

A model of the ocean migration of Pacific salmon

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Abstract

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Salmon migration on the high seas is poorly understood in comparison with freshwater migration. This thesis describes a model of the oceanic phase of adult Pacific salmon homing migration that combines advection by ocean currents with fish swimming behavior to model trajectories of salmon. The behavior rules are based on possible responses to components of the earth's magnetic field, and the ocean currents are simulated by a numerical ocean model. The model is used to examine spring run Chinook salmon returning from the high seas to the Columbia River, including the effects of interannual variability in ocean currents and what variability among stocks in arrival timing suggests in terms of probable ocean distributions. Examining the parameter sensitivity, the strength of response to the magnetic field (how directly north or south a fish swims in response to departures from the home value) is an important determinant of successfully navigating back to the river mouth from a wide variety of locations, while the migration initiation date is the key parameter determining the east-west center of successful starting locations. Comparing potential components of the magnetic field to use as directional mechanisms, inclination outperforms intensity due to smaller navigational errors from secular variation, more stable isocline bearings, and less sensitivity to home angle. However, both components succeed in returning fish to the river mouth from a wide spatial range and are plausible direc-

tional mechanisms. The number of years spent at sea is a predictor of relative arrival timing. Thus age composition is an important factor in timing at the stock level and potentially also at the run level. Early stocks have more compact timing than later stocks, which could be due to a distribution of migration initiation dates with greater variance for the later stocks.

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Chapter 1

INTRODUCTION

Pacific salmon (*Oncorhynchus spp.*) are anadromous fish, spawning in freshwater habitats along the west coast of North America (as well as parts of Asia) and migrating to sea to grow, before returning to their natal stream to reproduce (Figure 1.1). Salmon have a complex life cycle that varies between and within species and begins with embryos developing in gravel in freshwater. In the spring, fry emerge from the gravel and may go to sea immediately or rear in freshwater habitats ranging from streams to lakes up to a year or more. Most growth takes place after migration to the ocean, with residence time ranging from a few months to several years. Salmon then complete a return migration to their natal stream where they spawn and die. Although the chemical-cue-based olfactory system salmon use to migrate in freshwater from the river mouth to their natal site is well understood, there is less experimental evidence for which sensory mechanisms salmon use for ocean migration (Dittman and Quinn, 1996). The goal of this thesis is to explore the sensory mechanism used by adult salmon migrating homeward in the ocean.

The Columbia River is home to most species of Pacific salmonids: Chinook salmon (*O. tshawytscha*), chum salmon (*O. keta*), coho salmon (*O. kisutch*), sockeye salmon (*O. nerka*), and steelhead (*O. mykiss*). This thesis focuses on Chinook salmon in particular. Chinook salmon populations are found in the upper and lower Columbia River, the Willamette River, and the Snake River. Chinook salmon have a varied life cycle with some populations (“ocean-type”) immediately going to sea the same year they emerge and others (“stream-type”) rearing in freshwater for one year before migrating. After spending one to five years at sea, some maturing Chinook salmon

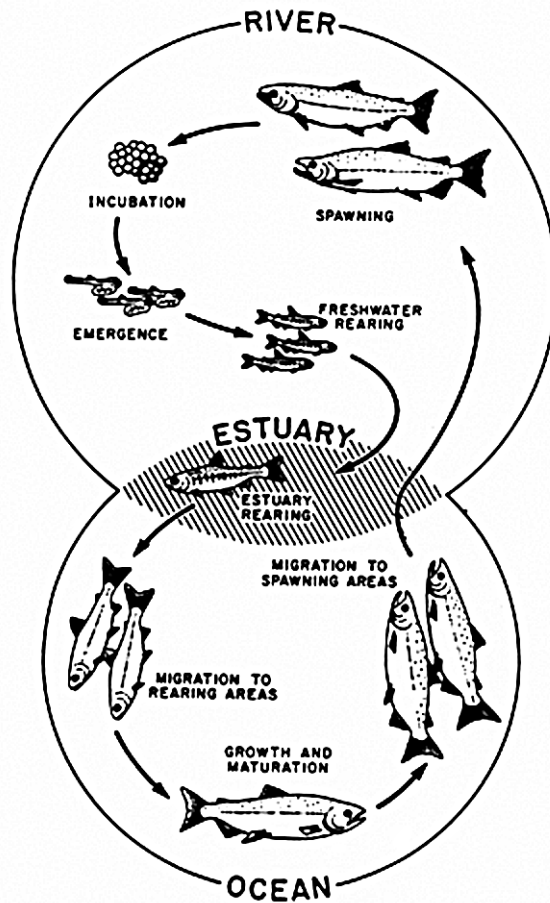


Figure 1.1: The salmon life cycle. Source: University of Washington Research & Teaching Hatchery (<http://www.fish.washington.edu/hatchery>).

populations return early—spring run (February to May) and summer run (June to July)—and others return later—fall run (August to October), though all are fall spawners. In general, spring Chinook are stream-type, and fall Chinook are ocean-type (Quinn, 2005).

The northward flowing Alaska Coastal Current (which may combine with the Davidson Current) is strongest in the winter and weakest in the summer, and is out of phase with the southward California Coastal Current. The coastal shelf surface currents from Point Conception to the Strait of Juan de Fuca flow southward from

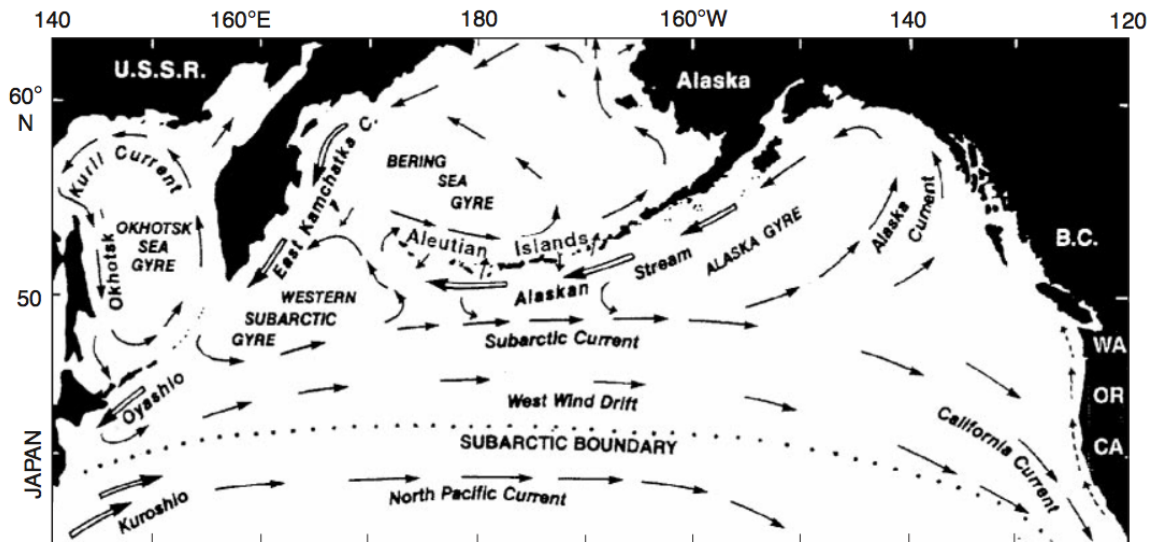


Figure 1.2: Schematic surface circulation of the North Pacific relative to 1000 db (i.e., assuming no flow near a depth of 1000 m) showing the Alaska and California Current systems. (From Hickey and Royer (2001), adapted from Thomson (1981).)

early spring to summer and northward the rest of the year (Hickey and Royer, 2001; Figures 1.2 and 1.3). Run types of Chinook salmon returning in the spring, summer, and fall encounter different coastal currents due to intraannual variability. Stream-type juveniles migrating out to the ocean in the spring encounter rapidly changing conditions in the ocean. Ocean-type juveniles, on the other hand, may rear for extended periods in the river and estuary, so they do not necessarily enter the ocean in the spring.

1.1 Spring Chinook Ocean Distribution

Healey (1983) hypothesized that spring Chinook are distributed mostly beyond the continental shelf in the open ocean during ocean residence, while fall Chinook have a more coastal distribution along the continental shelf. Partly supporting this, Sharma (2009) found that the ocean distribution of interior populations (upper Fraser, upper

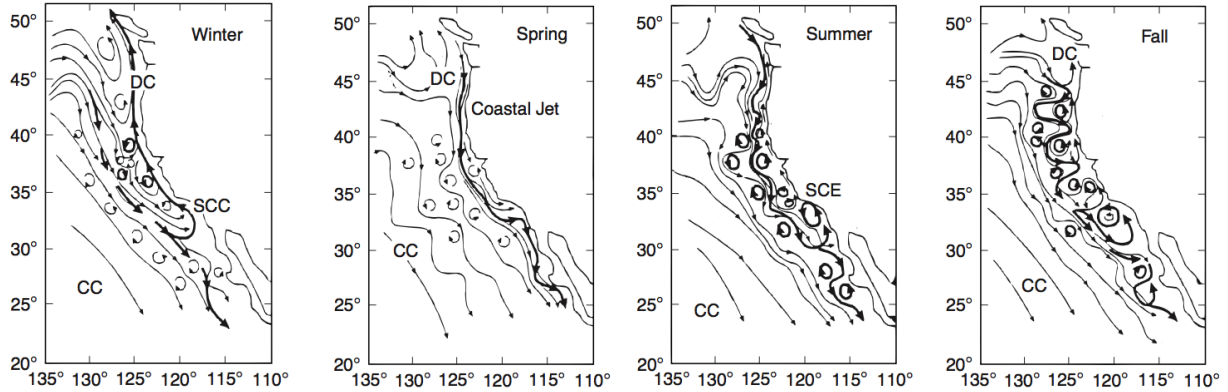


Figure 1.3: Schematic illustrating seasonal variation of large-scale boundary currents and coastal currents off the west coast of North America. CC, California Current; DC, Davidson Current; SCC, Southern California Countercurrent; SCE, Southern California Eddy. (From Hickey and Royer (2001), adapted from Strub and James (2000).)

Columbia, and Snake) of spring Chinook was primarily oceanic, while coastal and downriver populations overlapped more with fall Chinook and had a more coastal ocean distribution. The marine fisheries in the Pacific Northwest are along the continental shelf and thus catch coastal-oriented fish, while the terminal fishery in the Columbia River catches both coastal- and ocean-oriented fish. In fact, 100% of recoveries for upper Columbia (Leavenworth Hatchery) and Snake River (Dworshak hatchery) from 1977–2000 brood years were in the terminal fishery (Sharma, 2009). However, the ocean distribution of interior Columbia River spring Chinook is not so clear cut. In a mark-recovery study covering two brood years of Columbia River spring Chinook, Wahle et al. (1981) found recoveries of 48.5% in coastal marine fisheries, 6.4% in terminal fisheries, and 45.1% at hatcheries for Snake River salmon (though the recoveries for upper Columbia River were 7.4%, 67.8%, and 24.8% respectively). Using coastwide harvest data from the Pacific States Marine Fisheries Commission, Waples et al. (2004) found, like Sharma (2009), all interior stream-type (spring-run) populations range widely offshore, while ocean-type (fall-run) populations tend to

remain on the continental shelf. Additionally, marine distribution patterns appear to be the most genetically invariant, with more limited evolvability than run timing or smolt age (Waples et al., 2004). Different recovery patterns of transplant and local hatchery stocks released at the same location provide further evidence for the genetic control of marine distribution (Weitkamp, 2010). Even for the lower Columbia Chinook, where the spring run has a more similar ocean distribution to their nearby fall run counterparts (Waples et al., 2004; Sharma, 2009), only the spring run fish have been found in the bycatch of the Alaska groundfish fishery in the Bering Sea, Aleutian Islands, and Gulf of Alaska (NMFS, 2008). However, finding Columbia River Chinook in the Bering Sea is a rare occurrence, and they are considered to be generally located in the Gulf of Alaska, closer to their natal river (NMFS, 2008; Myers et al., 1987).

Where in the open ocean are spring Chinook salmon when starting their homeward migration? This thesis seeks to shed some light on that mystery. A better understanding of the navigational mechanisms salmon employ could clarify the direction of return as well as the ocean location and date when they begin their return migration. This could be useful both for a better understanding of the natural history of the species as well as for management, where predictions of run timing and size are important. Currently, with only information on arrival timing in the river available, space and time are confounded. An early distant migration start cannot be differentiated from a late nearby migration start, as both could arrive in the river on the same date.

In order to investigate the possible ocean distribution and migration mechanisms, assuming an offshore rather than a coastal ocean distribution, we can employ a model. To be informative, the model needs to include both advection by ocean currents as well as fish swimming behavior to model salmon trajectories. Before going into detail on the model, let us first consider previous models that have been used.

1.2 Previous Models

Royce et al. (1967) conceived one of the earliest descriptive models of salmon ocean migrations, discussing probable migratory paths of pink salmon (*O. gorbuscha*) and Bristol Bay sockeye salmon based on catch and tag data from the 1950's and 1960's. They described circular migration routes following the major currents and speculated on possible guidance mechanisms, favoring orientation to electromagnetic cues over a sun compass or orientation to current. Additionally, they thought migration was oriented rather than random and inherited rather than learned. French et al. (1976), also based on 1950's and 1960's research surveys, provided descriptive models for different sockeye salmon populations and hypothesized a counterclockwise circuit around the Gulf of Alaska each year at sea. Major et al. (1978) described the ocean distribution of Chinook salmon as primarily coastal during the first summer and fall at sea and then widely distributed. For example, a maturing Chinook salmon tagged near Adak Island was recovered in the Columbia River, a distance of 3800 kilometers.

Saila and Shappy (1963) proposed a random search model for the return migration of salmon, which Jamon (1990) updated to incorporate a one-dimensional random search once the coast is encountered. However, Quinn (1991) strongly critiqued the random search model for being inconsistent with empirical information on salmon migration, such as evidence indicating non-random movement by maturing salmon, observations that salmon make landfall in specific locations rather than broad swaths of coast, and that they never wind up on the Asian coast as an initial random angle would predict. Instead, Quinn (1991) argued that any model of salmon ocean migration should result in a well-timed arrival in a specific coastal region with a high rate of travel starting from a wide distribution in the ocean, and that current patterns and interannual variations should also be considered.

More recently, several computer models were created for salmon migration. NerkaSim (Rand et al., 1997) is a spatially-explicit, individual-based model of Fraser River

sockeye salmon in the eastern North Pacific which combines information on current, sea-surface temperature (SST), and zooplankton density with a bioenergetic model, alternative migration strategies, and mortality processes. Walter et al. (1997) used NerkaSim to examine possible behavioral mechanisms underlying salmon migration in the ocean. Walter et al. (1997) considered ocean currents and fish swimming behavior when modeling ocean migration of Fraser River sockeye salmon, and compared it to the standard accepted model of French et al. (1976). They found their model of a northwest heading the first four months, followed by random swimming to be as good as French et al.'s annual loops at agreeing with the (admittedly spotty) empirical data, casting doubt on French et al.'s assumption of annual circuits around the Gulf of Alaska. However, they considered only alternate models that assume the salmon maintain various compass headings at different times of year, and did not include any other possible navigational cues. In a complementary study, Thomson et al. (1992) examined the effect of ocean currents on the landfall latitude of home-migrating Fraser River sockeye salmon. They considered several swimming speeds, compass orientations, and migration start dates, and found that a stronger Alaska Gyre resulted in a more northerly deflection. Their results did not support random-swimming or a weak orientation as a homing mechanism, but argued instead the need for some type of navigation to enable salmon to complete their ocean migration. Thomson et al. (1992) also hypothesized that a single compass orientation is not sufficient unless specific stocks have different distributions in the Gulf of Alaska, due to the large impact of start location and migration timing on landfall location. A similar study (Thomson et al., 1994) examined the effect of ocean currents on run timing and found migration start location to be an important factor. Dat et al. (1995) also modeled the homeward migration of Fraser River sockeye salmon. They concluded that compass orientation was a sufficient guidance mechanism and found that the model that delayed migration until the last month at sea provided the most accurate homing and most bioenergetically efficient estimated swimming speed.

Healey et al. (2000) evaluated the effect of the Sitka eddy on migrating salmon (a mesoscale eddy not modeled by OSCURS, see Section 2.2) and found that fish modeled with compass orientation alone (as opposed to bicoordinate navigation or rheotaxis) took a bioenergetically near-optimal path through the eddy and that the eddy minimally deflected salmon. Because the Sitka eddy is another factor contributing to return time variance (both interannually and intraannually, with the former depending on whether it forms and the latter depending on the route different fish take), they also concluded that some mechanism must exist to maintain the fairly tight run time window. More recently, Booker et al. (2008) modeled the trajectories of fifteen Atlantic salmon (*Salmo salar*) with known release and recapture points, and investigated three direction-finding mechanisms: random-walk, rheotaxis (aligning movement to the prevailing current), and thermotaxis (moving to the preferred temperature along the temperature gradient), all with a constant velocity. Both rheotaxis and thermotaxis performed much better than random-walk, with rheotaxis more closely corresponding to recapture sites than thermotaxis.

1.3 Salmon Sensory Abilities

Previous models have assumed various navigational mechanisms, such as compass orientation, bicoordinate navigation, thermotaxis, and rheotaxis. Let us now turn to what evidence exists for these and other salmon sensory abilities, to determine which to include when developing a behavior-driven model.

1.3.1 Magnetoreception

The earth’s magnetic field can provide two types of information: compass information, which allows an animal to maintain a particular heading (e.g., north), and geographical position, which allows an animal to navigate complex routes or find home. Geographical position could in theory be determined from inclination angle or field intensity, or by the animal learning the local anomalies in its location. There are three

hypotheses for how magnetoreception works in animals, as summarized by Johnsen and Lohmann (2005): electromagnetic induction, magnetic field-dependent chemical reactions, and biogenic magnetite. However, direct evidence does not exist for any hypothesis. The mechanism for magnetoreception believed to be used by salmon, biogenic magnetite, comes in two types: single-domain magnetite, which are permanently magnetized crystals that rotate into alignment with the earth's magnetic field, and superparamagnetic magnetite, which are smaller crystals that are not permanently magnetized so they will not rotate, but the crystal's magnetic axis tracks the ambient field's axis. Single-domain magnetite mechanisms can detect polarity, while superparamagnetic magnetite mechanisms cannot. However, both can detect small changes in intensity as the basis of a magnetic map sense. The evidence for magnetoreception in salmon is based on juvenile salmon studies, but compass orientation has been used in many models of adult salmon. Several (Neave, 1964; Larkin, 1975; Quinn, 1982; Walker et al., 1997) have proposed magnetic map sense for salmon based on the complexity as well as how well-timed and well-directed their migration is. However, some models have achieved good results with compass orientation alone (Pascual and Quinn, 1991; Dat et al., 1995). Lohmann et al. (2008) proposes a variation on the magnetic map sense in which salmon imprint on the inclination or intensity of the magnetic field at the mouth of their home river, which provides the y coordinate on the North-South axis, while the coastline determines the x coordinate on the East-West axis. Imprinting on the magnetic field at a critical juncture before heading to sea is also proposed by Quinn (1982) as an alternative to a magnetic map based on inclination and declination.

A magnetic map sense has been demonstrated with displacement studies in animals such as lobsters (Boles and Lohmann, 2003), newts (Phillips et al., 2002), and sea turtles (Lohmann et al., 2001). Sharks have been shown to detect earth-strength magnetic fields (Meyer et al., 2005). Additionally, Wiltschko and Wiltschko (2005) give examples of birds and turtles using field inclination and/or intensity as a 'sign-

post' in navigation. The evidence for salmon is not as clear and little work has been done with maturing salmon migrating homeward from the open ocean. Biogenic magnetite has been found in a variety of salmon species (including Chinook salmon, sockeye salmon, chum salmon, and Atlantic salmon) in ethmoid tissues, the lateral line, and parts of the head and inner ear (see references in Yano et al., 1997). Studies conducted in tanks of out-migrating juvenile salmon showed direction changes when exposed to a magnetic field (Quinn, 1980; Quinn et al., 1981; Quinn and Brannon, 1982), though not always in the expected magnitude and direction (Quinn and Groot, 1983). Yano et al. (1997) altered the magnetic field around the head (including the inner ear) of adult chum salmon in the western North Pacific and followed them using telemetry before and after the magnetic field was activated. They did not find any effect on orientation when the magnetic field was modified, but this could be due to the salmon using alternate cues or due to a temporary response to trauma such as the delay in resumption of regular diving behavior observed in tagging studies (Friedland et al., 2001).

1.3.2 Celestial Compass

In addition to information from the earth's magnetic field, another possible source for compass orientation is the sun, by means of natural or polarized light. Evidence for a celestial compass comes from tank studies of juvenile sockeye salmon (Quinn, 1980; Quinn and Brannon, 1982). In the studies, salmon maintained an appropriate heading even when the magnetic field was rotated 90° during the day with tanks open to the sky, but not at night or with covered tanks during the day. Evidence from temperature data storage tags from maturing chum salmon tagged in the Bering Sea also supports the idea of a celestial compass: salmon made the most progress (as measured by crossing temperature gradients) during the day, while night temperatures were similar and suggested salmon were near the surface (Friedland et al., 2001). Large ranges in day-time temperatures suggest the salmon could be determining headings during dives and

ascents based on either the sun or polarized light as suggested by Novales Flamarique and Hawryshyn (1993), who determined that there was sufficient UV light at depths of 15 m for navigation off the coast of Vancouver Island and that polarization was maintained under some types of cloud cover. Polarized light is an intriguing potential mechanism, as it would not be affected by cloud cover, though polarization sensitivity has not been conclusively demonstrated in salmonids (Horváth and Varjú, 2004, as cited by Cheng et al. 2006). Juvenile salmonids, including anadromous steelhead, can detect polarized light with UV light being one possible mechanism (Parkyn et al., 2003). However, Cheng et al. (2006) showed UV-sensitive cones have changed to blue sensitivity by the time salmon migrate to the ocean, suggesting the UV component of polarized light would be difficult for salmon to detect. They concluded it is unlikely UV cones play a role in polarization sensitivity of salmonid fish.

1.3.3 *Rheotaxis*

Although the idea of salmon aligning with prevailing ocean currents (rheotaxis) as a navigational strategy has long been considered (Royce et al., 1967) and continues to be incorporated into models (Booker et al., 2008), it has met with skepticism due to lack of an explanation of how salmon would detect the speed and direction of the bulk flow (Walter et al., 1997). Riverine fish salmon have been known to align to the current. However, none of the riverine cues, such as relative ground position and acceleration, are present in the open ocean. Chagnaud et al. (2008) have proposed a mechanism for the detection of flow speed and direction by fish involving the lateral line: though lateral line afferent neurons respond to flow fluctuations rather than the constant flow component, bulk flow direction and velocity might still be inferred from the cross-correlation of multiple afferent neurons. In pairs of afferent neurons that showed significant correlation, the time shift of the correlation peak decreased as flow velocity increased, and reversing flow direction resulted in a corresponding reversal of the sign of the optimal time shift. Therefore, the time shift of the correlation

between neurons can be used as a proxy for the speed and direction of the bulk flow. However, whether this mechanism translates from the laboratory to the turbulent ocean remains to be demonstrated.

1.3.4 Day Length

Salmon are known to be sensitive to daylight and display different day and night behaviors (Friedland et al., 2001). The well-timed nature of their return migration suggests an internal clock (Neave, 1964; Quinn, 1982). Archival tags (a type of tag attached to marine animals that record and store data) are able to provide geopositional estimates with an error of 140 km based on a record of light intensity levels over time, by estimating times of dawn and dusk and thus estimating latitude and longitude (Welch and Eveson, 1999). Similarly, salmon could use day length to estimate latitude, perhaps combined with a calendar based on the number of days since the summer or winter solstice, and could also estimate longitude by comparing the times of dawn and dusk to an internal clock calibrated to their home stream. Thus, dawn and dusk times could be an alternative form of bicoordinate navigation instead of or in addition to a magnetic map sense. Salmon could also use day length or the rate of change of day length (adjusted for latitude) or the count of days since the solstice as a cue for when to start their homeward migration.

1.3.5 Temperature and Salinity

Orientation to gradients of environmental variables such as temperature and salinity has also been proposed as the mechanism for salmon migration (Leggett, 1977). However, there are several problems with this hypothesis: (1) Gradients are not generally in a smooth shoreward direction; Salmon populations diverge from a common area at sea to many locations and converge from a wide area at sea to home. (2) Salmon can maintain a straight heading in the open ocean; and (3) vertical movements can cause much larger temperature swings than horizontal movements (Quinn, 2005).

Others have proposed temperature or salinity as a boundary on salmon distribution (Azumaya et al., 2007). Welch et al. (1998) examined thermal boundaries of sock-eye salmon distribution and found that salmon distribution followed a step-function response to temperature at the thermal limit. They asserted that the mechanism behind the observed step-function response to temperature is not growth maximization, but avoidance of temperatures where metabolic losses exceed gains from consumption (i.e., starvation), as salmon's basal metabolic rate increases with temperature. Thus increasing thermal limits would be expected with increasing productivity, with salmon maintaining growth at higher temperatures due to an increased food supply. On the other hand, Rand (2002) suggested that the same step-function response to temperature can be obtained under a growth-maximization hypothesis, based on a statistical model of food availability derived from salmon stomach contents data. Welch et al. (1995, 1998) argue that physiological factors keep salmon in colder waters, though Carmack (2007, p. 2594) suggests it could also be the importance of the "special suite of environmental cues-maintained by freshwater mixtures in and above the permanent halocline" to navigation. Carmack (2007) recommends an alpha/beta ocean conceptual framework, where alpha oceans are found at subtropical latitudes and are characterized by being temperature stratified, while beta oceans are found at subarctic latitudes and are instead salinity stratified. The alpha/beta ocean boundary corresponds roughly to the 10° winter isotherm, and could represent the southern boundary for salmon, which are only found in beta oceans where temperatures are 6° to 10° or colder.

Beyond these abiotic sensory inputs, salmon are believed to perform their ocean migration to access better growing conditions, which requires finding prey and avoiding predators. The spring plankton bloom could also be a migration initiation cue, and thus relate to arrival timing. Though the Gulf of Alaska does not have a classic spring phytoplankton bloom, production peaks in spring. In contrast, the coastal area from British Columbia to California is a characteristic upwelling-dominated eastern

boundary current system with production peaking in early summer and continuing through the end of the year (Longhurst, 1995). The center of abundance and life cycle timing of zooplankton vary between warm, low-productivity years and cool, high-productivity years in both the oceanic and coastal areas of the Northeast Pacific (Mackas et al., 2007), with similar patterns for phytoplankton abundance (Lipsen et al., 2007). Though an interesting potential cue, the timing of the spring bloom would only be a useful mechanism if it is correlated with the river conditions needed for migration, and it is not considered farther here.

1.4 Understanding Columbia River Spring Chinook Migration

Taking these earlier models and what is known about salmon sensory abilities, what can a model of salmon migration in the ocean that combines advection by ocean currents with behavior rules accomplish? This model gives a framework for examining hypotheses about how salmon find their way to their home river from the high seas. Though there is not enough data available on salmon during their ocean residence to conclusively determine the distribution of salmon and how they navigate homeward, it is possible to evaluate whether a proposed homing mechanism is plausible or not.

One possible use of the model is to better understand ocean migration in order to improve run timing estimates, which are important for management. To preserve genetic diversity by distributing the harvest throughout the run, it is necessary to have a forecast of the run timing and size (Anderson and Beer, 2009). Timing estimates can be also used to differentiate a small early run from a late large run, and set harvest appropriately (Keefer et al., 2008). Additionally, knowledge of migration routes could allow the implementation of a test fishery to improve preseason estimates of run timing and size. A better understanding of ocean migration would also be useful for investigating potential responses to climate change. Crozier et al. (2008) examined potential evolutionary and plastic responses of salmon to climate change, such as heat tolerance and timing of migration and spawning, but found too little is known about

ocean migration routes to conjecture which changes may occur. Predicted changes in the North Pacific from climate change include: increasing stratification in the upper ocean due to increasing temperatures; variations in the timing and intensity of upwelling due to changing wind patterns; changing food web composition due to ocean acidification; and shifts in the ocean regions most favorable for growth and survival of salmon (Crozier et al., 2008). Examining the effect of ocean environment on migration timing and the impact of possible changing migration routes are both possible from a model.

The model can also be used to examine facets of the proposed navigational mechanisms. For example, are salmon of different stocks and ages also in different locations when they start their directed migration homeward? Can the fish get back to the right location in the right window in time from anywhere in the central North Pacific? What impact do ocean currents have on the approach path or arrival timing? Given these important questions and the available information, this model seeks to provide insight into where in the ocean the spring Chinook start, their migration route, and what factors might affect timing.

Chapter 2

MODEL DEVELOPMENT

2.1 Introduction

The model is spatially explicit and uses a Eulerian-Lagrangian-agent method (ELAM) framework. An ELAM model is useful for its ability to combine multiple scales, from large-scale oceanographic processes to the small scales of individual fish decision-making, and is well-suited to modeling the dynamics of fish movement (Goodwin et al., 2006). The Eulerian framework refers to a mesh or grid where the value for a set of variables is known at each node in the mesh for each time step. Time is discrete, so calculations are made at each time step, for example, a day. These variables are quantities like current velocity, temperature, or day length. The Lagrangian framework is used to compute the continuous trajectory of the fish through space. Finally, the agent framework consists of the behavior rules that govern the fish's decision of which way to swim. At each time step, the fish determines current sensory conditions and processes these inputs according to its behavior rules, which results in an updated swimming direction. This swimming direction is combined with the ocean currents interpolated to the fish's position from the Eulerian mesh to compute its new position (Figure 2.1).

The model can calculate either a forward-in-time-trajectory (FITT) or a backward-in-time-trajectory (BITT). BITT models have been used in the atmospheric sciences to determine pollutant sources and in the oceanic sciences to determine source sites for plankton settlement locations (Batchelder, 2006). In the case of salmon migration, very good data exists for the distribution of arrival dates in freshwater (i.e., counts at Bonneville Dam), but there is much less data on ocean distribution. Using a

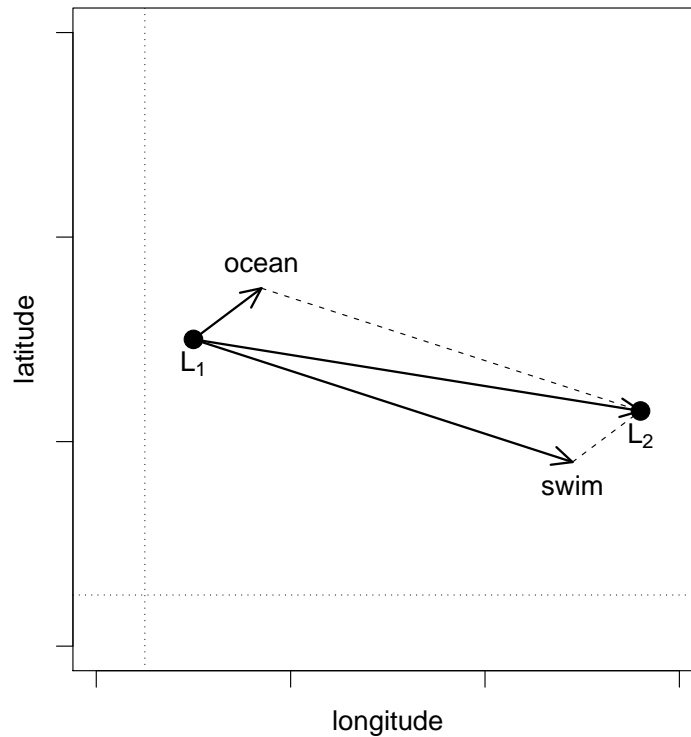


Figure 2.1: From location L_1 , the next location L_2 is computed by interpolating the ocean vector at L_1 from the Eulerian grid (shown by dotted lines) and combining it with the swimming vector, determined using the behavior rules.

BITT model, the fish begins at the known arrival time and location, then the model can run backwards to obtain a probability distribution of starting locations. The resulting distribution on the high seas can also be viewed as the relative density of salmon at different locations in the ocean when starting their homeward migration. When interpreting the probability distribution of starting locations, it is important to keep in mind that BITT models, which include stochastic processes, experience information loss, so the spread of starting locations is related to the length of the simulation (Christensen et al., 2007). Processes that are reversible, such as advection or time-dependent growth, are good candidates for BITT models, while non-reversible processes, such as diffusion, reproduction, and mortality, are better left to FITT

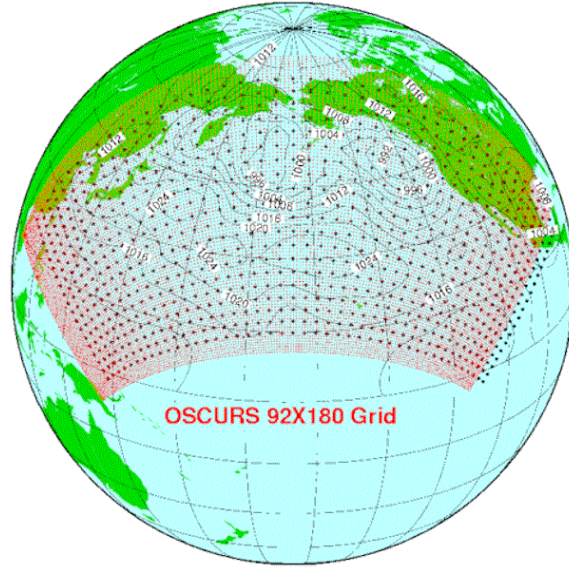


Figure 2.2: OSCURS grid. Larger dots are the 20×44 grid of daily sea level pressure, and small dots are the OSCURS 92×180 computational grid (Ingraham, 1997).

models (Batchelder, 2006). Thus only reversible behavior rules can be run backwards.

2.2 Ocean Model

The OSCURS (Ocean Surface Current Simulations) model provides daily ocean surface currents (the near surface mixed layer which extends to a depth of about 10–30 m in summer and 50–100 m in winter) for a 90 km wide grid of the North Pacific from 1901 to present (Ingraham and Miyahara, 1988, 1989). The surface currents in the model are calculated from sea surface pressure measurements used to compute wind velocities and in turn wind-induced current velocities. Those are then combined with long-term mean geostrophic currents. The model is calibrated with data derived from satellite-tracked drifters. The model does not include small-scale features such as mesoscale eddies and tides.

The OSCURS model operates on a daily time step. Though it would be possible to update the fish's trajectory more frequently, there would still be step-changes

across day boundaries without a finer-scaled ocean model. An interesting area for future research would be to calculate a continuous trajectory for each time step of the ocean model. This may or may not be feasible depending on the exact nature of the behavior rules, and whether they could be written in the form of a solvable differential equation. If not, a continuous trajectory could be approximated with very small time steps, though this could increase the simulation time. However, given the distance scale encompassed by the model and the use of a daily time step by successful previous models of salmon migration and the OSCURS model, a daily time step is used in the present model.

Though Walter et al. (1997) used the OSCURS model for the surface current inputs to their model, they found it to not be representative for continental shelf currents due to the lack of small-scale features. Instead, they used either no water movement or weak currents moving northwest parallel to the coast for points east of 155°W . West of 155°W they used the OSCURS model which accurately modeled the Alaskan stream found there. Given that spring Chinook are not thought to be coastally oriented (Healey, 1983), this deficit of the OSCURS model has less impact on the present model. In order to account for the coastal currents not being well modeled, when fish are within 50 km of the river mouth, they are considered to have arrived, rather than computing their trajectory all the way to the river mouth. For fish trajectories that intersect land, the fish are deflected back to sea if the location is west of 130°W , otherwise that location on the coast is considered the end location, though an adjusted arrival time is also computed for the river mouth based on the distance away.

The OSCURS model normally outputs the track of a particle; however, it internally calculates the surface current velocities at each point on its 92×180 grid (Figure 2.2) which are used in the present model. I ran the OSCURS model to generate daily estimated surface current velocities. Next I transformed from OSCURS's grid space to latitude-longitude, and then combined the resulting ocean vector component with

the fish swimming behavior vector component to form the fish movement vector.

2.3 Behavior Rules

The behavior rules describe how the fish processes sensory inputs in order to decide on a direction and possibly also a speed to swim. The behavior rules must be both realistic—derived from empirical knowledge of salmon sensory capabilities—and useful—allowing the salmon to complete their oceanic migration. A behavior rule can be designed in two ways: it can depend only on current conditions or it can integrate recent conditions experienced by the fish. For example, for a fish responding to temperature, the behavioral rule could be implemented as either as depending on the current temperature or as depending on the degree of change from the recent average temperature. Behavior rules depending only on current conditions have the advantage of being simpler and can be used in both FITT and BITT models. Behavior rules depending on integrating past conditions, on the other hand, can only be used in FITT models since BITT models do not have the information necessary on previous conditions experienced by the fish. However, the idea that signals, such as sound or images, must stand out from the background to be detected is well-established and known as the Weber–Fechner law (Weber, 1846; Fechner, 1907). Given a stimuli, s , the change in perception, p , can be described as $dp = k \frac{ds}{s}$. Therefore, the smallest detectable difference depends on the ratio of the change in stimuli to the background level of stimuli; the higher the background level, the larger a change must be to be detected.

2.3.1 Migration Initiation

After departing the Columbia River, juvenile spring Chinook salmon proceed rapidly northward along the coast towards Alaska (Trudel et al., 2009). After their first summer moving north along the coast, little is known about the distribution of spring Chinook salmon in the ocean. It is believed that spring Chinook are distributed in

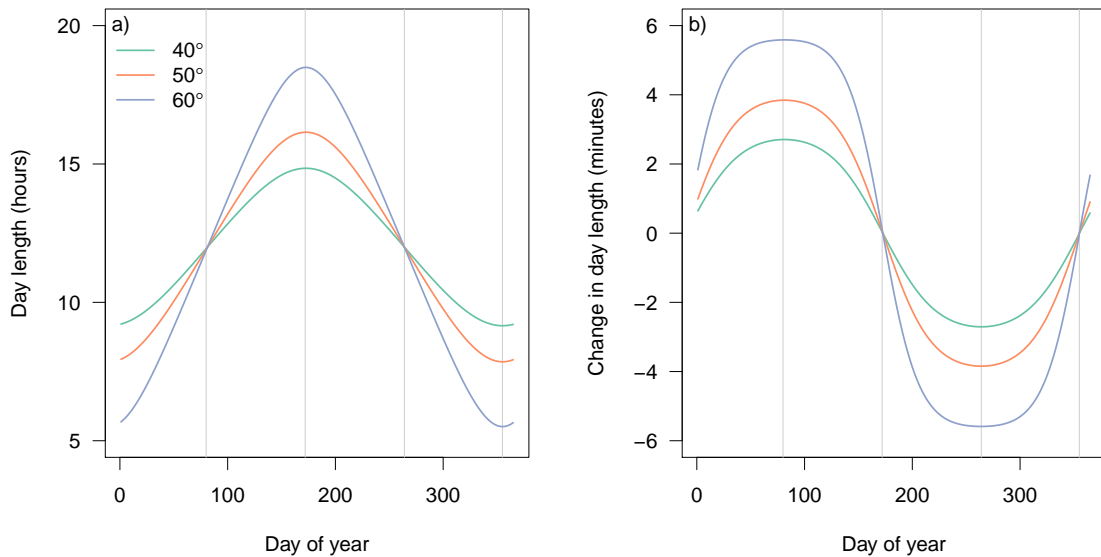


Figure 2.3: The day length (a) and rate of change in day length (b) at latitudes 40° , 50° , and 60° by day of year. The equinoxes and solstices are shown with light gray lines.

the Gulf of Alaska, moving more northwards in summer and southwards in winter (Myers et al., 2007). During this time, the salmon swim, but not in a highly directed manner, so this is modeled as passive drift with the ocean currents. At some point salmon must switch to a directed migration, during which they rapidly move towards their home river mouth (Quinn, 2005; Healey and Groot, 1987). This is modeled as a binary switch from non-directed motion to active swimming according to the behavior rules described in this section.

In order to complete their migration home, salmon must have a means of navigation as well as a means for knowing when to leave. There is evidence of both genetic control of migration timing (Quinn et al., 2000) as well as population-specific timing (Quinn et al., 2000; Waples et al., 2004). The mechanism behind migration initiation, or when a fish begins actively swimming home, is unknown. It is hypothesized that migration initiation is controlled by an internal calendar, based on circannual rhythms

and synchronized by day length (or rate of change of day length), adjusted for latitude as necessary, and is population-specific and potentially location-specific (Quinn, 1982). Note that rate of change in day length is maximized at the equinoxes regardless of latitude (Figure 2.3), which could be a cue for spring-migrating populations that does not necessitate knowing latitude.

2.3.2 *Homing*

In addition to a mechanism for the timing of migration initiation, the model also requires a mechanism by which the fish choose a swimming direction. As discussed earlier, both a compass orientation and magnetic map sense have been proposed as a mechanism for homeward migration. This model examines the version proposed by Quinn (1982) and Lohmann et al. (2008), in which salmon imprint on an element of the magnetic field at the mouth of their home river, which provides the y coordinate on the North–South axis, while the coastline determines the x coordinate on the East–West axis.

The model supports latitude, as well as magnetic inclination and total intensity as directional mechanisms. Magnetic inclination refers to the angle of the magnetic field with respect to the surface of the earth. For example, the magnetic field comes straight out of the earth at the magnetic south pole (-90°), is parallel near the equator (0°), and heads straight into the earth at the magnetic north pole (90°). Magnetic intensity refers to the total strength of the field. Latitude can be estimated from the angle and altitude of the sun at noon or from day length. In fact, archival tags are able to provide geositional estimates with an error of 140 km based on a record of light intensity levels over time by estimating times of dawn and dusk and thus estimating latitude and longitude (Welch and Eveson, 1999). However, day length is similar across latitudes near the spring and fall equinoxes, making estimation of latitude from day length problematic at that time, though archival tags provide good estimates of latitude outside a two week window around the equinox (Welch and

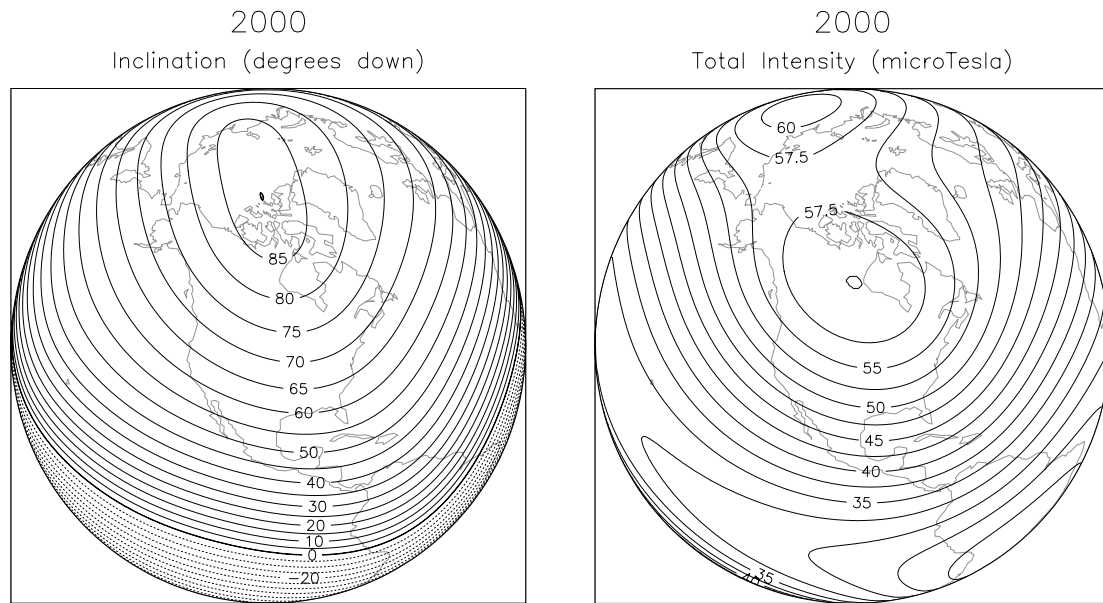


Figure 2.4: Magnetic field inclination and total intensity calculated from the IGRF model. Source: USGS (<http://geomag.usgs.gov>).

Eveson, 1999).

In the North Pacific, both inclination and intensity have isoclines that run approximately east–west and have values that increase northwards (Figure 2.4), referred to as isoclinics for inclination and isodynamics for intensity. The International Geomagnetic Reference Field (IGRF) model is an empirical representation of the earth’s magnetic field from which it is possible to get a variety of field elements, including inclination and total intensity (Macmillan and Maus, 2005). Although the magnetic field changes at a particular location over time, those changes would only cause an average navigational error of 6 km (inclination) or 31 km (total intensity) for Columbia River salmon spending 3 years at sea (Lohmann et al., 2008).

The model constrains the fish to swim generally east at an angle of 0° – 180° (measured clockwise from north), assuming salmon have a celestial compass or magnetic compass to maintain a rough heading. The directional mechanism, such as latitude,

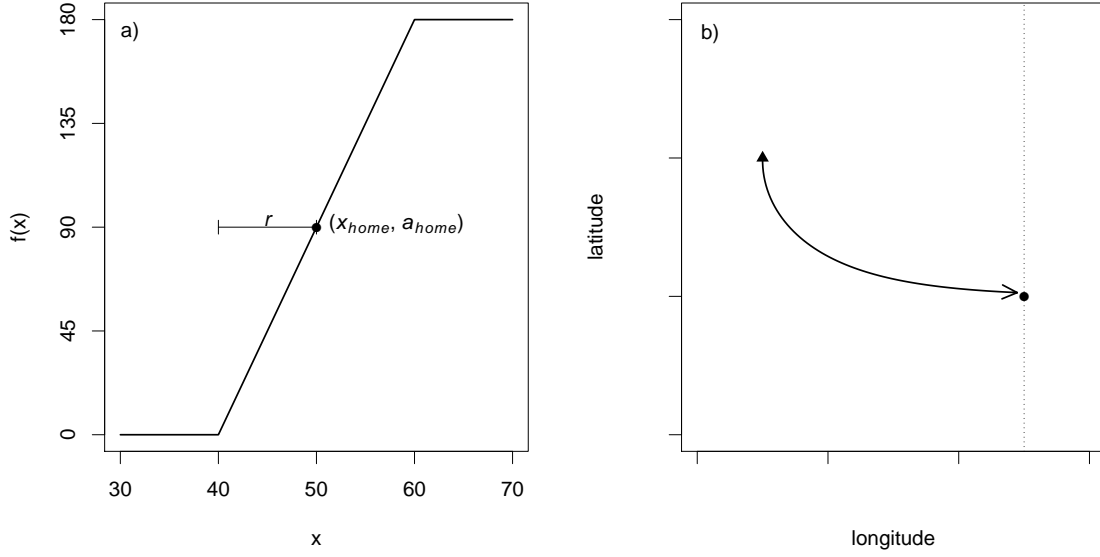


Figure 2.5: The determination of swimming angle. a) The equation for swimming angle, $f(x)$, calculated from the value of a hypothetical directional mechanism, x , when $x_{home} = 50$, $a_{home} = 90^\circ$, and $r = 10$. b) The trajectory of a fish from the starting point (triangle) to the river mouth (circle) on the coast (dotted line) for those parameters.

magnetic inclination, or magnetic intensity, is what salmon use to navigate homeward by comparing the currently detected value to the remembered home value. The home value, or target, is the value at the mouth of the river which juvenile salmon imprinted during the outward migration. The model uses the *range* parameter to determine the swimming direction from the value at the present location, and it determines how large a departure from the home value can occur before the fish will swim straight north or south. The home angle specifies the direction the fish swims when at the home value. The following equation describes the determination of the swimming angle,

$$f(x) = \begin{cases} 180 & \text{if } x > x_{home} + (180 - a_{home}) \frac{r}{a_{home}} \\ 0 & \text{if } x < x_{home} - r \\ \frac{a_{home}}{r}x - \frac{a_{home}}{r}x_{home} + a_{home} & \text{otherwise} \end{cases} \quad (2.1)$$

where $f(x)$ is the swimming angle in degrees measured clockwise from north, x is the current value which is assumed to increase to the north, x_{home} is the home value, a_{home} is the home angle, and r is the range. In the simple case where $a_{home} = 90^\circ$, the equation for swimming angle reduces to

$$f(x) = \begin{cases} 180 & \text{if } x > x_{home} + r \\ 0 & \text{if } x < x_{home} - r \\ \frac{90}{r}x - \frac{90}{r}x_{home} + 90 & \text{otherwise} \end{cases} \quad (2.2)$$

and is shown in Figure 2.5.

While introducing random variation to the heading was considered to account for error in the fish's perception as well as maintaining a heading, it was not included in the model for two reasons. First, including variation by adding white noise (such as normally distributed error with a mean of zero) does not change the trajectory of a track, but only makes it more jagged so overall progress is slower. The effect is no different than decreasing swimming speed. Second, the limited empirical evidence available shows very little variation in heading on a daily time-scale like that employed in the model. Instead, most variation in heading is on a much smaller time-scale, on the order of minutes (Sturlaugsson et al., 2009).

2.4 Parameters

Table 2.1 lists all parameters used in the model, some of which are discussed in further detail below.

2.4.1 Swim Speed

For the active migration portion, fish swim speed is constant and depends on the age of the fish, since age is correlated with length and swim speed is generally a function of length. One method of representing salmon ages is two numbers separated by a period. The first number denotes the number of winters spent in fresh water, while

Table 2.1: Parameters and their most common values used in the model.

Parameter	Value
Start location	Various (42°N–60°N, 128°W–180°W)
Direction mechanism	Inclination and intensity
Home value	Value at (46.25°N, 124.05°W) in out migration year
Home angle	110° for inclination and 117° for intensity
Range	1° for inclination and 1000 nT for intensity
Variance	0
Migration initiation	March 21 (Dworshak Hatchery) April 21 (Lookingglass Hatchery)
Swim speed	30 km/d (age 1.1), 40 km/s (age 1.2), 50 km/d (age 1.3)

the second number denotes the number of winters spent in the ocean. Thus a fish designated 1.2 spent one winter in freshwater followed by two years at sea and is four years old. Based on age and length studies at Bonneville Dam (Kelsey and Fryer, 2001, 2002, 2003; Miranda et al., 2004, 2005; Whiteaker and Fryer, 2006, 2007, 2008), the average length of a spring Chinook age 1.1 (also called a jack) is generally 50 cm. Similarly, the average length of adults age 1.2 and 1.3 are generally 70 cm and 85 cm respectively. The commonly used most efficient swimming speeds of one body length/s (based on laboratory studies of sockeye salmon by Brett, 1983) are 43.2 km/day, 60.5 km/day, and 73.4 km/day for age 1.1, 1.2, and 1.3 respectively. However, the model calculates distance swum on a daily time-step, ignoring small course variations within a day, so I assumed length-proportional swim speeds of 30 km/day, 40 km/day, and 50 km/day for 1.1, 1.2, and 1.3 age fish based on swim speeds used in previous models (Table 2.2). These speeds are also in line with empirical studies (Table 2.3).

Table 2.2: Swimming speeds used in previous models.

Paper	Value	Species	Notes
Booker et al. (2008)	0.2 m s ⁻¹	Atlantic	Juvenile postsmolts, corresponds to 1.6 body length/s
Dat et al. (1995)	0–88 km day ⁻¹	Sockeye	Optimum speed was 18 km day ⁻¹ (active migration total time), 16 km day ⁻¹ 60 day active migration), and 33 km day ⁻¹ (30 day active migration)
Healey et al. (2000)	10–85 km day ⁻¹	Sockeye	Bioenergetic optimal speed: 36.33 km day ⁻¹ , both fixed-speed and variable-speed navigation
Pascual and Quinn (1991)	mean 2.4 km h ⁻¹	Sockeye	From Quinn (1988), used a Gamma distribution for swim speed at each step
Thomson et al. (1992, 1994)	18, 30, 48 km day ⁻¹	Sockeye	Chosen to represent reasonable low, medium, and high speeds
Walter et al. (1997)	0.3 body length s ⁻¹	Sockeye	Length increased linearly from 20 cm to 50 cm over 21.5 month simulation

Table 2.3: Swimming speeds estimated by empirical studies.

Paper	Value	Species	Notes
Brett (1983)	0.8 length s ⁻¹	Sockeye	Lab studies of efficient sustained swim speed
Ogura and Ishida (1995)	0.54 m s ⁻¹ (0.88 length s ⁻¹)	Sockeye	Average ground speed determined via telemetry
	0.66 m s ⁻¹ (0.98 length s ⁻¹)	Chum	of salmon in the Bering Sea. Chinook salmon
	0.59 m s ⁻¹ (1.17 length s ⁻¹)	Pink	were thought to be immature, potentially
	0.34 m s ⁻¹ (0.49 length s ⁻¹)	Chinook	explaining slower speed.
Quinn (1984)	40–60 km day ⁻¹	Sockeye	Review of other studies, particularly Hartt 1966
Quinn (1988)	66.8 cm s ⁻¹	Sockeye	Speed through water during coastal migration?
Hartt, 1966; French et al., 1976; Groot and Quinn, 1987	35 and 70 cm s ⁻¹	Sockeye	from Thomson
Tanaka et al. (2005)	36.4 ± 15.2 km day ⁻¹	Chum	Horizontal swimming speed through water of single fish from data logger

2.4.2 *Migration Initiation*

As described above, the model uses a calendar date to initiate the active homing migration of the salmon, which is assumed to be cued from the change in day length or from the rate of change of day length (Figure 2.3). The dates for migration initiation are March 21 for the early Dworshak Hatchery stock (assumed to be triggered by the equinox) and April 21 for the late Lookingglass Hatchery stock (assumed to be triggered by the equinox with some delay). These stocks are discussed in more detail in the next chapter. These dates give a 30 day active migration period for the average mean arrival time across years, which had been found to give the most realistic and efficient swimming speeds in a previous model (Dat et al., 1995). Additionally, earlier and later migration initiation times are discussed in Section 4.3.3.

2.5 *Calculations*

This section details some of the calculations internal to the model.

2.5.1 *Interpolation*

Because the ocean currents are estimated only at grid points, the values must be interpolated to the coordinates of fish positions. Interpolation is done using a C^2 interpolating cubic spline (Shikin and Plis, 1995) in the same manner as the OSCURS model. A spline is a function defined piecewise with polynomials on the disjoint subintervals defined by the points t_1, \dots, t_k , called the knots, where the function values are known. The C^2 indicates the smoothness of the spline, meaning at a knot t_i the 0th, 1st, and 2nd derivative values are the same for the polynomial pieces on either side of t_i , and cubic refers to the degree of polynomial used. Splines are useful for interpolation as the result is smoother than bilinear interpolation and avoids the problem with polynomial interpolation, especially with higher degree polynomials, of giving drastically different results from small perturbations in the data.

Interpolations are first done for two grid points on each side of the target point, then those four points are used to interpolate horizontally to estimate the value. Interpolations are done separately for the \vec{u} and \vec{v} components of the current vector. After translating the latitude and longitude coordinates of the target point into the ij -space of the ocean grid, the i th C^2 interpolating cubic spline is evaluated at the target point x which is located between t_{i-1} and t_i with the following formula:

$$\begin{aligned} S_i(x) = & \frac{f''(t_i)(x - t_{i-1})^3}{6(t_i - t_{i-1})} + \frac{f''(t_{i-1})(t_i - x)^3}{6(t_i - t_{i-1})} \\ & + \left[\frac{f(t_i)}{t_i - t_{i-1}} - \frac{f''(t_i)(t_i - t_{i-1})}{6} \right] (x - t_{i-1}) \\ & + \left[\frac{f(t_{i-1})}{t_i - t_{i-1}} - \frac{f''(t_{i-1})(t_i - t_{i-1})}{6} \right] (t_i - x) \end{aligned} \quad (2.3)$$

where $f(t_i)$ are the values of the function at the i th knot, and $f''(t_i)$ are the values of the second derivative at the i th knot. The second derivatives are estimated as

$$f''(t_i) \approx \frac{f(t_{i+1}) - 2f(t_i) + f(t_{i-1}))}{(t_{i+1} - t_i)(t_i - t_{i-1})}. \quad (2.4)$$

2.5.2 Coordinate System

The trajectories of the fish are stored as latitude and longitude coordinates using decimal degrees. The model needs to calculate distances between a fish's position and a new point given a heading and a speed. The model uses the World Geodetic System 1984 (WGS 84), a georeferencing standard, for the reference ellipsoid. A reference ellipsoid is a mathematical approximation of the geoid, the equipotential surface which best fits the earth's global mean sea level, with a flattened spheroid that is wider at the equator than the poles. The model computes distances using Vincenty's inverse algorithm, which computes the ellipsoidal distance along the geodesic between two points, and computes new locations using Vincenty's direct algorithm, which computes an end point given the beginning point and the geodetic azimuth and ellipsoidal distance between the points (Vincenty, 1975).

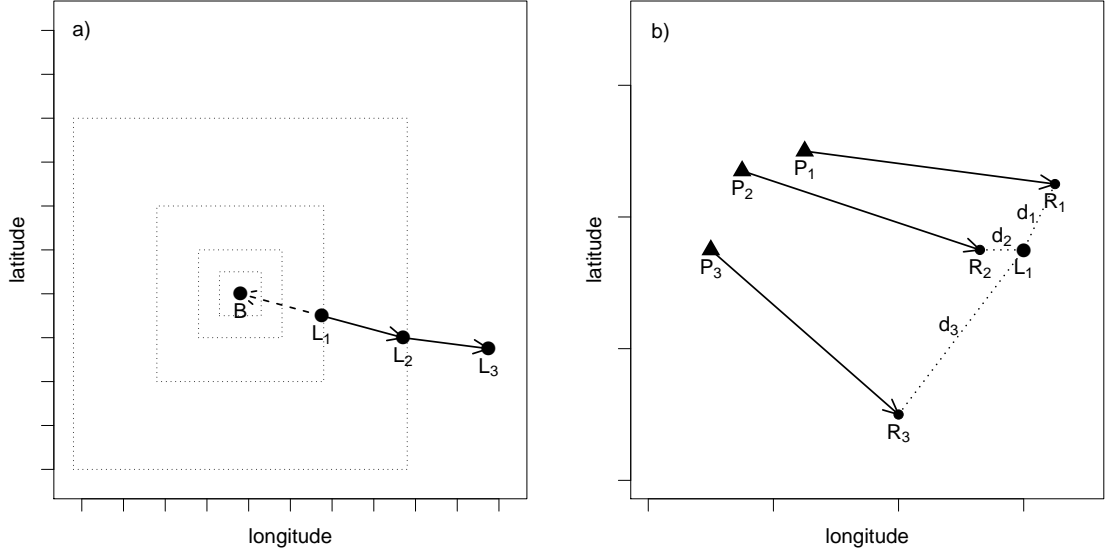


Figure 2.6: Backwards calculation of the model. a) For trajectory L_1, L_2, L_3 , to find preceding location L_0 , first reverse the vector $\overrightarrow{L_1 L_2}$ to find point B . Increasing search regions around B are shown with dotted lines. b) Potential preceding locations P_1, P_2, P_3 in the search area have their next location calculated, R_1, R_2, R_3 . The model seeks to minimize the distance from those next locations to L_1 (dotted lines d_1, d_2, d_3) when selecting the next set of potential points.

2.5.3 Optimization

The calculations for running the model forwards are straightforward, but finding the previous location when running the model backwards involves solving for more unknowns than equations, so a direct solution is not possible and optimization techniques must be used. Additionally, given the interaction between ocean currents and behavior rules, more than one previous location is possible. The model searches for potential previous locations by first calculating what the fish's movement vector would be at then present location (Figure 2.6a, point L_1) and then reversing that vector to determine a search area (Figure 2.6a, point B). The optimization algorithm selects points in the search area (Figure 2.6b, points P_1, P_2, P_3). For each point, the model computes the ocean current vector and fish swimming behavior vector to determine

the next location of the fish if it had started there (Figure 2.6b, points R_1 , R_2 , R_3). Then the distance between that location and the present location is computed (Figure 2.6b, lines d_1 , d_2 , d_3), and this distance is minimized by the optimization algorithm to determine the next set of points. Finally the minima returned by the optimization algorithm are evaluated, and if no valid previous locations are found, search area is widened and the process is repeated. When a point or point is found where its next computed location is L_1 (within some tolerance), then that point or points is designated the previous point, L_0 , and the model moves another step backward in time. It is an error condition if no possible previous location is able to be found.

The model uses the EvA2 (an Evolutionary Algorithms framework, revised version 2) java package (EvA2 team., 2008). Evolutionary algorithms are one optimization technique that can be used for multi-modal optimization, and are based on natural selection. Potential solutions are evaluated for fitness, and those selected for reproduction are recombined and mutated to create the next generation of candidate solutions. Evolutionary strategy is a type of evolutionary algorithm for real-valued problems. The model uses a technique called cluster-based niching to ensure multiple minima are retained. This means that the diversity of the population is maintained by retaining solutions from different niches, where the biological analogue would be speciation. Finally, the possible solutions are refined using hill climbing, in which a small changes are made iteratively to improve the solution.

2.6 *Running the Model Backwards*

This section investigates the performance of running the model backwards as described above. The first item to check is that running the model backwards, then forwards from those end locations, results in approximately the same trajectory. The trajectory is only approximate because the behavior rules cannot be inverted, so optimization techniques must be used to run the model backwards. The threshold for accepting a backwards point is 100 m, and the threshold is widened if the previous point cannot

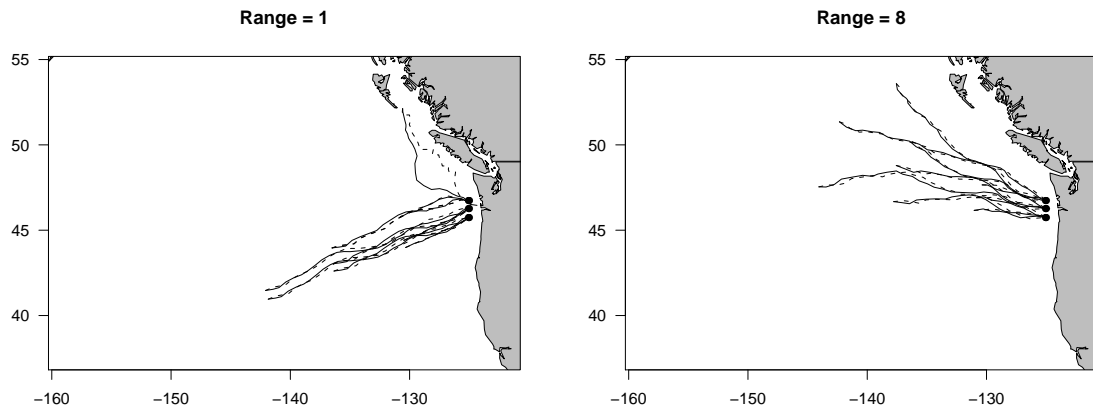


Figure 2.7: Comparison of running the model backwards then forwards for different values of the range parameter using inclination as the direction mechanism. Points indicate starting locations for the backwards runs, shown with dashed lines, started on three dates and three locations. The model was then run forwards starting from the end locations of the backwards runs, shown with solid lines.

be found. Though 100 m is a very small error for a fish that is nearly a meter long and swims approximately 40 km a day, it is enough that the trajectories will not match perfectly, given that the ocean currents and behavior rules vary slightly. In this case, the forwards and backwards trajectories match well for several starting locations and dates (Figure 2.7), except for the one of the trajectories with a range of 1° , which is due to the simple method used to deflect fish from the coast. In general, the fish run forwards end up at the starting location of the backwards runs on the same date along very similar trajectories.

The next thing to check is that running the model forwards from a variety of starting locations, then backwards from those ending locations, also results in approximately the same trajectory. In this case, results vary considerably depending on the range parameter (Figure 2.8), which is an important parameter in determining the fish trajectories (see Chapter 4 for a more complete sensitivity analysis of the parameters). For larger range values (i.e., 8° and 15°), the results are reasonable

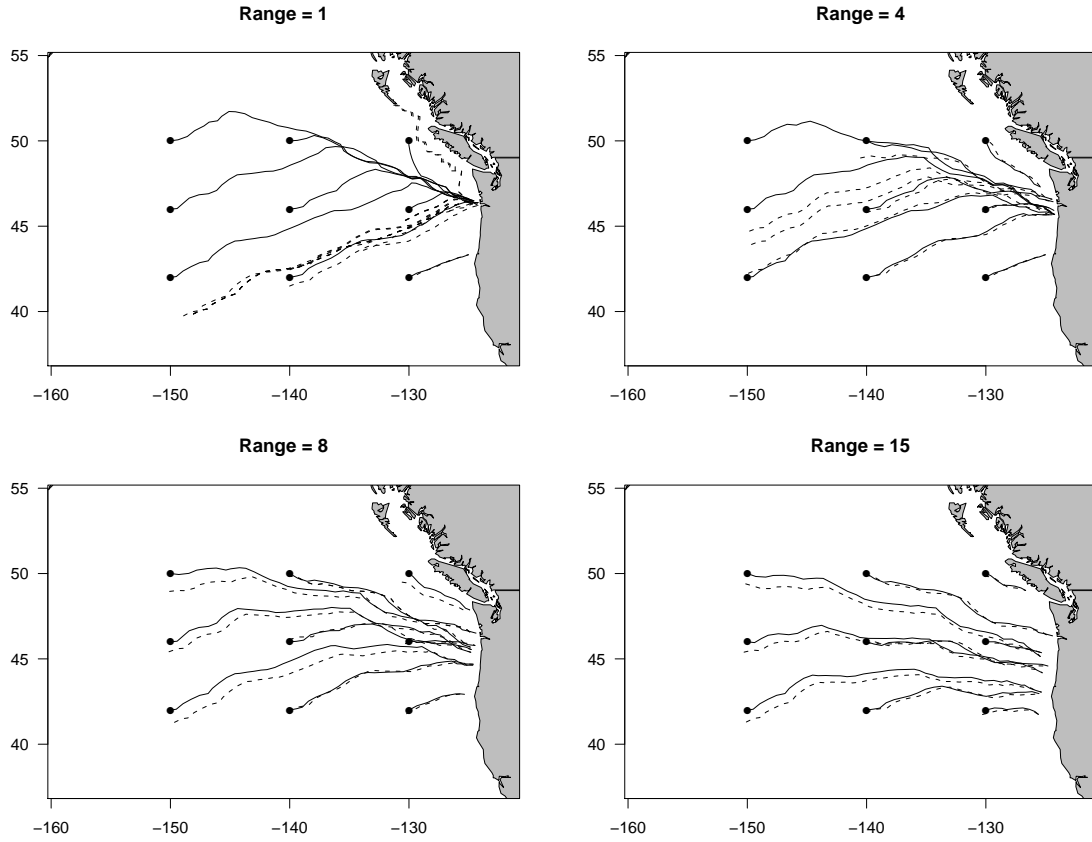


Figure 2.8: Comparison of running the model forwards then backwards for different values of the range parameter using inclination as the direction mechanism. Points indicate starting locations for the forward runs, shown with solid lines. The model was then run backwards starting from the end locations of the forward runs, shown with dashed lines.

accurate, with larger errors for the longer trajectories. This is expected since small differences in computing each backward step have longer to compound. However, for smaller values of range, performance is markedly worse. Results are mixed for a range of 4° , with most starting locations accurate and two completely off, and then deteriorate completely for a range of 1° , with only two starting locations accurately returned to when running backwards.

The issue with running backwards with small values of range is that the response

is very steep for any value not the home value. This means that any small deviation from the home isocline will be accentuated by the behavior rules, as seen with the trajectories for $\text{range} = 1^\circ$, which very quickly veer north or south of the isocline. I attempt to account for this in the model by using a multi-modal optimization technique, so that multiple previous locations can be returned. If more than one previous point is found, the model continues to track backwards from each of them, allowing for one backwards trajectory to diverge into many. In practice, multiple backwards trajectories for a single run sometimes occur, but the trajectories are generally so similar as to be virtually indistinguishable. Looking into this issue closer, there generally is just one possible previous location at the scale of a single step, so the problem is not the optimizer missing other potential solutions. Rather, the divergence between the backwards and forwards routes is due to small differences which are then magnified by the behavior rules that drive the backwards trajectory further from the isocline once it is north or south of it. Because running the model backwards is unique in animal behavior models and seems promising, future work could consider investigating if more directed search areas or other self-correcting backwards search techniques would improve performance for small range values and by extension, other strongly spatially varying behavior rules.

Chapter 3

APPLYING THE MODEL TO COLUMBIA RIVER SPRING CHINOOK

3.1 Introduction

Each salmon run is made up of multiple stocks, and there is evidence for stock-specific arrival timing (Keefer et al., 2004; Anderson and Beer, 2009) that has a genetic basis (Quinn et al., 2000; Waples et al., 2004). In the lower Columbia River, as well as in coastal rivers and the Fraser River, Chinook populations are genetically more similar to those in the same geographic area than those elsewhere with the same run timing (spring, summer, or fall), indicating parallel evolution of run timing and related life history characteristics (Waples et al., 2004). On the other hand, in the interior Columbia Basin, comprising the middle and upper Columbia and Snake Rivers, the spring Chinook populations are genetically divergent from the summer and fall Chinook populations, suggesting colonization from a single spring-run lineage rather than parallel evolution. This genetic divergence is possibly a consequence of geographic isolation in the interior Columbia Basin, with spring-run populations spawning in upper tributaries while fall-run populations generally spawn in main stem rivers (Waples et al., 2004).

Stock composition can have a confounding effect when looking at interannual variation in timing for the entire run. A more abundant early stock can shift the mean of the entire run earlier and vice versa. This difficulty can be avoided by examining the interannual variation in timing for specific stocks rather, rather than the entire run. A subset of juvenile fish in the Columbia River system are tagged with passive integrated transponder (PIT) tags, which are detected when fish pass

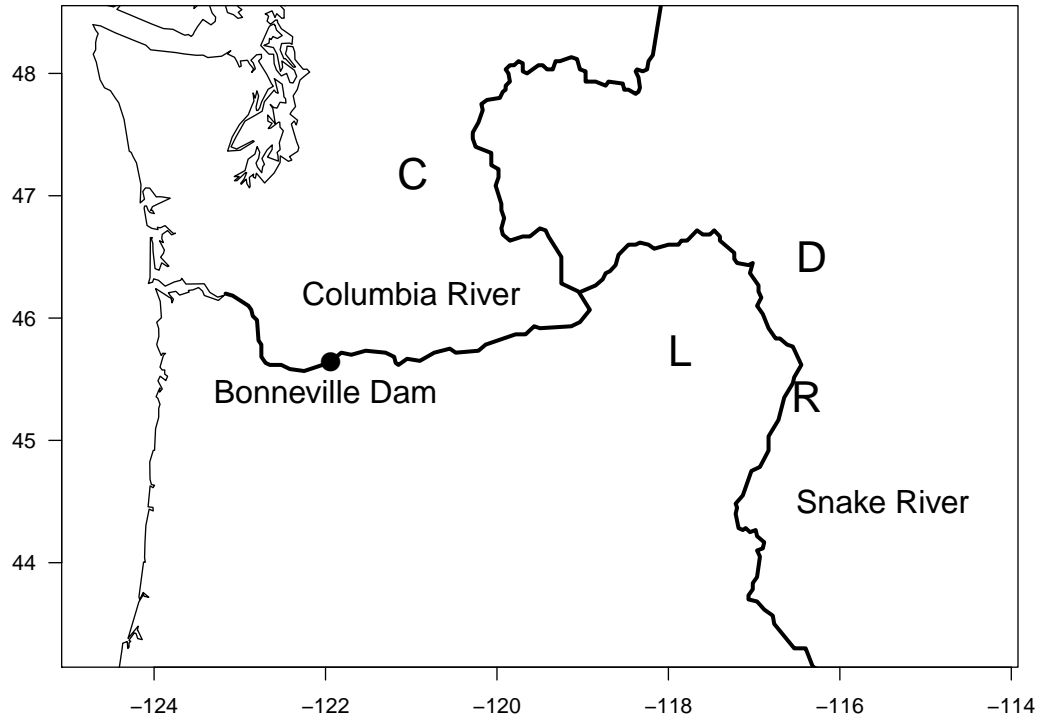


Figure 3.1: Hatchery locations. D, Dworshak Hatchery; R, Rapid River Hatchery; C, Cle Elum Hatchery; L, Lookingglass Hatchery.

by dams during their return migration upstream as adults. This enables them to be assigned to a stock. Of the wild and hatchery populations for which PIT tag data is available, four hatchery stocks have the best sample sizes for returning adults in the years 2001–2009. There are three early stocks (Dworshak Hatchery on the Clearwater River, Rapid River Hatchery on a tributary of the Little Salmon River, and Cle Elum Hatchery on the Yakima River) and one late stock (Lookingglass Hatchery on a tributary of the Grande Ronde River, Figure 3.1). All are located on tributaries of the Snake River, except Cle Elum Hatchery. One early stock, Dworshak, and one late stock, Lookingglass, are used as examples for the remainder of this chapter.

3.2 *Arrival Timing*

Though there are few data on Columbia River spring Chinook distribution in the ocean, there are excellent data on arrival timing in the Columbia River due to the hydropower system. Bonneville Dam is located 235.1 km upstream of the river mouth, and fish are counted there as they pass through the dam. During data collection at the dam, fish are classified as either jacks (age 1.1 for spring Chinook) if they are between 30 and 56 cm in length or adults (generally ages 1.2 and 1.3 for spring Chinook) if they are greater than 56 cm in length. Fish are also assigned to one of the following runs based on passage date: Spring (March 15 – May 31), Summer (June 1 – July 31), or Fall (August 1 – November 15). Daily counts of spring run Chinook salmon are available from Columbia River DART (<http://www.cbr.washington.edu/dart/dart.html>).

The model is focused on the salmon's ocean migration and requires arrival timing at the river mouth. Since Bonneville Dam is located several hundred kilometers upstream, it is necessary to compute an arrival day at the river mouth from the arrival day at Bonneville Dam. Salinger and Anderson (2006) represented the upriver migration time of Chinook salmon between Bonneville and Lower Granite dams as a broken linear model of swim speed as a function of temperature and flow. As part of this work, they were able to derive and fit an equation for ground speed as follows,

$$V = \begin{cases} 27.3 + 2.0\theta - 1.5F & \text{if } \theta \leq 16.3 \\ 100.7 - 2.5\theta - 1.5F & \text{if } \theta > 16.3 \end{cases} \quad (3.1)$$

where V is the ground speed in km day^{-1} , θ is the river temperature in degrees celsius, and F is the river flow in $10^3 \text{ m}^3 \text{ s}^{-1}$. Daily average river flow and temperature values measured by the Army Corps of Engineers at Bonneville Dam were used to calculate monthly averages for March and April, when spring Chinook migrate through the lower Columbia River. These values are then used in Equation 3.1 to calculate travel times from the river mouth to Bonneville Dam (Table 3.1), which ranged from about

Table 3.1: Average temperature (θ) and flow (F) at Bonneville Dam; calculated fish ground speed (V) and travel time from the river mouth (ΔT).

Year	April θ	May θ	April F	May F	April V	May V	April ΔT	May ΔT
2000	10.04	13.03	7.87	7.66	35.56	41.88	6.61	5.61
2001	9.11	13.80	3.44	4.08	40.36	48.79	5.83	4.82
2002	8.98	11.99	6.41	6.92	35.65	40.90	6.59	5.75
2003	9.85	12.44	6.05	7.32	37.93	41.20	6.20	5.71
2004	10.74	13.85	5.03	6.91	41.23	44.63	5.70	5.27
2005	9.28	13.64	4.19	6.69	39.57	44.55	5.94	5.28
2006	9.04	13.08	8.73	9.79	32.28	38.77	7.28	6.06
2007	8.99	13.06	6.72	7.63	35.21	41.96	6.68	5.60
2008	8.17	12.11	4.73	8.93	36.54	38.13	6.43	6.17
2009	8.56	12.20	6.57	7.84	34.56	39.93	6.80	5.89

Table 3.2: Calculated arrival timings at the Columbia River mouth in Julian days.

Year	Dworshack Hatchery				Lookingglass Hatchery			
	N	Mean	Median	SE	N	Mean	Median	SE
2000	30	107.32	103.39	11.88	41	130.68	132.39	26.25
2001	109	106.47	105.17	10.77	246	153.91	159.17	25.59
2002	299	110.92	113.41	9.49	428	147.61	149.41	15.19
2003	412	99.04	98.30	18.65	297	140.03	141.80	21.94
2004	276	108.49	106.30	9.23	338	141.90	144.30	21.62
2005	20	115.16	113.06	10.63	161	140.29	143.06	19.35
2006	146	122.12	122.72	7.13	24	143.84	150.22	20.09
2007	192	116.81	115.32	13.22	28	142.50	144.32	27.08
2008	473	118.80	118.57	11.59	50	144.25	149.57	21.60
2009	376	118.91	118.20	10.58	117	150.66	153.20	21.19

5 to 7 days. The April travel time is used for Dworshak Hatchery and the May travel time for Lookingglass Hatchery, since that is when the respective populations migrate, to calculate arrival date at the river mouth for both stocks (Table 3.2). Note that the variance in arrival timing is much greater for the later stock (Table 3.2); one hypothesis is that environmental conditions compress or expand the length of the entire run each year with greater impact on the earlier stocks (CBR, 2008). Although it is possible that the returning salmon delay in the Columbia River estuary, there is no empirical data available on that behavior. Therefore, this model assumes there is no delay in migration from the ocean to proceeding upriver.

3.3 Ocean Conditions

The reason for including the ocean model is that ocean conditions vary from year to year, which can affect fish migration timing as well as route (Thomson et al., 1992, 1994). Ocean conditions can be characterized by a variety of indices (Table 3.3, Figure 3.2). Upwelling refers to the wind-driven transport of surface waters, generally warmer and nutrient depleted, offshore, which are then replaced by upwelled cooler, denser, nutrient rich subsurface waters. Upwelling waters are an important driver of primary production, and the timing of the onset of upwelling is key to the spring production cycle of phytoplankton. The January upwelling index at 42°N is a direct measure of the volume of upwelled water along the coast, and is the best predictor of salmon arrival timing compared with all other months and latitudes (Anderson and Beer, 2009). The spring transition refers to the switch from a winter downwelling system to a summer upwelling system which is driven by a change from southwesterly winds that predominate in the winter to northerly winds. There are multiple ways of indexing the date of the spring transition, which occurs sometime between March and June and is more distinct in some years than others. The Logerwell et al. (2003) method takes the first day when the value of the 10-day running average for upwelling is positive and the 10-day running average for sea level is negative. The CBR mean

Table 3.3: Ocean indices.

Year	Spring Transition ^a	Spring Transition ^b	Upwelling ^c	ENSO ^d	PDO ^e
2001	61	64	-54	-0.25	0.45
2002	80	81	-34	-0.21	-0.27
2003	112	105	-215	1.22	1.78
2004	110	89	-172	0.43	0.51
2005	145	106	-54	0.80	0.87
2006	112	108	-85	-0.27	0.58
2007	74	71	49	0.38	-0.10
2008	89	36	-7	-1.01	-0.83
2009		67	8	-1.00	-1.51

^a Day of year of spring transition using the method of Logerwell et al. (2003). Source: http://cbr.washington.edu/data/trans_data.html.

^b Day of year of spring transition using the method of CBR mean. Source: http://cbr.washington.edu/data/trans_data.html.

^c January upwelling at 42°N from Pacific Fisheries Environmental Laboratory (units are m³ per second per 100 m of coastline). Source: <http://www.pfeg.noaa.gov/products/PFEL/modeled/indices/PFELindices.html>.

^d Average of January – March values for the Multivariate ENSO Index (MEI). Source: <http://www.esrl.noaa.gov/psd/people/klaus.wolter/MEI/table.html>.

^e Average of January – March values for the Pacific Decadal Oscillation (PDO). Source: <http://jisao.washington.edu/pdo/PDO.latest>.

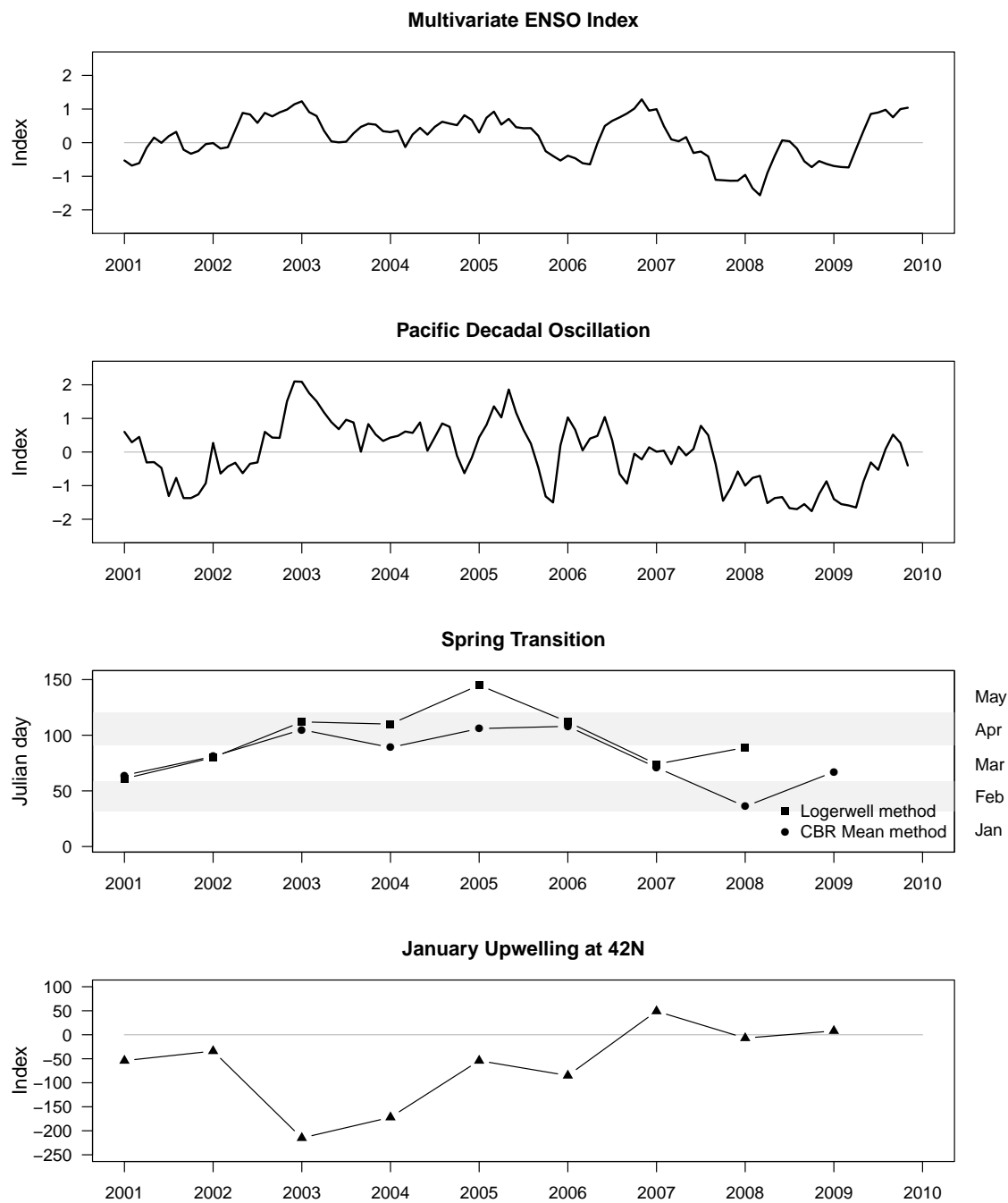


Figure 3.2: Ocean indices. Sources in Table 3.3.

method (CBR, 2007) averages daily deviations from the long term mean upwelling at three locations along the Pacific Northwest coast, smoothes the average deviation with a 15 day central mean, then takes the spring minima of the series.

The climate of the North Pacific can be summarized by the Pacific Decadal Oscillation (PDO). Mantua et al. (1997) define the PDO as an index based on variations of sea surface temperature in the Pacific north of 20°N and correlated with sea level pressure, winter land surface air temperature and precipitation, and stream flow. The PDO consists of warm and cool regimes with a warm regime 1925–1947, then a cool regime 1947–1977, followed by a warm regime after 1977. Recently there have been reversals on a smaller time scale with a cool phases in 1998–2001 and 2007–2009. Additionally, the PDO is correlated with adult salmon returns, with Columbia River spring Chinook returns being positively correlated with cool PDO regimes, though the reverse is true of Alaska populations (Mantua et al., 1997). Conditions in the North Pacific can also be influenced from far away, for example, by the El Niño-Southern Oscillation (ENSO). An El Niño phase is characterized by warming surface waters in the tropical eastern Pacific and high surface pressure in the tropical western Pacific, while conditions are reversed in a La Niña phase with cooling surface waters and low surface pressure. During an El Niño event, warm, high salinity equatorial waters are transported north to the Pacific Northwest coast. A measure of the ENSO cycle is the Multivariate ENSO Index (MEI), which combines six measured variables from the tropical Pacific: sea-level pressure, zonal and meridional components of the surface wind, sea surface temperature, surface air temperature, and total cloudiness fraction of the sky (Wolter and Timlin, 1998). The MEI is correlated with the PDO with more El Niño events during PDO warm regimes. However, the timescales for oscillations are different: interannual for the MEI but interdecadal for the PDO.

Keefer et al. (2008) examined a variety of environmental predictors of Columbia River spring Chinook run timing, including the PDO and North Pacific Index (NPI) as measures of ocean conditions (the NPI is based on sea-level atmospheric pressure

and measures the intensity of the mean wintertime Aleutian Low). In general, arrival timing was weakly negatively correlated with PDO, and positively correlated with NPI, in particular the January value which appeared in several of their regression models. Interestingly, the NPI is correlated with upwelling and productivity (Keefer et al., 2008), and January upwelling was also used by Anderson and Beer (2009) to represent ocean conditions because they hypothesized it correlated with the ocean currents experienced by migrating fish.

Ocean conditions also play important roles influencing physiological processes such as growth and mortality and therefore salmon behavior as they seek to maximize fitness. Comparing Chinook salmon growth on a basin scale (using stream-type and ocean-type fish from Alaska, the Puget Sound, and California), Alaska fish do better with a strong Alaska current, California fish do better with a strong California Current, and Puget Sound fish do best when neither current dominates (Wells et al., 2008). Examining Columbia River Chinook returning after two years at sea, stream-type Chinook return size is negatively correlated with the previous winter's PDO and the fall MEI when entering the ocean (ocean-type return size is also correlated with the previous winter's PDO as well as the spring PDO before return), showing there is not a simple story of how ocean environment affects return size (Wells et al., 2006). In general, both stream-type and ocean-type Columbia River Chinook grow larger when cooler conditions prevail, indicated by negative values for MEI and PDO (Wells et al., 2006). Ocean conditions can fluctuate on various time scales, and McGowan et al. (1998) examine the effect of climate variation on North Pacific ecosystems on an interannual and interdecadal scale. Looking at sea surface temperatures correlated with the Southern Oscillation Index (another ENSO index, based on the air pressure anomaly between Tahiti and Darwin, Australia), they find warm anomalies (El Niños) and cool anomalies (La Niñas) lasting 6–12 months with approximately equal and opposite amplitudes. The biological response to warming El Niño episodes is a northward shift of species and a decrease of population.

In summary, the model takes into account in-river environmental influences in timing by using river temperature and flow to calculate the day of arrival at the river mouth from the day of arrival at Bonneville Dam. The model takes into account regional ocean environmental influences on timing by incorporating ocean currents. Other possible ocean environmental influences, including the impact of ocean conditions on growth, are not currently incorporated in the model.

Chapter 4

BEHAVIOR RULE EXPLORATION

4.1 Introduction

Given the lack of empirical data, the behavior rules described in Section 2.3 seek to assess plausibilities of hypothesized direction-finding mechanisms of salmon and known sensory abilities of other species. The rules incorporate several parameters (Table 2.1), with swim speed being the only parameter that has been measured directly in field and laboratory experiments. Thus it is important to look at the model's sensitivity to those parameters. The behavior rules are based on the salmon imprinting on a value of the magnetic field when entering the ocean, and then using that value to locate the river mouth during the directed homing migration. This chapter examines variations of this basic concept to explore the sensitivity of different parameters as well as the efficiency of different versions of the rules. Behavior rules using both inclination and intensity as directional mechanisms are considered, and their relative performance is evaluated.

Assuming that ocean conditions do not completely control arrival timing year to year, there is likely some interannual variation in ocean distribution at the start of return migration. Due to the use of arrival window as one of the criteria of success, it is expected that not every location in the range distributions over years would qualify as successful every year. For example, in a year with an early return, some close locations will be successful that would not be in a year with a late return, and vice versa. However, given that we do not know the ocean distribution, arrival timing is the best information available.

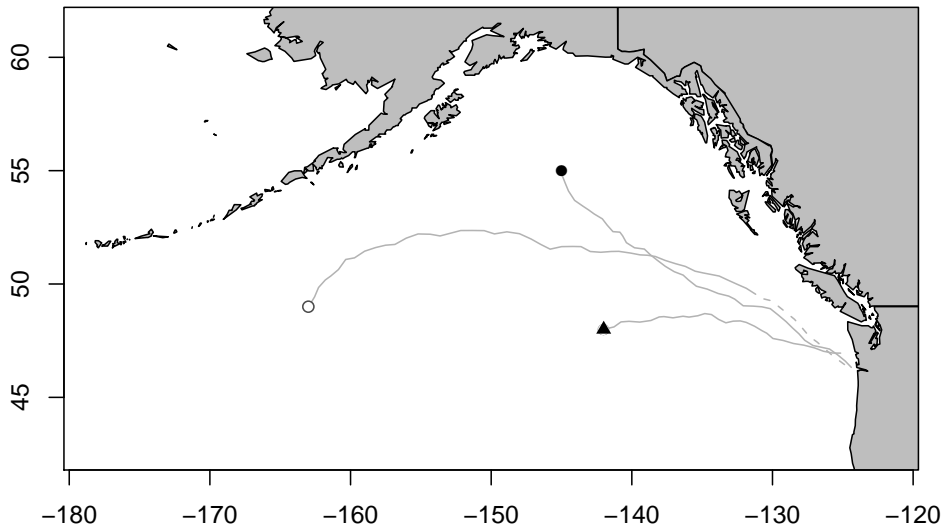


Figure 4.1: Three starting locations with different results. 1) A successful trajectory where the fish arrives within 100 km of the river mouth in the middle 80% of the stock (closed circle). 2) An unsuccessful trajectory where the fish arrives in the middle 80% of the stock, but over 100 km from the river mouth (triangle). 3) An unsuccessful trajectory where the fish arrives within 100 km of the river mouth, but after the middle 80% of the stock, indicated by the dashed line trajectory (open circle).

4.2 Figures

To determine if the modeled fish successfully make it home, both space and time are important. Success in space is defined as reaching the coast within 100 km of the Columbia River mouth. Success in time is defined two ways, using arrival timing for Dworshak Hatchery: the time window at the river mouth for the middle 80% of the arrivals, and the more generous time span between the 2nd and the penultimate fish (to exclude extreme outliers). While including the first and last fish does not alter the results in most years, some years would have an overly large arrival window, as

Dworshak Hatchery fish reached Bonneville Dam as early as February 26 and as late as August 27. All figures in this chapter reflect the middle 80% arrival window criteria for success, except Figures 4.7 and 4.8 which show both criteria. Figures also show the home isoclinic or isodynamic (the isocline of the inclination or intensity value at the river mouth).

For example, consider the three different trajectories in Figure 4.1. Two of the fish (open and closed circles) are successful in space, arriving at the coast within 100 km of the river mouth. However, only one of those (closed circle) is also successful in time, arriving in the middle 80% of the stock. The other fish (open circle) arrives too late, as shown by the trajectory turning to a dashed line after the middle 80% window has passed. It is also possible to be successful in time but not space, as shown by the fish arriving over 100 km from the river mouth (triangle). In addition to plots showing trajectories for individual starting locations, other plots show the number of times a starting location was successful aggregated across the years 2001–2009.

4.3 Sensitivity Analysis

This section examines the model's sensitivity to range, symmetry, migration initiation date, and home angle. Because there is more empirical evidence for estimating swim speed, and since swim speed and migration initiation are conflated (distance = velocity \times time), variation in swim speed is not examined here.

4.3.1 Range

Recall from Equation 2.1, that the range parameter, r , controls the steepness of response to the magnetic field: the smaller the value of the range, the more directly north or south the fish will swim when not on the home isocline, while the larger the value of range, the more eastward the fish swim. Values for r are also specific to the magnetic field component used for x , which is discussed further in Section 4.4.1. In general, smaller range values allow salmon to successfully migrate home in time and

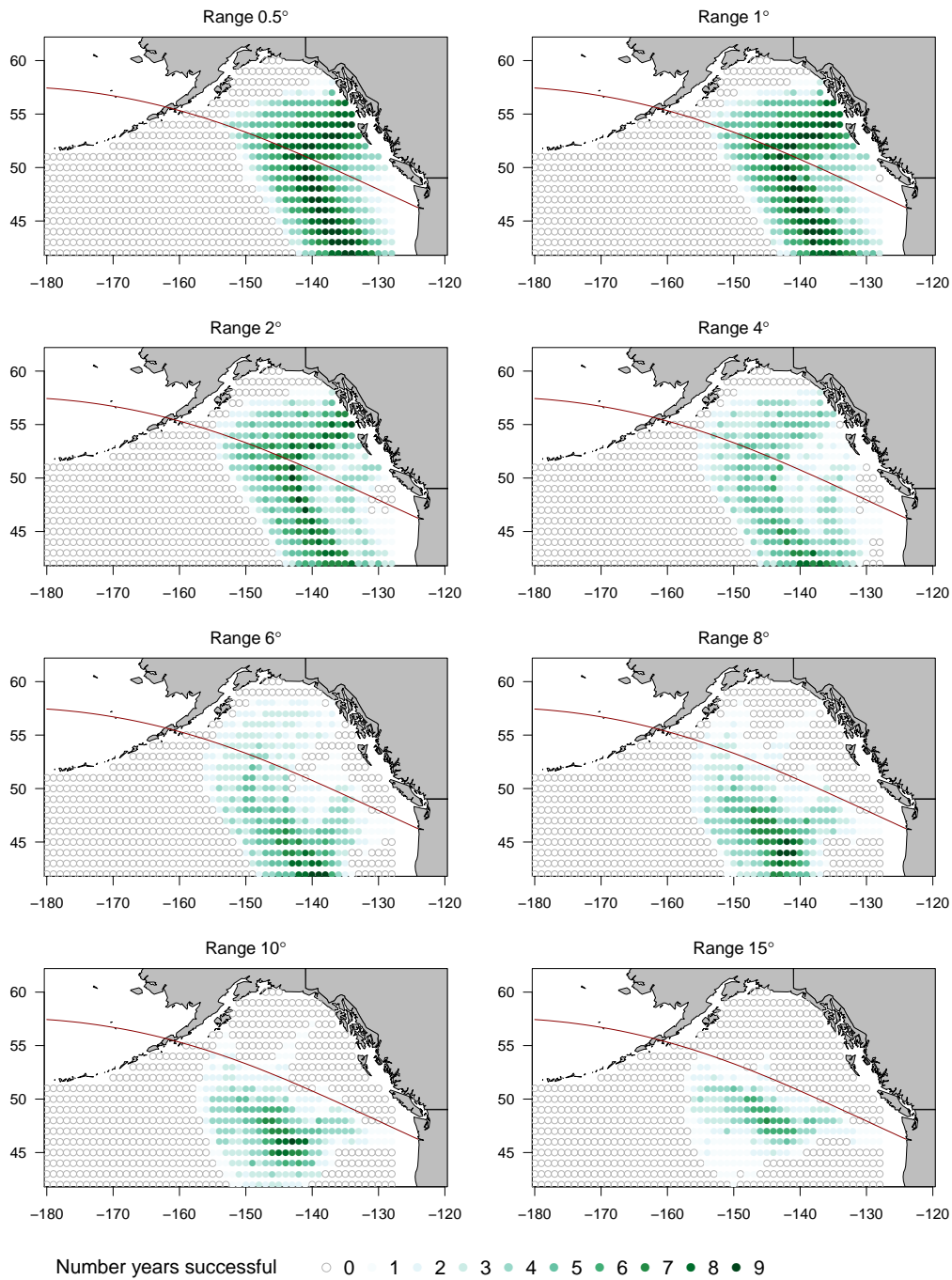


Figure 4.2: Inclination: number of years each starting position was successful, using the inclination component of the magnetic field, for a variety of range values. Line shows home isoclinic. Parameters: home angle = 110° , start date = March 21.

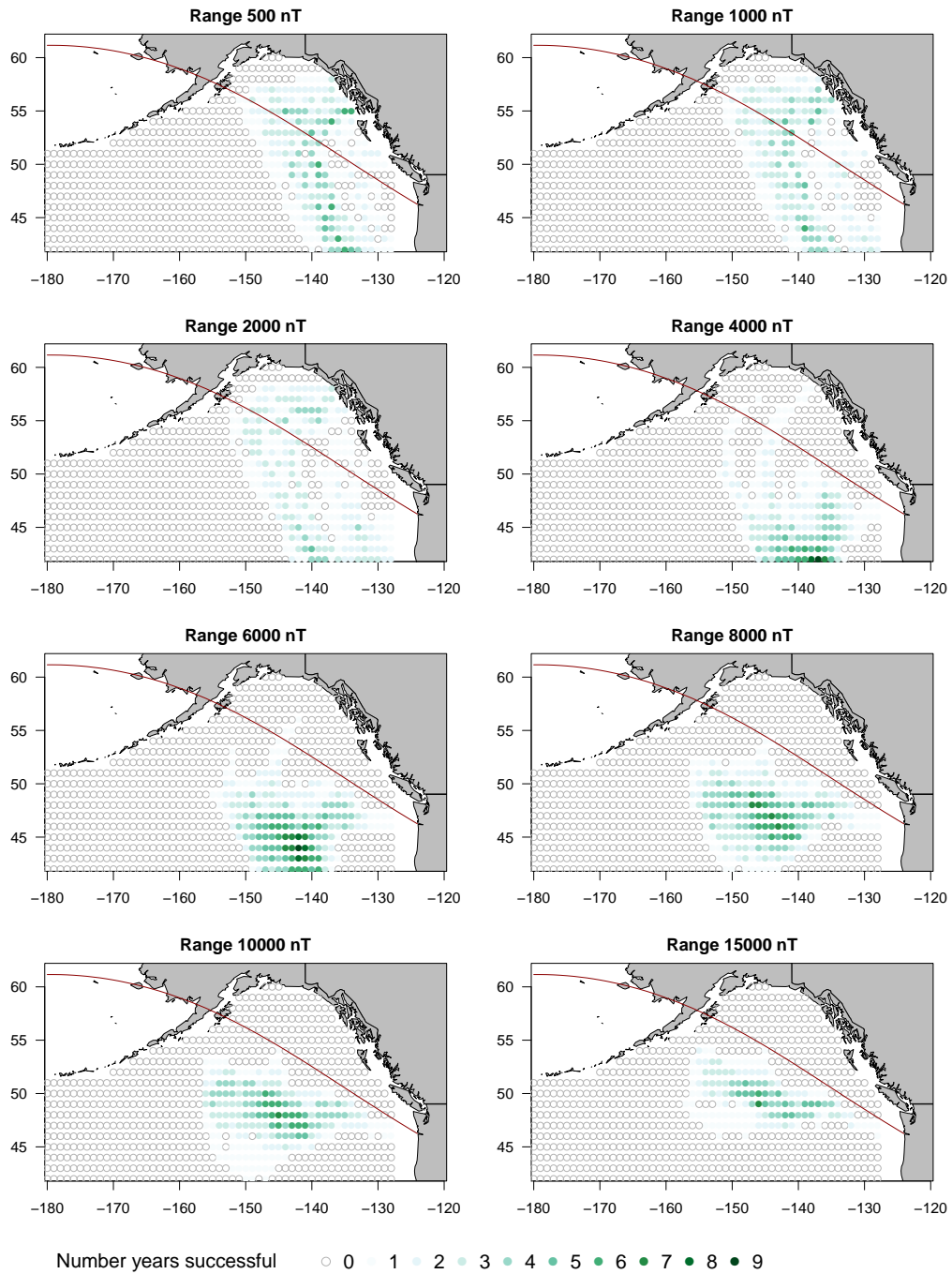


Figure 4.3: Intensity: number of years each starting position was successful, using the inclination component of the magnetic field, for a variety of range values. Line shows home isodynamic. Parameters: home angle = 117° , start date = March 21.

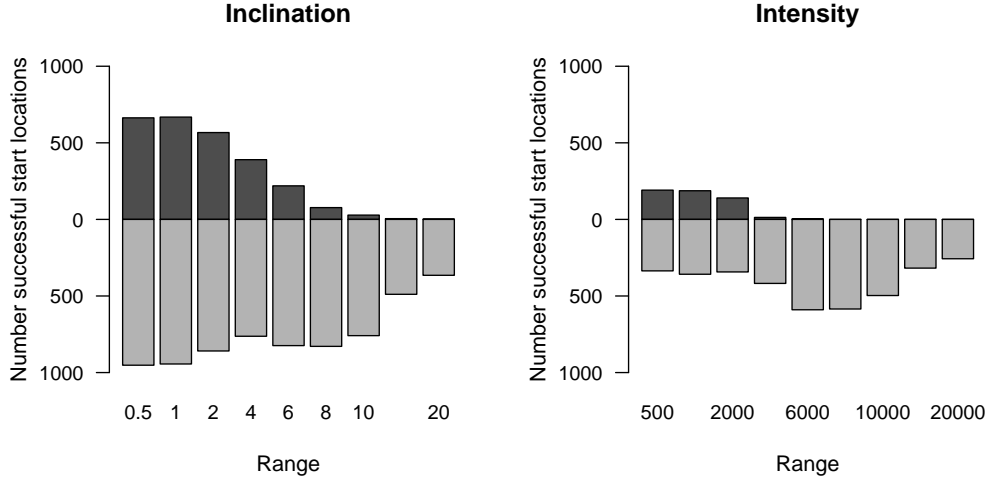


Figure 4.4: The distribution of successful starting locations north (dark gray) and south (light gray) of the home isocline for different values of range shown in Figures 4.2 and 4.3.

space using both inclination and intensity components of the magnetic field.

Inclination was modeled with range values from 0.5° to 15° (Figure 4.2), and intensity was modeled with range values from 500 nT to 15,000 nT (Figure 4.3). The figures show the results for each starting location summed across years, where a success means the fish arrived within 100 km of the river mouth in the middle 80% of the Dworshak run for that particular year. The successful starting locations are arranged in approximately concentric circles from the river mouth (more apparent for smaller values of range), which shows the effect of timing: a later start or slower swimming speeds would shift the successful zone closer, while an earlier start or faster swimming speed would shift the successful zone farther away. Additionally, different range values shift the north–south distribution of successful starting locations (Figure 4.4). The east–west distribution of successful starting locations is controlled by the migration initiation date, as discussed later. While there are more possible starting locations south of the home isocline, as range increases virtually no fish successfully

return to the river mouth from north of the home isocline. For inclination, range values of 0.5° and 1° are clearly the most successful, with 1° having a slight edge (Figure 4.2). For intensity, range values of 1000 nT and 6000 nT were the most successful, but with very different distributions: successful locations are spotty and dispersed for 1000 nT but clumped south of the river mouth for 6000 nT (Figure 4.3).

For smaller values of range, the fish swim more directly to the home isocline, and then follow that isocline homeward. Taking inclination, for example, compare the tracks for a range value of 1° to values of 6° and 15° (Figure 4.5); results are similar for intensity. Proceeding directly to the isocline is more robust to starting location than the more gradual tracks seen with larger values of range. The fish have a higher chance of reaching the home isocline before reaching the coast, even if this results in a slightly longer and less direct swimming trajectory. The adaptive value of precise homing from a wide variety of locations would outweigh any inefficiency in not taking the shortest path, especially as salmon are thought to be able to continue to feed during the ocean portion of their return migration.

Range is an important parameter in the model controlling behavior, but unfortunately there is not empirical evidence available to help estimate it. Tagging studies that provide trajectories, whether calculated from the measured headings of the fish or light-based geositional estimates, would be one way to determine an approximate value for the range parameter. Although the fish in the Sturlaugsson et al. (2009) study were released less than 200 km from the river mouth, a similar study carried out farther from the home river would be more useful in estimating r . However, looking at the distribution of end points along the coast (Figure 4.5), larger values of range, such as 15° for inclination, can be eliminated. Spring Chinook are rarely caught in coastal fisheries (Sharma, 2009; Waples et al., 2004). Trajectories for large values of range encounter the coast across a broad range from Vancouver Island to southern Oregon with little direct homing to the river mouth. While a larger range value could be a successful strategy if after reaching the coast, the fish proceeded along it to

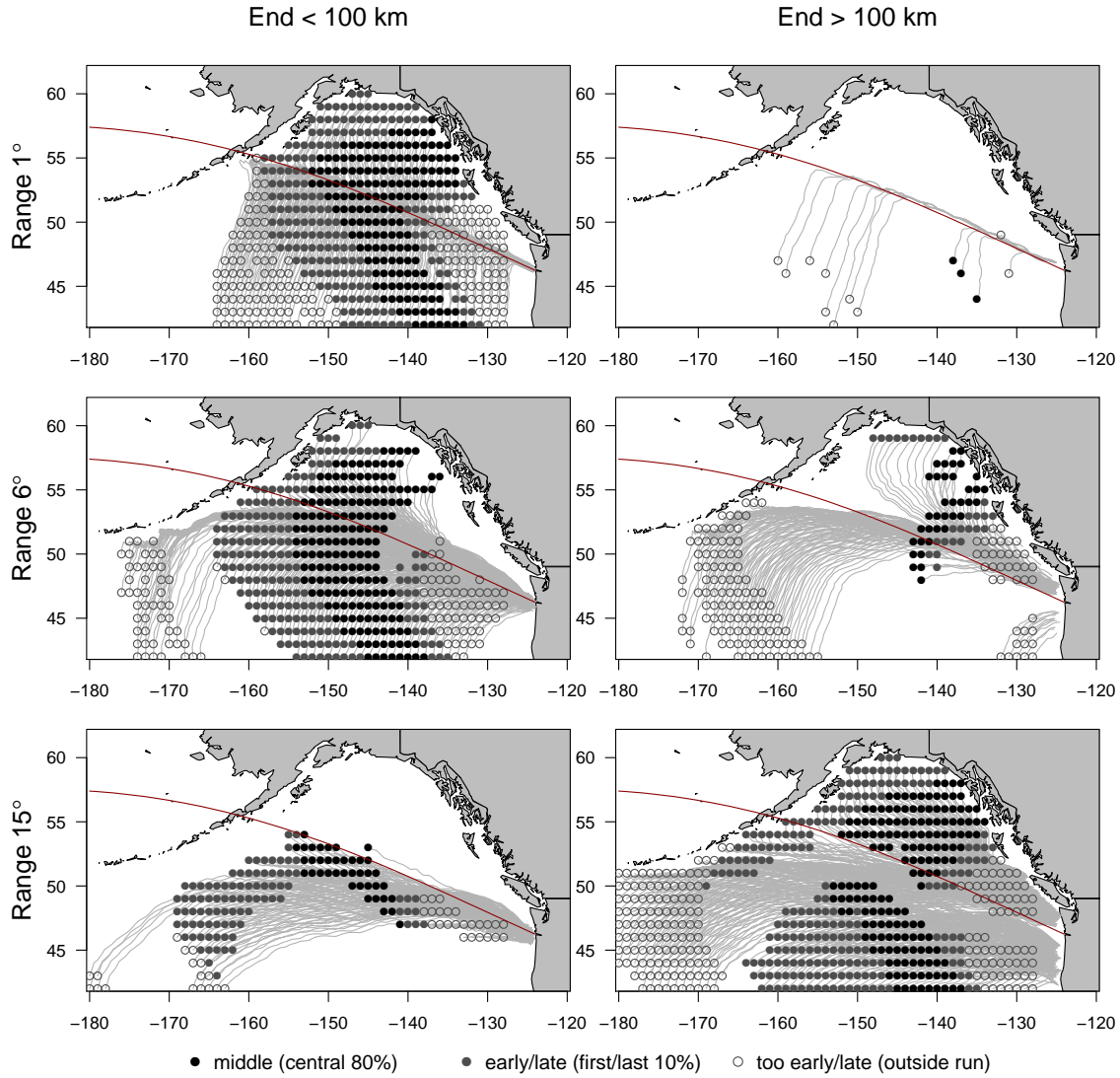


Figure 4.5: Start locations and tracks in 2006 using inclination as the directional mechanism for range values of 6° and 15° , divided into fish that ended within 100 km of the river mouth (top) and fish that ended over 100 km from the river mouth (bottom) (starting locations for fish still at sea July 1 not shown). Line shows home isoclinic. Parameters: home angle = 110° , start date = March 21.

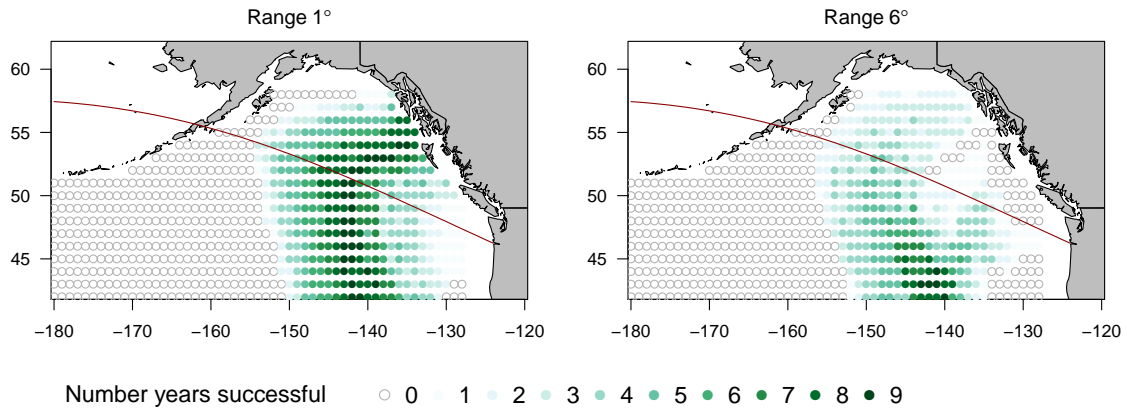


Figure 4.6: Symmetry of response: number of years each starting position was successful, using a symmetric response following the isoclinic. Line shows home isoclinic. Parameters: home angle = 110° , start date = March 21.

the river, the lack of catch in coastal fisheries are inconsistent with this possibility. Taking the small and medium values of range of 1° and 6° , both are plausible, though the smaller value is superior in terms of number of successful starting locations that arrive within 100 km of the river mouth at the right time. Though more starting locations end up over 100 km from the river for the medium range value, they are much fewer and less widely distributed than the large range value. Hence, a medium range value could still be consistent with the lack of coastal catch. The different range values produce different trajectories, with the medium range value resulting in more direct routes and the small range value yielding trajectories that proceed directly to the home isocline and then along it.

4.3.2 Symmetry of response

If the home angle in Equation 2.1 is not 90° , the response will be asymmetric. That is, the fish will swim straight north at a smaller departure from the home value than it will swim straight south. One way to make the rule symmetric about the home angle

is to cut off more southward directions once the same difference between home value and straight northward swimming is reached. Then, the fish would not be allowed to swim straight south. This accomplished by changing Equation 2.1 to the following (assuming $a_{home} > 90^\circ$):

$$f(x) = \begin{cases} 180 & \text{if } x > x_{home} + (180 - a_{home})\frac{r}{a_{home}} \\ 2a_{home} - 180 & \text{if } x < x_{home} - (180 - a_{home})\frac{r}{a_{home}} \\ \frac{a_{home}}{r}x - \frac{a_{home}}{r}x_{home} + a_{home} & \text{otherwise.} \end{cases} \quad (4.1)$$

The results from the symmetric response (Figure 4.6) can be compared with the asymmetric response (Figure 4.2) for values of range of 1° and 6° , using inclination as the directional mechanism. Though a symmetric response is more successful, the difference is slight. This suggests that whether the fish use a symmetric or asymmetric response is probably not critical. Further simulations use a symmetric response.

4.3.3 Migration initiation date

The model runs above all assumes a standard migration initiation date of March 21. This is the spring equinox when the rate of day length change is the fastest (Figure 2.3). However, earlier and later days are also possible. Comparing earlier dates (March 1 and March 11, Figure 4.7) and later dates (March 31 and April 10, Figure 4.8) to the standard date (March 21, Figure 4.6), and assuming fish follow the isoclinic with a range value of 1° , it is apparent that earlier dates move the center of distribution westward while later dates move the center of distribution eastward.

Again, it is difficult to separate starting location from migration initiation based solely on arrival time. Salmon migrating home in extremely early years, such as 2003, and late years, such as 2009, presumably had a different ocean distribution. This variation contributes to arrival disparity, as seen when summing successful starting locations across years. However, one can still recognize that these simple rules successfully get the salmon to the river mouth from a wide swath of the North Pacific, as

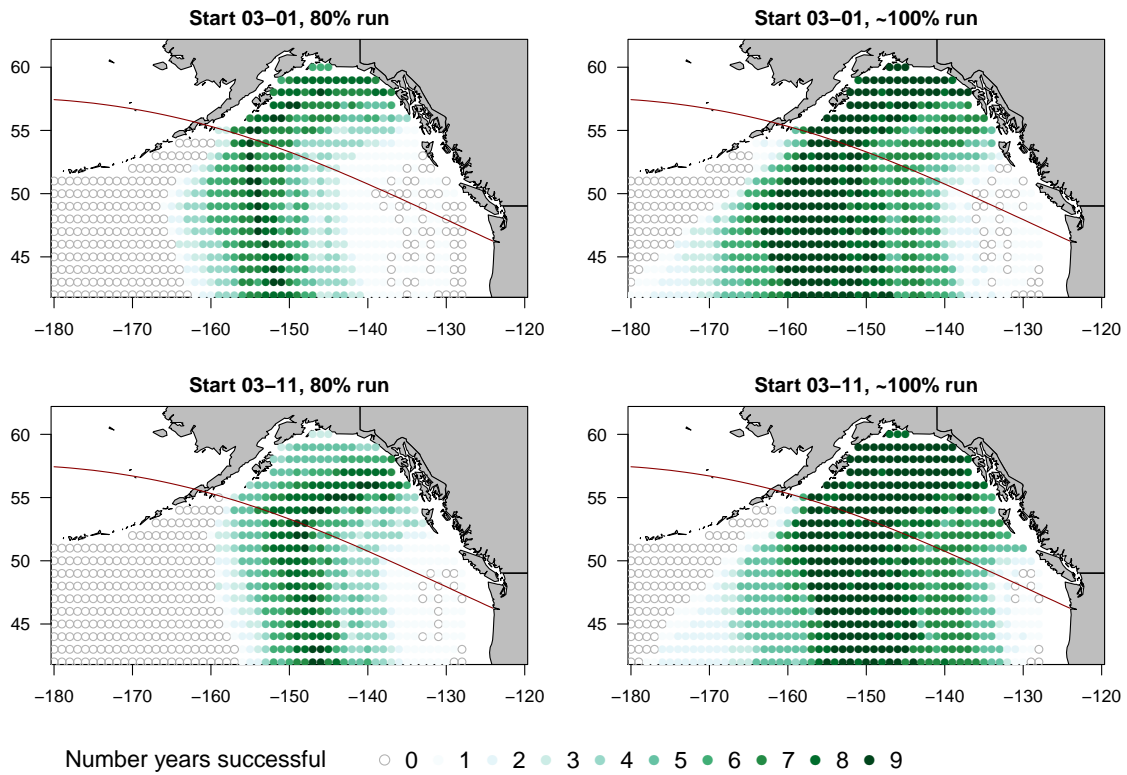


Figure 4.7: Migration initiation: number of years each starting position was successful for earlier migration initiation dates using a range of 1° . Left panels show success based on the middle 80% of the run, while right panels show success based on the entire run, omitting the first and last fish. Line shows home isoclinic. Parameters: range = 1° , home angle = 110° .

well as analyze the effect of different migration initiation dates. Whether all salmon start homeward on the same date is discussed in Section 5.3.

Compared with March 21, an earlier start date of March 11 is slightly more successful than other dates. One reason that later start dates are less successful is that, as the center of distribution of successful locations moves eastward, it runs into the coast. Thus the area of successful start locations shrinks for later start dates. A start date in mid-March would be the most generally successful, assuming fish have

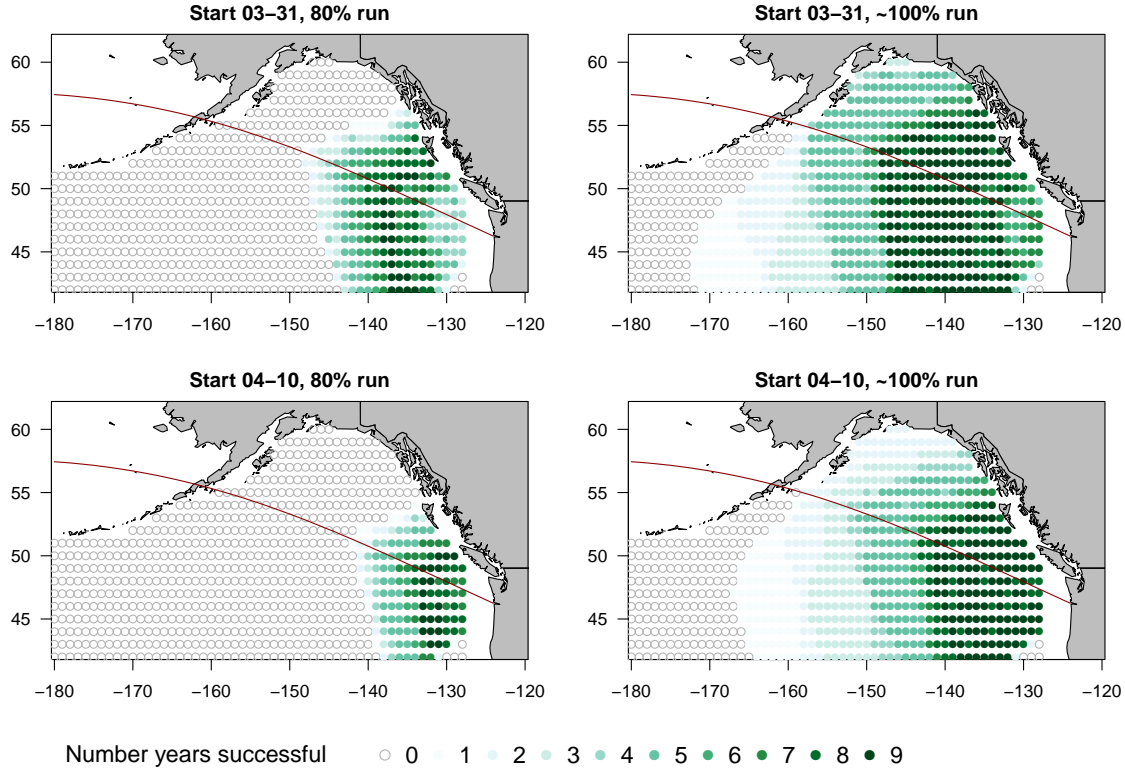


Figure 4.8: Migration initiation: number of years each starting position was successful for later migration initiation dates using a range of 1° . Left panels show success based on the middle 80% of the run, while right panels show success based on the entire run, omitting the first and last fish. Line shows home isocline. Parameters: range = 1° , home angle = 110° .

no knowledge of longitude with which to time their migration initiation date based on distance from home river.

4.3.4 Home angle

The earlier results assumed that once fish located the home isocline, they swam along it, which requires maintaining a heading, or home angle, of 110° or 117° (the average angle of the isocline or isodynamic in the area of the river mouth for the years 2001–

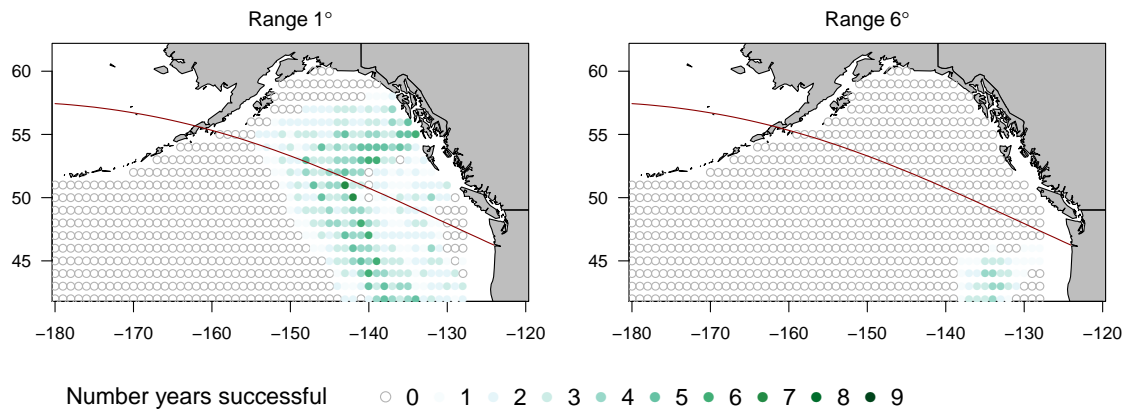


Figure 4.9: Home angle: number of years each starting position was successful, using east as the home angle and inclination as the directional mechanism. Line shows home isocline. Parameters: home angle = 90° , start date = March 21.

2009, as the angle of the home isocline can vary from year to year as the magnetic field shifts). However, other behavioral responses are possible, with one of the simplest being to head east when $x = x_{home}$, whether by magnetic or sun compass (other possibilities are discussed in Section 4.4.2). Following the isocline is a dramatically better strategy as shown by comparing a home angle of 90° along the isocline (Figure 4.9) to a home angle of 110° also along the isocline (Figure 4.2). While heading east is somewhat successful for smaller ranges, the success rate falls off dramatically to near zero as range increases.

4.4 Directional Mechanism

This section compares using the inclination and intensity components of the magnetic field as the directional mechanism. The directional mechanism is used to determine the salmon's heading during the home migration. The salmon imprint on the value of the directional mechanism (i.e., either inclination or intensity) at the river mouth when they enter the ocean, then compare the value at the current location to that

reference value during their return migration. The optimal values for range, 1° for inclination and 1000 nT for intensity, are used in this section. Larger values for range are clearly inconsistent, with the majority of trajectories ending along the coast rather than homing precisely to the river mouth. However, it is not possible to distinguish among smaller values of range. Thus, the optimal range values are used in this section since no empirical information exists to choose otherwise, such as trajectories from tagging experiments.

4.4.1 *Magnetic field component*

The isoclines for both the inclination and intensity of the magnetic field are roughly parallel in the Gulf of Alaska (Figure 2.4) and can be used as the latitudinal coordinate with the coastline potentially providing the longitudinal coordinate to locate the river mouth. However, the earth's magnetic field is always changing, so the secular variation, or the non-periodic change in the field over time, is also important. There is greater secular variation for intensity compared to inclination in the Pacific Northwest (Lohmann et al., 2008). This suggests that inclination would be a more robust mechanism, which is indeed the case (Figures 4.2 and 4.3). For the years examined, 2001–2009, assuming 2 years at sea, the navigation error was consistently ≈ 6 km for inclination and ≈ 29 km for intensity. In both cases it was always biased to the north (calculated using the IGRF-10 model). However, the maximum navigation error: the maximum navigation error is much larger for intensity, especially as the number of years at sea increases (Table 4.1). As the error is almost always to the north (at least in the last century), it is possible that the fish could compensate for this by biasing their heading to the south. This is discussed further in Section 4.4.2.

Secular variation is not the only disadvantage to intensity compared to inclination. The behavior rules are based on using a heading that follows the average isocline near the river mouth for 2001–2009: 110° for inclination and 117° for intensity. While this angle is consistent for inclination, there is more variation in the angle of the

Table 4.1: Navigational error in km due to secular variation in the earth’s magnetic field, assuming no compensation, for varying number of years at sea calculated for out migration years 1900–2005 calculated using the IGRF-10 model.

Years	Inclination			Intensity		
	Min	Max	Mean	Min	Max	Mean
1	0.01	3.46	1.45	1.96	14.65	8.42
2	0.02	7.52	3.23	4.39	31.80	18.68
3	0.03	11.51	4.98	6.78	49.18	29.04
5	0.17	18.99	8.52	13.10	84.31	50.14

isocline for intensity, thus no particular heading performs well in all years. Over the years 1900–2009, at the Columbia River mouth the inclination isocline has a mean of 111.5° with a standard error of 0.7° . The intensity isocline has a mean of 126.0° with a standard error of 4.6° . However, if the fish have some other mechanism for swimming along the isocline rather than maintaining a compass heading, this could be less of a problem. Additionally, while isoclines for both inclination and intensity are generally southeast-northwest (Figure 2.4), the isoclines for intensity are more north-south than those for inclination (by an average of 7° the last ten years). Therefore, trajectories are longer and less efficient for fish starting south of the home isocline.

Tracks of fish from starting locations towards home in a particular year shows reflect of these issues (Figure 4.10). In 2006, Dworshak had average to late arrival timing. 2006 also happened to be a more successful year than usual for intensity. Almost all the inclination starting locations ended within 100 km of the river mouth, which was not the case for intensity. Additionally, though neither gives a direct route home, the inclination mechanism results in fish initially south of the isocline not having to swim quite as far north. Intensity has more starting locations that ended at

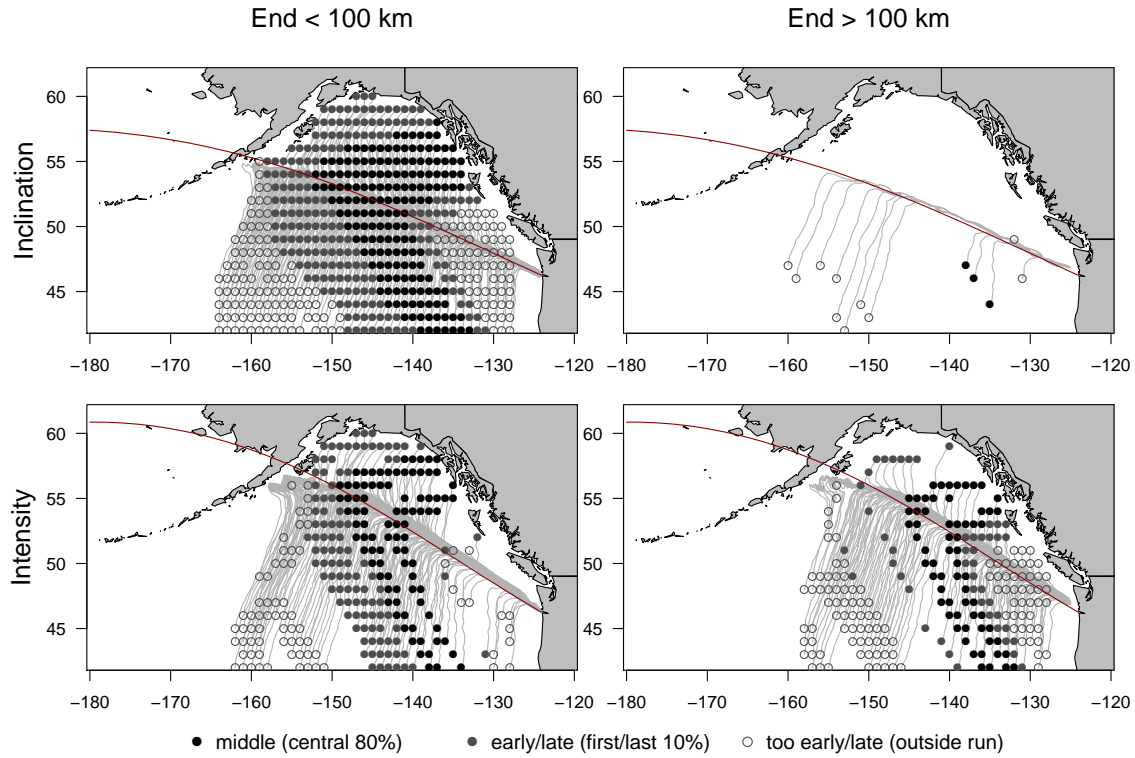


Figure 4.10: Start locations and tracks in 2006 using inclination and intensity as the directional mechanism, divided into fish that ended within 100 km of the river mouth (top) and fish that ended over 100 km from the river mouth (bottom) (starting locations for fish still at sea July 1 not shown). Line shows home isocline. Parameters: Range = 1° (inclination), 1000 nT (intensity); home angle = 110° (inclination), 117° (intensity); start date = March 21.

sea or later than the arrival timing window. However, though intensity is less accurate in the spatial dimension and has longer tracks, it is still a successful mechanism, especially if some coastal searching is allowed; even those starting locations that ended over 100 km from the river mouth were still along the central Washington coast.

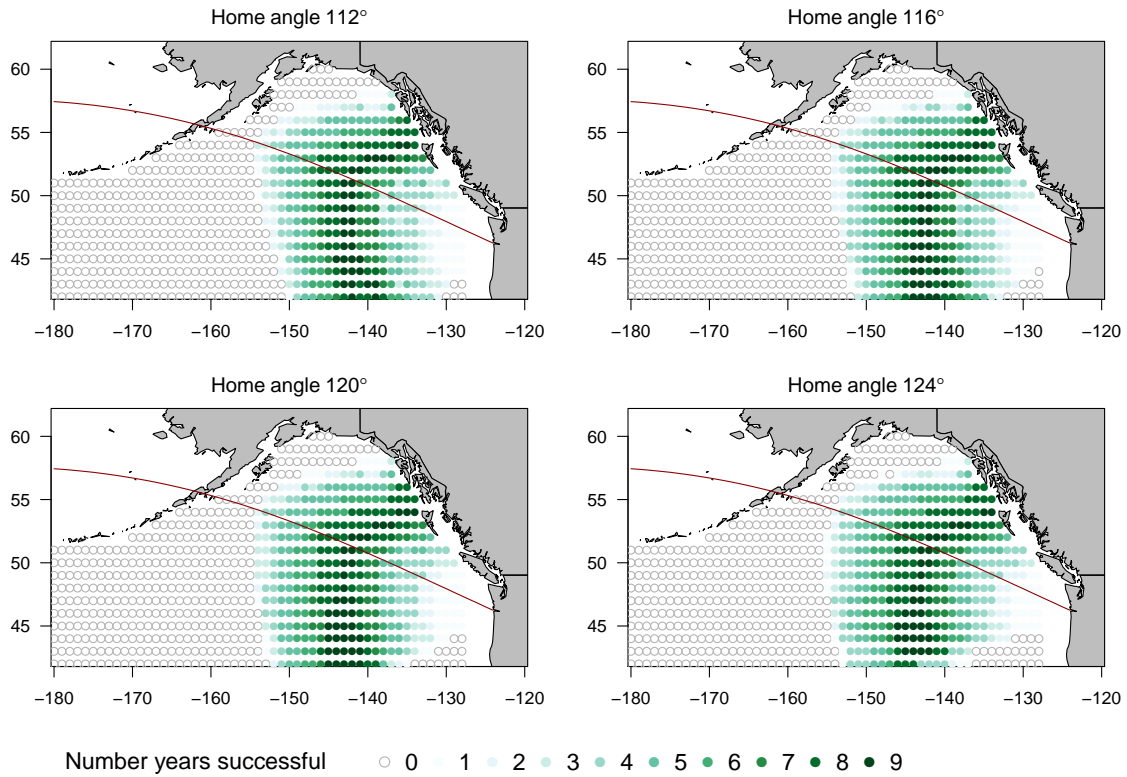


Figure 4.11: Inclination: number of years each starting position was successful, using the inclination component of the magnetic field, for a variety of home angle values. Line shows home isoclinic. Parameters: range = 1° , start date = March 21.

4.4.2 Southward bias in home angle

Rather than shifting the home angle eastward as above, another possibility is a southward bias to the home angle since the error due to secular variation for both inclination and intensity is northward (at least for the last century). Additionally, since intensity has a greater error due to secular variation, a stronger southward bias in heading might be able to compensate. Recall from Equation 2.1 that home angle is the direction the fish swims when at the home value, i.e. the inclination or intensity of the magnetic field when entering the ocean as a smolt. Inclination (Figure 4.11) and

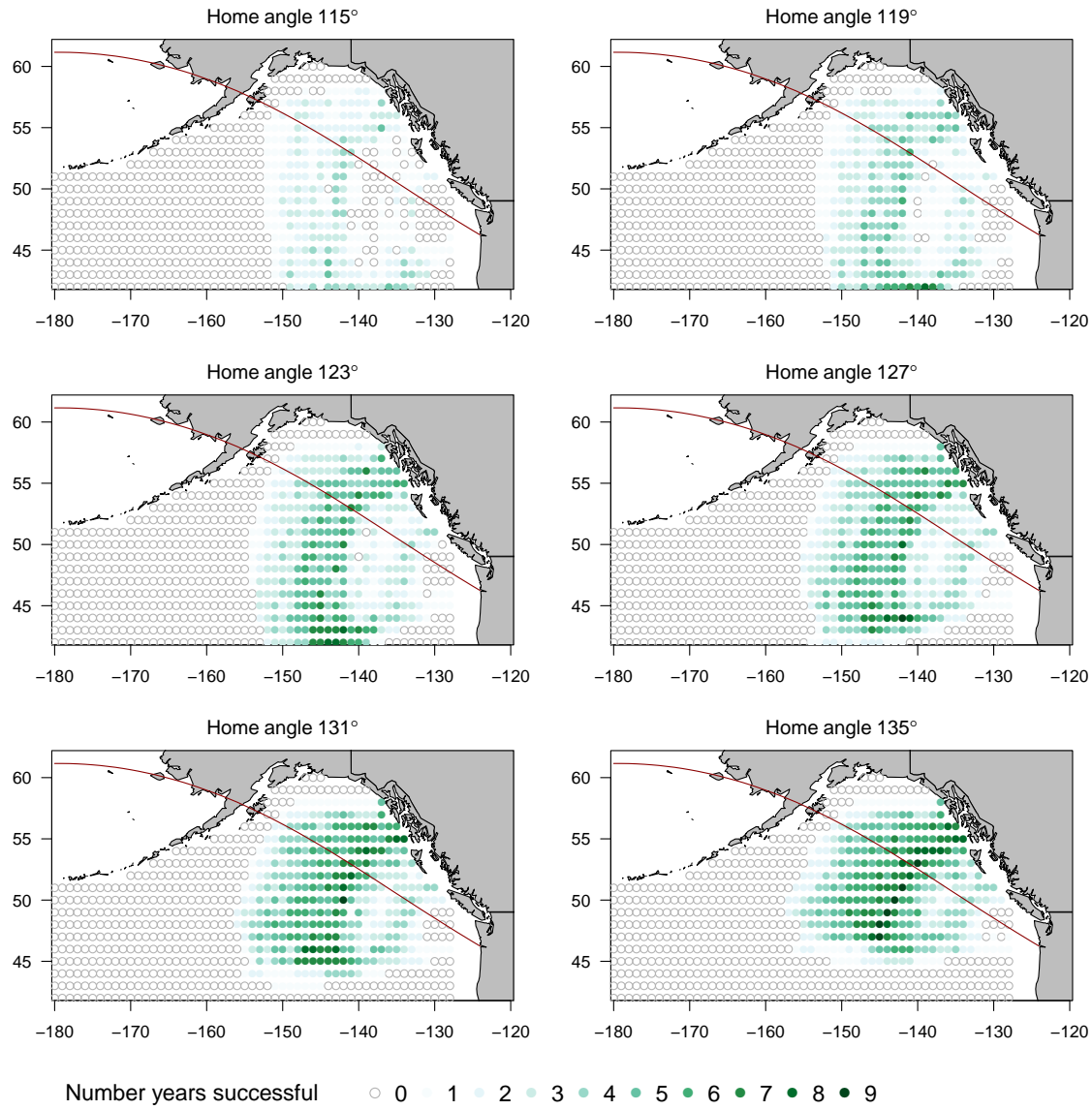


Figure 4.12: Intensity: number of years each starting position was successful, using the inclination component of the magnetic field, for a variety of home angle values. Line shows home isodynamic. Parameters: range = 1000nT, start date = March 21.

intensity (Figure 4.12) were examined in increments of 2° for the home angle, using 1° and 1000 nT for the range, respectively. A southward bias was more successful for both.

For inclination the most successful home angle is 120° , and for intensity the most successful home angles are 131° and 133° . Similar to the results above with a 90° home angle, home angles eastward of the average isocline have diminishing success. Southward of the average isocline, success increases to the optimum angle between east-southeast and southeast, then decreases as the home angle becomes more southward. However, what is striking is how much more robust inclination is to home angle than intensity is. There is only an 9% increase in success from the average isoclinic angle (110°) to the optimum heading (120°), and all angles in that range perform well. For intensity, on the other hand, there is a 82% increase in success from the average isodynamic angle (117°) to the optimum heading ($131\text{--}133^\circ$), and even the optimum heading is still much less successful than using inclination as the directional mechanism.

Recall that the number of successful starting locations north of the home isocline fell dramatically as range increased (Figure 4.4), due to fish starting north of the home isocline reaching the coast north of the river mouth with a weaker response to the magnetic field (Figure 4.5). Different values for home angle can also affect the distribution of successful starting locations north and south of the home isocline (Figure 4.13). Surprisingly, for inclination a southwardly biased home angle increases the number of successful starting locations south of the home isocline, while for intensity there are more successful starting locations both north and south of the home isocline. For intensity, secular variation is a major issue (Table 4.1), so a southward bias in heading increases success for locations north and south of the home isocline. For inclination, on the other hand, secular variation is less of an issue, but a southward biased heading makes trajectories starting from south of the home isocline slightly more direct.

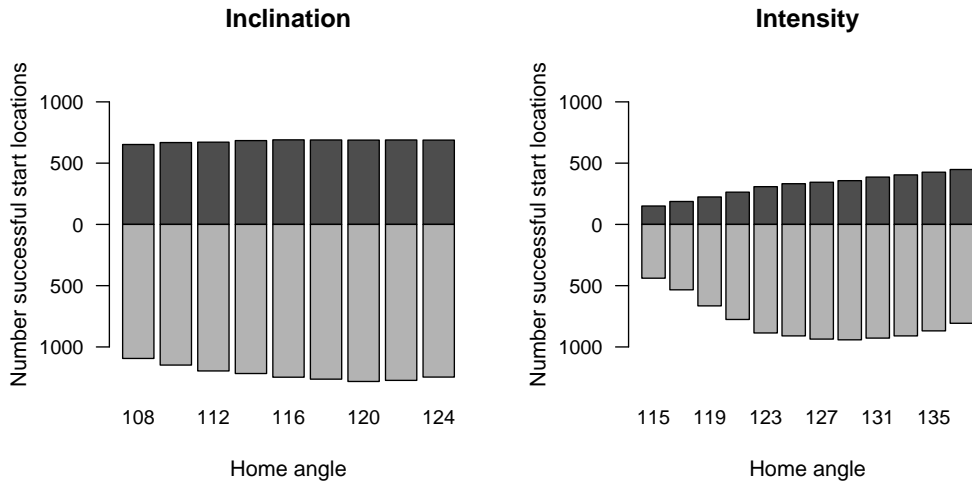


Figure 4.13: The distribution of successful starting locations north (dark gray) and south (light gray) of the home isocline for different values of home angle shown in Figures 4.11 and 4.12.

In conclusion, comparing inclination to intensity, inclination is both stable with respect to secular variation and the angle of the isoclinic through time, and is more tolerant of variability in the precise heading fish use to swim toward home. However, both perform well enough to be considered plausible mechanisms for oceanic navigation in salmon.

Chapter 5

AGE EFFECTS ON STARTING LOCATION AND DATE

5.1 *Introduction*

The majority of Chinook salmon return to freshwater after two years in the ocean, but some also return after one or three years at sea. Chinook are known to spend even longer in the ocean, but no PIT-tagged Columbia River spring Chinook has spent more than three years at sea. The investigation in Chapter 4 was based on 2 ocean¹ fish swimming 40 km/day, but recall from Section 2.4.1 that swim speed depends on size and thus age. Not only do fish of different ages swim at different speeds, they also arrive at the river mouth at different (but overlapping) times. Generally, the 3 ocean fish are the first to arrive, followed by the 2 ocean fish, then the 1 ocean fish, in line with their respective swimming speeds (Figure 5.2). Therefore, it seems possible that the fish all start from similar locations with arrival timing determined by swimming speed. However, we cannot exclude the possibility that fish of different ages start from different locations.

Because age affects arrival timing, the overall arrival timing for different years can also be affected by the relative composition of different age classes across years. For example, consider the mean arrival timing of the four spring Chinook hatchery populations with the largest numbers of returning fish: Lookingglass, Cle Elum, Rapid River, and Dworshak (Figure 5.1). The mean arrival timing for Dworshak and Rapid River moved in lockstep with Cle Elum but one to two weeks behind, except in 2007 and 2008. In 2007, Cle Elum had a mere four fish return, all 3 ocean fish, while 46 of 51 returning fish to Rapid River are 1 ocean fish. This explains why Rapid River

¹Meaning salmon that spend 2 winters at sea, so they would be age 1.2.

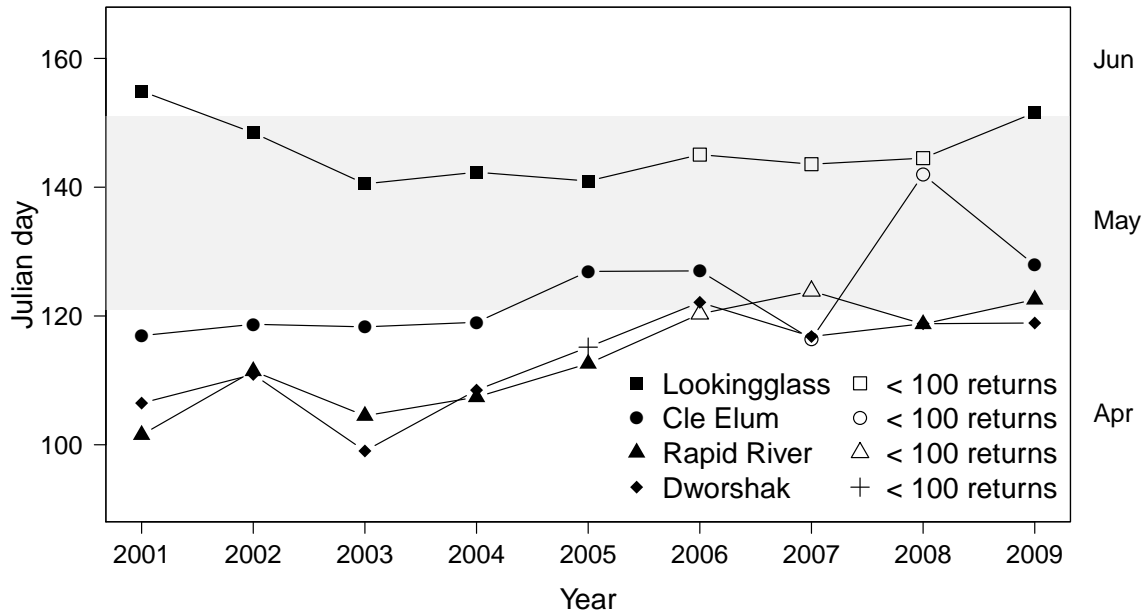


Figure 5.1: Estimated mean arrival times at the Columbia River mouth for four stocks.

lagged Dworshak in 2007. 2008 was even more dramatic, with the mean arrival at Cle Elum over three weeks later than Dworshak and Rapid River. This is not surprising, because all 63 fish returning to Cle Elum in 2008 spent one year in the ocean.

This appears to be an excellent problem to look at by running the model backwards, as every PIT-tagged fish is of a known age and can be run backwards from the river mouth starting at the known arrival date. Unfortunately, the poor performance of running backwards with small values for range prevents this. Instead, the following results are shown for running the model forward as in the previous chapter.

In the following analysis, fish are grouped into 5 categories based on arrival time: too early (before the 2nd fish), early (the first 10% of the arrivals), middle (the middle 80% of the arrivals), late (the last 10% of the arrivals), and too late (after the penultimate fish). The 2nd and penultimate fish arrival times are used to bound the successful arrival times to exclude extreme outliers (such as fish arriving in August).

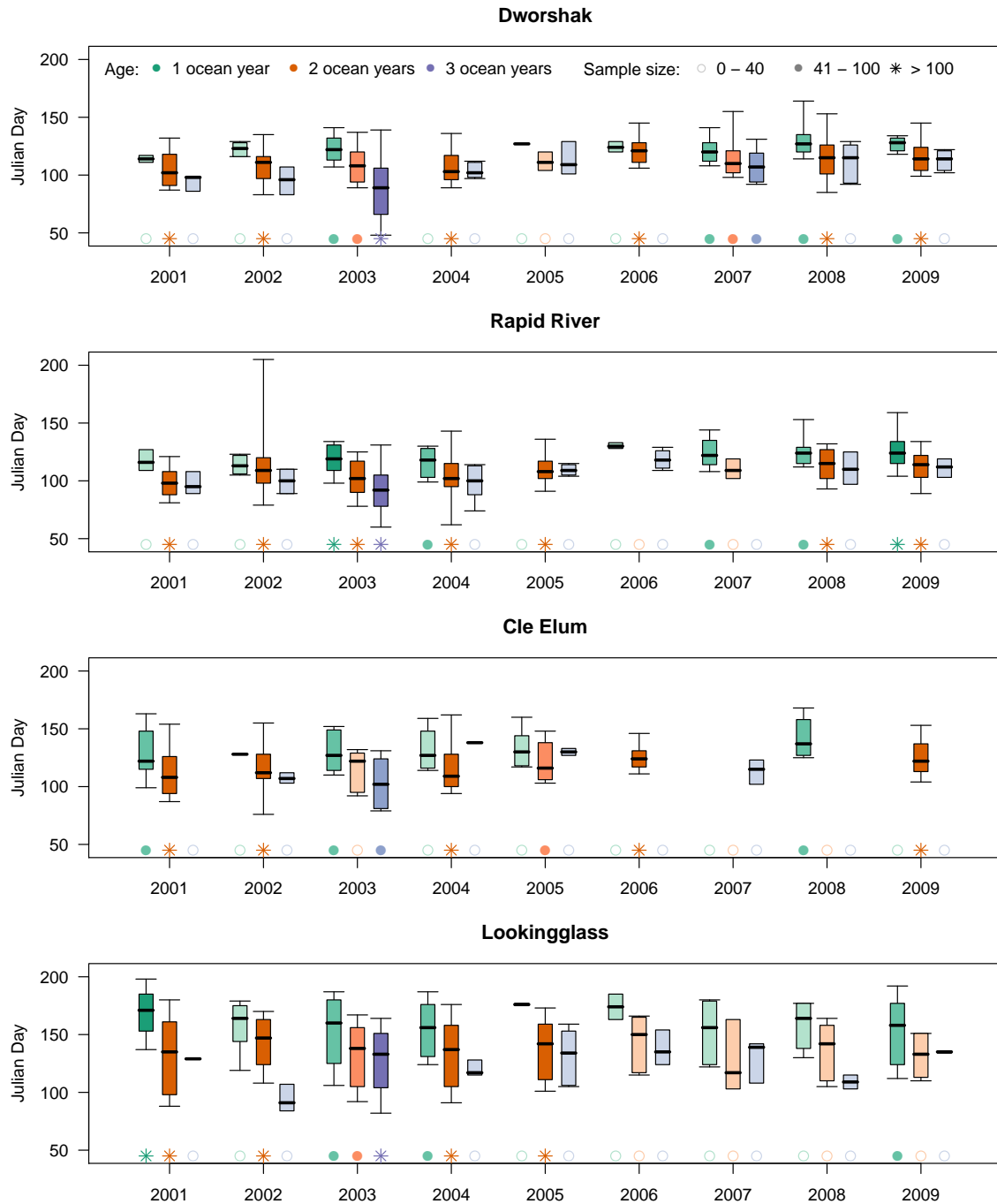


Figure 5.2: The arrival distribution and sample size by age at the Columbia River mouth for four stocks. The boxes show the middle 80% of the arrivals, with the whiskers extending to the 2nd and the next to last fish (the same divisions as those used in Chapter 4).

Additionally, fish are grouped into categories based on arrival location, either the number of kilometers from the Columbia River mouth when it reaches the coast or *sea* if the fish is still at sea at the end of the model run July 1. Though salmon could swim along the coast the rest of the way to the river mouth, I only consider those that reach the coast within 100 km of the river mouth successful because of the offshore distribution presumption discussed earlier. Based on the results of Section 4.3.3, I used a migration initiation date of March 11 for the early stocks (Dworshak, Rapid River, and Cle Elum), and a date of April 11 for the late stock (Lookingglass). I compared two home angles, along the isocline (110°) and at the optimum heading (120°). The differences between them were similar to Section 4.4.2 for all ages classes and stocks with the optimum heading being more successful, so only results using 120° for the home angle are shown.

5.2 Migration Start Location

Because age affects swimming speed as well as time available to spread out, it is important to take age into account when considering start location. However, the data limits which years and stocks can be examined. Most years have no or very few returns for at least one age class (Figure 5.2). An additional concern is that the age distribution in some years might be impacted by the number of releases in prior years. For example, an unusually high number of releases might result in a large number of jacks the next year, a large number of 2 ocean fish the year after that, and so on. Releases for Cle Elum and Lookingglass are relatively consistent. Though releases at Dworshak and Rapid River varied by a factor of two, there does not appear to be a strong correlation between number of releases and numbers of fish returning over the next three years for the observed release sizes (Figure 5.3). In fact, the most striking pattern is that 2 ocean fish return in the highest numbers, followed by 1 and 3 ocean fish. To examine all three age classes using a sufficient sample size of returns, two years fit the criteria: 2003 (Dworshak, Rapid River, and Lookingglass) and 2007

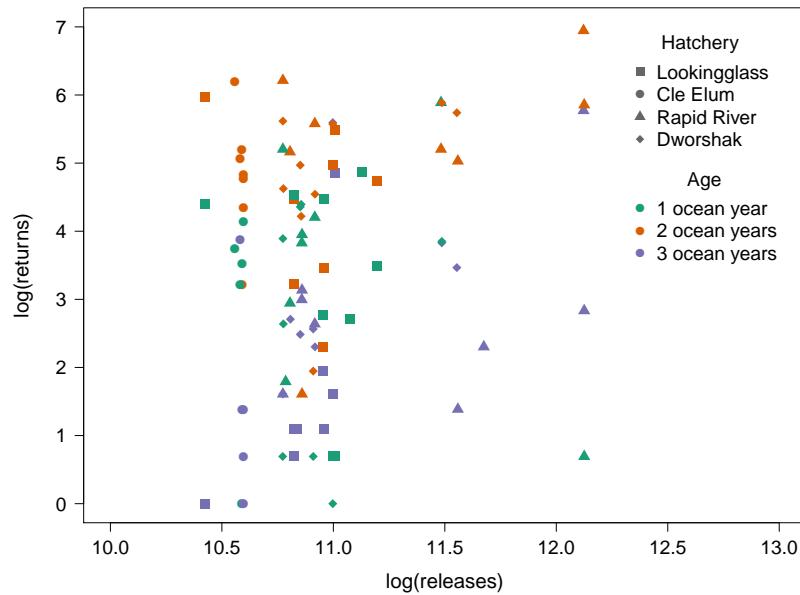


Figure 5.3: Number of hatchery returns by age by the number released the year each cohort out migrated on a log-log scale.

(Dworshak).

In 2003, Dworshak (Figure 5.4) and Rapid River (not shown) have similar arrival timing and thus similar results; Rapid River has a slightly earlier arrival window for 2 ocean fish, so there are slightly fewer locations possible for the last 10% of arrivals (i.e. closed squares turning to open squares) and more locations for the first 10% of arrivals (i.e. open triangles turning to closed triangles). Comparing ages for Dworshak in 2003, several things are apparent. Recall that fish of different ages not only swim at different speeds, but also have different ranges that define early, middle, and late timing. First, using the southward biased home angle rather than an isocline-based home angle is more successful for all ages, not just the 2 ocean fish examined in the last chapter (results for home angle of 110° not shown). This was true whether the starting location was north or south of the home isocline. Distributional differences are apparent across ages. The successful locations are the most compact for jacks (1

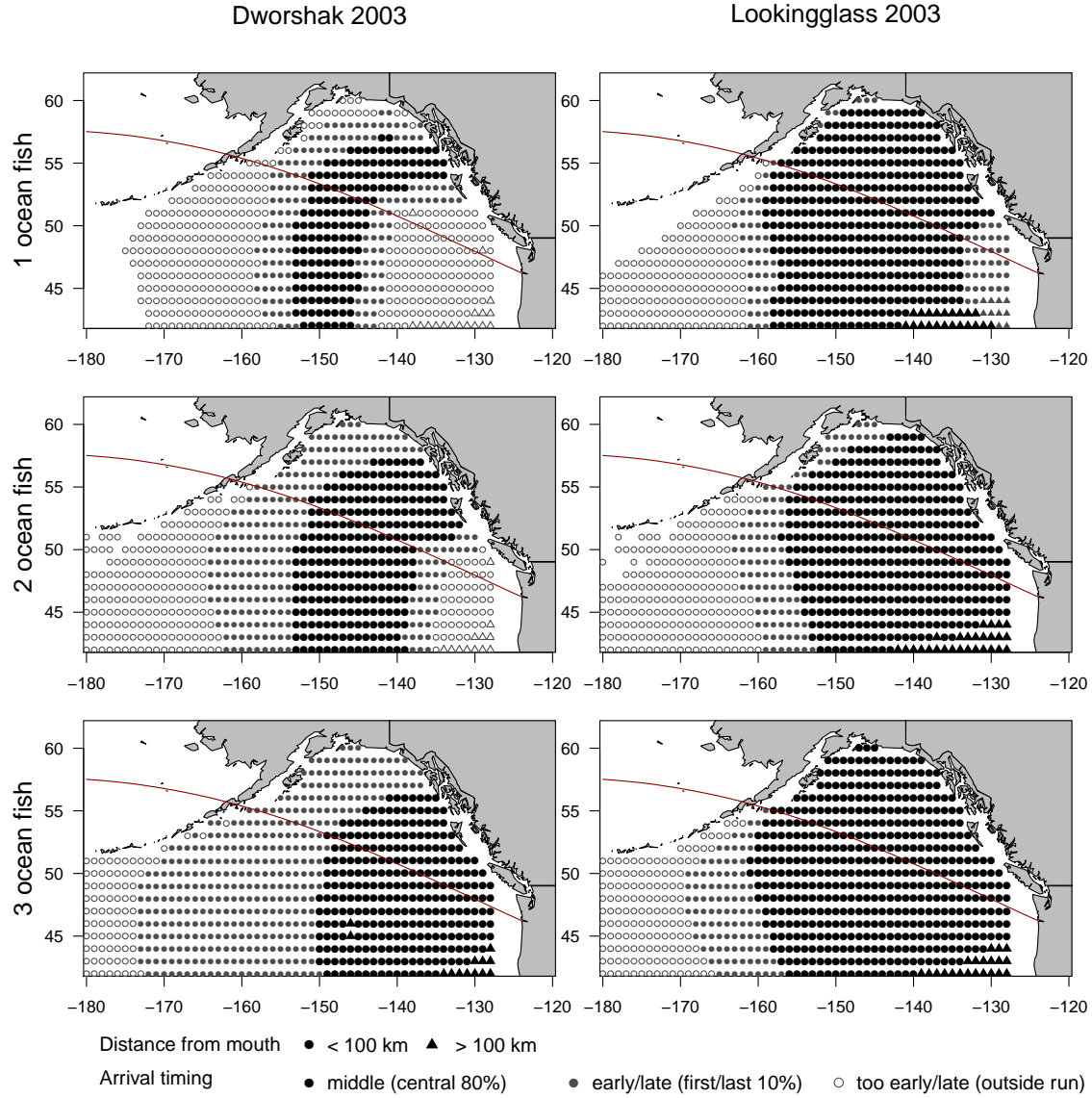


Figure 5.4: Starting locations showing success in space and time for three age classes for 2003 comparing Dworshak and Lookingglass. Line shows home isoclinic. Parameters: range = 1° ; home angle = 120° , start date = March 11 (Dworshak), April 11 (Lookingglass).

ocean) and the least compact for 3 ocean fish. This could be due in part to differences in swimming speed, with older, faster fish able to make it home from a wider range in starting locations. This spread could be explained by the diffusion of an age class for a particular stock being a function of time, such that fish are more spread out the longer they spend in the ocean. Juvenile Columbia River spring Chinook (0 ocean) rapidly disperse over the coastline north and are found along to coast of central and southeast Alaska by summer (Trudel et al., 2009). They could then move southward over the winter and remain relatively clumped, while salmon remaining in the ocean longer disperse as they move north and south seasonally in broad fronts (Myers et al., 2007). In a study of coastal recoveries of Chinook from the west coast of North America, the observed spacial variation was primarily due to natal region followed by ocean age, and the differences among years were slight with no discernible pattern (Weitkamp, 2010). In addition to the size of the successful area varying by age class, there is also a spatial location difference. The 3 ocean fish are the closest, followed by the 2 ocean fish, and finally the 1 ocean fish are the farthest out. We can quantify overlap as the count of locations in the intersection of successful starting locations across ages divided by the count of locations in the union of successful starting locations across ages, that is

$$overlap = \frac{\left| \bigcap_{i=1}^n S_i \right|}{\left| \bigcup_{i=1}^n S_i \right|} \quad (5.1)$$

where S_i is the set of successful starting locations for the fish who spent i years in the ocean ($i \in \{1, 2, 3\}$). With this measure, there is an overlap of 30% across 1, 2, and 3 ocean fish. Therefore, the difference in arrival time is not accounted for solely by swim speed, but also appears to have a spatial component under the assumption of a fixed start date.

The above description is just for a single stock and a single year. While 2003 is an early return for Dworshak, 2007 is one of the later years (Figure 5.1). Comparing

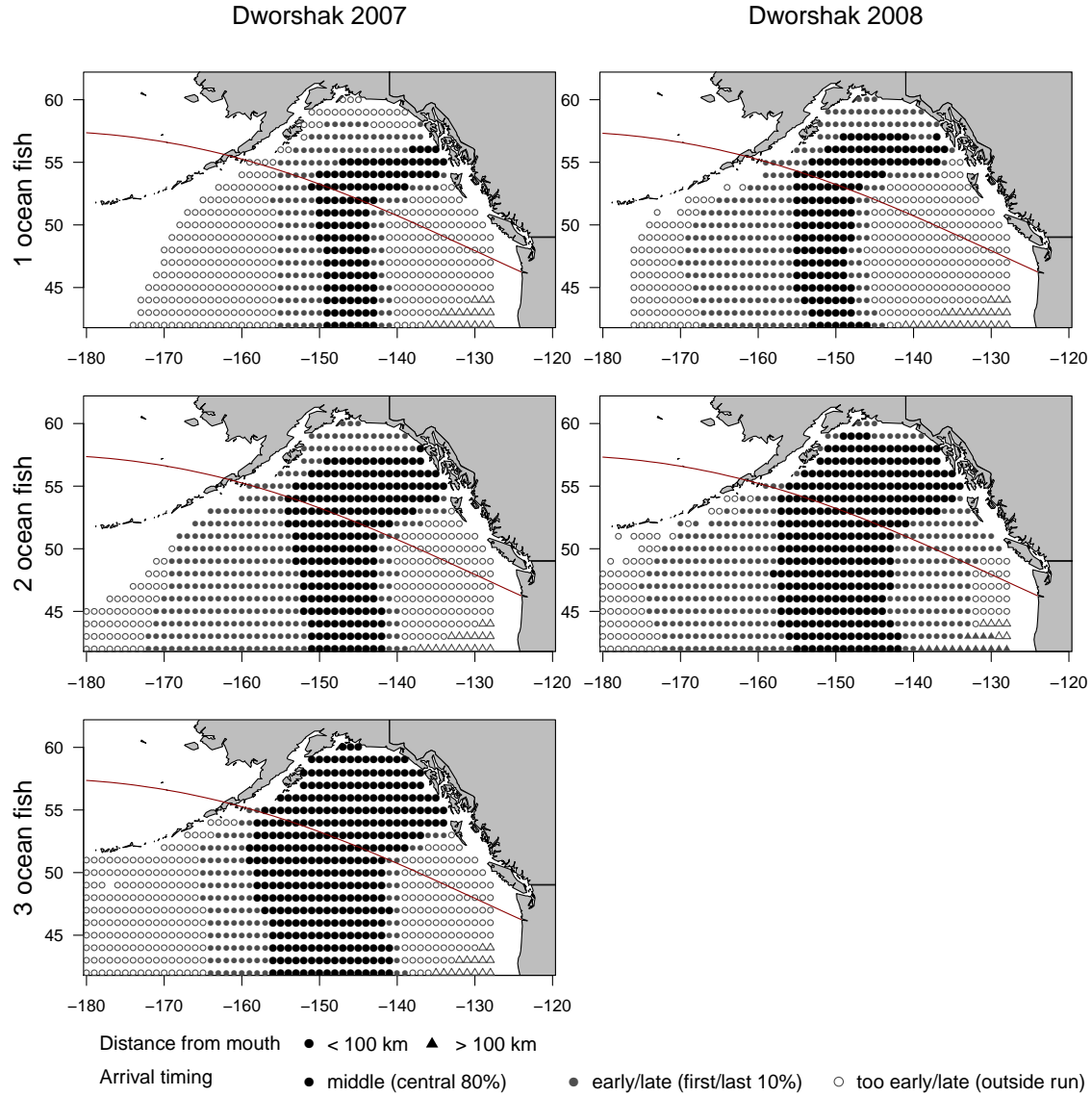


Figure 5.5: Starting locations showing success in space and time for Dworshak comparing 2007 and 2008. Line shows home isocline. Parameters: range = 1° , home angle = 120° , start date = March 11.

2007 and 2008 (Figure 5.5) to 2003 (Figure 5.4), the distribution of 3 ocean fish shifts dramatically, while the distribution of 1 and 2 ocean fish remains quite similar. In 2007 the overlap among ages is 38%, while the overlap in 2008 is 51%, though that only includes 1 and 2 ocean fish since so few 3 ocean fish returned that year. Looking closely, one can see that the distribution of 1 and 2 ocean fish is slightly farther from the river mouth in 2007, though it still noticeably overlaps with the 2003 distribution. For 3 ocean fish, on the other hand, the distributions are almost completely disjoint. So it is possible for the location of one age class, as determined from the arrival timing for that age class, to alter the overall arrival timing for the stock earlier or later. While this discussion focuses on start location, recall that changing the migration initiation date will also shift the successful start locations (Section 4.3.3). For example, an earlier migration initiation date would shift the distribution of successful starting locations farther from the river mouth, but would not change the relative differences in distribution among age classes. Another possibility is that the migration initiation date varies by year. This is unlikely if the trigger for directed homeward migration is physical, like the rate of change of day length, but possible if the trigger is biological, like the spring plankton bloom. However, the fact that the distribution of 1 and 2 ocean fish changed very little between early and late years argues against that possibility.

Next we compare two different spring Chinook stocks in the same year (2003): an early stock, Dworshak, and a late stock, Lookingglass (Figure 5.4). The late stock has a much wider arrival window (Figure 5.2) and thus a much larger distribution of successful starting locations. The fish can home precisely to the river mouth from just about anywhere in the Gulf of Alaska. This was also true for the early stocks based on success in space, but not in time. A large contrast between the early and late stocks is the near complete overlap of successful starting locations in the late stock, not seen in the early stock. The overlap among ages in 2003 is 73% for Lookingglass compared to only 30% for Dworshak. The jack's success is slightly different on the

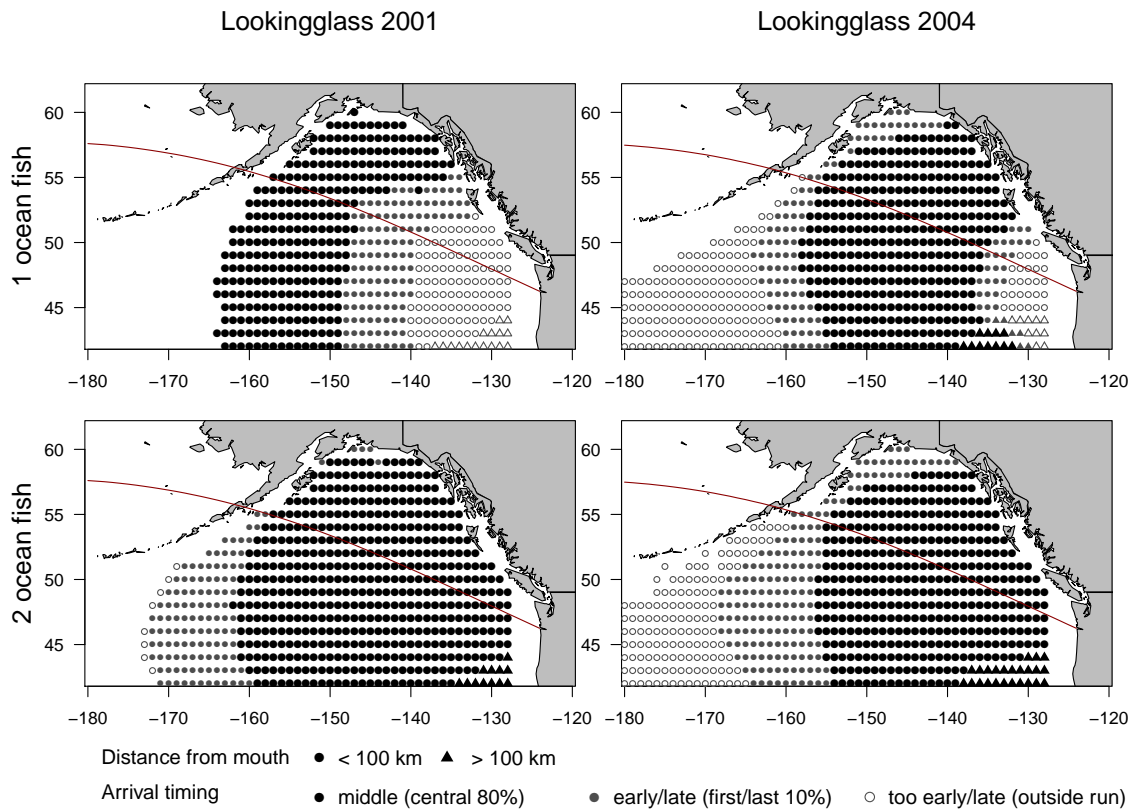


Figure 5.6: Starting locations showing success in space and time for two age classes for Lookingglass comparing 2001 and 2004 using April 11 for the migration initiation date. Line shows home isoclinic. Parameters: range = 1° , home angle = 120° , start date = April 11.

margins, with fewer successful starting locations far from the river mouth and starting locations close to the mouth being early rather than the middle of the run, but the distribution is still broadly similar. To see if this broad distribution of successful starting locations invariant to age class holds across years, we can examine 2001 and 2004, when there were sufficient returns of 1 and 2 ocean fish, though not of 3 ocean fish (Figure 5.6). Indeed, there is a broad distribution of successful starting locations, except for jacks in 2001. Though the successful starting area is still larger than that of the early Dworshak stock jacks, it forms a more distinctive band than 2003 or 2004.

This is also seen comparing the overlap of successful starting locations for 1 and 2 ocean fish, which is 49% in 2001 and 80% in 2004.

Thus, age composition can affect timing on a stock level when using PIT tag data, and should be taken into consideration when using arrival timing information based on this data. For example, Keefer et al. (2008) examines correlations between environmental predictors, such as river flow, temperature, and ocean indices, and median arrival timing of nine PIT-tagged Columbia River spring Chinook stocks. While the correlations mirror those seen with the overall run timing, all stocks have some years with small sample sizes (minimums range from 10 to 68). We have seen above how age composition can skew the mean and median arrival date for years with small sample sizes or even just years with a very unbalanced age composition.

5.3 Single Migration Initiation Date Per Stock

Previous chapters assume a single migration initiation date for an entire stock; that is, every fish begins a directed homeward migration on a single date. Thus the variation in arrival time is explained by differences in swimming speed and the spread of starting locations. However, another possibility is that there is a distribution of migration initiation dates, with some salmon departing earlier than others. The trigger would still be calendar based, such as day length or rate of change in day length, but the fish would have some plasticity in their response.

Looking back to the examination of different migration initiation dates (Section 4.3.3), a migration initiation date around March 11 to March 21 was the most successful for the early stocks (Dworshak and Rapid River). It is instructive to look at the distribution of starting locations for a particular year. For Dworshak, comparing 2003 (Figure 5.4), 2007, and 2008 (Figure 5.5), a single migration initiation date seems plausible. The only exception is 3 ocean fish in 2003, where there are no starting locations for which the fish arrive in the first 10% of the run. Since 10% of the 3 ocean fish had arrived by March 11, even a fish directly offshore of the Columbia

River cannot arrive prior to the migration initiation date of March 11. In fact the earliest modeled fish arrived March 17, i.e., in this case the observed data contradict the assumptions. For Lookingglass, comparing 2001 (Figure 5.6), 2003 (Figure 5.4), and 2004 (Figure 5.6), a single migration initiation date seems less plausible. Only the jacks have starting locations where they arrive in the first 10% of the run. The 2 and 3 ocean fish have a wide region of starting locations for fish that arrive in the middle 80% of the run, but no starting locations for fish that arrive in the first 10% of the run, even directly off the coast at the river mouth. Again, 3–5% of 2 and 3 ocean fish arrived before the migration initiation date of April 11 in those years, and the earliest modeled fish arrived April 17 or 18.

Using an earlier migration initiation date of March 1 for Dworshak and April 1 for Lookingglass, the distribution of successful starting locations shifts west farther from the river mouth (Figures 5.7 and 5.8). However, the overlap of successful starting locations across ages shifts only a few percentage points. Even with the westward shift due to an earlier start date, for Dworshak in 2003, there are still only two locations where the 3 ocean fish arrive in the first 10% of the run. Rather than posit an earlier start date overall, perhaps the 3 ocean fish were unusually close to the river mouth or started migrating unusually early in the particular year. For Lookingglass, on the other hand, the earlier migration initiation date provides starting locations with the whole range of arrival times, except for 2 ocean fish in 2004. However, the distribution of 1 ocean fish in 2001 is fairly skewed to the west. Rather than being solely a function of spread in starting location, the arrival distribution might also be partly a function of spread in migration initiation date. In that case, there would be a commensurate shrinking of the spread in starting locations, perhaps to something more similar to Dworshak.

We have seen larger arrival windows (i.e., variance in arrival timing) for Lookingglass compared to the early stocks. In general for Columbia River spring and summer Chinooks, for both wild and hatchery populations, early runs are more compact than

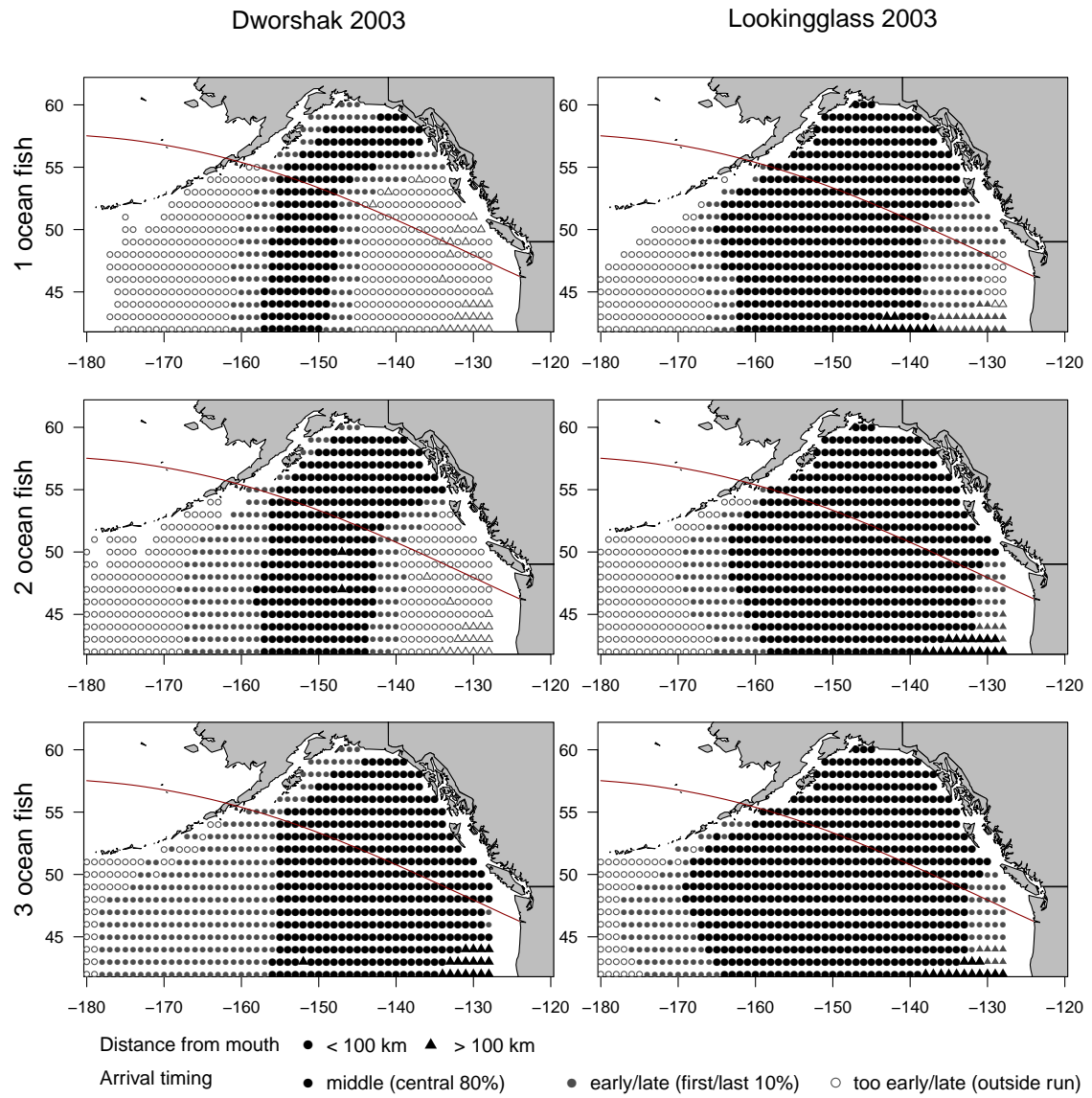


Figure 5.7: Starting locations showing success in space and time for three age classes for 2003 comparing Dworshak and Lookingglass using an earlier migration initiation date. Line shows home isocline. Parameters: range = 1° ; home angle = 120° , start date = March 1 (Dworshak), April 1 (Lookingglass).

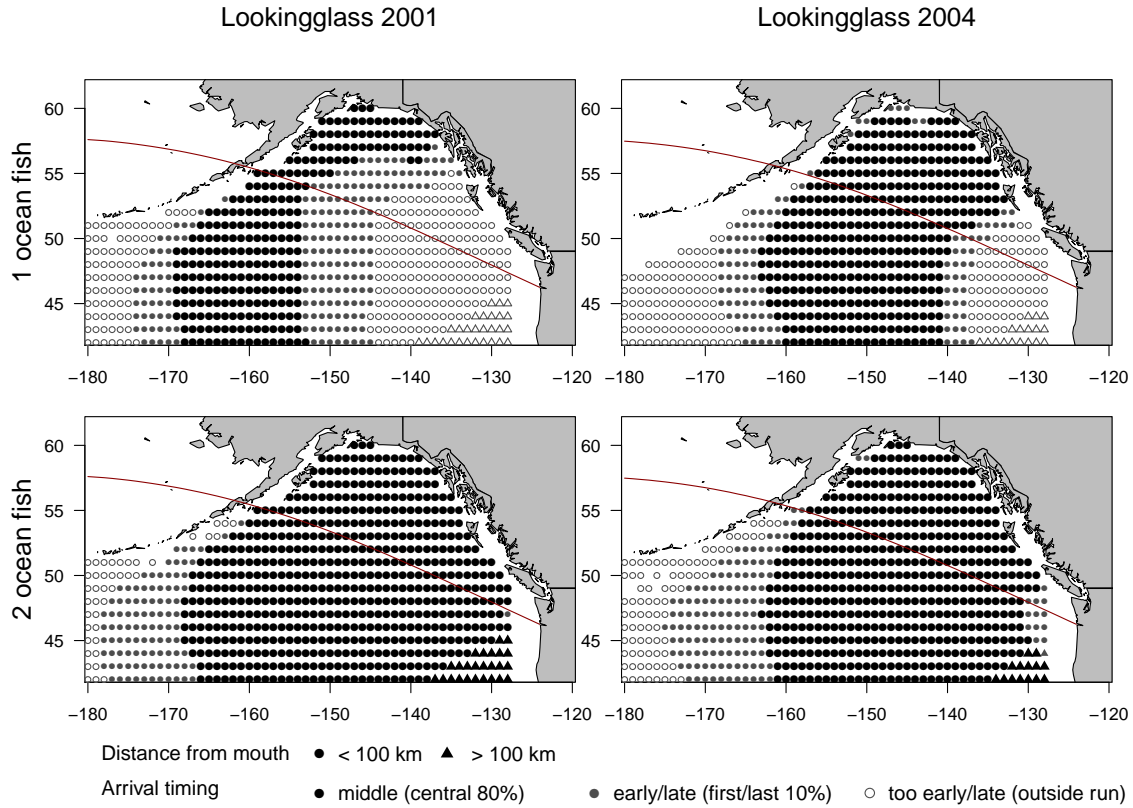


Figure 5.8: Starting locations showing success in space and time for two age classes for Lookingglass comparing 2001 and 2004 using an earlier migration initiation date. Line shows home isocline. Parameters: range = 1° , home angle = 120° , start date = April 1.

late runs (though this does not hold for fall stocks, possibly implying a different migration initiation mechanism) (CBR, 2008). One explanation is that there is a distribution of migration initiation dates, but the spread of starting dates is narrower for early stocks and wider for later stocks. For the ultimate reason behind differing variation in migration initiation dates, we could speculate that the cue (such as rate of change in day length) is less strong for later stocks, or that precise timing is less useful for later stocks and thus under less selective pressure.

5.4 Correlation with Run Timing

Given how the age composition in a given year could alter the mean arrival timing for a particular stock, the next question is whether the age composition in a given year influences the overall run timing. When considering the run at large, age information is not available as it is for PIT tagged fish. Fish are classified as jacks (age 1.1) or adults (age 1.2 and up) based on size when passing Bonneville Dam, so there are no direct data on the proportions of ages of adult fish. However, studies of age and length composition based on sampling enable one to estimate the ratio of 2 ocean to 3 ocean fish (John Whiteaker, pers. comm.; Hooff et al., 1999a,b; Kelsey and Fryer, 2001, 2002, 2003; Miranda et al., 2004, 2005; Whiteaker and Fryer, 2006, 2007, 2008; Torbeck et al., 2009). Additionally, fish are divided into spring, summer, and fall runs based on the date of passage at Bonneville Dam. Because the runs can overlap and vary from year to year, another method is to fit three normal distributions to the three runs (Anderson and Beer, 2009). Comparing the mean adult arrival from Anderson and Beer (2009) to the estimated percentage of adults aged 1.2 results in a correlation of 0.47 (Figure 5.9).

Though the correlation is weaker when the percentage of age 1.2 adults is higher, age composition might provide useful information as one predictor in a more complete run timing model, such as Anderson and Beer (2009) or Keefer et al. (2008). For example, Anderson and Beer (2009) describe a mechanistically derived model that predicts run timing as a combination of genetic factors and distal and proximal environmental conditions. The predictors include jack arrival timing, January upwelling, and April flow, all for the prior year, as well as January upwelling and March flow. It would be interesting to see whether the relationship holds, if data can be found for earlier years or for alternate estimates of age composition. However, if the goal is to predict run timing in advance of the run, an estimate of age composition is needed that does not rely on sampling at Bonneville Dam throughout the run.

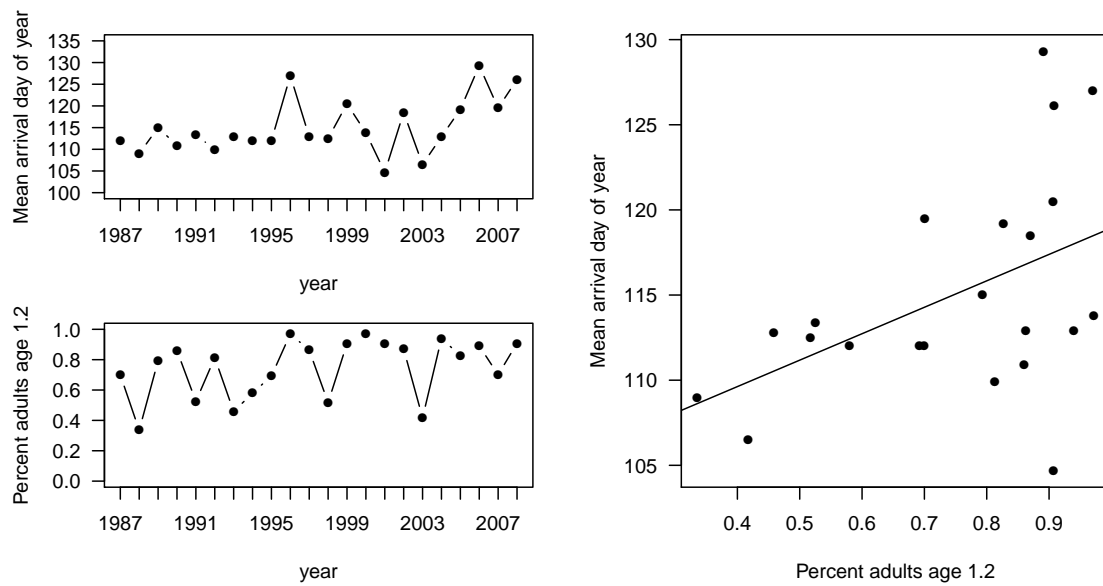


Figure 5.9: Left panels show the time series for estimated mean arrival day (top) and estimated adult age composition (bottom). The right panel shows age composition as a predictor for mean arrival day as well as the regression equation $d = 15.53a + 103.41$, where d is the mean arrival date and a is the percent of adults age 1.2 ($r^2 = 0.22$, $p = 0.03$).

Chapter 6

CONCLUSION

Models are an excellent way of examining hypotheses that are difficult and expensive to address experimentally. The ocean migration of Pacific salmon is a good example. Quinn (1982) and Lohmann et al. (2008) hypothesize that salmon imprint on the inclination or intensity of the magnetic field at the mouth of their home river on out migration as juveniles. When returning as adults, the magnetic field component provides the y coordinate on the North–South axis, while the coastline determines the x coordinate on the East–West axis. The difficulties in experimentally evaluating this are tremendous. Adult Chinook salmon are widely distributed in the Gulf of Alaska and average nearly a meter in length, making laboratory studies challenging if not impossible. Models, on the other hand, allow evaluation of the feasibility of proposed mechanisms in the context of realistic ocean conditions.

In examining the sensitivity of the model to various parameters, the range parameter is an important determinant of the rate of success, where success is defined as the salmon making it to the river mouth during the appropriate window in time from a variety of starting locations. Range controls the steepness of response to the magnetic field; the smaller the value of the range, the more directly north or south the fish will swim when not on the home isocline, while for larger range values, the fish will swim more eastward. Smaller values of range, where fish swim directly towards the isocline and then along it, are more successful, while larger values of range tend to work only for starting locations already near the home isocline. Additionally, a swimming angle that is symmetric around the angle of the home isocline is more successful than an asymmetric response. The migration initiation date is the key parameter determining

the east–west center of successful starting locations. If one imagines concentric circles centered on the river mouth, an earlier migration initiation date moves the successful locations towards the outer circles, while a later migration initiation date moves the successful locations inward.

Comparing the magnetic field components of inclination and intensity as directional mechanisms, both are successful in getting the fish to the Oregon/Washington coast near the Columbia River mouth from almost any starting location in the Gulf of Alaska. However, when narrowing the definition of success to arriving within 100 km of the river mouth in the middle 80% of the arrival window for a particular year, inclination clearly outperforms intensity for several reasons. First, the change in the magnetic field over time, known as secular variation, results in a smaller navigational error for inclination than intensity. The average navigational error is only 3 km for inclination compared to 19 km for intensity for fish that spend 2 years in the ocean. Also, the bearing of the inclination isoclines varies less than that of the intensity isoclines, which would be advantageous if fish attempt to maintain a compass heading along the isocline towards home. Because the inclination isoclines have a more east–west bearing than intensity isoclines, the route homeward from starting locations south of the home isocline is more direct using inclination rather than intensity. Perhaps most importantly, a wide variety of home angles result in a high rate of success for inclination, making the precise heading to which the fish orient less important. Even with a southward bias, which corrects for the navigational error to the north from secular variation, inclination has higher success across a broad range on angles than the optimum angle for intensity.

Because swim speed is a function of length, and length is a function of age, there is a pattern to the arrival timing by age with the oldest fish arriving first, then the bulk of the run which spends two years at sea, and finally the early maturing jacks that spend a single winter in the ocean. Age composition is thus an important factor in run timing at the stock level. There is the suggestion that age composition may also

be an important predictor at the run level, which needs further investigation. A single date for migration initiation looks more plausible for early stocks than late stocks. With the timing of early stocks generally being more compact than late stocks, one possibility is that there is a distribution of migration initiation dates. The late stocks would have a larger variance for the distribution than early stocks, which would also reduce some of the large spread seen in possible starting locations for the late stocks.

6.1 Next Steps and Possible Applications

While the present results are useful, there are also some shortcomings with the model in its current form. One issue is separating time and space effects. Because we have a single piece of empirical information, the arrival timings at Bonneville Dam, it is not possible to disentangle the two. Either a closer fish that starts migrating later or a farther fish that starts migrating earlier are equally valid explanations of an observed arrival time and are impossible to distinguish. Additionally, both scenarios could be affected by the swimming speed assumed in the model, though more empirical evidence exists to constrain swimming speed than the start location or date. It is possible that additional information could be used to help separate time and space. For example, if a maturing Columbia River spring Chinook, or ideally several of them, were tagged at sea with archival data storage tags, recovery data could be used to constrain the model. A return trajectory could be reconstructed from either a tag with light-based geopositional information or a tag that recorded magnetic information (Welch and Eveson, 1999; Sturlaugsson et al., 2009). Even a simpler depth and temperature tag could be used to narrow down the potential trajectories (Friedland et al., 2001). By further constraining the model, it may be possible to determine the migration initiation date and location, as well as refine the estimated swimming speed. These parameters could then be used for a variety of starting locations and a distribution of dates to determine probable ocean distribution.

While the OSCURS model is quite accurate in the open ocean, it does not incor-

porate small-scale features, and is known to be inaccurate near shore (Walter et al., 1997). To extend the present model to Chinook with different life history characteristics, different life stages, or even other salmon species, it would be advantageous to use an ocean model that incorporates coastal features. For example, fall ocean-type Chinook are thought to be more coastally oriented and are caught in large numbers in coastal marine fisheries. Additionally, out-migrating juvenile Chinook salmon proceed northward along the coast during their first year. Juvenile coho salmon also have a primarily coastal ocean distribution. The present model could easily be applied to all of the above, but would need a coastal ocean model to accurately simulate the coastal trajectories of salmon. Additionally, it would be interesting to compare coastal and open ocean models as part of a sensitivity analysis to see how use of a different ocean model influences the results.

The behavior rules currently implemented are very simple, in order to demonstrate whether simple rules can successfully return salmon to the river mouth from a wide variety of starting locations. However, more complex rules can also be used with the model. One possible extension would be to include bioenergetics (i.e., Rand et al., 1997). Indeed, this would be critical if the modeling duration were extended beyond the directed homeward migration to accurately model swimming speed as the fish are growing. Representing the spatial distribution of prey density is a challenge for bioenergetic models. While Booker et al. (2008) modeled juvenile Atlantic salmon trajectories using an ocean model and behavior rules, they created a separate non-spatial model to investigate bioenergetics in the marine phase (Smith et al., 2009).

There are many interesting directions to take this model. One could start applying it to other Pacific salmon species, both in the Columbia River or other locations, as well as fall Chinook salmon. Another possibility is to incorporate other data if they become available, such as tagging data, to refine the model and parameter values. Adding a bioenergetic model would allow longer time spans to be modeled and additional questions to be considered.

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