Overwintering habitats of coho salmon (*Oncorhynchus kisutch*) and other juvenile salmonids in the Keogh River system, British Columbia

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Catches of overwintering juvenile coho salmon (*Oncorhynchus kisutch*) in the Keogh River system, Vancouver Island, were higher in two small (8 and 25 ha), shallow (mean depth 2–3 m) lakes and their outlet and inlet streams than in the main river, where steelhead trout (*Salmo gairdneri*) were predominant. Dolly Varden char (*Salvelinus malma*), cutthroat trout (*Salmo clarki*), and threespine stickleback (*Gasterosteus aculeatus*) were also present in the lakes. The distribution of coho salmon in the lakes was restricted largely to areas close to the bank, with few fish being captured in offshore areas or in mid-water. Apparent differences in the abundance of coho salmon between the two lakes may have been related to differences in fish community composition, with sticklebacks being particularly numerous in Misty Lake, where catches of coho salmon were lower than in Long Lake. The population density and biomass of coho salmon overwintering in Long Lake were estimated to be 176 fish/ha and 1.14 kg ha^{-1}, respectively. The mean length of coho salmon in the lakes was greater than that of coho salmon in the tributary streams and main river, and the mean length of the salmon in the lakes generally increased with distance away from shore.

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Les résultats d'un échantillonage dans le bassin du Keogh, dans l'île de Vancouver, ont démontré que les Saumons coho (*Oncorhynchus kistuch*) juvéniles qui passaient l'hiver en deux petits lacs (8 et 25 ha) peu profonds (profondeur moyenne 2–3 m) et dans leurs tributaires étaient plus nombreux que ceux du cours principal où dominait la Truite "steelhead" (*Salmo gairdneri*). Les lacs contenaient aussi de la Dolly Varden (*Salvelinus malma*), de la Truite fardée (*Salmo clarki*) et de l'Epinoche à trois épines (*Gasterosteus aculeatus*). Les saumons des lacs occupaient surtout les zones situées près des rives et peu de saumons ont été capturés plus loin des rives ou au large. Les différences de densité des saumons dans les deux lacs sont probablement attribuables aux différences dans la composition des communautés de poissons des deux lacs : les épinoches étaient particulièrement abondantes dans le lac Misty où les saumons étaient moins nombreux que dans le lac Long. La densité des Saumons coho qui ont passé l'hiver dans le lac Long a été évaluée à 176 poissons/ha et la biomasse, à 1,14 kg ha^{-1}. La longueur moyenne des saumons des lacs était supérieure à celle des saumons des tributaires ou du cours principal et, dans les lacs, les poissons les plus longs se trouvaient loin des rives.

[Traduit par la revue]

Introduction

There has been a growing realisation recently of the critical role that the winter period can play in determining the freshwater production of juvenile anadromous salmonids (Bustard and Narver 1975; Swales *et al.* 1986; Tschaplinski and Hartman 1983). Many juvenile salmonids show a marked habitat shift between the summer rearing period and the start of the overwintering period in autumn–early winter (Cederholm and Scarlett 1981; Rimmer *et al.* 1983). Such redistributions seem to be an avoidance response to unfavourable winter conditions in summer rearing areas. This shift in habitat preference is well defined in populations of juvenile coho salmon (*Oncorhynchus kisutch*), which in the autumn and early winter migrate from predominantly main channel summer rearing areas to overwinter in tributaries, side-channels, back-channels, riverine ponds, and other off-channel wetland habitats (Bustard and Narver 1975; Cederholm and Scarlett 1981; Peterson 1982*b*; Swales *et al.* 1986; Tschaplinski and Hartman 1983). In coastal streams and rivers such movements probably serve to avoid the effects of high winter discharges in the main channel (Bustard and Narver 1975; Tschaplinski and Hartman 1983), while in colder, interior (noncoastal) rivers it may be more important to avoid the effects of severe icing and low temperatures (Swales *et al.* 1986).

Juvenile coho salmon show a marked preference for still or slow-moving waters with abundant cover, such as pools, side-channels, and off-channel riverine ponds (Chapman and Bjornn 1969; Hartman *et al.* 1982; Lister and Genoe 1970; Peterson 1982*b*; Swales *et al.* 1986). However, little attention has so far been paid to lakes as overwintering areas. The presence of juvenile coho salmon in lakes has been noted during the spring and summer (Blackman *et al.* 1985; Foerster and Ricker 1953; Mason 1976; Russell *et al.* 1981), but lakes are generally not recognised as major rearing or overwintering areas. The aim of this study was to investigate the use of two small lakes in the Keogh River drainage in northern Vancouver Island, British Columbia, as overwintering areas for juvenile coho salmon and other salmonids, and to compare and contrast population characteristics of fish stocks in lake inlet and outlet streams and main river channel habitats.

Study area

Long Lake and Misty Lake are two small, shallow lakes that drain into the Keogh River, a small coastal river in northeastern Vancouver Island (50.6° N, 127.4° W) (Fig. 1). The

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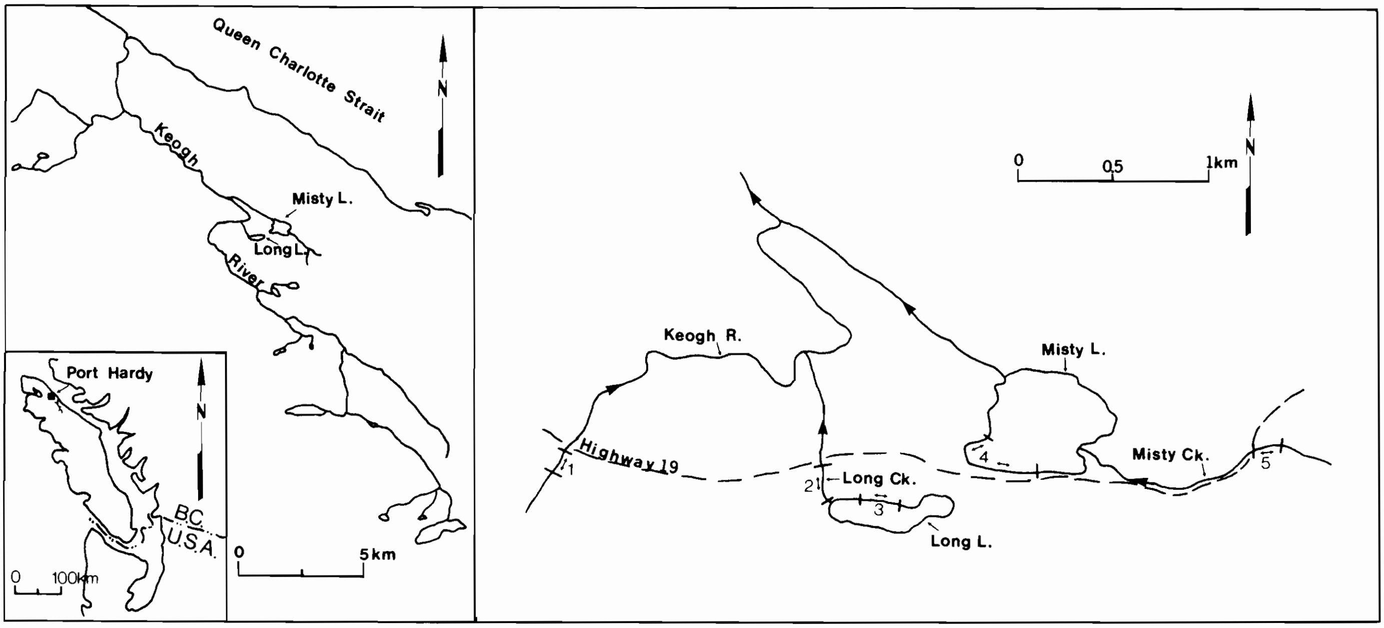

FIG. 1. Location of study sites (1–5) showing area sampled (↔) on routine sampling occasions.

TABLE 1. Study site characteristics

	Long L.	Misty L.	Long Ck.[b]	Misty Ck.[b]	Keogh R.[b]
Mean depth (m)	2.5	2.0	0.25	0.50–1.00	0.50–1.50
Mean width (m)	—	—	1–2	2–3	6–10
Mean flow (cm s^{-1})	—	—	40	25	—
Area (ha)	8.3	25.0	0.02	0.04	0.08
Shoreline length (km)	1.83	2.75	0.2	0.2	0.1
Shoreline development index (SDI)[a]	1.79	1.55	—	—	—
Mean winter temperature, 1985–1986 (°C)	4	4	5	3	4
Winter temperature range (°C)	1–9	3–9	3–8	1–7	2–7

[a]SDI = $L/2(\pi A°)^{1/2}$, where L = shoreline length, A° = lake surface area (Wetzel 1975).
[b]Measurements are only for area sampled.

Keogh River drains 129 km^2 of predominantly coniferous forest and is characterised by a highly variable discharge (0.1–225 $m^3\ s^{-1}$). Winters in this area are typically mild, with high rainfall and little snowfall. The river is humic stained and low in nutrients (Johnston *et al.* 1986). In addition to the lakes, we also investigated their tributary streams (Long and Misty creeks) and the main Keogh River 2 km upstream of the confluences of the two lake outlet streams (Fig. 1, Table 1).

The Keogh drainage supports populations of pink salmon (*Oncorhynchus gorbuscha*), coho salmon, chum salmon (*Oncorhynchus keta*), kokanee salmon (*Oncorhynchus nerka*), steelhead trout (*Salmo gairdneri*), cutthroat trout (*Salmo clarki*) and anadromous Dolly Varden char (*Salvelinus malma*), sculpins (*Cottus asper* and *Cottus aleuticus*), lampreys (*Entosphenus tridentatus*), and threespine stickleback (*Gasterosteus aculeatus*). Annual escapement estimates for the anadromous salmonid populations are highly variable, and for coho salmon in recent years range from 200 to 2000. The Keogh River is also enhanced by annual stockings of hatchery-reared juvenile steelhead trout, and by stream fertilisation (Johnston *et al.* 1986).

Methods

Fish were sampled from November 1985 to March 1986 using Gee wire mesh minnow traps (Cuba Specialty Manufacturing Co., Ontario) at all sites, enabling comparisons to be made among sites. The extensive marginal vegetation, ice, and soft substrate conditions in both lakes meant that conventional sampling techniques such as netting were ineffective. Traps were constructed from galvanised wire mesh (mesh size 6 mm) and consisted of two halves, each with a tapered funnel entrance 15 mm in diameter, that interlocked to form the completed trap, which measured 42 × 22 cm. Gee traps have been found effective in capturing most juvenile salmonids within the size range 50–130 mm (Bloom 1976; Swales 1987). Trap catches can provide estimates of relative abundance of juvenile salmonids in their winter habitat in terms of catch per unit effort (CPUE) (Swales *et al.* 1986). In this study we assume equal trappability for traps in all habitats sampled. It is possible, however, that traps are not equally effective in all habitats, because differences in habitat characteristics between sites may affect trappability. However, we felt that the advantage of using the same sampling method at all sites outweighed possible disadvantages due to differences in trappability.

Traps baited with salmon roe (~2·g) were normally set on the substrate and attached to the bank by an anchoring rope. The standard soak-time (the interval between setting and retrieval) at each site was 24 h, and the CPUE was defined as the catch within this period. The number of traps set at each site ranged from 15 to 30. In both lakes, traps were set along one shore, at 5-m intervals close to the bank (Fig. 1). In the stream and river sites, traps were set at approximately 5-m intervals in a variety of habitats. All sites were sampled approximately biweekly over the study period.

TABLE 2. Trap catches and mean fork lengths of juvenile salmonids captured at each site over the study period

Site	No. of traps set	Coho salmon				Dolly Varden char				Cutthroat trout				Steelhead trout				Stickleback			All species	
		C	%	CPUE	$\bar{L}$	C	%	CPUE	$\bar{L}$	C	%	CPUE	$\bar{L}$	C	%	CPUE	$\bar{L}$	C	%	CPUE	C	CPUE
Long L.	329	743	66	2.3	85.8	270	24	0.8	107.9	21	2	<0.1	134.6	9	1	<0.1	88.2	88	8	0.3	1131	3.4
Misty L.	235	244	25	1.0	83.7	19	2	0.1	124.7	1	<1	<0.1	116.0	5	1	<0.1	91.4	692	74	2.9	961	4.1
Long Ck.	138	224	63	1.6	82.1	83	23	0.6	104.2	20	6	0.1	115.9	2	1	<0.1	105.5	25	7	0.2	354	2.6
Misty Ck.	184	276	57	1.5	81.6	112	23	0.6	112.4	59	12	0.3	112.6	6	1	<0.1	113.2	30	6	0.2	483	2.6
Keogh R.	141	141	35	1.0	74.5	30	7	0.2	100.2	4	1	<0.1	89.0	227	56	1.6	91.6	1	<1	<0.1	403	2.9

NOTE: C, total catch; %, proportion of the total catch; CPUE, mean catch per unit effort; $\bar{L}$, weighted mean length (mm).

On January 14 and February 14 traps were also set along transects parallel and perpendicular to the shore to investigate fish distribution patterns in the lakes. In parallel transects, up to 25 traps were set at 5-m intervals along each of three lines, at 0, 5, and 10 m from the shore. In perpendicular transects, two lines of traps 10 m apart were set out from the shore at 5-m intervals to a distance of 75 m from the shore (in Misty Lake) or across the lake (in Long Lake). At each trap site, water depth was measured and one trap was set on the substrate and one in mid-water, suspended from a buoy at the surface.

On each sampling occasion, the catch in each trap was identified and enumerated, and all salmonids were measured (fork length) to the nearest 1 mm. The fish were then returned alive to the water. A subsample of juvenile coho salmon was taken at each site once per month, preserved in 10% formalin and returned to the laboratory for age determination (scale-reading), stomach contents analysis, and sex determination.

The number of juvenile salmonids in Long Lake in March 1986 was estimated by the mark–recapture technique. A total of 130 traps were set around the shores of the lake. Traps were retrieved and reset every day for 5 days and all salmonids captured were fin-clipped (upper lobe of caudal fin) and returned to the lake. A subsample of juvenile coho was measured (fork length) to the nearest 1 mm and weighed to the nearest 0.1 g. The same sampling intensity was used 1 week later, and the numbers of marked and unmarked fish were recorded. Population estimates were made using the modified Peterson estimate (Ricker 1975).

The surface area and perimeter length of each lake were measured using aerial photographs. Water temperature at each site was monitored using pocket and maximum–minimum thermometers.

Results

Trap catches

Four species of juvenile salmonids (coho salmon, Dolly Varden char, steelhead trout, and cutthroat trout) and one non-salmonid (threespine stickleback) were captured during the study. Catches of most species were generally low (Table 2). Coho salmon formed the greatest proportion of the total catch over the study period in Long Lake (66%), Long Creek (63%), and Misty Creek (57%) (Table 2), but a lower proportion of the total catch at the Misty Lake and Keogh River sites (25 and 35%, respectively). The CPUE of coho salmon was consistently higher in Long Lake than in Misty Lake, except during January, when similar values were recorded (Fig. 2). The CPUEs of coho salmon at the stream and river sites were comparable over most of the sampling period (Fig. 2). There was little indication of any trends in CPUE at most sites, although at Long Creek, CPUE of coho salmon increased gradually during the study (Fig. 2). CPUE of coho salmon often varied considerably between sampling occasions at most sites (Fig. 2). The highest mean CPUE recorded over the study period was in Long Lake (Table 2). Mean CPUEs of coho salmon recorded in lake inlet and outlet streams were similar, with the lowest value overall being recorded at the Keogh River site (Table 2). There was no significant difference in mean CPUEs of coho salmon between sites over the study period ($P > 0.05$).

Dolly Varden char was the second most abundant salmonid at most sites, forming around 24% of the total catch in Long Lake, Long Creek, and Misty Creek (Table 2). CPUE was generally low at most sites, but was consistently higher in Long Lake than in Misty Lake (Fig. 2). Differences in CPUE between sites were significant (Kruskal–Wallis ANOVA, $H = 29.4$, $P < 0.01$).

Steelhead and cutthroat trout were uncommon at most sites, with the notable exception of the Keogh River, where steel-

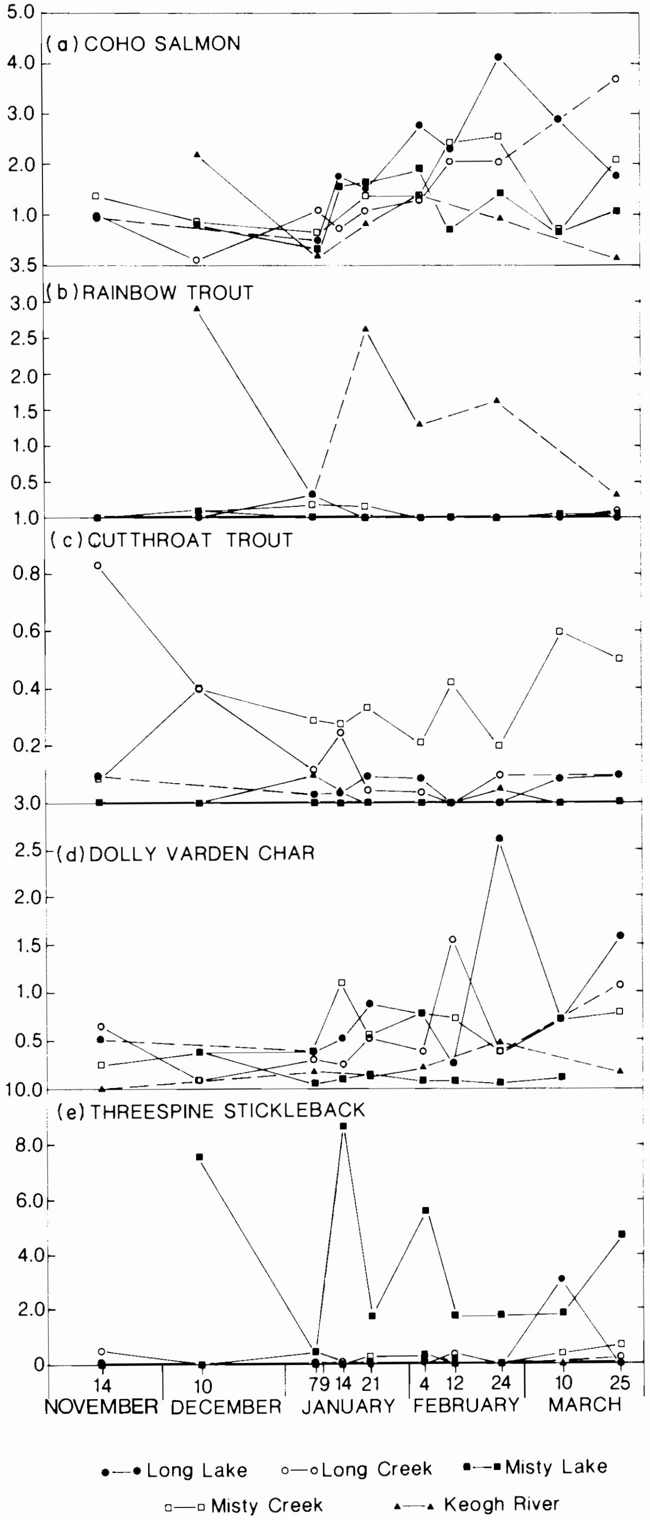

FIG. 2. Variation in mean CPUE of each species over the study period in all five study sites.

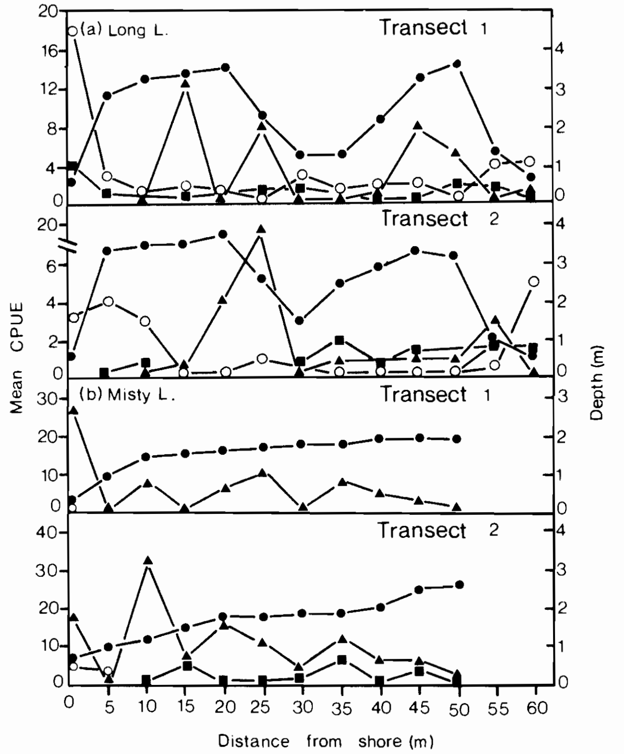

FIG. 3. Mean CPUE of coho salmon (○—○), Dolly Varden char (■—■), and sticklebacks (▲—▲) along transects set perpendicular to the shore in (*a*) Long L. and (*b*) Misty L. ●—● indicates depth profile.

head trout formed 56% of the total catch (Table 2). CPUE at this site was generally high over the study period (Fig. 2). Sticklebacks were also scarce at most sites except Misty Lake, where CPUE was high throughout the study, forming 74% of the total catch (Fig. 2, Table 2).

Lake distribution

The highest CPUEs of coho salmon in both Long and Misty lakes occurred in traps set adjacent to the shore, with few coho salmon being captured in offshore areas (Fig. 3). Although coho salmon were most abundant close to the shore in Long Lake, small numbers were also taken in offshore areas, particularly in a shallow area near the centre of the lake. In Misty Lake, no coho salmon were captured from offshore areas. Dolly Varden char and sticklebacks did not show a marked association with shoreline areas in either lake (Fig. 3).

The results from transects set parallel to the shore further emphasise the association of juvenile coho salmon with the shoreline (Table 3). The highest CPUEs of coho salmon in Long Lake were recorded from traps set as close as possible to the shore, with successively lower catches at 5 and 10 m from shore. This distribution pattern was not evident for other species. Mean length of coho salmon sampled in Long Lake increased significantly with distance from shore in both January and February (January, $t = 2.9$, $P < 0.01$; February, $F = 6.14$, $P < 0.01$). In Misty Lake, however, coho salmon decreased in length with distance from shore, although sample sizes were small.

Population and biomass estimates

Juvenile coho salmon in Long Lake exhibit fairly low levels of abundance in terms of numbers and of weight per unit area (Table 4). Because coho salmon were restricted mainly to bankside areas, abundance estimates may be more meaningful when expressed as number of fish per linear metre of shoreline (Table 4). Dolly Varden char were considerably less abundant than coho salmon (Table 4). Although this species was not as closely associated with bankside areas as coho salmon, population estimates are also given on a linear basis for comparative purposes (Table 4). Population estimates of cutthroat trout could not be made because of low recapture rates.

TABLE 3. Catches of juvenile salmonids and sticklebacks in traps set along parallel transects in Long Lake and Misty Lake

	Distance from shore (m)	No. of traps set	Coho salmon			Dolly Varden char			Cutthroat trout			Sticklebacks		All species	
			C	CPUE	$\bar{L} \pm$ SD	C	CPUE	$\bar{L} \pm$ SD	C	CPUE	$\bar{L}$	C	CPUE	C	CPUE
Long lake															
86-1-14	0	47	84	1.8	87.3±12.8	25	0.5	113.1±15.2	2	<0.1	149.0	0	0	117	2.4
	5	27	19	0.7	91.0±12.9	17	0.6	111.7±12.3	2	<0.1	138.0	1	<0.1	39	1.4
	10	10	2	0.2	107.0	2	0.2	125.0	0	0	—	7	0.7	11	1.1
86-2-14	0	15	35	2.3	86.0±9.9	4	0.3	106.5±10.6	0	0	—	4	0.3	43	2.9
	5	15	20	1.3	92.0±10.6	6	0.4	124.5±21.8	0	0	—	3	0.2	29	1.9
	10	15	23	1.5	94.7±9.1	5	0.3	117.4±16.8	1	<0.1	—	9	0.6	38	2.5
Misty Lake															
86-1-14	0	20	31	1.6	83.7±8.9	2	0.1	124.0	0	0	—	172	8.6	205	10.3
	10	20	5	0.3	81.3±7.1	0	0	—	0	0	—	45	2.3	50	2.5
86-2-14	0	36	25	0.7	84.0±7.9	3	<0.1	121.5	0	0	—	62	1.7	90	2.5
	5	15	6	0.4	77.5±7.3	0	0	—	0	0	—	44	2.9	50	3.3
	10	9	4	0.4	93.0±14.9	0	0	—	1	0.1	136.0	24	2.7	29	3.2

NOTE: C, catch; CPUE, mean catch per unit effort; $\bar{L}$, mean length (mm).

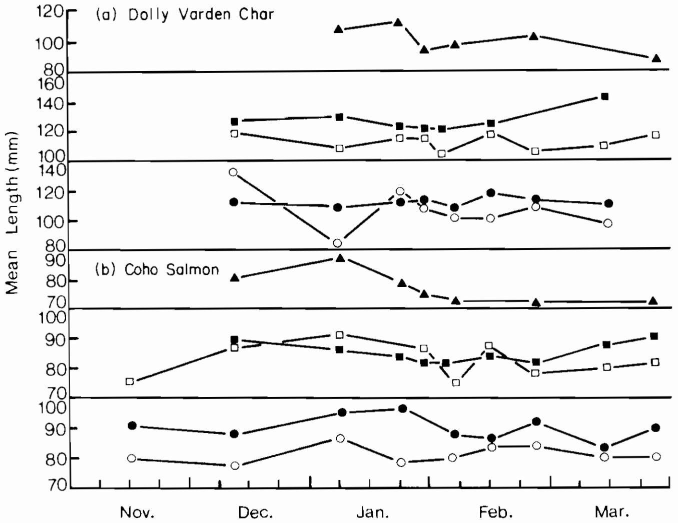

FIG. 4. Variation in mean length of (*a*) Dolly Varden char and (*b*) coho salmon at each site over the study period. ●—●, Long Lake; ○—○, Long Creek; ■—■, Misty Lake; □—□, Misty Creek; ▲—▲, Keogh River.

Size variation

The range in mean length of coho salmon captured over the study period (75–85 mm) was smaller than that recorded for other salmonids (Table 2). There was little evidence for any increase in length of either coho salmon or Dolly Varden char over the study period (Fig. 4). Length–frequency histograms of coho salmon captured at each site over the study period appear unimodal in distribution at most sites (Fig. 5). Coho salmon of ages 0+ and 1+ were present at all sites, with the 0+ age-group being generally predominant (Table 5). The 1+ age-group formed 30–50% of the population at most sites, declining to a low of 17% at the Keogh River site. There was a significant difference in the mean lengths of 0+ coho salmon between sites (F = 3.65, P < 0.01). A comparison of mean lengths of 0+ coho recorded at each site over the study period using orthogonal contrasts showed that lake fish were significantly larger than fish captured in lake inlet and outlet streams (F = 8.1, P < 0.005) (Table 5).

Discussion

The low catches of juvenile coho salmon recorded in the main Keogh River compared with the lakes and tributary streams suggests that main channel habitats were less important as overwintering areas for coho in the system than off-channel habitats. The winter distribution of juvenile salmonids that we recorded may be similar to the summer rearing distribution, or it may reflect a prewinter migration away from summer rearing areas to overwintering habitats. Although there is no evidence from the Keogh River to support either hypothesis, studies in other systems have documented autumn migrations of juvenile coho salmon to off-channel habitats in tributaries (Cederholm and Scarlett 1981; Scarlett and Cederholm 1984), side-channels, sloughs, wetland areas (Bustard and Narver 1975; Brown 1985; Tschaplinski and Hartman 1983), and off-channel riverine ponds (Peterson 1982*a*, 1982*b*).

Lakes have not previously been documented as significant overwintering areas for juvenile coho salmon. This may be more a reflection of the absence of lakes from the river systems

TABLE 4. Poulation size and biomass estimates of juvenile coho salmon and Dolly Varden char in Long Lake, March 1986 (numbers in parentheses are 95% confidence limits)

	Coho salmon	Dolly Varden char
Population size		
No.	1459 (1285–1670)	343 (291–411)
Density (no./m²)	0.017 (0.015–0.020)	0.004 (0.003–0.005)
Density (no./m)	0.800 (0.70–0.91)	0.190 (0.16–0.22)
Biomass		
In kg	9.480 (8.35–10.91)	5.800 (4.90–7.00)
In g m⁻²	0.114 (0.100–0.121)	0.070 (0.06–0.08)
In g m⁻¹	5.180 (4.55–5.50)	3.160 (2.67–3.82)

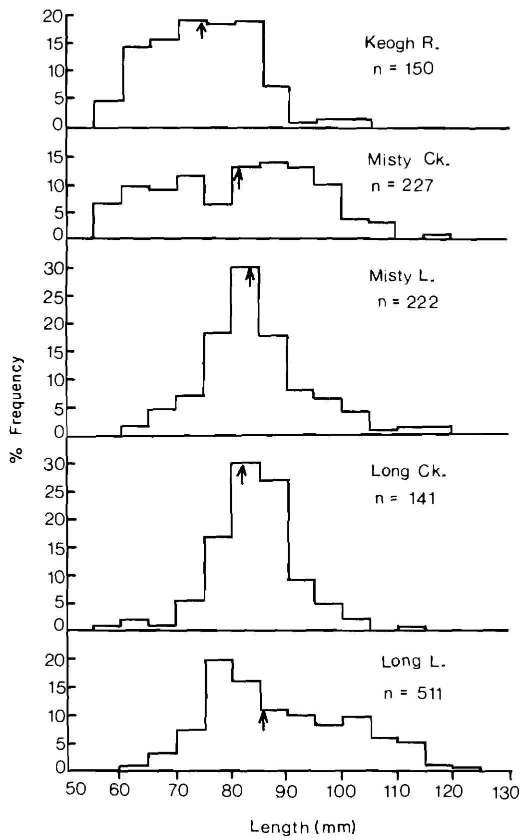

FIG. 5. Length–frequency distributions of juvenile coho salmon captured at each site over the study period. The mean length of each sample is indicated by an arrow.

previously investigated, or that lakes were present but not sampled, rather than a habitat preference or fish distribution factor. Juvenile coho salmon appear to prefer overwintering areas away from the main channel, which are slow-moving or still, and have adequate water depth, cover, and food (Bustard and Narver 1975; Hartman 1965; Swales *et al.* 1986). In river systems without ponds, lakes, or other wetland areas, juvenile coho salmon may have no alternative but to overwinter in suitable main channel areas and in tributaries.

Trap catches suggested that the density of juvenile coho salmon in Long Lake was more than double that in Misty Lake. The factors producing such a large difference in abundance in lakes which appear to be of similar morphometry could be environmental and (or) biological. Major differences in fish community composition between the two lakes are perhaps crucial. Sticklebacks were much more abundant in the littoral area of Misty Lake than in Long Lake, while Dolly Varden char were most abundant in Long Lake. The population of Dolly Varden char in Long Lake may prey on the stickleback population, as has been recorded in other lakes (Armstrong and Morrow 1980). The stickleback population in Misty Lake may, in turn, limit the coho salmon population because of competitive interaction for food and space. Sticklebacks in British Columbia lakes generally feed on planktonic crustaceans and insects (Manzer 1976), as did juvenile coho salmon in Long Lake and Misty Lake. Some possibility for interspecific competition may exist, particularly as both species were captured close to shore.

TABLE 5. Mean lengths ± standard deviation of the 0+ and 1+ age-groups in subsamples of coho salmon taken at each site over the study period

	0+ age-group			1+ age-group		
	N	%	$\bar{L} \pm$ SD	*N*	%	$\bar{L} \pm$ SD
Long Lake	52	52	77.3±6.6	48	48	98.0±7.8
Long Creek	10	67	73.2±10.2	5	33	95.6±6.3
Misty Lake	26	68	77.6±4.6	12	32	92.8±6.3
Misty Creek	39	46	72.8±8.7	45	54	92.9±5.6
Keogh River	24	83	73.1±6.2	5	17	96.5±5.7
All sites	151	57	75.3±7.0	115	43	95.3±6.6

NOTE: *N*, sample size; %, percentage occurrence; $\bar{L}$, mean length (mm). Proportions of age-groups in the samples aged are not necessarily representative of age distribution in the population.

The size of the overwintering coho salmon population may also have been affected by the presence of other salmonids in the lakes. Large Dolly Varden char and cutthroat trout were captured in fyke nets installed overnight in Long Lake. However, in most lakes fish appear to be an insignificant food of Dolly Varden (Armstrong and Morrow 1980). It has also been suggested that juveniles of these species interact minimally in the winter (Glova 1986; Armstrong and Morrow 1980). However, we captured almost all coho salmon and Dolly Varden char in traps set on the substrate, and few in mid-water, which suggests that interspecific competition may occur during the winter in these lakes.

Alternatively, differences in the relative abundance of coho salmon between lakes may be an effect of fish recruitment rather than of habitat suitability or competition. Fry may move into the lakes shortly after hatching and remain there for most of their freshwater residence. If so, the size of the coho salmon population in the lakes may largely be a function of the spawning escapement.

Juvenile coho salmon in both lakes showed a strong association with shoreline areas, and were almost absent from offshore and mid-water areas. Much of the shoreline area in the lakes, particularly Long Lake, consisted of sedges and other emergent grasses, which can provide juvenile fish with valuable cover and food in the form of invertebrates that browse on the periphyton associated with the vegetation. This strong association of juvenile coho salmon with bankside areas has been well demonstrated in streams and rivers (Bustard and Narver 1975; Lister and Genoe 1970; Mason 1976). This habitat preference may be most marked during winter, when fish are least active and rely heavily on concealment for protection from predators (Swales *et al.* 1986; Tschaplinski and Hartman 1983). Thus, lake morphometry may dictate the size of the overwintering coho salmon population.

Long Lake had a higher shoreline development index (a measure of the relationship between the length of the perimeter of a lake and its surface area (Wetzel 1975)) than Misty Lake. This indicates that bankside habitats are more abundant in the former than in the latter, suggesting that this may be a factor in explaining the differences in coho salmon abundance between the two lakes. The contribution of the shoreline to the total lake area generally decreases as lake size increases, so it might be expected that coho salmon would be more abundant in small ponds and lakes than in larger lakes. The evidence that is available supports this theory, with previous studies recording up to 4000 coho salmon/ha overwintering in small riverine ponds (Peterson 1982*a*; Swales *et al.* 1986), compared with less than 200/ha in Long Lake. Also, it might be expected that shallow lakes with a large littoral area would support larger coho salmon populations than deep lakes with a relatively small littoral area. In Great Central Lake (max. depth 200 m, surface area 51 km^2), the density of juvenile coho salmon in the lake during the summer was estimated to be less than 10 fish per hectare, or 0.55 fish per metre of shoreline (Mason 1974).

The finding that coho salmon in the lakes were larger than those in the inlet and outlet streams suggests either differences in growth rates, if winter distribution reflects summer rearing areas, or differential immigration of larger fish into the lakes. Cederholm and Scarlett (1981) also found that the average length of juvenile coho salmon emigrating from the Clearwater River into small tributary streams in autumn increased significantly with distance upstream from the confluence with the main river. The authors concluded that overwinter survival in juvenile coho salmon increased with size, and that smaller fish were selected against during the winter because they were restricted to downstream areas prone to high winter discharge. The difference in mean size of coho salmon from the main Keogh River and those from the lakes and their tributary streams suggests that similar factors may be operating in this system. Mason (1976) found that the lipid reserves of juvenile coho salmon declined considerably over the winter, with the reduction being much greater in fish less than 60 mm than in larger fish. Cederholm and Scarlett (1981) suggested that smaller coho salmon may not have the energy reserves necessary to make long upstream migrations into smaller tributaries. In a comparison of published estimates of winter mortality in salmonids, Murphy *et al.* (1984) showed that in stream fish, winter mortality ranged from 46 to 94% of late summer standing crop, with mortality being higher in mainstream locations than in tributaries and off-channel areas.

Juvenile salmonids have often been classified as either stream- or lake-dwelling species. It is becoming increasingly apparent that many species are more flexible in their choice of lotic or lentic environment than was previously thought, and that lakes can play a vital role in juvenile life histories (e.g., trout (Irvine and Northcote 1982; Swales 1986), sockeye salmon (Foerster 1968), Atlantic salmon (*Salmo salar*) (Chadwick and Green 1985; Pepper *et al.* 1985)). In Newfoundland it has been found that lakes provide better conditions for parr growth and survival than the riverine environment, and that smolt production occurs almost entirely within lakes, which represent important overwintering habitat (Hutchings 1986). The extensive use made of lakes by salmon in Newfoundland appears to reflect the relative abundance of lake habitat in this area (Ryan 1985). Our study suggests that lakes can represent important overwintering habitats for juvenile coho salmon. It may also be the case that, as in Atlantic salmon, juvenile coho salmon not only overwinter in lakes but rear in lakes for a major part of their freshwater residence. Further investigations are needed to identify the extent of lake use by juvenile coho salmon, both as overwintering and rearing habitat.

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