THE USE OF ESTUARIES AS REARING HABITATS
BY JUVENILE COHO SALMON

Peter J. Tschaplinski
Biological Consultant
1146 Union Road
Victoria, British Columbia   V8L 2S1

INTRODUCTION

The use of the Carnation Creek watershed by juvenile coho salmon (*Oncorhynchus kisutch*) is not limited to fresh water. The upper intertidal zone of the stream is also inhabited by coho fry and smolts. Fry rear in the estuary generally between April and October. Yearlings co-occur with these fry for variable periods of time in spring and early summer before the processes involved with the smolt transformation are completed and new smolts subsequently emigrate to marine habitats.

Comprehensive research on the ecology of estuary coho was undertaken to describe for the first time

(1) their population dynamics and life histories;

(2) the physiological adaptation of coho fry to the brackish estuarine environment; and,

(3) their food resources and feeding behavior. Comparative stuides on populations of juvenile coho salmon inhabiting the stream and estuary at Carnation Creek were conducted in the field between1979-1981 and in the laboratory between 1981-1984. The population dynamics of stream and estuary coho were compared for 1979-1980. Seasonal numbers, habitat preferences, distribution, survival, and growth rates of both stream and estuary fish were determined in detail and summarized elsewhere (Tschaplinski, 1982, 1987). Investigations on comparative physiology and on the physiological adaptation of coho fry to the estuarine environment were undertaken in 1981-1982 and also detailed

previously (Tschaplinski, 1982,1987). The salient points of these analyses will be reviewed presently together with a synthesis of some of the research conducted on the food resources and feeding ecology of stream and estuary coho.

Specifically, studies of estuary-dwelling coho were undertaken to determine whether (a) estuaries are able to support significant numbers of coho salmon fry; (b) coho fry displaced seaward could adapt physiologically and behaviourally to estuarine conditions and consequently take advantage of high environmental productivity and grow rapidly; and, (c) rapidly growing, estuary-reared fry could contribute important numbers of recruits to adult populations and the coho fishery.

In turn, the objectives of studies on the food resources and feeding relationships of stream-dwelling and estuarine coho were to first identify and quantify potential sources of coho food, namely aquatic drift, benthic macroinvertebrates, and terrestrial prey. Second, analyses were performed to determine which of these food resources were the most important to young coho both temporally and between environments. Ultimately, these studies revealed whether the secondary production assumed available to coho was estimated accurately from drift, terrestrial, and benthos samples, and whether environmental differences in food abundance and availability could account for differences in growth rates and production observed between stream and estuary fry.

The objectives of the trophic analyses were met through procedures in which (a) the numbers and

distribution of potential prey species in Carnation Creek and its estuary were quantified and compared from spring to late summer; (b) the species and quantities of prey actually consumed by stream and estuary coho were assessed on both diel and seasonal bases; and, (c) the stomach contents of coho predators were correlated statistically with the species and quantities of invertebrate prey found in drift, terrestrial, and benthos samples.

Revealing how the prey preferences and feeding behavior of young coho vary in response to changes in prey availability in different environments under different conditions of stream dishcarge (e.g., freshets), tidal cycling (estuaries), terrestrial vegetation, season, and time of day is important not only to elucidate the trophic ecology of this species, but also for resource managers and fish culturists concerned with maintaining optimum conditions for coho growth in both natural habitats and artificial rearing structures such as estuarine pens (Heard and Crone,1976) or streamside channels (Mundie, 1974). The present investigation on coho juveniles inhabiting two environments differing widely in physical and chemical conditions, as well as biological productivity, has contributed information interrelating the processes which determine their numbers, distribution, growth, and production in natural populations. The understanding of these interrelationships supports the general objectives of research at Carnation Creek which are to (a) identify and comprehend the biological and physical processes operating within a coastal watershed system; (b) reveal ways in which forest removal changes these processes; (c) allow managers to make reasonable and useful decisions about land use and fish populations; and, (d) employ these results in evaluating logging regulations applied in the past.

METHODS

Procedures and materials employed in studies of seasonal population numbers, distribution, survival, growth rates, and adaptive physiology are detailed elsewhere (Tschaplinski, 1982, 1987). However, a brief summary of methods employed to determine the seasonal food resources and feeding habits of stream and estuary coho is included presently (see Tshaplinski, 1987, for detailed descriptions).

Frequent and "simultaneous" sampling of both juvenile coho and their prey was undertaken between 1979-1981 to determine the trophic dynamics of stream and estuary populations. Three sources of prey were identified in both the stream and estuary: (1) populations of benthic macroinvertebrates; (2) drifting invertebrates ("drift") consisting mainly of benthic, aquatic invertebrates and terrestrial insects carried downstream by the current; and, (3) terrestrial invertebrates, mainly aerial insects, associated with the air-water interface.

Benthic populations were compared approximately monthly by taking five to eight bottom samples in each environment using a ~0.3m^2 modified, Hess sampler. Coho fry and yearlings were collected for stomach-content analyses also at near-monthly intervals from late June to early October, 1979, late May to early October in 1980, and on 1-2 May 1981. At the "same time" that fish were seined, drift samples were collected at each study site using four drift nets of 250μm mesh and and 15cm X 15cm aperture. Additionally, terrestiral invertebrates active at the water surface were sampled at each site using six 0.5m X 0.5m sticky traps constructed from transparent polyvinyl sheets which were oriented at the air-water interface and anchored to the channel bottom using four iron rods.

In each monthly study, coho and their potential prey were sampled "simultaneously" over 24-hour (diel) periods at 4-hour intervals in 1979 and at 3-hour intervals in 1980 and 1981. Each sample, of coho included 8-12 individuals of sizes representing those present in each population. High tides interrupted continuous sampling in most estuary studies; otherwise, investigations on coho diet were designed such that predators and potential prey were sampled continuously.

To assess the potential food resources in both the stream and estuary, (1) benthic populations were quantified in terms of no./m^2 and compared parametrically between environments using $log_{10}(x+1)$ transformations (Student's t, two-sample analysis of variance; p≤0.05); while (2) drift was quantified in terms of no./m^3•h; and, (3) surface-trapped, terrestrial prey were expressed in terms of of no./m^2•h. Both drift and surface-trapped invertebrates were compared nonparametrically between environments (Mann-Whitney, two-sample tests; p≤0.05).

To quantify the food organisms actually consumed by stream and estuary fry and yearlings, each prey item contained within the foregut (cardiac region of the stomach) was enumerated, classified to the lowest

possible taxon, and identified as either aquatic, "estuarine-aquatic" (unique to estuarine or marine habitats), or terrestrial in origin. Diel or diurnal feeding frequencies were determined as no. of prey/fish•3 h sampling interval and estimated directly from the numbers of loosely-compacted (undigested), recently-consumed prey items in the foreguts of sampled fish. Feeding rates were then compared parametrically between stream and estuary coho (two-sample analysis of variance; $p \leq 0.05$).

Ranking prey by percent numerical abundance (% N) usually provided the most accurate representation of the relative importance of different food organisms in the diets of stream and estuary coho. Other indices such as percent frequency of occurrence (% F), volume (% V), or IRI (Index of Relative Importance = % F(% N + % V); Pinkas et al. 1971) added information largely redundant to that already provided by numbers because (a) numerically important prey also displayed high frequency of occurrence percentages (i.e., were consumed by most individuals); and, (b) most prey fell within a narrow range of sizes. Over 95% of all prey eaten by estuary coho were between 0.250-8.157 mm long X 0.150-1.270 mm wide. Correspondingly, >95% of the prey of stream coho were between 0.250-6.831 mm long X 0.150-1.575 mm wide.

The taxonomic composition of the coho diet was thus quantified numerically and compared with the numerical proportions of species occurring in samples of drifting, benthic, and terrestrial invertebrates. Comparisons were made using the index of Moriseta (1959) modified by Horn (1966) to determine the overlap between diet and potential food resources. This index sums all "potential" and "actual" prey species within the same habitat and is given as S where "S" is the total number of food

$$C_\lambda = \frac{2\sum_{i=1}^{S} x_i y_i}{\sum_{i=1}^{S} x_i^2 + \sum_{i=1}^{S} y_i^2}$$

categories (taxa), "x_i" is the proportion (numerical %) of the total diet of predator species "x" taken from food category "i", and "y_i" is the numerical proportion of the total drift (benthos, or terrestrial prey) also composed of category "i". The amount of overlap (C_λ) varies from an upper limit of 1 when the species

proportions of the diet are the same as those of an environmental sample, to 0 when the respective populations have no species in common. The overlap values are the same as the average of the alpha (α) competition values used by MacArthur and Levins (1967); accordingly, it has generally been accepted that any value of $C_\lambda \geq 0.60$ demonstrates "significant" overlap although the index is descriptive.

After the overlap values between diet and benthic, drifting, and terrestrial prey sources were determined, the source showing the highest significant C_λ value was selected for statistical analyses of prey "preference". The "Linear Index of Food Selection" (Strauss, 1979, 1982) was used to determine whether stream or estuary coho were feeding upon individual prey species in proportion to the numerical abundance of each prey type in the environment or whether some prey items were being taken preferentially over others. The index compares linearly and statistically, the proportion of each individual prey type occurring in the diet with the proportion occurring in a prey "community", and is given as: $L = r_i - p_i$, where "r_i" is the numerical proportion (percent) of prey species "i" in the diet and "p_i" is the corresponding proportion sampled from the prey community. "Selection" values range from -1 when prey species are avoided or are temporally or spatially unavailable to +1 when prey are "preferred" or are more readily available than others. Values near 0 indicate that predators are consuming prey in proportions the same as those occurring in the environment; that is, no prey selection is occurring.

The Linear Index has been used frequently because "L_i" has the advantage of being normally distributed (Strauss, 1979, 1982; Ready, et al. 1985) thus allowing statistical comparisons (Student's t-tests) to be made between values. Because "L_i" is a linear combination of "r_i" and "p_i", it has a variance equal to the sum of the variances of "r_i" and "p_i": $S^2(L_i) = S^2(r_i) + S^2(p_i)$. Because multiple samples were used to estimated "r_i" and "p_i", the prey proportions used to calculate these values are the mean "r_i" and "p_i" weighted by the total number of prey in each sample (see Ready et al. 1985, Tschaplinski, 1987).

These analyses combined illustrated which source of invertebrate prey was the most important for stream and estuary fry, whether some prey were sought preferentially over others, and therefore, whether coho were able to use different prey sources and species efficiently in either environment.

RESULTS AND DISCUSSION

Life History, Habitat Preferences and Population Ecology

Estuary-dwelling coho salmon consist mainly of fry which emerge annually in large numbers from coastal streams between early spring and midsummer. Fry first emigrated downstream and inhabited the estuary within one week after they were first observed to emerge from the stream gravels. Observations of fry numbers, distribution and behavior from late February to mid-March (1981) provided no evidence of density-dependent causes for this early emigration. Numbers of stream fry were low in early spring. Many pools and other low-velocity sites, which are prime habitats for coho fry, contained few or no individuals. The overall density of fry during the first week of emergence was > 16-times lower than the 11-yr average recorded for late-summer populations in Carnation Creek. By 30 April (1981) > 9 000 fry emigrated from the stream although numbers were low and no aggressive interactions were observed among them even after populations had increased to 0.71 fry/m² in one study section.

The seasonal peak of fry emigration coincided with (1) the emergence of large numbers of coho into high-velocity riffles and runs; and, (2) the onset of seasonally high discharge volumes including freshets of 3 m³/s between March and early April. Over 90% of all emigration in 1981 occurred during that period. The co-occurrence of these events infers that fry were physically displaced downstream by the actions of rapid currents. These conclusions are corroborated by the results of other investigations in Carnation Creek (Holtby and Hartman, 1982) and elsewhere (Au, 1972).

Observations made from 1979-1981 revealed that the numbers and distribution of coho fry were stongly space-limited. The total length of the estuary was 490 m when the lengths of the main channel and all side channels were summed. However, only the uppermost 250 m contained habitats suitable for juvenile coho. From May to late September/early October, fry inhabited all low-velocity sites of this upper zone which consisted of an alternating sequence of riffles and pools at low tide. The upper estuary is sheltered from the open waters of Barkley Sound by high, vegetated banks, and contains complex salinity and temperature gradients both horizontally and vertically in the water column. Measurements made at both low and high tides

revealed that salinities ranged from 0-21°/oo, and temperatures varied from 8.9-19.0°C from June to late September.

These salinities and temperatures neither limited nor determined coho distrubution: based upon pool area at low tide, overall densities of fry in the estuary in 1980 were found to approximate those occurring upstream in fresh water. Late-summer densities varied from 1.06-1.53 fry/m² and were statistically equal to the 11-year mean. However, the distribution of estuarine coho was very irregular and depended upon habitat structure. Habitat space was the prime factor determing the numbers and distrubution of both fry and yearlings.

Preferred habitats of estuary coho were defined by water depths, current velocities, and overhead cover, and were the same as those of their stream-dwelling counterparts. The largest numbers of fry were always found in sites containing at low tide (1) low-velocity water averaging 8.7 cm/s and ranging between 0-32 cm/s; (2) pools usually 45-225 cm deep; and, (3) cover in the form of (a) undercut banks, often with vegetation overhanging the channel, and (b) masses of large debris (partially-submerged tree roots, logs, and fallen trees). Large, woody debris provides important structural habitat for coho fry occurring in estuaries by creating pools, furnishing shelter, and reducing water velocities and substrate movements. Estuary sections containing these features supported fry at densities varying up to 5 fry/m² during summer. Based on pool area, these sections held up to 17-times more fry than did broad, shallow reaches devoid of cover. Clearly, coho fry do not change their habitat preferences after they emigrate from streams to estuaries.

In 1979-1980, 1,205 and 2,453 fry remained in the estuary by late summer, amounting respectively to ~9-12% of the total numbers inhabiting the stream. Estuaries can thus provide additional habitats for coho fry, thereby retaining seaward-displaced fish that appear otherwise to be lost to the populations rearing in coastal watersheds. After emigrating to the estuary, coho fry rapidly outgrew their stream-resident counterparts by 1.8-2.3 fold during their first summer and were 16-18 mm longer on average by late September 1979-1980. As a consequence of accelerated growth, estuary fry comprised a greater proportion of the total population rearing in the watershed in terms of biomass than they did numerically. Between ~20-24% of the total-stream biomass was accounted for by fry rearing intertidally

over the same two years.

The estuary population demonstrated its greatest importance trophically in terms of net production which summed to 6.92 kg during May-September 1979 and amounted to 26.0% of the 26.6 kg produced by fry upstream. The estuarine production rate increased further to ~10.3 kg in 1980, comprising 38.0% of that recorded for stream fry notwithstanding the unusually high numbers inhabiting the stream in that year (20,953). These data demonstrate that even small estuaries can support important populations of rapidly growing coho. Increased growth in the estuary population was well illustrated by the observation that 50% of all fry that had inhabited the estuary from April/May to September were about as large as the one-year-old smolts leaving Carnation Creek for the sea in spring.

Physiological Acclimation to the Estuarine Environment

Coho fry leave the estuary with the onset of autumn freshets in late September-November. No overwintering occurs in the estuary, and only small numbers returned to fresh water to overwinter in a small tributary flowing into the intertidal zone of the stream at Carnation Creek. The overwinter survival rates of estuary fry leaving the intertidal zone in autumn have yet to be determined. However, laboratory and field studies in 1981-1982, together with the available literature, demonstrate that coho fry which emigrate from streams and reside in estuaries can (1) adapt physiologically to brackish estuarine waters during summer; (2) select salinities and temperatures within their ranges of preference and tolerance at which optima for survival, swimming activity, feeding, and growth are approached (Otto and McInerney, 1970); and, (3) acclimate temporally to waters of progressively higher salinity.

Samples of stream and estuary coho fry (N=10-12 each) collected monthly (May to November) and tested for salinity tolerance showed marked seasonal differences in their abilities to osmoregulate when immersed for 72 hours in brackish (15 °/oo,) water or 24 hours in high-salinity (30 °/oo,) water at 15°C in the laboratory.

Osmoregulatory performance in coho fry was determined by the concentration of sodium ions (Na^+) in their blood plasma. Juvenile coho in fresh water, and smolts in sea water, are able to maintain their plasma Na^+ concentrations 170 mM. Early in the season, neither stream nor estuary fry of equal (or near equal) body length and weight could osmoregulate fully in 15 °/oo, brackish water (a salinity level slightly higher than that found on average in the estuary at high tide). From May to July, mean sodium ion concentrations ranged between ~177-182 and 183-188 mM in the plasma of estuary and stream fry respectively. However, a consistent trend for lower Na^+ concentrations in estuary fry became statistically significant by August (analysis of variance, Student's t; $p < 0.05$). From August to October/November, estuary coho maintained their plasma Na^+ concentrations ≤170 mM, eventually osmoregulating at a level statistically equal ($p > 0.05$) to that of control fry in fresh water.

Unlike estuary coho, stream fry never previously exposed to saline water were unable to achieve similarly low levels of plasma sodium between mid-summer and autumn, notwithstanding a progressive, growth-associated trend toward lower levels which culminated seasonally in a mean of ~179 mM in early November.

These tests on coho fry revealed that (1) complete adaptation to brackish water in "pre-smolt", estuary coho is a gradual process which can be apparent midway through their first summer of growth; (2) estuary fry are able to physiologically regulate their plasma Na^+ concentrations when immersed aburptly into brackish water after they have achieved this seasonal acclimation in their environment; and, (3) regardless of body size, short-term (72 h) adaptation is not possible at any time during summer in fry not previously exposed to brackish water. Moreover, the high survival rates of all experimental fry (no mortality in estuary coho, and only 1.4% in stream fry) show clearly that stream coho displaced into estuaries at any time are able to withstand at least 15 °/oo brackish water without incurring high mortality due to osmoregulatory failure. Moderately elevated plasma Na^+ levels did not impair the swimming or feeding activities in experimental coho in any obvious way. After entering estuaries, steam coho require a long-term period (e.g. > 30 days; Otto, 1971) to adapt fully to the salinity regime of the upper estuary.

The temporal development of mechanisms imparting tolerance to brackish water in estuary coho also resulted in seasonally increased tolerance to 30 °/oo sea water in that population. Estuary fry immersed in high-salinity water were able to progressively reduce their plasma Na^+ concentrations from spring to

autumn ($p < 0.05$) and maintained significantly lower levels than stream fry by August. These trends notwithstanding, at no time between spring and autumn were estuary fry able to osmoregulate fully in 30 °/oo sea water: their plasma Na^+ concentrations were always ≥ 186 mM on average. However, swimming and feeding activities appeared unchanged from the controls and mortality was only 1.4%.

In contrast with estuary fry, about 12% mortality was observed in stream coho immersed in 30 °/oo sea water. Sodium ion concentrations in the plasma of stream fry never decreased below 200 mM on average.

Estuary fry apparently developed their ability to osmoregulate in brackish water and survive in sea water as a consequence of long-term exposure to intermediate-range salinities occurring intertidally. Although the smolt-sized fry leaving the Carnation Creek estuary in autumn were unable to fully osmoregulate in 30 °/oo sea water, other tests demonstrated that these fry were able to maintain plasma Na^+ concentrations in water of 26 °/oo, salinity that were statistically equal to levels measured in fish held in 15 °/oo water. Therefore, it is concluded that coho fry leaving the estuary in autumn are able to physiologically tolerate the brackish conditions of the near-shore, surface waters of (for example) Barkley Sound over winter.

The capability of coho fry to devleop salinity resistance early in their life history is widespread in light of observations consistent among many different investigations, and is confirmed by the uniformity of the present experimental data both between years and among samples of coho collected from Carnation Creek and the Goldstream and Big Qualicum Rivers on Vancouver Island (Tschaplinski, 1982, 1987). Rapid growth and long-term exposure to water of intermediate-range salinity have both been identified as agents promoting salinity adaptation in coho fry (see Clarke et al., 1981, Conte et al., 1966). The present results are thus consistent with those of several other laboratory investigations which have shown that coho fry removed from fresh water, and reared for long periods in water of low or intermediate salinity, increase their tolerance to sea water at least six to seven months before they demonstrate the morphological and behavioral changes associated with the smolt transformation (Clarke et al., 1978, Conte et al., 1966).

Numerous studies have shown that coho fry reared in laboratory conditions where growth, salinities, temperatures, and photoperiods are variously optimized can transform into smolts in as few as 12 weeks (see Clarke et al. 1978, Folmar and Dickhoff, 1980). Furthermore, fry raised in estuarine impoundments under natural conditions can grow rapidly and can transform into smolts in only 90 days (Garrison, 1965). These smolts have been shown to return to their watershed as adults after spending a two-year period in the ocean.

Such studies demonstrate unequivocally that estuaries are not physiologically hostile environments for coho fry, and have important and direct implications for the conservation and artifical culture of estuary populations. The strong, positive relationship between growth rates and acclimation to sea water infers that rapid growth in estuary fry at Carnation Creek was at least partly responsible for their acclimation to 15 °/oo, brackish water and concurrently improved osmoregulation in 30 °/oo sea water. Conversely, slow growth in stream fry may have impeded their seasonal acclimation to brackish water, and prevented any development of hypo-osmoregulation in sea water regardless of their lack of prior exposure to estuarine salminities. Several observations discounted the converse notion that the high rates of growth and production in estuary coho were caused by decreased metabolic costs of osmotic regulation in waters of low and intermediate salinity. Instead, all data indicated strongly that increased food abundance and availability in the estuary permitted the accelerated growth observed in emigrant fry.

Food Resources and Feeding Ecology of Stream and Estuary Coho

Increased growth efficiencies due to temperature optima could not be invoked to explain the large differences between the growth rates of stream and estuary coho at Carnation Creek because (a) the means and ranges in daily and seasonal water temperature were similar between the two environments; and, (b) coho growth in nature at temperatures between 5-17°C depends largely upon food abundance (see Averett, 1969). Additionally, experiments with coho fry in the laboratory have shown that potential increases in growth efficiencies in brackish waters resulting from decreased costs of osmotic regulation can account for < 10% of the

increased growth in esutary fry during April-September at salinities measured in the upper estuary at Carnation Creek (Canagaratnam, 1959, Otto, 1971).

High environmental productivity ultimately caused increased rates of growth, production, and biomass-energy turnover in estuary coho compared with their stream-dwelling counterparts (Tschaplinski, 1987). Primary production alone is several times greater in the estuary than in the stream (Stockner and Shortreed, 1976). Additionally, production based on detrital food webs dominates over primary production in many shallow-water estuaries (Odum, 1980). The large populations of benthic macroinvertebrates supported by these webs are in turn the chief foods of fish predators incuding young coho.

All of the food organisms potentially available (Hyatt, 1979) to estuarine fry were numerically more abundant (p <0.05) than those available to stream-dwelling coho at Carnation Creek between spring and autumn when fish grow the most rapidly. Benthic invertebrates alone were 6-6.5-fold more abundant monthly and annually in the estuary. Numbers in that environment ranged on average between 46,222 - 61,755 invertebrates/m^2 while only 7,140-11,387 invertebrates/m^2 were quantified from reaches upstream between June 1979 and late September 1980 (Table 1).

Similarly, invertebrate drift rates in the estuary exceeded those in the stream by wide margins (3-6 fold) diurnally except during freshetts (Figure 1). Aquatic (drifting benthic species) and terrestrial drift components were respectively 2-6-fold and 4-6-fold more abundant in the estuary in six of eight monthly studies conducted from July 1979 to May 1981 (Figure 1). Stream drift rates rose to equal those occurring intertidally only when discharge volumes were high in the watershed.

Although stream drift was sampled over complete diel cycles, that collected "diurnally" between 03:00-21:00 hours was concluded to best represent the potential drift prey of coho in the Carnation Creek system. Coho were primarily diurnal and crepuscular predators and ate few prey at night. Therefore, nocturnal drift was largely unavailable to either stream or estuary coho and was excluded from comparisons of food abundance between environments.

The highest drift rates observed diurnally in both the estuary and stream occurred during twilight periods, and especially at dusk (Figure 1). However, high rates also occurred in the estuary in association with tidal cycling. Peak drift rates were always recorded intertidally in the 3-hour period immediately following a flood tide. Tidal currents and the turbulence associated with the mixing of fresh and saline waters likely disturbed the sediments and dislodged many macroinvertebrates from the benthos, causing them to drift when the tide receeded. Visual observations also disclosed that saline water stimulated swimming activity in some estuarine crustaceans. Consequently, estuary drift enumerated diurnally between 03:00-21:00 hours exceeded the total numbers drifting in the stream over entire diel periods by factors of 2-3.5 whenever streamflows were low and stable (see Figure 1).

Finally, terrestrial prey caught on sticky traps at the air-water interface of pools were ~2-4-fold more numerous intertidally than in the stream in six of the same eight monthly analyses in which drift was quantified (Figure 2). Most terrestrial prey were aerial insects which were especially active above the surfaces of pools during midday periods and at dusk when coho fed frequently. Diverse and abundant coniferous and deciduous vegetation surrounding the estuarine channels might have accounted for the high numbers of terrestrial insects sampled in that environment.

Diel and seasonal data on coho predation showed clearly that greater temporal availability of prey combined with greater prey abundance promoted (1) increased duirnal feeding activity in estuary coho which (2) ultimately resulted in increased food consumption and growth in that population compared with coho upstream. Stomach-content analyses demonstrated that estuary coho consumed diurnally 28-71% more prey than their stream-dwelling counterparts (Figure 3; p < 0.05). These data were substantiated unequivocally by direct observations of feeding behavior which showed that estuary fry fed more frequently than stream coho during most times of the day, and daily made upward of twice as many feeding movements.

Estuary coho ate significantly more prey than stream fry and yearlings in every analyses. Averaging the data for each diurnal study, the stomachs of estuary coho contained between 54.3±7.5 to 65.2±8.6

Table 1. Comparative numbers of benthic macroinvertebrates in the stream and estuary at Carnation Creek during "summer" in 1979 and 1980. Means for each period were determined from eight bottom samples collected from riffles near the 100-m and 950-m sites in the stream and from sections 5 and 8 in the

STREAM		ESTUARY	
1979		1979	
Date	Numbers/m^2	Date	Numbers/m^2
30 June	7 140 ± 835	30 June	57 388 ± 5 064
17 September	10 012 ± 991	17 September	59 608 ± 5 395
1980		1980	
10 May	11 387 ± 2 635	10 May	46 222 ± 7 577
26 June	8 086 ± 2 277	17 June	53 454 ± 11 085
27 September	9 537 ± 2 352	27 September	61 755 ± 10 820

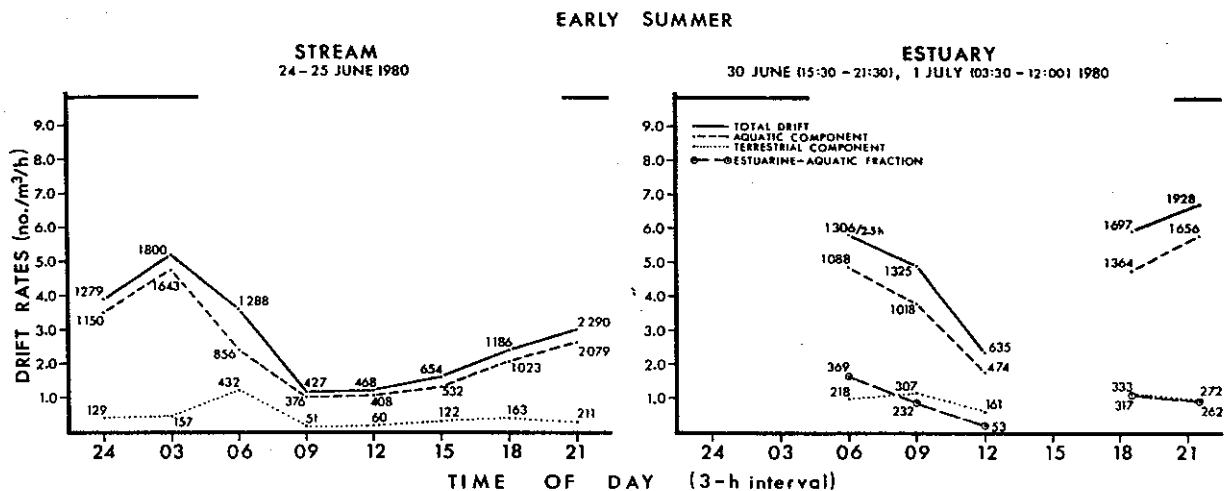EARLY SUMMER

Figure 1. Comparative drift rates for the stream and estuary at Carnation Creek. High tides prevented continuous sampling in the estuary; however, diurnal rates (03:00-21:00 h) in the estuary, for the month exemplified here, exceeded those in the stream by factors of 1.6-4.3 over all 3-hour intervals (Mann-Whitney U, p <0.05). Numbers of prey captured in each sample are also given.
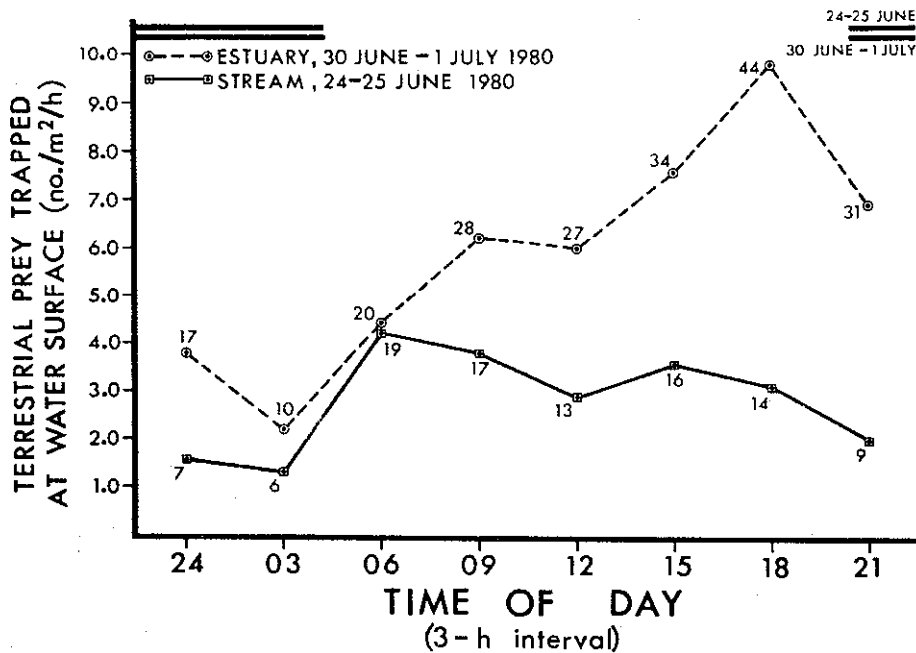
Figure 2. Comparative numbers of terrestrial invertebrates trapped at the air-water inteface in the stream and estuary at Carnation Creek. Estuary capture rates (no./m^2•h) and numbers for the period exemplified here, exceeded those in the stream by factors of 1.1-3.5 depending on each 3-hour sample (Mann-Whitney U, p <0.05).

prey/fish•3h (Figure 3). In comparison, stream-dwelling salmon consumed only 34.0 ± 5.3 to 42.4 ± 8.4 prey/fish•3h throughout the day.

Temporal analyses of drift abundance and coho diet, combined with direct observations of feeding behavior, revealed that drifting invertebrates represented the most important immediate source of prey for stream and estuary juveniles. These studies showed that (1) most of the prey coho consumed originated from the drift, and (2) the diurnal feeding patterns of stream and estuary coho were linked closely to the temporal availability of drifting invertebrates. Estuary fry (and yearlings) consumed more prey than did stream coho because they had more opportunities to feed upon drift at all times of the day except at dusk.

Drift was generally less available to stream coho because maximum drift rates occurred nocturnally in that environment — from 33-61% of all stream drift sampled over 24 hours was collected at 24:00 and 03:00 h when coho were unable to feed upon it. Consequently, stream coho were limited to feeding

intensively mainly at dusk when drift was the most abundant during daylight hours. Stream coho collected at 18:00 and 21:00 h consumed between 32.5 ± 10.7 to 79.0 ± 27.9 prey/fish•3h seasonally. Feeding frequencies were lower and relatively uniform at most other times of the day when stream fry and yearlings sometimes consumed as few as ~14 prey/fish•3h.

In contrast to the stream, estuary drift was especially abundant diurnally due to tidal cycling. Maximum drift rates, feeding activity, and food consumption were always temporally coincident and associated with tidal currents irrespective of time. Food consumption in estuary coho increased abruptly during flooding and high tides and peaked in the 3-hour period immediately following a tidal maximum (Figure 3). High predation rates during receding tides when drift rates were maximal accounted statistically for all differences in food consumption observed between stream and estuary coho in all months but one. Estuary coho sampled during periods of rapidly receding tide had consumed as many as 75.3 ± 18.9 prey/fish•3h at the same time that stream coho fed
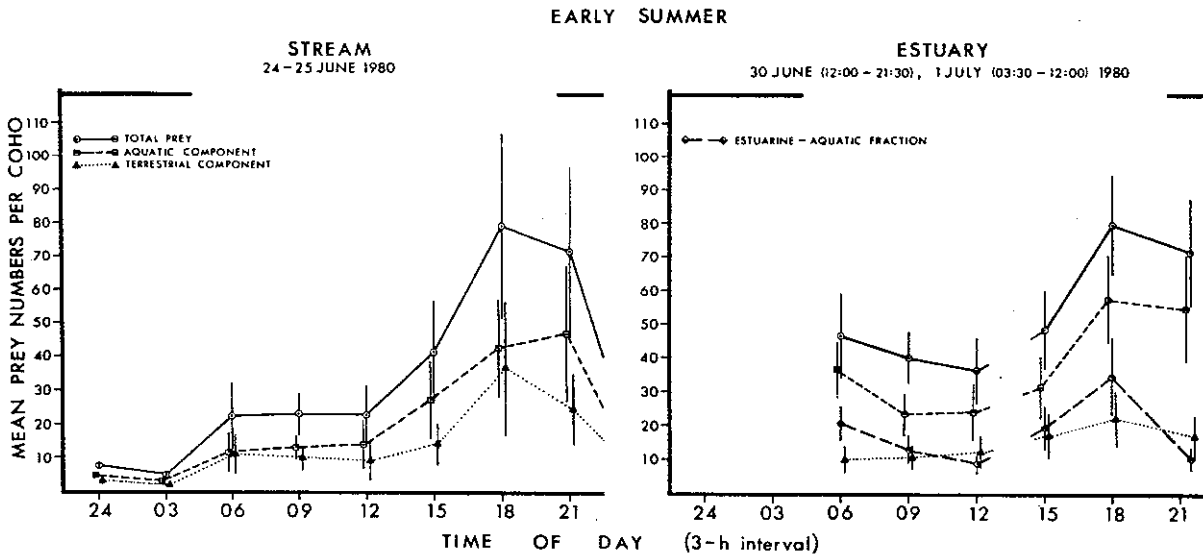
Figure 3. Numbers of prey contained within the stomachs of stream and estuary coho. High tides interrupted continuous sampling in the estuary; however, in the example given, estuary coho diurnally contained on average 54.3 ± 6.5 prey/fish•3h while similar-sized stream coho contained only 42.4 ± 8.4 prey/fish•3h (p <0.05). All means include 95% confidence limits.

moderately or infrequently. Direct observations of feeding behavior corroborated these data by showing that coho feeding activity was significantly elevated by tidal cycling. The numbers of feeding movements made by estuary coho during periods of flooding/high tide and during the first hour of the receding tide exceeded those made simultaneously by stream coho by 3.6 fold on average (see Tschaplinski, 1987).

Increased feeding activity in estuary coho was not due solely to increased availability of drifting prey. Estuary juveniles were also able to feed directly upon the benthos, especially during periods of flooding and high tide. Stream coho directed < 4% of their daily feeding movements toward epibenthic prey. On the other hand, estuary fry at the same time made upward of 17% of their feeding movements toward the benthos. Moreover, one-half of all the feeding activity of estuary coho on two occasions was directed benthically during brief periods of flooding and high tide when saline water intruded over the sediments. Coho in the estuary were thus able to

feed directly upon the most abundant prey occurring in the Carnation Creek watershed whereas benthic invertebrates were spatially unavailable to stream fry and yearlings.

Quantitative comparisons between the species proportions of the coho diet and those of drift, benthic, and surface-trap samples revealed that the greatest amount of overlap occurred consistently between the diet and drift in both the stream and estuary. The index of Moriseta (1959), modified by Horn (1966), demonstrated that "significant" overlap $(C_\lambda \geq 0.6)$ occurred in each monthly comparison of diet and drift, and confirmed other data showing that drifting invertebrates were the most important immediate source of prey for stream-dwelling and estuarine juveniles (Table 2). Only the drift contained both aquatic and terrestrial invertebrates which together comprised the broad prey specturm of stream and estuary populations. Both the benthos and surface-trap samples thus lacked an important food component used regularly by young coho.

132

Table 2. Values of the index of Moriseta (1959) modified by Horn (1966) measuring the overlap (C_λ) between the taxonomic composition of prey found in coho stomachs with the overall taxonomic composition of prey sampled from the drift, benthos, and air-water interface. Overlap values range from 0 to 1. By convention, values > 0.6 are considered to represent "substantial" overlap.

Environment	Date	Drifting Prey	Benthic Prey	Terrestrial Prey at Air-Water Interface
Stream	1-2 May 1981	0.82	0.55	0.27
	28-29 May 1980	0.86	0.44	0.21
	24-25 June 1980	0.59	0.48	0.32
	23-24 July 1980	0.90	0.46	0.24
	6-7 October 1980	0.95	0.65	0.20
Estuary	1-2 May 1981	0.80	0.40	0.47
	28 May - 7 June 1980	0.80	0.66	0.43
	30 June - 1 July 1980	0.82	0.81	0.18
	29-30 July 1980	0.87	0.89	0.03
	18/23 September 1980	0.77	0.67	0.18

Seasonally, C_λ values for correlations between drift and diet ranged from 0.77 to 0.87 in the estuary, and between 0.59 and 0.95 in the stream. Correlations between coho diet and benthos showed that overlap was usually limited in the stream (C_λ = 0.44-0.55) except in autumn when an overlap of 0.65 was observed (Table 2). However, the significant overlap occurring in October did not reflect direct predation upon the benthos because stream coho made few benthic feeding movements. Instead, the increased overlap was due to (a) the similarity between the taxonomic composition of the benthos and the aquatic component of the stream drift, and (b) the low numbers of terrestrial insects available in the drift in autumn.

In contrast with the stream, substantial overlap occurred between the composition of the coho diet and estuary benthos in most analyses (Table 2). Overlap values for 1980 ranged between 0.66-0.89 and resembled those determined between the diet and drift. Although the taxonomic composition of the estuary benthos corresponded closely to that of the drift, the high overlap between coho diet and benthos was caused partly by coho feeding directly on the bottom fauna in that environment.

The least amount of overlap between any food source and the coho diet was observed for terrestrial prey caught on sticky traps at the air-water interface (Table 2). Overlap was uniformly low in all months in the stream, ranging seasonally between 0.20-0.32. In the estuary, overlap coefficients fell to as low as 0.18-0.03 from mid-to-late summer. All observations suggested that neither fry nor yearlings were able to capture the numerous, large-sized aerial insects which were active just above the surfaces of pools. Although these insects were abundant and contacted pool surfaces frequently, both stream and estuary coho captured most of their terrestrial prey from the drift.

The diets of stream and estuary coho were highly varied and included almost all of the species identified from benthic, drift, and surface-trap samples. Over 340 prey categories including the larvae, pupae, and adults of numerous insect species were consumed by coho in both environments. Most taxa, especially terrestrial species, weere eaten in small numbers, and many occurred sporadically in both the coho diet and environmental samples throughout the season. Only 26 species in the stream and 30 in the estuary each formed at least one

percent of the coho diet in the respective environments in any of the monthly studies. All prey important in the coho diet were also present in drift samples in similar or identical numerical rankings (Tschaplinski, 1987). Because coho appeared to feed expediently on the most abundant prey items and usually did not differentiate between species, the diets of stream and estuary coho were described and analyzed seasonally after combining most prey species and genera into common families or even broader taxonomic categories (Tables 3, 4).

Ranked numerically in descending order, the insect orders Diptera (flies), Ephemeroptera (mayflies), Collembola (springtails), Plecoptera (stoneflies), and Trichoptera (caddisflies) collectively formed 89% of the prey of stream coho at all times. The Diptera, consisting of both aquatic (larvae and pupae), and terrestrial life stages (mainly aerial adults) together composed 48% of the coho diet numerically, 30% of it by volume, and 39% by IRI in mid-summer (Tschaplinkski, 1987).

The Chironomidae were by far the most abundant dipterans in the stream benthos and drift, and in turn this family was the most important one used for food by stream coho. Seven principal species plus numerious rare ones together formed 28-44% of the coho diet monthly. Aquatic larvae and pupae composed respectively 10-20 and 1-9% of the diet of stream fry and yearlings, while aerial adults simultaneously formed 10-16% throughout the season.

Mayfly nymphs were the most common aquatic prey of stream coho by all measures, forming 14-37% of the diet monthly. The Baetidae (mainly *Baetis tricaudatus*) which formed 5-28% of the diet, and *Paraleptophlebia sp.* (Leptophlebiidae) which composed 1-15% of all items counted from the stomachs of stream coho, were the dominant mayflies in all months. Additionally, *Ameletus* sp (Siphlonuridae) was consumed in substantial numbers when it was available in the drift in spring (Table 3).

Other prey formed important fractions fo the coho diet when they were available in the drift. For example, stonefly nymphs (mainly *Alloperla sp.* group), which were abundant benthically but usually present in the drift and diet in low or moderate numbers, composed 16% of diet numerically in early spring at the same time that they formed 12% of the stream drift.

Like their stream-dwelling counterparts, estuary coho fed opportunistically on any available invertebrate prey. However, only two invertebrate orders, the Diptera and Amphipoda, together formed 61-89% of the diet of estuary fry in both 1980 and 1981 (Table 4). The Diptera alone were overwhelmingly the most important food source of estuary coho, forming upward of 61% of the diet numerically, 34% of it by volume, and 52% by IRI. In turn, most dipterans were aquatic and aerial chironomids. Collectively, chironomids formed 31-51% of the coho diet monthly (Table 4). Aquatic larvae and pupae composed respectively 8-35 and 3-10% of the prey consumed by estuary fry and yearlings throughout the study, while aerial adults simultaneously formed 9-21% of their diet.

All data lead to the conclusion that juvenile coho are generalist predators, readily able to feed upon whatever prey was spatially or temporally available. Generalized feeding habits allowed emigrant coho from the stream to adapt to most prey species occurring intertidally. Consequently, "estuarine-aquatic" species consisting mainly of intertidal crustaceans (amphipods and isopods) formed 30-33% of the coho diet monthly in 1980. These percentages were extraordinarily invariant throughout the season and indicated clearly that coho fry were able to prey effectively upon estuarine invertebrates soon after emigrating from the stream regardless of the complex salinity and temperatures regimes occurring intertidally. Estuarine-aquatic species formed 39-50% of the benthic fauna and ~15-23% of the drift monthly; therefore, coho fed upon them efficiently in amounts equalling or exceeding the proportions composed by these species in environmental samples.

Corophium spinicorn (Corophiidae) and *Eogammarus confervicolus* were the two estuarine-aquatic species most frequently used for food by juvenile coho. *Corophium*, a tube-dwelling amphipod, was seasonally the most important prey species in the estuary, forming 19-24% of all prey which coho consumed in 1980. In comparison, the amphipod *E. confervicolus* composed numerically 5-13% of the coho diet throughout the study. The isopod *Gnorimosphaeroma oregonense* made up the remainder of the estuarine-aquatic prey consumed by coho fry and yearlings (Table 4).

The diets of juvenile coho salmon in both the stream and estuary at Carnation Creek remained largely

Table 3a. Seasonal prey of juvenile coho salmon in Carnation Creek. Prey items are ranked by percent numerical abundance. Statistics were determined from samples of coho collected at 3-hour intervals between 06:00 and 21:00 h. Each sample consisted of 10-12 coho. All prey numbers were determined from pooled data. Most prey items are given at the family level and most taxa comprising <1% of the diet are omitted. Only major genera and species are listed below (L = larvae, P = pupae, N = nymphs, A = adults, AQ = aquatic, T = terrestrial).

| | 1-2 MAY 1981 | | 28-29 MAY 1980 | | 24-25 JUNE 1980 | | 23-24 JULY 1980 | | 6-7 OCTOBER 1980 | |
TAXON	Numbers	Percent of Total	Numbers	Percent of Total	Numbers	Percent of Total	Numbers	Percent of Total	Numbers	Percent of Total
COPEPODA: Cyclopoida: Cyclopidae: Eucyclops serrulatus (AQ)	0	0	6	0.2	0	0	5	0.2	11	0.5
Harpacticoida: Canthocamptidae: Bryocamptus (2 spp.) (AQ)	0	0	5	0.2	2	0.1	22	0.9	14	0.7
ARACHNIDA: ACARINA: (A) Trombidiformes (All; AQ)	43	1.9	272	10.4	102	3.7	123	5.0	94	4.6
1. Hygrobatidae (2 spp.)	16	0.7	34	1.3	8	0.3	25	1.0	15	0.7
2. Arrenuridae: Arrenurus sp.	11	0.5	126	4.8	80	2.9	14	0.6	0	0
3. Torrenticolidae (2 spp., mainly Torrenticola sp.)	9	0.4	77	2.9	9	0.3	44	1.8	56	2.8
4. Aturidae: Aturus sp.	1	< 0.1	18	0.7	0	0	17	0.7	9	0.4
(B) Oribatei (All; AQ/T)	14	0.6	15	0.6	8	0.3	11	0.4	12	0.6
(C) Others (Prostigmata, Astigmata, Mesostigmata)	7	0.3	7	0.3	1	< 0.1	3	0.1	8	0.4
INSECTA: (A) Collembola (All; AQ/T)	135	6.0	221	8.4	326	11.9	257	10.4	82	4.0
1. Hypogastruridae	38	1.7	53	2.0	135	4.9	88	3.6	7	0.3
2. Isotomidae	42	1.9	31	1.2	75	2.7	67	2.7	51	2.5
3. Sminthuridae	53	2.3	137	5.2	104	3.8	96	3.9	24	1.2
(B) Ephemeroptera (All, A/N)	584	25.8	373	14.3	656	23.8	683	27.6	760	37.3
Nymphs (AQ)	578	25.6	361	13.8	643	23.4	675	27.3	757	37.1
1. Baetidae (N; 4 spp., mainly Baetis 3 spp.)	203	9.0	278	10.6	134	4.8	348	14.1	568	27.9
2. Siphlonuridae (N; mainly Ameletus sp.)	130	5.8	37	1.4	41	1.5	16	0.7	9	0.4
3. Heptageniidae (N; All)	56	2.5	30	1.2	61	2.2	79	3.2	17	0.8
(a) Cinygmula reticulata and C. ramaleyi	17	0.8	8	0.3	29	1.1	56	2.3	16	0.8
(b) Epeorus (Iron) sp.	39	1.7	22	0.8	25	0.9	23	0.9	1	0.1
4. Leptophlebiidae: Paraleptophlebia (2 spp.; N)	133	5.9	16	0.6	402	14.6	232	9.4	163	8.0
(C) Plecoptera (All, A/N)	357	15.8	24	0.9	95	3.5	84	3.4	110	5.4
Nymphs (AQ)	353	15.6	24	0.9	95	3.5	84	3.4	110	5.4
1. Chloroperlidae (N; 3 spp.)	291	12.9	24	0.9	92	3.4	77	3.1	92	4.5
(a) Alloperla sp. grp.	225	10.0	21	0.8	82	3.0	73	3.0	67	3.3
(b) Kathcoperla perdita	66	2.9	3	0.1	8	0.3	4	0.2	25	1.2
2. Leuctridae: Leuctra sp. grp.	57	2.4	0	0	0	0	7	0.3	0	0
(D) Psocoptera (A/N, T; 2 fam., 2 spp.)	15	0.7	39	1.5	30	1.1	43	1.7	18	0.9

135

Table 3b. Seasonal prey of juvenile coho salmon in Carnation Creek. Prey items are ranked by percent numerical abundance. Statistics were determined from samples of coho collected at 3-hour intervals between 06:00 and 21:00 h. Each sample consisted of 10-12 coho. All prey numbers were determined from pooled data. Most prey items are given at the family level and most taxa comprising <1% of the diet are omitted. Only major genera and species are listed below (L = larvae, P = pupae, N = nymphs, A = adults, AQ = aquatic, T = terrestrial).

TAXON	1-2 MAY 1981 Numbers	Percent of Total	28-29 MAY 1980 Numbers	Percent of Total	24-25 JUNE 1980 Numbers	Percent of Total	23-24 JULY 1980 Numbers	Percent of Total	6-7 OCTOBER 1980 Numbers	Percent of Total
(E) Hemiptera (A/N, T; 11 spp.)	4	0.2	1	< 0.1	0	0	6	0.2	0	0
(F) Homoptera (A/N, T; mainly Aphididae; 12 spp.)	19	0.8	5	0.2	12	0.4	24	1.0	6	0.3
(G) Coleoptera (A/L; AQ/T)	27	1.2	22	0.8	49	1.8	47	1.9	31	1.5
(H) Trichoptera (All; L/P/A)	12	0.5	38	1.5	89	3.2	61	2.5	36	1.8
Larvae and pupae (AQ)	12	0.5	38	1.5	86	3.1	61	2.5	36	1.8
1. Limnephilidae (7 spp.)	3	0.1	6	0.2	25	0.9	19	0.8	5	0.3
2. Hydroptilidae (Agraylea sp.)	5	0.2	9	0.3	22	0.8	13	0.5	0	0
(I) Diptera: 1. Dixidae: Dixella sp. (L/P, AQ)	0	0	8	0.3	18	0.7	13	0.5	2	0.1
2. Ceratopogonidae (All; 14 spp.)	138	6.1	147	5.6	233	8.5	135	5.5	5	0.3
(a) larvae (AQ)	25	1.1	4	0.2	14	0.5	7	0.3	0	0
(b) pupae/emerging adults (AQ)	17	0.8	0	0	18	0.7	20	0.8	0	0
(c) adults (T)	96	4.2	143	5.5	201	7.3	108	4.4	5	0.3
3. Chironomidae (All; 31 spp.)	699	30.9	1 163	44.4	766	27.8	723	29.2	686	33.7
(a) larvae (AQ)	223	9.9	511	19.5	337	12.3	271	11.0	416	20.4
(b) pupae/emerging adults (AQ)	171	7.6	229	8.8	21	0.8	122	4.9	74	3.6
(c) adults (T)	305	13.5	423	16.2	408	14.8	330	13.3	196	9.6
4. Simuliidae (L/P/A; AQ/T; mainly Simulium sp.)	21	0.9	37	1.4	21	1.1	12	0.5	8	0.4
5. Sciaridae (A,T; 6 spp.)	33	1.5	25	1.0	74	1.6	44	1.8	20	1.0
6. Cecidomyiidae (A/L; T; 9 spp.)	64	2.8	59	2.3	119	4.3	87	3.5	35	1.7
7. Empididae (L, P, A; AQ/T; 12 spp.)	15	0.7	48	1.8	41	1.5	36	1.5	22	1.1
(J) Hymenoptera (A, T; 15 fam., > 20 spp.)	36	1.6	51	2.0	30	1.1	49	2.0	34	1.7
Total Aquatic Prey	1 559	68.9	1 669	63.8	1 635	59.4	1 602	64.7	1 592	78.1
Total Terrestrial Prey	703	31.1	949	36.3	1 119	40.6	873	35.3	446	21.9
Number of Coho in Sample	60		65		65		65		60	

Table 4a. Seasonal prey of juvenile coho salmon in the Carnation Creek estuary. Prey items are ranked by percent numerical abundance. Statistics were determined from samples of coho collected at 3-hour intervals between 06:00 and 21:00 h. Each sample consisted of 8-12 coho. All prey numbers were determined from pooled data. Only major genera and species are listed below. (L = larvae, P = pupae, N = nymphs, A = adults, AQ = aquatic, AQ-MAR = "marine" or estuarine-aquatic, T = terrestrial).

	1-2 MAY 1981		28 MAY-7 JUNE 1980		30 JUNE-1 JULY 1980		29-30 JULY 1980		18-23 SEPTEMBER 1980	
TAXON	Numbers	Percent of Total	Numbers	Percent of Total	Numbers	Percent of Total	Numbers	Percent of Total	Numbers	Percent of Total
ANNELIDA: POLYCHAETA: Nereidae: Nereis (2 spp.; AQ-MAR)	3	0.1	11	0.3	8	0.3	7	0.2	13	0.4
OLIGOCHAETA: Enchytraeidae (AQ)	15	0.5	3	0.1	10	0.3	2	0.1	11	0.3
COPEPODA: Cyclopoida: Cyclopidae: Eucyclops serrulatus (AQ)	10	0.3	0	0	3	0.1	1	< 0.1	4	0.1
Harpacticoida: Canthocamptidae: Bryocamptus (2 spp., AQ)	0	0	42	1.3	28	0.9	38	1.1	2	0.1
Harpacticidae: Harpacticus uniremis (AQ-MAR)	4	0.1	9	0.3	29	1.0	50	1.4	27	0.8
ISOPODA: Sphaeromatidae: Gnorimosphaeroma oregonense (AQ-MAR)	7	0.2	12	0.4	95	3.1	177	4.9	148	4.5
AMPHIPODA: 1. Anisogammaridae: Eogammarus confervicolus (AQ-MAR)	426	13.4	173	5.1	241	7.9	189	5.3	150	4.6
2. Corophiidae: Corophium spinicorne (AQ-MAR)	134	4.2	811	24.1	625	20.6	673	18.8	744	22.8
ARACHNIDA: ACARINA: (A) Trombidiformes (All; 9 fam., 13 spp.)	97	3.1	27	0.8	21	0.7	16	0.5	14	0.5
(B) Oribatei (All, AQ/T)	26	0.8	8	0.2	11	0.4	22	0.6	17	0.5
(C) others (Prostigmata, Astigmata, Mesostigmata)	17	0.5	3	0.1	3	0.2	13	0.4	4	0.1
INSECTA: (A) Collembola (All; AQ/T)	285	9.0	14	0.4	184	6.1	281	7.8	375	11.5
1. Hypogastruridae	96	3.1	10	0.3	46	1.5	57	1.6	104	3.2
2. Isotomidae	122	3.9	3	0.1	79	2.6	100	2.8	67	2.1
3. Sminthuridae	67	2.1	1	< 0.1	59	1.9	124	3.5	202	6.2
(B) Ephemeroptera (All; A/N)	244	7.7	14	0.4	0	0	2	0.1	7	0.2
Nymphs (AQ)	236	7.4	14	0.4	0	0	2	0.1	7	0.2
1. Baetidae (N; Baetis 2 spp.)	111	3.5	12	0.4	0	0	2	0.1	0	0
2. Siphlonuridae: Ameletus sp. (N)	39	1.2	2	0.1	0	0	0	0	0	0
3. Heptageniidae: Cinygmula reticulata and C. ramaleyi (N)	33	1.0	0	0	0	0	0	0	0	0
4. Leptophlebiidae: Paraleptophlebia (2 spp.; N)	53	1.7	0	0	0	0	0	0	7	0.2

137

Table 4b. Seasonal prey of juvenile coho salmon in the Carnation Creek estuary. Prey items are ranked by percent numerical abundance. Statistics were determined from samples of coho collected at 3-hour intervals between 06:00 and 21:00 h. Each sample consisted of 8-12 coho. All prey numbers were determined from pooled data. Only major genera and species are listed below. (L = larvae, P = pupae, N = nymphs, A = adults, AQ = aquatic, AQ-MAR = "marine" or estuarine-aquatic, T = terrestrial).

TAXON	1-2 MAY 1981 Numbers	Percent of Total	28 MAY-7 JUNE 1980 Numbers	Percent of Total	30 JUNE-1 JULY 1980 Numbers	Percent of Total	29-30 JULY 1980 Numbers	Percent of Total	18-23 SEPTEMBER 1980 Numbers	Percent of Total
(C) Plecoptera (All; A/N)	77	2.4	12	0.4	7	0.2	6	0.2	9	0.3
Nymphs (AQ)	68	2.1	12	0.4	7	0.2	6	0.2	9	0.3
1. Chloroperlidae (N; 3 spp.)	40	1.3	12	0.4	5	0.2	1	< 0.1	9	0.3
(a) Alloperla sp. grp.	40	1.3	12	0.4	5	0.2	1	< 0.1	9	0.3
2. Leuctridae: Leuctra sp. grp.	28	0.9	0	0	2	0.1	5	0.1	0	0
(D) Psocoptera (A/N; T; 2 fam., 2 spp.)	42	1.3	8	0.2	18	0.6	30	0.8	61	1.9
(E) Thysanoptera: Aeolothripidae: Aeolothrips annectens (A/N; T)	18	0.6	3	0.1	14	0.5	24	0.7	88	2.7
(F) Hemiptera (A/N, T; 5 fam., 6 spp.)	9	0.3	3	0.1	6	0.2	15	0.4	43	1.3
1. Miridae	9	0.3	2	0.1	6	0.2	14	0.4	43	1.3
(G) Homoptera (A/N, T; 5 fam., 10 spp.)	144	4.5	100	3.0	37	1.2	52	1.5	164	5.0
1. Aphididae (mainly Aphis sp. and Macrosiphum spp.)	140	4.4	92	2.7	37	1.2	50	1.4	157	4.8
(H) Coleoptera (A/L; AQ/T)	64	2.0	25	0.7	40	1.3	27	0.8	34	1.0
(I) Trichoptera (L; AQ)	8	0.3	5	0.2	2	0.1	3	0.1	0	0
(J) Diptera: 1. Ceratopogonidae (All; 12 spp.)	181	5.7	136	4.0	62	2.0	33	0.9	42	1.3
(a) larvae (AQ)	3	0.1	14	0.4	0	0	0	0	0	0
(b) pupae/emerging adults (AQ)	34	1.1	0	0	0	0	0	0	0	0
(c) adults (T)	144	4.5	122	3.6	62	2.0	33	0.9	42	1.3
2. Chironomidae (All; 28 spp.)	1 160	36.6	1 718	51.0	1 442	47.4	1 786	49.8	1 026	31.4
(a) larvae (AQ)	266	8.4	708	21.0	846	27.8	1 260	35.2	511	15.6
(b) pupae/emerging adults (AQ)	317	10.0	296	8.8	132	4.3	191	5.3	93	2.8
(c) adults (T)	577	18.2	714	21.2	464	15.3	335	9.3	418	12.8
3. Mycetophilidae (A, T; 5 spp.)	21	0.7	36	1.1	16	0.5	4	0.1	5	0.2
4. Sciaridae (A, T; 4 spp.)	47	1.5	15	0.5	23	0.8	10	0.3	8	0.2
5. Empididae (All; AQ/T; 12 spp.)	59	1.9	105	3.1	48	1.6	26	0.7	15	0.5
(a) pupae/emerging adults (mainly AQ)	4	0.1	56	1.7	10	0.3	0	0	3	0.1
(b) adults (T)	55	1.7	49	1.5	38	1.3	26	0.7	12	0.4
(K) Hymenoptera (A, T; 15 fam., 30 spp.)	40	1.3	31	0.9	38	1.3	67	1.9	208	6.4
1. Mymaridae	27	0.9	0	0	18	0.6	45	1.3	55	1.7
2. Pteromalidae	0	0	3	0.1	7	0.2	8	0.2	71	2.2
3. Platygasteridae	7	0.2	0	0	12	0.4	10	0.3	74	2.3
Total Aquatic Prey	1 856	58.5	2 246	66.7	2 209	72.6	2 752	76.8	1 868	57.1
Total "Marine" or Estuarine Prey	589	18.6	1 019	30.3	998	32.8	1 096	30.6	1 082	33.1
Total Terrestrial Prey	1 316	41.5	1 120	33.3	832	27.4	833	23.3	1 401	42.9
Number of Coho in Sample	60		55		56		55		60	

unchanged seasonally between May and September/October (Tables 3, 4). The ranking of the principal families, genera, and species in the diets of juvenile coho displayed no clear seasonal patterns in either environment; nevertheless, all monthly shifts in the species used for food conformed most closely with changing patterns of relative abundance of the same invertebrate taxa occurring in the drift.

Values of the Linear Index of Food Selection (L) applied to the same food categories used to describe the seasonal prey of stream and estuary coho revealed that the proportions of the coho diet formed by each prey taxon corresponded closely to the percentages these invertebrates formed in the drift. No selection values > -0.23 or +0.14 were determined for any estuary prey taxon between the coho diet and drift, and none occurred outside the range bounded by -0.21 and +0.15 in the stream (Tschaplinski, 1987). Therefore, most prey species were neither strongly preferred nor avoided by coho because most "L" values were close to zero in both environments (Tschaplinski, 1987). Stream and estuary coho were clearly feeding opportunistically upon most invertebrates in direct proportion to the numerical abundance these prey formed in drift samples.

Some taxa such as fish (or fish larvae) and oligochaete worms were nevertheless avoided by coho or unavailable to them, and were thus associated with negative (and significant) L values. At no time were Carnation Creek coho predators of other fish species. Additionally, several L values determined between the coho diet and benthic taxa were negative and significant in both environments (see Tschaplinski, 1987). This trend implies strongly that most invertebrates living within the benthic sediments were spatially unavailable to coho despite observations revealing that estuary fry fed frequently on the bottom fauna. Many benthic prey must first enter the drift before stream or estuary coho are able to use them for food.

The results of this investigation show emphatically that most species in the drift were available to stream and estuary coho. Given that (1) the potential prey of estuary coho were several fold more abundant than those available to coho upstream, and (2) aquatic drift abundance is partly a function of production rates in benthic invertebrate populations (Muller,1974), it is concluded that the ability of estuary coho to use most of these invertebrates in proportion to their abundance directly links the increased growth rates of estuary coho to the increased secondary productivity occurring in that environment compared to the stream.

Coho fry in the estuary were clearly not food limited. The late-summer population in 1980 was double that in 1979; however, estuary fry grew equally rapidly in the two years. Mean instantaneous growth rates (in length) in 1979 were 0.133 ± 0.029 (i.e. 13.3% per month), and were no less than 0.124 ± 0.012 in 1980 (Tschaplinksi, 1987). In comparison, mean monthly increments in the stream zone were only 0.084 and 0.064 in 1979 and 1980 respectively. Moreover, Holtby and Hartman (1982) reported that the instantaneous growth rates of stream coho were density-dependent during summer, and low rates in years such as 1980 were associated with populations that were unusually large. Low growth rates in the stream were also negatively correlated with the number and duration of minimum stream flows during summer (Holtby and Hartman, 1982), intimating strongly that reductions in the abundance and availability of drifting food organisms underlay poorer seasonal growth in stream-resident coho populations. Estuary food resources were sufficiently abundant that similar density-dependent growth reductions were not observed between years in that environment.

IMPLICATIONS FOR COHO MANAGEMENT, ENHANCEMENT AND PRESERVATION

Only limited numbers (300) of estuary coho fry leaving the watershed after their first summer of growth have presently been marked. Consequently, only small numbers (9) have been found to return to the watershed in subsequent years, and all returns have been jacks (small-sized, sexually mature males, < two years old). The numbers of estuary-reared juveniles returning to the watershed to spawn have yet to be determined accurately. Despite this limitation, this investigation has demonstrated that coho salmon fry occur naturally in estuaries, adapt readily to the physiological rigors and abundant food resources of the intertidal zones of streams, rapidly outgrow their stream-dwelling counterparts, and can contribute some spawners for the following generation.

Recent data from Porcupine Creek, Alaska has revealed that estuary-reared coho form upward of 30% of all coho rearing in that watershed and can comprise up to 50% of the adults returning to spawn (see Thedinga and Koski, 1984). The estuary at

Porcupine Creek forms only 27% of the total rearing habitat in that watershed. Small estuaries therefore appear to be potentially important rearing areas for coho fry as observed in several streams on Vancouver Island and elsewhere on the Pacific coast, and should be considered by biologists, fisheries managers, and land-use planners.

Data on estuary coho at Carnation Creek are unavailable for most of the years that the watershed has been studied. Therefore, the historical contribution that estuary coho have made toward both juvenile and adult populations is unknown but should not be discounted simply because the information has not been gathered. Population surveys have shown that most emigrant fry do not become established as estuary residents. Less than 23 and 9% of the total numbers leaving the stream in 1979 and 1980 respectively remained in the estuary by the end of summer. Although late-summer populations in the estuary amounted roughly to 10% of those upstream, there are several important implications for the use of estuaries as rearing areas for juvenile salmonids. In some watersheds, populations of large, rapidly-growing estuarine coho fry might (a) provide significant numbers of smolts to ocean-dwelling populations, especially in years when low numbers of smolts are produced upstream, and (b) augment the numbers of adults returning to the watershed to spawn. Additionally, all estuaries appear to provide salmonid smolts with a transition zone between freshwater and marine environments in which they may reside in deep pools for variable periods of time, complete the fry-smolt transformation, and acclimate to saline water.

With reference to habitat preservation, logging-related practices which may destroy or alter estuarine habitats should be avoided or minimized. Reducing the harmful effects of log storage, siltation, or the input of wood chips and other small debris, not only maintains the integrity of the structural habitats which coho require, but also is important to preserve the stability and composition of benthic substrates which support large populations of invertebrate food organisms. Similarly, deciduous and coniferous vegetation essential for stabilizing banks and providing shelter for coho must also be maintained to (1) provide leaves and other organic material as a source of energy for detritus-based food webs which lead to the production of benthic invertebrates, and (2) directly contribute terrestrial insects as a source of food.

Since 1981, the Carnation Creek estuary has supported few fry. Populations have been reduced by 90% or more compared to levels assessed in 1980. Habitat destruction is directly responsible for these reduced numbers. Sedimentation and gravel movements have filled in side channels or have isolated them from the main channel. Main-channel pools which contained most of the estuary fry have virtually been eliminated due to the same substrate movements. Severe freshets have (1) caused bank collapse, (2) swept away large debris essential for the reduction of water velocities, and (3) caused associated changes in substrate distribution. Because estuaries may receive the sum of logging-related effects occurring upstream in the watershed, substantial damage to estuarine habitats appears to have been caused after logging and can be related to similar processes of habitat destabilization occurring at sites in the stream.

Because the habitat requirements of stream and estuary coho are similar, and because many of the physical processes affecting stream populations ultimately extend downstream to the estuary, common practices can be employed in streams and estuaries to manage, preserve, and enhance their coho populations. Ensuring that sources of large, woody debris are available in both environments will preserve optimum habitats by creating pools and reducing water velocities. Stabilizing flow regimes will also ensure the availability of drifting food organisms for coho. Juvenile coho fed upon both aquatic and terrestrial invertebrates in direct proportion to their availability in the drift. Therefore, enhancing prey availability should increase coho growth rates and production. Management techniques designed to provide optimum conditions for coho growth must ensure that (1) benthic invertebrate production is maintained or enhanced, and (2) sources of terrestrial invertebrates are provided or conserved.

Estuary populations might be enhanced by excavating stable secondary channels alongside major estuarine reaches to provide more habitat space in order to retain larger numbers of spring emigrants intertidally throughout the summer.

The conditions necessary for benthic invertebrate production can be ensured by allowing both tidal and fresh water to enter the new channels. Other channels might also be excavated in areas remote from tidal influence in order to provide sheltered habitats which fry might use optionally for

overwintering sites instead of moving seaward in autumn. The permanent weir at Carnation Creek might presently inhibit estuary fry from overwintering upstream, as most fry do in Porcupine Creek (Murphy et al. 1984). Nutrient enrichment or other methods for enhancing food production are likely inappropriate and unnecessary for both artificial and natural estuarine channels. High rates of primary and secondary production already occur in estuaries.

If enough space is available for constructing supplementary estuarine channels, complete with stabilized banks and shelter provided by large, woody debris (e.g., logs, fallen trees, root masses), coho production in small coastal watershed could be multiplied several fold without incurring the expenses required for nutrient addition or supplemental feeding.

Stream and estuary populations were considered separately, but may also be viewed as a single population of trophic generalists adapting behaviorally to feed upon different species of invertebrates in environments of contrasting salinities, flow patterns, food abundance, and prey availability. The seaward emigration of fry in spring does not have to be viewed as a disadvantage to juvenile coho. Rather, these movements can improve the feeding opportunities for coho fry and permit stream populations to disperse so that all habitats and food resources available in the watershed are fully used.

REFERENCES CITED

Au, D.W.K. 1972. Population dynamics of the coho salmon and its response to logging in three coastal streams. Ph.D. Thesis, Oregon State University, Corvallis, OR. 245 p.

Averett, R.C. 1969. Influence of temperature on energy and material utilization by juvenile coho salmon. Ph.D. Thesis, Oregon State University, Corvallis, OR. 74 p.

Canagaratnam, P. 1959. Growth rates of fishes in different salinities. J. Fish. Res. Board Can. 16: 121-130.

Clarke, W.C., J.E. Shelbourn, and J.R. Brett. 1978. Growth and adaptation to sea water in "underyearling" sockeye (*Oncorhynchus nerka*) and coho (*O. kisutch*) salmon subjected to regimes of constant or changing temperature and day length. Can. J. Zool. 56: 2413-2421.

Clarke, W.C., J.E. Shelbourn, and J.R. Brett. 1981. Effect of artificial photoperiod cycles, temperature, and salinity on growth and smolting in underyearling coho (*Oncorhynchus kisutch*), chinook (*O. tshawytscha*), and sockeye (*O. nerka*) salmon. Aquaculture 22: 105-116.

Conte, F.P., H.H. Wagner, J.C. Fessler, and C. Gnose. 1966. Development of osmotic and ionic regulation in juvenile coho salmon (*Oncorhynchus kisutch*). Comp. Biochem. Physiol. 18: 1-15.

Folmar, L.C. and W.W. Dickhoff. 1980. The parr-smolt transformation (smoltification) and seawater adaptation in salmonids. A review of selected literature. Aquaculture 21: 1-37.

Garrison, R.L. 1965. Coho salmon smolts in ninety days. Prog. Fish-Cult. 27: 219-220.

Heard, W.R. and R.A. Crone. 1976. Raising coho salmon from fry to smolts in estuarine pens, and returns of adults from two smolt releases. Prog. Fish-Cult. 38: 171-174.

Holtby, L.B. and G.F. Hartman. 1982. The population dynamics of coho salmon (*Oncorhynchus kisutch*) in a west coast rain forest stream subjected to logging. In Proceedings of the Carnation Creek workshop, A 10-year review. 24-26 February, 1982. Edited by G.F. Hartman. Pacific Biological Station, Nanaimo, B.C. pp. 308-347.

Horn, H.S. 1966. Measurement of "overlap" in comparative ecological studies. Am. Naturalist 100: 419-424.

Hyatt, K.D. 1979. Feeding strategy. In Fish physiology. Volume VIII. Edited by W.S. Hoar, D.J. Randall, and J.R. Brett. Academic Press. New York. pp. 71-119.

MacArthur, R.H. and R. Levins. 1967. The limiting similarity, convergence, and divergence of coexisting species. Am. Naturalist 101: 377-385.

Morisita, M. 1959. Measuring the interspecific association and similarity between communities. Memoirs of the Faculty of Science Kyushu University Series E (Biology) 3: 65-80.

Muller, K. 1974. Stream drift as a chronobiological phenomenon in running water ecosystems. Ann. Rev. Ecol. Syst. 5: 309-323.

Mundie, J.H. 1974. Optimization of the salmonid nursery stream. J. Fish. Res. Board Can. 31: 1827-1837.

Murphy, M.L., J.F. Thedinga, K.V. Koski and G.B. Grette. 1984. A stream ecosystem in an old-growth forest in southeast Alaska: Part V: Seasonal changes in habitat utilization by juvenile salmonids. In Fish and wildlife relationships in old-growth forests. Proceedings of a symposium held 12-15 April 1982, Juneau, Alaska. Edited by W.R. Meehan, T.R. Merrell Jr., and T.A. Hanley. American Institute of Fishery Research Biologists. pp. 89-98.

Odum, E.P. 1980. The status of three ecosystem-level hypotheses regarding salt marsh estuaries: tidal subsidy, outwelling, and detritus-based food chains. In Estuarine perspectives. Edited by V.S. Kennedy. Academic press, New York, London, Syndey, Toronto, and San Francisco. pp. 485-495.

Otto, R.G. 1971. Effects of salinity on the survival and growth of presmolt coho salmon (Oncorhynchus kisutch). J. Fish. Res. Board Can. 28: 343-349.

Otto, R.G. and J.E. McInerney. 1970. Development of salinity preference in pre-smolt coho salmon, Oncorhynchus kisutch. J. Fish. Res. Board Can. 27: 293-300.

Ready, R.C., E.L. Mills, and J.L. Confer. 1985. A new estimator of, and factors influencing, the sampling variance of the linear index of food

selection. Trans. Am. Fish. Soc. 114: 258-266.

Stockner, J.G. and K.R.S. Shortreed. 1976. Autotrophic production in Carnation Creek, a coastal rainforest stream on Vancouver Island, British Columbia. J. Fish. Res. Board Can. 33: 1553-1563.

Strauss, R.E. 1976. Reliability estimates for Ivlev's electivity index, the forage ratio, and a proposed linear index of food selection. Trans. Am. Fish. Soc. 108: 344-352.

Strauss, R.E. 1982. Influence of replicated subsamples and subsample heterogeneity on the linear index of food selection. Trans. Am. Fish. Soc. 111: 517-522.

Thedinga, J.F. and K.V. Koski. 1984. A stream ecosystem in an old-growth forest in southeast Alaska. Part VI: The production of coho salmon, Oncorhynchus kisutch smolts and adults from Porcupine Creek. In Fish and wildlife relationships in old-growth forests. Proceedings of a symposium held 12-15 April 1982, Junea, Alaska. Edited by W.R. Meehan, T.R. Merrell Jr., and T.A. Hanley. American Institute of Fishery Research Biologists. pp 99-108.

Tschaplinski, P.J. 1982. Aspects of the population biology of estuary-reared and stream-reared juvenile coho salmon in Carnation Creek: A summary of current research. In Proceedings of the Carnation Creek workshop, A 10-year review. 24-26 February 1982. Edited by G.F. Hartman. Pacific Biological Station, Nanaimo, B.C. p. 289-307.

Tschaplinski, P.J. 1987. Comparative ecology of stream-dwelling and estuarine juvenile coho salmon (Oncorhynchus kisutch) in Carnation Creek, Vancouver Island, British Columbia. Ph.D. Thesis, University of Victoria, Victoria, British Columbia. xviii + 530 p.