Simulation of juvenile sockeye salmon (*Oncorhynchus nerka*) migrations in the Strait of Georgia, British Columbia

RANDALL M. PETERMAN,1 SILVIO G. MARINONE,2,4 KEITH A. THOMSON,2 IAN D. JARDINE,2 ROBERT N. CRITTENDEN,1,5 PAUL H. LEBLOND2 AND CARL J. WALTERS3

1School of Resource and Environmental Management, Simon Fraser University, Burnaby, British Columbia, Canada V5A 1S6
2Department of Oceanography, University of British Columbia, Vancouver, British Columbia, Canada V6T 1Z4
3Fisheries Centre, University of British Columbia, Vancouver, British Columbia, Canada V6T 1Z4
4On leave from Centro de Investigacion Cientifica y de Educacion Superior de Ensenada, Baja California, Mexico
5Present address: Crittenden Biometric, Suite 1401-1801, 1001 Cooper Point Road SW, Olympia, Washington, USA 98502

ABSTRACT

Previous research has documented two main migratory routes of juvenile sockeye salmon (*Oncorhynchus nerka*) through the Strait of Georgia, British Columbia, Canada, and large interannual variability in marine survival rates of the Chilko Lake stock. Simulation models were used to explore the influence of surface currents on the migratory route of juvenile sockeye salmon (smolts) through the Strait of Georgia. We used a model of downstream migration to generate daily numbers of Chilko Lake sockeye salmon smolts entering the Strait of Georgia, based on daily counts of smolts leaving the rearing lake. A numerical hydrodynamic model (driven by surface wind, tide, and Fraser River discharge) hindcasted surface currents in the Strait of Georgia on a 2 km x 2 km grid. A smolt migration model simulated fish moving through the Strait with different compass-oriented migratory behaviours (i.e. swimming speed and directional orientation) within the time-varying surface advection field. Results showed that surface currents within the Strait of Georgia can affect the migratory route of sockeye salmon smolts in spite of their large size (8 cm). Wind is the forcing mechanism primarily responsible for determining which migratory route would be used. Under prevailing wind conditions (i.e. toward the north-west), most sockeye salmon smolts would use the eastern migratory route; however, relatively brief south-eastward wind events (lasting about 2 days) would force most smolts into the western migratory route. Given the heterogeneity of flow for salmon within the Strait, we hypothesize that wind-driven variability in the annual proportion of smolts that use the western and eastern migratory routes in the Strait of Georgia affects early marine survival rates of Fraser River sockeye salmon.

Key words: fish migration, sockeye salmon smolts, biophysical models, surface currents

INTRODUCTION

Large year-to-year variability is common in the abundance of recruits of fish populations (coefficients of variation average 80% – Hennemuth et al., 1980; Myers et al., 1990). The paucity of causal explanations for this variability makes forecasting and setting of management regulations difficult for short-lived marine fishes and Pacific salmon (*Oncorhynchus* spp.). For some salmon species, maturing adults (recruits) constitute most, if not all, of the fishable biomass each year. In their search for mechanisms that affect interannual variability in recruitment, researchers have found support for a number of physical processes such as wind-driven transport of surface waters or upwelling (Garrod and Colebrook, 1978; Cushing, 1982; Rothschild, 1986; Sinclair, 1988; Beamish and McFarlane, 1989; Kruse and Tyler, 1989; MacCall, 1990). One recently emerging theme has been that events on small spatial and temporal scales (e.g. <10 km and daily or hourly) can influence distribution and survival of larval fishes (e.g. Frank and Leggett, 1982; Peterman and Bradford, 1987; Taggart and Leggett, 1987; Wroblewski and Richman, 1987; Helbig et al., 1992), which may in some cases also affect recruitment. If this is true, then analysis of annual data such as year-class strengths and mean annual upwelling indices may not reveal causal relationships because of inadequate resolution of the data. To our knowledge, such small-scale analyses have not been applied in the marine environment to juvenile sockeye salmon (*O. nerka*), one of the most economically valuable species on the west coast of North America. In
part, this is because the size of juveniles entering the ocean (8-12 cm long) has been thought to make them much less vulnerable to oceanographic phenomena such as currents and turbulent mixing than the small larvae of pelagic marine species (usually <2 cm long).

Therefore, our purpose was to test the general hypothesis that the distribution of juvenile sockeye salmon (smolts) in the early phase of their ocean life is influenced by the variability of surface wind, tides, and river discharge on small spatial and time scales. The long-term objective of this research is to improve forecasts of abundance through better understanding of year-to-year variation in recruitment of Pacific salmon by investigating physical processes on small spatial and time scales. We examined the early marine life stage because previous work on Pacific salmon has strongly suggested that components of fishable adult biomass (body size and survival rate) are most affected by processes in that early marine stage (reviews: Peterman, 1987; Pearcy, 1992).

Our analysis focused on the Chilkoot Lake sockeye salmon stock in British Columbia, Canada, because of its relatively unique data set. Since 1951, this stock has shown up to 20-fold variation among years in smolt-to-adult survival rates of annual cohorts. Adults spawn in the interior of British Columbia and their offspring migrate approximately 600 km down the Chilkoot, Chilcotin, and Fraser Rivers to the Strait of Georgia between mid-April and late May. Smolts are enumerated daily as they leave Chilkoot Lake and they reach salt water in about 6 to 7 days (Williams, 1969; Crittenden 1994). Chilkoot sockeye salmon smolts average 8 cm in length when entering the Strait of Georgia (Henderson and Cass, 1991).

We focused on the migratory routes of juvenile sockeye salmon in their first month in salt water within the Strait of Georgia. Seine surveys from 1982 to 1985 (Groot et al., 1985) have shown that juvenile sockeye salmon from the Fraser River take about 1 month after entering salt water to exit from the north end of the Strait on their way to the north-east Pacific Ocean (Groot and Cooke, 1987). Within the Strait, most smolts were found within 10 m of the surface. These surveys showed that groups of juveniles migrate to sea either along the eastern or the western edge of the Strait (Fig. 1) and that the relative usage of these two migratory routes likely differed among years. Groot and Cooke (1987) speculated that the number of fish using the different routes might be affected by tidal currents and the magnitude of freshwater discharge from the Fraser River. The observation that there are two migratory routes is particularly important because St. John et al. (1992) have shown that there is considerable spatial heterogeneity of food for juvenile salmon in the Strait of Georgia at the time when juvenile sockeye salmon are present. Their samples showed a five-fold range in mean concentration of amphipods, euphausiids, copepods and larval fish.

Because of the heterogeneity in food supply (and possibly also in predators) across the Strait, interannual variations in migratory routes could affect the between-year variability in smolt-to-adult survival rate of the Chilkoot sockeye salmon stock. The analysis reported here focused only on the first step in this link: between the physical environment and the migratory route. Specifically, we hypothesized that surface currents in the Strait of Georgia (driven by winds, tides and Fraser River discharge) at the time of smolt migration into the Strait influence the proportion of juvenile Chilkoot Lake sockeye salmon taking these two migratory routes.

To investigate this hypothesis, we simulated the migration of juvenile Chilkoot Lake sockeye salmon in the Strait of Georgia using an individual-based smolt migration model of the type used in other fish studies (e.g. Huston et al., 1988). In contrast to other such modelling studies of salmon (e.g. Pascual and Quinn, 1991; Thomson et al., 1992), we focused on migration of juveniles rather than returning adults. Compass-oriented migratory behaviour was modelled with different swimming speeds and directional orientations. Surface advection fields within the Strait and number of smolts entering the Strait were provided by a hydrodynamic model and downstream migration model, respectively (Fig. 2).

**METHODS**

**Hydrodynamic model**

The Strait of Georgia is a large, deep (up to 100+ m) water body on the coast of British Columbia (Fig. 1) with a two-layer, positive estuarine circulation. Freshwater enters from a number of rivers and inlets around the Strait, 70% of which is accounted for by the Fraser River. The brackish surface layer flows out of the Strait through narrow passages to the north (e.g. Discovery Passage) and south (e.g. Juan de Fuca Strait), where vigorous tides mix the surface layer with saline, inward-flowing subsurface waters from the ocean (Thomson, 1981; LeBlond, 1983).

We used the Georgia-Fuca, Version 4 (GF4) numerical hydrodynamic model (Crean et al., 1988) to hind-cast hourly surface currents in the Strait of Georgia for the period when Fraser River sockeye salmon smolts were present (April to July). The GF4 model is a vertically integrated, buoyant-spreading upper layer
Figure 1. The Strait of Georgia, British Columbia, showing the eastern and western migratory routes of juvenile sockeye salmon from the Main Arm of the Fraser River to the north end of the Strait on their way to the north-east Pacific Ocean (adapted from Groot and Cooke, 1987).

The model of the Strait of Georgia, that uses a semi-implicit scheme for the numerical formulation of the basic equations for volume, salt, and momentum conservation in the upper layer on a 2 km × 2 km grid.

Velocities in the upper layer of the model were driven by surface winds, freshwater discharge, and tides. Wind stress, calculated from surface wind observations by Environment Canada at 14 stations around the Strait, was applied at the sea surface. The sole source of fresh water in the GF4 model was the Fraser River. Daily mean Fraser River discharge, measured by Environment Canada at Mission (60 km upstream from the river mouth), was apportioned between the North Arm (15%) and the Main Arm (85%), based on best available estimates; the flow at the river mouth was modulated by changing tidal elevations in the Strait. Velocities of the underlying layer were derived from harmonic constants of the barotropic tide obtained from prior calculation (Crean et al., 1988).

The interfacial boundary between the upper and underlying layers was formulated to permit the upper layer to vary in thickness due to entrainment (resulting from the fast-flowing turbulent upper layer near the river mouth) and mixing (particularly near constricted
passages at the north and south ends of the Strait). The thickness of the surface layer varied from less than 1 m to over 10 m (Crean et al., 1988).

The GF4 model satisfactorily simulated the basic circulation in the Strait of Georgia under a variety of prevailing wind conditions (Crean et al., 1988). Extensive field observations of surface current drifters (drogued at 2 m depth) were conducted over a 12 month period in 1981 and 1982 to compare with the model's output of surface currents. The phasing and directions of modelled surface flow features agreed well with observations, although the modelled speeds tended to be slightly less than those observed (this is likely due to the absence of free surface gradients associated with deep water renewal). The GF4 model was therefore considered a useful tool for examining the effects of surface advection on juvenile salmon migratory routes within the Strait.

**Downstream migration model**

To generate abundance of Chilko Lake sockeye salmon smolts entering the Strait of Georgia each hour, we used a model of smolt migration from Chilko Lake to the mouth of the Fraser River that was developed by Crittenden (1994). This model was driven by the annual observed daily counts of smolts leaving Chilko Lake (Dr. J. Wooden, International Pacific Salmon Commission, Vancouver, BC, personal communication, 1991) and daily river discharge provided by Environment Canada. A velocity/discharge relationship was used to calculate water velocity in the rivers along this freshwater migration path; the average movement rate of fish was proportional to this velocity. The model applied one-dimensional diffusion to spatially spread fish along the length of the river, and all modelled smolts entered the Strait via the Main Arm. The downstream migration model interpolated the daily Fraser River discharge data to hourly values and used hourly surface current velocities at the mouth of the Fraser River (from the GF4 model) to modulate the hourly movement of smolts into the Strait (Crittenden, 1994).

**Smolt migration model for the Strait of Georgia**

The smolt migration model moved fish through the Strait of Georgia using hourly surface current vector fields from the GF4 model and a smolt migratory behaviour. A Lagrangian particle-tracking algorithm simulated the migration of each smolt released at Sand Heads Lightstation, located on the edge of the mud flats at the end of a 9 km spit on the Main Arm of the Fraser River (Fig. 1). Each model smolt was assigned a number (obtained from the downstream migration model) to represent the number of smolts entering the Strait at a given hour. The hourly speed and direction of migration for model smolts was calculated as the vector sum of a surface current vector (obtained by interpolation from the GF4 model grid) and a smolt swimming vector (i.e. swimming speed and compass orientation). This smolt migration model was similar to Walters et al. (1992) model, although the simulated fish actively swam and diffusion was not included.

There was only one year (1984) in which field observations on the spatial and temporal distribution of smolts was sufficiently detailed to provide a comparison with our smolt migration simulations (Groot et al., 1989). However, we also wished to determine how conditions in other years might affect salmon migratory routes. Therefore, we examined the hypothesis that surface advection in the Strait of Georgia affects the migratory route of juvenile sockeye salmon smolts with simulation experiments using two different physical
Effects of advection on migration of sockeye salmon smolts

Table 1. Wind/discharge scenarios used for simulations of smolt migration routes with constant physical forcing.

<table>
<thead>
<tr>
<th>Surface wind* (km h⁻¹)</th>
<th>Fraser River discharge (m³ s⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>750</td>
</tr>
<tr>
<td>0</td>
<td>6000</td>
</tr>
<tr>
<td>20 south-eastward</td>
<td>750</td>
</tr>
<tr>
<td>20 south-eastward</td>
<td>6000</td>
</tr>
<tr>
<td>20 north-westward</td>
<td>750</td>
</tr>
<tr>
<td>20 north-westward</td>
<td>6000</td>
</tr>
</tbody>
</table>

*Directions are those toward which winds move.

forcing regimes (combination of surface winds, Fraser River discharge, and tides): (1) constant wind/discharge scenarios, and (2) 1984 physical forcing data.

Simulations of migration with constant wind/discharge scenarios

Simulations of smolt migration were conducted using six constant wind/discharge scenarios each during a spring tide and a neap tide to examine the relative importance of surface wind events, Fraser River discharge, and the fortnightly and diurnal tidal cycles in forcing salmon smolts along either of the two migratory paths in the Strait of Georgia (Table 1). Model smolts were released each hour over a 48 h period during a spring tide and a neap tide, and the migratory path of each smolt was simulated for 48 h.

We chose constant wind scenarios (Table 1) that were representative of the two different wind regimes that typically occur when Chilkok Lake sockeye salmon smolts enter the Strait of Georgia (April to June); north-westward and south-eastward winds (we will use the convention of describing the direction toward which winds and currents move). As well, we examined periods of relative calm. The prevailing winds (1967 to 1980) in the central Strait of Georgia (measured at Sand Heads Lightstation) during April and May are toward the north-west with a mean speed of 20.3 km h⁻¹ (Environment Canada, 1982). Variability of surface winds is primarily along the axis of the Strait (i.e. south-east–north-west). The frequency of occurrence of winds toward the north-west is 22% (56% to the west, north-west, and north); winds toward the south-east occur 18% of the time (34% toward the east, south-east, and south) with a mean speed of 22.7 km h⁻¹. Sustained wind speeds of about 20 km h⁻¹ for periods of 48 h or more toward the north-west or south-east are common.

The constant Fraser River discharge scenarios used were the minimum and maximum values that occurred at the beginning of May in a 40 year record: 750 m³ s⁻¹ and 6000 m³ s⁻¹. The Fraser River freshet occurs between May and August of each year due to snow melt from the mountains of British Columbia. The onset of the freshet generally occurs at the beginning of April and peaks in mid-June (mean mid-June discharge: 7500 m³ s⁻¹, maximum mid-June discharge: 12700 m³ s⁻¹), although the timing of these events may vary by several weeks between years.

Smolts migratory paths were simulated for the 48 h after smolts entered the Strait of Georgia using a constant smolt migratory behaviour and surface current vector fields from scenario-specific runs of the GF4 model. For these simulations of constant physical forcing only, we assumed that all fish had a swimming speed of 8 cm s⁻¹ within the Strait and a compass orientation of 304 degrees true (i.e. north-westwards along the axis of the Strait). This migratory behaviour was consistent with an optimum cruising speed of one body length per second (BL s⁻¹) and a smolt migration directed to the north-west (Groot and Cooke, 1987). For each wind/discharge scenario, the GF4 model was run for 2 weeks with the specified constant wind and constant Fraser River discharge, and tidal harmonics from 1984, and hourly surface current vector fields were recorded for a full spring–neap tidal period. Surface currents from 27–30 April were used for the neap tide smolt migration simulations, and currents for 5–8 May were used for the spring tide migration simulations. These two periods were selected as the first neap and spring tides occurring after 25 April, the date that juvenile Chilkok Lake sockeye salmon started to enter the Strait of Georgia in 1984.

Simulations of migration with 1984 physical forcing data

These simulations for 1984 were conducted to evaluate the modelled migratory behaviours by comparing our results with the observations of Groot and Cooke (1987) and Groot et al. (1989). As well, the model runs examined the influence of the temporal variability of surface currents in the Strait of Georgia that year on the distribution of smolts and their migratory paths.

Chilkok Lake sockeye salmon smolt migrations through the Strait of Georgia were simulated for 1984 using surface currents from the GF4 model, the time series of smolts entering the Strait (from the downstream migration model), and several different migratory behaviours. Hourly surface current fields were hindcast with the GF4 model for the period from 1 April to 31 July 1984 using hourly surface wind observations from 14 stations around the Strait, Fraser River discharge observations at Mission, and tidal harmonics.
The Sand Heads winds (Fig. 7b) are representative of surface winds in the Strait of Georgia but are not representative of winds in the northern portion of the Strait (north of Texada Island), where prevailing winds are toward the south-east during this period (Thomson, 1981; Environment Canada, 1982). Crittenden’s (1994) downstream migration model generated the number of Chilko Lake sockeye salmon smolts predicted to have entered the Strait of Georgia each hour (Fig. 3) using 1984 daily counts of smolts leaving Chilko Lake, 1984 freshwater discharge data, and surface currents at Sand Heads Lightstation from the GF4 model.

There is considerable uncertainty about the swimming speed and preferred direction of orientation of sockeye salmon smolts once they enter the Strait of Georgia, although a north-west orientation (315 degrees true) is close to directly up the Strait of Georgia (304 degrees true). Groot and Cooke (1987) suggested that a north or north-west orientation was likely and also reviewed literature on swimming speed, noting that values up to 3–4 BL s⁻¹ were feasible. To determine which fish behaviours were most consistent with the field observations, we explored eight types of fish migratory behaviour: zero swimming speed (i.e. passive drifters); 4 cm s⁻¹ towards the west, north-west, and north; 8 cm s⁻¹ (i.e. 1 BL s⁻¹) towards the west, north-west, and north; and 24 cm s⁻¹ towards the north-west.

The migration of sockeye salmon smolts through the Strait was simulated by releasing a model smolt in the migration model at Sand Heads every hour from 1 April to 31 July 1984 (2400 smolts) and following each smolt’s progress until (a) the smolt exited the north end of the Strait in the vicinity of Discovery Passage, (b) the smolt exited the south end of the Strait, or (c) it had not moved more than 10 m in a 12 h period. The spatial distribution of sockeye salmon smolts was modelled by assigning each model smolt a weighting based on the abundance of smolts entering the Strait each hour, as calculated by the downstream migration model (i.e. each model smolt represented a group of fish).

Simulation results for each smolt migratory behaviour (i.e. swimming speed and compass orientation) were compared with the field surveys of juvenile sockeye (Groot and Cooke, 1987; Groot et al., 1989) in three ways: (1) general migratory patterns in the Strait of Georgia, (2) time to exit the Strait via the north end, and (3) proportion of annual abundance of juveniles using the western migratory route. The hourly locations of model fish were used to calculate daily distribution maps (i.e. 24 h average) and average migration time to the north end of the Strait. The movement of sockeye salmon smolts between and around the Gulf Islands could not be modelled because these intricate passages are smaller than the resolution of the grid in the GF4 model. The proportion of juveniles using the western migratory route was obtained by dividing the number of simulated sockeye salmon that entered that route by the
total number of simulated salmon that entered the Strait of Georgia from the Fraser River that year. Model
smolts with migratory paths that came within 2 km of the western side of the Strait south of Nanaimo were
tabulated as having entered the western migratory route.

RESULTS
Simulations of migration with constant wind/discharge
scenarios
The surface current velocity fields generated by the G4 model for two constant wind/discharge scenarios (Fig.
4) show distinct surface circulation patterns; these result from the combination of winds, tides, and water
flowing from the Fraser River. South-easterly winds can divert the main Fraser River outflow from the
mouth across the Strait toward the Gulf Islands (Fig. 4a), a direction similar to the initial part of the western
migratory route for sockeye salmon smolts shown in Fig. 1. In contrast, the prevailing north-westward winds can
drive a strong current that flows north-westward from the Fraser River along the eastern side of the Strait (Fig.
4b), quite similar to the eastern migratory route for smolts in Fig. 1. The magnitude of simulated surface
currents between Nanaimo and the mouth of the Fraser River was frequently greater than 50 cm s\(^{-1}\).

Spatial distributions of simulated smolts obtained for constant wind/discharge scenarios illustrate the importance
of surface advection on juvenile salmon migrating through the Strait of Georgia (Fig. 5). For south-east
winds, all simulated sockeye salmon were pushed across the Strait into the western migratory route. For north-westward winds, all model smolts were pushed to the north into the eastern migratory route. For periods of calm, most of the model fish were advected towards the eastern migratory route or part way across the Strait towards the western migratory route, with the exception of the simulated sockeye salmon that exited the Fraser River during high discharge on an ebb tide. The dispersion of smolts within each of the six scenarios in Fig. 5 is due to the diurnal tides. Very similar distributions to those in Fig. 5 were obtained for simulations of migrations during a neap tide. Hence, diurnal and fortnightly tides had relatively minor influence on the smolt migration routes.

These simulations, using the range of winds and freshwater discharges that could be encountered by
Fraser River sockeye salmon smolts in April and May, illustrate that surface advection in the Strait of Georgia
is sufficient to generate the two main migratory routes observed in the field by Groot and Cooke (1987) and
Groot et al. (1989). Wind is the principal physical
mechanism for driving the surface circulation patterns
that advect salmon smolts along either route; Fraser
River discharge and tidal phase (diurnal and fortnightly) are of secondary importance. The prevailing
winds (north-westward) during the period of smolt migration through the Strait would force sockeye salmon
smolts along the eastern migratory route, whereas south-eastward wind events would force them towards
the Gulf Islands into the western migratory route.

Simulations of migration with 1984 physical forcing data
Evaluation of different migratory behaviours
We initially evaluated the plausibility of different assumed migratory behaviours based on whether simulated 1984 Chilko Lake sockeye salmon smolts generally moved northward and whether at least some migrated through the eastern Strait past Sechelt (north-west of Vancouver). This is because Groot et al. (1989) showed fish from their juvenile surveys moving generally northward and Chilko smolts appeared in both western and eastern routes, especially the latter. If a simulated migratory behaviour did not show the eastern route, we considered that behaviour to be inconsistent with field observations.

All simulated migratory behaviours showed migration generally towards the north end of the Strait of
Georgia (e.g. Fig. 6 for 4 cm s\(^{-1}\) NW) and the eastern migratory route was present in all simulations that used a north-westward or northward orientation. However, for those that used a westward orientation, that route was only present for smolts swimming at 4 cm s\(^{-1}\); at 8 cm s\(^{-1}\) and above, there was no eastern migratory route. Therefore, it appears unlikely that a westward orientation is used by salmon smolts, unless they use it with relatively slow swimming speeds ($<1$ BL s\(^{-1}\)).

Simulations with different swimming speeds and directional orientation generated a wide range of times
for fish to exit from the north end of the Strait of Georgia. Their migration times show the northward assistance provided by the mean surface circulation in the Strait, mean migration times from simulations that included effects of surface currents were less than migration times would have been without currents (Table 2). Smolts that swam at 4 cm s\(^{-1}\) and oriented to the west, north west, or north, and those that swam at 8 cm s\(^{-1}\) to the west, had mean migration times to reach the north end of the Strait (21 to 38 days, Table 2) close to the field estimate of 1 month (Groot and Cooke, 1987). Passive drifters took too long (42 days) and the 24 cm s\(^{-1}\) swimming speed, noted as plausible in literature reviewed by Groot and Cooke (1987), appeared too rapid (7 days), as did the 8 cm s\(^{-1}\) swimming speed when oriented to the north-west or north.
Figure 4. Surface current velocity maps for the Strait of Georgia (from Discovery Passage in the north down to just above the San Juan Islands) obtained from the UF-4 simulations with constant wind/discharge scenarios during a spring flood tide with low (750 m$^3$ s$^{-1}$) Fraser River discharge: (a) for 20 km h$^{-1}$ south-eastward winds, and (b) for 20 km h$^{-1}$ north-westward winds. The arrow at the top right of the figure indicates the length of a 100 cm s$^{-1}$ velocity vector.
Figure 5. Envelopes of 48-hour-long migration paths of simulated juvenile sockeye salmon in the Strait of Georgia (from the southern tip of Texada Island in the north down to just above the San Juan Islands). Results shown are for the six constant wind/discharge scenarios during a spring tide (directions toward which winds are blowing are indicated). These juveniles were swimming at 8 cm s$^{-1}$ (i.e. about 1 body-length s$^{-1}$) and were oriented north-westwards. Each envelope comprises the hourly positions (dots) of 48 simulated model smolts, released from the Main Arm of the Fraser River at hourly intervals. The large dot with a white centre indicates the release point of each smolt, which was Sand Heads Lightstation, at the end of a 9 km spit.
These criteria for comparing the simulations of smolt migration with the field observations (presence of the eastern migratory route and about 1 month of travel in the Strait) ruled out all migratory behaviours examined except those with swimming speeds of 4 cm s\(^{-1}\) (8 cm s\(^{-1}\) showed no eastern route). A speed of 4 cm s\(^{-1}\) with an orientation to the north-west gave the mean migration time through the Strait (24 days) that was closest to the field-estimated migration time.

**Effects of 1984 physical forcing** The effects of temporal variations in surface winds on the distribution of juvenile Chilko Lake sockeye salmon in the Strait can be seen by comparing the occurrence of south-eastward wind events in the 1984 wind data with the daily proportions of 1984 simulated salmon entering the western migratory route (Fig. 7). Most of the model smolts that entered the western route did so during two periods when sustained south-eastward winds of 20–30 km h\(^{-1}\) occurred during the early days of their life in the Strait of Georgia - the periods of 23–29 April and 26–30 May 1984. For example, smolts that entered the Strait beginning on 19 April were still only part way up the Strait when the strong south-eastward winds began, resulting in currents that pushed most fish to the western side of the Strait. These strong south-eastward wind events had similar effects for all the simulated migratory behaviours. The distribution maps in Fig. 6 also show the effect of these winds on advection of model smolts southward from Sand Heads and westward to the Gulf Islands.

The effect of migratory behaviour on the influence of physical forcing can also be seen in the total proportion of smolts entering the western migratory route and their mean time to enter that route after exiting from the Fraser River (Table 3). For a given swimming speed, the proportion of model smolts entering the western migratory route was larger for fish with westward orientation. Regardless of swimming speed, those with westward orientation also had shorter times to enter that route, as expected. However, northward-oriented fish that entered the western route took less time, on average, to reach that route than smolts with north-westward orientation. This was because relatively few northward-oriented smolts ever entered the western route and they only got there because strong or sustained south-eastward winds pushed them there quickly. This was in contrast to the larger number of smolts with north-westward orientation that came into the western route and that moved there through the cumulative effect of several small daily movements toward the west. This gave a longer average time to enter that route than the northward-oriented fish.

Fraser River discharge and tides had no discernible effect on the proportion of model smolts entering the western route. Daily Fraser River discharge generally increased over the simulated migration period, with a local minimum in the period 27 April to 8 May 1984 (Fig. 3). This period included times when some smolts moved into the western route and others did not (Fig. 7). Furthermore, if anything, the relatively low discharge should have tended to allow more fish, not fewer, to move into the eastern migratory route (compare bottom with top panels in Fig. 5). The two periods when a high proportion of smolts entered the western route (Fig. 7) occurred near a neap tide in the fortnightly cycle; however, such tides cannot account for the westward movement of model smolts because the same phase of the tide occurred during the middle of May and June when there was no similar movement of model smolts into the western route.

**Proportion of migrants by route** Unfortunately, it was impossible to use Groot et al.'s (1989) data to estimate the annual proportion of fish migrating via the western route in one year. This was because they did not sample randomly throughout the Strait (that was not their intention); "... sampling generally proceeded from south to north with time of season" (Groot et al., 1989). Thus, they could have sampled the same group of fish at more than one location and time as the group moved through the Strait (Dr K. Groot, Canada Dept of Fisheries and Oceans, Nanaimo, BC, personal communication, 1991). Furthermore, it is not possible with their data on stock composition to separate the contribution of relative stock abundance from the shift in migratory routes through the season.

However, given these caveats, stock composition data from the seine surveys (Groot et al., 1989) provide at least a crude, qualitative confirmation of the simulated effects of 1984 conditions. Groot et al.'s (1989) data for 1984 (only available from 15 May to 70 June)

---

**Figure 6. (Opposite)** Distribution maps of simulated 1984 juvenile Chilko Lake sockeye salmon in the Strait of Georgia (from Discovery Passage in the north down to just above the San Juan Islands). Fish were swimming at 4 cm s\(^{-1}\), oriented to 304 degrees true (i.e. 0.5 body-length s\(^{-1}\) directed roughly north-westwards along the axis of the Strait). Top panel: 24 April to 14 May; bottom panel: 21 May to 11 June 1984.
Table 2. Mean migration time between the mouth of the Fraser River and the north end of the Strait of Georgia, as simulated under 1984 physical forcing. The standard deviation is in parentheses. The migration time without currents was calculated for each swimming speed assuming a straight-line migration path from the Fraser River to the north end of the Strait.

<table>
<thead>
<tr>
<th>Swimming speed (cm s⁻¹)</th>
<th>Orientation</th>
<th>Mean migration time (days)</th>
<th>Migration time (days) without currents</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>–</td>
<td>42 (16)</td>
<td>–</td>
</tr>
<tr>
<td>4</td>
<td>West</td>
<td>38 (13)</td>
<td></td>
</tr>
<tr>
<td>4</td>
<td>North-west</td>
<td>24 (7.7)</td>
<td>58</td>
</tr>
<tr>
<td>4</td>
<td>North</td>
<td>21 (4)</td>
<td></td>
</tr>
<tr>
<td>8</td>
<td>West</td>
<td>25 (6)</td>
<td></td>
</tr>
<tr>
<td>8</td>
<td>North-west</td>
<td>17 (6.7)</td>
<td>29</td>
</tr>
<tr>
<td>8</td>
<td>North</td>
<td>14 (1)</td>
<td></td>
</tr>
<tr>
<td>24</td>
<td>North-west</td>
<td>7 (1.0)</td>
<td>10</td>
</tr>
</tbody>
</table>

showed that Chilko Lake sockeye salmon smolts (as identified by presence of parasite assemblages) generally appeared in the western route less frequently than expected (based on relative abundance of different stocks’ spawners) and more frequently in the eastern route. This relatively infrequent use of the western route corresponds roughly with the small proportion of the entire simulated population of 1984 Chilko Lake sockeye salmon smolts migrating via the western route, which was 10%, using a swimming speed of 4 cm s⁻¹ and an orientation to the north-west.

**DISCUSSION**

These simulation results support the hypothesis that the magnitude and variability of surface currents can influence migration patterns of even relatively large (8 cm) and fast-swimming juvenile sockeye salmon. Observed surface currents within the Strait can attain speeds of over 50 cm s⁻¹, which is likely to be 6 to 12 times the swimming speed of these fish.

The most important physical factor that influences the migratory route of juvenile sockeye salmon is the direction and strength of surface winds. Fraser River discharge and tidal influences are less important. This finding contrasts with Groot and Cooke (1987), who suggested that Fraser River discharge and tides affected the usage of the eastern or western migratory route. Our results (Fig. 5) indicate that this would only be true if the surface winds were light. We have shown that strong south-eastward wind events (sustained for periods of about 2 days) are responsible for driving the surface currents that would force juvenile sockeye salmon smolts into the western migratory route. This, in combination with the spatial heterogeneity in food supply (St. John et al., 1992), suggests that year-to-year variation in wind intensity and direction during the early marine life stage has the potential to influence survival rates and subsequent year-class strength of these fish by exposing various portions of year classes to different regimes of food (and possibly predators) in the Strait of Georgia.

Of primary importance is the degree of overlap (in space and time) between strong south-eastward wind events and the timing of smolt entry into the Strait from the Fraser River. Each year most smolts migrate from Chilko Lake in one to three major pulses of a few days each, between mid-April and late May. However, the timing and relative abundance of these pulses varies from year to year (summarized by Crittenden, 1994), as does the frequency of occurrence and timing of south-eastward winds in the Strait. The degree of overlap of these processes will affect the distribution of sockeye salmon smolts migrating through the Strait of Georgia. For example, if in one year, strong south-eastward winds only occur near the start of the migration of Chilko Lake sockeye salmon smolts into the Strait, then relatively few fish would migrate via the western route that year. In another year, if such winds occurred when the majority of those fish were in the lower Strait, a higher proportion would migrate via the western route. Such interannual variations in the timing of the two components affecting the wind-driven proportion of smolts using the western migratory route may have commensurate effects on the growth or survival of smolts. This importance of overlap in space and time of small-scale
physical and biological events is directly analogous to findings for larvae of marine fishes (e.g., Petelman and Bradford, 1987; Taggart and Leggett, 1987). The simulated sensitivity of fish as large as Chilko Lake sockeye salmon smolts (8 cm) to winds should stimulate further research on new mechanisms by which physical oceanographic processes affect variability in recruitment of other stocks and species of Pacific salmon, some of which enter the ocean at <4 cm in length.

This work has helped to refine the subset of plausible smolt migratory behaviours in the Strait by showing which combination of swimming speed and orientation is most consistent with field observations (Groot and Cooke, 1987). We discount the possibility that smolts are passive drifters largely because with a swim speed of zero, the simulated time to exit the north end of the Strait was much greater than that observed (Table 2). We further ruled out directed swimming speeds of 24 cm s\(^{-1}\) and higher because the simulated time to exit the Strait was about one-quarter of the field estimate. A swimming speed of 4 cm s\(^{-1}\) appears most plausible of those we tested. Studies of preferred compass orientation have been done for sockeye salmon smolts in freshwater, but none has been done on smolts that have...
Table 3. Proportion of model smolts that entered the western migratory route (came within 2 km of the western side of the Strait south of Nanaimo) and their mean time to enter the western route after exiting from the Fraser River, as simulated under 1984 physical forcing. The range of daily mean times is in parentheses.

<table>
<thead>
<tr>
<th>Swimming speed (cm s⁻¹)</th>
<th>Orientation (true)</th>
<th>Proportion of smolts entering the western route</th>
<th>Mean time to reach western route (days)</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>West</td>
<td>0.17</td>
<td>20.5 (1.5–53.8)</td>
</tr>
<tr>
<td>4</td>
<td>West</td>
<td>0.15</td>
<td>4.8 (1.1–9.7)</td>
</tr>
<tr>
<td>4</td>
<td>North-west</td>
<td>0.10</td>
<td>7.0 (1.3–17.8)</td>
</tr>
<tr>
<td>4</td>
<td>North</td>
<td>0.02</td>
<td>5.6 (2.8–11.6)</td>
</tr>
<tr>
<td>8</td>
<td>West</td>
<td>0.25</td>
<td>3.5 (0.8–6.7)</td>
</tr>
<tr>
<td>8</td>
<td>North-west</td>
<td>0.05</td>
<td>4.2 (1.3–8.3)</td>
</tr>
<tr>
<td>8</td>
<td>North</td>
<td>0.01</td>
<td>3.9 (1.9–6.1)</td>
</tr>
<tr>
<td>24</td>
<td>North-west</td>
<td>0.06</td>
<td>1.3 (0.8–3.1)</td>
</tr>
</tbody>
</table>

reached salt water (Dr C. Groot, personal communication). The simulations have helped narrow the most likely range of orientation to northward or northwestward.

However, we cannot completely rule out other behaviours because the addition of assumptions such as salinity preferences, vertical diet migration, 'tide-hopping', or variation among individuals that would lead to 'spatial diffusion' may change the dynamics predicted with a particular set of simulated behaviours. Diffusion would increase the spread over space in the distributions of fish shown in Figs. 5 and 6. 'Tide-hopping' behaviour is suggested by Groot et al.'s (1985) data, which show a significantly higher catch rate in samples taken on flood tides (heading northward) than ebb tides, reflecting the tendency of fish to be up near the surface when the current is moving in their preferred migratory direction.

Furthermore, the compass orientation we used was too simple because some simulated migrating fish became trapped in the complex coastal inlets of the Strait of Georgia. Actual smolts must therefore have some mechanism for avoiding such areas, perhaps in a manner similar to that postulated by Pascual and Quinn (1991) for returning adult salmon to avoid these same inlets.

However, all of these simplifications of our analysis will not change our general conclusion that the migration route of juvenile Chilko Lake sockeye salmon can be influenced by the interaction in time and space between surface currents and migration of fish into the Strait of Georgia.

Future analyses will extend the results presented here to hindcast, from 1951 to the present, the proportion of Chilko Lake sockeye salmon smolts migrating via the western route, and allow comparison of proportion with the smolt-to-adult survival rate. In addition, our results from the 1984 and constant wind/discharge simulations will help define an appropriate index for predicting the smolt-to-adult survival rate. Such an index would be based on the occurrence of south-eastward wind events relative to the timing and abundance of smolt entry into the Strait of Georgia.

Another future step could take into account trophic dynamics so that the smolt migration model includes predator and prey effects on smolts within the Strait of Georgia (e.g. Parsons and Kessler, 1986). This would provide a means of calculating the dynamics of differential survival and growth of fish that migrate through different parts of the Strait. A first step in this direction has been made by St. John et al. (1993), who simulated the dynamics of nutrients and primary productivity in the Strait. Further work is needed to add the next trophic levels to this model.

ACKNOWLEDGEMENTS

Funding was provided by the Ocean Production Enhancement Network, one of Canada’s Networks of Centres of Excellence, with grants to R. Peterman, P. LeBlond, and C. Walters. Very fruitful discussions with K. Cooke, C. Groot, P. Harrison, M. Henderson, C. Levings and M. St. John helped develop our hypotheses and define the simulation experiments. We also thank Josh Korman and the anonymous reviewers for useful comments on the manuscript.
REFERENCES


Match/mismatch predictions of spawning duration versus recruitment variability

G. Mertz AND R. A. Myers
Science Branch, Department of Fisheries and Oceans, Northwest Atlantic Fisheries Centre, PO Box 5667, St. John's, Newfoundland, Canada A1C 5X1

ABSTRACT
According to the match/mismatch hypothesis, larval fish survival and eventual recruitment is dependent on the offset time between the peaks of abundance of larvae and their planktonic prey. A rudimentary larval food supply model is developed to determine the dependence of food availability on the mismatch between peaks. The model predicts that recruitment variability should increase as spawning duration decreases, a result which is moderately supported by an analysis of Atlantic cod (Gadus morhua) data.

Key words: Atlantic cod, larvae, recruitment, match/mismatch hypothesis

INTRODUCTION
The match/mismatch hypothesis of Cushing (1969, 1982, 1990) has proved to be an influential guide to thinking about year class success and its variability in marine fish populations. Cushing posits that the closeness of the temporal match between the abundance peaks of larvae and their planktonic prey controls larval mortality, either because of the vulnerability of first-feeding larvae to starvation or due to the fact that poorly fed larvae grow slowly and are more susceptible to predation. Since larval mortality is thought to be very high, the larval stage may be the principal determinant of year class strength. This picture seems very plausible, and it enjoys some empirical support (review: Cushing, 1990).

Cushing (1990) has noted that the effect of variable and unpredictable timing of the plankton peak will be mitigated if a fish stock spreads its spawning effort over a broad temporal window. In order to evaluate how effective this measure might be in reducing the variability of plankton available to the larval fish, we will develop a rudimentary food supply model. This corollary of the match/mismatch hypothesis also suggests that there might exist a relationship between the width of the spawning window (the standard deviation of the estimated egg production versus time curve), for a given stock, and its recruitment variability.

Following a discussion of the data required for our study, the food supply model will be developed. Next we will apply the model to assessing the likely significance of stock-to-stock variations in the width of the spawning window. We will also empirically test for a relationship between recruitment variability and the width of the spawning window. Crude model-based estimates of the variability of larval stage cumulative mortality will be compared with corresponding estimates derived from research surveys. In the final section the results will be summarized.

DATA AND ANALYSIS
For the applications of the model which follow in a later section, we will require information on the temporal widths of the curves of plankton abundance and spawning intensity and estimates of the interannual variability in the timing of the peaks of these curves. We will limit our study to fish stocks and plankton species of the North Atlantic and environs. Many of the standard fishing zones referred to below are shown in Fig. 1: these are NAFO (Northwest Atlantic Fisheries Organization) zones. (The region shown has been selected to identify the less familiar fishing zones.) The methods for extracting the required quantities are described in this section.

Spawning data
Here, we will assume that the temporal width of the larval production curve can be represented by the width of the egg production curve. (The dates of the egg and larval peaks may jointly vary from year to year, perhaps under the influence of temperature, an effect which will inflate the width estimate; this factor is discussed at the end of this subsection.) Proxy egg production as a function of time will be estimated from maturity data or from planktonic egg surveys. We will exclusively exam-