Migrating sockeye salmon in spawning colors.

HOMING BEHAVIOUR OF ADULT SOCKEYE SALMON (*ONCORHYNCHUS NERKA*) PRESENTED WITH DILUTIONS OF HOMESTREAM WATER

by

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A B S T R A C T

HOMING BEHAVIOUR OF ADULT SOCKEYE SALMON (ONCORHYNCHUS NERKA) PRESENTED WITH DILUTIONS OF HOMESTREAM WATER

by Michael R. Fretwell

The upstream migration of adult sockeye salmon (*Oncorhynchus nerka*) in the home river system and selection of the homestream for spawning is believed to be based on a mechanism of positive rheotaxis in the presence of the appropriate odour cue. Results are presented here which support the hypothesis that the homing migration of sockeye salmon, after entering fresh water, entails more than merely positive rheotaxis in the presence of the homestream odour or sequence of odours, and that salmon are capable of relatively complex "decision-making" processes in locating the homestream.

Adult sockeye salmon, tested in a water source preference apparatus, discriminated between homestream water and mixtures of homestream water diluted by as little as 10 percent with water from a tributary stream. The basis of the discrimination was the olfactory sense and was a preference for the greater concentration of homestream water rather than avoidance of the dilutant water.

Field observations of homing sockeye salmon at a hydroelectric installation yielded evidence parallel to that obtained in the preference apparatus. After encountering homestream water discharging from a powerhouse, upstream migration was not always sustained in the presence of homestream water diluted by a tributary stream. These observations diverge from the conventional view of the olfactory hypothesis which would predict positive rheotaxis in the

presence of the mixture of homestream and tributary water, providing that the concentration of homestream water was detectable to the fish. The simplistic olfactory hypothesis, whereby positive rheotaxis occurs in the presence of homestream odour, is re-examined and expanded to incorporate a more complex "comparative" model.

Pink salmon (Oncorhynchus gorbuscha) did not exhibit a preference for the homestream water over mixtures of homestream and tributary water. It was speculated that, having reached the spawning grounds, the fish were no longer in an active migratory state.

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TABLE OF CONTENTS

LIST OF TABLES

Page

LIST OF FIGURES

LIST OF PLATES

INTRODUCTION

The homing migration of adult Pacific salmon from the ocean to their natal stream is generally subdivided into two discrete phases on the basis of the mechanisms utilized by the fish for orientation, navigation and homing. The oceanic phase is the least understood part of the salmon's migration. A variety of methods of orientation and navigation proposed to accomplish migration 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 with which salmon return from oceanic migrations of several thousand kilometers to very specific locations implies a degree of sophistication of navigation and measurement of time beyond that possible utilizing most of the above means of orientation either singly or in combinations. The current view is that some type of bi-coordinate map system is required to accomplish this feat of timing and precise location (Quinn, 1982). Magnetic-compass orientation is likely involved, possibly along with other mechanisms.

When adult salmon approach the home river system olfaction apparently becomes the dominant homing mechanism, although the precise odour cue(s) and the mechanism by which the fish are attracted have not been established. A large body of evidence supports the hypothesis that juvenile salmon imprint to an odour or odours present in the homestream, and that the returning adults respond to the presence of the imprinted chemical(s) during the return migration (Hasler, 1966; Hasler et al., 1978; Hasler and Scholz, 1983). An alternative to the "imprinting hypothesis" is the "pheromone hypothesis", which holds 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* L.). Although there is some indication that 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 during which 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 homing migration and therefore upon the likely success of many enhancement and rehabilitation projects. Some imprinting is believed to occur before or during smoltification. However, earlier imprinting during the incubation or emergence period may be necessary, at least in the case of salmon (such as sockeye) which move to sea from a rearing area remote from the homestream from which they emerged and to which they must ultimately return to spawn (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 hours (Novotny, 1980).

The homestream odour hypothesis, as stated by Hasler and others, is based on the following tenets: (1) that each stream possesses a characteristic odour detectable by salmon, (2) that salmon are able to discriminate between the odours of different streams, and (3) that salmon are able to retain the "memory" of the homestream odour during the one to several years of oceanic residence (Hara, 1975). The chemical basis of the homestream odour or odours 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 homestream odour in each stream may originate from the flora of the stream, geochemical nature of the watershed of the homestream, 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 and the homestream odour or sequence of odours, implicit in the olfactory hypothesis is the necessity for positive rheotaxis to occur in the presence of the appropriate odour cue (Hara, 1975; Hasler and Scholz, 1983; Johnsen, 1982; Johnsen and Hasler, 1980).

Results are presented here which suggest that the homing migration of salmon after entering fresh water entails more than mere positive rheotaxis in the presence of the homestream odour or sequence of odours and that salmon are capable of a relatively complex "decision-making" process in locating their homestream.

Field observations of homing sockeye salmon (*Oncorhynchus nerka*) at a hydroelectric installation indicated that, after encountering their homestream water discharging from a powerhouse, upstream migration (positive rheotaxis) was not sustained in the presence of homestream water naturally diluted by a tributary. The foregoing observation is not compatible with the conventional view of the olfactory hypothesis, which would predict positive rheotaxis in the presence of the homestream water and tributary mixture providing that the concentration of homestream water was high enough to be detectable by the fish.

The hypothesis that migrating salmon are capable of detecting the difference between and choosing the greater of two concentrations of their homestream water arose from the foregoing observations. It follows that the simple olfactory hypothesis, whereby positive rheotaxis is released by the presence of the homestream odour, must be expanded to incorporate a more complex "comparative" or "decision-making" model.

SUBJECT POPULATIONS AND STUDY AREA

I. Sockeye Salmon

Of the five species of Pacific salmon found in North America sockeye salmon exhibit what is probably the most rigidly structured life history, with the most specific requirements for the various aspects of the freshwater phase of their life cycle. In particular, the near-obligatory requirement for a 1-2 year lacustrine rearing period (Foerster, 1968) substantially limits the number of river systems and tributaries which can support sockeye populations. The lake rearing phase also obliges the sockeye during its life to perform three relatively precisely-timed migrations, the success of which are critical to the animal's survival and ultimate reproductive success. Juvenile sockeye salmon, upon emergence, move to the rearing lake and begin feeding. This is accomplished by the appropriate innate rheotactic and olfactory responses (Bodznick, 1978a; Brannon, 1972). One or two years later the smolt must locate the lake outlet, possibly using rheotactic cues and compass orientation (Groot, 1965 and 1982; Quinn, 1981). As previously discussed, the extensive oceanic migrations require further sophisticated means of orientation and navigation, likely involving some type of bi-coordinate "map" system. A basic directional orientation might be accomplished with reference to any one of many simple directional cues. Navigation, if it happens, requires a more complex integration of location and time to return the migrating fish to a predetermined location at a precise time of year. Quinn (1982) provides a convincing case for the need for a time-compensated method of navigation to explain the return of salmon from divergent locations at sea by routes not previously traversed. The return migration of the mature salmon to its natal stream to spawn is accomplished principally using olfactory cues along with positive rheotaxis and vision (Hasler and Scholz, 1978; Hasler *et al.*, 1978; Johnsen and Hasler, 1980).

Although the precision of homing for the various species of Pacific salmon is not well documented, it is likely, based on the unique lake requirement, that sockeye should be the most site-specific homers. Since only a small proportion of watersheds contain suitable lakes, a high degree of selection against straying would be expected in sockeye.

In the event that the normal return migration of the salmon is blocked by natural obstructions or by man-made dams or diversions, the specific nature of the homing mechanism can operate to the detriment of the fish. That appears to be the case at Seton Creek where a diversion of homestream water can interrupt the spawning migration of two races of sockeye salmon which spawn and rear in the Seton-Anderson system upstream of a diversion dam and hydroelectric installation operated by B.C. Hydro and Power Authority (Figs. 1 and 2). The Gates Creek adult sockeye salmon migrate upstream into the Seton-Anderson system during the period July 20-August 31 and spawn in Gates Creek and an artificial spawning channel at the head of Anderson Lake during August and September. A later run to Portage Creek enters Seton Lake from September 20-November 10 and spawns in October and November.

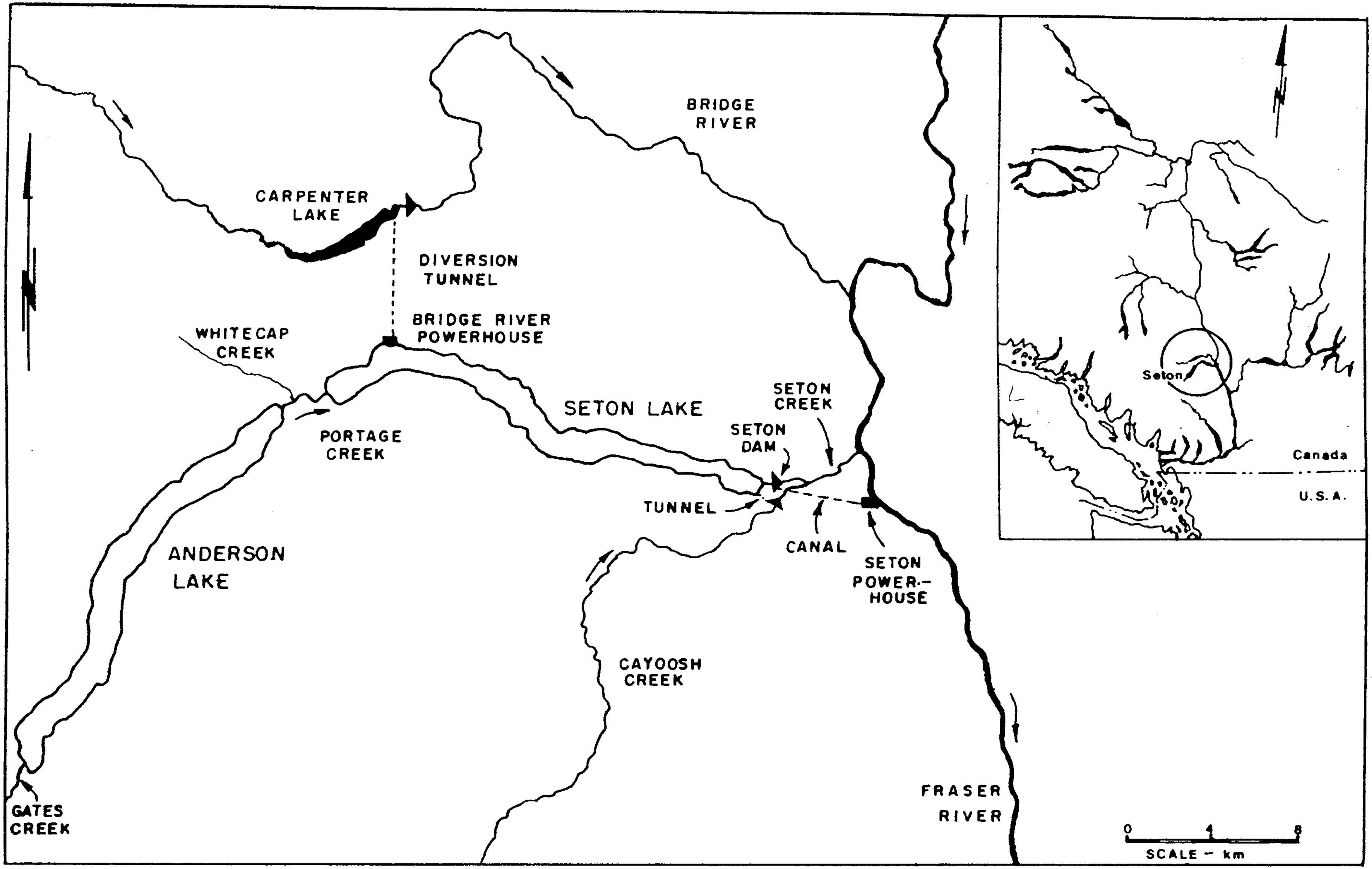

FIGURE 1. Seton-Anderson Lake system in relation to the Fraser River watershed.

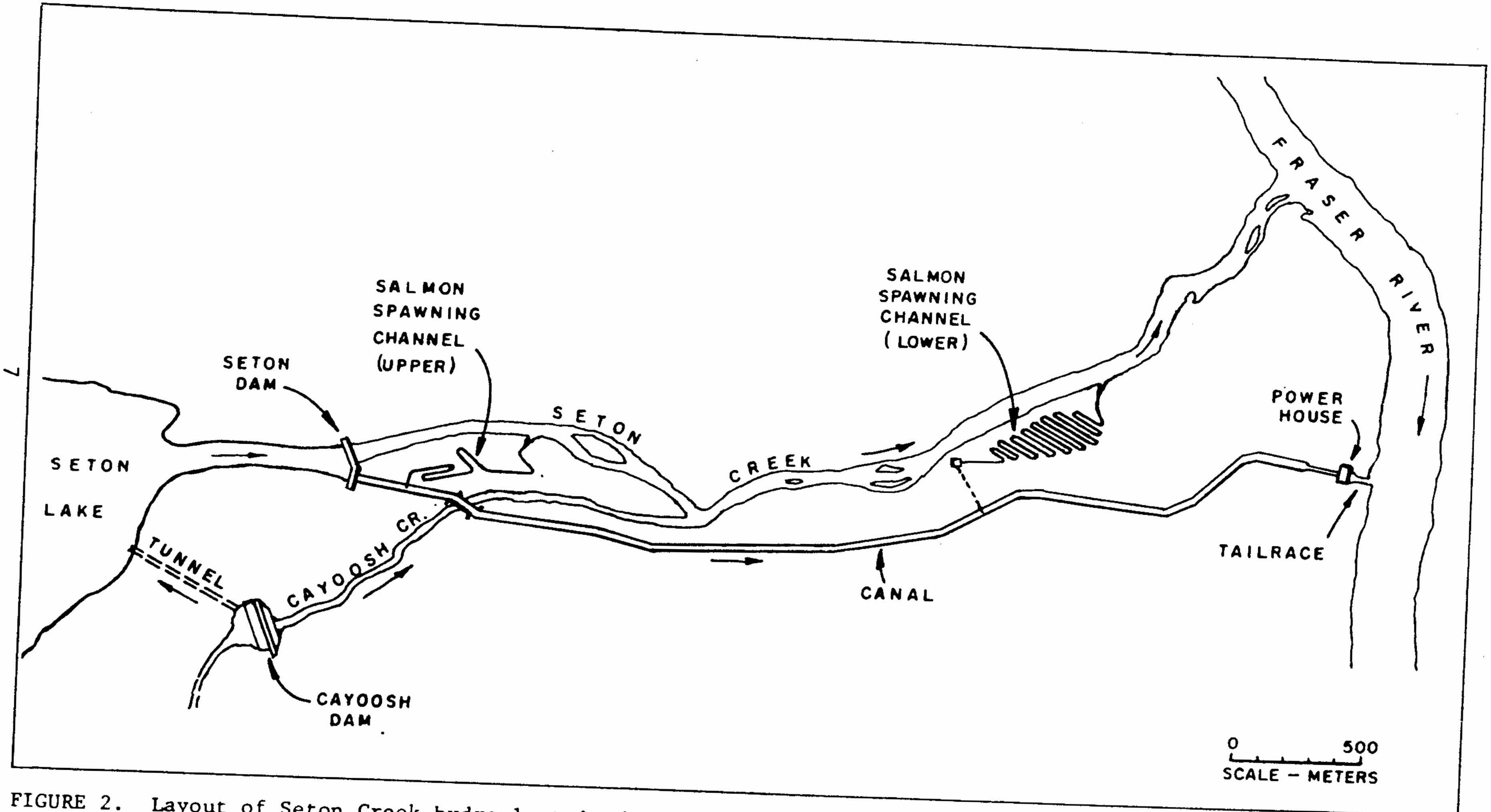

FIGURE 2. Layout of Seton Creek hydroelectric development in relation to Seton and Cayoosh Creeks.

Young of both races rear predominantly in Seton Lake for one year and emigrate as smolts during the April-June period (Andrew and Geen, 1958; Fretwell, 1981). Normal operation of the hydroelectric plant results in approximately 95% of the discharge from Seton Lake passing through Seton powerhouse (Fig. 2). During periods of downstream migration the majority of the sockeye salmon smolts migrate downstream through the power canal and powerhouse and emerge into the Fraser River at that point. Since at least 1972 there has been accumulation and loss of returning adult sockeye salmon which are attracted to the discharge of Seton Lake water from the powerhouse (Anonymous, 1976) (Plate 1).

It was originally believed that the delay of fish at the powerhouse resulted from a physical break in continuity of the olfactory cue which interrupted the return migration (Anonymous, 1976). It was concluded that the dissipation and dilution of the plume of Seton Creek between the mouth of the creek and the point of delay at the tailrace caused a dislocation of the odour trail of Seton Lake (homestream) water. Since there was no observable continuity between the tailrace and the plume of Seton Creek, it was believed that the fish would not venture upstream past the tailrace to Seton Creek.

Contrary evidence was obtained during preliminary radio-telemetry investigations in 1978 when it was noted that adult Portage Creek sockeye salmon, equipped with miniature radio transmitters, frequently returned downstream when released in Seton Creek (Fretwell, 1979). This ultimately led to the hypothesis that migrating adult salmon are capable of a more complex response to their homestream water than a simple upstream movement (positive rheotaxis). It was hypothesized that these fish were capable of

PLATE 1. Seton Lake water discharged into the Fraser River at Seton powerhouse.

comparing relative concentrations of their homestream odour and choosing the greatest concentration thereof.

II. Pink Salmon

Pink salmon (*Oncorhynchus gorbuscha*) represent what may be the opposite extreme, compared to sockeye, in terms of specific freshwater requirements. Pink salmon have minimal freshwater rearing requirements since they migrate to sea almost immediately after emergence, with little or no feeding in freshwater. Possibly the major limitation on the distribution of pink salmon, other than suitable spawning substrate, is the distance and difficulty of the adult migration since pink salmon are considered to be less capable swimmers than other species of Pacific salmon even when their generally smaller size is considered (Brett, 1982). On the basis of the general nature of their freshwater requirements it might be assumed that pink salmon would possess less precise homing than other species of Pacific salmon.

Included in the present study is a population of pink salmon which spawn in odd years from September 20-October 30 in the Seton-Anderson system. Most of the natural production results from spawning which occurs in Seton Creek between Seton Dam and its confluence with Cayoosh Creek (Fig. 2). Additional natural production occurs in Seton Creek below its confluence with Cayoosh Creek, in Seton Creek between Seton Dam and Seton Lake, in Cayoosh Creek and in Portage Creek. A substantial proportion of the production from the area is from two spawning channels adjacent to Seton Creek which are supplied with Seton Lake water from the B.C. Hydro power canal.

Returning adult pink salmon, like sockeye, are attracted to the discharge of Seton Lake water from the tailrace of Seton powerhouse.

METHODS AND MATERIALS

The hypothesis that migrating sockeye and pink salmon are capable of discriminating between different concentrations of homestream odours was examined by two methods: (1) testing salmon for a preference when they were presented with a choice of their homestream water and various dilutions of their homestream water in an experimental situation, and (2) observing the behaviour of radio-tagged adult salmon presented with similar choices in the field during their spawning migration.

I. Water Source Preference Experiments

1. Water Preference Apparatus

The apparatus used to test the preference of migrating salmon for various mixtures of homestream water was similar to that described by Sutterlin and Gray (1973) for testing the homing of Atlantic salmon (*Salmo salar*) to a hatchery. The test apparatus was located on the bank of Cayoosh Creek approximately 1200 m downstream from the outlet of Seton Lake. The preference apparatus consisted of two troughs through which test and control water were discharged into a central pool (Fig. 3). The rectangular fibreglass troughs were 305 cm long, 76 cm wide and 46 cm deep. The central round fibreglass 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 direct sunlight.

Water was supplied through 5.1 cm I.D. flexible polyethelene pipe into

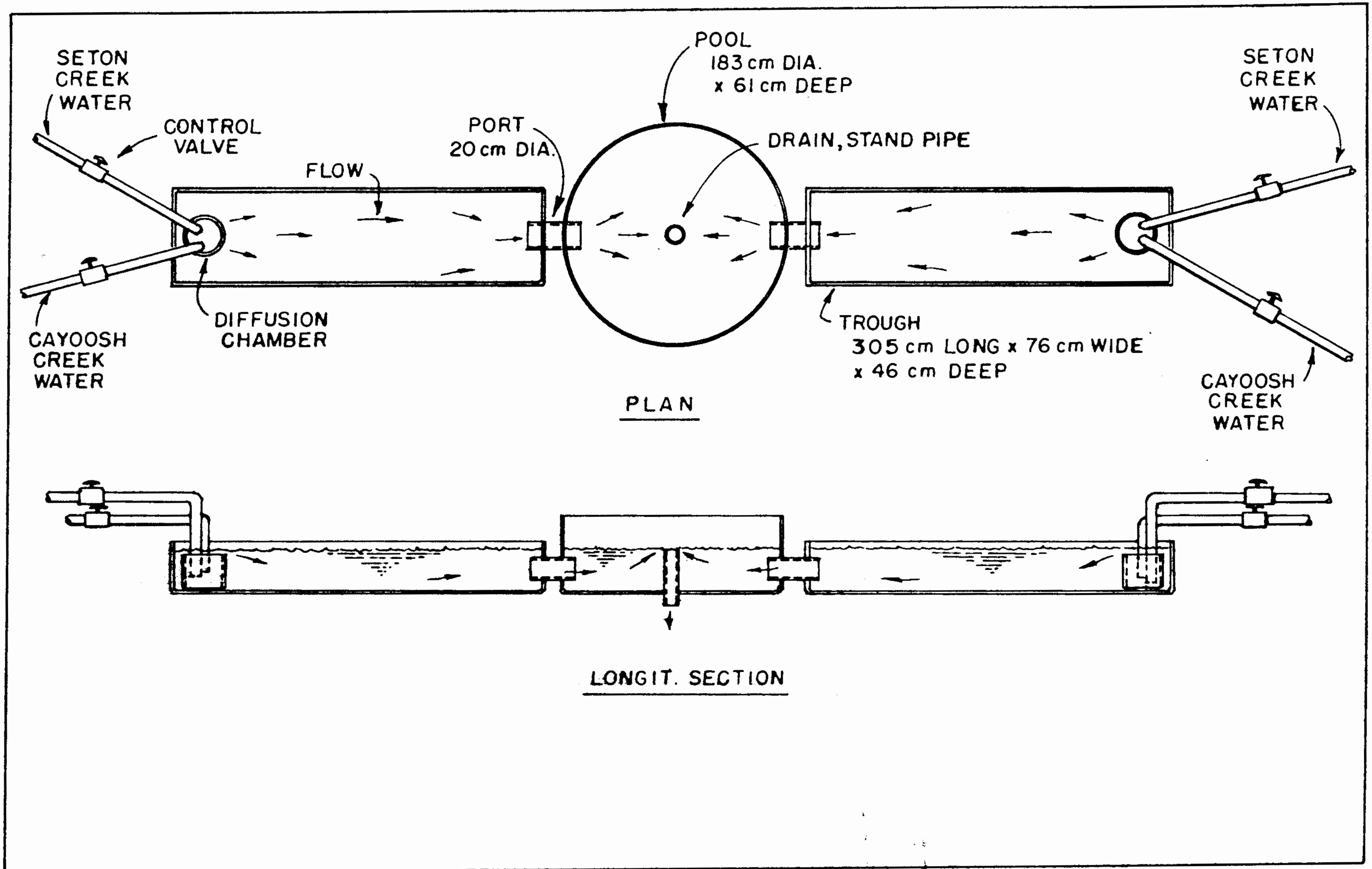

FIGURE 3. Water source preference apparatus.

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). Discharges were calibrated volumetrically by controlling the flow from each water source through a gate valve. After introduction into the diffusion chamber the water flowed the length of the rectangular trough, passed through the port into the circular pool and drained through a 7.6 cm stand-pipe at the center. Seton Lake water was obtained from the Seton Generating Station power canal by a siphon hose. Cayoosh Creek water was obtained by gravity feed from Cayoosh Creek.

The temperatures of the test mixture and control were recorded to the nearest 0.1°C. Water samples were obtained from 4 sites at intervals throughout the 1981 migrations to determine whether changing responses of fish to test procedures might be attributed to changing water chemistry parameters. Samples were forwarded for analysis to a laboratory operated by the Inland Waters Directorate and were analysed for conductance, alkalinity, hardness, calcium, fluoride and sulphate.

2. Capture and Handling of Fish

Adult sockeye and pink salmon were captured by brail-net in the tailrace of Seton Generating Station, or for certain trials, were obtained from the fishway at Seton Dam. Captures were made throughout the daily period when maximum light was available in the tailrace, 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. The fish were transported by truck in a 900-L fibreglass tank in oxygenated 0.3%

saline solution to reduce transportation stress (Mazeaud and Mazeaud, 1981).

3. Test Procedure

The fish were placed in the center pool in Seton Lake water for a 15-min acclimation period before the water flow into the rectangular troughs was started. Seton Lake water was chosen for the acclimation medium because that was the water in which the fish were captured. 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 choice troughs and to return to the central pool during the course of the test (Plate 2). The numbers of fish in each trough as well as the number remaining in the center pool were recorded after 1 hour.

Fish were returned to the central pool after it had been refilled with Seton Lake water. The rectangular troughs were then drained, the water supplies exchanged end-for-end, and the test repeated. In this way each group of fish was tested twice 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 3 times, the test mixture (a mixture of water from Seton Lake and Cayoosh Creek) and the

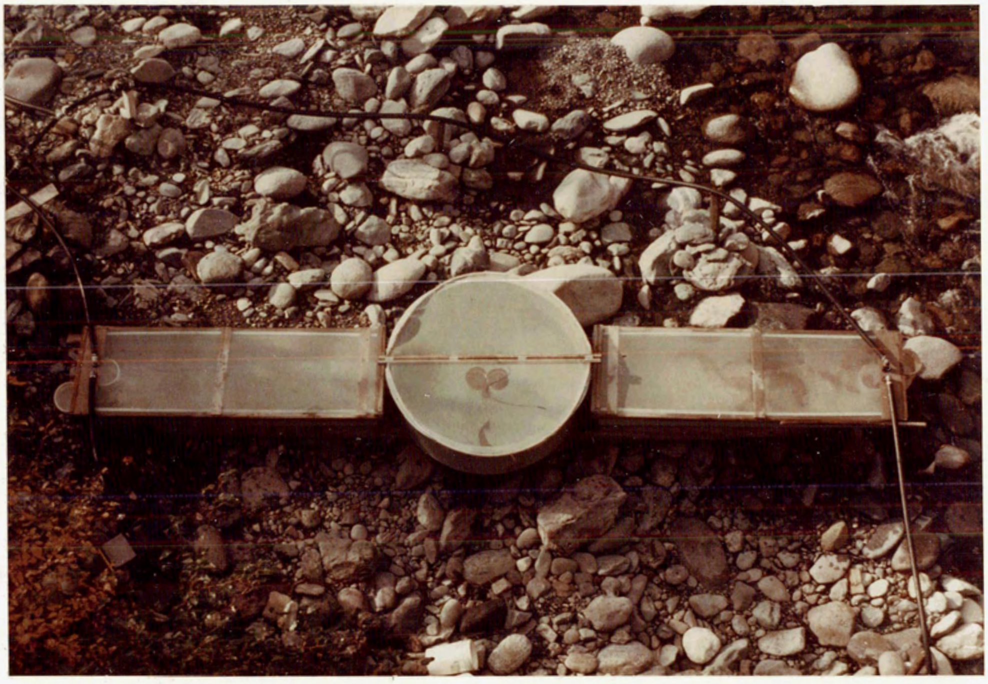

PLATE 2. Water source preference apparatus with fish congregated near the source of the control water (right-hand trough).

control (Seton Lake) water supplies being exchanged end-for-end after each trial. 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.

Previous workers have noted avoidance of water containing extract of mammalian skin (Brett and MacKinnon, 1954; Idler *et al*., 1961). Precautions were taken against introducing this bias by wearing rubber gloves during operation or manipulation of the test apparatus.

4. Water Mixtures Tested

During preliminary experiments in 1980, test mixtures ranged from 0-100% Cayoosh Creek water. In 1981 and 1982 test mixtures paired against Seton Lake water ranged from 5 to 20 % Cayoosh Creek water, depending upon the response elicited in the earlier trials.

During the 1981 Gates Creek sockeye salmon migration, two test mixtures containing different proportions of Cayoosh Creek water were paired against each other to determine whether Cayoosh Creek water elicited an avoidance response. It was reasoned that the preference apparently shown for Seton Lake water over test mixtures could have resulted from avoidance of Cayoosh Creek water in the test mixture. If the choice was based on avoidance, presentation of two test mixtures should result in the majority of fish remaining in the central pool rather than moving "upstream" to either test mixture.

A further experiment was conducted in 1981 to assess the possibility that Cayoosh Creek water contained come unique substance causing an avoidance reaction. Cayoosh Creek water was replaced in the test mixture by water from another stream, Dickie Creek. This small, precipitous creek flows into the Fraser River approximately 8 km upstream of Seton Creek. Consequently Seton-Anderson fish would be expected to be naive to this water, except as an extremely dilute constituent of the Fraser River. Water from this creek was transported in a stainless steel tank normally used to transport drinking water. It was delivered into the test troughs through the same polyethelene pipe used to deliver the Cayoosh Creek component of the test mixtures.

The results of the preference studies were analyzed by two-way chi-square to test for a preference between the control (Seton) and test (Seton and Cayoosh mixture) waters. Three-way chi-square was not generally done to test for divergence from a random distribution between the three possibilities (control water, central pool (no choice) and test mixture) because the distribution of fish was so obviously non-random. In all but a few special cases, which will be discussed later, only a small proportion of fish remained in the "no choice" pool.

5. Number of Fish Used in Experiments

Because of the time required for setting up and conducting each test it was advantageous to test fish in groups. To determine whether each fish in a group test was responding independently and could be considered as an individual data point, a series of trials with single fish was run using 1981 adult Gates Creek sockeye salmon. The fish were presented with a test mixture of Seton Lake water diluted 20% with Cayoosh Creek water. To minimize the time required for calibration of water flows, individually tested fish were utilized for only one trial and the test was terminated after 30 min or as soon as each fish had made a choice. Several fish were tested in succession before the control and test mixtures were exchanged end-for-end. Responses of groups of 5-12 different 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).

6. Response of Fish with Obstructed Nares

To verify that the outcome of the preference trough tests was indeed based on olfaction, 1981 adult Portage Creek sockeye salmon, captured in the tailrace, were tested after their anterior nares had been blocked. This was accomplished by inserting a 1 cm length of cotton covered Q-tip permeated with K-Y jelly, a water soluble lubricant. Groups of those fish were exposed to a test mixture which had previously been distinguished from Seton Lake water by groups of untreated fish.

7. Directional Preference

The end-for-end reversal of the test mixture and the control water between tests ensured that any directional preference shown by the fish would be cancelled. Any preference for the test mixture or the control water emerging from the tests would therefore be independent of any innate directional preference. However, if a directional preference existed, the proportion of fish choosing the preferred water source might be greater when it was paired with the preferred direction, and less when paired with the non-preferred direction. Consequently, throughout the studies, the direction chosen by the fish was recorded and the data analysed to determine whether a directional preference existed in addition to any preference for particular water sources.

8. Temperature Preference

Since fish are well known to be capable of discerning small differences in temperature and of choosing a preferred temperature, it was reasoned that temperature might be a critical factor in the choice made by fish in the preference tests. Generally the Cayoosh Creek water was colder than the Seton Lake water and, as a result, the test mixture was usually colder than the control water. Occasionally, due to solar heating of the supply pipes, the reverse was true.

A pair of tests was conducted in which control water was paired against an artificially cooled source of control water, 0.6-1.1°C cooler. This was accomplished through a simple heat exchange process, by passing one source of Seton Lake water through several hundred meters of pipe bathed in the cooler Cayoosh Creek water.

The results of all of the water source preference tests were examined for a temperature bias by subdividing test groups according to the relative temperature of the test and control water: 1) control water warmer, 2) control water colder, and 3) no difference. The water mixture treatments which resulted in a preference for the control water were examined separately to determine if the preference existed regardless of relative temperature. In a similar manner, water mixture treatments which did not result in a preference were examined to determine if the lack of preference was consistent for all relative temperatures.

II. Radio-Telemetry Studies

To study the behaviour of sockeye in the field setting in response to various mixtures of Seton Lake water diluted by Cayoosh Creek water, adult migrants were implanted with miniature radio transmitters. Various mixtures of Seton and Cayoosh Creek waters were produced by controlling the spill discharge at Seton Dam and the discharge of Cayoosh Creek (Fig. 2) by diverting part of it through a tunnel into Seton Lake (Fretwell 1980).

Radio-telemetry equipment utilized during these studies was supplied by AVM Instrument Co., Champaign, Illinois, U.S.A. Transmitting modules consisted of an SM-1 transmitter, tuned loop antenna and single Hg-675 battery potted in dental acrylic (Plate 3). 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 using LA-12 manual receivers operated either from a vehicle equipped with an omni-directional whip antenna or on foot using a portable M-Yagi directional antenna.

Fish utilized in radio-telemetry studies were captured in a brail net in the tailrace of Seton powerhouse and were handled and transported as previously described for preference experiments. The radio transmitter was inserted orally into the fish's gut (Plate 4) and the fish was marked with coloured Petersen discs to facilitate subsequent visual identification and recovery 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 least every 2-4 hr from 0700-2400 hr and more frequently when individual fish were actively migrating.

PLATE 3. Miniature radio transmitters used in migration studies.

PLATE 4. Insertion of radio transmitter into fish's gut.

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 only about 100 m on the west bank of the Fraser River was required for the fish to encounter the visually apparent plume of Seton Creek, the only possible migration route to the spawning grounds. The foray was considered a success if the fish continued to migrate upstream to Seton Dam and a failure if the fish ultimately 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 dis-charges of Seton and Cayoosh Creeks above their confluence, as recorded at Water Survey of Canada gauges.

RESULTS

I. Water Source Preference Experiments

Upon placement into the test apparatus, the fish at first appeared agitated, but within a short time (1-2 min) adopted a pattern of behaviour of slowly circling the holding pool and at times lying relatively motionless against the wall of the container. Often the fish would remain in small groups of 2-4 individuals for several minutes before resuming the slow swimming pattern. During the test period, when test and control water mixtures were flowing into the central pool, fish could be observed "exploring" the area of the inflow ports, frequently passing below the ports which were raised about 5 cm above the bottom of the tank. The fish sometimes would continue swimming away from the port, and on other occasions would return to continue "searching". Upon entry into the test or control container, the fish usually proceeded to the water source at the distal end and probed around the base and sides of the diffusion container. Particularly in the control trough, considerable activity often developed in the area of the water source, with several fish simultaneously attempting to swim into the diffusion bucket or into the 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 the trough through the port into the central holding pool if it was encountered. The number of fish located in each of the test and control troughs and the central pool at the end of each hour-long test therefore represents a "snap-shot" of the distribution of fish at that point in the test.

1. Preliminary Experiments

Since it was not known what threshold of dilution of the test water might be detected by the fish the 1980 preliminary tests were begun by comparing Cayoosh Creek and 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 the fish for the control (Seton) water (Table 1). 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% no preference for the control (Seton water) was indicated, although it must be noted that the numbers of fish tested under these conditions was relatively small.

TABLE 1. Preliminary water source 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	Numbers of Fish: Control (Seton)	No Choice	Test Mixture	n*	X^2	Level of Significance
100% Cayoosh Cr.	17	0	0	17(2)	17.0	$P < .005$
50% Cayoosh Cr.	11	0	1	12(1)	8.333	$P < .005$
33% Cayoosh Cr.	17	1	0	18(1)	17.0	$P < .005$
20% Cayoosh Cr.	48	2	14	64(4)	18.645	$P < .005$
10% Cayoosh Cr.	10	1	9	20(1)	0.053	n.s.
0% (100% Seton)	6	0	4	10(1)	0.4	n.s.

* Number of pairs of tests in brackets.

2. Gates Creek Sockeye Salmon

Groups of Fish

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 2). 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 pure Seton Lake water but the results were not significant.

Individual Fish

To determine whether the response of each fish tested in a group could be utilized as an independent data point, additional 1981 Gates Creek sockeye were tested individually at a test mixture of 20% dilution with Cayoosh Creek water (Table 2). The results of the pooled individual responses were nearly identical to the results of the group tests. The results of the individual and group testing procedures were compared using a heterogeneity chi-square test which indicated that there were no significant differences in response (Table 3). 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.

To assess the consistency of the preference behaviour of the fish, preference trough experiments were continued during the 1982 Gates Creek migration. Precocious (3_2) male sockeye, 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 adult Gates Creek sockeye salmon (Table 4). Jack sockeye presented with a choice of Seton Lake water and Seton water diluted 20% with Cayoosh Creek water showed a significant pre-

TABLE 2. Water source 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.

	Numbers of Fish					
	Control (Seton)	No Choice	Test Mixture	n*	X^2	Level of Significance
I. <u>Fish tested singly with test mixture of 20% Cayoosh Cr.</u>						
Fish from Seton powerhouse tailrace	15	1	7	23		
Fish from Seton Dam fishway	17	6	6	29		
Total	32	7	13	52	8.022	$P < .005$
II. <u>Fish tested in Groups</u>						
Test mixture 20% Cayoosh Cr.	39	18	18	75(4)	7.737	$P < .01$
Test mixture 15% Cayoosh Cr.	54	12	38	104(5)	2.783	n.s.

* Number of pairs of tests in brackets.

TABLE 3. Comparison of results of exposing 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.

	Numbers of Fish						
	Control (Seton)	Test Mixture	n		D.F.	X^2	Level of Significance
Individual Fish	32	13	45		1	8.022	$P < .005$
Groups of Fish	39	18	57		1	7.737	$P < .01$
				Total	2	15.759	
	71	31	102	Pooled	1	15.686	$P < .005$
	Heterogeneity chi-square				1	0.073	n.s.

TABLE 4. Water source 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.

Test Mixture	Numbers of Fish Control (Seton)	No Choice	Test Mixture	n*	X^2	Level of Significance
20% Cayoosh Cr.	28	3	14	45(3)	4.667	$P < .05$
10% Cayoosh Cr.	26	1	19	46(5)	1.09	n.s.

* Number of pairs of tests in brackets.

ference for Seton Lake water ($P < .05$). No significant preference was shown for Seton Lake water over test mixtures including 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.

Possible Avoidance of Cayoosh Creek Water

It was hypothesized that the apparent preference for Seton Lake water over various dilutions of Seton Lake water by Cayoosh Creek water observed in the foregoing experiments could have been a result of an active avoidance of Cayoosh Creek water rather than selection for the higher of the two concentrations of Seton Lake water. To examine the possibility that avoidance was the mechanism determining the choice between the test and control waters the following two experiments were carried out with 1981 Gates Creek sockeye.

i. Response to a choice of two test mixtures

Sockeye from the 1981 Gates Creek migration were presented with a choice of two test mixtures of Seton Lake water and Cayoosh Creek water: Seton Lake water diluted 20% and 50%, respectively, by Cayoosh Creek water. It was reasoned that if the observed preference for Seton Lake water were actually due to an active avoidance of Cayoosh Creek water fish would avoid both choices. That is, they would not exhibit a positive rheotaxis, swimming "upstream" toward either water source, but would remain in the center circular pool or become randomly distributed amongst the 3 containers. There did not appear to be avoidance since most of the fish made a choice:

Numbers of Fish					
Control (Seton)	No Choice	Test Mixture	n	X^2	Level of Significance
27	6	3	36	19.2	$P < .005$

The choice was significant in favor of the lower dilution ($P < .005$). The proportion of these fish (30 of 36 = 83.3%) making a choice rather than remaining in the center "no choice" container was even greater than 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 2). The strong preference shown by fish for the lower dilution of the two test mixtures may have been due to the 30% difference between these two dilutions. In comparison the difference between the single test water and the Seton control was only 20%.

ii. Response to a novel dilutant

A second experiment was conducted to test the possibility that the Cayoosh Creek water contained a unique substance causing a graded avoidance response proportional to its concentration. The Cayoosh Creek water was replaced by water from another creek, Dickie Creek, to which the fish had not previously been exposed. Only one set of paired trials was possible because it was necessary to transport the water by tanker truck to the trough apparatus. Consequently, a relatively high proportion of Dickie Creek water was incorporated in the test mixture so that if a response occurred the results would be clear:

Numbers of Fish					
Control (Seton)	No Choice	Test Mixture	n	X^2	Level of Significance
13	1	2	16	8.067	$P < .005$

The fish showed 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 indicates that, since the preference shown for homestream water over dilutions by Cayoosh Creek water can be duplicated with a novel dilutant, the effect of Cayoosh Creek water as a dilutant is not unique and therefore not likely based on a learned avoidance.

3. Portage Creek Sockeye Salmon

Preference trough experiments were conducted throughout the 1981 Portage Creek migration to determine whether the sensitivity of these fish to dilution of their homestream water changed with time during the migration. Test mixtures presented were 5, 10, 15 and 20% dilutions of Seton Lake water with Cayoosh Creek water (Table 5).

During passage of the first third of the fish (September 28-October 12) they exhibited a preference for Seton Lake water over test mixtures containing 20, 15 and 10% dilutions of Cayoosh Creek water ($P < .005$ in all cases). A test mixture containing a lower dilution (5% Cayoosh Creek water) did not result in a preference for Seton Lake water.

During the second third of the migration (October 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 numerical majority of the fish chose the Seton water.

During the last third of the Portage Creek sockeye salmon migration (October 31-November 6) no preference was shown for Seton Lake water over 10 or 15% dilutions. During that period Seton Lake water was significantly preferred over a test mixture of Seton water diluted 20% with Cayoosh Creek water ($P < .025$).

TABLE 5. 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	Numbers of Fish: Control (Seton)	No Choice	Test Mixture	n*	X^2	Level of Significance
20% Cayoosh Cr.						
first third of migration	28	11	7	46(5)	12.6	P < .005
last third of migration	46	7	25	78(4)	6.211	P < .025
15% Cayoosh Cr.						
first third of migration	62	7	21	90(5)	20.253	P < .005
last third of migration	14	1	11	26(1)	0.36	n.s.
10% Cayoosh Cr.						
first third of migration	85	27	40	152(7)	16.2	P < .005
second third of migration	45	9	24	78(4)	6.391	P < .025
last third of migration	32	6	32	70(3)	0	n.s.
5% Cayoosh Cr.						
first third of migration	26	4	36	66(3)	1.613	n.s.
second third of migration	42	8	32	82(4)	1.351	n.s.

* Number of pairs of tests in brackets.

The foregoing suggests that the response of the 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 (October 7-21) only a test mixture of 20% Cayoosh water resulted in a preference for Seton Lake water (Table 6). During the last half of the migration (October 30-November 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.

Fish with Obstructed Nares

During the middle portion of the 1981 Portage Creek migration several groups of sockeye salmon were exposed to test mixtures of 20% Cayoosh Creek water after their anterior nares had been blocked. At this time fish without blocked nares exhibited a preference for Seton Lake water over test mixtures containing as low as 10% Cayoosh Creek water (Table 5). Fish with blocked nares did not exhibit a preference between the control and test waters:

Numbers of Fish					
Control (Seton)	No Choice	Test Mixture	n	X^2	Level of Significance
29	28	27	84 (4)*	0.071	n.s.
			3-way chi-square	0.071	n.s.

* number of pairs of tests.

TABLE 6. 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	Numbers of Fish Control (Seton)	No Choice	Test Mixture	n*	X^2	Level of Significance
20% Cayoosh Cr.						
first half of migration	71	10	17	98(6)	33.136	$P < .005$
15% Cayoosh Cr.						
first half of migration	31	8	25	64(3)	0.64	n.s.
last half of migration	44	6	22	72(3)	7.33	$P < .01$
10% Cayoosh Cr.						
first half of migration	33	2	25	60(4)	1. 103	n.s.
last half of migration	27	6	13	46(2)	4.9	$P < .05$

* Number of pairs of tests in brackets.

Furthermore, the fish did not exhibit positive rheotaxis since they were randomly distributed in the three chambers, instead of being predominantly in the test or Seton troughs as was the case in all previous tests.

4. Pink Salmon

Seton Creek pink salmon were exposed to Seton Lake water and test mixtures of 20, 50 and 100% Cayoosh Creek water (Table 7). In none of these experiments was a significant preference shown, although in all cases a numerical preference was shown for the test mixture. 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 random, and that was because the greater proportion of the fish remained in the center pool (three-way chi-square = 16.829, $P < .005$).

5. Directional Preference

All of the data were analysed for possible directional preferences. The alignment of the preference trough apparatus during the preliminary tests in 1980 with Portage Creek sockeye was approximately east-west. A significant preference was shown for the west end of the apparatus (Table 8). Throughout the 1981 and 1982 tests the apparatus was aligned along a north-south axis. Tests of 1981 Gates Creek sockeye salmon with control water supplied at both ends elicited no directional response (Table 8). Throughout both the 1981 and 1982 Gates Creek sockeye salmon tests there was a small, but non-significant numerical preference for the north end of the test apparatus. In contrast during both Portage Creek migrations there was a strong statistical preference for the north end ($P < .005$). Taken as a group the sockeye data indicate a significant preference for the northerly

TABLE 7. 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	Numbers of Fish: Control (Seton)	No Choice	Test Mixture	n*	X^2	Level of Significance
20% Cayoosh Cr.	14	23	23	60(3)	2.189	n.s.
			3-way chi-square		2.7	n.s.
50% Cayoosh Cr.	21	22	27	70(4)	0.75	n.s.
			3-way chi-square		0.886	n.s.
100% Cayoosh Cr.						
- fish from tailrace	15	25	22	62(3)	1.324	n.s.
			3-way chi-square		2.548	n.s.
- fish from fishway	12	39	19	70(3)	1.581	n.s.
			3-way chi-square		16.829	P < .005

* Number of pairs of tests in brackets.

TABLE 8. Analysis for possible directional preference of sockeye and pink salmon in preference apparatus.

Test population	Directions		X^2	D.F.	Level of Significance
I. East vs West Trough	East	West			
1980 Portage Cr. Sockeye Salmon	48	72	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 Water	20	21	0.02	1	n.s.
(ii) All Tests	137	125	0.55	1	n.s.
1982 Gates Cr. Sockeye Salmon	48	39	0.93	1	n.s.
Total Gates Cr. Sockeye Salmon	185	164	1.26	1	n.s.
2. Portage Creek Sockeye Salmon					
1981 Portage Cr. Sockeye Salmon					
(i) Obstructed Nares	36	20	4.57	1	P < .05
(ii) All Tests	366	298	6.96	1	P < .01
1982 Portage Cr. Sockeye Salmon	178	130	7.48	1	P < .01
Total Portage Cr. Sockeye Salmon	544	428	13.84	1	P < .005
3. All 4 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	62	3.32	1	n.s.

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.).

6. Temperature Preference

There was generally a substantial difference between the temperatures of Seton Lake and Cayoosh Creek waters, with Seton Lake water frequently being several °C warmer. Although the test mixtures generally contained only 5-20% Cayoosh Creek water the 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 during passage through 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. This was accomplished through a simple heat exchange process by passing one source of Seton Lake water through several hundred meters of pipe bathed in the cooler Cayoosh Creek water. Although relatively few fish were tested in this way there was no preference shown for either temperature:

Test Mixture	Number of Fish 16.6°C	Number of Fish 17.2-17.7°C	X^2	Level of Significance
Seton Lake vs Seton Lake	9	9	0	n.s.

Since the temperature difference between these waters was as great or greater than the difference 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.

Possible biasing of the results of water source preference tests because of a temperature preference was further examined by subdividing test groups according to the relative temperature of the test and control water: 1) control (Seton Lake) 0.1-1.2°C warmer, 2) control (Seton Lake) 0.1-1.1°C colder, and 3) no difference in temperatures. For those water mixture treatments 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 9). 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.

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. If all of these data are pooled a significant preference is shown for the control (Table 10, $P < .05$). Grouped according to relative temperatures, only for the "Seton colder" category was there a significant preference ($P < .05$). A numerical preference for Seton water was maintained when there was no measurable temperature difference. However, when the Seton water was warmer a slight, but non-significant, numerical 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 was observable only when the

TABLE 9. Analysis for temperature preference among groups of sockeye salmon which showed a preference for control (Seton Lake) water over various test mixtures.

Relative Temperatures	Numbers of Fish: Seton Lake Water	Test Mixture	X^2	D.F.	Level of Significance
	1. 1981 Gates Creek Sockeye Salmon				
Seton water 0.1°C colder	8	0	8.0	1	$P < .005$
Same temperature	25	6	11.65	1	$P < .005$
Seton water 0.3-1.1°C warmer	46	17	13.35	1	$P < .005$
	2. 1981 Portage Creek Sockeye Salmon				
Seton water 0.1-.3°C colder	26	6	12.5	1	$P < .005$
Seton water 0.1-1.2°C warmer	240	111	47.41	1	$P < .005$
	3. 1982 Gates Creek Sockeye Salmon				
Seton water 0.1-.3°C colder	23	14	2.19	1	n.s.
Seton water 0.2°C warmer	5	0	5.0	1	$P < .05$
	4. 1982 Portage Creek Sockeye Salmon				
Seton water 0.1-1.2°C warmer	142	52	41.75	1	$P < .005$
	5. All 4 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-.3°C colder	57	20	17.78		$P < .005$
Same temperature	25	6	11.65		$P < .005$
Seton water 0.1-1.2°C warmer	433	180	104.42		$P < .005$

TABLE 10. Analysis for temperature preference among groups of sockeye salmon which showed no preference between control (Seton Lake) water and various test mixtures.

Relative Temperatures	Numbers of Fish: Seton Lake Water	Test Mixture		X^2	D.F.	Level of Significance
	1. 1981 Gates Creek Sockeye Salmon					
Seton water 0.3-1.1°C colder	31	25		0.64	1	n.s.
Same temperature	16	3		8.89	1	$P < .005$
Seton water 0.6°C warmer	7	10		0.53	1	n.s.
	2. 1981 Portage Creek Sockeye Salmon					
Seton water 0.1-.4°C colder	61	48		1.55	1	n.s.
Same temperature	14	16		0.13	1	n.s.
Seton water 0.1-.7°C warmer	36	39		0.12	1	n.s.
	3. 1982 Gates Creek Sockeye Salmon					
Seton water 0.1-.7°C colder	14	9		1.09	1	n.s.
Same temperature	12	10		0.18	1	n.s.
	4. 1982 Portage Creek Sockeye Salmon					
Seton water 0.1-.5°C colder	19	11		2.13	1	n.s.
Same temperature	10	5		1.67	1	n.s.
Seton water 0.1-.7°C warmer	35	34		.01	1	n.s.
	5. All 4 1981 and 1982 Sockeye Salmon Migrations					
			Total	16.94	11	n.s.
	255	210	Pooled	4.35	1	$P < .05$
			Heterogeneity	12.59	10	n.s.
	TOTALS					
Seton water 0.1-1.1°C colder	125	93		4.70		$P < .05$
Same temperature	52	34		3.77		n.s.
Seton water 0.1-.7°C warmer	78	83		0.16		n.s.

difference between water mixtures was slight. Heterogeneity chi-square analyses indicate homogeneity among the temperature treatments in both Tables 9 and 10. It can be concluded that the relatively small differences observed between the temperature of the test and control waters did not significantly bias the results.

7. Water Chemistry

The results of analysis of water samples do not indicate any consistent basis for the discrimination, by the fish, between Seton Lake and Cayoosh Creek waters (Figs. 4-6). None of the parameters measured showed a consistent difference between Seton Lake and Cayoosh Creek water: either there was no difference (within the accuracy of the methods used), or the relative levels reversed over time.

II. Radio-Telemetry Experiments

1. Sockeye Salmon

Radio-tagged fish were released at two locations during Gates and Portage Creek sockeye salmon migrations from 1978-82: 1) in the tailrace of Seton powerhouse to observe the behaviour of fish delayed at that point; and 2) in Seton Creek or its plume in the Fraser River to examine the response of fish to various dilutions of Seton Lake water by Cayoosh Creek.

Fish Released in the Powerhouse Tailrace

During the 1979, 1980 and 1981 Gates Creek sockeye salmon migrations the behaviour of 48 radio-tagged sockeye was observed at the tailrace. This included 39 fish released in the tailrace and a further 9 fish, released upstream in Seton Creek, that had moved downstream to the tailrace. Those fish were observed making 158 forays upstream from the tailrace into Seton Creek or its plume (Table 11). The success of each of those forays (defined

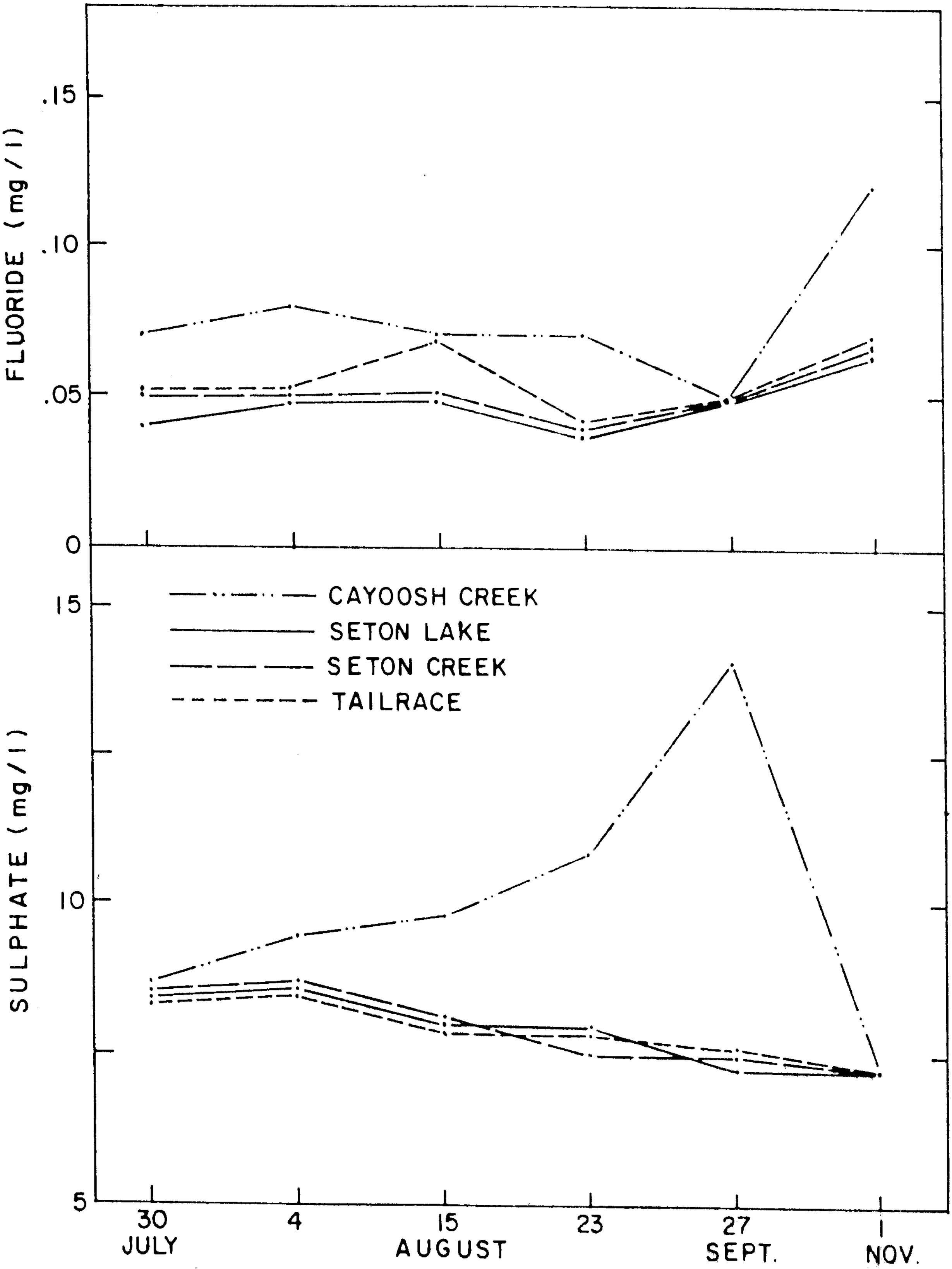

FIGURE 4. Sulphate and fluoride in water sampled in Cayoosh Creek, Seton Lake, Seton Creek and the tailrace.

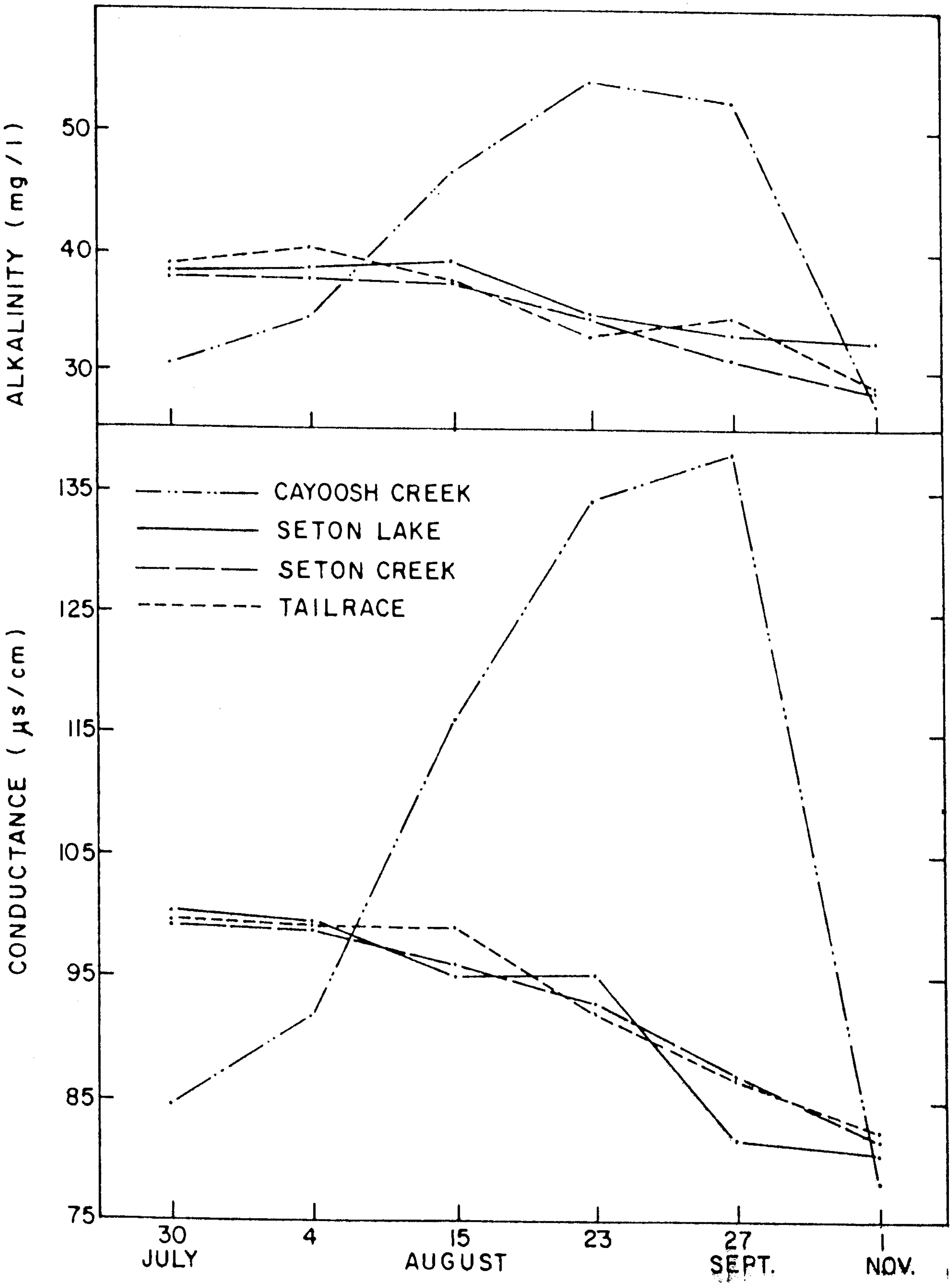

FIGURE 5. Conductance and alkalinity of water sampled in Cayoosh Creek, Seton Lake, Seton Creek and the tailrace.

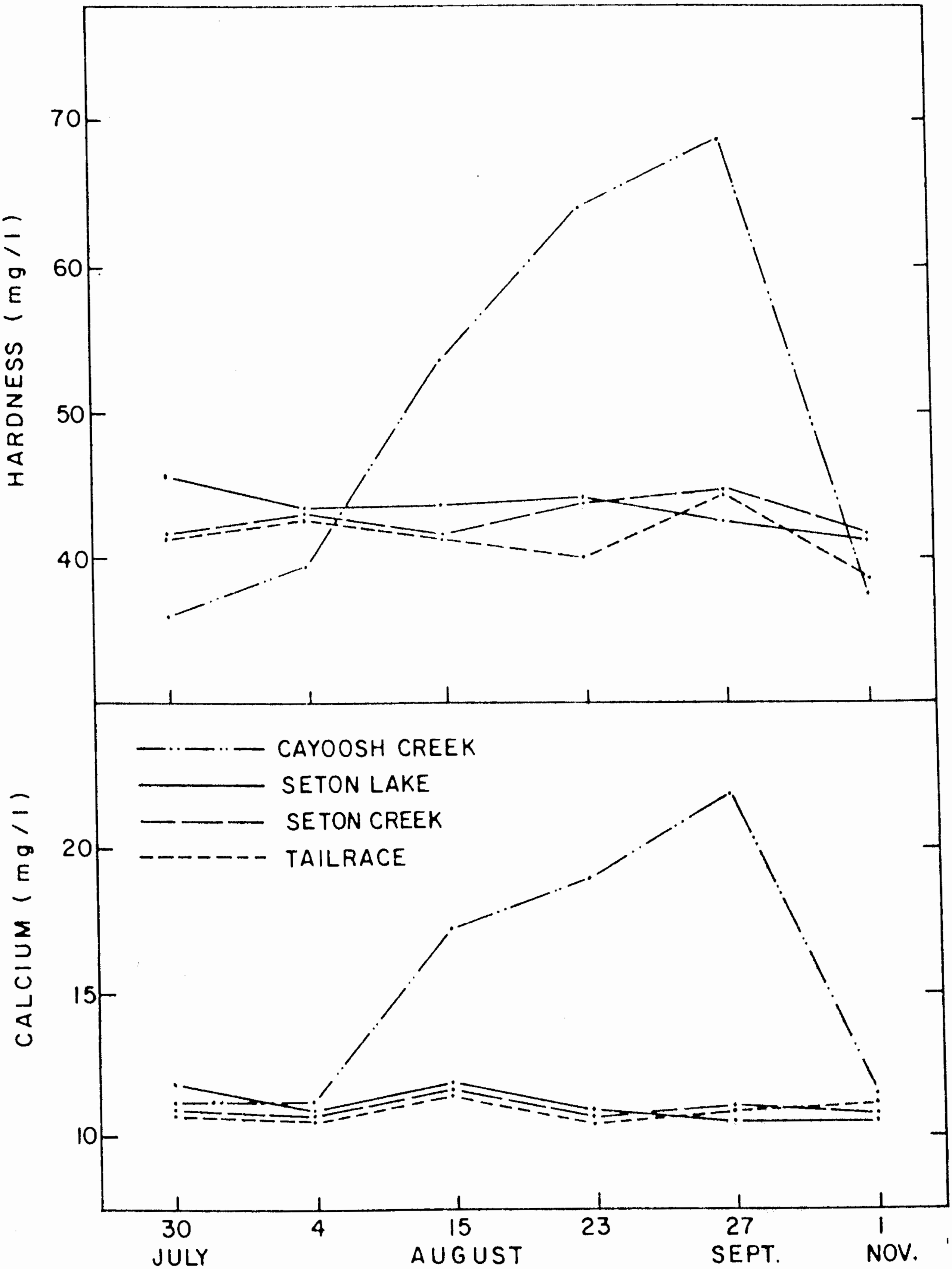

FIGURE 6. Calcium and hardness of water sampled in Cayoosh Creek, Seton Lake, Seton Creek and the tailrace.

TABLE 11. 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 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		

$Z = 8.53$ $P < .001$

as continued migration upstream to Seton Dam) was examined in relation to the mixture of Seton Lake and Cayoosh Creek water in Seton Creek. Fish, which moved upstream from the tailrace to Seton Creek but failed to continue upstream, returned to the tailrace. When 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 in Seton Creek 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).

During the 1978-82 Portage Creek migrations the tailrace delay of 139 radio-tagged sockeye was studied (Table 12). Amongst those fish 307 forays upstream to Seton Creek or its plume were documented. The success of the forays was greater when the Cayoosh Creek component was less than about 10% (50.2%) than when it exceeded 10% of Seton Creek (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 11 and 12). Forays were made more frequently by Gates Creek fish than by Portage Creek fish.

Fish Released in Seton Creek

The response of radio-tagged fish to various mixtures of Seton Lake and Cayoosh Creek waters in Seton Creek was further examined by releasing fish in Seton Creek (or its plume) downstream of the Cayoosh Creek confluence. Again success (defined as upstream migration to Seton Dam) was related to the proportion of Cayoosh Creek water in Seton Creek (Table 13). During the

TABLE 12. Response of radio-tagged Portage Creek sockeye salmon during forays upstream from the tailrace of Seton powerhouse, to various mixtures of Seton Lake water diluted by Cayoosh Creek water in 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
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 < .01	

* Includes two data groupings which overlap to 11%.

migration of Gates Creek sockeye salmon all forays were successful when the Cayoosh Creek component was less than 20% and none were 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 the results. However, 99 percent confidence limits were calculated for those proportions (Woolf, 1968). The confidence limits did not overlap (10/10 confidence limits = 6.9-10.0 of 10; 0/10 confidence limits = 0-3.1 of 10) and the results can therefore be considered significantly different.

During the Portage Creek sockeye salmon migrations the upstream migration success of radio-tagged fish released in Seton Creek was 86% (37/43) when the Cayoosh Creek component was less than 10% of 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 all observations made under those 2 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% of Seton Creek (Table 13). Those proportions were significantly different ($z = 3.71$, $P < .01$). The migration success rate was lowest (37.5%) when the Cayoosh Creek component exceeded 40% of Seton Creek discharge.

On some occasions the 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. To examine the possibility that the increased attraction of fish to Seton Creek when the Cayoosh Creek component was low

TABLE 13. Response of radio-tagged sockeye salmon released in Seton Creek (or its plume) downstream of the Cayoosh Creek confluence at various mixtures of Seton Lake water diluted by Cayoosh Creek.

	Percent Cayoosh Creek Water in Seton Creek %	Numbers of Fish Released	Migrated Upstream
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%)
	(99% conf. limits = 6.9-10.0/10)		
	> 20	10	0 (0%)
	(99% conf. limits = 0-3.1/10)		
II. Portage Creek Sockeye Salmon			
1978	10-20	1	1 (100%)
	20-30	6	3 (50%)
	30-40	2	1 (50%)
	> 40	8	3 (37.5%)
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%.

might be related to the increased total discharge of Seton Creek on those occasions, 9 fish were released in Seton Creek above the Cayoosh Creek confluence. Those releases were done 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). In all cases upstream migration resulted, indicating that high discharge was not a requirement for successful migration.

2. Pink Salmon

Four pink salmon, captured during their migration, were radio-tagged during the course of the study. These fish all migrated from the tailrace of the powerhouse to Seton Creek within 8 hr and none returned to the tailrace. Although too few pink salmon were radio tagged to permit detailed comparisons with the behaviour 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 when they encountered it during forays from the tailrace.

DISCUSSION

The olfactory hypothesis of salmon homing states that: 1) each stream possesses a characteristic odour which is imparted by local geochemistry, flora or fauna and is detectable by salmon, 2) salmon are able to discriminate between the odours of different streams, and 3) salmon are able to retain the memory of the homestream odour during the oceanic residence and utilize the odour as a homing cue to return to their homestream (Hara, 1975; Hasler and Wisby, 1951; Hasler *et al*., 1978). The foregoing investigators have postulated a mechanism of imprinting whereby the distinctive homestream odour(s) are learned by the juvenile salmon at, or prior to, emigration from the rearing area to the sea. Recently, others (Nordeng, 1971 and 1977; Stabell, 1984) have proposed a mechanism by which homing might be explained by a genetically-based attraction to pheromones excreted or secreted by conspecific juveniles present in the homestream. Evidence for the latter mechanism appears strongest for Atlantic salmon, and less convincing as an explanation for homing in Pacific salmon. In the cases of both sockeye and pink salmon, conspecific juveniles may be absent from the homestream during the spawning migration. Consequently, the following discussion will be based upon the assumption that the homing migration is predicated upon imprinting of the juvenile fish to the odour(s) of the homestream waters, although the discussion of migration behaviour would not be substantially altered if a genetically-based pheromone mechanism were active.

The foregoing investigators have hypothesized that the long-term "memory" of the imprinted homestream odour releases, in its presence, a positive rheotactic behaviour, causing the fish to swim upstream toward the homestream. Johnsen and Hasler (1980) studied the migratory behaviour of coho salmon imprinted to synthetic odours and concluded that upstream migration was controlled by the presence of the imprinting odours:

> "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 odour elicits rheotactic responses in the salmon so that localization of the odour occurs through positive rheotaxis rather than by detection of an increasing odour 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 odour releases positive rheotaxis. Scholz et al. (1972) observed a similar upstream behaviour in response to the ebb tide in an estuary.

The preference shown by sockeye salmon during the preliminary 1980 preference experiments (Table 1) for Seton Lake water over Cayoosh Creek water is consistent with the olfactory hypothesis which predicts that homing salmon are able to discriminate between their homestream water and non-homestream water and will exhibit positive rheotaxis in the presence of homestream water. The subsequently demonstrated ability of sockeye to discriminate between Seton Lake (homestream) water and various dilutions (as little as 10%) of Seton Lake water diverges from the conventional olfactory hypothesis concept since those fish failed to consistently exhibit a simple positive rheotaxis when exposed to Seton Lake water. Instead, the fish apparently were able to accomplish a more complex comparative or decision-making process by choosing the water source with the greatest concentration of homestream water. This finding was consistent for both Gates and Portage Creek sockeye salmon throughout the 3 years during which water source preference was tested in the experimental apparatus (Tables 1, 2, 4, 5 and 6), and through 5 years of radio-telemetry observations of sockeye in a field setting (Tables 11-13).

The behaviour of groups of sockeye salmon as compared to the behaviour of individual fish was studied to determine the appropriateness of testing the water source preference of the fish in groups. Since sockeye salmon are a schooling species it was logical to test them in groups. However, treatment of the data required an understanding of 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. Comparison of the results of 1981 Gates Creek sockeye tested singly and in groups showed that the responses were similar and that each fish's choice could therefore be considered as a separate result (Table 3). This permitted the testing of many more conditions than could otherwise have been achieved.

Experiments using sockeye with obstructed nares provided convincing evidence that the observed preference for Seton Lake water was based on olfaction. These 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 migration toward the test and control water sources can be considered analogous to upstream migration, it is evident that the stimulus for upstream migration was removed by obstructing the nares. Bodznick (1978a) observed a similar inability of sockeye fry with occluded nares to show a preference for lake water over stream water 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 behaviour 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 cauterization or severance of the olfactory nerve, which might cause 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 temporarily 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 conclusions 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, and that the "upstream" or migrational orientation of the fish was dependent upon the ability to detect the Seton Lake water.

Several possible alternative explanations for the observed preference behaviour were examined. It is well known that, given a choice, fish will consistently choose a "preferred" temperature, and it was reasoned that temperature might be the basis for the preference observed in the tank experiments. Artificially lowering the temperature of one control water source by an amount equal to or greater than any temperature differences observed during the experiments did not create a preference for either temperature of the homestream water. In such a situation sockeye salmon might be expected to detect and choose water of a preferred temperature since it is known that at least during some stages of the life cycle they carry out vertical migrations, which may function, among other things, as a form of behavioural thermoregulation which appears to optimize food conversion efficiency (Brett, 1971). One of the two temperature choices offered (16.1°C) is very close to the optimal temperature for growth and swimming performance of juvenile sockeye salmon (15°C). Consequently, if temperature were a primary factor in the choice made by the fish, the 16.1°C source should have been attractive and a preference for this source would have been expected.

Additional temperature analysis of all of the 1981 and 1982 water source preference experiments indicated that the results were free of a temperature bias. Water mixture treatments which resulted in a significant preference for Seton Lake water elicited this preference regardless of the relative temperature of Seton Lake water and the test mixture (Table 9). In addition, the results for these three relative temperature conditions were homogeneous, indicating that the strength of the preference for the homestream water did not vary with temperature. For water mixtures which did not individually result in a significant preference for the Seton Lake water there was, in nearly all cases, a numerical preference for Seton Lake water (Table 10). Only for one of the relative temperature groupings (Seton Lake water colder) was this preference significant ($P < .05$) but, the pooled results indicated a significant preference for Seton Lake water owing to the greatly increased sample size ($P < .05$). Again, the results indicated homogeneity among the results for the three relative temperature groupings (Seton warmer, colder or the same as the test mixture) indicating that the response was not altered by temperature. The evidence indicates that the preference consistently shown for Seton Lake water over various mixtures of Seton and Cayoosh Creek water was not based on a temperature preference.

The possibility that the preference for Seton Lake water was instead based upon an avoidance of Cayoosh Creek water was also investigated. Others have observed increased activity levels in fish exposed to water from streams nearby the homestream (Idler _et al_., 1961; Oshima et al., 1969). In these instances it is not certain whether the activity represented a positive or negative response to that water. It may be that a form of negative imprinting has evolved to ensure that fish do not accidentally enter unsuitable streams near the homestream. It is also possible that a negative response (i.e. avoidance) to Cayoosh Creek could be based upon a recognition that Cayoosh Creek contains primarily water 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 devoid of lakes. Bodznick (1978a) has observed that sockeye fry respond innately with the appropriate rheotaxis to lake or non-lake waters depending upon whether their rearing lake is upstream or downstream of their point of emergence. Bodznick proposes 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 water as non-lake water and therefore avoid it. It should also be noted that sockeye salmon commonly spawn in streams not fed by lakes, and it is therefore 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 Seton water.

No evidence was obtained that Cayoosh Creek water was actively avoided in the water source preference experiments. 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 ($P < .005$). If avoidance of Cayoosh Creek water were occurring a reduced percentage of the fish should have made a choice when Cayoosh Creek water was present in both ends and the majority of fish should have remained in the center pool. Whitman et al. (1982) observed that a reduced number of fish made a choice when ash caused an avoidance response. Such avoidance behaviour did not occur in the present study. In fact, a higher proportion of fish made a choice when presented with two test mixtures than when presented with only one test mixture and a Seton control.

The foregoing does not completely preclude the possibility that the observed results were based on a graded negative response to the Cayoosh Creek water in the test mixture, such that 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 behaviour.

The possibility that Cayoosh Creek contained a unique or unusual constituent which in some way masked the attractive odour of Seton water or caused an active avoidance was further investigated by examining the response to a test mixture containing a novel water to which the Seton-Anderson sockeye should be naive. A preference for Seton Lake water over this mixture indicated that the effect of the Cayoosh Creek water in the usual test mixture was in no way unique. It is therefore very unlikely that the observed preference for Seton Lake water actually resulted from avoidance of Cayoosh Creek water in the test mixture or in Seton Creek. Certainly Cayoosh Creek does not contain a material which causes a universal avoidance response among salmon, since large numbers of pink salmon spawn in Cayoosh Creek upstream of its confluence with Seton Creek (IPSFC records).

The possibility was also considered that the "recent experience" of the experimental fish, that is exposure to Seton Lake water in the tailrace, was a critical factor in the results of the water source preference experiments and radio-telemetry studies. Brett and Groot (1963) expressed similar concerns, and Oshima et al. (1969) noted that many behavioural 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 exhibited a preference for 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 behavioural evidence both for and against the hypothesis that the results of these types of experiments merely reflect an attraction to the odour of the water to which the fish were most recently exposed. In both cases the authors concluded that recent experience is not important and that during homing migration there is a substitution for, or inhibition of recent experience by the retained or long term memory which resulted from imprinting. In any event, in the present study homestream water was present in easily detectable concentrations in both choices presented to the fish. It is therefore clear, that choices were made on the basis of relative mixtures, not just presence or absence of homestream water or the most recently experienced water.

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 course of the migration. The Gates Creek sockeye, during tests in 1981 and 1982, consistently preferred Seton Lake water over test mixtures of Seton Lake water diluted 20% by Cayoosh Creek water (Tables 2 and 4). Lesser dilutions (10 or 15%) resulted in a numerical but statistically non-significant preferences for the Seton Lake water. In comparison, Portage Creek sockeye salmon showed a significant preference for Seton Lake water over test mixtures diluted from 10 to 20% by Cayoosh Creek water. During the 1981 experiments the 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 5). In 1982 the Portage Creek sockeye salmon exhibited the opposite trend over time in sensitivity to test mixtures (Table 6).

The reason for the apparent difference between Portage and Gates Creek sockeye salmon in sensitivity to various dilutions of Seton Lake water may be related to the relative proximity of the two spawning streams to Seton Creek. If the fish were also responding to constituents from their particular natal streams in Seton Lake water the difference in sensitivity might be understandable. Gates Creek comprises a lesser proportion of Seton Lake water than does Portage Creek since there is some local inflow to Anderson Lake between Gates Creek and Portage Creek. Therefore, it would be expected that Gates Creek sockeye would not be as strongly attracted to the Seton Lake water in the tailrace or to the control water in the preference experiment, 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 delay between the two races. Gates Creek sockeye salmon arrive at Seton Creek relatively silvery, ripen to sexual maturity rapidly in the summer water temperatures which generally exceed 16°C, 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 exhibit delay en route and on the spawning grounds prior to spawning (Fretwell and Hamilton, 1983).

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 there is a peak in the strength of the response to homestream odour 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 exhibited increased EEG response to 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 odours 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" in the classical sense that it is the water that the smolts are exposed to during the proposed 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 location. It is a moot point whether the peak period of sensitivity to Seton Lake water (if it exists) would correspond to the peak spawning period or to the time during the migration when Seton Creek would be encountered. Thus, the water source preference experiments in which the Portage Creek sockeye were able to discriminate a dilution of Seton Lake water by only 10% Cayoosh Creek water may correspond to the period of the migration schedule when peak numbers of these fish would be entering Seton Creek and would therefore be most receptive to 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 only the 20% Cayoosh Creek test mixture resulted in a preference for Seton Lake water (Tables 5 and 6). 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 as they encounter Seton Creek.

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 the change in response over time and between runs might have resulted from a change in those parameters. However, of the water chemistry characteristics examined (including hardness, calcium, fluoride, sulphate, conductance and alkalinity), none appeared to suit the pattern of changing response of the fish. The relative concentration of those parameters in Seton Lake and Cayoosh Creek waters was at times not measurably different, and in the case of certain parameters, reversed over time. Consequently, none of the parameters measured, at least singly, can explain the changing response of the fish during the experiments. This does not, however, prove that some change in the strength of cues present in the water might not have been responsible for the change in response of the fish.

It is assumed, by virtue of the design of the water source preference experiments, in which water supplies were reversed between each of the paired tests, that the results are independent of any innate directional preference exhibited by the fish. Analysis of the data indicated that such directional preferences did exist. A significant preference was shown by Portage Creek sockeye salmon in 1980 for the west end of the test apparatus over the east end. In 1981 and 1982 there was an overall preference shown for the north end over the south end and the results were homogeneous throughout the Gates and Portage Creek sockeye salmon migrations (Table 8). These directional preferences 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 period of migration up the Fraser River, or is simply the opposite of that learned during the juvenile migration to the outlet 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. However, it has been reported elsewhere (Groot, 1965; Quinn, 1981) 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 in which to locate their natal stream, to possess the opposite compass orientation to aid them during the return migration through the lake system. It is therefore logical to speculate that the northerly and westerly directional orientation exhibited by the Gates and Portage Creek sockeye salmon is a navigational aid in locating the north-westerly end of Seton Lake where Portage Creek enters. It may be further speculated that the directional orientation of Gates Creek fish subsequently changes to a preference for a south-westerly direction upon exposure to Anderson Lake or Gates Creek water. This directional preference would aid those fish in locating the mouth of Gates Creek at the south-westerly extremity of Anderson Lake.

The foregoing discussion regarding directional preference is speculative. It is possible that the directional preferences exhibited by the fish may instead have been the result of perception by the fish of nearby topographical features, vegetation, or variations in light intensity. The westerly preference of the fish in 1980 was away from the large cement power canal aqueduct, which stood 10-15 m above the east end of the test apparatus. The underside of this structure was in shadow and might therefore have been expected to attract the test fish since captive fish often seek areas of darkness or shadow. The nylon mesh which covered 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. Further possible bases for the directional preference include celestial cues and sound vibrations from nearby Cayoosh Creek.

The foregoing directional preference of the fish does not alter the conclusions regarding the water preference experiments. Since the olfactory tests were paired, any directional preference would merely have strengthened the olfactory preference in one direction, and weakened it in the other direction, thereby cancelling the effect.

Extension of the results of the preference studies to conclusions regarding choice-making among migrating fish depends upon some confidence that the fish in the test apparatus exhibited a degree of "normality" in their behaviour. It is recognized that the stress imposed by capture and transportation, as well as the artificiality of the test environment, would influence the response of the fish. However, the consistent nature of the results obtained indicates that the aforementioned divergences from the natural environment did not produce chaotic behaviour. The fish responded in a reasonably predictable fashion, consistent with the hypothesis that they would choose the mixture with the highest concentration of their homestream water.

The similarity of the results obtained using radio-tagged sockeye salmon in the river setting lends further credence to the results obtained in the preference apparatus. 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 Seton Creek: 92.6% of forays into Seton Creek or its plume were successful when Cayoosh Creek water comprised less than 20% of the discharge of Seton Creek (Table 11). In contrast, when Cayoosh Creek water comprised more than 20% of the 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 12). 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 delay. Radio-tagged Portage Creek sockeye salmon were successful 50.2% of the time when the Cayoosh Creek component was less than 10% of Seton Creek, but at greater dilutions the success of forays dropped significantly to 28.3%. Success was particularly low when the Cayoosh Creek component of Seton Creek exceeded 30%.

The release of radio-tagged sockeye salmon in Seton Creek or its plume produced results similar to the foregoing (Table 13). 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 were 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 the water source preference experiments with Portage Creek sockeye salmon.

In general the release of radio-tagged fish in Seton Creek or its plume resulted in higher success of upstream migration than did volitional forays by radio-tagged fish from the tailrace into Seton Creek. This may be because the fish released into the Creek could not possess a spatial awareness of the alternative water source in the tailrace. In contrast, fish making a volitional foray might possess a "short-term memory" of the similar water source at the tailrace, if such a faculty, as proposed by Cooper and Hasler (1973), exists. If the fish could not discriminate between the homestream odour concentration at the two locations they might sometimes return to the tailrace, especially if physical conditions there were "preferred".

The upstream migration of radio-tagged sockeye salmon released upstream of the Cayoosh Creek confluence, even at minimum discharge, indicated that the observed behaviour of the radio-tagged fish was governed primarily by the proportion of homestream water and not by the magnitude of discharge. This does not preclude the possibility that the behaviour of the fish in Seton Creek is affected by the magnitude of the discharge. The depths and velocities in Seton Creek are dependent upon the discharge level and it must be expected that the relative attractiveness of Seton Creek and the powerhouse tailrace to adult migrants will be a function not only of the concentrations of homestream odour, but of depths and velocities as well. The discharge of approximately 100 m^3/s from the powerhouse probably 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 of approximately 11 m^3/s. It could be speculated 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. This hypothesis could be tested but it would require a large number of radio-tagged fish and a great deal of flexibility on the part of B.C. Hydro in regulation of the flow at Seton Dam.

The potential effects, upon the fish, of capture and tagging and the presence of the radio tag in the gut must be considered in the evaluation of the foregoing telemetry studies. Petersen tags have been extensively utilized, with good success, to study salmon migration (IPSFC records). 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 (approximately 5 g) relative to the size of the fish being tagged, and comprised less than 0.2% of the weight of the fish. 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.

Pink salmon tested in the water preference apparatus showed no preference for either pure Seton Lake water or any dilution tested (Table 7). The random distribution in the 3 compartments of the test apparatus by all groups of pink salmon obtained from the powerhouse tailrace appeared indicative of fish no longer in an active migratory state. In effect the fish did not exhibit an "upstream" response. It is possible that the pink salmon failed to respond in a manner similar to the sockeye because of a greater susceptibility to handling stress. However, 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 3 test compartments was non-random in favor of the center pool: the fish were either 1) not sufficiently exploratory to distribute themselves randomly throughout all 3 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 behaviour of this latter group of pink salmon was similar to that of sockeye with obstructed nares, although the response observed in the two groups may have occurred for a different reason in each case. The migratory behaviour of the impaired sockeye was likely reduced or eliminated because of their inability to detect the odour of their homestream water. In the case of the pink salmon, the fish likely were able to detect the homestream water but did not exhibit positive rheotaxis because they had already reached the spawning grounds. Both waters tested, from Seton and Cayoosh Creek, are waters experienced by the pink salmon during incubation, emergence and/or downstream migration. It is probable (Horrall, 1981) that imprinting in pink salmon occurs during the period 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 passed their spawning grounds, would be expected to be even less responsive. It has been observed that Seton Creek pink salmon which pass the Seton Dam fishway, subsequently exhibit negative rheotaxis upon reaching Seton Lake (Fretwell, 1982). These fish are frequently observed schooling at the power canal intake screens, apparently attempting to move downstream.

Delay of pink salmon at the tailrace of the powerhouse is of shorter duration than delay of sockeye. This is evidenced by pink salmon tagged with Petersen discs in the tailrace for enumeration purposes. These fish are subsequently recovered on the spawning grounds upstream but are almost never recaptured in the tailrace (IPSFC records). The four pink salmon radio tagged during these studies delayed in the tailrace for only a very short period of time compared to the radio-tagged sockeye. Two explanations for this are possible. It has been hypothesized, based on their life history, that pink salmon may be the least specific in their homing precision of all Pacific salmon; they therefore should be more prone than sockeye to accept dilutions of their homestream water. Also, if imprinting occurs, pink salmon must imprint to water characteristics prior to and/or immediately after emergence, and it is likely that they would be imprinted to both Seton Lake and Cayoosh Creek waters or to a mixture of both. After being blocked in their migration at Seton powerhouse pink salmon might find the Seton Lake and Cayoosh Creek mixture in Seton Creek just as "attractive." The "willingness" of the pink salmon to leave the tailrace after a shorter delay than for sockeye may be related to lower "biological affordability" due to a rigid migration and spawning schedule. Fraser River pink salmon generally spawn within days of arrival on the spawning grounds whereas sockeye, particularly late-season races, frequently arrive on the grounds with many days or weeks to spare.

In light of the above observations on pink salmon, it might be postulated that if sockeye salmon smolts migrated downstream from Seton Lake via Seton Creek instead of primarily through the powerhouse they might also imprint to the Seton and Cayoosh Creek mixtures in Seton Creek. If such imprinting occurred, sockeye might respond in a similar manner to pink salmon, showing no preference for Seton or Cayoosh Creek water in the water source preference experiments and readily entering Seton Creek when it is encountered, rather than frequently returning to the tailrace. The fallacy of this argument was fortuitously demonstrated during the 1977 juvenile sockeye downstream migration and the subsequent adult return 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 must have emigrated via Seton Creek, thereby encountering a mixture of Seton and Cayoosh Creek waters. The adults returning in 1979 exhibited the usual delay in the tailrace of the powerhouse and radio-tagged sockeye frequently returned to the tailrace from forays upstream to Seton Creek (Tables 11-13). Evidently the short exposure of smolts to a mixture of Seton and Cayoosh Creek waters for approximately 1 hour or less (assuming passive drift) was not sufficient to imprint the juvenile sockeye to the Seton and Cayoosh Creek mixture at that stage in their development. Others have reported effective imprinting to occur at the smolt stage in as little as 4 hours (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 the adult salmon migration is dependent upon a sequence of odour cues encountered in the reverse order to that experienced as a juvenile. If the cues are encountered out of sequence it may be that the fish will 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 responding positively to a Seton-Cayoosh mixture which was "expected" to occur earlier in the sequence.

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. Hasler (1966) and Hasler et al. (1978) proposed that imprinting occurred in the natal stream to distinctive odours imparted by local flora, rocks and soils. Others have suggested that other fish, especially conspecifics, may provide all or part of the distinctive homestream odour (Døving et al., 1974; Nordeng, 1971, 1977; Selset and Døving, 1980; Solomon, 1973; Ueda et al., 1967) or that fish home on a "bouquet" of many odours (Liley, 1982). Implicit in this version of the olfactory hypothesis is a stimulus-response mechanism by which upstream migration is triggered in the adult salmon by detection of the presence of the odour or odours to which the fish imprinted as juveniles. The results of the preference studies and radio-telemetry observations presented here do not fully support the concept that upstream migration always results from an encounter with homestream water. A more complex response is suggested.

A second version of the olfactory hypothesis is that the downstream migrating juveniles imprint to a series of distinctive odours or combinations of odours 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 and is therefore not entirely supported by the results of the present study. It would be possible to test the sequential hypothesis utilizing the present preference trough apparatus and study populations. This could be done by testing the response of migrating Gates Creek sockeye salmon to the five water types which the fish encounter in sequence during the upstream migration: Fraser River, Seton Lake, Portage Creek, Anderson Lake and Gates Creek water. If fish were exposed in the preference trough apparatus to various pairs of the foregoing waters the effect of encountering water sources out of sequence could be ascertained.

A third, "generalized" odour hypothesis holds that streams near the homestream, due to similarities in flora, fauna and geochemistry, will have more similar odours than will geographically more remote streams. Therefore the homing fish, at each confluence, must simply choose the odour most similar to its homestream (Gleitman and Rozin, 1971). This would obviate the need for fish to be able to detect extremely small concentrations of homestream water which might be present 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 homestream excited migrants. Ueda et al. (1967) observed an elevated EEG response in chinook and coho salmon to water from tributaries near the homestream. Idler et al. (1961) observed a positive behavioural 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 which implies a comparative process on the part of the 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 it appeared that the fish could determine which of the two water sources contained the greater proportion of homestream odour. The fact that homestream water was present did not ensure that upstream movement resulted when the water mixture was encountered, as would be predicted by the conventional olfactory hypothesis as stated by Hasler (1966). It is recognized that there is ample experimental and field evidence indicating that upstream migration behaviour is released 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 upon 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 any lake or stream system are likely to be ubiquitous, albeit in varying concentrations in different watersheds. It is proposed, therefore, that the 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 that 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 project involving diversion or storage of water. Removal, or alteration of the flow of a tributary stream which contributes to the mixture of odours to which salmon are imprinted has the potential to impair the ability of the fish to return to the homestream.

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