

The influence of ocean currents on latitude of landfall and migration speed of sockeye salmon returning to the Fraser River

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ABSTRACT

We hypothesize that the interannual variability of the Northeast Pacific Ocean circulation affects the latitude of landfall and migration speed of adult sockeye salmon (*Oncorhynchus nerka*) returning to the Fraser River. The Ocean Surface Current Simulations (OSCURS) model was used to simulate the return migration paths of compass-orientated sockeye for two years: 1982, which had a weak Alaska Gyre circulation and low Northern Diversion Rate (defined as the percentage of sockeye returning around the north end of Vancouver Island instead of the south end); and 1983, with a strong circulation and high northern diversion rate. The majority of model sockeye made landfall further north in 1983 than in 1982. The difference in landfall between 1983 and 1982 depended on the migration start position, swim speed, direction of orientation, and migration start date. The currents assisted the shoreward migration of sockeye starting from south of 55° N and impeded the migration of sockeye starting from further north. The simulation results were consistent with our hypothesis and suggest that the effects of the Northeast Pacific currents must be included in sockeye migration models. We propose a conceptual model for the prediction of the Northern Diversion Rate that includes Blackbourn's (1987) temperature-displacement model, enhanced to include the effects of currents during the ocean phase of migration, and the use of two predictive formulas for the coastal phase

of migration: the formula of Xie and Hsieh (1989) for sockeye approaching Vancouver Island directly from the ocean, and a yet-to-be-developed formula for sockeye approaching from within the Coastal Downwelling Domain directly to the north of Vancouver Island.

Key words: sockeye migrations, ocean currents, sockeye behavior

INTRODUCTION

In this paper, we examine the effects of Northeast Pacific Ocean surface currents on the latitude of landfall and migration speed of adult sockeye salmon (*Oncorhynchus nerka*) returning to the Fraser River. Ocean tagging data collected between 1958 and 1983 provide a preliminary picture of the sockeye distribution during their ocean phase (Fig. 1). The homeward migration of mature adults can be divided into two parts: an ocean phase, which carries the fish from offshore feeding grounds to the coast, and a coastal phase, which carries the fish along the shore to their river (Healey and Groot, 1987). Little is known about the ocean phase of sockeye migration except that it is rapid, well directed, and well timed (Royce et al., 1968; French et al., 1976; Groot and Quinn, 1987; Burgner, 1991). Maturing Fraser River sockeye apparently move northeastward in May and June, then southeastward in July and August toward Vancouver Island (French et al., 1976). The point at which sockeye make landfall seems to be related to atmospheric and oceanographic conditions prior to or during the ocean phase of the migration (Wickett, 1977; Blackbourn, 1987; Groot and Quinn, 1987; Healey and Groot, 1987; Quinn, 1990). Catch data from the Alaskan and British Columbian coasts, particularly those relating to the Northern Diversion Rate, show that the point of landfall varies from year to year (Groot and Quinn, 1987).

The northern diversion rate (hereafter NDR) is defined as the percentage of adult sockeye returning to the Fraser River around the north end of Vancouver Island, rather than around the south end of the island.

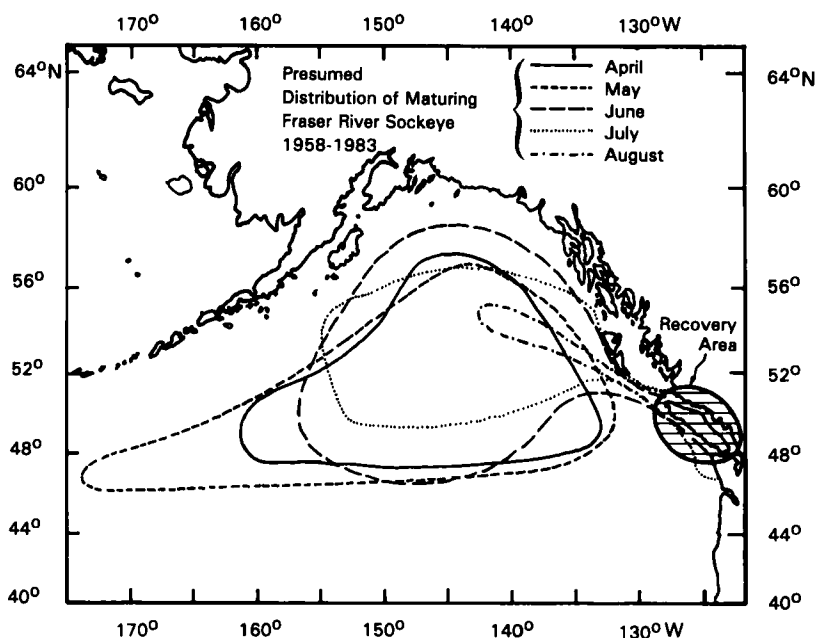


Figure 1. Presumed distribution of mature Fraser River sockeye, obtained from ocean tagging data between 1958 and 1983 (French et al., 1976), adapted from Groot and Quinn (1987). The "recovery area" encompasses Vancouver Island.

From the perspective of the fisheries manager who must allocate finite fisheries resources, and from the perspective of fishermen who must allocate costly vessel and personnel resources, the ability to reliably forecast the point of landfall and the NDR is very important. Fraser River sockeye is one of British Columbia's most valuable fisheries resources, with an average annual catch (1983–1986) of \$60 million to Canadian fishermen and \$17 million to U.S. fishermen. Wickett (1977), Groot and Quinn (1987), and Xie and Hsieh (1989) developed predictive formulae relating physical variables from coastal stations (e.g., Fraser River discharge and sea surface temperature) to the NDR. The limited predictive success of these formulas is likely due to the effects of offshore processes that cannot be examined in terms of coastal variables.

Healey and Groot (1987) reviewed three possible direction-finding mechanisms used by sockeye in their homeward migration: 1) piloting, the simple reliance on visual or other landmarks within familiar territory; 2) compass orientation, the ability to move in a particular compass direction even in unfamiliar territory by means of celestial or other reference clues; and 3) bicoordinate navigation, the ability to orientate toward a specific geographic goal from unfamiliar territory.

Saila and Shappy's (1963) Monte Carlo simulation of the ocean phase of salmon return migration suggested that only a weak homeward orientation (i.e., a

near-random drift) was required to produce the observed rates of return from ocean tagging studies. Quinn and Groot (1984), Healey and Groot (1987), and Quinn (1990) argued that compass orientation or bicoordinate navigation is necessary to explain the well-directed, well-timed, and rapid movements of sockeye in the open ocean.

Blackbourn (1987) proposed a temperature-displacement model to explain the interannual variation in run timing of sockeye salmon. He assumed that sockeye movements during and after the last marine winter fall into two types: 1) a relatively slow, non-directed migration in the first several months, in response to the seasonal changes in sea surface temperature or in the boundaries of ocean domains such as those discussed by Favorite et al. (1976); and 2) later, a rapid, directed migration toward the coast, largely independent of the boundaries of ocean variables, lasting no more than two months. According to the model, anomalously warm winter and spring sea surface temperatures displace sockeye farther to the north than usual in phase 1, requiring a longer migration to the Fraser River in phase 2, and result in late return times for Fraser River sockeye. Blackbourn's analysis implies differences among Fraser River sockeye stocks in their centers of winter distribution in the Gulf of Alaska and suggests that stock-specific compass orientation may be the direction-finding mechanism during phase 2 of ocean migration. This model is consistent

with models for predicting the coastal migration route of Fraser River sockeye (Groot and Quinn, 1987; Xie and Hsieh, 1989). In his review of salmon homing controversies, Quinn (1990) stated that there is no experimental evidence of navigation by adult salmon and that population-specific orientation may be the mechanism of some salmon during the ocean migration phase; however, the successful homing of some stocks is difficult to explain on the basis of fixed compass orientation.

Several investigators proposed that currents affect salmon migration routes. Royce et al. (1968) suggested that salmon accomplish their migrations within the Gulf of Alaska by orientating downstream or across currents. Hamilton and Mysak (1986) speculated that the Sitka eddy could deflect returning Skeena and Nass River salmon and that the interannual appearance and disappearance of the eddy might account for a portion of the variability of catches. Given the paucity of ocean current observations in the Northeast Pacific, these conceptual models could not be verified or developed into predictive models.

Hsieh and Lee (1989) developed a numerical model for studying the seasonal and interannual variability of the sea temperature and circulation fields of the Northeast Pacific, and suggested that such models, combined with observed coastal data (Wickett, 1977; Groot and Quinn, 1987; Xie and Hsieh, 1989), may improve the predictions of Fraser River sockeye return routes (e.g., NDR). Hsieh et al. (1991) found the interannual variability of the modeled sea surface temperature and circulation to be positively correlated with the NDR.

We hypothesize that interannual variations in the speed and pattern of the Northeast Pacific circulation acting on compass-orientated sockeye is sufficient to account for the variations in NDR. To investigate our hypothesis, we used daily surface current fields from an empirical model of the North Pacific and inserted an array of model sockeye given specific speed and direction characteristics. The simulations of sockeye migration paths focused on two years: 1) 1982, with a weak Alaska Gyre circulation and low NDR; and 2) 1983, with a strong circulation and high NDR. The migration paths of the model sockeye were simulated to their points of landfall, and the latitudes of landfall and migration speeds were determined.

In the following sections, we provide an overview of the Northeast Pacific Ocean circulation and its variability, describe the Ocean Surface Current Simulations (OSCURS) model and its depiction of the surface circulation, and present the rationale for the suite of sockeye behavioral scenarios used in the simula-

tions. We present the simulation results and specifically discuss their significance to the preceding models of the homeward migration of Fraser River sockeye.

NORTHEAST PACIFIC OCEAN CIRCULATION

The circulation of the Northeast Pacific is driven by surface winds and coastal runoff. The cyclonic (counterclockwise) surface winds associated with the Aleutian Low drive a long-term mean cyclonic flow around the Gulf of Alaska, called the Alaska Gyre. Ekman divergence of water in the upper-hundred meters results in the slow upwelling of deeper, saline water. This Ekman pumping in the central Gulf of Alaska and the lower salinities along the coasts of British Columbia and Alaska set up a cyclonic geostrophic flow around the Gulf in the upper 1000 m of the water column. The direct influence of the wind is superimposed on top of this geostrophic flow in the upper 100 m or so. In this surface layer, the currents are more variable and tend to flow slightly to the right of the local surface winds. There is a substantial seasonal and interannual variability in the strength of the Aleutian Low (Emery and Hamilton, 1985) and the Alaska Gyre (Hsieh et al., 1991).

The long-term mean circulation of the Alaska Gyre, as determined from climatological geostrophy (Dodimead et al., 1963; Thomson, 1981), comprises the Subarctic Current, a broad, slow eastward drift with speeds of about 5 to 10 cm/s; the Alaska Current, a broad, slow northward drift around 30 cm/s; and the Alaskan Stream, a narrow, southwestward boundary current with maximum speeds in excess of 100 cm/s. About 1500 km off the coast, between 45 and 50° N, the Subarctic Current bifurcates into the Alaska Current and the California Current, a broad, slow southward drift with mean speeds around 20 cm/s. Shoreward of this bifurcation zone, the ocean currents are poorly defined and variable.

The North Pacific Current flows parallel to the Subarctic Current and is part of the anticyclonic Central Pacific Gyre to the south of the Alaska Gyre. The North Pacific Current is a broad, slow eastward drift of about 5 to 10 cm/s. Its flow characteristics make it virtually indistinguishable from the Subarctic Current. The southern limit of the Subarctic Current, and thus the Alaska Gyre, is delineated by the Subarctic Boundary at around 40° N (Thomson, 1981). This boundary is identified by a salinity front, where the 34 ‰ isohaline separates the relatively saline surface waters to the south from the less saline surface waters of the

Alaska Gyre. It is frequently considered to be the southern limit of salmon distribution in the Gulf of Alaska (Favorite et al., 1976; Blackburn, 1987; Quinn, 1990).

Satellite-tracked drifters, drogued at depths of 100 and 120 m, have been used to investigate the variability of currents in the Northeast Pacific below the direct influence of the wind (Thomson et al., 1990). The mean Lagrangian flow was shown to be consistent with the geostrophic circulation pattern described previously. The individual drifter paths, however, show meanders and eddies occurring over much of the gyre, particularly in the bifurcation zone and Subarctic Boundary region. Significant differences in current variability have been found for drifters drogued at 30 m in the surface layer compared with those drogued at 100 and 120 m (McNally, 1981). The mean tracks of shallow drifters in the Northeast Pacific tend to follow time-averaged isobars of atmospheric pressure rather than geostrophy (Emery et al., 1985).

As the majority of sockeye in the Northeast Pacific Ocean are in the upper 15 m of the water column (French et al., 1976), we must model the circulation of the surface layer, not the subsurface geostrophic circulation, to study the influence of currents on migrating sockeye.

OCEAN SURFACE CURRENT SIMULATIONS (OSCURS) MODEL

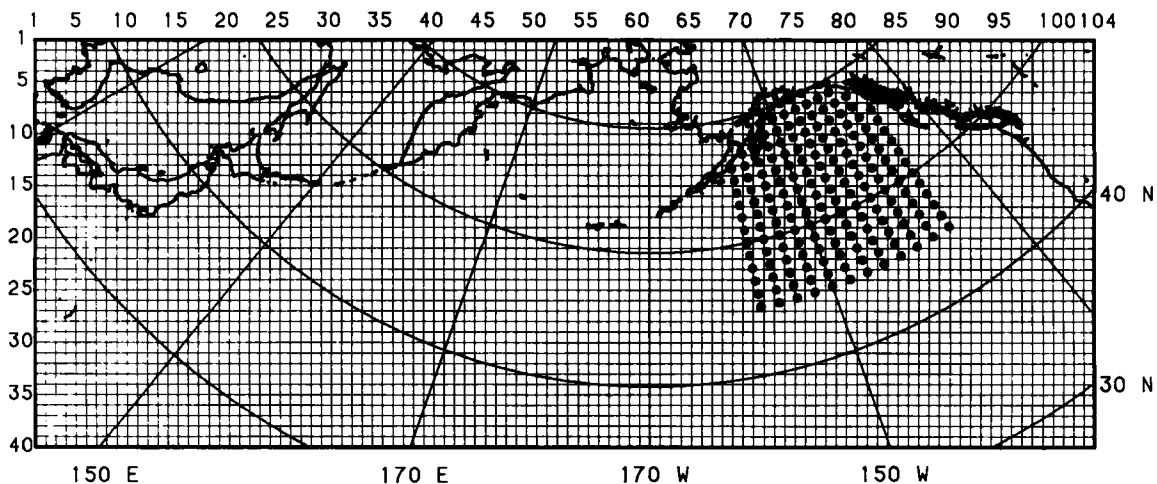
The Ocean Surface Current Simulations (OSCURS) model was used to simulate the surface currents in the

Northeast Pacific during the sockeye return migrations. OSCURS is an empirical model developed to examine the variability of Lagrangian drift in the North Pacific (north of 35° N) and Bering Sea (Ingraham and Miyahara, 1988; Ingraham et al., 1991).

The model computes currents as the vector sum of climatological geostrophic currents and daily surface wind drift with a spatial resolution of about 85 km (Fig. 2) and a time step of one day. The long-term mean temperatures and salinities of Bauer and Robinson (1985) were used to calculate geopotential anomalies (from 3000 m to the surface), from which surface geostrophic velocities were inferred. The barotropic currents are therefore uncertain due to the assumed level of no motion; however, the geostrophic circulation pattern and magnitudes were confirmed to be consistent with the descriptions of Favorite et al. (1976) and Reed and Schumacher (1987). The exception was in the Alaskan Stream, where the climatological calculations were low, presumably due to the relatively large grid spacing compared to the width of the stream. The grid size limitation was compensated for by scaling the geostrophic velocities at specified grid points (Ingraham and Miyahara, 1989).

The second, and generally the largest, component of the surface velocity, the wind-induced surface drift, was calculated using the daily atmospheric sea level pressure fields obtained from the U.S. Navy Fleet Numerical Oceanography Center on their standard 380 km grid. Details of the empirical formulas used to compute surface wind velocities and surface wind-induced drift (both speed and angle of deflection to the

Figure 2. Ocean Surface Current Simulations (OSCURS) model domain and grid. Longitude and latitude are labeled on the bottom and right sides of the figure; the grid indices are labeled on the left and top sides. The solid dots in the Northeast Pacific are the 174 start locations used for the sockeye migration simulations.



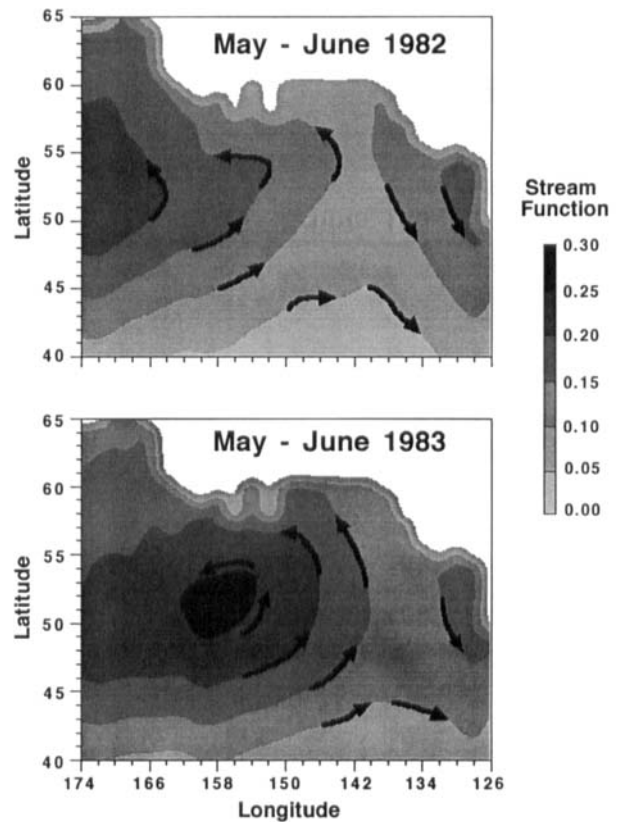
right of the wind) are presented in Ingraham and Miyahara (1989).

The model simulates the Lagrangian drift of a passive drifter in the surface layer by interpolating the geostrophic and wind drift vectors to the drifter location, summing the two vectors, calculating the drifter's 24 h displacement, and repeating the process at each new daily position. The resulting progressive vector diagram is the simulated drifter track. The geostrophic velocities, wind drift speed, and angle of deflection were tuned using a set of satellite-tracked drifters, drogued at 20 m, in the Gulf of Alaska (Reed, 1980). The tuned model simulates the observed drifter tracks with remarkably good visual agreement. The wind drift component dominates the modeled surface velocities, except in the Alaskan Stream, where geostrophic speeds are over 60 cm/s. Thus, the current patterns vary considerably from day to day, season to season, and year to year, due to the variability of the winds.

The strength of this model is in its ability to provide reasonable surface currents at any point and date on the model grid, and to integrate model sockeye displacements as they move through the time and space varying current regime. OSCURS does not, however, simulate circulation features that are driven by processes other than climatological geostrophy and local winds, specifically: the geostrophic mesoscale eddies observed by Thomson et al. (1990) in the bifurcation zone and Subarctic Boundary region; the topographically controlled Sitka eddy (Swaters and Mysak, 1985) centered near 57° N, 138° W; and coastal buoyancy-driven currents (Thomson et al., 1988). Regardless, OSCURS is clearly the best available model for providing currents on the time and space scales required to simulate sockeye migrating from the Gulf of Alaska to the coast. Given the model limitations, we defined the coast as the continental shelf break.

Prior to discussing the migration simulations, we will examine the year-to-year, month-to-month, and day-to-day variability of the surface currents modeled by OSCURS during the migration period. The May–June mean circulation patterns for 1982 and 1983 are shown in the stream function plots of Fig. 3. The stream function, a scalar representation of the current speed and direction (Pond and Pickard, 1983), was calculated from 61 d means of the daily surface current vector fields. Current vectors are everywhere tangent to the contours of the stream function, and vector magnitudes are proportional to the stream function gradients. If the currents were stationary in time such that Fig. 3 could be perceived as representing the “instantaneous” flow fields, surface drifters would follow the stream function contours with the stream function

Figure 3. Stream function plots of the mean Northeast Pacific circulation in 1982 and 1983 for the period from May 1 to June 30. The arrows show the direction of the mean surface current, but provide no indication of the current magnitude. See text for further details.



maximum to the left (as shown by the arrows) and have speeds inversely proportional to the distance between adjacent contours. In Fig. 3, 1983 can be seen to have the stronger and more northward surface circulation by the relative spacing and orientation of the stream function contours between 160 and 140° W. It is clear that at least part of the 1983 intensification is due to the eastward displacement of the Alaska Gyre. If we consider compass-orientated sockeye migrating toward Vancouver Island, it is apparent that the mean influence of the currents will vary depending on the migration start position. For the current fields in Fig. 3, currents assist the shoreward migrations of sockeye starting from the southern portion of their ocean distribution and impede those starting from the northern portion.

The surface circulation field, however, does not remain stationary over periods of months. The monthly variability of the long-term mean Lagrangian circulation pattern is illustrated in Fig. 4. The cyclonic cir-

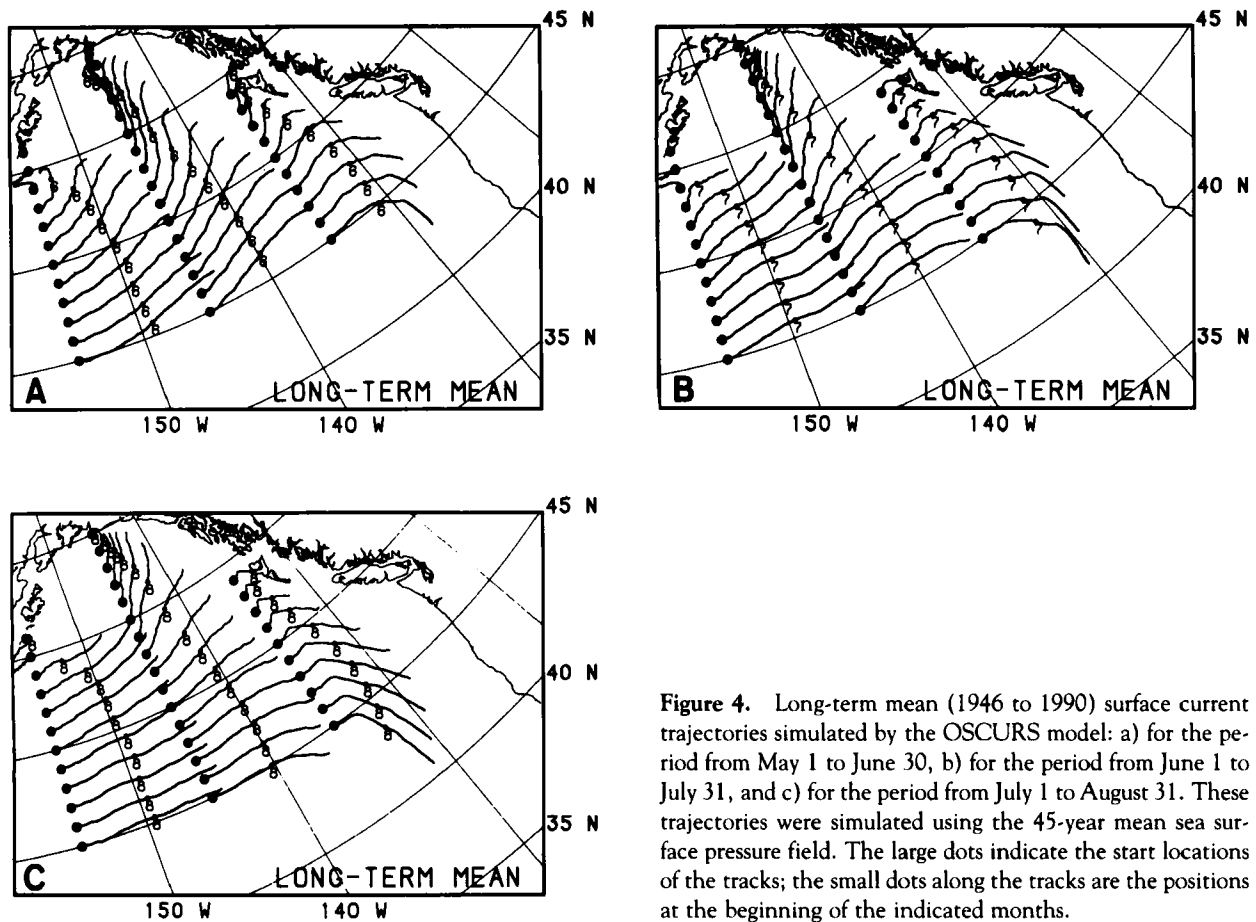


Figure 4. Long-term mean (1946 to 1990) surface current trajectories simulated by the OSCURS model: a) for the period from May 1 to June 30, b) for the period from June 1 to July 31, and c) for the period from July 1 to August 31. These trajectories were simulated using the 45-year mean sea surface pressure field. The large dots indicate the start locations of the tracks; the small dots along the tracks are the positions at the beginning of the indicated months.

ulation of the Alaska Gyre is discernable, as is the seasonal evolution of the Lagrangian pattern due to the displacement of the Aleutian Low by the North Pacific High. In June, the trajectories turn southward, a signature of the climatological wind shift due to the influence of the North Pacific High. This signature is greatest near the coast and diminishes offshore. The net northward displacement of each trajectory decreases as the start dates progress from May to July. We therefore expect the migration start time, sockeye swim speed, and timing of the seasonal wind shift (i.e., the progress of the migration relative to the wind shift) to modulate the current effects on the sockeye migrations.

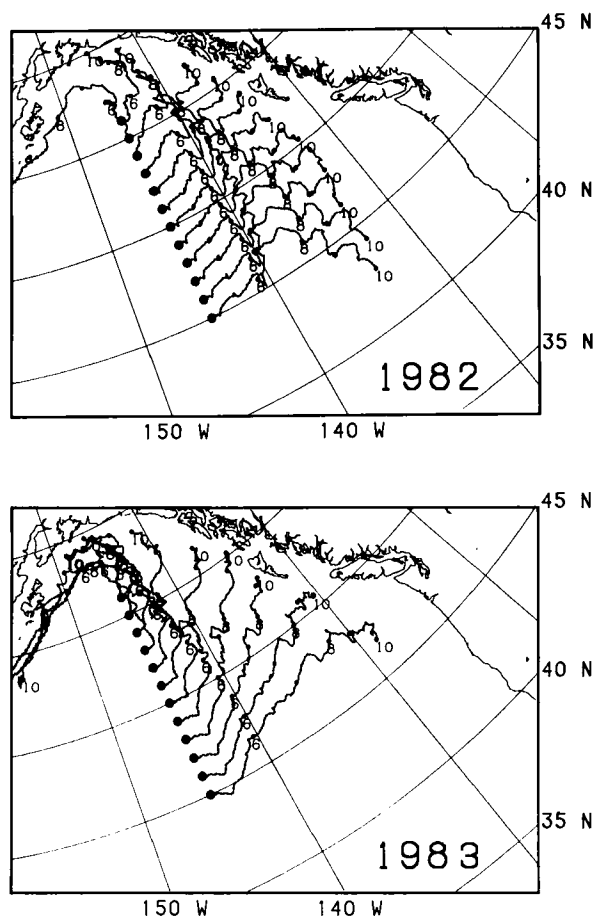
The daily variability of simulated passive drifter trajectories is shown in Fig. 5. Many wind-driven meanders are present, which can only be resolved with the daily vector fields. Also apparent is the cyclonic Alaska Gyre, the 1983 strengthening of the gyre (Fig. 3), and the seasonal evolution of the circulation field from May through July (Fig. 4).

SOCKEYE MIGRATION SIMULATIONS

The influence of Northeast Pacific Ocean currents on migrating sockeye was investigated by seeding the OSCURS model with an array of active drifters, to simulate swimming, compass-orientated sockeye. The simulations focused on 1982 and 1983 as years with representative weak and strong circulation patterns, respectively, and corresponding low and high NDRs. Comparisons of the between-year results will be made to test the validity of our hypothesis.

One hundred and seventy-four sockeye migration paths were modeled in each simulation. The array of these “release” points is shown in Fig. 2, consistent with the distribution of sockeye determined from ocean tagging data (Fig. 1). For each year, a suite of 27 behavioral scenarios was used to examine the importance of swim speed, orientation, and migration start date on the results. The range of behavioral scenarios was chosen to permit the timely return of salmon, from up to 2000 km offshore, in a 4 to 10 week

Figure 5. OSCURS-simulated surface current trajectories for the period from May 1 to October 1, for 1982 and 1983. The large dots indicate the start locations of the tracks; the small dots along the tracks are the positions at the beginning of the indicated months.



migration period, from any portion of their known ocean distribution. The behavioral scenarios were combinations of the following:

1) Sockeye swim speeds of 20.8 cm/s (18 km/d), 34.7 cm/s (30 km/d), and 55.6 cm/s (48 km/d). The term "swim speed" refers to the movement of a sockeye relative to the water, regardless of the water's motion. Laboratory studies of swimming energetics (Brett, 1983) indicate that the most efficient sustained swim speed for typical adult sockeye (61 cm) is about 0.8 lengths/s or 50 cm/s, and swimming is relatively efficient within the range of 28 to 72 cm/s. Ultrasonic tagging studies of coastal migrations have estimated the average swim speed as 66.8 cm/s (Quinn, 1988). Adult sockeye tagged on the open ocean and recovered in coastal waters had a mean migration speed (speed-

made-good over a great circle distance from release to capture) of 26.4 cm/s, with many migration speeds between 35 and 70 cm/s (Hartt, 1966; French et al., 1976; Groot and Quinn, 1987). The simulated swim speeds were chosen to represent reasonable low, medium, and high speeds.

2) Migration start dates of May 1, June 1, and July 1. These dates were used to be consistent with the ocean tagging data (French et al., 1976) and the unpublished analysis of Groot, which suggests that the sockeye are not actively migrating in April.

3) Compass orientations of 90° T (east), 112.5° T (east-southeast), and 135° T (southeast). Our choice of orientations permits sockeye to make landfall in the vicinity of Vancouver Island from any portion of their ocean distribution, in the absence of currents.

For each year, 1982 and 1983, and for each of the 27 behavioral scenarios, the migration paths of 174 model sockeye were simulated within the OSCURS model. The daily displacement of each fish was calculated as the vector sum of the displacement due to the given swim speed and orientation, and the displacement due to the surface current at the sockeye's position. The progressive vector diagram of these daily displacements is the simulated migration path. For each migration path, two landfall variables were computed: the latitude of landfall and the migration speed. We calculated migration speed as the great circle distance between the migration start position and the position of landfall, divided by the time required to make landfall. The migration speed of the model sockeye is a result of the sockeye swim speed and the net effect of currents along the entire migration path.

MIGRATION SIMULATION RESULTS

It is revealing to examine a small subset of the 9396 simulated sockeye migration paths (Figs. 6 and 7). For clarity, these figures show only the migration paths for model sockeye originating on the 150° W meridian.

In the absence of currents, the migration paths for sockeye shown in Fig. 6 would parallel the lines of latitude (great circle paths would appear as straight lines). Those for sockeye shown in Fig. 7 would appear to curve gently toward the top of the page. The most noticeable departures from expected "current-free" migration paths are the meanders due to the time and space varying currents. In particular, the four most northerly paths, in the vicinity of the southwest flowing Alaska Stream, have dramatic deflections to the south and southwest. In both figures, the signature of the seasonal shift in surface winds is apparent in the relative

Figure 6. Simulated sockeye migration paths, for 1982 and 1983, with a swim speed of 20.8 cm/s, a compass orientation of 90° T, and a migration start date of May 1. The map projection is polar stereographic. The large dots indicate the start locations. The small dots along the paths are the daily positions. The mid-sized dots along the paths are the positions at the beginning of the indicated months.

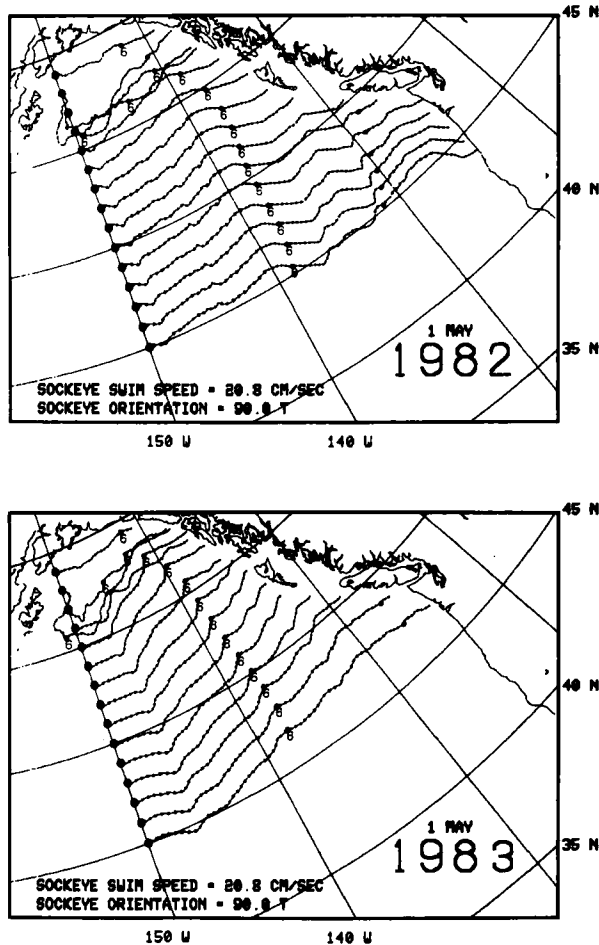
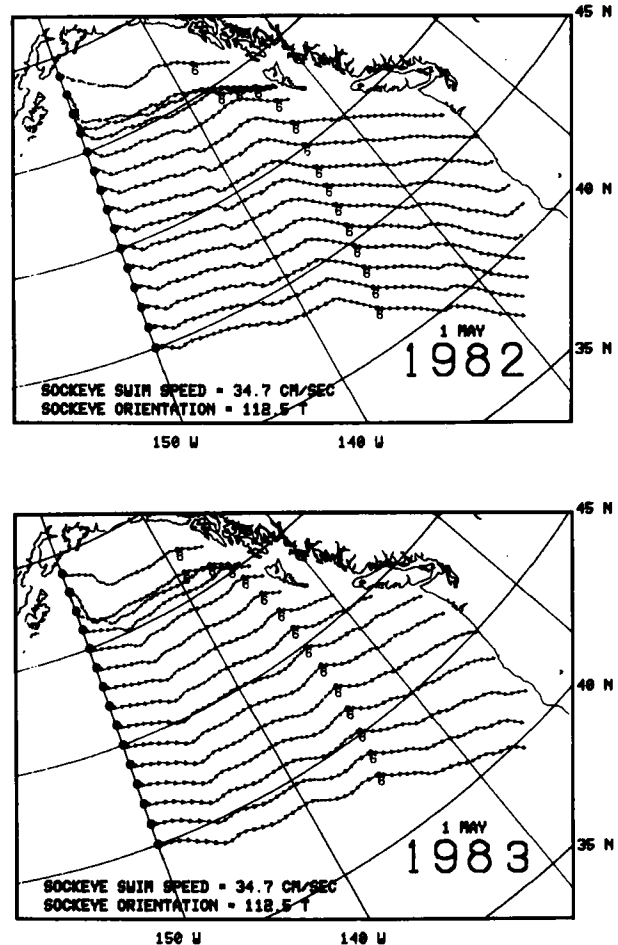


Figure 7. Simulated sockeye migration paths, for 1982 and 1983, with a swim speed of 34.7 cm/s, a compass orientation of 112.5° T, and a migration start date of May 1. The map projection is polar stereographic. The large dots indicate the start locations. The small dots along the paths are the daily positions. The mid-sized dots along the paths are the positions at the beginning of the indicated months.



southward deflection of paths near the beginning of June.

The strong 1983 circulation induced greater northward deflections than the weak 1982 circulation. In Fig. 6, the path originating at 50° N made landfall at about 49° N (a net southward deflection) in 1982, and at about 53° N in 1983. This is a difference of about 400 km between the two years, due solely to the different current fields. In Fig. 7, sockeye originating north of 54° N made landfall between 100 and 200 km farther north in 1983 than in 1982. These results are consistent with our hypothesis.

We note that an eastward orientation appears to be a reasonable strategy only for the sockeye swimming at

relatively slow speeds that start their migration south of about 55° N (Fig. 6). An east-southeastward orientation, on the other hand, appears to be reasonable only for sockeye swimming at speeds of about 35 cm/s, that originate north of 55° N (Fig. 7). Most sockeye originating farther south with the same orientation are "lost" in the California Current, particularly in 1982.

Influence of currents on latitude of landfall

As only a limited number of migration paths may reasonably be plotted in the format of Figs. 6 and 7, we developed a simple but revealing presentation for the qualitative analysis of sockeye landfall variables (e.g., Figs. 8 to 10). The results presented in each vertical

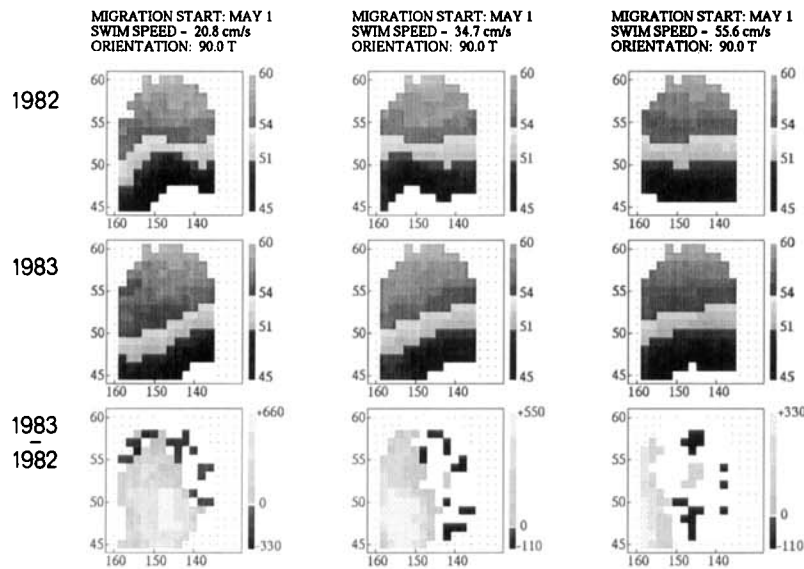


Figure 8. The effects of currents on the latitude of landfall of model sock-eye, with varying swim speeds. The top frames show the latitude of landfall in 1982 (in degrees north) as a function of migration start position. The center frames show the latitude of landfall in 1983. The bottom frames show the difference in latitude of landfall between 1983 and 1982 (in kilometers). A positive difference indicates that landfall was made farther north in 1983 compared with 1982. See text for further details.

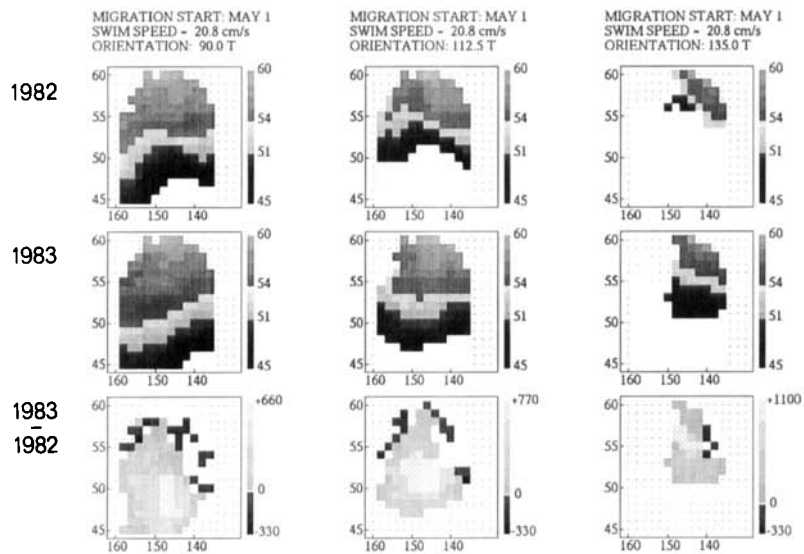


Figure 9. The effects of currents on the latitude of landfall of model sock-eye, with varying compass orientations. The top frames show the latitude of landfall in 1982 (in degrees north) as a function of migration start position. The center frames show the latitude of landfall in 1983. The bottom frames show the difference in latitude of landfall between 1983 and 1982 (in kilometers). A positive difference indicates that landfall was made farther north in 1983 compared with 1982. See text for further details.

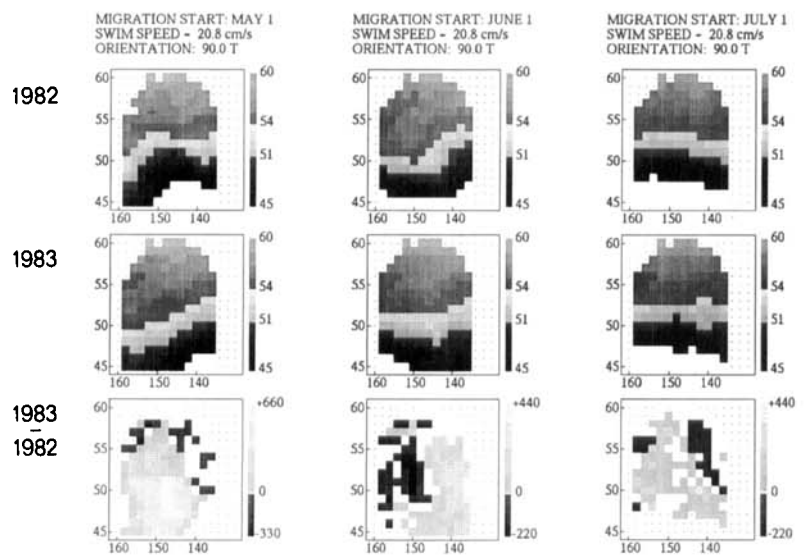


Figure 10. The effects of currents on the latitude of landfall of model sock-eye, with varying migration start dates. The top frames show the latitude of landfall in 1982 (in degrees north) as a function of migration start position. The center frames show the latitude of landfall in 1983. The bottom frames show the difference in latitude of landfall between 1983 and 1982 (in kilometers). A positive difference indicates that landfall was made farther north in 1983 compared to 1982. See text for further details.

vertical set of frames were obtained from simulations using a single behavioral scenario. In a given frame, the gray shade at a given latitude and longitude represents the value of the landfall variable, according to the gray scale shown to its right, for the model sockeye originating from that position.

Figures 8 to 10 map the latitudes of landfall for 1982 and 1983, and the differences between the two years, as a function of migration start position in the Northeast Pacific. Three gray-scale bands were used in the presentations of the 1982 and 1983 latitudes of landfall to highlight the portion of the British Columbia coast presumed to be targeted by returning Fraser River sockeye (i.e., the portion of the coast between 51 and 54° N shaded with the lightest gray band, which encompasses the Queen Charlotte Islands and Vancouver Island). Positions from which sockeye made landfall south of 45° N are shown as white, as the sockeye were considered to be lost. Two gray-scale bands are used in the presentation of the differences in landfall between 1983 and 1982 (labeled as "1983–1982" in the figures) to highlight the positive and negative differences. The light gray band represents a positive difference (i.e., the latitude of landfall was farther to the north in 1983 compared to 1982), and the dark band represents a negative difference. White indicates there was no difference in latitude of landfall between the two years.

The effects of different swim speeds on the latitude of landfall are illustrated in Fig. 8. The migration start date and orientation are fixed, while the swim speed increases from left to right. The light gray band in the 1982 and 1983 frames is a prominent feature. The progressive alignment of this band with the horizontal (i.e., lines of latitude) as the swim speed increases indicates that the influence of currents on latitude of landfall diminished with increasing swim speeds. The 1983–1982 frames show that the majority of sockeye made landfall farther north in 1983 than 1982, consistent with our hypothesis. There are, however, a number of locations in the eastern and northern portions of these frames where the differences in landfall were zero or negative. Figure 8 shows that the effect of currents on latitude of landfall was strongly dependent on the position from which sockeye start the ocean migration.

The effects of different orientations on latitude of landfall are shown in Fig. 9. The compass orientation shifts progressively southward from left to right, while the migration start date and swim speed are fixed. The light gray band in the 1982 and 1983 frames changes alignment as the compass orientation changes, illustrating that sockeye starting from different locations in the Northeast Pacific must use different orientations to make landfall between 51 and 54° N. Sockeye origi-

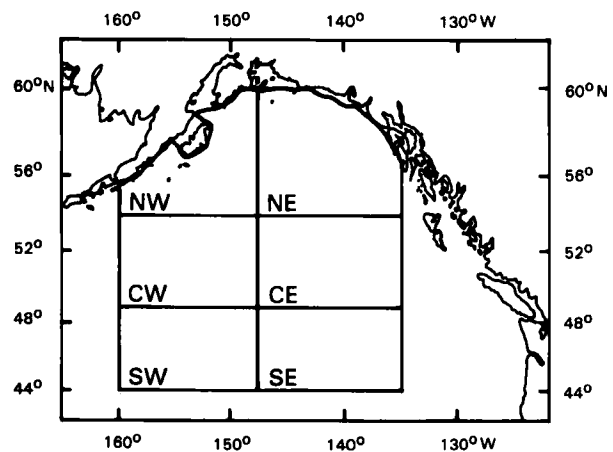
nating in the northern portions of the Gulf of Alaska required a southeastward orientation to make landfall on the British Columbia coast, whereas sockeye originating in the southern portion of the Gulf required an eastward orientation. The 1983–1982 frames illustrate that all but a few model sockeye made landfall farther north in 1983 than 1982, regardless of compass orientation.

In Fig. 10, the swim speed and orientation are fixed, and the migration start date becomes progressively later from left to right. The differences in landfall between the two years were again predominantly positive for all three migration start dates; however, the pattern of positive and negative differences varies. Clearly, the latitude of landfall depended on the migration start date and the progress of the migrating sockeye relative to the onset of the climatological wind shift in June. The positive–negative pattern of differences in landfall for sockeye starting on June 1 is significantly different from that for May 1 and July 1 start dates. The relative timing of the climatological wind shift between 1982 and 1983 presumably accounts for this anomalous pattern.

In light of the importance of the locations from which sockeye originate, we divided the start positions of our model sockeye into six areas (Fig. 11). The mean differences in landfall between 1983 and 1982 were calculated for these areas to examine the significance of migration start locations.

In Table 1, the mean landfall differences between 1983 and 1982 increased to the south, with the largest

Figure 11. Delineation of the six areas referenced in Tables 1 to 5: NW (Northwest), NE (Northeast), CW (Central West), CE (Central East), SW (Southwest), and SE (Southeast).



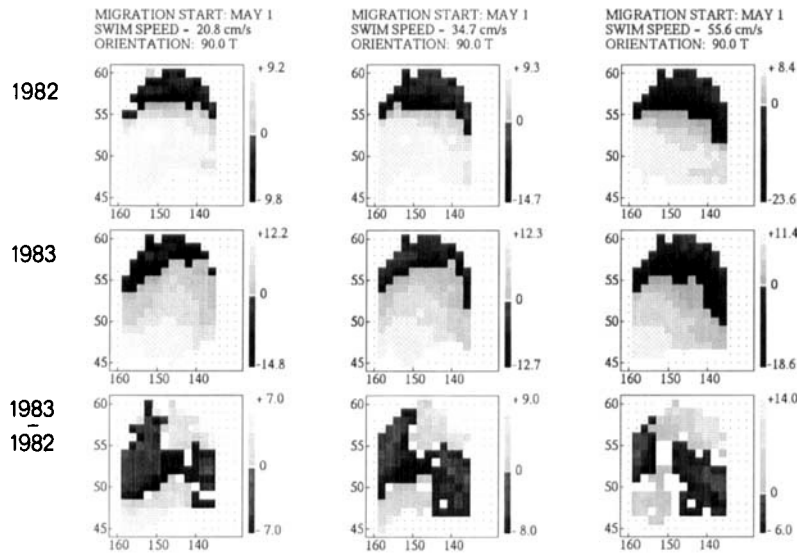


Figure 12. The effects of currents on the migration speed of model sockeye, with varying swim speeds. The top frames show the difference between migration speed and swim speed in 1982 (in centimeters per second) as a function of migration start position. A positive difference indicates the sockeye received a shoreward assist from the currents; a negative difference indicates the sockeye were impeded by the currents. The center frames show the difference between the migration speed and swim speed in 1983. The bottom frames show the difference in migration speeds between 1983 and 1982 (in centimeters per second). A positive difference indicates the sockeye received a relative shoreward assist in 1983 compared to 1982. See text for further details.

mean differences in the SW and SE (123 and 136 km, respectively). The northern areas, NW and NE, had significantly smaller landfall differences of 78 and 18 km, respectively. For the total area, the mean latitude of landfall was 84 km further north in 1983 than in 1982. This is significantly greater than zero, but is less than half the north–south extent of Vancouver Island and thus is likely to have only a minor impact on the NDR. The mean differences in landfall for the individual areas were frequently larger and thus more likely to have a significant impact on the NDR.

The mean difference in landfall between 1983 and 1982 for the total area significantly decreased, from 120 to 40 km, with increased swim speeds (Table 2). This trend was apparent for all areas except the NW and NE, where the values did not change significantly with swim speed. The largest mean differences occurred in the southern areas for all speeds and were for the most part, significantly greater than the means in the northern areas. All of the means were significantly positive with the exception of two: the NE with a swim speed of 34.7 cm/s was not significantly different from zero, and the NE area with a swim speed of 55.6 cm/s was significantly negative. The largest difference in landfall, 206 km, occurred for sockeye originating in the SE with a swim speed of 20.8 cm/s.

The mean landfall difference for the total area increased significantly, from 57 to 138 km, with increased orientation to the south (Table 3). This trend was also found for each area. All of the means were positive, with the exception of the NE area, with orientations of 90° T (negative) and 112.5° T (zero). The

largest difference, 283 km, occurred for sockeye with a 135° T orientation originating in the CW.

The mean landfall differences for the total area decreased significantly, from 144 to 40 km, with later start dates (Table 4). For the three western areas, the smallest mean differences occurred with a June 1 start. A June 1 start date also provided the largest differences for the three eastern areas. The anomalous pattern of landfall differences seen for a June 1 start date (compared with May 1 and July 1 start dates) in Fig. 10 is also apparent in Table 4, where the western means

Table 1. Mean differences in latitude of landfall between 1983 and 1982 (in kilometers) for the full suite of 27 behavioral scenarios. For each area, the bold value is the mean landfall difference (positive indicates the landfall in 1983 was north of 1982), the bracketed values are the 95% confidence interval of the mean, and the sample size (n) is shown. Sockeye that made landfall south of 45° N were not included.

NW	77.9 (57.9, 97.8) n = 510	NE	17.9 (4.6, 31.1) n = 739
CW	105.7 (84.9, 126.4) n = 481	CE	111.7 (95.4, 128.1) n = 632
SW	122.9 (98.4, 147.3) n = 248	SE	136.3 (119.0, 153.5) n = 289
Total Area: 84.2 (76.6, 91.8), n = 2899			

Table 2. Mean differences in latitude of landfall between 1983 and 1982 (in kilometers), using all orientations and migration start dates, for the three different swim speeds. See Table 1 for further details.

Swim Speed = 20.8 cm/s			
NW	64.6 (32.1, 97.1) n = 155	NE	47.3 (20.5, 74.1) n = 251
CW	136.3 (97.2, 175.4) n = 163	CE	176.2 (144.8, 207.6) n = 221
SW	161.1 (119.4, 202.7) n = 84	SE	205.8 (177.8, 233.9) n = 101
Total Area: 120.4 (106.2, 134.5) n = 975			
Swim Speed = 34.7 cm/s			
NW	107.6 (68.9, 146.2) n = 180	NE	20.6 (-3.9, 45.1) n = 246
CW	136.3 (95.0, 177.6) n = 163	CE	89.2 (64.6, 113.9) n = 212
SW	155.8 (106.2, 205.4) n = 84	SE	110.0 (61.2, 138.8) n = 91
Total Area: 90.8 (76.9, 104.8), n = 975			
Swim Speed = 55.6 cm/s			
NW	59.8 (27.9, 90.3) n = 175	NE	-15.5 (-30.8, -0.1) n = 242
CW	41.2 (19.0, 63.3) n = 155	CE	64.1 (38.3, 89.9) n = 199
SW	46.1 (18.8, 77.5) n = 80	SE	88.5 (60.4, 116.5) n = 97
Total Area: 40.3 (29.8, 50.7), n = 948			

were all negative and the eastern means were all positive. The largest positive difference, 292 km, occurred for sockeye migrating from the CW with a May 1 start date; the largest negative difference, -89 km, occurred for the same area but for a start date of June 1.

In summary, the mean differences in latitude of landfall between 1983 and 1982 depended on the area from which sockeye initiated their homeward migra-

Table 3. Mean differences in latitude of landfall between 1983 and 1982 (in kilometers), using all swim speeds and migration start dates, for the three different orientations. See Table 1 for further details.

Compass Orientation = 90° T			
NW	16.1 (2.6, 29.7) n = 232	NE	-11.3 (-18.6, -4.1) n = 252
CW	63.1 (43.6, 82.7) n = 270	CE	58.7 (42.9, 74.4) n = 270
SW	107.1 (81.4, 132.7) n = 225	SE	118.5 (98.6, 138.4) n = 220
Total Area: 57.1 (49.6, 64.6), n = 1469			
Compass Orientation = 112.5° T			
NW	101.1 (69.7, 132.6) n = 224	NE	-7.0 (-16.5, 2.5) n = 252
CW	155.8 (115.4, 196.3) n = 204	CE	126.7 (97.2, 156.1) n = 264
SW	277.4 (225.9, 328.8) n = 23	SE	192.5 (160.2, 224.8) n = 68
Total Area: 102.0 (88.1, 115.9), n = 1035			
Compass Orientation = 135° T			
NW	246.9 (134.8, 356.1) n = 54	NE	75.8 (36.8, 114.8) n = 235
CW	282.9 (228.5, 337.2) n = 7	CE	217.8 (170.3, 265.3) n = 99
SW	n = 0	SE	n = 0
Total Area: 138.4 (107.6, 169.2), n = 395			

tions, the swim speed, the compass orientation, and the migration start date. For the most part, the mean difference in landfall between the two years was positive, consistent with our hypothesis, and of sufficient magnitude to suggest that the influence of ocean currents accounts for at least a portion of the NDR.

Influence of currents on migration speed

Figure 12 maps the influence of currents on migration speed (using the same presentation format as Figs. 8 to

Table 4. Mean differences in latitude of landfall between 1983 and 1982 (in kilometers), using all swim speeds and orientations, for the three different migration start dates. See Table 1 for further details.

Migration Start Date: May 1			
NW	155.9 (121.6, 190.2) n = 175	NE	32.4 (7.0, 57.7) n = 248
CW	292.3 (259.9, 324.8) n = 181	CE	85.8 (56.2, 115.3) n = 218
SW	282.7 (249.5, 315.9) n = 107	SE	96.7 (54.4, 139.1) n = 83
Total Area: 143.5 (129.1, 157.9), n = 1012			
Migration Start Date: June 1			
NW	-59.7 (-84.1, -35.2) n = 166	NE	37.8 (22.0, 53.6) n = 250
CW	-89.4 (-99.6, -61.1) n = 167	CE	241.9 (219.2, 264.6) n = 221
SW	-23.8 (-46.0, -1.6) n = 88	SE	210.6 (191.6, 229.6) n = 129
Total Area: 63.4 (51.8, 74.9), n = 1021			
Migration Start Date: July 1			
NW	132.1 (97.8, 166.4) n = 162	NE	-17.8 (-44.3, 8.7) n = 241
CW	85.2 (62.7, 107.7) n = 133	CE	-8.0 (-28.1, 12.2) n = 632
SW	43.6 (21.1, 66.1) n = 53	SE	54.3 (37.8, 70.8) n = 77
Total Area: 39.6 (27.5, 51.9), n = 866			

10) for the three swim speeds, with a fixed orientation of 90° T and a fixed migration start date of May 1. The top frames map the effect of currents on migration speed in 1982, and the center frames map the effect on migration speed in 1983. The bottom frame maps the difference between the 1983 migration speed and the 1982 migration speed.

Each behavioral scenario exhibits a similar pattern:

the currents impeded the shoreward progress of sockeye originating north of about 55° N, and assisted the migration of sockeye originating to the south of 55° N. Sockeye originating in the northeast and southwest quadrants received a relatively greater shoreward assist in 1983 than in 1982. In the northwest and southeast quadrants, the reverse was true.

Table 5 shows the magnitude of these effects for each of the six areas defined in Figure 12. Over the total area, the currents provided a shoreward assist of less than 1 cm/s in both 1982 and 1983. Sockeye from the central and southern areas received a shoreward assist, while the two northern areas were impeded by the currents. In 1982, the sockeye from the SW area had the largest mean shoreward assist, 6.3 cm/s, while the NE area had the largest impediment, of 4.0 cm/s. In 1983, the shoreward assist for sockeye originating from the SW was 9.1 cm/s, significantly greater than in 1982, and the impediment to the NE sockeye was 3.3 cm/s, significantly smaller than in 1982. The differences in the effects of the currents on migration speed between 1983 and 1982 were all less than 3 cm/s. NE, SW, and SE sockeye had greater shoreward assists in 1983. The reverse was true for sockeye originating from the NW, CW, and CE.

In summary, the Northeast Pacific currents impeded the shoreward progress of sockeye that start their migration north of 55° N, and assisted the shoreward migrations of sockeye starting south of 55° N. The magnitude of these effects was as high as 50% of the swim speed of slow swimming sockeye, and as low as about 10% of the swim speed of fast swimming sockeye.

DISCUSSION

Our results show that the interannual variability of Northeast Pacific surface currents is sufficient to affect the latitude of landfall and migration speed of sockeye migrating to the Fraser River. Surface currents during years with anomalously strong Alaska Gyre circulations (e.g., 1983) deflect migrating sockeye farther to the north than currents in other years (e.g., 1982), and thus may contribute to an increased Northern Diversion Rate. We do not advocate that the interannual variability of ocean currents alone drives the observed NDR, but suggest that the ocean currents must be considered an important factor.

Saila and Shappy's (1963) arguments about random swimming or very weak orientation being a sufficient explanation for successful homing are less convincing in light of our results. Although the currents increased the migration speed of our model sockeye by up to 10 cm/s, the current magnitudes are not sufficient to

Table 5. Mean differences between migration speed and swim speed for 1982, for 1983, and between 1983 migration speed and 1982 migration speed (in centimeters per second). For each area, the bold value is the mean difference, the bracketed values are the 95% confidence interval of the mean, and the sample size (n) is shown. Sockeye that made landfall south of 45° N were not included.

1982 Migration Speed Minus Swim Speed			
NW	-3.0	NE	-4.0
	(-3.4, -2.6)		(-4.4, -3.6)
	n = 510		n = 739
CW	4.8	CE	2.6
	(4.6, 5.0)		(2.3, 2.9)
	n = 481		n = 632
SW	6.3	SE	4.8
	(6.0, 6.5)		(4.5, 5.1)
	n = 248		n = 289
Total Area: 0.6 (0.3, 0.8), n = 2899			
1983 Migration Speed Minus Swim Speed			
NW	-3.6	NE	-3.3
	(-3.9, -3.2)		(-3.6, -3.0)
	n = 510		n = 739
CW	3.6	CE	0.7
	(3.3, 3.9)		(0.3, 1.0)
	n = 481		n = 632
SW	9.1	SE	7.5
	(8.9, 9.4)		(7.3, 7.7)
	n = 248		n = 289
Total Area: 0.8 (0.6, 1.0), n = 2899			
1983 Migration Speed Minus 1982 Migration Speed			
NW	-0.7	NE	0.6
	(-1.0, -0.4)		(0.3, 0.9)
	n = 510		n = 739
CW	-1.4	CE	-2.3
	(-1.7, -1.2)		(-2.5, -2.0)
	n = 481		n = 632
SW	2.7	SE	2.4
	(2.3, 3.1)		(1.9, 2.9)
	n = 248		n = 289
Total Area: -0.3 (-0.4, -0.1), n = 2899			

bring sockeye to the coast with the observed timing. This is well illustrated by the relatively slow progress of passive drifters simulated by the OSCURS model (Fig. 5). These model drifters moved to the northeast and then southeast toward the coast, consistent with the general pattern of sockeye migration during the

ocean phase (French et al., 1976); however, the passive drifters did not approach the coast until October or later.

A single compass orientation appears to be an insufficient explanation for homing salmon, given the importance of start location and start time on the ultimate point of landfall. If stocks have different distributions in the Gulf of Alaska, as implied by Blackburn's (1987) analysis, then stock-specific orientation may be a sufficient explanation.

Our results also agree with some form of navigation as the direction-finding mechanism for sockeye during the ocean phase of their homeward migration. We anticipate that sockeye using bicoordinate navigation would be influenced by the interannual variability of currents similar to the compass-orientated sockeye in our simulations. Sockeye navigation would have to be very precise, and a forecast of currents to be encountered by migrating sockeye would almost be required, for the currents not to have an impact.

The simulation results are consistent with the temperature-displacement model of Blackburn (1987). In phase 1 of this model, it was assumed that the north-eastward movement of sockeye in May and June was in response to seasonal changes in sea surface temperatures. This migration phase can also be explained by random drift within the surface circulation patterns of the Gulf of Alaska. This is well illustrated by the long-term mean Lagrangian trajectories of passive drifters shown in Fig. 4a. In a year with anomalously strong currents (e.g., 1983), sockeye would be pushed farther to the north than in other years (e.g., 1982). This interannual effect can be seen clearly in our simulation of passive drifters (Fig. 5). In phase 2 of Blackburn's model, sockeye move in a rapid and directed migration toward the coast. Our simulation results show that compass-orientated sockeye (and presumably sockeye using bicoordinate navigation) have greater migration speed and make landfall farther north in years with an anomalously strong circulation. Thus, the mean pattern and interannual variability of Northeast Pacific currents have significant effects in both migration phases of the temperature-displacement model. We suggest that Blackburn's (1987) model could be enhanced, to provide more accurate predictions of sockeye run timing and to provide NDR predictions, by including the effects of currents.

We further suggest that the influence of ocean currents on the latitude of landfall of homeward migrating sockeye may impact the reliability of the NDR prediction formulas of Groot and Quinn (1987) and Xie and Hsieh (1989). These formulae use coastal data in the immediate vicinity of Vancouver Island (e.g., Fraser

River runoff and sea surface temperature on the west coast of Vancouver Island). While runoff from the Fraser River (and other rivers with similar flow characteristics) affects the surface salinity along much of the British Columbian coast and as far offshore as 1500 km (Thomson, 1981), the processes that drive the variability of surface temperature off the west coast of Vancouver Island do not have such far-reaching effects. Ware and McFarlane (1989) described two distinct oceanographic domains along the coast of British Columbia: the Coastal Upwelling Domain, including the continental shelf off the west coast of Vancouver Island, and the Coastal Downwelling Domain, encompassing the continental shelf immediately north of Vancouver Island. Sockeye salmon that make landfall to the north of the Coastal Upwelling Domain and approach Vancouver Island from within the Coastal Downwelling Domain may migrate around the north or south end of the island according to physical process in the Coastal Downwelling Domain, which are not accounted for by the variables in the models of Groot and Quinn (1987) and Xie and Hsieh (1989).

We propose a conceptual model for the observed NDR with an ocean component and a coastal component. The ocean component would comprise the Blackburn (1987) temperature-displacement model enhanced with the inclusion of the effects of the Northeast Pacific Ocean surface currents. The coastal component would use the predictive formula of Xie and Hsieh (1989), for sockeye making landfall in the vicinity of Vancouver Island, and a yet-to-be-developed predictive formula using coastal observations from the Coastal Downwelling Domain, for sockeye making landfall north of Vancouver Island.

SUMMARY

We hypothesized that the interannual variability of the surface circulation in the Northeast Pacific Ocean affects the latitude of landfall and migration speed of adult sockeye returning to the Fraser River. OSCURS, an empirical model that simulates the trajectories of shallow Lagrangian drifters, was seeded with arrays of compass-orientated "sockeye" with a range of behavioral scenarios (i.e., swim speed, compass orientation, and migration start date). The migration paths of sockeye were simulated for 1982, a year with a relatively weak Northeast Pacific circulation and low Northern Diversion Rate, and for 1983, a year with a strong circulation and high Northern Diversion Rate.

Our results are summarized as follows:

1) The latitude of landfall in 1983 compared with

1982 was generally farther to the north, due to the stronger Northeast Pacific circulation in 1983.

2) The difference in latitude of landfall between 1983 and 1982 increased for slower swim speeds, more southward orientations, and earlier migration start dates.

3) The difference in latitude of landfall between 1983 and 1982 was strongly dependent on the area from which sockeye initiate their migration. The landfalls of 1983 compared with 1982 were generally farther to the north for sockeye starting from the southern areas. The mean difference in latitude of landfall for these southern areas was as high as 292 km.

4) The shoreward migrations of sockeye starting north of 55° N were impeded by the currents. Sockeye starting south of 55° N were assisted in their shoreward migrations. These effects were as high as 50% of the swim speed of slow swimming sockeye and about 10% of the swim speed of fast swimming sockeye.

Our results confirm the viability of our hypothesis. The influence of the interannual variability of the Northeast Pacific currents on the model sockeye were consistent with the positive correlation between the ocean circulation and NDR reported by Hsieh et al. (1991).

The simulation results do not support Saila and Shappy's (1963) random drift hypothesis for sockeye migrating to the Fraser River from the Northeast Pacific. A single compass orientation appears to be an insufficient explanation for the sockeye migration. Our analysis of the simulated migration paths is consistent with stock-specific compass orientation and bicoordinate navigation.

We suggest that the influence of ocean currents must be accounted for in conceptual and predictive models of the NDR, and propose a two-part conceptual model that accounts for the influence of oceanographic variables in both the Northeast Pacific Ocean and coastal environment along the British Columbia coast. The influence of ocean currents in this model will likely enhance the predictive capabilities of Blackburn's (1987) temperature-displacement model and enhance the applicability of the coastal predictive formula of Xie and Hsieh (1989).

Our discussion is based on sockeye migration simulations for only two years. Further work is obviously required, specifically: 1) the simulation of the effects of currents over a greater range of years, 2) the development of an index of the surface circulation that may be used in predictive models, and 3) the examination of the effects of currents on sockeye using bicoordinate navigation. We have recently completed the simulations of compass-orientated sockeye for the period from

1946 to 1990, and have prepared stream function plots of the May–June mean circulation fields (e.g., Fig. 3). The analysis of these data is underway.

We support the hypothesis of Hsieh et al. (1991) that numerical ocean circulation models will benefit fisheries research (with hindcasts) and fisheries management (with predictions). At present, numerical models of the Northeast Pacific Ocean are inadequate for these purposes, particularly the latter. Until accurate numerical models are available for predicting the sea surface temperature and circulation fields, we may still make progress toward understanding the links between physical and fish variables with innovative analyses of historical data sets and empirical ocean models, such as OSCURS.

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