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UNIVERSITY OF CALIFORNIA, IRVINE

Model Estimation of the Effect of Wind-driven Flow and Freshwater Plumes on the Transport and Environmental History of Marine Invertebrates Larvae

MASTER'S THESIS

submitted in partial satisfaction of the requirements for the degree of

MASTER OF SCIENCE

in Engineering

by

Shukai Cai

Thesis Committee: Assistant Professor Kristen A. Davis, Chair and Primary Advisor Associate Professor Amir AghaKouchak Assistant Professor Cascade Sorte

2017

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DEDICATION

I would like to express my sincere thanks to my parents. Without their support, I could not have had an opportunity to continue my M.S study at UCI. Their support makes my life joyful and gives me a chance to do what I want to do.

I express my thanks to Professor Kristen Davis, Aryan Safaie and Emma Reid, who made my time staying at the Coastal Dynamics Lab enjoyable and help me to learn a lot. Professor Davis' guidance directed me from a student who had no idea what Matlab was to one that has the ability to conduct this entire research project by using Matlab. The memory of the scene in which she went through Matlab codes one line by one line with me two years ago is still vivid in my mind. Also, I need to thank her support for each option I have made in my career during my program at UCI.

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I thank Professor Davis for giving me the opportunity of being a Graduate Researcher, which gave me a chance to continue my research at UCI.

ABSTRACT OF THE THESIS

Model Estimation of the Effect of Wind-driven Flow and Freshwater Plumes on the Transport and Environmental History of Marine Invertebrates Larvae

By

Shukai Cai

Master of Science in Civil and Environmental Engineering University of California, Irvine, 2017 Assistant Professor Kristen A. Davis, Chair

This thesis investigates the physical processes that govern the transport and environmental history of marine invertebrates during their larval stage, focusing on the role of wind-driven flow and freshwater plumes. Additionally, this work examines how release location and swimming behavior modifies the path and environmental history of a larval particle. The research was conducted by using Regional Ocean Modeling System (ROMS) and a particle-tracking code to estimate the transport of larval-stage invertebrates and their environmental history over the larval duration period (particle paths) in parameters such as temperature, salinity and phytoplankton concentration. Results indicate that swimming particles are retained closer to shore and to their release location compared to passive particles (no swimming behavior). The freshwater plume affects alongshore dispersal of particles released to the south of the Columbia River during downwelling periods and weak upwelling periods, and particles released to the north of the river during downwelling periods. Furthermore, wind-driven circulation can influence the environmental exposure of larval stage marine invertebrates. Particles north of the Columbia River mouth saw greater variation in temperature and salinity, and higher phytoplankton concentration as upwelling index increased. As upwelling intensity increases, southern particles experience lower average temperature, higher salinity, and higher phytoplankton concentration conditions (however, lower phytoplankton concentrations than northern particles). This work suggests that wind-driven circulation and freshwater plumes can play an important role in the distribution and environmental history of larval stage marine invertebrates and this could influence their future persistence along the U.S. West Coast.

Chapter 1 Introduction

As an eastern boundary upwelling system, the west coast of the United States, has high productivity marine ecosystems (Chavez and Messie, 2009). The reason why it has high productivity is that an upwelling current, which is caused by an equatorward-flow under Coriolis force, current brings cool and nutrient-enriched water from the deep ocean to the surface of the ocean (Ryther et al., 1969). The upwelling of nutrients supports the growth of phytoplankton and increases primary productivity in the ocean (Bakun, 1990, Chavez et al., 1991). Bakun (1990) hypothesized that upwelling-favorable winds have been growing and intensifying as Greenhouse gases have accumulated, since accumulation of Greenhouse gases would intensify the land-sea pressure gradient because of the increasing land-ocean heating difference (Bakun, 1990). Narayan et al. (2010) support this hypothesis by analyzing Comprehensive Ocean Atmosphere Dataset (COADS) during 1960-2001, and results showed an increase of coastal upwelling in all major upwelling regions including California. Even though upwelling intensification will lead to an increase in the food source supply that sustains a population, concentration of food may decrease due to increased mixing (Snyder et al., 2003). Additionally, retention of particles near shore may be decreased because of increased offshore surface water transport (Snyder et al., 2003).

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Wind-driven circulation in the coastal ocean not only influences nutrient concentrations in the upper ocean, but also affects the distribution of marine larvae. Strong upwelling currents can sweep larvae far offshore making it harder for intertidal species to return to settle onshore (Alexander and Roughgarden 1996, Connolly et al. 2001). However, Shanks and Brink (2005), suggest that some slow-swimming ciliated larvae are not strongly influenced by surface currents. North et al. (2008), find that even though the swimming behavior of marine invertebrate is very weak (~1 to 10mm/s) compared to horizontal current velocities (>1m/s), their motion still effectively helps them maintain their depth against currents and influence their direction of transport and dispersal. Therefore, it is essential to take invertebrates' swimming behavior into consideration while using model to estimate their dispersal.

Besides the influence of wind-driven current on the west coast, freshwater plumes have a huge impact on this region. The surface mixed layer in coastal upwelling regions are typically 0-20 m thick, but in the Oregon shelf, the surface mixed layer is thin and strongly stratified due to the influence of freshwater plumes and weak wind stress (Lentz, 1992). The Columbia River, as the largest freshwater source on the west coast of North America, plays an important role in the physical, biogeochemical and ecological functioning of the Washington and Oregon coastal regions (Thomas and Weatherbee, 2006). The large annual discharge of the Columbia River is around 260 km³/ year, and its low salinity water plume can extend as far south as 38°N in summer (Thomas and Weatherbee, 2006). The seasonal variability of flow, which ranges from 3500 m³/s to 9000 m³/s drives downstream variability in the coastal dynamics on the continental shelves of the Pacific Northwest (MacCready et al. 2009). During summer, the freshwater plume extends primarily offshore and southward, and during winter, its orientation is more northward and close to shore (Thomas and Weatherbee, 2006). Additionally, the freshwater plume increases stratification and decreases the impact of upwelling since the stratification increases the amount of energy required to bring water from bottom of the ocean to the surface (MacCready et al. 2009).

It is important to examine the impact of freshwater plumes and wind-driven currents on the transport of marine larvae as these mechanisms will determine the distribution and environmental exposure of organisms in their larval stage and may influence their recruitment and survival (Morgan 2014; Sorte et al., 2017). Furthermore, these physical processes may influence the poleward transport of marine larvae, influencing their redistribution potential (Deutsch et al. 2008; Somero 2010; Sorte et al., 2017). Redistribution and evolutionary adaptation are two main mechanisms that help species react to the change of environmental conditions (Berg et al. 2010).

In terms of redistribution, marine invertebrates' distributions will be affected by increased temperatures in the ocean (Perry at al. 2005). Perry et al. (2005) found that in the North Sea increasing ocean temperature changed ocean species distribution by shifting the centroids and ranges of most species distributions poleward. Nearly two-thirds of fish in the North Sea have shifted in mean latitude to the northern direction or toward greater depths over 25 years because of increasing sea temperature (Perry et al. 2005). Climate change is causing species extinctions in the sub-polar regions (the tropics and semi-enclosed seas), while, species invasions in the Arctic Ocean and the South Ocean are becoming more intense (Cheung et al., 2009). The reason for this phenomenon is that the biological diversity gradient is decreasing from tropical to extratropical areas.

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However, species diversity and richness in cold regions is expected to increase due to increasing ocean temperature (Willig et al., 2003). The intensity of species redistribution also depends on species' dispersal abilities and habitat connectivity. For example, species with faster life cycles and small body sizes responded more strongly to climate change by shifting their habitat toward the northward in North Sea (Perry et al., 2005). That is the reason why we need to take species swimming behavior into consideration while we study the redistribution of marine invertebrates. Biological behaviors will also be shaped by global warming. Harley et al. (2006) shows that the change of ocean chemistry (e.g. pH) has more complex and significant impact on marine organisms' biological process compared to the change of ocean temperature.

Global warming can affect biological processes, as temperature influences molecular kinetic energy, and therefore, changes the rate of fundamental processes, like enzyme reaction and diffusion (Hoegh-Guldberg and Bruno 2010). In addition, climate change might decrease dissolved oxygen concentration in subsurface of the ocean based on the model output in Southern Ocean (Matear et al. 2000). The dissolved oxygen distribution in the ocean will critically change the site and rate of marine nitrogen transformation (Codispoti et al. 2001). Also, chemical components, like pH, pCO₂ and calcium carbonate saturation, are the factors that control the physiological performance, morphology and behavior of marine invertebrates (Gibson et al. 2011). Therefore, it is essential to study marine invertebrates' environmental history during the larval stage.

This thesis focus on understanding the physical processes that govern the environmental history and transport of marine invertebrates during their larval stage, focusing on the role of wind-driven flow and freshwater plumes. Additionally, this work examines how release location and swimming behavior modifies the path and environmental history of a larval particle.

Chapter 2 Modeling Methods

2.1 Regional Ocean Modeling System (ROMS)

ROMS is a free-surface, terrain-following, primitive equation ocean model used by a broad community for applications from basin to coastal and estuarine scales (Wilkin et al., 2005, Giddings et al. 2014). In this study, we use the "Cascadia" implementation of ROMS, which was developed by the Coastal Modeling Group at the University of Washington, and was forced with realistic atmospheric, tidal, river flow and boundary conditions (Giddings et al. 2014). The model domain (43-50°N, 127-122°W) encompasses the coastal ocean and estuaries of Washington, Oregon, and Vancouver Island, British Columbia with horizontal resolution ranging from 1.5 km at the coast to 4.5 km offshore. The model uses 40 vertical, terrain-following layers (s-coordinates) and vertical resolution is enhanced near the sea surface and at the bed (Davis et al. 2014). Further details on the physical and ecosystem models as well as comprehensive skill assessments can be found in Giddings et al. (2014), Davis et al. (2014), and Siedlecki et al. (2014).

2.2 Particle Tracking

The particle-tracking code used in this research was developed by Banas et al. (2009). It uses a Lagrangian particle tracking algorithm which has been developed for use with larval dispersal studies (Banas et al. 2009). The particle-tracking code includes advection of currents (velocity fields output by the ROMS model) in three dimensions plus a parameterization of vertical mixing by a random displacement model (North et al. 2008).



Figure 1. Locations of particle release in model runs. Blue points are release points of particles to the north of the Columbia River and red points are release points of particles to the south of the river.

In each particle-tracking experiment, 224 particles were released on the northern side and southern side of the Columbia River mouth and tracked each particle's trajectory for 30 days in each period, which is within the range of 3 to 5 weeks of the average larval duration of *Mytilus* mussels (Seed 1969). The reason of choosing *Mytilus* mussels as model study organism is that based on the genetic dispersal scale in Kinlan and Gaines (2003), the life history traits of invertebrates are more likely to represent the life history traits among taxonomic groups (macroalgae, invertebrates, and fish).

Particles were released along the coastline from Heceta Bank, Oregon (43°N) up to Vancouver Island, Canada (50°N). Particles reaching the model boundaries were not considered for analysis. Based on the latitude, longitude and depth of the positions of each particle in each hour, the surrounding environment conditions (e.g.., temperature, salinity and phytoplankton concentration) can be extracted from the output of the ROMS model.

2.3 Swimming Behavior Model

In this experiment, particle tracking was used to compare the effect of invertebrate swimming behavior to passive transport for the dispersion of particles. For passive transport, the particles were moved passively by physical advection and diffusion. For swimming particles, each particle swims vertically toward a target depth, with vertical swimming speed increasing exponentially with distance away from the target depth up to a maximum defined swimming speed. The depth-seeking swimming behavior can be represented by adding the following vertical velocity to the particle path, as done in Drake et al. (2013):

$$W_l = W_{max} sgn(d-z)(1-e^{-|d-z|/\lambda})$$

where W_{max} is the maximum swimming speed, sgn is the sign function, *d* is the target depth, *z* is the depth of the larvae, and λ is a shape parameter set to a value of 12 m. This experiment focus on the vertical swimming behavior since the horizontal swimming speed is far smaller than that of the current, regardless of whether the current is upwelling or downwelling. In this experiment, the target depth was set to 20 m, the mean depth of the coastal pycnocline. The maximum swimming speed was set to 2 mm/s to simulate *Mytilus edulis*'s maximum swimming speed (Sprung, 1984, Troost et al. 2008).

2.4 Meteorological Data

The particle-tracking experiments were run for time periods including winddriven upwelling periods and downwelling periods in 2005, August 2006, and June and September 2007. The upwelling and downwelling were caused by the direction of the Ekman layer transport, which depends on the direction of alongshore wind stress. Therefore, strong upwelling was caused by the strong southward wind velocity and strong downwelling was caused by the strong northward wind velocity. In this thesis, the upwelling and downwelling are quantified by using an 8-day weighted wind index (W_{8d}) which was developed by Austin and Barth (2002):

$$W_k(t) = \int_0^t \frac{\tau^s}{\rho_0} e^{\frac{t'-t}{k}} dt'$$

where, k is a relaxation timescale which was recommended as 8 days by Austin and Barth (2002), since the pycnocline relaxes back toward a rest state after an upwelling-favorable wind event in around 8 days. τ^{s} is the alongshore wind stress, and ρ is the water density, which was set to 1000kg/m³.



Figure 2. Daily Wind Index during 2005. The positive value means surface current is dominated by downwelling. Otherwise, the study period is dominated by upwelling surface current. Study periods highlighted by red are selected as downwelling study periods and those highlighted by blue are selected as upwelling study periods.

Year	Julian Days	Average Upwelling	Dominant
		Index during Study	Surface current
		Period (m^2/s)	
2005	91-120	43.61	Downwelling
	155-184	-5.75	Upwelling
	198-227	-30.37	Upwelling
	245-274	-20.20	Upwelling
	278-307	30.57	Downwelling
	336-365	24.51	Downwelling
2006	236-262	-28.41	Upwelling
2007	177-204	-2.75	Upwelling
	250-276	-19.94	Upwelling

Table 1. Wind Index of Each Study Period

Based on our available output data from ROMS and the average value of each period, this research selected the upwelling periods as Day 155-184, 198-227 and 245-274, the downwelling periods as Day 90-120, 278-307 and 336-365. The output data from ROMS is only available for certain months during year 2006 and 2007. Therefore, upwelling periods in this research are Day 155-184, Day 198-227 and Day 245-274 in 2005, Day 236- 262 in 2006, and Day177-204 and Day 250-276 in 2007. Downwelling periods are Day 91-120, Day 278-307 and Day 336-265 in 2005.



Figure 3. Wind Index during Study Periods

In addition, the wind index during each study period in shown in Fig 3. Except the study period of Day 177-203 in 2007, all study periods are dominated by one surface current during the whole period. The study period of Day 177-204 in 2007 was dominated by downwelling surface current in the first 11 days, and then shifted to upwelling surface current for rest of the period. The data from this study period will only be taken into consideration in section 3.2.

Chapter 3 Results and Discussion

3.1 Influence of Swimming Behavior on Particle Distribution

To consider the influence of swimming behavior on larval transport, this section compares the dispersal distance, or displacement, of passive and swimming particles. Particles were released at the first day of the upwelling study periods (Day 155-184, Day 198-227 and Day 245-274 in 2005) and downwelling study periods (Day 278-307 and Day 336-265 in 2005), and were continually tracked for 30 days. To avoid the edge effect, data was set to NaN after particles reached boundaries (43°N and 50°N). Some particles might be trapped by topography. To avoid this case, it assumed that if a particle stayed in the same latitude for 48 hours, this particle was trapped by the topography and data of this particle would be set to NaN after this time. This assumption only applies to this section. Fig. 4 (a) shows probabilities that particles stay within each longitude zone during their dispersal. The probability was defined as the sum of hours that all released particles were retained in each zone over total hours of all released particles distributed in all study periods. The particles' released zone is located within 44.2450–47.9670 °N, 124.7259-123.9500°W. Fig. 4 (a) shows that most of passive and swimming particles stay within the longitude zone 124-123.5°W. However, swimming particles have a higher probability of staying closer to shore compared to passive particles.

Fig. 4 (b) shows particles' latitude displacement between their initial latitude and final latitude at the end of the study period. Results show that swimming particles are more likely to remain closer to their initial release position than are passive particles. The swimming particles' poleward displacement during the downwelling period is positive, as would be expected with poleward wind, but also is greater in magnitude than displacement during the upwelling period. Latitude displacement of swimming particles during the downwelling period is farther than the latitude displacement during the upwelling period. Particles released to the south of the Columbia River move further north and further south during the downwelling period and the upwelling period respectively.

From Fig. 4 (c), regarding the difference in depth between swimming behavior and passive particles, it can be observed that passive particles are, on average, deeper in the water column than swimming particles. Swimming particles are more likely to maintain their depth near the defined target depth of 20 meters. Upwelling currents bring water from the deep ocean to the surface, which causes the particles to remain in the shallower layer. Considering the effect of the surface current on the change of particles' location, we can see the upwelling current drives particles to the south and shallower depth, and the downwelling current drives particles to the opposite direction.



Figure 4 Locations of Particles' Displacement. Probability that particles stay within each longitude zone during their paths, across all study periods including selected upwelling study periods (Day 155-184, Day 198-227 and Day 245-274 in 2005) and selected downwelling study periods (Day 278-307 and Day 336-265 in 2005). Blue color represents passive particles and red color represent swimming particles. (b) shows latitude displacement of passive particles and swimming particles released to the north of the Columbia River and to the south of the river during selected upwelling periods and selected downwelling periods during 2005. (c) shows passive and swimming particles' depth change during selected upwelling periods and selected downwelling periods. Grey lines represent each particle's path during over the whole study period.

Compared to passive particles, on average, swimming particles are more likely to stay closer to shore and their initial latitude (Fig. 4). The main reason swimming particles stay closer to shore is related to particles' vertical depth. For passive particles, the downwelling current pulls passive particles to over 50 meters in depth, which is below the Ekman layer (transports particles in the across-shore direction), while the upwelling current holds passive particles at 20 meters in depth, which may be still within the Ekman layer. Therefore, during the downwelling period, the bottom current pulls particles offshore, and during the upwelling period, the Ekman layer current sweeps particles offshore as well. Thus, passive particles are pulled offshore regardless of surface current conditions. Particles' vertical depth alone cannot explain why swimming particles remain closer to their initial latitude. As particles' depth increases, the influence of wind-driven currents decreases. Therefore, due to behavior alone, swimming particles should move further north during the downwelling period and further south during the upwelling period compared to passive particles. However, the result shows the opposite result. Therefore, freshwater plumes might play the key role in particles' alongshore displacement. In the next section, the experiment investigates the influence of freshwater plumes on particles' alongshore displacement.

3.2 Physical Processes Influencing Alongshore Distribution of Particles

This section explores the effect of wind-driven currents and freshwater plumes on alongshore displacement of swimming particles. Swimming behavior is used in all following analyses as this behavior is more realistic: invertebrates' motion effectively helps them maintain their depth against currents and influence their direction of transport and dispersal (North et al. 2008). In addition, particles' release locations are taken into consideration in this section.



Figure 5. Release Areas along Western Coast. Release locations along the shore are divided into 8 areas with equal number of particles released in each area (56 particles).

Released locations are the same as the previous experiment along coastal Washington and Oregon, but are further divided into 8 areas (See Figure. 5). Areas 1-4 are located to the north of the Columbia River mouth, and Areas 5-8 are located to the south of the river mouth. 56 particles were released daily from each area during whole study period. The model tracked particles from their released time until their landing time. Landed particles are defined as those that reached water depths less than 20 meters, the mean depth of the coastal pycnocline. In addition, the experiment analyzes particles dispersed in the ocean for over one week. 6,281 particles were tracked in this part of the experiment (see Table 2).

Year	Study	Number of	Dominant	Total
	Period	Particles	Surface	Number of
		Tracked	current	Particles
2005	91-120	739	Downwelling	6281
	278-307	690	Downwelling	
	336-365	1313	Downwelling	
	155-184	1075	Upwelling	
	198-227	540	Upwelling	
	245-274	615	Upwelling	
2006	236-262	549	Upwelling	
2007	177-204	301	Upwelling	
	250-276	459	Upwelling	

Table 2. Number of Particles are Tracked

In order to better visualize particle dispersal over the study period, Fig. 6 and Fig. 7 show particles' locations after they were redistributed for 10, 20 and 30 days during one of the upwelling period on Day 245-274 in 2005 (Fig. 6), and one of the downwelling periods on Day 278-307 in 2005 (Fig. 7). Sea Surface Salinity and Sea Surface Temperature (SST) are mapped in these figures. Salinity and SST can show the direction of freshwater plumes flow, and indicate how surface currents affect particles' distributions (e.g. high salinity and low temperature would be indicative of water brought from the ocean bottom to the surface by upwelling).

As graphs show, during the upwelling period, particles are more likely to be flushed in the southward and offshore direction. Based on salinity and SST maps (Fig. 6), particles released near to the mouth of the Columbia River are transported equatorward, and particles released to the south of the river are pushed offshore by the upwelling surface current. However, particles released to the north of the river tend to stay closer to shore during upwelling period. When looking into graphs of the downwelling period (Fig.7), particles are entrained in the freshwater plume and transported poleward (northward). Most of particles during the downwelling period are swept into the Strait of Juan de Fuca, where the estuarine environment has low salinity.



Figure 6. Particle distribution during an upwelling period. It shows particles' location after they distributed 10, 20 and 30 days since they were released during the upwelling period (day 245-274 in 2005). Pink dots represent particles released to the north of the Columbia River and red particles represent particles released to the south of the river. Four figures in the first row are mapped with sea surface salinity. The figures in the second row are mapped with sea surface temperature (SST).



Downwelling Period (Day 278 - 307 2005) Particles Distribution

Figure 7. Particle distribution during the downwelling period. It shows particles' location after they distributed 10, 20 and 30 days since they were released during the downwelling period (day 278-307 in 2005). Pink dots represent particles released to the north of the Columbia River and red particles represent particles released to the south of the river. Four figures in the first row are mapped with sea surface salinity. The figures in the second row are mapped with sea surface temperature (SST).

Figure 8 shows the relationship between average salinity and salinity variance over each particle's path during its dispersal and latitudinal displacement (i.e. difference between initial latitude and landing latitude). The value of the 8-day wind index represents the intensity of wind-driven surface currents (on average directed southward and offshore for upwelling favorable winds and northward and onshore for downwelling favorable winds). A positive 8-day wind index represents the surface current is dominated by the downwelling current, and a negative wind index represents the surface current is dominated by the upwelling current.

When analyzing the graph (Fig. 8 (a)) vertically, it shows that as the wind index increases, the latitude displacement moves to northward, which means that the downwelling current transports particles poleward. When analyzing the graph (Fig. 8 (a)) horizontally, it shows that the larger wind index (downwelling current), particle's path average salinity is smaller; and the smaller wind index (upwelling current), particles' average salinity is larger. This is reasonable, as seen in Fig. 6, during upwelling circulation, freshwater plumes are more diffuse, and transported offshore and may not come into contact with particles released at the coast as much as during downwelling.

When taking released locations into consideration, particles released to the north of the Columbia River (Area 1-3) concentrate around the diagonal line from left top to right bottom, see Fig. 8 (b). These particles move northward and experience lower salinity during the downwelling period, and they move southward and experience higher salinity during the upwelling period. Particles released to the south of the river (area 6-8) move northward during the downwelling period and move to southern direction during the upwelling period. Their average salinities are concentrated around 32 PSU during downwelling periods and week upwelling periods. During strong upwelling periods, particles released to the south of the river also experience higher salinity environment.

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Figure 8. Relationship between Salinity and Alongshore Displacement. (a) shows the relationship between particles' paths average salinity and their latitude displacement. Colors represent values of 8-day wind indexes. A positive 8-day wind index represents the surface current is dominated by downwelling current, and a negative wind index represents the surface current is dominated by upwelling current. (b) shows the relationship between particles' paths average salinity, their latitude displacement, and particles released areas. Area 1-8 are from northern part to the southern part. (see Fig.5) (c) shows the relationship between particles' paths salinity variance, their latitude displacement and their released areas. The number inside the circle represent the box number, which is used to categorize particles to better analyze in section 3.2. Box 2 and Box 4 are overlapped.

Since both surface currents and freshwater plumes can cause the salinity to change during particles' paths, salinity variance is taken into consideration. This experiment assumes that larger salinity variances are most likely caused by freshwater plumes. When comparing salinity variance in Fig. 8 (c), it shows that higher variance happened during downwelling period and weak upwelling period (Wind index between 0 $-10 \text{ m}^2/\text{s}$). Most of these particles are released to the south of the river during downwelling periods and weak upwelling periods. Particles have lower salinity variance during strong upwelling period and these particles are mostly released to the north of the river.

From this section, results show that particles released to the north part of the Columbia River experience lower salinity environments along their particle paths and larger salinity variance during downwelling period, see Fig.8 Box 1. The reason might be the freshwater plume flows to northward direction during downwelling period, and causes these particles' salinity paths to be lower and also causes these particles experience larger salinity variance. However, during the upwelling period, these particles experience higher salinity and lower salinity variance, see Fig.8 Box 2. Therefore, the freshwater plume does not play the key role on these particles, and upwelling current has large impact on them since the current brings high salinity water from deep ocean to the surface. For particles released to the south of the river, particle' path average salinities are closer to 32 PSU during downwelling periods and weak upwelling periods, see Fig.8 Box 3. During strong upwelling period, particles released to the south of the river experience higher salinity, see Fig.8 Box 4. In addition, from the Fig 8 (d), it shows that particles released to the south of the Columbia River experience higher salinity variance regardless

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the surface current, but these particles have more higher salinity variance during weak upwelling periods compared to downwelling periods, see Fig.8 Box 3. Hence, freshwater plume has larger impact on particles released to the south of the river. During weak upwelling periods, the freshwater plume produces a physical alongshore barrier (Banas et al. 2008) so these particles remain in a certain salinity. However, during strong upwelling periods, particles are still affected by the upwelling current.

The main conclusion from this work is that the only case that the freshwater plume does not hugely affect particles is when particles released to the north of the river during the upwelling period. During the weak upwelling period, the freshwater plume acts as a physical alongshore barrier for the particles released to the south of the river, then these particles experience lower average salinities and higher salinity variances. However, during strong upwelling, upwelling current also has large impact on these particles. The flow volume of the freshwater plume might influence the extent to which freshwater plumes influence particle paths, however this factor was not considered in this study.

3.3 Environmental History Along Particle Paths

In this experiment, the temperature, salinity, and phytoplankton concentration for each released particle was tracked from release time until landing time. This part of the experiment only considers particles released during 2005. In total, 2,230 particles were tracked during upwelling periods (Day 155-184, Day 198-227 and Day 245-274 in 2005) and 2,742 particles were tracked during downwelling periods (Day 91-120, Day 278-307 and Day 336-265 in 2005). For NaN values in environmental paths, linear interpolation is used to calculate values to replace NaN values. In Fig. 9, Fig.10 and Fig. 11, hourly average values of the environmental variables for particles released in the same area are shown.

From the Fig. 9, it shows environmental paths of particles during the study period. The temperature during the whole period of downwelling is higher than the temperature paths during the upwelling period. It is reasonable since the downwelling current brings surface water from the surface of the ocean to the deep ocean. It shows that temperature paths along particles' paths during the upwelling period have more fluctuations than the temperature paths they experienced during the downwelling period. Based on Bakun's hypothesis (1990), if upwelling-driven circulation intensifies in the future, marine invertebrates might experience higher temperature variations. The variations in temperature might help invertebrates to acclimate to the environment or selectively kill invertebrates if the temperature exceeds invertebrates' thermal tolerance (Sorte et al. 2017).

During downwelling-favorable circulation, the environmental history of along particle paths is similar regardless of release location. In addition, particles released further south experience higher mean temperatures along their path. However, during upwelling period, particles released to the south of the Columbia River experience lower temperature along their paths than those released to the north of the river, possibly due to the warmer waters of the fresh water plume (compared to upwelled deep ocean water).

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Figure 9. Particles' temperature paths during their dispersal. It shows it shows environmental paths of particles during the study period. Hourly average values of the environmental variables for particles released in the same area are shown. Different colors represent different released locations, grey lines are individual particle path during all study periods.

From Fig 10, particles' salinity paths during the upwelling period has more fluctuations than particles' salinity paths during the downwelling period. Area 4, which is the nearest area to the north of the Columbia River, has the lowest salinity paths in both upwelling period and downwelling period. The factor that decided the salinity level along particles' paths is their initial locations of particles. Also, the salinity paths of particles released south part of the Columbia River is higher than the salinity paths of particles released north of the river during both the upwelling period and the downwelling period. If the upwelling current is intensified in the future, invertebrates whose natal location is to the north of the river will experience more fluctuating salinity environments especially if their natal site is near to the north part of the river mouth.



Figure 10. Particles' salinity paths during their dispersal. It shows it shows environmental paths of particles during study periods. Hourly average values of the environmental variables for particles released in the same area are shown. Different colors represent different released locations, grey lines are individual particle path during all study periods.

From Fig 11. we can find that trends of phytoplankton level are very similar in all given study areas. However, the phytoplankton concentration of the particles released during the upwelling period is higher than phytoplankton concentration of particles which released during the downwelling period. This is because upwelling circulation brings nutrient-rich water into the euphotic zone of the coastal ocean, which fuels phytoplankton growth (Bakun, 1990, Chavez et al., 1991). However, the result of Snyder et al., (2003) that suggests that concentration of food source will decrease due to increased mixing is not shown in this experiment.

Environmental history along particle paths during downwelling periods was independent of particle release location. However, during the upwelling period, phytoplankton concentrations along particle paths for larvae released north of the Columbia River is higher than the phytoplankton concentrations of particles released south of the river, possibly because of dilution of surface waters rich in marine phytoplankton by freshwater plumes. If the intensity of upwelling increases, as predicted by some, it may provide more a supplemental food source for invertebrates whose natal sites along the Pacific Northwest coast are to the north of the Columbia River.



Figure 11. Particles' phytoplankton paths during their dispersal. It shows it shows environmental paths of particles during the study period. Hourly average values of the environmental variables for particles released in the same area are shown. Different colors represent different released locations, grey lines are individual particle path during all study periods.

Chapter 4 Conclusion

Results from the larval transport numerical studies completed here highlight the importance of considering swimming behavior in the larval transport studies. Compared to the passive particles, particles given some typical depth-seeking vertical swimming behavior are more likely to be retained closer to shore and to experience smaller overall dispersal distances. Dispersal distance is not uniform along the Pacific Northwest coast. The dispersal distance of particles released south of the Columbia River mouth is larger than for particles released north of the river. The Columbia River plume plays a role in this latitudinal gradient in dispersal distance.

Wind-driven currents and fresh water plumes both can influence the alongshore transport and displacement of marine invertebrate larvae. For particles released to the north of the river, wind-driven currents play an important role on particles alongshore displacement during upwelling period. However, the freshwater plumes dominate the displacement of particles released north of the river during downwelling periods and particles released to the south of the river during downwelling periods and weak upwelling periods. In addition, during strong upwelling periods, both the upwelling circulation and freshwater plumes impact particles' alongshore displacement. Further exploration of the relationship between flow volume of the freshwater plume and the upwelling intensity need to be conducted in future.

Our study of environmental history along particle paths reveals that the site of larval release can determine the exposure to different conditions during the larval duration period. For example, invertebrates whose natal sites are located to the north of the Columbia River mouth face more variability in temperature and salinity during their larval stage, according to our experiments. However, those released to the south of the river experience lower mean temperature and higher mean salinity conditions. Larvae released north of the river mouth see higher phytoplankton concentrations along their paths and this may further increase if upwelling intensifies in the future.

This research explores wind-driven currents and water plumes' effects on particle paths from data output from ROMS coupled with a Particle-tracking code. Further field observation is necessary to understand the drivers and impacts of environmental paths that invertebrates' experience in their larval stage. In addition, it is necessary to understand invertebrates' thermal and salinity tolerances to examine whether thermal and salinity fluctuations north of the river will strengthen the ability of invertebrates to cope with future climate change or, alternately, kill invertebrates by exceeding their tolerance limits.

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