

# Computer Simulations of the Influence of Ocean Currents on Fraser River Sockeye Salmon (*Oncorhynchus nerka*) Return Times

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Thomson, K.A., W.J. Ingraham Jr., M.C. Healey, P.H. LeBlond, C. Groot, and C.G. Healey. 1994. Computer simulations of the influence of ocean currents on Fraser River sockeye salmon (*Oncorhynchus nerka*) return times. *Can. J. Fish. Aquat. Sci.* 51: 441–449.

We hypothesized that the interannual variability of the northeast Pacific Ocean circulation affects the return times of Fraser River sockeye salmon (*Oncorhynchus nerka*). Homeward migrations were simulated for 1982 (with a relatively weak Alaska Gyre circulation) and 1983 (with a relatively strong circulation) in the context of three sequential return migration phases: a nondirected oceanic phase, a directed oceanic phase, and a directed coastal phase. Passive drifters were simulated to examine the influence of ocean currents during the nondirected oceanic phase: model fish south of 48°N were advected closer to Vancouver Island in 1983 compared with 1982; those north of 48°N were advected closer to Vancouver Island in 1982 than in 1983. Fish were simulated during the directed oceanic phase using a variety of behaviour scenarios: model fish starting south of 50°N had earlier return times in 1983 than in 1982; those starting north of 50°N had return times in 1983 that were generally the same as or later than in 1982. We inferred that ocean currents would modulate the environmental influences on return times during the directed coastal migration phase, by deflecting sockeye salmon into different oceanographic domains along the British Columbia coast.

Nous avons posé que la variabilité interannuelle de la circulation dans le nord-est de l'océan Pacifique a un effet sur le moment du retour du saumon rouge (*Oncorhynchus nerka*) du Fraser. Nous avons simulé les migrations de retour pour 1982 (circulation relativement faible du courant giratoire de l'Alaska) et pour 1983 (circulation relativement forte) dans le contexte de trois phases séquentielles : une phase océanique non dirigée, une phase océanique dirigée et une phase côtière dirigée. Nous avons employé des dériveurs passifs pour examiner par simulation l'influence des courants pendant la phase océanique non dirigée : les poissons du modèle, au sud de 48°N, étaient amenés par advection plus près de l'île de Vancouver en 1983 qu'en 1982; au nord de 48°N, ils étaient amenés par advection plus près de l'île de Vancouver en 1982 qu'en 1983. Nous avons simulé le déplacement des poissons pendant la phase océanique dirigée en suivant divers scénarios de comportement : les poissons partant du sud de 50°N revenaient plus tôt en 1983 qu'en 1982; ceux qui partaient du nord de 50°N revenaient en général en 1983 au même moment ou plus tard qu'en 1982. Nous pensons que les courants océaniques pourraient moduler les influences environnementales sur la période de retour pendant la phase de migration côtière dirigée en orientant les saumons rouges vers différents domaines océanographiques le long de la côte de Colombie-Britannique.

Received October 14, 1992  
Accepted August 25, 1993  
(JB657)

Reçu le 14 octobre 1992  
Accepté le 25 août 1993

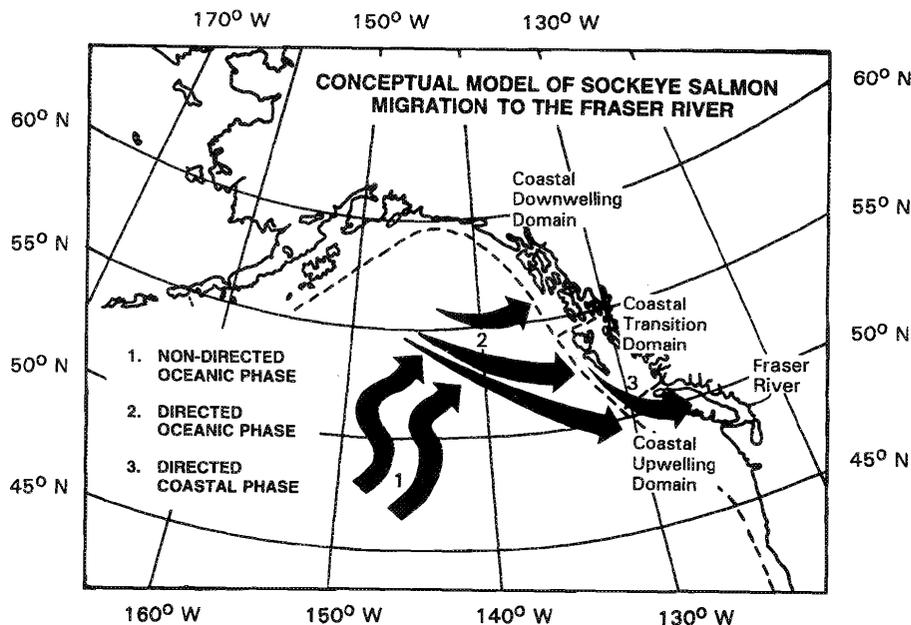


FIG. 1. Conceptual model of sockeye salmon time-sequenced return migration phases in the marine environment. Sockeye salmon swim speed, guidance mechanism, and response to environmental variables are thought to depend on the phase of return migration.

The Fraser River sockeye salmon (*Oncorhynchus nerka*) is one of British Columbia's most valuable fisheries resources, with an average annual catch (1983–86) of \$60 million to Canadian fishermen and \$17 million to U.S. fishermen. Reliable forecasts of the region of landfall, coastal migration route, and return times are very important to sockeye salmon fisheries management on the British Columbia coast (Healey 1993).

Sockeye salmon return migrations can be conceptualized as three time-sequenced phases: (1) a nondirected oceanic phase, (2) a directed oceanic phase, and (3) a directed coastal phase (Fig. 1). Few details are known about the ocean migration except that the directed phase is rapid, well directed, and well timed (Royce et al. 1968; French et al. 1976; Groot and Quinn 1987; Burgner 1991). Sockeye salmon coastal return migration route and return times seem to be related to atmospheric and oceanographic conditions in the winter, spring, and summer of the return year (Wickett 1977; Blackburn 1987; Xie and Hsieh 1989; Hsieh et al. 1991).

Blackburn (1987) proposed a temperature-displacement model to explain the interannual variation in stock-specific sockeye salmon return times. According to his model, anomalous warm winter and spring sea surface temperatures would displace sockeye salmon farther to the north than usual, requiring longer migrations to the Fraser River. Blackburn (1987) found significant positive correlations between sea surface temperatures in the central Gulf of Alaska and return times of seven Fraser River sockeye salmon stocks.

Mysak (1986) suggested that interannual variations in the surface circulation pattern of the northeast Pacific Ocean (Fig. 2) could affect the timing and location of return migrations. Hamilton and Mysak (1986) also speculated that in years when the Sitka eddy (57°N, 135°W) is present, pink (*Oncorhynchus gorbuscha*) and sockeye salmon returning to the Nass and Skeena rivers are deflected southward by the intense anticyclonic (i.e., clockwise) vortex. Hsieh et al.

(1991) found Chilko Lake sockeye salmon (a Fraser River stock) return times to be correlated with wind stress in the first marine year and sea surface temperature in the return year. However, no empirical relationship has been found between ocean surface currents in the return year and salmon run timing.

We used daily surface currents from an empirical model of the North Pacific Ocean to examine the potential influence of ocean currents. The return migrations of compass-orientated sockeye salmon were simulated for two years: 1982, with a relatively weak Alaska Gyre circulation, and 1983, with a relatively strong circulation. The influence of northeast Pacific Ocean currents on the latitude of landfall of salmon was reported in Thomson et al. (1992): the stronger circulation in 1983 deflected model fish as much as 550 km farther north than in 1982. In this paper, we examine the hypothesis that northeast Pacific Ocean surface currents affect Fraser River sockeye salmon return times.

### Sockeye Salmon Migration Simulations

We investigated the potential effects of northeast Pacific Ocean surface currents on sockeye salmon, during the non-directed and directed oceanic migration phases, by seeding the Ocean Surface CURrent Simulations model (OSCURS) with arrays of passive drifters (i.e., randomly moving fish) and active drifters (i.e., compass-orientated fish).

The applicability of OSCURS to the study of sockeye salmon migration is discussed in Thomson et al. (1992); we reiterate only those aspects of the model essential to understanding our discussion here. OSCURS is an empirical model developed to examine the variability of Lagrangian drift in the North Pacific Ocean and Bering Sea (Ebbesmeyer and Ingraham 1992). It computes surface currents as the vector sum of long-term mean geostrophic currents (Fig. 2) and daily surface wind drift (Ingraham and Miyahara 1988, 1989). Most sockeye salmon in the northeast Pacific Ocean

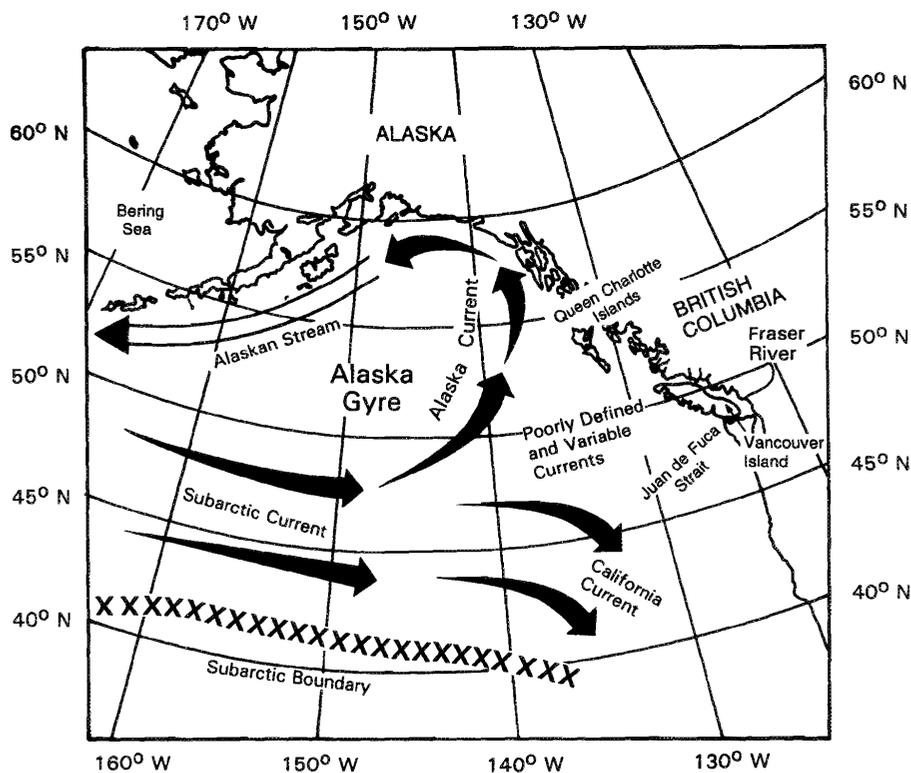


FIG. 2. Schematic of the long-term mean surface geostrophic circulation in the Gulf of Alaska (i.e., the prevailing surface currents), adapted from Dodimead et al. (1963) and Thomson (1981). Geostrophic currents are due to the slope of the sea surface, set up by the prevailing winds. These surface currents have magnitudes of about  $5\text{--}10\text{ km}\cdot\text{d}^{-1}$  in the Subarctic Current,  $30\text{ km}\cdot\text{d}^{-1}$  in the Alaska Current,  $20\text{ km}\cdot\text{d}^{-1}$  in the California Current, and over  $100\text{ km}\cdot\text{d}^{-1}$  in the Alaskan Stream. East of the Subarctic Current bifurcation, the ocean currents are poorly defined and variable. The southern limit of the Alaska Gyre is delineated by the Subarctic Boundary, a salinity front that has been frequently referred to as the southern limit of salmon distributions in the northeast Pacific Ocean.

are found in the upper 15 m of the water column (French et al. 1976; Burgner 1991). In this surface layer, the instantaneous wind-driven currents are stronger than the mean geostrophic flow, and tracks of surface drifters (i.e., drogued at 20 m depth) tend to follow time-averaged isobars of atmospheric pressure (Emery et al. 1985).

Our simulations focused on 1982 and 1983, years with representative weak and strong Alaska Gyre circulation patterns, respectively. For each simulation, 174 drifters were used (Fig. 3). Passive drifters were simulated to examine the potential influence of currents on randomly moving fish during the nondirected oceanic migration phase. For each year, the trajectories of passive drifters were simulated with start dates of 1 May, 1 June, and 1 July. Active drifters were simulated to examine the potential effects of currents on sockeye salmon during the directed oceanic migration phase. Compass-orientated fish were simulated with 27 behaviour scenarios using combinations of swim speed ( $18, 30,$  and  $48\text{ km}\cdot\text{d}^{-1}$ ), compass orientation ( $90^\circ\text{T}$  (east),  $112.5^\circ\text{T}$  (east-southeast), and  $135^\circ\text{T}$  (southeast)), and migration start date (1 May, 1 June, and 1 July). The rationale for choosing these behaviour scenarios and the array of migration start locations is described in Thomson et al. (1992).

The return date of arrival off Juan de Fuca Strait (Fig. 2) was calculated for each active drifter, using the simulated date and latitude of landfall (landfall was assumed to occur when a model fish reached the continental shelf) and a constant

migration rate along the coast. Sockeye salmon, during their homeward migration, take about 2 wk to travel along the coast from the Queen Charlotte Islands to Juan de Fuca Strait and 1 wk to travel the length of Vancouver Island (D. Blackburn and J. Woodey, personal communication). On the basis of this information, we used a coastal migration rate of  $38.7\text{ km}\cdot\text{d}^{-1}$ , which compares well with ultrasonic tag studies of sockeye salmon along the south coast of British Columbia (Quinn 1988).

Mean differences in return dates between 1983 and 1982 were calculated for simulated sockeye salmon originating from the six areas shown in Fig. 3. The 95% confidence limits of the population mean were used to determine whether or not the sample mean return time differed significantly between the two years.

### Migration Simulation Results

The simulated passive drifters moved to the northeast around the Alaska Gyre, for the most part. Figure 4 shows the difference in passive drifter trajectories between 1982 and 1983, as well as the meandering effects of wind-driven currents. The stronger currents in 1983, compared with 1982, would advect passive drifters farther around the Alaska Gyre. Simulated drifters started south of  $48^\circ\text{N}$  were advected closer to Vancouver Island in the first 2 mo of ocean drift in 1983, compared with 1982. However, simulated drifters

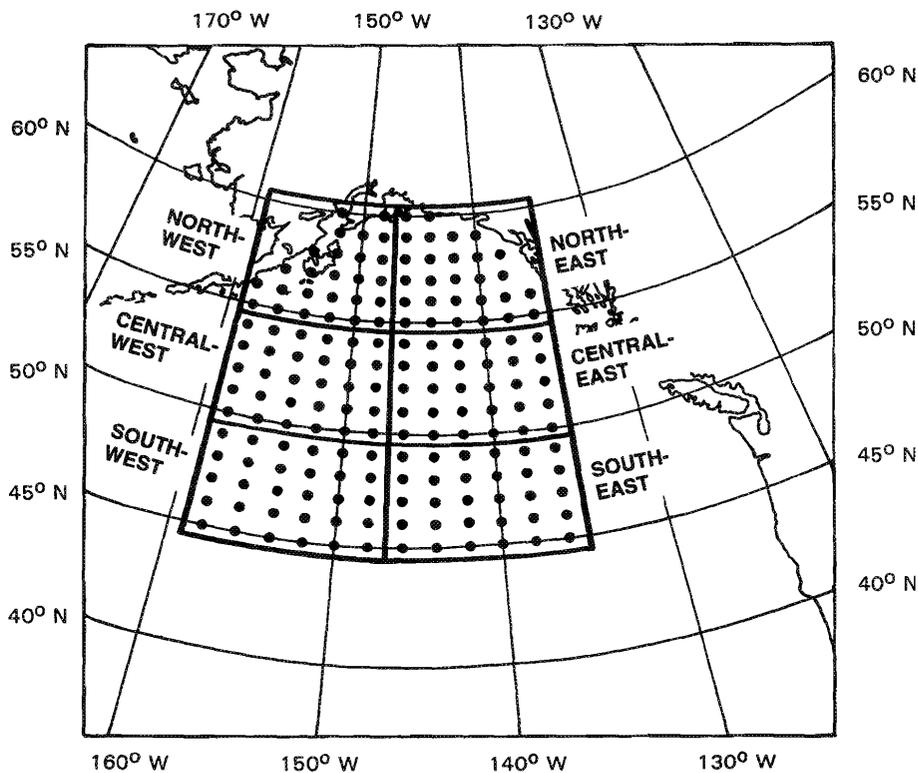


FIG. 3. Locations of the 174 migration start positions used in each simulation, and delineation of the six geographic areas referenced in Tables 1–4.

started north of 48°N were advected closer to Vancouver Island in 1982 than in 1983.

The trajectories of simulated active drifters (i.e., simulated compass-orientated sockeye salmon) made landfall earlier and farther north in 1983, compared with 1982. In Fig. 5, for example, the simulated sockeye salmon, started at 50°N, arrived on the coast about 2 wk earlier and about 400 km farther to the north in 1983 than in 1982. Although the model fish arrived at the coast earlier in 1983, a longer coastal swim to the Fraser River would be required than in 1982; a migration rate of about 35 km·d<sup>-1</sup> along the coast would result in no difference in return time to Juan de Fuca Strait between the two years.

The effect of ocean currents on simulated return times, during the directed oceanic phase, was strongly dependent on the geographic location from which model fish were started (Table 1). Simulated sockeye salmon originating from the southwest and southeast areas arrived off Juan de Fuca Strait nearly 1 wk earlier in 1983 compared with 1982, model fish from the central–east area arrived about 1 d earlier in 1983, and model fish from the northwest, northeast, and central–west areas arrived at about the same time in 1983 and 1982.

The influence of currents on simulated return times was also dependent on swim speed, compass orientation, and migration start date. The differences in mean return times between the two years decreased with increased swim speed (Table 2). With an 18 km·d<sup>-1</sup> swim speed, model fish from the southwest and southeast areas arrived about 1.5 wk earlier in 1983 compared with 1982; with a 48 km·d<sup>-1</sup> swim speed, these simulated sockeye salmon arrived about 2 d earlier in 1983.

Compass orientation affected the mean return time differences between 1983 and 1982 (Table 3); however, there

was no discernable relationship between orientation and return time differences. Simulated sockeye salmon with an eastward orientation, starting from the southwest and southeast areas, arrived almost 1 wk earlier in 1983 (compared with 1982), and model fish from the central–west area arrived a day or so later in 1983. Simulated sockeye salmon with an east–southeastward orientation, starting from the central–west and central–east areas, arrived a few days earlier in 1983 than in 1982, and model fish from the southeast area arrived almost 1 wk earlier in 1983. Model fish with a southeastward orientation did not differ in return time.

Migration start date affected return time differences between the two years (Table 4); however, there was no discernable relationship between migration start date and return time differences. For a migration start date of 1 May, simulated sockeye salmon arrived at Juan de Fuca Strait about 1.5 wk earlier in 1983 when starting from the southwest area, a day or so earlier when starting from the northeast area, and several days later when starting from the northwest area. For a 1 June migration start, model fish arrived about 1.5 wk earlier in 1983 when starting from the southeast area, about 0.5 wk earlier when starting from the southwest area, and about 2 d earlier when starting from the central–east area. From the areas to the north and west, the model fish starting 1 June arrived several days later in 1983 than in 1982. Simulated sockeye salmon from all areas with the exception of the central–east, starting their migration on 1 July, arrived up to several days earlier in 1983.

## Discussion

The simulation results illustrate that the interannual variability of northeast Pacific Ocean surface currents would

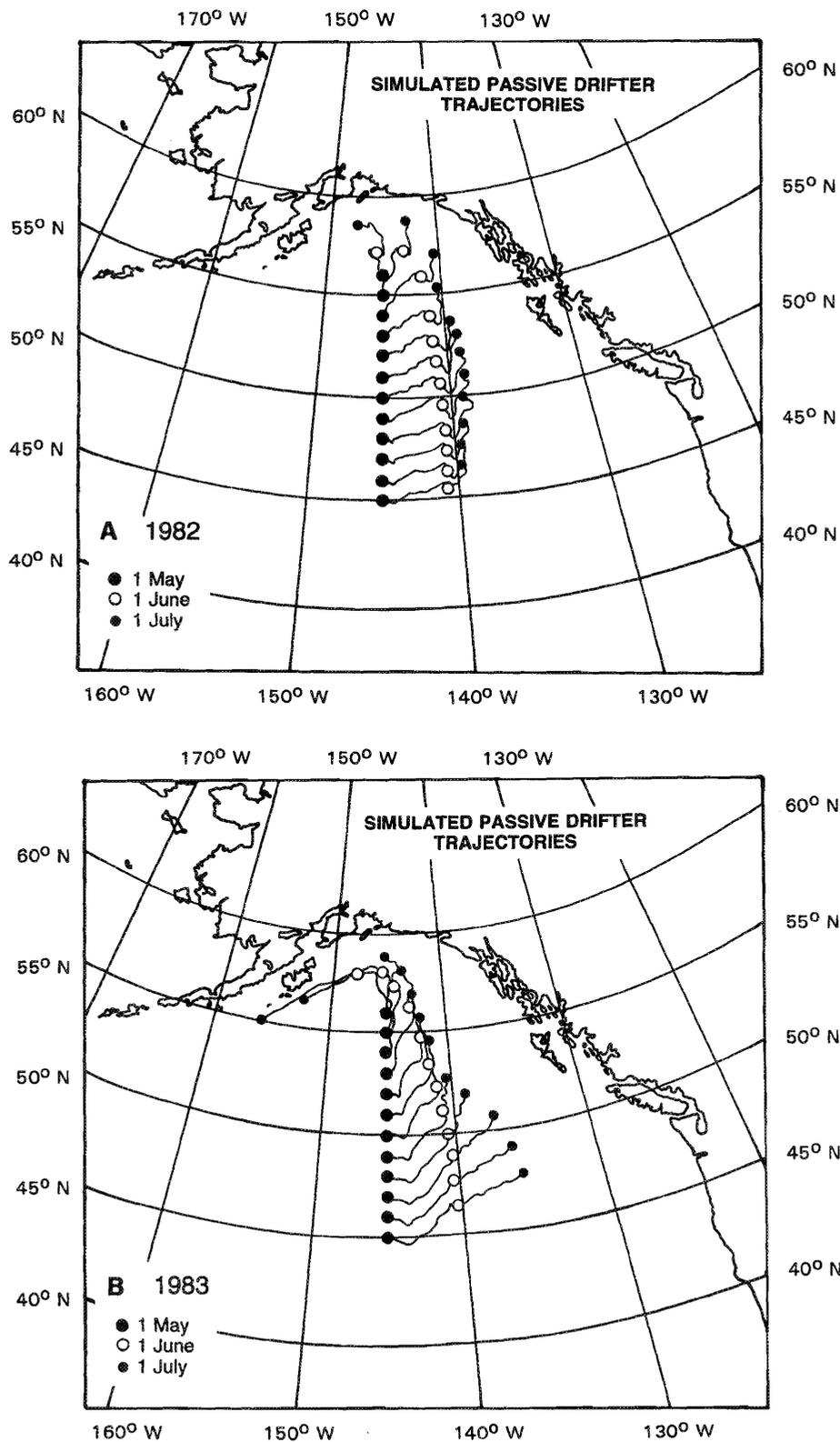


FIG. 4. OSCURS-simulated surface current trajectories from 1 May to 1 July for (A) 1982 and (B) 1983.

affect the return times of Fraser River sockeye salmon by up to 1.5 wk (i.e., three times the standard deviations of estimated annual peak return dates of seven Fraser River stocks (Blackbourn 1987)). To provide a perspective on the importance of these differences, we note that a few days' difference in the return time of any Fraser River sockeye salmon stock

is sufficient to impact the fisheries management plan and the commercial sockeye salmon fisheries along the British Columbia coast (D. Blackbourn, personal communication).

Unfortunately, we cannot compare run timing differences between our 1982 and 1983 simulations with differences between actual 1982 and 1983 timing data because there

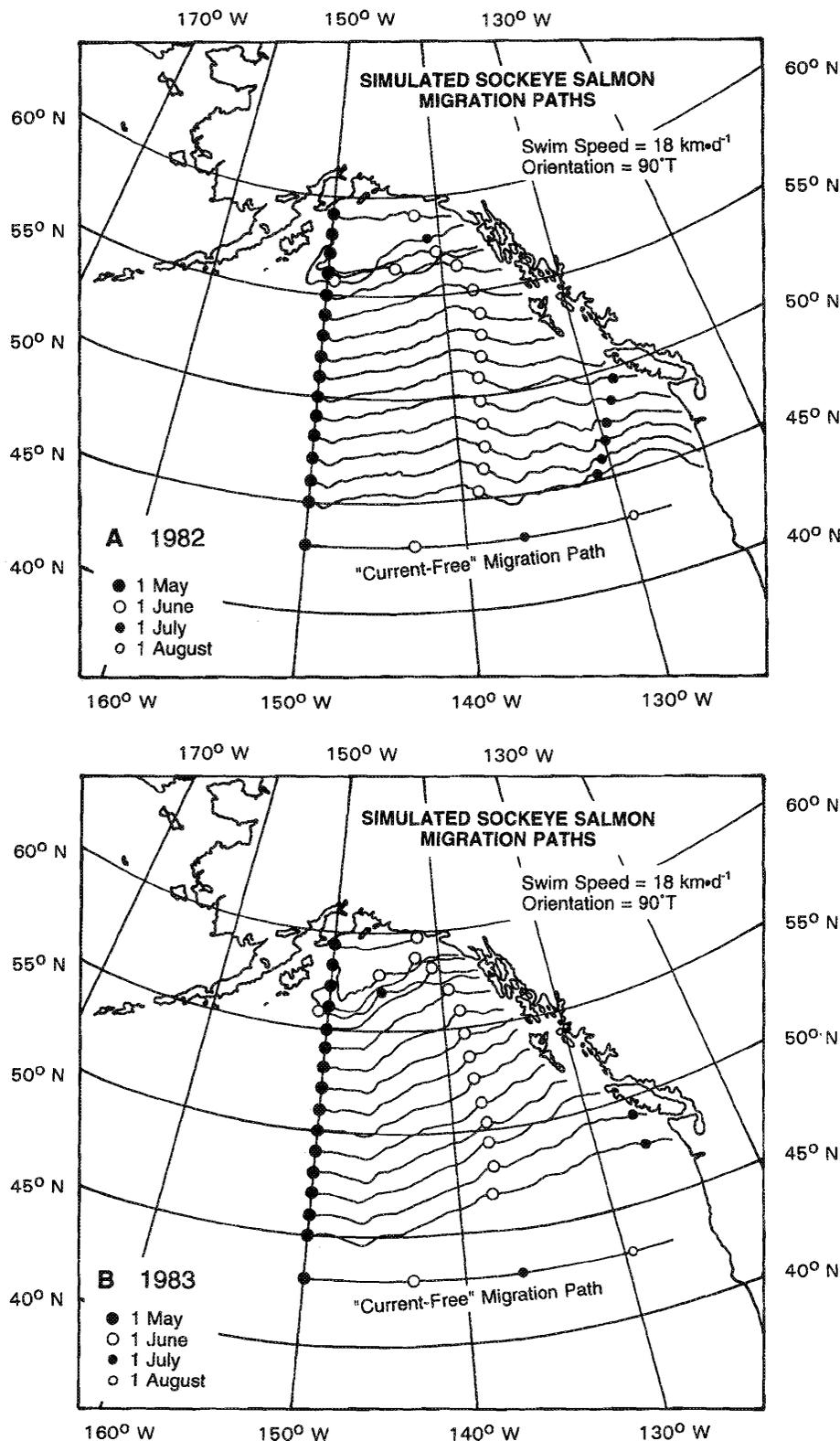


FIG. 5. Simulated sockeye salmon migration paths for (A) 1982 and (B) 1983, with a swim speed of  $18 \text{ km}\cdot\text{d}^{-1}$ , a compass orientation of  $90^\circ\text{T}$ , and a migration start date of 1 May. Departures from "current-free" migration paths (a sample is shown) and meanders are due solely to the time- and space-varying surface currents.

are no run timing data available for 1983 due to the high Northern Diversion Rate (defined as the percentage of sockeye salmon returning to the Fraser River around the north end of Vancouver Island rather than around the south end of the

island through Juan de Fuca Strait). Regardless, the simulation results permit an examination of the kinematics of ocean circulation effects on sockeye salmon return times in the context of the three return migration phases (Fig. 1). During

TABLE 1. Mean difference in return date between 1983 and 1982 (in days), using all 27 behaviour scenarios. Statistics are provided for each geographic area shown in Fig. 3. Mean differences in bold type are significantly different from zero. The bracketed values are the 95% confidence interval of the mean; *n* is sample size. Simulated sockeye salmon that made landfall south of 45°N are not included. A negative (positive) mean indicates that the return dates in 1983 were earlier (later) than in 1982.

Northwest:	0.4 (-0.4, 1.2) <i>n</i> = 471	Northeast:	-0.2 (-0.6, 0.2) <i>n</i> = 711
Central-west:	0.1 (-0.6, 0.8) <i>n</i> = 423	Central-east:	<b>-0.6</b> (-1.1, 0.1) <i>n</i> = 541
Southwest:	<b>-6.1</b> (-7.1, -5.1) <i>n</i> = 196	Southeast:	<b>-5.3</b> (-6.2, -4.4) <i>n</i> = 199
Total area:	<b>-1.0</b> (-1.3, -0.7), <i>n</i> = 2541		

the nondirected oceanic phase, randomly moving fish would be advected by surface currents within the Alaska Gyre (Fig. 2). The Subarctic Current would advect sockeye salmon to the east, the Alaska Current would advect sockeye salmon to the northeast and around the top of the Alaska Gyre, and the Alaskan Stream would advect sockeye salmon towards the southwest. Our simulations show that randomly moving fish would be advected closer to (or farther away from) the Fraser River, depending on their location within the gyre and the interannual variability of the currents; this would affect sockeye salmon return times by requiring shorter (or longer) travel distances in the directed oceanic and coastal migration phases.

The effects of ocean currents on simulated compass-orientated sockeye salmon, during the directed oceanic phase, were dependent on swim speed, compass orientation, migration start date, and, most importantly, premigration position. The Subarctic Current would assist sockeye salmon in their homeward migration dependent on the magnitude of the current in the surface layer: the stronger Alaska Gyre circulation in 1983, compared with 1982, resulted in earlier return times for model fish starting the directed oceanic migration phase within the Subarctic Current. Simulated sockeye salmon starting the directed return migrations in the Alaska Current or Alaskan Stream had return times in 1983 that were the same as or later than return times in 1982 due to (1) large northward deflections in the Alaska Current requiring longer migrations to the Fraser River within the coastal environment (Thomson et al. 1992) or (2) increased westward transport in the Alaskan Stream which impeded the eastward migration.

Our simulations imply that ocean currents would modulate the influence of the coastal environment on sockeye salmon run timing by deflecting fish into different marine environments along the British Columbia coast (e.g., see Fig. 1: Coastal Downwelling Domain, Coastal Transition Domain, and Coastal Upwelling Domain (Ware and MacFarlane 1989)). Sockeye salmon migrating through the Alaska Current would be deflected to the northeast with magnitudes depending on the year-to-year strength of the surface currents: the stronger Alaska Gyre circulation of 1983, compared with 1982, placed our model fish on the coast farther to the north (Thomson et al. 1992), thereby requiring longer migrations

TABLE 2. Mean difference in return date between 1983 and 1982 (in days) for three simulated swim speeds, using all orientations and migration start dates. Statistics are provided for each geographic area shown in Fig. 3. Mean differences in bold type are significantly different from zero. The bracketed values are the 95% confidence interval of the mean; *n* is sample size. Simulated sockeye salmon that made landfall south of 45°N are not included. A negative (positive) mean indicates that the return dates in 1983 were earlier (later) than in 1982.

<i>Swim speed = 18 km·d<sup>-1</sup></i>			
Northwest:	1.2 (-1.0, 3.3) <i>n</i> = 150	Northeast:	-0.5 (-1.6, 0.5) <i>n</i> = 242
Central-west:	-0.5 (-2.2, 1.2) <i>n</i> = 150	Central-east:	<b>-1.6</b> (-3.0, -0.2) <i>n</i> = 177
Southwest:	<b>-10.6</b> (-12.8, -8.4) <i>n</i> = 61	Southeast:	<b>-10.1</b> (-12.1, -8.1) <i>n</i> = 57
Total area:	<b>-1.8</b> (-2.5, -1.1), <i>n</i> = 837		
<i>Swim speed = 30 km·d<sup>-1</sup></i>			
Northwest:	0.5 (-0.6, 1.5) <i>n</i> = 161	Northeast:	0.0 (-0.6, 0.6) <i>n</i> = 234
Central-west:	0.3 (-0.8, 1.3) <i>n</i> = 135	Central-east:	-0.3 (-1.0, 0.4) <i>n</i> = 186
Southwest:	<b>-6.4</b> (-7.8, -5.1) <i>n</i> = 63	Southeast:	<b>-4.6</b> (-5.9, -3.3) <i>n</i> = 68
Total area:	<b>-0.8</b> (-1.2, -0.4), <i>n</i> = 847		
<i>Swim speed = 48 km·d<sup>-1</sup></i>			
Northwest:	-0.4 (-0.9, 0.1) <i>n</i> = 160	Northeast:	-0.1 (-0.4, 0.2) <i>n</i> = 235
Central-west:	<b>0.5</b> (0.1, 1.0) <i>n</i> = 138	Central-east:	0.1 (-0.4, 0.6) <i>n</i> = 178
Southwest:	<b>-1.9</b> (-2.6, -1.4) <i>n</i> = 72	Southeast:	<b>-2.2</b> (-3.2, -1.4) <i>n</i> = 74
Total area:	<b>-0.4</b> (-0.6, -0.2), <i>n</i> = 857		

to the Fraser River within the complex coastal environment (Thomson et al. 1989; Crawford and Thomson 1991; Jardine et al. 1993).

Our examination of the effects of ocean currents assumed that sockeye salmon are found in the same locations, each year, at the beginning of the directed and nondirected oceanic migration phases. This is probably not the case: sockeye salmon may have stock-specific distributions in the northeast Pacific Ocean, and sockeye salmon distributions may be displaced to the north (south) by anomalous warm (cold) sea surface temperatures (Blackbourn 1987). However, the run timing effects of spring/summer ocean currents on stock-specific sockeye salmon distributions, affected by winter/spring sea surface temperatures, can be inferred. The influ-

TABLE 3. Mean difference in return date between 1983 and 1982 (in days) for three simulated orientations, using all swim speeds and migration start dates. Statistics are provided for each geographic area shown in Fig. 3. Mean differences in bold type are significantly different from zero. The bracketed values are the 95% confidence interval of the mean; *n* is sample size. Simulated sockeye salmon that made landfall south of 45°N are not included. A negative (positive) mean indicates that the return dates in 1983 were earlier (later) than in 1982.

<i>Compass orientation = 90°T (eastward)</i>			
Northwest:	0.4 (-0.8, 1.6) <i>n</i> = 232	Northeast:	0.0 (-0.3, 0.3) <i>n</i> = 252
Central-west:	<b>1.2</b> (0.6, 1.9) <i>n</i> = 270	Central-east:	0.5 (-0.1, 1.0) <i>n</i> = 270
Southwest:	<b>-6.1</b> (-7.1, -5.1) <i>n</i> = 195	Southeast:	<b>-5.3</b> (-6.3, -4.4) <i>n</i> = 182
Total area:	<b>-1.2</b> (-1.5, -0.8), <i>n</i> = 1401		
<i>Compass orientation = 112.5°T (east-southeastward)</i>			
Northwest:	0.5 (-0.5, 1.5) <i>n</i> = 223	Northeast:	0.0 (-0.4, 0.4) <i>n</i> = 252
Central-west:	<b>-1.9</b> (-3.5, -0.4) <i>n</i> = 153	Central-east:	<b>-2.1</b> (-3.0, -1.1) <i>n</i> = 242
Southwest:	<i>n</i> = 0	Southeast:	<b>-5.3</b> (-8.3, -2.3) <i>n</i> = 17
Total area:	<b>-0.9</b> (-1.3, -0.4), <i>n</i> = 887		
<i>Compass orientation = 135°T (southeastward)</i>			
Northwest:	-0.8 (-9.7, 8.1) <i>n</i> = 16	Northeast:	-0.7 (-2.0, 0.5) <i>n</i> = 207
Central-west:	<i>n</i> = 0	Central-east:	1.7 (-2.7, 6.2) <i>n</i> = 29
Southwest:	<i>n</i> = 0	Southeast:	<i>n</i> = 0
Total area:	-0.5 (-1.7, 0.8), <i>n</i> = 252		

ence of ocean temperatures is consistent over the northeast Pacific Ocean (relatively warm temperatures would force relatively late return times) whereas the influence of ocean currents is due primarily to the Subarctic Current, and a relatively strong Alaska Gyre circulation would force relatively early return times for sockeye salmon stocks in the vicinity of the Subarctic Current (Fig. 2). For stocks in the northern portion of the Alaska Gyre (e.g., Adams River stocks; Blackburn 1987), the effects of currents on run timing would be minimal. For stocks in the vicinity of the northern boundary of the Subarctic Current (e.g., Horsefly River and Chilko River stocks; Blackburn 1987), the effects of ocean currents on run timing would augment the effects of ocean temperatures: warm temperatures would displace sockeye salmon northward away from the eastward drift of

TABLE 4. Mean difference in return date between 1983 and 1982 (in days) for three simulated migration start dates, using all swim speeds and orientations. Statistics are provided for each geographic area shown in Fig. 3. Mean differences in bold type are significantly different from zero. The bracketed values are the 95% confidence interval of the mean; *n* is sample size. Simulated sockeye salmon that made landfall south of 45°N are not included. A negative (positive) mean indicates that the return dates in 1983 were earlier (later) than in 1982.

<i>Migration start date: 1 May</i>			
Northwest:	<b>3.2</b> (1.6, 4.9) <i>n</i> = 153	Northeast:	<b>-1.3</b> (-1.9, -0.8) <i>n</i> = 239
Central-west:	0.0 (-1.5, 1.5) <i>n</i> = 142	Central-east:	-0.3 (-1.3, 0.6) <i>n</i> = 178
Southwest:	<b>-10.2</b> (-12.2, -8.1) <i>n</i> = 68	Southeast:	-1.3 (-3.0, 0.4) <i>n</i> = 60
Total area:	<b>-0.8</b> (-1.3, -0.2), <i>n</i> = 840		
<i>Migration start date: 1 June</i>			
Northwest:	<b>1.6</b> (0.3, 2.8) <i>n</i> = 160	Northeast:	<b>1.7</b> (1.1, 2.3) <i>n</i> = 240
Central-west:	<b>3.0</b> (2.3, 3.7) <i>n</i> = 161	Central-east:	<b>-1.9</b> (-3.1, -0.8) <i>n</i> = 182
Southwest:	<b>-4.2</b> (-5.3, -3.0) <i>n</i> = 82	Southeast:	<b>-10.8</b> (-11.9, -9.6) <i>n</i> = 73
Total area:	-0.4 (-0.9, 0.1), <i>n</i> = 898		
<i>Migration start date: 1 July</i>			
Northwest:	<b>-3.5</b> (-4.5, -2.5) <i>n</i> = 158	Northeast:	<b>-1.0</b> (-1.9, -0.1) <i>n</i> = 232
Central-west:	<b>-3.8</b> (-5.0, -2.6) <i>n</i> = 120	Central-east:	0.5 (-0.1, 1.1) <i>n</i> = 181
Southwest:	<b>-3.5</b> (-4.6, -2.5) <i>n</i> = 46	Southeast:	<b>-2.9</b> (-3.6, -2.4) <i>n</i> = 66
Total area:	<b>-1.9</b> (-2.3, -1.5), <i>n</i> = 803		

the Subarctic Current and cold temperatures would displace fish southward into the eastward flow.

The effects of ocean currents on stocks within the Subarctic Current (e.g., Early Stuart Lake stocks; Blackburn 1987) would depend on whether cold (warm) winter/spring temperatures lead strong (weak) spring/summer currents. If a strong (weak) Alaska Gyre circulation follows warm (cold) ocean temperatures, then the effects of currents on return times would tend to offset the effects of surface temperatures; however, if a weak (strong) Alaska Gyre circulation follows warm (cold) temperatures, the eastward drift of the Subarctic Current would reinforce the effects of ocean temperatures on run timing.

Would sockeye salmon using bicoordinate navigation, rather than compass orientation as we have modelled, be affected by ocean currents? Consider an aircraft attempting to navigate to an airport without a forecast of winds perpendicular to the intended route: the aircraft would reach its goal, but it would be deflected from the intended flight path regardless of navigational precision, requiring a longer period of time to reach its goal or more fuel to travel faster. Navigating sockeye salmon would be similarly affected by ocean currents; they would be deflected from their intended migration route and arrive later or require more energy to reach their goal at the intended time. To migrate along a "straight" line in the presence of ocean currents, sockeye salmon would require a positive rheotactic response (i.e., orientation into oncoming currents) in addition to compass orientation or bicoordinate navigation; we expect that ocean currents would still affect salmon return times or bioenergetics. The direction-finding mechanism used by sockeye salmon during the return migrations is unknown (Healey and Groot 1987; Quinn 1990). We suggest that interannual variations in northeast Pacific Ocean currents would affect sockeye salmon return times, regardless of the direction-finding mechanism used.

The results from our simulations are consistent with the hypothesis that ocean currents affect the return times of homeward migrating sockeye salmon. Since we examined only two years with insufficient run timing data available for verification, this must be considered a conceptual model. Incorporation of stock-specific effects of ocean currents on return times into fisheries forecasts may provide more reliable empirical relations for the management of Fraser River sockeye salmon stocks. An examination of ocean current and run timing data over many more years (i.e., 1950 to present) is required.

## Acknowledgements

This work was supported by grants to P.H. LeBlond and M.C. Healey from the Natural Sciences and Engineering Research Council of Canada and to P.H. LeBlond from the Canadian Department of Fisheries and Oceans subvention program. Partial support for K.A. Thomson's salary was provided by the Ocean Production Enhancement Network (OPEN), one of Canada's Networks of Centres of Excellence. W.J. Ingraham is indebted to T. Laevastu for his guidance in the development of the OSCURS model. C.G. Healey gratefully acknowledges support from a Natural Sciences and Engineering Research Council of Canada graduate scholarship and the Media and Graphics Interdisciplinary Centre, Department of Computer Science, University of British Columbia. Barbara Rokeby drafted several figures. The authors gratefully acknowledge fruitful discussions with D.J. Blackburn and J. Woodey and constructive, detailed reviews from G. Rose and an anonymous reviewer.

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