985	91.0	=	92.0	101.2	=	105.6	92.2	<*	93.6
1986	91.8	>***	85.6	106.8	=	105.0	92.9	>***	87.0
1987	93.7	=	95.4	111.6	=	114.1	96.9	=	98.7

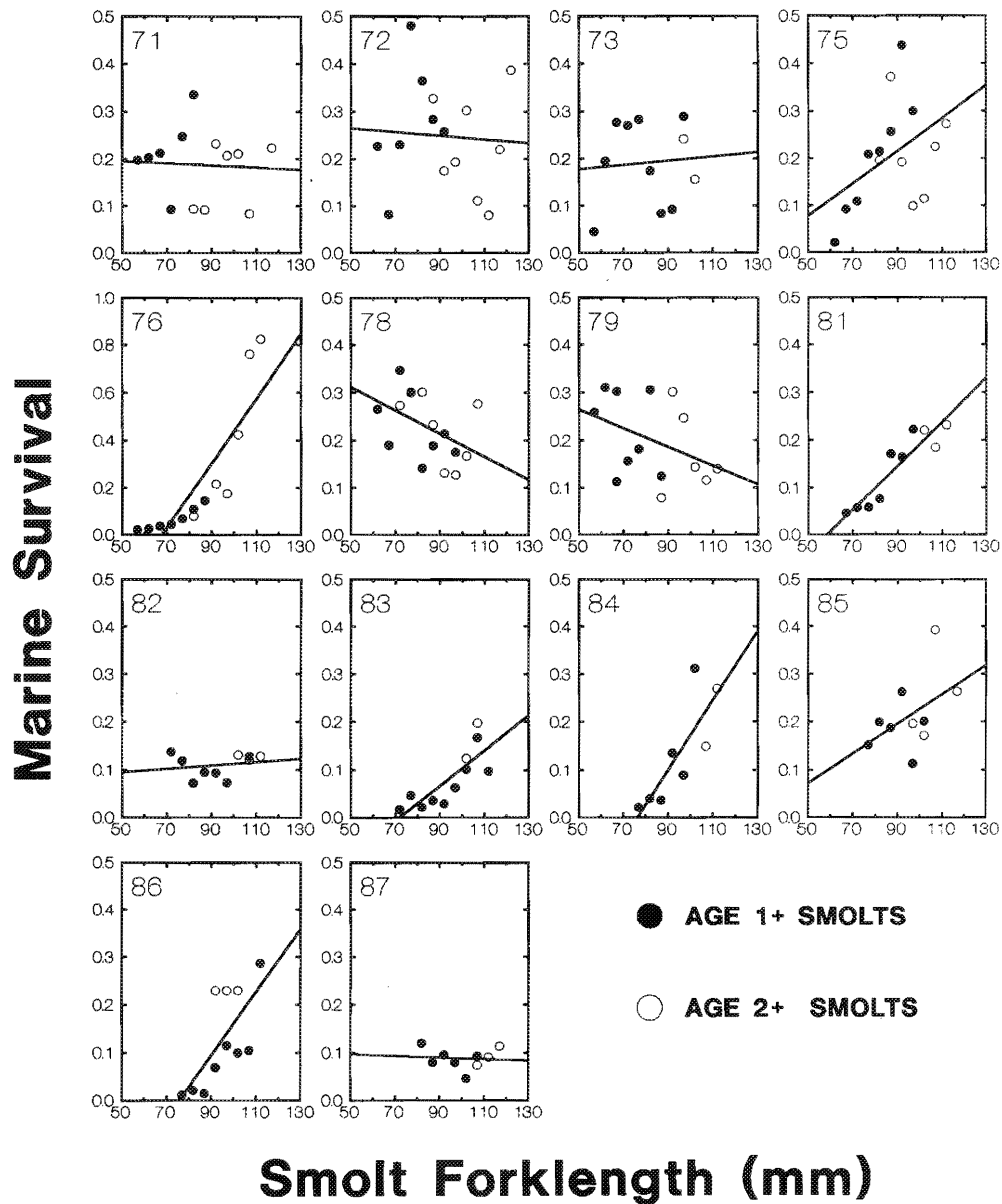*Can. J. Fish. Aquat. Sci., Vol. 47, 1990*

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FIG. 7. Marine survivals vs. smolt forklength in 5 mm FL classes. Regression lines shown were fitted to survival data for both freshwater age groups.

coastal upwelling at 51°N, 131°W, over the period June through August inclusive. We hypothesized that relatively strong upwelling coupled with onshelf transport of upwelled water indicated by high salinities and low temperatures near shore should have indicated favourable growth conditions for juvenile salmon off the west coast of Vancouver Island north of Barkley Sound. For both the spring and summer environmental time series, the averaging periods correspond to the approximate location of smolts migrating northward along the coast of Vancouver Island to rearing areas off the northwest coast of Vancouver Island.

Data Relevant to the Predation Intensity Hypothesis

If variation in predation intensity was an important factor in determining interannual variation in coho salmon survival then ecologically similar species of the same size and resident on the continental shelf should have been similarly affected. In

Barkley Sound, juvenile coho salmon are often found associated with schools of the considerably more abundant Pacific herring (*Clupea harengus pallisi*; K. Groot, Pacific Biological Station, Nanaimo, B.C. V9R 5K6, pers. comm.). Age 1 and 2 herring and coho salmon in thir first ocean summer are approximately the same size and probably have similar diets (Hourston 1959; Healey 1976, 1978). Thus, juvenile coho salmon may be ecologically similar to herring over their first few months in the ocean. Pacific herring are an important prey species of the major piscivorous fish on the west coast, and in particular Pacific cod (*Gadus macrocephalus*, Walters et al. 1986) and Pacific hake (*Merluccius productus*, Ware and McFarlane 1988).

Changes in the abundance of Pacific herring off the west coast of Vancouver Island are relevant to our thesis because it is believed that declines in herring numbers since the mid-1970's were the result of increased predation pressure (Ware and McFarlane 1988). Predation pressure has increased either

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TABLE 2. Regression of marine smolt survivals in 5 mm FL intervals on the mid-points of the intervals. r^2 has been adjusted for the degrees of freedom. P is the probability that the slope ($\hat{\beta}_{survival}$) is different from zero.

| Smolt year	Age 1+				Age 2+				Overall			
	$\hat{\beta}_{survival}$	n	P	$r^2_{adjusted}$	$\hat{\beta}_{survival}$	n	P	$r^2_{adjusted}$	$\hat{\beta}_{survival}$	n	P	$r^2_{adjusted}$
1971	0.0040	6	0.34	0.032	0.0024	7	0.36	0.002	−0.0002	13	0.86	0.0
1972	0.0045	7	0.38	0.0	0.0003	8	0.94	0.0	−0.0004	15	0.83	0.0
1973	0.0006	9	0.82	0.0	—	2	—	—	0.0005	11	0.82	0.0
1975	0.0098	8	0.002	0.81	−0.0010	7	0.81	0.0	0.0034	15	0.10	0.14
1976	0.0041	7	0.002	0.86	0.0269	6	<0.01	0.81	0.0136	13	0.71	<0.001
1978	−0.0027	8	0.23	0.10	−0.0030	8	0.21	0.13	−0.0024	16	0.15	0.08
1979	−0.0030	8	0.39	0.0	−0.0021	6	0.67	0.0	−0.0020	14	0.09	0.16
1981	0.0061	7	0.002	0.85	—	3	—	—	0.0046	10	<0.001	0.83
1982	−0.0004	7	0.68	0.0	—	3	—	—	0.0004	10	0.58	0.0
1983	0.0029	9	0.009	0.60	—	2	—	—	0.0037	11	0.003	0.60
1984	0.0098	6	0.041	0.61	—	2	—	—	0.0073	8	0.013	0.62
1985	0.0004	6	0.90	0.0	0.0050	4	0.57	0.0	0.0031	10	0.16	0.13
1986	0.0063	8	0.007	0.69	—	3	—	—	0.0066	11	0.016	0.44
1987	−0.0015	6	0.25	0.14	—	3	—	—	−0.0002	9	0.82	0.0
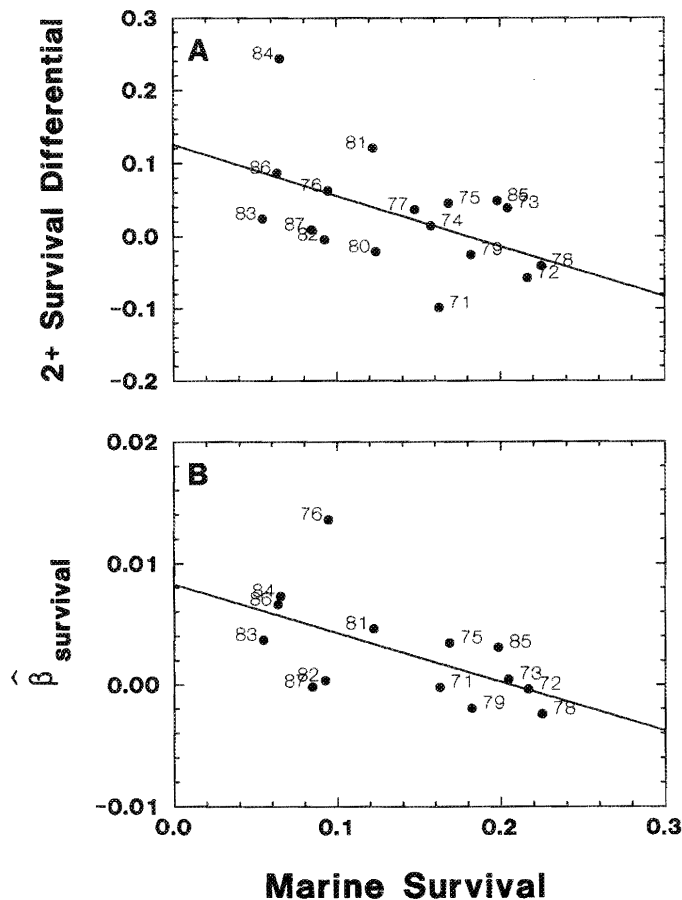
FIG. 8. (A) 2+ survival differential and (B) $\hat{\beta}_{survival}$ (both age groups) vs. marine survival for both freshwater age groups combined. Fitted lines are regression models 1 and 2, Table 3.

because of northward range extensions of hake associated with rising ocean temperatures, or because of increased abundances or predation rates of hake and other piscivorous fishes. Furthermore, Ware and McFarlane have calculated that the biomass of piscivorous fishes was sufficient to have accounted for all of the annual mortality in age 1 and older herring. Although salmon smolts are not known to be an important prey species of the above fish (e.g. Outram and Haegele 1972), the relative scarcity of juvenile salmon compared to herring would make it unlikely that salmon would constitute a significant fraction of any of the above piscivores' diets. Even if juvenile salmon were an incidental prey species, there was sufficient predator biomass to have caused substantial mortality of Carnation Creek coho salmon smolts.

We therefore compared the marine survivals of smolts with an index of age 1 and 2 herring survivals derived from the data of Haist et al. (1987) and Haist and Schweigert (1990). Age-specific herring abundances for the southwest coast of Vancouver, including Barkley Sound, were estimated using an age-structured model (Fournier and Archibald 1982; Stocker et al. 1983; Haist and Schweigert 1990). The abundance of age 1 herring was not measured but was back-calculated from measured abundances of age 2 and older herring using assumed constant natural survival rates. Consequently, survival rates of age 1 and 2 herring fluctuate around the assumed natural survival rate and must be considered as an index of survival only. The predation-intensity hypothesis would be supported if herring and salmon survival rates covaried.

Results

Importance of Smolt Size

Prior to clear-cut logging in the watershed (pre-1977 smolt year), Carnation Creek produced roughly equal numbers of age 1+ and age 2+ smolts (Fig. 4A). After 1977, the numbers of age 2+ smolts steadily declined, and from 1978 to 1987 at least 90% of the smolts were aged 1+. The 2+ smolts were, on average, longer and heavier than the 1+ smolts (Fig. 4B).

If smolt size was an important determinant of early marine survival and assuming that the two age-groups of smolts differed only in size, then 2+ smolts should have consistently survived better than 1+ smolts compared within smolt years. Although, on average, marine survivals of the 2+ smolts (average: 16.6%; range: 7.7–29.9%) were greater than those of 1+ smolts (average: 13.8%; range: 5.3–23.4%; Fig. 5A), the difference was not statistically significant (paired t-test: $t = -1.52$, df = 16, $P = 0.15$). The proportion of 1+ fish in the adults (average 0.730) was not significantly different from the same proportion in the smolts (average 0.752; paired t-test: $t = 1.33$, df = 16, $P = 0.17$; Fig. 5B). In addition, there was no significant

TABLE 3. Regression models referred to in text. P is the probability that the slope is different from zero. $\Delta d_{circulus}$ is the average inter-circular spacing over the first five ocean circuli, and is a measure of early ocean growth rate. SSSal is the mean sea-surface salinity at Kains Island from June through August.

| Regression model	$r^2_{adjusted}$	P	n
1. 2^+ survival differential $= 0.125 - 0.697 \times$ marine survival	0.21	<0.05	17
2. $\beta_{survival} = 0.00828 - 0.0403 \times$ marine survival	0.23	<0.05	14
3. 2^+ survival differential $= 0.137 - 0.787 \times$ age 1^+ marine survival	0.37	<0.01	17
4. $\beta_{survival} = 0.00840 - 0.0413 \times$ age 1^+ marine survival	0.3	0.01	14
5. Age 1^+ marine survival $= -0.838 + 26.3 \times \Delta d_{circulus} 1^+ (mm)$	0.77	<0.0001	14
6. Age 2^+ marine survival $= 0.174 - 0.101 \times \Delta d_{circulus} 2^+ (mm)$	0.00	≈ 1	14
7. Marine survival $= -0.695 + 22.0 \times \Delta d_{circulus} (mm)$	0.73	<0.0001	14
8. 2^+ survival differential $= 0.908 - 23.1 \times \Delta d_{circulus} (mm)$	0.41	<0.01	14
9. $\beta_{survival} = 0.0439 - 1.09 \times \Delta d_{circulus} (mm)$	0.33	<0.05	14
10. 2^+ survival differential $= 0.947 - 24.6 \times \Delta d_{circulus} 1^+ (mm)$	0.42	<0.01	14
11. $\beta_{survival} = 0.047 - 1.20 \times \Delta d_{circulus} 1^+ (mm)$	0.37	<0.05	14
12. $\Delta d_{circulus} (mm) = 0.00445 + 0.000368 \times FL (mm)$	0.40	<0.0001	877
13. Marine survival $= -1.86 + 0.0636 \times SSSal (‰)$	0.59	0.0005	17
14. $\Delta d_{circulus} (mm) = -0.0364 + 0.00236 \times SSSal (‰)$	0.47	0.005	14
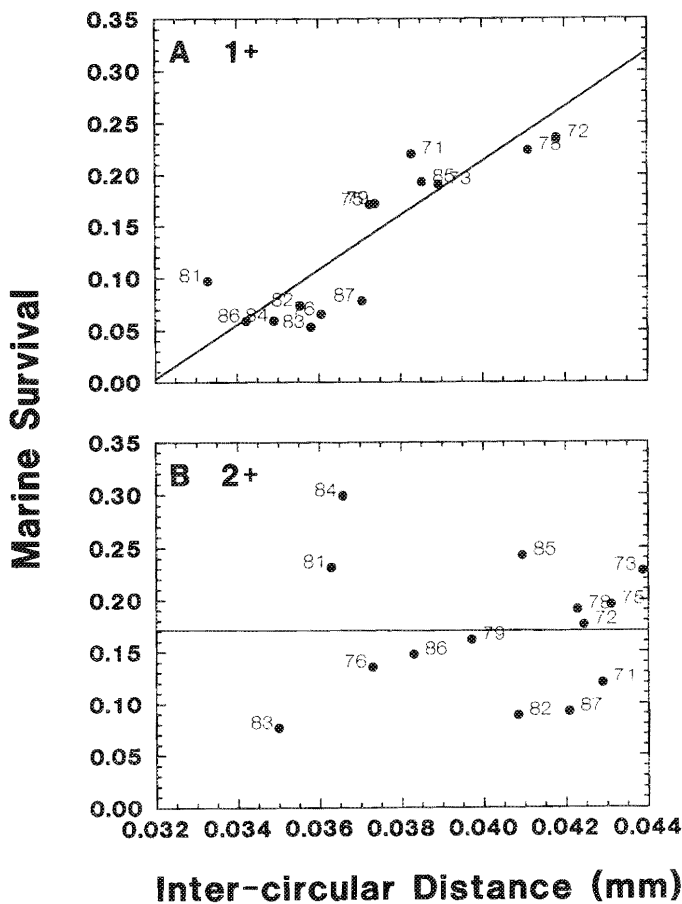
FIG. 9. Marine survival of (A) age 1^+ and (B) age 2^+ smolts vs. average inter-circular distance. Fitted lines are regression models 5 and 6, Table 3.

relationship between marine survival and smolt size ($r = 0.162$, $n = 34$, $P = 0.36$; Fig. 6).

We could not fully test our assumption that age 1^+ smolts differed only in size from 2^+ smolts, but we did examine two factors which could have contributed to different marine survivals, independent of smolt size. First, emigration dates could have been different for the two age-groups, leading to different marine survivals (Bilton et al. 1982). Holtby et al.

(1989) found that the median date of age 1^+ smolt emigration tended to be 0–6 d before the median data for age 2^+ smolts from 1971 to 1977. From 1978 to 1987 the median dates were on average the same. In view of the inter-quartile range in emigration date of 12–31 d, differences of a few days in the median emigration dates of the two age-groups were probably of no significance. Second, age 2^+ smolts may have grown more slowly in the ocean than age 1^+ smolts since they had grown more slowly in freshwater. Slower growth in the ocean might have diminished any advantage to ocean survival of larger initial size. We used average intercircular distance over the first five ocean circuli to compare early ocean growth rates of the two age-groups of smolts. The average inter-circular distance for age 2^+ smolts (0.0401 mm) was significantly greater than for 1^+ smolts (0.0371 mm; paired t-test: $t = 5.91$, df = 13, $P < 0.001$). We think that it was reasonable to assume that the principal difference between the two age-groups was average size.

If smolt survival was not size-dependent then the mean of the smolt size-frequency distribution back-calculated from the adult scales should have been the same as the mean of the size-frequency distribution observed for emigrating smolts. Expected and observed mean smolt sizes were compared in 14 yr (Table 1). For both smolt age-groups combined, small smolts were significantly over-represented in the return in 2 yr, in 6 yr there were no significant differences between the observed and expected mean sizes, and in the remaining 6 yr small smolts were significantly under-represented in the return. Similar differences between expected and observed mean sizes were found for the age 1^+ smolts considered alone (Table 1), but for the age 2^+ smolts the observed mean smolt size was generally equal to or less than the predicted mean size (Table 1).

To examine the effects of smolt size on survival within years in more detail, we calculated smolt survivals within 5 mm intervals of estimated smolt FL. We first compared survivals of age 1^+ and age 2^+ smolts in those intervals where both occurred and found no significant difference in survival rate (mean difference = 0.00224, age 1^+ survival greater; paired t-test: $t = 0.097$, df = 25, $P > 0.9$). Since smolts of the same size but of different age survived at the same rate, we used smolts of both ages in regressions of survival on smolt FL. (This result is further evidence of the validity of our assumption that smolts of different ages differed importantly only in size.) In 10 of 14
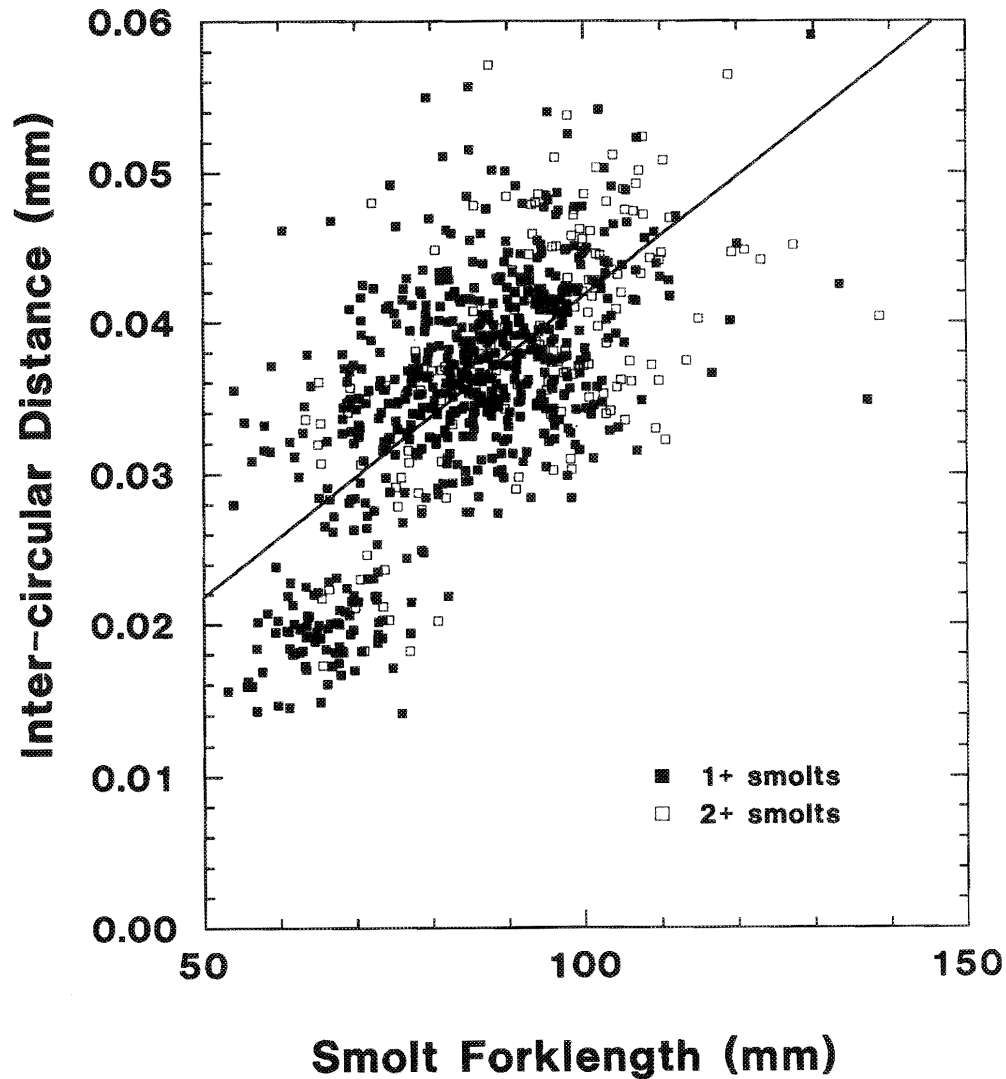
FIG. 10. Average inter-circular distance vs. smolt FL for the 14 smolt years of Table 1. Fitted line is from regression model 12, Table 3.

yr there was no significant relationship between size and survival (Fig. 7; Table 2). In the other 4 yr, large smolt size conferred a significant survival advantage. If only the age 1^+ smolts were used in the regression, then $\beta_{survival}$ was significantly greater than zero in six of 14 yr (Table 2). In those same years, mean smolt lengths back-calculated from adult scales were significantly greater than those expected from smolt length distributions (Table 1). In several years (e.g. 1975, 1976, 1983) a sigmoidal or saturating function of size would have been more appropriate than a linear model. However, we used linear models so that we could use the slope of the line ($\beta_{survival}$) as an indicator of the relative survival advantage of large smolt size.

Our two measures of the relative survival advantage of large smolt size (2^+ survival differential and $\beta_{survival}$) were significantly correlated ($r = 0.66$; $n = 14$; $P = 0.011$). Years in which large size was of advantage to survival tended to be the years in which age 2^+ smolts had a survival advantage.

The advantage to smolt survival of large size was inversely related to overall survival. Both the 2^+ survival differential and $\beta_{survival}$ varied inversely with smolt to adult survival (Fig. 8; models 1 and 2 of Table 3). As overall survival fell, the 2^+ smolts survived increasingly better than the 1^+ smolts and large

smolts survived better than small regardless of freshwater age. Both relationships were stronger when the survival of the age 1^+ smolts rather than overall survival was used (models 3 and 4 of Table 3), indicating that both relationships were being driven by variation in the survival of age 1^+ smolts.

Early Ocean Growth

Growth rates in the 2 mo after ocean entry were positively correlated with the marine survivals of 1^+ smolts (Fig. 9A) and of 1^+ and 2^+ smolts combined (models 5–7 of Table 3). The rate of growth was measured by the average inter-circular spacing over the first five circuli. The correlation between inter-circular distance and survival was strongest if only the age 1^+ smolts were considered (model 5 of Table 3). The survival of the age 2^+ smolts was not significantly correlated with inter-circular distance (model 6 of Table 3). Both the 2^+ survival differential and $\beta_{survival}$ were negatively correlated with the inter-circular spacing (models 8 and 9 of Table 3; Fig. 10). The latter correlations were stronger when the inter-circular distance of only the age 1^+ smolts was used (models 10 and 11 of Table 3), an indication that these relationships were being driven by variations within the younger, and consequently smaller, smolts.

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TABLE 4. ANOVAs for effects of freshwater age and smolt FL on inter-circular distance ($\Delta d_{circulus}$).

ANOVA dependent variable: $\Delta d_{circulus}$; categorical variable: freshwater age; covariate: smolt forklength

Source	SS	df	MS	F	P
Smolt forklength	0.0219	1	0.0219	555.6	<0.0001
Freshwater age	0.00002	1	0.00002	0.403	0.53
Error	0.0344	874	0.000039		

ANOVA dependent variable: $\Delta d_{circulus}$; categorical variable: smolt year; covariate: smolt forklength

Source	SS	df	MS	F	P
Smolt year	0.0131	13	0.00101	40.8	<0.0001
Smolt forklength	0.0076	1	0.0076	307.6	<0.0001
Error	0.0213	862	0.000025		

Post-hoc comparison of $\Delta d_{circulus}$ corrected for smolt length between years of low survival (<0.10) and high survival.

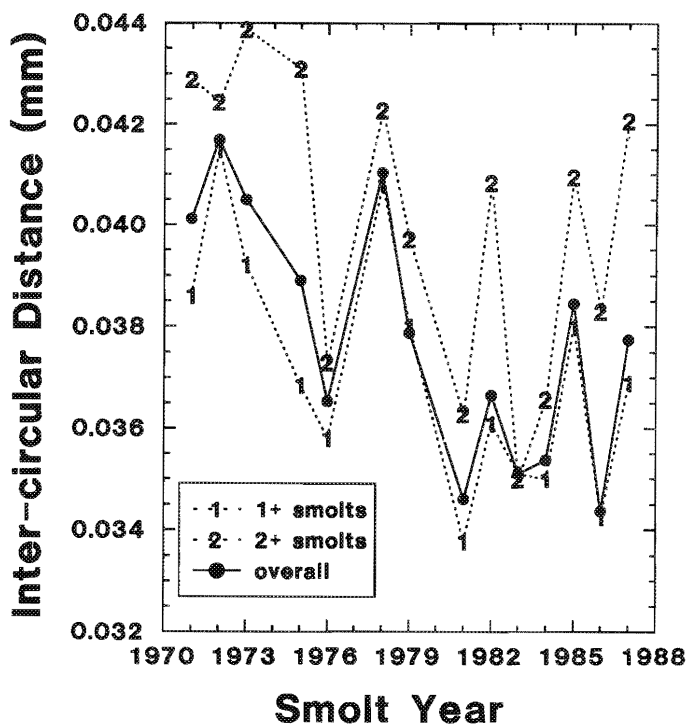| Source	SS	df	MS	F	P
Comparison	0.0053	1	0.0053	214.6	<0.0001
Error	0.0213	862	0.000025		

FIG. 11. Average inter-circular distance by freshwater age group against smolt year.

Inter-circular distances were positively correlated with smolt length at ocean entry (model 12 of Table 3; Fig. 10). This relationship underlies the significantly higher average growth rates of the age 2^+ smolts compared to the age 1^+ smolts noted earlier. To confirm this we did an analysis of covariance of inter-circular distance with freshwater age as the grouping variable and smolt FL as the covariate, and found no significant effect of age (Table 4). Because smolt size changed considerably over the study period (Fig. 4B), it was possible that the correlation between smolt survival and growth rate was a spurious result of a simultaneous, but coincidental, increase in both

survival and smolt size following 1977. However, relatively poor survivals (Fig. 5A) and slow growth (Fig. 11) occurred often in the 1980's while at the same time smolt size was relatively large (Fig. 4B). To further confirm that growth rate and survival were positively associated, independent of smolt size, we did an analysis of covariance on average inter-circular distance with smolt year as the categorical variable and smolt forklength as the covariate (Table 4). A post-hoc comparison between years of low (<10%) and high ($\geq$10%) survival (Table 4) confirmed that inter-circular distance differed significantly in years of low and high survival, independently of smolt size.

Density-Dependence

We could find no indication that smolt numbers affected either smolt survival or early ocean growth. Marine survival was not correlated with either the number of smolts leaving Carnation Creek (age 1^+: $r = -0.37$, $P>0.1$, $n = 17$; age 2^+: $r = -0.29$, $P>0.25$, $n = 17$), or with the number of coho smolts estimated to have entered the Sound ($r = -0.31$, $P>0.25$, $n = 17$). Similarly, the average inter-circular distance was not significantly correlated with either the number of smolts leaving Carnation Creek (1^+: $r = -0.42$, $P>0.1$, $N = 14$; 2^+: $r = 0.49$, $P = 0.08$, $n = 14$) or the estimated regional production ($r = -0.46$, $P>0.1$, $n = 14$). We were unable to detect density-dependent effects on survival and growth when the analysis was restricted to the 6 yr when overall smolt survival was less than 10% (smolt years 1976, 1982–1984, 1986, and 1987).

Ocean Conditions

The six environmental time series were selected as probable indicators of upwelling conditions at times and locations appropriate to the migration of coho salmon smolts up the west coast of Vancouver Island. Within both time period-locations, sea-surface salinities and temperatures were negatively correlated and sea-surface salinities and coastal upwelling indices were positively correlated (Table 5), but none of the correlations was statistically significant. The sign of the correlation between sea-

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TABLE 5. Product–moment correlations among the six environmental time series. SST is sea-surface temperature (°C), SSSal is sea-surface salinity (‰), and CUI is the coastal upwelling index. Summer values were averages from June through August. For all correlations n was 17. Significant departure from $r = 0$: **$P<0.01$; ***$P<0.001$.

Environmental variable	1.	2.	3.	4.	5.
1. May SST Amphitrite Point	—				
2. May SSSal Amphitrite Point	−0.111	—			
3. May CUI 48°N, 125°W	0.227	0.341	—		
4. Summer SST Kains Island	0.801***	−0.210	0.389	—	
5. Summer SSSal Kains Island	−0.316	0.607**	−0.091	−0.339	—
6. Summer CUI 51°N, 131°W	0.009	0.181	0.069	−0.079	0.327

TABLE 6. Relationships between marine survival and inter-circular distance with six environmental time series. Table entries are Pearson correlation coefficients, r. E_{sign} is the expected sign of r. For H_0: $r=0$, *$P<0.1$, **$P<0.05$, ***$P<0.01$, ****$P<0.001$.

Environmental variable	E_{sign}	Marine survival ($n = 17$)			Δcirculus ($n = 14$)		
		Age 1$^+$	Age 2$^+$	Both ages	Age 1$^+$	Age 2$^+$	Both ages
May SST Amphitrite Point	−	−0.31	−0.14	−0.30	−0.27	−0.54**	−0.38
May SSSal Amphitrite Point	+	0.49**	−0.29	0.51**	0.53*	0.64***	0.61***
May CUI 48°N, 125°W	+	0.02	−0.70***	−0.13	0.05	0.11	0.05
Summer SST Kains Island	−	−0.21	−0.27	−0.31	−0.19	−0.57**	−0.34
Summer SSSal Kains Island	+	0.75***	0.16	0.79***	0.70***	0.76****	0.72***
Summer CUI 51°N, 131°W	+	0.22	−0.11	0.25	0.24	0.43*	0.25

surface temperature and the coastal upwelling index was different in the two time period-locations (Table 5), indicating that mid-year sea-surface conditions were similar over the northwest coast of Vancouver Island.

For both survival and inter-circular distance we calculated 12 correlations (two age-groups × six environmental time series) and for each determined an expected direction based on the hypotheses previously outlined. For marine survivals nine of the 12 comparisons were of the expected sign and three were significant ($P<0.05$; Table 6). Assuming that values of r, the correlation coefficient, were randomly distributed around zero, the probability of finding 10 of 12 correlations with the expected sign was 0.075. Similarly, for inter-circular distances all 12 correlations were of the expected sign, an occurence with a probability of less than 0.001. Five of the 12 were statistically significant (Table 6). For both survival and growth the strongest and most consistent environmental correlate was the summer sea-surface salinity at Kains Island, near the northwest tip of Vancouver Island (models 13 and 14 of Table 3). In summary, relatively fast growth and high survival were associated with ocean conditions indicative of a strong upwelling along the northwest coast of Vancouver Island.

Although we used linear models to quantify the relationships between smolt survival, early ocean growth, and ocean conditions, linear models may not have been appropriate. For both survival and early ocean growth, a threshold model with two steps might have better described the observations (Fig. 12A, B). In such a model the dependent variable varies around one of two average values and jumps between the two values when a threshold value of some driving variable (or its correlate) is crossed. For Carnation Creek coho, overall survival fluctuated around values of ≈0.088 and ≈0.18 with a threshold summer salinity value of ≈31.5‰ (Fig. 12A). Similarly, the average inter-circular distance fluctuated around values of ≈0.036 mm and ≈0.40 mm with the same threshold summer salinity value (Fig. 12B).

Survival Variations in Age 1 and 2 Pacific Herring

Changes in the abundance of Pacific herring off the southwest coast of Vancouver Island since 1970 have been ascribed to changes in predation intensity (Ware and McFarlane 1988). Indexed survival rates of age 1 and 2 herring and the marine survival of Carnation Creek coho were positively correlated ($r=0.6$, df$=15$, $P<0.01$; Fig. 13) over our study period. Since age 1 and 2 herring and coho salmon smolts are similarly sized, are ecologically similar, and co-occur in Barkley Sound, it seems reasonable to infer that the covariation in their survival rates was not coincidental.

Discussion

The three general hypotheses explaining variations in the marine survival of coho salmon, "ocean-productivity," "density–dependence," and "predation–intensity," present two alternative views of the marine life histories of coho salmon. The "ocean–productivity" and "density–dependence" hypotheses both assume that the rate of predation on juvenile salmon depends on their initial size and on their growth rate in the ocean, and stems from a relatively constant number of predators. Both initial size and growth rate determine the length of time the juvenile salmon remain below some critical size threshold above which predation lessens. The two hypotheses differ in the mechanism that produces variations in the duration of maximum susceptibility. In contrast, the "predation–intensity" hypothesis as formulated by Fisher and Pearcy (1988) assumes that varying levels of size-independent predation accounts for variations in ocean survival.

We found no indication that either the survival or growth of coho salmon leaving Carnation Creek varied with numbers of juvenile coho salmon estimated to have entered Barkley Sound, even though increased hatchery production resulted in an approximate 2.4× increase in total coho numbers through the 1970's and early 1980's. The numbers of ecologically similar
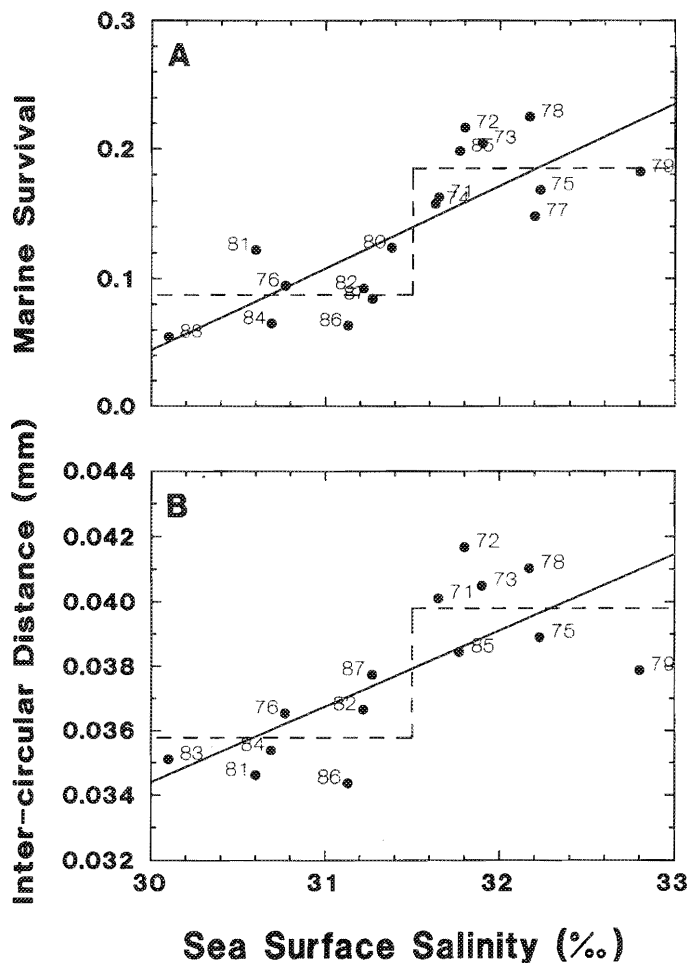
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FIG. 12. (A) Marine survival both age groups combined and (B) average inter-circular distance, both age groups combined versus summer sea-surface salinity at Kains Island. Dashed lines represent possible stepped models.
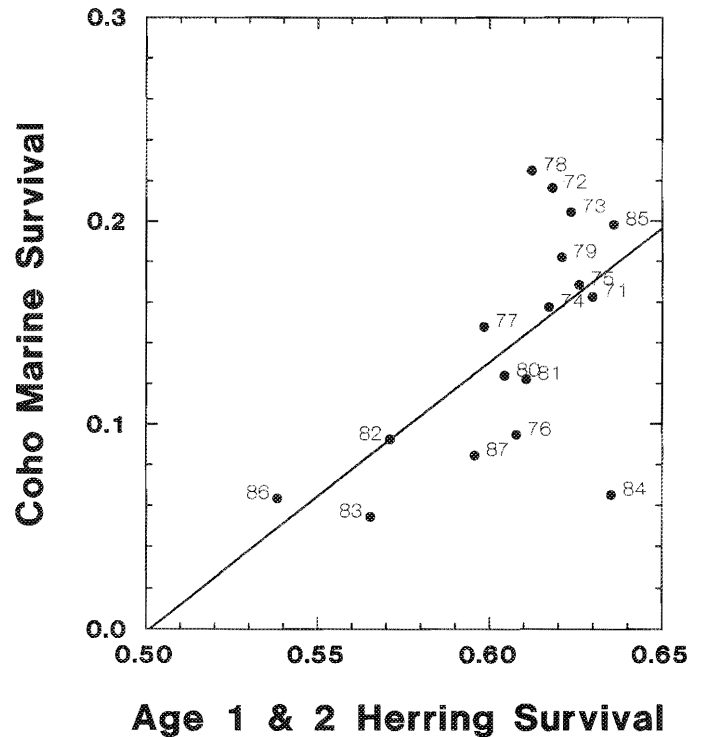

FIG. 13. Marine smolt survival of Carnation Creek coho salmon versus index of age 1 and 2 Pacific herring survival off southwest coast of Vancouver Island from 1971 to 1987.

marine species in and around Barkley Sound were probably far greater than the numbers of juvenile salmonids. For example, $\approx 1.1 \times 10^9$ age 1 and 2 Pacific herring were estimated to have resided in Barkley Sound and the neighboring coastal area of Vancouver Island (Haist et al. 1987). The total number of young herring off southern Vancouver Island has fallen substantially in the last two decades (Haist et al. 1987), suggesting that densities of small pelagic fishes, ecologically similar to coho salmon, were declining over our study period and were lowest in the same years that marine survivals of coho salmon were poorest. Consequently, within the estimated densities observed over the years of our study, we reject the density–dependent hypothesis as an explanation for variations in coho smolt survival at Carnation Creek.

Although large smolt size did not confer a consistent survival advantage among smolts leaving Carnation Creek, either between or within years, large smolts did have a measurable survival advantage in years when overall marine survivals were poor. Marine survival and early ocean growth were positively associated. One explanation of both observations would be that size-dependent mortality was a determinant of inter-annual variability in the marine survival of coho salmon smolts leaving Carnation Creek. Growth rates during early sea life determined the length of time that fish remained small and, presumably, most susceptible to predation. During years when growth rates

were particularly slow, mortality was high. It was only in years when mortality rates were high that the survival advantage associated with large size (superior escape ability, faster growth, and a shorter time to attain a size-threshold) became sufficiently large to be detected using our methods.

Thus, the "predation–intensity" hypothesis of Fisher and Pearcy (1988) is inconsistent with our observations. Whereas they found no evidence for either size-dependent mortality or for differences in growth rate between low and high survival years, we found considerable evidence that smolt size and early ocean growth were predictive of smolt survival. We note, however, that the average smolt sizes reported by Fisher and Pearcy (1988) ranged between 149–162 mm, 1.9 × the average size of 1^+ smolts and 1.6 × the size of 2^+ smolts observed at Carnation Creek. Assuming an average growth rate of 0.93 $mm \cdot d^{-1}$ (Fisher and Pearcy 1988), 2^+ smolts leaving Carnation Creek would have required 60 d to reach 150 mm. Using the same growth rate, the fifth ocean circulus was deposited at an average size of 145 mm, ≈ 45–51 d after leaving Carnation Creek. We suspect that Fisher and Pearcy did not observe consequences of either size-dependent mortality or growth because smolts produced by Oregon hatcheries were larger than the size threshold where such size-dependent processes were operative.

The observations that we have presented indicate that variability in the marine survival of Carnation Creek coho salmon was closely related to ocean conditions off the west coast of Vancouver Island over the first 4 mo of ocean life. Conditions favourable to upwelling and subsequent transport of the upwelled water onto the continental margin may have been conducive to fast growth for juvenile salmon migrating up the coast. Relatively fast growth was in turn associated with relatively high survival. Thus, our observations support the "ocean–productivity" hypothesis.

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The covariation of survivals of coho salmon smolts and Pacific herring suggest some common underlying factor. Since declines in herring abundance have been linked to changes in the distribution and abundance of a piscivorous fish (probably Pacific hake) around ·Barkley Sound (Ware and McFarlane 1988), the common factor may have been variations in predation intensity. A large and transient stock of Pacific hake arrive in the Barkley Sound region from the south in May. The northward and inshore movements of these fish are influenced by conditions around the time of the spring transition in the Vancouver Island Coastal Current (Smith et al. 1990). Early and abrupt transitions not only produce conditions favourable to upwelling along the coast but also delay the formation of, and weaken, the northward flowing Coastal Current, possibly delaying the northward movements of hake. In years of late or weak transitions southerly surface waters, and probably hake as well, move more strongly northward along the coast at the same time as migrating coho salmon smolts (Smith et al. 1990).

We propose that variations in the smolt survivals of Carnation Creek coho salmon were caused by changes in near-shore ocean productivity that affected salmon growth rates and consequently their susceptibility to predation, and by simultaneous changes in predation intensity caused by changes in some combination of predator distribution, abundance, or type. Further resolution of the mechanisms underlying variation in coho salmon smolt survival at Carnation Creek cannot be made from input or output data like ours, but must depend on the collection of observational data during the first months of sea life.

Acknowledgments

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