Patterns of Timing and Size of Wild Coho Salmon (*Oncorhynchus kisutch*) Smolts Migrating from the Keogh River Watershed on Northern Vancouver Island

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Coho salmon (*Oncorhynchus kisutch*) smolts leaving the Keogh River and its tributaries demonstrated consistent patterns in their timing and size. An initial early peak in the mean size of migrating smolts occurred several weeks before the peak in their timing, and in several years when smolt migration was monitored until July, a late peak in size occurred near the end of the smolt migration. Changes in the mean size of smolts were not related to their origin within the watershed, and varying age compositions were only partially responsible for the two peaks in mean size. Fish overwintering in tributary lakes grew faster than fish overwintering in tributary streams. A greater proportion of lake-origin smolts migrated to sea after only 1 yr in freshwater than stream-origin smolts. It appears that fish that wait until their second spring to smoltify are among the first to emigrate that spring. These relatively large 2+ smolts, combined with fast growing 1+ smolts that leave early during their first spring, cause the first peak in size. The small numbers of large smolts leaving the Keogh River at the ends of several of the smolt runs apparently left then because of minor flow increases in the river. As has been found with releases of coho smolts from nearby hatcheries, fish that left the Keogh River early in the smolt run generally had a more northerly marine catch distribution than later migrating smolts. A greater proportion of fish migrating to sea late in the smolt run were caught in the fishery than fish migrating early. Additional work examining the marine survival of early and late migrating wild smolts is recommended to enable detailed comparisons to be made between the optimal timing and size of wild and hatchery smolts.

Les tacons du saumon coho (*Oncorhynchus kisutch*) quittent le bassin de la Keogh selon un mode prévisible : plusieurs semaines avant les passages maximaux, la taille des poissons qui migrent est maximale et, quand les observations durent jusqu'en juillet, on observe un autre maximum de taille vers la fin de la migration. La taille n'est pas liée au lieu d'origine, et la composition démographique n'est que partiellement responsable des deux sommets de taille moyenne. Les poissons qui hivernent en lac grossissent plus vite que ceux qui hivernent en ruisseau, et une plus grande proportion des premiers que des seconds descend à la mer après un an seulement. Il semble que les poissons qui deviennent tacons au deuxième printemps sont parmi les premiers à émigrer cette année-là. Le premier passage de gros tacons est dû à ces poissons et aux tacons de première année qui ont grossi rapidement. Le petit nombre de gros tacons qui émigrent de la Keogh après plusieurs passages migratoires le font apparemment à cause de petits accroissements du débit de la rivière. Comme dans le cas des tacons de cohos relâchés de piscicultures voisines, les poissons qui quittent la Keogh tôt dans la saison sont généralement capturés plus au nord que ceux qui migrent plus tard. Les migrateurs tardifs sont pêchés en plus grande proportion que les migrateurs hâtifs. Il faudrait maintenant étudier la survie en mer des migrateurs hâtifs et tardifs afin de pouvoir comparer les données de migration et de grosseur relatives aux tacons sauvages et d'élevage.

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In their studies on the importance of various times and sizes at release for juvenile hatchery-raised coho salmon (*Oncorhynchus kisutch*), Bilton et al. (1982, 1984) hypothesized that it should be possible to manipulate release times and sizes to maximize growth and survival in the marine environment. If optimal release times and sizes do exist for hatchery stocks, it seems reasonable that natural selection pressures may have favoured stocks of wild coho with smolting tendencies similar to that observed for hatchery fish. Alternatively, other factors may control the timing and size of wild smolt migrations. However, there are few data on the migratory timing and sizes of wild coho smolts, and the impact of smolt size and timing on adult returns is poorly understood.

Salmonid populations have been investigated in the Keogh River on northern Vancouver Island (Fig. 1) since 1975 when a fish counting fence was installed to enumerate migrating adult steelhead (*O. mykiss*) (Ward and Slaney 1988). This 33-km long river drains an area of 129 km^2 and varies in flow between 0.1 and 254 $m^3 \cdot s^{-1}$. Hatchery outplants of coho to the Keogh have not been permitted although fish in the river have been impacted

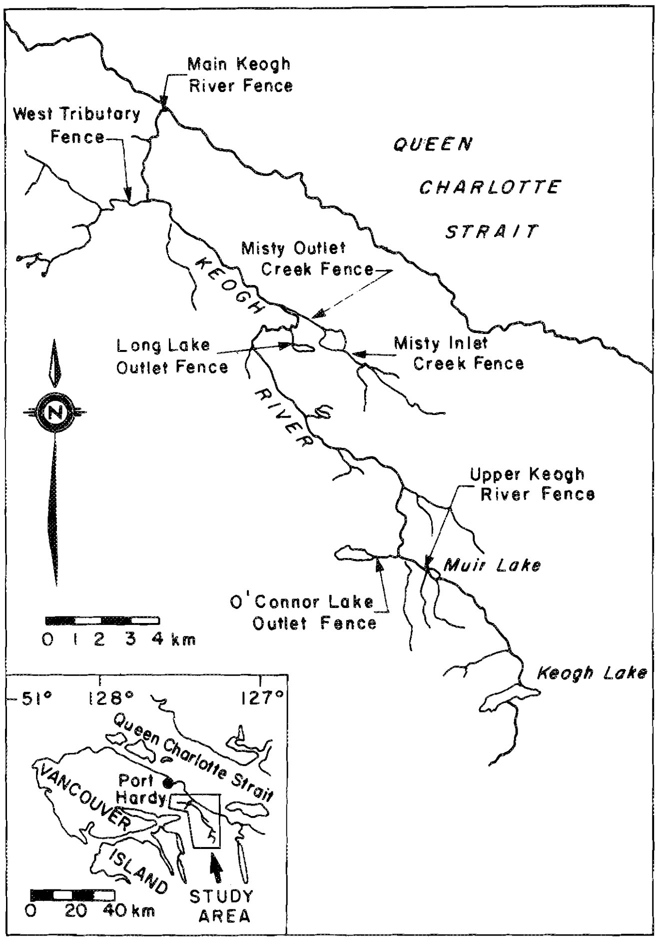

FIG. 1. Location of the fish counting fences in the Keogh River Watershed. Inset shows the location of the Keogh River Watershed on northern Vancouver Island.

by experimental stream fertilization (Perrin et al. 1987), instream enhancement structures (Ward and Slaney 1979, 1981), lake-pen rearing of steelhead smolts (Slaney and Harrower 1981), and logging. Between 55 000 and 105 000 coho salmon smolts leave the system annually. Preliminary analysis of data on the coho smolts leaving the Keogh River between 1979 and 1985 demonstrated that consistent trends in the timing and sizes of smolts existed. Therefore, we initiated a study to investigate if different overwintering environments were responsible for producing these trends. In this paper we discuss the patterns in size and timing for wild coho salmon smolts in the Keogh River in relation to their overwintering environment and age structure. Coded-wire tag data from commercial and sport fish catches are used to compare the marine distribution of fish that left the Keogh River early and later during the smolt run.

Methods

Coho salmon smolts were enumerated every spring between 1978 and 1987 at the main fish counting fence about 300 m upstream of the Keogh River mouth (Fig. 1). Smolt enumeration was only conducted during spring as earlier studies (e.g. Shapovalov and Taft 1954) indicated that most coho smolts migrate to the sea during spring. As well, smolt trapping in the Keogh River during the autumn and winter of 1975 and 1976 failed to capture any coho salmon smolts, although some coho parr were caught. During the enumeration of smolts leaving the Keogh River, the river was normally diverted away from the main fence via an overflow channel. Smolts were collected in trap boxes after passing over a large horizontal screen (expanded metal mesh, 9.9 × 22.2 mm). Occasionally, during freshets when it was not possible to divert all the river down the overflow channel, smolts were also collected using inclined-plane traps along the main fence (Mottram 1977). Trap efficiency tests were conducted usually twice per season. These tests consisted of capturing large (>120 mm) coho smolts in the trap boxes, clipping a corner of the caudal fin of 500 of these fish, and then releasing them about 50 m above the main fence. Subsequently, smolts captured in the trap boxes were examined for clipped fins. Trapping efficiency was usually about 90%.

Between 1977 and 1980, smolt traps were operated in various tributaries of the Keogh River as well as the upper mainstem river. These traps, similar in design to the main fence, are described by de Hrussoczy-Wirth (1979) and Smith and Slaney (1980). Lake-origin smolts were captured in 1977 and 1978 at the outlet of O'Connor Lake; predominantly stream-origin fish were captured in West Tributary in 1977 and 1978. Fish originating from a combination of lake and stream environments were captured in the upper Keogh River near the outlet of Muir Lake each year between 1977 and 1980 and in Misty Outlet Creek in 1977 (Fig. 1). To assist in distinguishing between differences in the timing and sizes of coho smolts that overwintered in lake and stream habitats, smolts were again trapped in 1986 at the outlet of O'Connor Lake, as well as at the outlet of Long Lake, and the inlet of Misty Lake (Fig. 1). There are no streams containing salmon upstream of O'Connor or Long Lake and no lakes upstream of the Misty Inlet Creek trapping site. The O'Connor Lake trap was operated continuously between 14 April and 27 May. The traps in Long Lake Outlet and Misty Inlet Creeks were operated intermittently between 20 March and 17 July, the number of 24-h periods per week depending upon the size of the smolt run and the availability of personnel. All traps were 100% efficient in capturing migrating smolts.

During the early part of the smolt migration, significant numbers of coho parr were often caught. These fish generally had parr marks and usually were smaller than the more silver smolts. Any coho less than 75 mm was considered a parr and all parr were excluded from the data analysis.

At each trap site, smolts were sampled randomly for fork length and weight; scales were taken from a subsample of these fish for subsequent age determination.

In 1977 and 1978, coho smolts captured at the main fence were coded-wire tagged (de Hrussoczy-Wirth 1979) and results were analyzed to assess the relationship between timing of smolt migration and catch in the commercial and sport fisheries. In 1977, three tag codes were used, corresponding to the early, peak, and late portions of the smolt migration. In 1978, fish migrating during the first half of the migration period had one tag code, while fish migrating during the second half of the migration had a separate code:

Year	Timing	Capture period	Approximate number tagged
1977	early	20 April–11 May	9 558
1977	middle	12 May–27 May	24 116
1977	late	28 May–21 June	7 862
1978	early–mid	30 April–13 May	9 489
1978	mid–late	13 May–21 June	18 856

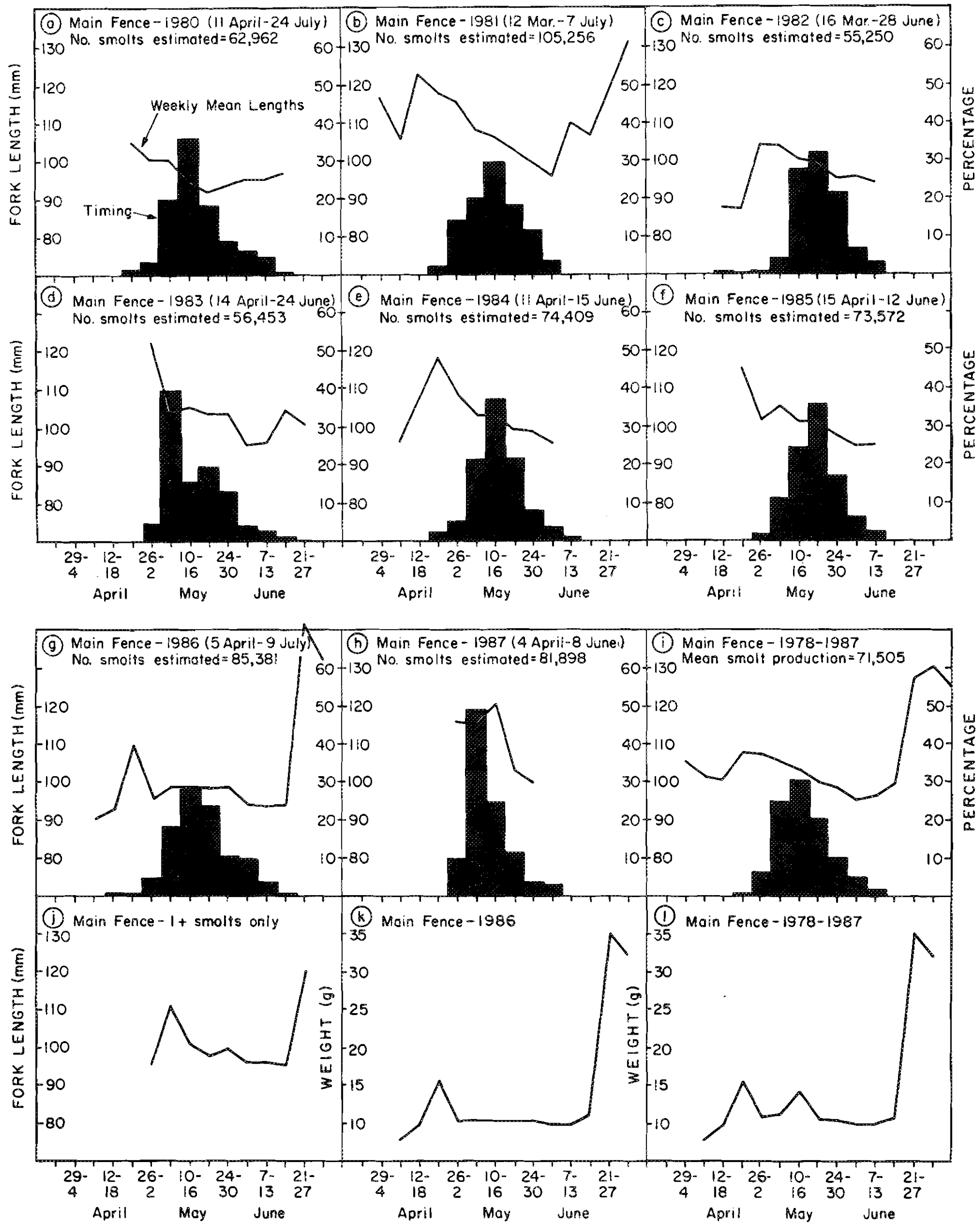

FIG. 2. Weekly mean lengths and timing of migration for coho smolts captured at the main fish counting fence on the Keogh River during 1980–87 (a–i), for 1+ smolts only (j), and weekly mean weights (k–l). The period the fence was operated each year is indicated in brackets. Sample size was always greater than 25 smolts measured each week; otherwise weekly means are not given. Weekly mean lengths in (i), and (j), and weights in (l) are not weighted by year.

The numbers of tagged fish captured in the commercial and sport fisheries in Alaska, British Columbia, Washington, and Oregon were obtained through the Mark Recovery Program. As commercial catches were sampled at a target intensity of 20% (Kuhn et al. 1988), the number of observed recoveries of tagged fish in the commercial fishery was multiplied by five. Approximately 25% of clipped coho caught by the sport fishery in the Strait of Georgia (body of water between Vancouver Island and mainland) in 1980–81 were reported (DPA 1982) so the number of reported recoveries in the sport catch was multiplied by four to obtain the estimated number in the sport catch.

Results

Size and Timing of Smolts at Main Fence

For each of the years for which adequate numbers of fish were measured throughout the smolt migration, there was a peak in the length distribution near the beginning of the run, usually in late April (Fig. 2 a–i). This was invariably followed by a decrease in the mean length of migrating smolts. In several of the years when smolt migration was monitored until late June (1981, 1983, and 1986), the mean length of migrating smolts again increased about this time. The same pattern was illustrated when the mean weights of migrating smolts were plotted by weekly intervals (Fig. 2 k–l).

The timing of the run was consistent. The peak migration period was usually in mid-May and never before 3 May or after 23 May. The first peak in mean smolt length was between 1 and 4 wk before the peak in timing (Fig. 2 a–i).

These consistent patterns in the size and timing of smolts at the main fence were examined by plotting length-frequency distributions by weekly intervals for each year. Results are

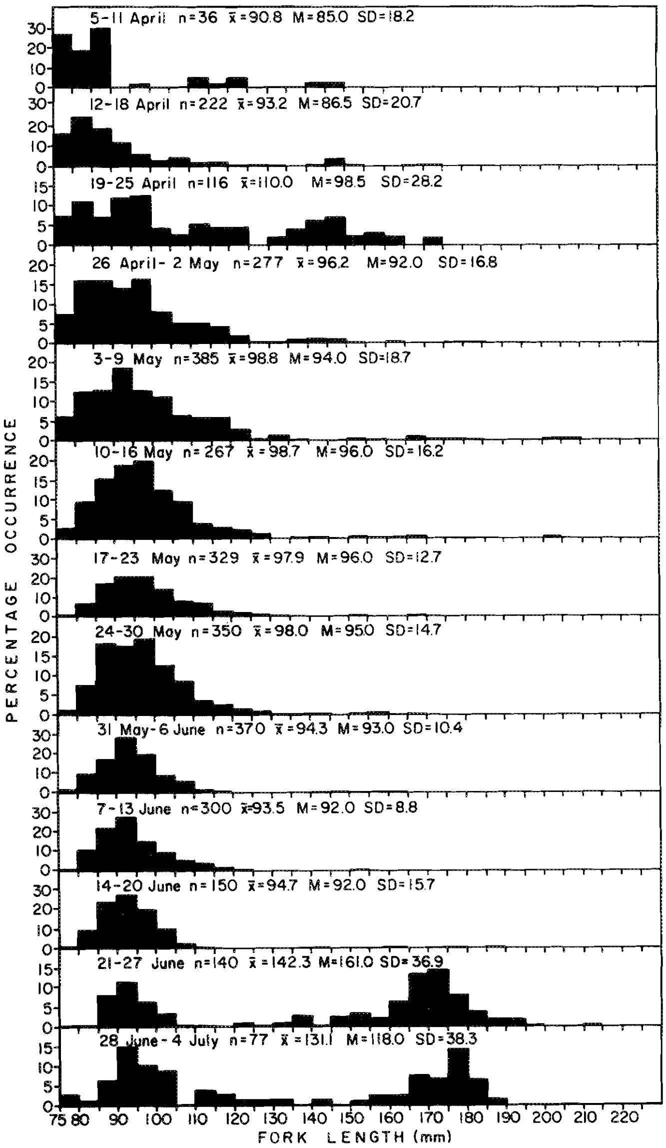

FIG. 3. Length-frequency distributions by weekly intervals for coho smolts captured at the main fish counting fence on the Keogh River during 1986. Mean ($\bar{x}$), median (M), and standard deviation (SD) are given for each weekly interval.

presented here for 1986, the year that the most intensive smolt sampling occurred (Fig. 3). In the early part of the run, the length–frequency distribution was skewed right because the smolts were predominantly small. As well, many of the coho leaving the river at this time were parr less than 75 mm which were excluded from the analysis.

The peak in the mean size of smolts during 19–25 April 1986 was at least partly attributable to the relatively high proportion of large 2+ smolts in the run. After mid-May, less than 10% of the smolts aged were 2+, while before 10 May, the proportion of 2+ smolts was generally much higher (Table 1).

As the run approached and then passed its peak in timing, the reduction in the proportion of 2+ smolts reduced the mean length of the smolts. However, the mean size of the younger cohort also declined and the frequency distribution approached normality. Late in the 1986 run (21 June–4 July), the frequency distribution was bimodal (Fig. 3). This resulted in an increased mean size of smolts. Interestingly, it appears that both modes were composed of predominantly 1+ fish (Table 1).

The weekly length-frequency distributions of the smolts at the main fence, and the age distributions of these smolts, partially explained the consistent patterns in mean smolt lengths. However, these patterns still existed when only lengths of 1+ smolts were examined (Fig. 2j). The possibility therefore existed that the timing and size of smolts migrating from different parts of the watershed were important in producing these patterns.

Size and Timing of Smolts Upstream of the Main Fence

There were no consistent differences in the timing of migration from various habitats (i.e. stream, lake, or stream/lake combination) (Fig. 4). The peaks in timing from the tributaries were about 1 wk before the peak at the main counting fence; in 1986, the peaks in timing from O'Connor Lake, Long Lake Outlet, and Misty Inlet Creek were during 3–9 May while the peak at the main fence was during 10–16 May. In most cases, a peak in the mean length of migrating smolts occurred before the peak of the smolt run timing.

Consistent differences existed in the size of smolts from the different habitats. In 1977, there were significant differences among the mean lengths of smolts leaving O'Connor Lake, the upper Keogh River, Misty Outlet Creek, and West Tributary ($p<0.01$; Kruskal-Wallis test). O'Connor Lake fish were significantly larger than the others ($p<0.01$), and West Tributary fish were smaller ($p<0.01$); differences among the lengths of fish leaving the upper Keogh River and Misty Outlet Creek were not significant ($p>0.05$) (nonparametric multiple comparisons using a STP test). In 1977, there were significant differences among the lengths of smolts from the four sites during the weeks between 26 April and 30 May ($p<0.05$; Friedman's test); i.e. the effect of time on smolt size was significant. In 1978, there were again significant differences among the mean lengths of smolts leaving the tributaries ($p<0.01$; Kruskal-Wallis test). Significant differences ($p<0.05$; STP test) existed between each group (O'Connor, upper Keogh River, and West Tributary). In 1978, there were no significant differences among the sizes of smolts leaving during the 5 wk between 26 April and 30 May. That year, 88% of the smolts leaving O'Connor Lake were 1+ (age determination sample size, $n=49$) 81% of the smolts leaving West Tributary were 1+ ($n=21$) and 96% of those captured in the upper Keogh River were 1+ ($n=55$) (de Hrussoczy-Wirth 1979). Therefore, the large size of smolts leaving O'Connor Lake was not a result of their age but rather their rapid growth. In 1986, there were significant differences among the sizes of smolts captured at O'Connor Lake, Misty Inlet Creek, and Long Lake Outlet ($p<0.01$; Kruskal-Wallis test). O'Connor Lake fish were significantly larger than fish from Misty Inlet Creek and Long Lake Outlet ($p<0.05$; STP test), but there were no significant differences among the sizes of fish from Misty Inlet Creek and Long Lake Outlet. The reason that the Misty Inlet Creek fish (stream origin) in 1986 were not smaller than the lake origin fish (Long Lake) was the high proportion of 2+ smolts leaving Misty Inlet Creek. Of 55 smolts aged from Misty Inlet Creek, 49% were 1+ ($\bar{x}$ length = 90.9 mm) and 51% were 2+ ($\bar{x}$ length = 101.4 mm). Of 122 smolts aged from Long Lake Outlet, 91% were 1+ ($\bar{x}$ length = 99.6 mm), and only 9% were 2+ ($\bar{x}$ length = 116.8 mm).

Relation between Timing of Smolt Migration and Catch

Fish tagged as smolts leaving the Keogh River contributed more to the commercial troll fishery than the commercial net

TABLE 1. Weekly mean lengths ($\bar{x}l$), standard deviations (SD), and sample sizes (n) indicative of proportions of 1+ and 2+ coho smolts captured at the main fish counting fence on the Keogh River.

		1977			1978			1986		
Week	Age	n	$\bar{x}l$ (mm)	SD	n	$\bar{x}l$ (mm)	SD	n	$\bar{x}l$ (mm)	SD
19–25	1+							11	90.6	10.4
April	2+							13	146.0	13.6
26 April –	1+	45	101.3	25.7				78	93.0	12.0
2 May	2+	10	116.4	12.3				5	112.0	5.3
3–9	1+	65	116.4	16.5				24	95.8	13.3
May	2+	14	127.1	21.1				4	115.0	36.5
10–16	1+	137	105.9		412	100.6		42	98.9	10.6
May	2+	15	121.9		47	124.3		5	123.0	25.6
17–23	1+							50	97.8	8.9
May	2+							3	118.3	11.1
24–30	1+	81	99.5	15.8	89	105.0	21.3	89	94.7	8.4
May	2+	9	116.1	17.9	5	136.4	31.0	5	123.4	16.0
31 May –	1+	108	93.8	10.1	92	100.5	19.5	36	95.9	7.7
6 June	2+	10	117.0	15.6	1	129.0		0		
7–13	1+	120	92.4		79	104.4	26.2	36	94.4	6.7
June	2+	4	122.0		4	146.0	15.3	0		
14–20	1+	90	98.8	14.2	86	92.1	21.5	23	93.3	15.1
June	2+	6	121.8	14.2	2	150.0	77.8	1	193.0	
21–27	1+							19	120.5	28.8
June	2+							1	169.0	
28 June–	1+							4	141.0	36.8
4 July	2+							0		

or sport fisheries (Table 2). With the exception of 10 fish originating from the mid–late group of smolts in 1978, all fish captured in the fishery were 3 yr old. The association between release timing and type of fishery (troll, net, or sport) was not significant (contingency table chi-square; $p>0.5$ for each year). However, a larger proportion of fish tagged as smolts migrating late in the smolt run was caught than of fish tagged early in the smolt run. An estimated 3.5% (333) of those smolts tagged leaving the Keogh River early in the smolt run of 1977 were captured, 3.4% (816) of the middle group were captured, and 5.5% (430) of the latest migrating fish were captured. Of those fish leaving the Keogh River in 1978, an estimated 6.3% (594) of the early group were captured, and 8.4% (1575) of the late group turned up in the commercial and sport catches.

The association between release timing in 1977 and 1978 and location of capture (Fig. 5) was significant (contingency table chi-square; $p<0.05$ for each year). A greater proportion of early migrating smolts was caught in northern areas than later migrating smolts. Late migrating smolts were caught more frequently in southern areas than earlier migrating smolts.

Discussion

Consistent patterns were found when 9 yr of coho smolt length data from the mainstem Keogh River were analyzed. There appeared to be two maxima in the mean length of smolts. The first was several weeks before the peak date for smolt output and a second maximum was found in late June in three of the years that smolt sampling extended this late in the season. The two peaks in mean size were only partially attributable to varying age compositions in the migrating smolts. It was found that 1+ smolts, which constituted approximately 90% of the total smolts, also exhibited a similar pattern of length and timing except that the first peak in mean size appeared to occur closer to the climax in numbers. In those years that a second size maximum was found, late-occurring minor flow increases may have been responsible for the small pulse of large smolts which caused this second maximum.

Smolts captured in tributaries to the Keogh River and the Keogh River near its headwaters also exhibited similar characteristics with large smolts leaving before the climax of the run. There were no significant differences in the timing of migration of smolts from various tributaries, but there were significant differences in the sizes of smolts from different locations. Smolts produced in O'Connor Lake were significantly larger than smolts originating from a combination of stream and lake environments (Misty Outlet Creek and upper Keogh River), while fish produced in the predominantly lotic environment of West Tributary were smallest. Lake-origin smolts from Long Lake were not bigger than stream-origin smolts from nearby Misty Inlet Creek, but this was due to the high proportion of 2+ smolts produced in Misty Inlet Creek. In a separate investigation, Swales et al. (1988) documented that underyearling coho in Misty Inlet Creek and Long Outlet Creek were significantly smaller than coho in Misty Lake and Long Lake. The overwintering location of smolts captured at the main enumeration fence on the Keogh River could not be identified by the size or timing of migrating smolts captured there.

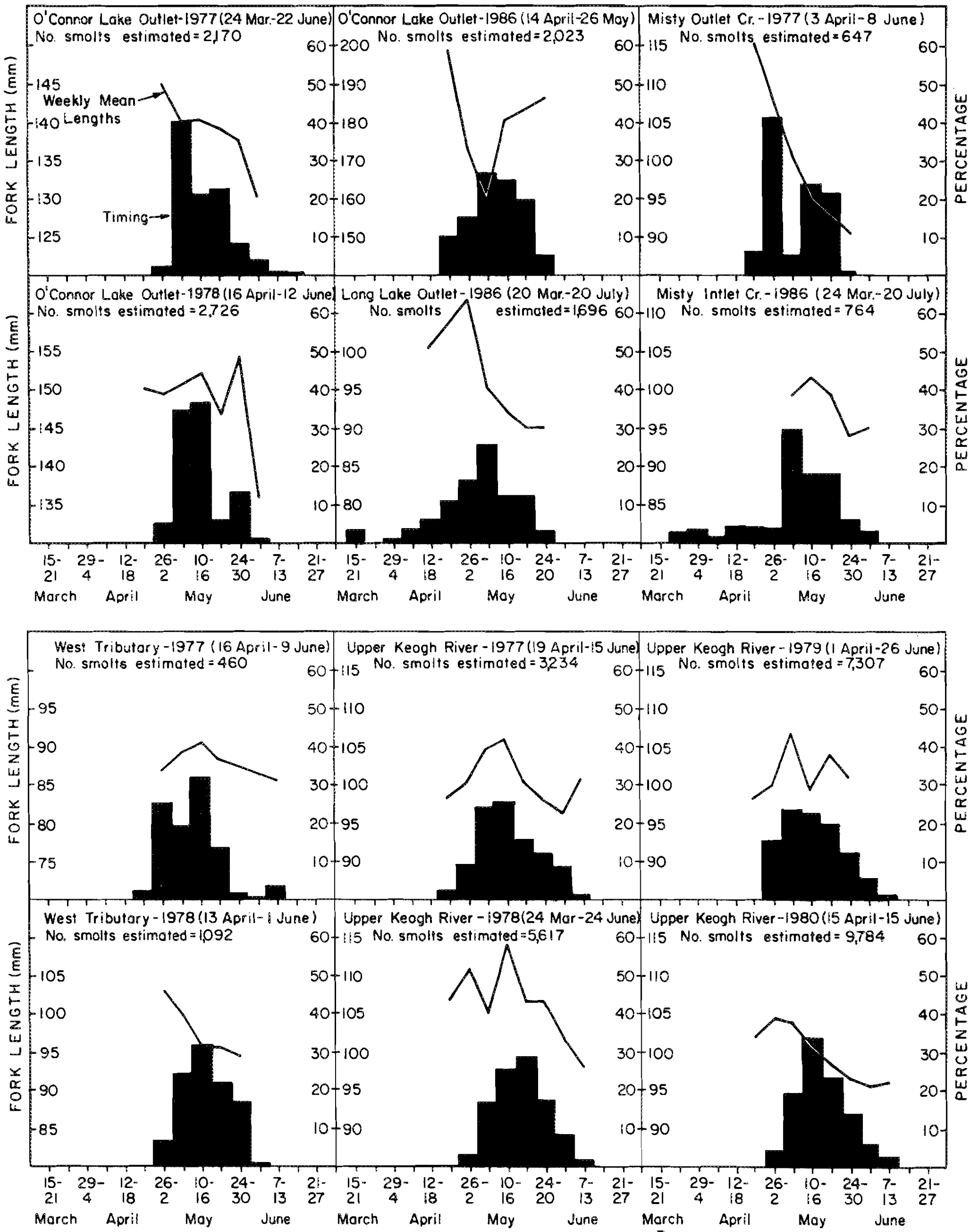

FIG. 4. Weekly mean lengths and timing of migration for coho smolts captured at fish counting fences operated in tributaries to the Keogh River and in the upper Keogh River. The period the fences were operated each year is indicated in brackets. Sample size was always greater than 15 smolts measured each week; otherwise weekly mean lengths are not given.

These paradigms in size and timing are not unique to coho leaving the Keogh River. For example, an initial peak in the mean size of steelhead smolts leaving the Keogh River about 10 May is followed by a relatively constant decline in mean size until late June when the size of smolts increases (B. R. Ward, unpubl. data). Steelhead smolts from the Keogh River average 70 mm longer than coho (Ward and Slaney 1988), and their peak timing is almost 2 wk later, occurring about 25 May. Weekly mean lengths of coho smolts leaving Carnation Creek on the west coast of Vancouver Island also varied consistently for many years, although the pattern was not as distinct as for coho leaving the Keogh River. Examination of 14 yr of data provided in Anderson (1983a, 1983b, and 1985) and Narver and Anderson (1974) revealed that for 1+ smolts, there was always an increase in mean smolt lengths until the end of April, although this increase sometimes continued until early June. In 8 yr there appeared to be a decrease in smolt size during the last half of May and June. Saunders (1967) found that older Atlantic salmon (*S. salar*) smolts (3+ and 4+) tended to migrate before young smolts. Ewing et al. (1984) reported that larger chinook salmon (*O. tshawytscha*) juveniles migrated before small ones and probably swam faster. These patterns of smolt size and migration timing have implications for the sampling of smolts in streams. We must be cautious when we compare lengths of smolts from different systems, particularly if the smolts are not all captured at the same time of year.

Apparently, similar pressures operate in different environments, which can produce the patterns of smolt size and migration timing that were found in the Keogh River. Folmar and Dickhoff (1980) stated that increasing photoperiod and water

TABLE 2. Estimated numbers (percentages in brackets) of coho salmon from the Keogh River that were captured in the troll, net, and sport fisheries. Smolts were coded-wire tagged in 1977 and 1978 according to their timing in the smolt migration.

	Release year				
	1977	1977	1977	1978	1978
Timing	early	middle	late	early–mid	mid–late
Troll fishery	261 (78.4)	603 (73.9)	307 (71.4)	471 (79.3)	1235 (78.4)
Net fishery	64 (19.2)	190 (23.3)	103 (24.0)	110 (18.5)	300 (19.1)
Sport fishery	8 (2.4)	23 (2.8)	20 (4.7)	13 (2.2)	40 (3.2)

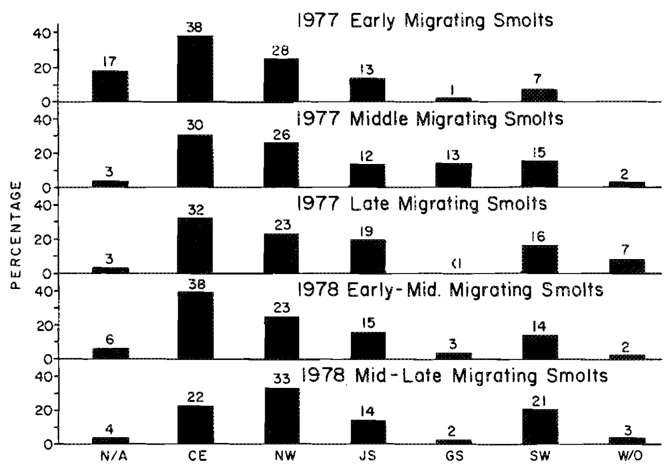

FIG. 5. Catch distributions of different groups of wild coho smolts migrating from the Keogh River during 1977 and 1978. N/A = northern (statistical areas 1–5) and Alaska; CE = central (areas 6–12 and 30); NW = northwest coast Vancouver Island (areas 25–27); JS = Johnstone Strait (areas 12 and 13); GS = Strait of Georgia (areas 13–18); SW = southwest coast Vancouver Island (areas 21, 23, and 24); W/O = Washington and Oregon.

temperature appeared to regulate the beginning and synchronization of smoltification and migration, but they also cited studies documenting the importance of an endogenous factor, manifested as critical size, which may be important in the timing of seaward migration. When fish, because of various environmental priming factors, are physiologically ready to smoltify, external releasing factors such as a heavy rain can trigger migration (Baggerman 1960; Grau 1981). When the lengths of 2+ smolts from the Keogh River were backcalculated to give their lengths 1 yr previously, these lengths were significantly less than those of 1+ smolts (J. R. Irvine, unpubl. data). These fish apparently had not reached their proper state of readiness to migrate during their first spring, but were generally among the first to emigrate the next spring.

It is of interest that the critical size for smoltification varies in different systems. We have shown how smolts produced in different environments in the Keogh River watershed emigrated at different sizes. Age 1 smolts in tributaries of the Cowichan River on Vancouver Island ranged between 74 and 100 mm (Argue et al. 1979). Drucker (1972) gives the average fork lengths of coho smolts for a variety of systems between Alaska and California. Average lengths of 1+ smolts ranged between 83 and 120 mm. The reason large 1+ smolts migrate before the peak of the outmigration is probably because, due to their large size, they are receptive to external releasing factors earlier than most smaller fish.

As mentioned earlier, the large smolts that left the Keogh River at the end of several of the runs may have left then because of minor freshet events in the river. These late-migrating large smolts, few in number, migrated well after the peak in migratory timing when many investigators have stopped enumerating smolts. In 1986, we maintained smolt enumeration fences in Long Lake Outlet and Misty Inlet Creek until early July, and large smolts were not captured in these tributaries late in the run. Flows were low in these tributaries in June and July. The large smolts captured at the main fence in June 1986 presumably originated from the main river, in which there was a small increase in flow in June. It has been shown that coho held in hatcheries can also smolt well after the peak in their normal run timing. Zaugg (1981) found that hatchery coho which had exhibited the silvery colouration and enzyme activity levels characteristic of smolts lost these traits after the normal smolt migration period. However, when these fish were released into the Columbia River in June or July, enzyme activity levels increased, silvery colouration returned, and the fish rapidly migrated to sea. As the large smolts that left the Keogh River in June were bigger than fish leaving in April or May, it does not seem possible that these fish could have waited until the following spring to emigrate. They apparently left in June because an increase in flow occurred then, and they presumably would have left later in the summer or fall if that is when the next postspring freshet occurred.

Although it was not possible in this study to compare smolts from different parts of the run in the returning adult escapement, it was possible to make comparisons in the commercial and sport fisheries. Fish originating from the Keogh River watershed were caught from Alaska to Oregon with most being caught by the commercial troll fishery near the North end of Vancouver Island. This gives us an indication of the extent of oceanic migration for coho salmon from the Keogh River. Some coho salmon spend their entire marine lives in "inside" waters (Milne 1957) while others migrate long distances offshore (Hartt and Dell 1986). The fact that a greater proportion of early migrating coho salmon smolts from the Keogh River were caught in northern areas than later migrating smolts implies that early migrating smolts may have different oceanic migration routes than later migrating smolts. Fish from early releases from the Quinsam Hatchery also had a more extended northward distribution than fish from later releases (Bilton et al. 1984; Morley et al. 1988). There is a need for further studies which focus on smolt run timing in relation to oceanic migration routes and timing.

We could not determine differences in natural mortality between early and late migrating smolts because adult escapement was not monitored when tagged fish returned to the Keogh River. A larger proportion of fish that had left the Keogh River after the peak in smolt timing were caught in the fishery than earlier migrating fish. This may indicate increased marine survival to the time of the fishery by late-migrating smolts, or it may simply reflect a difference in migratory routing and/or timing which affected the susceptibility of different groups of fish to fishing pressure.

The peak in timing of coho smolts leaving the Keogh River was earlier than the optimal release times recommended by Bilton et al. (1982, 1984) and Morley et al. (1988) for hatchery-raised coho smolts. In the Keogh, the peak in timing was mid-May. Although natural smolt migrations occur later in more northerly systems (Drucker 1972), May timing peaks have been reported for other Vancouver Island populations (Anderson 1983a; Argue et al. 1979). Bilton and his colleagues examined the influence of time and size at release of coho from two hatcheries on the east coast of Vancouver Island. Results of experiments at Rosewall Creek Hatchery suggested that maximum returns (escapement plus catch) would be obtained by releasing 25.1-g juveniles on 22 June (Bilton et al. 1982). Coho smolts leaving the Keogh River in late June averaged 35 g. When Green and Macdonald (1987) analysed the data provided by Bilton et al. (1982), maximum returns were predicted by the late release of small, rather than large individuals. Results from a more northerly hatchery, the Quinsam, were obtained from releases made in 3 yr. Results from the first year (1980) suggested that maximum adult returns would be obtained from the release of 15.7-g juveniles on 4 June although size at release was less important than time (Bilton et al. 1984). Results from releases made in 1981 and 1983 confirmed that a tight "time window" for release centered at about 5 June, and that size at release was much less important than time (Morley et al. 1988). The release of smaller juveniles (14–30 g) was recommended, chiefly to reduce the incidence of jacking associated with large release sizes. Coho released from the Quinsam Hatchery migrated very quickly downstream to the estuary (Macdonald et al. 1987).

Although it is difficult to conclude from hatchery experiments what the optimal size at release of hatchery fish should be, it is of interest that most wild coho smolts that leave the Keogh River are much smaller than those released from hatcheries. Only during their two peaks in size were Keogh River smolts within the size range common for hatchery smolt releases. During the peak of their migration, Keogh River smolts averaged only 10.7 g. The importance of size for wild coho smolts is not understood.

Most wild smolts do not migrate at what appears to be the optimal time for survival in the ocean of hatchery fish, perhaps because the external releasing factors that initiate wild smolt migrations from freshwater occur earlier. Alternatively, downstream migration may be mainly passive and associated with changing stream flows. Perhaps if wild smolts were to delay their migration timing, they would fare better in the marine environment than they currently do, but instream survival would be poor. It is equally likely that late releases of hatchery coho do best because they do not have to compete with many wild smolts, and also perhaps because marine predators have not evolved to capitalize on the late arrival of these smolts. Further work examining the marine survival of early and late migrating wild smolts is underway to enable more detailed comparisons to be made between the optimal timing and size of wild and hatchery coho salmon smolts.

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