

LOCOMOTOR RESPONSES OF JUVENILE AND ADULT SOCKEYE SALMON

(ONCORHYNCHUS NERKA)

TO ACUTE CHANGES IN TEMPERATURE AND SALINITY.

By

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ABSTRACT

The locomotor responses of juvenile and adult sockeye salmon (Oncorhynchus nerka) to concurrent changes in temperature and salinity were examined in a controlled laboratory setting. I hoped to better understand how these environmental factors influence the coastal movements of migrating salmon.

Juvenile sockeye were captured during the downstream migration from Great Central Lake on Vancouver Island, British Columbia, Canada. The fish were acclimated for 1 wk at 10°C, 20 ppt, and then tested in annular activity tanks. Spontaneous locomotor movements were recorded during concomitant changes in temperature and salinity using infra-red photometry.

Raising the water temperature by 4°C in 1 h caused a dramatic increase in locomotor activity. Decreasing temperature by 4°C or varying salinity by 10 ppt from the control levels did not influence routine swimming speed and there was no interaction between factors.

Adult sockeye homing to the Fraser River, British Columbia, Canada were captured along the nearshore migration route in two oceanographically distinct regions. Three groups of fish were collected from the cold, saline waters of Queen Charlotte Strait, near the northern end of

Vancouver Island. Two groups of sockeye were captured within 60 km of the Fraser River in the warmer, less saline waters of the Strait of Georgia. The adults were acclimated 2 - 5 days at 12°C, 30 ppt and locomotor activity was tested in annular activity tanks.

Routine swimming speed and turning rate rose when the water temperature was raised by 4°C in 2 h, however, locomotor activity was not influenced by decreasing temperature. In addition, decreasing salinity by 10 ppt in 2 h had no effect on swimming activity of adult sockeye and there was no interaction between the two factors. Fish taken from the Strait of Georgia generally showed a less dramatic response to increasing temperature than adults captured in Queen Charlotte Strait.

Results indicate that warm coastal temperatures may influence the nearshore migration of both juvenile and adult sockeye salmon.

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## INTRODUCTION

The coastal migration is an important phase in the life history of anadromous Pacific salmon (Oncorhynchus sp.). Temperature and salinity gradients have been proposed to influence the nearshore movements of both juvenile and adult salmon (Baggerman 1960a, McInerney 1964, Hurley and Woodall 1968, Tully et al. 1960). However, it has also been hypothesized that other factors such as tidal currents or odor cues exert a greater influence on migration (LaBar et al. 1979, Stabell 1982). At present, the ways in which oceanographic conditions affect the migratory behavior of salmon is poorly understood (Groot and Quinn 1987).

This thesis examined the locomotor responses of juvenile and adult sockeye salmon to acute changes in temperature and salinity. Both of these factors may play a role in the coastal movements of migrating salmon. With respect to the juvenile migration, McInerney (1964) suggested that temporal changes in salinity preference could regulate the seaward migration of young salmon through estuaries. Experiments in vertical gradient tanks led Hurley and Woodall (1968) to conclude that time-varied changes in preference for temperature and salinity direct juvenile pink salmon (O. gorbuscha) during the outmigration. Similarly, Straty and Jaenicke (1980) found that sockeye smolts oriented to salinity and temperature gradients while

in nearshore waters. Quinn and Groot (1983) concluded that compass orientation and preference for saline water could direct juvenile chum salmon (O. keta) during the feeding migration.

Several researchers have questioned the role of temperature and salinity on juvenile salmon migration (e.g. Fried et al. 1978). LaBar et al. (1979) concluded that migration patterns of Atlantic salmon smolts were not affected by any environmental variables other than water current. Similarly, McCleave (1978) attributed the estuarine movements of juvenile Atlantic salmon to passive drift, dependent on tidal flow.

Studies relating the return migration of adult salmon to oceanographic variables are often based on statistical correlations using fisheries catch records (reviewed by Leggett 1977). One of the more recent studies examined the homing migration of sockeye salmon (O. nerka) to the Fraser River, British Columbia (Groot and Quinn 1987).

Each year, between 2 and 20 million sockeye salmon return to the Fraser River (IPSFC 1954-1984). Access to the river is by one of two possible routes. Historically, the majority of migrants approached the Fraser River from the southern end of Vancouver Island (southern route). The fish adopting this route approach south and then east through Juan de Fuca Strait before turning north to the Fraser River

(Groot and Quinn 1987). The remainder of the sockeye would return between the northern tip of Vancouver Island and the mainland coast (northern route) and approach the river south through Johnstone Strait (Groot and Quinn 1987). Since 1977, greater proportions of returning sockeye have used the northern route than had previously done so (Mysak et al. 1986, Hamilton 1985). A number of hypotheses have been proposed to explain the interannual variability in diversions through the northern passage (known as the Johnstone Strait Diversion).

Tully et al. (1960) and Royal and Tully (1961) suggested that the relatively high JSD of 1958 (35%) could have been a result of warm water intrusions from the south deflecting migrants farther north so that they migrated through Johnstone Strait. Favorite (1961), on the other hand, hypothesized that Fraser River water emanating north through Johnstone Strait could act as an attractant to returning adults (see also Wickett 1977). Groot and Quinn (1987) showed that from 1953 to 1977 Fraser River discharge was significantly correlated with sockeye returns through Johnstone Strait, however, since 1977 the relationship has broken down. Groot and Quinn (1987) concluded that temperature and salinity gradients around the northern tip of Vancouver Island do not guide the movements of Fraser River sockeye but reflect ocean conditions that may directly influence behavior during the homing migration (i.e.

preference/avoidance responses) or indirectly, prior to the migration, by affecting food supply.

The locomotor responses of migrating sockeye salmon to concurrent changes in temperature and salinity have not been analyzed in the laboratory. Few experiments have focussed on the effects of temperature and salinity corresponding to actual conditions that may be encountered in coastal waters. In addition, it is not known how responses to temperature and salinity fit into the general scheme of fish migratory mechanisms (e.g. Neill 1979, 1984). In this study, I examined the swimming activity of migrating sockeye salmon during concomitant changes in temperature and salinity, within a range that could be encountered in nearshore waters. The hypothesis I tested was that rapid changes in temperature and salinity have a direct effect on locomotor behavior and could thereby influence coastal migration patterns of juvenile and adult sockeye.



## LITERATURE REVIEW

This review will consist of two sections. First, I will discuss the general life history of Pacific salmon, stressing the influence of environmental factors on migratory behavior. The second section will review the physiological and behavioral responses of migratory fish to temperature and salinity, including relationships to season and stage of maturation.

### 1. THE LIFE HISTORY OF PACIFIC SALMON

Pacific salmon typically migrate from freshwater lakes and rivers to oceanic waters, and, after one to seven years, return to spawn and die in the natal stream. The dramatic environmental changes that salmon encounter require appropriate physiological and behavioral adaptations. In addition, directional information gained from environmental cues may also guide migratory movements.

#### A. ENVIRONMENTAL INFLUENCE ON THE BEHAVIOR OF YOUNG SALMON

The environment affects the behavior of Pacific salmon soon after the egg has hatched. The first response of newly emerged salmon is to wriggle down beneath rocks and gravel (Bams 1969); probably as a reaction to light (Hoar

1955, 1958, Heard 1964). In addition, developing alevins exhibit a 'righting response' that persists through yolk absorption (Dill 1982).

Hoar (1958) showed that oriented responses to environmental cues lead populations of salmon fry to their respective rearing areas. However, the early behavior of fry shows marked interspecific and interpopulation differences (Hoar 1958, Brannon 1972) implying genetic control (Raleigh 1971).

Pink salmon fry begin the seaward migration soon after yolk absorption (Hoar 1956), and downstream movements result from a negative rheotaxis in response to low light intensity (McDonald 1960). Chum fry also begin the downstream migration within a few weeks of emergence and riverine movements may depend on negative rheotaxis in response to high water temperature (Keenleyside and Hoar 1953). In addition, a relationship may exist between compass orientation and rheotactic behavior. Quinn and Groot (1984) showed that chum fry exhibited unimodal compass orientation in high water flow, and bimodal directional tendencies in low flow.

Coho (O. kisutch) fry remain in river systems for approximately 18 to 30 months, during which time distribution is a function of social interactions (Hoar 1958) and rearing channel temperature (Glova 1986). Chinook (O. tshawytscha) may proceed directly to the estuary, or

spend up to a year in the homestream (Reimers 1973, Healey 1980, 1982). Sockeye salmon generally spend the first year or two of life in freshwater lakes. The migration to these rearing areas is probably aided by orientation to odors and water flow (Brannon 1972). Vertical distribution of sockeye during lake residence appears to be dependent on metabolic responses to temperature in relation to food availability (Brett 1971).

## B. JUVENILE MIGRATION

### (i) LACUSTRINE AND RIVERINE MOVEMENTS

Prior to the downstream migration, salmon undergo a number of morphological, physiological and behavioral changes that are requisite for an ocean existence. These processes have been collectively termed smoltification (reviewed by Hoar 1976, Folmar and Dickoff 1980, Wedemeyer et al. 1980). The smolting process is partially under endogenous control and regulated by the neuroendocrine system. In addition, the process appears to be synchronized both by photoperiod (Hoar 1976) and temperature (Clarke and Shelbourn 1985). In particular, seasonal fluctuations in water temperature appear to be important for initiating the downstream migration (Foerster 1937, 1968, Brett 1983, Rogers 1980). Jonsson and Ruud-Hansen (1985) suggested that temperature changes in relation to acclimation temperature

are important for the development of a migratory disposition in young salmon.

The migration of juvenile sockeye salmon out of lake systems appears to be directed by solar and magnetic factors. Groot (1965) found that sockeye smolts exhibit time-varied directional preferences involving celestial orientation (see also Quinn and Brannon 1982), resulting in an active, well oriented migration out of the lake rearing areas (Groot and Wiley 1965, Groot 1972).

Riverine movements of juvenile salmon may be facilitated by compass orientation (Healey 1967, Quinn and Groot 1983), while passive responses to current may also play a role in downstream movements, especially in the lower reaches of the river (Fried et al. 1978, Thorpe et al. 1981). MacDonald (1960) proposed that decreasing light levels are important for maintaining negative rheotaxis during the downstream migration (see also Hoar 1958). In addition, temperature may influence migratory behavior in conjunction with other environmental factors such as water flow (White 1939), climate (Solomon 1978), and lunar cycle (Grau 1982).

#### (ii) ESTUARINE MOVEMENTS

The environmental conditions encountered in the river estuary impose significant physiological stress on

migrating salmon (Healey 1982, Simenstad et al. 1982). Exposure of pink and chum fry to high salinity water results in a transitory decrease in swimming activity (Houston 1957) that may inhibit predator avoidance (Houston 1959). The timing of the downstream migration corresponds to high biological productivity in the neritic zone (Simenstad 1982), however, the first few weeks in saltwater probably account for a large proportion of the overall salmon mortality (Brett 1983).

Estuaries serve several roles for young salmon, and the duration of coastal residence shows marked interspecific differences. Sockeye and chum salmon move swiftly through nearshore areas (Brett 1983, Quinn and Groot 1983), while chinook and pink salmon may inhabit coastal waters for a number of months (Healey 1980, Hurley and Woodall 1968). Progressive changes in preference for colder temperatures and more saline waters has been cited as a potential orientation mechanism for migrating smolts (Hurley and Woodall 1968, McInerney 1964, Baggerman 1960b). However, it appears that other environmental factors may be of greater importance for the coastal migration of some salmonid species. Tracking studies of Atlantic salmon (Salmo salar) smolts through estuaries have shown that current plays a major role in seaward movements (Labar et al. 1979). Eriksson (1984) found that juvenile Atlantic salmon exhibited negative rheotaxis in fresh and brackish water,

however, migratory behavior was influenced mainly by water current.

#### C. OCEAN RESIDENCE OF MATURING SALMON

The coastal migration of young Pacific salmon has been reviewed by Hartt and Dell (1986), while the offshore distribution of maturing sockeye salmon in the northeast Pacific has been reviewed by French et al. (1976). Favorite and Hanavan (1956) noted that sea surface conditions did not significantly affect oceanic distribution of salmon, however, specific water masses seemed to delimit their range in both a southerly and northerly direction. Favorite et al. (1976) suggested that sockeye salmon distribution was bounded by identifiable water masses- the Subarctic Boundary in the north, and the Transitional Domain in the south.

During ocean residence, seasonal changes in environmental parameters may affect the distribution of maturing salmon. Royce et al. (1968) suggested that currents in the ocean (in particular the Alaskan gyre) were responsible for seasonal variations in the distribution of Bristol Bay sockeye. Burgner (1980) concluded that salmon rearing areas were primarily determined by genetic factors. However, French and Bakkala (1974) found that both temperature and food supply were important in determining movements and distribution of maturing sockeye. This view

was endorsed by Leggett (1977) who suggested that ocean temperatures may affect food availability and thus influence migratory patterns (see also McAlister 1969, Andrievskaya 1957, Ito 1964). Watanabe (1954) reported that high seas salmon fishing concentrated at areas bounded by cold northern surface waters, and warm water intrusions from the south. Horizontal gradients of temperature and salinity, associated with upwelling, appeared to increase catch efficiency. Similar reports by Nakai and Honjo (1954) related increased salmon catches to areas of high primary production.

#### D. HOMING MIGRATION

##### (i) OPEN OCEAN MOVEMENTS

A number of hypotheses have been proposed to explain the homing migration of salmon. Leggett (1977) concluded that salmon may gain directional information from polarized light, sun, or geomagnetic cues. Hasler (1971) proposed the use of a sun-compass mechanisms during the open-sea migration. Quinn (1984) suggested that salmon may have a bicoordinate map that permits navigation using the sun or magnetic fields.

Saila and Shappy (1963) developed a computer model that depicted the homeward migration of Pacific salmon as a random walk accompanied with a slight directional bias. The

authors concluded that well-oriented behavior was not a prerequisite for successful homing. This model was criticized by Quinn and Groot (1984) who showed that many of the model's assumptions were inaccurate. Quinn and Groot (1984) showed that at the optimum cruising speed and observed rate of travel, salmon must migrate with a high degree of orientation to be consistent with known levels of homing success.

Patten (1964) concluded that appropriate 'low-level' behavioral responses to environmental gradients would allow salmon to home with sufficient accuracy. Balchen (1976) extended this view and concluded that migration results from a constant attempt to maintain an optimal physiological state and responses to environmental conditions based on stage of maturation ultimately determine the expression of migratory behavior (see also Neill 1979, 1984). Leggett (1977) endorsed the 'optimisation of comfort' hypothesis, but stressed that additional research is required before applying it to open-sea migrations. Quinn and Groot (1984) emphasized that any migration mechanism must account for known rates of travel in relation to the optimum swimming speeds and the relatively weak gradients of temperature and salinity in the sea.



(ii) COASTAL AND RIVERINE MOVEMENTS

The return migration through nearshore waters once again provides salmon with a wide variety of potential orientation cues (Quinn and terHart 1987). Hasler and Scholz (1983) showed that homestream odors provide the major directional stimulus during the spawning migration. However, the chemical nature of these odors and the extent of their influence on movements through coastal waters is unknown. Stabell (1982) extended the scope of Nordeng's (1977) pheromone hypothesis by suggesting the entire return migration of Atlantic salmon was dependent on orientation to population-specific odors released by migrating juveniles. Evidence indicates that Pacific salmon can identify population-specific odors (Quinn and Tolson 1986, Groot et al. 1986), however, their role in migration remains uncertain.

Recent work has shown that environmental gradients may be important for locating odors during the homestream approach. Doving et al. (1985) proposed that adult Atlantic salmon attempt to gain directional cues by concentrating activity around steep gradients of temperature and salinity--the most likely location for obtaining chemical cues. Quinn and terHart (1987) concluded that the preference of Fraser River sockeye salmon for stratified depths was a potential mechanism for odor location, however, the responses of fish

to tide and horizontal environmental gradients were not easily characterized.

The return migration terminates in the natal stream, where Pacific salmon spawn and subsequently die. During the spawning migration, directional information is gained primarily from homestream odors (reviewed by Hasler and Scholz 1983). Other environmental stimuli that control different stages of the upstream migration include; waterflow, temperature, photoperiod, and tidal action (Gilhousen 1960, Weaver 1963, Banks 1969). The tight energy budget imposed on some migrating salmon (Idler and Clemens 1959), necessitates accurate homing with minimal metabolic cost. Methods to reduce energy expenditure include an ability to distinguish between minor variations in water flow and choose routes that provide the greatest energetic efficiency (Brett 1983).

## II. INFLUENCE OF TEMPERATURE AND SALINITY ON METABOLISM AND BEHAVIOR

Changes in temperature and salinity often have a dramatic influence on the metabolism and activity of fish (reviewed by Brett 1970) and species that undergo diadromous migrations naturally encounter steep gradients of both factors. Physiological stress imposed by the environment has been proposed to affect the distribution of many fish species (reviewed by Leggett 1977). Therefore, it is

important to review some physiological principles of temperature and salinity related to behavioral responses and possible influences on migration.

Temperature influences the activity of poikilotherms by governing the rate of metabolism (e.g. Brett 1967, 1982). Within the thermal tolerance limits, fish operate within a zone of efficiency in which internal metabolism accommodates a range of temperature (Crawshaw 1977). Outside of this range, regulatory or compensatory processes are required (Brett 1970). Instances of physiological temperature regulation in fish are rare and apparently limited to certain scombrid species and lamnid sharks (e.g. Carey and Teal 1969, Carey et al. 1971). In the vast majority of fish, responses to adverse temperature are dependent on behavioral thermoregulation (reviewed by Crawshaw 1977), and to a lesser extent, on physiological compensation (Dizon et al. 1978, reviewed by Hazel and Prosser 1974).

Many studies have dealt with the concept of temperature preference and behavioral thermoregulation (see compilation by Coutant 1977, reviewed by Reynolds and Casterlin 1979). Fish exposed to rapidly changing temperatures exhibit the least activity at the acclimation temperature (e.g. Sullivan 1954, Olla and Studholm 1971). Ivlev (1960) showed that activity levels of young Atlantic salmon were directly related to the absolute difference between preferred and experimental temperatures. Similarly,

Peterson and Anderson (1969) found that Atlantic salmon fry exhibited a rapid increase in activity and oxygen consumption as temperatures departed from acclimation levels.

In a rapid thermal shift, fish show the least activity at the preferred temperature. If, however, fish are exposed to a gradual temperature change, and can equilibrate with the environment, then spontaneous activity is greatest over a temperature range that permits the maximum metabolic scope (Fry 1971). In other words, fish placed in a constant heterothermal environment sequentially select and adapt to temperatures that provide optimum physiological benefits. The point where acclimation and selected temperatures meet represents the species-specific final temperature preferendum (Fry 1971, Reynolds and Casterlin 1979).

Fry (1971) described salinity as a masking factor, essentially adding to the cost of metabolism through the need for regulation. Rao (1968) showed that the metabolic cost for respiration in rainbow trout (S. gairdneri) increased 20% as salinity rose from isosmotic (7.5 ppt) to 15 ppt. However, total metabolism only increased from 20% to 27% as salinity was raised from 15 ppt to 30 ppt. Glova (1972) found that the sustained swimming speed of juvenile coho salmon was affected slightly by salinities ranging from 1 ppt to 20 ppt, but noted that tolerance to salinity

decreased during smoltification. Brett (1970) reported that the metabolic rate of sockeye smolts decreased by 20 to 30% upon transfer from fresh to salt (28 ppt) water.

Although oxygen consumption appears to be lowest at isosmotic concentrations (Farmer and Beamish 1969), selected temperatures may vary considerably with changes in salinity (Beamish 1970). In addition, Job (1959) and Hickman (1959) showed that routine metabolism may also be influenced by salinity and thereby affect spontaneous activity.

Early work showed that some fish can select very narrow temperature and salinity ranges (e.g. Bull 1938), introducing the possibility of a directive influence (reviewed by Brett 1956, 1970). Recent studies have shown that salinity gradients, in concert with temperature, may provide localized areas for migrating fish to obtain other directional cues (Doving et al. 1985, Quinn and terHart 1987). In addition, behavioral responses of fish to salinity may often be dependent on physiological state and can be modified by other external and internal factors (reviewed by Holliday 1971, Woodhead 1975).

Temperature and salinity may direct fish behavior under the influence of internal drive or environmental stress (Holliday 1971). For migratory fish, seasonal variations in environmental stimuli have been shown to influence migrations, often associated with maturational changes (reviewed by Leggett 1977). Laboratory and field

investigations led Norris (1963) to conclude that seasonal temperature changes were directly responsible for the onshore movements of opaleye (Girella nigerens). Olla et al. (1985) tested locomotor responses of juvenile bluefish (Potatomus saltatrix) to vertical temperature gradients, and found a temporal shift in avoidance of cold water that coincided with the southerly fall migration. Nyman (1972) determined that yellow (immature) eels (Anguilla anguilla) were attracted to a rising temperature gradient, whereas silver (mature) eels were attracted and later repelled by the same temperature conditions (see also Westin and Nyman 1979). Westin and Nyman (1977) hypothesized that a seasonal change in the behavioral response to temperature was the single factor that allowed silver eels to migrate back to the Sargasso Sea.

Baggerman (1957, 1960a) noted the influence of maturational stage on the salinity preference of sticklebacks (Gasterosteus aculeatus), but could not demonstrate a significant change in temperature preference. Other studies showed that gulf killifish (Fundulus grandis) exhibit a temporal change in salinity preference, modulated both by the neuroendocrine system (Fivizzani and Meier 1978) and by temperature (Miller et al. 1983).

The role of temperature and salinity in the coastal migration of salmon is not well understood. Both factors could direct movements in nearshore areas by influencing

preference/avoidance behavior (Straty and Jaenicke 1980, Hurley and Woodall 1968, Tully et al. 1960, Royal and Tully 1961). Alternatively, migrations may be controlled by other environmental factors not related to nearshore temperature and salinity gradients (Groot and Quinn 1987, McCleave 1978, LaBar et al. 1976, Tytler et al. 1978). In order to gain a better understanding on how environmental conditions influence the coastal migration, I tested the locomotor responses of adult and juvenile sockeye salmon to horizontal gradients of temperature and salinity, within a range that could be encountered in nearshore waters.

## MATERIALS AND METHODS

This study examined the spontaneous locomotor movements of juvenile and adult sockeye salmon during concurrent changes in temperature and salinity. All behavioral tests were conducted at the Pacific Biological Station, Nanaimo, British Columbia, between June 1 and September 20, 1986.

### I. JUVENILE EXPERIMENTS

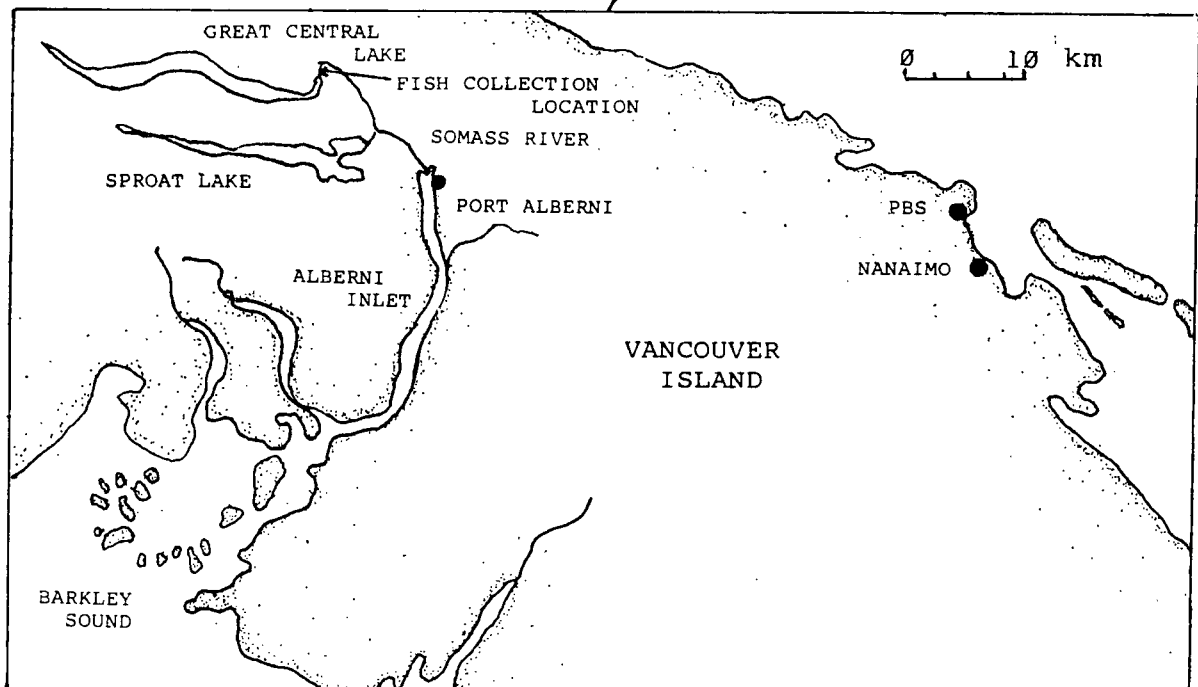
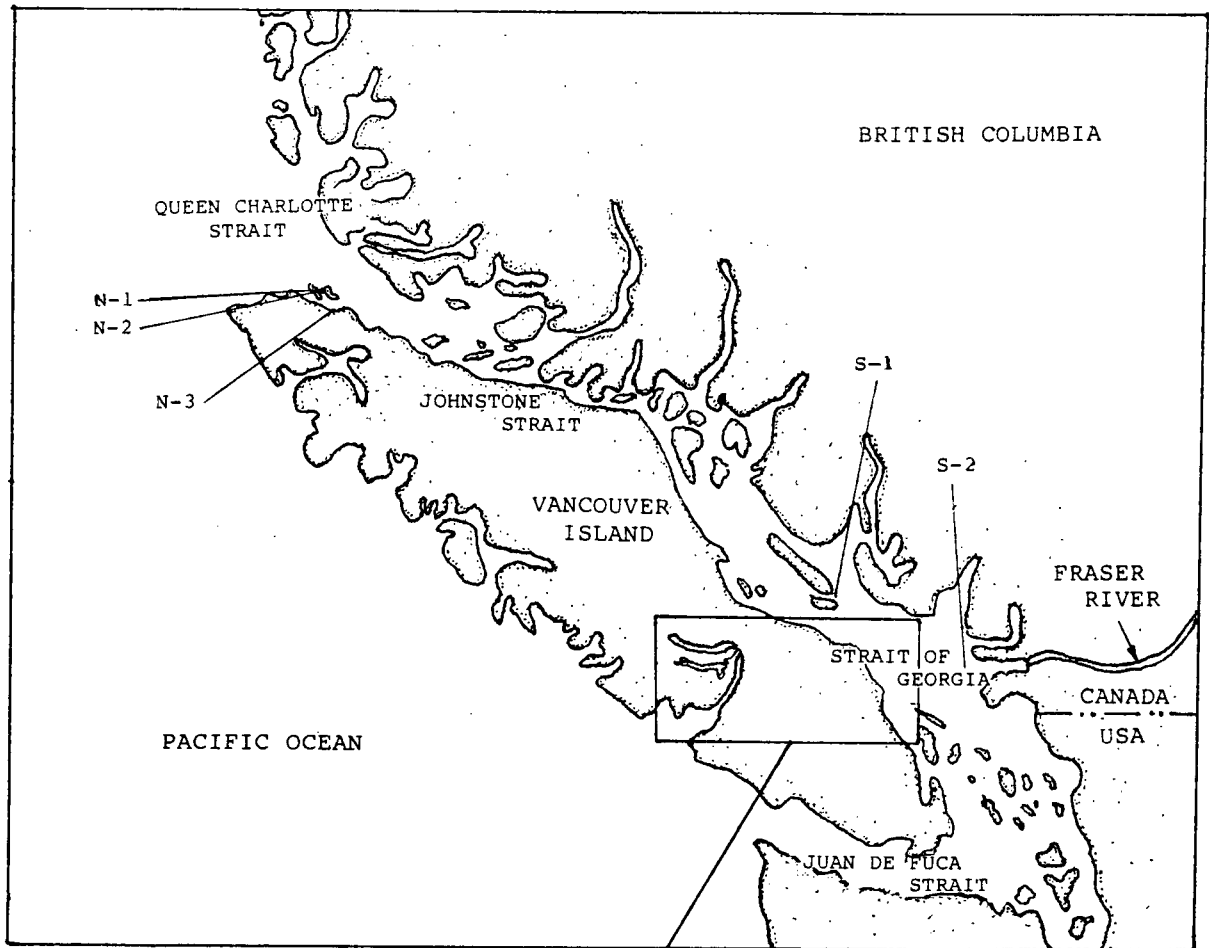
Sockeye smolts from Great Central Lake, British Columbia were used for the juvenile behavior experiments. This stock leaves the lake between early April and early June (Groot et al. 1986). The fish migrate through the Stamp and Somass Rivers and into Alberni Inlet, where they encounter seawater for the first time (Figure 1).

#### A. FISH COLLECTION

On May 7, 1986, approximately 450 juvenile sockeye salmon were collected from a small creek near the head of the Stamp River. The capture site was a shallow area, located approximately 2 km from Great Central Lake (Figure 1). The sockeye were caught using a long-handled dip net and quickly placed in two 40 l transport tanks that had been



Figure 1. Coastal migration area of Great Central Lake and Fraser River sockeye salmon. Adults used in activity experiments were collected at three locations near the northern tip of Vancouver Island (N-1 - N-3), and from two areas near the Fraser River (S-1 - S-2). Location where the juvenile sockeye were collected is shown in relation to Alberni Inlet.



filled with river water ( $11.7^{\circ}\text{C}$ ) and connected to a compressed air supply. Ice packs were periodically added or removed during transport to maintain the container water temperature at  $10^{\circ}\text{C}$  ( $\pm 0.5^{\circ}\text{C}$ ).

#### B. HOLDING CONDITIONS

At the Pacific Biological Station, groups of approximately 60 juvenile sockeye were transferred to 8 separate 30 l holding tanks. The fish were acclimated to dechlorinated city water ( $10^{\circ}\text{C}$ ) for a period of 1 wk. Initial mortalities were severe. During the first day over 100 fish succumbed- likely due to scale loss incurred during collection. After 2 d in captivity mortalities decreased significantly and only 5 fish died during the remainder of the experimental period.

Maintaining sockeye smolts in freshwater for extended periods of time may result in extensive mortalities (C. Groot, Pacific Biological Station, Nanaimo, British Columbia; pers. comm.); therefore, the juveniles were transferred to diluted seawater ( $10^{\circ}\text{C}$ , 20 ppt) on May 24, and acclimated for a period of 1 wk. I chose acclimation and test conditions that could normally be encountered by sockeye migrating through the Somass River estuary (Tully 1949, Morris and Leany 1980). The temperature and salinity of holding tanks were midway between the upper and lower

test levels, and also provided control conditions during the experiments.

The juvenile sockeye commenced feeding after 2 d in captivity and were fed frozen euphausiids ad libitum every morning. The tanks were cleaned of feces and food remains once per week. Overhead fluorescent lamps were connected to a timer that was adjusted weekly to simulate the local photoperiod.

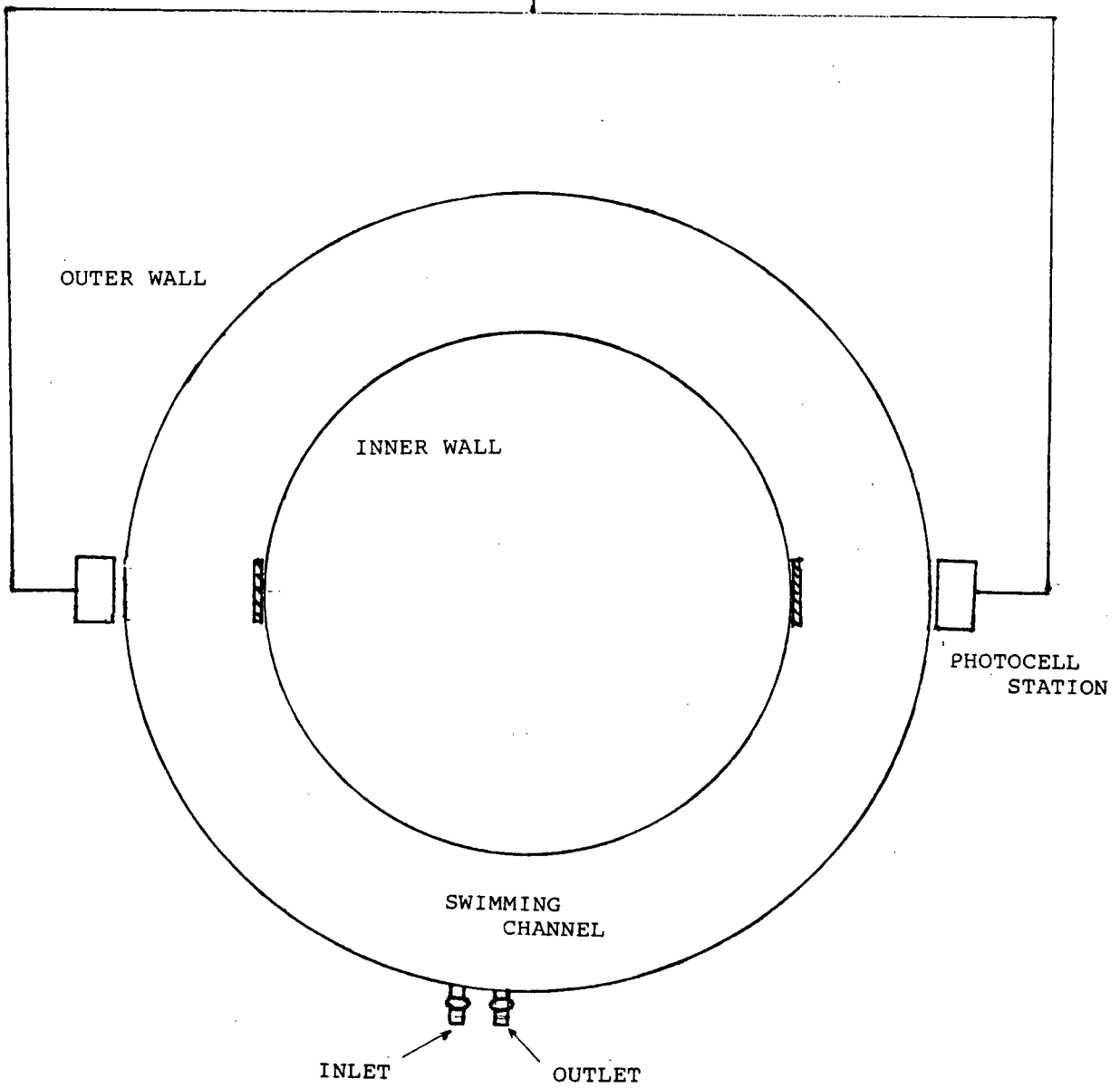
### C. EXPERIMENTAL APPARATUS

Each of the 6 annular activity tanks used in the present study consisted of 2 PVC rings fixed with fiberglass resin to a waterproofed, plywood bottom (Figure 2). The 2 rings formed a swimming chamber that had an outer circumference of 250 cm, and an inner circumference of 160 cm. External standpipes were used to maintain water depth at 10 cm. Excess glare was eliminated by painting the bottom of the swimming chambers with black, rust-oleum paint. Both control and experimental water was added through 0.63 cm PVC valves connected to the sides of the tanks.

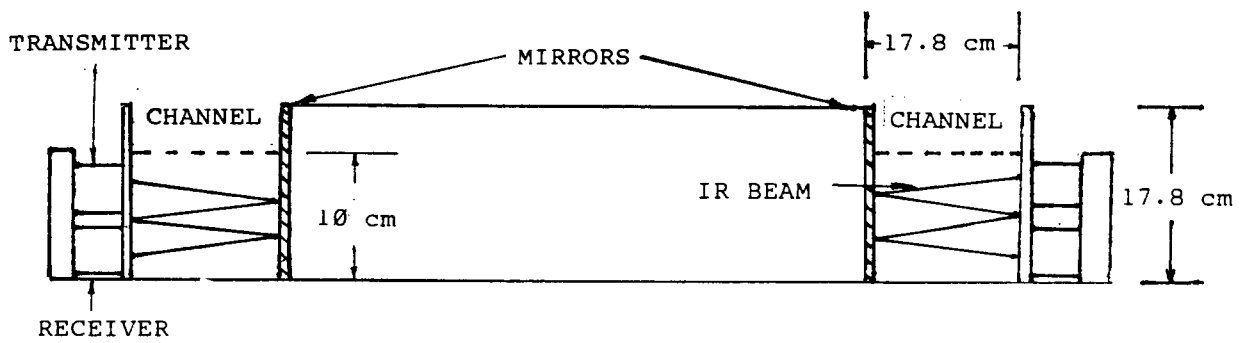
Fresh (1 ppt) and salt (31 ppt) water was available at temperatures of 4, 10 and 28°C. (+/- 1.0°C for each). The test conditions were produced by premixing 2 or more water sources at different rates in 30 l fiberglass tanks

Figure 2. Top and side views of activity tank used to measure locomotor responses of juvenile sockeye salmon to rapid changes in temperature and salinity. At each photo-cell station, an infra-red beam was focussed through a plexiglass plate, reflected on a mirror, and collected by a receiver positioned underneath the emitter.

TOP VIEW



SIDE VIEW



(Table 1). The experimental water was then gravity fed to the test apparatus at a rate of 2 l/min. Slight fluctuations in water temperature (up to 1°C) over the 6 wk test period necessitated weekly flow adjustments in order to maintain consistent levels of temperature and salinity. Therefore, the flow rate between tanks varied between 1.9 and 2.1 l/min. However, water flow to the tanks was constant during the experiments.

#### D. DATA COLLECTION

Juvenile salmon held in annular tanks exhibit constant unidirectional swimming behavior (Byrne 1968, Godin et al. 1978). In preliminary experiments, Great Central Lake smolts exhibited similar behavior, however, turning and periods of inactivity were also quite common.

Locomotor activity data were collected using infra-red photo-metric sensors (Amseco Ltd, Houston, Texas - model EBP-2503) interfaced with an Apple II+ microcomputer. There were 2 photo-cell stations per tank (each station consisting of 1 emitter and 1 receiver) positioned on opposite sides; thus, dividing the apparatus into equal halves (Figure 2). The infra-red beam was focussed through a plexiglass window on the outer tank wall, reflected off mirrors on the inner and outer tank walls, and collected by the receiver positioned below the emitter. The infra-red

Table 1. Combinations of water sources used to produce test conditions in the juvenile sockeye activity experiments. Flow rates of each water source and total flow are included in the table. Ranges of each parameter were the minimum and maximum recorded during the experimental period. Test conditions were produced by mixing water sources together in 30 L tanks. C= Cold (4°C), N= Normal (10°C), H= Hot (28°C), F= Fresh (1 ppt), S= Salt (31 ppt).

Temperature ( 0.2 C)	Salinity ( 1 ppt)	Flow Rate of Test Water Source ( 0.1 L/min)						Total Flow Rate ( 0.2 l/min)
		CF	CS	NF	NS	HF	HS	
6.0	10	1.4	-	-	0.6	-	-	2.0
6.0	20	-	1.4	0.6	-	-	-	2.0
6.0	30	-	1.4	-	0.6	-	-	2.0
10.0	10	-	-	1.4	0.6	-	-	2.0
10.0	20	-	-	0.6	1.4	-	-	2.0 -control-
10.0	30	-	-	-	2.0	-	-	2.0
14.0	10	0.8	-	0.5	-	-	0.7	2.0
14.0	20	-	0.8	0.5	-	0.7	-	2.0
14.0	30	-	0.8	-	0.5	-	0.7	2.0



field provided sufficient coverage so that a photo-cell station could not be passed by a juvenile sockeye without triggering the receiver.

A mechanical switch located within the receiver relayed a continuous high ('connected') or low ('broken') signal to the computer. An analog to digital converter (12 bit, 16 channel- Applied Engineering Ltd., Carrollton, Texas) was used to interface the activity recorders with the microcomputer. In total, 12 photo-cell units (2 for each tank) were used for data collection.

An Applesoft (Apple Computer Inc., Cupertino, California) BASIC program was written for data acquisition and storage. The algorithm involved sequential monitoring of the 12 channels (i.e. photo-cells) in a continuous loop. When a 'broken' signal was received, the program branched to a subroutine that recorded the time and channel number to a 1 dimensional array. The subroutine then returned to the main program and continued sequential monitoring.

Preliminary experiments showed that fish would often change their vertical position while passing through the infra-red field, causing repetitive signal recordings. Therefore, the program was modified so that once a 'broken' signal was established for a given photo-cell, that unit could not be recorded again until a period of 2 s had passed (allowing the fish to pass through the station), and the signal had returned to a 'connected' state.

The recording accuracy of the apparatus was also determined. The number of photo-cell breaks recorded by a single fish during 30 min exposure to control conditions was monitored visually and electronically. The mean number of counts obtained by the two methods were statistically compared using chi-square analysis.

#### E. EXPERIMENTAL PROCEDURE

The juveniles were not fed 1 d prior to testing, and the experiments were conducted twice daily (morning and afternoon). Prior to the tests, the annular tanks were filled with control water (10°C, 20 ppt) and maintained at a flow rate of 2 l/min. A single fish was introduced into each experimental tank and covered with a translucent sheet to prevent startling. The smolts were observed visually through 10 cm wide areas that had been cut over the photo-cell stations.

For a period of 1 h, the smolts were allowed to adjust to the experimental tanks. Activity during this period was monitored (but not recorded) both visually and on the computer screen. The sockeye often did not move during the first few minutes after transfer, however, most became mobile within 15 min. Fish that remained immobile for 45 min were removed and that tank was not used in the test.

Each experiment was divided into a 1 h control

phase, followed by a 1 h water turnover period and concluding with a 1 h test phase. During the initial hour, swimming activity was recorded in control conditions ( $10^{\circ}\text{C}$ , 20 ppt) to determine baseline levels. At the start of the second hour, the control water valve was shut off and experimental water was introduced into the test apparatus. Overflow samples were obtained at 10 min intervals during the turnover phase to determine temperature, salinity, and water flow. Although water turnover was not linear, both temperature and salinity stabilized at experimental levels within 45 to 50 min. During the final hour, activity was recorded during exposure to the treatment conditions. Upon completion of the test, fork lengths of the fish were recorded. Prior to the next test, tanks were rinsed and refilled with control water.

#### F. TEST CONDITIONS AND STATISTICAL ANALYSIS

In total, there were 8 experimental conditions and 1 control (Table 1). The juvenile sockeye were subjected to control conditions for 1 h. In the second hour, temperature was increased to  $14^{\circ}\text{C}$ , decreased to  $6^{\circ}\text{C}$ , or held constant. Thirty minutes after introducing warm or cold water, temperature had changed by  $\pm 1.8^{\circ}\text{C}$ , and after 60 min, water temperature had increased or decreased by  $4^{\circ}\text{C}$ . In the final hour, temperature remained constant at the treatment

level.

After the initial 60 min in control conditions, salinity was increased to 30 ppt, decreased to 10 ppt, or held constant at 20 ppt. During the first 30 min of water turnover, test tank salinity was altered by  $\pm 6$  ppt. Sixty minutes after test water introduction, salinity had increased or decreased by 10 ppt. Salinity remained constant during the final 60 min of testing.

Activity of the sockeye smolts was converted into average swimming speed for comparison between treatment groups. Preliminary experiments showed that, even in control conditions, fish would occasionally stop moving for periods of up to 5 min. Therefore, to decrease variability in the calculation of swimming speed, only active behavior was included in the analysis. This was calculated as follows. There were 2 photo-cell stations for each tank. Preliminary tests showed that in control conditions active fish usually swam  $1/2$  the distance around the tank (i.e. between stations) within 10 to 15 s. Activity data were recorded when the fish swam between stations within 30 s. Intervals of more than 30 s and instances when fish turned back through the same station were not included in the analysis.

Activity in each 30 min period was converted to average swimming speed. Total excursions under 30 s were multiplied by the average distance for 1 excursion

(difference between the outer and inner walls of the swimming chamber). This result was divided by the total time (in seconds) to complete all excursions, and divided by the fork length of the fish. The value calculated was average routine swimming speed in fork lengths per second (fl/s).

Responses to temperature and salinity were the main effects tested by the statistical analyses. However, Byrne (1968) showed that juvenile sockeye entrained to a 12:12 L/D cycle exhibited significant diurnal variations in locomotor activity. While experiments were coordinated with the peak activity period for young sockeye (i.e. morning and afternoon- Byrne 1968), the time of experiment was also incorporated into the statistical analysis. A single factor ANOVA was used to test for differences in mean swimming speed during the 60 min control (i.e. pre-treatment) phase, for sockeye tested in either the morning or afternoon.

The mean swimming speed of juvenile sockeye during the final 60 min exposure to test conditions was analyzed using a two factor ANOVA. The experiment was designed so that treatment effects could be compared as well as any possible interactions. When sample sizes were unequal, an F-max test (Sokal and Rohlf 1969) was used to assess homogeneity of variance prior to the ANOVA. If heterogeneity existed, a  $\ln(x+1)$  transformation (Zar 1980) was conducted on the data, and the results were then

subjected to parametric analyses. Newman-Keuls multiple range test (Zar 1980) was used as an a posteriori comparison of between treatment effects.

Behavioral responses of young salmon to temperature and salinity may change over time (e.g. Hurley and Woodall 1968, McInerney 1964). In the present study, experiments were conducted during a 6 wk period. In the event of a significant effect from the two factor ANOVA, possible temporal changes in locomotor response were analyzed between fish tested in the first 3 wk and the final 3 wk using a single factor ANOVA.

In addition to testing responses in the final 1 h of the experiments, activity was also analyzed at 30 min intervals during the control, water turnover, and test phases. Mean swimming speeds of the smolts were statistically tested using a repeated measures ANOVA (Zar 1980). Unequal sample sizes prohibited the use of 1 large multivariate block analysis. Rather than using statistical methods to estimate 'missing data' (e.g. Zar 1980), the experimental results were analyzed separately and interactions were not tested. The analyses were designed such that a single fish constituted 1 block and swimming speed was averaged over 30 min periods during exposure to test conditions. In total there were five 30 min intervals (1 control, 2 water turnover, and 2 test) for which mean swimming speed was calculated.

## II. ADULT EXPERIMENTS

From August 10, 1986 to September 20, 1986, the locomotor responses of migrating adult sockeye salmon to rapid changes in temperature and salinity were tested.

All adult sockeye used in the present study were assumed to be migrating to the Fraser River. The capture area extended from Queen Charlotte Strait at the northern end of Vancouver Island to the Strait of Georgia near the Fraser River estuary (Figure 1). During the summer months, Queen Charlotte Strait is slightly stratified, with little vertical change in temperature and salinity (Thomson et al. 1985). The Strait of Georgia, however, is a more strongly stratified region with distinct variations in temperature and salinity over the top 30 m. (Thomson et al. 1985).

Although other local rivers do contain small sockeye runs, in 1986 the Fraser River accounted for over 90% of sockeye production in the study area (B. Tasaka, Pacific Salmon Commission, Vancouver, British Columbia; pers. comm.). The 2 principle runs that constituted the majority of spawners in 1986 were from the Adams Lake and Chilko Lake systems. Lesser contributions were made by runs to Birkenhead River and Weaver Creek (B. Tasaka, Pacific Salmon Commission, Vancouver, British Columbia; pers. comm.). The race of individual fish was determined using discriminate

scale sample analysis by staff of the Pacific Salmon Commission, Vancouver, British Columbia (Table 2).

#### A. FISH COLLECTION

Adult sockeye were collected at 5 locations along the nearshore migration route (Figure 1, Table 2). Three samples (total of 44 fish) were taken from Queen Charlotte Strait (Sets N1 - N3) on August 7th, 14th, and 21st, and two (total of 34 fish) from the Strait of Georgia (Sets S1 - S2) on September 4th and 10th.

The salmon were collected by purse seine in areas that were historically known to be prime fishing locations. Prior to sampling, surface seawater was pumped into the vessel's hold. After the set was made, the net was brought close to the boat and the adult sockeye were transferred to the hold by dip net. Oxygen was provided for the fish using an air compressor. Surface temperatures were recorded immediately after capture.

The seiner brought the samples to shore within 2 h of collection and water was pumped from the hold of the boat into a large fiberglass tank (1200 l) located on the back of a truck. In general, most salmon were relatively docile during transport. Oxygen was provided for the fish by adding compressed air. Water in the transport tank was maintained at 12°C (+/- 1°C) by periodically adding or



Table 2. Contributions of sockeye from four Fraser River races to the adult activity tank experiments. Location, date of capture, and totals from each set are included for male (M) and female (F) fish.

Set	Capture	Location	Chilko	Adams	Birk'head	Weaver	?	?	Total
	Date		River	River	River	Creek			
			M	F	M	F	M	F	
N1	24/07/86	Goletas Channel	1	5	2	1	0	0	10
N2	1/08/86	Goletas Channel	2	5	1	4	1	1	16
N3	21/08/86	Qu'n Ch't Strait	4	2	1	5	2	0	18
S1	4/09/86	Sabine Channel	2	2	4	3	1	1	17
S2	10/09/86	Gulf of Georgia	2	0	6	5	1	2	17

removing ice packs during the drive to the Pacific Biological Station in Nanaimo. Transport time (seiner plus truck) varied from 7 h for fish taken from Queen Charlotte Strait to 2 h for fish caught in the Strait of Georgia. Recovery from capture was excellent; all 79 fish sampled survived transport and only 1 died after arrival at the Pacific Biological Station.

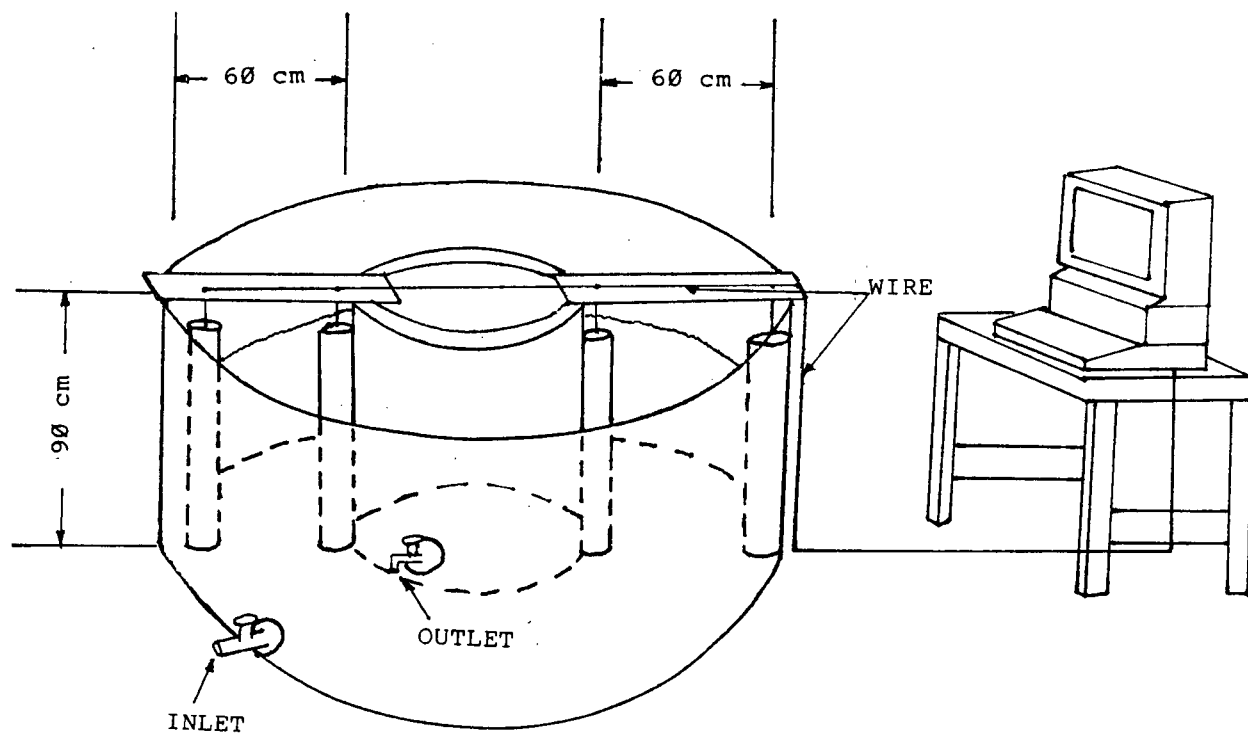
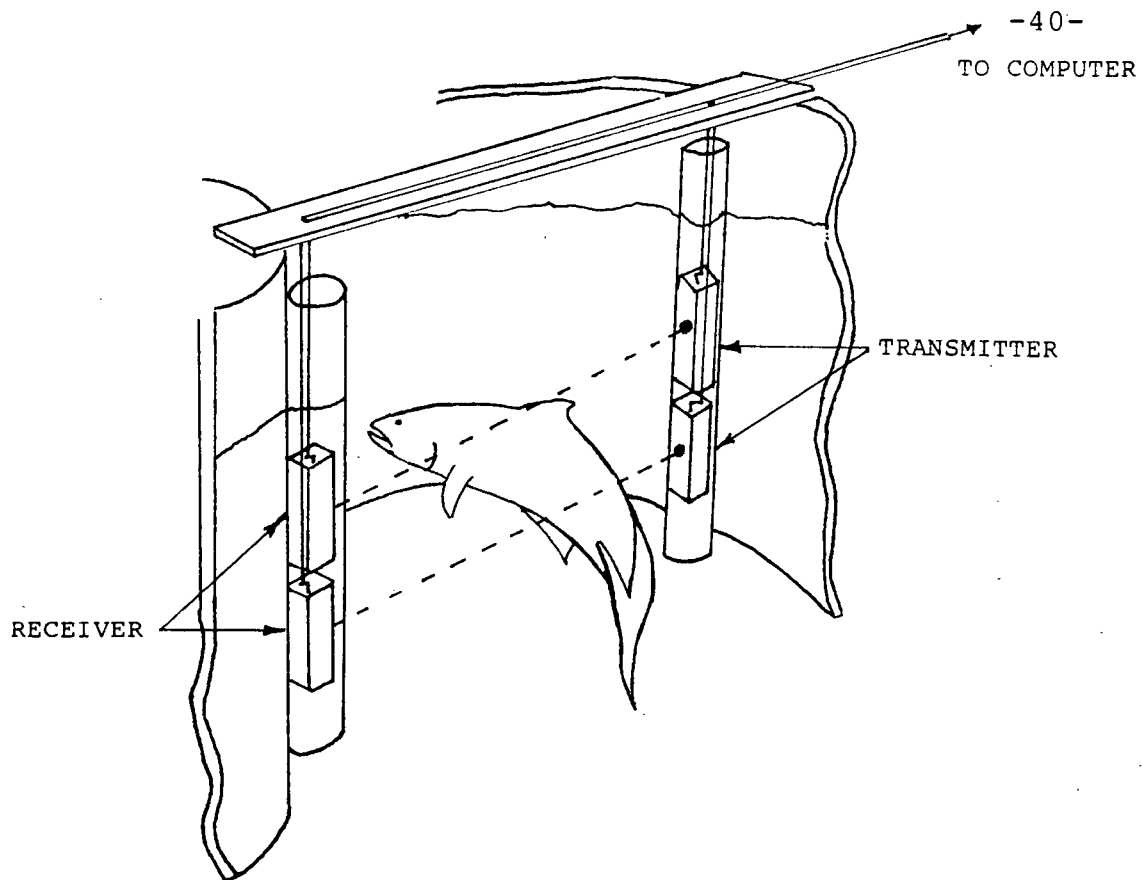
#### B. HOLDING CONDITIONS

The sockeye were acclimated for 1 d prior to the experiments and subsequently tested for 2 to 5 d. Twenty fish were held in two 800 l fiberglass tanks with water (12°C, 30 ppt) flowing at 15 l/min. Overhead fluorescent lamps were connected to a timer (adjusted weekly) corresponding to local photoperiod. Tanks were covered with PVC sheeting (0.02 cm) to prevent injuries caused by jumping. The adult sockeye were not fed at any time during the experiments.

#### C. EXPERIMENTAL APPARATUS AND DATA COLLECTION

Three 800 l, circular, fiberglass tanks were fitted with a center fiberglass annulus (diameter= 60 cm) to provide a swimming channel of 60 cm between the outer tank wall and the annulus (Figure 3). The circumference of the

Figure 3. Experimental apparatus used to measure locomotor responses of adult sockeye salmon to rapid changes in temperature and salinity. At each photo-cell station, two emitters were placed end to end in a plexiglass tube. The infra-red beams were focussed onto two receivers positioned on the opposite side of the swimming channel.



outer wall was 570 cm and the circumference of the annulus was 190 cm. External standpipes provided a water depth of 45 cm.

Locomotor activity was recorded by 2 photo-cell stations located on opposite sides of the test tanks. Each station consisted of 2 emitters placed end to end in clear PVC tubes (12 cm diameter) and fixed with marine caulking to the inner side of the tank wall (Figure 3). Similarly, tubes containing the 2 receivers were fixed to the outer side of the annulus. The 2 photo-cell units provided sufficient coverage so that at least 1 beam would be broken if an adult salmon passed by.

Filtered seawater (4, 12, 28°C, 30 ppt) or dechlorinated city water (12, 28°C, 1 ppt) were used as control and experimental sources. Up to 3 water types were combined at different rates in 40 l mixing containers before being gravity fed to the experimental tanks (Table 3). The experimental design of the adult tests consisted of a factorial combination of 3 temperatures (8°C, 12°C, 16°C) by 2 salinities (20 ppt, 30 ppt).

The activity of the fish was monitored both visually and electronically for 60 min during exposure to control conditions to determine the recording accuracy of the infra-red sensors. The mean number of counts obtained by both methods were compared using a single factor ANOVA.

Table 3. Combinations of water sources used to produce test conditions in the adult sockeye activity experiments. Flow rates of each water source and total flow are included in the table. Ranges of each parameter were the minimum and maximum recorded during the experimental period. Test conditions were produced by mixing water sources together in 40 L tanks. C= Cold (4°C), N= Normal (12°C), H= Hot (28°C), F= Fresh (1 ppt), S= Salt (31 ppt).

Temperature ( 0.2 C)	Salinity ( 1 ppt)	Flow Rate of Test Water Source ( 1.0 L/min)						Total Flow Rate ( 1.0 L/min)
		CF	CS	NF	NS	HF	HS	
8.0	20	-	10.0	3.8	-	-	1.2	15.0
8.0	30	-	7.5	-	7.5	-	-	15.0
12.0	20	-	-	5.0	10.0	-	-	15.0
12.0	30	-	-	-	15.0	-	-	15.0 -control-
16.0	20	0.8	-	-	10.0	4.2	-	15.0
16.0	30	-	-	-	11.2	3.8	-	15.0

#### D. EXPERIMENTAL PROCEDURE

Prior to an experiment, the test tanks were filled with the same water that was used in the holding tanks ( $12^{\circ}\text{C}$ , 30 ppt). A single fish was then transferred from the holding tank to an experimental chamber and acclimated for 1 h. Most adults began swimming immediately and fish that did not become active 45 min after introduction were excluded from the test.

When the experiment commenced, baseline activity was recorded for 1 h during exposure to control conditions. In the second hour, the control water was shut off and experimental water was introduced at 15 l/min. At 30 min intervals, temperature and salinity were recorded from the overflow pipe. The turnover phase took approximately 120 min. In the final hour, activity was recorded during exposure to treatment conditions. After the experiment finished, the total length of each fish was recorded. The tanks were then drained, rinsed, and refilled for the next test.

During the 5 wk of testing, experimental and ambient temperatures ranged by a maximum of  $\pm 0.2^{\circ}\text{C}$ . In addition, salinity varied by about 1 ppt, and flow rate was accurate to within  $\pm 1$  l/min (Table 3).

In addition to swimming behavior, activities such as the number of turns made (i.e. reversals of direction), the

number of 'noses' ("lifting the nose or head out of the water as far as the operculars"- see Groot et al. 1986) and 'fins' (moving the dorsal surface out of the water) were recorded for 10 min intervals before, during, and after introduction of the test water.

#### E. TEST CONDITIONS AND STATISTICAL ANALYSIS

The adult experiments were divided into 3 phases. After the initial 60 min in control conditions, water temperature was increased or decreased by 4°C, or held constant at 12°C. Concurrently, salinity was decreased by 10 ppt or maintained at 30 ppt. Activity was converted into average swimming speed by calculating the total number of excursions between stations, multiplied by the average distance for 1 excursion, and divided by the total time to complete all excursions. The resulting value was divided by the total body length of the fish, giving average swimming speed in total lengths per second (tl/s). The time required for swimming between stations was usually 20 - 30 s, however, adults would occasionally stop moving; therefore, the value used as the upper level for making an excursion was set at 60 s.

In the statistical analysis, a number of tests were initially conducted to identify any inherent differences between the experimental animals that may have influenced



results of the main design. Mean swimming speeds in control conditions were compared in relation to sex (single factor ANOVA), race (single factor ANOVA), and time of day (single factor ANOVA).

The mean swimming speeds of adult sockeye during the final 60 min test period were compared using a two factor ANOVA. Tests for homogeneity of variance (F-max test) were used, and the Newman-Keuls multiple range test was utilized to examine between group differences using the results of the ANOVA.

Fish came from 2 distinct oceanographic regions and were acclimated for varying amounts of time prior to testing. Therefore, when significant effects were obtained from the main treatment model, mean swimming speeds were compared during the final hour of testing based on area of capture and number of days acclimated to control conditions.

A repeated measures ANOVA in a mixed block design (fish as blocks, periods as treatments) was used to test differences in mean swimming speed between 1/2 hour intervals. The first 30 min period in control water was not used in the analysis. Comparisons were made between the other seven 30 min intervals for each experimental condition. In the event of a significant main effect, multiple range testing (Newman-Keuls) was used to compare average swimming speeds between the 30 min periods.

Other behaviors (i.e. nosing, finning, turning) were

analyzed between treatment groups using a repeated measures ANOVA. The analyses compared mean events in 10 min intervals during the control period, the first 30 min of water turnover, and the first 30 min at test levels. An alpha level of 0.05 was used for all statistical tests.

## RESULTS

### JUVENILE EXPERIMENTS

In total, 214 juvenile sockeye were tested over a 6 wk period (mean fork length= 10.39 cm, SD= 0.66 cm). The sample size was originally to be 240 (30 fish for 8 conditions), however, equipment malfunctions resulted in the exclusion of 8 tests from the data analysis. In addition, 18 juveniles remained motionless for most of the experiment and were not included in the statistical tests.

Analyses were conducted on each of the 6 experimental tanks to determine the accuracy of recording equipment. Chi-square analysis showed no difference between the mean number of photo-cell breaks recorded by visual or electronic methods in 30 min tests (Table 4).

The experiments were run twice daily- once in the morning and once in the late afternoon (~ 4 h difference between tests). The average swimming speed of juvenile sockeye from morning experiments was not different from fish tested in the afternoon (Table 5).

The swimming speeds of juvenile sockeye averaged over the last hour of testing are shown in Figure 4. Fish exposed to decreasing temperature, and increasing or decreasing salinity had mean swimming speeds that were close to control values. However, fish tested in 14°C showed

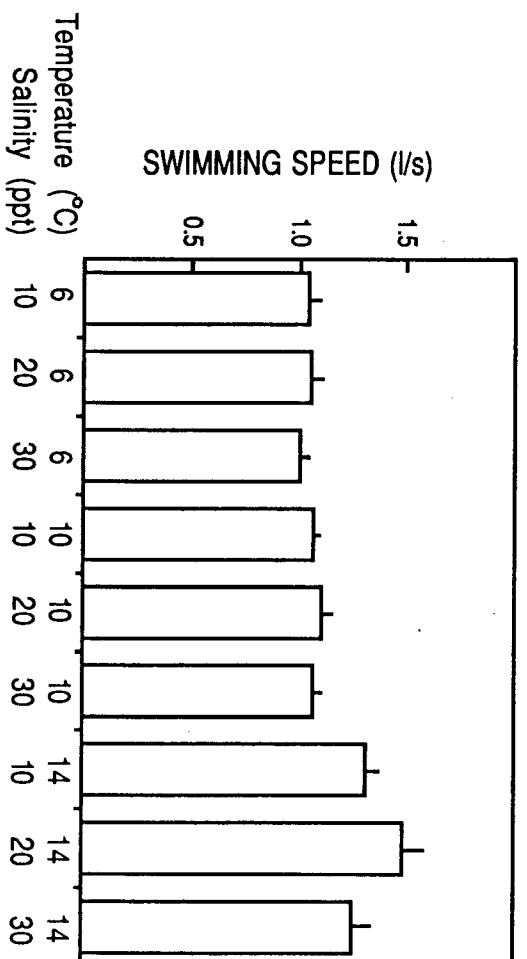
Table 4. The number of passes through photo-cell stations recorded for juvenile sockeye during 30 minutes exposure to control (10°C, 20 ppt) conditions. Data collected by electronic and visual observations were not significantly different (chi-square= 0.11, P> 0.05).

Observation	Number of counts					
Method	per 30 minute interval					
	Tank 1	Tank 2	Tank 3	Tank 4	Tank 5	Tank 6
Electronic	112	86	84	103	91	41
Visual	108	87	86	110	90	39

Table 5. The average swimming speed of juvenile sockeye salmon exposed for 30 minutes to control conditions (10°C, 20 ppt) in morning or afternoon tests (~ 4 hours difference). Statistical analysis (single factor ANOVA) showed no significant difference between mean values.

Time of Day	N	Mean Swimming	SD	F	P > F
		Speed (1/s)	(1/s)		
Morning	107	1.02	0.15	0.11	-
Afternoon	107	1.01	0.20		

Figure 4. Average swimming speeds ( $\pm$ -SEM) of juvenile sockeye salmon during the final 60 minutes exposure to test levels. Fish were initially subjected to control conditions ( $10^{\circ}\text{C}$ , 20 ppt) for one hour, and water turnover took approximately 60 minutes.



elevated swimming speeds in each of the 3 salinity conditions. The highest average speed was found for fish exposed to 14°C and 20 ppt.

There were an unequal number of juvenile sockeye tested in each experimental condition (Table 6). In addition, variances were found to be heterogeneous (F-max test-  $F = 9.00$ ,  $P < 0.05$ ). The conservative approach suggested by Zar (1980) was adopted, and the swimming speed data were transformed ( $\ln(x+1)$ ).

The two factor ANOVA on the transformed data, showed that temperature was the only significant treatment effect ( $F = 22.07$ ,  $P < 0.001$ ). There was no influence due to salinity ( $F = 1.43$ ,  $P = 0.24$ ) or interaction between factors ( $F = 1.07$ ,  $P = 0.37$ ). For comparative purposes, I also conducted a two factor ANOVA on the untransformed swimming speeds (Table 7). F values were similar to those derived from the transformed data, and statistical conclusions were the same- temperature was the only factor that influenced locomotor activity. Due to the equivalent results of the two statistical tests, I felt justified in using the untransformed data in the a posteriori analysis. Newman-Keuls multiple range test showed that increasing temperature was the only factor that affected swimming activity (Table 6).

Additional tests were performed to assess changes in locomotor activity based on the number of weeks in

Table 6. The mean swimming speeds of juvenile sockeye salmon during the final 60 minutes exposure to test levels. Fish were initially subjected to control conditions (10°C, 20 ppt) for one hour, and water turnover took approximately 60 minutes. Results from Newman-Keuls multiple range test are also included in the table (NS= not significant, \*= < 0.05, \*\*= < 0.01).

Temperature ( C)	Salinity (ppt)	N	Mean Swimming Speed (l/s)	SD (l/s)	Newman-Keuls
6	10	19	1.04	0.11	NS
6	20	21	1.05	0.19	NS
6	30	25	1.00	0.15	NS
10	10	24	1.07	0.11	NS
10	20	22	1.10	0.18	-control-
10	30	29	1.07	0.15	NS
14	10	25	1.31	0.18	*
14	20	26	1.48	0.33	**
14	30	20	1.20	0.27	*

Table 7. Results of the two factor ANOVA comparing the mean swimming speeds of juvenile sockeye salmon subjected to experimental conditions for 60 minutes (see Table 6).

Source	SS	DF	MS	F	P > F
Temperature	3.01	2	1.50	18.79	< 0.001
Salinity	0.22	2	0.11	1.35	0.260
Temp*Sali	0.36	4	0.09	1.13	0.345
Error	15.40	198	0.08		



captivity. The previous analysis showed that increasing temperature was the only factor influencing swimming activity (Table 7). Therefore, results were restricted to fish tested in 14°C, 20 ppt. A single factor ANOVA showed that the mean swimming speed of fish tested in weeks 1 to 3 was not different from fish tested in weeks 4 to 6 (Table 8).

For each experimental condition, the swimming speeds of juvenile sockeye were averaged over 30 min intervals during the control, water turnover, and experimental periods. Juveniles subjected to decreasing temperature and decreasing, constant, or increasing salinity maintained a consistent activity level throughout the experiment (Figure 5, Figure 6). Fish tested in 14°C water increased locomotor activity in each of the 3 salinity conditions (Figure 7). After introduction of the experimental water, there was an initial rise in average swimming speed, followed by a period of relatively constant activity during temperature stabilization. However, locomotor activity continued to increase somewhat towards the end of the experiments despite constant temperatures.

The only effect detected by the repeated measures ANOVA was due to increasing temperature (Table 9). Newman-Keuls multiple range test showed that swimming activity increased above control levels after 30 min exposure to test conditions. In addition, for fish exposed

Table 8. The mean swimming speeds of juvenile sockeye salmon during 60 minutes exposure to water of 14°C and 20 ppt. Data was pooled from fish tested in the first 3 weeks (1 - 3) or the last 3 weeks (4 - 6) of the experimental period. Results from the statistical analysis (single factor ANOVA) are included in the table.

Week of Test	N	Mean Swimming Speed (l/s)	SD (l/s)	F	P > F
1 - 3	13	1.49	0.34	0.35	-
4 - 6	13	1.46	0.29		

Figure 5. Mean swimming speeds ( $\pm$ -SEM) of juvenile sockeye salmon during exposure to (A) 6°C, 10 ppt; (B) 6°C, 20 ppt; and (C) 6°C, 30 ppt. Values were calculated at 30 minute intervals for control conditions (T0), one hour of water turnover (T0 - 60), and one hour at test levels (T60 - T120). Approximate changes in temperature and salinity are included in the upper portion of each figure.

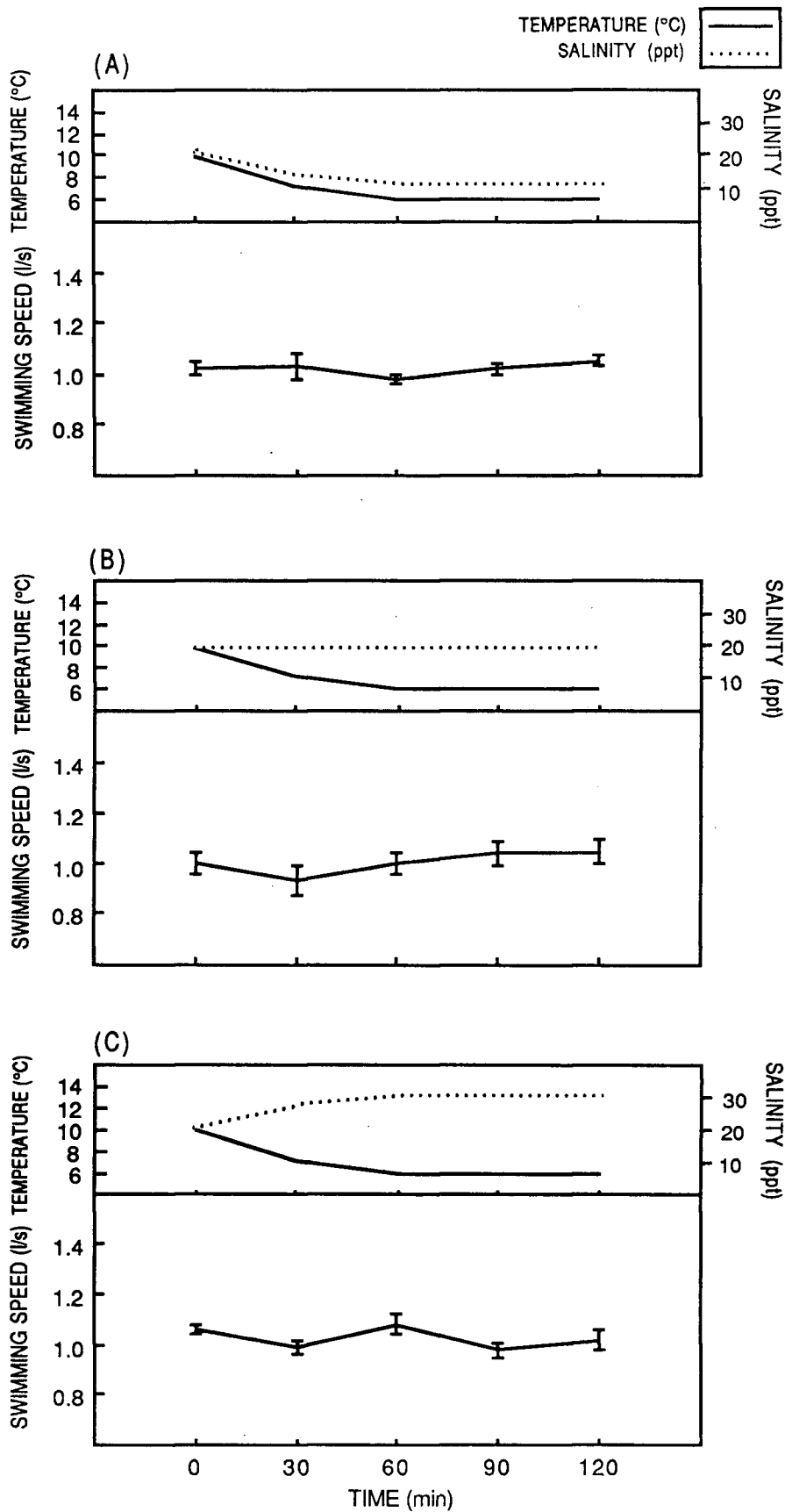


Figure 6. Mean swimming speeds ( $\pm$ -SEM) of juvenile sockeye salmon during exposure to (A)  $10^{\circ}\text{C}$ , 10 ppt; (B)  $10^{\circ}\text{C}$ , 20 ppt; and (C)  $10^{\circ}\text{C}$ , 30 ppt. Values were calculated at 30 minute intervals for control conditions (T0), one hour of water turnover (T0 - 60), and one hour at test levels (T60 - T120). Approximate changes in temperature and salinity are included in the upper portion of each figure.

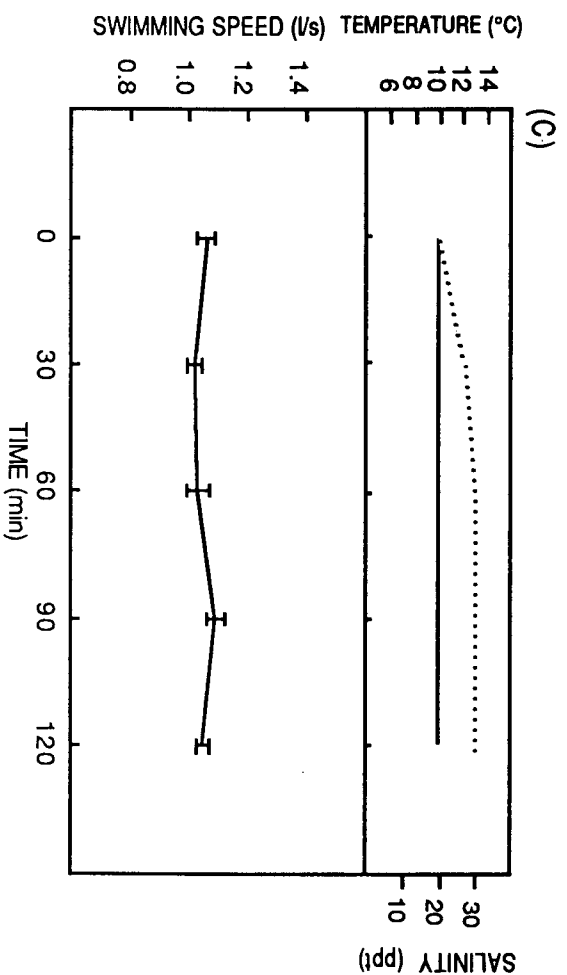
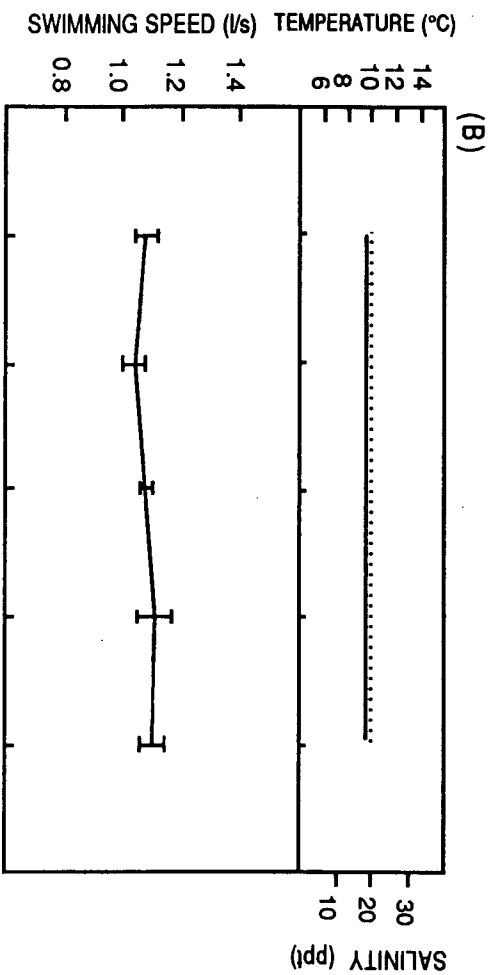
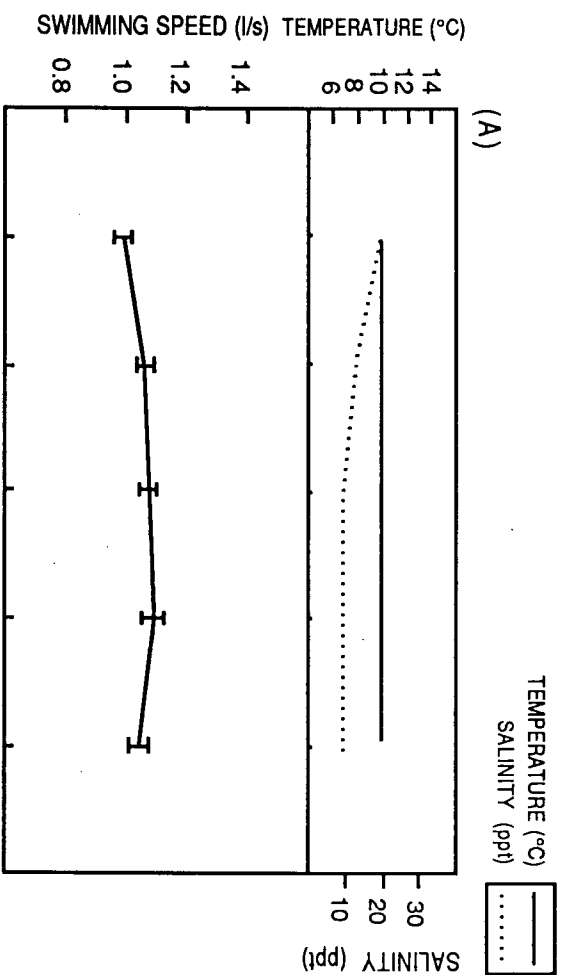


Figure 7. Mean swimming speeds ( $\pm$ SEM) of juvenile sockeye salmon during exposure to (A) 14°C, 10 ppt; (B) 14°C, 20 ppt; and (C) 14°C, 30 ppt. Values were calculated at 30 minute intervals for control conditions (T0), one hour of water turnover (T0 - 60), and one hour at test levels (T60 - T120). Approximate changes in temperature and salinity are included in the upper portion of each figure.

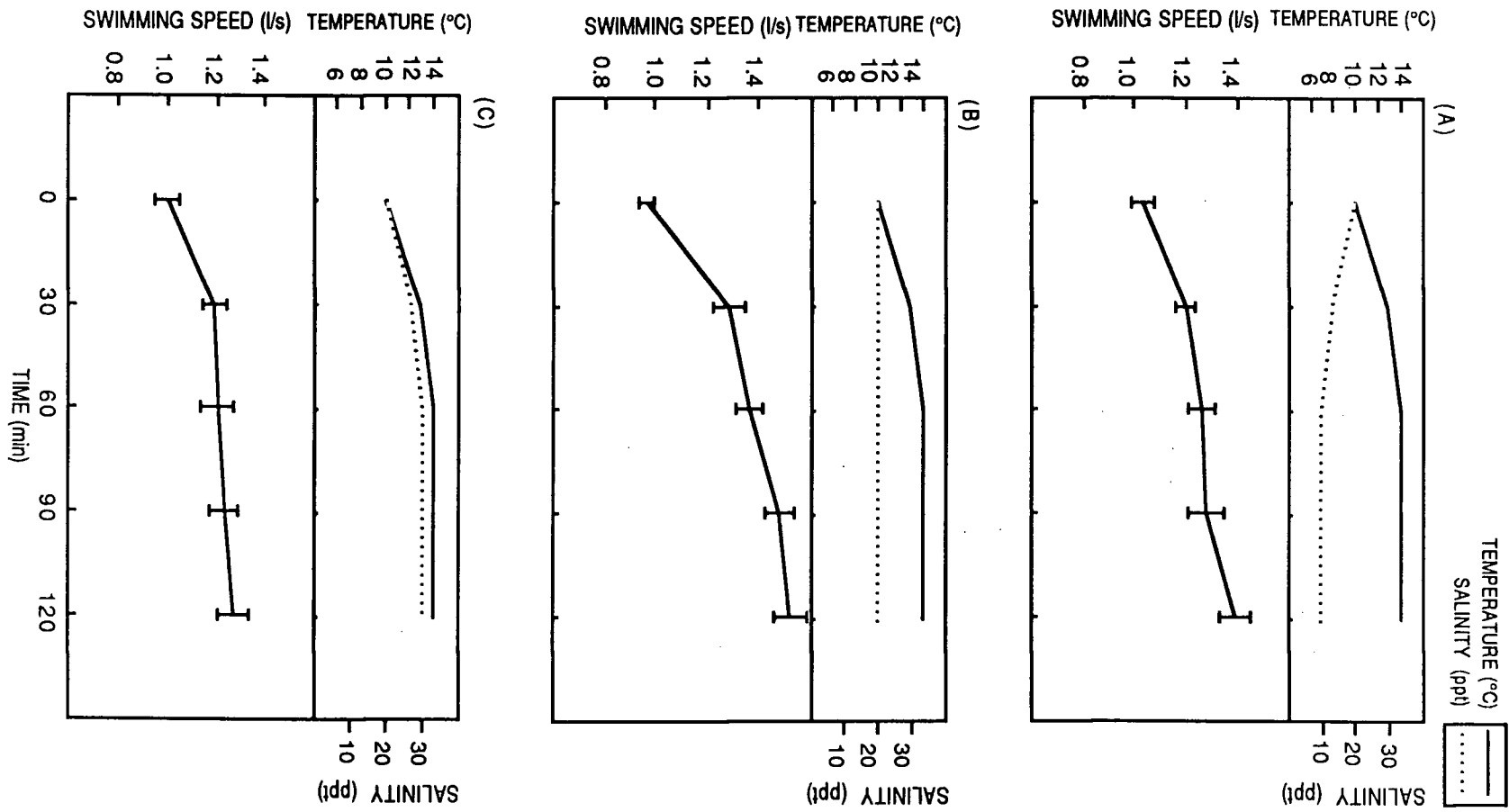




Table 9. Mean swimming speeds of juvenile sockeye calculated over 30 minute intervals during 1/2 hour in control conditions (T0), one hour of water turnover (T0 - T60) and one hour at test levels (T60 - T120). Results of statistical tests (repeated measures ANOVA) are included for each condition.

Temperature ( C )	Salinity (ppt)	N	Mean Swim Speed (l/s) per 30 Minute Interval (SD in brackets)					F	P > F
			T0	T30	T60	T90	T120		
6	10	19	1.02 (0.14)	1.03 (0.21)	0.98 (0.10)	1.02 (0.10)	1.05 (0.10)	0.71	0.468
6	20	21	1.00 (0.17)	0.93 (0.27)	1.00 (0.17)	1.04 (0.21)	1.05 (0.21)	1.40	0.253
6	30	25	1.06 (0.10)	0.99 (0.15)	1.08 (0.20)	0.98 (0.17)	1.02 (0.21)	1.21	0.321
10	10	24	0.99 (0.13)	1.06 (0.15)	1.08 (0.16)	1.09 (0.18)	1.04 (0.13)	1.04	0.290
10	20	22	1.08 (0.19)	1.04 (0.21)	1.08 (0.11)	1.11 (0.26)	1.10 (0.18)	0.64	-
10	30	29	1.06 (0.17)	1.02 (0.17)	1.03 (0.21)	1.09 (0.19)	1.05 (0.11)	0.56	-
14	10	25	1.03 (0.20)	1.20 (0.20)	1.26 (0.24)	1.28 (0.33)	1.34 (0.29)	9.28	< 0.001
14	20	26	0.97 (0.16)	1.28 (0.28)	1.36 (0.23)	1.44 (0.28)	1.52 (0.35)	22.80	< 0.001
14	30	20	1.00 (0.23)	1.19 (0.26)	1.20 (0.30)	1.23 (0.25)	1.27 (0.27)	10.80	< 0.001

to 14°C, 10 ppt and 14°C, 20 ppt, average swimming speed was higher 120 min after test water introduction, compared to the initial 30 min exposure.

#### ADULT EXPERIMENTS

The adult experiments were originally designed to test 8 sockeye from northern waters, and 8 from the south in each of the 6 conditions (total of 96 fish). However, only 76 fish were used in the analysis. Of the 79 adults collected, 1 died prior to experiments and 2 were excluded from tests because they failed to move during the control period. The mean total length was 61.4 cm (SD= 2.6 cm).

The number of passes through photo-cell stations was recorded for 60 min by electronic and visual means. Results are shown in Table 10. Chi-square analysis failed to demonstrate a difference between the two methods of data collection.

Statistical tests were performed to identify any variations in locomotor activity due to time of day, race, or sex. Results showed no difference in average swimming speed between sockeye tested in the morning and afternoon (Table 11). In addition, the analyses did not detect a difference in locomotion between the 4 races of sockeye (Table 12), or between males and females (Table 13).

Swimming speeds of adult salmon exposed to

Table 10. The number of passes through photo-cell stations recorded for adult sockeye during 60 minutes exposure to control (12°C, 30 ppt) conditions. Data collected by electronic and visual observations were not significantly different (chi-square= 0.038, P> 0.05).

Observation	Number of counts		
Method	per 30 minute interval		
	Tank 1	Tank 2	Tank 3
Electronic	91	96	168
Visual	93	94	163

Table 11. The average swimming speed of adult sockeye salmon exposed for 30 minutes to control conditions (12°C, 30 ppt) in morning or afternoon tests (~ 4 hours difference). Statistical analysis (single factor ANOVA) showed no significant difference between mean values.

Time of Day	N	Mean Swimming	SD	F	P > F
		Speed (1/s)	(1/s)		
Morning	38	0.41	0.23	0.19	-
Afternoon	38	0.38	0.21		

Table 12. The difference in average swimming speed between four races of adult Fraser River sockeye. Activity of fish was recorded during exposure to control conditions (12°C, 30 ppt) for 30 minutes. Statistical analysis (single factor ANOVA) showed no significant difference between mean values for each of the four groups.

Population	N	Mean Swimming Speed (l/s)	SD (l/s)	F	P > F
Chilko River	25	0.38	0.21	0.70	-
Adams River	32	0.46	0.21		
Birkenhead	9	0.46	0.26		
Weaver Creek	8	0.40	0.24		

Table 13. The mean swimming speeds of male and female sockeye salmon subjected to control conditions (12°C, 30 ppt) for 30 minutes. Statistical tests (single factor ANOVA) showed no difference between mean values.

Sex	N	Mean Swimming Speed (l/s)	SD (l/s)	F	P > F
Male	36	0.38	0.23	0.29	-
Female	40	0.39	0.22		

decreasing salinity or decreasing temperature were comparable to the controls (Figure 8). However, exposure to  $16^{\circ}$ , 20 ppt and  $16^{\circ}\text{C}$ , 30 ppt caused an elevation in locomotor activity (Table 14). A two factor ANOVA showed that temperature was the only factor influencing average swimming speed during the final hour of testing (Table 15). In addition, Newman-Keuls multiple range test demonstrated that the effect was solely due to increasing temperature (Table 14).

Since fish were obtained from oceanographically distinct regions and were acclimated for different periods of time, additional analyses were required to identify effects due to area of capture and/or number of days in captivity. Prior tests had indicated that decreasing temperature did not influence swimming activity (Table 14); thus, the analyses were restricted to fish tested in  $16^{\circ}\text{C}$ . Salinity was also found to have no effect on locomotor activity (Table 15); therefore, to increase sample size for testing effects due to days in captivity, data were pooled from  $16^{\circ}\text{C}$ , 20 ppt and  $16^{\circ}$ , 30 ppt.

The average swimming speeds of adult sockeye tested in  $16^{\circ}\text{C}$  were compared by area of capture and salinity condition. The two factor ANOVA did not detect an effect on mean speed due to area of capture and there was no interaction between response to salinity and sampling

Figure 8. Average swimming speeds ( $\pm$ SEM) of adult sockeye salmon during the final 60 minutes exposure to test levels. Fish were initially subjected to control conditions ( $12^{\circ}\text{C}$ , 30 ppt) for one hour, and water turnover took approximately 120 minutes.

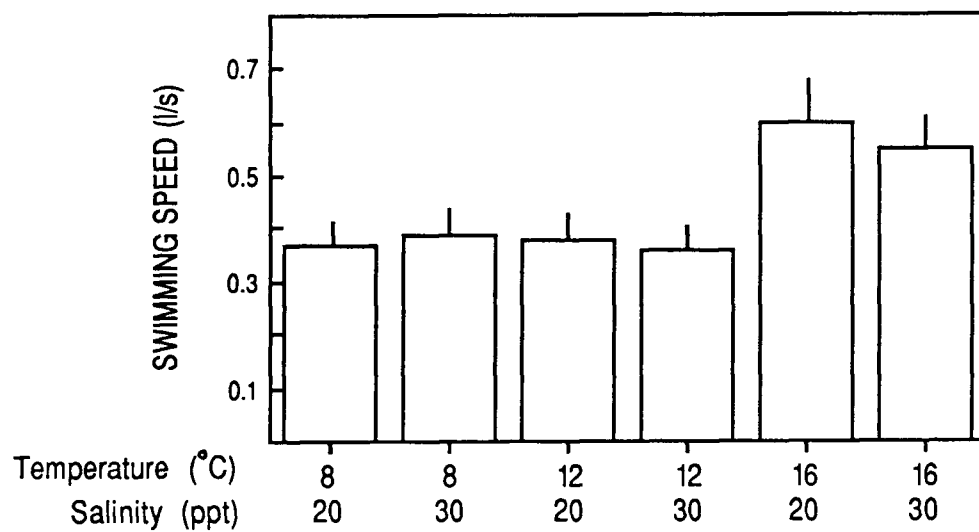


Table 14. The mean swimming speeds of adult sockeye salmon during the final 60 minutes exposure to test levels. Fish were initially subjected to control conditions (12 °C, 30 ppt) for one hour, and water turnover took approximately 120 minutes. Results from Newman-Keuls multiple range test are also included in the table (NS= not significant, \* =  $< 0.05$ , \*\* =  $< 0.01$ ).

Temperature ( C )	Salinity (ppt)	N	Mean Swimming Speed (l/s)	SD (l/s)	Newman-Keuls
8	20	10	0.37	0.13	NS
8	30	14	0.39	0.19	NS
12	20	15	0.38	0.15	NS
12	30	11	0.36	0.14	-control-
16	20	15	0.60	0.26	**
16	30	11	0.55	0.18	*

Table 15. Results of the two factor ANOVA comparing the mean swimming speeds of adult sockeye salmon subjected to experimental conditions for sixty minutes (see Table 14).

Source	SS	DF	MS	F	P > F
Temperature	8.11	2	4.11	7.49	0.001
Salinity	0.26	1	0.26	0.47	-
Temp*Sal	0.27	2	0.14	0.25	-
Error	41.64	76	0.55		



region (Table 16).

Sockeye taken from the northern area were tested in 16°C water 2 - 5 d after collection. Analyses did not detect a difference in average swimming speed between the 4 d (Table 17). Fish caught in the southern area were tested in 16°C water 2 - 4 d after capture and also there was no effect of days in captivity on mean swimming speed (Table 17).

Locomotor activity was compared between each test condition during control, water turnover, and test phases. Fish tested in decreasing temperature, and either decreasing or constant salinity maintained consistent levels of swimming activity throughout the experiment (Figure 9a-b). Similar results were obtained for fish exposed to decreasing salinity (Figure 10a) compared to the controls (Figure 10b).

The locomotor activity of adult sockeye tested in 16°C water tended to follow the pattern of temperature change (Figure 11). For fish exposed to 16°C, 20 ppt swimming activity increased steadily during the first hour of water turnover, followed by a plateau period, and concluding with a slight rise in swimming speed during the final hour of testing (Figure 11a). Fish exposed to 16°C, 30 ppt exhibited a similar pattern of locomotor activity (Figure 11b), however, the change in swimming speed did not appear as pronounced.

The repeated measures ANOVA demonstrated that the

Table 16. The average swimming speeds of adult sockeye salmon subjected to 16°C 20 ppt or 16°C 30 ppt during the final hour of testing. Standard deviations are given in brackets beside each mean value. Mean speeds were pooled for fish taken in the northern sampling sets (N1, N2, N3) and the southern sets (S1, S2). Results from the statistical analysis (two factor ANOVA) are also included in the table.

Area of Capture	N	Salinity	Mean Swimming Speed (l/s)	Source of Variation	F	P > F
North	9	20	0.61 (0.23)	Area	0.80	-
North	7	30	0.58 (0.18)	Salinity	0.36	-
South	6	20	0.56 (0.17)	Area*	0.21	-
South	4	30	0.54 (0.22)	Salinity		

Table 17. The mean swimming speeds of adult sockeye during the final hour of exposure to 16°C water. Average values are pooled for fish from northern and southern sets based on the number of days acclimated at control conditions. Results of the statistical analyses (single factor ANOVA) conducted on northern and southern samples are also included.

Days Acclimated	Area Caught	N	Mean Swimming Speed (l/s)	SD (l/s)	F	P > F
2	North	4	0.62	0.27	0.70	-
3	North	4	0.55	0.15		
4	North	4	0.64	0.23		
5	North	4	0.61	0.27		
2	South	4	0.47	0.28	0.40	-
3	South	3	0.60	0.19		
4	South	3	0.46	0.34		

Figure 9. Mean swimming speeds ( $\pm$ SEM) of adult sockeye salmon during exposure to (A) 8°C, 20 ppt; and (B) 8°C, 30 ppt. Values were calculated at 30 minute intervals for control conditions (T0), two hours of water turnover (T0 - 120), and one hour at test levels (T120 - T180). Approximate changes in temperature and salinity are included in the upper portion of each figure.

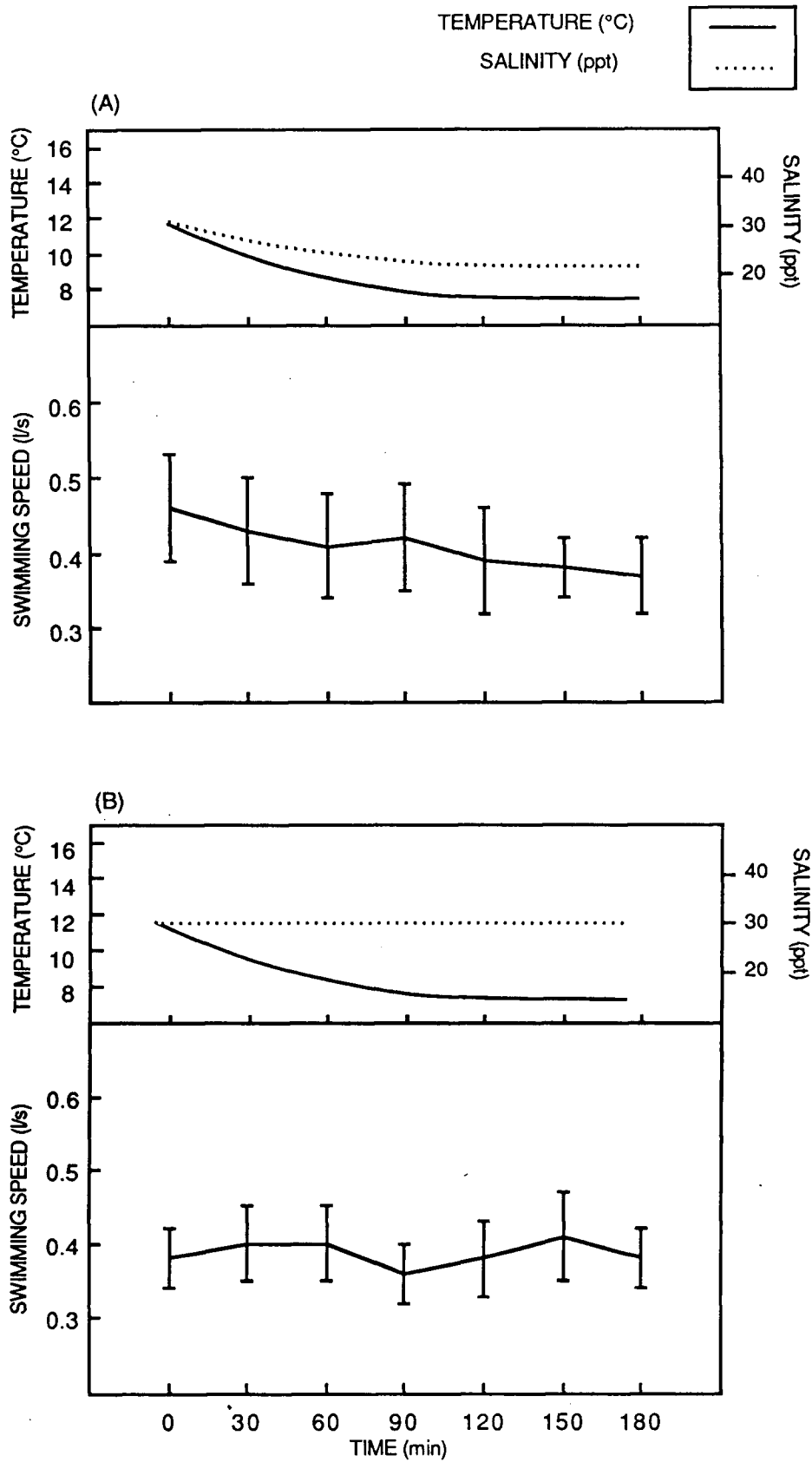


Figure 10. Mean swimming speeds ( $\pm$ SEM) of adult sockeye salmon during exposure to (A) 12°C, 20 ppt; and (B) 12°C, 30 ppt. Values were calculated at 30 minute intervals for control conditions (T0), two hours of water turnover (T0 - 120), and one hour at test levels (T120 - T180). Approximate changes in temperature and salinity are included in the upper portion of each figure.

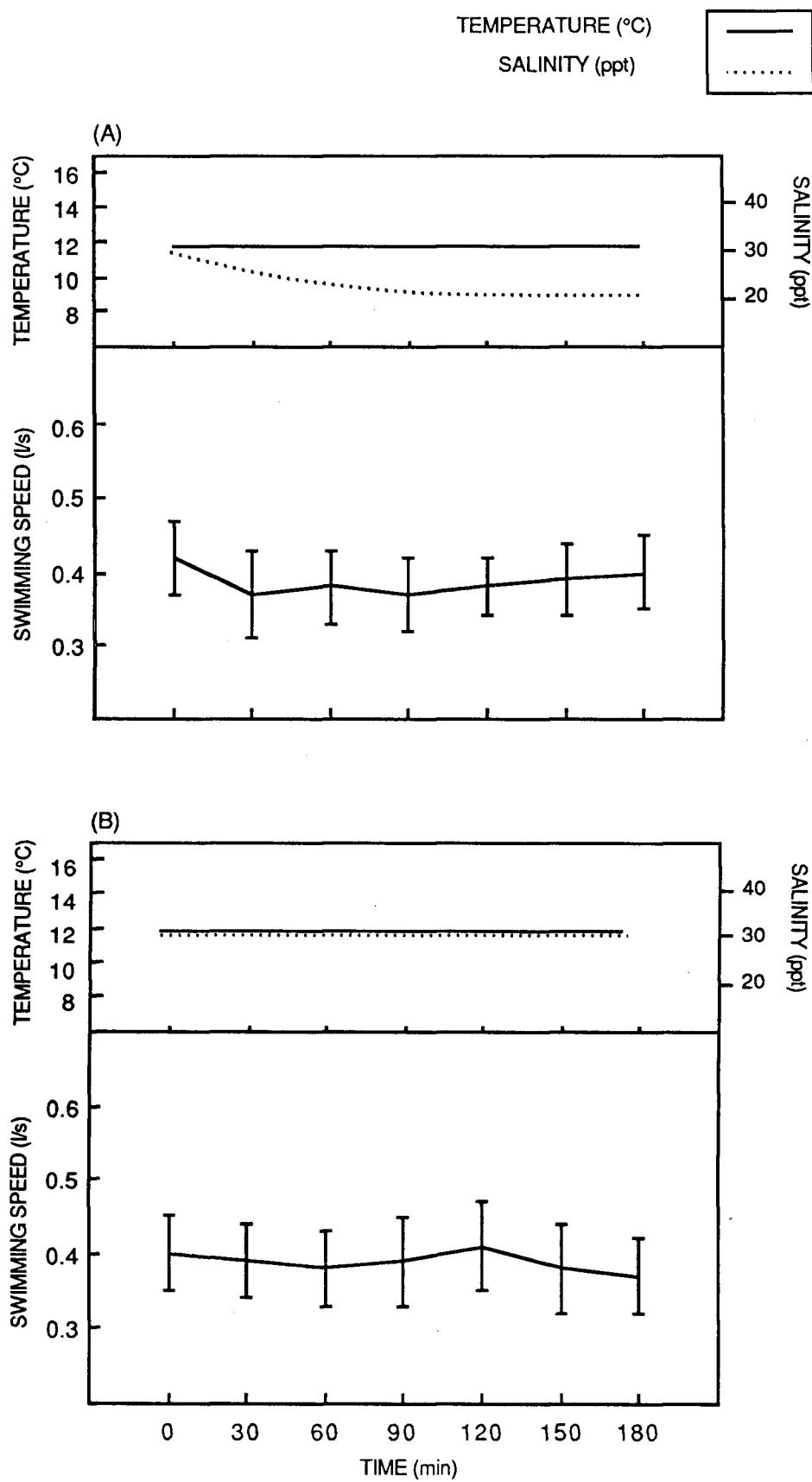
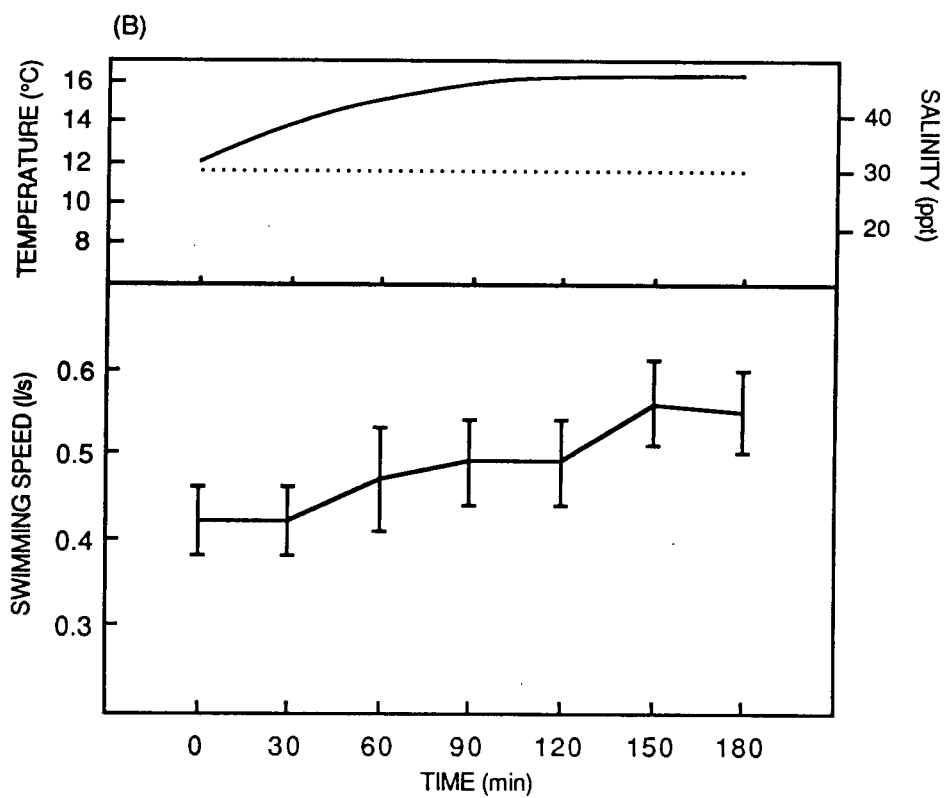
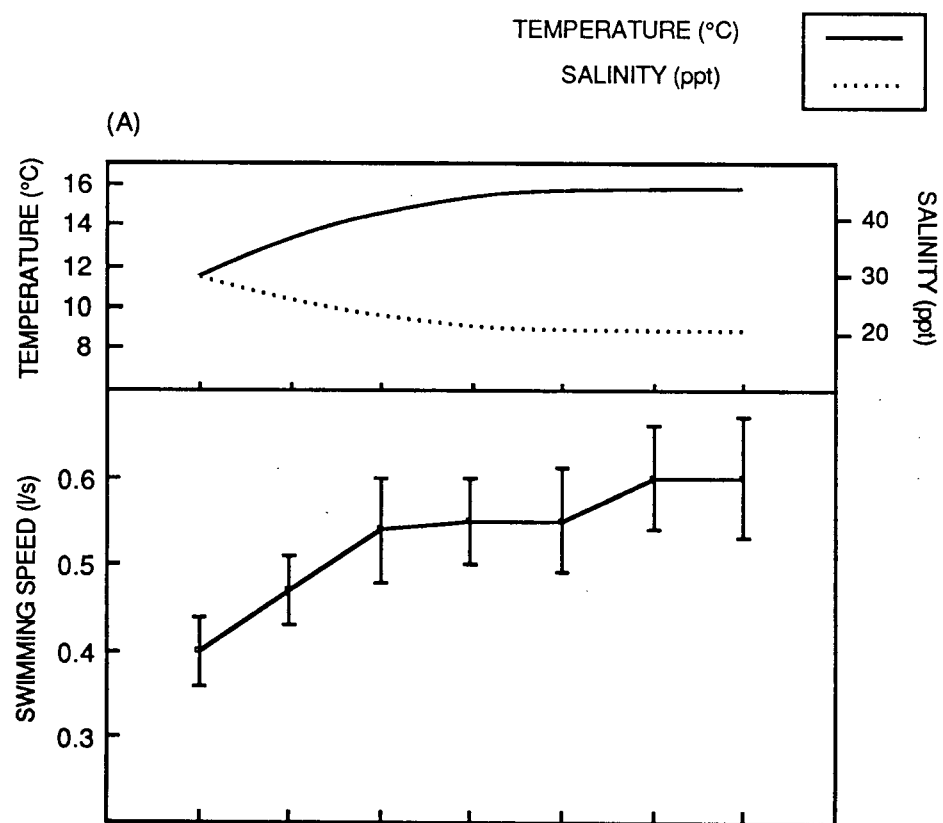


Figure 11. Mean swimming speeds ( $\pm$ SEM) of adult sockeye salmon during exposure to (A) 16°C, 20 ppt; and (B) 16°C, 30 ppt. Values were calculated at 30 minute intervals for control conditions (T0), two hours of water turnover (T0 - 120), and one hour at test levels (T120 - T180). Approximate changes in temperature and salinity are included in the upper portion of each figure.





average swimming speeds of adult sockeye were not affected by decreasing temperature or by salinity (Table 18).

However, locomotor activity increased during exposure to  $16^{\circ}\text{C}$ , 20 ppt and  $16^{\circ}\text{C}$ , 30 ppt. Additional a posteriori analysis (Newman-Keuls multiple range test) showed that the average swimming speed of adult sockeye was higher after 60 min exposure to  $16^{\circ}\text{C}$ , 20 ppt, and after 90 min exposure to  $16^{\circ}\text{C}$  30 ppt (Table 18).

The influence of capture area on swimming activity in  $16^{\circ}\text{C}$  water was also examined. Fish from the northern areas had a more pronounced locomotor response to increasing temperature (Figure 12). Mean swimming speeds of fish from each sampling set were subjected to a repeated measures ANOVA. Set N1 had only 2 fish tested in  $16^{\circ}\text{C}$ , and therefore was pooled with set N2. Previous analyses had shown no effect due to salinity (Table 15). Therefore, to increase sample size data were pooled from fish subjected to  $16^{\circ}\text{C}$ , 20 ppt and  $16^{\circ}\text{C}$  30 ppt.

The ANOVA demonstrated that fish from each of the northern sets had highly significant responses to increasing temperature, while fish from southern sets did not (Table 19). When sets S1 and S2 were pooled together, the effect of increasing temperature was significant at the 0.05 level (Table 19).

In addition to electronic recording of swimming activity, adult salmon were observed visually for 10 min

Table 18. Mean swimming speeds of adult sockeye calculated over 30 minute intervals after 1/2 hour in control conditions (T0), two hours of water turnover (T0 - T120) and one hour at test levels (T120 - T180). Results of statistical tests (repeated measures ANOVA) are included for each condition.

Temp. ( C )	Sali. (ppt)	N	Mean Swimming Speed (l/s) for each 30 minute interval (SD in brackets)							F	P > F
			T0	T30	T60	T90	T120	T150	T180		
8	20	10	0.46 (0.21)	0.43 (0.25)	0.41 (0.23)	0.42 (0.23)	0.39 (0.21)	0.38 (0.12)	0.37 (0.18)	0.48	-
8	30	14	0.38 (0.13)	0.40 (0.18)	0.40 (0.17)	0.36 (0.15)	0.38 (0.21)	0.41 (0.22)	0.38 (0.14)	0.55	-
12	20	15	0.42 (0.18)	0.37 (0.21)	0.38 (0.18)	0.37 (0.17)	0.38 (0.13)	0.39 (0.18)	0.40 (0.19)	0.50	-
12	30	11	0.40 (0.16)	0.39 (0.16)	0.38 (0.14)	0.39 (0.19)	0.41 (0.20)	0.38 (0.21)	0.37 (0.16)	0.45	-
16	20	15	0.40 (0.15)	0.47 (0.16)	0.54 (0.22)	0.55 (0.18)	0.55 (0.22)	0.60 (0.23)	0.60 (0.26)	7.75	<0.001
16	30	11	0.42 (0.12)	0.42 (0.12)	0.47 (0.23)	0.49 (0.15)	0.49 (0.17)	0.56 (0.18)	0.55 (0.16)	4.25	<0.001

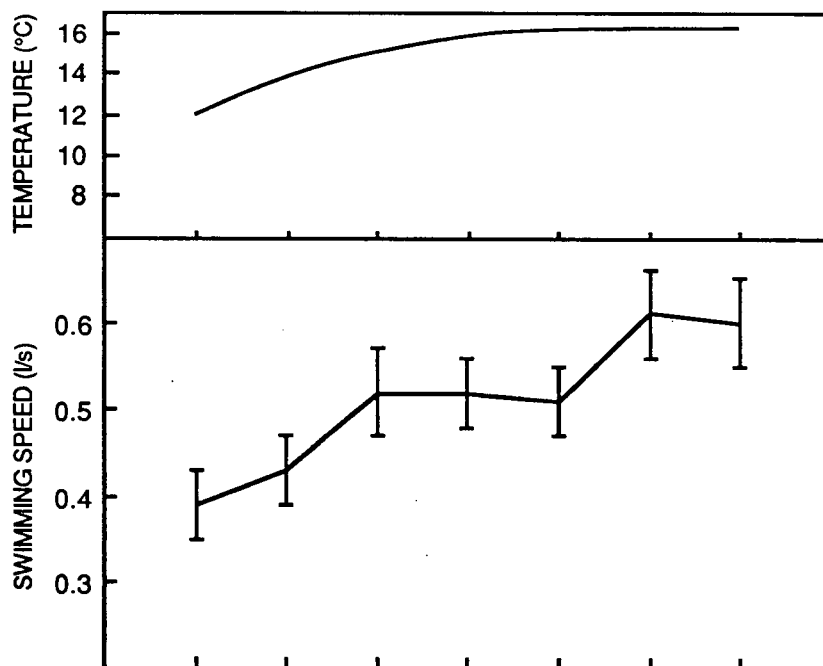
Figure 12. Mean swimming speeds ( $\pm$ -SEM) of adult sockeye salmon during exposure to 16°C pooled for fish taken from (A) northern sets- N1, N2, N3 (n= 16), and (B) from southern sets S1 and S2 (n= 10). Values were calculated at 30 minute intervals for control conditions (T0), two hours of water turnover (T0 - 120), and one hour at test levels (T120 - T180). Approximate changes in temperature and salinity are included in the upper portion of each figure.

TEMPERATURE (°C)

SALINITY (ppt)



(A)



(B)

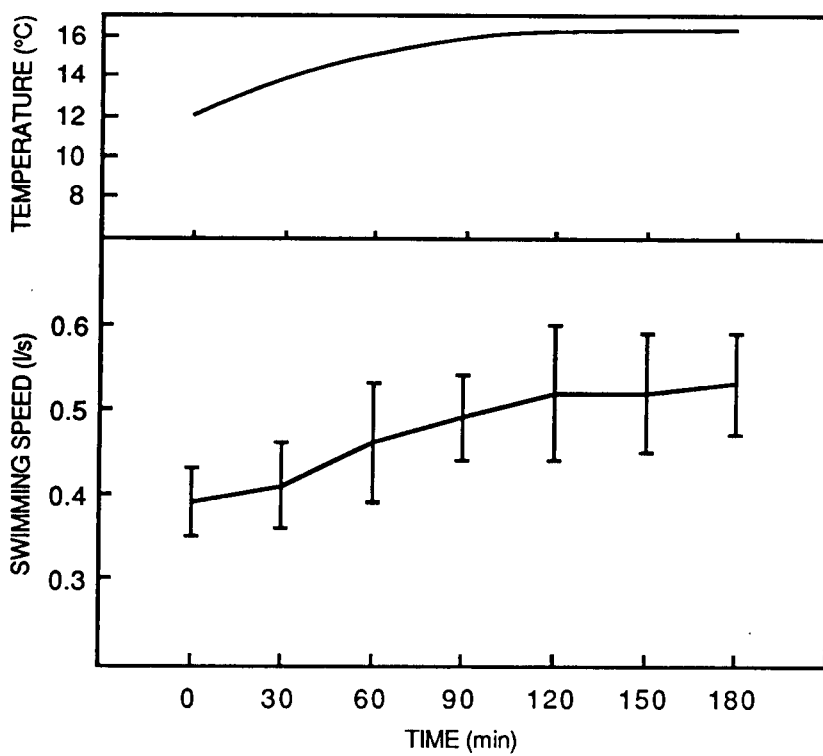


Table 19. Average swimming speeds of adult sockeye salmon calculated over 30 minute intervals after 1/2 hour in control conditions (T0), 2 hours of water turnover (T0 - T120) and 1 hour exposure to 16°C (T120 - T180). Mean values are given for the different sampling sets and for pooled data from northern and southern areas. Results from statistical tests (repeated measures ANOVA) are included for separate and pooled samples.

Set number	N	Mean Swimming Speed (l/s) for each 30 minute interval (SD in brackets)							F	P > F
		T0	T30	T60	T90	T120	T150	T180		
N1/N2	10	0.46 (0.19)	0.46 (0.14)	0.54 (0.24)	0.54 (0.24)	0.57 (0.22)	0.67 (0.22)	0.60 (0.24)	5.88	<0.001
N3	6	0.31 (0.16)	0.36 (0.10)	0.47 (0.16)	0.50 (0.12)	0.41 (0.08)	0.51 (0.13)	0.61 (0.19)	5.14	<0.001
S1	5	0.41 (0.17)	0.37 (0.15)	0.50 (0.25)	0.53 (0.22)	0.54 (0.20)	0.45 (0.20)	0.54 (0.27)	2.00	0.105
S2	5	0.38 (0.09)	0.43 (0.11)	0.42 (0.21)	0.44 (0.14)	0.51 (0.14)	0.58 (0.28)	0.53 (0.24)	1.77	0.150
North pooled	16	0.39 (0.13)	0.43 (0.13)	0.52 (0.21)	0.52 (0.18)	0.51 (0.19)	0.61 (0.20)	0.60 (0.22)	10.60	<0.001
South pooled	10	0.39 (0.13)	0.41 (0.18)	0.46 (0.22)	0.49 (0.18)	0.52 (0.24)	0.52 (0.24)	0.53 (0.24)	2.64	0.025

periods during the control, water-turnover, and test phases. The conditions for which data were recorded include: 8°C, 30 ppt; 10°C, 20 ppt; 10°C, 30 ppt; and 16°C, 30 ppt. This allowed for the main effects (temperature and salinity) to be examined, but interactions between factors were not compared. Fish were not separated by geographical area.

Results for fish maintained in control conditions are included in Table 20. Statistical tests detected no difference in the 4 parameters that were recorded. In addition, analyses showed no effect of decreasing temperature (Table 21) or salinity (Table 22) on any of the observed behaviors. Nosing and finning were not influenced by increasing temperature. However, both swimming activity and turning rate increased within 30 min exposure to 16°C water (Table 23). In the final hour of testing, locomotor activity had stabilized. Turning rate appeared to decrease, however, Newman-Keuls test failed to detect a significant result.

The electronic and visual methods of data collection both showed an effect of increasing temperature on locomotion. However, there was some variation in swimming activity recorded by the two methods (Table 24). The swimming speed of sockeye during the initial 30 min exposure to 16°C water was low compared to the rate of locomotor activity and turning that was measured by visual means.

Table 20. Activity of adult sockeye salmon during exposure to control temperature (12°C) and control salinity (30 ppt). There were four activity parameters, each recorded for ten minute intervals, at various times in the experiment. Data collection corresponded to the experimental periods. These included; the initial control phase (Time 1), ten minutes during the first 1/2 hour of water turnover (Time 2), and ten minutes during the first 1/2 hour at test levels (Time 3). Mean values are events per ten minute interval. Standard deviations (in brackets below means) and results from statistical (repeated measures ANOVA) analyses are included in the table.

	Activity	Turns	Noses	Fins
	(per 10 min)	(per 10 min)	(per 10 min)	(per 10 min)
Time 1	11.78 (11.96)	8.60 (10.70)	1.78 (4.30)	0.67 (2.00)
Time 2	15.90 (9.70)	3.22 (3.07)	0.67 (1.12)	1.00 (1.80)
Time 3	14.00 (14.70)	3.78 (4.92)	0.33 (0.50)	0.22 (0.44)
N	9	9	9	9
ANOVA F	0.82	1.55	0.77	0.53
P > F	0.80	0.24	-	-

Table 21. Activity of adult sockeye salmon during exposure to decreasing temperature (8°C) and constant salinity (30 ppt). There were four activity parameters, each recorded for ten minutes in control conditions (Time 1), ten minutes during the first 1/2 hour of water turnover (Time 2), and for ten minutes during the first 1/2 hour at test levels (Time 3). Mean values are events per ten minute interval. Standard deviations (in brackets below means) and results from statistical analyses (repeated measures ANOVA) are included in the table.

	Activity	Turns	Noses	Fins
	(per 10 min)	(per 10 min)	(per 10 min)	(per 10 min)
Time 1	10.30 (10.70)	2.14 (5.24)	1.18 (3.21)	0.43 (1.62)
Time 2	14.14 (11.05)	5.42 (8.79)	0.68 (1.05)	0.91 (1.33)
Time 3	13.71 (14.51)	2.28 (4.11)	0.92 (1.83)	1.26 (1.46)
N	7	7	7	7
ANOVA F	0.24	0.80	0.63	0.81
P > F	-	-	-	-



Table 22. Activity of adult sockeye salmon during exposure to control temperature (12°C) and decreasing salinity (20 ppt). There were four activity parameters, each recorded for ten minutes in control conditions (Time 1), ten minutes during the first 1/2 hour of water turnover (Time 2), and for ten minutes during the first 1/2 hour at test levels (Time 3). Mean values are events per ten minute interval. Standard deviations (in brackets below means) and results from statistical analyses (repeated measures ANOVA) are included in the table.

	Activity	Turns	Noses	Fins
	(per 10 min)	(per 10 min)	(per 10 min)	(per 10 min)
Time 1	13.33 (9.43)	4.25 (5.07)	1.50 (3.34)	1.17 (2.29)
Time 2	13.33 (9.37)	1.83 (2.12)	0.50 (1.45)	0.67 (1.37)
Time 3	16.08 (8.50)	3.25 (5.94)	1.67 (5.77)	1.83 (3.61)
N	12	12	12	12
ANOVA F	0.59	0.76	0.34	1.15
P > F	-	-	-	0.33

Table 23. Activity of adult sockeye salmon during exposure to increasing temperature (16°C) and control salinity (30 ppt). There were four activity parameters, each recorded for ten minutes in control conditions (Time 1), ten minutes during the first 1/2 hour of water turnover (Time 2), and for ten minutes during the first 1/2 hour at test levels (Time 3). Mean values are events per ten minute interval. Standard deviations (in brackets below means) and results from statistical analyses (repeated measures ANOVA) are included in the table.

	Activity	Turns	Noses	Fins
	(per 10 min)	(per 10 min)	(per 10 min)	(per 10 min)
Time 1	8.43 (6.74)	5.21 (5.45)	1.36 (3.71)	1.07 (3.20)
Time 2	19.43 (19.67)	18.71 (18.13)	3.93 (6.74)	2.07 (2.43)
Time 3	22.21 (8.44)	10.57 (8.86)	0.79 (1.81)	0.93 (1.90)
N	10	10	10	10
ANOVA F	22.41	5.14	2.14	1.33
P > F	< 0.001	0.01	0.14	0.28

Table 24. The mean swimming speeds, locomotor activity and turning rate of adult sockeye salmon during exposure to increasing temperature and control salinity. Standard deviations are included in brackets under each mean. Swimming speed was calculated at 1/2 hour intervals during control (Time 1), water turnover (Time 2), and test (Time 3) intervals. Activity and turning rate were recorded visually for 10 minute intervals during each of the three time periods.

Time	N	Mean Swimming	Activity	Turns
Period		Speed (l/s)	(per 10 min)	(per 10 min)
1	17	0.38 (0.12)	11.4 (5.3)	4.8 (5.3)
2	17	0.40 (0.13)	18.9 (9.2)	16.4 (18.0)
3	17	0.58 (0.21)	23.9 (13.4)	10.2 (9.1)

## DISCUSSION

This study was undertaken to gain a better understanding of how environmental factors may influence the nearshore migration of sockeye salmon. The only factor that affected the locomotor activity of juvenile and adult sockeye was increasing temperature. Swimming speed was not influenced by salinity or decreasing temperature, and there was no interaction between factors. Differences between test fish based on race, sex, area of capture, and time of experiment did not affect locomotor behavior.

Both juvenile and adult sockeye increased swimming speed during exposure to warm water (Figure 7, Figure 11). Because the juvenile behavior was not recorded visually, turning behavior could not be assessed. However, the adults showed an increase both in turning rate and locomotor activity (Table 23).

The behaviors demonstrated by test fish were consistent with previously described mechanisms of animal orientation. Fraenkel and Gunn (1961) suggested that an increase in locomotor activity (orthokinesis) when conditions are poor, coupled with a decrease in activity when conditions are favourable leads to an aggregation of animals in a preferred temperature range. Fraenkel and Gunn (1961) also suggested that an elevation in turning rate (klinekinesis) when an unfavourable environment is

encountered increases the probability of finding the preferred area. When favourable conditions are relocated, turning immediately decreases and the animal maintains position in the desired field. If favourable conditions are not located, 'adaptation' occurs and turning rate gradually declines. In this way the animal increases its area of search and raises its chance of finding the preferred conditions (Fraenkel and Gunn 1961).

Few studies have applied the mechanisms described by Fraenkel and Gunn (1961) to salmon orientation. Neill (1979) tested a computer simulation of Fraenkel and Gunn's (1961) hypotheses using Ivlev's (1960) Atlantic salmon data. Neill's (1979) model failed to show that strict orthokinesis allowed adequate avoidance of lethal temperatures. Although klinekinetic responses were more effective, he showed that a klinekinesis 'with avoidance' produced results comparable to those given by Ivlev (1960). In his model, Neill (1979) assumed that turning rate was dependent on the interaction between two variables- recent temperature stress and rate of thermal change. Thus, turning rate increased when a combination of these parameters exceeded some pre-set tolerance limit.

In the present study, turning rates of adult sockeye exposed to 16°C declined during the final hour of testing, while swimming speeds remained high (Table 19, Table 23). This may have resulted from 'adaptation' similar to the

mechanism described by Fraenkel and Gunn (1961). However, the results could also be in accordance with Neill's (1979) model of klinekinesis based on recent thermal experience and rate of temperature change (i.e. during tests, the rate of temperature change decreased throughout the water turnover period). The decline in turning rate was not statistically significant, and random variation was high (Table 23); therefore, I hesitate to make any conclusions regarding the present data set.

Orientation to salinity gradients is considered to involve the kinetic mechanisms described by Fraenkel and Gunn (1961). McInerney (1964) hypothesized that juvenile salmon maintain position in a salinity field using klinekinetic rather than orthokinetic behavior. Holliday (1971) also suggested that klinekinetic responses allow fish to maintain position in a salinity gradient. In the present study, turning rates of juvenile sockeye were not recorded, however, there was no orthokinetic response to test salinities (Table 9). Similarly, the adult salmon I tested did not exhibit orthokinetic or klinekinetic responses to decreasing salinity (Table 22).

Both juvenile and adult sockeye were able to withstand a 4°C decrease in temperature without influencing locomotor activity (Figure 5, Figure 9). The lack of a behavioral response suggests that sockeye salmon may utilize physiological means to deal with decreasing temperatures.

One mechanism that has been reported for a number of fish species involves molecular temperature compensation (Dizon et al. 1978, Stevens and Fry 1972, Glova 1972, Conner et al. 1964). Temperature compensation may involve an enhanced affinity of certain enzymes for their substrate at low temperature ('positive thermal modulation'), as well as the use of enzyme variants (reviewed by Hazel and Prosser 1974, Hochachka and Somero 1970). Other workers have suggested that some eurythermal species have an enhanced ability to regulate myofibrillar ATPase activity over a wide range of temperatures (Heap et al. 1986). Behringer (1969) showed that migrating pink salmon maintained high levels of energy conversion over an extensive thermal range, and suggested that enzyme/substrate modulation and decreased allosteric inhibition at low temperatures were the most likely mechanisms involved.

In the field, migrating sockeye swim faster than the fish I tested (Quinn and terHart 1987, Quinn 1988), and may show a different response to decreasing temperature. However, the results do suggest that some mechanism of adaptation is involved. The ability of sockeye salmon to withstand a wide thermal range is emphasized by the vertical migrations of both juveniles and adults. In summer, the daily vertical migration in lakes may expose sockeye fry to temperature ranges of 10°C (Brett 1971, Barraclough and Robinson 1972), while homing adults may move through thermal

gradients of  $8^{\circ}\text{C}$  in a matter of minutes (Quinn and terHart 1987).

Temperature compensation may be an important component of the salmon migratory strategy. At various stages of their life history salmon encounter dramatic temperature gradients that could potentially compromise locomotor movements. Since adult sockeye migrate on a relatively tight energy budget (Brett 1983) and at a constant rate (Groot and Quinn 1987), it would not be conducive to survival if cold temperatures dramatically decreased swimming activity. Migrating silver eels that encounter excessively cold autumn temperatures halt the migration and hibernate until the following spring (Westin and Nyman 1977). An alternative strategy of temperature compensation would allow sockeye a greater degree of freedom in their movements, and, in effect increase the thermal zone of efficient operation (Crawshaw 1979).

Juvenile and adult sockeye responded to elevated temperatures by increasing locomotor activity (Figure 4, Figure 8). This may reflect a lesser ability to compensate at high temperatures compared to low temperatures (eg. Hochachka and Somero 1971, Peterson and Anderson 1969). For a mobile animal, elevated activity with increasing temperature would be an appropriate component of behavioral thermoregulation (Crawshaw 1979), whereas decreasing locomotion with decreasing temperatures would not.



When exposed to 16°C, a number of juvenile and adult sockeye continued to increase their swimming speeds even though temperatures had stabilized (Table 9, Table 18). The results were similar to the 'overshoot' reported by Peterson and Anderson (1969). They noted that at low temperatures and a modest rate of water turnover juvenile Atlantic salmon initially increased activity, followed by a plateau period, and a subsequent rise in swimming speed. At higher rates of water turnover the fish tested by Peterson and Anderson (1969) showed a more pronounced overshoot, and a corresponding increase in oxygen consumption. It appears likely that a similar mechanism influenced the locomotion of fish I tested; although, the adaptive significance of this behavior is not known.

The juvenile sockeye did not show a locomotor response to salinity changes (Figure 6, Table 7), however, there may have been an interaction between salinity and temperature at 14°C (Figure 11). The average speeds of juvenile sockeye tested in 14°C, 10 ppt and 14°C, 30 ppt, were somewhat lower than for fish exposed to 14°C, 20 ppt. It is possible that salinity challenge at higher temperatures may have compromised metabolic functions of the smolts and caused a decrease in volitional swimming activity. Brett (1970) reported a 20 - 30% drop in standard metabolism for sockeye smolts passing from fresh to saltwater. Houston (1959) noted a significant decrease in

locomotor activity of juvenile salmon undergoing seawater transition.

The adult sockeye taken from the northern area exhibited a more pronounced locomotor response to increasing temperature than did fish collected near the Fraser River (Figure 12). However, the small and unequal sample sizes make interpretation of the results difficult. It is possible that acclimation state had some influence on activity responses to increasing temperature. Fish taken from the southern region had access to warmer temperatures, and Quinn et al. (1988) showed that Fraser River sockeye spend at least some time in the warmer surface layers of the Strait of Georgia. If acclimation was a factor affecting behavior, then locomotor responses might change as a function of time in captivity. This was not the case (Table 17); although, conditioning to a new temperature may take weeks (Brett 1970), and the fish I tested were only held for a few of days.

It is also conceivable that developmental changes during the homestream approach had some influence on locomotor responses to temperature. A relationship between maturational state and behavioral response to environmental gradients has been demonstrated for a number of fish species (eg. Norris 1963, Baggerman 1957). The sockeye caught near the Fraser River had significantly higher levels of sex steroids (unpublished data), however, it was not possible to

separate the influence of other factors such as acclimation state. For the present study, no conclusions can be made regarding the affect of maturational state on activity responses to test temperatures.

It has been hypothesized that estuarine migrations depend on orientation to temperature and salinity gradients (McInerney 1964, Baggerman 1960b). Hurley and Woodall (1968) concluded that time-varied changes in preference for nearshore temperature and salinity gradients lead pink salmon smolts to ocean feeding areas. Straty and Jaenicke (1980) suggested that the run timing and distribution of Bristol Bay sockeye smolts was influenced by direct responses to both temperature and salinity.

Opposing views contend that temperature and salinity are not the main factors affecting smolt migrations. Ultrasonic tracking studies (LaBar et al. 1978) indicated that environmental factors other than temperature and salinity influenced the migratory movements of juvenile Atlantic salmon. Similarly, McCleave (1978) reported that responses to current were the main factor affecting the estuarine migration of Atlantic salmon smolts.

Some of the discrepancy concerning the role of environmental parameters relates to the behavior of the species in question. For example, pink salmon typically move downstream soon after yolk absorption, but may spend months in estuaries prior to migrating offshore (Hurley and

Woodall 1968). Therefore, temporal changes in preference for colder, more saline water could play a role in the seaward movement of pink salmon (Hurley and Woodall 1968).

Orientation to temperature and salinity gradients may be of less importance to migrating Atlantic salmon smolts. Telemetry studies have shown that Atlantic salmon move directly seaward and do not require extensive periods of acclimation (McCleave 1978). The smolts tracked by LaBar et al. (1978) moved from fresh water to 29 ppt in less than 48 h (see also Tytler et al. 1978). If sequential changes in temperature and salinity preference do influence the migration, it would be difficult to identify behavioral responses in such a short transition period.

The seaward movements of sockeye smolts is generally direct and rapid (Brett 1983); thus, the use of nearshore gradients as an orientation mechanism must be relatively brief. The juvenile sockeye I tested did not exhibit a temporal change in locomotor response to increasing temperature (Table 8) and the fish were able to withstand 10 ppt deviations in salinity. Acclimation to 10°C, 20 ppt for 1 wk prior to the experiments may have increased tolerance to salinity challenge, and decreased the need for behavioral avoidance. Otto and McInerney (1970) reported that preference/avoidance responses to salinity gradients would not be an effective directing mechanism for juvenile coho salmon once the fish were acclimated to intermediate

salinities.

Changes in temperature influenced the swimming activity of juvenile and adult sockeye, and locomotor responses were consistent with known kinetic mechanisms of orientation. I will now consider the possible ecological significance of these results on the coastal migration of sockeye salmon.

Great Central Lake sockeye begin the downstream migration in April or May (Groot et al. 1986). Robinson and Barraclough (1972) reported that GCL smolts migrating in the spring have been exposed to waters of 2 - 6°C for the previous 5 mo. Therefore, prior to the downstream migration it is probably safe to assume that the salmon are conditioned to relatively cold temperatures.

The smolts move out of the Somass River (Figure 1) and through the inner estuary, which extends about 5 - 6 km from the river mouth. Tully (1949) showed that sockeye migrating through Alberni Inlet in spring would encounter temperatures of 13 - 15°C at the surface, and 9 - 10°C at a depth of 10 m (see also Morris and Leany 1980). Tully (1949) also reported that maximum surface temperatures were located near the estuary and progressively decreased towards Barkley Sound.

Given the behavior of the smolts I tested, and the arrangement of temperature gradients in Alberni Inlet, it is possible that locomotor responses to temperature aid the

migration to oceanic waters. However, it is unlikely that orthokinesis is the only factor involved. Pickard (1963) showed that over the length of Alberni Inlet temperatures at 10 m depth differed by only about 3°C. It remains to be seen if gradients of this magnitude are sufficient to facilitate oriented movements, or if additional guidance mechanisms are also required.

During an El Nino event, sockeye homing to the Fraser River may be exposed to anomalous coastal temperatures 2°C above normal (Dodimead 1985). The present study showed that adult sockeye respond to temperature changes of this magnitude by increasing locomotor activity and turning rate. Therefore, it is possible that orthokinetic and klinekinetic responses to warm temperatures influence the nearshore migration of Fraser River adults. The results support the hypothesis of Tully et al. (1960) and Royal and Tully (1961) that avoidance of warm waters emanating from the south cause a higher than average diversion of sockeye through Johnstone Strait.

Groot and Quinn (1987) hypothesized that the ocean distribution prior to the nearshore approach influences the location where sockeye make landfall, and thereby determines the route taken to the Fraser River. If adult sockeye maintain consistent speed and compass direction while homing (Quinn and Groot 1984), then the location prior to the onset of migration will determine where, when, and if the fish

encounter steep environmental gradients. It may be that both oceanic distribution and locomotor responses to gradients encountered enroute act synergistically to influence the path taken to the Fraser River. More information on ocean movements in relation to environmental parameters is required to better understand the relative importance of each factor.

The present study showed that sockeye respond to elevated temperatures by increasing swimming activity, however, additional work is required to assess the use of vertical avoidance as a potential orientation mechanism. Quinn et al. (1988) found that adult sockeye swam deeper in the warm waters of Georgia Strait than did fish tracked in colder, northern waters. Vertical temperature avoidance was also reported by Olla et al. (1985) who showed that juvenile bluefish faced with cold temperatures increased their swimming speed and changed vertical distribution.

The hypothesis posed in this study was that rapid changes in temperature and salinity have a direct influence on the behavior of juvenile and adult sockeye and could thereby affect the nearshore migration. There was no locomotor response to decreasing temperature or changing salinity, however, I conclude that warm temperatures could affect the movements of sockeye in coastal waters. For Great Central Lake smolts, elevated locomotor activity and avoidance of warm temperatures may facilitate the migration

out of Alberni Inlet and Barkley Sound. The homing migration of Fraser River adults could be affected by anomalous temperatures off of the British Columbia coast, however, the location where temperature influences migration is not known. Adults appear to utilize a combination of orthokinetic and klinekinetic responses to unfavourable temperatures, but potential vertical avoidance mechanisms require greater study.

In developing a predictive model of sockeye migration, it is important to identify the factors involved, and to understand how these factors may affect migratory movements. The present study, and concurrent field investigations (Quinn 1988, Quinn et al. 1988, Quinn and terHart 1987) have better characterized how a number of environmental parameters may influence the nearshore migration of sockeye salmon. Future work should be directed to oceanic regions to determine when and where these factors exert the greatest influence.



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