

Yearling Chinook salmon ecology and behavior during early-ocean migration

Brian Joseph Burke

A dissertation
submitted in partial fulfillment
of the requirements for the degree of

Doctor of Philosophy

University of Washington

2014

Reading Committee:

James J. Anderson, Chair

David A. Beauchamp

John W. Ferguson

Program Authorized to Offer Degree:
School of Aquatic and Fishery Sciences

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Brian Joseph Burke

University of Washington

Abstract

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Brian Joseph Burke

Chair of the Supervisory Committee:
James J. Anderson
School of Aquatic and Fishery Sciences

High mortality rates of Pacific salmon (*Oncorhynchus* spp.) in the nearshore ocean environment of the Columbia River (Northwest USA) is one of several key factors limiting recovery of these threatened and endangered fish. Several studies describe correlative relationships between environmental or biological factors and fish abundance. However, few mechanistic descriptions exist that describe the causes of growth and mortality during the early ocean life stage (i.e., the first two to four months in the ocean). Similarly, salmon navigation and behavior during early ocean migration is poorly understood. The purpose of this study was to build a spatially-explicit individual-based model (IBM) of yearling Chinook salmon migration in the nearshore ocean environment that mechanistically describes the biologically-relevant processes impacting salmon movement and growth during the early ocean life-history stage. The model domain covers about 1000 km of shoreline from northern California to Vancouver Island, BC and extends about 300 km offshore. Specific objectives were to:

1. Model yearling Chinook salmon spatial distribution through time as a function of environmental and geospatial covariates. Covariates were chosen and grouped according to the types of sensory capabilities salmon use to detect them. Results can therefore inform the behaviors and external cues used during migration.
2. Construct a spatially-explicit IBM that includes many of the basic ecological processes of early ocean migration and growth, relying on an existing external hydrodynamic model for environmental variables. The model tracked individual fish through space and time, recording location, size, and state (alive or dead, energetic content, etc.) for the first several months of ocean life. Several different migration strategies were simulated and compared to existing empirical estimates of spatially-explicit abundance data from a ten-year ocean cruise dataset. Only one strategy, defined here, was able to characterize the observed spatial temporal distribution of fish.
3. Validate and fine-tune the model using existing empirical estimates of growth and migration rates derived from otolith microchemistry from about 200 individuals. For this validation, I used the behavior that was shown to be most reasonable in Objective 2 to test against empirical data.

Chapter 1 provides a general background for the analyses described above and some of the reasoning that went into the project design.

Chapter 2 describes the use of a zero-inflated Generalized Linear Model assuming a negative binomial error structure to describe catches of yearling Chinook salmon as a function of both environmental and geospatial covariates. I found that both types of information were associated with salmon abundance, but that the geospatial information was slightly more informative in the model. I conclude that environmental conditions experienced during out-

migration can alter the genetically-driven, stock-specific migration patterns observed in the marine environment. By applying the model to multiple stocks over three months, I was able to show that spatial distributions vary among stocks and change through time.

Chapter 3 compares catch data collected during May and June in three different years to simulations of fish distributions generated with five distinct migration strategies. Only two strategies produced fish distributions similar to those observed in May and only one of these mimicked the observed distributions through late June. In the strategies that result in matches with empirical data, salmon distinguish North from South (i.e., they must have a compass sense), and control their position relative to particular landmarks such as the river mouth (i.e., they must have a map sense). Salmon with these two abilities could follow spatially-explicit behavior rules and avoid entrapment in strong southward currents or advection offshore. To fit the relatively consistent interannual spatial distributions observed over the migration season, simulated swimming speed needed to vary among years, suggesting that salmon also have a clock sense to guide the timing of their migration.

In Chapter 4, I applied the spatially-explicit individual based model of early marine migration designed in Chapter 3 on two stocks of yearling Chinook salmon to quantify the influence of external forces on estimates of swimming speed and consumption. Swimming speeds required in the model were higher than those estimated without taking into account ocean currents (and assuming a straight-line migration from the river mouth to the capture location). Moreover, the estimated variance in swimming speeds was significantly lower than the variance in movement rates, suggesting that ocean currents mask salmon behaviors and the role of genetically-determined movement may be more important in marine migration than previously thought. There was also a stock-specific response, as fish from the Snake River Basin swam

faster than salmon from the Mid and Upper Columbia River. By taking into account experiences of individual fish, this approach incorporates both individual behavior and the influence of external physical factors such as ocean currents, allowing a more accurate estimation of biological parameters.

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Acknowledgements

In 2006, Ed Casillas began discussions about how we might model some of the data coming from NOAA's ocean program. These discussions led to an introduction to Jim Anderson and it quickly became clear that we had highly overlapping views of what would be a good approach to better understanding the marine ecology of salmon. John Williams and John Ferguson joined the discussion and pushed for a close collaboration between NOAA and UW. Without a little prodding from Ed, Jim, John W., and John F., this work would not have been done. I want to thank these four people for creating this opportunity.

Jim Anderson was quite receptive to the ideas I had for modeling ocean migration and was very supportive and influential throughout the last six years. He created an environment in his lab that spurred a great combination of critical thinking and creativity. I learned a great deal more in Jim's "whiteboard" sessions than I contributed, and will be forever grateful for that.

I also want to thank the rest of my committee. John Ferguson has been uniquely supportive, both as a Division Director at NOAA Fisheries and as a committee member. His feedback and interest in my progress has helped immensely. David Beauchamp and Julie Keister both provided crucial feedback at a very early stage. Although they may not have realized it, particular comments from each of them have driven me to look particularly hard at model assumptions and design. And at the last minute, when I needed to fill a hole in my committee, Neil Banas graciously agreed to serve as the GSR. Thank you!

Even though Jim is fond of saying things like "We're modelers – data just get in the way", this project would never have begun without the amazing data sets generated by NOAA's ocean program. I started working with this group in 2006 and have enjoyed every bit of it. I probably shouldn't list names because I will inevitably leave some important ones off, but I specifically want to thank Ed Casillas, Kurt Fresh, Bill Peterson, Brian Beckman, David Teel, Jessica Miller, Cheryl Morgan, Laurie Weitkamp, Bob Emmett, Jen Zamon, and Kym Jacobsen. António Baptista deserves his own sentence in this list, as the bulk of this dissertation is centered around using the output from his hydrodynamic model – he has been extremely helpful throughout. I hope I can continue working with this amazing group of scientists.

I need to put in a plug for the funding agencies. Bonneville Power Administration funded much of the ocean work that supplied the data for these analyses. In addition, they funded me to travel for project meetings and some regional science meetings as well. NOAA Fisheries supplied me with a salary! I would not have even considered going back to school without that support.

Last but not least, my family. There are a lot of reasons I decided to go back to school. One of them is so that I can show my kids, Claire and Derry, the value of a good education. Many times, after hitting a writing block or a particularly hard day, I would look at their picture and remember this fact. They've provided much more motivation than they will ever know. And I want to thank my wife, Aimee Fullerton. Yesterday evening was typical – I was working on my laptop after dinner, she got the kids ready for bed (read them books, brushed their teeth, etc.) and never asked whether I was going to help. I can't count the number of times she's covered for me while I was working. Nor can I count the times I used Aimee as a sounding board for some half-baked ideas. I couldn't ask for a better wife or colleague (let alone both of these in one person). Thank you!!!

Dedication

For Ba, my late grandfather, who inspired critical thinking and always set a high priority on education. Thank you for everything.

Chapter 1 Introduction

1.1 Background

A key attribute of salmon (*Oncorhynchus spp.*) life history is the migration and residence in the marine environment. Chinook salmon (*O. tshawytscha*) in particular spend an extensive period in the ocean (one to five years), before returning to freshwater to spawn (Groot and Margolis 1991). For most individuals, ocean residence represents the longest stage of their life history. However, relative to other life-history stages, our understanding of the behavior and ecology of salmonids during ocean residence is limited (Healy 1980). Due to the size of the Pacific Ocean and the time lag between when fish enter the ocean and when they return to freshwater, direct observation and manipulative studies are difficult at best. Almost everything known about the importance of this life-history stage comes from correlative studies. Fortunately, the growing evidence that growth and survival in the ocean environment affect population dynamics has resulted in an increase in marine research in recent years.

The early portion of the marine residence period is particularly critical to salmon survival (Parker 1968, Hartt 1980, Pearcy and McKinnell 2007) and for setting year-class strength (Beamish and Mahnken 2001, Mueter et al. 2005). Mortality of salmon tends to be highest during the first few months at sea (Bax 1983, Fisher and Pearcy 1988, Cross et al. 2008). For example, Wertheimer and Thrower (2007) released several groups of chum salmon (*O. keta*) at different times and conditions (fed/unfed) and showed that mortality rate decreased with days at sea. Anecdotal evidence also supports this hypothesis; in most years, there is a strong relationship between the number of precocious male salmon (i.e., jacks) and adult returns the following year, suggesting that year-class strength is set early in ocean life. Finally, a spate of research shows that abiotic (ocean conditions, river flow, temperature, etc.) and biotic (prey indices, competitor abundance, etc.) factors during the early marine residence period impact salmon growth (Holtby et al. 1990, Beauchamp et al. 2007, Wells et al. 2008) and survival rates (Fisher and Pearcy 1988, Mueter et al. 2005, Pearcy and McKinnell 2007; also see <http://www.nwfsc.noaa.gov/research/divisions/fed/oeip/a-ecinhome.cfm> for detailed

correlations between ocean conditions and salmon survival). It should be noted that although most evidence suggests that mortality is greatest just after entering the ocean and declines with size, Beamish and Mahnken (2001) suggest that there are two main periods of mortality during the first ocean year – one immediately after entering the ocean and one during the first fall/winter. This hypothesis is supported by data from Moss et al. (2005) and points to growth during the first summer at sea as an important factor determining year-class strength. Moreover, the good ocean conditions in 2011 off the coast of Washington and the unexpected low returns of spring Chinook salmon to the Columbia River in 2013 (from the 2011 outmigration) suggest that environmental factors after the first summer can sometimes have a strong influence on cohort strength.

The mechanism behind the observations of high early marine mortality is likely related to size-dependent mortality (Holtby et al. 1990, Moss et al. 2005, Cross et al. 2008). If the old paradigm “bigger is better” holds for juvenile salmon after entering the marine environment, the optimal strategy would be to grow fast. Empirical estimates of marine growth rates are difficult to obtain, but data suggest that marine growth rates are high. For example, Tomaro et al. (2012) estimated mean growth rates of almost 1 mm/d and Trudel et al. (2007) estimated extremely high salmon growth rates in the coastal environment, sometimes exceeding 2.5 mm/d.

Although salmon growth is variable among locations and years (Cross et al. 2008, McKinnell and Reichardt 2012), there are several lines of evidence that suggest salmon take advantage of good growing conditions when they can. On a small scale (meters to kilometers), when spring Chinook salmon are near areas of high prey patchiness, they tend to aggregate near prey patches (J. Zamon, NOAA Fisheries, pers. comm.). Brodeur and Pearcy (1987) documented diel feeding patterns (peaks of stomach fullness near dawn and dusk), probably in response to the vertical migrations of prey species (Blaxter and Holliday 1963, Orsi et al. 2007). On a larger spatial and temporal scale, yearling Chinook salmon have evolved a general northward migration (Miller et al. 1983, Fisher et al. 2007, Morris et al. 2007, Tucker et al. 2011). This migration pattern puts them further north than many of their competitors (Orsi et al. 2007), such as Clupeids and squid. Moreover, day length during summer increases with latitude, allowing more time

to feed each day in northern regions. Brodeur et al. (2007) found a higher incidence of full stomachs in salmon caught off of Alaska than fish in more southern areas, indicating good conditions for feeding and growth. Similarly, Trudel et al. (2007) estimated higher salmon growth rates in northern regions as compared to southern regions.

However, Trudel et al. (2007) also showed that average salmon size decreased with increasing latitude, contrary to expectations. To complicate the picture, a portion of salmon emigrating from the Columbia River each year does not undertake a northward migration and some even migrate short distances south (particularly subyearling Chinook and coho salmon; Morris et al. 2007). The factors affecting whether an individual fish migrates north or not are unknown.

Although general migration patterns and behaviors have been documented and several environmental correlates determined, we do not have a comprehensive understanding of the ocean ecology of juvenile salmon. One of the more difficult aspects of studying juvenile salmon ocean ecology is the temporal and spatial variability. For example, the Pacific Decadal Oscillation (a correlate with salmon survival) has fluctuated rapidly in the past ten years (<http://jisao.washington.edu/pdo/>). Even within years, the various indices of ocean condition change from week to week (A. Baptista, Oregon Health and Science University, pers. comm.; <http://www.stccmop.org/datamart/columbiariver-climatologies>). Brodeur et al. (2007) found greater spatial variation in salmon diet than temporal variation (both among and within years). Of particular importance for early marine growth of fish migrating through this dynamic seascape is the spatial and temporal overlap with predators and prey, both of which can be patchily-distributed and ephemeral.

Management of salmon populations has focused primarily on the freshwater environment (Ford et al. 2010). The dearth of data on salmon performance in the ocean and the effect of spatial and temporal variability on salmon growth and survival have forced some managers to base decisions on incomplete knowledge of factors affecting stocks across the life cycle. For example, many juvenile salmon are barged downstream in an attempt to reduce in-river mortality. These fish arrive in the Columbia River estuary earlier than fish traveling in the river, with unknown consequences. The timing

of barged fish releases may or may not match well with good ocean conditions (e.g., high prey abundance, cool temperatures, etc.), but certainly affects survival to some degree (Scheuerell et al. 2009). Similarly, hatcheries throughout the Columbia River basin release millions of fish annually without the benefit of knowing the state of ocean productivity at the time smolts enter the marine phase of their life. Another aspect of salmon management that would benefit from a greater understanding of ocean ecology is harvest management. Most pre-season estimates of run size come from correlative studies, such as jack counts, and are often inaccurate. Managers of multi-million dollar salmon fisheries could make more informed decisions if they had a better understanding of the complex interactions between salmon and their environment. Fish size, timing of ocean entry, migration behavior, and marine growth rates all interact to affect salmon survival rates. We currently lack the tools necessary to describe these dynamics in any detail.

1.2 Purpose and Concepts

Although we have some data on where juvenile salmon go after emigrating from the Columbia River (Fisher et al. 2007, Morris et al. 2007, Weitkamp 2010, Fisher et al. 2014), the behavioral decisions and information-processing mechanisms fish use to migrate are unknown. For example, are fish locating themselves as to optimize their growth rates? What is the relative role of predator abundance versus prey abundance in driving migration? Do proximate cues and environmental gradients lead to a generally northward migration or can this only be described by a longer-term evolutionary mechanism? Imprecise fish abundance information and sparse environmental data are not sufficient to address these complex questions. Due to the paucity of empirical data, we therefore require a theoretical tool that tracks the whole environment, allows individual organisms to adapt to their local environment in a dynamic way, and describes fish decisions based on current conditions and possibly even past experiences. Fortunately, because these are all attributes of an individual-based model (IBM), my approach should be able to address some of these questions.

One of my goals was to model several ‘decision rules’ that fish might use to migrate in the nearshore ocean environment. Fish make thousands of individual decisions based on their environment, condition, and genetic makeup. When we catch a

fish, we do not know how long it has been at that location, or where it was prior to arriving. To correlate fish attributes with the environmental conditions at the capture location ignores all of the history that culminated in the fish being in that location. With an individual-based model, I can track the history of individual fish as they move through a dynamic environment. By integrating over the time series of environmental conditions experienced by fish that use various decision mechanisms, I can evaluate which rule sets produce logical and realistic situations and result in reasonable final states (fish condition and location). This is currently not possible empirically.

Another potential emergent property of this particular individual-based model (though not explored in this dissertation) is the relative role of proximate versus ultimate motivations for migration. If fish maximize their growth rate at each time step by responding directly to ambient conditions (a logical objective, given that mortality is size-dependent), would this strategy result in the growth rates and spatial distributions we observed empirically? Or is a long-term and coarse spatial scale trait required to get fish to migrate north, suggesting that fish have evolved a strategy to migrate north regardless of local conditions? Although Alaskan coastal waters tend to be more productive than Oregon and Washington coastal waters, it is unclear what information is available to fish entering the ocean from the Columbia River that would indicate this fact and so induce them to migrate north. However, it is also difficult to conceive that fish do not make short-term decisions during their migration that yield immediate benefits. For example, do fish alter migration behavior in response to local conditions, such as slowing swim speeds when feeding conditions are favorable and speeding up when they are not? Using this IBM, it may be possible to explore the mechanisms and potential trade-offs fish make in balancing immediate and long-term gains in fitness (see Hinrichsen 1994 for an example of this modeling approach).

1.3 Objectives

Currently, the state of knowledge concerning nearshore ocean ecology of salmonids is a patchwork of correlative studies. By creating a spatially-explicit model of salmon movement and growth, I collated available data into a mechanistic tool to increase our collective understanding of the system. I proposed to run the model under various environmental conditions and with a range of assumptions to describe model

behavior. Sensitivity analyses of model parameters can point to areas that need further research while model predictions can generate testable ecological hypotheses. This comprehensive approach to ecology has proven effective in determining patterns, processes, and mechanisms that are not apparent with correlative studies alone. In the ocean environment, where research is difficult and expensive, modeling the system is a relatively quick and cost-effective way to describe ecological interactions, summarize complex datasets, and guide future research. Specific objectives are described below with a reference to the chapter in which the results can be found.

Objective 1 (Chapter 2). Model yearling Chinook salmon spatial distribution through time as a function of environmental and geospatial covariates. I proposed to select covariates based on the types of sensory capabilities salmon use to detect them so that results could inform the behaviors and external cues employed in a migration model.

Objective 2 (Chapter 3). Construct a spatially-explicit individual-based model that includes many of the basic processes of early ocean migration and growth, relying on an existing external hydrodynamic model for environmental variables. The model can track individual fish through space and time, recording location, size, and state (alive or dead, energetic content, etc.) for the first several months of ocean life. In addition to passive movement, virtual fish can make behavioral ‘decisions’ based on a suite of alternate rule sets.

Objective 3 (Chapter 4). Validate the model using existing empirical estimates of fish distribution and performance. For this objective, I proposed to use growth and migration rate estimates derived from otolith microchemistry (Tomaro et al. 2012). In this modeling effort, fish use the behavior selected as the most reasonable from Objective 2, in an effort to describe the decision processes fish use during migration. I proposed to use maximum likelihood and model averaging methods to summarize results from the individual based model.

1.4 Anticipated Future research

This model accepts multiple data types from various sources and synthesizes a description of the ecological processes acting on salmon, the interactions among those processes, and how they result in observable salmon distributions. Exploration of the

large number of potential applications that this model could address is beyond the scope of this dissertation. However, I see at least four possible expansions of the scope and application that would not be possible without this initial effort:

My collaborators working with the SELFE (Semi-implicit Eulerian–Lagrangian Finite-Element) model are designing a simulation of the most likely future climate scenarios described by the Intergovernmental Panel on Climate Change (IPCC 2007). Using results from this simulation, one could estimate how the various changes expected in the physical environment due to climate change might affect salmon migration and growth in the nearshore environment. For example, with increased rainfall in the Pacific Northwest, increased Columbia River flow may result in larger spring plume volumes. One could compare the relative influence of altered plume dynamics and the larger-scale changes in coastal currents.

The SELFE model extends about 65 km upstream into the Columbia River. Using data currently being collected on salmon distribution and movement (McMichael et al. 2011, McMichael et al. 2013), one could model salmon growth and migration through the Columbia River estuary. At the time of this writing, a PhD student is beginning to explore these ideas in the Columbia River estuary (Ian Brosnan, Cornell University, personal communication).

Although I modeled yearling Chinook salmon, data exist for other runs and species, such as coho and subyearling Chinook salmon. The model could be applied to these groups with slight modifications.

I made simplifying assumptions about the impact of mortality (both realized and perceived) on salmon spatial distribution. With more detailed information, one could explicitly model mortality and behavioral modifications due to perceived threats of mortality.

Chapter 2 Environmental and geospatial factors drive juvenile Chinook salmon distribution during early ocean migration

Published as:

Burke, B. J., M. C. Liermann, D. J. Teel, and J. J. Anderson. 2013. Environmental and geospatial factors drive juvenile Chinook salmon distribution during early ocean migration. *Canadian Journal of Fisheries and Aquatic Sciences* 70(8):1167-1177.

Abstract

Migrating animals rely on a variety of cues to guide them, but the relative importance of those signals may vary with size, life stage, or location. During their initial ocean migration, yearling Chinook salmon from the Columbia River have stock-specific spatial distributions that shift through time. I used a two-process mixture model to examine how the distribution of yearling migrants from three Chinook salmon stocks varies as a function of geospatial (e.g., latitude and distance from shore) and environmental (e.g., chlorophyll *a* and temperature) covariates. In this framework, one process described the probability of being inside the spatial, temporal, and environmental boundaries of the migration route, and one process described the patchy distribution of salmon abundance within that route. I found that both environmental and geospatial covariates explained substantial portions of observed spatial patterns in abundance, suggesting that these stocks responded to multiple cues during migration. However, model selection criteria indicated that fish distributions were more affected by geospatial than by environmental covariates. I conclude that during migration, behavioral responses to environmental variation are secondary to responses to geospatial variation, sometimes resulting in suboptimal environmental conditions. This may have sub-lethal effects on growth and could ultimately influence stock-specific responses to large-scale climate changes.

2.1 Introduction

The evolution of migration is often described in terms of the beneficial attributes of the destination habitat relative to those of the origin. However, long-distance migrating animals must maximize fitness over the entire course of migration, not just after migration is complete (Moore and Simons 1992). Behavior and performance during migration can have at least as great an impact on population level production as conditions at the destination location (Newton 2006). Many animals have evolved mechanisms for processing multiple types of external stimuli during migration, including birds (Wiltschko and Wiltschko 2005), butterflies (Mouritsen and Frost 2002), turtles (Lohmann et al. 2008, Sherrill-Mix et al. 2008), and insects (Chapman et al. 2010). The particular cues an animal uses may depend on its size (DeRobertis et al. 2000), life stage (Salmon and Lohmann 1989), condition (Brodersen et al. 2008), or location (Fransson et al. 2001). To understand the relationship between a migrant and its environment, it is critical to characterize the cues that are important in directing migration behavior.

Long-distance migrations are particularly important for Pacific salmonids (*Oncorhynchus* spp.), with many species undergoing some phase of migration during most of their lives. Migration strategies employed by salmon during the high-mortality, early marine portion of their life cycle result in ocean distributions that vary among species and life history types (Healey 1983, Trudel et al. 2009, Weitkamp 2010, Tucker et al. 2011). For example, in Chinook salmon (*O. tshawytscha*), two generalized early marine life history strategies have been described: subyearling life history types, which enter the ocean during their first year of life and tend to favor shallow coastal waters, and yearling types, which enter the sea after a year in fresh water with many populations migrating north faster and farther offshore than the subyearling type (Miller et al. 1983, Hartt and Dell 1986, Fisher and Pearcy 1995).

However, within a particular salmon species and life-history type, spatial distributions of the individuals during migration are relatively consistent among years (Weitkamp 2010, Tucker et al. 2012). This consistency in ocean distribution, even among years with variable environmental conditions, suggests a genetic response to large-scale geospatial cues, such as the Earth's magnetic field (e.g., Quinn et al. 2011, Bracis and Anderson 2012), and a relatively inflexible response to environmental stimuli. On the other hand, there is evidence of a relationship between salmon abundance and environmental characteristics (De Robertis et al. 2003, Pool et al. 2012). Thus, evidence suggests that for salmon, both environmental (proximal)

and geospatial (proximal or distal) cues shape the migratory route and resulting distribution within that route.

A number of studies have investigated the relationship between Chinook salmon spatial distribution in marine waters and local environmental characteristics; most of these used relatively simple approaches that may have missed information available in the data. For example, Peterson et al. (2010) used Spearman rank correlations between catch per unit effort of Chinook and coho salmon and temperature, salinity, depth, and chlorophyll *a* concentration. Bi et al. (2007) applied a logistic regression model to quantify how environmental factors influence the presence or absence of Chinook and coho salmon. Others have modeled the entire catch distribution with a generalized linear mixed model (Bi et al. 2011) or generalized additive model (Yu et al. 2012).

However, only small subsets of the available data have been used in these analyses, potentially introducing bias in the catch distributions. For example, many analyses have focused solely on yearling Chinook salmon caught during June, even though considerable numbers of these fish enter the ocean from late March through mid-June or later (Peterson et al. 2010, Tomaro et al. 2012). Catch numbers tend to be highest in June, but these fish are widely distributed throughout the sample areas in spring and summer, with their presence diminishing through September (Fisher and Pearcy 1995, Peterson et al. 2010, Tucker et al. 2011). Furthermore, there is consistent evidence that different stocks or population groups exhibit unique distributions in the marine environment (Fisher et al. 2007, Weitkamp 2010, Tucker et al. 2011, Fisher et al. 2014), but previous analyses have lumped these populations together. Thus, to date there has been no comprehensive analysis of stock-specific spatial distribution and habitat associations over the entire temporal distribution of migrating juvenile Chinook salmon in the marine environment.

Here I present a comprehensive analysis of yearling Chinook salmon from the Columbia River from 2001 through 2009, improving upon previous efforts in three ways. First, I directly addressed the temporal changes in spatial distribution by including catch per unit effort (CPUE) throughout the spring and summer. This allowed me to more accurately describe the migration process, rather than the distribution at a single point in time. Second, I chose an analytical tool specifically designed for overdispersed data with a large number of zeros. Although relatively

uncommon in ecology, the zero-inflated negative binomial model is quickly becoming a standard approach for handling data with excess zeros (Zuur et al. 2012) and has been used to study the abundance of snapper around marine reserves (Smith et al. 2012), tree recruitment in managed plots (Zhang et al. 2012), and earthworms in soil samples (Sileshi 2008). Using this framework, I examined alternate hypotheses using environmental and geospatial variables as predictors of migration behavior. By quantifying the relationships between salmon catch and geospatial and/or environmental variables, I aimed to identify the relative importance of these drivers to migration behavior.

Finally, I applied the models to three genetically distinct stocks of yearling Chinook salmon from the Columbia River Basin (Interior Basin spring-run, Interior Basin summer/fall-run, and Lower River spring-run Chinook salmon) to investigate variability in response to migration cues among salmon stocks. These stocks differ in marine distribution, both as juveniles (Trudel et al. 2009) and adults (Waples et al. 2004, Weitkamp 2010). Given the diversity in their observed distributions, I hypothesized that migratory responses to environmental and geospatial cues would be significantly different and would change asynchronously throughout the season. For example, if fish use large-scale geographic cues to navigate (e.g., the Earth's magnetic field or the sun), one might expect catches to be more related to static geospatial attributes such as latitude or distance offshore. Alternatively, if local environmental variables were the main driver of salmon migration routes, one might expect a strong relationship between these local variables and catches of salmon.

2.2 Methods

2.2.1 Data

The data I used come from an ongoing study of juvenile salmon distributions off the Washington and Oregon coasts. In May, June, and September of 2001 through 2009, juveniles were sampled at 6-7 stations along transects extending outward from the coast (Fig. 1). At each station, a Nordic 264 pelagic rope trawl (30 m wide x 20 m high x 200 m long) with a cod-end liner of 95 mm stretch mesh was towed at a speed of 6 km·h⁻¹ for approximately 30 min. (see Brodeur et al. 2005 for complete details). Yearling Chinook salmon were differentiated from younger (subyearling) and older (sea entry in earlier years) age classes based on fish size and month of capture, following the method of Peterson et al. (2010). In May, any Chinook salmon

between 121 and 250 mm was designated a yearling migrant. In June, the size range was 141 and 280 mm. Catch per unit effort was based on the number of fish caught per kilometer towed (estimated with GPS coordinates at the beginning and end of each tow), assuming a constant height of the net mouth (about 25m). We collected temperature, salinity, and transmissivity down to 100 m (or within 5 m of the bottom) and recorded Secchi depth and water depth at each station with a Sea-bird CTD. We also collected water samples at 3-m depth using a 1-L Niskin bottle for later analysis of chlorophyll a concentration (Morgan et al. 2005). Any stations with missing environmental data were removed from the analysis, resulting in a final dataset that contained 569 trawls at 33 fixed sampling stations along 5 transects.

2.2.2 Models

To evaluate which factors influenced salmon distribution, I fit counts of yearling Chinook salmon to a series of models with spatial, temporal, and environmental factors using individual trawls as the sampling unit. Due to the dynamic nature of salmon in Washington's coastal waters, the probability of encountering a fish depends on gear efficiency (which I assume to be relatively constant and did not model here), whether or not one is sampling in the migratory route, and on the proximal and distal cues that influence fish location within the route. The concept underlying this probability is that even though environmental conditions of a sampling site may be ideal for fish, no fish may be observed because the sample site is outside the migratory route or because the site was sampled prior to or after the fish moved through the habitat. Thus, the number of fish captured in a trawl was modeled as a dual process involving: 1) the probability of sampling within the spatial/temporal boundaries of the migratory route and 2) the probability of encountering a specified number of fish, given that the trawl sample was within the migratory route. The partitioning of samples into habitats inside and outside of the migration route resulted in a distribution of counts of surveyed yearling Chinook salmon that was heavily skewed toward extra zeros (Fig. 2).

This two-process problem can be formulated in terms of a zero-inflated model (e.g., Zuur et al. 2009), in which one population consists only of zeros (samples outside the migration route) and the other population consists of both zero and non-zero counts (samples within the route). Thus, the chance of collecting y fish in a trawl depends on the chance p of sampling outside the migration route (sampling from the zero population) plus the probability $1 - p$ of sampling

within the migration route (zero or non-zero population) multiplied by the probability of capturing y fish within that population. Although I used this framework to design and construct the model, I acknowledge that it oversimplifies the sources of variability in the data and stress that individual trawls are assigned to the two populations in a probabilistic manner (i.e., I do not attempt to describe the migratory route on a trawl-specific basis).

Formally, if I let $Z = 0$ when sampling occurs outside the migration route with probability p (i.e., $p = P(Z = 0)$) and $Z = 1$ when sampling occurs inside the route, then the probability function for a zero-inflated model is:

$$(1) \quad P(Y = y) = p * P(Y = y | Z = 0) + (1 - p) * P(Y = y | Z = 1),$$

which translates into two components, representing zero and non-zero catches:

$$(2) \quad P(Y = 0) = p + (1 - p) * P(Y = 0)$$

when $y = 0$, and

$$(3) \quad P(Y = y) = (1 - p) * P(Y = y)$$

when $y > 0$. Here, P is the catch distribution within the migratory route and can be specified as any number of probability distributions. The probability p of sampling outside the migratory habitat and the probability distribution P of catch within the habitat can both be functions of spatial, temporal, and environmental covariates.

To describe catch distribution within the migratory habitat (i.e., $P(Y = y)$), I considered both Poisson and negative binomial models (Zuur et al. 2009). The Poisson distribution assumes complete spatial randomness, resulting in a variance that is equal to the mean. In contrast, the negative binomial model has one additional parameter, allowing the variance to be greater than the mean (in our case, due to the patchy distribution of Chinook salmon). I explored four permutations of these models: the Poisson and negative binomial models alone, and each of these models with a zero inflated component. However, I limit my discussion to the zero-inflated negative binomial model for two reasons. First, it is unlikely that salmon are completely random in their distribution (Peterson et al. 2010). Second, the negative binomial distribution has been

shown to fit Pacific salmon catch data well (Bi et al. 2011), and my initial models strongly favored the zero-inflated negative binomial.

Within the migratory habitat, the negative binomial model describing the catch distribution is

$$(4) \quad P(Y = y) = \frac{\Gamma(y+k)}{\Gamma(k)\Gamma(y+1)} \left(\frac{k}{k+\mu}\right)^k \left(\frac{\mu}{k+\mu}\right)^y,$$

where y is the number of occurrences of an event (i.e. number of a target species in a trawl), μ is the average rate at which events occur, and k is a dispersion parameter (a value of 1 would reduce the negative binomial distribution to a geometric distribution and a value of infinity would indicate that the patchiness in counts had been accounted for by the covariates and would reduce the negative binomial model to the Poisson). Covariates affect the mean rate of occurrence, μ , such that

$$(5) \quad \mu = d + e^{(\alpha_a + \beta_a X_a)},$$

d is the length of the tow in kilometers (modeled as a constant offset), α_a is the intercept (the subscript a , for abundance, distinguishes this intercept from the intercept in Eq. 6), and β_a is a vector of coefficients for the matrix of covariates X_a , which may include temporal, geospatial, and environmental attributes of each trawl. I described the probability of sampling outside the migration habitat p with a logit link:

$$(6) \quad p = \frac{e^{(\alpha_{zi} + \beta_{zi} X_{zi})}}{1 + e^{(\alpha_{zi} + \beta_{zi} X_{zi})}},$$

where α_{zi} is the zero-inflation intercept and β_{zi} is a vector of zero-inflation coefficients for the covariates X_{zi} . Covariates included were the same as those used to describe catch within the migration habitat, except for year and month interaction terms, which were not significant in any of the models.

2.2.3 Environmental versus geospatial covariates

I took a two-step approach to selecting covariates for μ and p . First, I divided potential covariates into three groups based on the type of information they provided: 1) temporal, 2) environmental, or 3) geospatial. Temporal covariates were month and year; environmental

covariates were average temperature, temperature range (from a depth of 0 to 20 m), chlorophyll *a* concentration, Secchi depth, and salinity; geospatial covariates were latitude, distance from shore, and water depth. By including or excluding entire groups in potential models, I greatly reduced the number of parameter combinations to compare. This allowed me to focus directly on assessing the relative importance of geospatial vs. environmental cues for salmon migration. The second step in selecting covariates was to examine correlations among covariates within each group. Highly correlated covariates were identified, and their relative performance was compared in the zero-inflated negative binomial model (see supplementary material). Based on these comparisons, I dropped Secchi depth from the environmental model and water depth from the geospatial model. The data showed no support for including salinity or transmissivity in any of my initial models, so these two covariates were dropped from all models.

To evaluate the importance of geospatial vs. local environmental cues on fish movement decisions, I fit a suite of competing models using the three groups of covariates defined above (Table 2.1). Using the zero-inflated negative binomial distribution, I first fit a null model with only an intercept to characterize the magnitude of variance in the data. I then fit a temporal model that included month and year as factors to account for changing abundance through time. This model run was for basic comparisons only; however, the change in abundance through summers and among years was large enough that I included month and year as factors in all other models.

Thus, my final environmental model included temperature (both mean and range in the top 20-m of the water column, see supplementary material) and chlorophyll *a* concentration as covariates, in addition to the temporal factors. Likewise, the final geospatial model candidate included latitude and distance from shore as continuous covariates, as well as month and year. I also examined a full model, which included all final covariates from the temporal, environmental, and geospatial models (Table 2.1). In all models, predictor variables were centered and scaled (divided by their standard deviation) prior to analysis to improve performance of the estimation process and to allow direct comparison of model parameters (Gelman et al. 2003).

2.2.4 Genetic stock differences

In addition to combining all fish into one analysis (Table 2.2), I wanted to analyze particular Chinook salmon stocks individually because of behavioral heterogeneity (e.g., emigration timing, ocean migration patterns) and size differences among stocks (Table 2.3). To estimate stock origin of each fish, my collaborator, Dr. David Teel - NOAA Fisheries, used population data from a standardized microsatellite DNA database (Seeb et al. 2007) and the genetic stock identification program ONCOR (Kalinowski et al. 2007). Individuals from eight Evolutionarily Significant Units, ESUs (Waples 1991), in the Columbia River Basin were identified in the catch data (Table 2.2). These ESUs included yearlings from populations with spring, summer, or fall adult run timing (returns to freshwater). Using this timing and genetic information, as well as life-history and geographic information (Waples et al. 2004, Matala et al. 2011), I condensed the eight ESUs into the following three stocks: Interior Basin spring-run (IBS), Lower River spring-run (LRS), and Interior Basin summer/fall-run (IBSF) Chinook salmon (Table 2.2).

I theorized that the known genetic and behavioral differences among these three stocks in freshwater (Waples et al. 2004) would be accompanied by behavioral differences in the marine environment. To test this proposition, I ran null, temporal, environmental, spatial, and full models on each of the three stocks. Note that for the Interior Basin spring stock, I modeled only May and June because only two fish from this stock were collected in September of any year, and this low catch rate precluded parameter estimation.

All models were run in a Bayesian framework using JAGS software (Plummer 2008), implemented in the R2jags package (<http://www.R-project.org>). For each model, I ran 60 000 iterations with three chains and dropped the first 30 000 iterations as the burn-in period. I used a thinning rate of 10 based on initial checks for convergence, resulting in 3 000 iterations for calculating the posterior distributions. I calculated the deviance information criterion (DIC) for each model as the deviance evaluated at the mean joint posterior plus the effective number of parameters as estimated by the mean posterior deviance minus the deviance calculated using the mean posterior parameter values (Spiegelhalter et al. 2002). To evaluate the importance and direction of the effect of model covariates, I compared the posterior parameter distribution for each covariate to zero. Finally, for each stock, I used the posterior parameter distributions and

observed covariate data to predict mean response for the fitted model and obtain 90% confidence intervals for the fit.

2.3 Results

2.3.1 Spatial/temporal distribution of stocks

Salmon that entered the ocean from the Columbia River in April and May were widespread in study transects during May (Figure 2.3). Fish from the Interior Basin spring stock were smaller than fish in the other two stocks (Table 2.3), but showed a clear and targeted northward migration out of the sampling area, with only two fish caught in the September cruises. Fish in the Lower River spring stock were significantly larger and had a slightly more dispersed distribution among months, with a less clear north/south migration pattern. The Interior Basin summer/fall fish (intermediate in size) exhibited a more protracted migration from the Columbia River (and entry into our sampling area), with few fish found in the north part of our survey area during May and the highest catches observed in June.

Annual variation in abundance was high, with CPUE varying from less than 0.2 fish/km in 2005 to almost 2.25 fish/km in 2008. Moreover, abundance declined throughout the sampling season within each year, and the inclusion of month as a factor in the model was supported in both the abundance and the zero-inflation parts of the models. For the abundance part of the model, the month interaction with each environmental covariate greatly improved model fit, suggesting that habitat associations evolved throughout spring and summer. Moreover, catches decreased with latitude in May, but increased with latitude in June, particularly for the Interior Basin spring stock, reflecting the expected shift in spatial distribution as fish migrated north.

2.3.2 Relative importance of geospatial and environmental variables

The full model fit the data better than either the environmental or geospatial models, regardless of whether I analyzed individual stocks or all stocks together (Table 2.4). Given the moderate correlation between some predictor variables in the geospatial model and variables in the environmental model, these two models most likely fit some of the same variance. But the substantial improvement in model fit when both types of covariates were included (i.e., the full

model) relative to either submodel suggests that fish responded to some degree to both types of information.

When comparing the two types of predictor variables, yearling Chinook salmon spatial distribution was more closely associated with geospatial than environmental information for all three stocks (Table 2.4). Applying the models to different stocks of fish showed that the relative importance of geospatial and environmental variables differed by stock. In particular, the Lower River spring stock showed relatively little response to environmental variables but a strong response to geospatial variables. For this stock, ΔDIC was about six times greater for the environmental than for the geospatial model, whereas it was only about three times larger for both the Interior Basin spring and Interior Basin summer/fall stocks. In fact, an alternative method for estimating DIC (Gelman et al. 2003) showed that the catch data for the Lower River spring stock, which migrated primarily near shore, was best fit by the geospatial model and the addition of environmental variables did not substantially improve model fit. In contrast, environmental variables were strongly supported by the data for the Interior Basin spring and Interior Basin summer/fall stocks.

2.3.3 Responses to cues

2.3.3.1 Environmental cues

I found several differences among stocks in terms of response to external cues. Both interior basin stocks showed a strong affiliation for warmer water in May, but this affinity switched by June and September to an association with cooler water (Figure 2.4), particularly for the Interior Basin spring stock. Interestingly, the Lower River spring stock was associated with cooler water even in May. The Interior Basin spring and summer/fall stocks were associated with a large range in temperature in May, but this dissipated for both stocks in later months.

Chlorophyll *a* was important for all three stocks, both in the zero-inflation and abundance model components (Table 2.8 in the supplemental material). The direction of response to chlorophyll *a* by Lower River spring and Interior Basin summer/fall fish was consistent between components (i.e., increased chlorophyll was associated with a higher probability of catching fish and a higher expected abundance, given a non-zero catch). However, results from the two components showed opposite directions for the Interior Basin spring fish, resulting in a non-linear response (Figure 2.4).

2.3.3.2 Geospatial cues

The Interior Basin spring stock showed two major distributional differences from the other two stocks. First, there was a positive effect of distance from shore in May and June (Figure 2.4), demonstrating the more offshore distribution of the Interior Basin spring stock relative to the other two stocks, both of which showed a consistent negative effect of distance from shore. Second, all three stocks showed a negative association with latitude in May, due in part to their recent migration from the Columbia River. Yet by June, the Interior Basin spring stock showed a significant positive association with latitude, while the other two stocks showed no relationship with latitude (Figure 2.4).

2.3.4 Catch overdispersion

Results showed that yearling Chinook salmon were not randomly distributed, but displayed a significant amount of spatial and temporal patchiness. Out of 569 trawls, just under half (286 trawls) contained at least one yearling Chinook salmon. The distribution of counts dropped off quickly with only one third of trawls having more than two fish and 10% having more than 10 fish. However, there was a large tail in the count distribution, with the largest catch being 65 yearling Chinook salmon.

When analyzing stock-specific counts, over-dispersion and the proportion of zeros was even higher, because trawls with yearling Chinook from one stock did not necessarily have fish from another stock. However, the frequency distribution of counts within each stock was similar (Figure 2.2). Of the 2181 yearling Chinook in the genetic analysis, the largest proportion (about 38%) was from the Interior Basin spring stock (Table 2.2). We caught fish from a given stock in less than one third of the trawls, resulting in a high proportion of zeros in all three subsets of the data. Therefore, between 60 and 78% of trawls yielded zero fish from a given stock (Figure 2.2).

The use of a zero-inflated component and the ability of the negative binomial distribution to account for over-dispersion allowed these models to fit the catch data well (Figure 2.5). However, there was a slight tendency to underestimate the number of small catches (i.e., 2-5 fish) in the Lower River spring stock. The dispersion parameter, k , ranged from 0.27 in the null model to 0.67 in the full model, suggesting that some of the overdispersion can be accounted for by covariates, but even the full model showed a large amount of overdispersion.

2.4 Discussion

This study suggests that environmental conditions experienced during out-migration can modulate the genetically-driven, stock-specific migration patterns observed in the marine environment (Weitkamp et al. 2012, Fisher et al. 2014). This effort extends the results from previous analyses (Bi et al. 2007, Bi et al. 2008, Yu et al. 2012), which demonstrated the associations between salmon abundance and biotic and abiotic habitat characteristics. Although I did not have lower trophic level covariates (such as copepod abundance, as in these previous studies), two key additions to those analyses (multiple months and multiple stocks) allowed a more complete characterization of the dynamic aspect of salmon spatial distribution during migration. I found that associations with the environment were stock specific and that these associations change as fish migrate up the coast. Future advances in our understanding of the marine life-history stage will most likely come from studies that explicitly incorporate this dynamic aspect of salmon ecology.

2.4.1 Relative importance of geospatial and environmental variables

I found that the spatial structure of the environmental data made it difficult to partition the variance in CPUE into strictly geospatial or environmental components (see Table 2.7 for correlations among environmental and geospatial covariates). However, because the sum of Δ DICs from the environmental and geospatial models were below the Δ DIC of the simpler temporal model, I conclude that both environmental and geospatial factors contribute to the distribution of salmon during early ocean migration. Furthermore, the effects of mean temperature, temperature range, and chlorophyll *a* were consistent in the environmental model and the full model, which included environmental, geospatial and temporal factors (Table 2.8 in the supplemental material). Thus, my overall results suggest that even though temperature and chlorophyll *a* were spatially structured, the effect of these variables on salmon distribution was not driven solely by that structure, but persisted even when the association with spatial factors was explicitly considered (i.e., in the full model).

2.4.2 Responses to cues

In their northward migration, two of the three yearling Chinook salmon stocks (Interior Basin spring and Interior Basin summer-fall) were associated with warm water in May (greater than 12°C), but cooler water later in the summer and fall. In contrast, the Lower River spring stock, which had the largest mean size (Table 2.3), was associated with cold water even in May.

This finding of a size-based temperature optimum makes sense bioenergetically, because the optimal temperature for growth is higher for small fish than for large fish (Beauchamp 2009).

Additionally, fish were found in higher abundance in May at locations with a large vertical temperature range. This may indicate that fish made vertical migrations to thermoregulate (Hinke et al. 2005), intermittently inhabiting the colder subsurface water to optimize growth rates. By June and September, when salmon were larger and their thermal preferences lower, oceanic surface water generally was warmer than the fish's optimal temperature. Under this scenario, the utility of a large range in temperatures was no longer beneficial and fish probably avoided such areas. The Lower River spring stock, which consistently showed a smaller response to average temperature than the other two stocks, showed only a moderate response to temperature range (Figure 2.4).

Chlorophyll *a* concentration is often used as a surrogate for prey resources because salmon prey are rarely sampled directly (Brodeur et al. 2011). As I and others have observed (Bi et al. 2007, Peterson et al. 2010, Pool et al. 2012, Yu et al. 2012), chlorophyll *a* concentration is often a significant covariate of salmon abundance. Although not completely spurious, I caution against interpreting these findings as a mechanistic causal relationship related to trophic transfer of biomass from primary producers to salmon for two reasons. First, salmon prey are at least one trophic level above chlorophyll *a* (Miller et al. 2010b) such that the temporal lag between chlorophyll *a* production and salmon prey (larval fish or crab megalopae) is too large to assume the association with chlorophyll *a* represents direct trophic transfer to salmon.

Second, there was spatial structure in the chlorophyll *a* data that was not captured by the geospatial covariates, which could bias parameter estimates. Specifically, high chlorophyll *a* concentration bounded the study area: the Columbia River plume to the south and the Juan de Fuca eddy to the north (Hickey and Banas 2008). Chlorophyll *a* was most significant in our June samples, when most yearling Chinook salmon were between these two areas; therefore, it is plausible to assume part of the association between chlorophyll *a* and salmon catch (Figure 2.4) is related to a coincidental spatial/temporal overlap of migration and phytoplankton blooms rather than a biological preference for chlorophyll *a*. Interestingly, the Interior Basin spring stock, which had the most directed northward migration, did not have a strong relationship with

chlorophyll *a* (Figure 2.4), suggesting a possible trade-off between migrating and optimizing local environmental conditions.

2.4.3 Behavioral diversity and resilience

Salmon have evolved a wide range of behaviors and life-history strategies that enable them to persist in spite of considerable variation in environmental conditions (Quinn 2005). Schindler et al. (2010) and Moore et al. (2010) illustrated that diversity among populations and associated freshwater habitats can lead to more stable populations. My results demonstrate that behavioral diversity is not limited to the freshwater environment, but also extends to the marine environment.

To date, there was no evidence of behavioral heterogeneity among yearling Chinook salmon upon entering saltwater, yet my results suggest that fish may employ a variety of migration strategies during this time. Unlike subyearling Chinook salmon, which disperse both north and south of the Columbia River and can remain in the coastal waters for months to years, yearling migrants from the Columbia River have been shown to migrate north rapidly (Fisher and Percy 1995, Tucker et al. 2011, Fisher et al. 2014). Yet, the presence of Interior Basin summer/fall fish throughout the sampling range and their persistence through September (Figure 2.2) suggests that at least some of these fish spend some time near the river mouth prior to migrating north. This sets up two competing hypotheses: (1) some stocks of yearling Chinook salmon reside near the Columbia River mouth prior to initiating a northward migration; and (2) there exists heterogeneity in migration speeds and some fish swim more slowly than others (Tomaro et al. 2012). Unfortunately, I cannot distinguish between these hypotheses without a more detailed analysis of the outmigration timing of Interior Basin summer/fall yearlings or direct information on the movement of individual fish.

As management strategies to increase diversity and resilience progress, it is important to consider the marine environment as well as freshwater systems, as the consequences of freshwater management strategies can be partially realized in the marine environment. Strategies that bring fish to the ocean early (e.g., barging) may extend the time fish spend in the plume environment, which has been shown to be associated with high mortality rates (Rechisky et al. 2013). Alternatively, a delayed arrival to the ocean has also been associated with increased mortality (Scheuerell et al. 2009). These results likely shift from year to year as environmental

conditions change. Moreover, we now know there is behavioral heterogeneity among salmon stocks and a single management strategy will not benefit all stocks equally.

The larger size of fish from the Lower River spring stock suggests that maybe this stock had a higher proportion of hatchery fish (which tend to be larger on average than wild fish). Differences between wild and hatchery fish are rarely documented in the marine environment (Daly et al. 2012), but can have politically-relevant consequences. Unfortunately, I did not have information for many of these fish regarding whether they had hatchery or natural origins. However, we can estimate the proportion of wild fish in the sample using the proportion of marked fish in our catches relative to the proportion released from various hatcheries. An analysis of this sort suggested that the vast majority (>90%) of yearling salmon in our catches of each of the stock groups analyzed here are hatchery fish (David Teel, unpublished data). Although I cannot suggest how results may have been different between hatchery and wild fish, I can at least rule out fish origin as a factor driving the differences among stock observed in this analysis.

The degree to which fish will be able to contend with rapid changes in climate or environmental conditions depends on the strength of genetic control of early ocean migration. Weitkamp (2010) implied that consistent migration patterns in variable ocean conditions infers a genetic component to migration. I posit that if the migratory path is predominantly determined through a genetic response to temporal or geospatial cues (which do not change with climate), then the ability of individual fish to respond to conditions may be limited. However, as fish face increasingly altered oceanic conditions, a more flexible behavioral response and a greater reliance on environmental variables may confer improved survival benefits. Columbia River yearling Chinook salmon from the lower river exhibit high life history diversity in freshwater (Waples et al. 2004). Therefore, I expected this flexibility to translate into increased behavioral heterogeneity in the marine environment. Contrary to our expectations, yearling Chinook salmon from the lower river exhibit a weaker behavioral response to environmental variables than those from the interior basin. Therefore, lower river stocks may experience lower or more variable marine survival as ocean conditions change. Yet even with highly plastic responses to local environmental conditions, yearling Chinook salmon are unlikely to arrest migration based on conditions within the migration route.

2.4.4 Model design

By allowing model covariates to separately influence the presence and abundance of salmon in a zero-inflated model framework, I was able to more accurately assess the relationship between salmon and their environment. For example, the probability of catching zero salmon increased with distance from shore for all three stocks (Table 2.8 in the supplemental material), partly due to our sampling strategy, which promoted continued sampling along each transect until we were outside of the salmon migration route. Had I used a model that could not account for zero-inflation, results would have suggested that all stocks were less abundant offshore. However, I showed that while in the migration route, the abundance of the Interior Basin spring stock was higher offshore than inshore (Table 2.8 in the supplemental material), demonstrating the importance of matching data with an appropriate analytical tool.

2.4.5 Limitations of results

As with most studies with large spatial extents and limited data, several factors could have influenced my results. First, it is possible that the differences in response to local conditions observed among stocks were the result of local environmental conditions not included in my model, such as predator or prey distributions. Bi et al. (2011) showed that copepod abundance (a surrogate measure of Chinook salmon prey) was related to spatial distribution of salmon during June. However, Chinook salmon prey were not directly sampled during this study and copepod data from other studies were insufficient for inclusion in my model.

Second, there are two potential limitations to the CPUE data. I restricted my analyses to yearling Chinook salmon, which I distinguished from smaller, subyearling Chinook salmon and larger ocean-age 1 fish using a length-based cutoff (Fisher and Pearcy 1995, Peterson et al. 2010). When data were available, I used either coded-wire tags (Trudel et al. 2009) or otoliths (J. A. Miller, unpublished data) to validate these size-based cutoffs. Although I found little overlap in the size distributions of the two life-history types, some of the largest subyearling fish were inevitably included in my analysis while some of the smallest yearling Chinook salmon were erroneously excluded.

The other potential limitation of the CPUE data concerns whether we have adequately sampled the full distribution of depths used by juvenile salmon. Relatively little depth-specific sampling has been conducted during the early ocean stage of salmon life history. Thus, we are

currently unable to estimate the proportion of Chinook salmon that we may have missed if fish were deeper than our sampling gear, which extended from the surface down to about 20m. There is a distinct trend towards fish using deeper water later in the season and as they get larger (Orsi and Wertheimer 1995). However, Emmett et al. (2004) found that most Chinook salmon at this early stage of ocean migration are shallower than 20 m. Two additional circumstantial lines of evidence suggest that we adequately sampled the appropriate depth distribution: 1) mean salmon length was larger in our surface trawl than that from nearby purse-seine sampling (which samples a greater proportion of the water column; L. A. Weitkamp, unpublished data), suggesting that larger fish were not necessarily deeper than smaller fish this soon after out-migration and 2) in an analysis of Chinook salmon abundance and depth-specific temperature data, I found the highest correlations when using temperature data from the top 20 m (see supplementary material). Unfortunately, I do not know how my results may have been biased if some proportion of the larger fish were deeper than we sampled, particularly if this proportion changed through time or was associated with some environmental variable. This represents an important gap in our understanding of the early ocean ecology of juvenile salmon, which would be vastly improved with additional depth-specific sampling.

Finally, some yearling Chinook salmon were still out-migrating from the Columbia River during our first sampling period in late May and others, particularly for the Interior Basin spring stock, had migrated north of the study area by our second survey in late June. A more comprehensive temporal sampling regime, which was not feasible, may have provided slightly different results. Similarly, mortality, which is known to be high during the early northward migration (Welch et al. 2011), influenced spatial distribution to some extent and may have biased my results. Although mortality is probably not uniform over the sampling area, I currently have no evidence that mortality affects the spatial distribution of salmon in this area.

2.4.6 Concluding remarks

I have shown clear, stock-specific behavioral associations with both local environmental factors and broad-scale geospatial factors during migration. Habitat conditions experienced during this time are important and can influence survival and population dynamics. Salmon are not unique to this situation; for many animals, migration takes weeks or longer to complete and can be associated with high mortality (Sillett and Holmes 2002, Newton 2006). Further study of

the cues directing ocean migration of salmon and other organisms is important, both for management purposes and for general ecological understanding.

2.5 Acknowledgements

This work has been published in the Canadian Journal of Fisheries and Aquatic Sciences 70(8):1167-1177, and I thank the coauthors for all their hard work – Martin Liermann, David Teel, and Jim Anderson. Thanks to Andre Punt for initial discussions regarding model design. Chinook salmon catch data were obtained during a survey funded by the Bonneville Power Administration. Many people assisted with the project organization and data collection, including but not limited to Ed Casillas, Bill Peterson, Ric Brodeur, Bob Emmett, Kym Jacobson, Cheryl Morgan, Jen Zamon, Brian Beckman, Laurie Weitkamp, Don Van Doornik, David Kuligowski, Tom Wainwright, Joe Fisher, Susan Hinton, and Cindy Bucher. Andre Punt contributed to the initial design of the model. I also thank JoAnne Butzerin, James Faulkner, Bridget Ferris, Mark Scheuerell, Rich Zabel, Aimee Fullerton, and two anonymous reviewers for their constructive comments on earlier versions of this document.

2.6 Tables

Table 2.1. Covariates that were included in each of four candidate models. Variables included in the abundance (negative binomial) part of the model are indicated with mean rate of occurrence μ ($\mu[m]$ if there was a month interaction) and variables in the zero-inflated component are indicated with p (probability of sampling outside the migration habitat).

	Temporal	Environmental	Geospatial	Full
Month (n = 3)	μ, p	μ, p	μ, p	μ, p
Year (n = 9)	μ	μ	μ	μ
Average temperature	--	$\mu[m], p$	--	$\mu[m], p$
Temperature range	--	$\mu[m], p$	--	$\mu[m], p$
Chlorophyll a	--	$\mu[m], p$	--	$\mu[m], p$
Distance from shore	--	--	$\mu[m], p$	$\mu[m], p$
Latitude	--	--	$\mu[m], p$	$\mu[m], p$

Table 2.2. Number of fish per stock and ESUs included. 429 fish (19.7%) were not genotyped, and were therefore not included in any of the stocks, but were included in the All Fish dataset.

ESUs included	Stock	May	June	Sep	All Months
Mid-Columbia River spring Upper Columbia River spring Snake River spring/summer	Interior Basin spring	459	372	2	833
Upper Willamette River spring Lower Columbia River*	Lower River spring	310	111	11	432
Upper Columbia River summer/fall Snake River fall Deschutes River summer/fall	Interior Basin summer/fall	87	343	57	487
All Fish		948	977	256	2181

*Only fish assigned to spring-run populations were included.

Table 2.3. Mean yearling Chinook salmon size (mm) by month for fish sampled off the coast of Washington and Oregon in May, June, and September 2001-2009.

	All Fish	Interior Basin spring (IBS)	Lower River spring (LRS)	Interior Basin summer/fall (IBSF)
May	176.9	156.1	204.3	188.8
June	188.7	171.7	210.8	199.8
September	299.1	259	331.9	293.7

Table 2.4. Model comparison for each data set from the zero-inflated negative binomial model. IBS = Interior Basin spring-run, LRS = Lower River spring-run, and IBSF = Interior Basin summer/fall-run Chinook salmon.

Model	# Params	ΔDIC			
		All Fish	IBS	LRS	IBSF
Full	35	0	0	0	0
Geospatial	23	46.4	11.8	14.2	22.7
Environmental	27	90.2	39	97.7	73.3
Temporal	15	225.7	80.1	155.7	189
Null	3	353.2	113.6	274.4	246.6

2.7 Figures

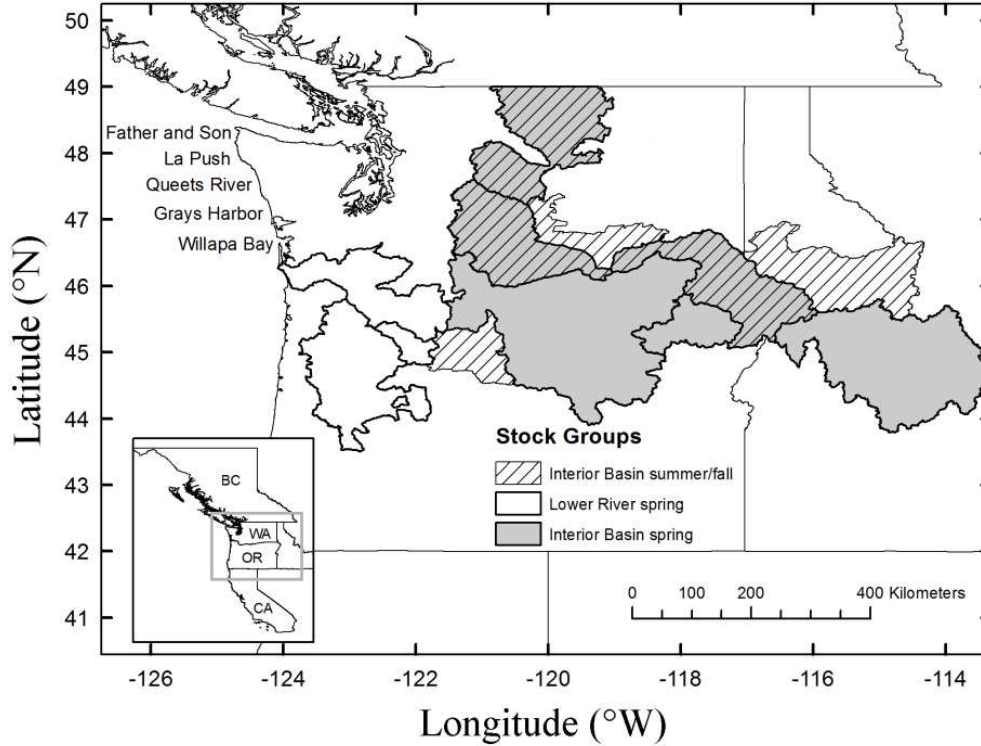


Figure 2.1. Map of stock origins and ocean survey transects.

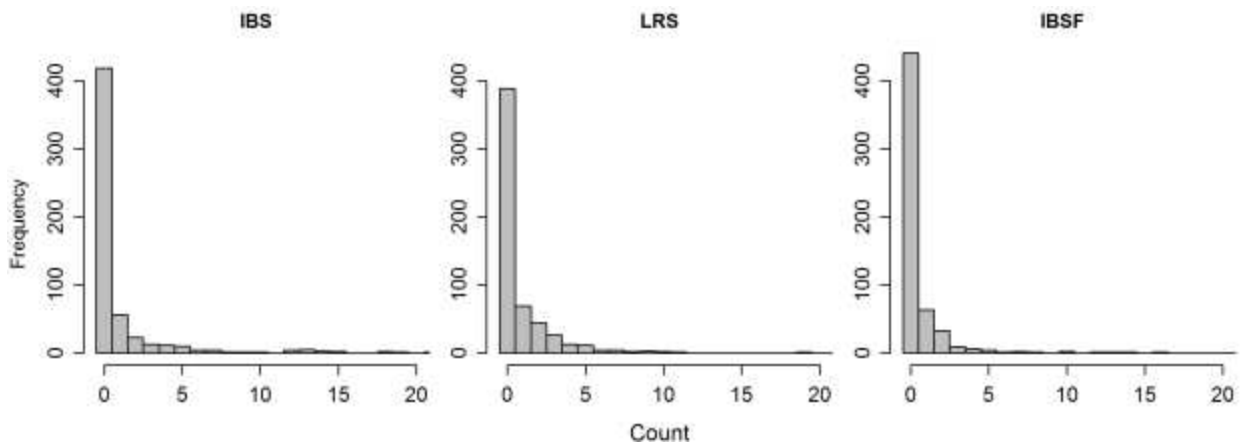


Figure 2.2. Frequency distribution of salmon counts, by stock, in all trawls analyzed. IBS = Interior Basin spring, LRS = Lower River spring, and IBSF = Interior Basin summer/fall Chinook salmon. Twelve trawls resulted in more than 20 fish from one stock and are not shown (9 from IBS and 3 from LRS).

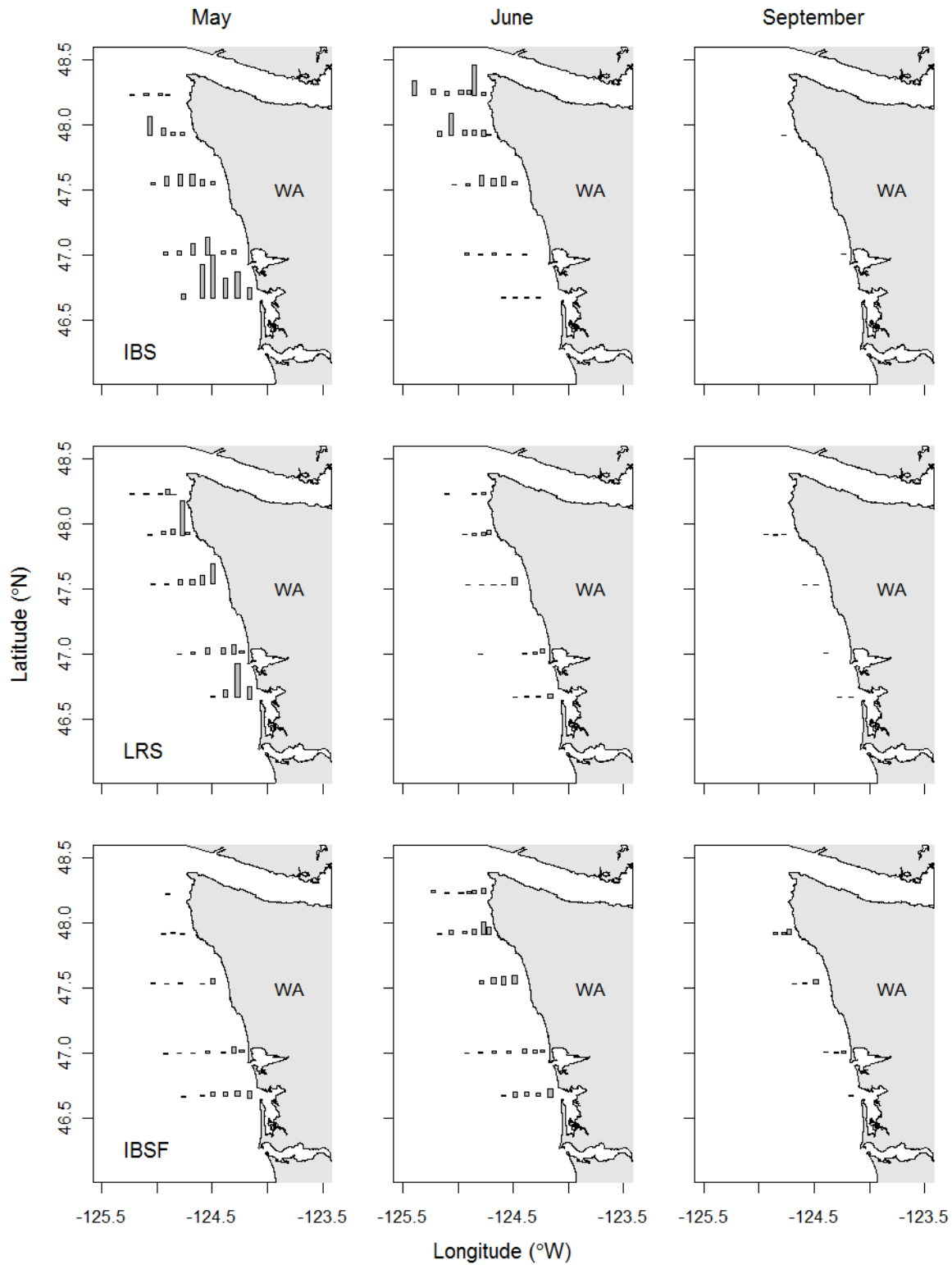


Figure 2.3. Maps of mean catch per station of for the different stocks (rows) and months (columns). IBS = Interior Basin spring, LRS = Lower River spring, and IBSF = Interior Basin summer/fall Chinook salmon.

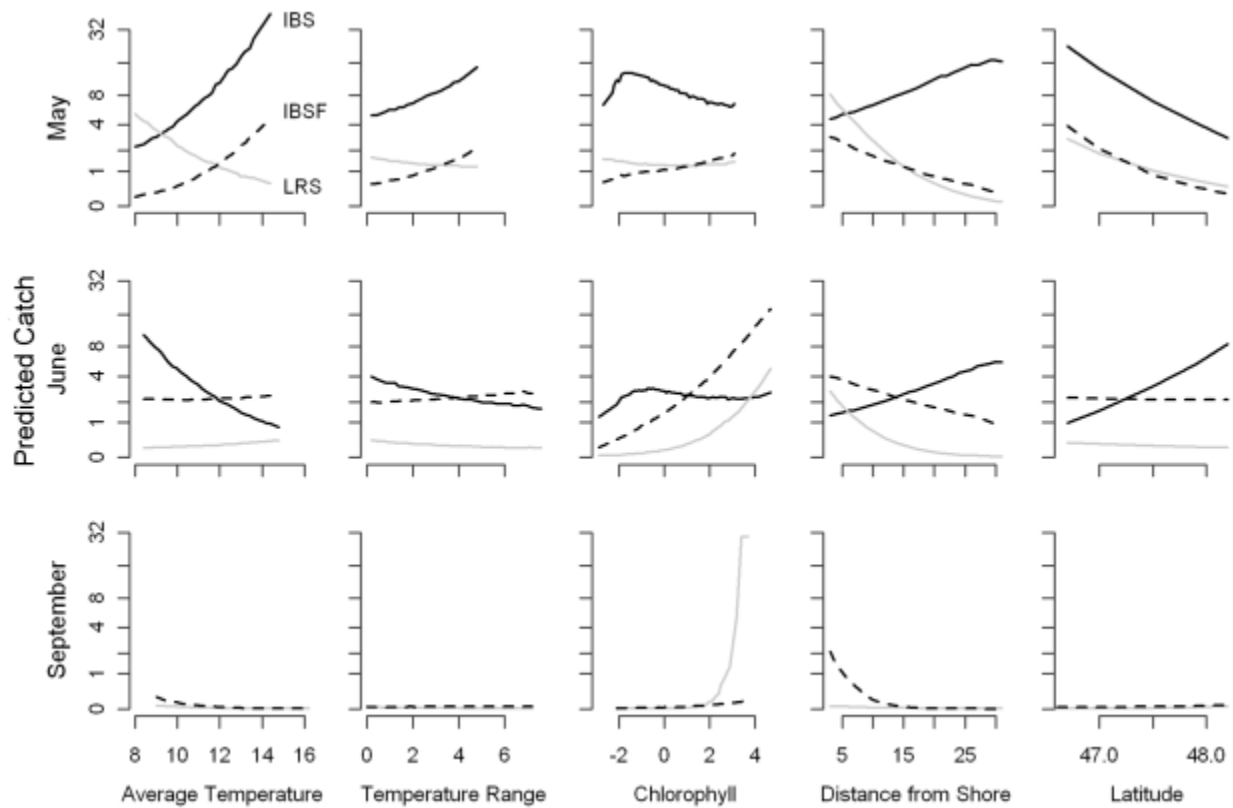


Figure 2.4. Relationship between each of the covariates and mean predicted catch of each stock using the full model. IBS = Interior Basin spring, LRS = Lower River spring, and IBSF = Interior Basin summer/fall Chinook salmon.

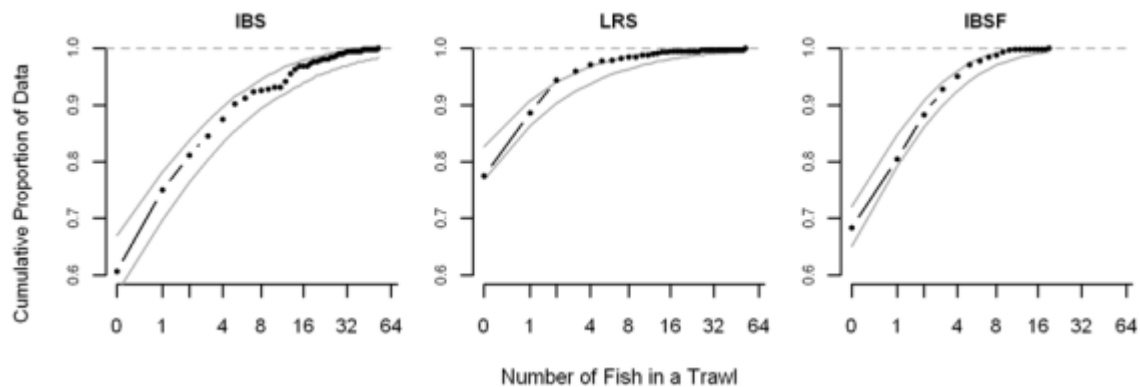


Figure 2.5. Observed cumulative catch distribution (black) and posterior predicted 90% credible intervals (grey lines) for each stock produced from the full zero-inflated negative binomial model. IBS = Interior Basin spring, LRS = Lower River spring, and IBSF = Interior Basin summer/fall Chinook salmon.

2.8 Supplemental Material for Chapter 2

2.8.1 Independent Variable Selection

In previous studies, copepod abundance has been shown highly correlated with salmon catches (Bi et al. 2007, Bi et al. 2011, Yu et al. 2012). However, these previous analyses used June catch data only, while my analyses used catch data from May, June, and September. Because no zooplankton data were available for the May and September cruises, I could not consider copepods as an independent covariate. Analyses using salinity or transmissivity showed no support for the catch-per-unit-effort data, and these variables were dropped from all models.

Based on the correlation among the remaining potential predictor variables, I identified two sets of variables that were highly correlated: water depth was correlated with distance from shore ($r = 0.88$; Figure 2.6), and chlorophyll *a* concentration was correlated with Secchi depth ($r = -0.81$; Figure 2.7). Therefore, rather than including both variables from these sets in the models, I ran competing models with each of the two candidates from each set to determine which variable to include in the final models. I used differences in the deviance information criterion (ΔDIC) to determine which model best fit the data. Although I ran comparisons with multiple distributional assumptions, I report results for the zero-inflated negative binomial (the best fit) model only.

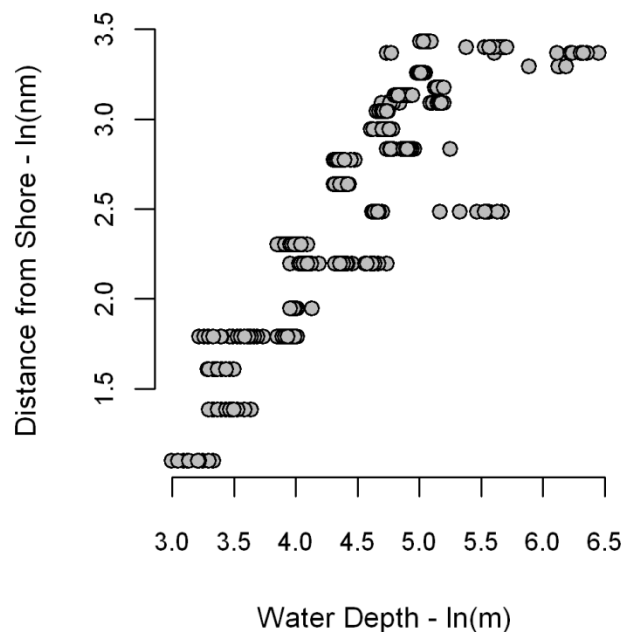


Figure 2.6. Relationship between distance from shore and water depth, $r = 0.88$. Distance from shore was log-transformed to aid in comparisons with water depth (for both the plot and the correlation analysis), but the model using log-transformed distance was not supported by the catch data.

2.8.1.1 Depth/Distance

The distribution of depth values was highly right skewed due to the presence of multiple canyons along the Washington coastline. I therefore natural-log transformed the depth data. For all comparisons, I ran models with all of the other variables included to evaluate whether depth or distance from shore accounted for more of the variability left *after all other variables had been accounted for*. Among these competing models, β_a (in Eq. 5 of Chapter 2) included average temperature, temperature range, chlorophyll a , latitude, month, and year while β_{zi} (in Eq. 6) included average temperature, temperature range, chlorophyll a , latitude, and month. The only difference was whether β_a and β_{zi} included depth or distance from shore.

Distance from shore and water depth were both good predictors of salmon abundance for particular subsets of the data, depending on the stock group modeled. I chose to include distance from shore in all further models for two reasons. First, distance from shore had the lowest DIC for three of the four data sets (Table 2.5). Although the catch data for the Interior Basin spring group was better explained by water depth than distance, the magnitude of the difference was small, suggesting no overwhelming support for either metric over the other. It

should be noted that stock-specific comparisons made in Chapter 2 were affected by this decision. However, the two variables were too highly correlated to draw meaningful conclusions about the mechanistic drivers of east-west distribution for yearling Chinook salmon.

Table 2.5. Model comparison (Δ DIC) using different measures of east-west location. Models with Δ DIC of zero fit the data better than the other model.

	All Fish	Interior Basin spring	Lower River spring	Interior Basin summer/fall
Distance from shore	0	0	0	2.0
Water depth	0.7	7.6	11.2	0

2.8.1.2 Chlorophyll *a*/Secchi Depth

Secchi depth was highly correlated with chlorophyll *a* (after each was natural-log transformed; Figure 2.7). Similar to the above analysis with depth and distance from shore, I compared models using Secchi depth and chlorophyll *a* to determine which was the better predictor of juvenile salmon abundance.

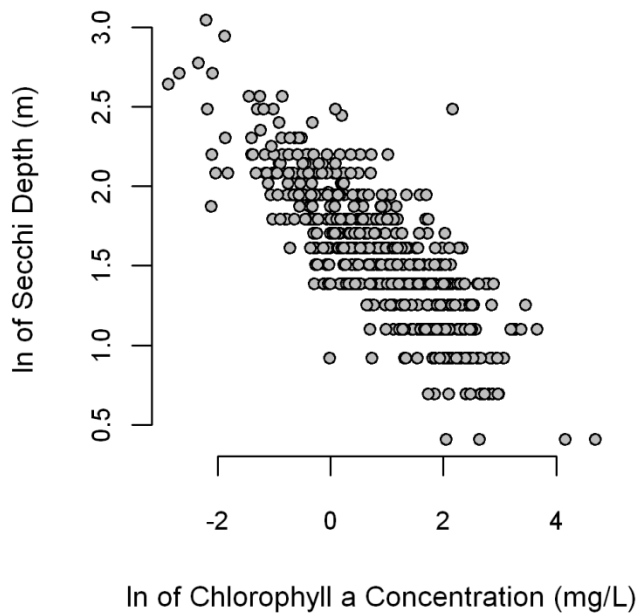


Figure 2.7. Relationship between Secchi depth and chlorophyll *a* concentration (both natural-log transformed), $r = -0.81$.

For no data set did the models strongly suggest one variable over the other (Table 2.6). However, for three of the four data sets, models that included chlorophyll *a* resulted in marginally lower DIC. I therefore used chlorophyll *a* in all future analyses. Chlorophyll *a* is at least two trophic levels away from Chinook salmon prey, suggesting that the correlation between chlorophyll *a* and Chinook salmon abundance is likely not mechanistic. There may be a link between chlorophyll *a* and zooplankton and another link between zooplankton and larval and juvenile fishes, which are the primary prey for Chinook salmon (Daly et al. 2009). However, the temporal scale at which these linkages operate are broader than would be required to make a bottom-up trophic mechanism likely. Interestingly, Secchi depth does have a reasonable mechanistic explanation in that turbidity is often used as a predator refuge. Turbidity in this area was not high enough to impact salmon feeding, but the efficiency of piscivorous fish predation was likely affected by turbidity.

Table 2.6 Model comparison (Δ DIC) using different measures of water clarity in the full model. Models with Δ DIC of zero fit the data better than the other model. Both variables were log-transformed prior to analysis.

	All Fish	Interior Basin spring	Lower River spring	Interior Basin summer/fall
Chlorophyll <i>a</i>	0	6.2	0	0
Secchi Depth	0.1	0	4.9	6.0

After removing Secchi depth from the environmental model and water depth from the geospatial model, there was very little correlation among the remaining predictor variables (Table 2.7). The highest correlation among all of my predictor variables was -0.66 (between chlorophyll *a* and average temperature in May). However, the correlation between the posterior parameter values for these two variables was weaker ($r = 0.50$). Interestingly, I found the largest correlations in posterior parameter values between latitude and chlorophyll *a* in September ($r = 0.57$), but the correlation in the raw data between these two variables was -0.15.

Table 2.7 Correlation among predictor variables included in the final models. Correlations greater than 0.5 (in magnitude) are shown in boldface shaded cells.

		Temp. Average	Temp. Range	Chl	Dist. from Shore	Latitude
May	Temp. Average	1				
	Temp. Range	-0.2	1			
	Chl	-0.66	0.03	1		
	Dist. from Shore	0.32	-0.13	-0.51	1	
	Latitude	-0.36	-0.19	0.34	-0.18	1
June	Temp. Average	1				
	Temp. Range	0	1			
	Chl	-0.57	0.01	1		
	Dist. from Shore	0.51	-0.13	-0.59	1	
	Latitude	-0.23	-0.24	0.06	-0.17	1
Sept.	Temp. Average	1				
	Temp. Range	-0.04	1			
	Chl	-0.24	0.16	1		
	Dist. from Shore	0.27	0.11	-0.43	1	
	Latitude	-0.16	-0.3	-0.15	-0.17	1

2.8.1.3 Temperature selection

Yearling Chinook salmon are found primarily near the surface during their first ocean year (Orsi and Wertheimer 1995, Emmett et al. 2004, Krutzikowsky and Emmett 2005). Even older fish are often found near the thermocline in coastal waters, which is usually shallow (~10-15m). Behavioral thermoregulation could influence growth rates and ultimately survival rates.

If thermoregulation is an important ecological driver of vertical distribution, the absolute range of temperatures available may also be important. Rather than simply using surface temperature in the model, which is associated with high variance and observation error, I systematically searched for an optimal way to summarize the temperature information. Previous research has used temperature at 3m as a predictor variable (Morgan et al. 2005, Bi et al. 2007), so this was my default temperature metric. Against this, I compared models that used the temperature within a particular depth range. I included temperatures from the surface down to a variable depth (0-4m, 0-6m, etc.) with a maximum depth range of 0-40 m. For each new input data set, I ran three full zero-inflated negative binomial models: one with average temperature, one with temperature range, and one with both (all calculated using the depth range for that iteration).

The best model resulted from using average temperature and temperature range from the surface down to about 20m (Figure 2.8). For models that included only one of these predictor variables, average temperature was best down to about 20m, but temperature range was best using data down to about 13-14m. For simplicity, however, I used the top 20m for both average temperature and temperature range in all further models. I concluded from this that yearling Chinook salmon used the top 15-20m of water on a regular basis, at least through September of their first ocean year. This result is particularly interesting given that our net fished the top 20m of water, suggesting that we fished the full depth range that yearling Chinook salmon used. An obvious criticism is that fish used a greater depth range, but our catches were most associated with this range because that is all we fished; however, without further depth-specific sampling, I cannot explore this idea.

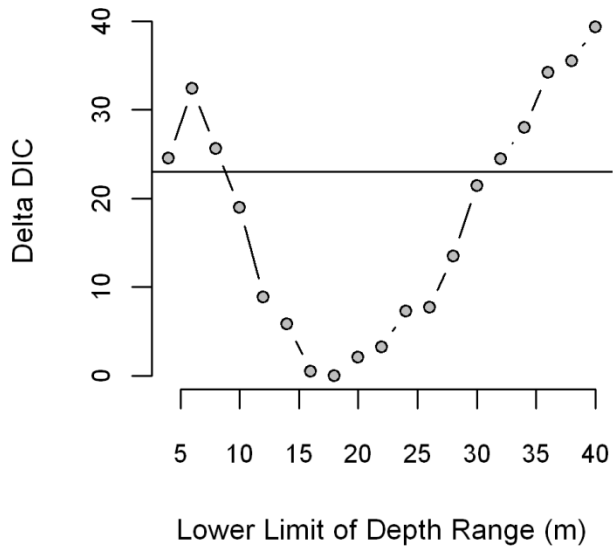


Figure 2.8. Delta DIC for a zero-inflated negative binomial model using temperature at 3 m (horizontal line) and from models using a range of depths from the surface down to a variable depth (points).

Table 2.8 Parameter importance and direction by stock for environmental vs. geospatial models as judged by the proportion of the posterior distribution that is greater/less than zero. Parameters that had more than 5% of posterior values on the opposite side of zero than the mean (i.e., not different than zero) are indicated with a bullet (•). Plus or minus symbols indicate the direction of the gradient with increasing covariate values (e.g., for the abundance component of the model, a plus sign indicates that as the covariate increased, the expected number of fish caught also increased). In the zero-inflated component, a plus sign indicates that as the covariate increased, the probability of zero catch increased. Categorical variables that had more than 5% of posterior values on the opposite side of zero are shown with an asterisk. Blank indicates a parameter was not in the model. Stock abbreviations: IBS, Interior Basin Spring; IBSF, Interior Basin Summer/fall; LRS, Lower River Spring.

	Environmental				Geospatial				Full				
	All	IBS	LRS	IBSF	All	IBS	LRS	IBSF	All	IBS	LRS	IBSF	
Within habitat (negative binomial component)													
K	+	+	+	+	+	+	+	+	+	+	+	+	
alpha	•	•	•	—	•	•	—	—	•	•	—	—	
month	*	*	*	•	*	*	*	*	*	*	*	*	
year	*	*	*	*	*	*	*	*	*	*	*	*	
average temp.	May	•	+	•	+				•	+	—	+	
	June	—	—	•	•				•	—	•	•	
	Sept	—		•	—				•		•	—	
temp. range	May	+	+	•	+				•	•	•	•	
	June	•	—	•	•				•	•	•	•	
	Sept	•		•	•				•		•	•	
chl a	May	•	•	•	•				•	•	•	•	
	June	+	—	+	+				+	•	+	+	
	Sept	•		+	•				•		+	•	
distance from shore	May					—	+	—	—	—	+	—	—
	June					—	•	—	—	—	+	—	—
	Sept					—		—	—	—		•	—
latitude	May					—	—	—	—	—	—	—	—
	June					+	+	•	•	+	+	•	•
	Sept					•		•	•	•		•	+
Outside habitat (zero inflated component)													
alpha	—	—	—	—	—	—	—	—	—	—	—	—	
month	*	*	•	*	•	•	*	•	*	•	*	•	

average													
temp.	+	•	•	•					+	•	•	•	
temp.													
range		•	•	•	•				•	•	•	•	
chl <i>a</i>	-	-	•	-					-	-	•	•	
distance													
from shore						+	+	•	•	+	+	•	+
latitude						•	•	•	•	•	•	•	•

Chapter 3 Evidence for multiple navigational sensory capabilities by Chinook salmon

Published as:

Burke, B. J., J. J. Anderson, and A. M. Baptista. 2014. Evidence for multiple navigational sensory capabilities by Chinook salmon. *Aquatic Biology* 20:77-90.

Abstract

To study the complex coastal migrations patterns exhibited by juvenile Columbia River Chinook salmon as they enter and move through the marine environment, I created an individual-based model in a coupled Eulerian-Lagrangian framework. I modeled five distinct migration strategies and compared the resulting spatial distributions to catch data collected during May and June in three years. Two strategies produced fish distributions similar to those observed in May but only one strategy produced the observed June distributions. In both strategies, salmon distinguish north from south (i.e., they have a compass sense) and they control their position relative to particular landmarks, such as the river mouth. With these two abilities, I posit that salmon follow spatially-explicit behavior rules that prevent entrapment in strong southward currents and advection offshore. Additionally, the consistent spatio-temporal distributions observed among years suggest that salmon use a clock sense to adjust their swimming speed, within and among years, in response to progress along their migration.

3.1 Introduction

Relative to other life-history stages, our understanding of salmonid behavior and ecology during ocean residence is limited (Hartt and Dell 1986, Quinn 2005). However, for most individuals, ocean residence represents the longest stage of the life history. For example, Chinook salmon (*Oncorhynchus tshawytscha*) typically spend the first year in freshwater and then one to five years in the Pacific Ocean before returning to spawn. Yearling Chinook salmon from the Columbia River enter the ocean and quickly migrate north (Peterson et al. 2010). Although general migration patterns are known (Weitkamp 2010, Tucker et al. 2011) and environmental correlates have been proposed (Bi et al. 2007, Burla et al. 2010a, Peterson et al. 2010, Burke et al. 2013), missing is a comprehensive understanding of the early ocean ecology and migration behavior of these juvenile salmon.

One of the more difficult aspects of studying juvenile salmon ocean ecology is understanding the behavioral responses of these fish to external stimuli. For example, what cues do salmon use as aids during migration? Do fish make behavioral decisions based on local environmental conditions, so as to maximize their short-term growth rate? This would be a logical objective, given that mortality during early ocean residence is often size-dependent (Healey 1982, Good et al. 2001, Moss et al. 2005, Cross et al. 2009)? Or have salmon evolved a northward migration strategy that relies on large-scale navigational aids, such as has been shown for other animals (Wiltschko and Wiltschko 1995, Papi 2006)?

The ability of salmon to consistently migrate to relatively specific locations, both as smolts and adults, has driven a large body of research. Salmon appear to use multiple cues, depending on their availability and the stage of migration (Dittman and Quinn 1996, Quinn 2005). Groot (1965) first demonstrated that salmon use celestial cues for orientation, but switch to ‘some as yet unknown set of reference cues’ as cloud cover increased. A series of experiments on sockeye salmon fry and smolts (Quinn 1980, Quinn et al. 1981, Quinn and Brannon 1982) then revealed that, in the absence of alternative information, salmon oriented using the Earth’s magnetic field; an ability also found in a wide range of animals (Wiltschko and Wiltschko 1995, Papi 2006, Lohmann et al. 2007). Indeed, recent work has identified magnetite-based magnetoreceptors in both salmon and trout (Kirschvink et al. 1985, Walker et al. 1988, Walker et al. 1997) as well as the use of the magnetic field in adult salmon during their return migration (Bracis and Anderson 2012, Putman et al. 2013). Yet, as discussed by Friedland et al.

(2001), our understanding of the relative role of these reference systems is still limited, particularly in the marine environment.

Willis (2011) distinguishes two general processes involved in migration; navigation is movement toward a goal outside of the sensory environment of an animal and orientation as a directional response to local conditions (it should be noted that multiple definitions exist in the literature). By this definition, navigation requires a compass sense, while orientation may only require knowledge of ambient environmental conditions (e.g., an animal could orient relative to a temperature or salinity gradient). Burke et al. (2013) found that the response to (unspecified) large-scale variables, such as the sun or Earth's magnetic field, was stronger than the response to local environmental cues, which suggests that salmon primarily use navigation in their migrations. However, orientation to local conditions is also suggested by the high correlation between yearling Chinook salmon catches and local environmental conditions (Bi et al. 2007, Burla et al. 2010a, Yu et al. 2012, Burke et al. 2013).

To explore in more detail the importance of global navigation and local orientation in salmon migration behavior, I simulated fish movement through a virtual environment using an individual-based model in a coupled Eulerian-Lagrangian framework (similar models were reviewed in North et al. 2009, Kishi et al. 2011, Willis 2011, Byron and Burke In Press). An individual fish makes thousands of behavioral decisions every day based on its environment, condition, and genetic makeup. I simulated these decisions and the resulting movement of individual fish using prescribed behaviors in response to a dynamic physical environment. By integrating specific behavioral responses over a time series of environmental conditions experienced by the fish, I identified which behaviors produced realistic fish trajectories and final locations.

Using this tool, I tested a suite of plausible behaviors to characterize the effect of various orientation and navigation cues on the spatio-temporal distribution of juvenile salmon in the marine environment. Because of the complexity of migratory behavior and cues that direct migration, my aim was to eliminate some behaviors and cues as infeasible, while identifying others that may be significant. In this way, my goal was to reduce the set of possible factors that need to be considered when studying salmonid migration and how existing migratory patterns may respond to local and global changes in the marine environment.

3.2 Methods

A number of movement-modeling frameworks (e.g., reaction-diffusion equations) are inadequate to represent the complex coastal currents and concomitant ocean migration behaviors employed by salmon. I therefore used a combination of Eulerian and Lagrangian frameworks to simulate fish movement through a virtual environment (Willis 2011). Specifically, I used output from a Eulerian hydrodynamic model as the virtual environment (rather than dynamically simulating fish movement within the hydrodynamic model) and created a Lagrangian individual-based model (IBM) that generated individual fish movements and behaviors within the environment.

After modeling fish with individualized responses to the environment, I summarized the set of modeled individuals to determine population-level spatio-temporal distributions. Simulations were implemented in the Python language (PSF 2013). Below, I describe the salmon data used in the simulations, the hydrodynamic model that generated the virtual environment, the details of the IBM, and finally, how I analyzed results.

3.2.1 Salmon Catch data

Several distinct stocks of Chinook salmon from the Columbia River Basin migrate as yearlings (Waples et al. 2004, Quinn 2005, Burke et al. 2013). On entering the ocean, these stocks generally initiate a rapid northward migration (Peterson et al. 2010) (Figure 3.1) against prevailing coastal currents (Hickey and Royer 2001). Although the stocks exhibit distinct spatio-temporal distributions (Burke et al. 2013), I consider the aggregate Chinook salmon run for our analysis and not stock-specific differences.

I used yearling Chinook salmon catch data from an ongoing NOAA Fisheries survey (Peterson et al. 2010) in which juvenile salmon were collected using a pelagic rope trawl with a mouth opening of 30 m wide by 20 m deep. The survey includes 3-10 east-west transects from La Push, Washington to Newport, Oregon. Stations along each transect were sampled annually for 12 years in late May, late June, and late September. Further details on the survey methods are available in Brodeur et al. (2005).

I restricted the analysis to ocean entry years 2003, 2004, and 2008, which represent a range of both salmon survival rates and oceanographic conditions (Tomaro et al. 2012), for several reasons. First, the simulations take a long time to run and three years was about all I

could envision (if I wanted to finish this decade). When I started the modeling, 2004 was the most recent year for which the hydrodynamic model results were available. By the time the model was operational, 2008 was the most recent year available. Since I had done much testing on 2003 and 2004, I kept those years in the analysis. I also included 2008 as a comparison since it was a year in which we caught a large number of juvenile salmon in the trawls. Finally, knowing I was going to run similar simulations for the next part of this project (Chapter 4), I wanted to use years in which we had a lot of otolith data available. The three years included in this study provided matched all of these criteria. It should be noted that many more years are now available and the model described here could be used in future studies to make a broader interannual comparison.

3.2.2 Hydrodynamic modeling system

Understanding the ocean migration routes of Columbia River salmon requires quantitative knowledge of the circulation during their residence in the coastal marine habitat. I defined ocean circulation near the Columbia River and the coastal ocean from March 1st through September 30th using the Virtual Columbia River modeling system (CMOP 2013), which provides a high-resolution description of 3-D river-to-ocean circulation and water properties in the Columbia River and plume (Baptista et al. 2008, Burla et al. 2010b).

I used simulations archived as database DB22 in the Virtual Columbia River. State variables of DB22 (water level, temperature, salinity, and 3D velocities) were computed every 90 seconds and stored every 15 minutes, in either the centers (water level, vertical velocity), the nodes (salinity, temperature), or the side centers (horizontal velocity) of the triangular elements of the computational grid. Grid element areas varied from less than 0.002 to over 480 km² (mean 8.5 km²). The computational grid extended from Beaver Army Terminal near Quincy, OR (in the tidal freshwater part of the Columbia River estuary) to marginally beyond the Oregon and Washington continental shelves (Zhang and Baptista 2008); this domain encompasses the rectangular box bounded by 42.0°N and 125.5°W and 49.0°N and 124.0°W used in this study. Because simulated fish could exist anywhere in a continuous volume, I interpolated oceanic conditions to the fish locations.

The computational engine underlying the Virtual Columbia River modeling system was SELFE (semi-implicit Eulerian-Lagrangian finite-element), a baroclinic circulation model based

on the solution of 3D shallow water equations (Zhang and Baptista 2008). These consisted of a continuity equation; conservation equations for momentum, salinity and heat; and an equation of state, which used a finite-element method applied on an unstructured, 3-node triangular grid. The skill of these simulations had been previously assessed through quantitative comparison against observations of water level, salinity, and temperature from the Science and Technology University Research Network (SATURN) collaboratory (Baptista et al. 2005, Burla et al. 2010b).

3.2.3 Individual Based Model

I describe the individual-based model using the overview, design concepts, details (ODD) protocol of Grimm et al. (2006), Grimm et al. (2010). The overview portion includes the purpose of the model, the state variables and scales used, and an overview of the processes and scheduling. I then describe the details of initialization, model input, and several submodels.

3.2.3.1 Overview

Purpose: After salmon leave the Columbia River, there is little known about the routes taken during their initial migration, and even less is known about the behaviors they employ during this stage. This model is intended to 1) distinguish between feasible and unrealistic behaviors, given the constraints of coastal currents, fish size, and post-smolt migration timing and 2) evaluate various migration behaviors by comparing simulated spatio-temporal distributions to observed distributions.

State variables and scales: Environmental state variables included temperature, salinity, three-dimensional flow, distance from shore, and water depth.

Fish were assigned an ocean entry date and an initial 3D location, which was updated at every 15-minute time step of the simulation. Fish size was also updated at every time step using a standard bioenergetics model with parameters for Chinook salmon (Hewett and Johnson 1992). Consumption was modeled using a proportion of maximum daily consumption, or P-value (a size- and temperature-dependent variable), and each fish kept its randomly assigned P-value for the duration of the simulation. Similarly, if a simulation employed active swimming (Table 3.1), assigned swimming speeds (body lengths (BL) per second) were maintained for the duration of the simulation, such that speed relative to the water increased as fish grew.

Process and scheduling: Each simulation started at 12:15 a.m. on April 1st and ran through midnight on July 1st. During each time step, fish first grew according to the bioenergetics model, local temperature, and assigned P-value. Fish then moved to a new location, where they stayed until the next time step. Growth and movement of each fish was independent of that of other fish, as there was no direct or indirect interaction among individuals. While mortality is high during the early ocean stage (Pearcy 1992, Beamish and Mahnken 2001), I had insufficient information to partition mortality spatially or temporally. Therefore, all simulated fish were considered survivors of the first 3 months in the marine environment.

3.2.3.2 Design concepts

Basic Principles: Optimal swimming speed for both travel and foraging is size-dependent (Ware 1978), as are many ecological processes acting on individuals (Arendt 1997, Sogard 1997). I included a bioenergetics model to allow individual growth throughout the simulation, such that all size-dependent processes in the model (e.g., growth and swimming speed) affected fish appropriately.

As this model describes the migration of animals through a dynamic environment, I tested behaviors related to both movement theory and habitat selection. Among the behavioral rules, I included passive drift, diffusion, and directed migration. In other rules, I explicitly tested habitat selection using multiple temperature-based behaviors as well as some involving distance from shore (Table 3.1).

Adaptation: Columbia River yearling Chinook salmon are consistently captured in a narrow east-west band (mean distance from shore = 28.5 km, SD = 7.6 km) along the Washington coast (Peterson et al. 2010), but my efforts to mechanistically model such a narrow migration corridor were unsuccessful. As the northward migration was my primary focus, I simplified the model by imposing an attraction to a specific east-west location. For simulations involving behavior SX (behaviors are described below and in Table 3.1), I used an Ornstein–Uhlenbeck process to adjust the swimming angle. In this framework, the greater the distance between a fish and the line of attraction, the more its swimming angle was shifted back toward the line. This resulted in swimming angles of about 320° for fish on the shoreline and about 45° for fish 80 km offshore. Although the mechanism by which fish maintain their east-west location is unknown, inclusion of this line of attraction was necessary to keep simulated fish

from migrating into land or far offshore. Mean distance from shore for yearling Chinook salmon sampled over 12 years (Peterson et al. 2010) was 28.5 km, and I used this as the line of attraction.

Sensing and Prediction: Ambient conditions such as temperature and flow were used to determine fish behavior. Simulated fish had no explicit knowledge of environmental conditions at any spatial coordinates other than their immediate location, with the exception of vertical structure used to optimize vertical temperature (OT) and flow (F2). For these behaviors, fish selected specific attributes from within the water column. The thermocline was usually shallow (~10 m) and it is certainly feasible that fish regularly make short vertical movements within a 15-minute time step to determine vertical temperature or flow profiles.

On a larger temporal and spatial scale, I postulated that fish are inherently inclined to migrate north, which implies a genetically selected propensity to migrate to regions that have historically allowed higher growth and/or survival. For these simulations, I made two assumptions regarding spatial information: 1) fish had a compass sense and therefore knew what direction was north (Quinn and Groot 1983, Quinn 1991) and 2) fish knew their distance from shore. For the latter assumption, I did not know the nature of the cue, but it is likely to involve one or more oceanographic features.

Stochasticity: I started all simulations with the same random number seed in the Python language, so that all randomly drawn variables (initial length, ocean entry date, P-value, initial depth) were identical among simulations. Therefore, each simulation (within a year) tested the same initial set of 10,000 randomly drawn fish with the only difference among simulations being fish behavior (see *Initialization*).

Observation: I stored all initial data (length, location, P-value, swimming speed) to files. Every 12 hours of simulated time, I recorded location and length of all fish. All data were imported into R software for analysis (R Development Core Team 2011).

3.2.3.3 Details

Initialization: At the start of a simulation, I generated 10,000 virtual fish and assigned initial values for all state variables. Fish sizes ($\mu = 155$ mm, $SD = 15$ mm) and ocean entry dates ($\mu = \text{May } 15^{\text{th}}$, $SD = 10$ days) were drawn randomly from normal distributions (Table 3.2),

roughly matching empirical data collected in the Columbia River estuary (Weitkamp et al. 2012). Fish initiated migrations just inside the Columbia River mouth (Longitude -124.0759, Latitude 46.2482) at randomly (uniformly) assigned depths within the top 10m. The proportion of the maximum daily consumption rate (P-value) of each fish was drawn from a log-normal distribution ($\mu = \log(0.5)$, $SD = 0.5$).

Input: All input data were obtained from the hydrodynamic modeling system described above (Zhang and Baptista 2008).

Growth submodel: I modeled fish growth using a standard bioenergetics model parameterized for Chinook salmon (Hewett and Johnson 1992). In each 15-minute time step, fish first instantaneously grew and then moved. As most bioenergetics models are parameterized for a 24-hour time step, I divided all rate constants (e.g., consumption) by 96 to match the 15-minute time step. To maintain a widening gap between the largest and smallest fish throughout the simulation, maximum daily consumption (P-values) did not change within a simulation. This also reduced the stochasticity of the model and allowed comparisons of individual fish among simulations (results not shown), where the only difference between the fish was the assigned behavior (Table 3.1).

Movement submodel: I defined five distinct behavioral rules (Table 3.1). Swimming through water is energetically expensive and our set of migration strategies was chosen to determine whether simple and efficient behaviors were sufficient to simulate the observed fish distributions or whether more complex and energetically costly behaviors were required. The null behavior, passive particle (PP), assumed fish were passive in three dimensions (Willis and Hobday 2007, Brochier et al. 2008) and served as a particle tracer of ocean currents.

For the optimum temperature behavior (OT), fish maintained the optimum temperature for growth, which we assumed to be 12 °C based on results from Hinke et al. (2005), via vertical movement during each time step. Horizontal movement for this behavior was passive. Similarly, there was no active horizontal movement for the optimizing flow behavior (F2), in which fish selectively adjusted their depth within the top 20 m to maximize northward movement (see Burke et al. 2013 for justification of the 20-m cutoff). Essentially, fish move vertically into slow water when flows are southerly and into fast water when flows are northerly, thus

maximizing net northward displacement without active horizontal swimming (Lacroix and McCurdy 1996). Using local currents to aid movement has been shown for many migrating species ranging from moths (Alerstam et al. 2011) to Atlantic salmon *Salmo salar* (Thorstad et al. 2012). To employ the selection of northward currents in this behavior, animals required a compass sense.

I simulated two behaviors that involved active horizontal movement. The PR (positive rheotaxis) behavior was similar to that used in other coupled oceanographic and individual-based models, which have shown that swimming with or against currents could be a successful migration strategy (Booker et al. 2008, Mork et al. 2012). During the positive rheotaxis simulations, fish maintained a swimming speed of 0.5 BL/s directly into the prevailing current. Although I report results only for positive rheotaxis, I also ran simulations using negative rheotaxis. However, ocean currents in this region are predominantly southern in the springtime (Hickey and Royer 2001), and therefore negative rheotaxis was obviously not a viable strategy.

Finally, I simulated active northward swimming (SX), independent of local environmental conditions. Three swimming speeds were individually simulated (0.3, 0.5, and 0.9 BL/s) at a mean angle of 8° west of north (approximately along the coastline), adjusted each time step according to the Ornstein-Uhlenbeck model described above. Like the behavior to optimize flow, the active northward migration behavior required that fish have a compass sense.

3.2.4 Analysis

Final locations of simulated fish were compared to the spatial distribution of yearling Chinook salmon caught during the NOAA Fisheries surveys Figure 3.1 (sampling protocol described in Brodeur et al. 2005). To select feasible behaviors, I used a combination of visual comparisons and simple summary metrics (e.g., mean final latitude). My goal was to provide relative support for or against migration behaviors rather than to prove that salmon use any particular behavior. Moreover, the simulated data (a point process) and the observed data (density estimates at discrete locations) were not directly comparable quantitatively (most spatial statistics require either a point process or a density estimate (Bivand et al. 2013) – I am not aware of statistical methods to compare the two types directly).

I summarized simulated data from May 26th and June 26th, corresponding to the middle dates of research cruises each year. For these summaries, I calculated the centroid of the population, defined as the mean location of the 10,000 fish in each simulation, and the spread about the centroid. To account for anisotropy in final locations, I estimated variance in the final location in two directions. For this estimate, I used principal component analysis to determine the axis with the greatest variance (Woillez et al. 2007), which was often somewhat parallel with the coastline, and calculated the variance in this direction as well as the direction perpendicular to it. Spatial metrics were calculated in meters, the unit of the hydrodynamic model (Oregon State Plane projection for spatial coordinates, epsg: 32026, units = m), and converted to latitude and longitude for reporting and mapping. Because the final depth of simulated fish from all behaviors was primarily near the surface (data not shown), and this depth matched the depths observed in trawl samples, no further analyses or comparisons were done with fish depth.

To better understand the relationship between the final location of fish and model variables, I compared final locations on June 26th of each year to several model parameters, such as initial length, ocean entry date, and the bioenergetics P-value. Fish length (and therefore, any parameters related to growth) by definition had no effect on location for any behaviors where fish were not actively swimming (i.e., passive particle, optimal temperature, and optimal flow). Migration date had the potential to influence final location in all simulations, as currents near the mouth of the Columbia River and coastal ocean vary considerably on daily and weekly time scales (Hickey et al. 2005, Burla et al. 2010b, Hickey et al. 2010).

3.3 Results

The behaviors that produced spatial distributions most similar to those observed were different in May and June. For May, behaviors of optimized flow and active northward swimming fit the observed distributions relatively well (Figure 3.2). This suggested that salmon either used a depth modification behavior to avoid the strongest southward ocean currents or actively migrated north. For simulations using active northward swimming, the swimming speed required to match empirical data differed by year. In 2003, when southward currents were relatively strong, a swimming speed of 0.9 BL/s (S9) matched well with observed distributions. In contrast, in 2004 and 2008, swimming speeds of only 0.3 and 0.5 BL/s (S3 and S5) were required to match observed distributions (however, see Model Sensitivity below).

Although optimizing northward flow (F2) allowed a substantial number of simulated fish to move north as late as May, when coastal currents were relatively weak, it was not a sufficient strategy to maintain northward movement through June. Only active northward swimming produced a reasonable spatial overlap with the observed distributions (Figure 3.2; Appendix A). Additionally, swimming speeds that produced the best results in June matched those that did so in May within each year simulated.

The Ornstein-Uhlenbeck process was employed to keep simulated fish from migrating too far inshore or offshore during simulations of active northward swimming, and resulted in a realistic east-west distribution off the Washington coastline (mean distance from shore observed over 12 years of sampling was 28.5km (Peterson et al. 2010) with a SD of 7.6 km). Swimming angles varied considerably within and among years (Figure 3.3) and were highly dependent upon location (particularly whether fish were north or south of the Columbia River). Although I expected this variability given the complex nature of the Columbia River plume (Hickey et al. 2005, MacCready et al. 2009), this aspect of the model was not directly validated, and results should not be treated as direct evidence of a particular behavior.

As is true most years during spring and summer, ocean currents were predominately southward in the three years included in this study, and simulated fish with passive particle behavior mostly ended up south of the Columbia River (Figure 3.4; Table 3.3). By June, most simulated fish were more than two degrees latitude south of the centroid of the observed distribution. For all passive particle comparisons (year-month combinations), variability in north-south location was 2-5 times greater for simulated fish than for observed fish.

Simulated fish that adjusted vertical depth to a temperature of optimum growth (OT) ended up much further south than fish in the observed distributions in both months and all years (Table 3.3). While most of these fish remained in the top 40 m of the water column, suggesting that the behavior was logistically feasible, their final locations in May and June strongly suggested that movement based on optimal temperature for growth is not a feasible behavior for migrating yearling Chinook salmon. Similarly, positive rheotaxis resulted in most simulated fish moving south of the Columbia River (Figure 3.4). However, the difference in mean latitude between observed and simulated fish was less for fish using the positive rheotaxis than that for

fish using the optimal temperature behavior. In both cases, I did not see a large effect of fish size on movement and distribution.

In all simulations, including those that best matched observed spatial patterns, some fish were pushed south of the Columbia River just after ocean entrance. Although the proportion of fish pushed south varied by year and behavior (Figure 3.4), very few fish were able to counter the strong southward flows, upwelling-driven offshore currents, and eddies that carried them offshore. In some cases, these advected fish had a large influence on summary metrics, such as mean final location (Table 3.3; Appendix A). Interestingly, the subset of fish advected south was not influenced to a large extent by length, growth, or ocean entry date (Appendix B).

3.4 Discussion

The simulations suggest that Columbia River yearling Chinook salmon use at least two sensory modalities during migration: a compass sense and a clock sense. In addition, there is some tentative evidence that fish use a map sense, although other modalities may be involved. Evidence for each modality arises from different aspects of the simulations, as described below.

3.4.1 Compass sense

For most of the behaviors modeled, the predominantly southward flowing coastal currents prevented simulated fish from migrating north. In fact, most behaviors resulted in fish moving quite far south and offshore of the Oregon coast. Counter to my initial expectations, positive rheotaxis alone was insufficient to produce northward migration since the coastal currents were too complex to produce a consistent cue for northward movement. The only behaviors that produced the observed northern distributions of fish were optimization of northward flows via vertical migration (F2) and/or active northward swimming (SX). Since both of these behaviors require that fish sense the direction north, I concluded that salmon use a compass sense during their marine migration.

3.4.2 Clock sense

The observed interannual variability in the spatial distribution of yearling Chinook salmon has been relatively small (Peterson et al. 2010, Weitkamp 2010), particularly in May, shortly after they entered the marine environment (Figure 3.1). However, in the years included in this study, the strength and direction of ocean currents varied considerably (see the passive particle simulation results in Appendix A to get a sense of this variability). I propose that to

achieve a stable spatial distribution within a highly variable current regime requires that fish have a sense of time, i.e. clock sense, enabling them to adjust swimming behavior to achieve a consistent rate of migration. As expected under this scenario, I found that the swimming speed and swimming angle required to match observed distributions varied among years. Given the abundant evidence on biological clocks in animal movement (e.g. Brady 1982, Pastor and Artieda 1996), it is not surprising that salmon also employ a clock sense during migration.

3.4.3 Map sense

Growing evidence suggests that salmon have the capability to detect and respond to the Earth's magnetic field during ocean migration (Bracis and Anderson 2012, Putman et al. 2013). In addition to a compass and clock sense, my results provide two indications that post-smolt salmon perceive their location in the ocean relative to some geo-referenced cues. First, yearling Chinook salmon maintain a relatively constant distance from shore, even though the east-west component of flow is highly variable. Because of this, the swimming angle necessary for simulated fish to maintain a particular distance from shore was also highly variable (Figure 3.3). However, it is unclear how salmon are able to maintain their narrow east-west distribution ($SD = 7.6$ km). Moreover, wind-driven upwelling events occur frequently and result in strong offshore currents, yet we rarely caught fish at our outermost sampling locations (Figure 3.1), suggesting salmon counteract the effect of upwelling-driven offshore currents. It is unclear whether salmon detect the eastward or westward movement of water directly or whether they are initially advected by the currents and detect their resulting change in location. The former could potentially be accomplished via small-scale movements to determine vertical gradients in flow, whereas the latter would indicate direct knowledge of position and support the notion of a map sense. Either way, the low variability in offshore distance is compelling evidence that fish behaviorally compensate for the dynamic east-west component of coastal currents.

A similar location-induced behavioral compensation could explain the apparent sharp southern boundary of yearling Chinook salmon from the Columbia River. Despite consistent sampling as far south as Newport, Oregon, very few fish from these stocks have been captured south of the river (Peterson et al. 2010, Burke et al. 2013). However, many simulated fish were caught in an eddy south of the Columbia River and quickly transported south and offshore. Even

fish migrating at the fastest speeds tested (0.9 BL/s) could not counter these ocean currents at times.

The presence of simulated fish south of the Columbia River mouth resulted in a latitudinal variance that was generally higher than that for observed fish (Table 3.3). One possible explanation for the discrepancy between simulated and observed latitudinal variance is that observed fish exhibit more control than the modeled fish of their northward migration in relation to their geo-spatial position. For example, real fish may increase their swimming speed (> 0.9 BL/s) if they are driven south of their migratory route. However, in this scenario, they must also decrease their speed once they return to the migration route and on schedule. Otherwise, the increased swimming speed would have simulated fish exceed the position of fish observed in June. Supporting this scenario, Tomaro et al. (2012) observed variable swimming speed with early migrating individuals swimming slower than average and later migrants swimming slightly faster. In effect, I suggest that to avoid entrapment in large scale eddies, fish require some perception of their position so they can adjust their swimming speed and direction to maintain a migration schedule northward along the coast.

Unfortunately, the mechanisms driving the hypothesized adjustments in swimming speed are unclear. Similar to the east-west component of their distribution described above, salmon may either detect the strong southward currents directly, and alter behavior to avoid them, or they may detect that they have been advected south through the use of a map sense and increase northward movement. Of the two explanations, I believe that the use of positional information and a map sense is more likely for two reasons. First, the consistency in spatial distribution (Weitkamp 2010) requires that fish respond to the complex and highly dynamic ocean currents in and near the Columbia River plume in a precise manner. The Columbia River plume is particularly variable and often shifts direction on weekly or even daily time scales (Hickey et al. 2005, Burla et al. 2010b, Hickey et al. 2010). Error in response to changing currents would propagate through time, resulting in fish dispersing farther off course throughout the migration, which is not supported by the empirical data. Second, salmon have been shown to possess the magnetoreceptors necessary for this sensory ability (Kirschvink et al. 1985, Walker et al. 1988) and evidence exists that adult salmon use a map sense during their homing migration in the ocean (Putman et al. 2013). If salmon indeed use a map sense to restrict movement away from

the southern areas, it need only be a single-coordinate system (Lohmann et al. 2007). For example, if salmon can detect the magnetic field inclination, they could determine whether they were North or South of the Columbia River by comparing the inclination at their present location to the inclination imprinted at the Columbia River mouth (see Putman et al. 2013). Although there is much literature on these sensory capabilities (Wiltschko and Wiltschko 1995, Walker et al. 1997, Papi 2006, Lohmann et al. 2007), I cannot distinguish among particular mechanisms (e.g., magnetic versus sun or celestial maps). Therefore, any conclusions from the present work about salmon using a map sense during migration are still speculative and require further research.

3.4.4 Model Sensitivity

I did not perform a complete sensitivity of model parameters, as this would have been prohibitively time consuming. However, several aspects of the model were allowed to vary and provide some information regarding sensitivity of the model. For example, initial location when fish were released varied only in the vertical direction. But after only a few hours, fish distribution was well mixed both inside and outside of the river mouth, suggesting the precise latitude and longitude of release location was not driving model results.

Initial fish length and date of release were both estimated from empirical data (Weitkamp et al. 2012). Neither of these variables had a noticeable impact on final latitude of simulated fish (Appendix B).

Swimming speed is an interesting variable. The slowest fish were often advected south of the Columbia River. In contrast, at least in some simulations, the fastest fish exited the study area (hit the northern edge of the model domain) and were removed from the spatial analysis. Both of these situations suggest that swimming speed is indeed a sensitive parameter. A caveat to swimming speed results is that this application of the model was not designed to test swimming speeds per se and multiple swimming speeds could theoretically result in a similar spatial distribution. A comparison of results among years suggested the mean swimming speed varied in response to ocean currents, but I reserve statements on precise estimates of swimming speed (until Chapter 4, where I use information on individual fish movements).

3.4.5 Behaviors that did not work

Coastal currents are highly dynamic in space and time, and my simulations indicated that a simple response to currents (e.g., rheotaxis) would not guarantee northward movement. My analysis suggests that the consistent distributions of juvenile salmon along the coast of Washington in spring and summer can only be achieved if fish use northward-biased migration behaviors, at least as a component of their migratory behavior.

There seemed to be a limit to how much selective transport could aid in migration. In optimal flow (F2) simulations, fish adjusted their depth to maximize northward movement, and the resulting distributions matched the observed distribution of salmon for May but not for June. This is primarily because southward flow intensified during the spring and summer and eliminated the ability to passively move north at most depths. Simulations therefore tended to clump the fish that had moved north into a very small cluster off the coast of southern Washington in June, contrasting with the larger spread in observed distributions.

In simulations not included here, I evaluated a “selective transport” behavior involving larger vertical migrations, wherein fish were able to move further north by May and June. However, fish must make use of the entire water column to match June distributions (e.g., hold station at the bottom during southward moving phases and move to the surface during the northward phases). Because these ocean migrants primarily use the surface waters (Emmett et al. 2004), I ruled out “selective transport” as a sole migration strategy.

This study is limited by not combining behaviors and I therefore limit my conclusions to the feasibility of the tested behaviors as the sole drivers of migration. It is possible that vertical migration, for example, is a component of a more complex migration strategy, used for example in avoiding strong southward flows, or in combination with other behaviors, such as rheotaxis or actively swimming north. Similarly, it is likely that during migration fish seek, to some extent, to optimize local conditions for growth, such as thermoregulating via vertical migrations (Hinke et al. 2005). Studies conclusively show that yearling Chinook salmon are associated with particular environmental characteristics, which indicates some level of behavioral adjustment to local conditions (Bi et al. 2007, Peterson et al. 2010, Burke et al. 2013). However, given the limitations of my data and the added complexity of modeling the effects of multiple interacting behaviors, I limited my analysis to the effects of individual behaviors.

An additional limitation was the testing of only one swimming speed in simulations of positive rheotaxis. It is possible that these simulations might have matched the observed distributions more accurately using faster swimming speeds. However, the migration paths of fish using positive rheotaxis were quite circuitous, and often generating distributions with far greater spatial extent than was observed in the catch data.

Of particular importance is a lack of prey resources and predator abundances in my simulations. Unfortunately, spatially-explicit data on salmon prey and predator populations do not exist, representing one of the largest gaps in salmon marine ecology. Salmon diet data exist (Brodeur et al. 2007, Daly et al. 2009), but not at the temporal or spatial resolution required for this type of modeling. Still, these findings add to the continuing debate on the nature of navigation/orientation cues used by salmon (Quinn and Groot 1984, Quinn 1991, Quinn 2005, Byron and Burke In Press) and lend support to the hypothesis that salmon have and use both a compass and clock sense when migrating as post smolt in nearshore marine environments. Future efforts should explore the effect of more complex behaviors, perhaps with multiple components, on fish distribution and incorporate additional data as it becomes available.

The coupling of oceanographic and individual-based models is rapidly becoming an important and efficient way to explore potential behaviors by many species in environments where direct observation is not feasible (North et al. 2009, Kishi et al. 2011, Willis 2011, Byron and Burke In Press). While outside the scope of this work, I recognize a growing need to characterize the effects of modeling uncertainty in both hydrodynamic (Putman and He 2013) and individual-based models (Simons et al. 2013) and to understand the repercussions of various behavioral rules (Wilson et al. 2013). Nevertheless, I demonstrated the utility of the combined Eulerian-Lagrangian approach in finding support for certain migration behaviors (and sensory capabilities) and clear evidence against other behaviors.

As hydrodynamic models improve and collections of empirical data on animal distribution and physiology expand, application of these tools will contribute greatly to our understanding of migration ecology. Moreover, such tools are critical to evaluating the implications of behavioral adjustments to climate-driven changes in the ocean, such as responses to changes in predator or prey distributions and whether the sensory mechanisms animals have evolved will continue to function in an altered environment (Anderson et al. 2013). For

example, results from this model add to growing evidence that yearling Chinook salmon from the Columbia River exhibit directed northward migratory behavior and that local conditions and experiences have only a secondary influence on fish distribution. As the climate changes and ocean conditions are altered in a spatially-explicit manner, it is unclear whether migration strategies that evolved over centuries will remain successful. Due partially to the dearth of information regarding salmon ecology in the marine environment, management of salmon populations has focused primarily on the freshwater environment (Ford et al. 2010). Information gleaned from models such as the one described here can provide managers additional insight into how various management approaches might affect the entire life cycle of salmon.

3.5 Acknowledgements

This work has been published in *Aquatic Biology*, and I thank the coauthors for their hard work –Jim Anderson and António M. Baptista. Chinook salmon catch data were obtained during a survey funded by the Bonneville Power Administration. Many people assisted with the project organization and data collection, including but not limited to Ed Casillas, Bill Peterson, Ric Brodeur, Bob Emmett, Kym Jacobson, Cheryl Morgan, Jen Zamon, Brian Beckman, Laurie Weitkamp, David Teel, Don Van Doornik, David Kuligowski, Tom Wainwright, Joe Fisher, Susan Hinton, and Cindy Bucher. I also thank JoAnne Butzerin, Chris Harvey, Steve Smith, Mark Scheuerell, Beth Sanderson, Rich Zabel, and three anonymous reviewers for their constructive comments on earlier versions of this document.

3.6 Tables

Table 3.1. Simulated movement behaviors.

Simulated Behavior ID	Behavior	Description
PP	Passive particle	No active swimming, passively drift horizontally and vertically with ocean currents
OT	Optimize temperature	Migrate vertically each time step to the depth closest to 12° C; optimal temperature during the first summer at sea is probably between river temperatures (~ 15° C) and temperatures observed for subadults (8 - 12° C, Hinke et al. 2005); passive in the horizontal direction
F2	Optimize flow	Similar to selective tidal transport; migrate vertically each time step to depth of greatest northward flow within the top 20m; passive in the horizontal direction
PR	Positive rheotaxis	Swim at a constant rate each time step in the same horizontal direction as the ocean current; passive in the vertical direction
SX	Active northward biased migration	Actively swim northward along the coast; passive in the vertical direction. Separate simulations were run using swimming speeds of $X = 0.3, 0.5, \text{ or } 0.9 \text{ BL/s}$. Mean swimming direction was 8° west of north. An Ornstein-Uhlenbeck process was used to alter the swimming angle each time step to bring fish back towards the center of the migration route at 28.5 km-from-shore.

Table 3.2. Model parameters and variables.

Attribute	Value or Distribution	Source
Release date	$\sim N(\mu = \text{May } 15, \text{ SD} = 10 \text{ d})$	(Weitkamp et al. 2012)
Fish length	$\sim N(\mu = 155 \text{ mm}, \text{ SD} = 15 \text{ mm})$	(Weitkamp et al. 2012)
Energy content	$0.0000152 * \text{Length}^{2.9648}$	(Hewett and Johnson 1992)
Bioenergetics P-value	$\sim \text{LN}(\mu = \log(0.5), \text{ SD} = 0.5)$	
Initial location	Latitude = 46.248 Longitude = -124.076 Depth ~ uniform (0-10m)	

Table 3.3. Mean Latitude (degrees) and standard deviation in the north-south direction (km; in parentheses) of observed salmon and simulated fish. For observed data, I calculated mean and SD by weighting the station locations by CPUE.

	2003		2004		2008	
	May	June	May	June	May	June
Observed	46.5 (59.0)	47.3 (80.1)	46.4 (43.8)	47.0 (98.2)	46.4 (49.1)	47.5 (82.4)
Passive particle	45.2 (135)	44.8 (194)	45.6 (100)	44.7 (211)	45.5 (110)	44.2 (198)
Optimize temp	44.8 (122)	44.1 (139)	45.5 (94)	44.6 (112)	45.3 (91)	43.8 (123)
Optimize flow	45.6 (150)	45.0 (130)	46.5 (92)	47.3 (175)	46.3 (110)	46.0 (186)
Positive rheotaxis	45.3 (116)	44.8 (135)	46.0 (58)	45.6 (128)	45.7 (86)	45.2 (143)
Active northward migration (BL/s)						
0.3	45.4 (129)	45.5 (132)	46.3 (93)	46.8 (206)	45.9 (114)	45.4 (206)
0.5	45.6 (136)	45.7 (115)	46.7 (83)	47.3 (165)	46.2 (107)	46.3 (215)
0.9	46.0 (140)	45.7 (132)	47.2 (73)	48.0 (74)	47.0 (76)	47.7 (125)

3.7 Figures

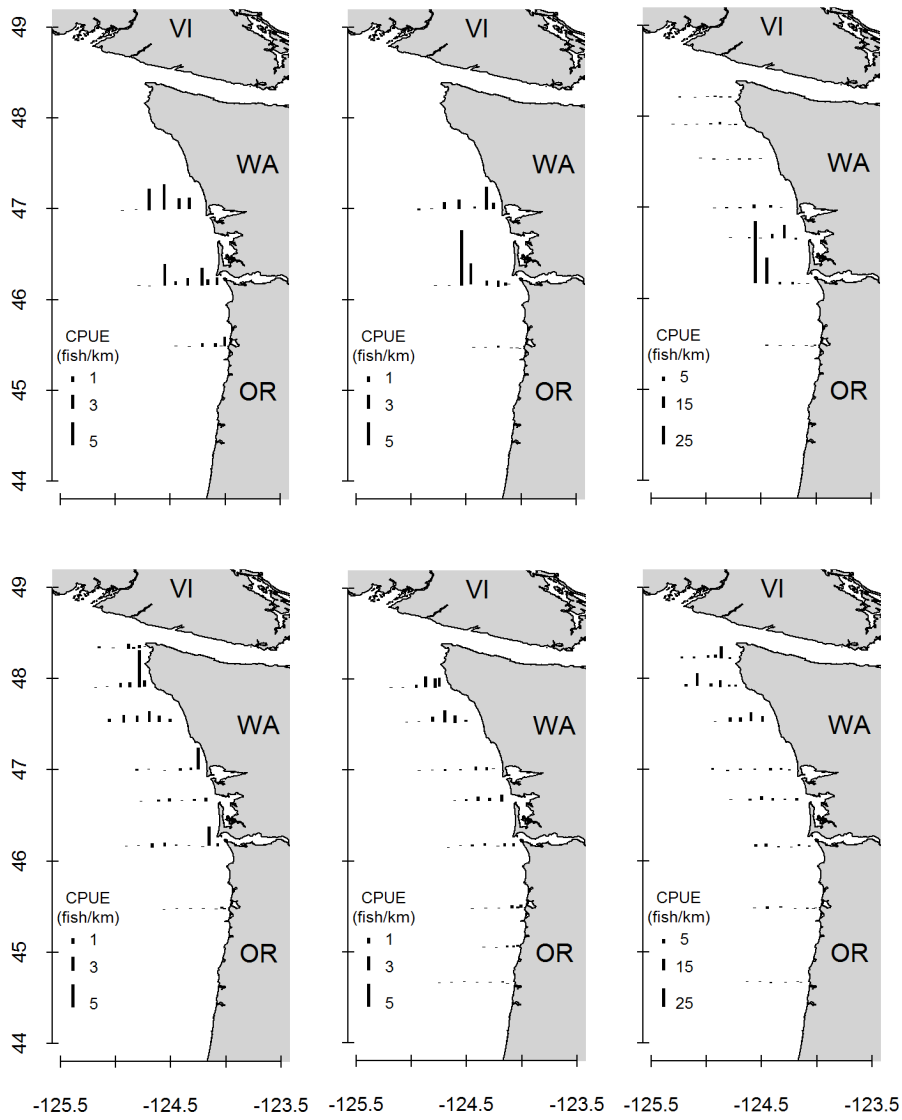


Figure 3.1. CPUE of yearling Chinook salmon in May (top) and June (bottom) of 2003 (left), 2004 (middle), and 2008 (right).

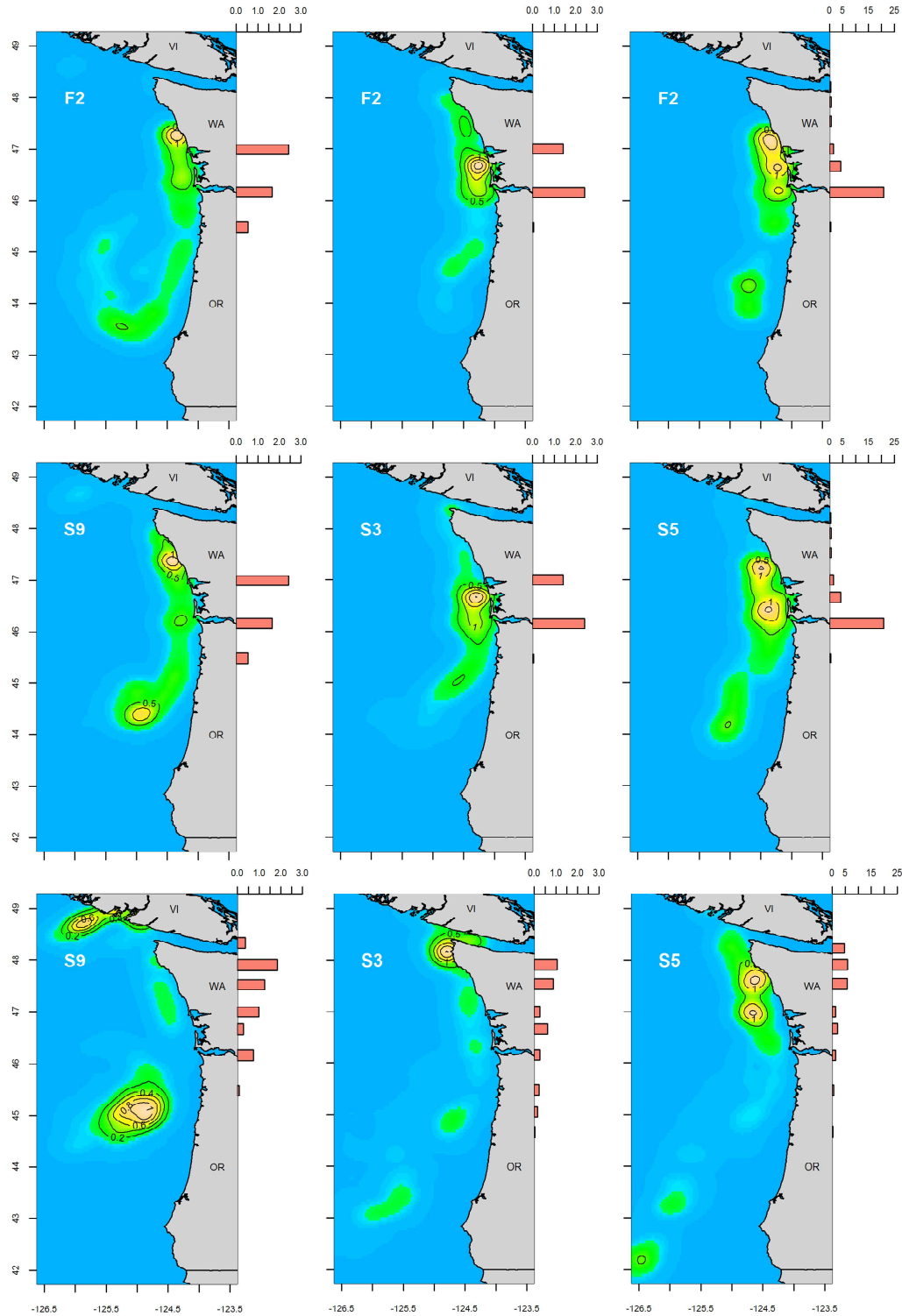


Figure 3.2. Density of simulated fish from the best models for May (top and middle) and June (bottom) for 2003 (left), 2004 (center), and 2008 (right). Bars represent the average CPUE for each transect from the trawl survey. Respective active northward migration rates were 0.9, 0.3, and 0.5 BL/s for 2003, 2004, and 2008.

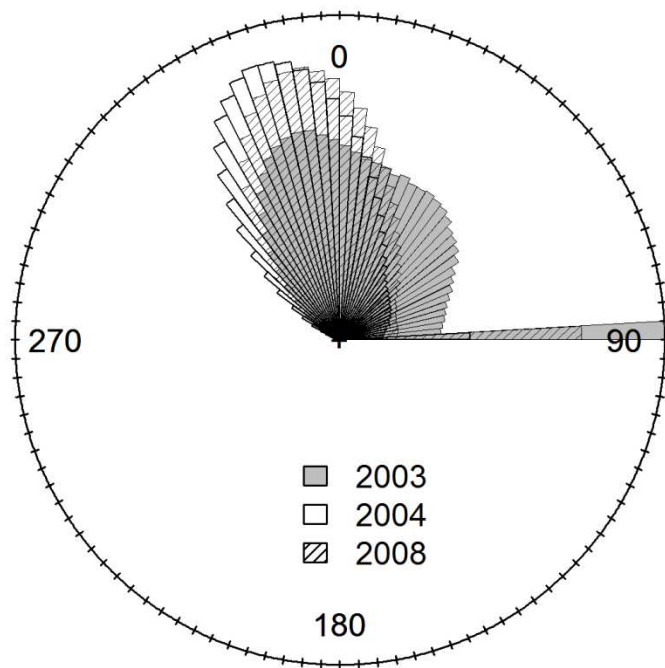


Figure 3.3. Frequency of turn angles by fish throughout the entire simulation. Results are from simulations using the active northward migration behavior and the best swimming speed for each year: 0.9 BL/s in 2003, 0.3 BL/s in 2004, and 0.5 BL/s in 2008. The large proportion of fish swimming at 90° is due to fish south of the Columbia River that were advected offshore and were trying to compensate.

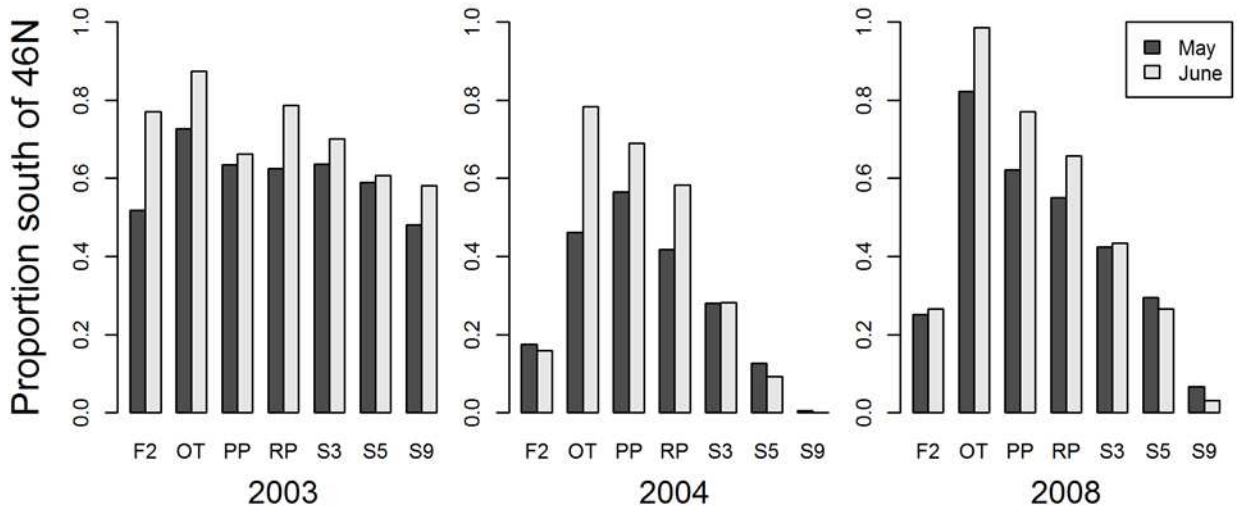


Figure 3.4. Proportion of simulated fish south of latitude 46 °N by behavior for 2003, 2004, and 2008.

3.8 Appendix A

Density of simulated fish in May and June of 2003, 2004, and 2008 for each behavior.

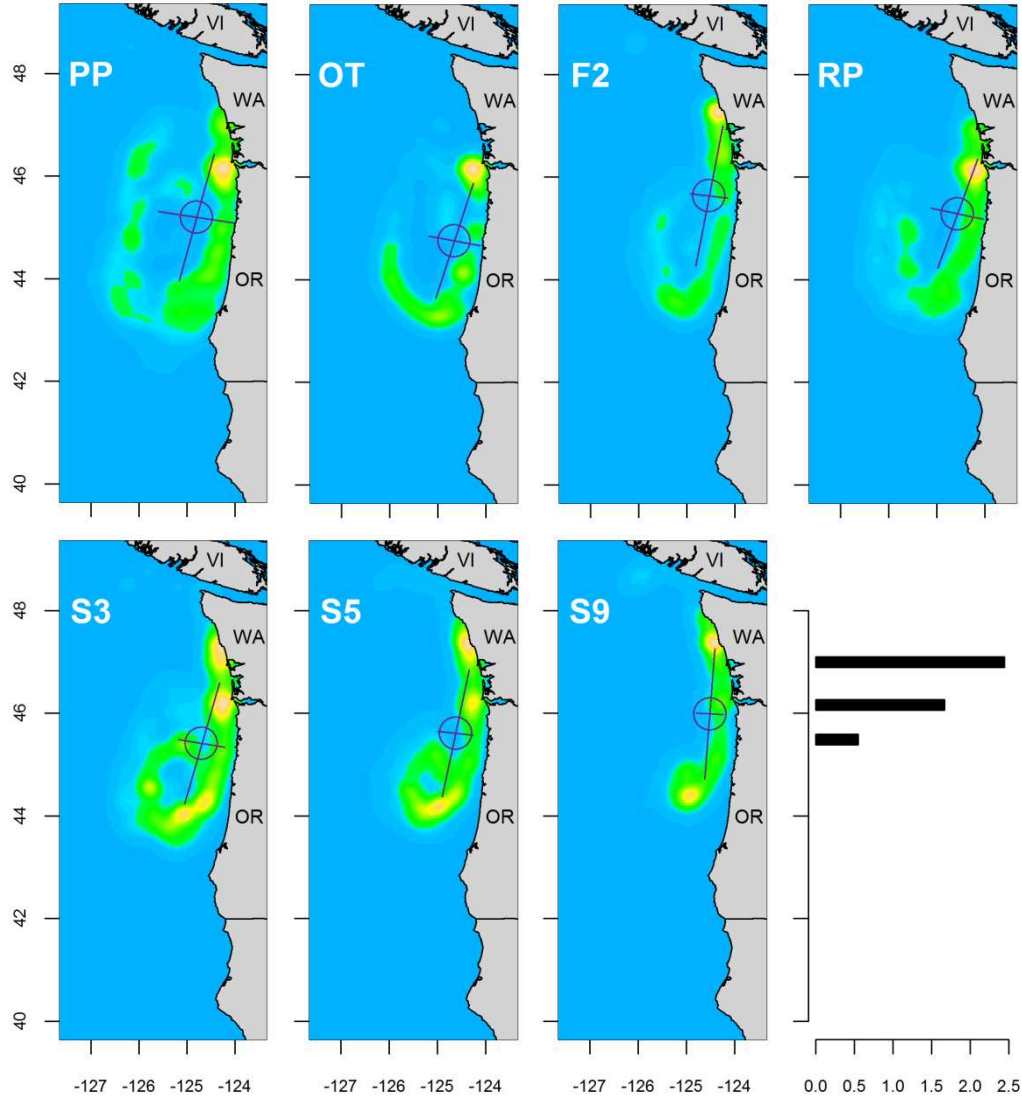


Figure 3.5. Density distribution of simulated fish in May 2003. Circles show the mean location of simulated fish and lines represent the variance in two directions. Black histogram shows the mean CPUE (fish / km trawled) for each transect from the trawl survey.

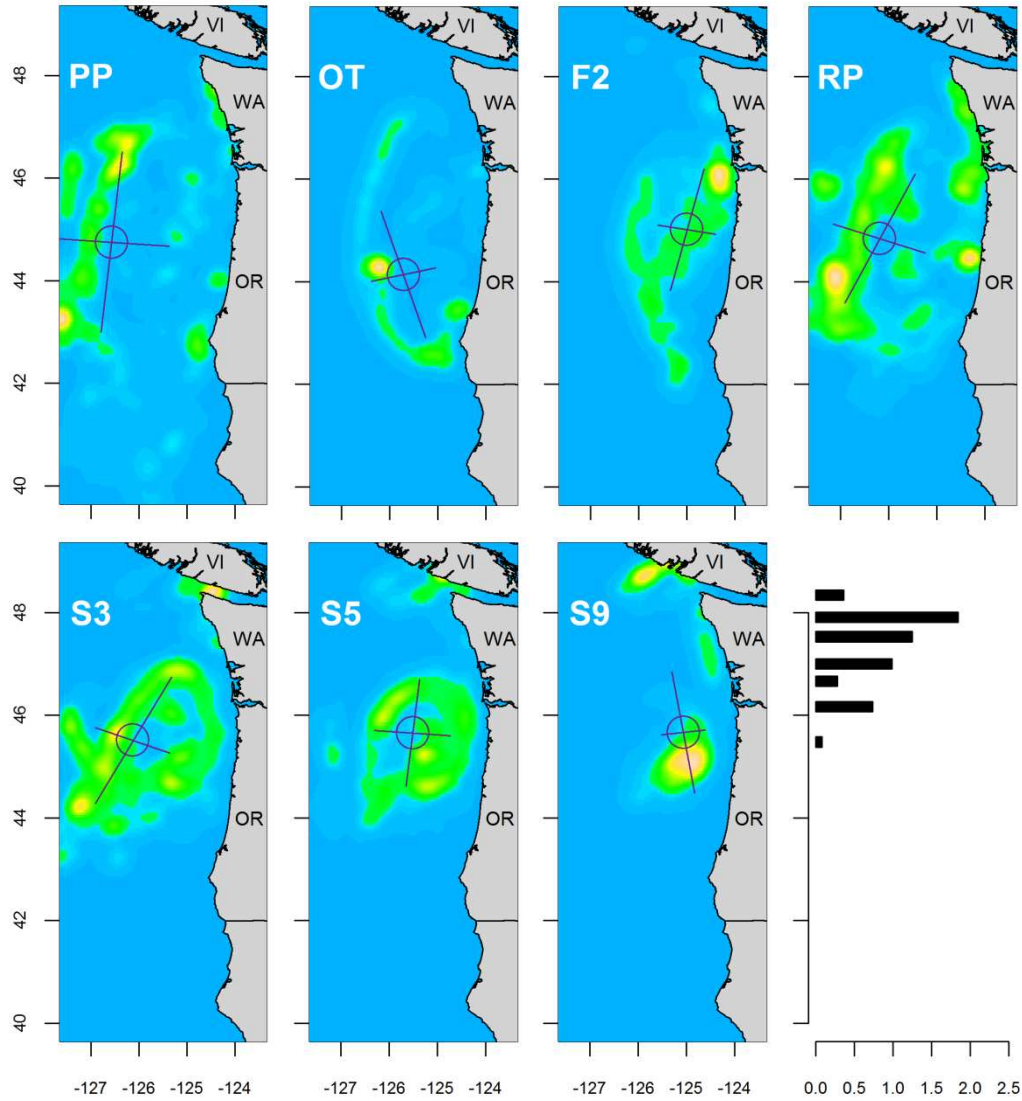


Figure 3.6. Density distribution of simulated fish in June 2003. Circles show the mean location of simulated fish and lines represent the variance in two directions. Black histogram shows the mean CPUE (fish / km trawled) for each transect from the trawl survey.

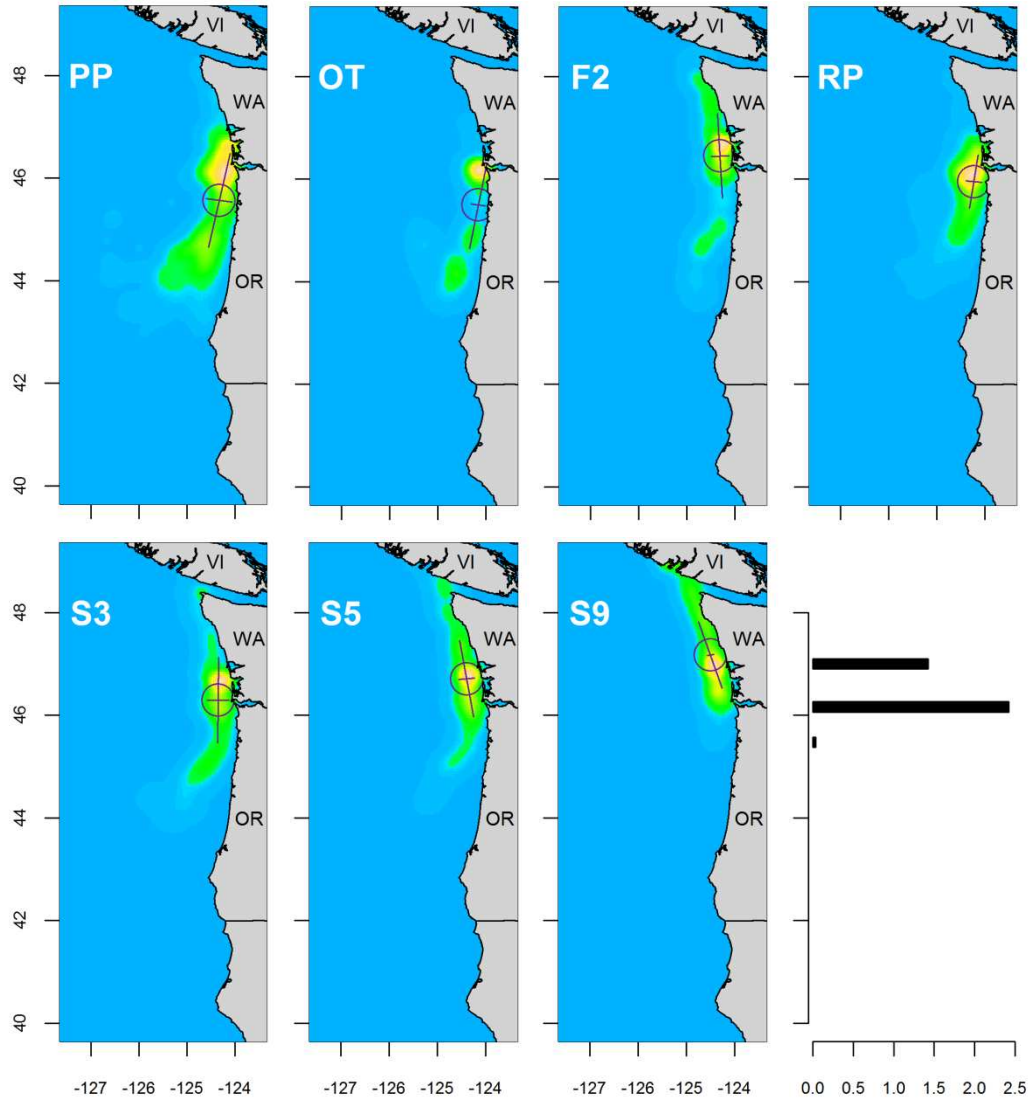


Figure 3.7. Density distribution of simulated fish in May 2004. Circles show the mean location of simulated fish and lines represent the variance in two directions. Black histogram shows the mean CPUE (fish / km trawled) for each transect from the trawl survey.

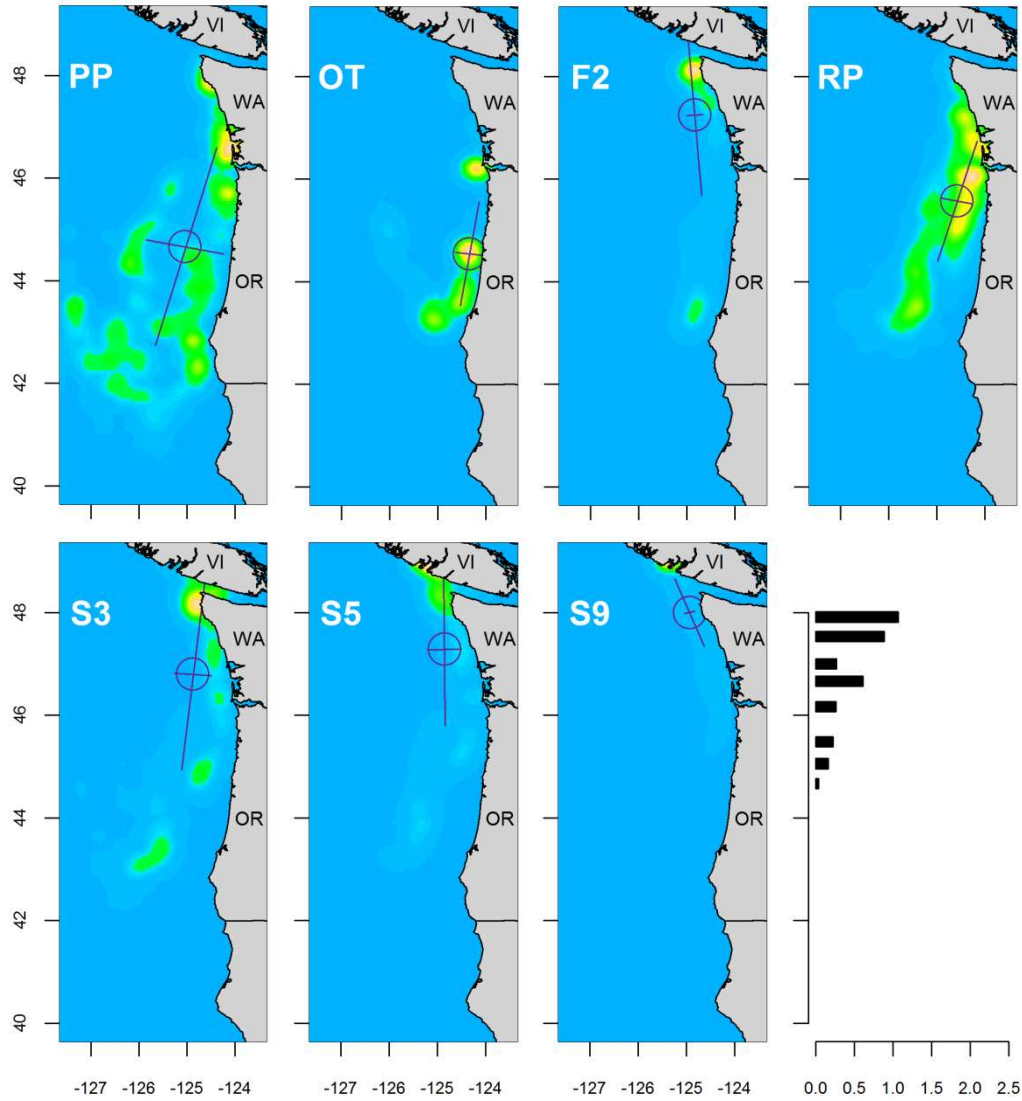


Figure 3.8. Density distribution of simulated fish in June 2004. Circles show the mean location of simulated fish and lines represent the variance in two directions. Black histogram shows the mean CPUE (fish / km trawled) for each transect from the trawl survey.

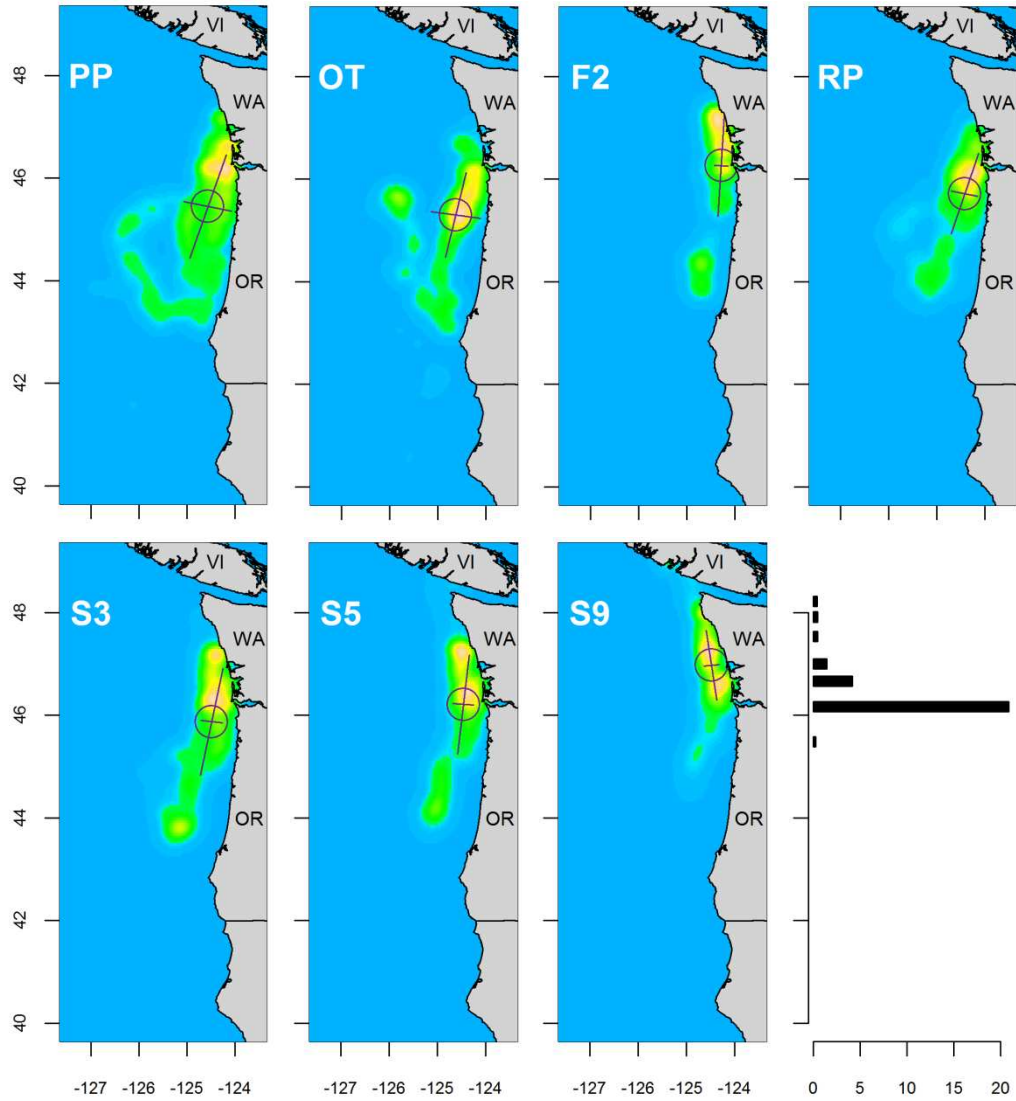


Figure 3.9. Density distribution of simulated fish in May 2008. Circles show the mean location of simulated fish and lines represent the variance in two directions. Black histogram shows the mean CPUE (fish / km trawled) for each transect from the trawl survey (note the different scales between 2008 and the other two years).

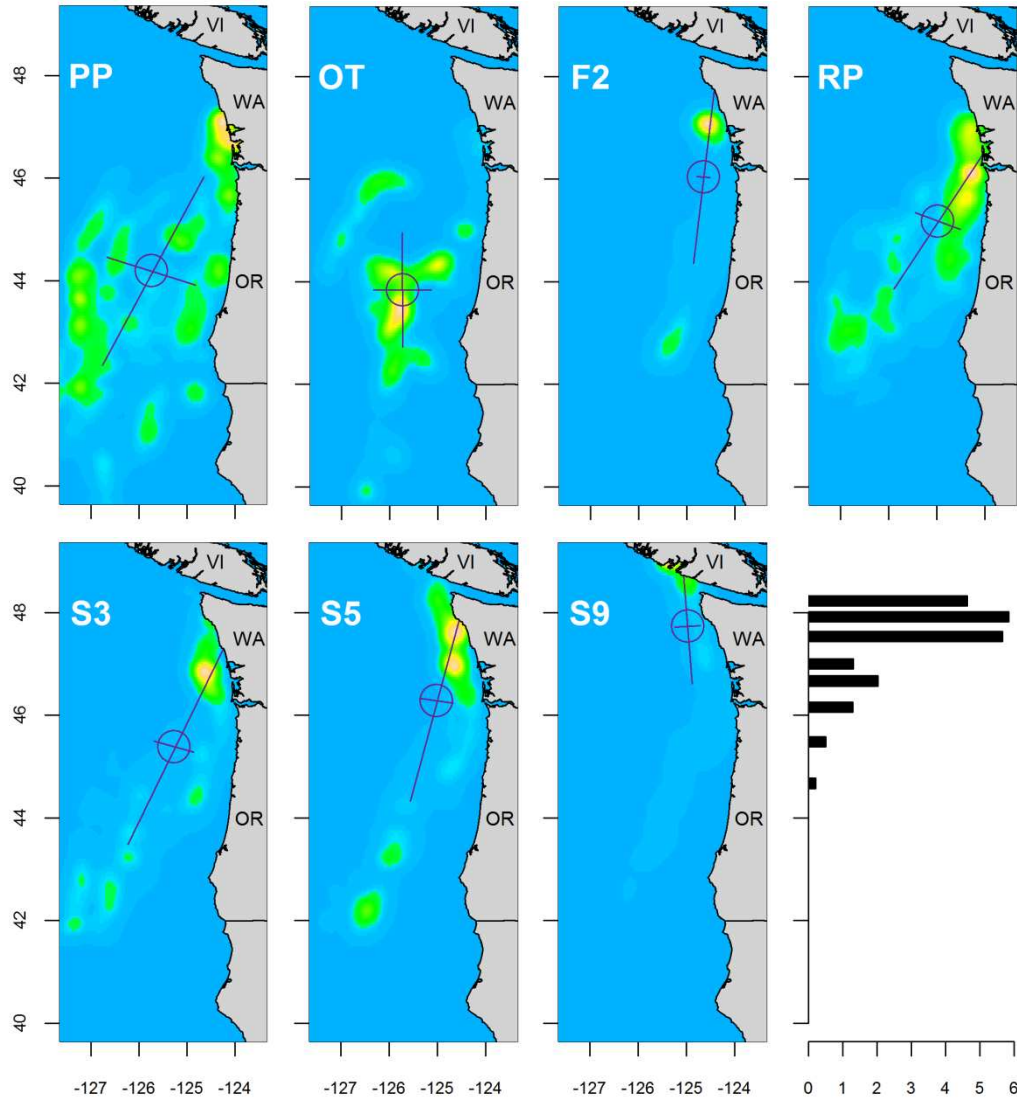


Figure 3.10. Density distribution of simulated fish in June 2008. Circles show the mean location of simulated fish and lines represent the variance in two directions. Black histogram shows the mean CPUE (fish / km trawled) for each transect from the trawl survey (note the different scales between 2008 and the other two years).

3.9 Appendix B

Sensitivity of initial values to final latitude.

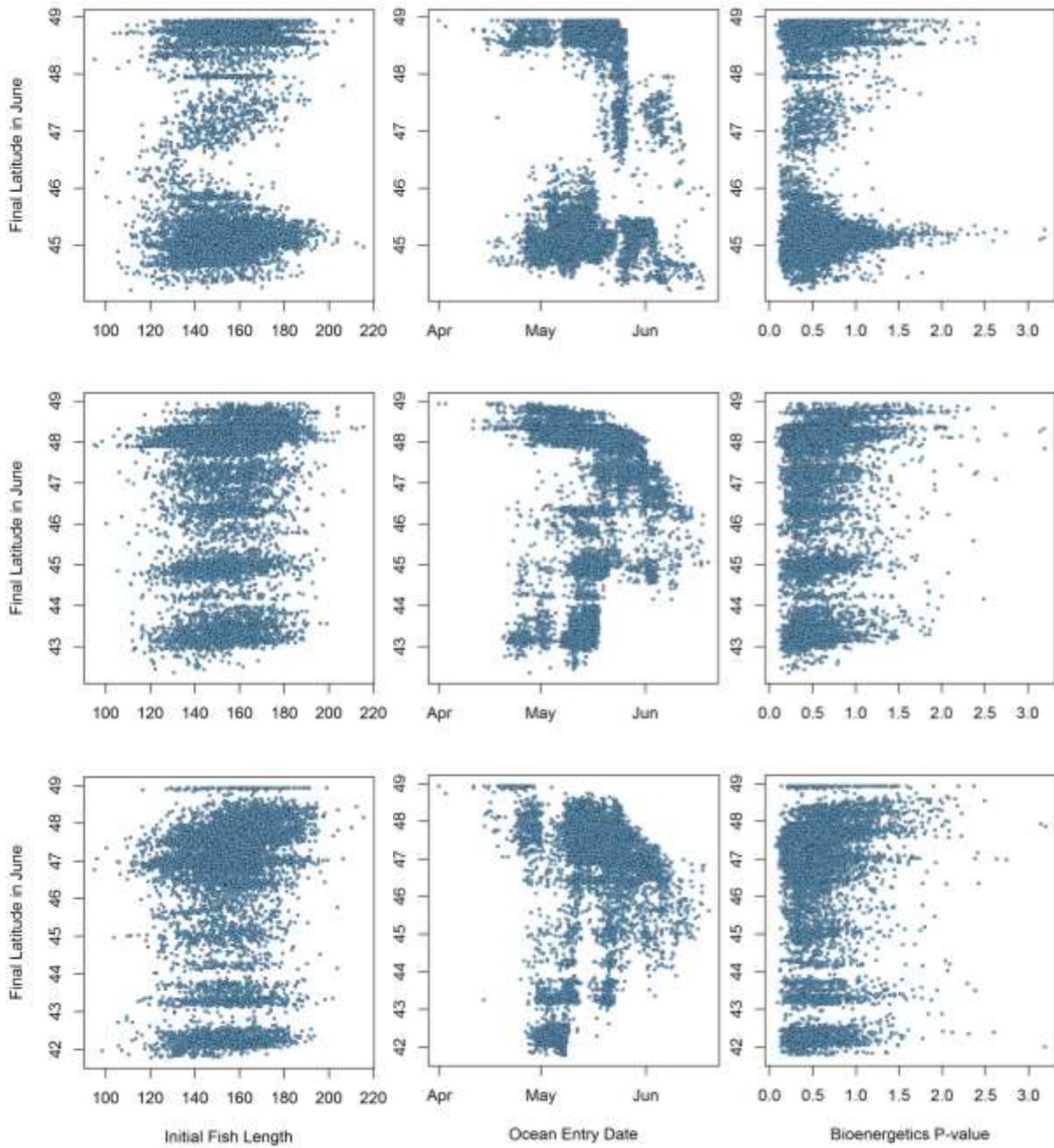


Figure 3.11. Relationship between initial length (left), ocean entry date (middle), or P-value for the bioenergetics model (right) and final latitude for each of 10,000 simulated fish in 2003 (top), 2004 (center), and 2008 (bottom). All data come from the best-fit simulations of active northward migration, where swimming speeds (BL/s) were 0.9 in 2003, 0.3 in 2004, and 0.5 in 2008.

Chapter 4 Influence of coastal currents on our understanding of fish behavior during marine migration

Abstract

High-resolution data of animal movement in the marine environment are scarce, typically resulting in analysts making simplifying assumptions regarding movement paths and behavior. Yet, the influence of ocean currents or temperatures experienced during migration can be substantial. I used a spatially-explicit individual based model of early marine migration of two stocks of yearling Chinook salmon to quantify the influence of external forces on estimates of swimming speed and consumption. Swimming speeds required in the model were higher than those estimated without taking into account ocean currents. Moreover, the estimated variance in swimming speeds was significantly lower than the variance in net movement rates, suggesting that ocean currents add a substantial amount of noise to movement data. Unfortunately, most marine movement data includes this masking effect of ocean currents, biasing estimates of swimming speed and restricting our understanding of movement ecology. Model results suggest that salmon behaviorally compensate for changes in the strength and direction of ocean currents. In a variety of model outputs there was a stock-specific result; for example, fish from the Snake River Basin swam faster than fish from the Mid and Upper Columbia River. How fast or far an animal swims can differ from how fast or far it moves, because the swim vector and ocean current vectors are additive. Results suggest that migrating Columbia River salmon have a total travel (track) distance that is twice as far as they swim (relative to the water) and three times as far as their net movement (straight-line distance). By taking into account experiences of individual fish, this approach incorporates both individual behavior and the influence of external physical factors such as ocean currents, allowing a more informed understanding of juvenile salmon behavior upon enter the marine phase of the their life cycle.

4.1 Introduction

Movement by marine organisms is often complex and highly dynamic. To understand the behaviors employed or stimuli used by migrating animals, these dynamics must be estimated with fairly high precision. Unlike marine mammals, which can be tracked with satellite tags, most fish movement is estimated as the net distance and speed between capture/recapture locations. Such information on net movements, although useful for characterizing spatial distributions, poorly resolves the ecological processes involved in fish moving between the two locations.

Similarly, it is currently not feasible to directly measure fish swimming speed over long distances in the ocean. Therefore, most estimates of marine migration are of net movement (e.g., Thorstad et al. 2007, Welch et al. 2009, Welch et al. 2011, Tomaro et al. 2012). Due to the difficulty of obtaining frequent (e.g. hourly or daily) estimates of fish location, migration speeds are therefore estimated assuming a straight-line movement trajectory. Although necessary, it is not clear how assumptions of straight-line movement affect our understanding of fish behavior.

There are several important ramifications from assumptions of movement (straight-line or otherwise). First, the abiotic conditions experienced by an animal during migration can have a large impact on growth and survival (Anderson et al. 2013). To estimate these impacts, one needs to know or estimate the fish's experiences with respect to the abiotic environment. For example, temperature can have a large influence on fish growth (Brett 1971, Beauchamp 2009) and swimming performance (Lee et al. 2003). Temperatures experienced by two hypothetical fish – one moving in a straight line and another moving in a more circuitous route - can be quite different. Moreover, the swimming speeds required for these two hypothetical fish to arrive at the same destination at the same time likely differ, which could in turn affect their energetic demand and ultimately their growth and survival. Finally, the suite of predators and prey encountered by these fish may be quite different, demonstrating the importance of knowing, at least in a gross sense, the tracks animals take during migration.

Much of the literature on animal movement refers to animal *tracks* as the observed path taken, and the *track vector* as the observed speed and direction of movement (Chapman et al. 2011). The track vector can be broken down into two components: the *swim vector* is the speed (in body lengths per second; BL/s) and direction that an animal swims relative to the water and

the *flow vector* is the speed and direction of the current (or wind) (Gaspar et al. 2006, Chapman et al. 2011) (Figure 4.1). I further define the *net vector* as the net speed and direction of an animal relative to the ground, essentially the straight line distance between two points. Therefore, the swim vector can be independent of ocean currents, while the track vector and net vector are both combinations of behavior and advective processes.

Here, I use an individual-based model of fish movement and behavior to estimate swimming speeds and consumption rates. I then compare these values to empirical estimates of net speed and growth to determine the influence of physical factors, such as ocean currents and temperature, on our understanding of fish behavior and ecology.

4.2 Methods

4.2.1 Yearling Chinook Salmon Data

Empirical data come from an ongoing study of juvenile salmon distributions off the Washington and Oregon coasts. Six or seven stations along transects extending outward from the coast were sampled from May 20th through May 29th and June 22nd through July 3rd of 2003, 2004, and 2008. At each station, a Nordic 264 pelagic rope trawl (30 m wide x 20 m high x 200 m long) with a cod-end liner of 9.5 mm stretch mesh was towed at a speed of 6 km·h⁻¹ for approximately 30 min. (see Brodeur et al. 2005 for complete details).

I selected three years (2003, 2004, and 2008) to include in this modeling study for multiple reasons. First, hydrodynamic model output was limited for many of the years for which we had fish data. Two years (2003 and 2004) were complete and I had been using them to build the model, so I included those two years. When deciding which other year(s) to include, many of the otoliths (see below) had not yet been analyzed. Due to the large catches of salmon in 2008, we had more fish and otolith data for that year than any other, so that year was also included. I chose to limit the study to three years primarily because of the hard drive space required to store the hydrodynamic model output and the computing time required to run the simulations.

4.2.1.1 Genetic Stock Differences

Stock origin of each fish was identified by David Teel (NOAA Fisheries) using population data from a standardized microsatellite DNA database (Seeb et al. 2007) and the genetic stock identification program ONCOR (Kalinowski et al. 2007). Using this genetic

information, as well as life-history and geographic information (Waples et al. 2004, Matala et al. 2011), fish were categorized into three evolutionarily significant units (ESUs): Mid-Columbia River spring Chinook salmon, Upper Columbia River spring Chinook salmon, and Snake River spring-summer Chinook salmon. Due to similarities between the Mid and Upper Columbia River stocks, I combined these two ESUs in a single group (referred to as Mid & Upper Columbia River spring Chinook salmon) for analyses.

4.2.1.2 Otolith Analysis

A subsample of the juveniles was selected for otolith structural and chemical analyses (by Jessica Miller, Oregon State University) to determine size at and timing of freshwater outmigration as well as marine migration rate and growth. Sagittal otoliths were removed, cleaned, and polished using wet-or-dry paper (240-2500 grit) and lapping film (1- 30 μm) using standard procedures for elemental analysis (Miller 2009). Otolith Sr and Ca were measured along the dorsal-ventral growth axis using laser ablation-inductively coupled plasma mass spectrometry. The laser was set at a pulse rate of 7 Hz and translated across the sample at 5 $\mu\text{m s}^{-1}$ with a spot size of 30 or 50 μm . Normalized ion ratios were converted to molar ratios using standard procedures (Kent and Ungererz 2006, Miller 2009). Instrument precision (mean percent relative standard deviation) was <5% for Ca and Sr across all samples and days ($n = 65$) and accuracy for Sr:Ca was 4% ($n= 10$) based on USGS MACS-1.

Image analysis was combined with Sr:Ca data to determine otolith size at freshwater outmigration and to estimate the date of marine entry (Neilson and Geen 1982). For each individual, the otolith width at the time of marine entry (OW_M) was determined by the initial and abrupt increase in otolith Sr:Ca ratio, which indicates exit from freshwater, prior to stabilizing at marine values (Miller et al. 2010a, Miller et al. 2011). The number of increments deposited after the initial and abrupt increase in otolith Sr:Ca was used to determine residence in brackish/ocean waters. To determine date of marine entry (day of year), the duration of marine residence was subtracted from the date of capture. Here, I assumed date of marine entry was only negligibly different from date of entry into brackish/ocean water, as yearling Chinook have been shown to migrate about 60 km/d through the estuary (McMichael et al. 2013). Marine migration distance was conservatively estimated as the linear distance between the mouth of the Columbia River (N 46.253, W 124.059) and the capture station plus 32.1 km to account for travel through the

estuary. I divided the migration distance (km) by the marine residence time (d) to calculate the mean migration rate (km d^{-1}) for each fish, which was converted to body lengths per second (BL s^{-1}) based on estimated size at marine entry.

Juvenile length at marine entry was estimated using a direct back-calculation model based on yearling sp/su Chinook salmon from the interior Columbia River basin that were collected from 1999-2008 ($r^2 = 0.82$, $n = 362$, $p < 0.001$; Eq. 1 in Tomaro et al. 2012).

$$\ln(\text{FL}_M) = 1.126 (\pm 0.028 \text{ SE}) \cdot \ln(\text{OW}_M) - 3.69 (\pm 0.21 \text{ SE}) \quad (1)$$

where FL_M = fork length (mm) at marine entry, and OW_M = otolith width (μm) at marine entry. Marine growth rates ($\% \text{ d}^{-1}$, mm) were determined by subtracting estimated size at marine entry from size at capture, dividing by size at marine entry, and multiplying by 100.

4.2.1.3 Oceanographic Data

Understanding the ocean migration routes of Columbia River salmon requires quantitative knowledge of the circulation encountered by the fish as they enter the marine environment. I described ocean circulation near the Columbia River and the coastal ocean from March 1st through September 30th of each year using the Virtual Columbia River modeling system (CMOP 2013). This system provides a high-resolution, spatially explicit description of 3-D river-to-ocean circulation and water properties in the Columbia River and plume (Baptista et al. 2008, Burla et al. 2010b). In this study, I used the same archived simulations as Burke et al. (2014) – further details regarding the oceanographic model can be found in that paper or in Chapter 3.

4.2.2 Migration Model

I quantified the complex interaction between fish and the environment using a combined Eulerian-Lagrangian approach (detailed in Burke et al. 2014; Chapter 3). For each fish with otolith data ($N = 125$), I modeled 10,000 simulated fish, which individually differed in swimming speed, consumption rate, and initial migration timing.

Following behavior SX from Chapter 3 and Burke et al. (2014), all fish swam at a constant speed in a generally northward direction along the coastline. An Ornstein-Uhlenbeck process modulated the swimming angle, such that the farther a fish was from a central line (28.5

km from the coast, based on empirical data), the more its angle changed towards that line, allowing most fish to stay within the boundaries of the empirical data.

Each simulated fish swam at a fixed swimming speed randomly assigned from a lognormal distribution ($\mu = \log(0.5)$, $SD = 0.5$), which they maintained for the duration of the simulation. The parameters of the distribution spanned the range of potential swimming speeds, from near 0 to over 2 BL/s (Brown et al. 2006), which ensured that at least some of the simulated fish reached the capture location and time of the real fish.

The location of the salt wedge in the Columbia River estuary varies considerably over a tidal cycle and is affected by river flow, resulting in imprecise knowledge of the exact location of freshwater exit. Randomly assigning fish an initial location in the estuary resulted in some fish getting 'stuck' at the edge of the model domain (this only occurred in the estuary environment, where boundaries and flows were complex). Therefore, rather than initiating migration at different locations, I jittered the timing of initiation, drawing from a normal distribution of time with mean centered at noon on the estimated freshwater exit day of year and a standard deviation of 10 hours (chosen somewhat arbitrarily to allow a day or two deviation in either direction for the timing of freshwater exit).

Fish growth during migration was simulated with a bioenergetics model (Hanson et al. 1997) parameterized for Chinook salmon (Hewett and Johnson 1992). Growth during each time step was based on the fish's temperature, size, and consumption index (PC_{max} , or a proportion of maximum consumption given their body size and ambient temperature (Hanson et al. 1997); $\mu = \log(0.5)$, $SD = 0.5$). The distribution of PC_{max} provided a broad range of consumption values (in many cases, greater than theoretical maximum consumption), such that some simulated fish matched the final size of each of the real fish. To maintain a widening gap between the largest and smallest fish throughout the simulation, PC_{max} for each fish was fixed over the simulation. If the consumption indices were time varying, variance in growth among fish would have declined over the course of the simulation, as the large number of random draws for the value of PC_{max} would have resulted in convergence.

In this application, the goal was not to estimate consumption per se, but rather to simulate fish growth at realistic rates to ensure that swimming speeds (in BL/s) resulted in appropriate

movement. This required two simplifying assumptions: 1) the prey caloric density remained constant (1000 cal/g) and 2) half of consumed biomass consisted of invertebrates and half was fish (Daly et al. 2009), which influenced the proportion of consumption that was digestible. While bioenergetic models' rate parameters and output are generally expressed in a daily step, all rate constants (e.g., consumption) were scaled to the 15-minute time step of the simulation.

4.2.3 Analyses of Model Results

The simulated mean speed and consumption rate corresponding to each of the 125 real fish were calculated from the weighted average of the respective 10,000 simulations. Simulated swimming speeds and consumption rates were assigned to fish independently, so some simulated fish may have matched the final size of the real fish, but ended up in a distant location while others ended up in the right place, but grew at much faster or slower rates than the real fish. To ensure that the highest-weighted fish were ones that did well with both metrics, weights were calculated combining the two values according to the formula:

$$W = \frac{1}{(L^2 + S^2)},$$

where L is the error in final location (Euclidian distance between capture location and final simulated fish location) and S is the error in final size (total length). Both error measurements were scaled to one standard deviation of the mean prior to calculating the weight. Resulting weights for each fish (within a simulation) were then used to calculate a weighted mean for all variables of interest (e.g., weighted mean swimming speed, weighted mean track distance, etc.).

I used linear models with categorical covariates (month, year, and stock) to characterize swimming speeds. I compared swimming speeds to net speeds using linear models (here, I used the difference between the two speed estimates for each fish as the response variable) to determine the magnitude of the error between what I observed (net speed) and the behavior of migrating salmon (swimming speed). Similarly, I wanted to characterize errors in estimates of distances moved, both actively and passively, so I compared swimming distance to both track distance and net distance. In each model, I specifically tested whether the differences in swimming speed or distance varied by month, year, or stock group. I used the Akaike Information Criterion (AIC) for model comparison and use the Akaike weights to perform model averaging (Burnham and Anderson 2010).

4.3 Results

I used genetic and otolith information for 125 fish; 60 from the Mid & Upper Columbia River spring Chinook salmon ESUs and 65 from the Snake River spring-summer Chinook salmon ESU (Table 4.1; Figure 4.2). There was a fairly even number of fish across years and months, though I had no fish from the Mid & Upper Columbia River ESUs in May of 2003 or June of 2008.

4.3.1 Speed, Direction, and Distance

4.3.1.1 Mean Swimming Speed

The vast majority of simulated fish had low weights, either because they ended up too far from their respective real fish's capture location or their simulated growth did not match the empirical data. Therefore, for each of the 125 fish, the weighted mean swimming speed of the 10,000 simulated fish (hereafter referred to as simply swimming speed) and weighted mean consumption rate were primarily determined by a small proportion of the 10,000 simulated fish.

Results suggest that fish behaviorally compensate for increased southward flows by increasing swimming speed. The mean swimming speeds required to get simulated fish to their respective capture location at the correct time varied significantly by year (Table 4.2), with the highest mean swimming speeds in 2003 ($\bar{x} = 0.65$ BL/s), followed by 2008 ($\bar{x} = 0.57$ BL/s) and 2004 ($\bar{x} = 0.50$ BL/s) (Figure 4.3). These swimming speeds directly reflect the North-South component of ocean currents experienced by simulated fish, with the strongest southerly flows occurring in 2003 (Figure 4.4).

Mean swimming speed also varied significantly by month and stock (Table 4.3, Table 4.4). Swimming speeds tended to increase through time (Figure 4.5) and were therefore higher for fish caught in June than for those caught in May (Figure 4.6). As I did not test any behaviors where fish altered their swimming speed during a migration, I cannot determine if the month-specific response is because all fish increased their swimming speed with time or if there was some other difference between the fish caught in May versus those caught in June. Swimming speeds were higher for Snake River fish than for Mid & Upper Columbia River fish in both May and June (Figure 4.6).

Weighted mean swimming speeds were higher than net speeds for fish caught in May, but not for those caught in June (Figure 4.7, Table 4.2, Table 4.5) and these differences were consistent across years. Interestingly, the magnitude of the difference varied by stock, with a difference in May-caught fish of 0.23 BL/s for Mid & Upper Columbia River spring Chinook salmon and 0.12 BL/s for Snake River spring-summer Chinook salmon (Table 4.5; Figure 4.7).

4.3.1.2 Variance

Model results imply more consistency in swimming speed during marine migration than suggested by other methods. For example, the estimated variance in swimming speeds was significantly lower than the variance in net speeds (F test, $p < 0.001$; Figure 4.3). This was true for most combinations of year, month, and stock (Table 4.6). For comparisons with adequate sample sizes, the variance in net speeds was about 1.9 to 9 times higher than for swimming speeds.

4.3.1.3 Swimming Angle

Mean weighted swimming angles were fairly consistent among years and stocks, with fish averaging a northwest swimming angle (Figure 4.8). However, for fish caught in June of 2003, the mean swimming angle was more northerly and many fish averaged a northeast swimming angle (Figure 4.8). The likely cause of this change was the east-west component of simulated ocean currents, which showed anomalously strong westward currents (Figure 4.4). Although these ocean current data were simulated, they are supported by two data sources: 1) wind speed and direction as measured by a buoy off of the Washington coast (http://www.ndbc.noaa.gov/station_page.php?station=46041) showed slightly stronger winds and a slight shift north in wind direction in June 2003 and 2) an index of upwelling (http://www.pfeg.noaa.gov/products/pfel/modeled/indices/upwelling/NA/data_download.html) showed an increase in the strength of upwelling from May to June 2003, resulting in the strongest upwelling during any of the months I simulated. This strong upwelling resulted from the westward movement of surface water (Bakun 1973), which corroborates the increased westward component of the simulated current data.

4.3.1.4 Distance traveled

Most fish swam a shorter distance (relative to the water) than they moved (track distance, relative to the ground; Figure 4.9). On average, simulated fish swam 208.2 km to get to the

capture location, yet they had a track distance of over 341 km, resulting in distance traveled being 1.64 times longer than fish swam. However, this extra distance was not all towards the capture location (see plots in Supplemental Material). The net distance averaged just over 119 km. Therefore, fish swam 1.74 times farther than their net distance would suggest, but the circuitous course taken resulted in a much greater travel distance than their swimming distance (Figure 4.9).

The track distance was significantly longer than swimming distance ($p < 0.001$), particularly in June. The largest difference between the two distances was in June of 2003, whereas the smallest was June of 2008 (Figure 4.10). The difference between track distance and net distance had a similar difference, with the exception that there was a stock-specific response with Snake River spring-summer Chinook salmon having a smaller difference in distances (i.e., closer to a straight line trajectory) than Mid & Upper Columbia River spring Chinook salmon.

4.3.2 Consumption and growth rates

I found significant interannual variability in consumption rates, with rates in 2003 and 2008 averaging about 21% higher than rates in 2004 (Figure 4.12). There was no difference in consumption between the two stocks except for in 2008, when Snake River fish consumed more than Mid & Upper Columbia River fish ($p < 0.001$; Figure 4.12). Although the mean consumption for fish caught in May was about 12% lower than consumption for those caught in June, month of capture was only marginally informative to the model (Table 4.4), indicating that (after the effects of year and stock had been taken into account) there was little difference in consumption between fish caught in May and those caught in June.

4.4 Discussion

4.4.1 Swimming speed and net speed

The analysis clearly shows that interannual variation in coastal currents (e.g., Burla et al. 2010b) not only influences the mean location of yearling Chinook salmon (Yu et al. 2012), but results in altered migration behavior. If salmon have the ability to know where they are in space (i.e., a map sense; Putman et al. 2013, Burke et al. 2014, Putman et al. 2014), these results suggest that fish respond to that knowledge by altering their swimming speed to mediate the southward component of coastal currents. In years with strong southerly flows, fish may behaviorally compensate by increasing northward swimming speed. Similarly, as evidenced by

the change in swimming angle for fish caught in June of 2003, when winds shift surface currents farther west, fish seem to respond by altering their swimming angle eastward. This dynamic behavioral response to ambient conditions is required for fish to maintain the relatively consistent spatial distribution observed among years (Peterson et al. 2010, Weitkamp 2010).

Unlike most shallow freshwater environments, where fish have a visual reference for movement relative to the ground, fish in the ocean (particularly surface oriented fish) must reference their movement relative to some other aspect of their environment (Lohmann et al. 2008, Putman et al. 2014). For salmon and other marine-migrating species, movement must be referenced to stimuli such as temperature, food resources, or the Earth's magnetic field. Therefore, when alongshore currents intensify or winds shift and alter the surface current trajectory, salmon must either detect these changes directly or sense the changes in their position relative to external cues (Chapman et al. 2011). Recent evidence from tagging studies imply the latter, where fish are temporarily advected by strong currents and adjust behavior as a response (McMichael et al. 2013). Although this modeling exercise cannot distinguish among particular sensory capabilities, it does suggest that fish respond to shifts in the environment with dynamic behavior, and that these behavioral adjustments can be stock-specific.

There also seems to be a time-dependent aspect to behavior, with swimming speeds increasing throughout the spring and summer. This result corroborates findings by Tomaro et al. (2012) and (Miller et al. In Prep.). However, it is not clear whether individual fish increase swimming speed through time or if fish that out-migrate later have higher (but constant) swimming speeds. In general, prey organisms in northern latitudes have higher fat reserves than taxa in more tropical systems (Lee and Hirota 1973, Armstrong et al. 1994). The longer a fish resides in Washington's coastal environment, the more motivation it may have to actively migrate north. This could result in fish with a later out-migration date swimming faster on average than those out-migrating early and/or individual fish increasing swimming speed through time.

There are several aspects of behavior I intentionally left out for simplicity. As noted above, I did not include a dynamic swimming speed, which appears to be likely. Second, I simulated fish swimming 24 hours per day at their predetermined speed. If there is a diel pattern to swimming behavior and more active swimming occurs during the day, the mean swimming

speed estimated here may be slower than actual daytime swimming speeds. Moreover, due to the complex influence of currents on movement, the effects of diel migration behavior on migration route and timing cannot be estimated without explicitly modeling that behavior. Similarly, salmon may switch between multiple behavioral modes, such as migrating and feeding. Unfortunately, these cannot be teased apart without more precise location and movement data. Ideally, one could combine prey information with this type of individual-based model to explicitly ask how migration behavior is driven by optimal foraging theory (e.g., maximizing growth potential each time step). However, the lack of spatially and temporally explicit prey data precludes this type of analysis.

Most estimates of marine migration rate come from point location data (e.g., Thorstad et al. 2007, Welch et al. 2011). Although informative for understanding migration behavior, these estimates are relative to the ground and tell us little about the energetic and physiological aspects of fish movement. Results from this modeling exercise suggest that yearling Chinook salmon swim much farther relative to the water than indicated by their net movement relative to the ground, further confirming results from Chapter 3 and Burke et al. (2014) that these fish do not migrate passively. This is particularly relevant to any study looking at the energetics of movement or migration, as swimming speed is a major component of the energetic budget of fish (Brett 1995, Brown et al. 2006). Therefore, assuming straight-line movement or failing to account for the influence of ocean currents on movement can dramatically affect estimates of behavior and growth.

The question of whether fish are predetermined to migrate to a certain place by a certain time is also informed by the variability in behavior among individuals. Data on movement are usually a combination of the movement process and noise (which can be the result of some random process or observational noise). If the magnitude of the observational noise is large enough (say, because our movement data did not incorporate ocean currents), then the underlying process is obscured, preventing us from accurately determining migration behavior. Judging by net travel speeds, which historically has been the only data available, variance among individuals may be orders of magnitude higher than variance in swimming speeds. This suggests that yearling Chinook salmon from a given ESU may have a characteristic swimming speed, perhaps determined over evolutionary time scales, that guides their migration. My results

suggest that the effect of ocean currents has been one of masking fish behavior, and that yearling Chinook salmon may have much more consistent behavior than estimated with other methods (e.g., Welch et al. 2011).

Similarly, estimates of migration route can be obscured. The estimated total distance traveled was twice as far as the distance fish swam and three times as far as their net movement. To understand migration, one must estimate the environmental experiences of individual organisms. By failing to account for the difference between track movement and net movement, we are inherently adding noise to our understanding of the environments that fish experience (Gaspar et al. 2006).

4.4.2 Consumption and growth rates

In 2004, I estimated that fish not only swam the slowest, but also consumed the least. This was somewhat contrary to our expectations, since optimal foraging theory states that one reason to slow swimming speed during migration is an abundant food supply (or higher quality food, which we could not test for lack of data). An alternative explanation for this result is that in 2004, fish experienced less southward transport of northern cold water. Under this scenario, fish would have to swim less to achieve northward movement and would not have access to the higher quality food that often accompanies northern waters (Keister et al. 2011). Or maybe they swam less *because* they ate less and therefore had less energy.

For simplicity, I used a constant energetic density for prey organisms in all simulations. In reality, I know the quality of food resources shifts annually (Brodeur et al. 2007) and seasonally (Daly et al. 2009). I fully recognize the possibility that differences in estimated consumption were due to differences in the relative abundance of high quality food in the diet among years and months. Prey quality is particularly influential in bioenergetics models (Beauchamp et al. 1989) and could have large impacts on results. Therefore, results from the bioenergetics modeling should be taken with caution.

The bioenergetics component of this model did not provide results entirely different than estimated growth rates derived directly from the otoliths. This could either be due to the relative insensitivity of growth to temperature in the range experienced during the simulations (Beauchamp 2009) or it could indicate that the temperatures experienced were not highly

variable. However, I stress the importance of the bioenergetics submodel in this type of individual-based model. Many aspects of behavior are size-dependent and having fish grow at realistic rates throughout a simulation can dramatically influence movement rates and, therefore, how we characterize behavior. I did not run simulations using a constant growth rate (rather than a bioenergetics model), but such simulations could estimate the effect of assumptions regarding growth – for another day perhaps.

This effort is intended to provide a first estimate of some biological variables. However, results are dependent on accuracy of both the hydrodynamic model and the otolith analysis that were used as inputs to the model. Errors in either of these components can propagate through the model and bias results. Ideally, similar models could be run using an alternative hydrodynamic model; initial efforts using a Regional Ocean Modeling System (ROMS) model resulted in qualitatively similar conclusions. However, at the time of testing that model, not enough ROMS output was available to make quantitative comparisons. As accuracy in hydrodynamic models increases, efforts such as the one described here can provide more confidence in estimates of swimming speed and migration routes.

4.4.3 Conclusions

Individual-based models have significantly contributed to our understanding of ecology (DeAngelis and Gross 1992, Grimm and Railsback 2005). In many individual-based models, emergent properties of populations (as more than a group of individuals) have provided useful information. In others, such as this effort, the usefulness stems from the inability to otherwise account for the complex and highly dynamic environment experienced by individuals. I have clearly shown how ocean currents can mask our understanding of salmon migration behavior. By accounting for this external factor, one can better estimate swimming speeds, movement paths, and the stock-specific dynamics of movement. Moreover, the low variance in swimming speeds suggested by the model furthers our conceptual understanding of the role of evolutionary processes in salmon migration.

This initial use of the model was not designed to directly address management issues. However, results provide some clues to how management strategies might affect ocean migration. For example, the timing of ocean entry significantly affects the conditions a fish experiences. Alongshore currents shift seasonally and migrating salmon must alter behavior to

account for these changes. As the season progressed, estimated swimming speeds increased, suggesting that fish out-migrating later responded to ocean conditions differently than fish out-migrating earlier. Therefore, existing management strategies that affect ocean entry timing (hatchery releases, barging, etc.) have a high likelihood of impacting the behavior and experiences of salmon when they enter the ocean. Models such as this can help elucidate the potential effects of current and proposed management approaches on salmon ocean ecology.

Future modeling efforts should focus on 1) incorporating prey information and some sort of mortality agent, as much as possible given available data, 2) combining behaviors and/or allowing spatially-explicit behavior, as the results suggested here, and 3) simulating more years and more species or runs of Chinook salmon. Variability in spatial distribution among stocks is substantial (Weitkamp 2010, Tucker et al. 2012) and the differences in behavior required to create this variability can help us understand the forces driving marine migration.

4.5 Acknowledgements

Chinook salmon catch data were obtained during a survey funded by the Bonneville Power Administration. Many people assisted with the project organization and data collection, including but not limited to Ed Casillas, Bill Peterson, Ric Brodeur, Bob Emmett, Kym Jacobson, David Teel, Cheryl Morgan, Jen Zamon, Brian Beckman, Laurie Weitkamp, Don Van Doornik, David Kuligowski, Tom Wainwright, Joe Fisher, Susan Hinton, and Cindy Bucher. I thank Jim Anderson, Lisa Crozier, Eric Buhle, James Faulkner, and Mark Scheuerell for helpful discussions related to data analysis.

4.6 Tables

Table 4.1. Number of Chinook salmon by year, month, and stock. Mid&Upp. C.R. = Mid. & Upper Columbia River spring Chinook salmon, Snake R. = Snake River spring-summer Chinook salmon.

	May		June		Total
	Mid&Upp. C.R.	Snake R.	Mid&Upp. C.R.	Snake R.	
2003	-	9	24	10	43
2004	8	6	3	4	21
2008	25	6	-	30	61
Total	33	21	27	44	125

Table 4.2. Mean swimming and net speeds for fish caught in May and June (along with their standard deviation).

	May		June	
	Swimming speed (SD)	Net speed (SD)	Swimming speed (SD)	Net speed (SD)
2003	0.61 (0.06)	0.47 (0.17)	0.66 (0.12)	0.62 (0.30)
2004	0.50 (0.04)	0.28 (0.19)	0.52 (0.14)	0.66 (0.33)
2008	0.52 (0.12)	0.32 (0.18)	0.63 (0.12)	0.69 (0.32)

Table 4.3. Results from model averaging, with AIC weights for model with a Δ AIC less than 4 and an AIC weight greater than 0.05. M = month, Y = year, S = stock.

Swimming Speed:					
	df	logLik	AICc	Delta	Weight
M+Y+S	6	101.04	-189.37	0	0.3
M+Y+S+M*S	7	102.12	-189.29	0.08	0.29
M+Y	5	98.97	-187.43	1.94	0.11
M+Y+S+(M*S)+(Y*S)	9	103.49	-187.42	1.95	0.11
M+Y+(M*Y)	7	100.67	-186.38	2.98	0.07
M+Y+S+(M*Y)	8	101.8	-186.36	3.01	0.07
M+Y+S+(M*S)+(M*Y)	9	102.73	-185.89	3.48	0.05
Swimming Speed minus Net Speed:					
	df	logLik	AICc	Delta	Weight
M+S	4	14.61	-20.88	0	0.6
M+S+(M*S)	5	14.66	-18.8	2.08	0.21
M	3	11.74	-17.27	3.61	0.1
Track Distance minus Swimming Distance:					
	df	logLik	AICc	Delta	Weight
M+Y+(M*Y)	7	-708.5	1431.96	0	0.46
M+Y+S+(M*Y)	8	-707.7	1432.64	0.68	0.33
M+Y+S+(M*Y)+(M*S)	9	-707.43	1434.43	2.47	0.13
M+Y+S	6	-711.35	1435.4	3.44	0.08

Track Distance minus Net Distance:					
	df	logLik	AICc	Delta	Weight
Y+S	5	-796.13	1602.76	0	0.51
M+Y+S	6	-796.11	1604.94	2.18	0.17
S	3	-799.47	1605.13	2.37	0.16
M+Y+S+(M*Y)	8	-794.57	1606.37	3.61	0.08
M+S	4	-799.15	1606.63	3.87	0.07

Consumption Rate:					
	df	logLik	AICc	Delta	Weight
Y+S+(Y*S)	7	246.94	-478.92	0	0.27
Y+S	5	243.97	-477.43	1.49	0.13
M+Y+S	6	245.01	-477.31	1.61	0.12
M+Y+S+(M*Y)	8	247.18	-477.13	1.8	0.11
M+Y+S+(Y*S)	8	246.95	-476.67	2.26	0.09
M+Y+(M*Y)	7	245.71	-476.46	2.46	0.08
M+Y+S+(M*Y)+(M*S)	9	247.93	-476.29	2.63	0.07
M+Y+S+(M*S)	7	245.52	-476.08	2.84	0.07
M+S	4	242.13	-475.94	2.99	0.06

Growth Rate:					
	df	logLik	AICc	Delta	Weight
Y+S+(Y*S)	7	-59.64	134.27	0	0.16
M+Y+S+(M*Y)+(M*S)	9	-57.38	134.38	0.12	0.16
M+Y+(M*Y)	7	-59.87	134.72	0.46	0.13
Y+S	5	-62.1	134.73	0.46	0.13
M+Y+S+(M*S)	7	-59.96	134.92	0.65	0.12
M+Y+S+(M*Y)	8	-59.12	135.52	1.25	0.09
M+Y+S	6	-61.46	135.65	1.38	0.08
M+Y+S+(Y*S)	8	-59.54	136.36	2.09	0.06

Table 4.4. Model averaged parameter weights for the six models. Response variables are: Swimming speed, the difference between swimming speed and net speed, the difference between track distance and swimming distance, the difference between track distance and net distance, consumption rate (g/g/d), and growth rate (BL/s).

Factor	Parameter Weights					
	Swimming speed	Swimming - Net	Track - Swimming	Track - Net	Consump.	Growth
Month	1.00	1.00	1.00	0.33	0.60	0.71
Year	1.00	0.09	1.00	0.77	0.94	1.00
Stock	0.82	0.90	0.54	1.00	0.92	0.87
Month x Stock	0.45	0.21	0.13	--	0.14	0.32
Month x Year	0.19	--	0.92	0.08	0.26	0.45
Year x Stock	0.11	--	--	--	0.36	0.30

Table 4.5. Mean difference between swimming speed and net speed. Mid&Upp. C.R. = Mid. & Upper Columbia River spring Chinook salmon, Snake R. = Snake River spring-summer Chinook salmon.

	Mid & Upper		
	All Stocks	C. R.	Snake R.
May	0.19	0.23	0.12
June	-0.02	0.04	-0.05

Table 4.6. F test p-values for test of differences in variance between swimming speed and net speed by year, month, and stock. Mid&Upp. C.R. = Mid. & Upper Columbia River spring Chinook salmon, Snake R. = Snake River spring-summer Chinook salmon.

	May		June	
	Mid&Upp. C.R.	Snake R.	Mid&Upp. C.R.	Snake R.
2003	NA	0.007	> 0.001	0.003
2004	0.051	0.001	0.012	0.144
2008	0.123	0.113	NA	> 0.001

4.7 Figures

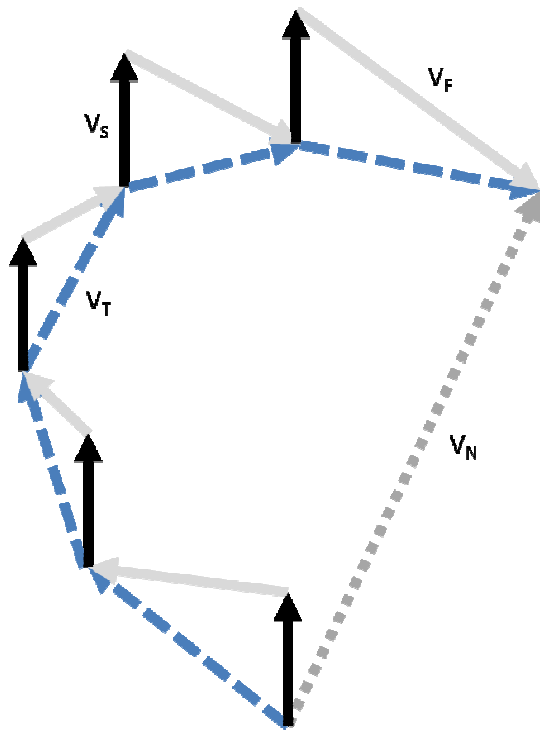


Figure 4.1. Vector diagram. In this example diagram, a fish swarm directly north at a constant speed and direction (V_S = swim vector) during 5 distinct time steps. It was initially advected west, but that changed to a northeast and then southeast direction (V_F = flow vector), resulting in a change to its track (V_T = track vector), and ultimately its net movement (V_N = net vector). As in Figure 7, $V_N < V_S < V_T$.

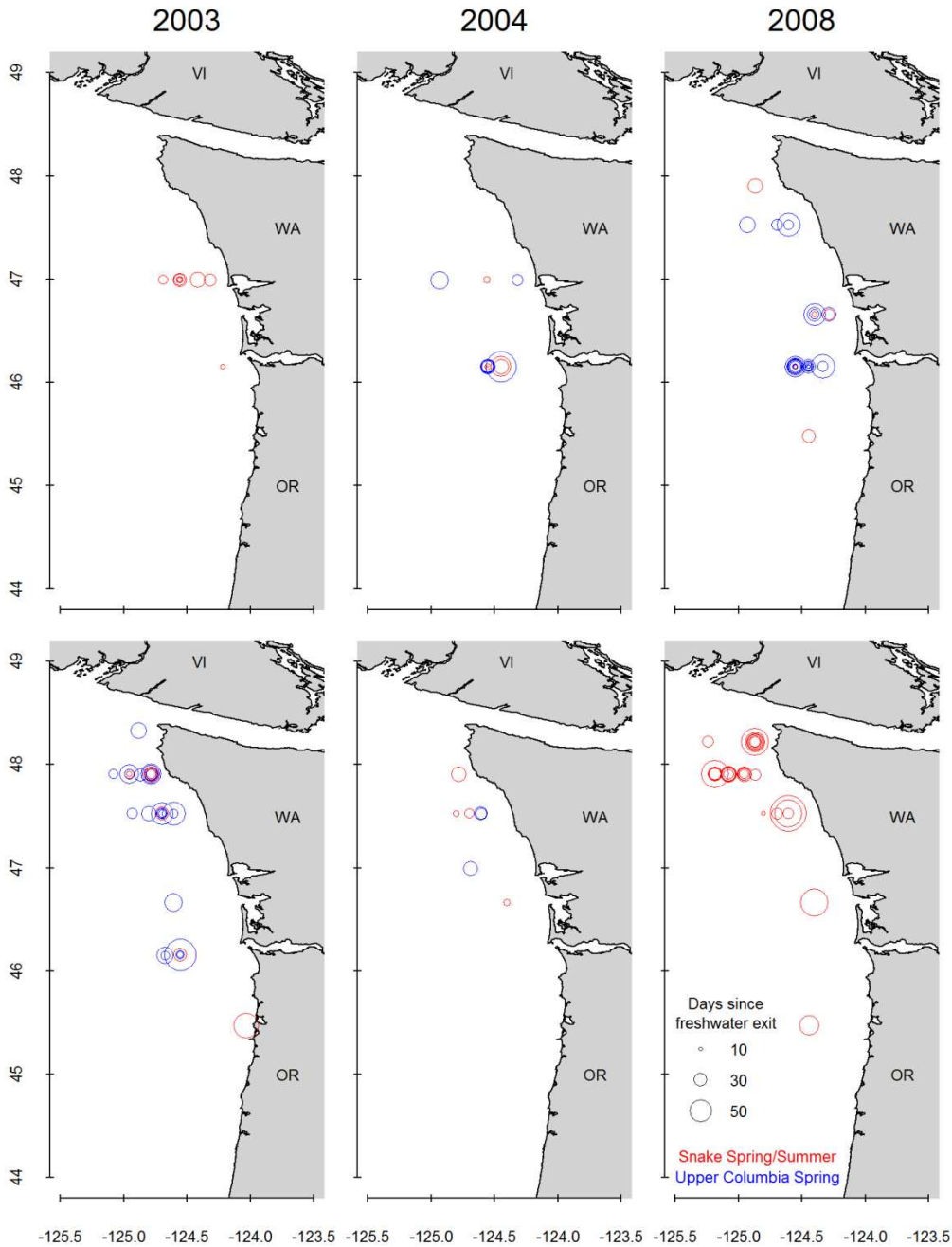


Figure 4.2. Spatial distribution of yearling Chinook salmon caught in during the last 10 days of May (top) and the last 10 days of June (bottom) for which I have otolith data. Distributions do not necessarily represent CPUE from the trawl survey. Size of the circle represent the days since freshwater exit. Snake River spring-summer Chinook salmon are in red and Mid & Upper Columbia River Chinook salmon are in blue.

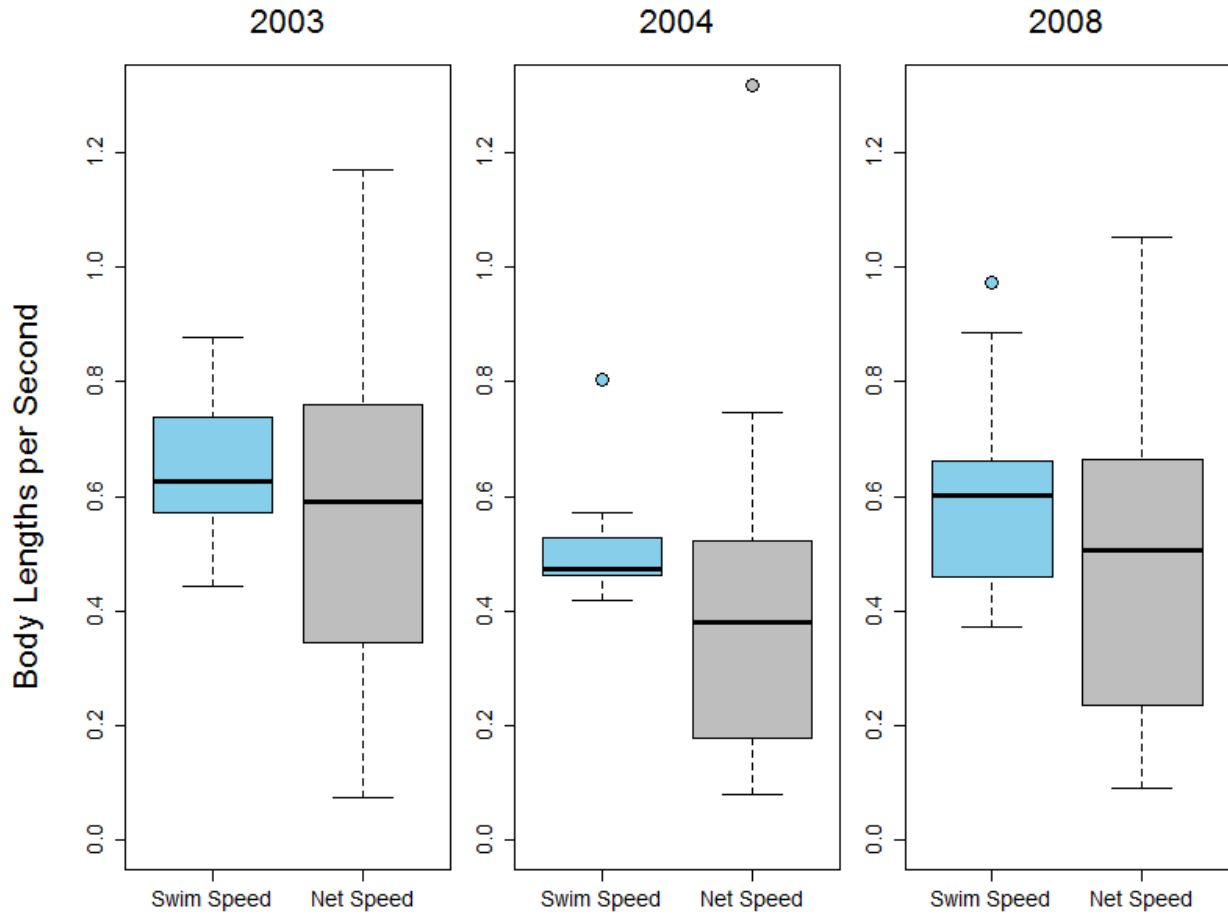


Figure 4.3. Swimming speed and net speed (BL/s) by year. Dark line represents the median speed, while the box represents the first and third quartile of the data.

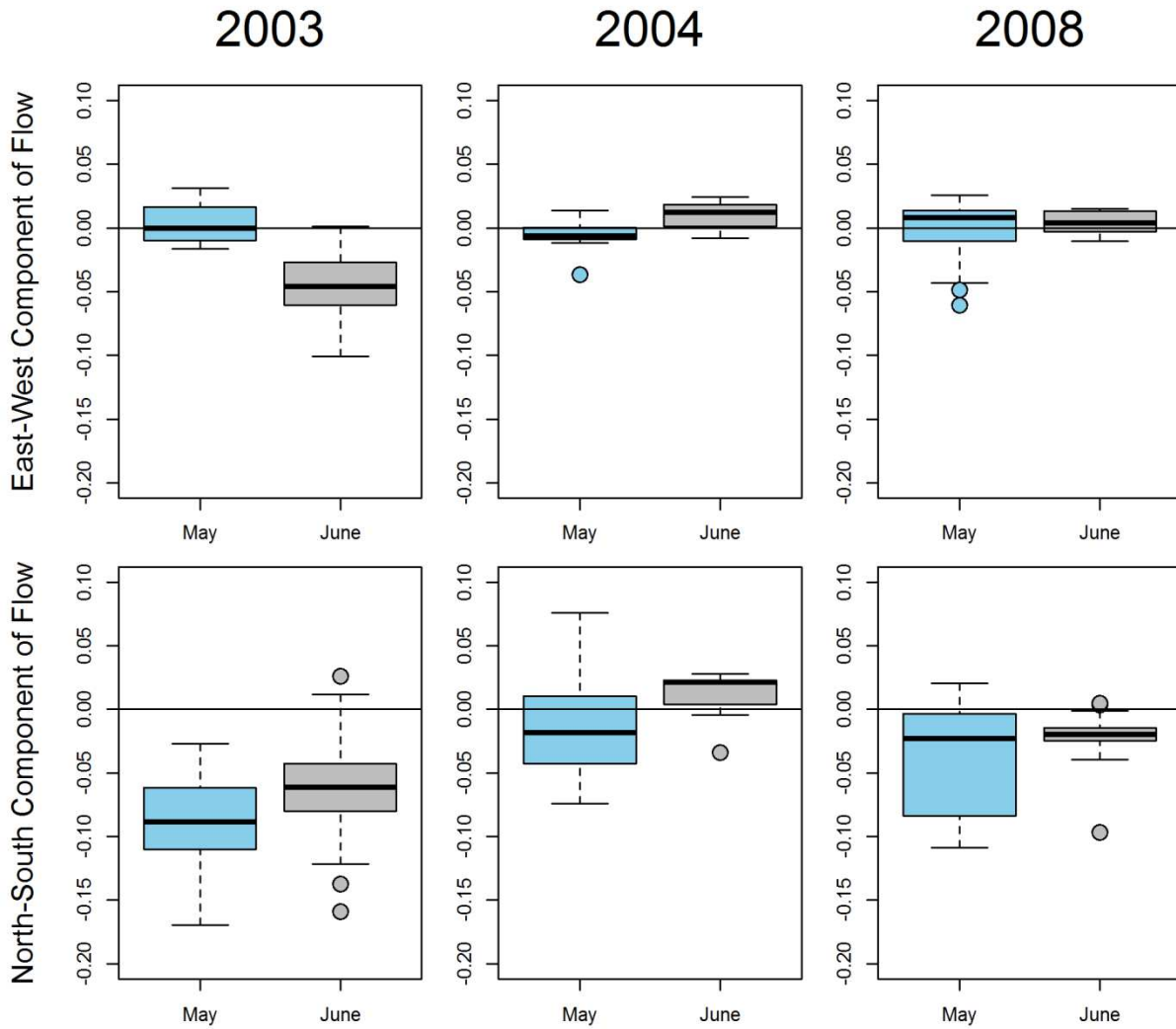


Figure 4.4. The distribution of weighted mean ocean currents experienced by simulated fish, separated into the east-west and north-south components. Negative values indicate stronger westward flow (top panel) or southward flow (bottom panel).

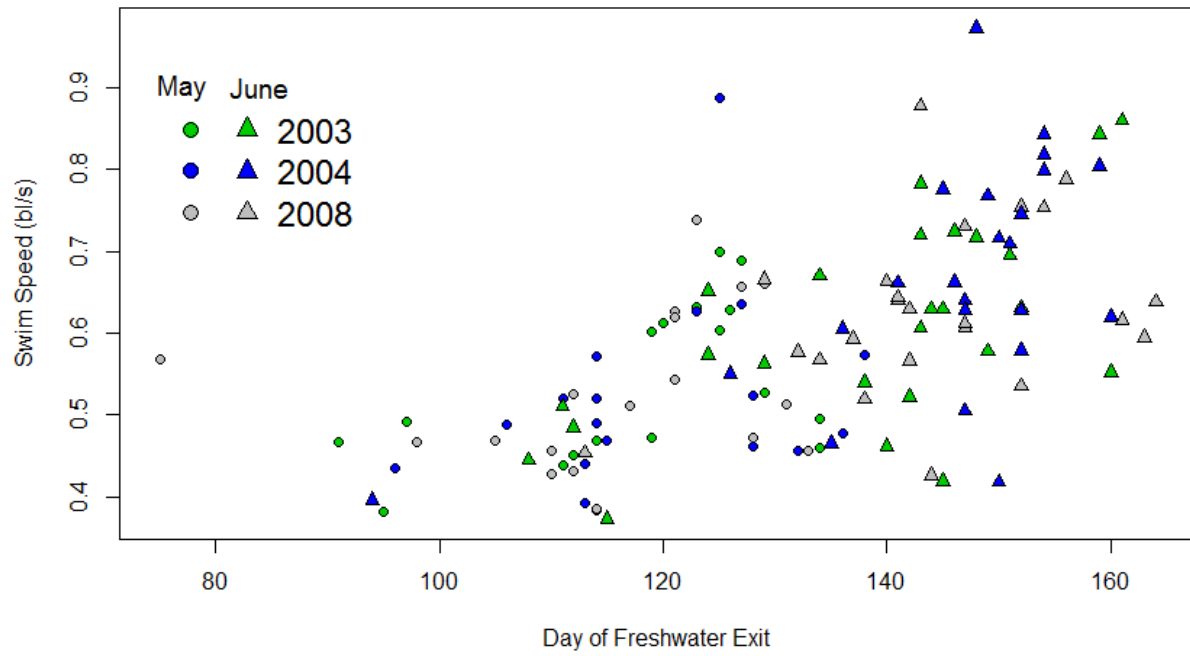


Figure 4.5. Swimming speed versus day of freshwater exit, by month of capture and year.

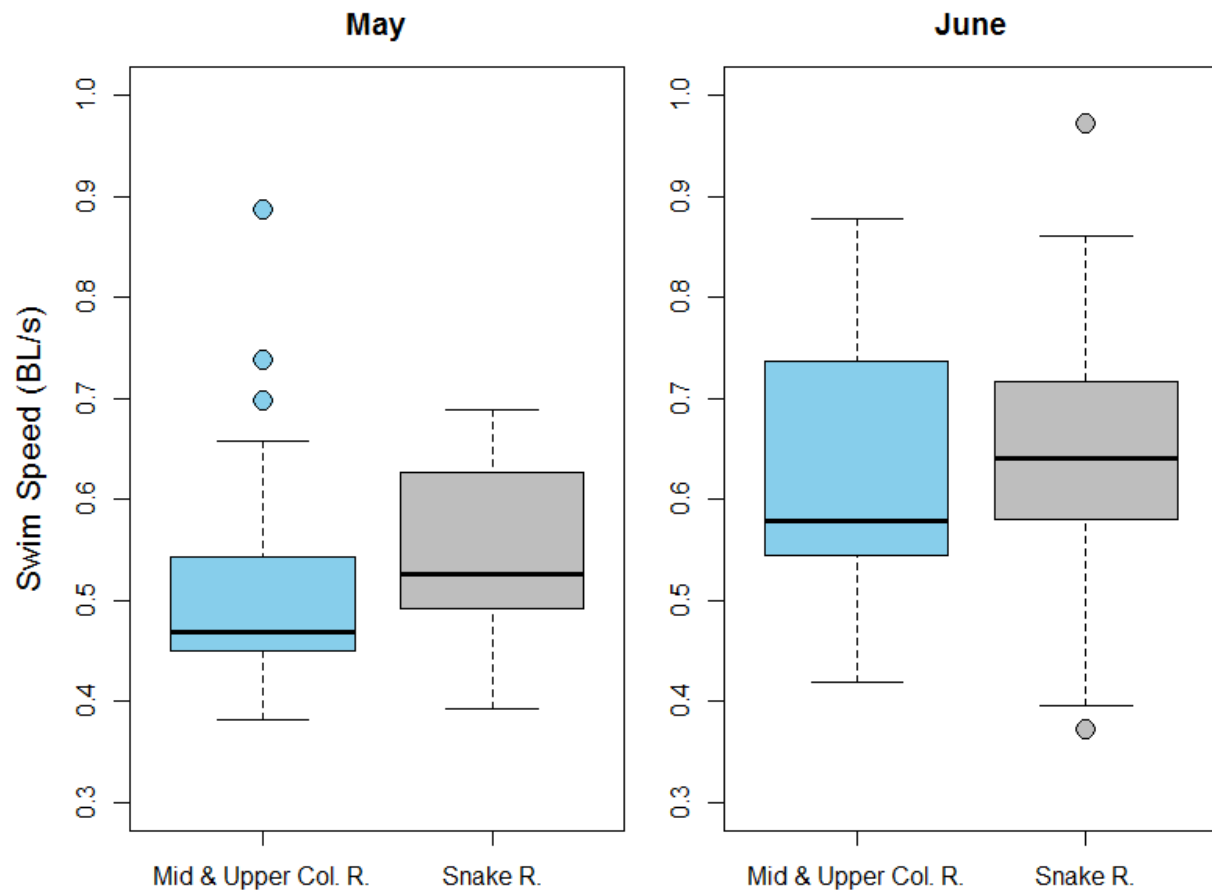


Figure 4.6. Swimming speed (BL/s) by month and stock. Both month and stock were significant factors in the model.

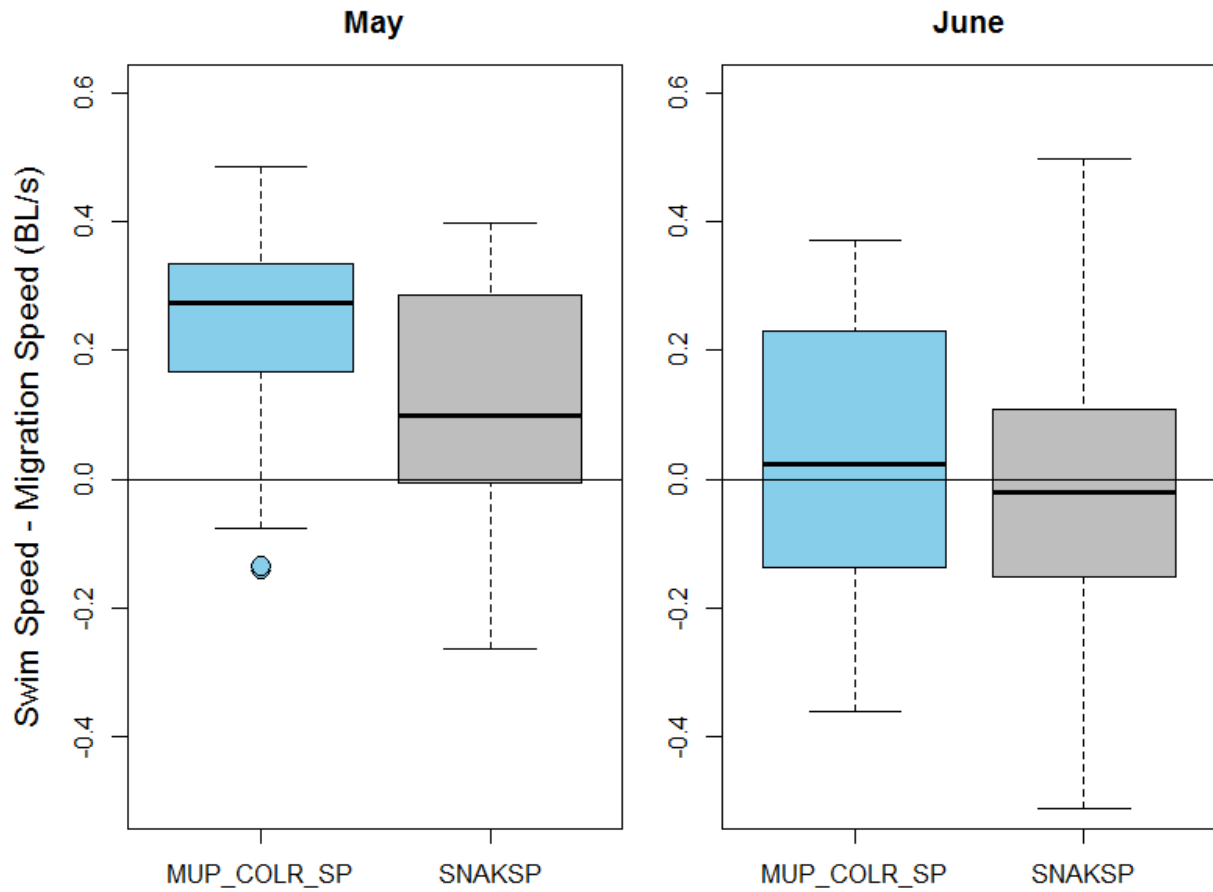


Figure 4.7. Month- and stock-specific differences between swimming speed and net speed (in BL/s). Positive values indicate swimming speeds were higher than net speeds. One value not shown for Snake River spring Chinook salmon in June (difference = -1.13). Mid&Upp. C.R. = Mid. & Upper Columbia River spring Chinook salmon, Snake R. = Snake River spring-summer Chinook salmon.

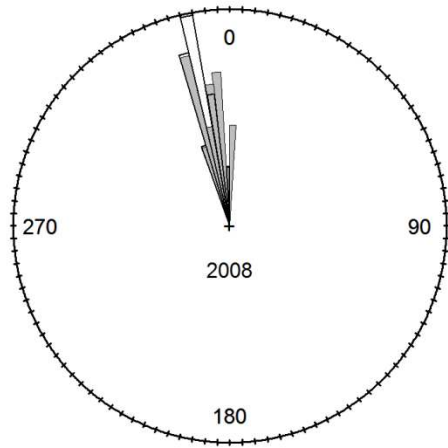
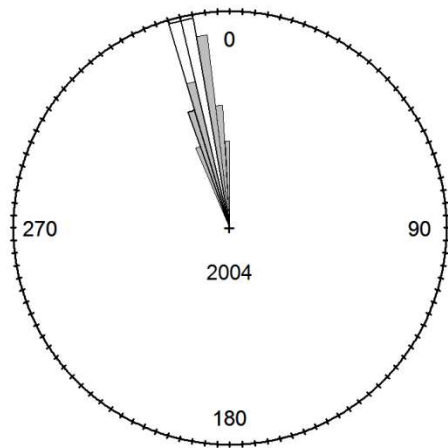
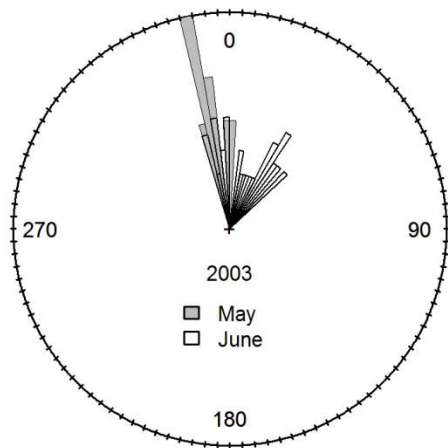


Figure 4.8. Weighted mean swimming angle for each of the simulated fish. There was considerable variability in swimming angle within each fish, as ocean currents were highly dynamic. However, that variability is not represented in these mean angle plots.

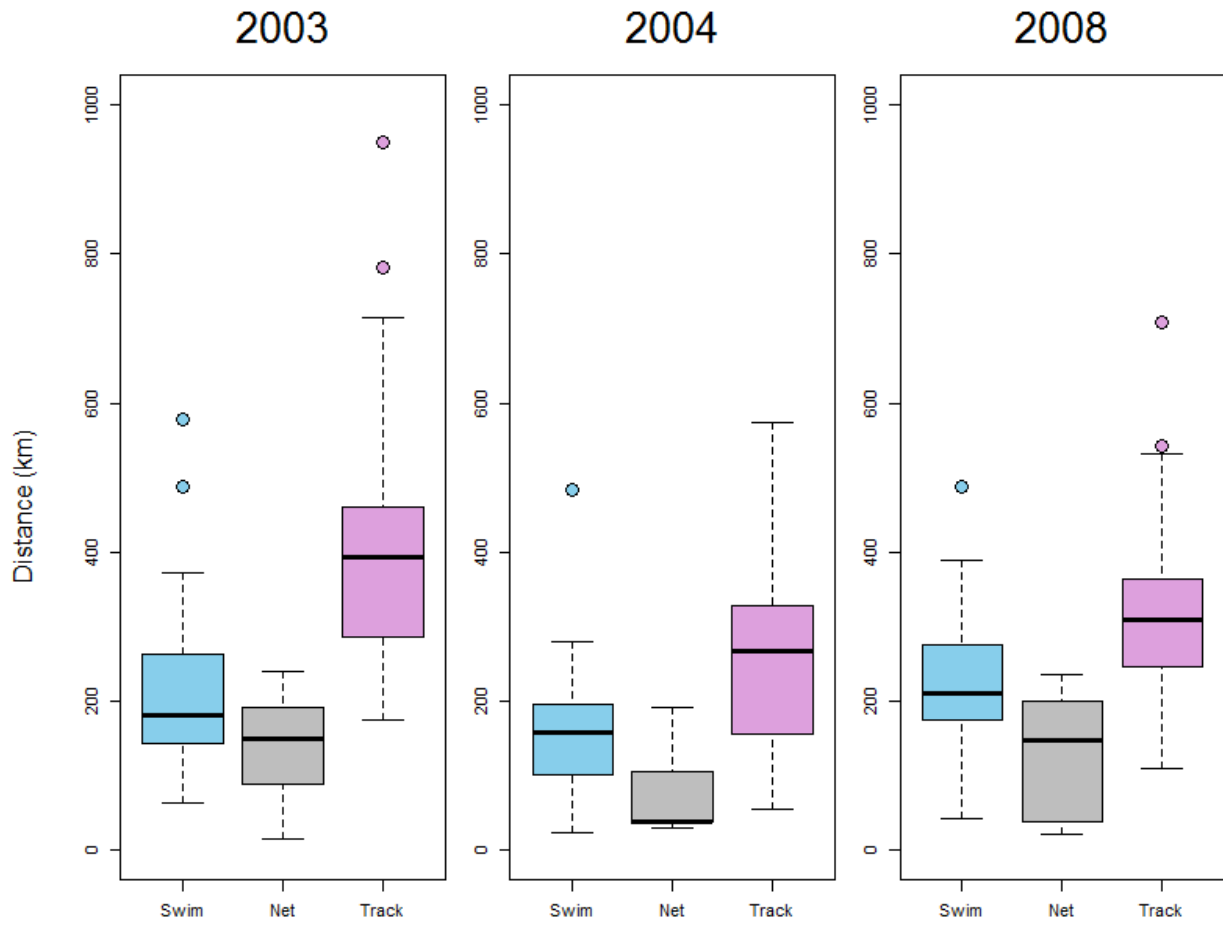


Figure 4.9. Swimming, net, and track distances for 2003, 2004, and 2008.

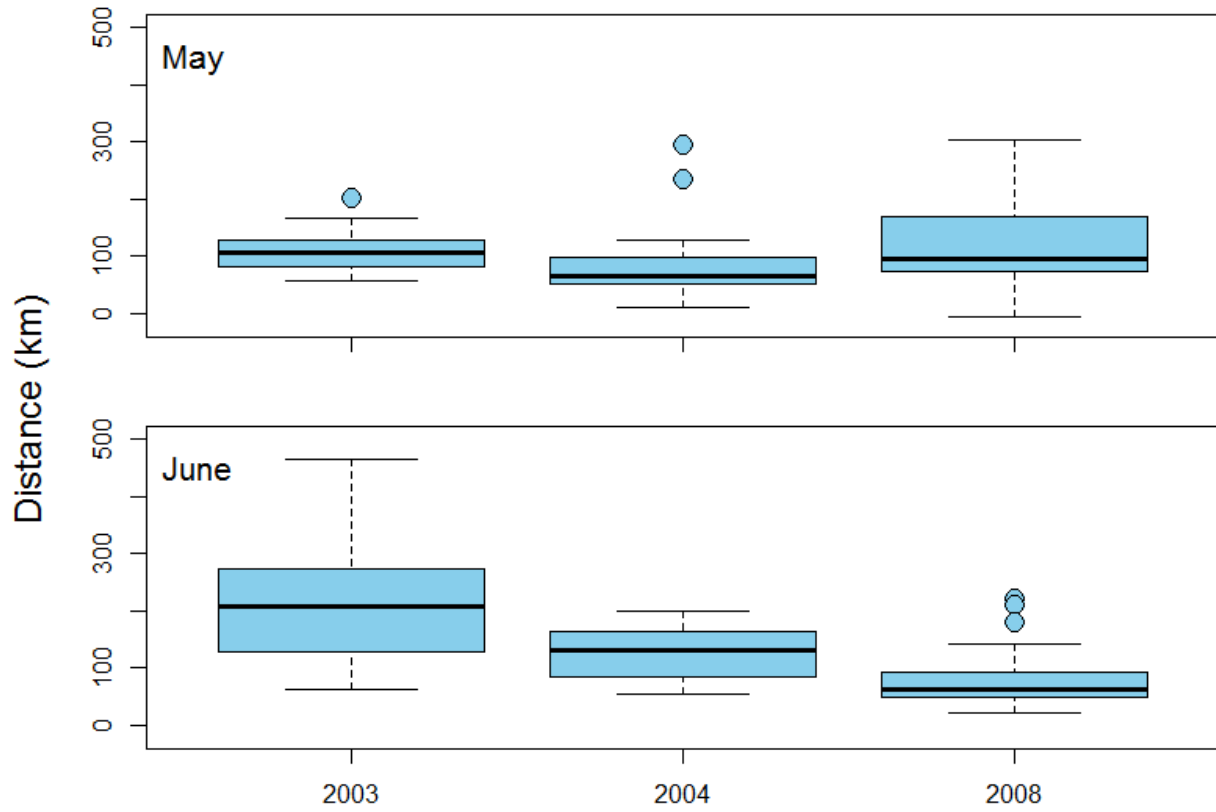


Figure 4.10. Difference between track distance (relative to the ground) and swimming distance (relative to the water) for May (top) and June (bottom) of 2003, 2004, and 2008.

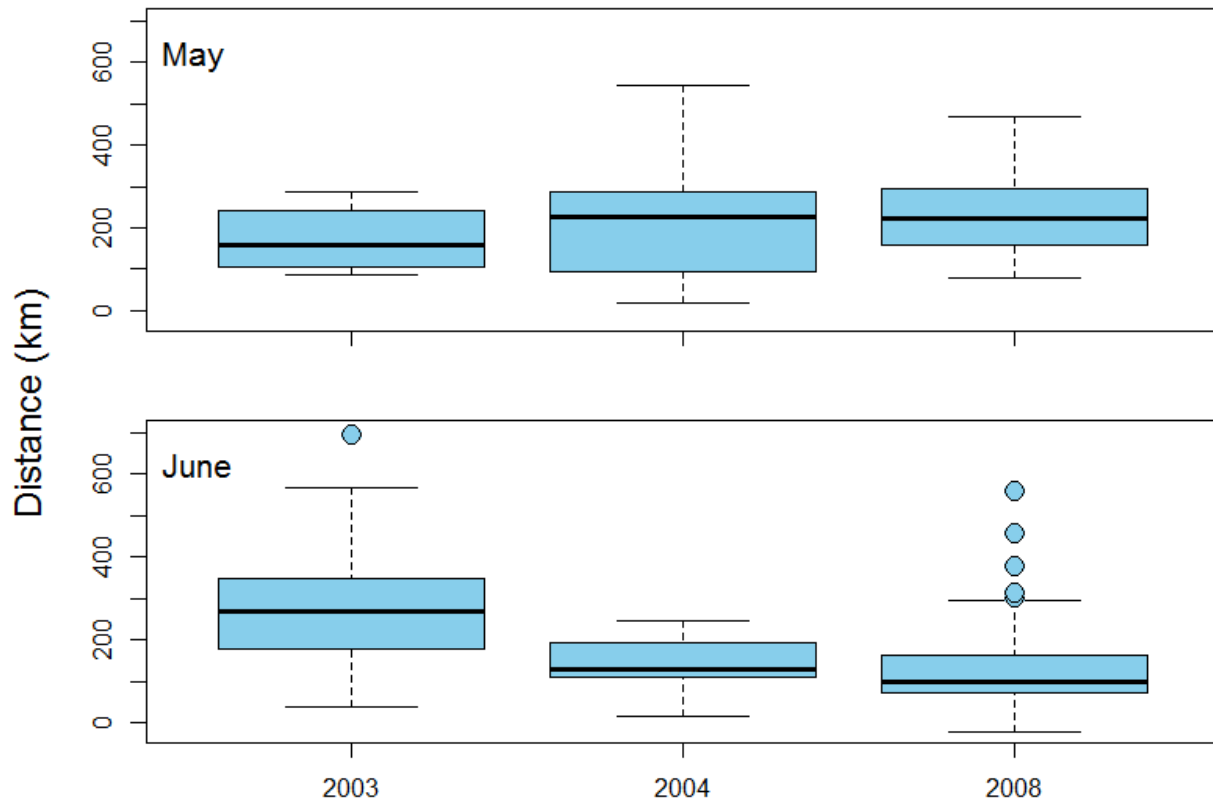


Figure 4.11. Difference between track distance (relative to the ground) and net distance (relative to the ground) for May (top) and June (bottom) of 2003, 2004, and 2008.

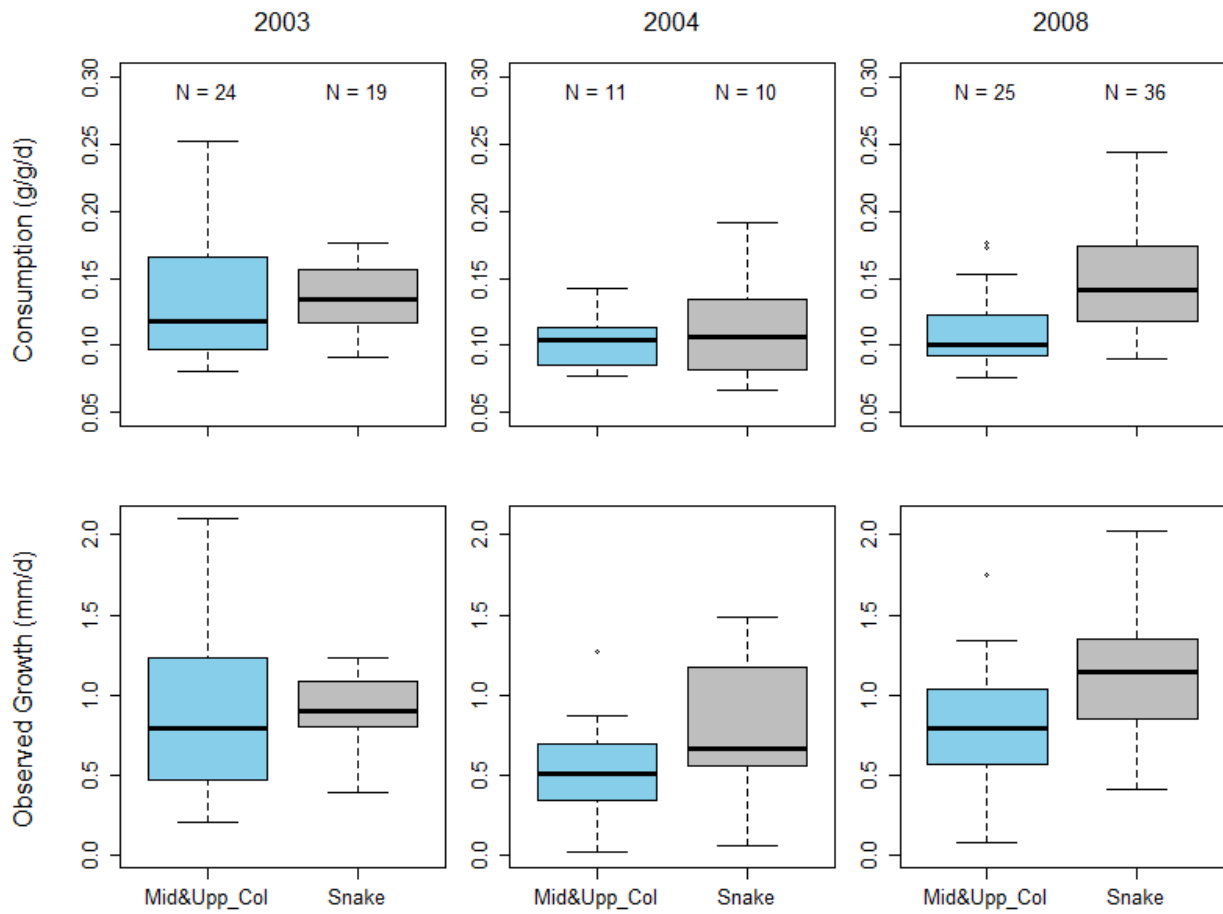
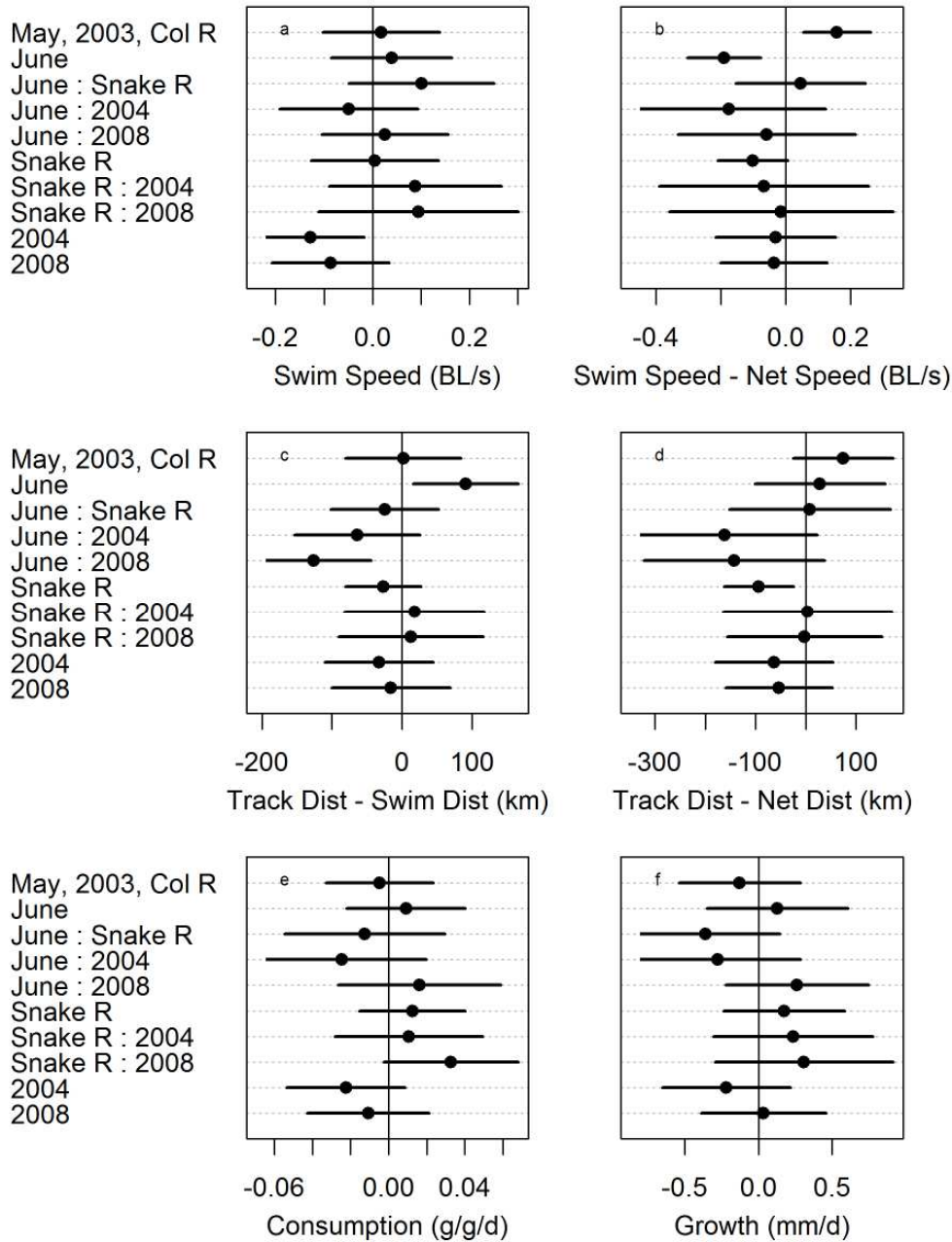


Figure 4.12 Stock-specific consumption (g/g/d) and growth (mm/d) rates from 2003, 2004, and 2008. N is the sample size for each group.

4.8 Supplementary Material for Chapter 4

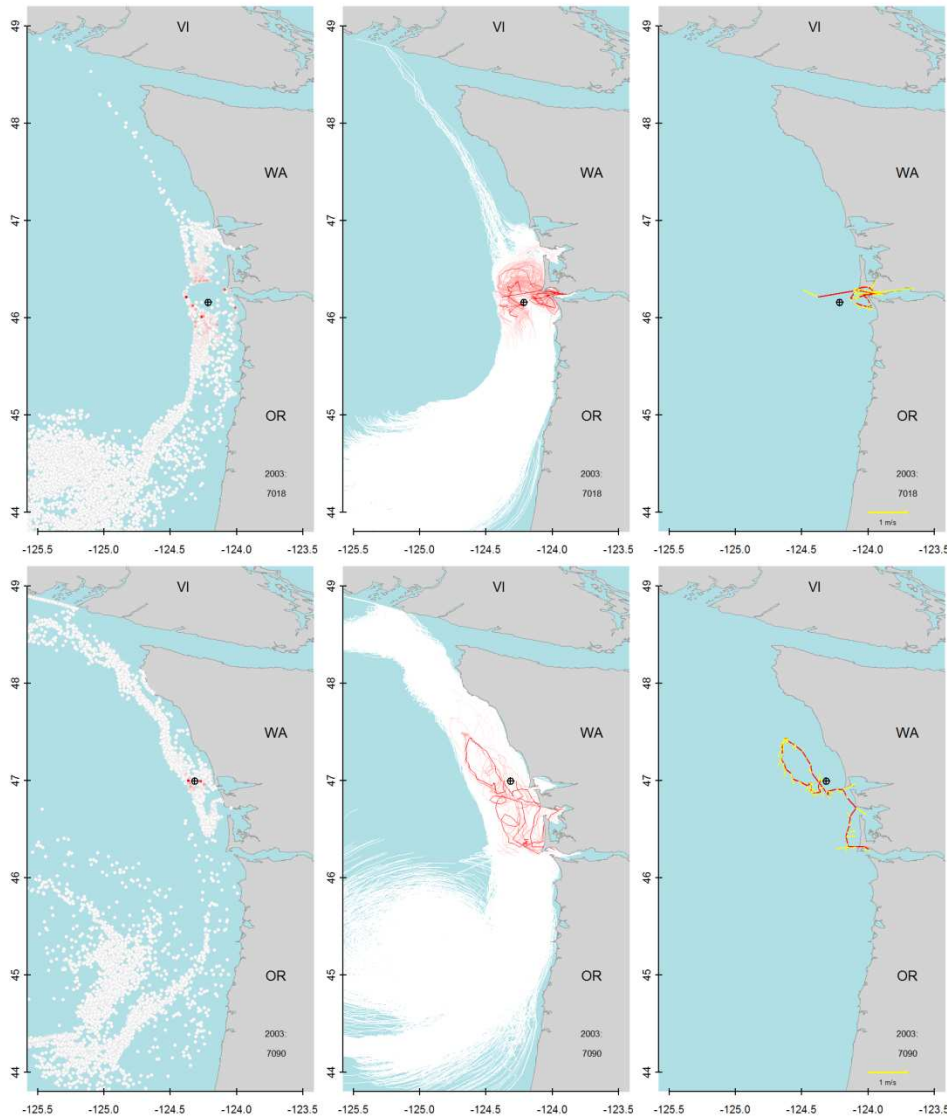
4.8.1 Model results

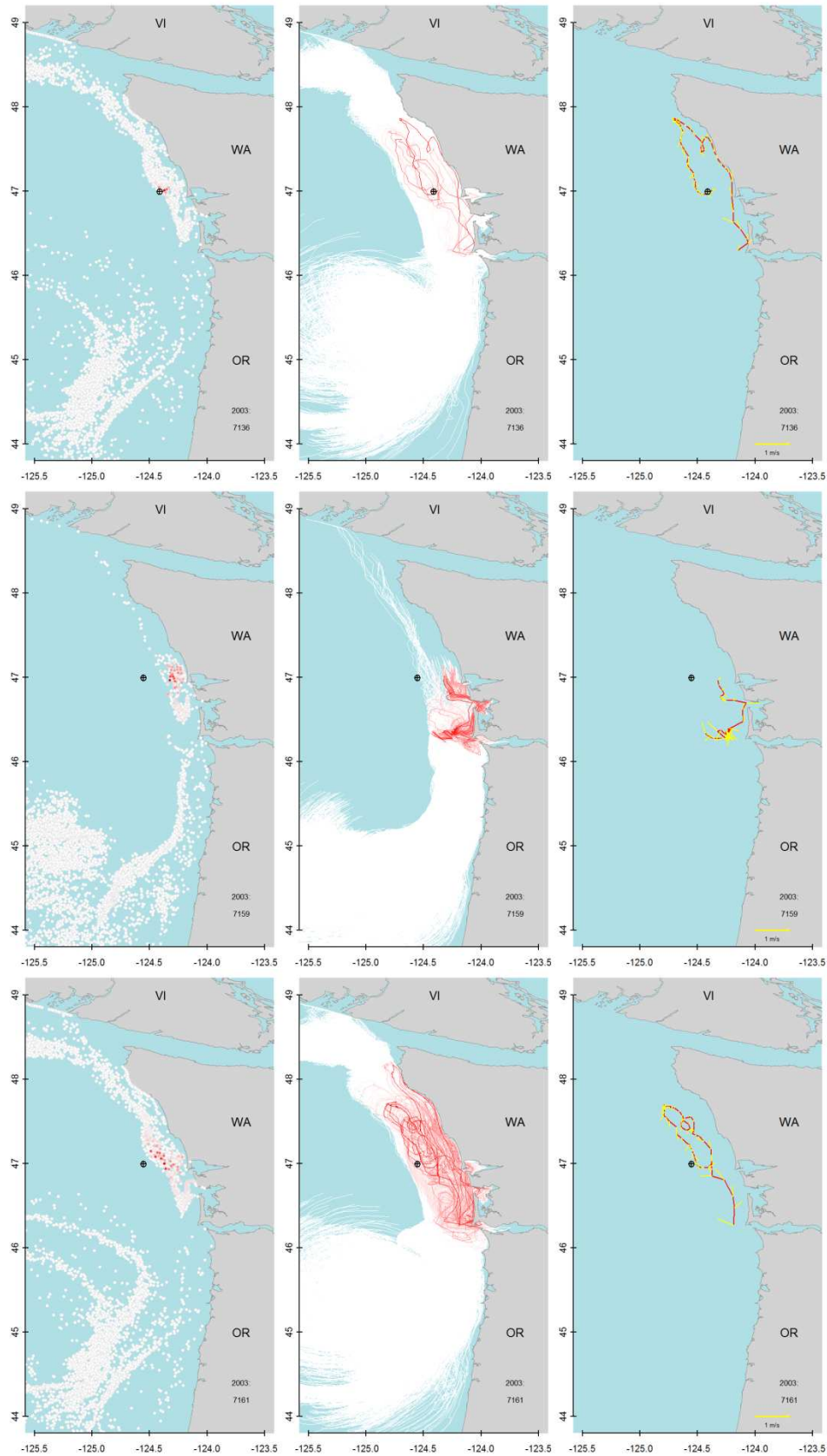


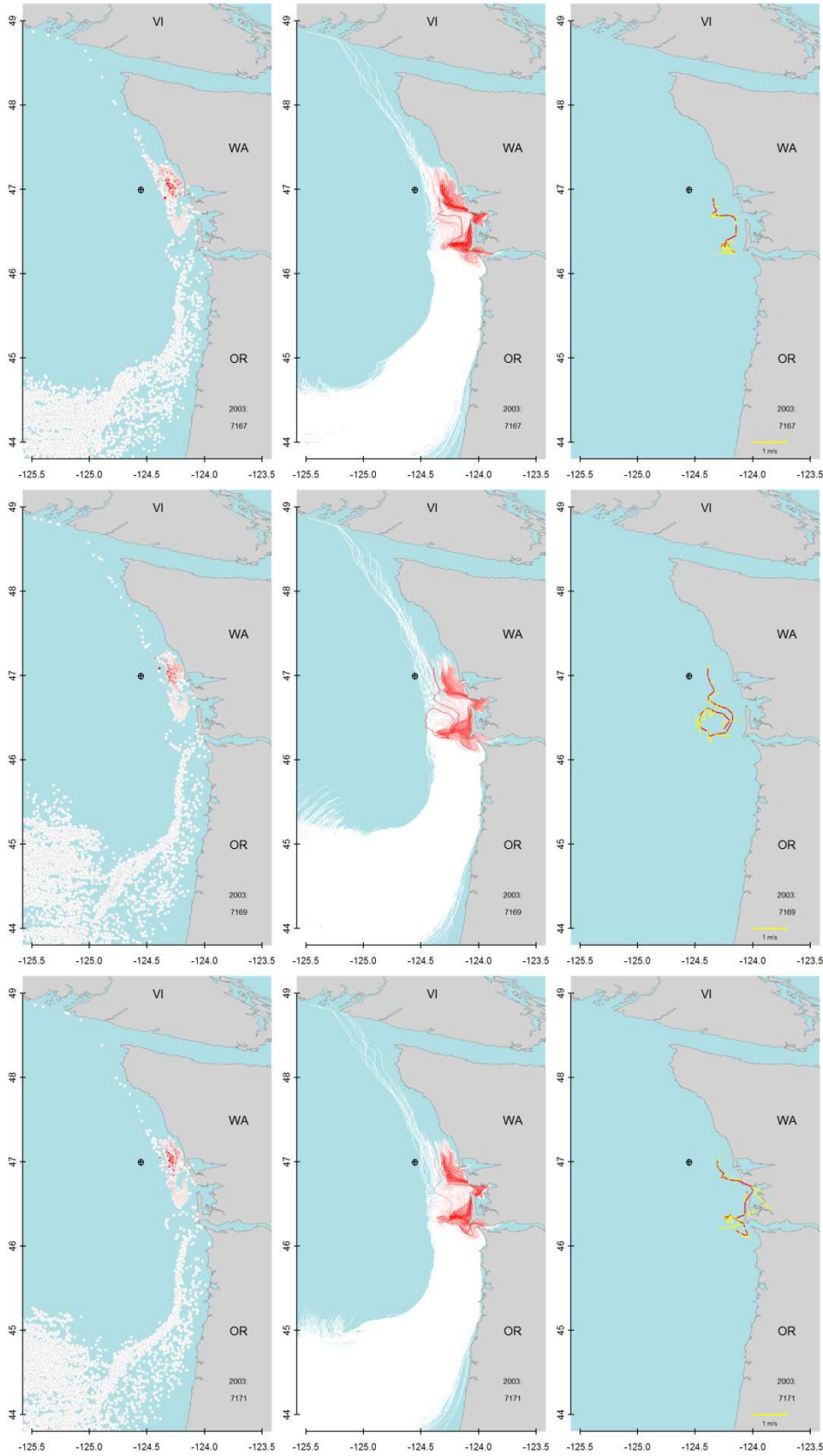
Model coefficients and 95% confidence intervals for a) swimming speed, b) the difference between swimming speed and net speed, c) the difference between track distance and swimming distance, d) the difference between track distance and net distance, e) consumption rate, and f) growth rate. The first point in each plot represents the offset (from the global mean) for Mid & Upper Columbia River ESUs during May of 2003. Each point after that details which variables have changed from that default set (and the corresponding offset from the global mean).

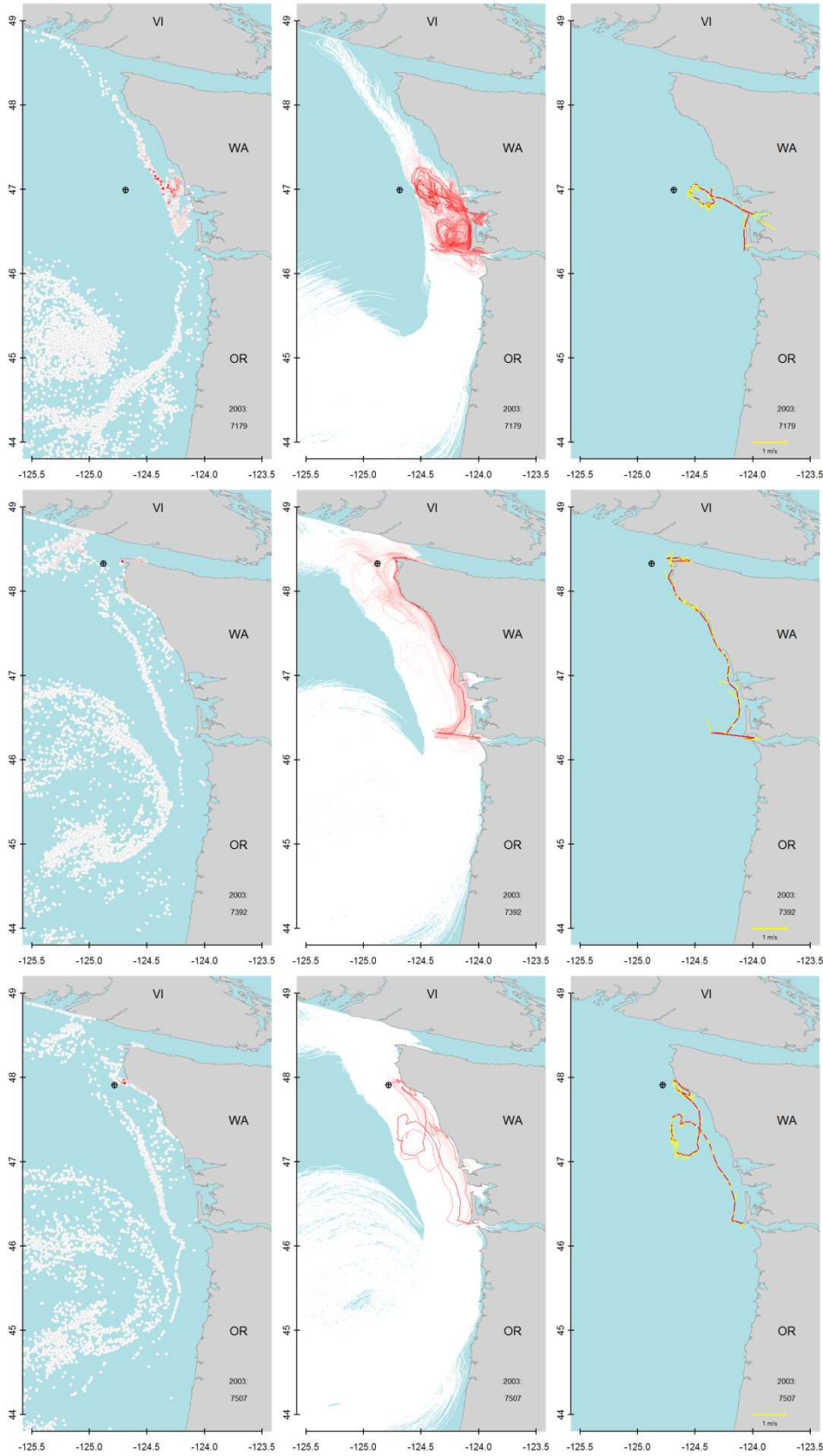
4.8.2 Individual fish tracks

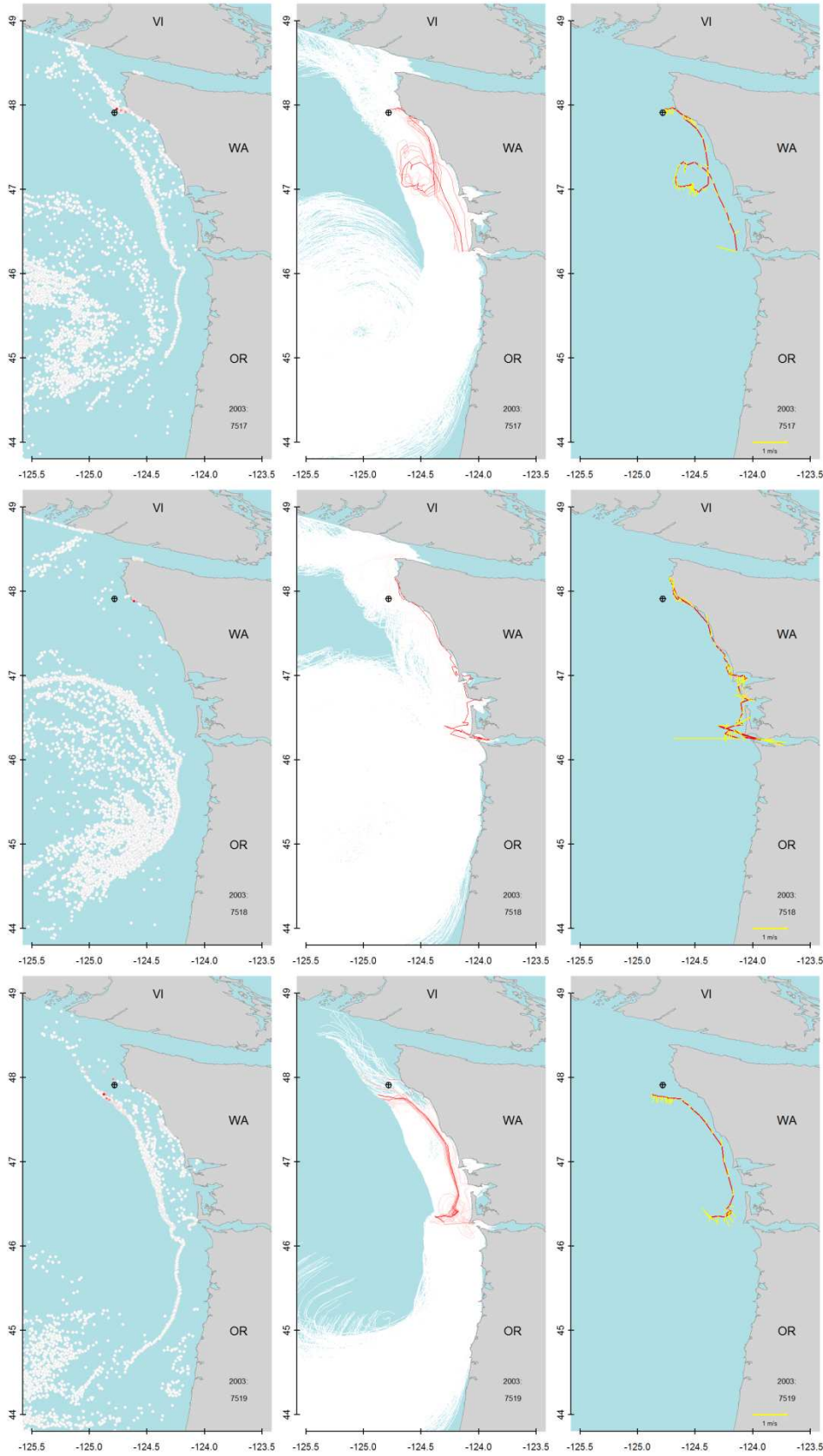
Simulation results for each of the 125 fish. Each row shows the final location of the 10,000 simulated fish (left) and the tracks taken by those fish (center; data were output every 12 hours, not every model time step). In both plots, the color indicates weight with the redder the color, the higher the weight. The plot on the right shows the track of the highest weighted fish (red) and the strength and direction of the ocean current every 12 hours (yellow). The year and fish ID number are listed in the bottom right of each plot.

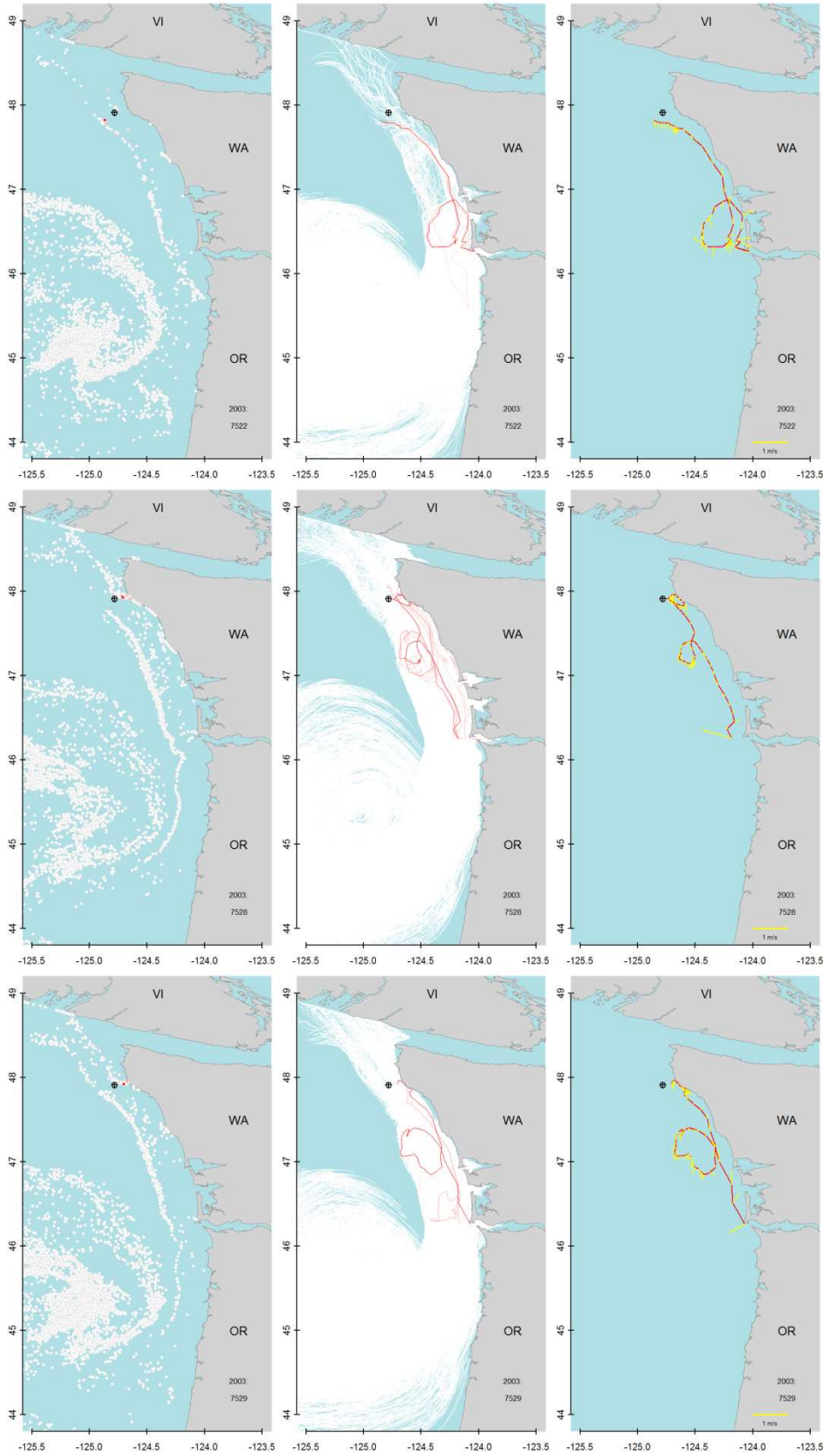


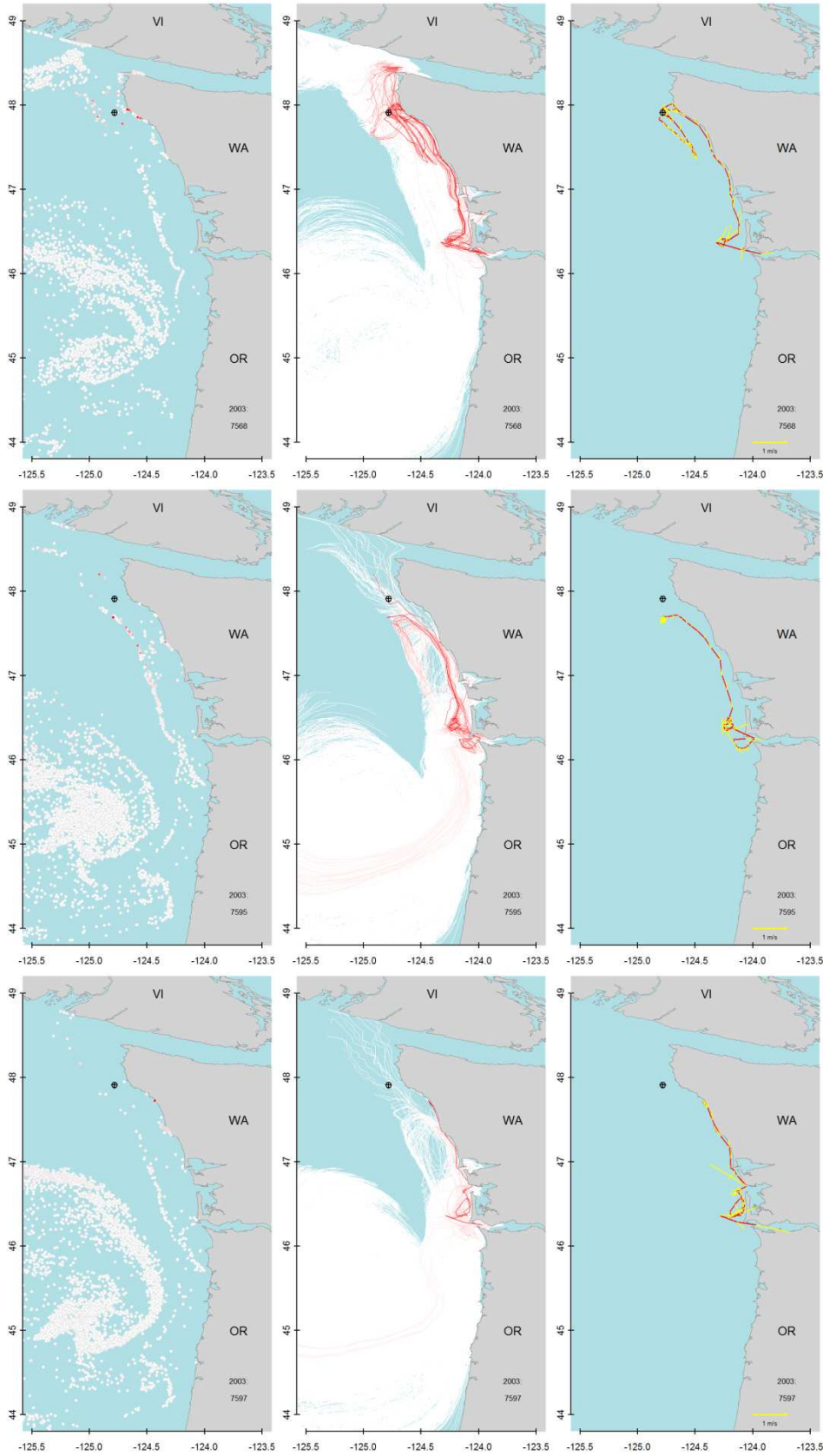


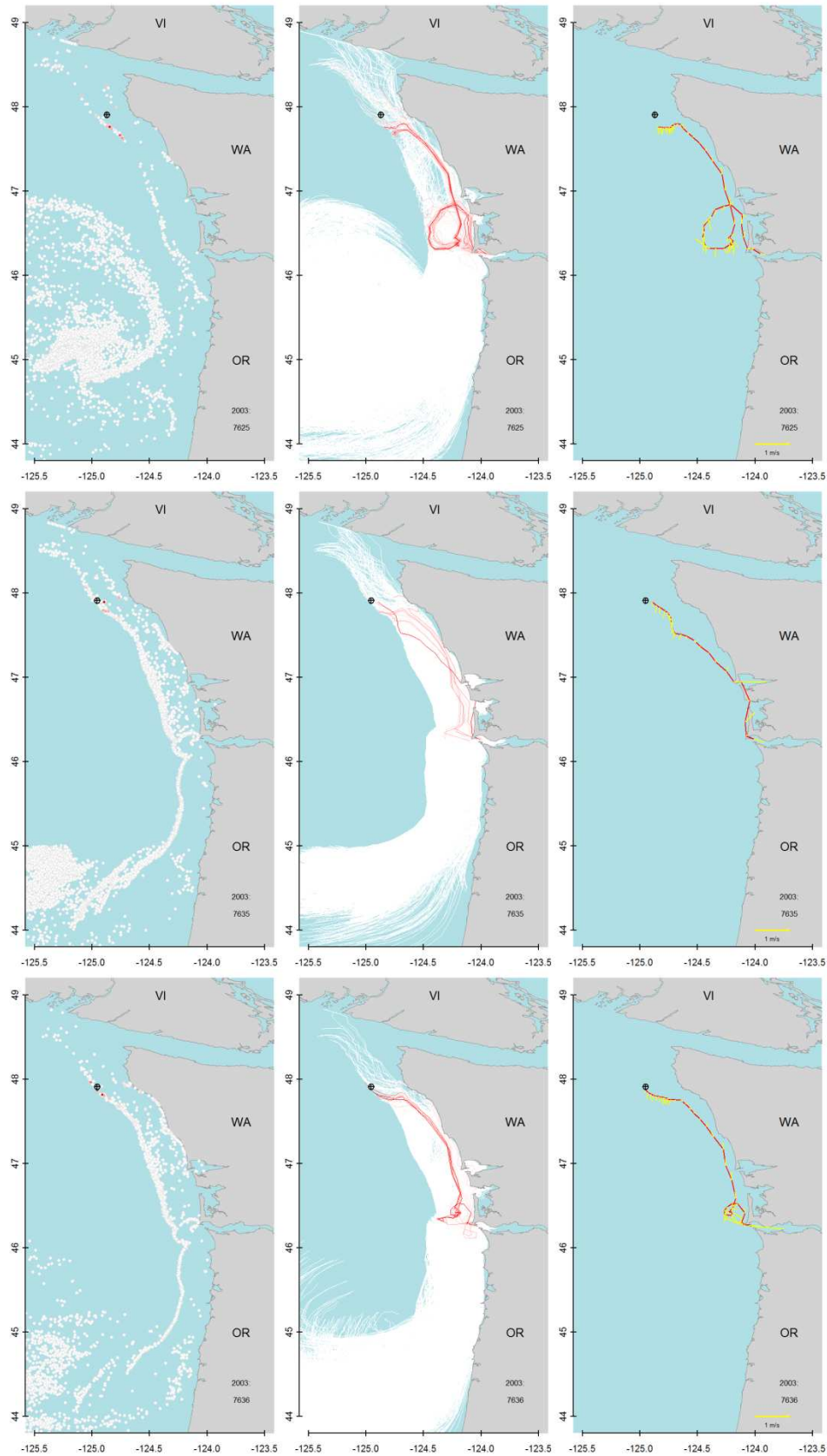


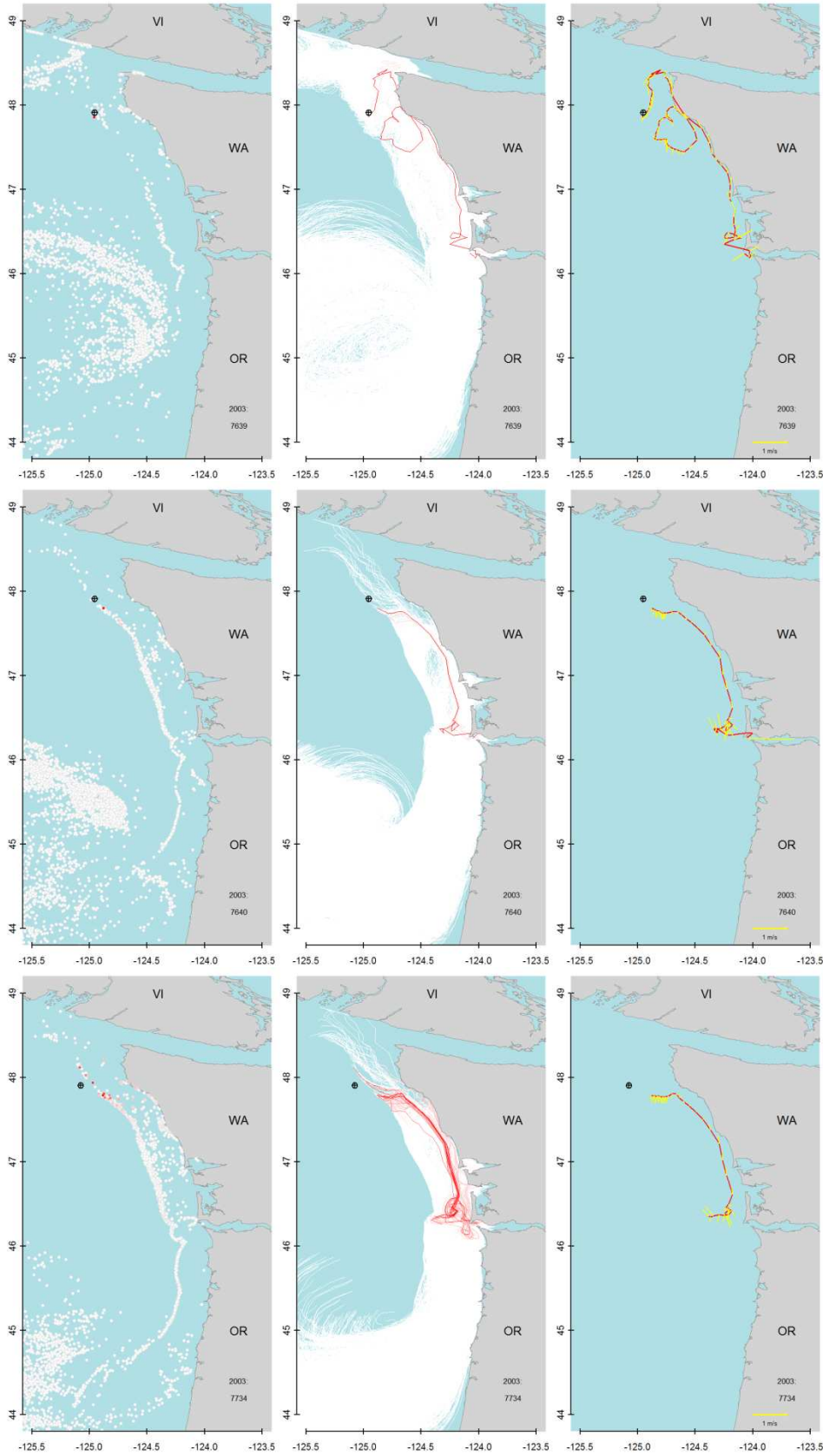


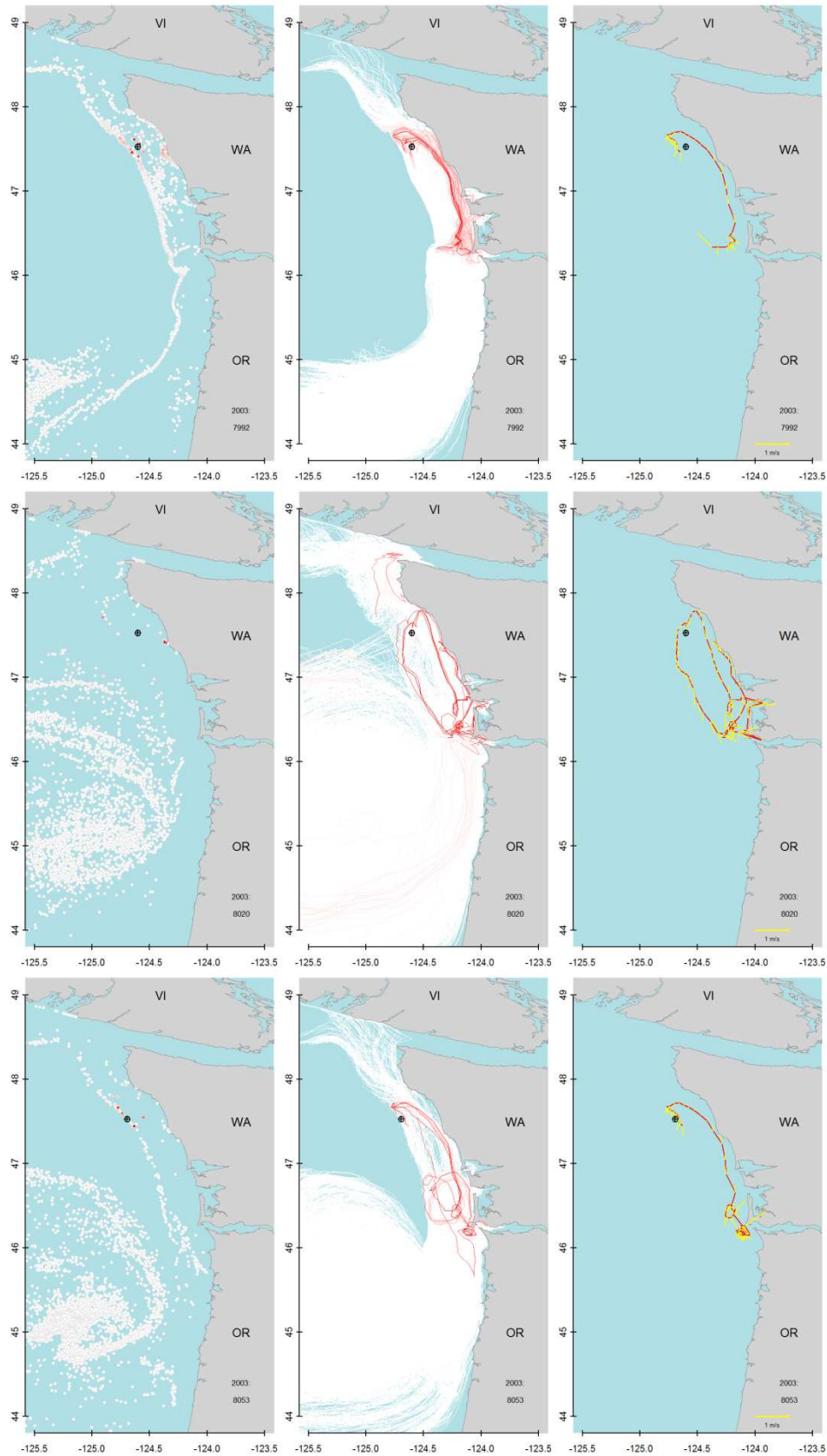


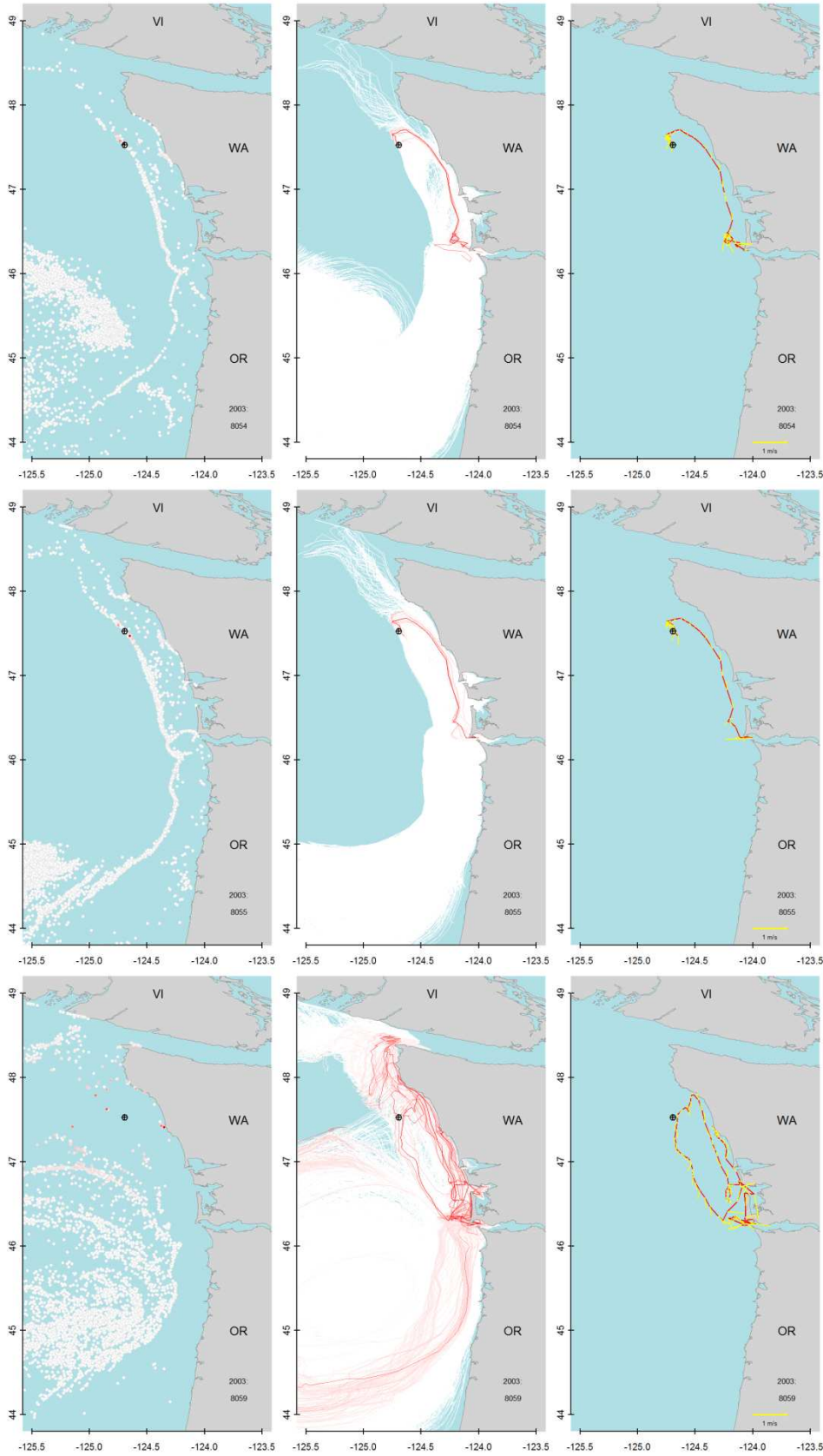


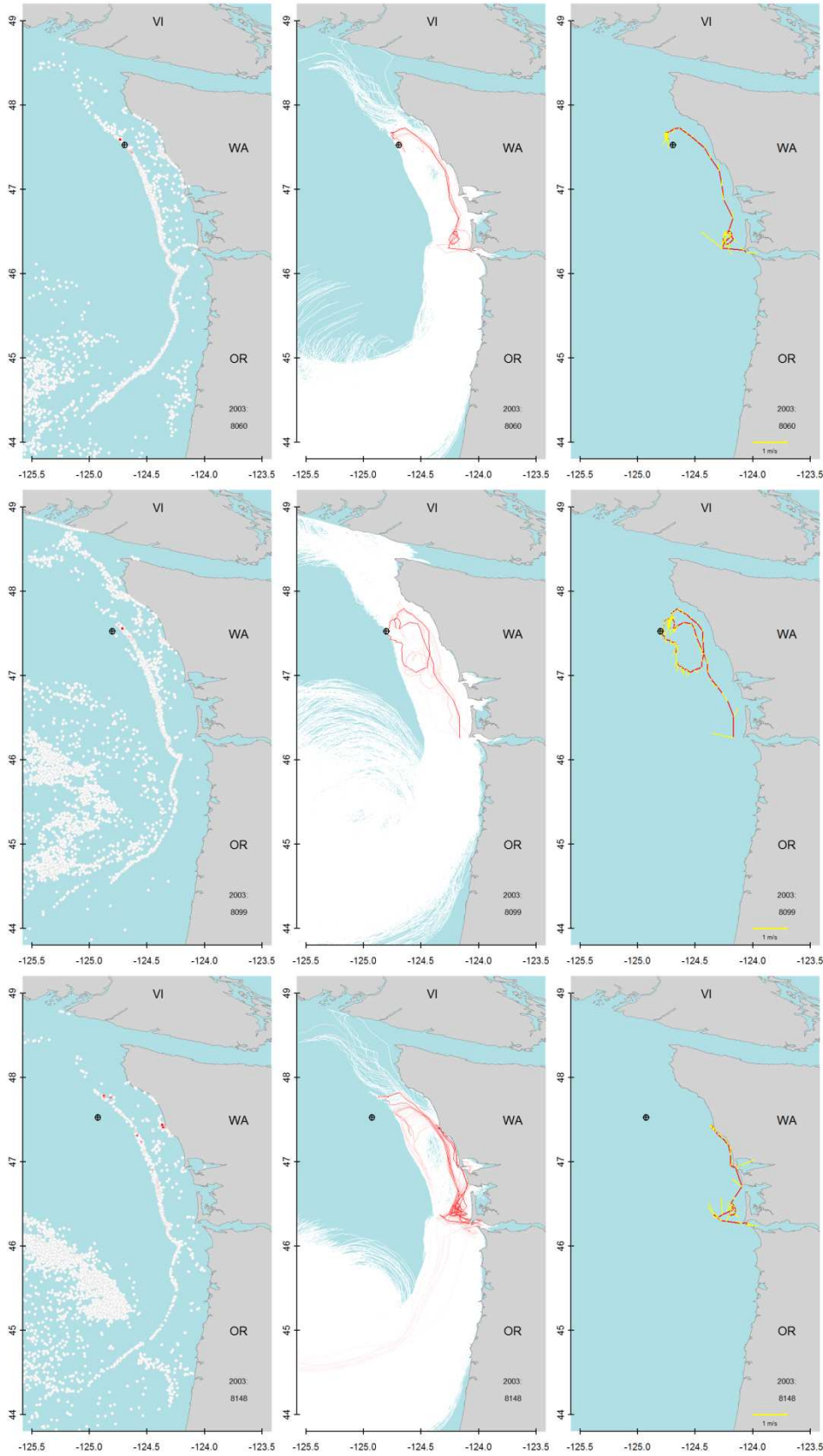


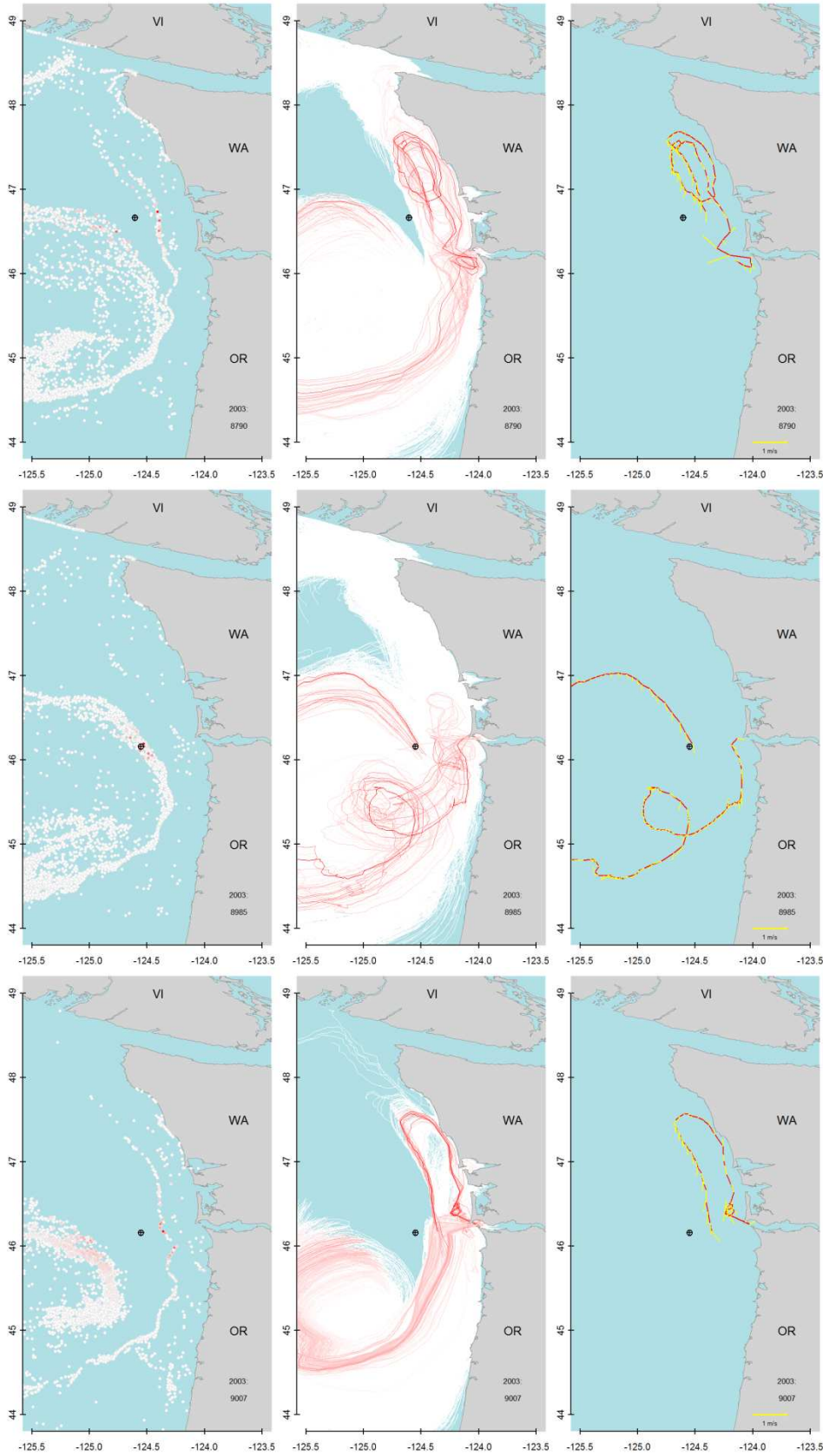


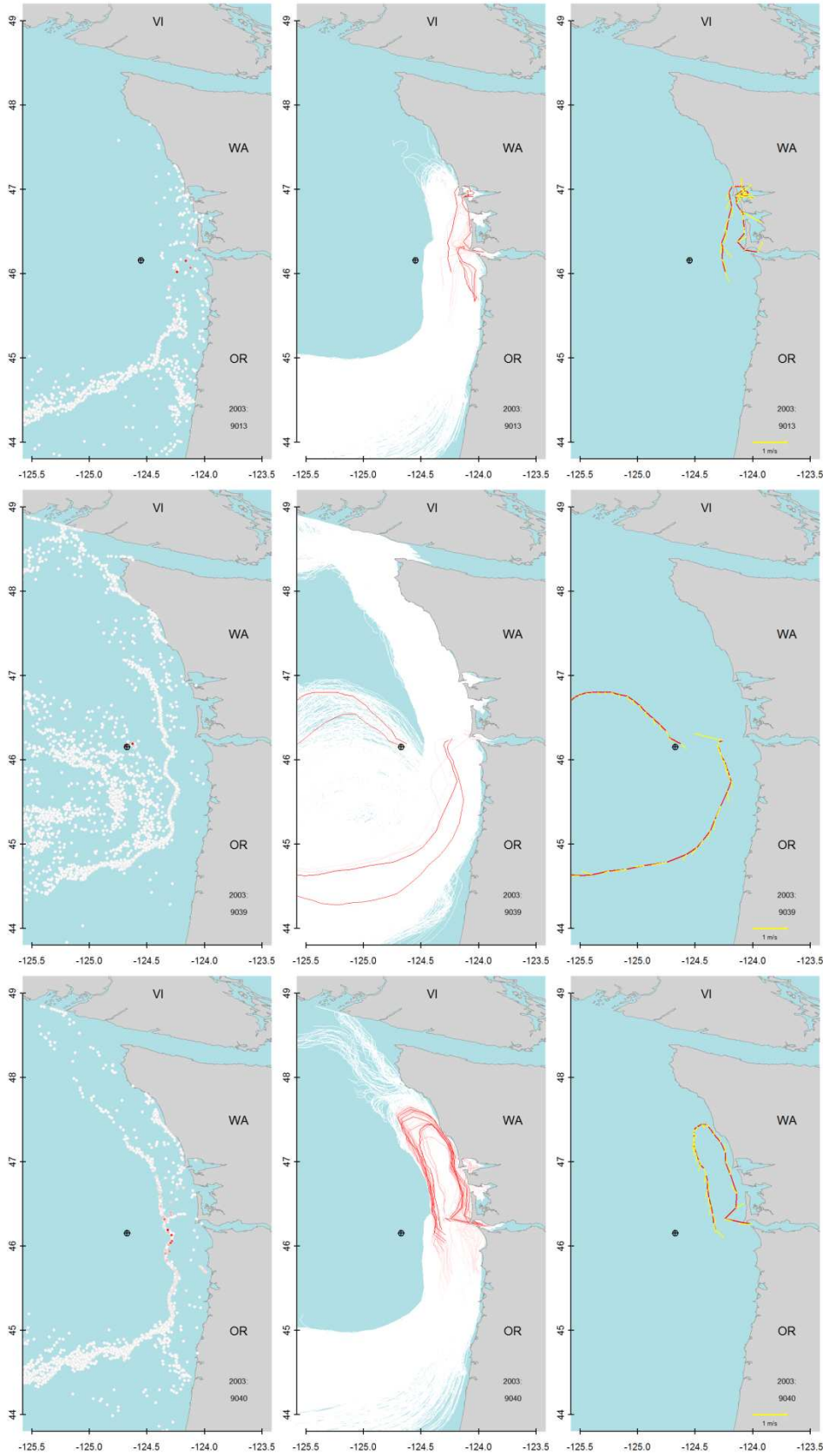


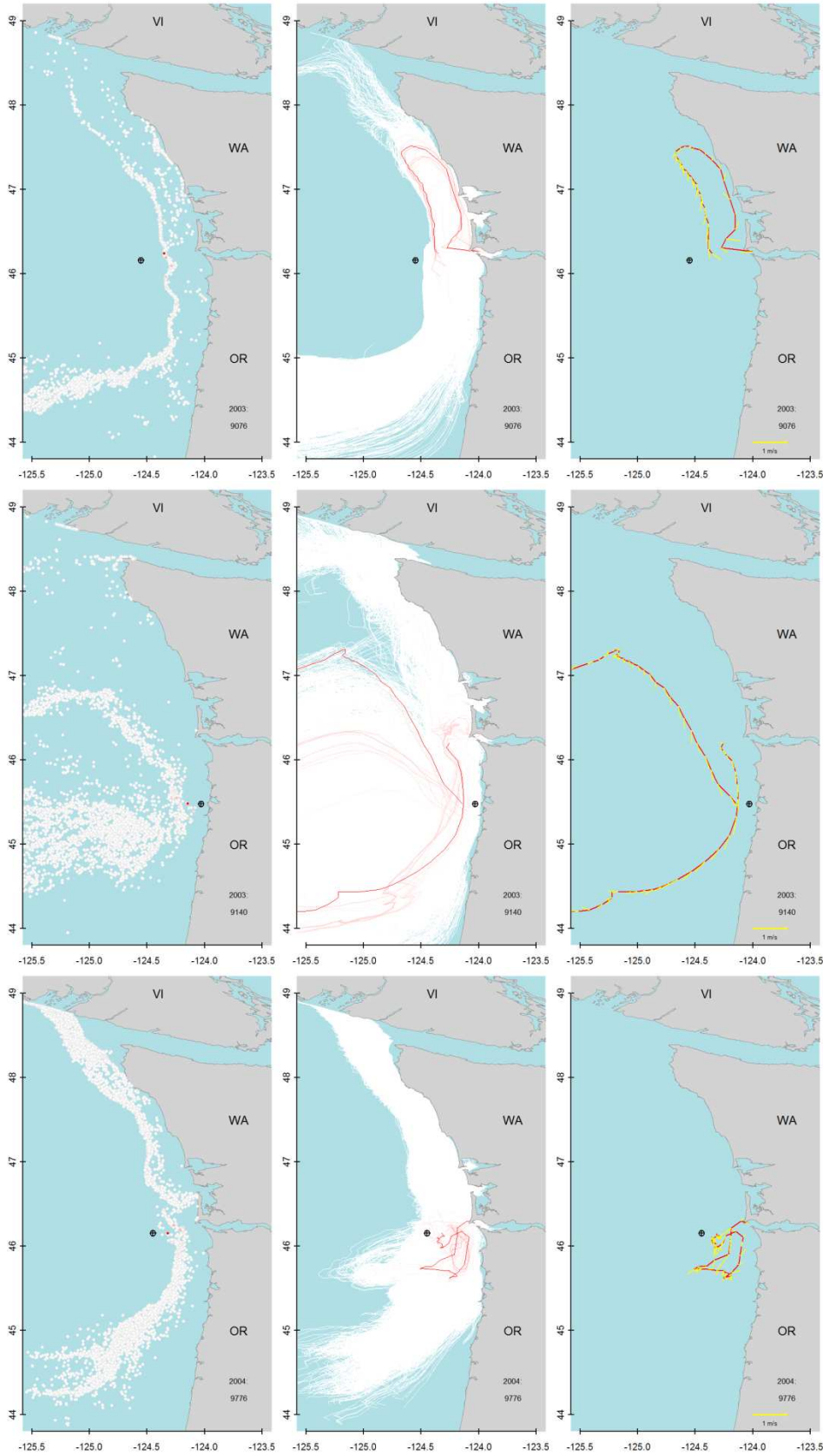


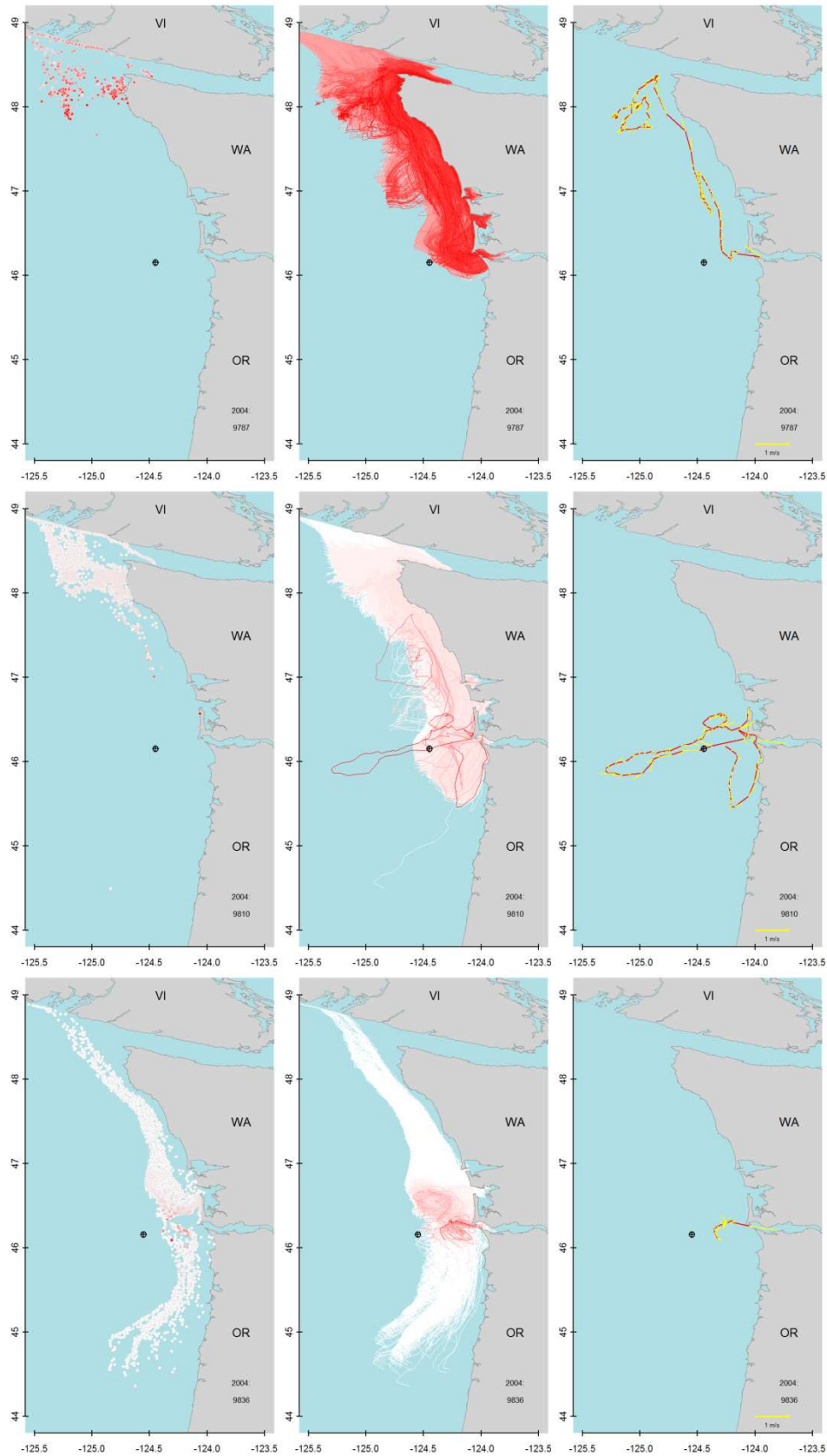


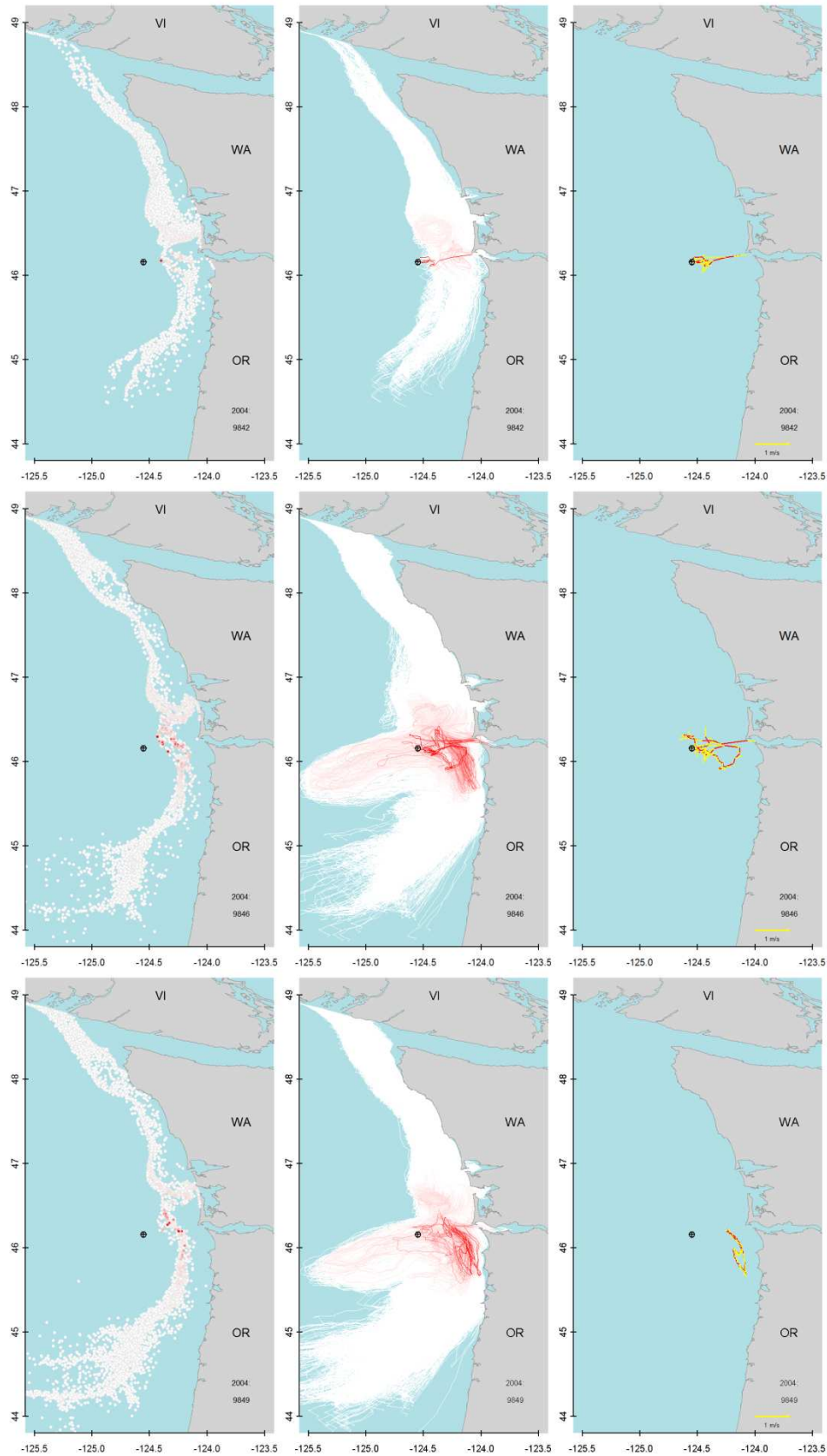


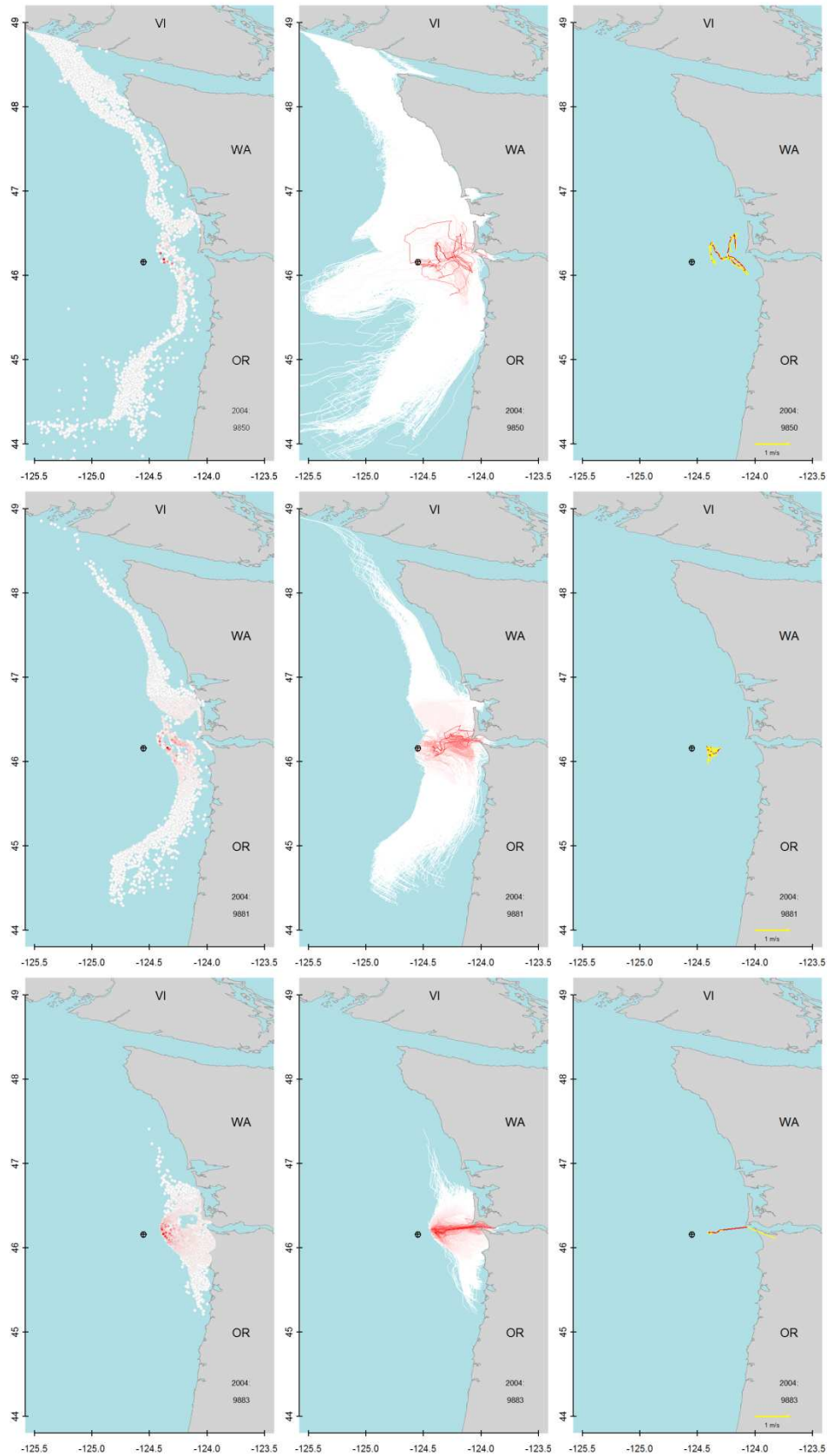


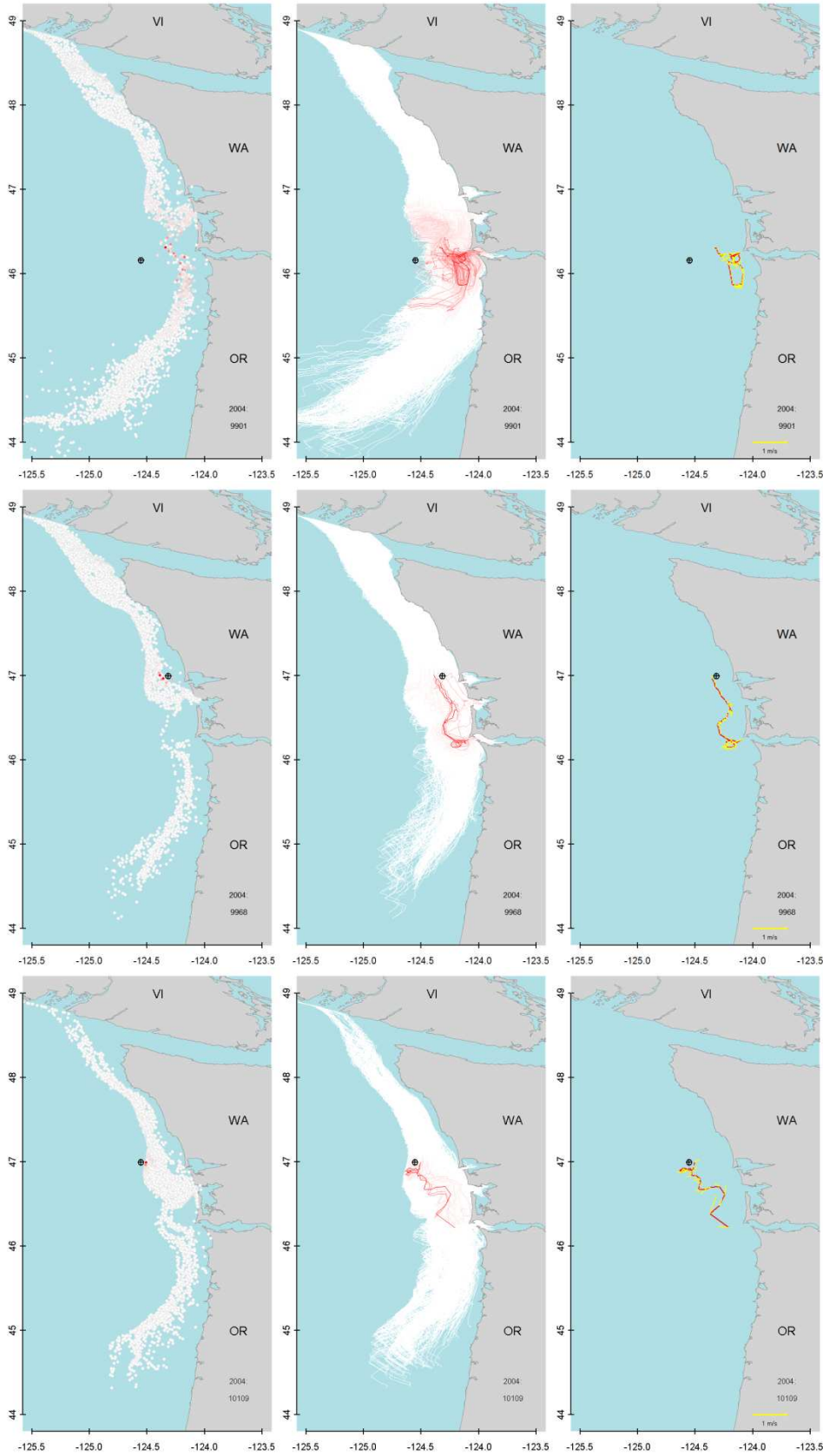


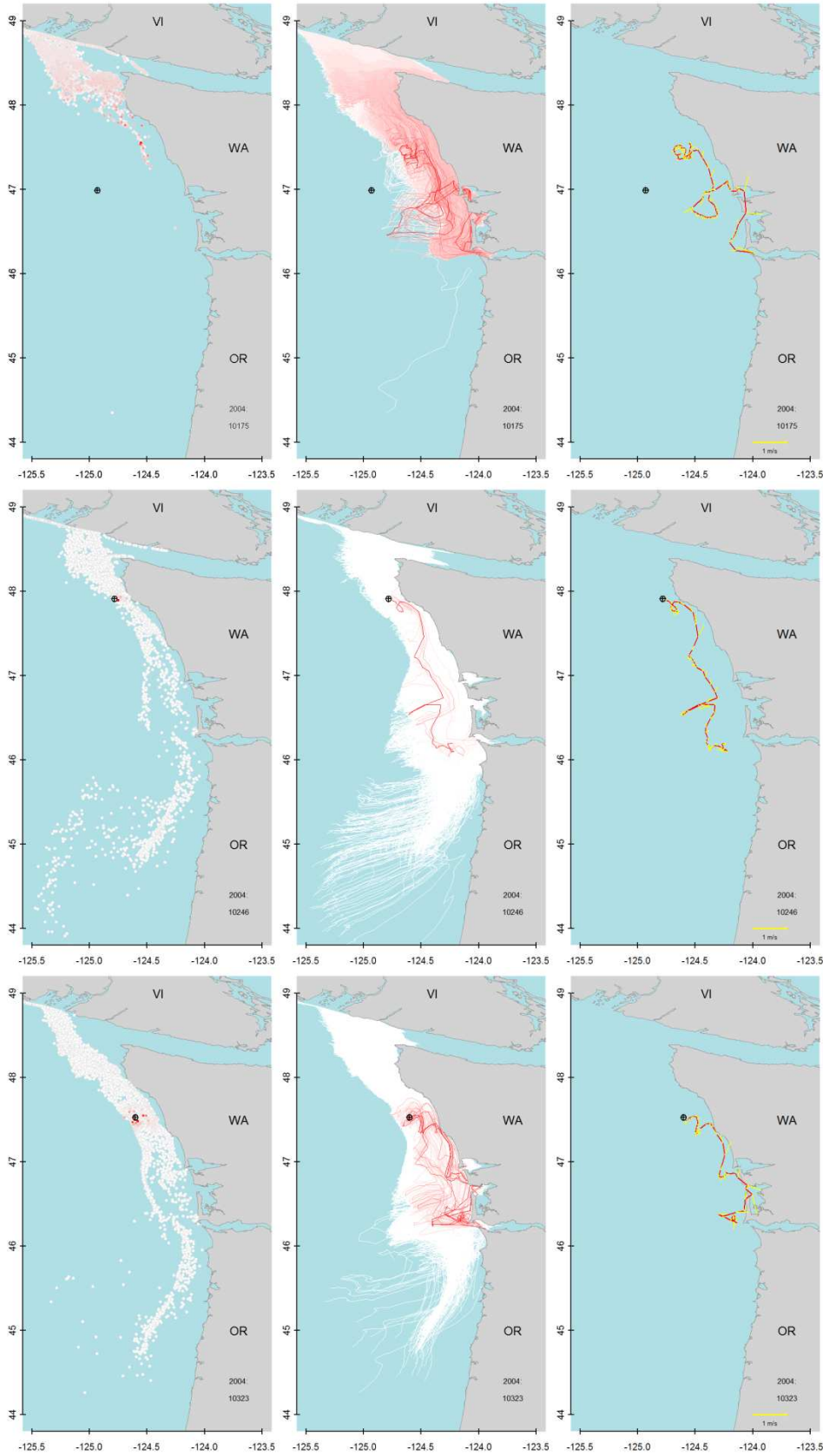


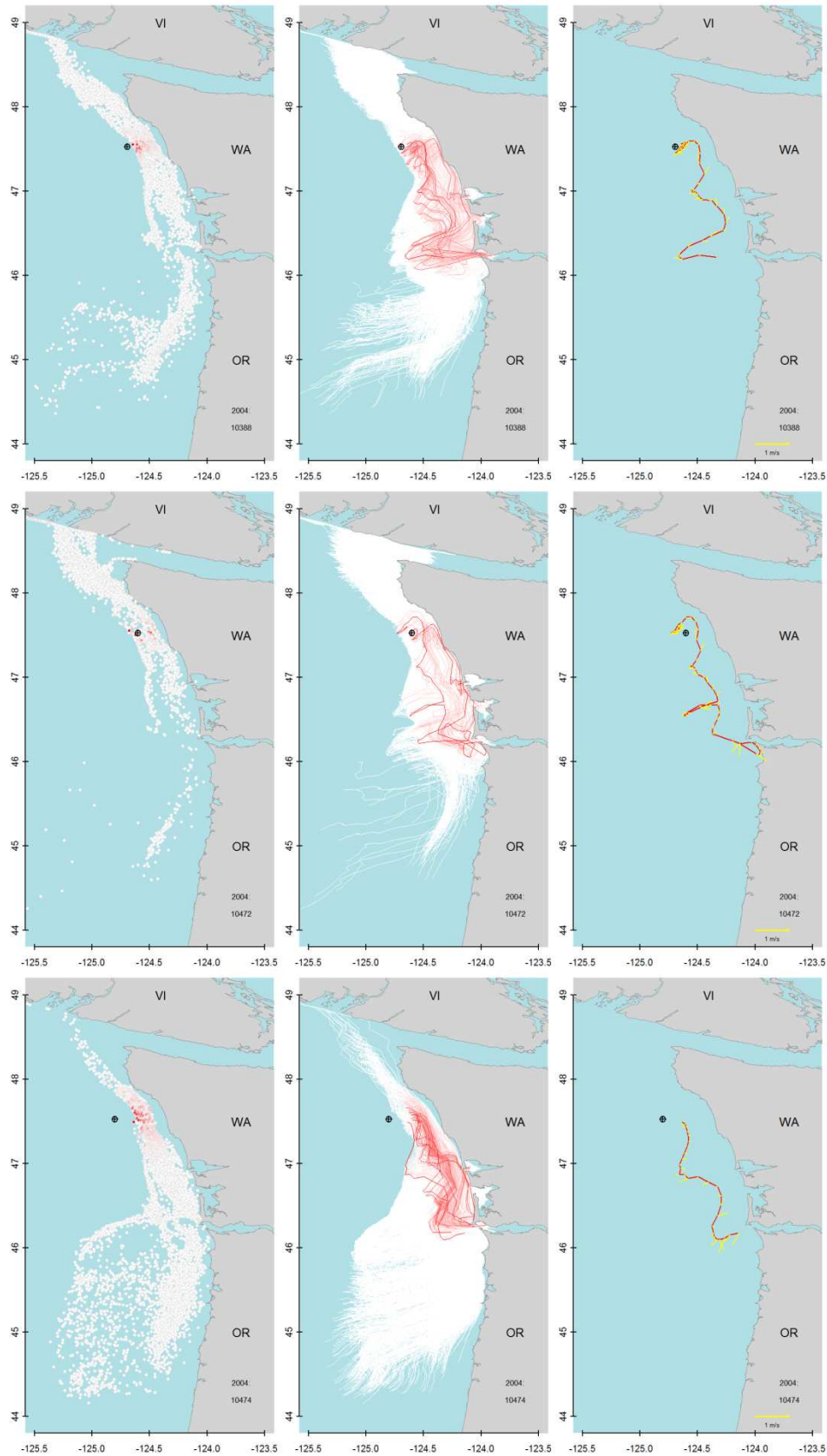


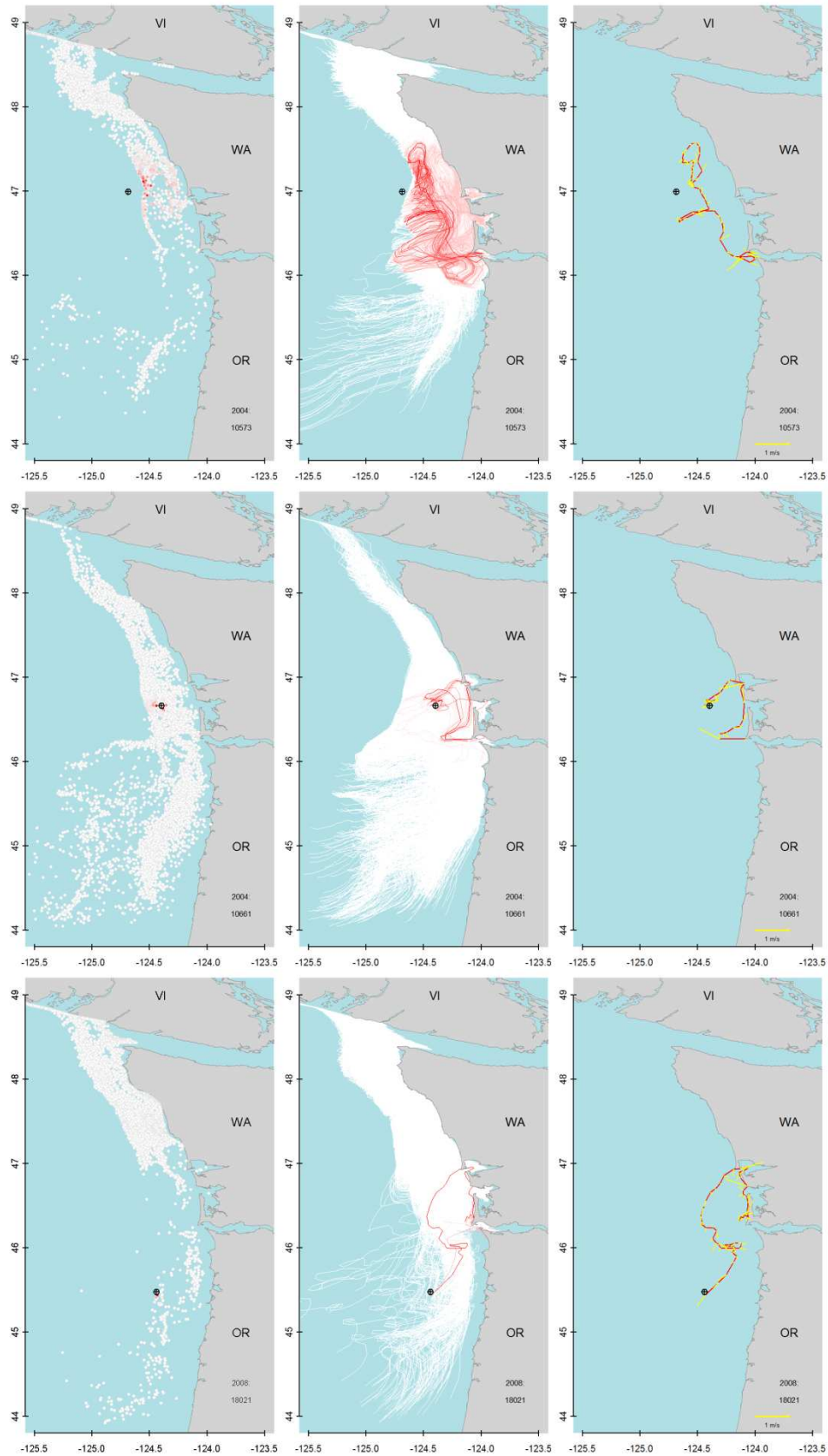


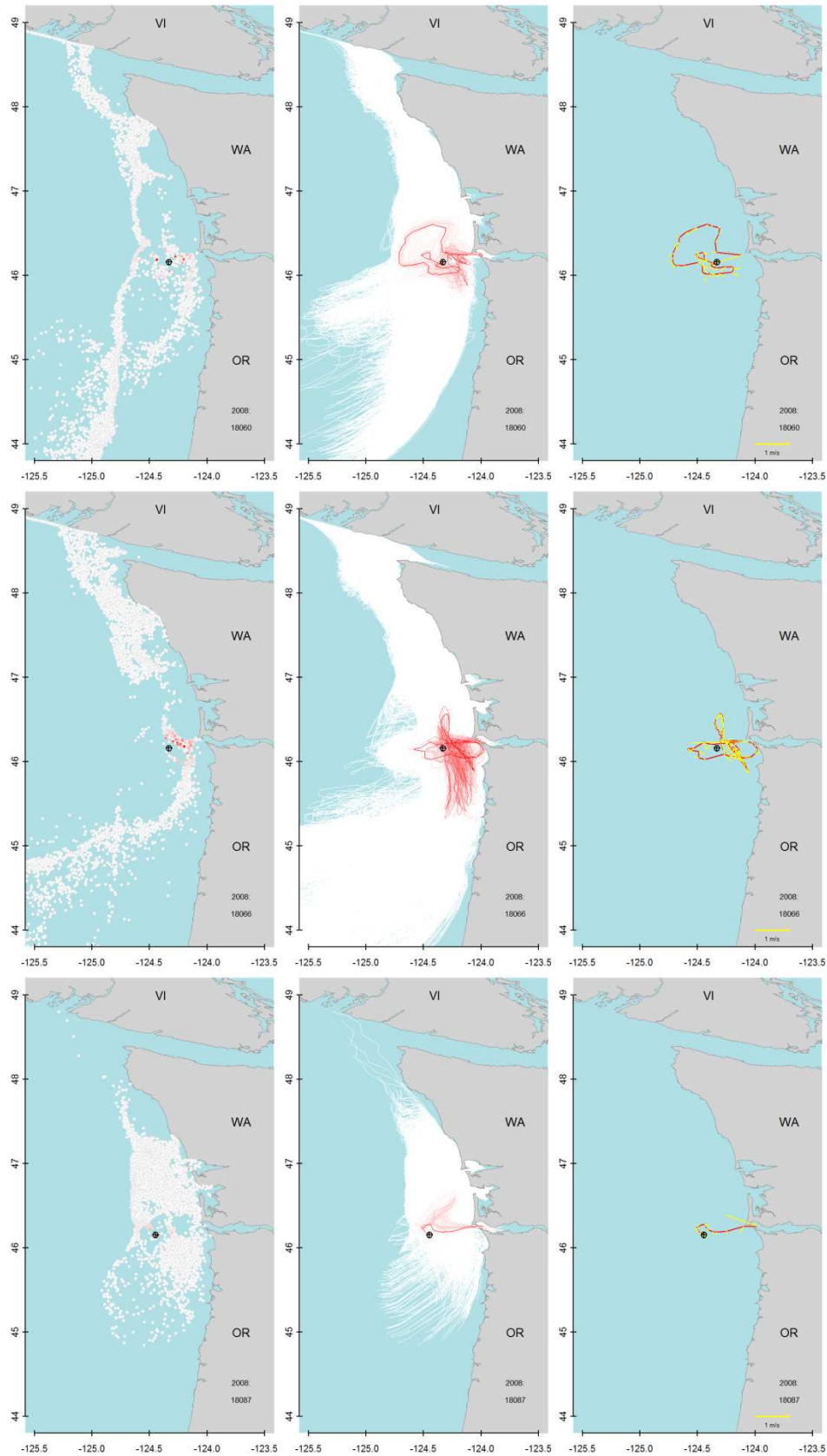


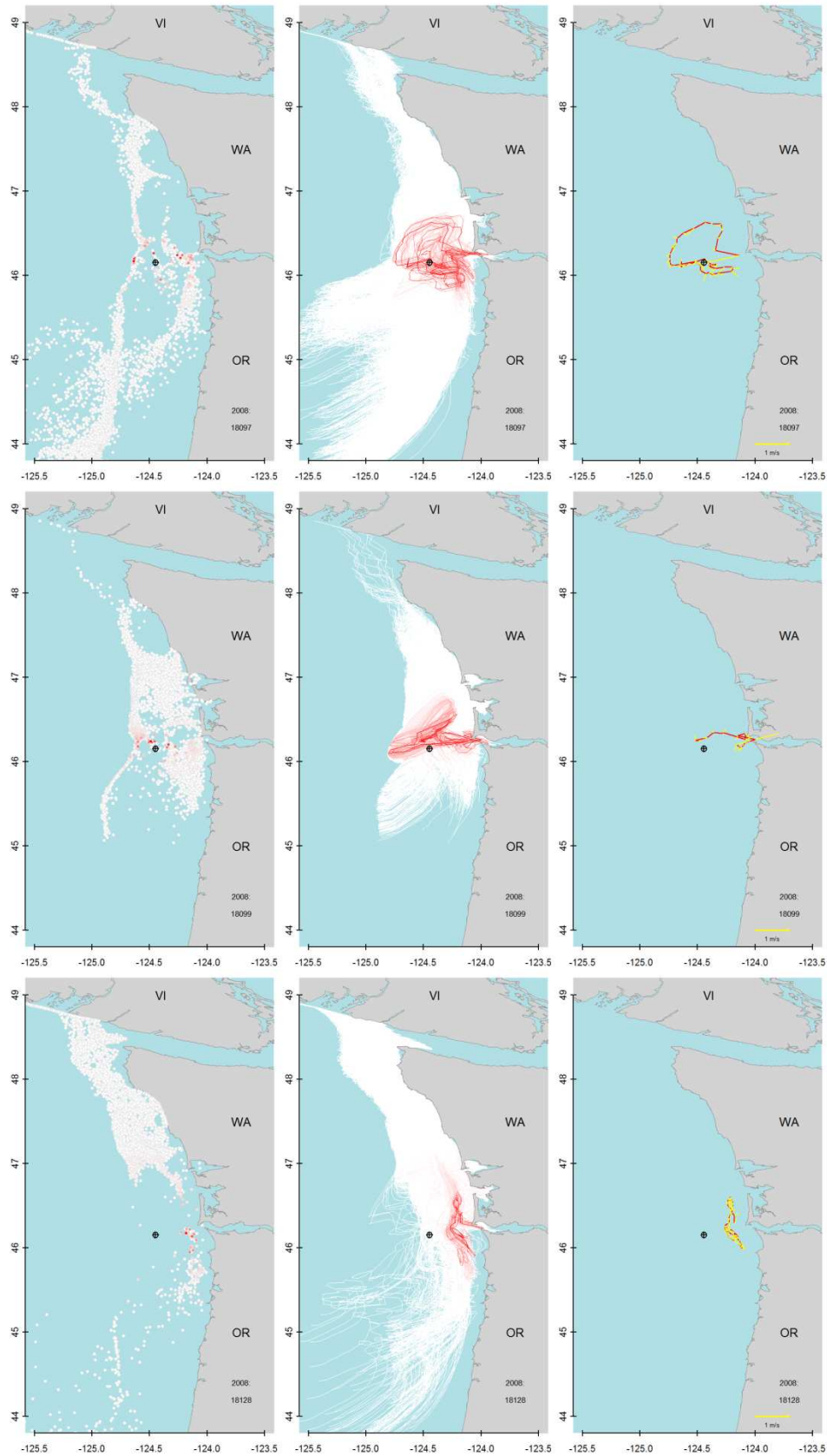


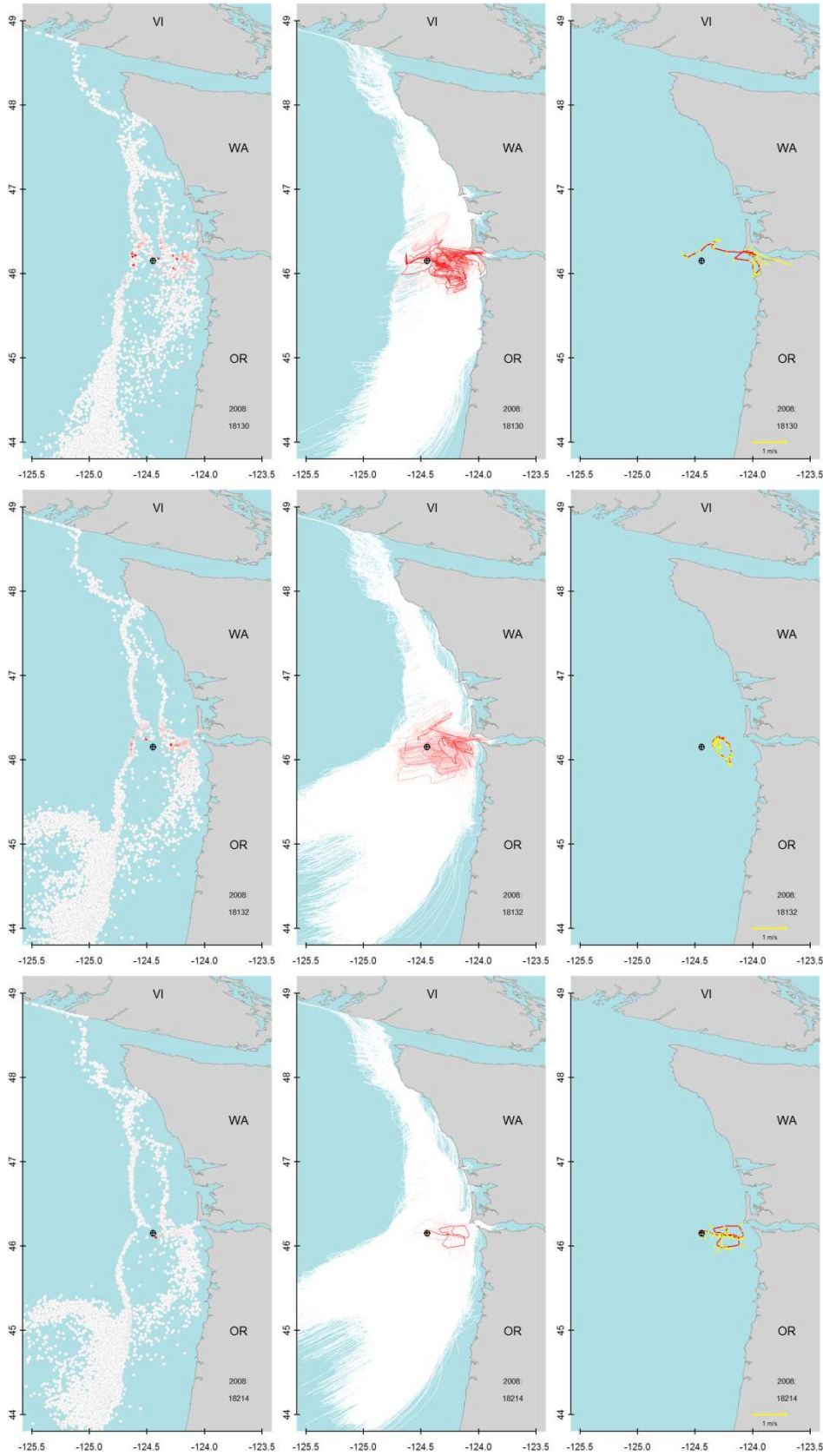


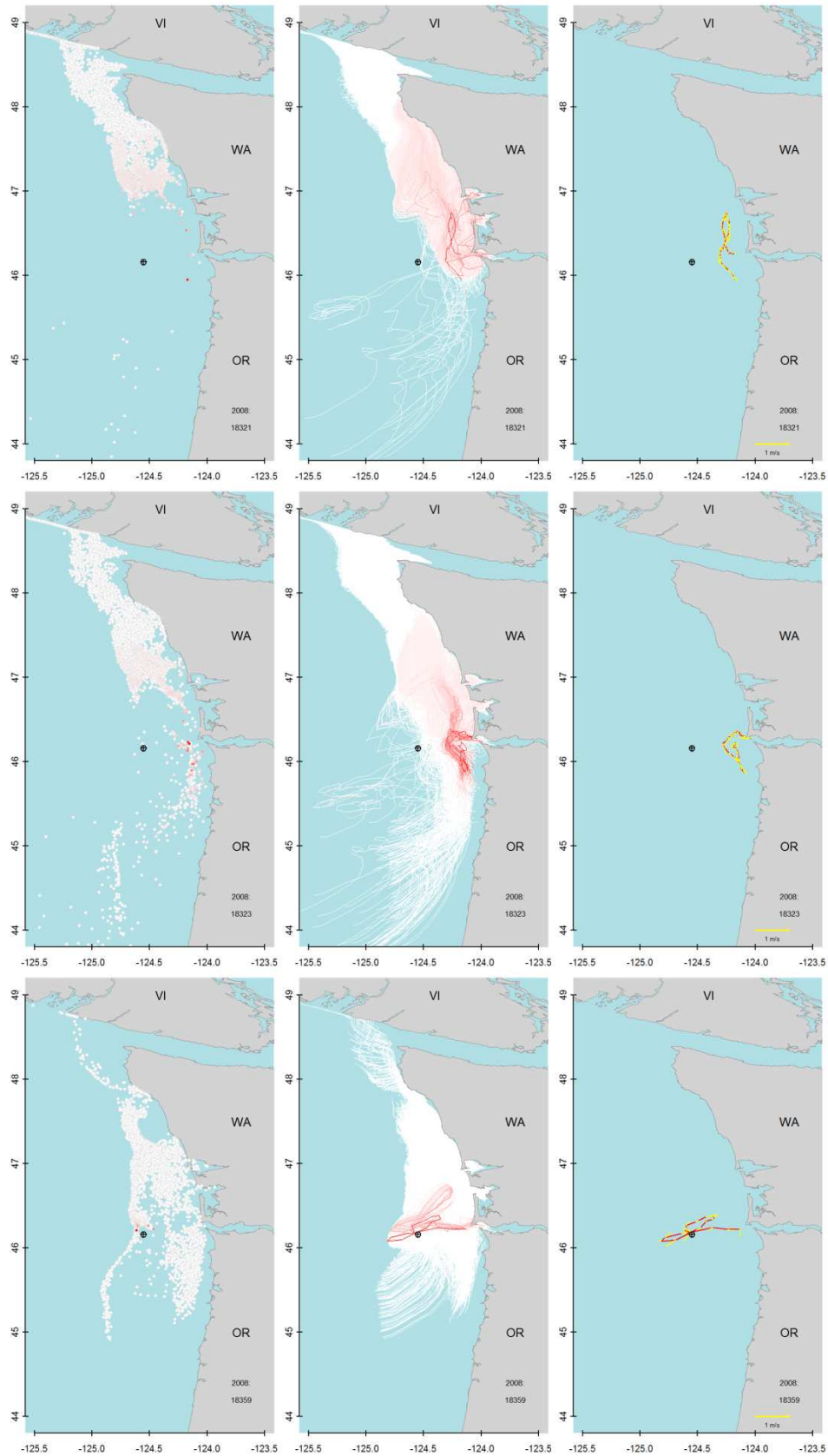


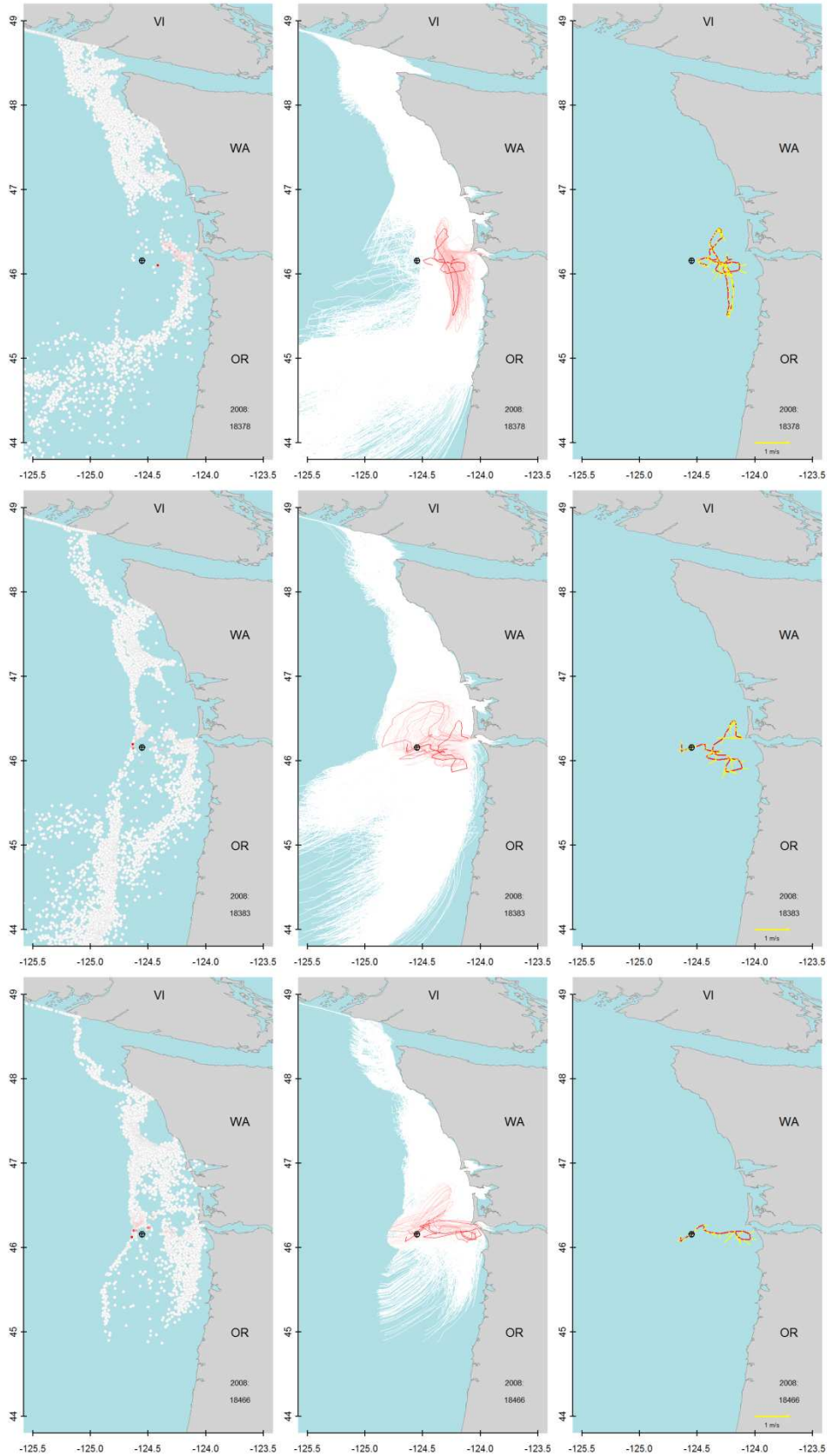


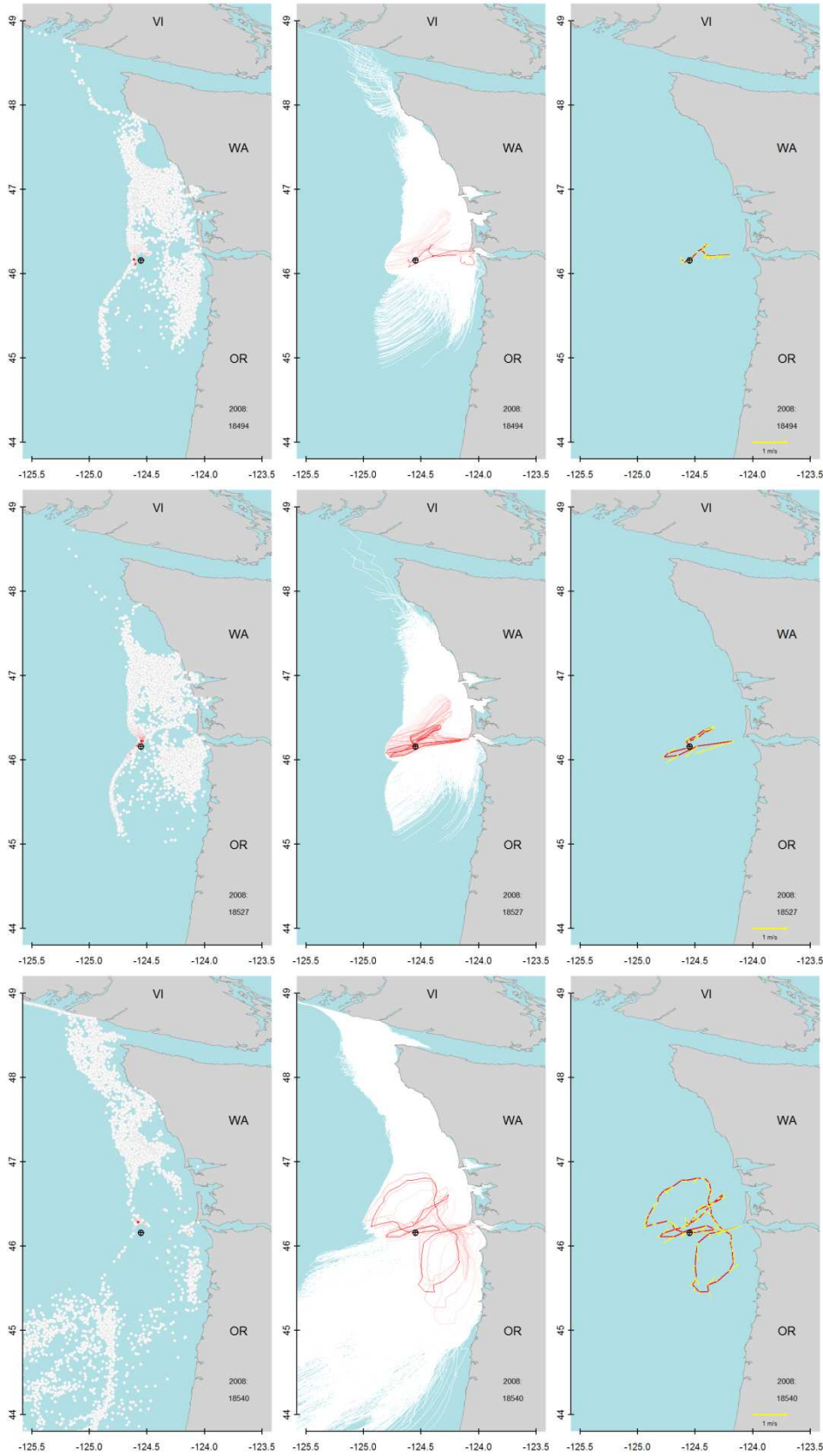


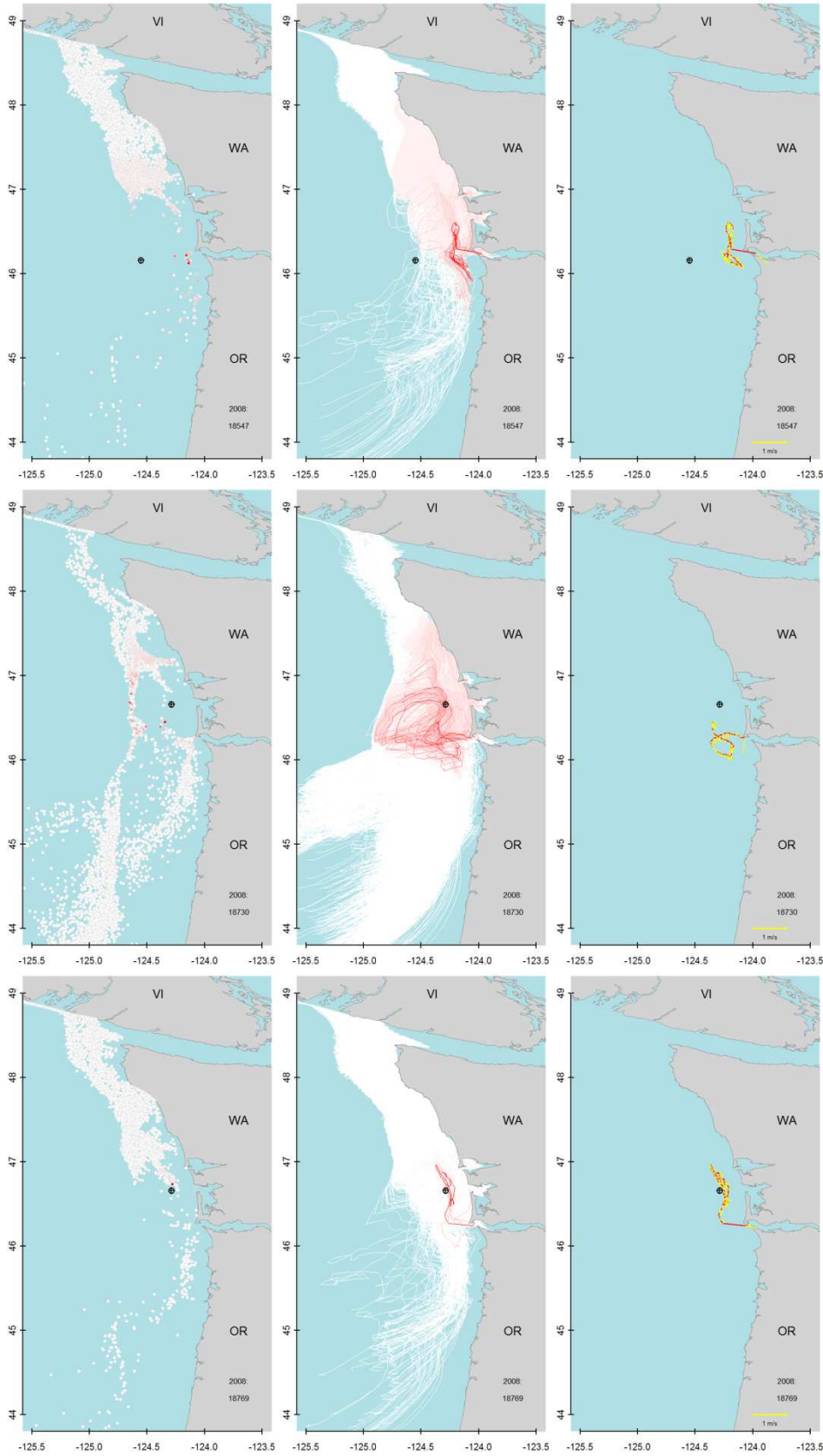


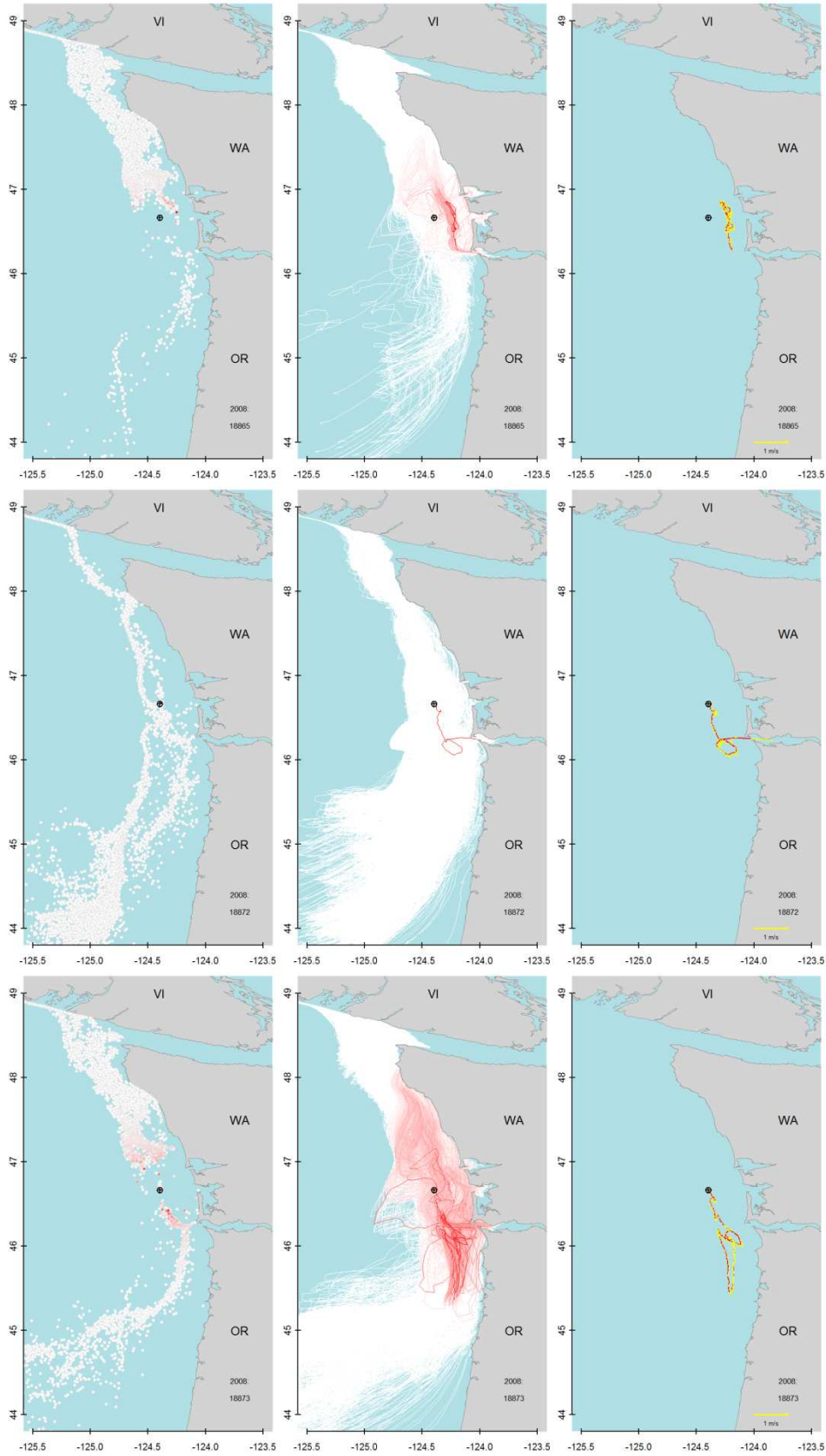


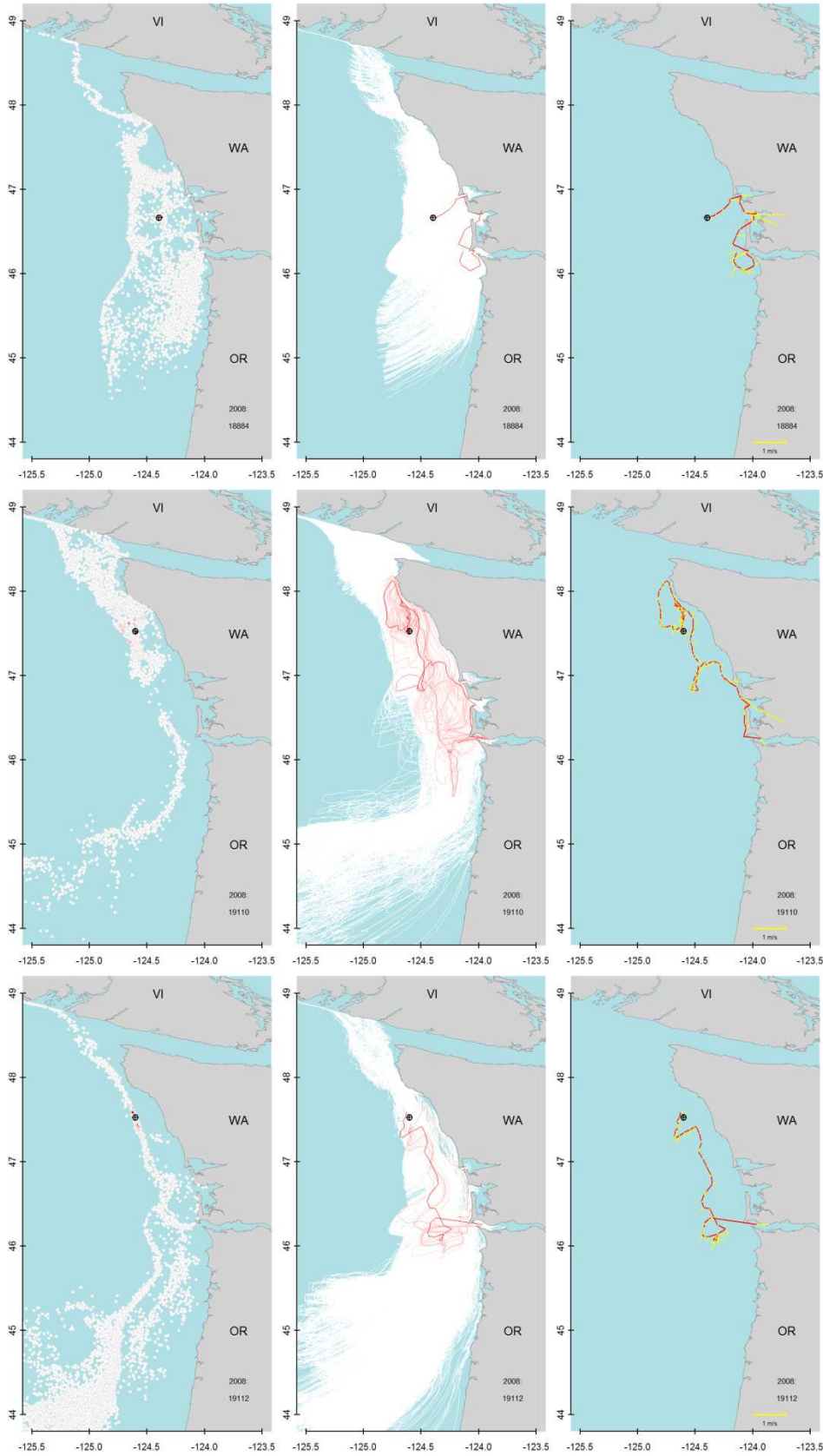


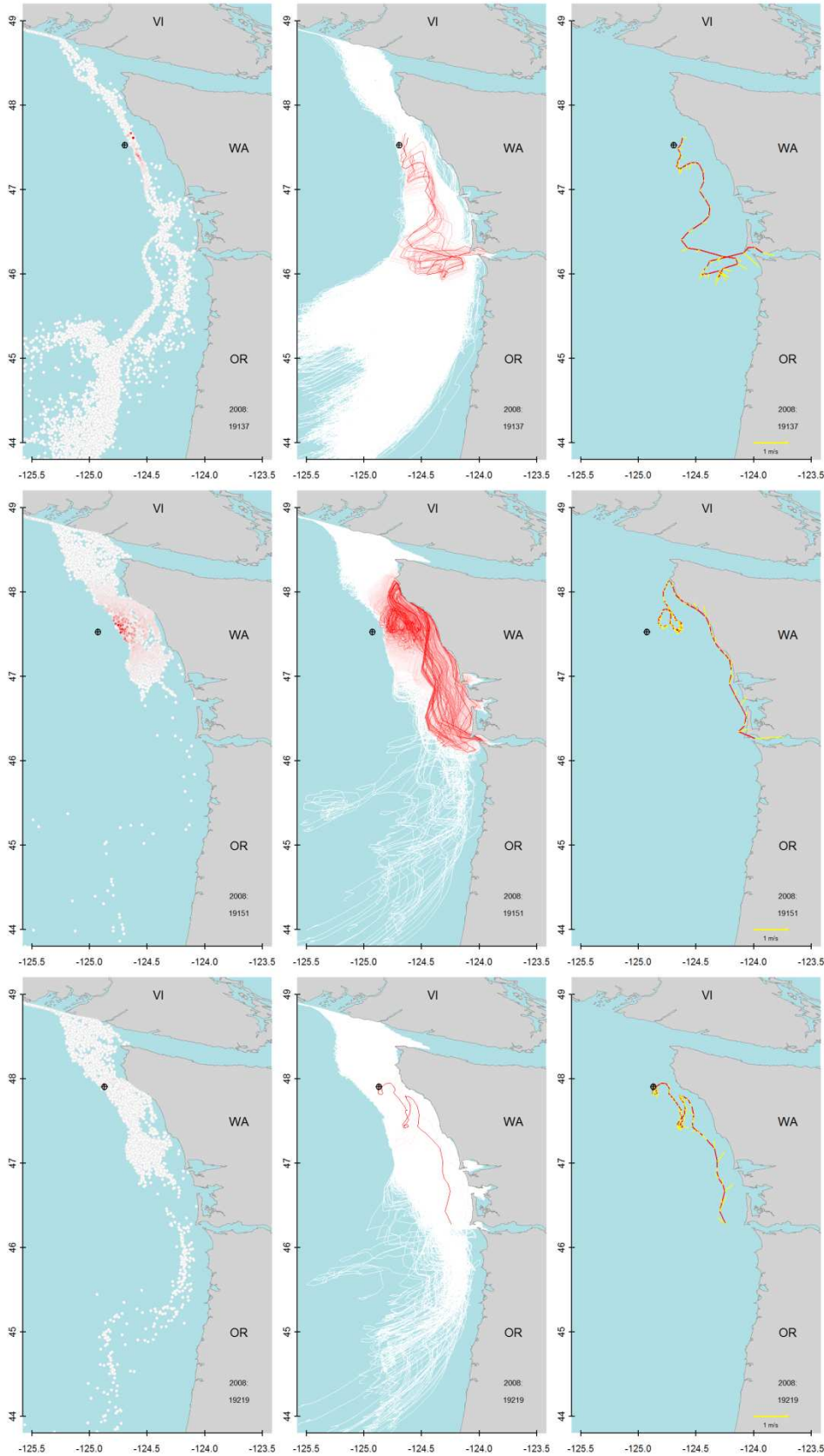


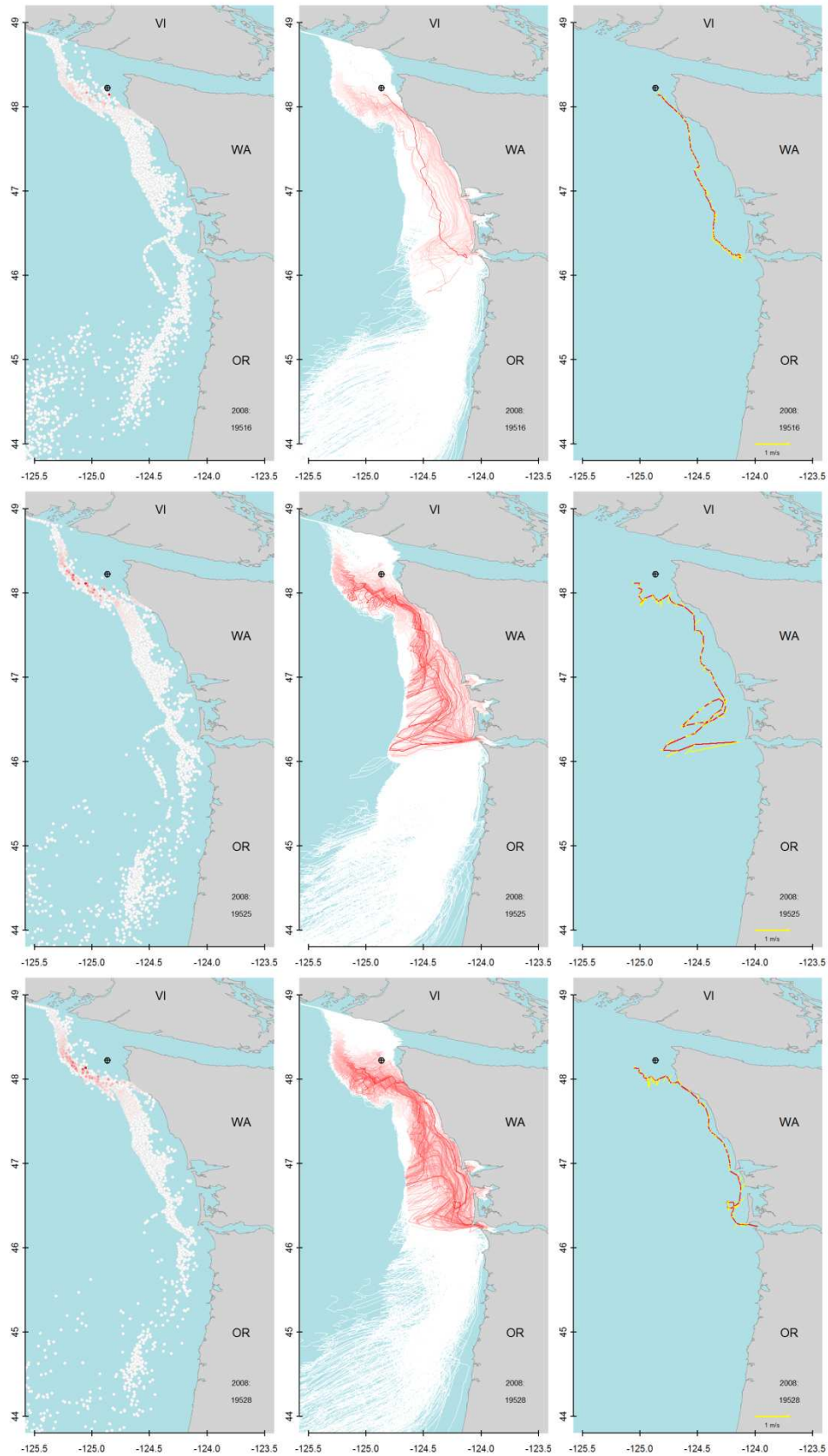


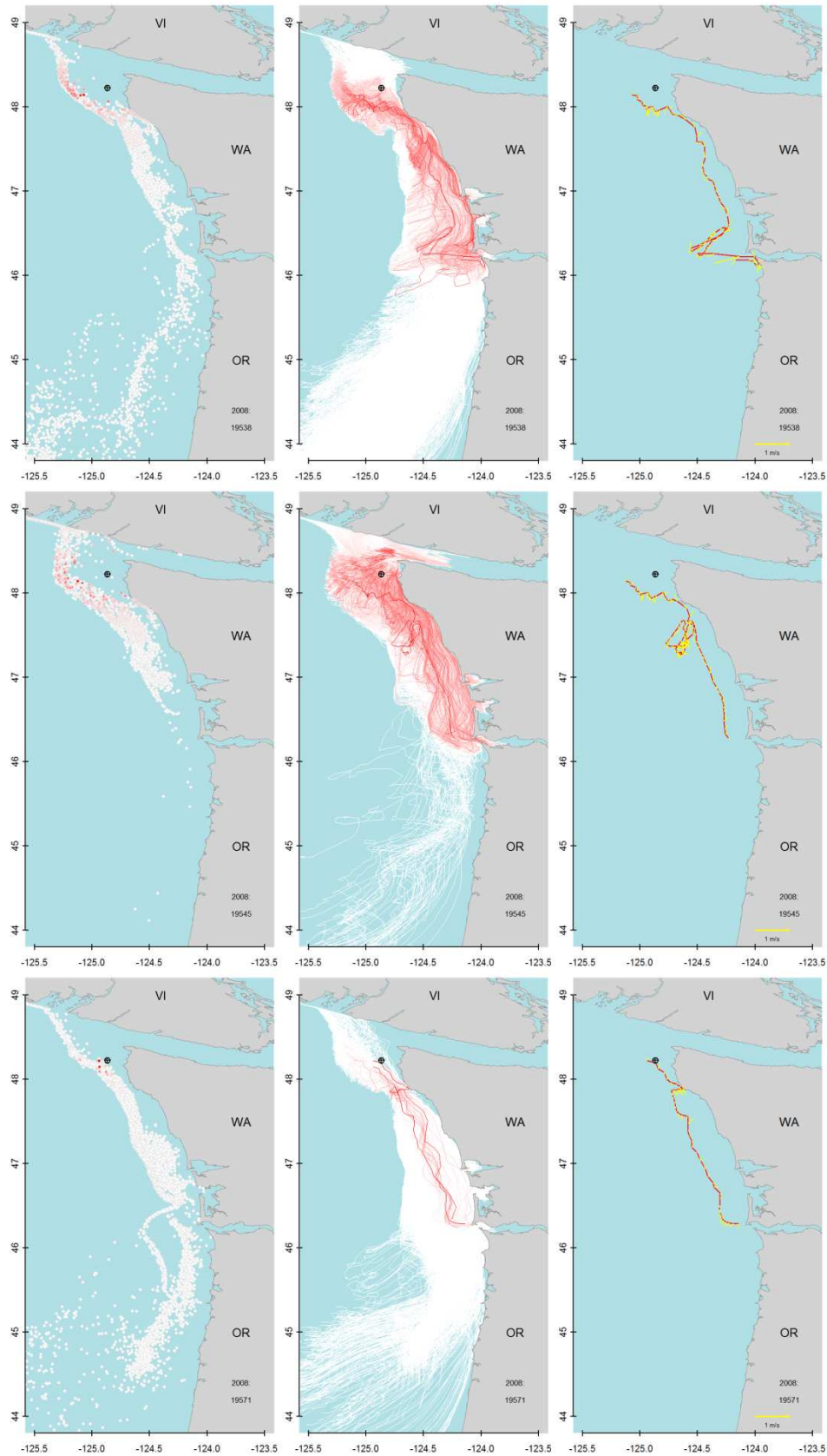


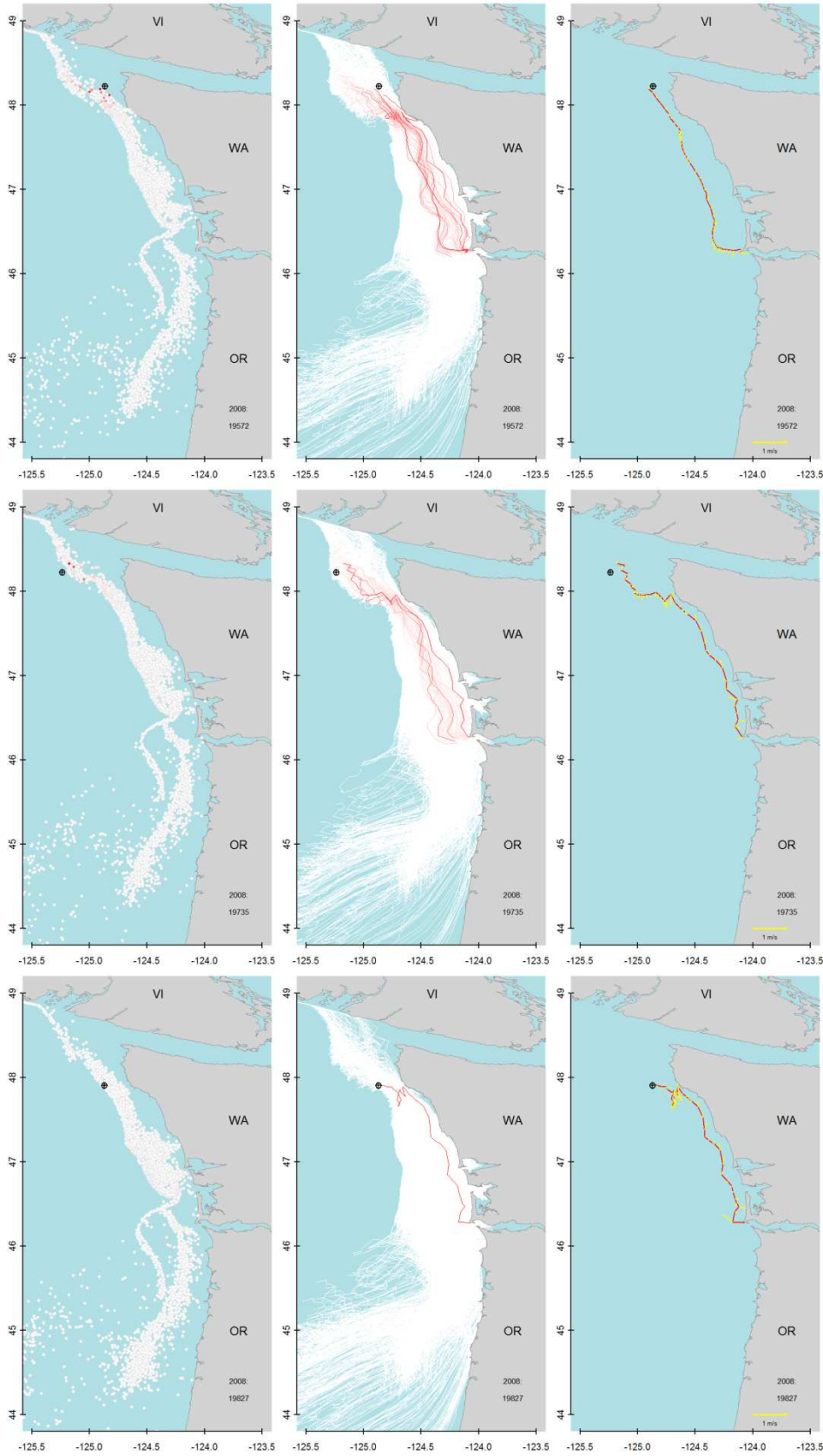


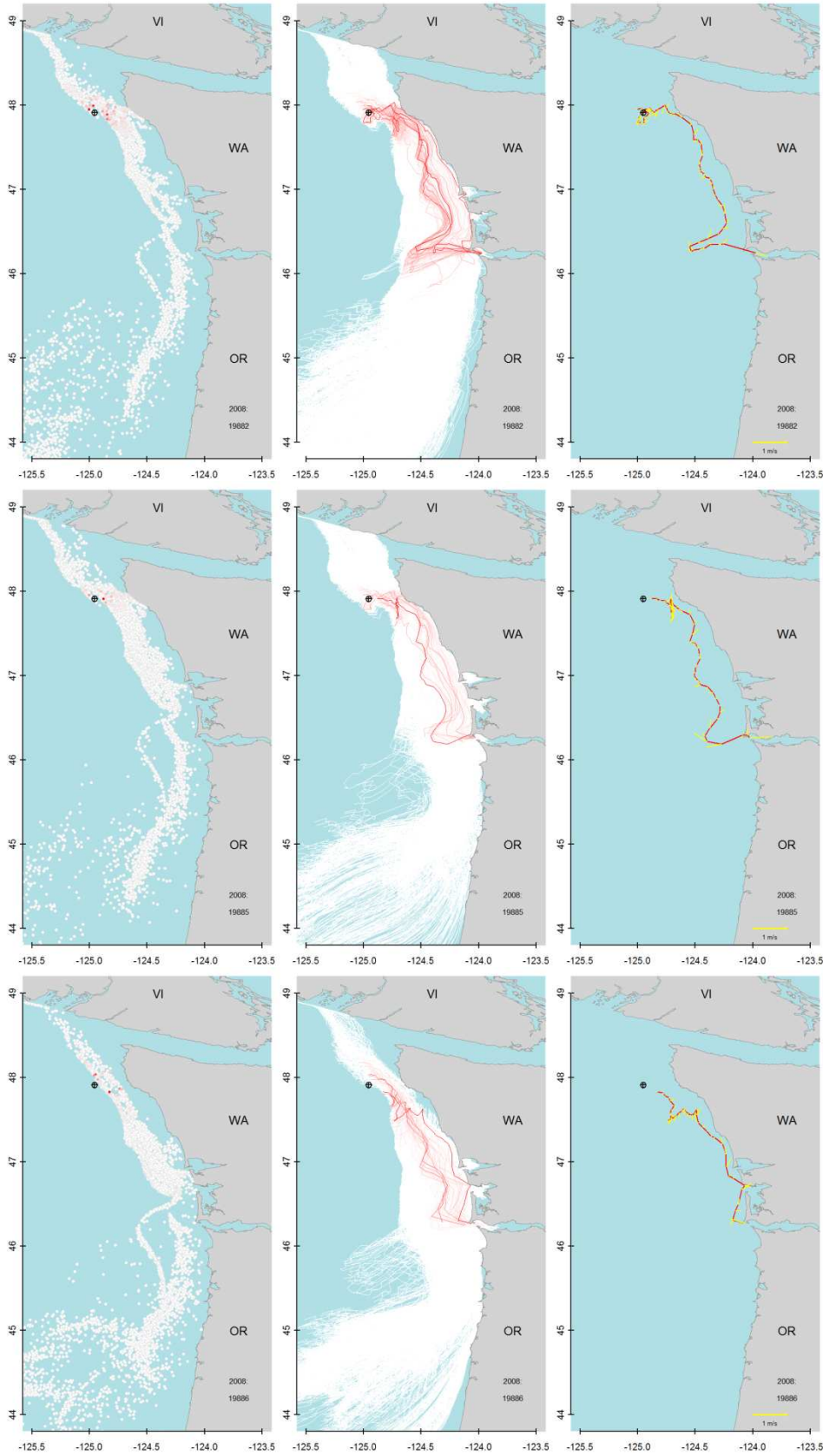


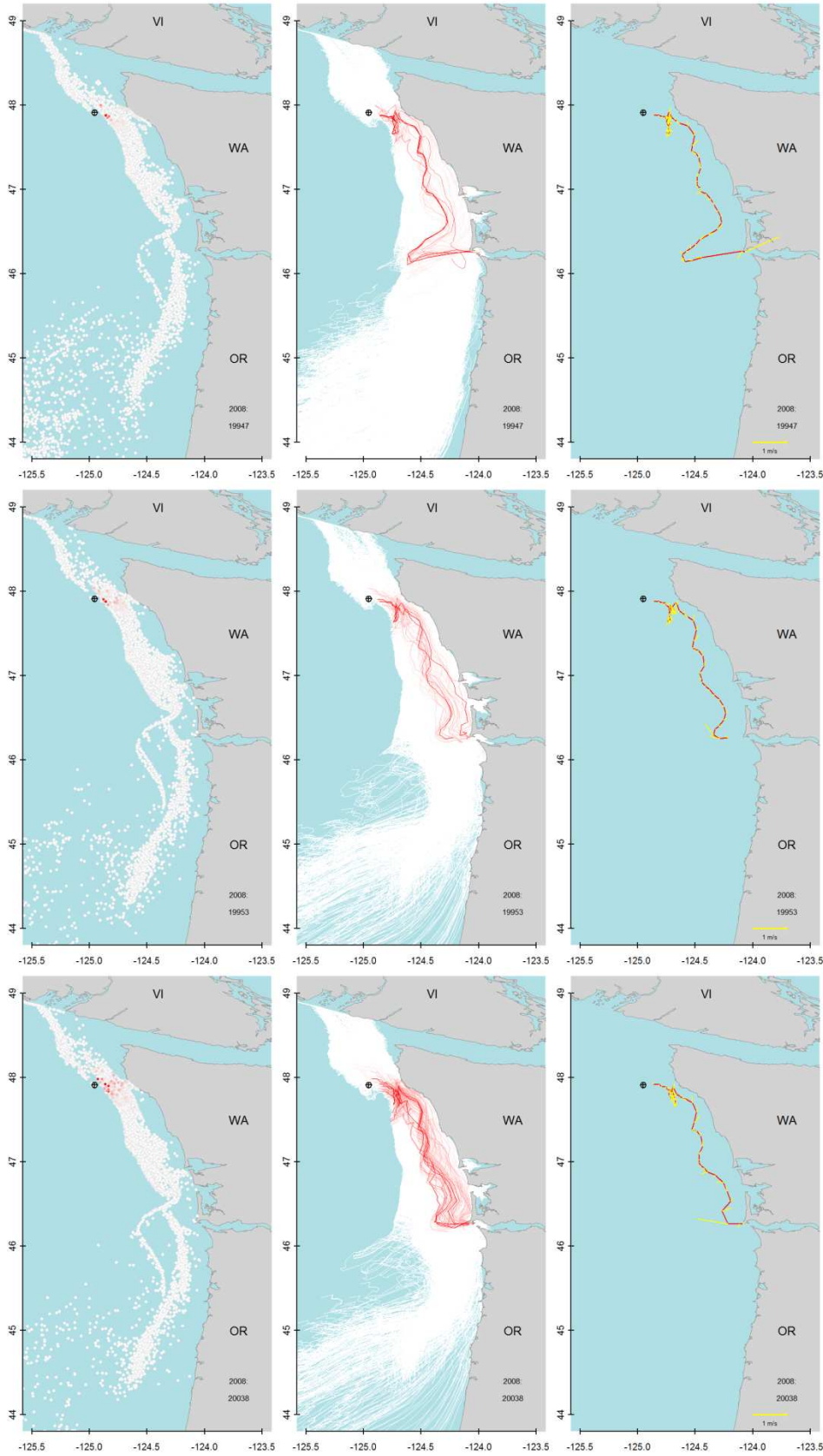


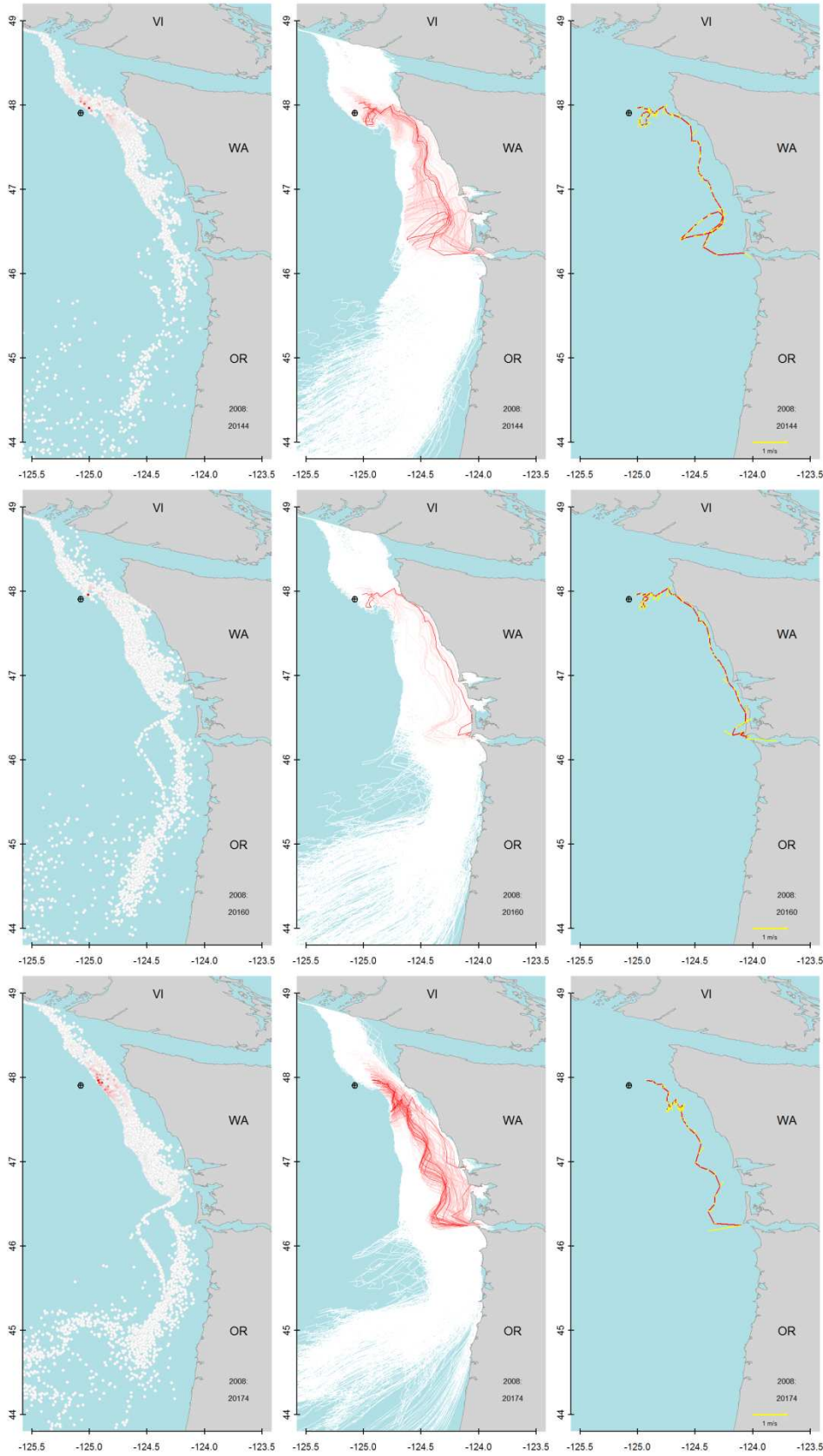


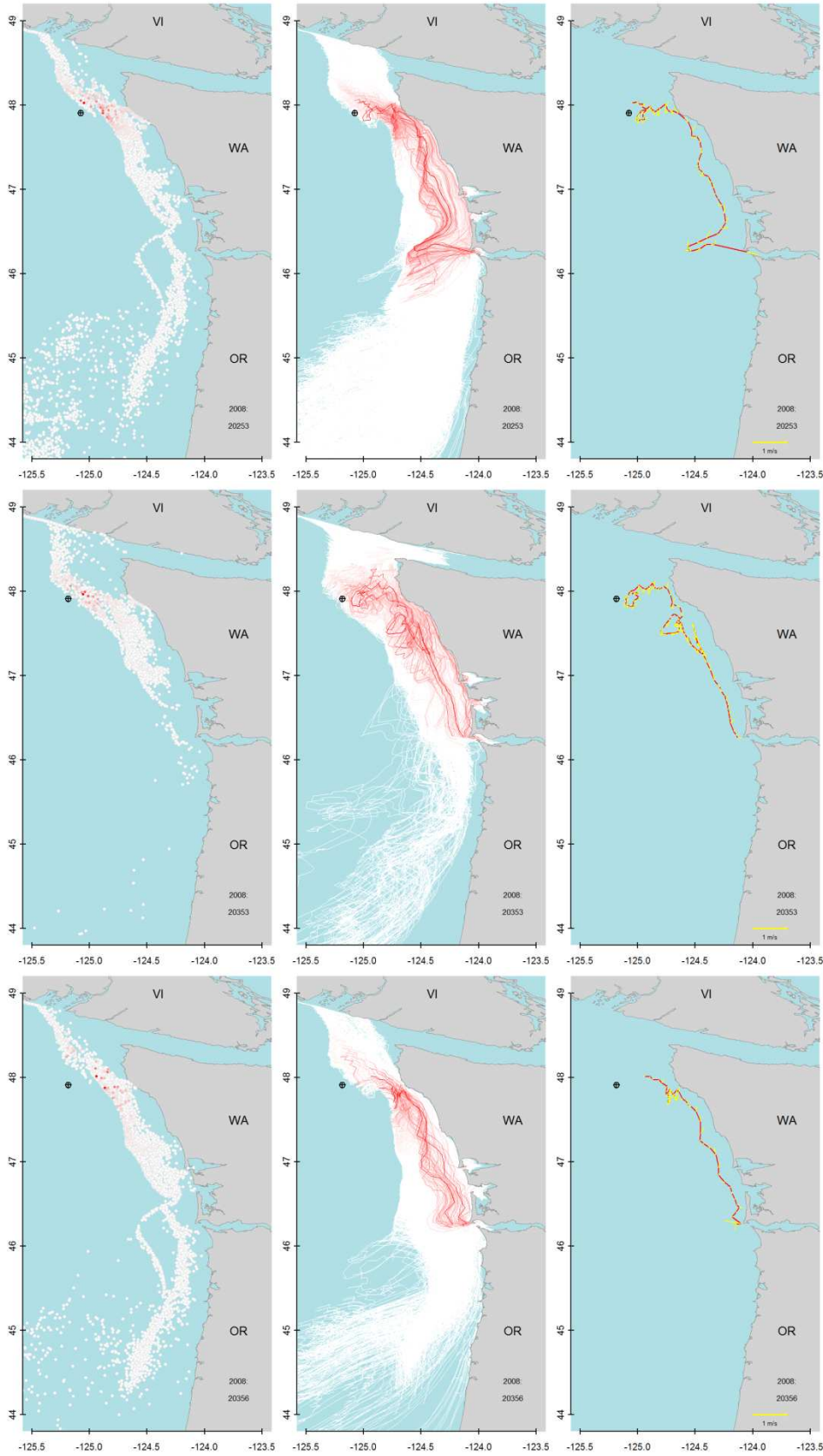


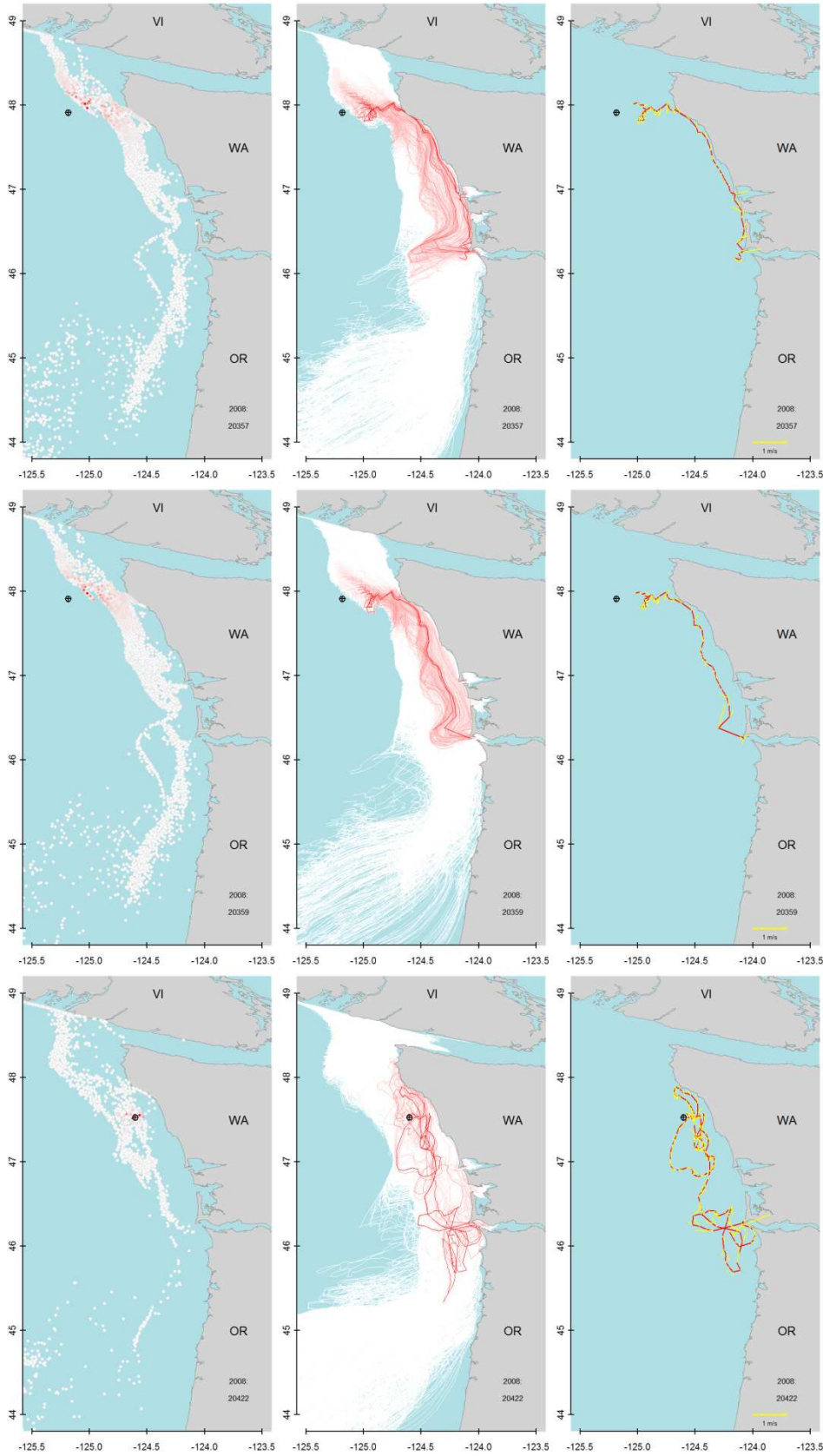


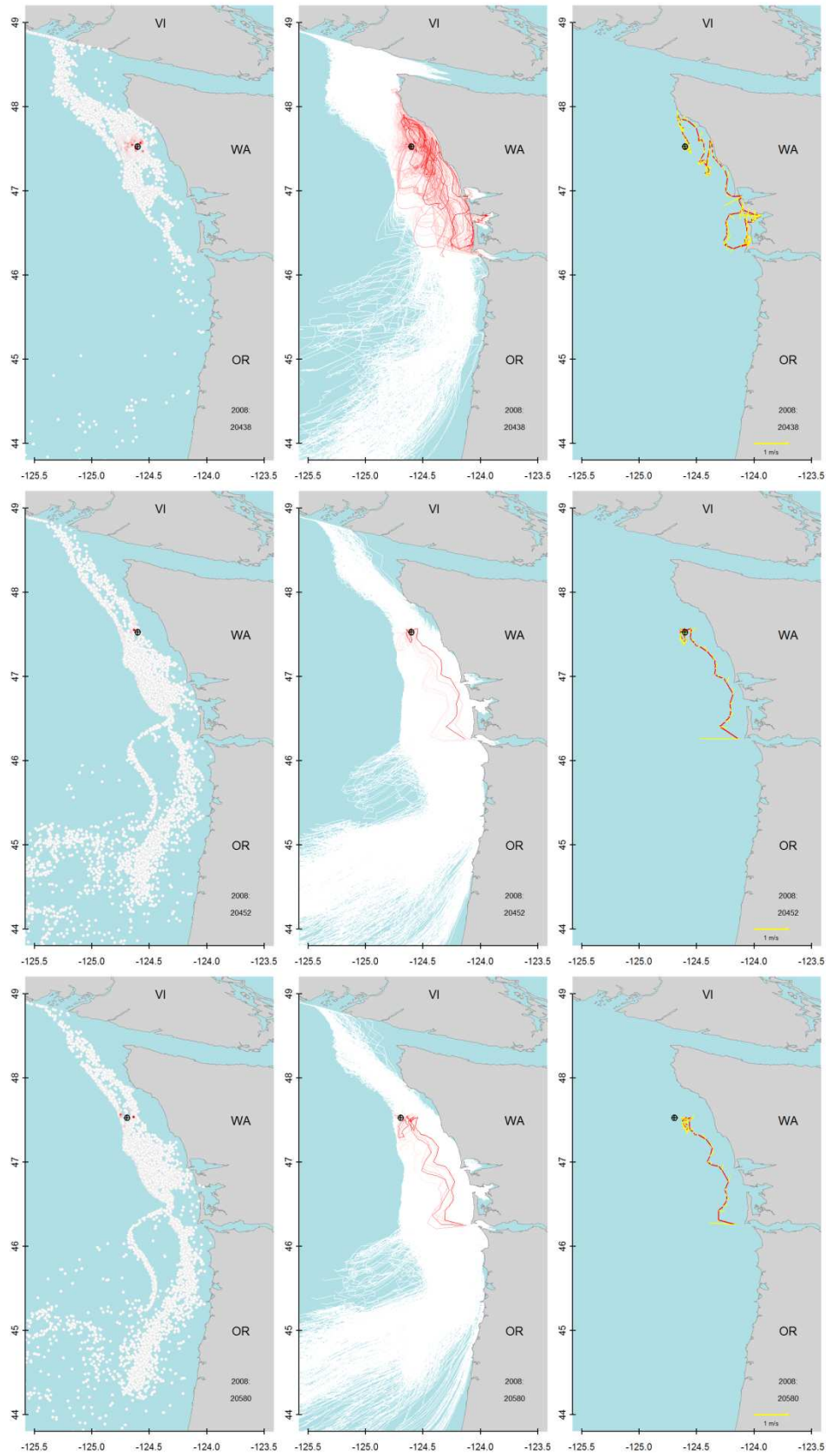


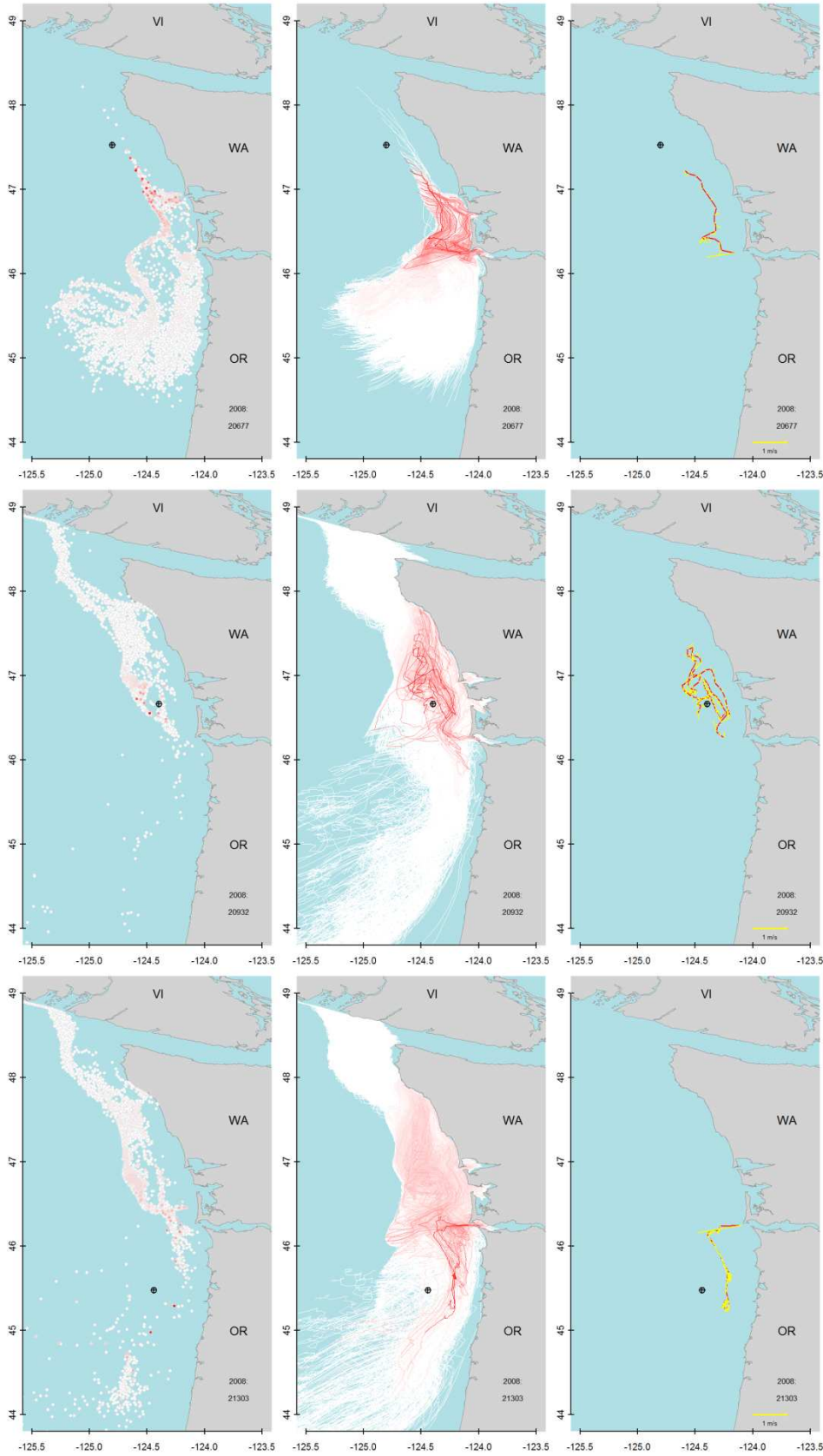












Chapter 5 Epilogue

In the early part of the 20th century, it was generally accepted that salmon go to sea, migrate only short distances, and randomly return to a stream nearby (Jordan 1904). Without direct evidence to the contrary, this seemed a logical assumption. Due primarily to the work of Charles Henry Gilbert and his students, the idea of homing began to spread, and was debated throughout the 1930's (Huntsman 1937, Rich 1937).

The concept of homing was debated for various reasons. First, it was unknown where fish migrate in the ocean. If salmon migrated long distances and then returned to their natal stream, the mechanism, which would have involved highly refined sensory capabilities, was difficult to fathom. In contrast, a random return to a nearby stream required just rheotactic behavior. But more than that, it was just such an amazing concept – that every fish could somehow know where to migrate, in the middle of the ocean, or at each fork in the river, over hundreds and even thousands of kilometers! Homing is quite extraordinary and this was an exciting time in salmon science.

We are now at another exciting time in the science of Pacific salmon. Within the past 15 years, the marine environment has gone from what most scientists considered a black box to an amazing source of information and understanding about salmon life history. Combining the current work with that of others (Weitkamp 2010, Tucker et al. 2012, Fisher et al. 2014) creates a clear picture showing that, just like the stock-specific behavior observed in the freshwater environment, salmon behavior and spatial distribution in the marine environment is stock-specific and consistent among years. Even within a freshwater life history strategy (e.g., yearling Chinook salmon), there are distinct marine behaviors and spatial distributions (David Teel, NOAA Fisheries, unpublished data). The sensory abilities required to maintain these distributions go beyond responding to their immediate biotic and abiotic environment. Salmon have a compass sense and can determine their specific swimming direction. They have a clock sense, adjusting behavior throughout the season (this we already knew, as they also arrive at their natal stream with great temporal precision). Salmon also have some sort of map sense, avoiding

particular areas and consistently aggregating in others. And each of these attributes is stock-specific!

With recent advances in technology, such as the miniaturization of acoustic and other tagging techniques, tracking salmon during their marine migration will continue to provide a wealth of information. New tools, such as the individual-based model described here, will allow us to integrate the data and ideas coming from new technologies. Soon, the ocean 'black box' will be just another stage in the well understood ecology of the salmon life cycle.

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