Evidence for Navigational Sensory Capabilities of Yearling Chinook Salmon

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Yearling Chinook salmon (*Oncorhynchus tshawytscha*) from the Columbia River enter the ocean after one year in freshwater and quickly migrate north (Peterson et al. 2010). Although general migration patterns have been suggested (Weitkamp 2010; Tucker et al. 2011) and several environmental correlates determined (Bi et al. 2007; Burla et al. 2010a; Peterson et al. 2010; Burke et al. 2013; Miller et al. 2013), we do not have a comprehensive understanding of the early ocean ecology of these juvenile salmon. One of the more difficult aspects of studying juvenile salmon ocean ecology is the behavioral responses to environmental stimuli. For example, what cues do salmon use to orient during migration? If fish make decisions so as to maximize their growth rate (a logical objective, given that mortality is size-dependent (Arendt 1997)), would this strategy result in the growth rates and spatial distributions we observed empirically? Although waters off of Alaska tend to be more productive than areas near Oregon and Washington, fish leaving the Columbia River have no cognitive knowledge of this fact. Is a northward migration therefore an evolved strategy? If so, what role does local environmental variability play in migration?

As a first step towards addressing these complex questions, we created an individual-based model in a coupled Eulerian-Lagrangian framework to simulate fish movement through a virtual environment (Willis 2011; Burke et al. In Review). Specifically, we used the output from a Eulerian hydrodynamic model as the virtual environment and created a Lagrangian individual-based model (IBM) that allowed individual fish movements and behaviors. This model is intended to (1) distinguish between feasible and unrealistic behaviors, under constraints of coastal currents, outmigration timing, and fish size and (2) evaluate various feasible migration behaviors by comparing simulated spatial distributions to observed distributions.

The model was driven by environmental and individual fish-level variables. Environmental input data (three-dimensional flow, temperature, salinity, bathymetry) were obtained from the Virtual Columbia River modeling system (Baptista et al. 2008), which is based on the 3D finite element circulation code SELFE (Zhang and Baptista 2008) run with realistic bathymetry and river, ocean, and atmospheric forcing (Burla et al. 2010b). Chlorophyll *a* concentration was obtained from a satellite via the NOAA CoastWatch Program and NASA's Goddard Space Flight Center, OceanColor Web (http://coastwatch.pfel.noaa.gov, "Chlorophyll-a, Aqua MODIS, NPP, 0.05 degrees, Global, Science Quality*" downloaded March 13, 2012).

Mortality was high in this stage of the salmon life cycle, but we had insufficient information to parameterize mortality mechanistically. Therefore, all simulated fish are survivors of the first three months in the marine environment.

Each simulation started 12:15 am on April 1 and ran through midnight on July 1. At the start of a simulation, we generated 10,000 virtual fish and assigned initial values for outmigration date and a three dimensional location. Fish sizes (μ = 155 mm, SD = 15 mm) and outmigration dates (μ = May 15, SD = 10 days) were drawn randomly from normal distributions, roughly matching data collected in the Columbia River estuary (Weitkamp et al. 2012). Starting locations were just inside the Columbia River mouth (46.2482 °N, 124.0759 °E) at randomly and uniformly assigned depths within the top 10 m. The model time step was 15 min.

We defined five distinct behavioral rules (Table 1) to determine whether simple and efficient behaviors were sufficient to match simulated fish distributions with empirical data or whether more complex and energetically costly behaviors were required. The null behavior, PP, assumes fish are passive (Willis and Hobday 2007; Brochier et al. 2008) and serves as a particle tracer of ocean currents. Two behaviors allow for vertical migration: OT maintains fish at the depth closest to their optimum temperature for growth (we used 12°C, which was the upper range found by Hinke et al. (2005)) and OF allows fish to selectively adjust depth within the top 20 m to maximize passive northward movement. To tests results from similarly coupled oceanographic and IMB models that showed swimming with or against the currents could be a successful strategy (Booker et al. 2008; Mork et al. 2012), we tested rheotaxis (RP). Although we report results for just positive rheotaxis, we also ran simulations using negative rheotaxis. However, ocean currents in this region are predominantly southern in the springtime and negative rheotaxis was obviously not a viable strategy. Finally, behavior SX simulates active northward swimming (three swim speeds were simulated: 0.3, 0.5, and 0.9 bl·s⁻¹) independent of the local environmental conditions.

Table 1. Simulated movement behaviors.

Behavior ID	Behavior	Description
PP	Passive Particle	No active swimming, passively drift with ocean currents
OT	Optimize Temperature	Migrate vertically each time step to the depth closest to 12°C. Optimal temperature during the first summer at sea is probably between river temperatures (~ 15°C) and temperatures observed for subadults (8 - 12°C, Hinke et al. 2005)
OF	Optimize Flow	Similar to selective tidal transport; migrate vertically each time step to depth of greatest northward flow within the top 20 m
RP	Rheotaxis (positive)	Swim at a constant rate (0.5 bl·s^{-1}) each time step in the same horizontal direction as the ocean current
SX	Active Northward Biased Migration	Actively swim northward along the coast. Separate simulations were run where using swim speeds of X = 0.3, 0.5, or 0.9 bl·s^{-1}. Mean swim direction was 8° west of north. An Ornstein-Uhlenbeck process was used to alter the swim angle each time step to bring fish back towards the 28.5 km-from-shore migration route.

Yearling Chinook salmon from the Columbia River are consistently captured in a longitudinal band less than 0.5° wide along the Washington coast, but our efforts to mechanistically model such a narrow migration corridor were unsuccessful. As the northward migration was our primary focus, we simplified the model by creating an attraction to a specific east-west location (28.5 km from shore) using an Ornstein-Uhlenbeck process. In this framework, fish swam at a mean angle of 8° west of north (approximately along the coastline), but this angle was adjusted at each time step back towards the attraction location.

We used yearling Chinook salmon catch data from an ongoing NOAA Fisheries survey (Peterson et al. 2010) to test the model. This survey is conducted annually in May, June, and September. Few yearling Chinook salmon are caught in September, so we compared simulated spatial distributions to survey data from May 26th and June 26th (the midpoints of survey cruises). We calculated a kernel density of simulated fish locations using the kde2d function in the MASS package of R (Venables and Ripley 2002; R Development Core Team 2011) to summarize model results. Due to limitations of the time to run simulations and the quantity and quality of data on juvenile salmon distribution, we restricted the analysis to migration years 2003, 2004, and 2008, which represent a range of both salmon survival and oceanographic conditions (Tomaro et al. 2012). Details on survey methods and gears used to obtain the fish distributions are available in Brodeur et al. (2005).

Out of five biologically possible migration behaviors for yearling Chinook salmon during their first three months at sea, our analysis indicates only one or two are plausible. Ocean currents off the coast of Washington in spring, which are predominantly from the north, prevent fish with most of the behaviors from heading north. In fact, most behaviors resulted in fish moving south and far offshore of the Oregon coastline in a large offshore eddy, with very few able to counter the strong southward flows.

The behavior sets that produced spatial distributions most similar to observed distributions were month-specific. For May, OF (optimize flow) and SX (active northward biased migration) fit the observed distributions equally well (Fig. 1), suggesting that salmon modified depth to avoid the strongest southerly ocean currents. For June, only active swimming produced a reasonable spatial overlap with observed distributions (Fig. 1); the OF strategy could not maintain northward movement in June. Interestingly, for a given year, the best swim speed was the same in both months.

The swim speed required to match empirical distributions varied among years. In 2004, when southward currents were relatively mild, swimming at 0.3 bl·s^{-1} matched quite well the observed distributions. In contrast, swimming 0.9 and 0.5 bl·s^{-1} was required to match observed distributions in 2003 and 2008. The consistent distributions of juvenile salmon along the coast of Washington in spring and summer can only be achieved if using year-specific, northward-biased migration behaviors. This suggests that in addition to a compass sense, salmon have a map sense of location and adjust their speed to achieve a consistent migration rate independent of the ocean current speed.
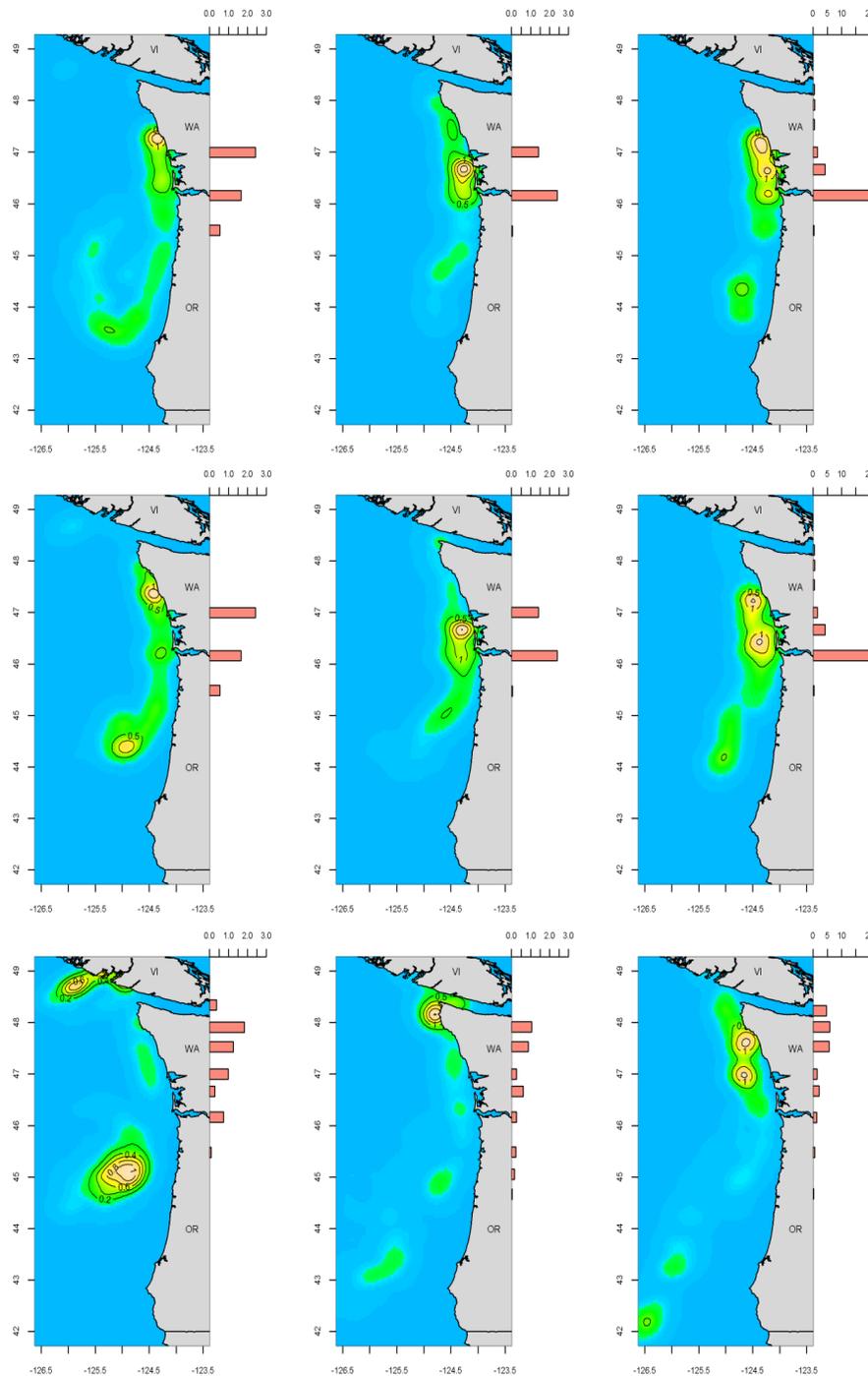
Fig. 1. Best models for May (top row, middle row) and June (bottom row) for 2003 (left column), 2004 (middle column), and 2008 (right column). Black bars represent the mean catch of yearling Chinook salmon in our surveys.

The spatial variance of the simulated fish was higher than for the observed fish (data not shown) suggesting actual fish have greater control of their migration behavior than expressed in our model. For example, simulated fish caught in an eddy south of the Columbia River were quickly transported south and offshore, yet it is quite rare to find yearling Chinook salmon from the Columbia River south of the river mouth (Peterson et al. 2010). This suggests that fish out-migrating from the Columbia River make location-specific behavioral adjustments to avoid entrapment in such eddies. Additionally, yearling Chinook salmon may increase their swim speed through time (Tomaro et al. 2012), reducing overall variance in location as later migrants catch up to early migrants (a behavior not in the model).

We did not test an exhaustive list of behaviors. For example, simulating positive rheotaxis with much higher swim speeds may bring simulated fish further north. Nor did we combine behaviors. It is plausible that salmon minimize southward movement through vertical migrations (avoiding the highly dynamic surface water when it flows south strongly) as a minor component of their migration strategy. Combining behaviors would not change our conclusion that salmon must swim north, but it could alter the swim speeds required to match observed spatial distributions. It is also likely that fish optimize local conditions to some extent, such as thermoregulation via vertical migrations. Studies conclusively show yearling Chinook salmon associated with certain environmental characteristics, which indicates some level of behavioral adjustment to local conditions (Bi et al. 2007; Yu et al. 2012; Burke et al. 2013). However, we did not test for combinations of behaviors and cannot currently estimate the impact of multiple behaviors on spatial distributions.

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