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# Coho Salmon (Oncorhynchus kisutch) Use of Lakes and Streams in the Keogh River Drainage, British Columbia

#### Abstract

Seasonal patterns of freshwater habitat use by coho salmon were documented in two small watersheds on northern Vancouver Island over a three-year period to assess the importance of small lakes and non-natal tributaries as rearing and over-wintering areas. Spawning occurred at a limited number of locations in these systems. Newly-emerged coho fry moved both upstream and downstream from spawning areas in the Misty Lake system towards Misty Lake. The capture of fry in Long Lake and its outlet stream, where spawning was not observed, indicated upstream dispersion of fry from the Keegh River. The lakes provided both summer rearing and overwintering habitat for juvenile coho salmon, but their use varied between years. The mainstem Keegh River was used primarily for rearing during summer. Coho fry generally grew fastest in the lakes and their outlet streams. Cohorts of large fry (mean FL > 80 mm) did not show over-winter growth, but the mean sizes of cohorts of small fry (mean FL < 70 mm) increased over winter, suggesting size-differential mortality. The utilization of small tributary lakes and streams as both summer rearing and over-wintering habitat by juvenile coho salmon suggests that more emphasis should be placed on the preservation and management of such areas. Because use of these habitats may be temporally variable, their importance is easily underestimated.

## Introduction

In the Pacific Northwest, juvenile coho salmon live in freshwater for one to three years before seaward migration as smolts (McPhail and Lindsey 1970, Drucker 1972). Because of their long period of freshwater residency, patterns of freshwater habitat use are particularly important in the management of coho salmon. However, studies documenting the seasonal importance of various habitat types are uncommon.

The distribution of spawning habitat for coho salmon is often clumped within a watershed, requiring the dispersion of fry away from spawning areas. Major episodes of fry dispersal within freshwater include movements during spring in both downstream (Chapman 1962) and upstream (Gribanov 1948) directions, as well as pre-winter movements into small tributaries and riverine ponds (Skeesick 1970, Bustard and Narver 1975, Peterson 1982). Downstream dispersion in spring may partly result from displacement of fry by larger, social dominants (Chapman 1962, Mason and Chapman 1965). Habitat quality also influences fry density, and thus dispersion, through the relationship between territory size and food resources (Mason 1976a, Dill et al. 1981).

The importance of fry dispersal to the production of smolts and adult coho remains largely un-

known. In many coastal river systems, significant numbers of fry migrate to sea (Mason 1975, Crone and Bond 1976, Hartman et al. 1982), but apparently make little contribution to adult returns (Pritchard 1936, Mason 1975, Crone and Bond 1976). Nomadic fry establish residence where space permits (Chapman 1962), and live in a variety of habitats (Dolloff 1987, Murphy et al. 1989). Growth and production vary considerably among habitat types (Bilby and Bisson 1987, Dolloff 1987).

We undertook this study to document seasonal patterns of habitat use by juvenile coho in two small watersheds, one of which was believed to be colonized by fry, and to determine the growth of juvenile coho in stream and lake habitats within the watersheds.

## **Materials and Methods**

Study Site

The use of tributary streams and lakes by coho salmon was examined in the Misty Lake and Long Lake drainages of the Keogh River, a small coastal river on northern Vancouver Island (Fig. 1). Descriptions of the Keogh River watershed and its fish fauna are given in Johnston *et al.* (1986, 1987b), Swales *et al.* (1988), Ward and Slaney (1988), Irvine and Ward (1989), and Bailey and

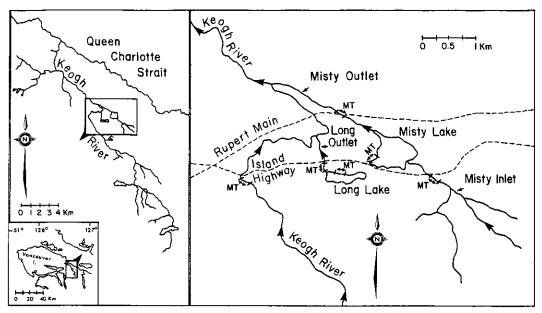


Figure 1. The Keogh River drainage, and the Misty Lake and Long Lake sub-drainages, showing the minnow trapping locations (MT). Large arrows indicate the direction of flow. Insets show the location of the study area within the Keogh drainage and the location of the Keogh River drainage on northern Vancouver Island.

Irvine (1991). The Koogh River is 32 km long and drains a partially-logged, conifer-forested watershed of about 130 km<sup>2</sup>. Large flow variations occur during the autumn-winter rainy season. Mean annual discharge is 5.3 m<sup>3</sup>·s<sup>-1</sup> and mean summer flow is 1.6 m<sup>3</sup> • s<sup>-1</sup>. The maximum estimated flow is 254 m<sup>3</sup>·s<sup>-1</sup>. Between 55,000 and 105,000 (mean = 71,000) coho salmon smolts emigrate from the Keogh River system annually (Irvine and Ward 1989). Other fish species found in the drainage include pink salmon (O. gorbuscha), chum salmon (O. keta), steelhead and rainbow trout (O. mykiss), Dolly Varden char (Salvelinus malma), cutthroat trout (O. clarki), kokanee (O. nerka), coast range sculpin (Cottus aleuticus), prickly sculpin (C. asper), threespine stickleback (Gasterosteus aculeatus), and Pacific lamprey (Lampetra tridentatus).

The Misty Lake and Long Lake systems drain into the mainstem Keogh River about 11 km and 13 km upstream of the confluence of the Keogh River and Queen Charlotte Strait (Fig. 1). The Misty Lake watershed comprises Misty Lake and its inlet and outlet streams, Misty Inlet and Misty Outlet. The Long Lake watershed consists of Long Lake and its outlet stream, Long Outlet. The lakes are small and shallow, and the streams are small (Table 1). Riparian vegetation is primarily a shrub

TABLE 1. Physical characteristics of the Misty Lake and Long Lake sub-drainages recorded during the study.

Parameter	Misty Inlet	Misty Lake	Misty Outlet	Long Lake	Long Outlet
Mean width (m)	2	_	3	_	2
Mean depth (m)	0.5	2.0	0.5	2.5	0.3
Mean velocity (em•s-1)	25	_	45	_	40
Area (ha)	_	25.0	_	8.3	_
Shoreline length (km)	5.3	2.8	2.3	1.8	0.9
Mean gradient (%)	1.5	_	1.0	_	< 0.5
Temperature range (°C)	1-19	2-20	2-15	1-19	3-19

community of salal (Gaultheria shallon), Red Alder (Alnus rubra), and willow (Salix spp.). Away from the streambank, the vegetation is dominated by Western Hemlock (Tsuga heterophylla), Western Red Cedar (Thuja plicata), and Sitka Spruce (Picea sitchensis). During summer, canopy closure exceeds 50 percent for each of the streams. Approximately 40 percent of the Keogh River

watershed has been logged during the past 40 years. Logging has not occurred at any of our study sites although the Misty Inlet watershed upstream of our sampling sites has been logged.

#### Adult Salmon

To estimate numbers of adult coho salmon, nine visual surveys were conducted during the fall of 1986 in Misty Outlet downstream of the Rupert Main road crossing, and in the 250 m section of Long Outlet upstream of the Island Highway crossing (Fig. 1). The lower-most sections of Misty Inlet also were surveyed periodically. During overview surveys in Misty Outlet upstream of the Rupert Main bridge, and in Long Outlet downstream of the highway crossing, adult coho salmon were not seen and little or no spawning habitat was found. Therefore, regular spawner surveys were not conducted in these regions.

Survey methods for adult coho salmon followed those of Johnston *et al.* (1987a), with either two or three observers walking downstream, using 2 m long poles to probe for fish. Carcasses found were sexed, measured, and slashed to avoid recounting.

Coho escapements were estimated as peak daily counts of live fish, peak daily counts of live fish plus accumulated carcass counts to that date, total carcass counts, and the area under the curve (AUC) of counts of live fish divided by the time in days that fish were estimated to survive in the stream. The AUC estimate used a stream life of 11.4 d obtained from mark-recapture data for Keogh River coho the previous year (Johnston et al. 1986).

#### Juvenile Salmon

Major changes in relative abundance, measured as catch per unit effort (CPUE), and sizes of juvenile coho salmon were estimated with data collected through a standardized minnow trapping program. Misty Inlet, Misty Lake, Long Lake, Long Outlet, and the mainstem Keogh River about 100 m above the Island Highway crossing were sampled at 2 to 4 week intervals from November 1985 to April 1987, and at irregular intervals thereafter to August 1988; Misty Outlet was similarly sampled commencing October 1986 (Fig. 1). Minnow traps were used as they could be deployed by staff who had minimal fisheries training, and also because this technique enabled us to sample pools and

areas of dense cover where other techniques were impractical.

The minnow traps and trapping methods were described in detail in Swales et al. (1988). On every sampling occasion, between 15 and 35 traps (6 mm mesh, 15 mm diameter opening) were spaced at 3-5 m intervals at each site. Traps were set on the substrate and a rope extended between each trap and the bank. Traps were baited with salmon roe and fished overnight (about 20 h). Swales (1987) showed that minnow trap catches of juvenile coho in the Keogh River drainage increased to an asymptote at about 24 h. According to Bloom (1976), minnow traps are non-selective by size of coho over the range from 51 to 100 mm forklength (FL). In spring 1987, some traps were lined with fine-mesh hardware cloth (1 mm mesh) to retain newly-emerged fry. Fish captured were anaesthetized in 2-phenoxyethanol, FL was measured to the nearest mm, and the fish were released. Age-at-length was estimated from length-frequency analyses (Macdonald 1987), and from scale-aging samples of fish.

The efficiency of minnow traps in capturing juvenile coho may vary both seasonally and among the various habitat types sampled. Therefore, differences in CPUE are not necessarily directly proportional to differences in relative abundance. Nevertheless, the presence of juvenile coho in traps at a particular location confirms the use of that site at a particular time of year. Comparisons between the CPUE and mean sizes of juvenile coho salmon obtained from our minnow trapping and the densities and mean sizes of coho estimated from electrofishing surveys at the Keogh River site (B. R. Ward, B. C. Fisheries Branch, unpublished data), suggest that mean sizes and interannual changes in abundance are adequately represented by the minnow trap data.

To examine the movements of newly-emerged fry, upstream-downstream fry traps similar to those used by Northcote (1969) were operated between 18 March and 13 April 1987 and from 17 March to 13 May 1988 in Misty Inlet and Misty Outlet. Fry traps (1 mm mesh) were operated along the stream margins about 400 m downstream of the minnow trapping sites (Fig. 1). Approximately 20 percent of the stream width was sampled by the traps in each instance. These fry traps were checked daily or on alternate days depending on rate of capture. All coho were counted. Fork lengths were measured on each occasion, to a

maximum of 25 fry moving in each direction at each site. Downstream migrating fry were released at least 1 m below the traps, and upstream migrating fry were released at least 1 m above the traps. In 1988, approximately half the fry captured moving upstream at Misty Outlet were marked (by the removal of the left pelvic fin) to determine if these fry were destined for Misty Inlet. All fry captured at Misty Inlet were examined carefully for clipped fins.

#### Results

We found adult coho salmon in the lower-most 1.5 km of Misty Outlet from late October until 2 December 1986. Adult coho were never seen in the upper portion of Misty Outlet, in Misty Inlet, or in Long Outlet.

Estimates of the coho escapement into Misty Outlet in 1986 ranged between 31 and 48 fish. The peak daily count was only 25 live fish, but the peak daily count of live fish plus accumulated carcasses was 31 fish, and the total carcass count was also 31 fish. If an observer efficiency for live coho of about 75 percent (Solazzi 1984, Johnston *et al.* 1987a) is assumed, the expanded daily peak count of live fish plus accumulated carcass counts produced an escapement estimate of 39 fish. The AUC estimate was 48 fish.

Newly-emerged coho fry caught in upstreamdownstream traps in the Misty Lake drainage in early spring showed directional movement towards the lake (Table 2). Coho fry caught in Misty Outlet were predominantly moving upstream in both 1987 and 1988. In Misty Inlet, migrating fry were only caught in 1988 and were predominantly moving downsteam. These data imply that adult coho spawned in Misty Inlet during the fall of 1987 but not during the fall of 1986. The few parr caught in the upstream-downstream traps in 1988 were also moving upstream in Misty Outlet, but parr movements were random in Misty Inlet. In 1988, yolked fry were caught in Misty Outlet during late March and early April, indicating that fry emergence occurred during this period, while fry emerged slightly later in Misty Inlet (median dates of capture of yoked fry = 9 April and 11 April respectively), and at a slightly smaller size (Table 2, Student's t-test, p < 0.001). Few fish other than coho were caught in the upstream-downstream traps.

In 1988, upstream-moving fry at Misty Outlet (mean FL = 40.4 mm) were significantly larger than downstream-moving fry (mean FL = 38.8 mm) (t-test, p < 0.001), but upstream- and downstream-moving fry did not differ in size at Misty Inlet (t-test, p = 0.38). Although 436 fry migrating up Misty Outlet in 1988 were marked, none of these fry were recaptured in Misty Inlet.

Major scasonal trends in the pattern of habitat use by juvenile coho salmon can be inferred from the minnow trap CPUE data (Fig. 2). Both lakes were used during winter, but the importance of the lakes for summer rearing varied between years. Declining CPUE in Long Lake between late winter and early summer probably resulted from the exodus of coho smolts (Irvine and Ward 1989). All stream sites were used for both summer rearing and over-wintering, although CPUE in the mainstem Keogh River during winter was very low. During summer, CPUE in streams were consistently greater than CPUE for lake sites. Increases at each stream site during the spring of 1987 were the result of catches of newly-emerged fry, more of

TABLE 2. Catches of newly-emerged coho salmon fry and parr in upstream-downstream traps in Wisty Outlet and Wisty Inlet in spring 1987 and 1988, and the probability of random movement from the binomial distribution.

Year	Site	Mean FL (mm)	Numbers Moving		
			Down	Lp	Probability
fry:					
1987	Misty Outlet	35.2  (SD = 2.1)	3	55	< 0.001
	Misty Inlet		0	0	
1988	Misty Outlet	39.9  (SD = 2.4)	213	878	< 0.001
	Misty Inlet	38.0 (SD=1.5)	64	17	< 0.001
parr:					
1988	Misty Outlet	72.8  (SD = 12.1)	7	22	0.004
	Wisty Inlet	81.4  (SD = 14.2)	10	16	0.163

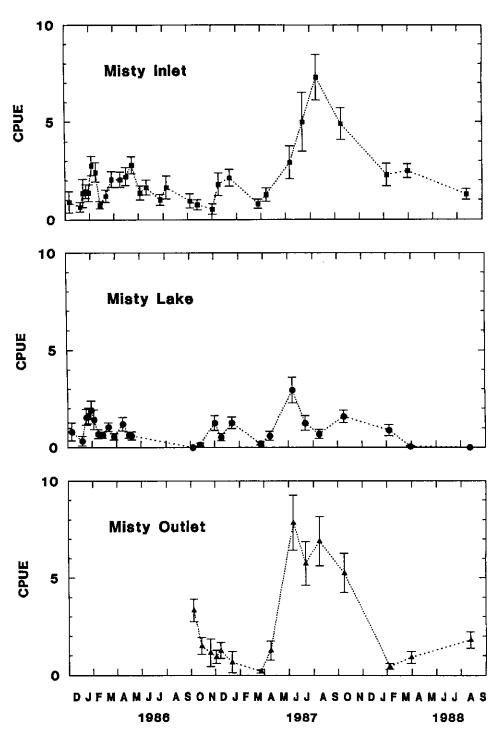


Figure 2(a). CPUE (fish\*trap-night\*\* ± SE) of juvenile coho salmon in minnow trap catches in lake and stream habitat in the Keogh River drainage (see next page for continuation of figure). In spring 1987, some traps were lined with fine-mesh hardware cloth which may have increased catches of newly-emerged fry.

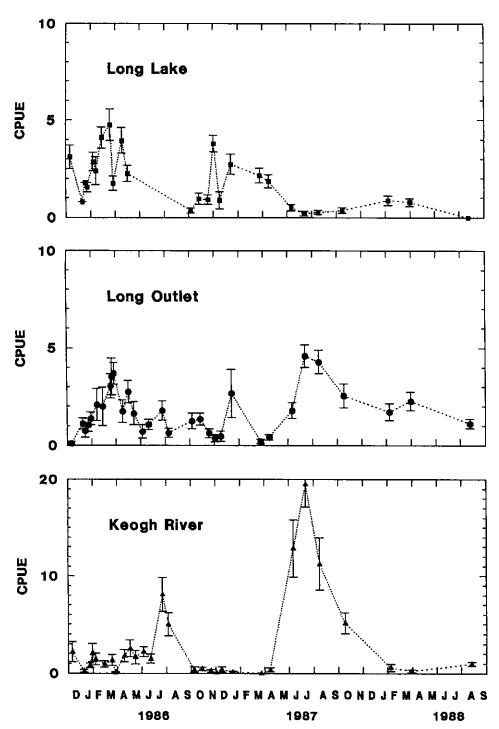


Figure 2(b). CPUE (fish\*trap-night\*\* ± SE) of juvenile coho salmon in minnow trap catches in lake and stream habitat in the Keogh River drainage (see previous page for beginning of figure). In spring 1987, some traps were lined with fine-mesh hardware cloth which may have increased catches of newly-emerged fry.

which were retained than in spring 1986 because of the smaller mesh size used in the minnow traps in 1987.

Although coho salmon were generally the most numerous species captured in the minnow traps and the only species for which detailed results are presented in this paper, other species of fish were captured. Rainbow trout were common in samples from the mainstem Keogh River but were rare elsewhere. Dolly Varden char and cutthroat trout were relatively common in Misty Inlet, Long Outlet, and Long Lake but were scarce elsewhere. Threespine stickleback were the most frequently captured fish in Misty Lake, and were also common in Long Lake. Sculpins were occasionally captured at several sites. No evidence of predation on juvenile coho salmon in our minnow traps was seen.

Changes in the mean sizes of coho in the minnow trap catches suggested considerable variation in growth rates among sites and among years (Fig. 3). Growth rates tended to be greatest in the two lakes and their outlet streams. Growth rates were lowest at Misty Inlet, where the size-frequency distributions and scale aging showed two distinct agegroups to be present. The among-site differences in apparent summer growth rates may partly result from differences in water temperature, which were generally higher in the two lakes and lower at Misty Inlet than elsewhere (J. R. Irvine, unpub. data). Growth rates in 1987 were lower than in 1986.

For cohorts of fry whose fall mean size exceeded about 80 mm FL, there was little indication of over-winter growth at any site prior to March-April (Fig. 3). The mean size of smaller fry (<70 mm), however, appeared to increase over the winter despite low water temperatures.

## Discussion

Small tributary lakes and stream areas not used for spawning nevertheless are important summer rearing and over-wintering areas for juvenile coho salmon in the Keogh River drainage. Coho fry in two tributaries dispersed from isolated spawning sites to rear in both lake and stream habitats throughout the year.

The mechanisms controlling the directional movement by coho fry towards lakes in the Keogh River drainage are not known. Gribanov (1948) reported coho fry moved 10 to 15 km upstream to reach lakes in which they reared over summer.

Mason (1976b) found that fry emerging from simulated redds exhibited a strong upstream response. Upstream movement of coho fry was not found in Carnation Creek, British Columbia (Hartman et al. 1982) which lacks tributary lakes. Downstream movements of coho fry soon after emergence are well-known (Chapman 1962, Crone and Bond 1976, Hartman et al. 1982), and have been attributed to the aggressive displacement of smaller fry by larger, territorial fry (Chapman 1962, Mason and Chapman 1965, Hartman et al. 1982). Downstream displacements of small fry can be induced when coho are stocked at high densities (Mason 1976a, Bilby and Bisson 1987). In contrast, increased food availability may offset the effects of high population density, allowing more fish to coexist (Mason 1976a). Size-based aggressive displacement of fry is unlikely to account for the movements inferred from our fry trap and minnow trap data because the mean sizes of fry migrating upstream towards Misty Lake were the same as or larger than those of downstream-moving fry. Positive rheotaxis (Hoar 1951) cannot be invoked to account for the observed fry dispersal since movement was primarily upstream in Misty Outlet but downstream in Misty Inlet.

Coho fry moved towards lakes in the Keogh River drainage soon after emergence (April), and were found in near-shore lake habitat from early June onward. Other studies have also recorded the presence of juvenile coho in lakes during the summer (Gribanov 1948, Foerster and Ricker 1953, Mason 1974, Russell et al. 1981, Hyatt et al. 1984, Fielden and Holtby 1987, Swain and Holtby 1989). Large numbers of juvenile coho salmon rear in small lakes in some watersheds. Murphy et al. (1989) estimated that about 26 percent of the juvenile coho in the lower Taku River, Alaska reared in beaver ponds. Because juvenile coho in ponds and lakes are most abundant in shallow nearshore areas (Mason 1974, Swales et al. 1988, Swales and Levings 1989), the ratio of lake perimeter to stream length can be used as an index of the relative potential importance of these habitats for coho rearing in a watershed.

The apparent growth of coho fry was fastest in the lakes and their outlet streams. Similarly, Fielden and Holtby (1987) found the largest coho at lake sites within the Cowichan River system, British Columbia. Bailey and Irvine (1991) documented significant differences in body

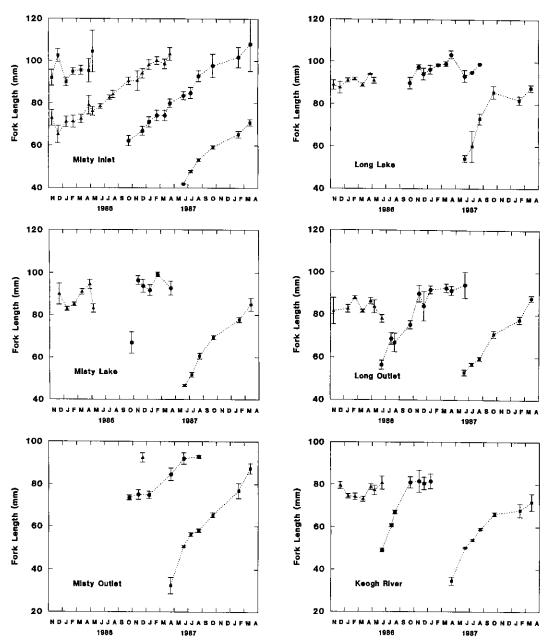


Figure 3. Mean FL (±SE) of cohorts of juvenile coho salmon in minnow trap catches in lake and stream habitat in the Keogh River drainage. A different symbol is used for each cohort. Small fry were captured during spring 1987 because the minnow traps were fined with hardware cloth.

morphology among groups of coho salmon fry from various riverine environments within the Keogh River watershed. However, they were unable to demonstrate a relationship between the morphology of fish from a particular location, and the habitat characteristics of that location. The growth rates of juvenile salmonids vary directly with temperature (Iwama and Tautz 1981), and inversely with density (Mason 1976a, Scrivener and Andersen 1984). The higher summer water temperatures and lower relative abundance of coho observed in tributary lakes in the Keogh River

system may permit coho fry rearing in littoral areas to attain larger sizes before winter than stream-rearing fry. Alternatively, fry in lakes may grow quicker because of reduced energetic costs associated with living in environments with minimal current. Large size is adaptive since over-winter survival improves with increased body size in coho (Holtby and Hartman 1982), as does smolt-to-adult survival (Hager and Noble 1976). Growth rate also influences the duration of freshwater residence. The slower-growing coho smolts emigrating from Misty Inlet were comprised of equal proportions of age 1+ and 2+ fish while 91 percent of the faster-growing smolts emigrating from Long Lake were 1+ (Irvine and Ward 1989).

A reduction in CPUE between fall and winter in the Keogh River suggested a movement of juvenile coho out of the mainstem river (Fig. 2). Other studies have documented autumnal migrations of juvenile coho from mainstem rearing habitat into riverine ponds and small tributaries (Skcesick 1970, Bustard and Narver 1975, Peterson 1982, Tschaplinski and Hartman 1983, Swales et al. 1986, Brown and Hartman 1988) which are believed to serve as refuges from unfavourable winter conditions such as high discharge, low water temperatures, and reduced food abundance. Low water temperature functions as a cue for juvenile coho to seek areas of low water velocity (Taylor 1988).

Over-winter survival may be greater in lake-fed tributaries than in mainstem rivers because tributaries tend to be less variable. Large increases in discharge in the mainstem Keogh River are associated with winter rains (Ward and Slaney 1988). Fluctuations in water depth were relatively smaller in tributary streams such as Misty Outlet (Johnston et al. 1987b, their Fig. 2). Coho fry were virtually absent from the mainstem Keogh River sampling site during winter (Fig. 2), but remained abundant in the lakes and tributaries. Over-winter survivals of 49 to 87 percent have been reported for coho salmon in ponds (Bustard and Narver 1975, Peterson 1982. Swales et al. 1986), but survival in stream habitat was much lower (Bustard and Narver 1975). Consequently, small lakes may be major contributors to smolt production in some watersheds. In 1986, Long Lake produced about 1.700 smolts (0.94 • m<sup>-1</sup> of shoreline) compared to about 765 (0.14•m<sup>-1</sup>) produced by Misty Inlet (Irvine and Ward 1989).

Swales et al. (1986) suggested that coho overwintering in riverine ponds may continue to grow. Certainly, juvenile coho can feed at low (2.5°C) water temperatures (McMahon and Hartman 1989). Our data showed a continuous increase over the winter in the mean size of cohorts of coho whose initial size was less than about 70 mm FL, but little change in the mean lengths of cohorts whose mean FL was greater than 80 mm. This difference may result from higher over-winter mortalities of the smaller fish. The physiological costs of adaptation to winter conditions are relatively more severe for small coho fry. Mason (1976a) found that coho less than 60 mm FL largely depleted their lipid reserves over winter whereas larger coho lost only a small proportion of their lipid reserves.

The utilization of small tributary lakes and streams as both summer rearing and over-wintering habitat by juvenile coho salmon suggests that more emphasis should be placed on the preservation and management of such areas. Use of these habitats is temporally variable and, therefore, it is easy to underestimate their importance. For instance, adult coho salmon spawned in Misty Inlet during 1987, and have been observed in this stream during other high flow years (P. A. Slaney, B.C. Fisheries Branch, 2204 Main Mall, Vancouver, B.C., pers. comm.), but apparently did not spawn in this stream during 1986. Misty Lake was more important for juvenile coho salmon during the summer of 1987 than the summer of 1988. To protect and manage the freshwater environment of coho salmon, it is necessary to improve our understanding of the complex patterns of freshwater use of this species.

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#### Literature Cited

- Bailey, R. E., and J. R. Irvine. 1991. Morphological differences among juvenile coho salmon Oucorhynchus kisutch living in nearby tributaries of a small coastal watershed. Can. Tech. Rep. Fish. Aquat. Sci. 1780, 15 p.
- Bilby, R. E., and P. A. Bisson. 1987. Emigration and production of hatchery coho salmon (*Oncorhynchus kisuteh*) stocked in streams draining an old-growth and a clearcut watershed. Can. J. Fish. Aquat. Sci. 44:1397-1407.
- Bloom, A. M. 1976. Evaluation of minnow traps for estimating populations of juvenile coho salmon and Dolly Varden. Prog. Fish-Cult. 38:99-101.
- Brown, T. G., and G. F. Hartman. 1988. Contribution of seasonally flooded lands and minor tributaries to the production of cobo salmon in Carnation Creek, British Columbia. Trans. Amer. 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. Bd. Can. 32:667-680.
- Chapman, D. W. 1962. Aggressive behavior in juvenile cohosalmon as a cause of emigration. J. Fish Res. Bd. Can. 19:1047-1080.
- Crone, R. A., and C. E. Bond. 1976. Life history of coho salmon, Oncorhynchus hisutch, in Sashin Creek, southcastern Alaska. Fishery Bull. 74:897-923.
- 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.
- Dolloff, C. A. 1987. Scasonal population characteristics and habitat use by juvenile coho salmon in a small southeastern Alaska stream. Trans. Amer. Fish. Soc. 116:829-838.
- Drucker, B. 1972. Some life history characteristics of coho salmon of the Karluk River system, Kodiak Island, Alaska, Fishery Bull, 70:79-94.
- Fielden, R. J., and L. B. Holtby. 1987. Standing crop and habitat characteristics of juvenile salmonids at sites in the Cowichan River system, Can. MS Rep. Fish. Aquat. Sci. 1950. 65 p.
- Foerster, R. E., and W. E. Ricker, 1953. The coho salmon of Cultus Lake and Sweltzer Creek, J. Fish, Res. Bd. Can. 10:293-319.
- Gribanov, V. I. 1948. The coho salmon (Oncorhynchus kisutch Walbaum)—a biological sketch. Trans. Scr. Fish. Res. Bd. Can. 370, 83 p.
- Hager, R. C., and R. E. Noble. 1976. Relation of size at release of hatchery-reared coho salmon to age, size, and sex composition of returning adults. Prog. Fish-Cult. 38:144-147.
- 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.
- Hoar, W. S. 1951. The behavior of chum, pink, and coho salmon in relation to their seaward migration. J. Fish. Res. Bd. Can. 8:241-263.
- Holtby, L. B., and G. F. Hartman. 1982. The population dynamics of coho salmon (Oncorhynchus kisutch) in a west coast rain forest stream subjected to logging. In G. F. Hartman (ed.) Proceedings of the Carnation Creek workshop, a ten year review. Pacific Biological Station, Nanaimo, B.C. Pp. 308-347.

- Hyatt, K. D., D. Rutherford, T. Gjernes, P. Rankin, and T. Cone. 1984. Lake enrichment program: juvenile sockeye unit survey guidelines. Can. MS Rep. Fish. Aquat. Sci. 1796. 84 p.
- Irvine, J. R., and B. R. Ward. 1989. Patterns of timing and size of wild coho salmon (Oncorhynchus kisutch) smolts emigrating from the Keogh River watershed on northern Vancouver Island. Can. J. Fish. Aquat. Sci. 46:1086-1094.
- Iwama, G. K., and A. F. Tautz. 1981. A simple growth model for salmonids in hatcheries. Can. J. Fish. Aquat. Sci. 38:649-656.
- Johnston, N. T., J. R. Irvine, and C. J. Perrin. 1986. A comparative evaluation of fence count, mark-recapture and Bendix sonar estimates of salmon escapements in the Keogh River, a variable-flow coastal B.C. stream. Can. Tech. Rep. Fish. Aquat. Sci. 1453, 44 p.
- Johnston, N. T., J. R. Irvine, and C. J. Perrin. 1987a. Instream indexing of coho salmon (*Oncorhynchus kisutch*) escapement in French Creek, British Columbia. Can. Tech. Rep. Fish. Aquat. Sci. 1573, 37 p.
- Johnston, N. T., J. R. Irvine, and C. J. Perrin. 1987b. Coho salmon (Oncorhynchus kisutch) utilization of tributary lakes and streams in the Keogh River drainage, British Columbia. Can. MS Rep. Fish Aquat. Sci. 1973. 54 p.
- Macdonald, P. D. M. 1987. Analysis of length-frequency distributions. In R. C. Summerfelt and G. E. Hall (ed.) Age and growth of fish. Iowa State University Press, Ames, IA. Pp. 371-384.
- Mason, J. C. 1974. Aspects of the ecology of juvenile cohosalmon (Oncorhynchus kisutch) in Great Central Lake, B.C. Tech. Rep. Fish. Res. Bd. Can. 438, 37 p.
- Mason, J. C. 1975. Seaward movement of juvenile fishes, including lunar periodicity in the movement of cohosalmon (Oncorhynchus kisutch) fry. J. Fish. Res. Bd. Can. 32:2542-2547.
- Mason, J. C. 1976a. Response of underyearling coho salmon to supplemental feeding in a natural stream. J. Wildl. Manage, 40:775-788.
- Mason, J. C. 1976b. Some features of coho salmon, Oncorhynchus kisutch, fry emerging from simulated redds and concurrent changes in photobehavior. Fishery Bull. 74:167-175.
- Mason, J. C., and D. W. Chapman. 1965. Significance of early emergence, environmental rearing capacity, and behavioral ecology of juvenile coho salmon in stream channels. J. Fish. Res. Bd. Can. 22:173-190.
- McMahon, T. E., and G. F. Hartman. 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.
- McPhail, J. D., and C. C. Lindsey. 1970. Freshwater fishes of northwestern Canada and Alaska. Fish. Res. Bd. Can. Bull. 173, 381 p.
- Murphy, M. L., J. Heifetz, J. F. Thedinga, S. W. Johnson, and K. V. Koski. 1989. Habitat utilization by juvenile Pacific salmon (Oncorhynchus) in the glacial Taku River, southeast Alaska. Can. J. Fish. Aquat. Sci. 46:1677-1685.
- Northcote, T. G. 1969. Lakeward migration of young rainbow trout (*Salmo gairdneri*) in the upper Lardeau River, British Columbia. J. Fish. Res. Bd. Can. 26:33-45.

- Peterson, N. P. 1982. Immigration of juvenile coho salmon (*Oncorhynchus kisutch*) into riverine ponds. Can. J. Fish. Aquat. Sci. 39:1308-1310.
- Pritchard, A. L. 1936. Facts concerning the coho salmon (Oncorhynchus kisutch) in the commercial catches of British Columbia as determined from their scales, Fish, Res, Bd. Can. Prog. Rep. Pacific 29:16-20.
- Russell, R., C. C. Graham, A. G. Sewid, and D. M. Archibald. 1981. Distribution of juvenile chinook, coho, and sockeye salmon in Shuswap Lake 1978-1979; biophysical inventory of littoral areas of Shuswap Lake, 1978. Fish. Mar. Serv. MS Rep. 1479, 54 p.
- Scrivener, J. C., and B. C. Andersen. 1984. Logging impacts and some mechanisms that determine the size of spring and summer populations of coho salmon fry (*Oncorhynchus kisutch*) in Carnation Creek, British Columbia, Can. J. Fish. Aquat. Sci. 41:1097-1105.
- Skeesick, D. G. 1970. The fall immigration of juvenile coho salmon into a small tributary. Res. Rep. Oregon Fish. Comm. 2:90-95.
- Solazzi, M. F. 1984. Relationship between visual counts of coho, chinook, and chum salmon from spawning fish surveys and the actual number of fish present. Oregon Dep. Fish Wildl. Info. Rep. (Fish) 84-7, 22 p.
- Swain, D. P., and L. B. Holtby. 1989. Differences in morphology and behavior between juvenile coho salmon (Oncorhynchus kisutch) rearing in a lake and its tributary stream. Can. J. Fish. Aquat. Sci. 46:1406-1414.

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- Swales, S. 1987. The use of small wire-mesh traps in sampling juvenile salmonids. Aquaculture and Fish. Manage. 18:187-195.
- Swales, S., F. Caron, J. R. Irvine, and C. D. Levings. 1988. Overwintering habitats of coho salmon (Oncorhynchus kisutch) and other juvenile salmonids in the Keogh River system, British Columbia. Can. J. Zool. 66:254-261.
- Swales, S., R. B. Lauzier, and C. D. Levings. 1986. Winter habitat preferences of juvenile salmonids in two interior rivers in British Columbia. Can. J. Zool. 64:1506-1514.
- Swales, S., and C. D. Levings. 1989. Role of off-channel ponds in the life cycle of coho salmon (*Oncorhynchus kisuteh*) and other juvenile salmonids in the Coldwater River, British Columbia. Can. J. Fish. Aquat. Sci. 46:232-242.
- Taylor, E. B. 1988. Water temperature and velocity as determinants of microhabitats of juvenile chinook and coho salmon in a laboratory stream channel. Trans. Amer. Fish. Soc. 117:22-28.
- 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.
- Ward, B. R., and P. A. Slaney. 1988. Life history and smoltto-adult survival of Keogh River steelhead trout (Salmo gairdneri) and the relationship to smolt size. Can. J. Fish. Aquat. Sci. 45:1110-1122.