INTERNATIONAL PACIFIC SALMON FISHERIES COMMISSION *

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BULLETIN XXV

HOMING BEHAVIOR OF ADULT SOCKEYE SALMON IN RESPONSE TO A HYDROELECTRIC DIVERSION OF HOMESTREAM WATERS AT SETON CREEK

MICHAEL R. FRETWELL

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MICHAEL ROBERT FRETWELL
1951 - 1988

A 1974 graduate in biological science from the University of British Columbia, the author was employed by the International Pacific Salmon Fisheries Commission from 1977 until its dissolution on December 31, 1985, when he transferred to Canada Department of Fisheries and Oceans. He prepared a first draft of this report in 1985 after completing a thesis on the same subject, for which he received a Master of Science degree from Simon Fraser University. He lost his life in a helicopter crash on September 27, 1988 while engaged in spawning ground enumeration on Nechako and Stuart Rivers. He was an outstanding scientist, having a brilliant mind and a keen dedication to his work in conserving the fishery resource.

ABSTRACT

The spawning migration of sockeye and pink salmon was disrupted by a hydroelectric diversion of Seton Creek that caused the fish to be attracted to the tailrace of the power plant, where they were delayed and some were seriously injured in attempting to swim into the draft tube. The problem was examined by means of radio-telemetry and by field-laboratory studies of fish preference for various dilutions of their homestream water. Sockeye preferred to remain in the discharge from the powerhouse because it had a higher concentration of homestream water than Seton Creek, which was diluted by inflow from Cayoosh Creek. They failed to migrate upstream in Seton Creek unless the proportion of homestream water (Seton Lake outflow) was increased to at least 80% for the summer-run population (Gates Creek sockeye) and at least 90% for the fall-run population (Portage Creek sockeye). The required concentration of homestream water was obtained by diverting Cayoosh Creek to Seton Lake and occasionally it was also necessary to increase the spill discharge at Seton Dam. Pink salmon were not affected as severely as sockeye and the stipulated corrective measures for sockeye were sufficient to avoid serious pink salmon delay and injury. Observations indicating an ability of sockeye to choose the higher concentration of two mixtures of homestream water and the failure of radio-tagged sockeye to migrate upstream in Seton Creek after having encountered a higher concentration of homestream water in the tailrace suggested that sockeye possess a more complex decision-making ability than embraced by conventional olfactory hypotheses.

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NOTE: The first draft of this report was extensively reviewed by Dr. Ernest Brannon and Dr. Richard Thompson. After the author's death, Mr. Fred Andrew volunteered to complete the final draft.

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INTRODUCTION

The Seton Creek hydroelectric installation is located on Seton Creek, a tributary of the Fraser River near Lillooet, British Columbia (Fig. 1). It was completed in 1956 by British Columbia Electric Company, which was later taken over by British Columbia Hydroelectric and Power Authority. It consists of a low diversion dam on Seton Creek 750 m downstream from the outlet of Seton Lake and a concrete-lined canal that transports water 3.8 km from this dam to a 58,500 hp generating station on the Fraser River 1.2 km downstream from the natural mouth of Seton Creek (Fig. 2). During the first years of operation, the plant discharge was augmented by water diverted from Cayoosh Creek to Seton Lake by means of a low timber dam on Cayoosh Creek and a 500 m tunnel to Seton Lake. The diversion discharge from the Bridge River system to Seton Lake was later increased, which provided enough water for full operation of the Seton plant, and therefore the Cayoosh dam was removed and the tunnel was blocked off.

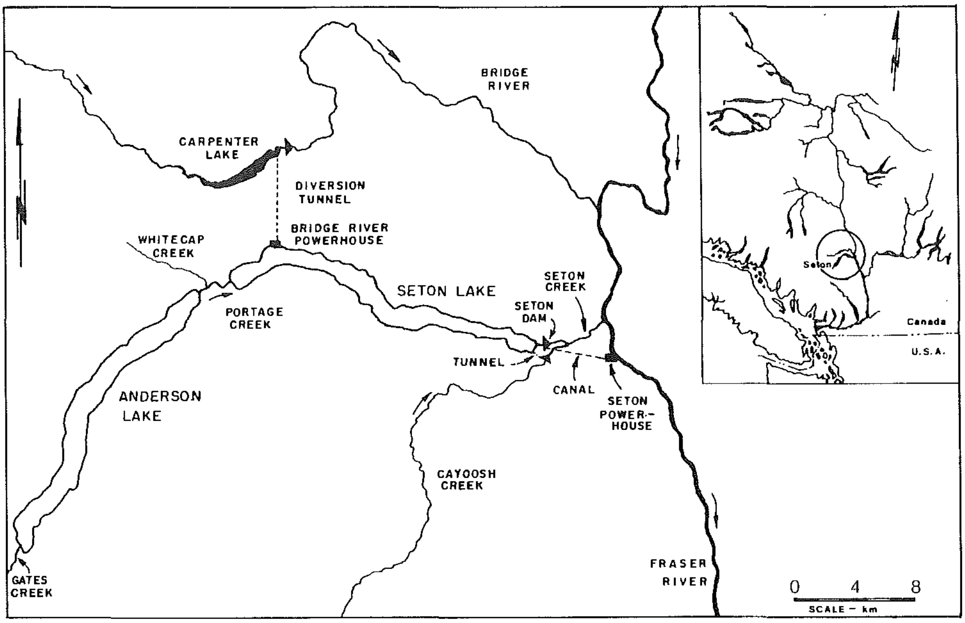

FIGURE 1—Seton-Anderson Lake system in relation to the Fraser River watershed.

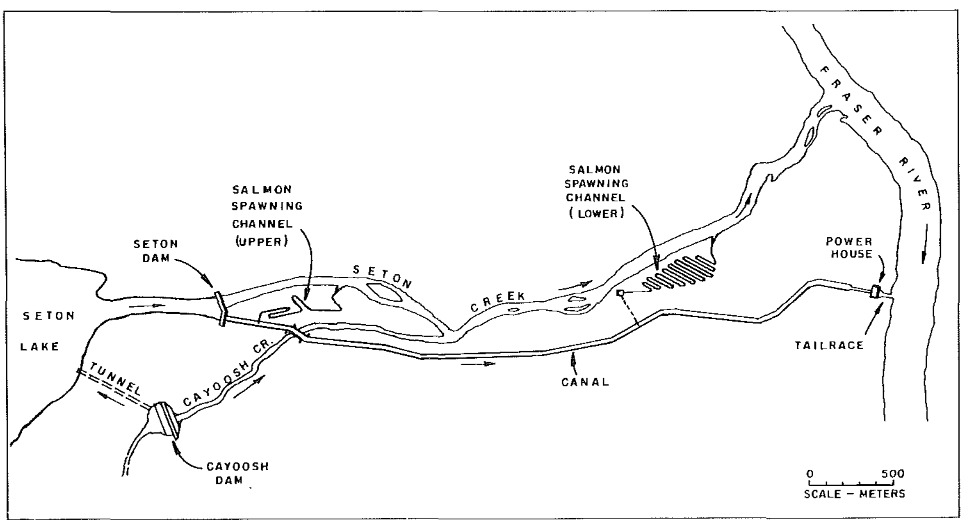

FIGURE 2—Layout of Seton Creek hydroelectric development in relation to Seton and Cayoosh Creeks.

Discharge of the Seton plant at full load varies from about 100 - 125 m^3/s depending on elevation of the tailrace, which is controlled by Fraser River discharge (Fig. 3). A minimum discharge of 11.3 m^3/s for protection of fish in Seton Creek is spilled at Seton Dam during salmon migration and spawning periods and 5.7 m^3/s at other times. With efficient control of flows from the Bridge River system, spilling of surplus water seldom occurs at Seton Dam but there is no flow control on Cayoosh Creek. During the salmon migration and spawning period, about 90% of the outflow from Seton Lake is diverted to the powerhouse. When the plant began operating, with practically all of Cayoosh Creek diverted to Seton Lake, the Cayoosh component in the outflow of Seton Creek at the Fraser River was only about 5% but after the Cayoosh diversion was closed, the Cayoosh component increased substantially, frequently exceeding 50% of the flow in lower Seton Creek during the period of salmon migration.

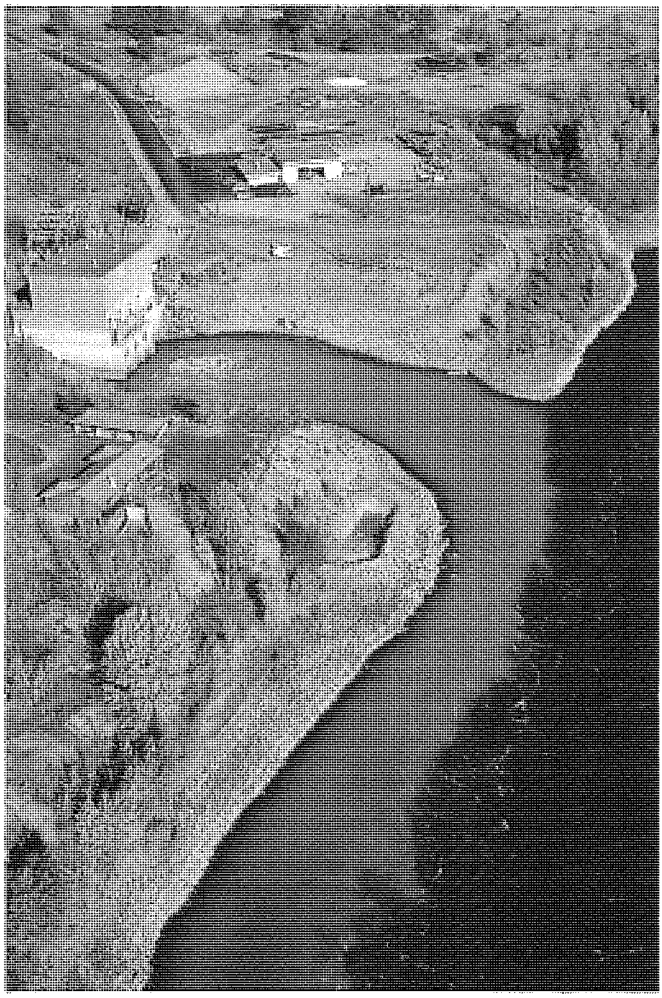

FIGURE 3—Seton Lake water discharged into the Fraser River at Seton powerhouse.

Two sockeye (*Oncorhynchus nerka*) populations and a very large pink (*O. gorbuscha*) population spawn in the Seton system. Up to 29,000 sockeye migrate up Seton Creek from about July 20 to Aug. 30 and spawn in Gates Creek and a spawning channel on that stream. Up to 32,000 Portage Creek sockeye migrate up Seton Creek from about Sept. 20 to Nov. 15. Pink salmon arrive in Seton Creek about Sept. 20 and the spawning populations consist of up to 1,300 in Gates Creek, 52,000 in Portage Creek, 51,000 in Cayoosh Creek and 564,000 in Seton Creek and two spawning channels on that stream (IPSFC records for the period 1957 - 1985 inclusive).

Sockeye and pink salmon fry produced in the Seton system migrate downstream immediately after emerging from the spawning gravel, predominantly in the period March 15 - May 15. The pinks go directly to sea but the sockeye remain in Anderson and Seton Lakes for a year. Geen and Andrew (1961) studied juvenile migration patterns in relation to lake productivity and found that despite much higher abundance of zooplankton in Anderson Lake, most of the Gates Creek fry and all of the Portage Creek fry migrate directly to Seton Lake. Scale analysis of six year-classes of adults returning to Gates Creek showed that about 15% had reared in Anderson Lake, the remainder migrating to Seton Lake as fry. Those that remained in Anderson Lake apparently migrated to Seton Lake during the fall and winter months and they migrated out of Seton Lake in April and May along with those that spent all of their rearing period in Seton Lake. The yearling smolts migrated downstream via the power canal and through Seton Dam (spillways and fishway) in proportion to the water flows in these two routes.

Sockeye smolts and pink salmon fry are exposed to somewhat different water mixtures during their respective early life periods. Sockeye smolts that exit Seton Lake via the Seton Dam spillways or fishway encounter a variable concentration of Cayoosh Creek water in Seton Creek below the Cayoosh confluence, depending on the discharges of the two streams. Approximately 95% of the sockeye smolts exit Seton Lake via the power canal and do not encounter Cayoosh Creek water except in a very dilute concentration in the Fraser River below the tailrace.

Fry from pink salmon spawning populations in Gates and Portage Creeks and in Seton Lake and Seton Creek upstream from Seton Dam experience a variable exposure to Cayoosh Creek water during their seaward migration similar to sockeye smolts. Pink salmon fry incubated in Seton Creek between Seton Dam and the Cayoosh confluence and those from the two spawning channels on Seton Creek are incubated in water from the Seton Lake outflow but they are exposed to a Seton-Cayoosh mixture for a few hours during their seaward migration below the Cayoosh confluence. Fry incubated in Cayoosh Creek and those incubated in Seton Creek below the Cayoosh confluence are exposed to Cayoosh water during incubation and to a Seton-Cayoosh mixture during their seaward migration in Seton Creek.

The fish-protective facilities at Seton Dam consist of a vertical-slot fishway, an adjustable gate for maintaining the required minimum flows and a coarse wire screen across the canal intake at this dam to prevent adult salmon from being swept downstream into the power canal. To compensate for the area of pink salmon spawning ground lost as a result of the construction of Seton and Cayoosh dams, the B.C. Electric Company provided land for construction of a pink salmon spawning channel on Seton Creek. The company also agreed to provide additional fish-protective measures if the need was indicated by studies after the plant was in operation. The first investigations were undertaken in 1956 and 1957, revealing two major problems: (1) seaward-migrant sockeye suffered a mortality rate of about 10% in passing through the turbine and 1 - 7% in the Seton Dam spillways, and (2) adult sockeye and pink salmon were delayed in migrating upstream past the powerhouse to the natural mouth of Seton Creek (Andrew and Geen 1958). There was an average one-day delay of pink salmon in the powerhouse tailrace and some pink salmon and Portage Creek sockeye were believed to be delayed for substantially longer periods. There was no evident injury of pinks or Portage Creek sockeye adults in the tailrace during these preliminary investigations but the sockeye runs were very small during the study period and it was therefore recommended that "the problem of delay of upstream migrants, particularly of sockeye, in the powerhouse tailrace requires further study" (Andrew and Geen 1958).

Subsequent observations did not reveal a serious migration blockade until 1972, when it was noted that the number of Gates Creek sockeye counted through the Seton Dam fishway was much lower than had been expected on the basis of the estimated numbers that had passed through the commercial fisheries. Other sockeye races migrating through the fisheries concurrently did not exhibit similar losses. In addition, late timing of the run through the fishway and a high frequency of extensive head injuries suggested that the fish had suffered a long delay in the tailrace and that they had made repeated attempts to swim into the draft tube. It was not recognized at that time or in studies conducted from 1968 to 1975 that the closure of the Cayoosh diversion had resulted in substantial dilution of the homestream odor in lower Seton Creek (from the Cayoosh confluence to the Fraser River), as compared to the flow from the powerhouse (Anon. 1976). Instead, the observed accumulation of fish in the tailrace was attributed to the apparent lack of a continuous stream of Seton Lake water in the Fraser River between Seton Creek and the tailrace. It was reasoned that an observed break in the Seton Creek plume caused by Fraser River turbulence just upstream from the tailrace caused the fish to lose their olfactory cue and to tend to remain in the tailrace. However, when fish behavior was later studied in much more detail by the use of radio-telemetry, it was found that sockeye frequently migrated from the tailrace and into lower Seton Creek and then returned to the tailrace (Fretwell 1979). This observation and subsequent studies led to the conclusion that migrating adult salmon, upon encountering two streams containing their homestream odor, are capable of identifying the stream with the highest concentration and that they exhibit positive rheotaxis in the high-concentration stream and negative rheotaxis in the low-concentration stream.

The problem of delay and injury of salmon in the Seton tailrace was examined by two methods: (1) testing salmon for a preference when they were presented with a choice between their homestream water and various dilutions of their homestream water in an experimental situation, and (2) observing the behavior of radio-tagged adult salmon during their natural migration. This report gives the results of those studies, discusses the implications of the findings with respect to the homing behavior of salmon and discusses the application of the findings to resolution of the Seton tailrace delay and injury problem.

SALMONID HOMING

The homing migration of adult Pacific salmon from the ocean to their natal stream is generally subdivided into the oceanic and freshwater phases on the basis of the sensory mechanisms utilized by fish for orientation, navigation and homing. Methods of orientation and navigation that may be used by salmon at sea include passive drift, random searching, keying on specific temperatures and salinities, celestial orientation, orientation to polarized light and magnetic-compass orientation (Neave 1964, Quinn 1981, Royce et al. 1968). The relatively precise timing of salmon migrations of several thousand kilometers to very specific locations implies a higher degree of ability in navigation and time measurement than seems possible utilizing the above means of orientation either singly or in combination. The current view is that some type of bi-coordinate map-compass, calendar-clock system is required to accomplish this feat of timing and precise location (Quinn 1982).

When adult salmon approach the mouth of their home river watershed, olfaction apparently becomes the dominant guiding mechanism. One hypothesis is that juvenile salmon imprint to an odor or odors present in the homestream and when returning as adults they respond to the presence of those imprinted odors (Hasler 1966, Hasler et al. 1978, Hasler and Scholz 1983). An alternative to the "imprinting hypothesis" is the "pheromone hypothesis," which postulates that the returning adults are inherently attracted to the homestream by pheromones released by juveniles of the same population (Stabell 1984). The pheromone hypothesis has been directed mainly toward homing of Atlantic salmon (*Salmo salar*). Throughout this report, Seton Lake outflow is referred to as homestream water for sockeye and pinks originating in the Seton system since it appears to contain the olfactory cue or cues that the adults "home" to.

Although some aspects of the return to the homestream may be under genetic control in Pacific salmon (Bams 1976), the most widely held view is that homing of Pacific salmon is at least partly dependent upon some form of imprinting to chemical constituents of the homestream water. The mechanism by which imprinting is accomplished and the precise time it occurs is not completely understood (Cooper et al. 1976, Hasler et al. 1978, Jensen and Duncan 1971, Novotny 1980). Numerous attempts have been made to clarify the imprinting mechanism since it has a significant bearing on the route and timing of migration and therefore upon the likely success of many enhancement and rehabilitation projects as well as management of harvesting fisheries. Some imprinting is believed to occur before or during smoltification. However, earlier imprinting during the incubation and emergence periods may also occur, at least in the case of salmon (such as sockeye) which move to sea from a lake rearing area remote from the spawning area from which they emerged and to which they must ultimately return (Horrall 1981). The length of time required for effective imprinting at the smolting stage is also only partially known but in some instances may be as little as 4 hr (Novotny 1980).

The homestream odor hypothesis is based on the following tenets: (l) that each stream possesses a characteristic odor detectable by salmon, (2) that salmon are able to discriminate between the odors of different streams, and (3) that salmon are able to retain the "memory" of the homestream odor during the one to several years of oceanic residence. The chemical basis of the homestream odor or odors has not been identified but is thought to be, in part, volatile organic compounds (Idler et al. 1961). It has also been variously suggested that the distinctive odor in each stream may originate from its flora and the geochemical nature of the watershed or from race-specific pheromones excreted or secreted by related juveniles in the homestream (Hasler 1966, Hasler et al. 1978, Nordeng 1971 and 1977).

Regardless of the imprinting mechanisms, implicit in the olfactory hypothesis is the necessity for a positive rheotactic response in the presence of appropriate odor cues (Hara 1975, Hasler and Scholz 1983, Johnsen 1982, Johnsen and Hasler 1980). Results presented in this report suggest that the homing migration of salmon after entering fresh water entails more than positive rheotaxis in the presence of the homestream odor or sequence of odors and that salmon are capable of a "decision-making" process in locating their homestream.

WATER SOURCE PREFERENCE STUDIES

APPARATUS AND METHODS

The apparatus used to test the preference of migrating salmon for various concentrations of homestream water was similar to that described by Sutterlin and Gray (1973) for testing the behavior of Atlantic salmon returning to a hatchery. The test apparatus was located on the bank of Cayoosh Creek approximately 900 m upstream from its confluence with Seton Creek. The preference apparatus consisted of two troughs through which test and control waters were discharged into a central pool (Fig. 4). The rectangular fiberglass troughs were 305 cm long, 76 cm wide and 46 cm deep. The central, round fiberglass pool was 183 cm in diameter and 61 cm deep. The troughs were joined to the round pool by means of 20.3 cm diameter ports constructed of plastic. These were sealed with silicon specified by the manufacturer as non-toxic to fish. The entire apparatus was covered with a fine nylon mesh to prevent fish from jumping out. The mesh also provided partial shade from sunlight.

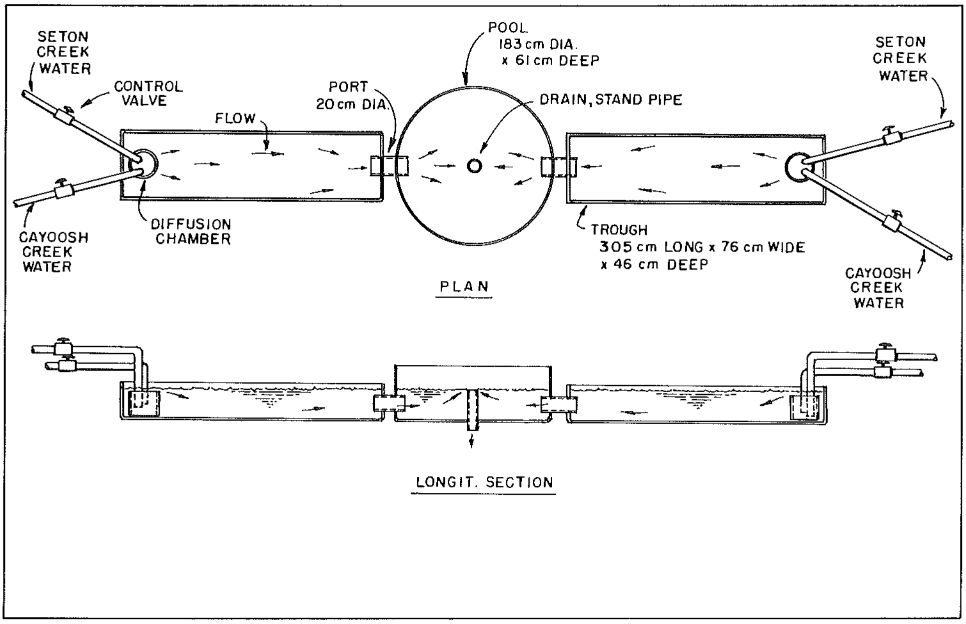

FIGURE 4—Water source preference apparatus.

Water was supplied through 5.1 cm (inside diameter) flexible polyethylene pipe into a diffusion chamber at the distal end of each of the rectangular troughs. Total discharge into each trough was 68.2 L/min. Seton Lake water was presented in one trough (referred to as the control) and a mixture of Seton Lake water and Cayoosh Creek water in the other trough (referred to as the test mixture). Water from both sources was piped to the upstream end of both troughs so that the test mixture and control water could be exchanged end-for-end in alternating tests. Discharges were controlled with valves on the incoming supply pipes. After the water entered the diffusion chambers, it flowed the length of the rectangular troughs, passed through the ports into the circular pool and drained through a 7.6 cm standpipe in the middle of the central pool. A removable plug in the port at the downstream end of each trough prevented the test and control mixtures from entering the central pool prior to the start of each test. Seton Lake water was obtained from the Seton Generating Station power canal by a siphon hose. Cayoosh Creek water was obtained by gravity flow from Cayoosh Creek.

Adult sockeye and pink salmon were captured by means of a power-operated 3-m-square brail net in the tailrace of Seton Generating Station or, for certain trials, they were captured by hand-operated dip net from the fishway at Seton Dam. Captures were made from approximately 0800-1500 hr. Fish were not sorted according to sex except during the 1982 Gates Creek sockeye migration, when only precocious males were utilized in order to avoid any adverse effect on production of a very small escapement. The fish were transported by truck in an oxygenated 900-L fiberglass tank. A 0.3% saline solution was used to reduce transportation stress (Mazeaud and Mazeaud 1981).

The fish were placed in the central pool in Seton Lake water (the same water they had been taken from, whether captured in the tailrace or fishway) for a 15-min acclimation period before the water flow into the rectangular troughs was started. A further 15 min elapsed before the troughs were filled. This 30-min pre-test acclimation period was comparable to that used elsewhere (Emanuel and Dodson 1979, Quinn et al. 1983). When the troughs were filled, the plugs separating them from the central holding pool were removed by means of a cord drawn by an observer situated 15 m directly above the apparatus. Removal of the plugs signalled the beginning of the experiment.

Fish were allowed 1 hr to choose between the trough discharging control (Seton Lake) water and the trough discharging test (Seton Lake plus Cayoosh Creek) water. Fish were free to move from the central pool to the troughs and to return to the central pool during the course of the test (Fig. 5). The numbers of fish in each trough as well as the number remaining in the center pool were recorded after 1 hr.

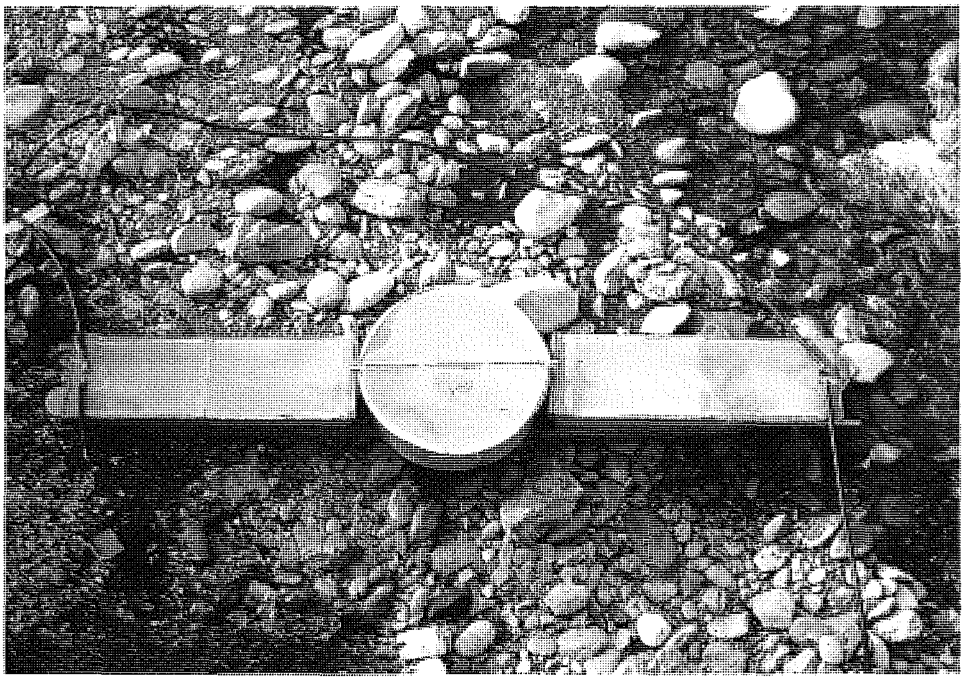

FIGURE 5—Water source preference apparatus with fish congregated near the source of the control water (right-hand trough).

Fish were returned to the central pool after it had been refilled with Seton Lake water. The rectangular troughs were then drained, the water sources switched end-for-end, and the test repeated. In this way each group of fish was tested twice (in "pairs") and any directional or end preference was eliminated.

Preliminary experiments were conducted in 1980 using Portage Creek sockeye salmon. Initially, each group of fish was tested three times, as explained above. Relatively consistent results were obtained during the first two tests. However, by the beginning of the third test, 4 hr or more had elapsed since the fish had been captured and they became aggressive and easily excited by the test procedures. Subsequently, each group of fish was limited to two trials (one pair of tests).

Previous workers have noted that salmon avoid water containing extract of mammalian skin (Brett and MacKinnon 1954, Idler et al. 1961). Therefore, as a precaution against introducing this bias, all operators wore rubber gloves during operation or manipulation of the test apparatus.

Water temperatures were recorded to the nearest 0.1 °C. Water samples were obtained from four sites at intervals throughout the 1981 season to determine whether changes in responses of fish might be attributed to changes in water chemistry. Samples were forwarded for analysis to a laboratory operated by the Inland Waters Directorate, Environment Canada, and were analyzed for conductance, alkalinity, hardness, calcium, fluoride and sulphate.

RESULTS OF PREFERENCE STUDIES

Behavior of Fish in the Test Apparatus

Upon placement into the test apparatus, the fish at first appeared agitated, but within one to two minutes began slowly circling the holding pool and at times lying relatively motionless against the wall of the container. Often the fish would remain motionless in small groups of 2-4 individuals for several minutes before resuming the slow swimming pattern. After the test and control mixtures began flowing into the central pool, the fish sometimes continued swimming without apparent reference to the ports, and on other occasions would "explore" or "search" the area of the ports. Upon entry into the test or control trough, the fish usually proceeded to the water source and probed around the base and sides of the diffusion chamber. Considerable activity often developed in the area of the water source, particularly in the control trough, with several fish simultaneously attempting to swim into the diffusion chamber or into an adjacent corner of the trough. Some fish also attempted to leap out of the trough at that point. After several minutes of activity near the water source, the fish frequently would swim in a "searching" pattern along the sides of the trough, sometimes returning to the area of the water source and sometimes exiting through the port into the central holding pool.

Table 1. Distribution of 1980 Portage Creek sockeye in the preference testing apparatus with a test mixture containing 20% Cayoosh water.

	Fish Distribution				
Elapsed Time	Seton Lake Water		Center Pool	Test Mixture	
(min.)	Number	%*	Number	Number	%*
0	0	-	64	0	-
15	36	62	6	22	38
30	39	67	6	19	33
45	40	68	5	19	32
60	48	77	2	14	23

* Percentage calculated from the total number of fish making a choice.

The distribution of fish gradually changed with all of the fish in the central pool at the start of the test and, in most tests, few fish in the central pool at the end of the test. Most choices were made during the first 15 min of the test with only gradual reinforcement of that distribution occurring throughout the remaining 45 min. The change in distribution during preliminary tests with 1980 Portage Creek sockeye exposed to a test mixture containing 20% Cayoosh water was typical of results obtained throughout (Table 1).

Preliminary Experiments

Since it was not known what threshold of dilution of test water might be detected by the fish, the 1980 preliminary tests were begun by comparing 100% Cayoosh Creek and 100% Seton Lake water. Subsequently the proportion of Cayoosh Creek water in the test mixture was reduced to 50, 33, 20, 10 and 0%. The test mixtures containing 100, 50, 33 and 20% Cayoosh Creek water all elicited a strong preference by Portage Creek sockeye for the control (Seton) water (Table 2). The preference for Seton Lake water was significant ($P < .005$ in all cases). When the proportion of Cayoosh water in the test mixture was reduced to 10 and 0%, the fish showed no preference for the control water.

Groups of 1981 Gates Creek sockeye were exposed to Seton Lake water and test mixtures of Seton Lake water diluted 20 and 15% with Cayoosh Creek water (Table 3). A highly significant preference was shown for Seton Lake water over a 20% dilution ($P < .01$). A test mixture diluted 15% with Cayoosh Creek water attracted fewer fish than 100% Seton Lake water but the results were not significant.

Table 2. Preliminary preference experiments utilizing 1980 Portage Creek sockeye salmon exposed to Seton Lake water and test mixtures of Seton Lake water diluted with various proportions of Cayoosh Creek water.

Test Mixture	Fish Distribution: Seton Lake Water Number	% *	Center Pool Number	Test Mixture Number	% *	Total	Number of Test Pairs	Chi-Square	Level of Significance
100% Cayoosh Cr.	17	100	0	0	0	17	2	17.0	P < .005
50% Cayoosh Cr.	11	92	0	1	8	12	1	8.333	P < .005
33% Cayoosh Cr.	17	100	1	0	0	18	1	17.0	P < .005
20% Cayoosh Cr.	48	77	2	14	23	64	4	18.645	P < .005
10% Cayoosh Cr.	10	53	1	9	47	20	1	0.053	n.s.
100% Seton Lake	6	60	0	4	40	10	1	0.4	n.s.

* Percentage calculated from the total number of fish making a choice.

Table 3. Preference of 1981 Gates Creek sockeye salmon exposed singly or in groups to Seton lake water and test mixtures of Seton Lake water diluted with Cayoosh Creek water.

	Fish Distribution: Seton Lake Water Number	% *	Center Pool Number	Test Mixture Number	% *	Total	Number of Test Pairs	Chi-Square	Level of Significance
I. Fish tested singly with test mixture of 20% Cayoosh Cr.									
Fish from Seton powerhouse tailrace	15	68	1	7	32	23	11		
Fish from Seton Dam fishway	17	74	6	6	26	29	14		
Total	32	71	7	13	29	52	25	8.022	P < .005
II. Fish tested in Groups									
Test mixture 20% Cayoosh Cr.	39	68	18	18	32	75	4	7.737	P < .01
Test mixture 15% Cayoosh Cr.	54	59	12	38	41	104	5	2.783	n.s.

* Percentage calculated from the total number of fish making a choice.

Comparison of Response of Groups and Individuals

The behavior of groups as compared to the behavior of individual fish was studied to determine the appropriateness of testing the fish in groups. The reliability of the conclusions depended on whether each fish within a group could be considered a separate observation or whether the result of each test of a group of fish comprised only one data point.

To determine whether individual fish were responding independently and if each could be treated as an individual data point, single-fish trials were run using 1981 adult Gates Creek sockeye. Individual fish were presented with a test mixture of Seton Lake water diluted 20% with Cayoosh Creek water. To minimize test duration, each fish was utilized for only one trial and the test was terminated after 30 min or as soon as a choice had been made. Also, several individual fish tests were run in succession before the control and test mixtures were exchanged end-for-end. Responses of groups of 5-12 sockeye were subsequently tested under similar conditions and the responses of the single fish and groups were compared by means of heterogeneity chi-square analysis (Woolf 1968).

The results of the pooled individual responses were nearly identical to the results of the group tests (Table 3). The statistical tests indicated that there were no significant differences in response (Table 4). Consequently, all subsequent testing was done with groups of fish and the response of each fish in the group was treated as if it were an independent data point.

Table 4. Comparison of results of exposing 1981 Gates Creek sockeye salmon singly or in groups to Seton Lake water and a test mixture of Seton Lake water diluted 20% with Cayoosh Creek water.

	Fish Distribution							
	Seton Lake Water		Test Mixture			D.F.	Chi-Square	Level of Significance
	Number	%*	Number	%*				
Individual Fish	32	71	13	29		1	8.022	P < .005
Groups of Fish	39	68	18	32		1	7.737	P < .01
					Total	2	15.759	
	71	70	31	30	Pooled	1	15.686	P < .005
			Heterogeneity chi-square			1	0.073	n.s.

* Percentage calculated from the total number of fish making a choice.

Comparison Between Years

To assess the consistency of the observed preference behavior, preference trough experiments were continued during the 1982 Gates Creek sockeye migration. Jack sockeye (precocious 3-year-old males) caught in the fishway at Seton Dam were utilized since very few adult sockeye were available. Results were similar to those achieved during tests of 1981 Gates Creek sockeye (Table 5). Jack sockeye presented with a choice of Seton Lake water and Seton water diluted 20% with Cayoosh Creek water showed a significant preference for Seton Lake water (P < .05). No significant preference was shown for Seton Lake water over test mixtures with 10% Cayoosh Creek water although the majority of fish did select the Seton Lake water. Due to the low abundance of fish an intermediate test mixture of 15% was not tested.

Table 5. Preference of 1982 Gates Creek jack sockeye salmon exposed to Seton Lake water and test mixtures of Seton Lake water diluted 10 and 20% with Cayoosh Creek water.

	Fish Distribution						Number of		
Test Mixture	Seton Lake Water		Center Pool	Test Mixture		Total	Test Pairs	Chi-Square	Level of Significance
	Number	%*	Number	Number	%*				
20% Cayoosh Cr.	28	67	3	14	33	45	3	4.667	P < .05
10% Cayoosh Cr.	26	58	1	19	42	46	5	1.09	n.s.

* Percentage calculated from the total number of fish making a choice.

Possible Avoidance of Cayoosh Creek Water

The apparent preference for Seton Lake water over various dilutions of Seton Lake water with Cayoosh Creek water could have been a result of an avoidance response to Cayoosh Creek water rather than selection for the higher of the two concentrations of Seton Lake water. To examine the possibility that such avoidance was the mechanism affecting the choice between the test and control waters, two experiments were carried out.

Sockeye from the 1981 Gates Creek migration were presented with a choice of two test mixtures: Seton Lake water diluted 20% with Cayoosh Creek water and a 50:50 mixture of the two waters. It was reasoned that if the observed preference for Seton Lake water was actually due to avoidance of Cayoosh Creek water, fish would avoid both choices. That is, they would not swim "upstream" toward either water source, but would remain in the center circular pool or become randomly distributed in the three areas.

There did not appear to be avoidance since most of the fish made a choice (Table 6). The choice was significant in favor of the 20% dilution (P < .005). The proportion of these fish (30 of 36 = 83.3%) making a choice rather than remaining in the center "no choice" pool was almost the same as in the previous tests of groups of fish exposed to Seton Lake water and a test mixture of 20% Cayoosh Creek water. In those cases 76% of group-tested fish made a choice (57 of 75 = 76%, Table 3). The strong preference shown by fish for the lower dilution of Seton Lake water may have been due to the 30% difference between these two dilutions. In comparison, the difference between the proportion of Cayoosh Creek water in the single test water and the Seton control was only 20%.

Table 6. Preference of 1981 Gates Creek sockeye exposed to two dilutions of Seton Lake water.

Fish Distribution							
20% Cayoosh Water		Center Pool	50% Cayoosh Water		Total	Chi-Square	Level of Significance
Number	%*	Number	Number	%*			
27	90	6	3	10	36	19.2	P < .005

*Percentage calculated from the total number of fish making a choice.

A second experiment in 1981 tested the possibility that the Cayoosh Creek water contained a unique substance causing an avoidance response proportional to its concentration. The Cayoosh Creek water was replaced by water from Dickie Creek, a small precipitous stream flowing into the Fraser River 8 km upstream of Seton Creek. Only one set of paired trials was possible because of difficulty in transporting the water in a stainless steel drinking-water tank to the trough apparatus. Consequently, a relatively high proportion of Dickie Creek water was used as the test mixture so that if a response occurred the results would be clear. The water was delivered into the test troughs through the same polyethylene pipe that had been used to deliver the Cayoosh Creek component of the test mixtures.

As shown in Table 7, the fish had a highly significant preference for the Seton Lake water over the test mixture of Seton Lake water diluted 50% with Dickie Creek water (P < .005). This result indicated that, since the preference shown for homestream water over dilutions by Cayoosh Creek water was duplicated with a new and different dilutant, the response to Cayoosh Creek water was not unique and therefore not likely based on a learned avoidance.

Table 7. Preference of 1981 Gates Creek sockeye exposed to Seton Lake water and a 50% dilution with Dickie Creek water.

Fish Distribution							
Seton Lake Water		Center Pool	50% Dickie Creek		Total	Chi-Square	Level of Significance
Number	%*	Number	Number	%*			
13	87	1	2	13	16	8.067	P < .005

*Percentage calculated from the total number of fish making a choice.

Other investigators have observed increased activity levels in fish exposed to water from streams nearby the homestream (Idler et al. 1961, Oshima et al. 1969). It is not known whether the activity represented a positive or negative response to that water. It may be that a form of negative imprinting has evolved in salmon, which ensures that they do not accidentally enter unsuitable streams near the home stream. It is also possible that Cayoosh Creek water was not chosen because the fish recognized that Cayoosh Creek water is primarily of non-lacustrine origin. There is a small lake (Duffy Lake) at the head of Cayoosh Creek but much of the flow is contributed by precipitous tributaries below the lake. Brannon (1972) and Bodznick (1978a) observed that newly emerged sockeye fry respond innately with the appropriate migration to lake or non-lake waters depending upon whether their rearing lake is upstream or downstream of their incubation area. Bodznick proposed that the discrimination between lake and non-lake water may be based in whole or in part upon differential levels of calcium ions (Bodznick 1978b). It is possible that Gates and Portage Creek adult sockeye recognize Cayoosh Creek as non-lake water and therefore do not choose it. However, since sockeye salmon commonly spawn in streams that are not fed by lakes but flow into lakes, it is unlikely that the similar response to Dickie and Cayoosh Creek waters can be attributed to a difference between those non-lacustrine streams and lake-fed water.

No evidence was obtained that salmon actively avoided Cayoosh Creek water. Table 6 shows that when mixtures of Seton Lake and Cayoosh Creek waters were present in both ends of the preference apparatus, the fish chose the mixture with the lowest proportion of Cayoosh Creek water. Since the center pool contained 100% Seton water at the start of the test and since both of the incoming flows contained a high proportion of Cayoosh water (one 80:20 mix and one 50:50 mix), the fish would be expected to remain in the center pool if they chose to avoid Cayoosh water. Whitman et al. (1982) observed that a reduced number of fish made a choice when ash caused an avoidance response. Such avoidance behavior did not occur in the present study. In fact, a higher proportion of fish chose the water with the lowest dilution when presented with two test mixtures than when presented with only one test mixture and a Seton control.

The possibility that the observed results were based on a negative response to the Cayoosh Creek water in the test mixture cannot be completely disregarded. Perhaps when Cayoosh Creek water was present in both choices, the fish chose the "lesser of two evils." However, that possibility appears unlikely on the basis of the evidence presented.

Hara (1981) described several ways in which pollutants might interact with chemoreceptors and result in disturbance of salmon homing behavior. The possibility that Cayoosh Creek contained a unique or unusual constituent which in some way masked the attractive odor of Seton water or caused an active avoidance was further investigated by examining the response to a test mixture containing Dickie Creek water to which the Seton-Anderson sockeye should be naive. A preference for Seton Lake water over this mixture indicated that the reactions to the Cayoosh Creek water were in no way unique. It is therefore very unlikely that the observed preference for Seton Lake water resulted from a specific avoidance of Cayoosh Creek water. Certainly, Cayoosh Creek does not contain a material which causes a universal avoidance response among salmon since large numbers of pink salmon spawn in Seton Creek below the Seton-Cayoosh confluence as well as in Cayoosh Creek upstream of the confluence.

Variation in Response Over Time

Preference trough experiments were conducted throughout the 1981 Portage Creek migration to determine whether or not the sensitivity of these fish to dilution of their homestream water changed during the migration. Test mixtures presented were 5, 10, 15 and 20% dilutions of Seton Lake water with Cayoosh Creek water (Table 8).

During the first third of the run (Sept. 28-Oct. 12), the fish preferred Seton Lake water over test mixtures containing 20, 15 and 10% dilutions of Cayoosh Creek water ($P < .005$ in all cases). A lower dilution (5%) of Cayoosh Creek water resulted in no preference.

During the second third of the migration (Oct. 23-27), a test mixture of 10% Cayoosh Creek water resulted in a significant preference for Seton Lake water ($P < .025$). A test mixture of 5% Cayoosh Creek water did not result in a significant preference for Seton Lake water, although a majority of the fish chose the Seton water.

During the last third of the run (Oct. 31-Nov. 6), no preference was shown for Seton Lake water over test mixtures containing 10 or 15% Cayoosh Creek water. During that period Seton Lake water was significantly preferred over a test mixture of Seton water diluted 20% with Cayoosh Creek water ($P < .025$).

These results suggest that responses of Portage Creek sockeye salmon changed during the course of the migration. During the first two-thirds of the migration the fish discriminated between Seton Lake water and test mixtures of Seton Lake water diluted 10% or more with Cayoosh Creek water. Near the end of the migration, test mixtures containing less than 20% Cayoosh Creek water were not discriminated from Seton Lake water.

The response of the 1982 Portage Creek sockeye also changed during the course of the migration but in a manner chronologically opposite to that in 1981. During passage of the first half of the 1982 Portage Creek sockeye migration (Oct. 7-21), only a test mixture of 20% Cayoosh water resulted in a preference for Seton Lake water (Table 9). During the last half of the migration (Oct. 30-Nov. 9), test mixtures containing both 10 and 15% Cayoosh Creek water resulted in a significant preference for Seton Lake water. The 20% mixture was not tested.

Table 8. Water source preference of 1981 Portage Creek sockeye salmon exposed to Seton Lake water and test mixtures of Seton Lake water diluted 5, 10, 15 and 20% with Cayoosh Creek water.

Test Mixture	Fish Distribution: Seton Lake Water		Center Pool	Test Mixture		Total	Number of Test Pairs	Chi-Square	Level of Significance
	Number	%*	Number	Number	%*				
20% Cayoosh Cr.									
first third of migration	28	80	11	7	20	46	5	12.6	P < .005
last third of migration	46	65	7	25	35	78	4	6.211	P < .025
15% Cayoosh Cr.									
first third of migration	62	75	7	21	25	90	5	20.253	P < .005
last third of migration	14	56	1	11	44	26	1	0.36	n.s.
10% Cayoosh Cr.									
first third of migration	85	68	27	40	32	152	7	16.2	P < .005
second third of migration	45	65	9	24	35	78	4	6.391	P < .025
last third of migration	32	50	6	32	50	70	3	0	n.s.
5% Cayoosh Cr.									
first third of migration	26	42	4	36	58	66	3	1.613	n.s.
second third of migration	42	57	8	32	43	82	4	1.351	n.s.

* Percentage calculated from the total number of fish making a choice.

Table 9. Water source preference of 1982 Portage Creek sockeye salmon exposed to Seton Lake water and test mixtures of Seton Lake water diluted 10, 15 and 20% with Cayoosh Creek water.

Test Mixture	Fish Distribution: Seton Lake Water		Center Pool	Test Mixture		Total	Number of Test Pairs	Chi-Square	Level of Significance
	Number	%*	Number	Number	%*				
20% Cayoosh Cr.									
first half of migration	71	81	10	17	19	98	6	33.136	P < .005
15% Cayoosh Cr.									
first half of migration	31	55	8	25	45	64	3	0.64	n.s.
last half of migration	44	67	6	22	33	72	3	7.33	P < .01
10% Cayoosh Cr.									
first half of migration	33	57	2	25	43	60	4	1.103	n.s.
last half of migration	27	68	6	13	32	46	2	4.9	P < .05

* Percentage calculated from the total number of fish making a choice.

Response of Fish With Obstructed Nares

During the middle portion of the 1981 Portage Creek migration, several groups of sockeye salmon were tested with mixtures of 20% Cayoosh Creek water after their anterior nares had been blocked by inserting into the nares a 1 cm length of cotton swab permeated with K-Y jelly, a water-soluble lubricant. At this time, untreated fish exhibited a preference for Seton Lake water over test mixtures containing as low as 10% Cayoosh Creek water (Table 8). As shown in Table 10, fish with blocked nares did not exhibit a preference between the control and test waters.

Table 10. Exposure of 1981 Portage Creek sockeye with blocked nares to Seton Lake water and Seton Lake water diluted 20% with Cayoosh Creek water.

Fish Distribution						Number of		
Seton Lake Water		Center Pool	Test Mixture			Test	Chi-	Level of
Number	%*	Number	Number	%*	Total	Pairs	Square	Significance
29	52	28	27	48	84	4	0.071	n.s.
					3-way chi-square		0.071	n.s.

*Percentage calculated from the total number of fish making a choice.

These experiments showed that the preference for Seton Lake water was based on olfaction since anosmic fish showed no preference for water sources which elicited a strong preference in unimpaired fish. Furthermore, they did not distribute predominantly in the "upstream" troughs containing the control or test mixtures, as observed in all other sockeye experiments, but were randomly distributed amongst the three compartments. If movement into the test troughs can be considered analogous to upstream migration, it would appear that the stimuli for upstream migration were removed by obstructing the nares. Bodznick (1978a) observed a similar inability of sockeye fry with occluded nares to select lake water over stream water, as had been demonstrated by unimpaired fry. Also, as in the present situation, Bodznick noted that fewer impaired fry than unimpaired fry made a choice. Others have noted that the trauma of olfactory occlusion may affect the animal's behavior to a greater extent than simple removal of the olfactory sense (Hasler et al. 1978, Peters 1971). In many instances, occlusion was achieved by relatively traumatic methods, such as cauterizing or cutting the olfactory nerve, which might have caused inhibition of the migratory state independent of the loss of the olfactory sense. In the present studies, little or no damage was done to the fish in the process of obstructing the nares beyond the act of handling them, which was common to all fish tested.

It is recognized that the foregoing experiment lacks certain controls which would have been desirable if logistics and fish availability had permitted. There is no guarantee that the fish were rendered truly anosmic by the treatment and it is possible that they were responding (or not responding) due to physical or chemical irritation of the olfactory apparatus. However, that eventuality would not change the conclusion regarding the importance of the olfactory sense for detecting homestream water. It is therefore concluded that the ability of the non-occluded fish to choose the control over the test mixtures was based on the olfactory sense.

Pink Salmon

Seton Creek pink salmon were tested with Seton Lake water and mixtures of 20, 50 and 100% Cayoosh Creek water (Table 11). In none of these experiments was a significant preference shown. The most noteworthy aspect of these tests was that in only one of the four groups of tests was the distribution of fish in the three chambers significantly different from

Table 11. Water source preference of 1981 Seton Creek pink salmon exposed to Seton Lake water and test mixtures of Seton water diluted 20, 50 and 100% with Cayoosh Creek water.

Test Mixture	Fish Distribution: Seton Lake Water Number	% *	Center Pool Number	Test Mixture Number	% *	Total	Number of Test Pairs	Chi-Square	Level of Significance
20% Cayoosh Cr.	14	38	23	23	62	60	3	2.189	n.s.
						3-way chi-square		2.7	n.s.
50% Cayoosh Cr.	21	44	22	27	56	70	4	0.75	n.s.
						3-way chi-square		0.886	n.s.
100% Cayoosh Cr.									
— fish from tailrace	15	41	25	22	59	62	3	1.324	n.s.
						3-way chi-square		2.548	n.s.
— fish from fishway	12	39	39	19	61	70	3	1.581	n.s.
						3-way chi-square		16.829	P < .005

*Percentage calculated from the total number of fish making a choice.

random, and that was because the greater proportion of the fish remained in the center pool (three-way chi-square = 16.829, P < .005). The random distribution in the three compartments by all groups of pink salmon obtained from the powerhouse tailrace suggested that the fish were no longer in an active migratory state. Possibly pink salmon failed to respond similarly to sockeye because of a greater sensitivity to handling stress but this possibility is considered unlikely since pink salmon appear to withstand handling and tagging for enumeration purposes equally as well as sockeye (IPSFC records).

The group of pink salmon obtained from the Seton Dam fishway apparently exhibited a further reduction in their migratory tendency since their distribution in the three test compartments was non-random in favor of the center pool. This indicated that the fish were either: 1) not sufficiently exploratory to distribute themselves randomly throughout all three compartments, or 2) avoiding the inflowing water mixtures. The latter is unlikely since those fish were incubated in one or both of those waters and presumably had homed to them.

The behavioral responses of this latter group of pink salmon were similar to those of sockeye with obstructed nares, although the responses may have occurred for different reasons. The impaired sockeye responses were likely reduced or eliminated because of their inability to detect the odor of their homestream water. In the case of the pink salmon, the fish may have detected the homestream water but made no selection because they had already reached the spawning grounds. Both waters tested, from Seton and Cayoosh creeks, are waters experienced by the pink salmon during incubation or migration. It is probable (Horrall 1981) that imprinting in pink salmon occurs immediately before and/or after emergence. Therefore, pink salmon could be imprinted to both Seton and Cayoosh Creek waters and, having achieved their spawning site, would have a low level of "migratory motivation." The fish obtained from the fishway, having been exposed to both a Seton-Cayoosh mix as well as 100% Seton water, would be expected to be even less responsive. It has been observed that Seton Creek pink salmon that migrate past Seton Dam frequently school at the power canal intake screens, apparently attempting to move back downstream (Fretwell 1982). This behavior may be indicative of a low level of migrational motivation.

Directional Preference

All of the data were analyzed for possible preference in compass direction. The alignment of the preference trough apparatus in 1980 with Portage Creek sockeye was approximately east-west. A significant preference was shown for the west end of the apparatus (Table 12). In both 1981 and 1982, the apparatus was on a north-south axis. Tests

Table 12. Analysis for possible directional preference of sockeye and pink salmon in preference apparatus.

Test population	Fish Distribution				Chi-Square	D.F.	Level of Significance
	Number	%	Number	%			
I. East vs. West Trough	East		West				
1980 Portage Cr. Sockeye Salmon	48	40	72	60	4.8	1	P < .05
II. North vs. South Trough	North		South				
1. Gates Creek Salmon							
1981 Gates Cr. Sockeye Salmon							
(i) Control vs. Control	20	49	21	51	0.02	1	n.s.
(ii) All Tests	137	52	125	48	0.55	1	n.s.
1982 Gates Cr. Sockeye Salmon	48	55	39	45	0.93	1	n.s.
Total Gates Cr. Sockeye Salmon	185	53	164	47	1.26	1	n.s.
2. Portage Creek Sockeye Salmon							
1981 Portage Cr. Sockeye Salmon							
(i) Obstructed Nares	36	64	20	36	4.57	1	P < .05
(ii) All Tests	366	55	298	45	6.96	1	P < .01
1982 Portage Cr. Sockeye Salmon	178	58	130	42	7.48	1	P < .01
Total Portage Cr. Sockeye Salmon	544	56	428	44	13.84	1	P < .005
3. All four 1981 and 1982 Sockeye Salmon Migrations:				Total	15.92	4	P < .005
				Pooled	14.21	1	P < .005
				Heterogeneity	1.71	3	n.s.
4. 1981 Pink Salmon	84	58	62	42	3.32	1	n.s.

of 1981 Gates Creek sockeye salmon with control water at both ends resulted in no directional response. In the 1981 and 1982 Gates Creek sockeye salmon tests, there was a small but non-significant preference for the north end. In contrast, Portage Creek sockeye salmon showed a strong preference for the north end (P < .005). As a group, the sockeye showed a significant preference for the northerly direction. Analysis of the results from the four runs indicate homogeneity of these data according to heterogeneity chi-square analysis (heterogeneity chi-square = 1.71, n.s.). Pink salmon were also numerically oriented toward the north although the preference was not significant (chi-square = 3.32, n.s.).

It was assumed in the design of the preference experiments, in which water sources were alternated in paired tests, that the results would be independent of any innate directional preference exhibited by the fish. Analysis of the data indicated that such directional preferences did exist. The preference shown by Portage Creek sockeye salmon in 1980 for the west end of the test apparatus and the overall preference shown for the north end in 1981 and 1982 are consistent both with the migration direction the fish had followed for approximately 160 km from Hope to Lillooet in the Fraser River and with the direction the fish would be required to migrate during passage through Seton Lake. The data do not enable a conclusion to be drawn as to whether the directional preference was that learned during the immediately preceding migration up the Fraser River or the opposite of that imprinted on the juveniles in their migration out of Seton Lake. It is difficult to imagine the usefulness of a compass orientation in a river setting where the overwhelming directional cue must be the current, except at river confluences, where odor appears to be the main cue for water selection. However, Groot (1965) and Quinn (1981) have reported that juvenile salmon possess an innate compass orientation which enables them to locate the outlet of their rearing lake in the absence of significant current cues. It would be equally important for adult salmon, with limited time to reach their natal stream, to possess compass orientation abilities to aid them during the return migration through a lake system. It is therefore logical to speculate that the northerly preference of Portage Creek sockeye salmon is the result of a compass orientation ability that enables them to locate the north-westerly end of Seton Lake where Portage Creek enters. The lack of a significant preference for northerly orientation by Gates Creek fish may be related to the fact that these fish must migrate south-westerly after passing through Portage Creek.

This discussion of directional preferences is speculative. It is possible that the directional preferences of the fish may have resulted from their perception of nearby topographical features, vegetation, or variations in light intensity. The westerly preference of the fish in 1980 was away from the large canal aqueduct, which was 10-15 m above the east end of the test apparatus. However, since this structure was in shadow, one would expect the test fish to be attracted to that direction since captive fish often seek areas of darkness or shadow. The nylon mesh covering the test apparatus would be expected to substantially reduce the ability of the fish to perceive clearly any nearby objects such as trees or the power canal aqueduct and it is likely that only general indications of light and shadow would have been detectable. Since tests were conducted throughout the day from about 0800-1600 PST on both clear and overcast days, a wide variety of light conditions existed. There was no evident trend in response of fish to any of these conditions. It is also possible that the directional preferences were influenced by celestial cues or sound vibrations from nearby Cayoosh Creek.

These directional preferences do not alter the conclusions reached on the basis of the water preference experiments. Since water sources in the olfactory tests were alternated, any directional preference would have strengthened the olfactory preference in one direction and weakened it in the other direction, thereby cancelling the effect.

Temperature Preference

The temperatures of Seton Lake and Cayoosh Creek waters generally differed, with Seton Lake water frequently being the warmest. Although the test mixtures generally contained only 5-20% Cayoosh Creek water, the resultant mixture was often 0.1-1.2°C cooler than the control (Seton Lake) water. Occasionally the reverse effect occurred when there was slight solar warming of the Cayoosh Creek water in the supply pipe.

The effect of temperature was examined in several ways. During one pair of tests, 1981 Gates Creek sockeye were tested with control (Seton Lake) water in both ends but with the temperature of one source reduced by 0.6-1.1°C. The cooling was accomplished through a heat exchange process by passing one source of Seton Lake water through several hundred meters of the supply pipe immersed in Cayoosh Creek. Although relatively few fish were tested in this way, there was no preference shown for either temperature (Table 13). Since the temperature difference between these waters was as great or greater than the difference

Table 13. Exposure of 1981 Gates Creek sockeye to two temperatures of Seton Lake water.

Test Mixture	Fish Distribution				Chi-Square	Level of Significance
	16.6°C		17.2-17.7°C			
	Number	%	Number	%		
Seton Lake vs. Seton Lake	9	50	9	50	0	n.s.

existing during the other tests, temperature is not likely to have been a critical factor in the preference for Seton Lake water over Seton-Cayoosh mixtures.

The possible bias caused by temperature preference was further examined by subdividing test groups according to the relative temperatures of the test and control waters. Test results that showed a preference for the control water (Seton Lake) were examined separately to determine if the preference existed regardless of relative temperature. In a similar manner, results that did not show a preference were analyzed separately to determine if the lack of preference was consistent for all relative temperatures. For those water source mixtures which resulted in a significant preference for the Seton Lake water, the preference was evident regardless of the relative temperature of the test and control waters (Table 14). The one exception occurred during the 1982 Gates Creek sockeye migration when the colder Seton Lake water was chosen by a majority of fish but the result was not significant to the .05 level.

Table 14. Analysis for temperature preference among groups of sockeye salmon which showed a preference for control (Seton Lake) water over various test mixtures.

Relative Temperatures	Fish Distribution: Seton Lake Water Number	%	Test Mixture Number	%	Chi-Square	D.F.	Level of Significance
1. 1981 Gates Creek Sockeye Salmon							
Seton water 0.1 °C colder	8	100	0	0	8.0	1	P < .005
Same temperature	25	81	6	19	11.65	1	P < .005
Seton water 0.3-1.1 °C warmer	46	73	17	27	13.35	1	P < .005
2. 1981 Portage Creek Sockeye Salmon							
Seton water 0.1-0.3 °C colder	26	81	6	19	12.5	1	P < .005
Seton water 0.1-1.2 °C warmer	240	68	111	32	47.41	1	P < .005
3. 1982 Gates Creek Sockeye Salmon							
Seton water 0.1-0.3 °C colder	23	62	14	38	2.19	1	n.s.
Seton water 0.2 °C warmer	5	100	0	0	5.0	1	P < .05
4. 1982 Portage Creek Sockeye Salmon							
Seton water 0.1-1.2 °C warmer	142	73	52	27	41.75	1	P < .005
5. All four 1981 and 1982 Sockeye Salmon Migrations							
				Total	141.85	8	P < .005
				Pooled	132.43	1	P < .005
				Heterogeneity	9.42	7	n.s.
TOTALS							
Seton water 0.1-0.3 °C colder	57	74	20	26	17.78		P < .005
Same temperature	25	81	6	19	11.65		P < .005
Seton water 0.1-1.2 °C warmer	433	71	180	29	104.42		P < .005

For water mixture treatments which individually did not result in a statistically significant choice between the test mixture and control, there was generally a numerical preference for the control (Seton Lake) water over the various mixtures. When all of these data were pooled, a significant preference was shown for the control (Table 15, $P < .05$). Grouped according to relative temperatures, only for the "Seton colder" category was there a significant preference ($P < .05$). The fish preferred Seton water when there was no measurable temperature difference. However, when the Seton water was warmer, a slight but non-significant preference was shown for the colder test water. Superficially, this suggests that there may have been a tendency for fish to choose the cooler water, although this tendency was small and occurred only when the difference between water mixtures was slight. Heterogeneity chi-square analyses indicated homogeneity among the temperature treatments in both Tables 14 and 15. It was concluded that the relatively small differences between the temperature of the test and control waters did not significantly bias the results.

Table 15. Analysis for temperature preference among groups of sockeye salmon which showed no preference between control (Seton Lake) water and various test mixtures.

Relative Temperatures	Fish Distribution: Seton Lake Water Number	%	Test Mixture Number	%	Chi-Square	D.F.	Level of Significance
1. 1981 Gates Creek Sockeye Salmon							
Seton water 0.3-1.1°C colder	31	55	25	45	0.64	1	n.s.
Same temperature	16	84	3	16	8.89	1	P < .005
Seton water 0.6°C warmer	7	41	10	59	0.53	1	n.s.
2. 1981 Portage Creek Sockeye Salmon							
Seton water 0.1-0.4°C colder	61	56	48	44	1.55	1	n.s.
Same temperature	14	47	16	53	0.13	1	n.s.
Seton water 0.1-0.7°C warmer	36	48	39	52	0.12	1	n.s.
3. 1982 Gates Creek Sockeye Salmon							
Seton water 0.1-0.7°C colder	14	61	9	39	1.09	1	n.s.
Same temperature	12	55	10	45	0.18	1	n.s.
4. 1982 Portage Creek Sockeye Salmon							
Seton water 0.1-0.5°C colder	19	63	11	37	2.13	1	n.s.
Same temperature	10	67	5	33	1.67	1	n.s.
Seton water 0.1-0.7°C warmer	35	51	34	49	0.01	1	n.s.
5. All four 1981 and 1982 Sockeye Salmon Migrations							
Total					16.94	11	n.s.
Pooled	255	55	210	45	4.35	1	P < .05
Heterogeneity					12.59	10	n.s.
TOTALS							
Seton water 0.1-1.1°C colder	125	57	93	43	4.70		P < .05
Same temperature	52	60	34	40	3.77		n.s.
Seton water 0.1-0.7°C warmer	78	48	83	52	0.16		n.s.

Magnitude of Discharge

During natural migration, salmon probably respond, at least to some degree, to the volume of the river or stream in addition to the odor qualities of the water. In a multi-channel stream, fish prefer the larger channels with their greater range of depths and velocities. In the preference apparatus, discharges from the two troughs were equal and since only the source of the waters differed, the choices made in those experiments were independent of the magnitude of the discharge.

Water Chemistry

The results of analysis of water samples are presented in Figures 6-8. Oxygen levels were not measured as part of the water chemistry analysis since all waters to which fish were exposed were from free-flowing sources and would therefore be expected to be at or near saturation.

The possibility was considered that the ability of the fish to discriminate between the various mixtures of Seton and Cayoosh Creek waters might have been based on various measurable water chemistry parameters and that any change in response over time and between runs might have resulted from changes in those parameters. However, of the water chemistry characteristics examined (including hardness, calcium, fluoride, sulphate, conductance and alkalinity), none correlated with the changing responses of the fish. Concentrations of chemical parameters in Seton Lake and Cayoosh Creek waters were usually not measurably different and, in the case of certain parameters, reversed over time. Consequently, none of the parameters measured, at least singly, explained the changing response of the fish during the experiments.

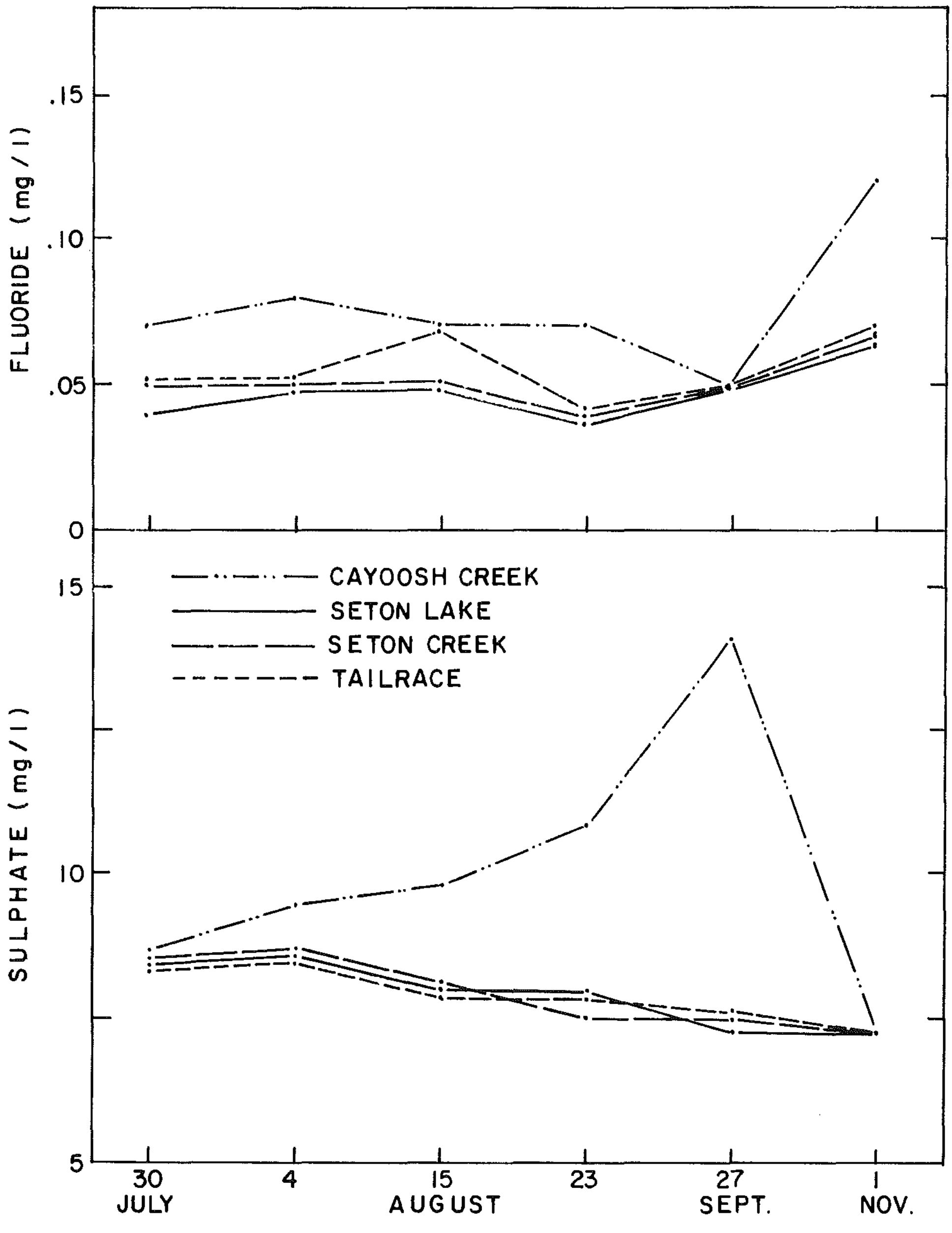

FIGURE 6—Sulphate and fluoride in water sampled in Cayoosh Creek, Seton Lake, Seton Creek and the tailrace in 1981.

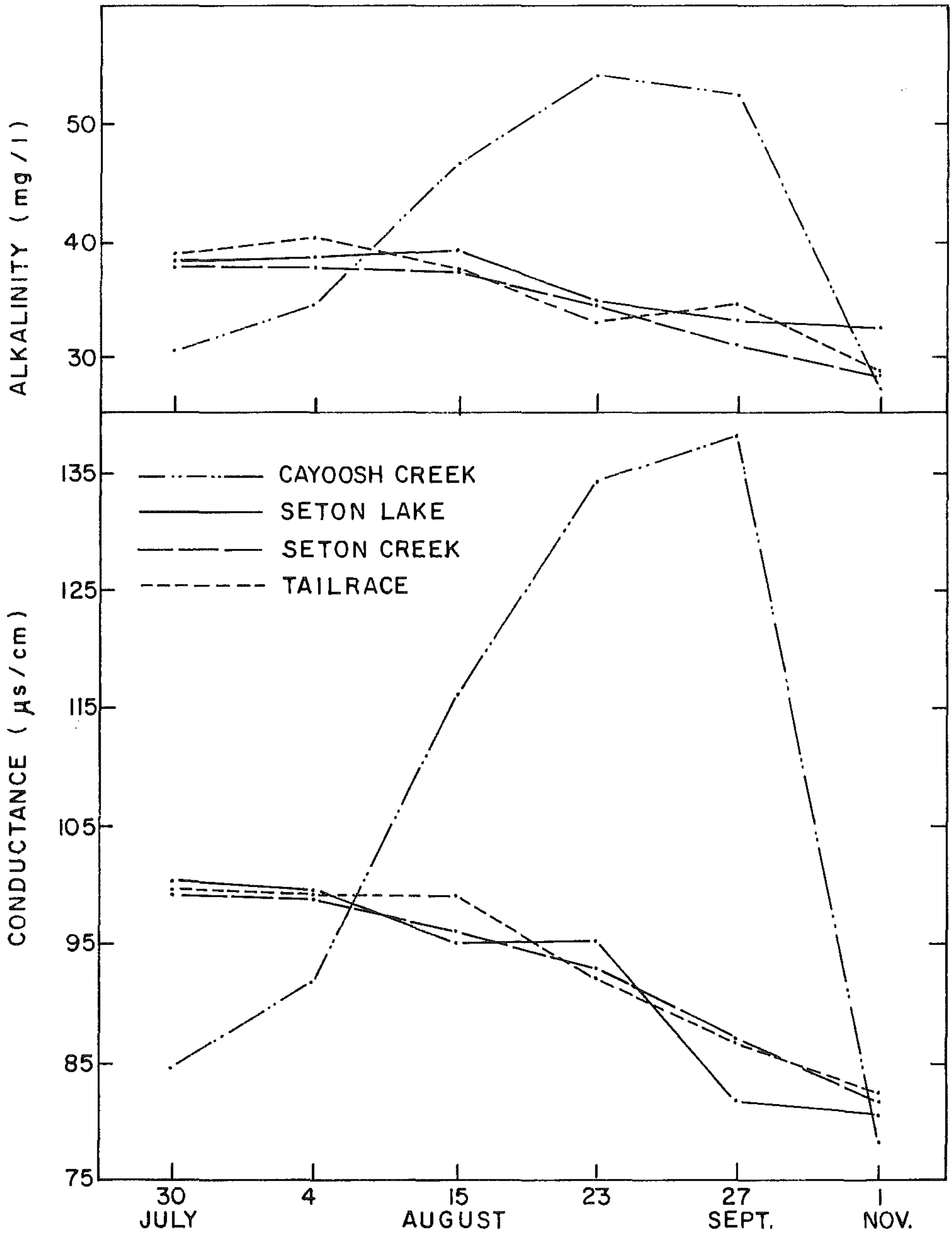

FIGURE 7—Conductance and alkalinity of water sampled in Cayoosh Creek, Seton Lake, Seton Creek and the tailrace in 1981.

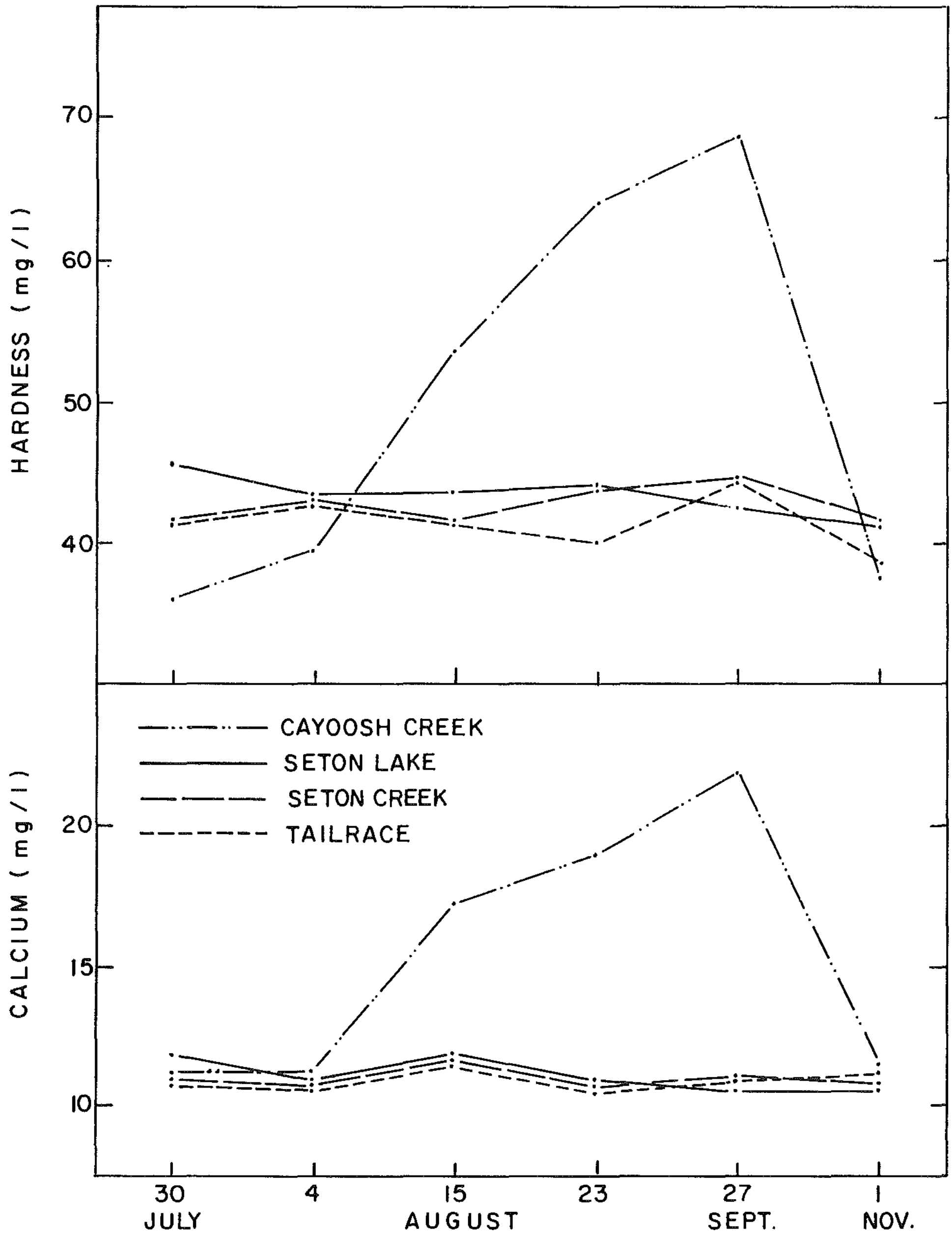

FIGURE 8—Calcium and hardness of water sampled in Cayoosh Creek, Seton Lake, Seton Creek and the tailrace in 1981.

RADIO-TELEMETRY STUDIES

APPARATUS AND METHODS

To study the behavior of salmon in the natural setting in response to various mixtures of Seton Lake water diluted by Cayoosh Creek water, miniature radio transmitters were implanted in adult migrants and these fish were released in the tailrace or in Seton Creek. Various mixtures of Seton and Cayoosh Creek waters were produced below the Seton-Cayoosh confluence by controlling the spill discharge at Seton Dam and the discharge of Cayoosh Creek, part of which was diverted through the tunnel into Seton Lake.

Radio-telemetry equipment utilized during these studies was supplied by AVM Instrument Co., Champaign, Illinois, U.S.A. The radio tags consisted of an SM-1 transmitter, tuned loop antenna and single Hg-675 battery potted in dental acrylic (Fig. 9). This unit weighed approximately 4.5 gm in air prior to application of several coats of beeswax for waterproofing. Transmitters operated on individually distinguishable frequencies within the 49.3-49.6 MHz range. Tracking was accomplished with LA-12 receivers operated either from a truck equipped with an omni-directional whip antenna or on foot using a portable M-Yagi directional antenna.

Fish for the radio-telemetry studies were captured in the tailrace of Seton powerhouse, handled and transported as previously described for the preference experiments. The radio transmitter was inserted through the mouth into the stomach (Fig. 10) and each fish was then tagged with colored Petersen discs to facilitate visual identification of the fish and recovery of the transmitter module on the spawning grounds.

Radio-tagged fish were released at each of three locations: in the tailrace of Seton powerhouse, in Seton Creek near its mouth and in Seton Creek upstream of the Cayoosh Creek confluence. During initial studies in 1978-79, tracking was done on a 24-hr basis. Limited activity of fish from approximately 2400-0600 hr allowed a reduction in effort during that period. Subsequently, fish were located at intervals not greater than 4 hrs from 0700-2400 hr and much more frequently when any of the tagged fish were actively migrating.

Radio-tagged fish, delayed in the tailrace of Seton powerhouse, were considered to have made a "foray" when they moved upstream in the Fraser River from the tailrace. Upstream movement of about 100 m on the west bank of the Fraser River was required for the fish to encounter the plume of Seton Creek, which was visible to the observers. This was the only possible migration route to the spawning grounds. A foray was considered successful if the fish continued to migrate up Seton Creek to Seton Dam and a failure if the fish returned to the tailrace. The mixture of Seton Lake water and Cayoosh Creek water present in Seton Creek during each foray was calculated from measurements of the discharges of Seton and Cayoosh Creeks above their confluence, as recorded at Water Survey of Canada gauges.

RESULTS OF THE RADIO-TELEMETRY STUDIES

Fish Released in the Powerhouse Tailrace

During the 1979, 1980 and 1981 Gates Creek sockeye salmon runs, the movements of 48 radio-tagged sockeye were monitored as they migrated out of the tailrace. These included 39 fish released in the tailrace and nine fish that had moved downstream to the tailrace after being released in Seton Creek just above its mouth. These 48 fish were observed making 158 forays upstream from the tailrace into Seton Creek or its plume (Table 16). The success of each of those forays (defined as continued migration upstream to Seton Dam) was examined

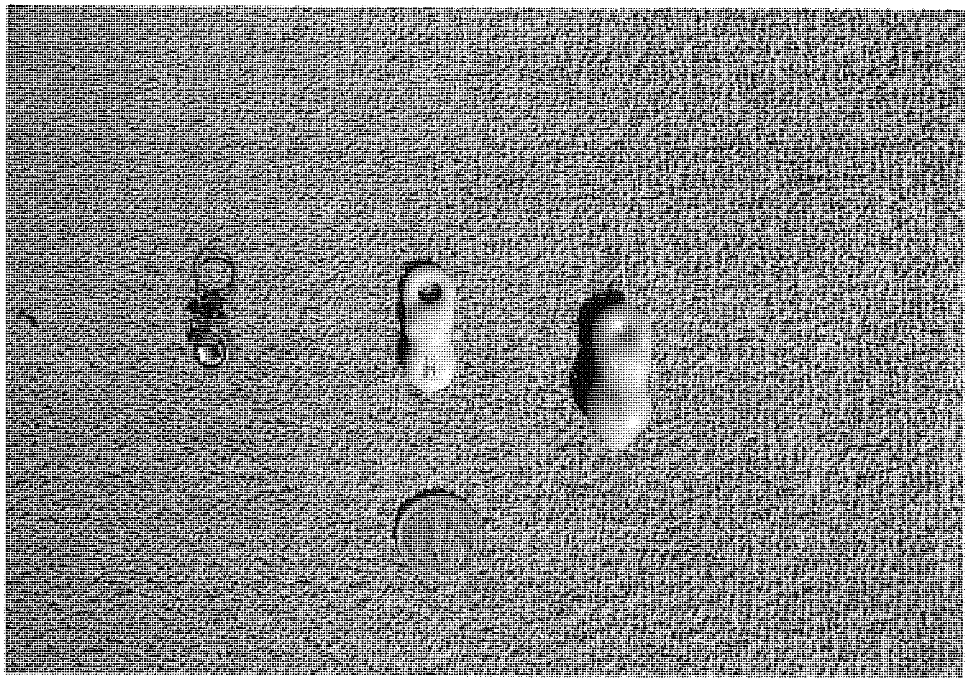

FIGURE 9—Miniature radio transmitters used in migration studies.

FIGURE 10—Insertion of radio transmitter into fish's gut.

Table 16. Response of radio-tagged Gates Creek sockeye salmon during forays upstream from the tailrace of Seton powerhouse in relation to various mixtures of Seton Lake water diluted by Cayoosh Creek water in lower Seton Creek.

Year	Percent Cayoosh Creek Water in Seton Creek	Number of Forays	Number Successful	Percent Successful	Frequency of Forays (forays/day)	Number of Fish
1979	20-30	25	8	32.0	1.8	23
	30-35	45	7	16.0		
	≥ 50	61	2	3.3		
1980	15-17	17	15	88.2	2.8	15
1981	5-6	6	6	100.0	1.4	10
	14	4	4	100.0		
Summary	< 20	27	25	92.6		
	> 20	131	17	13.0		
			z =	8.53	P < .001	

in relation to the mixture of Seton Lake and Cayoosh Creek water in lower Seton Creek. Fish that moved upstream from the tailrace but failed to continue upstream to the Seton-Cayoosh confluence always returned to the tailrace. When lower Seton Creek contained less than 20% Cayoosh Creek water, 92.6% of the forays were successful whereas only 13% were successful when the proportion of Cayoosh Creek water exceeded 20%. A "z" statistic, calculated to measure the significance of the difference between proportions, indicated that there was a significant difference between the success of forays which occurred when Seton Creek contained less than, as compared to more than, 20% Cayoosh Creek water ($z = 8.53$, $P < .01$) (Dixon and Massey 1969).

The movements out of the tailrace of 139 radio-tagged sockeye were studied during the 1978-82 Portage Creek migrations (Table 17). These fish were observed making 307 forays upstream to Seton Creek or its plume. The success of the forays was greater when the Cayoosh Creek component was less than about 10% (50.2%) than when it exceeded 10% (28.3%). This difference was significant ($z = 3.69$, $P < .01$).

The frequency of forays from the tailrace was recorded and is presented as forays/day (Tables 16 and 17). Forays were made more frequently by Gates Creek fish than by Portage Creek fish.

Table 17. Response of radio-tagged Portage Creek sockeye salmon during forays upstream from the tailrace of Seton powerhouse in relation to various mixtures of Seton Lake water diluted by Cayoosh Creek water in lower Seton Creek.

Year	Percent Cayoosh Creek Water in Lower Seton Creek	Number of Forays	Number Successful (Reached Seton Dam)	Percent Successful	Frequency of Forays (forays/day)	Number of Fish
1978	10-20	6	4	66.7	0.6	14
	20-30	9	5	55.6		
	30-40	3	0	0		
	40-50	1	0	0		
	50-60	23	1	4.3		
1979	8-11	44	27	61.4	1.4	27
1980	< 10	44	19	43.2	0.7	27
	10-20	9	6	66.7		
	> 20	8	2	25.0		
1981	< 10	59	25	42.4	0.7	41
	10-20	35	11	31.4		
	> 20	7	1	14.3		
1982	< 11	54	30	55.6	0.5	30
	16-25	5	0	0		
Summary	< 10*	201	101	50.2		
	> 10	106	30	28.3		
			z =	3.69	P < 0.01	

*Includes two data groupings which overlap to 11%.

Fish Released in Lower Seton Creek

The response of radio-tagged fish to various mixtures of Seton Lake and Cayoosh Creek waters in lower Seton Creek was further examined by releasing fish in Seton Creek downstream of the Cayoosh Creek confluence or in the Seton plume in the Fraser River. Again, success (defined as reaching Seton Dam) was related to the proportion of Cayoosh Creek water in Seton Creek (Table 18). All forays of Gates Creek sockeye were successful when the Cayoosh Creek component was less than 20% and none was successful when the Cayoosh Creek component exceeded 20%. Because the number of fish released was small (10 for each condition) and the results deviated substantially from 50% success, it was not appropriate to calculate a "z" value to determine the significance of the difference between

Table 18. Response of radio-tagged sockeye salmon released in lower Seton Creek (or its plume) at various mixtures of Seton Lake water diluted by Cayoosh Creek.

	Percent Cayoosh Creek Water in lower Seton Creek	Number Released	Migrated Upstream to Seton Dam	
			Number	%
I. Gates Creek Sockeye Salmon				
1979	27	5	0	0
	52	5	0	0
1981	14-15	10	10	100
Summary	< 20	10	10	100
	> 20	10	0	0
II. Portage Creek Sockeye Salmon				
1978	10-20	1	1	100
	20-30	6	3	50
	30-40	2	1	50
	> 40	8	3	38
1979	8-11	18	18	100
1980	23	9	5	55
	9	5	5	100
1981	< 10	20	14	70
	10-20	10	9	90
Summary	< 10*	43	37	86
	10-20	11	10	91
	< 20	54	47	87
	> 20	25	12	48
	z = 3.71		P < .01	

*Includes 1 data grouping which overlaps to 11%.

the results. However, 99% confidence limits were calculated for those proportions (Woolf 1968). The confidence limits did not overlap: (for proportions less than 20%, 10/10 confidence limits = 6.9-10.0; for proportions over 20%, 0/10 confidence limits = 0-3.1) and the results can therefore be considered significantly different.

Portage Creek sockeye salmon released in Seton Creek were successful 86% (37/43) of the time when the Cayoosh Creek component was less than 10% in lower Seton Creek and the success rate was 91% (10/11) when the Cayoosh component was 10-20%. These proportions were not significantly different (z = 0.44) and therefore all observations made under those two conditions were combined for a success rate of 87% (47/54). The success rate was only 48% (12/25) when the Cayoosh Creek component exceeded 20% (Table 18). Those proportions were significantly different (z = 3.71, P < .01). The success rate declined from an average of 87% with less than 20% Cayoosh dilution to 53% with 20-40% Cayoosh and to 38% when the Cayoosh component exceeded 40%.

Fish Released in Seton Creek Above the Cayoosh Confluence

On some occasions, lower proportions of Cayoosh Creek water in Seton Creek were achieved partly through a diversion of most of Cayoosh Creek water into Seton Lake and partly through unusually high spill discharge into Seton Creek at Seton Dam. The possibility that higher success rates were attained when the Cayoosh Creek component was low because of increased total discharge of Seton Creek was tested by releasing nine fish in Seton Creek above the Cayoosh Creek confluence. Those releases occurred at relatively low discharges and most (6/9) were at the minimum discharge permissible during the period of adult sockeye migrations (11.3 m^3/s). All fish succeeded in reaching the dam, indicating that high discharge was not a requirement for successful migration.

Pink Salmon

Four pink salmon captured in the tailrace were radio-tagged. These fish all migrated from the tailrace to Seton Creek within 8 hr during periods when the Cayoosh concentration below the Seton-Cayoosh junction was 10%. Each fish made only one foray from the tailrace and none returned to the tailrace. Although not enough pink salmon were tested to permit detailed comparisons with the behavior of sockeye salmon, it appeared that pink salmon were less prone to delay in the tailrace and less inclined to reject the water mixture in Seton Creek.

DISCUSSION

RELATIVE SENSITIVITY TO TEST WATERS IN PREFERENCE APPARATUS

The sensitivity of the Gates Creek and Portage Creek sockeye salmon to dilutions of their homestream water differed and the sensitivity of the Portage Creek fish varied during the migration. The Gates Creek sockeye, during tests in 1981 and 1982, consistently preferred Seton Lake water over 20% dilutions by Cayoosh Creek water (Tables 3 and 5). Lesser dilutions (10 or 15%) resulted in numerical but statistically nonsignificant preferences for the Seton Lake water. In comparison, Portage Creek sockeye preferred Seton Lake water over test mixtures diluted from 10 to 20% by Cayoosh Creek water. During the 1981 experiments Portage Creek fish were able to discriminate Seton Lake water from test mixtures diluted by as little as 10% Cayoosh Creek water, at least during the first two thirds of the migration. During the last third of the migration, test mixtures diluted 10 and 15% by Cayoosh Creek water did not elicit a preference; only the test mixture containing 20% Cayoosh Creek water resulted in a preference for the Seton Lake water (Table 8). In 1982, Portage Creek sockeye salmon exhibited the opposite trend over time in sensitivity to test mixtures (Table 9).

The difference between responses of Portage and Gates Creek sockeye to various dilutions of Seton Lake water may be related to the relative proximity of their spawning streams to Seton Creek. The results suggest that the fish may respond to constituents from their particular natal streams in Seton Lake water. Gates Creek water comprises a lesser proportion of Seton Lake outflow than does Portage Creek since there is inflow to Anderson Lake between Gates Creek and Portage Creek. Therefore, Gates Creek sockeye may not be as strongly attracted to the Seton Lake water in the tailrace or to the control water in the preference tests and therefore would not be as persistent in choosing it over mixtures of Seton and Cayoosh Creek water.

The greater sensitivity of the Portage Creek sockeye salmon may also be a reflection of different "biological affordability" of migration delay between the two races. Gates Creek sockeye salmon arrive at Seton Creek while still silver in color, ripen to sexual maturity in Anderson Lake and spawn soon after reaching the spawning grounds. Portage Creek sockeye salmon, in contrast, arrive at Seton Creek in spawning colors, mature slowly in the cold waters (generally less than 15°C) and migrate slowly to the spawning grounds (Fretwell and Hamilton 1983). The lower water temperatures and consequent slower maturation and reduced migration speed may demand that Portage Creek sockeye be more sensitive to their homestream odor in order to avoid unnecessary diversions and energy expenditure on their migration route.

The within-year variation in sensitivity of Portage Creek sockeye salmon to dilution of Seton Lake water may be related to the changing hormonal and maturational state of the fish. Cooper and Hasler (1973) and Scholz et al. (1973) concluded that the peak response to homestream odor occurs at the period of peak spawning and that this phenomenon may be hormone-mediated. Scholz et al. observed that during the peak of spawning coho salmon exhibited peak EEG responses to those chemicals to which they had been artificially imprinted as juveniles and tracked fish showed greater orientation to homestream water. The change in strength of response to homestream odors noted by these investigators may be analogous to the variation in sensitivity over time of Portage Creek sockeye salmon to various dilutions of Seton Lake water. Seton Lake water is "homestream water" since it is the water that the smolts are exposed to during their smolt imprinting period. However, these sockeye must also possess a "memory" of an earlier homestream water, Portage Creek, to accomplish the return migration to that specific location. It is a moot point whether the peak period of sensitivity of Portage Creek sockeye to Seton Lake water would correspond to the peak spawning period or to the time during the migration when Seton Creek would be encountered. Thus, the selection by Portage Creek sockeye of pure Seton Lake water instead of Seton Lake water diluted by only 10% Cayoosh Creek water may correspond to the period of the migration schedule when most of these fish would be entering Seton Creek and would be most sensitive to odor-cues from Seton Lake water. Before and after this optimum time the fish might be less responsive to Seton Lake water and it may have been during such periods that the fish showed no rejection of a 10% Cayoosh Creek test mixture (Tables 8 and 9). Such a temporal change in sensitivity, in combination with the fortuitous timing of the tests, may have caused the differing trend in sensitivity between years. It is also possible that the differences in sensitivity between the Gates and Portage Creek runs may reflect differences in their hormonal states at the time they enter Seton Creek.

RESPONSE OF RADIO-TAGGED FISH

The radio-tagging studies supported the results obtained in the preference apparatus with sockeye salmon. Gates Creek sockeye salmon tested in the preference apparatus did not discriminate between Seton Lake water and test mixtures diluted by less than 20% Cayoosh Creek water. Radio-tagged Gates Creek sockeye released in the tailrace of Seton powerhouse responded in a similar way to mixtures of Seton Lake and Cayoosh Creek water in lower Seton Creek: 92.6% of forays into Seton Creek or its plume were successful (reached the dam) when Cayoosh Creek water comprised less than 20% of the discharge of lower Seton Creek (Table 16). In contrast, when Cayoosh Creek water comprised more than 20% of the lower Seton Creek discharge, only 13.0% of forays from the tailrace were successful.

The response of radio-tagged Portage Creek sockeye was similar to that of Gates Creek fish although the success of forays by Portage Creek fish was generally lower (Table 17). It is believed that the reduced frequency and success of forays of Portage Creek fish may be related to their reduced level of activity and slower rate of maturation, associated with lower water temperatures and a resulting general tendency to migrate slower. Radio-tagged Portage Creek sockeye salmon reached the dam 50.2% of the time when the Cayoosh Creek component was less than 10% of lower Seton Creek but with higher proportions of the Cayoosh Creek component the success of forays dropped significantly to 28.3%. Success was particularly low when the Cayoosh Creek component exceeded 30%.

The release of radio-tagged sockeye salmon in lower Seton Creek or its plume produced similar results (Table 18). Gates Creek fish migrated upstream 100% of the time when Seton Creek was diluted less than 20% by Cayoosh Creek but when the dilution exceeded 20%

none of the fish was successful. Again, the results for Portage Creek sockeye were less clear but followed a similar trend. In this case there was no discernible difference between the response of fish released when Cayoosh Creek comprised less than 10% of Seton Creek (86% successful) and when it comprised 10-20% (91% successful). Consequently, those results were combined (87% successful). In comparison, only 48% of the fish migrated successfully when the Cayoosh Creek component exceeded 20% of the Seton Creek discharge. The threshold between high and low success rates in this test appeared to be about 20% Cayoosh Creek dilution, in contrast to a threshold of 10% for forays from the powerhouse tailrace. This change of threshold may be a result of a change in responsiveness of the fish during the course of the migration, as observed in preference tests with Portage Creek sockeye salmon.

In general, radio-tagged fish released in Seton Creek or its plume had higher success rates in reaching Seton Dam than did radio-tagged fish released in the tailrace. This may be because the fish released into the creek did not possess odor cues or a spatial awareness of the alternative water source in the tailrace. In contrast, fish making a volitional foray might retain a "short-term memory" of the 100% Seton Lake water in the tailrace, if such a faculty, as proposed by Cooper and Hasler (1973), exists. If the fish could not discriminate between the homestream odor concentration at the two locations they might return to the tailrace, especially if physical conditions there were "preferred".

The consistent upstream migration of radio-tagged sockeye salmon released in upper Seton Creek (upstream of the Cayoosh Creek confluence) showed that the minimum discharge of $11.3 m^3/s$ was sufficient to provide successful migration conditions when there was no influence of Cayoosh Creek water. This does not preclude the possibility that the behavior of fish in Seton Creek may be affected by the magnitude of the discharge. Depths and velocities in Seton Creek are dependent upon discharge and it must be expected that the relative attractiveness of Seton Creek and the powerhouse tailrace to adult migrants is a function not only of the concentrations of homestream odor but of flow volumes as well. The discharge of approximately $100 m^3/s$ from the powerhouse provides a broad range of depths and velocities which are more attractive than the lesser magnitude and range of depths and velocities found in Seton Creek during minimal discharge conditions. It is probable that increasing the discharge of Seton Creek while maintaining the relative concentration of Seton Lake and Cayoosh Creek water would increase the attractiveness of Seton Creek in comparison to the powerhouse tailrace. However, solution of the tailrace delay problem through substantial increases in spill discharge would be a highly unsatisfactory alternative from the point of view of B.C. Hydro since the loss of hydroelectric generating potential would be costly.

EFFECTS OF HANDLING, TAGGING AND "RECENT EXPERIENCE"

Extending results of the preference studies to conclusions regarding choice-making among migrating fish requires confidence that the fish in the test apparatus were able to exhibit "normal" behavior. Stresses imposed by capture and transportation as well as the artificiality of the test environment could influence the response of the fish. However, the consistent results obtained indicate that the divergence from the natural environment did not produce unrepresentative behavior. The fish responded in predictable fashion, consistent with the hypothesis that they would choose the mixture with the highest concentration of their homestream water.

The potential effects of capture and tagging, and the presence of the radio tag in the gut must also be evaluated. Care was taken during the present study to minimize the handling of fish and to return them to the water as quickly as possible. The radio transmitters used in this study were very small relative to the size of the fish and less than 0.2% of the fish weight. Petersen-disc tags have been used extensively with good success to study salmon migration (IPSFC records). Consequently, although it is recognized that any capture or handling of fish imposes some stress, the extent of those adverse effects is thought to be equivalent to, or less than, that accompanying other similar migration studies.

The effect of exposure of the fish to Seton Lake water in the tailrace prior to the preference tests and radio-telemetry studies was also considered. Brett and Groot (1963) had similar concerns in their study and Oshima et al. (1969) noted that many behavioral and electrophysiological experiments utilized fish which had been captured in their homestream and therefore had recently experienced test water, including homestream water and nearby tributaries. Bodznick (1978a) found that sockeye fry preferred recently encountered water over foreign water. In contrast, Sutterlin and Gray (1973) found that mature Atlantic salmon did not become sensitized to or show a preference for non-homestream water in which they were held. Cooper and Hasler (1973) and Scholz et al. (1973) reviewed electrophysiological and behavioral evidence both for and against the hypothesis that the results of these types of experiments merely reflect an attraction to the odor of the water to which the fish were most recently exposed. In both cases the authors concluded that recent experience was not important and that during homing migration there is a substitution for, or inhibition of, recent experience by the imprinted or long-term memory. In the present study, homestream water was present in detectable concentrations in both choices presented to the fish. It is therefore clear that choices were made on the basis of relative concentrations, not just presence or absence of homestream water or the most recently experienced water.

PINK SALMON

Pink salmon are delayed at the tailrace of the powerhouse for shorter periods than sockeye. The radio tagging and preference studies gave similar results in that they both suggested that pink salmon are less precisely oriented than sockeye to the Seton Lake "homestream" odor.

The Seton Creek pink salmon enumeration program involves a major effort in capturing fish in the tailrace for Petersen-disc tagging. The tagged fish are released at the point of capture but they are almost never recaptured in the tailrace (IPSFC records), indicating very little tailrace delay. Similarly, the four pink salmon radio tagged during these studies delayed in the tailrace for a much shorter time than radio-tagged sockeye. Two explanations for this are possible. It has been hypothesized that pink salmon may be the least specific of all Pacific salmon in their homing precision and they would therefore be more prone than sockeye to accept dilutions of their homestream waters. Also, if imprinting occurs, pink salmon fry must imprint to water characteristics prior to and/or immediately after emergence from the gravel of their redd and it is likely that they would be imprinted to both Seton Lake and Cayoosh Creek waters or to a mixture of both. Therefore, after being blocked at Seton powerhouse, pink salmon might find the Seton Lake and Cayoosh Creek mixture in Seton Creek just as "attractive" as Seton Lake water.

The tendency of pink salmon to leave the tailrace after a shorter delay than sockeye may also be related to lower "biological affordability" due to a more rigid migration and spawning schedule. Fraser River pink salmon generally spawn within days of arrival on the spawning grounds whereas both the Gates and Portage Creek sockeye populations usually arrive in Seton Creek with many days to spare prior to spawning.

SOCKEYE SALMON IMPRINTING

In light of the above observations on pink salmon, it might be postulated that if, as occurred prior to construction of Seton Dam, sockeye salmon smolts migrated downstream from Seton Lake via Seton Creek instead of primarily through the canal and powerhouse, they might also imprint to the Seton and Cayoosh Creek mixtures in lower Seton Creek. If such imprinting occurred, sockeye might be expected to respond in a manner similar to pink salmon, showing no preference for Seton or Cayoosh Creek water in the preference tests and readily entering Seton Creek when it is encountered, rather than frequently returning to the tailrace. The failure of sockeye to respond in this manner was fortuitously demonstrated during the 1977 juvenile sockeye downstream migration and the subsequent return of these fish as adults in 1979. The Seton Generating Station was not operated from April to August 1977, encompassing nearly the entire period of smolt migration (B.C. Hydro records). Consequently, the smolts had to emigrate via Seton Creek, thereby encountering a mixture of Seton and Cayoosh Creek waters. The adults returning in 1979 delayed as usual in the tailrace. Radio-tagged sockeye in 1979, as in other years, frequently returned to the tailrace from forays upstream to Seton Creek (Tables 16-18). Evidently the short exposure of smolts to the mixture of Seton and Cayoosh Creek waters in lower Seton Creek for approximately 1 hour or less (assuming passive drift) did not imprint the juvenile sockeye to the Seton and Cayoosh Creek mixture. Other researchers have reported that effective smolt imprinting occurred in as little as 4 hr (Hasler et al. 1978, Novotny 1980). Even if some imprinting to Cayoosh Creek water took place it may have been masked by a much longer period of imprinting to Seton Lake water. An alternative possibility is that homing may depend upon a sequence of odor cues encountered in the reverse order to that experienced as a juvenile. If the cues are encountered out of sequence, the fish may not respond to or recognize those cues that were by-passed. In that case, exposure to Seton Lake water (in the tailrace) might prevent the fish from subsequently responding positively to a Seton-Cayoosh mixture which was "expected" to occur earlier in the sequence.

OLFACTORY HYPOTHESIS

Many investigators have hypothesized that the long-term "memory" of the imprinted homestream odor releases a positive rheotactic behavior causing the fish to swim upstream toward the home stream. Johnsen and Hasler (1980) studied the migratory behavior of coho salmon imprinted to synthetic odors and concluded that upstream migration was controlled by the presence of the imprinting odors:

"Apparently the upstream movement was a positive rheotactic response released in the presence of the imprinting odour .... Thus, the segregation of fish imprinted to different odours appears to be based on differential rheotactic responses in the presence or absence of the imprinting odour. This provides a possible mechanism for the successful migration to a homestream in a dendritic river system by different stocks of salmon".

Hara (1975) concluded that the attractant odor elicits rheotactic responses in the salmon so that localization of the odor occurs through positive rheotaxis rather than by detection of an increasing odor gradient. Arnold (1974), Brannon (1982), Brett and Groot (1963), Groot (1982) and Johnsen (1982) have also supported the concept that the presence of the imprinted homestream odor releases positive rheotaxis. Scholz et al. (1972) observed a similar upstream behavior in response to the ebb tide in an estuary.

Within the framework of the olfactory hypothesis at least three sub-hypotheses have been proposed to explain the mechanism by which natural imprinting and subsequent homing take place. In the original version, Hasler (1966) and Hasler et al. (1978) proposed that imprinting occurred in the natal stream to distinctive odors imparted by the local environment. Others have suggested that other fish, especially conspecifics, may provide all or part of the distinctive homestream odor (Doving et al. 1974, Nordeng 1971, 1977, Selset and Doving 1980, Solomon 1973, Ueda et al. 1967) or that fish home on a "bouquet" of many odors (Liley 1982). Implicit in this version of the olfactory hypothesis is a stimulus-response mechanism by which upstream migration is triggered by detection of the odor or odors to which the fish imprinted as juveniles.

A second version of the olfactory hypothesis is that the downstream migrating juveniles imprint to a series of distinctive odors or combination of odors throughout the course of the downstream migration. During the return migration the fish recognize this sequence of distinctive olfactory cues, perhaps necessarily in the correct reverse order (Barnett 1977, Oshima et al. 1969). This version of the hypothesis also would predict upstream migration in the presence of diluted Seton Lake water.

A third, "generalized" odor hypothesis holds that streams near the homestream, due to similarities in flora, fauna and geochemistry, will have more similar odors than will geographically more remote streams. Therefore the homing fish, at each confluence, must choose the odor most similar to its home stream (Gleitman and Rozin 1971). One strength of this hypothesis is that it would obviate the need for fish to be able to detect extremely small concentrations of homestream water at the mouth of a large river. Gleitman and Rozin suggest that their hypothesis is supported by studies showing that the presence of water from tributaries near the home stream "excited" olfactory nerve actions of migrants. Ueda et al. (1967) observed elevated EEG responses in chinook and coho salmon to water from tributaries near the homestream. Idler et al. (1961) observed a positive behavioral response by sockeye salmon to water from nearby tributaries. However, these observations could also be interpreted as support for the sequential imprinting hypothesis. In the case of Ueda et al. (1967), the interpretation of the EEG response may be open to question since other investigators have reported non-specific EEG responses to waters never previously encountered (Cooper 1982, Hara and Brown 1979, Oshima et al. 1969).

The generalized response hypothesis is the only one of the three that implies a comparative process on the part of salmon in choosing the most appropriate water source. In this respect the generalized response hypothesis is best supported by the present studies: in both the preference tests and the radio-telemetry studies, the fish determined which of two water sources contained the greater proportion of homestream odor. The fact that homestream water was present did not ensure positive rheotaxis as would be predicted by the conventional olfactory hypothesis stated by Hasler (1966). It is recognized that there is ample experimental and field evidence indicating that upstream movement occurs in the presence of homestream water. However, the present studies indicate an additional capacity on the part of the fish to discriminate the quality or concentration of the homestream water.

If the fish responded to a single unique compound to which they were imprinted, there would be no need for this discriminatory ability. However, for each race to be imprinted to a single unique compound is extremely unlikely since most of the chemicals present in the waters of any lake or stream are likely to be ubiquitous, albeit in varying concentrations in different watersheds. It is proposed, therefore, that homing salmon respond to a mixture or sequence of mixtures of chemicals present in the waters along the migration pathway. Changes in discharge of various tributary streams between the time of the downstream juvenile migration and the return migration of the adults will obviously alter the various mixtures of waters and olfactory cues. The homing fish must therefore be capable of choosing the mixture most similar to the one to which it imprinted as a juvenile. This mechanism would explain the ability of sockeye salmon in the present study to select the water source containing the greatest concentration of Seton Lake water over various dilutions of that water. This hypothesis has implications with respect to any water-use project involving diversion or storage. Diversions or alterations of a tributary stream contributing to the mixture of odors to which salmon are imprinted have the potential to impair the ability of salmon to return to their home stream.

SIGNIFICANCE OF RESULTS IN RESOLVING THE TAILRACE DELAY PROBLEM

Considerable confidence can be placed upon the results of this study based on the consistent and similar responses obtained over several years in both the preference tests and the radio-telemetry studies in the natural environment.

Gates Creek sockeye consistently discriminated between Seton Lake water and test mixtures containing 20% Cayoosh Creek water. Test mixtures containing lesser proportions of Cayoosh Creek water generally resulted in numerical but non-significant preferences for the Seton Lake water. Results of radio-tracking studies with Gates Creek sockeye clearly showed a similar divergence in response at the 20% dilution threshold. Forays upstream from the tailrace and releases of fish in lower Seton Creek were highly successful when Seton Creek contained less than 20% Cayoosh Creek water. In contrast, migration was seriously interrupted with higher proportions of Cayoosh Creek water. As a result of these studies, it has been recommended to, and accepted by, B.C. Hydro that during the Gates Creek adult sockeye migration period the proportion of Cayoosh Creek water in lower Seton Creek should be maintained below 20%.

Results of the Portage Creek sockeye studies are somewhat more variable than for Gates Creek sockeye, but the trend is similar. The Portage Creek sockeye tested in the preference apparatus were capable of discerning between Seton Lake water and test mixtures diluted by as little as 10% with Cayoosh Creek water. Responses varied during the course of the migrations and at times the threshold of sensitivity was as high as 20%. Radio-tagged Portage Creek sockeye responded similarly: success of forays from the tailrace and success of fish released in lower Seton Creek was significantly higher when the Cayoosh Creek component was less than 10%. Based on these results, recommendations were accepted by B.C. Hydro that the Cayoosh Creek component of Seton Creek should be limited to less than 10% during the Portage Creek adult sockeye migration. This control of the proportion of Cayoosh Creek water in lower Seton Creek can be achieved by diverting the majority of Cayoosh Creek through the existing tunnel to Seton Lake. At the present time, this diversion is accomplished by constructing a temporary rock and gravel dam in Cayoosh Creek following the high water period each year. However, a permanent dam is required because building the dam causes downstream siltation each year and in some years the flow is so high that the dam cannot be built until late in the migration period. Also, increasing the spill discharge at Seton Dam in order to achieve the required proportion of Seton Lake water in lower Seton Creek is not satisfactory because the very high spill discharge required in some years may seriously erode good spawning gravels in Seton Creek and interfere with production of trout and other resident species.

These temporary measures were implemented by B.C. Hydro, beginning in 1982, and their unqualified success in reducing delay and eliminating injuries to fish was verified in 1982 (Fretwell and Hamilton 1983). Subsequently, cursory observations have supported the efficacy of the measures insofar as there have been no indications of injuries to fish or losses en route. Although fish are initially attracted to the tailrace discharge, accumulations of fish at that point are now much less than observed previously.

The effectiveness of the measures described appears to be associated with several aspects of the biology of the two races of sockeye and pink salmon which have been discussed in this report. The Gates Creek sockeye migration is typical of the early summer-run stocks, as characterized by Killick (1955), which enter the Fraser River in a relatively "green" condition, migrate rapidly, and ripen and spawn very soon after arrival on the spawning grounds. It is believed that these characteristics, along with relatively warm water temperatures at the time of migration, contribute to the behavior observed among Gates Creek fish in preference tests and radio-telemetry studies: high level of activity with frequent forays from the tailrace, relatively high "threshold" of Cayoosh water in Seton Creek (20%) and consistently short tailrace delay under favorable conditions.

In comparison, the Portage Creek sockeye typify the other extreme of Killick's groupings: migrate late in the season, enter the Fraser in a more advanced state of maturity, migrate more slowly, have a propensity to delay, and may arrive on the spawning grounds with surplus time. Low water temperatures during migration may contribute to lethargic behavior and the slow rate of further maturation. In conjunction with these characteristics, Portage Creek sockeye make less frequent forays from the tailrace and generally delay longer in the tailrace than Gates Creek fish.

Evidence gathered during present studies supports previous conclusions (Andrew and Geen 1958) that delay of pink salmon in the tailrace is not prolonged and that this may be related to the fact that these fish have achieved their spawning destination. Also, they appear to have no preference for either Seton or Cayoosh Creek waters, possibly because they encountered both water sources during imprinting at the emergence stage.

SUMMARY

1. Migratory behavior of adult sockeye salmon in the vicinity of the Seton Creek Generating Station was studied by field observations, field-laboratory source-water preference tests and radio-telemetry during five years. The behavior of pink salmon was similarly studied during one year.
2. Migrating adult Gates and Portage Creek sockeye salmon were attracted to large discharges of homestream (Seton Lake) water from the Seton Generating Station, where the fish were delayed and seriously injured.
3. Radio-telemetry studies showed that delayed fish frequently made exploratory "forays" upstream in the Fraser River to the natural mouth of Seton Creek. They continued their migration when the concentration of a tributary stream (Cayoosh Creek) in Seton Creek was very low but at higher concentrations they dropped downstream to the tailrace, even after migrating up Seton Creek for some distance.
4. Water source preference experiments showed that adult sockeye were capable of discriminating between Seton Lake water (homestream) and Seton Lake water diluted by Cayoosh Creek water.
5. The threshold of sensitivity to test mixtures differed between summer-run Gates Creek sockeye and fall-run Portage Creek sockeye.
6. Gates Creek sockeye consistently discriminated between Seton Lake water and a test mixture diluted 20% with Cayoosh Creek water. Lesser dilutions resulted in a numerical but statistically non-significant preference for Seton Lake water.
7. Portage Creek sockeye exhibited a similar ability to discriminate between Seton Lake water and test mixtures but the sensitivity varied over time. During both the 1981 and 1982 migrations the threshold of sensitivity of Portage fish varied between 10% and 20% dilutions of Seton Lake water with Cayoosh Creek water.
8. Radio-tagged Gates Creek sockeye released in the powerhouse tailrace made more frequent "forays" upstream in the Fraser River to lower Seton Creek than did Portage Creek sockeye, apparently reflecting differences in level of maturation and ambient water temperature.
9. A higher proportion of Gates Creek sockeye migrated to Seton Dam from the tailrace when the concentration of Cayoosh Creek water was less than 20% than when it was greater than 20%.
10. Radio-tagged Gates Creek sockeye released in lower Seton Creek migrated upstream to Seton Dam only when Cayoosh Creek water comprised less than 20% of Seton Creek.
11. A higher proportion of Portage Creek sockeye migrated to Seton Dam when the concentration of Cayoosh Creek water was less than 10% than when it was greater than 10%.
12. Olfaction was determined to be the sensory mechanism by which fish detected the water source with the greatest concentration of homestream water. Anosmic fish did not choose the homestream water source.
13. The ability of the fish to choose the homestream water over test mixtures was not specific to the presence of Cayoosh Creek water. Preference tests with a dilutant from a foreign source showed the same preference for homestream water, demonstrating that the choice of Seton water rather than Seton-Cayoosh mixtures was not based upon a specific avoidance of Cayoosh Creek water.
14. The effect of discharge on upstream migration was eliminated in the preference tests since the preference shown by sockeye salmon for homestream water over test mixtures was independent of discharge. Also, radio-tagged fish released in Seton Creek migrated upstream regardless of the magnitude of discharge provided there was no influence from Cayoosh Creek water.
15. Seton Creek pink salmon did not exhibit a preference between Seton Lake water and either Cayoosh Creek water or mixtures of the two in the preference apparatus. It was speculated that this result occurred because the fish had already reached their spawning

ground and/or because they had been imprinted as fry to both Seton and Cayoosh waters.

16. The behavior of radio-tagged pink salmon indicated only limited delay in the tailrace of Seton powerhouse, consistent with the water preference studies.
17. Sockeye tested in the water preference apparatus exhibited a directional preference for the westerly and northerly ends, consistent with their direction of migration in the Fraser River and Seton Lake.
18. The observations indicating an ability of sockeye to choose the higher concentration of two mixtures of homestream water and the failure of radio-tagged fish to continue migrating upstream in the presence of the lower of two concentrations of homestream water suggested that sockeye possess a more complex decision-making ability than embraced by conventional olfactory hypotheses.
19. The problem of delay and injury of adult sockeye salmon in the tailrace of Seton Generating Station was mitigated by reducing the concentration of Cayoosh Creek water in Seton Creek to less than 20% during the Gates Creek migration and less than 10% during the Portage Creek migration. Sockeye continue to be attracted to Seton Lake water discharged at the tailrace but the probability of continued upstream migration in Seton Creek was substantially increased with reduced concentrations of Cayoosh Creek water in lower Seton Creek.
20. Control of the Cayoosh concentration in lower Seton Creek has been achieved since 1982 by building a temporary rock and gravel dam each year to divert most of the flow of Cayoosh Creek to Seton Lake during the adult salmon migration period. Since it has been demonstrated that the problem of delay and injury of salmon can be avoided by diversion of Cayoosh Creek flow to Seton Lake, consideration should now be given to building a permanent diversion structure in order to overcome three shortcomings of the present system: 1) building and removing temporary dams each year causes downstream siltation, 2) in high discharge years, the temporary dam cannot be completed prior to the start of the sockeye migration period, and 3) when high flows prevent completion of the temporary dam, the spill flow at Seton Dam must be increased to achieve the necessary reduction in Cayoosh concentration, causing potential erosion of valuable spawning beds and threatening the productivity of trout and other resident species.

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