HOMING MIGRATION OF SOCKEYE SALMON, *ONCORHYNCHUS NERKA*, TO THE FRASER RIVER

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ABSTRACT

Adult sockeye salmon, *Oncorhynchus nerka*, return to the Fraser River via either of two routes: a northern route through Queen Charlotte Strait, Johnstone Strait, and the Strait of Georgia between the mainland and Vancouver Island, and a southern route along the west coast of Vancouver Island and through Juan de Fuca Strait. The proportions of the total run of sockeye salmon using the two routes varies substantially from year to year. Understanding the factors influencing the migratory routes of Fraser River sockeye salmon provides a basis for forecasting the coastal migrations of salmon as they make the transition between oceanic and riverine environments. Our analysis of west coast troll catch and high seas tag-recovery data indicates that the salmon make landfall in different coastal regions from year to year. If the majority of Fraser sockeye approach the coast of Vancouver Island, then most will migrate via the Strait of Juan de Fuca. However, when landfall occurs north of Vancouver Island in the Queen Charlotte Sound area, most homeward migrating Fraser sockeye will travel through Johnstone Strait. Northern diversion rates of Fraser River sockeye salmon for the period 1953-77 were positively correlated with Fraser River discharge. For the period 1978-85 a strong positive correlation was evident with sea surface temperature (SST) along the northwest coast of Vancouver Island (Kains Island lighthouse). We conclude that Fraser River discharge and SST in the vicinity of Kains Island do not guide sockeye salmon in any direct way during their coastal approach, but that they reflect oceanographic conditions that affect salmon migrations directly or indirectly by acting on the feeding distribution, distance, or direction they must travel to reach home.

The Fraser River in British Columbia, Canada, is among the most important producers of sockeye salmon, *Oncorhynchus nerka*, in North America. Forty to sixty separate stocks, inhabiting the different lakes of its watershed, produce 2 to 20 million adults yearly (IPSFC 1954-1985). Sockeye salmon from the Fraser River system generally spend 1 year in nursery lakes after emergence and then migrate to sea as smolts. Most spend two winters in the ocean, returning to spawn in their home river as 4-yr-olds. To reach the Fraser River from their ocean feeding grounds they can take either of two routes around Vancouver Island (Fig. 1). From 1953 until 1977, the majority homed via the southern route through the Strait of Juan de Fuca (average 84%, range 65-98%). Since 1978, a larger proportion of sockeye have migrated via the northern route through Johnstone Strait (average through Juan de Fuca Strait 56%, range 20-78%) (IPSFC 1954-1986).

In 1958 a relatively high proportion (35%) of Fraser River sockeye salmon returned via the northern route. A large number of fish did not make landfall off the west coast of Vancouver Island but rather arrived in the more northerly Queen Charlotte Sound area (Tully et al. 1960) (Fig. 1). This coincided with anomalously high water temperatures off the coast of British Columbia. Tully et al. (1960) and Royal and Tully (1961) suggested that intrusion of warm water from the south in 1958 directed the homing sockeye salmon northward and closer to the mainland. Moreover, the fish appeared 10 days later in the fishery around Vancouver Island and over a longer period than usual, suggesting that they might have detoured around the area of warm water and made their coastal approach in the cooler nearshore waters. Alternatively, they might have initiated their homeward migration later or from a more distant area than usual.

Favorite (1961), on the other hand, took the view that the unusual extent of dilute seawater of Fraser River origin offshore from Queen Charlotte Sound in 1958 determined the location where the migrating sockeye entered coastal water. He assumed that homeward migrating salmon are attracted to dilute seawater contain-

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Manuscript accepted April 1987.
FISHERY BULLETIN: VOL. 85, NO. 3, 1987.

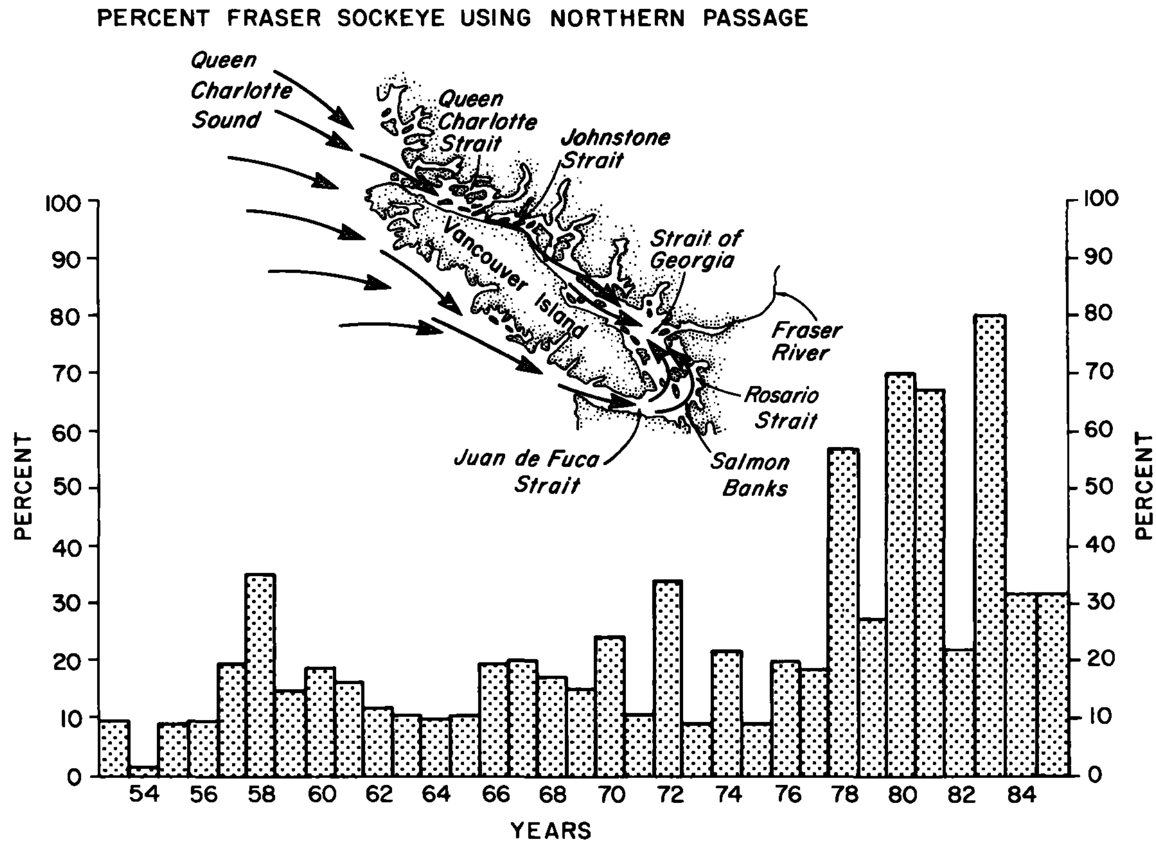


FIGURE 1.—Migratory routes of adult sockeye salmon returning to the Fraser River around Vancouver Island. The bar graph indicates the proportion of the total run that was estimated to have used the northern route (data from IPSFC annual reports).

ing homestream odors. Wickett (1977) extended this hypothesis by using indices of oceanographic processes to indicate the extent of dilute water plumes off Queen Charlotte Sound from 1953 to 1976. He concluded that the large proportion of Fraser River water discharged into the ocean northwest of Vancouver Island increased the rate of Fraser sockeye migrating through Johnstone Strait. The assumptions by Favorite (1961) and Wickett (1977) were influenced by the proposal of Hasler and Wisby (1951) that riverine odors learned during sensitive juvenile stages guide the homeward migration of adults in nearshore and river environments (Hasler 1966; Hasler and Scholz 1983).

We evaluated the extent to which oceanographic conditions in offshore waters influence the migratory routes of returning Fraser River sockeye around Vancouver Island. Nine more years of data (1977-85) have become available since Wickett's (1977) publication and four of these show unprecedented (57% to 80%) diversion rates via Johnstone Strait.

COASTAL MIGRATORY PATHWAYS OF FRASER RIVER SOCKEYE

INPFC Data

Under the auspices of the International North Pacific Fisheries Commission, Canada, the United States and Japan tagged 99,576 sockeye salmon in the North Pacific Ocean east of long. 165°E between 1956 and 1983. Of these, 4,842 were recovered, mostly (99.4%) along the coast of British Columbia and Alaska (INPFC 1984). We isolated data on Fraser River sockeye salmon from this larger data set to determine the migratory routes of these salmon. In the waters around Vancouver Island, 745 sockeye salmon were recovered. Since sockeye salmon home accurately (Ricker 1972; Foerster 1968; Quinn 1985), the high seas tagging locations of the recovered fish give information on the distribution of Fraser River sockeye in the ocean. Southern British Columbia sockeye (of which at least 90% are Fraser River fish) were distributed in the Gulf of Alaska southward to lat. 45°N and westward to long. 178°E, a distance of 6,600 km from the Fraser River. The monthly changes in distribution of tagged fish from April to August and recovered in the year of tagging suggest that during spring and summer there is first a shift northeastward in May and June and then southeastward in July and August along southeast Alaska and the Queen Charlotte Islands towards Vancouver Island (Fig. 2). The findings are in accordance with the migration model for southeast British Columbia sockeye salmon presented by French et al. (1976).

Further indications of the coastal approach routes of Fraser River sockeye salmon can be derived from the rate of travel and the assumed direction of movement. From the positions and the dates of tagging and recovery, the rate of travel along the shortest route can be calculated for each fish. The rates ranged up to 98 km/day (4.1 km/hour or about 2 body lengths/second). Sonic tracking studies by Madison et al. (1972), Stasko et al. (1976), and Quinn and terHart (in press) showed that sockeye salmon travel at average speeds of 1.8 to 2.2 km/hour (about 1 body length/second) when migrating, which approximates the optimum sustained swimming speed for mature sockeye in endurance tests (Brett 1983).

For 373 sockeye salmon that were tagged 1,000 km or more away from the Fraser River and recovered around Vancouver Island, 86 (or 23%) travelled at speeds greater than 45 km/day (1.9 km/hour or about 1 body length/second) (Fig. 3). These estimates of swimming speed discount any effect of currents. Current direction and speed vary considerably in the regions through which

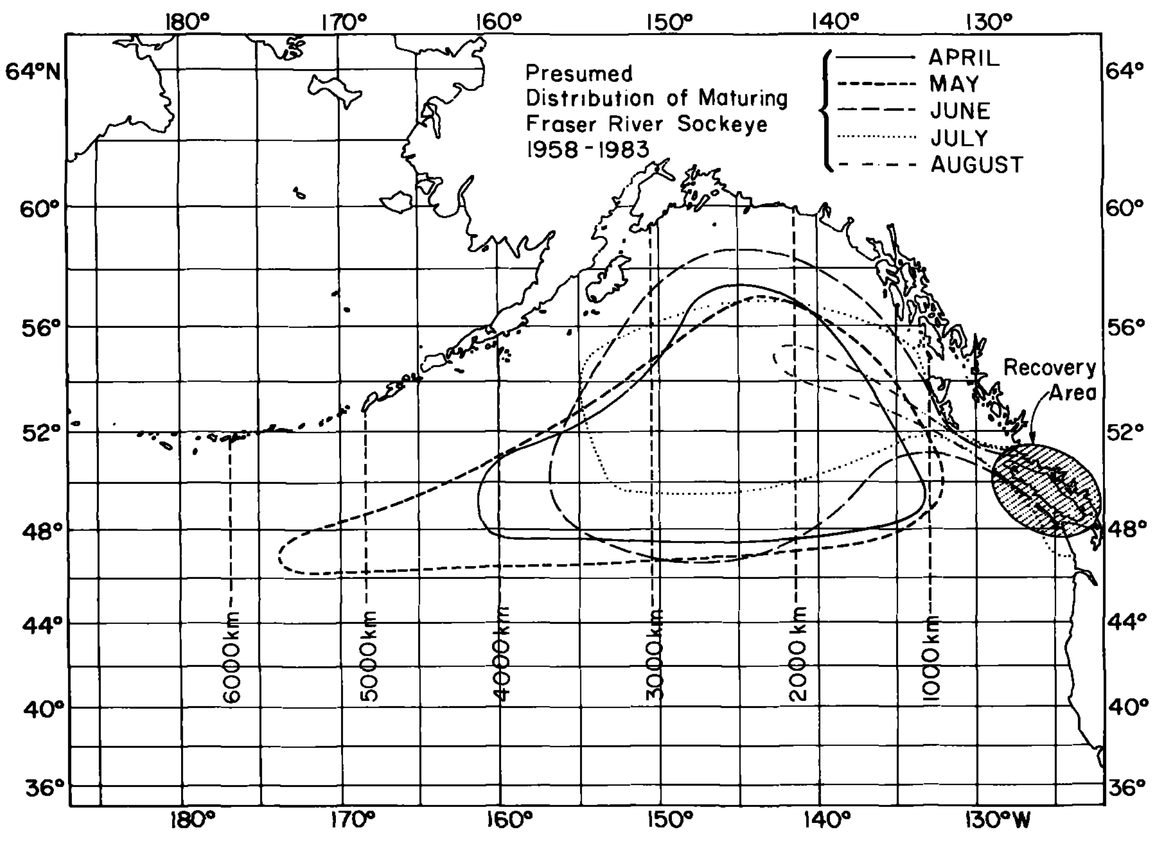


FIGURE 2.—Distributions in the Gulf of Alaska of releases of sockeye salmon from April through August that were recovered during the year of tagging around Vancouver Island, 1953-85.

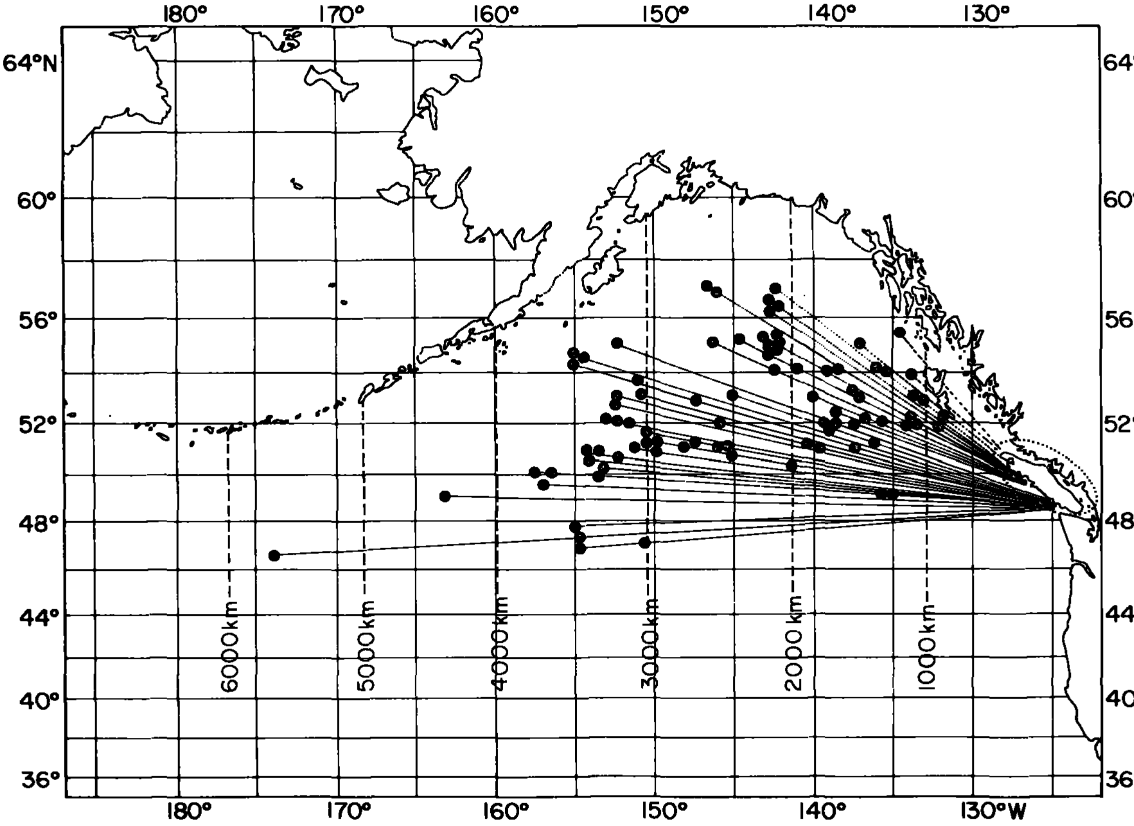


FIGURE 3.—Locations where maturing sockeye salmon were tagged and recovered in the Vancouver Island area. Only recoveries farther than 1,000 km away from the entrance of the Fraser River and with speeds over 45 km/day are illustrated.

the sockeye migrate but are usually less than 0.4 km/hour (Favorite et al. 1976; Tabata 1984). We assume that these fish must have travelled on relatively direct courses, day and night, based on the optimum speed of sockeye salmon (~2 km/hour) and the fact that substantial divergence from straight-line travel would have required the salmon to exceed their fatigue speed of 5 km/hour to accomplish the observed displacements (Quinn 1984; Quinn and Groot 1984). Connecting the tagging positions of these 86 sockeye salmon with the mouth of the home river shows that they must have approached Vancouver Island from a westerly or northwesterly direction (Fig. 3). The sockeye salmon that were about 3,000 km or more from the Fraser River (mostly tagged in April and May) were generally distributed farther to the south than those tagged later in the season at distances from 1,000 to 2,300 km. The former must have travelled almost due east, while most of the latter may have moved northeast first and then later in the season turned southeast towards Vancouver Island.

Thus, sockeye salmon returning to the Fraser River from their ocean feeding grounds approach Vancouver Island from the west and the northwest and, depending on their homing course, generally make landfall along the west coast of Vancouver Island or farther north in Queen Charlotte Sound (Fig. 1).

West Coast Troll Fishery

To derive information on areas of landfall for different years, we used records of troll fishing off the west coast of Vancouver Island. The Canadian west coast fishery has usually been open during the period that sockeye salmon arrive on the coast. Only during 1978, 1982, 1983, and 1985 were there short nonretention periods for sockeye salmon. We assume, therefore, that in general the catches reflect the migratory patterns of these fish in nearshore waters. The troll catches and boat efforts are recorded on a weekly basis for the different statistical areas by the Department of Fisheries and Oceans of Canada (F. Wong[3]). The west coast sockeye salmon catches generally reflect the annual variability in the total Fraser River run (Henry 1961); therefore, most sockeye salmon captured along the west coast are considered to be returning to this river. Small proportions of the catch are of Barkley Sound (Vancouver Island) and Lake Washington (USA) origin.

In 1979 and 1982 peak catches of sockeye salmon occurred near the middle of Vancouver Island in areas 24-26 (Fig. 4). The relatively low diversion rates (27 and 22% respectively during

[3]F. Wong, Pacific Biological Station, Nanaimo, B.C. V9R 5K6, Canada, pers. commun. 1984.

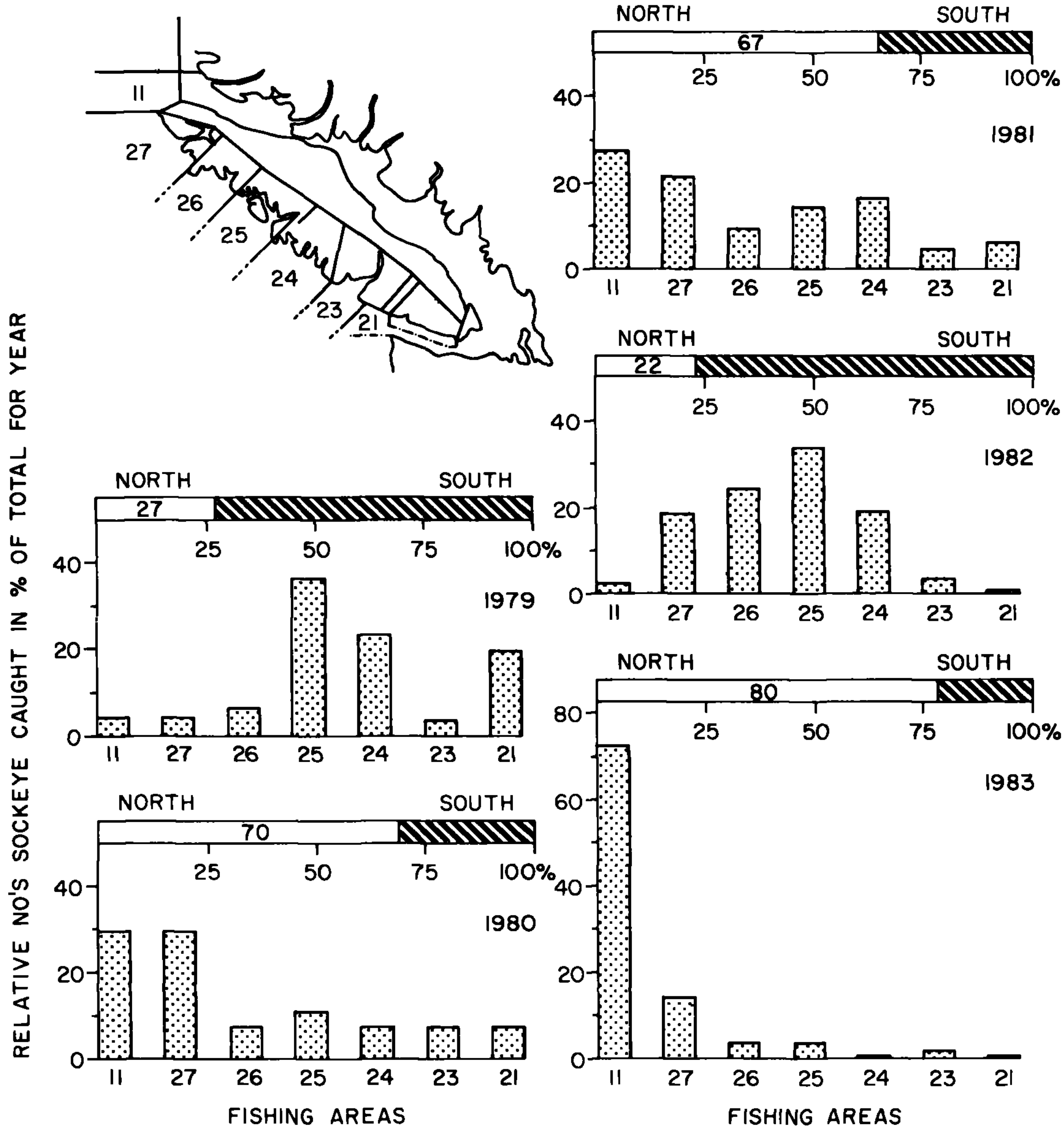


FIGURE 4.—Vertical bar graphs illustrate the proportions of the total troll catch of sockeye salmon off the west coast of Vancouver Island caught in different statistical areas (see map insert) for the years 1979-83. Horizontal bars indicate the proportions of sockeye salmon migrating to the Fraser River via the northern and southern routes.

these years) indicate that most sockeye may have migrated southwest from a relatively southerly position offshore and returned to the Fraser River via the Strait of Juan de Fuca. In 1980 and 1981 the largest sockeye catches were made near the north of Vancouver Island in areas 11 and 27 (Fig. 4). In these years 70 and 67% of the Fraser sockeye migrated through Johnstone Strait. In 1983 an extreme situation prevailed: most of the sockeye salmon were caught in area 11 (Queen Charlotte Sound) and 80% of the fish migrated via the northern route (Fig. 4).

From these results we conclude that the proportions of Fraser River sockeye salmon returning via the northern and southern routes are generally associated with the area where the fish make their landfall (see also Tully et al. 1960; Henry 1961; IPSFC 1979-1984). If the majority of Fraser sockeye approach the coast west of Vancouver Island, then most will continue to migrate via the Strait of Juan de Fuca. However, when landfall occurs north of Vancouver Island in the Queen Charlotte Sound area, most homeward migrating Fraser sockeye will travel through Johnstone Strait.

North Coast Salmon Tagging Project

During 1982 and 1983, Canada and the United States tagged sockeye salmon along the coast of northern British Columbia and southeastern Alaska to determine interception rates in the commercial fisheries of both countries near the boundary. The results of these studies provide additional information on migratory routes of this species along the North American coast. In 1982, 40,556 and in 1983, 23,052 maturing sockeye salmon were tagged in several places in southeastern Alaska and northern British Columbia (Fig. 5) (B. Riddell[4]). Most of these fish were heading for spawning rivers in southeastern Alaska and the Nass and Skeena Rivers of northern British Columbia. However, a number of sockeye salmon, 24 in 1982 and 126 in 1983, were recovered in the commercial fishery around Vancouver Island. We assume that most of these were Fraser River fish because more than 90% of sockeye salmon captured in southern British Columbia belong to Fraser River stocks.

Of the sockeye salmon tagged in the north, 9 times more were recovered in the Vancouver Island area in 1983 than in 1982 (Fig. 5), despite the fact that the total run of sockeye to the Fraser River in 1982 (13,933,000) was more than twice as large as in 1983 (5,167,000; IPSFC 1983, 1984). This indicates that in 1983 a greater proportion of Fraser River sockeye made landfall north of Vancouver Island than in 1982. This was reflected in the diversion rates through Johnstone Strait of 80 and 22% respectively for the 2 years (Figs. 1, 4). The results also show that relatively 9 (1982) to 13 (1983) times more sockeye were recovered in the Vancouver Island area from the outside (Noyes and Queen Charlotte Islands, and Cape Muzon) than from the inside (Clarence Strait and Areas 3, 4, and 5) tagging operations (Fig. 5). We suggest that the southern British Columbia sockeye primarily migrated along the west coast of the Queen Charlotte Islands during their migration south. However, some entered Dixon Entrance in 1983 and travelled through Hecate Strait towards the Fraser River, as indicated by recoveries from inside tagging locations.

The findings from the North Coast Tagging Project support the evidence presented earlier that coastal migratory routes of Fraser River sockeye can vary considerably from year to year and that during years of high diversion through Johnstone Strait the returning sockeye make landfall farther north. Analysis of catches, run timing, and stock composition led the Pacific Salmon Commission to a similar conclusion several years ago (IPSFC 1983).

In summary, our analysis of the INPFC, West Coast Troll, and North Coast Tagging data sets indicates that Fraser River sockeye salmon returning from ocean feeding grounds approach Vancouver Island from the west and northwest. The area of landfall varies yearly from the west coast of Vancouver Island to more northern regions in Queen Charlotte Sound. Moreover, the area where most salmon reach the coast is strongly correlated with the proportion that enters the Strait of Georgia via the southern or northern routes.

Migratory Routes and Oceanographic Conditions

A coastal approach north of Vancouver Island results in a higher proportion of fish moving through Johnstone Strait, while an approach farther south, along the west coast of Vancouver Island, directs the fish to the Fraser River through

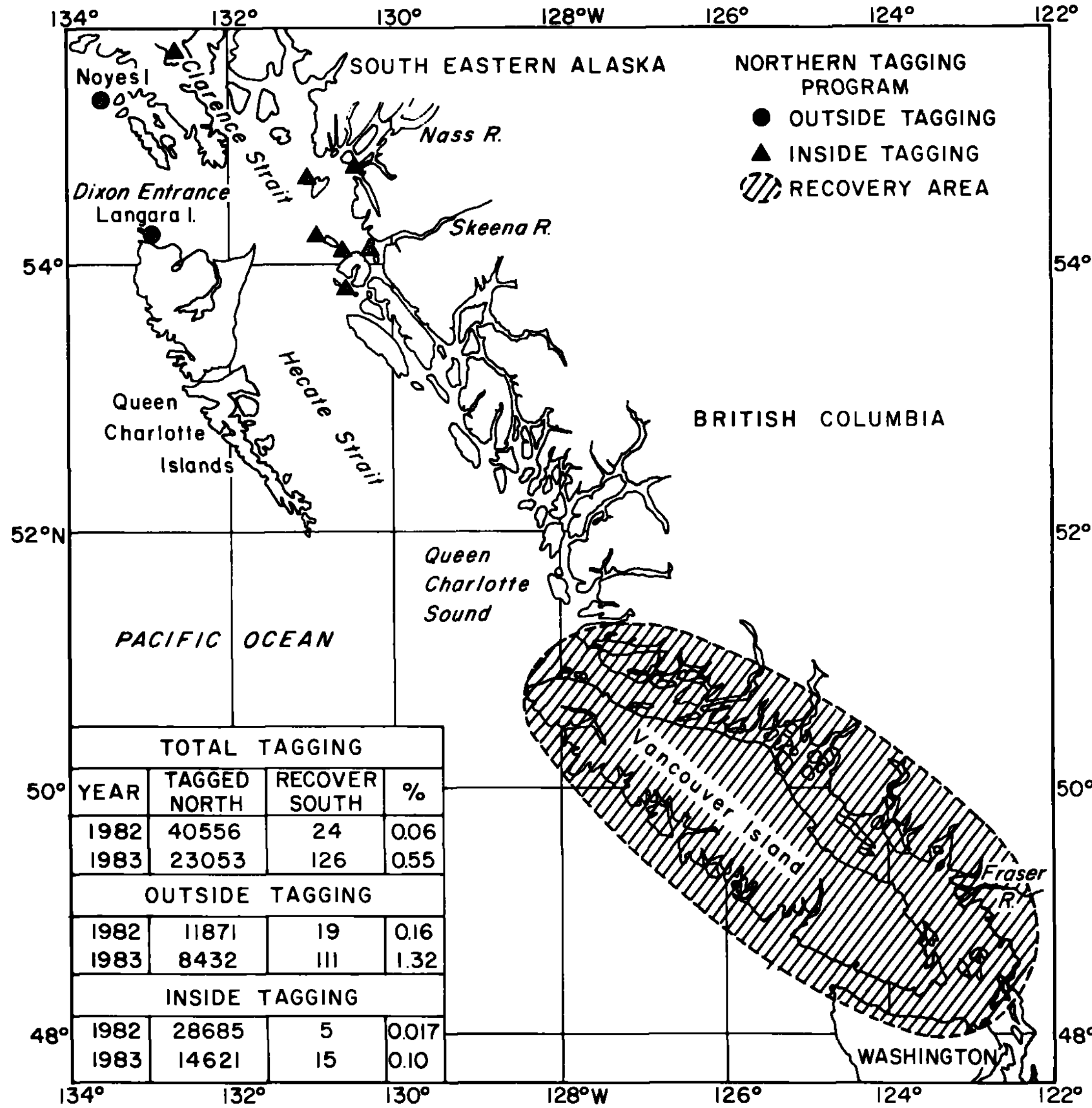
[4]B. Riddell, Pacific Biological Station, Nanaimo, B.C. V9R 5K6, Canada, pers. commun. 1985.

the Strait of Juan de Fuca. We propose that the coastal approach may be influenced by oceanographic conditions in the eastern Gulf of Alaska during the April-June period when the maturing sockeye perform their homing migrations from the high seas overwintering grounds to the coastal areas (French et al. 1976).

The following environmental factors were analyzed for correlation with diversion rates of Fraser River sockeye via the north:

1) Sea surface temperatures (SST) (average April-June) measured daily at four lighthouse stations along the British Columbia coast: Amphitrite Point, Kains Island, Cape Saint James, and Langara Island (Fig. 6) (Dodimead 1984; L. F. Giovando[5]). SSTs can be used as indications

[5]L. F. Giovando, Institute of Ocean Sciences, Patricia Bay, B.C. V8L 4B2, Canada, pers. commun. 1985.



YEAR	TAGGED NORTH	RECOVER SOUTH	%
TOTAL TAGGING			
1982	40556	24	0.06
1983	23053	126	0.55
OUTSIDE TAGGING			
1982	11871	19	0.16
1983	8432	111	1.32
INSIDE TAGGING			
1982	28685	5	0.017
1983	14621	15	0.10

FIGURE 5.—The numbers of sockeye salmon tagged in northern British Columbia and southeastern Alaska and recovered that year in waters around Vancouver Island. Tagging data are separated by location of tagging (inside vs. outside waters) and year (1982 vs. 1983).

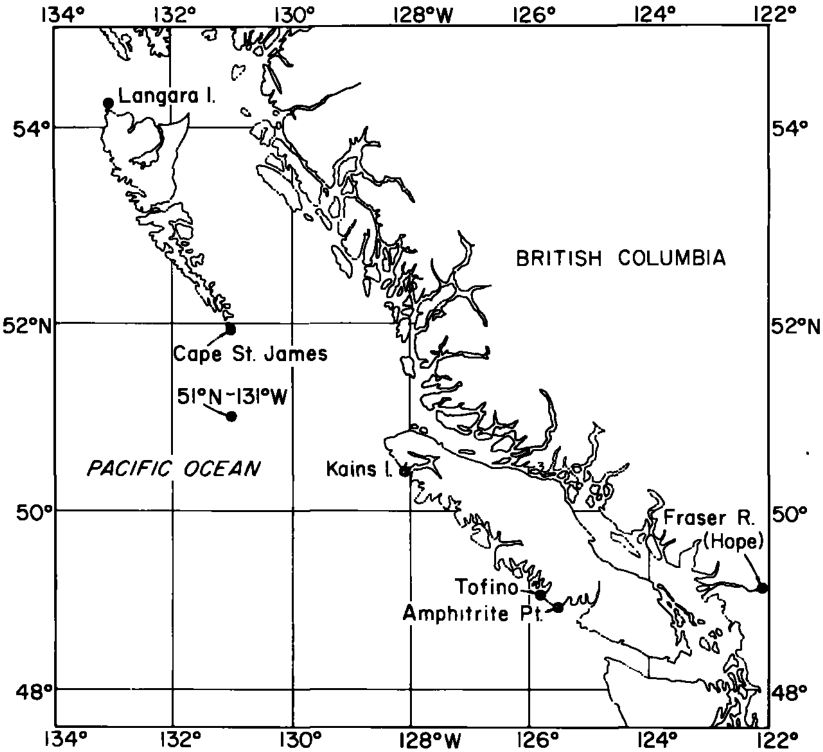


FIGURE 6.—Locations where environmental conditions were monitored for regression analysis with sockeye salmon migratory patterns: sea surface temperature and salinity at Amphitrite Point, Kains Island, Cape St. James, and Langara Island; sea level at Tofiño; Ekman transport at lat. 51°N, long. 131°W; and Fraser River discharge at Hope.

of the extent of warm water intrusion from the south along the coast.

2) Sea surface temperatures (average April-June) at ocean station P (50°N, 145°W) (see Figure 8) (S. Tabata[6]) as an indication of ocean conditions in the Gulf of Alaska. After sampling at this station was terminated in 1981, temperatures for this area in the Pacific Ocean were obtained from satellite and shipboard observations.

3) Monthly mean sea-levels (average April-June) recorded at Tofino, on the west coast of Vancouver Island (Fig. 6), as an indication of convergent and divergent conditions along the coast (A. Dodimead[7]). Also, high coastal sea levels indicate northward currents.

4) Ekman transport normal to the coast (average April-June) at 51°N, 131°W (Fig. 6) calculated from barometric pressure data (Dodimead 1984; Giovando fn. 5) to indicate the general pattern of circulation from wind-driven transport.

5) Fraser River discharge (average April-June) measured at Hope (Fig. 6) (LeBlond et al. 1983; Inland Waters Directorate[8]), as an indication of coastal run-off and extent of Fraser River homewater along nearshore areas.

Linear regression analysis of Fraser sockeye diversion rates from 1953 to 1985 with SST of lighthouse data from Amphitrite Point, Kains Island, Cape St. James, and Langara Island for the months of April to June showed significant correlations (Table 1). Since the correlation coefficient of diversion rates was highest with the data from the Kains Island lighthouse, these were selected for further analysis and averaged over April, May, and June.

Regression analysis between the northern diversion rates and the environmental variables

[6]S. Tabata, Institute of Ocean Sciences, Patricia Bay, B.C. V8L 4B2, Canada, pers. commun. 1985.

[7]A. Dodimead, Pacific Biological Station, Nanaimo, B.C. V9R 5K6, Canada, pers. commun. 1984.

[8]Inland Waters Directorate, 1001 West Pender Street, Vancouver, B.C. V6E 2M9, Canada, 1985.

TABLE 1.—Correlations (R) of sea surface temperature at four lighthouse stations along the British Columbia coast with the percentage of sockeye salmon returning to the Fraser River via Johnstone Strait during the years 1953-83.

Lighthouse stations	March		April		May		June	
	R	*N*	R	*N*	R	*N*	R	*N*
Amphitrite Pt.	0.65	31	0.69	31	0.59	31	0.59	31
Kains Island	0.65	31	0.65	31	0.65	31	0.63	31
Cape St. James	0.54	30	0.68	29	0.66	30	0.54	30
Langara Island	0.55	31	0.62	31	0.65	31	0.64	29

listed above for the years 1953-85 showed significant ($P < 0.01$) positive correlations with nearshore (Kains Island) SSTs, explaining 51% of the variance (Table 2; Fig. 7A).

TABLE 2.—Relationship (R and R^2) for linear regression analyses of average April-June SST at Kains Island lighthouse, sea level at Tofino, Ekman transport at lat. 50°N, long. 131°W, SST at Station P (50°N, 145°W), and Fraser River discharge at Hope with percentage sockeye salmon returning to the Fraser River via Johnstone Strait for the years 1953-85 ($N = 33$), 1953-77 ($N = 25$), and 1978-85 ($N = 8$). The level of significance was set at $P < 0.01$.

Factors	1953-85		1953-77		1978-85	
	R^2 (%)	R	R^2 (%)	R	R^2 (%)	R
SST Kains Island	51	0.71*	9	0.30	85	0.92*
Sea level Tofino		0.19	19	0.44	3.9	0.20
Ekman transport	4	0.29	4	−0.20	5	0.23
SST Station P	15	0.39	11	0.33	11	0.33
Fraser River discharge	2	0.14	45	0.67*	30	−0.55

*$P < 0.01$.

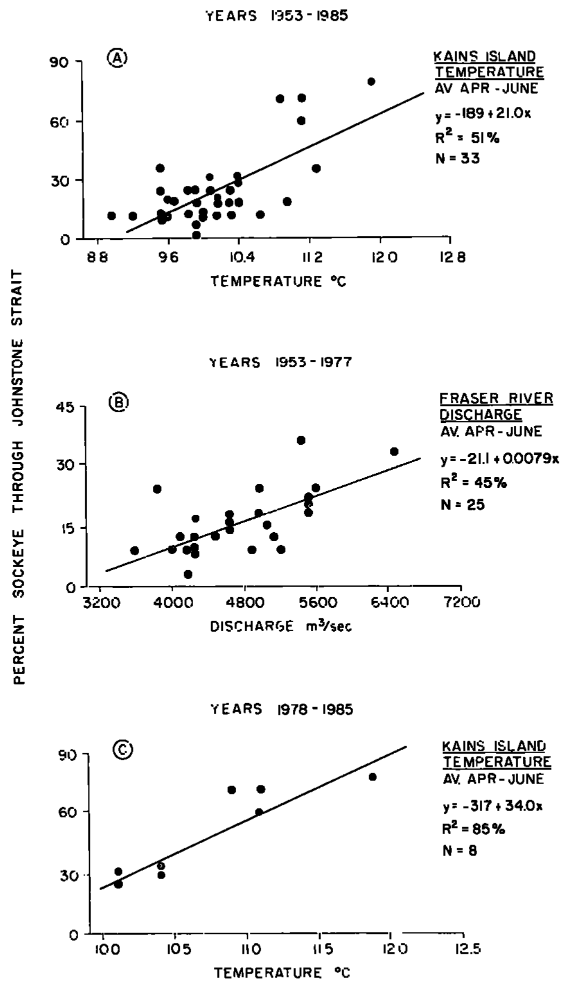


FIGURE 7.—Relationships between the proportion of Fraser River sockeye salmon migrating via the northern route (Johnstone Strait) and A) average sea surface temperature and salinity at Kains Island for April, May, and June for the years 1953-85; B) average Fraser River discharge for April, May, and June for the years 1953-77; C) average sea surface temperature at Kains Island for April, May, and June for the years 1978-85.

Inspection of the diversion rates over the last 33 years suggested that after 1977 a change occurred in the migratory patterns of Fraser River sockeye approaching the coast. During the period 1978-85, unprecedented rates of 70 to 80% have used the northern route (Fig. 1). This change in migratory behavior coincided with a remarkable prolonged warming period in the northeast Pacific Ocean (Chelton 1984; McClean 1984). The trend culminated in the extended warm-water anomaly of 1983 along the coast of British Columbia, which was associated with the 1982-83 El Niño event that occurred in the equatorial Pacific Ocean. This event was one of the most extreme of the century (Mysak 1985). We therefore carried out separate analyses for the two periods, 1953-77 and 1978-85.

The regression analyses for the 1953-77 period identified Fraser River discharge as the only significant ($P < 0.01$) factor, explaining 45% of the variance (Table 2; Fig. 7B). This positive relationship between northern diversion rates and Fraser River discharge was also suggested by Wickett (1977) for the same time period.

For the period 1978-85, the regression analyses indicated that SST at Kains Island was the only helpful predictor, explaining 85% of the variance (Table 2; Fig. 7C). A strong positive relationship between northern diversion rates of Fraser River sockeye salmon and SST at Kains Island was also noted for the years 1973-83 by staff of the Pacific Salmon Commission (IPSFC 1984).

DISCUSSION

We suggest that sockeye salmon returning to the Fraser River may have been influenced by year-to-year changes in ocean conditions during and between the periods 1953-77 and 1978-85. The relationships of sockeye migration to sea surface temperature and river discharge will be discussed separately.

Sea Surface Temperature and Sockeye Salmon Migration

Leggett's (1977) review of fish migration concluded that oceanic fish migrations largely represent the continuous optimization of physiologically important conditions. Temperature is an oceanographic feature whose importance in fish physiology is well established (Brett 1970). While evidence indicates that thermal conditions may be correlated with the timing of salmon migrations (Burgner 1980; Blackbourn in press) or the route of their return migration to coastal waters (this study), it is not clear how temperature affects salmon behavior. Temperature might directly influence salmon in some way or it might merely correlate with some other oceanographic feature influencing them such as eddies and currents (Mysak 1986), or the abundance or species composition of prey items (Fulton and LeBrasseur 1985). If so, a correlation of salmon behavior with temperature could mislead attempts to understand the control of migration.

Alternatively, temperature may indeed have a direct impact on sockeye salmon. There is considerable evidence that temperature is correlated with the distribution of marine fishes (Brett 1970; Laurs and Lynn 1977; Laurs et al. 1977; Magnuson et al. 1980). Manzer et al. (1965) and French et al. (1976) summarized the distribution of sockeye salmon in relation to sea surface temperature. While waters of certain temperatures were generally devoid of sockeye salmon, the apparent thermal preferendum was 3° to 5°C wide and changed seasonally. Manzer et al. (1965) reported that most sockeye were caught by research gill nets in the North Pacific Ocean and Bering Sea in waters of 4° to 6°C in May, 4° to 7°C in June, 8° to 12°C in July, and 9° to 12°C in August. Based on the occurrence of sockeye salmon in large areas of the North Pacific Ocean, French and Bakkala (1974) concluded that they are not exclusively associated with specific oceanic conditions.

To determine the ways in which temperature might directly affect sockeye salmon, we must ascertain the horizontal and vertical distribution of temperatures which they experience at sea on their homeward journey. An oceanographic survey of the North Pacific Ocean and Gulf of Alaska from 16 to 24 July 1959 (S.I.O.U.C. 1965) provide useful data to suit this purpose (Fig. 8). Temperatures at 0, 30, and 50 m depth were used to estimate the extent of horizontal and vertical gradients experienced by salmon migrating to the northern tip of Vancouver Island along the path which Fraser River sockeye seem to take.

If we assume that salmon swam 48 km/day on the surface along the route of the ship, they would have experienced total temperature changes of +3.68°C or a daily average of +0.10°C/day (Table 3). Averaged over the stations, vertical excursions from 0 to 30 m would have caused the fish to experience changes of −0.81°C. Dives from the surface to 50 m would have been accompanied by changes averaging −5.00°C. Earlier in the sum-

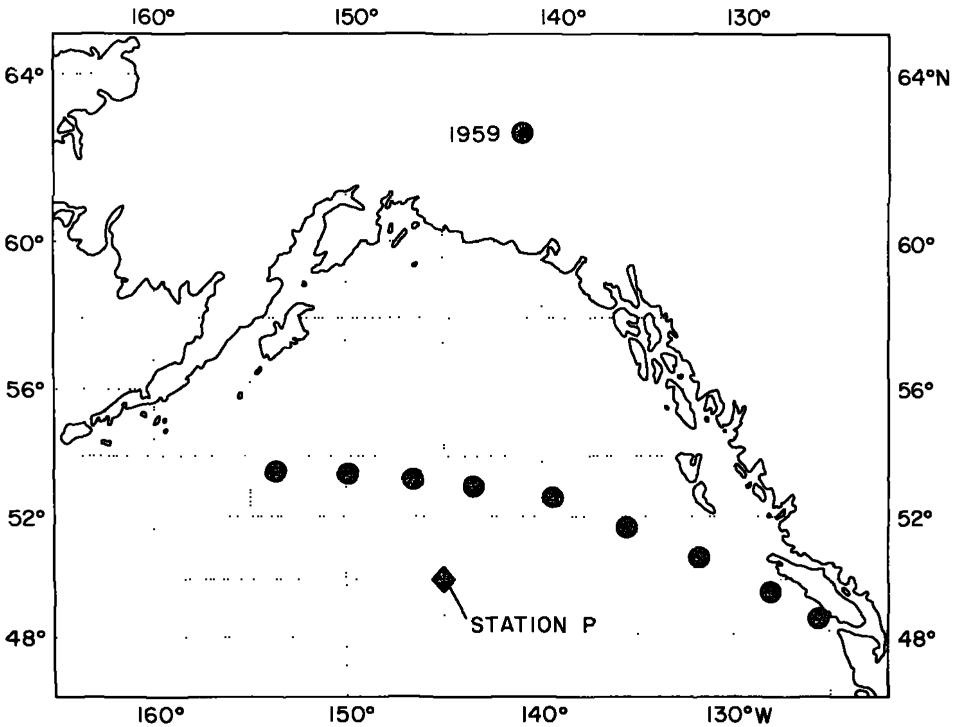


FIGURE 8.—Map of the North Pacific Ocean showing the sites sampled by an oceanographic cruise in 1959 (S.I.O.U.C. 1965) and Station P, where sea surface temperatures and salinities were also recorded.

TABLE 3.—Temperature at depth, recorded by the RV *Brown Bear*, 16-24 July 1959 (data from S.I.O.U.C. 1965).

Latitude (N)	Longitude (W)	0 m	30 m	50 m
53°56′	153°18′	10.52	9.98	4.80
53°42′	149°43′	10.54	9.49	4.60
53°30′	146°42′	10.82	9.94	4.80
52°58′	143°27′	11.20	10.90	6.82
52°18′	139°35′	10.90	10.70	6.79
51°40′	135°55′	12.39	12.12	8.58
50°40′	131°57′	13.59	10.60	8.18
49°30′	128°12′	14.20	13.96	9.59
48°44′	125°39′	[1]13.18	[1]8.90	[1]8.23

[1]Data not included in calculations of gradients.

mer when the sockeye salmon migrate through these areas, the vertical and horizontal gradients are presumably smaller.

Available information indicates that salmon in general and sockeye in particular do not restrict themselves to one depth but rather have a diel vertical movement pattern while at sea. Manzer (1964) reported that most sockeye were caught in gill nets at or near the surface during the night, but in the daytime they were caught in substantial numbers as deep as 48 to 60 m. Mishima and Shimazaki (1969) reported a more complex pattern: sockeye were most abundant on the surface at 13:00-15:00 h but a second peak of abundance occurred at 03:00-05:00 h. Whereas variations in diel movements and depth distribution may occur, it seems likely that sockeye experience temperature changes of 1°C during their daily movements, and may experience changes of 4° to 5°C if they dive below the mixed layer.

The slight changes in temperature associated with horizontal movement relative to vertical movement make it unlikely that the long-distance migration of homing sockeye is determined by physiological responses to temperature (Laevastu 1983). Moreover, the temperatures experienced by sockeye salmon at sea do not seem to reflect physiological optima (Brett 1974, 1983). Nevertheless, there is a west-east gradient of increasing temperature over much of the homeward path of Fraser River sockeye salmon. Therefore, "predictive behavioural thermoregulation" (Neill 1979) may play a role in homing, though "reactive behavioural thermoregulation" (e.g., Olla et al. 1975) probably does not. However, gradients are an inefficient aid to migration unless coupled with an independent sense of direction. Moreover, as the salmon near the coast, they may experience a decrease in temperature (Table 3).

We conclude that the relationship between sea surface temperatures at Kains Island and the diversion rate of sockeye salmon returning to the Fraser River via Johnstone Strait between 1978 and 1985 reflects the influence of ocean conditions on the behavior of fish, either on the feeding distribution prior to homing (see also Mysak 1986) or on the homing migration itself.

Fraser River Discharge and Sockeye Salmon Migration

Most of the fresh water along the British Columbia coast originates from the Columbia, Fraser, and Skeena Rivers and distinct tongues of dilute water (SSS of 32.6‰ and less) extend seaward from the Strait of Juan de Fuca and Queen Charlotte Sound several hundred kilometers offshore (Favorite 1961). Wickett (1977) suggested that it was the Fraser River water discharged in the ocean to the northwest of Vancouver Island that increased the percentage of Fraser River sockeye migrating through Johnstone Strait.

Fraser River sockeye migrating from their ocean feeding grounds towards the British Columbia coast pass through the areas of dilute surface water ("dilute domain") long before making landfall (Fig. 9). Interannual changes in river discharge and the resulting dilute extensions offshore could affect the coastal approach routes of Fraser River sockeye by causing more northerly landfall than usual during years of high levels of runoff (Favorite 1961; Wickett 1977).

What might be the mechanism that underlies a direct relationship between river discharge and migration route of adult Fraser River sockeye salmon? Two possibilities present themselves. First, returning sockeye salmon could prefer lower salinity water as they home, similar but

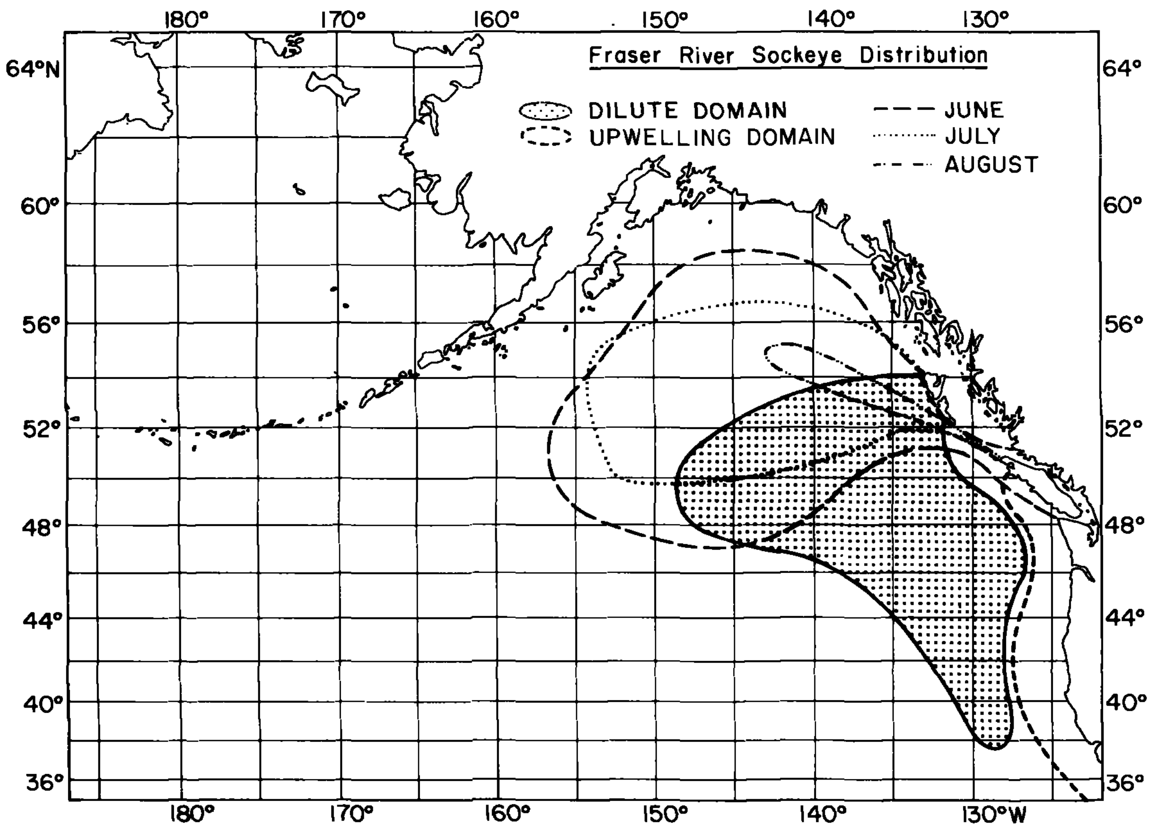


FIGURE 9.—The estimated distribution of maturing Fraser River sockeye salmon in June, July, and August in relation to regions of dilute water and upwelling.

opposite to the increasing saltwater preference documented by Baggerman (1960) and McInerney (1964) for juvenile salmon during the period of seaward migration. McInerney (1964) argued that the shift in salinity preference over time could gradually lead fish along the gradient of salinities found in coastal areas toward the open ocean.

Salinity measurements during the 1959 cruise (S.I.O.U.C 1965) mentioned previously showed that from the middle of the Gulf of Alaska to the tip of Vancouver Island, sea surface salinities decreased from 32.73 to 32.46‰ over a distance of about 1,757 km (Table 4). Fish swimming at a rate of 48 km/day would have met changes averaging 0.00015‰/km or 0.0074‰/day when approaching the coast. The threshold for recognition of salinity differences by sockeye salmon is unknown. However, if it is similar to that of minnows (*Phoxinus phoxinus*) of 0.003‰ (Glaser 1966), then it is about 20 times higher than the average difference that wil be encountered during a km of travel.

TABLE 4.—Salinity at depth, recorded by the RV *Brown Bear*, 16-24 July 1959 (data from S.I.O.U.C. 1965)

Latitude (N)	Longitude (W)	0 m	30 m	50 m
53°56′	153°18′	32.73	32.84	32.88
52°42′	149°43′	32.75	32.84	32.88
53°30′	146°42′	32.85	32.86	32.95
52°58′	143°27′	32.60	32.61	32.72
52°18′	139°35′	32.66	32.68	32.83
51°40′	135°55′	32.24	32.31	32.53
50°40′	131°57′	32.15	32.31	32.57
49°30′	128°12′	32.46	32.47	32.53
48°44′	125°39′	[1]31.35	[1]32.28	[1]32.73

[1]Data not included in calculations of gradients.

Moreover, salinity changes towards the coast do not occur in a smooth gradient (Table 4). Water masses of different salinities and temperatures form a dynamic patchwork that is continuously changing under the influence of wind and currents (Tabata 1984). We therefore consider it unlikely that a general preference for lower salinity water determines the approach direction of homing Fraser River sockeye migration. Smith (1985) concluded that for fishes in general ". . .there is little evidence that salinity is a guiding mechanism."

Second, the sockeye could react to home odors from the Fraser River in the offshore waters as suggested by Favorite (1961) and Wickett (1977). The sensitivity of salmonids to certain odors is high: 10^{-8} M for morpholine and 10^{-9} M for free amino acids (Brett and Groot 1963; Hara et al. 1984). However, it is questionable that, given the extensive mixing in the Fraser River and in the ocean, the already low concentrations of odors from the different nursery lakes would be above threshold. Moreover, odors generally act as releasers and not as directors of responses (Johnsen and Hasler 1980). It is difficult to understand how salmon could change their migration routes far offshore in the ocean, even if they could sense the aroma of their home water. We therefore conclude that the relationship between Fraser River discharge and diversion rate of sockeye salmon returning via the northern route is not a direct, but probably an indirect one.

CONCLUSION

We hypothesize that Fraser River discharge (1953-77) and SST at Kains Island (1978-85) primarily reflect certain atmospheric and related oceanographic conditions, which affect Fraser River sockeye salmon winter distribution and/or migration in the ocean. The weather conditions in the Gulf of Alaska are controlled by the locations and intensities of two major semipermanent atmospheric pressure cells; the Aleutian low and the North Pacific high (Favorite et al. 1976; Thomson 1981; Emery and Hamilton 1985). The interannual variations of these pressure cells affect precipitation and the extent of the snow pack during the winter, as well as temperature, salinity, and circulation patterns in the ocean (Favorite et al. 1976; Thomson 1981; Emery and Hamilton 1985).

Anomalous temperature conditions in the ocean, resulting from varying atmospheric conditions, may affect salmon migrations directly or indirectly by acting on their feeding distribution or on the distance or direction they must travel to reach home. When ocean conditions are warmer than usual, sockeye salmon tend to encounter the coast of British Columbia at the north of Vancouver Island. In such cases their approach to the Fraser River will be primarily through Johnstone Strait. Following cold winter conditions in the Gulf of Alaska, landfall usually occurs along the west coast of Vancouver Island and migration to the home river is primarily via the Strait of Juan de Fuca.

ACKNOWLEDGMENTS

We thank Lawrence Mysak, Kevin Hamilton, and David Blackbourn for valuable discussions. We also thank the following individuals for providing data used in this paper: Brian Riddell (North Coast Tagging), Fred Wong (West Coast Troll) and Colin Harris (updated information on INPFC tagging). Sherry Greenham and Laurie Mackie drew the figures. During the later stages of this study, T. P. Quinn was supported by NSERC Strategic Grant, G-1485.

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