

Behaviour, Habitat Use, and Movements of Coho Salmon (*Oncorhynchus kisutch*) Smolts during Seaward Migration¹

Thomas E. McMahon² and L. Blair Holtby

Department of Fisheries and Oceans, Biological Sciences Branch, Pacific Biological Station, Nanaimo, B.C. V9R 5K6, Canada

McMahon, T. E., and L. B. Holtby. 1992. Behaviour, habitat use, and movements of coho salmon (*Oncorhynchus kisutch*) smolts during seaward migration. *Can. J. Fish. Aquat. Sci.* 49: 1478–1485.

Coho salmon (*Oncorhynchus kisutch*) smolts formed aggregations in pools with large woody debris during their migration downstream and into the Carnation Creek estuary, British Columbia. Smolts utilized the estuary throughout the smolt run, with periods of high outmigration coinciding with spring tides which brought warmer, more saline water into the estuary. Smolt abundance in the stream and estuary was positively related to debris volume, and 82% of the 1260 smolts observed during underwater counts occurred within 1 m of debris. Debris volume and smolt density were significantly lower in clearcut than in buffered stream sections. Our observations support the need to retain and manage large woody debris for smolt habitat in streams and estuaries.

Des saumoneaux cohos (*Oncorhynchus kisutch*) se sont regroupés dans des fosses encombrées de gros morceaux de bois lors de la dévalaison vers l'estuaire du ruisseau Carnation, en Colombie-Britannique. Ils ont fréquenté cet estuaire pendant toute la durée de la dévalaison; un grand nombre l'ont quitté lors des marées de vives-eaux qui baignaient l'estuaire d'eau plus chaude et plus salée. L'abondance des saumoneaux dans le cours d'eau et l'estuaire était en corrélation positive avec le volume de morceaux de bois; ainsi, 82% des 1 260 saumoneaux observés au cours de dénombrements sous-marins étaient retrouvés en deçà de 1 m de débris de bois. Le volume de débris et la densité des saumoneaux étaient nettement inférieurs dans les tronçons du cours d'eau où les rives avaient été coupées à blanc que dans les tronçons où une marge tampon existait. Nos observations confirment qu'il est nécessaire de garder de gros morceaux de bois dans les cours d'eau et les estuaires afin qu'ils servent d'habitat aux saumoneaux.

Received March 26, 1991
Accepted January 13, 1992
(JA965)

Reçu le 26 mars 1991
Accepté le 13 janvier 1992

Parr-smolt transformation in coho salmon (*Oncorhynchus kisutch*) and other anadromous salmonids is accompanied by distinct changes in morphology, physiology, and behaviour (Hoar 1976; Wedemeyer et al. 1980). While the morphological and physiological changes that occur have been well documented, relatively few studies have examined behavioural changes during the shift from freshwater to marine habitats. Laboratory observations by Hoar (1951) suggested that during smoltification, coho salmon show a marked decline in aggression and associated territorial and hierarchical behaviour and form aggregations presumably adaptive for life in schools in the open ocean. In contrast, Mason (1966) and Paszkowski and Olla (1985) found that smolts continue to exhibit aggression and hierarchical behaviour in seawater. No direct underwater observations of coho smolts in the field have been reported to corroborate laboratory observations.

Prior to seaward migration, presmolts overwinter in protected sites of deep pools and undercut banks containing large woody debris (Bustard and Narver 1975; Tschaplinski and Hartman 1983), off-channel ponds, wetlands, sidechannels, and low-gradient tributaries (Peterson 1982; Brown and Hartman 1988), and lakes (Swales et al. 1988). Bustard and Narver (1975) and Tschaplinski and Hartman (1983) found that coho overwintering in off-channel sites moved back to the main channel of Carnation Creek, British Columbia, in early spring, up to 6 wk prior to the main period of smolt migration. How-

ever, the types of habitat utilized by coho salmon prior to and during the period of smoltification and migration to the sea have not been previously described.

Estuaries may be important for smolts as sites for completion of seawater adaptation and other smoltification processes (Iwata and Komatsu 1984; McCormick et al. 1985). Some species, notably chinook (*O. tshawytscha*) and chum salmon (*O. keta*), may spend several months in estuaries utilizing the abundant food resources there prior to moving out to sea (Healey 1982; Mason 1974; Macdonald et al. 1987; Murphy et al. 1988). Studies have shown that coho salmon parr utilize estuaries during spring and summer (Murphy et al. 1984; Tschaplinski 1988), but information is limited on estuarine utilization by coho smolts, particularly wild fish.

In this study we describe the behaviour, movement timing, and habitats utilized by wild coho salmon smolts prior to and during their migration downstream into the Carnation Creek estuary. We show that smolts are closely associated with large woody debris during seaward migration and discuss the implications of this association to habitat management for the species.

Methods and Materials

Carnation Creek empties into Barkley Sound on the west coast of Vancouver Island. The stream is ~8 km long of which the lower 3.2 km is accessible to anadromous salmonids. Coho salmon are the predominant salmonid rearing in the stream. The watershed is the site of a long-term study initiated in 1970 to

¹Contribution No. 163 of the Carnation Creek Fish-Forestry Project.

²Present address: Biology Department, Montana State University, Bozeman, MT 59717, USA.

examine the effects of logging on a coastal rainforest stream. Physical and biological characteristics of the stream have been described in detail elsewhere (Hartman and Scrivener 1990).

Three distinct sections of the watershed were delineated for this study: (1) a small, 500-m-long, "riverine-type" estuary bounded on its upper end by a permanent fish counting fence located near the uppermost limit of tidal influence and its lower end by Barkley Sound, (2) a "buffered" section (0–1300 m upstream from the counting fence) where a strip of trees was left intact along the stream margin after logging of 41% of the watershed during 1976–81, and (3) a "clearcut" section (1300–3200 m above the fence) where streamside trees had been removed during logging and much of the instream woody debris removed or lost during logging and subsequent freshets (Tschaplinski and Hartman 1983; Hartman and Scrivener 1990).

Eight 50-m-long study reaches were chosen to represent the characteristics of each section. In the estuary, a study reach was designated in the upper, middle, and lower part of the estuary based on differences in woody debris, streamside canopy, and salinity patterns (Table 1). Buffered and clearcut reaches were located downstream or adjacent to the mouths of off-channel ponds and tributaries utilized by coho salmon as overwintering sites (750, 1600, and 2600 m upstream from the main counting fence; Brown and Hartman 1988). Together, the eight study reaches comprised 30% of the total area of the estuary and 8% of the stream. Additional observations were made in Dicks Creek, a small tributary entering the estuary about 100 m below the main fish fence (see map, Bustard and Narver 1975).

Behaviour and habitat use by coho salmon smolts were determined from underwater counts and observations using a wet suit, mask, and snorkel. Dives were made at least biweekly at times between 1000 and 1500 h in each of the eight study reaches during March–June 1985. Temperatures during this

period ranged from 4 to 10°C. Dives were limited to high-visibility (>3 m) conditions, i.e. stream discharges <0.5 m³/s and low tides.

Observations were made by entering the downstream end of a study reach and slowly swimming upstream in a zigzag fashion through the entire reach. Fish could be approached quite closely (within 1 m) and were readily counted and observed. When fish were encountered, a diver made repeated counts over a 10-min period to insure as complete a count as possible. Counts of smolts located within dense cover were often facilitated by fish swimming out of cover to feed on benthic organisms purposely dislodged by the diver. Feeding, aggression, and aggregative behaviour were also noted. Following the definition of Cunjak and Power (1986, p. 1972), an aggregation was defined as "a group of (5 or more) fish in close association. . . , displaying a common behavioural pattern but lacking the spatial homogeneity and polarity of schooling fish." The number and location of fish were recorded on a map of the study site by an assistant on the bank. Smolts were distinguished from parr based on their size and colouration (McMahon and Hartman 1988). Distance of fish from cover was estimated within 1 m by the diver and later measured in relation to particular stream features noted during a dive. Four separate repeat counts of a study reach on the same or next day indicated that precision of visual estimates was ~10–15%. Accuracy of counts was not measured. However, previous comparisons of visual counts with pole-seine/electrofishing removals of juvenile coho salmon in Carnation Creek in sites similar to those used in the present study indicated that visual counts of coho were about 15% lower than removal estimates (Tschaplinski and Hartman 1983).

Physical habitat features of study reaches were mapped on the basis of 11 transects positioned 5 m apart along each reach. Habitat type (pool, riffle, or glide) and water depth were determined at 1-m intervals along each transect. Current velocity

TABLE 1. Physical habitat characteristics of the eight study reaches in Carnation Creek. All reaches were 50 m in length.

Location	Distance from fence (m)	Area (m ²)	Mean (max.) depth (m)	Pools/glides/riffles (%)	Woody debris			Site characteristics			
					Total vol. (range) (m ³)	Area (m ²)	No. of jams	Bank cover (m ²)	Canopy (%)	Vegetation	Salinity (ppt)
Clearcut											
A	1500	305	0.3 (1.4)	24/18/58	4.6 (0.2–4.4)	6.9	2	7.3	<10	Young alder and salmonberry	
B	1550	490	0.4 (1.2)	49/14/37	0.9 (0.1–0.8)	6.6	2	39.7	<10	Young alder and salmonberry	
C	1625	425	0.4 (1.1)	37/26/37	9.9 (—)	14.1	1	50.6	<10	Young alder and salmonberry	
Buffered											
A	530	465	0.4 (1.6)	36/36/28	25.4 (0.5–19.1)	20.7	4	50.2	~75	Mature forest	
B	630	545	0.5 (1.5)	53/24/23	29.6 (2.0–14.5)	39.2	4	52.3	~75	Mature forest	
Estuary											
Upper	–10	510 ^a	0.6 (1.8) ^a	52/19/29	34.9 (1.3–33.6)	31.8	2	43.9	~75	Mature forest	0–5 ^b
Middle	–60	420 ^a	0.6 (1.2) ^a	74/9/17	1.3 (—)	1.2	1	43.3	<20	Salt marsh, brush cover along one bank	0–5 ^c
Lower	–405	605 ^a	0.4 (1.6) ^a	32/24/44	21.2 (—)	14.1	1	0	<10	Salt marsh (<i>Spartina</i> sp.)	10–22

^aAt low tide.

^b≥ 10 ppt only during spring tides.

^c≥ 10 ppt only during high tides.

was measured with a Gurley Pygmy meter in areas inhabited by coho salmon smolts. Bank cover was measured with a tape and included overhanging vegetation and undercut banks. Woody debris cover was defined as the volume of water containing debris cover and determined by measuring the surface area and depth of a woody debris accumulation (Tschaplinski and Hartman 1983). Salinity and water temperatures were measured in the estuary following each census.

Movements of smolts from three tributaries used as overwintering sites were determined from small two-way fences erected near the tributary junctions with the main channel (Brown and Hartman 1988). Movements of smolts into the estuary were monitored at the main fish counting fence located near the upper limit of the Carnation Creek estuary (Andersen 1987). Potential triggers for seaward migration were examined by comparing smolt numbers at the main fish fence with stream discharge, water temperature, and lunar phase. Water temperature and stream discharge were recorded continuously at the hydrological weir located 500 m above the main fish counting fence.

Results

Downstream Movement

Movement of smolts began with the onset of emigration from upstream tributaries in late March and generally progressed over time in a downstream direction. The median date of emigration from tributaries (April 11) preceded peak counts of smolts in the buffered section (April 24), which in turn preceded the median date of the smolt run at the main fish fence (May 4) by about 10 d (Fig. 1). Smolts were present in the estuary below the fence throughout the smolt run, with peak counts lagging about 10 d behind the median date of migration at the fence. Most smolts had migrated from the estuary by early June.

The number of smolts (3-d average) migrating through the main fence was not influenced strongly by stream discharge ($r = 0.43$, $P = 0.12$). Temperatures during the main period of migration ranged from 6.5 to 8.5°C, with the number of migrants increasing significantly during declines in temperature ($r = -0.60$, $P = 0.02$). There was no significant trend between smolt numbers at the main fence and lunar phase (2-wk periods surrounding new and full moons) (Fig. 1C; $t = 1.79$, $P = 0.08$).

Sharp declines (high outmigration) in numbers of smolts in the estuary were associated with spring tides occurring during new and full moons (Fig. 1D). During three spring tidal cycles, smolt densities declined an average of 85.7 (± 4.6)% compared with an average increase of 344.0 (± 70.6)% during neap tides; this difference was highly significant (arcsine transformation, $t = 6.3$, $P = 0.003$). Incursions of warmer (+2–5°C), more saline (>20 ppt) water into the upper estuary accompanied spring tides (Table 1).

Relative Distribution and Habitat Use

Smolt density differed significantly ($P < 0.05$) (Kruskal-Wallis), between the three sections of Carnation Creek (Fig. 2). Few smolts were observed during underwater surveys in the clearcut section prior to and during the smolt run, despite emigration of 96 coho from adjacent or upstream tributaries (Fig. 1). Smolt density was about five times higher in the buffered section, where numbers increased after emigration from an adjacent tributary (Fig. 1B). Highest densities occurred in the estuary, where a total of 534 smolts were observed in aggregations of up to 136 fish (Fig. 1D).

Smolt densities were similar between study reaches within clearcut and buffered sections, but varied considerably between reaches and over time in the estuary (Table 2). No smolts were observed in the middle estuary reach compared with the relatively high utilization observed in upper and lower reaches. Use of the upper and lower reaches also varied: smolts utilized the upper estuary throughout the run whereas the lower estuary was utilized primarily in the latter half of the run (Table 2). In contrast with upstream reaches, no juvenile coho salmon were observed overwintering in the estuary prior to seaward migration (Fig. 1).

Large woody debris influenced the abundance of smolts in the stream and estuary. Smolt density was positively correlated with the total volume of large woody debris in a 50-m reach (Fig. 3A). Smolt density within 1 m of debris was also correlated with volume of individual debris jams (Fig. 3B), although this relationship was more variable and accounted for only 25% (r^2) of the variation in smolt density. The clearcut section had significantly less debris volume than did the buffered (5.2 \pm 2.6 versus 27.5 \pm 3.0 m³; $t = 6.0$, $P = 0.01$) (Fig. 3A; Table 1). Similarly, the middle estuary reach had little debris (Fig. 3A; Table 1) and no smolts (Table 2) compared with upper and lower estuary sites. Smolt density was not significantly associated with other habitat features such as debris area, bank cover, percent canopy, percent pools, and mean or maximum depth ($P > 0.20$; Table 1).

Smolt distribution was also highly clumped around debris. Over 80% of the 1260 smolts observed in Carnation Creek and Dicks Creek were within 1 m, and 95% within 2 m, of debris (Fig. 4). The distance between the 17 debris jams located in the eight study reaches averaged 21 m (range 5–50 m); the total area of these structures comprised about 3.5% of the total surface area surveyed (Table 1). These sites were characterized by deep (>1 m), slow-moving (<15 cm/s) water, overhead shade (low light intensity), and structurally complex cover afforded by root masses, deeply undercut banks, and submerged logs. Most smolts were observed in proximity to debris with volumes >14 m³ (Fig. 3B). Smaller accumulations and single logs generally supported few fish; the exception was the relatively high density of smolts observed near a small debris jam in the clearcut section where total debris was low (Fig. 3B). Smolts were notably scarce in areas affording deep pools or bankcover (e.g. clearcut and middle estuary reaches; Table 1) but lacking in large debris.

Behaviour

About 95% of smolts observed were aggregated in groups of >5 fish. Aggregation size increased significantly over the course of the smolt run and was significantly greater in the estuary than in the combined upstream sections (Table 3).

Smolts exhibited few agonistic interactions other than occasional nipping and chasing. Typically, fish were quite secretive, milling about in dark, low-velocity areas under cover with occasional forays to the edge of cover to feed on invertebrate drift or coho fry. Three instances of smolt predation on coho fry, one in the estuary and two in freshwater, were noted during snorkle surveys. Smolts exhibited a high degree of cohesiveness, moving together as a group if disturbed. Departures from this general pattern, however, indicated a degree of plasticity in behaviour. On several occasions, hierarchical behaviour, similar to that described by Paszkowski and Olla (1985), was observed among small numbers (≤ 5) of smolts vigorously defending feeding territories for short periods near the head of pools.

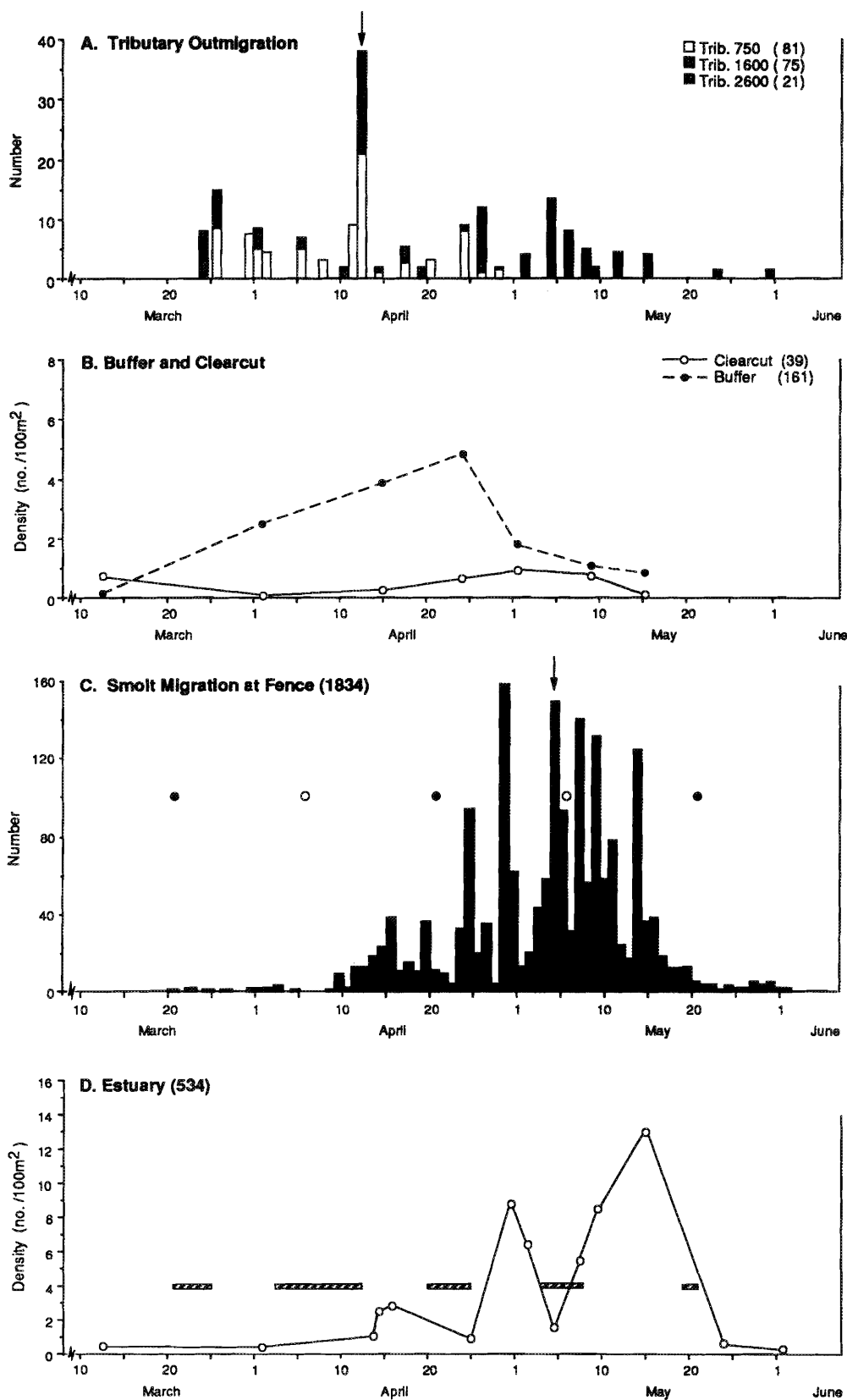


FIG. 1. Timing of movements and utilization of various sections by smolts in Carnation Creek during seaward migration. (A) Movement from upstream tributaries; tributary numbers refer to distance from the main fish fence; (B) density of smolts censused during snorkle counts in clearcut and buffer sections; (C) timing of downstream migration at the main fish counting fence located near the mouth of Carnation Creek; lunar phase indicated as full moon (open circles) and new moon (solid circles); (D) density of smolts censused during snorkle counts in the estuary below the fence; horizontal bars indicate spring tides >3.8 m. Vertical arrow indicates median dates of migration. Total number of smolts indicated in parentheses.

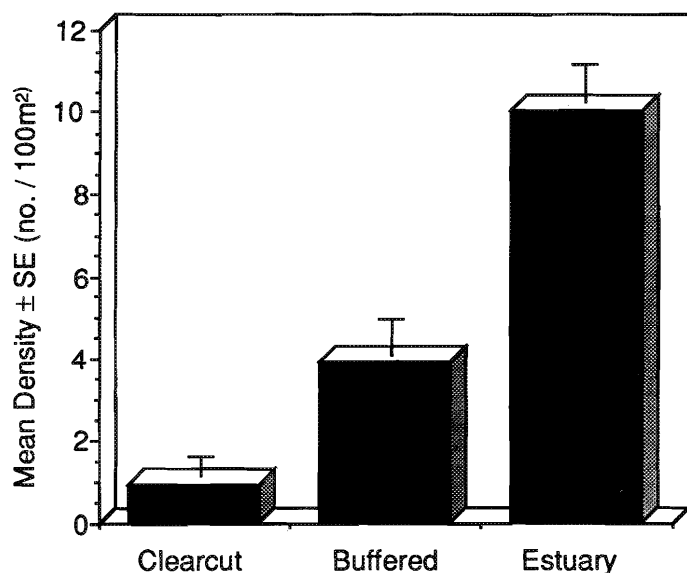


FIG. 2. Mean densities of smolts in clearcut, buffered, and estuary sections as calculated from three highest counts. Differences were significantly different ($P < 0.05$) among all three sections (Tukey's multiple comparisons test).

Discussion

Coho salmon juveniles formed aggregations near large woody debris in freshwater and estuarine sections of Carnation Creek during the period of parr-smolt transformation and seaward migration. Large aggregations of smolts have been reported beneath docks in Oregon estuaries (McAllister 1988). Moser et al. (1991) noted that smolts congregated for extended periods in areas of a Washington estuary having low water velocity and log pilings. These observations of smolts in the field are in agreement with Hoar's (1951) laboratory findings of strong aggregating and cover-seeking behaviours in smolts.

The results were not consistent with studies suggesting that a social system based on agonistic behaviour characterizes coho salmon following smoltification and entry into seawater (Mason 1966; Paszkowski and Olla 1985). We did observe aggression

among smolts (see also Hoar 1951, p. 257), but territorial-hierarchical interactions were infrequent and short-lived. Paszkowski and Olla (1985) suggested that contrasting observations of smolt behaviour may be attributable to aggression becoming more pronounced upon seawater entry. However, the highly clumped distribution and large size of aggregations of smolts we observed in the Carnation Creek estuary indicated that aggregative behaviour of smolts persists at least in brackish water. Our observations support Paszkowski and Olla's (1985) conclusion that smolts do not rigidly form schools but exhibit a degree of plasticity in behaviour dependent upon environmental conditions. The territorial behaviour we observed occasionally among small numbers of smolts feeding near the head of pools, where drift rates of invertebrates were presumably high (Smith and Li 1983), suggests that the combination of small group size and an abundant, localized food source, conditions similar to those provided in laboratory environments, may favour the expression of aggressive behaviour and development of feeding territories (Ryer and Olla 1991). The similarity in behaviour of smolts and lake-rearing coho salmon parr (Swain and Holtby 1989) likely reflects selection for a common behavioural pattern adaptive to open-water environments.

Aggregating and cover-seeking behaviour of smolts represents a continuation of, rather than a marked shift from, behaviour of coho salmon parr during winter. In winter, aggression declines and coho form aggregations near cover as temperatures decrease below 7°C (Bustard and Narver 1975; Tschaplinski and Hartman 1983; McMahon and Hartman 1989). We did not observe a return to territorial behaviour and a more dispersed distribution common to stream-dwelling coho during summer (Dill et al. 1981) as temperatures rose above 7°C in the spring, which suggests that behaviour of smolts was not solely under temperature control (Holtby et al. 1989).

Habitat utilization by smolts also parallels that of overwintering parr. In Carnation Creek, Bustard and Narver (1975) and Tschaplinski and Hartman (1983) showed that during winter, stream-dwelling coho occupy deep pools and undercut banks containing woody debris and are generally absent from habitats lacking cover. We observed a similar habitat use pattern by smolts. We also found a marked reduction in apparent carrying

TABLE 2. Comparisons of smolt density in eight 50-m study reaches and of the relative percentage of total density of smolts observed in the upper, middle, and lower estuary during the first (March 30 – May 3) and second half (May 4 – June 2) of the smolt run. n = total number counted; *differences in means significant at the $P < 0.05$ level; ns = not significant.

	Mean density (SE) (no./100 m ²)	n	% of total density	
			First half	Second half
Clearcut				
A	0.4 (0.2)	7		
B	0.2 (0.2)	7		
C	1.0 (0.3) ns	25		
Buffered				
A	2.9 (0.8)	82		
B	2.4 (0.8) ns	79		
Estuary				
Upper	8.4 (3.1)	260	93.5	53.9
Middle	0	0	0	0
Lower	7.5 (3.9)*	274	6.5	46.1

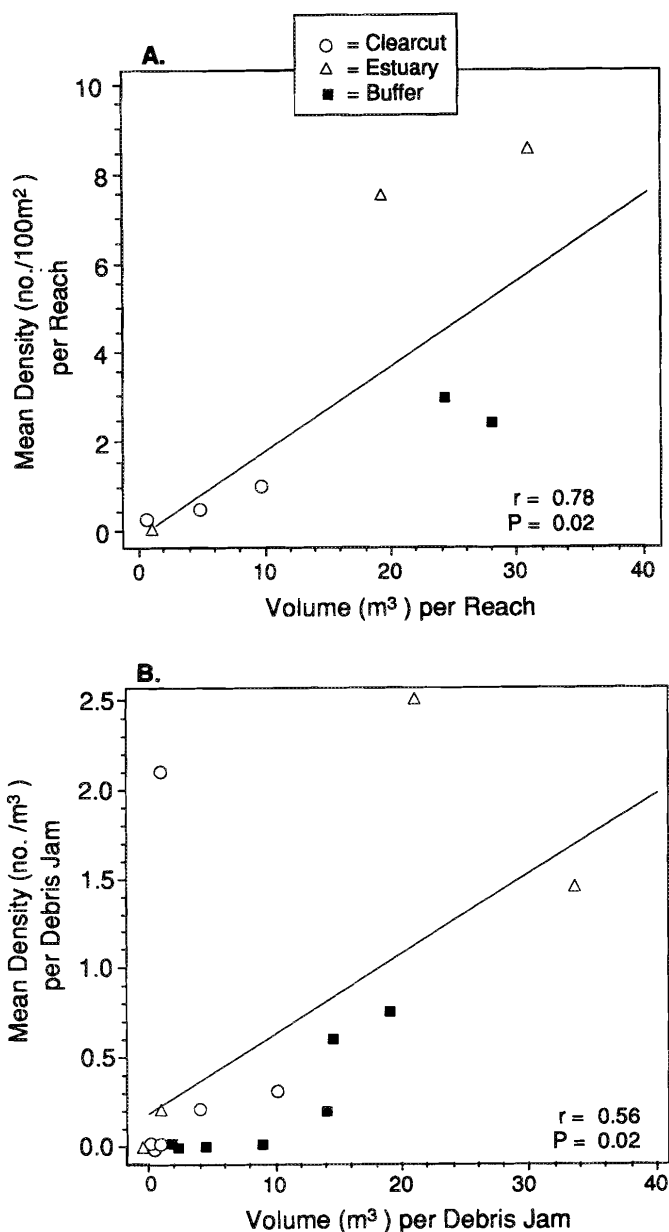


FIG. 3. Relationship between mean smolt density (no./100 m² or no./m³) and (A) volume of large woody debris per reach and (B) volume per debris jam. Location of site indicated by clearcut, buffer, or estuary symbol.

capacity for smolts in clearcut reaches of Carnation Creek, where debris volume and smolt abundance were significantly lower than in reaches bordered by a buffer strip of trees; Tschaplinski and Hartman (1983) noted a similar difference in winter carrying capacity for coho in these same sections. A notable difference between habitat use by overwintering parr and smolts was the high utilization of debris in the estuary by smolts whereas parr were absent from debris in the estuary in late winter (Fig. 2). In Carnation Creek, parr leave the estuary and return upstream in the fall with the onset of cooler temperatures and higher flows (T. G. Brown, Pacific Biological Station, Nanaimo, B.C. V9R 5K6, unpubl. data; see also Cunjak et al. 1989).

Our observations support previous experimental studies showing that woody debris creates the preferred habitat features of slow current velocities and low light intensity (McMahon

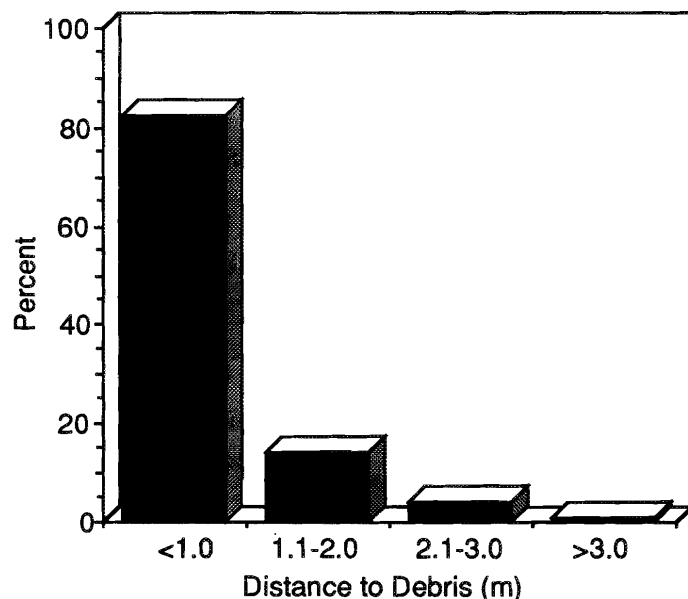


FIG. 4. Proximity of coho salmon smolts to large woody debris; $n = 1260$.

TABLE 3. Size of aggregations of coho salmon smolts observed during the first (March 30 – May 3) and second half (May 4 – June 2) of the smolt run and in the estuary relative to upstream sites (buffered and clearcut sections combined). n_a = number of aggregations observed; SE = standard error; * $P < 0.05$.

	Mean aggregation size (\pm SE)	n_a
Smolt run		
First half	22.8 \pm 4.5	24
Second half	50.8 \pm 12.1*	13
Location		
Upstream	10.6 \pm 1.8	13
Estuary	54.5 \pm 12.6*	12

and Hartman 1989; Shirvell 1990). As in winter, association with these cover features likely provides smolts with shelter from high current velocities and protection from predation. Shelter from high velocity during spring freshets (Hartman et al. 1982) and tidal flushing (Macdonald et al. 1987) is likely important to prevent premature displacement into the ocean prior to completion of smoltification, especially since smolts exhibit reduced swimming abilities (Flagg and Smith 1981). Predation risk from piscivorous birds and fishes appears particularly significant for seaward migrating smolts (Elson 1962; Larsson 1985; Wood 1987). Merganser broods were frequently seen feeding in Carnation Creek and we observed several freshly scarred smolts during underwater counts in the estuary.

The results clearly show that smolts utilize the estuary as a temporary rearing environment prior to ocean entry. The 2-mo (April–May) estuarine residency period for the smolt population migrating from Carnation Creek was similar to that observed in an Oregon estuary (Myers and Horton 1982). Although individual residence times were not determined in our study, even relatively short periods of residency could enhance survival of smolts. In Carnation Creek, 50% of smolts enter

the estuary prior to completion of smoltification (McMahon and Hartman 1988). Exposure to brackish water promotes development of salinity tolerance in salmonids (McCormick et al. 1985; Tschaplinski 1988) and complete physiological adjustment of coho smolts to salinities of 25–30 ppt may require at least 36–40 h (Conte et al. 1966; Miles and Smith 1968). Estuaries may also provide enhanced feeding opportunities (Macdonald et al. 1987). Tschaplinski (1988) reported six times greater numbers of benthic invertebrates in the Carnation Creek estuary compared with upstream. Murphy et al. (1988) observed rapid growth (1.6 mm/d) for coho smolts temporarily rearing in a small Alaska estuary. Rapid growth of smolts may decrease the window of availability to nearshore predators, a major source of ocean mortality for coho salmon (Holtby et al. 1990).

Distribution and movement of smolts in the estuary are likely related to seawater affinity and osmoregulatory ability. During smoltification, coho salmon show a marked preference for seawater (Baggerman 1960; McInerney 1964). The outmigration of smolts coincident with spring tides is consistent with McInerney's (1964) contention that salinity acts as a migratory orientation mechanism for smolts. The increase in use of the lower estuary during the latter part of the smolt run may reflect increased seawater tolerance of migrants. Rodgers et al. (1987) found that downstream migrants showed increased gill (Na + K)-ATPase activity (a measure of osmoregulatory ability) over the course of the smolt migration. McMahon and Hartman (1988) noted that the silvering index, another correlate of seawater tolerance, increased in smolts entering the Carnation Creek estuary as the run progressed.

The results of our study underscore previous research on the importance of large woody debris as a structural element of coho salmon habitat. The multiple functions of woody debris in streams have been well documented (e.g. Bisson et al. 1987); however, relatively little research has addressed its role as fish habitat in estuaries. Our findings show that debris functions as cover habitat for coho salmon during smoltification and seaward migration. In the Carnation Creek estuary, deep pools with debris also serve as holding areas for returning coho and chum salmon and steelhead trout (*O. mykiss*) adults prior to their movement upstream during freshets (T. E. McMahon, pers. observ.). As in streams, debris in many Pacific Northwest estuaries has been reduced through a long history of removal (Gonor et al. 1988) and reduction in source (Bisson et al. 1987). Management practices along streams now address the need for long-term maintenance of large debris by leaving buffer strips of conifers along streambanks during adjacent timber harvest (e.g. Oregon Forest Practice Rules 1988; Bilby and Wasserman 1989); by contrast, conifer buffer strips along estuaries are currently not required in some parts of the Northwest (e.g. Oregon Forest Practice Rules 1988). Our results suggest the need to retain and manage large woody debris for salmonid habitat in estuaries as well as in streams.

Acknowledgments

This paper is dedicated to Dr. Gordon Hartman, lifelong student of salmon behaviour and ecology, and former coordinator of the Carnation Creek Fish-Forestry Project. The original idea for the study grew out of discussions with him. We thank B. Andersen, S. Baillie, T. G. Brown, G. Hennig, T. Joe, D. Leahy, J. C. Scrivener, and P. Tschaplinski for field assistance and B. Bilby, B. Gould, S. Ireland, C. Kaya, J. Magee, and J. C. Scrivener for manuscript review. This study was made possible by a NSERC visiting fellowship to T.E.M.

References

- ANDERSEN, B. C. 1987. Fish populations of Carnation Creek and other Barkley Sound streams 1985–1986. Can. Data. Rep. Fish. Aquat. Sci. 657: 59 p.
- BAGGERMAN, B. A. 1960. Salinity preference, thyroid activity and the seaward migration of four species of Pacific salmon (*Oncorhynchus*). J. Fish. Res. Board Can. 17: 295–322.
- BILBY, R. E., AND L. J. WASSERMAN. 1989. Forest practices and riparian management in Washington state: data based regulation development, p. 87–94. In R. E. Gresswell, B. A. Barton, and J. L. Kershner [ed.] Practical approaches to riparian resource management. U.S. Department of the Interior, Bureau of Land Management, Billings, MT.
- BISSON, P. A., R. E. BILBY, M. D. BRYANT, C. A. DOLLOFF, G. B. GRETTE, R. A. HOUSE, M. L. MURPHY, K. V. KOSKI, AND J. R. SEDELL. 1987. Large woody debris in forested streams in the Pacific Northwest: past, present, and future, p. 143–190. In E. O. Salo and T. W. Cundy [ed.] Streamside management: forestry and fishery interactions. University of Washington, Seattle, WA.
- BROWN, T. G., AND G. F. HARTMAN. 1988. Contribution of seasonally flooded lands and minor tributaries to the production of coho salmon in Carnation Creek, British Columbia. Trans. Am. Fish. Soc. 117: 546–551.
- BUSTARD, D. R., AND D. W. NARVER. 1975. Aspects of the winter ecology of juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*Salmo gairdneri*). J. Fish. Res. Board Can. 32: 667–680.
- CONTE, F. P., H. H. WAGNER, J. L. FESSLER, AND C. GNOSE. 1966. Development of osmotic and ionic regulation in juvenile coho salmon (*Oncorhynchus kisutch*). Comp. Biochem. Physiol. 18: 1–15.
- CUNJAK, R. A., E. M. P. CHADWICK, AND M. SHEARS. 1989. Downstream movements and estuarine residence by Atlantic salmon parr (*Salmo salar*). Can. J. Fish. Aquat. Sci. 46: 1466–1471.
- CUNJAK, R. A., AND G. POWER. 1986. Winter habitat utilization by stream resident brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*). Can. J. Fish. Aquat. Sci. 43: 1970–1981.
- DILL, L. M., R. C. YDENBERG, AND A. H. G. FRASER. 1981. Food abundance and territory size in juvenile coho salmon (*Oncorhynchus kisutch*). Can. J. Zool. 59: 1801–1809.
- ELSON, P. F. 1962. Predator-prey relationships between fish-eating birds and Atlantic salmon. Bull. Fish. Res. Board Can. 133.
- FLAGG, T. A., AND L. S. SMITH. 1981. Changes in swimming behavior and stamina during smolting of coho salmon, p. 191–195. In E. L. Brannon and E. O. Salo [ed.] Salmon and trout migratory behavior symposium. School of Fisheries, University of Washington, Seattle, WA.
- GONOR, J. J., J. R. SEDELL, AND P. A. BENNER. 1988. What we know about large trees in estuaries, in the sea, and on coastal beaches, p. 83–112. In C. Maser, R. F. Tarrant, J. M. Trappe, and J. F. Franklin [ed.] From the forest to the sea: a story of fallen trees. U.S. For. Serv. Gen. Tech. Rep. PNW-GTR-229: 153 p.
- HARTMAN, G. F., B. C. ANDERSEN, AND J. C. SCRIVENER. 1982. Seaward movement of coho salmon (*Oncorhynchus kisutch*) fry in Carnation Creek, an unstable coastal stream in British Columbia. Can. J. Fish. Aquat. Sci. 39: 588–597.
- HARTMAN, G. F., AND J. C. SCRIVENER. 1990. Impacts of forestry practices on a coastal stream ecosystem, Carnation Creek, British Columbia. Can. Bull. Fish. Aquat. Sci. 223: 148 p.
- HEALEY, M. C. 1982. Juvenile Pacific salmon in estuaries: the life support system, p. 315–341. In V. S. Kennedy [ed.] Estuarine comparisons. Academic Press, London, England.
- HOAR, W. S. 1951. The behaviour of chum, pink, and coho salmon in relation to their seaward migration. J. Fish. Res. Board Can. 8: 241–263.
1976. Smolt transformation: evolution, behavior, and physiology. J. Fish. Res. Board Can. 33: 1243–1252.
- HOLTBY, L. B., B. C. ANDERSEN, AND R. K. KADOWAKI. 1990. Importance of smolt size and early ocean growth to interannual variability in marine survival of coho salmon (*Oncorhynchus kisutch*). Can. J. Fish. Aquat. Sci. 47: 2181–2194.
- HOLTBY, L. B., T. E. MCMAHON, AND J. C. SCRIVENER. 1989. Stream temperatures and inter-annual variability in the emigration timing of coho salmon (*Oncorhynchus kisutch*) smolts and fry and chum salmon (*O. keta*) fry from Carnation Creek, British Columbia. Can. J. Fish. Aquat. Sci. 46: 1396–1405.
- IWATA, M., AND S. KOMATSU. 1984. Importance of estuarine residence for adaptation of chum salmon (*Oncorhynchus keta*) fry to seawater. Can. J. Fish. Aquat. Sci. 41: 744–749.
- LARSSON, P.-O. 1985. Predation on migrating smolt as a regulating factor in Baltic salmon, *Salmo salar* L., populations. J. Fish Biol. 26: 391–397.
- MACDONALD, J. S., I. K. BIRTWELL, AND G. M. KRZYNSKI. 1987. Food and

- habitat utilization by juvenile salmonids in the Campbell River estuary. *Can. J. Fish. Aquat. Sci.* 44: 1233–1246.
- MASON, J. C. 1966. Behavioral ecology of juvenile coho salmon (*Oncorhynchus kisutch*) in stream aquaria with particular reference to competition and aggressive behavior. Ph.D. thesis, Oregon State University, Corvallis, OR.
1974. Behavioral ecology of chum salmon fry (*Oncorhynchus keta*) in a small estuary. *J. Fish. Res. Board Can.* 31: 83–92.
- MCALLISTER, T. 1988. Cormorants harassed to save smolts. *The Portland Oregonian*, May 15, 1988, Portland, OR.
- MCCORMICK, S. D., R. J. NAIMAN, AND E. T. MONTGOMERY. 1985. Physiological smolt characteristics of anadromous and non-anadromous brook trout (*Salvelinus fontinalis*) and Atlantic salmon (*Salmo salar*). *Can. J. Fish. Aquat. Sci.* 42: 529–538.
- MCINERNEY, J. E. 1964. Salinity preference: an orientation mechanism in salmon migration. *J. Fish. Res. Board Can.* 21: 995–1018.
- MCMAHON, T. E., AND G. F. HARTMAN. 1988. Variation in the degree of silvering in wild coho salmon, *Oncorhynchus kisutch*, smolts migrating seaward from Carnation Creek, British Columbia. *J. Fish Biol.* 32: 825–833.
1989. Influence of cover complexity and current velocity on winter habitat use by juvenile coho salmon (*Oncorhynchus kisutch*). *Can. J. Fish. Aquat. Sci.* 46: 1551–1557.
- MILES, H. M., AND L. S. SMITH. 1968. Ionic regulation in migrating juvenile coho salmon (*Oncorhynchus kisutch*). *Comp. Biochem. Physiol.* 26: 381–397.
- MOSER, M. L., A. F. OLSON, AND T. P. QUINN. 1991. Riverine and estuarine migratory behavior of coho salmon (*Oncorhynchus kisutch*) smolts. *Can. J. Fish. Aquat. Sci.* 48: 1670–1678.
- MURPHY, M. L., J. F. THEDINGA, AND K. V. KOSKI. 1988. Size and diet of juvenile Pacific salmon during seaward migration through a small estuary in southeastern Alaska. *Fish. Bull.* 86: 213–222.
- 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 5: Seasonal changes in habitat utilization by juvenile salmonids, p. 89–98. *In* W. R. Meehan, T. R. Merrell, Jr., and T. A. Hanley [ed.] *Fish and wildlife relationships in old-growth forests: proceedings of a symposium*. Amer. Inst. Fish. Res. Biol., Morehead City, NC.
- MYERS, K. W., AND H. F. HORTON. 1982. Temporal use of an Oregon estuary by hatchery and wild juvenile salmon, p. 377–392. *In* V. S. Kennedy [ed.] *Estuarine comparisons*. Academic Press, London, England.
- OREGON FOREST PRACTICE RULES. 1988. Northwest region. Available from Oregon Department of Forestry, 2600 State St., Salem, OR 97310.
- PASZKOWSKI, C. A., AND B. L. OLLA. 1985. Social interactions of coho salmon (*Oncorhynchus kisutch*) smolts in seawater. *Can. J. Zool.* 63: 2401–2407.
- PETERSON, N. P. 1982. Immigration of juvenile coho salmon (*Oncorhynchus kisutch*) into riverine ponds. *Can. J. Fish. Aquat. Sci.* 39: 1308–1310.
- RODGERS, J. D., R. D. EWING, AND J. D. HALL. 1987. Physiological changes during seaward migration of wild juvenile coho salmon (*Oncorhynchus kisutch*). *Can. J. Fish. Aquat. Sci.* 44: 452–457.
- RYER, C. H., AND B. L. OLLA. 1991. Agonistic behavior in schooling fish: form, function and ontogeny. *Environ. Biol. Fishes* 31: 355–363.
- SHIRVELL, C. S. 1990. Role of instream rootwads as juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*O. mykiss*) cover habitat under varying streamflows. *Can. J. Fish. Aquat. Sci.* 47: 852–861.
- SMITH, J. J., AND H. W. LI. 1983. Energetic factors influencing foraging tactics of juvenile steelhead trout, *Salmo gairdneri*, p. 173–180. *In* D. L. G. Noakes, D. B. Lindquist, G. S. Helfman, and J. A. Ward [ed.] *Predators and prey in fishes*. Dr. Junk Publishers, The Hague, The Netherlands.
- SWAIN, D. P., AND L. B. HOLTBY. 1989. Differences in morphology and behavior between juvenile coho salmon (*Oncorhynchus kisutch*) rearing in a lake and in its tributary stream. *Can. J. Fish. Aquat. Sci.* 46: 1406–1414.
- SWALES, S., F. CARON, J. R. IRVINE, AND C. D. LEVINGS. 1988. Population characteristics of coho salmon (*Oncorhynchus kisutch*) and other juvenile salmonids overwintering in lake, tributary stream and main river habitats in the Keogh River system, Vancouver Island, British Columbia. *Can. J. Zool.* 66: 452–461.
- TSCHAPLINSKI, P. J. 1988. The use of estuaries as rearing habitat for juvenile coho salmon, p. 123–142. *In* T. W. Chamberlin [ed.] *Proceedings of the workshop: applying 15 years of Carnation Creek results*. Pacific Biological Station, Nanaimo, B.C.
- TSCHAPLINSKI, P. J., AND G. F. HARTMAN. 1983. Winter distribution of juvenile coho salmon (*Oncorhynchus kisutch*) before and after logging in Carnation Creek, British Columbia, and some implications for overwinter survival. *Can. J. Fish. Aquat. Sci.* 40: 452–461.
- WEDEMEYER, G. A., R. L. SAUNDERS, AND W. C. CLARKE. 1980. Environmental factors affecting smoltification and early marine survival of anadromous salmonids. *Mar. Fish. Rev.* 42: 1–14.
- WOOD, C. C. 1987. Predation of juvenile Pacific salmon by the common merganser (*Mergus merganser*) on eastern Vancouver Island. I: Predation during the seaward migration. *Can. J. Fish. Aquat. Sci.* 44: 941–949.