Winter habitat preferences of juvenile salmonids in two interior rivers in British Columbia

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The winter distribution and abundance of juvenile salmonids was investigated in various main channel and off-channel habitats in the Coldwater and Nicola rivers in the southern interior region of British Columbia. Catches were generally low in all main channel habitats, with coho salmon and steelhead trout being most abundant and chinook salmon and Dolly Varden char being present in smaller numbers. Coho salmon and steelhead trout catches were generally highest in pools with abundant instream and riparian cover. Steelhead trout was the main species in riprap bank protected areas, although catches were generally low. Highest overall catches were recorded in side channels and off-channel ponds, where water temperatures were usually several degrees higher than in the main river. Coho salmon was the main species in the two Coldwater off-channel ponds with overwintering populations of approximately 4000 and 1000 in 1- and 0.1-ha ponds, respectively (0.4-1.5 fish/m^2): overwinter survival of coho salmon in the ponds was estimated to be 87 and 54%, respectively . High densities of coho salmon were also recorded in side channels on the Nicola River (1.5–1.8 fish/m^2), together with smaller numbers of chinook salmon and steelhead trout (0.2–0.3 fish/m^2). Growth in ponds and side channels appeared to be faster than in main channel habitats. We conclude that juvenile salmonids in the rivers investigated showed considerable habitat segregation during the winter. As in coastal rivers, juvenile coho salmon made extensive use of off-channel ponds, while rainbow trout and chinook salmon were generally most abundant in riprap and deep pools containing log debris, respectively.

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L'abondance et la répartition d'hiver des jeunes saumons a fait l'objet d'une étude dans les rivières Coldwater et Nicola, dans le sud de la Colombie-Britannique, à l'intérieur des terres; des habitats situés dans le canal central du cours d'eau et d'autres situés hors du canal central ont été échantillonnés. Les captures étaient généralement peu abondantes dans les habitats du canal central et elles étaient dominées par le saumon coho et la truite steelhead et contenaient aussi des nombres assez importants de Dolly Vardens et de saumons chinook. Le saumon coho et la truite steelhead étaient particulièrement abondants dans les bassins à couverture végétale importante à la fois dans le cours d'eau et sur les berges. La truite steelhead était l'espèce dominante dans les régions protégées à rives enrochées, bien que les captures aient été peu abondantes dans ces milieux. Les captures les plus riches ont été faites dans les canaux latéraux et les étangs isolés où la température de l'eau atteignait un point de plusieurs degrés plus élevé que l'eau du cours d'eau principal. Le saumon coho était l'espèce principale en deux étangs latéraux du bassin de la rivière Coldwater et la densité des populations d'hiver a atteint 4000 poissons dans l'étang de 1 ha (survie de 87%) et 1000 poissons dans l'étang de 0,1 ha (survie de 54%) (0,4–1,5 poisson/m^2). De fortes densités de saumons coho ont été enregistrées également dans les canaux latéraux de la rivière Nicola (1,5–1,8 poisson/m^2) où habitaient aussi des populations plus petites de saumons chinook et de truites steelhead (0,2–0.3 poisson/m^2). La croissance a semblé plus rapide dans les étangs et les canaux latéraux que dans le canal central. Il faut conclure que les jeunes salmonidés de ces rivières font preuve d'une forte ségrégation d'habitat au cours de l'hiver. Tout comme dans les cours d'eau côtiers, les jeunes saumons coho de ces régions préfèrent les étangs isolés, alors que la truite arc-en-ciel abonde dans les bassins à rives bien enrochées et le saumon chinook, dans les basins profonds contenant beaucoup de débris ligneux.

[Traduit par la revue]

Introduction

In coastal streams and rivers of the Pacific Northwest, juvenile salmonids often undergo a marked seasonal habitat redistribution in response to changes in environmental conditions. This relocation is often most apparent in juvenile coho salmon (*Oncorhynchus kisutch*). In spring and summer, juvenile coho salmon occupy a wide variety of main-channel habitats, but are usually most pronounced in slow-moving pools with abundant instream and bankside cover (Hartman 1965; Lister and Genoe 1970; McMahon 1983; Ruggles 1966). In contrast, juvenile rainbow trout and steelhead trout (*Salmo gairdneri*) fry usually occupy riffle areas during the summer, while larger fish live in pools (Hartman 1965; Raleigh et al. 1984). In autumn, as water temperatures decrease, juvenile coho salmon become less active and move into deeper, slower flowing water in or very near dense instream cover (Bustard and Narver 1975*a*; Hartman 1965). In many streams, particularly where such pools are lacking, coho salmon also move into tributaries, side channels, slough areas, and riverine ponds (Bustard and Narver 1975*a*; Cederholm and Scarlett 1981; Peterson 1982*a*, 1982*b*; Tschapalinski and Hartman 1983). Such shifts in distribution could be a behavioural response to avoid unfavourable high winter discharges, low water temperatures, and predation (Hartman et al. 1982). During winter, most juvenile salmonids appear to show restricted movements, with most fish being closely associated with instream cover areas such as log jams, root wads, and other instream organic debris (Bustard and Narver 1975*a*; Raleigh et al. 1984). It has been suggested that in some streams, the major factor limiting salmonid abundance may be the extent of overwintering habitat, rather than the amount of summer rearing habitat (Bustard and Narver 1975*a*; Hall and Knight 1981; Mason 1976).

In the Pacific Northwest, seasonal shifts in habitat distribution among juvenile salmonids are best known for coastal rivers.

Relatively little is known of the overwintering ecology of salmonids in streams and rivers of interior regions, which are less affected by coastal and oceanic influences. Interior rivers experience much harsher winter conditions than coastal rivers, with colder temperatures and heavier snowfall. In coastal rivers, winter is typically a period of high flows as a result of heavy rainfall, while interior rivers often freeze over and show very low flows until the spring snowmelt. Fish sampling difficulties related to the severe weather conditions may account for the few detailed studies on the winter ecology of juvenile salmonids in interior rivers. A recent study suggests that differences in mophological characteristics exist between inland coho salmon populations and those in coastal rivers, which may be linked to the often extensive freshwater migrations in interior river systems (Taylor and McPhail 1985). Consequently, interior populations of salmonids may exhibit ecological and behavioural characteristics that differ from those of coastal populations. There is a need for more information on the winter distribution and habitat requirements of juveile salmonids in interior rivers to identify the major factors limiting salmonid abundance during the freshwater rearing phase. The objective of this study was to investigate the distribution and abundance of juvenile salmonids in various main-channel and off-channel habitats in two interior rivers in southwestern British Columbia.

Study area and methods

Study area

The study was carried out on the Coldwater and Nicola rivers, tributaries of the Thompson River, which drains into the Fraser River at Lytton (Fig. 1). The Coldwater River has its origin at 1372 m above sea level in the Cascade Mountains of southern British Columbia and flows northeast for 94 km to its junction with the Nicola River near the town of Merritt at 579 m above sea level on the Thompson plateau. The river drains an area of 914 km^2. Annual precipitation ranges from 101 cm in the upper reaches of the river to 30 cm at Merritt. The valley of the Coldwater River above Kingsvale is presently the site of a major new highway being constructed between the towns of Hope and Merritt. Although some areas of the river are affected by construction works, the total length of river affected is small.

The Nicola River is in the interior dry belt, with an annual precipitation of 25–40 cm, and runs from above Nicola Lake to join the Thompson River at Spences Bridge, a total river length of 193 km. The region through which the rivers flow experiences a seasonal temperature range of 39 to −43°C and both rivers are frozen over between December and March each year. The Coldwater River is generally much colder than the Nicola River because of its high elevation (Wightman 1979). The Coldwater is also extremely nutrient poor compared with the Nicola, with a conductivity of 40–50 μmho cm^{-1} (1 mho = 1 s) in the upper reaches of the river, compared with 150–300 μmho cm^{-1} in the Nicola. The mean discharge of the Coldwater at Merritt during 1984 was 6.16 $m^3\ s^{-1}$, with a maximum daily discharge of 81.4 $m^3\ s^{-1}$ on January 5 and a minimum daily discharge of 0.64 $m^3\ s^{-1}$ on December 31 (Anonymous 1985). The period of highest flows usually occurs during snow melt (April–July), while minimum flows occur usually during the winter months, although flash floods can occur, as in January 1984.

The main fish species in the Coldwater and Nicola rivers are chinook salmon (*Oncorhynchus tshawytscha*), coho salmon, steelhead trout, Dolly Varden char (*Salvelinus malma*), and mountain whitefish (*Prosopium williamsoni*). In addition, large numbers of nonsalmonid species are present throughout the Nicola River, while pink salmon (*Oncorhynchus gorbuscha*) spawn in the lower reaches.

The study sites chosen represented a selection of the major mainstem and off-channel habitats present in or near the Coldwater River and included natural main channel pools, rock revetment (riprap; diameter, 0.5–1.5 m), main-channel areas, side channels, and off-channel ponds (Fig. 1). All sites were above Kingsvale, which is the main juvenile rearing area in the river (Wightman 1979). Additional study sites were situated on the Nicola River, where sampling was restricted to one off-channel pond and two side channels, which remained ice-free over the winter. The dimensions and main physical characteristics of each site are summarized in Table 1. The off-channel ponds were adjacent to the main river and probably originated as cutoff river meanders. Beaver dams on the outlet streams impounded groundwater inflow into the area, creating a shallow pond. The ponds supported a thriving aquatic community and water quality was good (dissolved oxygen concentration, 6–8 mg L^{-1}). Most main-river and side-channel sites were sampled on a biweekly basis over the period from November 1984 to April 1985, while off-channel ponds were sampled once each month. Air temperature recorded in the upper reaches of the Coldwater River over this period ranged from −30 to 5°C, while in the main river, water temperature ranged from 0 to 2°C, averaging around 0.5°C. The mean discharge at Brookmere, near Kingsvale, during December 1984 was 0.89 $m^3\ s^{-1}$, while at Merritt it was 1.04 $m^3\ s^{-1}$ (Anonymous 1985).

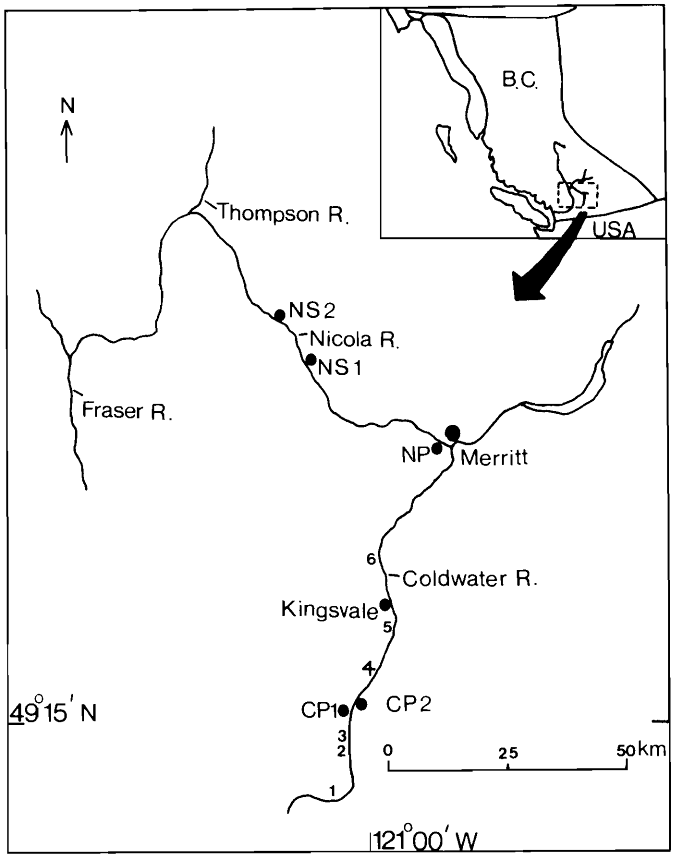

FIG. 1. Location of study sites on the Coldwater and Nicola rivers. Key to sites: 1–6, main-channel Coldwater River sites (1–3, natural pools; 4–6, riprap sites; 1 and 6 are also side-channel sites); CP1, off-channel pond No. 1; CP2, off-channel pond No. 2; NP, Nicola River off-channel pond; NS1 Nicola River side-channel No. 1; NS2, Nicola River side-channel No. 2.

Methods

Over most of the sampling period, both rivers were either completely or partially frozen over, making most conventional fish sampling methods impracticable. In such conditions, the fish-sampling technique we found to be most appropriate was trapping using Gee wire mesh minnow traps (42 cm long by 22 cm wide, with 5-mm mesh and 15-mm openings in funnels at each end; (Cuba Speciality Manufacturing Co., Ontario). In previous studies, Gee minnow traps were effective in providing relative estimates of juvenile salmonid abundance, capturing a representative sample of the population within the size range 50–130 mm (Bloom 1976; Shepherd 1977). We baited traps with salmon roe, inserted them into the river through holes made in the ice

TABLE 1. A summary of the dimensions and main physical features of the habitats sampled

Habitat	Area (m^2)	Depth (m)	Width (m)	Mean temp. (°C)	Substrate
Coldwater River					
Main-channel pools	500	0.5–1.5	4–10	0.5–1	Sand, gravel, cobbles, organic debris
Main-channel riprap	500	0.3–1.5	8–15	0.5–1	Cobbles, boulders (0.5–1.5 m diameter)
Side channels	250	0.3–1.5	3–8	1.5	Sand, silt, organic debris
Off-channel pond No. 1	9700	0.5–1.5	—	3	Decaying organic matter, mud
Off-channel pond No. 2	600	0.5–1.0	—	3	Decaying organic matter, mud
Nicola River					
Off-channel pond	5000	1–2	—	—	Decaying organic matter, mud
Side channel No. 1	500	0.5–1.5	5–7	7	Sand, gravel, organic debris
Side channel No. 2	500	0.5–1.5	4–5	8	Sand, gravel, organic debris

(either manually or using a powered ice auger), and anchored them to the bank. The traps were generally fished on the stream bed in a variety of habitat types, water depths, and flows. In main-channel sites, sampling was restricted to pools and other deep-water areas since riffles were too shallow for trapping. Usually, the traps were left overnight and retrieved the next day, with a standard soak time (the interval between setting and retrieving) of 24 h. Catch per unit effort (CPUE) was defined as the catch within this time period. The number of traps set per site varied from 8 to 12 at main-channel sites to over 60 in off-channel ponds.

All fish captured were anaesthetised, identified, enumerated, and measured (fork length) to the nearest 1 mm. A scale sample was taken for age determination. Fish weights and water current velocities could not be measured as low air temperatures made equipment inoperative. After processing, all fish were returned alive to the site of capture. Population estimates in ponds and side channels were made using Peterson or Schnabel mark–recapture methods (Younds and Robson 1978). Trapped fish were fin clipped (adipose and (or) caudal), returned to the water, and sampled again at a later date, when the numbers of marked and unmarked fish were noted. Instantaneous growth rates were calculated using the following formula (Bagenal and Tesch 1978):

$$G = (\log_e l_2 - \log_e l_1)/\Delta t$$

where G is the instantaneous growth in length, l_2 is the mean length at time 2, l_1 is the mean length at the time 1, and Δt is the time interval in days

Results

Variation in CPUE between sites

Coho salmon

In the Coldwater River, catches of juvenile coho salmon were generally much lower in main-channel sites altered by riprap bank stabilization than in natural pool areas (Table 2). In the latter, highest catches occurred when traps were in or very near dense instream cover such as submerged root wads, branches, logs, etc. and (or) were near overhanging cover such as ice and snow shelves, bankside vegetation, or undercut banks. While coho salmon appeared to have both flow and depth requirements, with highest catches being recorded in deep, slow-flowing areas, instream and riparian cover seemed, through subjective assessment, to be the main habitat features in determining trap catches. Catches in side channels were slightly higher than in main channel pools, with highest catches again being recorded when traps were in or near areas of cover. Maximum CPUE in the Coldwater River was recorded in two off-channel ponds in the upper reaches of the river, where mean CPUE was 3–5 times greater than in main- or side-channel pools and up to 50 times greater than in main-channel riprap areas. Catches in the larger pond No. 1 were, on average, twice as high as in pond No. 2. Both ponds were warmer than the main river, averaging 3°C over the study period compared with 1°C in the main river. Catches in the off-channel pond in the Nicola River were also high, with a mean CPUE similar to that recorded in pond No. 2 in the Coldwater River. The two side-channel sites on the Nicola River provided the highest catches at any site, with mean CPUE being almost twice as great as in pond No. 1 in the Coldwater River. Individual trap catches of up to 70 coho were recorded when traps were in or near dense instream cover. The water temperature in the two groundwater-fed side channels averaged around 7°C over the study period compared with 1°C in the main river.

Nonparametric analysis of differences in CPUE between sites using Kruskall–Wallis analysis of variance showed a significant difference in CPUE between sites on the Coldwater River. ($P < 0.05$, $H = 13.96$).

Chinook salmon

Chinook salmon CPUE was generally low in all habitats (Table 2). In the Coldwater River, catches were highest in natural main-channel pools containing large log debris and were very low in riprap areas and in side channels. Only small numbers of chinook salmon were caught in the two off-channel ponds on the Coldwater River and were absent from the Nicola River pond. Highest catches were recorded in the two Nicola side channels, although catches were 5 times lower than for coho salmon. Kruskall–Wallis analysis of variance showed a significant difference in CPUE between Coldwater sites ($P < 0.05$, $H = 28.5$).

Steelhead trout

In the Coldwater River, CPUE was generally low in natural main-channel pools and side channels, but was considerably

TABLE 2. Mean catch per unit effort of juvenile salmonids in the various habitats sampled

Habitat	Coho salmon	Chinook salmon	Steelhead trout	Dolly Varden	Total salmonids
Coldwater River					
Main channel	1.49	0.57	0.19	0.16	2.42
	(1.69,19)*	(0.68,19)	(0.21,19)	(0.15,19)	(2.19,19)
Riprap	0.16	0.23	1.73	0.02	1.82
	(0.27,15)	(0.32,15)	(0.92,15)	(0.07,15)	(1.25,15)
Side channels	2.28	0.43	0.36	0.61	3.69
	(2.06,14)	(1.32,14)	(056,14)	(1.31,14)	(2.93,14)
Off-channel pond No. 1	7.25	0.18	0.04	0.04	7.40
	(0.77, 5)	(0.08, 5)	(0.01, 5)	(0.01, 5)	(0.79, 5)
Off-channel pond No. 2	3.71	0.27	0	0.01	3.83
	(2.1,5)	(0.18, 5)	(—, 5)	(—, 5)	(2.20, 5)
Nicola River					
Off-channel pond	3.90	0	0	0	3.90
	(—, 1)	(—, 1)	(—, 1)	(—, 1)	(—, 1)
Side channel No. 1	15.10	3.33	3.95	0	22.70
	(4.71, 3)	(2.84, 3)	(1.55, 3)	(—, 3)	(5.50, 3)
Side channel No. 2	14.80	1.0	1.4	0	16.90
	(—, 1)	(—, 1)	(—, 1)	(—, 1)	(—, 1)

*Values in parentheses indicate standard deviation and number of sampling occasions, respectively.

TABLE 3. Estimated population size ($\hat{N}$) and densities ($\hat{D}$, fish/m^2) of overwintering juvenile salmonids in side channels and off-channel ponds

Site	Date*	Coho salmon			Chinook salmon			Steelhead trout		
		$\hat{N}$	95% CL	$\hat{D}$	$\hat{N}$	95% CL	$\hat{D}$	$\hat{N}$	95% CL	$\hat{D}$
Off-channel pond No. 1	9/26/1984	4300	3800–4900	0.44	—	—	—	—	—	—
	1/31/1985	3748	2810–4971	0.39	75	—	<0.01	—	—	—
Off-channel pond No. 2	10/2/1984	920	780–1110	1.53	—	—	—	—	—	—
	1/31/1985	493	343–755	0.82	15	—	<0.03	—	—	—
Nicola River side channel No. 1	1/31/1985	1397	1118–1759	2.80	156	72–312	0.31	115	52–287	0.23
Nicola River side channel No. 2	3/5/1985	1188	727–2049	1.50	15	5–75	0.02	156	43–1560	0.20

*Month/day/year.

higher in riprap areas, where rainbow trout was the dominant species (Table 2). Trout were only occasionally captured in the off-channel ponds on the Coldwater River and were absent from the Nicola pond. The highest CPUE was recorded in side channel No. 1 on the Nicola River, where mean CPUE was twice as great as in Coldwater riprap sites. Kruskall–Wallis analysis of variance showed a significant difference in CPUE between Coldwater sites ($P < 0.05$, $H = 16.9$).

Dolly Varden char

This species was largely restricted to main Coldwater sites where CPUE was generally very low (Table 2).

Side-channel and off-channel pond population estimates

Population estimates of juvenile salmonids in off-channel ponds No. 1 and No. 2 in the Coldwater River and side channels No. 1 and No. 2 in the Nicola River are shown in Table 3. In both off-channel ponds, coho salmon was the main species, with densities up to 1.53 fish m^{-2}. In the larger pond (No. 1), the late autumn coho salmon population was estimated at around 4300 (95% confidence level (CL), 3800–4900; 0.44 fish/m^2), while in the smaller and shallower pond (No. 2), the population was estimated at 920 (95% CL, 780–1110; 1.53 fish/m^2). Chinook salmon and rainbow trout were uncommon. The overwinter survival of coho salmon in the ponds, calculated from population estimates made in September 1984 and February 1985 (Table 3), was estimated to be 87% for pond No. 1 and 54% for pond No. 2. Large numbers of coho salmon were also found overwintering in the two Nicola River side channels, with estimates of 1400 (2.8 fish/m^2) and 1200 (1.5 fish/m^2) for side channels No. 1 and No. 2 in February, respectively. Chinook salmon and rainbow trout were also present in both side channels at fairly high densities (0.2–0.3 fish/m^2).

Population structure

Coho salmon populations showed considerable variation in size and age structure between sites (Fig. 2). In main- and side-channel habitats on the Coldwater River, two distinct modes were apparent in the length–frequency distributions, which scale reading showed corresponded to 0+ and 1+ age groups. In contrast, all off-channel pond and Nicola side

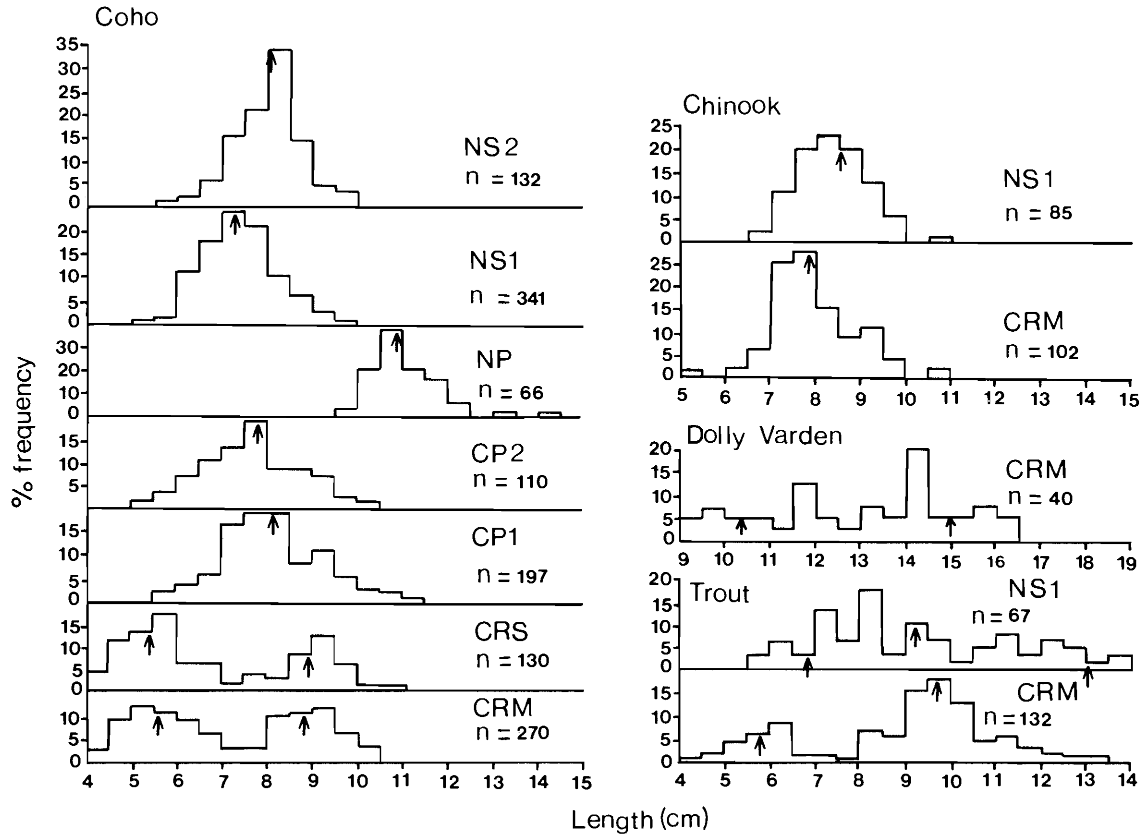

FIG. 2. Length–frequency distributions of coho and chinook salmon, Dolly Varden char, and steelhead trout in the various habitats sampled. Abbreviations are as in Fig. 1. CRM, Coldwater River, main channel; CRS, Coldwater River, side channels. Arrows indicate the mean lengths of each age group.

channel populations tended to be unimodal in distribution. Analysis of scales from the Coldwater pond populations revealed only one check in most fish, often indistinct, at the scale perimeter. This suggests that most fish were from the 1984 year class (0+ age group) that had spent only one winter in the ponds. However, small numbers of fish appeared to show two checks, suggesting that they were from the 1983 year class (1+ age group) and had spent two winters in the pond. The frequency distribution of the Nicola pond coho salmon population was shifted to the right compared with the Coldwater populations and was also unimodal. Scale reading showed a high proportion of 1+ fish, although there was considerable variation in scale growth patterns. The Nicola side channel coho salmon populations were composed mainly of 0+ fish, but 1+ fish were also present.

Chinook salmon populations in the Coldwater and Nicola rivers were all unimodal in distribution (Fig. 2) and scale analysis showed that all fish sampled were from the 1984 year class (0+ age group). The steelhead trout population in the Coldwater River showed two clear modes (Fig. 2), which scale analysis showed corresponded to 0+ and 1+ age-groups, with small numbers of 2+ fish. The main feature of the Dolly Varden char population in the Coldwater River was the absence of fish smaller than 9 cm, i.e., the 0+ age group.

Growth

Mean lengths at age of all species often showed considerable variation between sites (Table 4, Fig. 2). In the Coldwater River, 0+ coho salmon rearing in main channel pools were significantly larger (55.7 mm) than fish rearing in side channels (54.6 mm) ($P < 0.05$, $t = 0.95$, df = 205), although there was no significant difference in the lengths of 1+ fish ($P > 0.05$). Coho salmon rearing in all off-channel ponds were much larger than fish in the main Coldwater River and side-channel sites. Group 0+ coho salmon rearing in Coldwater pond No. 1 were significantly larger (82.0 mm) than fish in the main river (55.7 mm) ($P < 0.05$, $t = 17.0$, df = 234). There was no significant difference in the mean lengths of coho salmon in pond No. 1 (82.0 mm) and pond No. 2 (77.9 mm) ($P > 0.05$). In mid-January, coho salmon rearing in Nicola side channel No. 1 were significantly smaller (73.3 mm) than fish in Coldwater pond No. 1 (82.0 mm) ($P < 0.05$, $t = 14.24$, df = 222) and pond No. 2 (77.9 mm) ($P < 0.05$, $t = -5.04$, df = 232). Coho salmon in Nicola side channel No. 2 were significantly larger (80.0 mm) than in side channel No. 1 (73.3 mm) ($P < 0.05$, $t = 7.3$, df = 257), but this may have been due to differences in sampling times.

Catches of chinook salmon, steelhead trout, and Dolly Varden char were generally too low to allow meaningful statistical comparison between sites to be carried out. However, 0+ chinook salmon in Nicola side-channel No. 1 were significantly larger (85.0 mm) than in the main Coldwater River (78.8 mm) ($P < 0.05$, $t = 4.01$, df = 151).

Mean lengths of coho salmon in main- and off-channel habitats were compared to assess and compare winter growth. There was no significant difference in the mean lengths of 1+ coho in the main Coldwater River between the start (87.3 mm) and end (90.7 mm) of the sampling period ($P > 0.05$, $t = 0.49$, df = 62). Similarly, there was no significant difference in the mean length of coho in off-channel pond No. 1 in mid-January

TABLE 4. Weighted mean lengths (mm) of juvenile salmonids captured over the sampling period in each habitat

Habitat	Coho		Chinook,	Steelhead trout			Dolly Varden	
	0+	1+	0+	0+	1+	2+	1+	2+
Coldwater River								
Main channel	55.7	88.2	78.8	57.4	97.0	126.0	107.6	144
	(7.6, 131)*	(7.2, 126)	(9.2, 102)	(6.6, 35)	(9.2, 94)	(4.2, 7)	(11.6, 14)	(9.6,16)
Side channels	54.6	89.3	85.6	62.0	101.0	136.0	122.0	158
	(7.5, 76)	(6.8, 45)	(9.0, 10)	(11.0, 5)	(9.8, 18)	(—, 2)	(14.2, 6)	(18.1, 5)
Off-channel pond No. 1	82.0	—	84.6	—	—	—	—	—
	(12.6, 103)	—	(10.2, 8)					
Off-channel pond No. 2	77.9	—	85.4	—	—	—	—	—
	(12.0, 107)	—	(6.3, 5)					
Nicola River								
Off-channel pond	—	109.4	—	—	—	—	—	—
		(7.0, 66)						
Side channel No. 1	73.3	—	85.0	68.6	92.3	130.4	—	—
	(7.0, 127)	—	(8.4, 51)	(4.4, 5)	(7.4, 8)	(7.8, 5)		
Side channel No. 2	80.0	—	88.0	78.0	109.0	145.0	—	—
	(7.1, 133)	—	(6.5, 9)	(7.4, 10)	(—, 2)	(—, 1)		

*Values in parentheses indicate standard deviation and sample size, respectively.

(82.0 mm) and the end of March (84.7 mm) ($P > 0.05$, $t = 1.64$, df = 234). Although not statistically significant, this increase in mean length over a relatively short time period suggests that coho salmon in the pond may have continued to grow in length over the winter. The instantaneous growth rate, calculated using mean lengths in mid-January and the end of March, was 4.563×10^{-4}.

Discussion

The habitat preferences of juvenile salmonids in main-channel sites and the large number of fish overwintering in off-channel ponds and side channels are similar to the findings of other studies carried out in coastal streams and rivers of the Pacific Northwest. In Carnation Creek, a west coast Vancouver Island stream, juvenile coho salmon and steelhead trout were most abundant during winter in deep, slow-moving pools with abundant organic cover. However, coho salmon also use side pools, back channels, and beaver ponds, which are dry during the summer, but flooded in winter, as overwintering areas (Brown 1985; Bustard and Narver 1975*a*). Tschapalinski and Hartman (1983) confirmed that a major seasonal shift in distribution occurred in Carnation Creek, with many fish emigrating into low-velocity tributaries and valley sloughs. Less than half of the main stream coho salmon population remained by midwinter. In the Clearwater River in Washington, large numbers of 0+ and 1+ coho salmon and cutthroat trout (*Salmo clarki*) migrated during autumn into small tributaries and riverine ponds connected to the main river (Cederholm and Scarlett 1981). Densities of coho salmon in these ponds (Peterson 1982*b*) were similar to those in pond No. 1 on the Coldwater River. Also, in a small stream in Oregon, densities of coho were 3 times higher in an off-channel pond than in the best main-river habitat (Everest and Sedell 1983). Studies on the overwintering ecology of juvenile salmonids in interior rivers in British Columbia have been few, but investigations in the Morice River in northern British Columbia showed that side channels were an important overwintering area for juvenile chinook and coho salmon and steelhead trout (Bustard 1986).

The results of this and previous studies suggest that side channels, back channels, off-channel ponds, and other low-velocity, off-channel areas are the preferred overwintering habitats for juvenile coho salmon in many coastal and interior rivers. The relative scarcity of other salmonids in these habitats suggests that other species do not use these areas extensively. The main features that these habitats appear to have in common and that seem to be attractive to overwintering coho salmon are low water velocity, abundant cover, a high water temperature relative to the main river, a relative lack of predators, and an abundant food supply. Together, these factors probably account for the higher survival rates seen in these habitats compared with the main river. Overwinter survival estimates for juvenile coho salmon in the Coldwater River ponds (54 and 87%) are similar to those seen in riverine ponds on the Clearwater River in Washington (49 and 79%) (Peterson 1982*a*) and in beaver ponds on Carnation Creek (70%), where survival was twice that in the main river (Bustard and Narver 1975*a*). The difference is survival between the two Coldwater pond populations may be caused by differences in pond size and depth. Peterson (1982*a*) postulated that in the Clearwater ponds, survival and growth differences were attributable to differences in pond morphometry, predation effects, and times of immigration to the ponds. The much shallower waters in Coldwater pond No. 2 resulted in more severe icing than in pond No. 1 and may have produced an oxygen deficit in some areas of the pond, increasing fish mortality. The faster growth rate in the Coldwater pond coho salmon compared with main river fish probably reflects the better growing conditions in the ponds, with higher water temperatures and abundant food (large numbers of amphipods, *Gammarus lacustris*, were seen in the water column and on the aquatic plant community). Although it seems likely that the higher water temperatures and increased food availability in the ponds were the main factors responsible for the faster growth of coho salmon in the off-channel ponds than in the other habitats, it is also possible that other factors such as size-selective predation may also have been involved. Since the ponds were frozen over during winter, it is possible to discount birds and mammals as predators; however, fish predators such as Dolly Varden char may have been present in the ponds, which could have had a size-selective effect on the coho salmon population. In cold, unproductive rivers such as the Coldwater River, off-channel areas may be of considerable survival advantage to juvenile coho salmon overwintering in the system and may be a crucial factor in determining total smolt output. Previous studies in coastal rivers have suggested that coho salmon may move into ponds to avoid high winter flows in the main river, with immigration coinciding with increasing streamflow and decreasing water temperatures of autumn and early winter (Bustard and Narver 1975*a*; Cederholm and Scarlett 1981; Peterson 1982*b*). This survival advantage may not apply in interior rivers where winter is, typically, the period of lowest flows. Immigration into interior ponds probably still occurs during freshet conditions, but, because of climatic differences between coastal and interior regions, this usually occurs in spring and summer rather than in winter. Side channels may offer similar survival advantages to juvenile salmonids during the winter in that they provide low-velocity refuge areas, often with higher water temperatures than in the main river because of groundwater inflow.

The relatively low catches of juvenile coho salmon in main-channel sites provides further evidence that large numbers of fry and fingerlings had left the system or migrated into off-channel areas. The main-channel sites where coho salmon were most abundant (deep, slow-flowing pools with abundant instream and bankside cover) are similar to those found to be used in coastal rivers (Bustard and Narver 1975*a*; Tschapalinski and Hartman 1983). The microhabitat parameters that appeared to be of most importance in determining catches were water flow and cover, both organic cover in the form of submerged root wads, branches, riparian vegetation, etc., and nonorganic cover such as overhanging banks and ice and snow shelves. Coho salmon also appeared to congregate close to stream banks where cover was often most abundant. Using experimental channels in winter conditions, Bustard and Narver (1975*b*) also found that coho salmon showed a strong preference for side pools with overhanging bank cover. The importance of instream woody debris as a microhabitat parameter in juvenile salmonid ecology in west coast streams and the adverse consequences of its removal are now well established (Bryant 1983; Dolloff 1983). In Carnation Creek, areas containing adequate winter habitat in the form of deep pools, log jams, and undercut banks with tree roots and debris lost fewer fish during freshets and maintained higher numbers of coho salmon in winter than sections without these habitat characteristics (Tschapalinski and Hartman 1983).

The very low catches of juvenile chinook salmon at all sites suggest that many fish had already left the system for the ocean or were overwintering in other areas. There are known to be three life history modes for Fraser River chinook, based on time of seaward migration: "immediate," "ocean type," and "stream type" (Fraser et al. 1982). Scale analysis of returning Coldwater River adults has shown that in a sample of 39 fish, 94% had overwintered in freshwater as juveniles ("stream type"), while 6% migrated to sea during their 1st year (Berry and Kahl 1982). Since few fish were captured in the upper and middle regions of the Coldwater River, it would seem that most had either moved downstream, migrated out of the system to overwinter in downstream mainstem locations, or moved into areas not accessible to trapping. The relatively high numbers captured in one side channel on the Nicola River suggests that more fish may overwinter there than in the Coldwater River. Downstream migration of juvenile chinook salmon in fall from high, cold, headwater rearing areas to larger and generally warmer rivers, where overwintering takes place, may be a widespread and general winter survival mechanism in this species (Everest 1969). The few fish that remained in the river were mainly captured from deep pools with large organic debris and cobbles on the stream bed. It is widely felt that juvenile chinook salmon overwinter beneath rocks, rubble, and other large cover on the stream bed (Chapman and Bjornn 1969; Chapmann 1966; Edmundson et al. 1968; Everest and Chapman 1972). If chinook salmon do remain in the Coldwater River over the winter and move to stream bed shelter areas, it may be that these fish would be less prone to capture by trapping than other species in more accessible areas, and low trap catches may not be a true reflection of real levels of abundance in the river.

It is well known that water temperature affects the behaviour of salmonids, with activity decreasing at low temperatures. Gardiner and Geddes (1980) found that below a water temperature of 5°C, young Atlantic salmon (*Salmo salar*) sought shelter in the stream bed and reduced energy expenditure. At water temperatures of 6–7°C, young salmon came out of hiding and lay between stones, while at higher temperatures, fish swam actively near the stream bed. It has been suggested that this autumnal movement to stream bed cover areas explains the apparent decline in the population abundance of Atlantic salmon, which has often been recorded at this time of year, and that there is in fact little or no autumnal movement into pools or other deeper, warmer waters (Rimmer et al. 1983, 1984). The available evidence suggests that this may not be the case in coho salmon, where large numbers appear to leave summer rearing habitats to overwinter in off-channel areas, although it may occur to some extent in chinook salmon. This difference in behaviour between Atlantic and Pacific salmon species may be related to climatic and hydrologic factors. Both chinook and coho salmon do appear, however, to exhibit a shift in microhabitat preference during the winter, when they are closely associated with either pool debris and bank cover or stream bed shelter areas.

At most main-river sites, juvenile steelhead trout were often found in the same habitat as coho salmon, i.e., deep pools with abundant cover, although at lower densities. This supports previous findings that while the two species typically show habitat segregation during the summer, with coho salmon in pools and trout in riffles, both may coexist sympatrically during the winter (Hartman 1965; Raleigh et al. 1984). However, in the Coldwater River, trout were most abundant in main-channel riprap, where they were the main species present. This habitat preference is probably related to the winter "hiding behaviour" known to be exhibited by juvenile steelhead trout (Edmundson et al. 1968; Everest 1969; Hartman 1965). As water temperatures decrease with the onset of winter, juvenile trout move to the stream bed where they shelter beneath large rocks and rubble, often penetrating some distance into the substrate (Bjornn 1971; Bustard and Narver 1975*a*; Chapman and Bjornn 1969; Hartman 1965; Everest 1969). This movement is thought to be a behavioural response to avoid physical damage by ice scouring and to conserve energy. It seems likely that trout are attracted to riprap, since it provides abundant cracks and crevices in which they can shelter. Everest (1969) also found that the highest winter densities of juvenile steelhead trout in an Idaho stream were in highway riprap.

Sampling is probably the major difficulty in conducting studies of the winter ecology of juvenile salmonids in cold interior regions. While wire mesh traps were found to be useful in this study in providing estimates of relative abundance and for general fish capture, traps are known to be selective for size and, to a lesser extent, species (Craig 1980). Catch may also be influenced by environmental parameters such as water temperature and flow (Hamley and Howley 1985), which may vary between stations. The trapping technique used in this study also assumed equal catchability of all species in all habitats. The results of this and previous studies suggest that these assumptions may be violated to some extent during the winter, when it appears likely that species such as juvenile Atlantic salmon, chinook salmon, rainbow trout, and steelhead trout move to substrate chambers where they may remain relatively inactive and where the influence of nearby baited traps may not be detected. Also, some habitats such as shallow riffles, which were subject to severe icing, could not be sampled with traps and while it seems unlikely that conditions in such areas would be favourable to the survival of juvenile salmonids, the inability to sample these areas means that the possibility that fish were present in these areas cannot be entirely ruled out. These deficiencies must be borne in mind, but, in the absence of a more effective sampling technique, trapping is likely to remain the only feasible winter sampling method available.

The apparent habitat segregation between species recorded in this study could be explained merely in terms of habitat preferences, but it is also possible that other functional or biological factors may also be involved. For example, the dominance of coho salmon in the off-channel ponds and the virtual absence of other salmonids probably largely reflects the preference of coho salmon for deep, low-velocity areas with abundant cover. However, such habitat features are also attractive to other species, such as rainbow or steelhead trout parr (Raleigh et al. 1984), which were present in the ponds only in small numbers. It is possible that this may at least partly be attributable to coho salmon out competing these other species, leading to their aggressive displacement from these habitats. Similar factors may also be involved in the dominance of juvenile steelhead trout in riprap habitats.

In conclusion, this study suggests that as in coastal streams, side channels and off-channel ponds are the preferred overwintering habitats of juvenile coho salmon in small interior rivers. Although some chinook salmon overwinter in main-channel areas it seems likely that before the onset of winter conditions, many fish emigrate from tributary streams into deeper, warmer, downstream habitats. The study further suggests that the microhabitats occupied by coho and chinook salmon and steelhead trout over the winter period in small interior rivers are quite distinct. Coho salmon appear to overwinter in ponds and pools containing organic cover, while chinook salmon occupy deep pools with large debris cover. In contrast, steelhead trout appear to shelter in rock crevices or beneath large substrate material. The results of the study suggest that the habitat requirements and distribution of juvenile salmonids in small interior rivers during the winter may show marked differences from those recorded in other seasons and these must be borne in mind when developing management strategies for interior river salmonid populations.

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