Effect of Changes in Streamflow on the Microhabitat Use and Movements of Sympatric Juvenile Coho Salmon (*Oncorhynchus kisutch*) and Chinook Salmon (*O. tshawytscha*) in a Natural Stream

C.S. Shirvell

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

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The microhabitats at positions selected by juvenile coho (*Oncorhynchus kisutch*) and chinook salmon (*O. tshawytscha*) following a change in streamflow differed from microhabitats occupied at normal streamflows. At drought streamflow (37% mean seasonal streamflow (MSF)), juvenile coho salmon selected slower, darker, and higher sites above the streambed ($P < 0.05$) than sites selected at normal (75% MSF) or flood (159% MSF) flows. Juvenile chinook salmon microhabitat use changed similarly with changes in streamflow, but the differences were not significant. Up to one fifth of the fish chose positions with faster water velocities than those available either 30 cm above or 30 cm lateral to them. These fish chose positions inconsistent with the hypothesis of optimal position selection based on maximizing net energy gain. On average, fish moved 6.8 m following a change in streamflow. Juvenile coho salmon generally moved upstream in response to decreasing streamflows and downstream in response to increasing streamflows. Juvenile chinook salmon tended to move offshore and downstream in response to all streamflow changes. These results show that juvenile coho and chinook salmon will move to find suitable microhabitat following a change in streamflow and that the microhabitats are not the same at all streamflows.

Les microhabitats aux emplacements choisis par les jeunes saumons coho (*Oncorhynchus kisutch*) et quinnat (*O. tshawytscha*) après un changement de débit diffèrent des microhabitats occupés lorsque le débit est normal. Au débit de sécheresse (37 % du débit saisonnier moyen (DSM)), le jeune saumon coho choisit des sites plus sombres, plus élevés par rapport au lit du cours d'eau et où l'écoulement est plus lent ($P < 0,05$) qu'au débit normal (75 % DSM) ou au débit de crue (159 % DSM). L'utilisation du microhabitat par le jeune saumon quinnat varie également en fonction du débit, mais les différences observées sont non significatives. Jusqu'à un cinquième des poissons choisissent des emplacements où la vitesse d'écoulement de l'eau est plus élevée que ceux disponibles à 30 cm d'eux, en hauteur ou latéralement. Le choix des emplacements par ces poissons est contraire à l'hypothèse de la sélection optimale de l'emplacement basée sur l'optimisation du gain d'énergie nette. En moyenne, les poissons se déplacent de 6,8 m consécutivement à un changement de débit. Le jeune saumon coho se déplace en général vers l'amont en réponse à une diminution du débit, et vers l'aval en réponse à une augmentation du débit. Le jeune saumon quinnat a tendance à quitter le rivage et à se déplacer vers l'aval en réponse aux changements de débit de tout type. Ces résultats indiquent que les jeunes saumons coho et quinnat se déplaceront pour trouver un microhabitat adéquat consécutivement à un changement de débit, et que les microhabitats ne sont pas les mêmes quel que soit le débit.

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Changes in river discharge (referred to as "streamflow" herein) associated with flow regulation can have negative effects on fish and wildlife resources (Petts 1984; Burt and Mundie 1986). As a result, numerous "instream flow" assessment methods have been developed for use throughout North America to evaluate environmental impacts and minimize losses of fish habitat (Reiser et al. 1989). Some of these assessment methods incorporate attributes of the habitat used by fish (e.g., the Instream Flow Incremental Methodology (IFIM), Bovee, 1982). The requirement of specific levels of habitat attributes for these methods has stimulated investigations into the basis on which fish choose positions in streams (e.g., Shirvell 1990). Fausch (1984), Fausch and White (1986), Hughes and Dill (1990), and others have suggested that juvenile salmonids select stream positions that allow optimal foraging. Specifically, juvenile salmonids in streams are hypothesized to select positions in slow current close to faster water with an abundant food supply. Such a choice would allow the fish to maximize its net energy gain by reducing its energy expenditure. Positions with these characteristics can be considered for feeding to be "optimal positions" where the greater the water velocity gradient next to the position, the greater the potential for net energy gain. When streamflows change, the locations that allow maximum net energy gain will also change because of the shift in patterns of water velocity (Bravender and Shirvell 1989). If the hypothesis of optimal positions is correct, when stream locations that allow maximum net energy gain change because of changes in streamflow, fish should redistribute themselves and take up new optimal positions. Although instream flow assessment methods such as IFIM assume that fish have the same habitat preferences following a change in streamflow, no formal test of the correspondence between optimal locations and fish positions following a change in streamflow has been conducted.

The purposes of this paper were to (1) compare water depths and velocities used by the same juvenile coho (*Oncorhynchus kisutch*) and chinook salmon (*O. tshawytscha*) before and after a change in streamflow to determine whether their microhabitat use remained consistent, (2) compare the positions used before and after a change in streamflow to determine whether the fish moved to find new locations with suitable conditions, and (3) examine the specific water velocity gradients around positions the fish chose at three different streamflows to determine whether they selected positions in slow water close to faster water consistent with optimal stream position theory.

Methods

Study Area

The study was conducted in Kloiya Creek, a small coastal stream 12 km southeast of Prince Rupert, British Columbia. Kloiya Creek has a series of reservoirs and a short mainstem emptying directly into the Pacific Ocean. There is a dam with a fishway 3.2 km upstream from the ocean. The study area was a 235-m-long section of stream consisting of a series of five alternating pools and riffles approximately 800 m downstream of the dam. The pools were consecutive but in two groups: pools 1 and 2 formed the upstream group and were separated from pools 3, 4, and 5 by 100 m of stream. At the average annual streamflow the five pools averaged 47 m long, 21 m wide, 52 cm maximum depth, and averaged 18 $cm \cdot s^{-1}$. They had predominantly cobble substrate with gravel and sand along their margins. A complete physical description of the study area is given in Bravender and Shirvell (1989).

Kloiya Creek has annual spawning escapements of about 200 chinook salmon, 700 coho salmon, and populations of at least three other anadromous species (Shirvell 1990). Although the dam has a fishway, all the chinook salmon and about 30% of the coho salmon spawn downstream of the dam in two localized areas with spawning gravels. The study area used for this research was within the upper spawning area. After emerging from the gravel, the juvenile coho and chinook salmon remain and grow in the study pools for periods ranging from a few days to several months before they emigrate to sea.

Streamflow Manipulation

To investigate the consistency of water depths and velocities occupied by juvenile salmon at different streamflows, the flow in Kloiya Creek was experimentally altered. By storing or releasing water from the reservoir upstream of the dam, the flow in the study area could be regulated between 0.5 and 8.0 $m^3 \cdot s^{-1}$. Flow was manipulated at the dam to create alternating low, medium, and high levels in the study area.

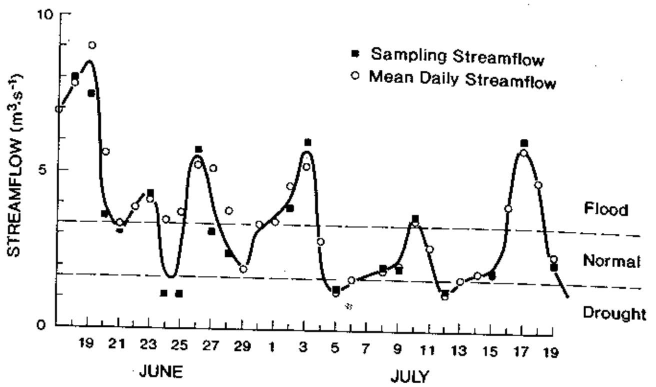

FIG. 1. Mean daily streamflow and instantaneous streamflows when fish habitat measurements were taken in Kloiya Creek, B.C., from June 17 to July 19, 1985 (redrawn from Shirvell 1990). Streamflow classifications were as follows: drought, <1.65 $m^3 \cdot s^{-1}$; normal, 1.65–3.35 $m^3 \cdot s^{-1}$; flood >3.35 $m^3 \cdot s^{-1}$.

The low flows averaged 1.25 $m^3 \cdot s^{-1}$ (range 1.17–1.64 $m^3 \cdot s^{-1}$), medium flows averaged 2.56 $m^3 \cdot s^{-1}$ (range 1.65–3.35 $m^3 \cdot s^{-1}$), and high flows averaged 5.42 $m^3 \cdot s^{-1}$ (range 3.36–8.02 $m^3 \cdot s^{-1}$). The experiment was conducted from June 18 to July 19, 1985. The mean seasonal streamflow (MSS) during June and July each year from 1975 to 1984 was 3.41 $m^3 \cdot s^{-1}$. For the experiment, I chose low, medium, and high streamflows that approximated drought (37% MSS), normal (75% MSS), and flood conditions (159% MSS) relative to the normal June and July flows. Over the 32-d study period, five floods, four normal flows, and three droughts were simulated (Fig. 1).

Measurement of Microhabitat Characteristics at Fish Positions

Typically, habitat used by a fish population is determined from measurements of conditions at positions occupied by a sample of different fish collected on different days and assumed to be representative of an entire population on each sample date. Because water depths and velocities used by fish are related to their size, samples composed of different fish could result in different mean depths and velocities due to random sample variation. To prevent habitat variation caused as an artifact from measuring conditions occupied by different fish on different sampling dates, in this study I measured the habitat conditions occupied by the same fish at different streamflows on different days.

Individual juvenile coho and chinook salmon were located in the study area by direct underwater observation. Twenty surveys lasting 7 h each were used to locate the fish and measure habitat attributes at their position. A diver with snorkel quietly entered one of the pools at its downstream riffle and carefully moved upstream until a juvenile salmon maintaining position in the stream was observed. The diver noted the location and position of the fish in relation to the substrate and then captured the fish alive in a small, handheld purse seine (Morantz et al. 1987).

Upon capture of the fish the following habitat attributes were measured at each fish position: (1) water depth, (2) vertical distance of the fish above the streambed, (3) water velocity at the fish's head (the focal point velocity), (4) light intensity at the focal point, (5) light intensity at the water surface, and (6) dominant substrate particle size. The location of the fish's position within the pool was determined by triangula-

TABLE 1. Description of juvenile salmon tagged and relocated following a change in streamflow in Kloiya Creek, B.C., 1985.

Species	Number tagged	Mean length, mm (SD)	Mean weight, g (SD)	Number never relocated	Number of times relocated									
					1	2	3	4	5	6	7	8	9	10
Coho	40	55.4 (7.1)	1.9 (1.1)	17	6	6	3	1	2	1	2	0	2	0
Chinook	37	53.8 (3.6)	1.7 (0.4)	27	4	3	1	1	1	0	0	0	0	0
Total	77			44	10	9	4	2	3	1	2	0	2	0

tion using measurements from the position to permanent metal pins marking the ends of transects used for hydraulic measurements (see Bravender and Shirvell 1989). The positions were later marked on scale maps of the study pools.

To test whether fish in the study pools chose positions consistent with the hypothesis of optimal position selection (Hughes and Dill 1990; Fausch 1984), (7) water velocity 30 cm lateral to the fish's position on the faster side of the position and (8) water velocity 30 cm above the fish's position were also measured. This distance was chosen because Wankowski (1981) found that the distance juvenile Atlantic salmon (*Salmo salar*) would move to capture prey varied seasonally from 1.9 to 9.9 body lengths. The juvenile coho and chinook salmon in this study were approximately 55 mm in length (Table 1); therefore, 30 cm represented 5.5 body lengths. All water velocity measurements were taken with an Ott current meter using a 3.0-cm propeller following the recommendations of Morantz et al. (1986). Light intensity was measured with a Licor integrating quantum photometer (model LI-212SB). The dominant particle size of the substrate at any location was visually determined and then a representative particle was measured and coded using the modified Wentworth classification (see Orth 1983).

Once the habitat measurements were taken, the fish was anaesthetized, weighed (nearest 0.1 g), and measured (fork length in millimetres). Each fish was then tagged with an individually colour-coded aluminum staple. These tags were attached to the fish by pinching the ends of the staple into the back of the fish on either side of the dorsal fin. When attached, the tag hung behind the dorsal fin and rested on the fish's back between the dorsal and adipose fins. Each tag was marked with a unique two- or three-colour code of enamel paint on the top of the staple. The colour code could be read underwater by the diver without capturing the fish. Following measurements and tagging, the fish was allowed to recover and was then released near its capture location.

On subsequent observations of tagged fish, the tag code was noted and all the habitat variables described above were remeasured at the position the fish was occupying. The distance and direction that tagged fish moved between subsequent observations were measured from their locations marked on scale maps of the study pools. The direction in which a fish moved between two observations was coded according to the numbers on a clock, where 12 = upstream, 6 = downstream, 3 = inshore, and 9 = offshore. Because fish may be influenced by the nearest shore when searching for new positions following a streamflow change, the coding for inshore and offshore was reversed for fish occupying locations on the right-hand side (facing downstream) of the thalweg. This transformation standardized code 3 to always represent inshore (generally shallower) and 9 to always represent offshore (generally deeper) for analysis of the direction the fish moved in regardless of which side of the thalweg the fish was initially on before the streamflow changed (see Fig. 4 for an example).

The change in streamflow between two consecutive observations of the same fish was calculated and paired with the distance and direction the fish had moved between the two observations. All observations were taken between 08:30 and 17:00 from June 18 to July 19, 1985.

Statistical Analysis

To test the variability of microhabitat conditions selected by the fish between different streamflows, the means of the habitat attributes at the positions selected for each of the three streamflows were analyzed for significant differences with Duncan's multiple range test (DMRT) at $P = 0.05$. Differences in habitat conditions selected by tagged versus untagged fish, differences between habitat conditions selected by coho and chinook salmon, and differences between water velocities at the fish's position and water velocities lateral or vertical to the fish's position were analyzed using t-tests or paired t-tests at $P = 0.05$. The existence of any relationship between the distance fish moved as a result of a streamflow change and the magnitude of the streamflow change was examined using linear regression. The directions fish moved in response to a streamflow change were plotted graphically, where the direction the fish most frequently moved in was normalized to 1. All other directions the fish moved toward were plotted as proportions relative to the most frequently used direction. The transformation of the direction of movement data to normalized proportions was done to allow comparisons between different changes in streamflow or comparisons between the coho and chinook when the sample sizes were unequal. All statistical analyses were conducted using SAS systems software (SAS Institute Inc. 1985).

Results

Effect of Tagging on Microhabitat Choice

To investigate whether tagging the fish affected their choice of microhabitat, the conditions at the locations where the fish were captured before they were tagged were compared with the conditions at the locations where the fish were located on their first observation following tagging. None of the habitat attributes investigated was significantly

TABLE 2. Microhabitat conditions occupied by juvenile coho salmon at three streamflows in Kloiya Creek, B.C.

Mean of habitat variable	Streamflow ($m^3 \cdot s^{-1}$) 1.25	2.42	5.38	All three streamflows
Depth (cm)	39.1 [29][a] (10.6)	37.9 [43] (9.6)	35.6 [49] (9.0)	37.3 [121] (9.6)
Distance above bottom (cm)	12.6 [29] (8.3)	11.2 [43] (9.4)	8.1[b] [49] (4.3)	10.3 [121] (7.6)
Focal point velocity ($cm \cdot s^{-1}$)	11.3 [29] (7.7)	16.4 [43] (7.4)	18.7 [49] (6.2)	16.1 [121] (7.5)
Lateral velocity ($cm \cdot s^{-1}$)	19.0 [29] (9.6)	25.4 [43] (8.5)	26.8 [49] (9.6)	24.5 [121] (9.6)
Vertical velocity ($cm \cdot s^{-1}$)	24.9 [29] (11.8)	34.8 [43] (14.5)	34.6 [49] (17.2)	32.3 [121] (15.6)
Light at fish's position ($lx \cdot 10^3$)	7.0 [28] (4.4)	13.8 [23] (9.0)	13.6 [37] (14.5)	11.6 [88] (11.1)
Light at surface ($lx \cdot 10^3$)	12.3 [28] (8.8)	26.0 [23] (19.7)	22.3 [37] (24.7)	20.1 [88] (20.1)
Substrate (cm)[c] (label)	6.4 (gravel)	15.7 (cobble)	3.3 (gravel)	6.4–25.0 (cobble)
Distance from shore (m)	4.6 [28] (2.6)	4.9 [40] (2.2)	3.9 [40] (2.2)	4.5 [108] (2.3)

[a] Sample size in square brackets; SD in parentheses.

[b] Underlined values are significantly different from the means at the other streamflows.

[c] Mode of frequency histogram.

different between the two locations for either species (coho $N = 23$, chinook, $N = 10$, $P > 0.05$, paired t-test) except for water velocities 30 cm above the fish's position ($P < 0.01$, paired t-test) and light intensities at the water surface above the fish positions ($P < 0.05$, paired t-test). These results show no difference in the microhabitat conditions at the fish's focal point before or after tagging, but some differences existed in the conditions above the fish after tagging. These results suggest that once juvenile coho and chinook salmon were tagged, they may have selected locations underlying faster water than before they were tagged. I speculate that this may be a fright reaction to the tagging procedure. Nevertheless, other than the fish possibly selecting positions under faster water, these results show that the tags appeared to have had no effect on the fish's swimming ability and subsequent choice of water velocities at the fish's position. It further suggests that habitat conditions used by the tagged fish were valid samples of habitat conditions that would be chosen by the population at different streamflows.

Juvenile Coho and Chinook Salmon Microhabitat Differences

A total of 40 juvenile coho and 37 juvenile chinook salmon were tagged (Table 1). Of these, tagged coho salmon were observed after a streamflow change on 66 occasions; some individuals were observed after as many as nine streamflow changes. Tagged chinook salmon were observed after a streamflow change on 22 occasions; some individuals were observed after as many as five streamflow changes. The average length of time between consecutive observations of the same fish was 5.1 d (SD = 3.8 d; min. = 1, max. = 22). There were substantially fewer juvenile chinook salmon relocated than juvenile coho salmon. This was because the chinook salmon were emigrating to the ocean during the study period. The coho will remain in freshwater for a year before emigrating. There was no significant difference between the length or weight of either species ($P = 0.24$, t-test; Table 1).

Comparisons between species showed that juvenile coho and chinook salmon chose different microhabitats for each streamflow tested in Kloiya Creek. Although the water depth ($P = 0.37$), water velocity at the fish's position ($P = 0.45$), water velocity 30 cm lateral to the fish's position ($P = 0.71$), and light intensity at the fish's position ($P = 0.17$) were not significantly different between locations chosen by either coho or chinook salmon, the water velocity 30 cm above the fish's position, distance above the streambed, and distance from shore were significantly different ($P < 0.05$) at different streamflows. Juvenile chinook salmon chose locations that were significantly farther from shore ($P = 0.04$ or less), closer to the streambed ($P = 0.0017$), and underneath significantly faster currents ($P = 0.0013$) at all streamflows.

Consistency of Habitat Use between Different Streamflows

Juvenile coho and chinook salmon each occupied different microhabitats at different streamflows. For coho salmon, the values of water velocity at their position, the water velocity 30 cm lateral to their position, and the water velocity 30 cm above their position were significantly lower at drought streamflow than at normal or flood streamflow, while they were higher for light intensity ($P < 0.05$, DMRT; Table 2). These attributes were not different between the positions coho salmon chose at normal and flood streamflows. The water depth, substrate size, and distance from shore at the positions chosen by coho salmon were consistent for all three streamflows ($P > 0.05$, DMRT; Table 2).

For juvenile chinook salmon, the water velocity 30 cm above their position was significantly lower at drought streamflow than at either normal or flood streamflow ($P < 0.05$,

TABLE 3. Microhabitat conditions occupied by juvenile chinook salmon at three streamflows in Kloiya Creek, B.C.

Mean of habitat variable	Streamflow ($m^3 \cdot s^{-1}$)			All three streamflows
	1.25	2.42	5.38	
Depth (cm)	37.0 [9][a] (10.7)	34.4 [19] (10.8)	36.1 [31] (12.7)	35.7 [59] (11.7)
Distance above bottom (cm)	$\underline{9.4}$[b] [9] (4.2)	5.3 [19] (2.1)	$\underline{7.3}$ [31] (4.0)	7.0 [59] (3.7)
Focal point velocity ($cm \cdot s^{-1}$)	12.1 [9] (7.7)	17.2 [19] (7.3)	18.7 [31] (10.3)	17.2 [59] (9.2)
Lateral velocity ($cm \cdot s^{-1}$)	17.7 [9] (12.1)	25.8 [19] (8.7)	24.4 [31] (11.8)	23.8 [59] (11.1)
Vertical velocity ($cm \cdot s^{-1}$)	$\underline{25.0}$ [9] (17.4)	43.9 [19] (12.9)	43.2 [31] (15.0)	40.6 [59] (16.0)
Light at fish's position ($lx \cdot 10^3$)	8.8 [9] (3.7)	17.0 [16] (5.1)	14.7 [28] (15.8)	14.4 [53] (12.1)
Light at surface ($lx \cdot 10^3$)	15.3 [9] (6.0)	30.0 [16] (9.9)	25.7 [28] (28.0)	25.2 [53] (21.6)
Substrate (cm)[c] (label)	3.3 (gravel)	15.7 (cobble)	15.7 (cobble)	6.4–25.0 (cobble)
Distance from shore (m)	7.1 [7] (3.0)	6.8 [15] (1.7)	5.9 [24] (2.8)	6.3 [46] (2.5)

[a] Sample size in square brackets; SD in parentheses.

[b] Underlined values are significantly different from the means at the other streamflows.

[c] Mode of frequency histogram.

TABLE 4. Correlation between streamflow, fish's distance above the streambed, and water velocity at the fish's position for juvenile coho and chinook salmon in Kloiya Creek, B.C.

Species	Streamflow (1.25 $m^3 \cdot s^{-1}$) (2.42 $m^3 \cdot s^{-1}$) (5.38 $m^3 \cdot s^{-1}$)	Variables (streamflow) (height above bottom) (water velocity)	Pearson correlation coefficient (R)	Probability (P)	Number of observations (N)
Coho, chinook	All	Flow, height	−0.25	0.0008	180
Coho, chinook	All	Flow, velocity	0.25	0.0009	180
Coho, chinook	2.42	Flow, height	−0.29	0.0244	62
Coho	All	Flow, height	−0.27	0.0032	121
Coho	All	Flow, velocity	0.32	0.0004	43
Coho	2.42	Flow, height	−0.30	0.0508	9
Chinook	1.25	Height, velocity	−0.62	0.0757	19
Chinook	2.42	Height, velocity	−0.40	0.0940	32
Chinook	5.38	Height, velocity	0.38	0.0319	32

NOTE: 27 other correlation analyses (8 distance above bottom with streamflow, 10 water velocity at fish position with streamflow, and 9 water velocity at fish position with distance above bottom) were conducted that had $P > 0.10$.

DMRT; Table 3). The mean water velocity at the position chosen by the chinook salmon, the mean water velocity lateral to their position, the mean light intensity above their position, the modal substrate size, and their mean distance from shore were different, but the difference was not statistically significant at $P < 0.05$. This may be due to the small sample size.

The size of the difference between the means of these variables and the size of their variances at different streamflows were the same for the chinook salmon as they were for the coho salmon. The only difference between the coho and chinook salmon data was that fewer chinook salmon positions ($N = 22$) were measured than coho salmon positions ($N = 66$). Therefore, had the sample size of the chinook data been larger, the differences in these habitat attributes used by juvenile chinook salmon at the different streamflows may have been significant as well.

Juvenile coho and chinook salmon changed their position in the water column and the water velocities they occupied in response to changes in streamflow. The height above the streambed occupied by coho during the flood streamflows was significantly less than what they used at normal or drought streamflow ($P < 0.05$, DMRT; Table 2). For juvenile chinook salmon, their distance above the streambed was significantly higher at drought streamflow than at either normal or flood streamflow ($P < 0.05$, DMRT; Table 3). The distance above the streambed occupied by coho and chinook salmon was negatively correlated with streamflow, but the water velocity at the positions they occupied was positively correlated with streamflow (Table 4). At drought

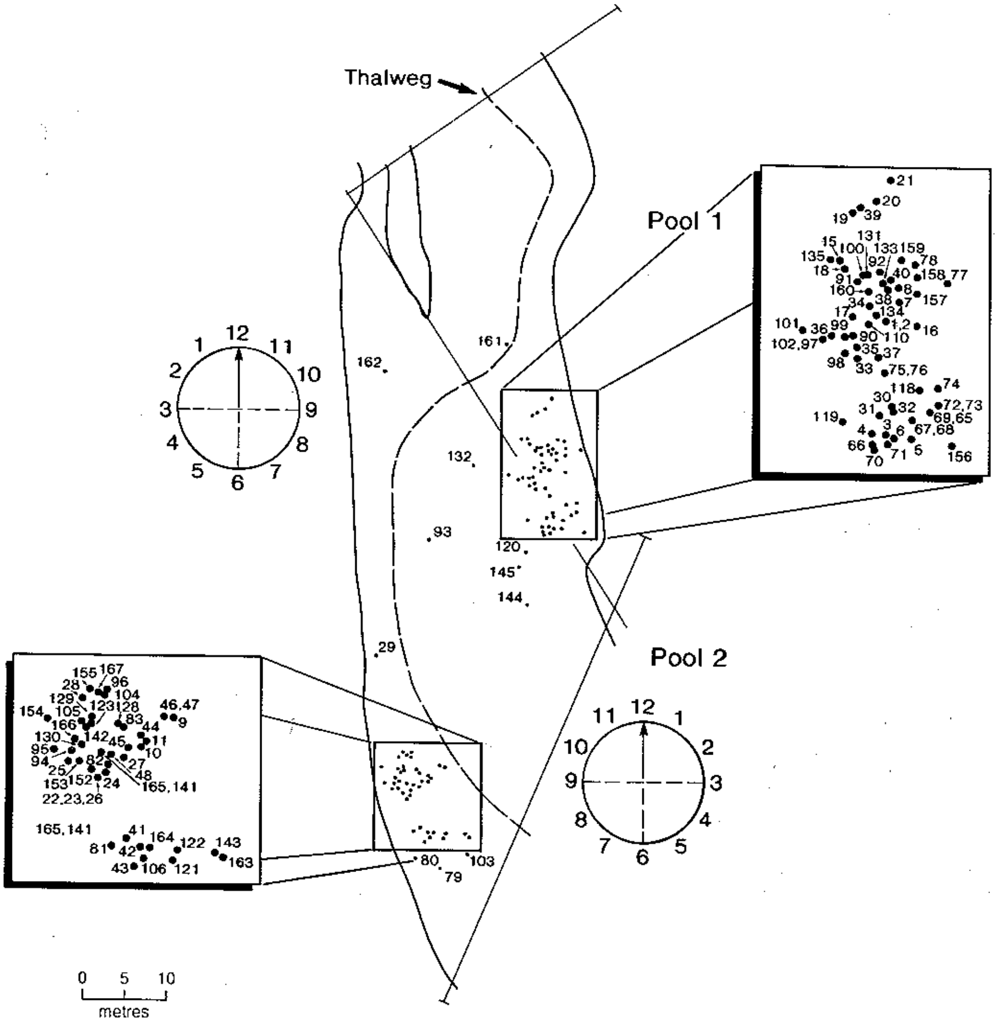

FIG. 2. Distribution of positions used by juvenile coho and chinook salmon in pools 1 and 2 of Kloiya Creek, B.C., at 1.25, 2.42, and 5.38 $m^3 \cdot s^{-1}$. The direction the fish moved in response to a streamflow change was coded according to clock positions (12 = upstream). Note the reversed clock numbers on the right side of the river (looking downstream). Numbers of individual fish positions are from Bravender and Shirvell (1990).

and normal streamflows, the water velocity at the position that juvenile chinook occupied was negatively correlated (Pearson correlation) with their distance above the streambed, but at flood streamflows, it was positively correlated.

Water Velocity Gradients around Fish Positions

The focal point velocity at positions chosen by both species was significantly slower than the water velocity both adjacent to and above the positions ($P < 0.06$, *t*-tests). Additionally, for both coho and chinook salmon, the mean water velocity 30 cm above the fish was significantly faster than the mean water velocity 30 cm lateral to the fish at all streamflows (coho $P = 0.001$, chinook $P = 0.001$).

The analyses above, because they use the mean of water velocities at many fish positions, do not detect inconsistencies in the patterns of water velocity gradients around individual fish. The positions selected by all juvenile coho and chinook salmon were not always slower than surrounding water velocities. Eighteen percent (21 of 121) of positions occupied by coho salmon had focal point water velocities that were faster than water velocities 30 cm lateral to the faster side of the fish (mean = 4.4 $cm \cdot s^{-1}$ faster, max. = 9.0 $cm \cdot s^{-1}$ faster) and 10% (13 of 121) had focal point water velocities that were faster than water velocities 30 cm above the fish (mean = 4.8 $cm \cdot s^{-1}$ faster, max. 12.0 $cm \cdot s^{-1}$ faster (Bravender and Shirvell 1990)). Two positions occupied by coho salmon had focal point water velocities that were faster than velocities both lateral and vertical to the fish's focal point. For positions occupied by juvenile chinook salmon, 19% (12 of 59) had velocities faster than velocities 30 cm lateral to the fish (mean = 3.4 $cm \cdot s^{-1}$ faster, max. = 10.0 $cm \cdot s^{-1}$ faster) and 2% (1 of 59) had velocities faster than velocities 30 cm above the fish.

Fish Movements

Juvenile coho and chinook salmon usually selected locations near the edge of the stream and distributed themselves in concentrated clumps. An example of their distribution in pools 1 and 2 is shown in Fig. 2. When streamflow changed, the fish moved to new locations. The average distance moved by both species for all streamflow changes was 7.2 m (N = 97, SD = 7.9 m). Juvenile chinook salmon generally moved

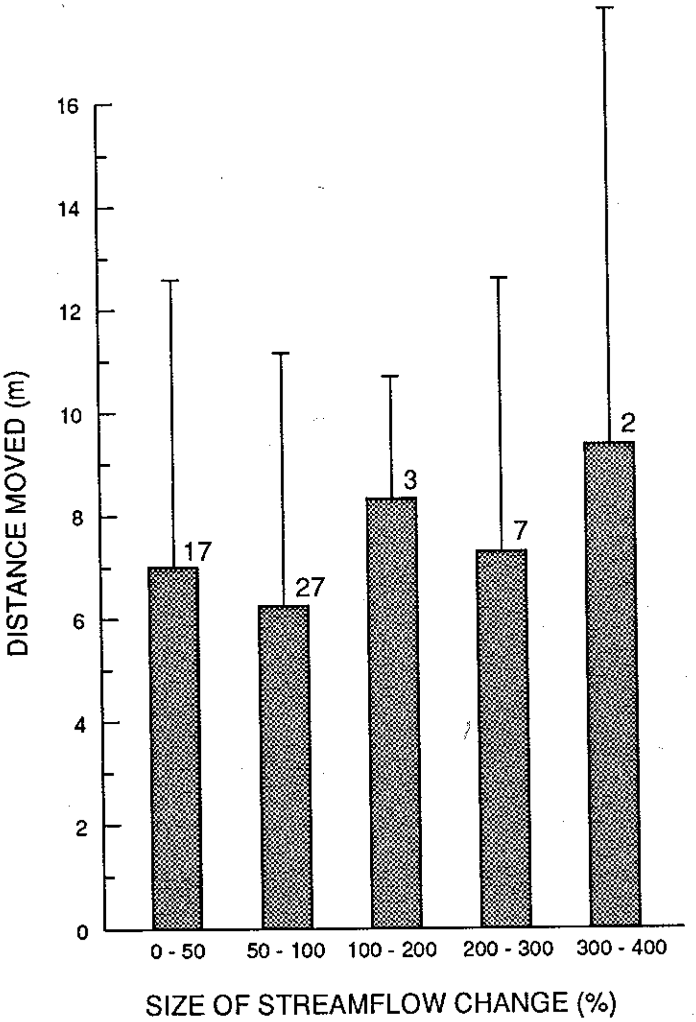

FIG. 3. Distance moved by juvenile coho and chinook salmon in Kloiya Creek, B.C., in response to changes in streamflow: Distance moved (m) = 5.91 + 0.57(% change in streamflow ($m^3 \cdot s^{-1}$)) ($R^2 = 0.55$, P that $b \neq 0$ is 0.15). The size of the streamflow change is expressed as a percentage of the initial streamflow. Error bars show 1 SD of the mean, and the numbers at the top of the bars are the sample sizes.

farther than coho salmon following a change in streamflow (mean distance of 8.6 versus 6.9 m, respectively); however, the difference was not significant ($P = 0.37$, t-test). The movements of each fish between successive observations are shown in Bravender and Shirvell (1990).

The mean distance the fish moved following a streamflow change was positively correlated with the size of the streamflow change, but only weakly (Fig. 3). Most fish remained in the pool where they were originally captured; only two coho and one chinook salmon moved to a different pool following a streamflow change. Two of these fish moved to a pool upstream. The mean distance moved by all three fish exceeded 50 m. Seventeen of the coho salmon that were tagged (43%) and 27 of the chinook salmon that were tagged (73%) were never observed again. These fish apparently left the pool where they were originally captured following a streamflow change. While it is unknown where these fish moved, it is probable that the chinook salmon, at least, went downstream into the estuary.

Juvenile coho and chinook salmon generally moved in different directions following a streamflow change. Juvenile coho salmon moved predominantly downstream and parallel to the water's edge with increasing streamflow and upstream parallel to the water's edge with decreasing streamflow (Fig. 4). In contrast, juvenile chinook salmon moved predominantly offshore and downstream regardless of the direction of the streamflow change, but especially with decreasing streamflow. With increasing streamflow, juvenile chinook salmon tended to move perpendicularly inshore.

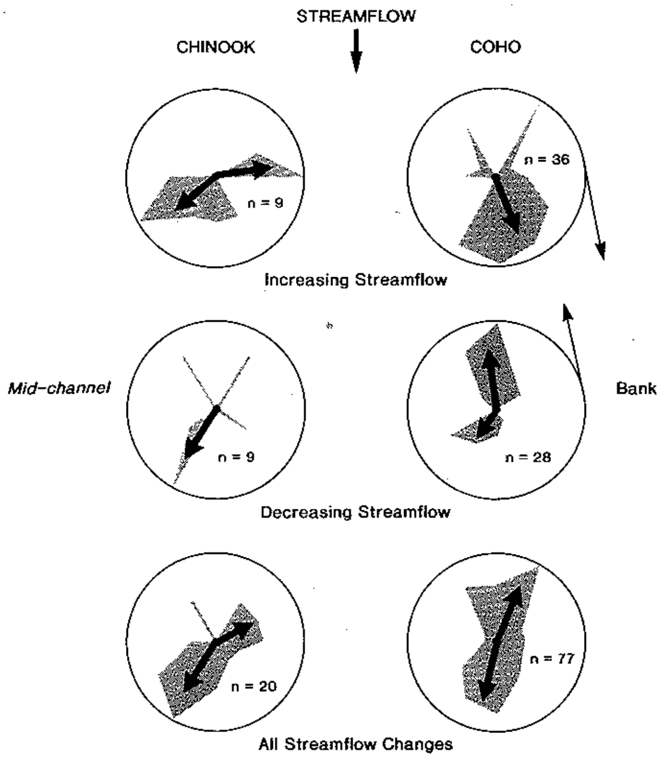

FIG. 4. Directions moved by juvenile coho and chinook salmon in Kloiya Creek, B.C., following changes in streamflow. The frequency of all directions in which the fish moved was normalized and shown in proportion to the most frequently used direction. "All streamflow changes" includes movements following increases and decreases in streamflow plus movements for intervals where the streamflow on the relocation date was the same as the streamflow at the previous observation. Arrows on the edges of the circles for coho salmon indicate the shift in the water's edge with increases or decreases in streamflow.

The direction moved by juvenile coho salmon appeared to be unrelated to the size of the streamflow change. Movements following both an increase and a decrease in streamflow greater than 60% from the previous streamflow were no different from movements made following an increase or a decrease in streamflow less than 60% from the previous streamflow. There were insufficient data to analyze the chinook salmon movements for any relationship with the size of the streamflow change.

The mean distance of the positions occupied by both the coho and chinook salmon relative to the water's edge was the same at all streamflows (4.5 and 6.3 m, respectively; Tables 1 and 2). However, because the shoreline shifted an average 2.0 m when streamflow increased from drought to normal streamflow and an additional 2.9 m when streamflow increased from normal to flood streamflow, the juvenile coho and chinook salmon must have also moved laterally by the same amount for their mean distance from shore to remain unchanged.

Discussion

Juvenile coho and chinook salmon occupied different microhabitats in Kloiya Creek. When they were the same size, the water depths and velocities they selected were similar (Tables 1 and 2), but the locations juvenile chinook salmon occupied were usually farther out from shore in brighter light and over larger substrate. Additionally, juvenile chinook salmon stayed closer to the streambed and were always beneath much faster currents than were juvenile coho salmon. Despite these differences, both species occupied the same general areas of the stream (e.g., Fig. 2). In Kloiya Creek, coho and chinook salmon shared the available habitat in the rearing areas in subtle ways. Lister and Genoe (1970) found similar habitat segregation between juvenile coho and chinook salmon during their first 3 mo following emergence in the Big Qualicum River, B.C., a comparable coastal stream. It appears that each species has different specific habitat preferences that allow them to intermingle in heterogeneous rearing areas without competing for the same microhabitats.

When streamflow changed, juvenile coho and chinook salmon moved to new locations characterized by their specific microhabitat preferences. The average distance moved by the fish exceeded the average distance that the isopleths of habitat conditions used by the fish at the former streamflow shifted (the fish moved an average of 6.8 m, while the depth and velocity contours shifted laterally an average of 2.0–2.9 m). While the fish demonstrated that they could discriminate between and select new positions with habitat conditions similar to their previous ones, they did not appear to be efficient at occupying the closest possible site with suitable conditions. I speculate that this inefficiency in occupying the closest suitable position may have been caused by the randomness of searching combined with behavioural interactions with other fish.

Movements made by juvenile salmon in response to rapid increases in streamflow in Kloiya Creek were voluntary and not due to their inability to swim against the increased current. For coho salmon, many of their movements after a streamflow change were upstream. Even when movements were downstream, such as those made predominantly by the chinook salmon, the distances were not great, generally less than 10 m. Furthermore, of all the fish relocated after a streamflow increase, only three left the pool where they were first observed. Both the coho and chinook salmon did not use the deepest water available to them, even at the highest streamflows. When streamflow increased to flood, neither species used positions much deeper than 40 cm (Tables 1 and 2) even though 40% of the study area had greater depths available (Bravender and Shirvell 1989). Heggenes (1988) suggested that, based on data from Tschaplinski and Hartman (1983) and Heggenes and Traaen (1988), young fish might be "washed-out" from streams by abrupt increases in stream discharge. While there was no evidence of this in Kloiya Creek, the coho and chinook salmon in this study were much larger than the fish studied by Heggenes and Traaen (1988) (54 versus 30 mm). The size of the streamflow increase used in this study was also much less than used by Heggenes (1988) (2 times increase versus 4–100 times increase, respectively). All movements and subsequent selection of habitat by the juvenile coho and chinook salmon in this study appeared to have been by choice.

Juvenile salmon in Kloiya Creek avoided displacement by high streamflows by moving to new locations with lower water velocities. When streamflows increased, both the juvenile coho and chinook salmon initially moved toward the stream bed (Tables 1 and 2) and then laterally (Fig. 4) to position themselves in suitable velocities. However, the juvenile chinook salmon moved greater distances on average to locate new "suitable" locations than did juvenile coho salmon (8.6 versus 6.8 m). A possible explanation for this might be that the centre of the stream was physically less heterogeneous than the edges of the stream. Because juvenile chinook salmon usually occupied the middle of the stream while the coho usually stayed along shore (see Shirvell 1990) the distances between physical structures that caused suitable reductions in the current (boulders or large pieces of wood?) may have been greater in the middle of the stream than they were near the shore.

Although the habitats used by juvenile coho and chinook salmon at the three streamflows were similar, they were not identical. The means of several of the habitat attributes at positions the fish occupied were significantly different between the low and the normal and high streamflows. This suggests that the fish may have had different habitat preferences at each of the streamflow levels assuming that the forces of social interaction remained constant between streamflows. It is not certain that these differences in habitat use were strictly due to different habitat preferences, however, because habitat use can be affected by the amount and kind of habitat that is available (Baldridge and Amos 1982). Nevertheless, the area of suitable habitat available in Kloiya Creek was so large that it seems reasonable that a surplus of appropriate habitat was available at all streamflows (Bravender and Shirvell 1989). If so, then the different habitat used at the three streamflows would reflect different habitat preferences.

Position selection by juvenile salmonids in streams has been suggested to be due to the fish's attempt to acquire food efficiently, i.e., they are hypothesized to select "optimal stream positions" in moderate currents near fast water where, by minimizing their energy expenditure near abundant food sources, they maximize their net energy gain (Fausch 1984). An alternative hypothesis is that the fish select positions with combinations of preferred levels of water velocity, depth, and substrate, where their probability of occurrence is 1.0 (Bovee 1982). If optimal position selection is correct, then selection of positions in streams would not be based on a preferred water velocity per se (the IFIM hypothesis), but would be based on locations with velocity gradients, where the stronger the gradient, the greater the potential for net energy gain. Fausch (1984) showed that juvenile coho salmon occupied positions with the highest potential for net energy gain available to them. However, Hughes and Dill (1990) showed that for solitary Arctic grayling (*Thymallus arcticus*), the position that allowed the maximum net energy gain was not necessarily in slow current next to strong velocity gradients because the Arctic grayling had to be close enough to the prey to detect it so that they could react.

Juvenile coho and chinook salmon usually selected positions in Kloiya Creek where water velocity increased in any direction away from them. However, because of the effect of streambed friction on waterflow in streams, it is normal that there is a positive water velocity gradient at increasing distance away from the streambed. Consequently, it is usual that any position near the streambed or banks would have the water velocity gradient of optimal position theory. However, coho and chinook salmon selected positions 18 and 19% of the time, respectively, in water that was faster than water velocities 30 cm lateral to them, and coho salmon selected positions 10% of the time in the water column that were faster than water velocities 30 cm above them. Similar position choice has been found for juvenile chinook salmon in the Nechako River (Nechako River Project 1987). There, 26% of the juvenile chinook salmon (78 of 304) selected positions that were faster than water velocities 30 cm lateral to them and 19% (58 of 299) selected positions in the water column faster than those 30 cm above them. Thus the juvenile salmon in Kloiya Creek selected positions that were inconsistent with the optimal stream position hypothesis. The juvenile coho salmon also selected different levels of focal water velocity, focal light intensity, and height above the bottom of Kloiya Creek at different streamflows. Therefore, they also selected positions that were inconsistent with the constant habitat preference hypothesis of IFIM.

While the lack of a positive velocity gradient around all positions selected by salmonids in streams does not refute an energetic basis for position selection some of the time, it suggests that the fish consider other needs besides feeding. As the predominant motivation changes from feeding to some other need, the microhabitat conditions required by the fish may also change, thus accounting for the different habitat use at different streamflows that occurred in Kloiya Creek. I propose that fish have different habitat preferences for different activities. As an example, when the primary purpose is feeding, fish would select optimal positions along velocity gradients, as found by Fausch (1984). When the primary purpose is avoidance of predators, fish would select optimal positions along light gradients, as found by Heggenes et al. (1993). Shirvell and Dungey (1983) found significant differences between the microhabitats used by brown trout (*Salmo trutta*) for feeding and spawning, while Shirvell (1990) found that different levels of water velocity were selected by steelhead (*Oncorhynchus mykiss*) parr depending on whether they were sheltering from current velocity (feeding?) or hiding from predators. Thus, fish have activity-specific habitat preferences. Because the activity a fish is engaged in can be affected by streamflow, the assumption that habitat use by juvenile coho and chinook salmon is constant for all streamflows is false, and this has important significance for models that attempt to predict the effects of streamflow change on fish habitat.

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References

BALDRIDGE, J.E., AND D. AMOS. 1982. A technique for determining fish habitat suitability criteria: a comparison between habitat utilization and availability, p. 251–258. *In* N.B. Armantrout [ed.] Acquisition and utilization of aquatic habitat inventory information. American Fisheries Society, Western Division, Bethesda, Md.

BOVEE. K.D. 1982. A guide to stream habitat analysis using the Instream Flow Incremental Methodology. Instream Flow Information Paper 12, U.S.D.I. Fish and Wildlife Service, Office of Biological Services. FWS/OBS-82/26. 248 p.

BRAVENDER, B.A., AND C.S. SHIRVELL. 1989. Depth, velocity, and substrate measurements of Pacific salmon habitat at three streamflows in Kloiya Creek, B.C. 1984–1985. Can. Data Rep. Fish. Aquat. Sci. 758: 67 p.

BRAVENDER, B.A., AND C.S. SHIRVELL. 1990. Microhabitat requirements and movements of juvenile coho and chinook salmon at three streamflows in Kloiya Creek, B.C. Can. Data Rep. Fish. Aquat. Sci. 802: 159 p.

BURT, D.W., AND J.H. MUNDIE. 1986. Case histories of regulated stream flow and its effects on salmonid populations. Can. Tech. Rep. Fish. Aquat. Sci. 1477: 98 p.

FAUSCH, K.D. 1984. Profitable stream positions for salmonids: relating specific growth rate to net energy gain. Can. J. Zool. 62: 441–451.

FAUSCH, K.D., AND R.J. WHITE. 1986. Competition among juveniles of coho salmon, brook trout, and brown trout in a laboratory stream, and implications for Great Lakes tributaries. Trans. Am. Fish. Soc. 115: 363–381.

HEGGENES, J. 1988. Effect of short-term flow fluctuations on displacement of and habitat use by brown trout in a small stream. Trans. Am. Fish. Soc. 117: 336–344.

HEGGENES, J., O.M.W. KROG, O.R. LINDAS, J.G. DOKK, AND T. BREMNES. 1993. Homeostatic behavioural responses in a changing environment: brown trout (*Salmo trutta*) become nocturnal during winter. J. Anim. Ecol. 62: 295–308.

HEGGENES, J., AND T. TRAAEN. 1988. Downstream migration and critical water velocities in stream channels for fry of four salmonid species. J. Fish Biol. 32: 717–727.

HUGHES, N.F., AND L.M.DILL. 1990. Position choice by drift-feeding salmonids: model and test for Arctic grayling (*Thymallus arcticus*) in subarctic mountain streams, interior Alaska. Can. J. Fish. Aquat. Sci. 47: 2039–2048.

LISTER, N.F., AND H.S. GENOE. 1970. Stream habitat utilization by cohabiting underyearlings of chinook (*Oncorhynchus tshawytscha*) and coho (*O. kisutch*) salmon in the Big Qualicum River, British Columbia. J. Fish. Res. Board Can. 27: 1215–1224.

MORANTZ, D.L., S.E. BARBOUR, AND R.K. SWEENEY. 1986. Source of error in water velocity measurement for aquatic studies. Can. J. Fish. Aquat. Sci. 43: 893–896.

MORANTZ, D.L., R.K. SWEENEY, C.S. SHIRVELL, AND D.A. LONGARD. 1987. Selection of microhabitat in summer by juvenile Atlantic salmon (*Salmo salar*). Can. J. Fish. Aquat. Sci. 44: 120–129.

NECHAKO RIVER PROJECT. 1987. Studies of juvenile chinook salmon in the Nechako River, British Columbia 1985 and 1986. Can. MS Rep. Fish. Aquat. Sci. 1954: 152 p.

ORTH, D.J. 1983. Aquatic habitat measurements, p. 61–84. *In* L.A. Nielsen and D.L. Johnson [ed.] Fisheries techniques. American Fisheries Society, Bethesda, Md.

PETTS, G.E. 1984. Impounded rivers perspectives for ecological management. John Wiley & Sons, New York, N.Y. 326 p.

REISER, D.W., T.A. WESCHE, AND C. ESTES. 1989. Status of instream flow legislation and practices in North America. Fisheries 14: 22–29.

SAS INSTITUTE INC. 1985. SAS user's guide: statistics, version 5 edition. SAS Institute Inc., Cary, N.C. 956 p.

SHIRVELL, C.S. 1990. Role of instream rootwads as juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*O. mykiss*) cover habitat under varying streamflows. Can. J. Fish. Aquat. Sci. 47: 852–861.

SHIRVELL, C.S., AND R.G. DUNGEY. 1983. Microhabitats chosen by brown trout for feeding and spawning in rivers. Trans. Am. Fish. Soc. 112: 355–367.

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.

WANKOWSKI, J.W.J. 1981. Behavioral aspects of predation by juvenile Atlantic salmon (*Salmo salar* L.) on particulate, drifting prey. Anim. Behav. 29: 557–571.