

# Numerical Simulations of Fraser River Sockeye Salmon Homing Migration Routes in a Dynamic Marine Environment

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Kolody, D., M. Healey. 1998. Numerical simulations of Fraser River sockeye salmon homing migration routes in a dynamic marine environment. N. Pac. Anadr. Fish Comm. Bull. No. 1: 118-128

A spatially-explicit individual-based model was used to simulate adult sockeye salmon return migration routes from the Gulf of Alaska to the Fraser River through temporally variable, spatially-explicit environmental fields. We wanted to examine whether coastal migration route variability could be explained by the interactions between simple behavior rules and a dynamic ocean environment described by historical temperature observations and estimated surface currents. Assuming that sockeye were broadly distributed throughout the central Gulf of Alaska prior to homeward migration, and that during homeward migration they oriented on a fixed compass bearing, the following mechanisms were invoked to produce migration route variations among years: 1) the distribution prior to homing was constrained by thermal limits, 2) sockeye were advected by surface currents during open ocean migration, and 3) sockeye tended to avoid high water temperatures. The behavioural component of the model was numerically optimized to maximize the fit between simulated and observed coastal migration routes, while maintaining swimming speeds and migratory timing consistent with the literature. The optimized model suggested that southern thermal limits and current advection could not explain much of the observed coastal migration route variability. The tendency to avoid high temperatures explained about 33% of the variation and suggested that coastal processes may be more important than offshore.



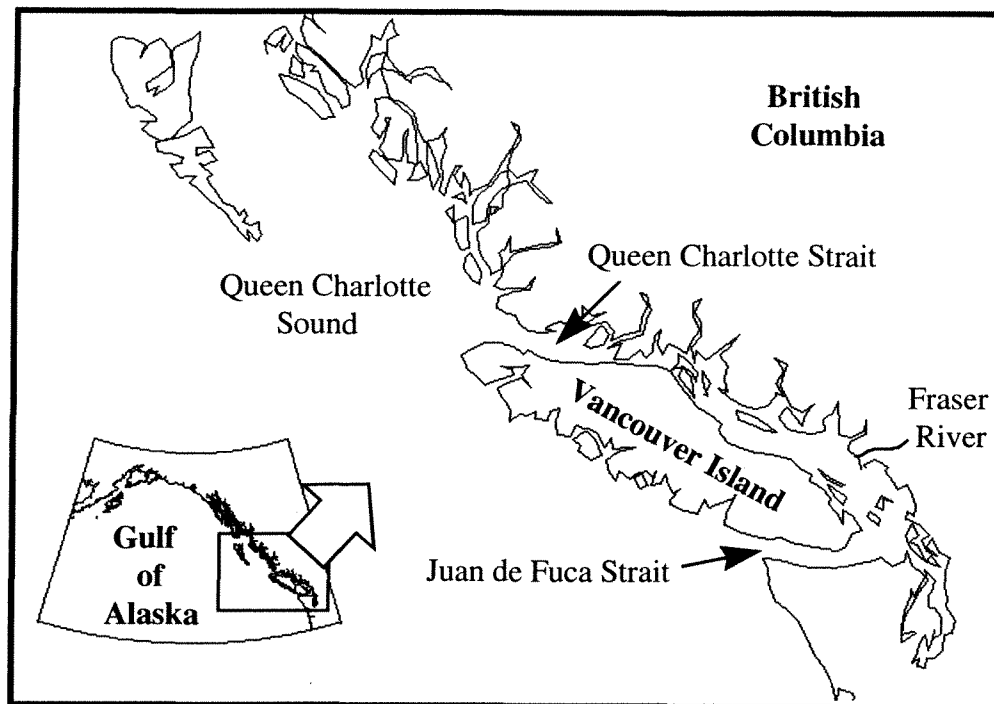
## INTRODUCTION

Adult sockeye salmon (*Oncorhynchus nerka*) can return from the Gulf of Alaska to the Fraser River by migrating around either the north or south end of Vancouver Island (Fig. 1). The proportion of fish using the northern route (northern diversion rate) varies considerably among years, and it is not known what factors cause this variation. This variability is of theoretical interest to behavioural ecologists studying the mechanisms of salmon migration, but also has practical implications for fisheries managers attempting to meet complex harvest allocation and escapement objectives.

A number of studies have looked for an association between diversion rate variability and oceanographic variability. The most common oceanographic factors explored have included: 1) sea surface temperatures (SST) offshore or in coastal waters near the north end of Vancouver Island (Groot and Quinn 1987, Hamilton 1985, Hsieh et al. 1991, Royal and Tully 1961, Tully et al. 1960, Xie and Hsieh 1989), 2) coastal salinity patterns and the

volume of Fraser River discharge (Favorite 1961, Groot and Quinn 1987, Hamilton 1985, Xie and Hsieh 1989), or 3) currents (Groot and Quinn 1987, Hsieh et al. 1991, Thomson et al. 1992). These studies have generally involved either regressing the northern diversion rate time series onto various environmental indices, or describing contrast in oceanographic conditions associated with specific high and low diversion years. None of these published relationships has been shown to be consistent for the entire duration of the historical record. The proposed biological and oceanographic interactions were often either poorly defined, or the physical data were indexed at points in time and space where the proposed interaction could not have been direct. Continued use of this approach is not likely to substantially improve our understanding of the underlying mechanisms, because there is a high probability of describing spurious relationships (e.g. Walters and Collie 1989), and the appropriate scale of interaction cannot be defined when temporally and spatially variable environmental factors are condensed into a single annual index.

Fig. 1 Map of the coastal approaches to the Fraser River showing important locations referred to in the text.



As an alternative investigative approach, we used a process-based model to explore explicit, testable hypotheses about the effects of oceanic conditions on Fraser sockeye coastal migration routes on temporal and spatial scales relevant to the decision processes of individuals. Specifically, we chose to explore how sockeye migration routes could be affected by 1) the initial distribution in the NE Pacific Ocean, 2) advection by open ocean surface currents, and 3) SST preference behaviours. Marine distributions and migration routes of sockeye salmon are not well known, but there is empirical evidence suggesting that temperatures and currents may affect the sockeye distribution prior to and during the homing migration. Mark and recapture studies have suggested that during the year prior to homing, Fraser sockeye are located throughout the Gulf of Alaska (French et al. 1976). Welch et al. (1995) observed that the southern limit of the offshore sockeye distribution is associated with SST. It is not known what effect SST has during the marine phase of the homing migration, but high river temperatures can delay salmon migration into and within rivers (e.g. Major and Mighell 1966, Alabaster 1990). Presumably, avoidance of high temperature could also result in deflected trajectories of sockeye in marine areas. Similarly, Thomson et al. (1992) have shown that ocean currents in the Gulf of Alaska are strong enough and variable enough to have a substantial effect on the latitude at which homing

sockeye reach the coast. The two years which they examined, 1982 and 1983, corresponded to low and high diversion years, respectively. A small sample of Fraser River sockeye tagged on the north coast of British Columbia during these years also suggested that the Fraser sockeye were less abundant in northern coastal waters in 1982 relative to 1983 (Groot and Quinn 1987). We used a spatially-explicit, individual-based model to explore the potential effects of these three factors on coastal migration routes. Numerical optimization of behavioural parameters was used to maximize the fit between modelled and observed diversion rate time series, subject to external constraints which were imposed to maintain consistency with other biological observations. The potential importance of individual and combined mechanisms is examined.

## METHODS

### *Northern Diversion Rate Time Series*

The Fraser River sockeye salmon northern diversion rate is estimated annually from commercial fisheries catch data and in-river escapement monitoring, but the estimation methodology has never been published (Jim Woodey, Pacific Salmon Commission, 600 - 1155 Robson St., Vancouver, B.C., Canada, pers. comm.). There has not been any formal attempt to quantify diversion rate

variability within years or among stocks. However, there is no pattern in the time series to suggest that diversion variability is related to the 4 year cycles of abundance characteristic of Fraser sockeye. While there is an unknown amount of estimation error in the time series, it is certain that the extreme high and low events, that we are most interested in, are not the result of estimation errors.

#### *Numerical Representation of the Physical Oceanography of the NE Pacific Ocean*

The model domain covered the NE Pacific Ocean from 44-61°N and 123-160°W and incorporated temporal and spatial variability of observed SST and estimated surface currents in the open ocean region. The land mask was approximated on a 0.18 × 0.18 degree grid corresponding to the SST grid resolution, and the coastal region was defined as all areas within approximately 50 km of the land mask.

Gulf of Alaska SST was described by weekly Advanced Very High Resolution Radiometry (AVHRR) images (1982-94), obtained from the Physical Oceanography Distributed Active Archive Center at Jet Propulsion Laboratory/California Institute of Technology. Calibration and image processing details are provided at the web site [http://podaac.jpl.nasa.gov:2031/DATASET\\_DOCS/avhrr\\_wkly\\_mcsst.html#17](http://podaac.jpl.nasa.gov:2031/DATASET_DOCS/avhrr_wkly_mcsst.html#17) (3 Oct 1997). Images were archived on an equal-angle grid with spatial resolution of approximately 0.18 × 0.18 degrees (19.5 × 19.5 km on the equator). Each weekly (approximately) image was a composite of numerous images produced during a week, and often considerable spatial interpolation was required to estimate temperatures beneath cloud cover. In our model, linear interpolation was used to estimate SST between the available image dates.

Surface currents within the model were approximated by hindcast output from the Ocean Surface Current Simulations (OSCURS) model described by Ingraham and Miyahara (1988, 1989). OSCURS currents are calculated as the vector sum of long term mean baroclinic geostrophic flow and daily wind driven surface flow. Sea level pressure fields are used to generate the wind driven current estimates over a rectangular grid of approximately 90 km resolution across the north Pacific Ocean. To reduce data storage requirements for our individual-based model, daily hindcast current observations (1982-94) were converted to monthly averages and interpolated onto a 1 degree grid. During simulations, bilinear spatial interpolation and linear temporal interpolation were used to estimate currents at specific points in time and space. Currents were reduced to 0 in coastal areas, because OSCURS does

not account for coastal geometry or tidal effects. There is at present no satisfactory means of hindcasting British Columbia coastal currents for the period of interest.

#### *Numerical Representation of Sockeye Salmon Homing Migration Behaviour*

Sockeye salmon homing migrations were simulated from the central Gulf of Alaska to the coastal approaches of the Fraser River. Fish that arrived at Queen Charlotte Strait or Juan de Fuca Strait were removed from the model and committed to either the northern or southern migration routes respectively. Fish which wandered out of the model domain or failed to reach Queen Charlotte Strait or Juan de Fuca Strait by the end of the simulation were not included in annual diversion rate calculations, but were recorded for homing success rate calculations. A complete run of the model involved simulating homing trajectories for years 1982-94 and calculating time series of annual diversion rates and homing success rates.

The model required a large number of parameters to describe behavioural interactions with the ocean environment and ensure reasonably successful homing rates (Table 1). These parameters contributed to one of the following roles: 1) establishing the initial sockeye distribution, 2) defining general orientation behaviour, 3) helping to avoid trapping in complex coastal geometry, or 4) describing interactions between sockeye and local SST.

The initial Fraser River sockeye distribution in the NE Pacific Ocean was described by the latitude, longitude and spread of the distribution. We assumed that the distribution was of uniform density and circular, roughly covering the central Gulf of Alaska as indicated by the French et al. (1976) summary of tagging studies. During the optimization procedure, the parameters describing the location and spread of the initial distribution were not constrained. However, one model scenario involved using seasonally-varying thermal limits to constrain the initial distribution. We assumed a simplified version of the seasonal thermal limits defined by Welch et al. (in press). Prior to Day-Of-Year (DOY) 170, the limit was 8°C, between DOY 170 - 190, the limit increased linearly to 12°C, and between DOY 190 and 250, the limit remained at 12°C. In the thermal limit scenario, fish were established according to the location and spread parameters, but as each simulation year was initialized, fish located in regions with SST exceeding the thermal limit were eliminated. The initial temperatures and thermal limits were averaged over the preceding 21 days under the assumption that fish take some time to

**Table 1. Range of valid parameter values in the spatially-explicit individual-based migration model.**

Parameter	min.	max.
latitude of initial distribution centre	48	55° N
longitude of initial distribution centre	140	150° W
radius of distribution	0	1000 km
initiation date for homing migration	150	190 DOY
swimming speed	20	60 km/d
open ocean compass bearing	0	360°
coastal compass bearing	0	360°
(inertial/compass) open ocean directional weighting	0	100
(inertial/compass) coastal directional weighting	0	100
open ocean directional precision	0	1
coastal directional precision	0	1
probability of reorienting to the compass (per timestep)	0	1
SST difference detection threshold	0	5°C
SST preference random factor	0	10°C
thermal limit adjustment factor	-4	4°C

react to changing temperatures and redistribute themselves.

During a simulated homeward migration, all sockeye used the same fixed compass bearing (which differed between open ocean and coastal regions) as the primary direction finding mechanism. Swim speeds were confined to limits suggested by tagging studies (French et al. 1976, Quinn 1988) and migration initiation dates were determined by the requirement for sockeye to return to the Fraser River during the interval DOY 170-250 (Killick and Clemens 1963).

A number of parameters were invoked largely to help fish migrate through complex coastal geometry that would trap individuals if they migrated on a compass bearing with perfect accuracy. These included: 1) a probability of reorienting to the compass bearing during a given time step, 2) an inertial directional component, which describes the tendency to keep migrating in the same direction, and 3) a coefficient of directedness, describing directional precision. These parameters provided a stochastic element to the orientation similar to those invoked by Pascual and Quinn (1991).

The interactions between fish and local SST consisted of a simple decision; whether or not to enter an adjacent SST box (0.18 × 0.18 degree AVHRR SST grid unit). On any given timestep, the fish had an initial migration direction. If the fish reached the border with an adjacent SST box, it either entered the box and continued swimming in the same direction, or it rebounded off the adjacent box like an elastic particle (if the fish struck land it always rebounded). The decision to enter or rebound was based on the relative difference in preference values between adjacent boxes. If the fish was moving from a lower preference value to a higher preference value it would always proceed, however,

if it was moving from higher to lower preference, the fish may have rebounded, depending on whether the magnitude of the difference exceeded a minimum detection threshold plus a stochastic decision element. All temperatures below the seasonally-varying thermal limit threshold were considered to be of equally high baseline preference value. Preference values for temperatures exceeding the thermal limit were lower than the baseline value by a factor proportional to the squared difference between the local SST and the thermal limit. The direct biological interpretation of this decision process was: fish detected physical conditions where they were at any given time, and could remember physical conditions experienced an average of ~10 km prior. The fish assessed water quality only in water masses that it directly experienced, and could only distinguish gradients over distances of ~18 km or less, and then only if a minimum detection threshold difference was exceeded. In this way, net migration from lower to higher preference water masses resulted from reactive movement away from undesirable areas, rather than a proactive movement into favourable areas.

#### *Numerical Optimization with a Floating Point Genetic Algorithm*

The migration model required many parameters, most of which could not be directly quantified from the literature. Therefore an objective optimization scheme was needed to test parameter combinations that potentially included all reasonable values. We used a floating point genetic algorithm (e.g. Michalewicz 1992) as a computationally intensive numerical method of fitting simulated and observed time series. This technique is merely an optimization tool, and we are not using it to imply anything about

salmon genetics or evolution. However, the floating point genetic algorithm is most easily described by functional analogy with genetic evolution. A single parameter is analogous to a gene, a complete set of model parameters is analogous to a genotype, and the superset of all genotypes can be thought of as the genepool. Genotype fitness in this case was calculated as the goodness of fit ( $R^2$ , coefficient of determination) between modelled and observed coastal migration routes described below. The genetic algorithm calculated a fitness value for all genotypes from an initial arbitrary genepool, and then selected genotypes with highest fitness for the next generation, while low fitness genotypes were removed from the genepool. The genotypes in the new generation were subjected to random perturbations of parameters (mutations) and switching of groups of parameters (crossovers). Fitness values of the new genotypes were then calculated and the whole process was repeated until maximum fitness values no longer increased from one generation to the next.

Genotype fitness was calculated as the goodness of fit between modelled and observed coastal migration routes, subject to the following constraints: 1) swimming speeds had to be consistent with tagging studies, 2) arrival timing in coastal fisheries had to fall within the period from late June to early September, and 3) homing success rates had to exceed 70%. While there is no way of knowing what the actual homing success rate is, a navigational failure rate of 30% is probably much too high. However, without introducing more complex navigational behaviour, we were not able to produce both consistently high success rates, and substantial interannual migration route variation. We felt that a 70% success rate represented a trade-off between describing trajectories of the majority of the fish, and allowing us to explore potential effects of interannual oceanographic variations by not overly constraining the initial positions and orientation behaviour of the fish.

The coefficient of determination ( $R^2$ ), was used as a comparative index of the goodness of fit between simulated and observed migration route time series:

$$R^2 = 1 - \text{ESS} / \text{TSS}$$

where:

ESS = Error Sums of Squares

$$= \sum_{i=1982}^{1994} (\hat{y}_i - y_i)^2,$$

TSS = corrected Total Sums of Squares

$$= \sum_{i=1982}^{1994} (\hat{y}_i - \bar{y})^2,$$

$\hat{y}_i$  = simulated northern diversion rate in year  $i$ ,

$y_i$  = observed northern diversion rate in year  $i$ , and

$\bar{y}$  = mean observed northern diversion rate 1982-94.

This value is equal to the familiar  $R^2$  in least squares linear regression. However, in this case, predicted and observed values of  $y$  are not related by a least squares linear regression fit, so the properties of  $R^2$  are slightly different.  $R^2 = 1$  indicates that the modelled and observed time series are identical,  $0 < R^2 \leq 1$  indicates that some of the variation around the mean diversion rate can be explained by the model, and  $R^2 < 0$  indicates that the mean diversion rate is a better fit to the time series than the model result. The coefficient of determination was used as a relative measure to evaluate and compare alternative models, but we did not attempt to assess the statistical significance of these models.

The genetic algorithm may not find a global optimum solution, because parameter combinations may become trapped in local optima, and the stochastic behaviour of the fish may obscure the true optimum. However, this method should identify solutions that are reasonably close to the global optimum if it exists over a reasonably large parameter space. Substantially different parameter combinations may yield similar goodness of fit values because two parameters may have offsetting effects. For example, a late initiation date and fast swimming speed may yield essentially the same result as an early initiation date and a slow swimming speed. In this study, the role of the numerical optimization was to quantify (approximately) how much coastal migration route variability could be explained by each behavioural/oceanographic mechanism. Thus, the relative explanatory power of each mechanism is of primary importance, while the actual parameter values are of secondary interest and not reported.

This method of optimization raises two important concerns: 1) because there are so many parameters in the model, the genetic algorithm may be able to produce good, but spurious, coherence between modelled and observed coastal migration routes using any mechanism, or conversely 2) the genetic algorithm may not be able to optimize the model adequately, so that the explanatory power of one or more mechanisms could be severely underestimated. If the first situation occurred, it would be obvious. If the second situation occurred, it would not be detectable, and the apparent effects of the different mechanisms would be the result of random events during optimization. We attempted to address this concern by using the migration model as a reference model. An arbitrary set of parameters was selected to produce a time series of coastal migration routes

with substantial interannual variability. Then the genetic algorithm was used to optimize the model from random initial conditions. This process was repeated a number of times and we found that the optimized model could consistently explain a substantial amount of the migration route variability ( $0.75 < R^2 < 0.97$ ). Individual parameters often varied substantially between the reference model and the optimized model, but the relative contribution of the different mechanisms changed relatively little. This gives us some confidence that the optimization procedure performs as we hoped, but we cannot be certain that it is effective in all situations.

#### *Stepwise Assessment of Mechanisms Potentially Affecting Coastal Migration Routes*

The effects of three mechanisms on coastal migration route variability were explored:

- 1) the Fraser sockeye distribution prior to migrating is constrained by thermal limits
- 2) sockeye salmon are advected by offshore surface currents in the Gulf of Alaska
- 3) sockeye tend to avoid water temperatures that are bioenergetically unfavourable.

The model was optimized several times, first to examine the effects of each mechanism independently, and then to examine the mechanisms in combination. The SST constraints and high SST avoidance behaviours were removed to optimize the model for current variability alone. To optimize the model for either SST constraints or high SST avoidance alone, year-specific monthly currents were replaced by monthly mean currents averaged over the years 1982-94.

### **RESULTS**

Sockeye orientation in the optimized models always included a somewhat eastward directional preference in offshore waters, and a south-eastward directional preference in coastal waters. Thus, successful sockeye always arrived at the coast somewhere north of Juan de Fuca Strait and then followed the coast south.

#### *Effects of Thermal Constraints on the Sockeye Distribution Prior to Homing*

Thermal constraints on the sockeye initial distribution did not explain very much of the northern diversion rate variability ( $R^2 = 0.07$ ). In the optimized model, thermal limit constraints had the greatest effect on the initial distribution in 1983, and no effect in several other years (Fig. 2). In a

few years, the distributions were marginally affected on the southern and eastern boundaries, while northern and western boundaries were always unaffected.

The model is not able to produce both high and low diversions with a single parameter combination because constraints essentially affect only the south-east boundary. As the distribution contracts along this boundary, the number of southern migrants decreases, resulting in an increase in the proportion of northern migrants. As the boundary extends southward, the number of southern migrants increases, but the number of northern migrants remains the same. Without a concurrent decrease in the number of northern migrants, the northern diversion rate cannot reach very low values. Of course, the northern diversion rate could take very low values if the preferred compass bearing was shifted to the south, but then the problem would be reversed and very high diversion rates would not be attainable.

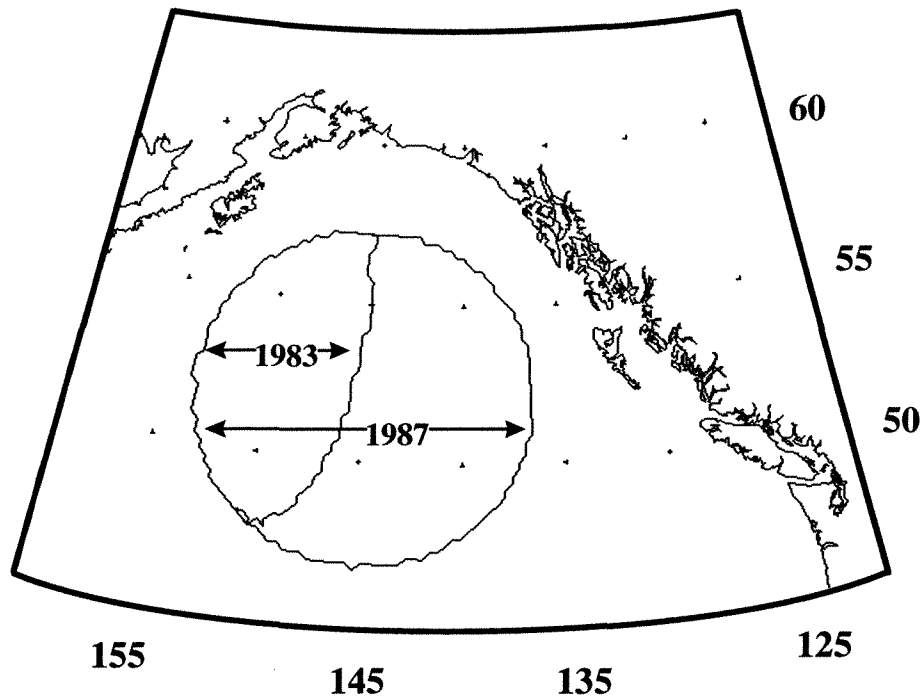
#### *Effects of Current Advection*

Current advection in the offshore oceanic region did not explain any of the observed coastal migration route variability ( $R^2 = 0$ ). Mean migration trajectories of salmon in offshore waters (Fig. 3) indicate that currents do not produce large route deviations relative to the width of the optimized initial distribution. Since offshore currents are the only mechanism introducing variability in this case, variability in the latitude of arrival in coastal waters determines the diversion rate. All fish are affected by interannual current variation, but when the initial distribution is broad, only a small proportion are positioned so that the current displacement causes them to switch between northern and southern routes. If the initial distribution is very narrow, then the proportion of fish which change routes may be much greater. However, the genetic algorithm could not identify any broad or narrow initial distributions that would indicate that current variability was consistent with the diversion rate time series.

#### *Effects of a Behavioural Tendency to Avoid High SST During Homing Migration*

The behavioural tendency to avoid high SST explained the most northern diversion rate variability ( $R^2 = 0.33$ ). The optimal parameter set was unexpected in that the initial distribution was essentially a point source (20 km diameter) and open ocean migration precision was essentially perfect (coefficient of directedness = 0.98). This resulted in a single mass of fish arriving simultaneously in the coastal waters north of Vancouver Island (Fig. 4).

**Fig. 2** Range of sockeye salmon initial distributions that resulted when the migration model was optimized with thermal limit constraints on the initial distribution. 1983 demonstrated the most restricted distribution, while 1987 (and some other years) were not affected by thermal limits.



**Fig. 3** Initial distribution and mean migration trajectories that resulted when the model was optimized with offshore current variability. The large circle outlines the initial distribution; each line connecting the distribution centre to the coast represents the mean open ocean trajectory of all individuals from a single year (1982-94).

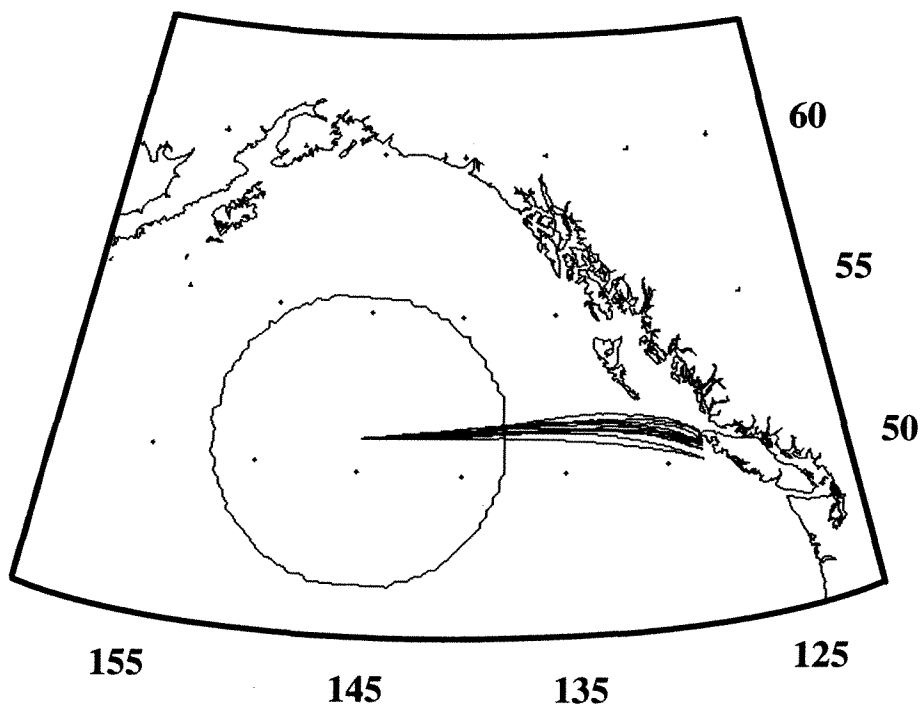
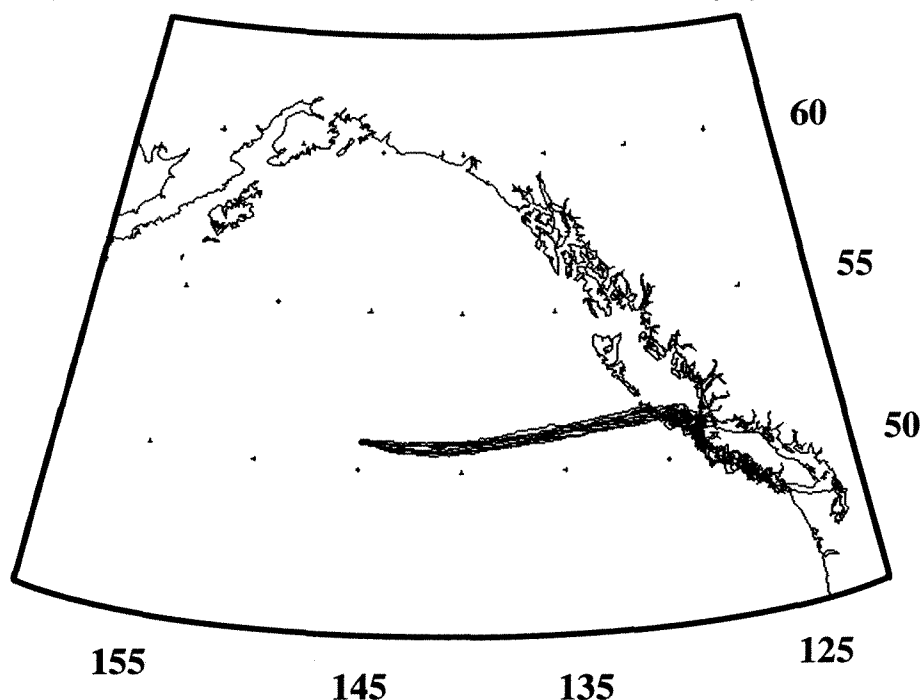


Fig. 4 Typical trajectories that resulted when the model was optimized with a behavioural tendency to avoid high SST. Ten trajectories from 1982 are shown, and are representative of the precise open ocean migration and more dispersed coastal migration observed in all years. The initial distribution was essentially a point source.



The open ocean trajectories did not differ much among years, and the fish rapidly dispersed in coastal waters (only 10 trajectories from a single year are shown because the overlapping paths are confusing and uninformative). The comparison of modelled and observed diversion rates (Fig. 5) indicates that the model did not produce much diversion variability.

The model did simulate higher than average diversions in the four high diversion years (1983, 1992-94), but not nearly as high as observed. Only 1990 appeared as a very low diversion year in the simulations, similar to the observed value. The highest and lowest diversion years in the simulations (1983 and 1990 respectively), were also two of the warmest years along the British Columbia coast. This demonstrates that the high SST avoidance behaviour can result in both high and low diversions depending on the fine scale SST spatial distribution. Thus, defining the appropriate scale of interaction between salmon and SST may be critical for understanding migration routes.

We also optimized this model with the additional constraint that the initial distribution had to be greater than 500 km in diameter, but in this case, much less diversion rate variability could be explained ( $R^2 = 0.12$ ).

#### Effects of Combined Mechanisms

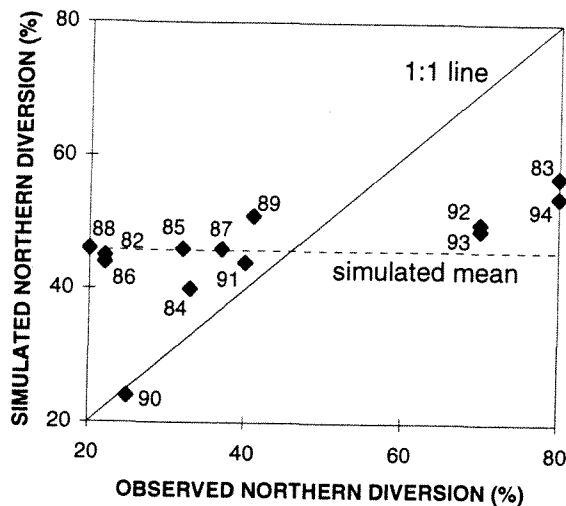
The northern diversion rate variability explained

by individual and combined mechanisms is summarized in Table 2. Combined mechanisms did not result in any increased explanatory power. When high SST avoidance and thermal limit constraints were combined, the thermal limits did not actually have any effect in the optimized models because the initial distribution was essentially a point source as described above. The slight decrease in explained variation resulting from the addition of currents to thermal limits or high SST avoidance further suggests that current variability does not covary with diversion rates, but may also indicate imperfect optimization.

Table 2. Goodness of fit between modelled and observed Fraser River sockeye salmon coastal migration routes (1982-94). Behavioural parameters were optimized independently for each individual mechanism and each combination of mechanisms.

Mechanism	$R^2 \times 100$
(1) thermal limit constraints on the initial distribution	7
(2) offshore current advection	0
(3) behavioural avoidance of high SST	33
(1) & (2)	5
(1) & (3)	33
(2) & (3)	29
(1) & (2) & (3)	29

**Fig. 5** Comparison of simulated and observed annual northern diversion rates (1982-94) generated when the model was optimized with a behavioural tendency to avoid high SST. Individual years are labeled.



### DISCUSSION

Our model was unable to reproduce the Fraser sockeye northern diversion rate time series well enough to demonstrate the viability of a causal hypothesis, or to be a useful predictive tool for fisheries management. The failure of the model to explain more of the northern diversion rate variability was most likely due to two main factors: 1) inappropriate representation of salmon behaviour, and 2) inappropriate representation of the NE Pacific oceanography. Incomplete optimization and errors in the observed northern diversion rate time series are probably of lesser importance. However, the model has provided insight into the workings of the system and the results suggest directions for additional modelling and field studies.

Our representation of salmon behaviour was obviously simplistic. We ignored interactions between behaviour and all environmental stimuli except for SST (and the static stimuli required for salmon to distinguish open ocean and coastal regions, land, and compass directions). Our representation of navigation behaviour was the simplest that we could conceive of, such that fish could reach the coastal approaches to the Fraser River from vastly different initial positions. However, the low homing success rates attained in some years (approaching 70 %), suggests that additional behaviours are likely important. Some kind of longer term memory could help fish avoid becoming trapped in coastal geometry or prevent substantial delays in regions of high water temperature which could be handled most efficiently with more directed swimming. With simple compass navigation, fish may bypass their coastal target, and fail to return

home because there is no provision for turning around (but we do not know if this is a problem in reality). The assumptions that the initial distribution was uniform, and that all stocks began migrating at the same time is also likely unrealistic. Different coastal migratory timing observed for different stocks (Clemens and Killick 1963) suggests that either the stocks occupy different areas of the ocean, they start migrating at different times, they swim at different rates or they follow different routes. The model would have to be optimized separately for each stock to account for this variability, but the biological data are not sufficient to describe stock-specific variations in any of these features.

Our results suggested that the offshore processes that we defined could not explain as much northern diversion rate variability as coastal processes. If all salmon orient on a similar compass bearing, and offshore distributions are as broad as field studies have suggested (French et al. 1976, Welch et al. 1995), then it is unlikely that thermal limits and offshore currents could produce both very high and very low diversion rates. Broad initial distributions also prevented SST avoidance behaviour from reproducing observed diversion rates, but we did not explore whether this behaviour was capable of producing arbitrarily high and low diversions. However, if all fish arrive north of Vancouver Island in a tight spatial distribution and narrow time window, then SST preference behaviours can reproduce a substantial amount of northern diversion rate variability. This supports the notion that initial conditions prior to migrating do not necessarily influence diversion rates. If the migration route decision is made at essentially the same coastal location by all fish, then offshore processes may be largely irrelevant. For this to occur, there would have to be some mechanism aggregating the fish. The most obvious aggregation occurs as sockeye swim eastward and 'pile up' on the coast. If the majority of the fish arrive on the coast north of Vancouver Island, they will all migrate through a relatively narrow corridor in the Queen Charlotte Sound area, although the timing will not be synchronous. Thus the coastal migration route decision process could be determined in a very confined area despite a broad and variable open ocean distribution.

We did not expect to explain much coastal migration route variability with coastal processes because the model timestep and physical oceanographic representation were more appropriate for open ocean processes. The AVHRR SST images probably provided adequate resolution in time and space for the offshore processes that we were describing. These images do not resolve mesoscale SST variability very well, and this is probably a more serious problem in coastal areas. Relative to offshore

waters, British Columbia coastal oceanography is characterized by steep SST gradients, and complex tidal, wind driven, and buoyancy-driven currents. This coastal heterogeneity was not well represented in our model, so we cannot confidently describe the potential interactions between salmon and oceanographic variability in the region north of Vancouver Island. Our model results demonstrated that high SST avoidance behaviours could explain some of the interannual migration route variability, and suggested that the system might be very sensitive to the scale of interaction. High annual temperatures could produce both high and low diversions, depending on the SST spatial distribution. If the important temporal and spatial patterns are not described with the appropriate resolution, substantial errors will likely eventually result from any predictive model, even if the underlying processes are essentially understood. In this system, predictive correlation models based on annual indices and vague understanding of important processes are probably doomed to predictive failure.

Our results suggest that further research into the mechanisms driving migration route variability should be focused on the coastal region, particularly around the north end of Vancouver Island. Seemingly small interannual variations in coastal SST distributions or Fraser River northward flow patterns may have a large effect on coastal migration routes. Simulation modelling of fine scale interactions between coastal oceanographic variability and fish behaviour may help to further define critical decision points in the migration route, however, the mechanisms that drive migration route variability will never be adequately described without additional field studies. Detailed observations of sockeye migration trajectories may help to quantify the important behaviours. It may be informative to observe how trajectories of individuals around the north end of Vancouver Island relate to mesoscale oceanographic variability, especially SST and salinity gradients. Although if the important factors are difficult to measure (e.g. Fraser River odours), individual trajectories may not be informative. If consistent behaviours could be identified, and quantitatively described, we could work toward understanding the spatial and temporal scales of interaction, and modify our migration models accordingly.

### CONCLUSIONS

- 1) Seasonally-varying thermal limits constraining the sockeye distribution in the Gulf of Alaska are not likely to be a sufficient mechanism to explain Fraser sockeye coastal migration route variability.
- 2) Offshore currents in the Gulf of Alaska do not appear to be sufficient to explain Fraser sockeye

coastal migration route variability.

- 3) A behavioural tendency for sockeye to avoid high SST while migrating could explain a substantial amount of Fraser sockeye coastal migration route variability, and it appears that this behaviour may be most important in the coastal region north of Vancouver Island.

### ACKNOWLEDGEMENTS

We thank David Welch and an anonymous reviewer for helpful suggestions, Leonardo Huato for his plotting code, Jim Ingraham for providing us with OSCURS current vectors, and James Scandol and Emily Walter for condensing the current vectors. This work was funded by an NSERC strategic grant to MH.

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