DISTRIBUTION OF ZOOPLANKTON AND DETRITUS WITHIN LANGMUIR CIRCULATION CELLS

by

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A THESIS

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Langmuir circulation cells are wind generated surface currents, which take the form of alternating clockwise and counter clockwise rotating helical cells. Models suggest that organisms and particles may be retained in the convergence and divergence zones depending on the relative settling and swimming velocity versus circulation velocity. Surface water in convergence and divergence zones of Langmuir circulations were sampled with plankton nets and zooplankton and fecal pellets were enumerated. Copepods did not differ significantly between zones. *Balanus glandula* cyprids, competent *Polydora* spp., and an unidentified late stage veliger were often significantly concentrated in convergence zones. These results suggest that late stage larvae may be exploiting Langmuir circulation as a transport mechanism to travel shoreward for settlement. Fecal pellets were more concentrated in divergence zones on four out of six

sample days. On the two days when pellets were more concentrated in convergence zones the swell was larger.

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CHAPTER I

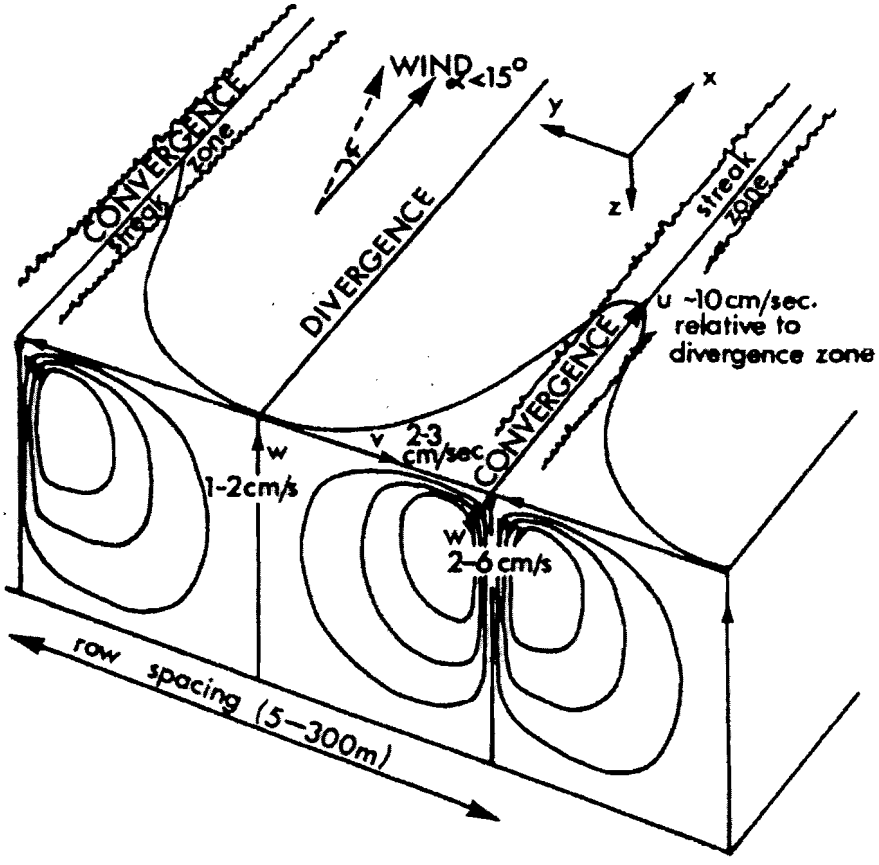
GENERAL INTRODUCTION

As wind blows on a calm ocean the surface water moves downwind and wind driven waves begin to form. Once the wind speed reaches approximately 1.5 m/sec an organized three-dimensional flow in the upper ocean is formed by the interaction of wind, Stokes drift (Stokes, 1847) and the surface wave field (Barstow, 1983). This flow is referred to as Langmuir Circulation (LC) (Leibovich, 1983). The existence of these wind induced helical cells was first described using a series of experiments by Irving Langmuir (1938).

Langmuir circulation covers the ocean surface with alternating clockwise and counter clockwise rotating helical cells oriented parallel to the wind (Leibovich, 1983) (Figure 1). Where two Langmuir cells come together they form a convergence zone, which is often delineated by a slick on the sea surface, containing high concentrations of foam, flotsam and seaweed (Faller & Auer, 1988). Beneath the convergence is a downwelling jet with observed near surface current speeds from two to seven cm s^{-1} (Weller & Price, 1988). Approximately mid-way between the convergence zones is a divergence zone characterized by diffuse upwelling. Vertical current speeds have been recorded at 0.8-1.5 cm s^{-1} (Weller & Price, 1988). As the water travels from a

divergence zone to a convergence zone it increases in speed due to momentum transfer from the wind, maximum downwind speed is observed at the convergence.

Figure 1: A schematic representation of the physical structure of Langmuir Circulations (Pollard 1979). Cells align parallel with the wind. The divergence zone is an area of diffuse upwelling. Water travels from the divergence zone to the convergence zone, where the water is then downwelled. Maximum downwind drift is at the convergence zone.



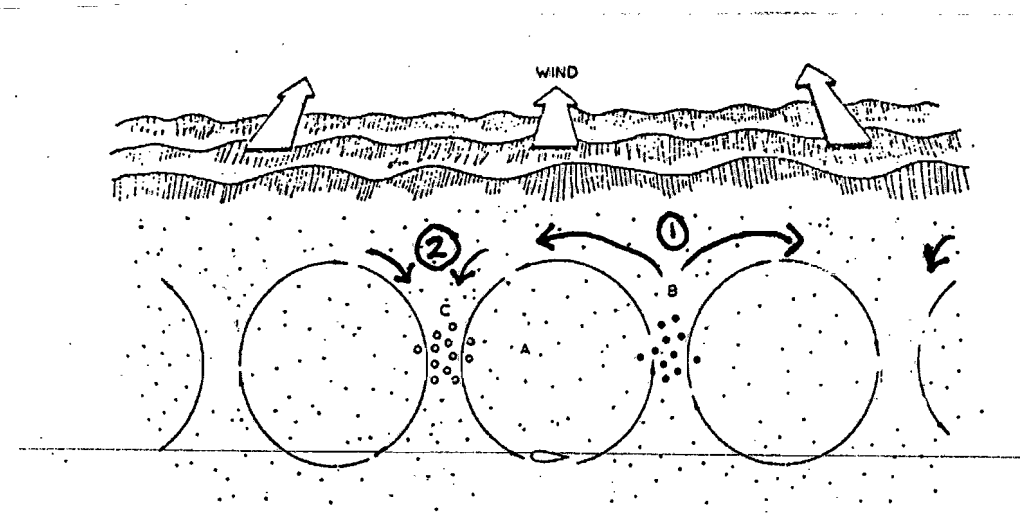
Langmuir circulation displays itself on the sea surface within tens of minutes of the onset of sufficient wind strength. Over time, energy is transferred from small to large LC cells (Faller & Auer,1988). This energy transfer leads to a range of LC cell spacing in any particular wind event. Cell spacing in the horizontal plane varies from a few

meters to hundreds of meters and tends to increase with increased wind speed and duration of the wind event (Leibovich, 1983). In the event of a wind shift the circulation will quickly reorient to the wind, so that the convergences run parallel with the wind. Cell depth varies with wind speed and duration of the wind event. Langmuir circulation affects the water column from the surface layer, down potentially to the thermocline.

This organized flow should play an important role in the transport of heat and momentum from the air-sea interface down to the top of the thermocline. LC is regarded as an important mechanism that mixes the epilimnion (Langmuir, 1938; Leibovich, 1983; Weller et al., 1985). Leibovich and Paolucci (1979) suggest LC is one of the main turbulent processes that establishes and maintains the mixed layer. The mixed layer is a main component in many studies of climate and biological productivity.

Langmuir circulation must be of biological significance. It was the observation of organized rows of *Sargassum natans* running parallel to the wind, which first drew Langmuir's attention to the phenomenon and caused him to seek out the mechanisms behind the circulation (Langmuir, 1938). Nees (1949) discovered that the concentration of zooplankton collected in plankton tows parallel with the wind were more variable than tows collected perpendicular to the wind. Based on this discovery, Stommel (1949) developed a hydrodynamic model to explain how LC could affect particle distribution. According to this model, particles could be retained due to the ratio of settling or swimming velocity to circulation velocity. Negatively buoyant particles may be retained in upwelling zones (divergence zones), while positively buoyant particles may be retained in zones of downwelling (convergence zones)(Figure 2).

Figure 2: Representation of particle distribution within Langmuir Circulations (modified from Ledbetter, 1979). (1) Marks the divergence zone. (2) Marks the convergence zone. (A) Marks where neutral buoyant organisms would concentrate. (B) Marks where organisms swimming downward would concentrate (C) Marks where organisms swimming upward would concentrate. Arrows indicate the path of water circulation.



The primary objective of this thesis is to examine the effect of Langmuir circulation on organisms and detritus in the surface waters. The study examines and describes the distribution of organisms and fecal pellets within the convergence and divergence zones of Langmuir circulation cells and compares the results to Stommel's model. Chapter II investigates the concentration of specific zooplankton in the convergence and divergence zones of the circulation. The main questions addressed are: 1) Does LC concentrate zooplankton in the convergence zones? 2) Does the circulation affect holoplankton and meroplankton differently? Within the context of these questions I hypothesized that: 1) Holoplankters will be evenly distributed between convergence and

divergence zones within LC cells. 2) Meroplankters will be distributed within LC cells based on taxonomic and ontogentic form; late stage larvae of intertidal and shallow subtidal benthic invertebrates will be found in a higher concentration in convergence zones, whereas early larval stages will not be present in the surface waters.

Chapter III examines the concentration of fecal pellets in the convergence and divergence zones of the circulation. The main question addressed is: Does LC concentrate fecal pellets in a specific zone of the circulation? I hypothesized that fecal pellets will be concentrated in the divergence zone due to the ratio of settling velocity to circulation velocity.

The results of Chapter II and III provide evidence to support Stommel's model that particles and organisms are held within zones based on the ratio of settling or swimming velocity to circulation velocity. Studying this circulation mechanism by which organisms and particles are advected within the mixed layer will help us to gain a better understanding of transport processes and nutrient cycling within the epilimnion.

CHAPTER II

DISTRIBUTION OF ZOOPLANKTON IN LANGMUIR CIRCULATION CELLS

Introduction

The basic mechanics and physics of Langmuir circulation are described in Chapter I of this Thesis. Langmuir circulation affects the water column from the surface layer, down potentially to the thermocline. Therefore the convergence and divergence zones of these circulations may be affecting organisms and particles throughout the mixed layer.

The surface water is inhabited by a variety of zooplankton including both holoplankton and meroplankton. The ecological characteristics or habitat needs of these two groups are quite different. Holoplankton are born in the water column and reside there for their entire life. Whereas, meroplankton are planktonic larvae of benthic invertebrates which spend only a portion of their life in the water column before settling into a benthic habitat. Zooplankton on the whole are weak swimmers and may be entrained and advected by currents. However, many zooplankters have the ability to vertically move to position themselves for feeding or advection. How does Langmuir circulation affect zooplankton in the surface water and does it affect holoplankton and meroplankton differently? Zooplankton have been described as "patchy": "mean ratios were far greater than would be expected if individual organisms were positioned

randomly within the sampled region"(Mackas et al., 1985). Langmuir circulation may have a role in zooplankton patchiness in the surface water.

Nees (1949) discovered that the concentration of zooplankton collected in plankton tows parallel with the wind were more variable than tows collected perpendicular to the wind. Based on this discovery, Nees suggested that organisms were concentrated in convergence zones and not in divergence zones. Tows collected parallel with the wind would be representative of either a convergence or a divergence zone, with high or low zooplankton concentrations, respectively. When these tows were averaged the variance would be high. Each tow collected perpendicular to the wind would pass through the convergence and divergence zones of the circulation, thus averaging the organismal density in all zones of the circulation, resulting in a lower variance.

Based on Nees' observations, Stommel (1949) developed a hydrodynamic model to explain how LC could affect zooplankton distribution. According to this model, organisms could be retained due to the ratio of buoyancy or swimming velocity to circulation velocity. Negatively buoyant or downward swimming organisms would be retained in upwelling zones (divergence zones), alternatively animals that are positively buoyant or swim upwards will be retained in zones of downwelling (convergence zones). Therefore, LC could sort zooplankton based on the organism's buoyancy, swimming strength and behavior. Although there has been a fair amount of modeling and hypotheses derived from Stommel's work, little field evidence has been collected.

It was the observation of organized rows of *Sargassum natans* running parallel to the wind, which first drew Langmuir's attention to the phenomenon and caused him to

seek out the mechanisms behind the circulation (Langmuir, 1938). Woodcock (1944) observed aggregations of *Physalia* spp. in Langmuir convergence zones. Woodcock (1950) also made detailed observations on the affect of LC currents on *Sargassum* spp. He noted that vertical currents in convergence zones pulled *Sargussum* spp. below the surface when winds were in excess of Force 3. Hamner and Schneider (1986) observed linear rows of medusae in convergence zones, where jellyfish were observed to be swimming upward against the downwelling current. These observations show that LC can affect the distribution of some algae and large zooplankton in the neuston. These organisms are quite large and are relatively buoyant or strong swimmers. Even so these studies have generated speculation that LC affects small zooplankton in the neuston.

There are only two studies, which directly address relatively small zooplankton distribution in LC cells. Jillet and Zeldis (1985) used aerial photography to observe that postlarval galetheid crabs were concentrated in convergence zones, which they attributed to Langmuir circulation. Kingsford et al. (1991) found within a coral reef lagoon that *Aurelia aurita* and associated juvenile postflexion crangids fish were concentrated in convergences of Langmuir circulation cells. Both studies yielded high variance in larval concentrations, which they attributed to difficulty in determining or maneuvering in and out of a convergence zone. Both of these studies focus on late stage larvae, which are strong swimmers, suggesting that LC can affect the distribution of larvae in the surface waters.

A more precise and thorough comparison of relatively small zooplankton in convergence and divergence zones of Langmuir cells still needs to be conducted. To test

Stommel's Retention Zone hypothesis, a study investigating if zooplankton are more concentrated and if so are the organisms holoplankton or meroplankton in the convergence zone should be conducted.

Studies have found larvae to be concentrated in convergences of other flow regimes. Larvae have been shown to concentrate in the neuston in convergences over internal waves (Zeldis & Jillet,1982; Shanks, 1983,1986,1987; Kingsford & Choat, 1986), in fronts and plumes (Lefevre, 1986; Govoni et al., 1989) and in upwelling fronts relaxing toward shore (Pineda, 1994; Shanks et al., 2003). Knowing that larvae are found in convergences of these flow systems strongly suggests that larvae will be found in high concentrations in LC convergences.

Langmuir circulation may not only shape larval distribution patterns in the neuston but also influence their direction of movement. LC cells are oriented parallel to the wind and the maximum downwind drift is at the convergence zone. If plankters are concentrated in the convergence zone, this will explain enhanced downwind transport.

A larva in the surface water is likely to be affected by the diurnal coastal air circulation, termed "sea breeze"(Sonu et al., 1973). The sea breeze is caused by differential heating of the land relative to the ocean. During the day, air over land warms faster than that over the adjacent ocean causing low pressure over the land (Atkinson, 1981). Air flows landward toward this low-pressure area, causing an onshore sea breeze (Simpson, 1994). At night, air over the land cools more rapidly than that over the ocean and this process is reversed causing the wind to blow toward the ocean, this is known as

offshore land breeze. The onshore sea breeze is typically stronger than the offshore land breeze (Simpson, 1994).

These diurnal wind patterns will shape LC cells to run in the same direction, on and offshore. Given that Langmuir circulation cells are oriented parallel to the wind and the sea breeze is stronger than the land breeze, water in LC convergences should be rapidly moving shoreward. Therefore, organisms in convergence zones would be traveling downwind and shoreward.

The life history stage of a meroplankter determines where it positions itself in the water column. Their pelagic period begins in the shallows where embryos and early stage larvae enter the water column. The larvae then disperse; the scale depending on water movement, larval behavior and length of pelagic stages (Day & McEdward, 1984). Typically, early stage larvae are advected offshore for a variable period of time dependent on the species. Once the organism is ready to settle, it needs to find a mechanism to travel shoreward for settlement. Larvae may be exploiting LC convergence zones as a mechanism for onshore transport required for settlement. Larvae in LC convergence zones would increase their downwind drift and during sea breeze, LC convergences would flow shoreward, allowing larvae to move shoreward.

The purpose of this study is to examine the distribution and concentration of holoplankton and meroplankton in convergence and divergence zones of LC. The main questions addressed are: 1) Does LC concentrate zooplankton in the convergence zones? 2) Does the circulation affect holoplankton and meroplankton differently? Given the potential physical forcing of Langmuir circulation and the basic habitat needs of

holoplankton (remain in the water column) and meroplankton (late stage migrate shoreward for settlement), I hypothesized the following: 1) Holoplankters will be evenly distributed between convergence and divergence zones within LC cells (unless the organism has persistent directional swimming behavior). 2) Meroplankters will be distributed within LC cells based on taxonomic and ontogentic form; late stage larvae of intertidal and shallow subtidal benthic invertebrates will be found in a higher concentrations in convergence zones, whereas early larval stages will not be present in the surface waters. I suspect that these late stage larvae will be in convergences so as to exploit the sea breeze, which would allow horizontal transport shoreward for settlement. To test these hypotheses, I conducted replicate neuston tows and vertical plankton tows (0-10m depth) in convergence and divergence zones of Langmuir circulation cells. I compare and report the concentrations of specific holoplankton and meroplankton in these two zones.

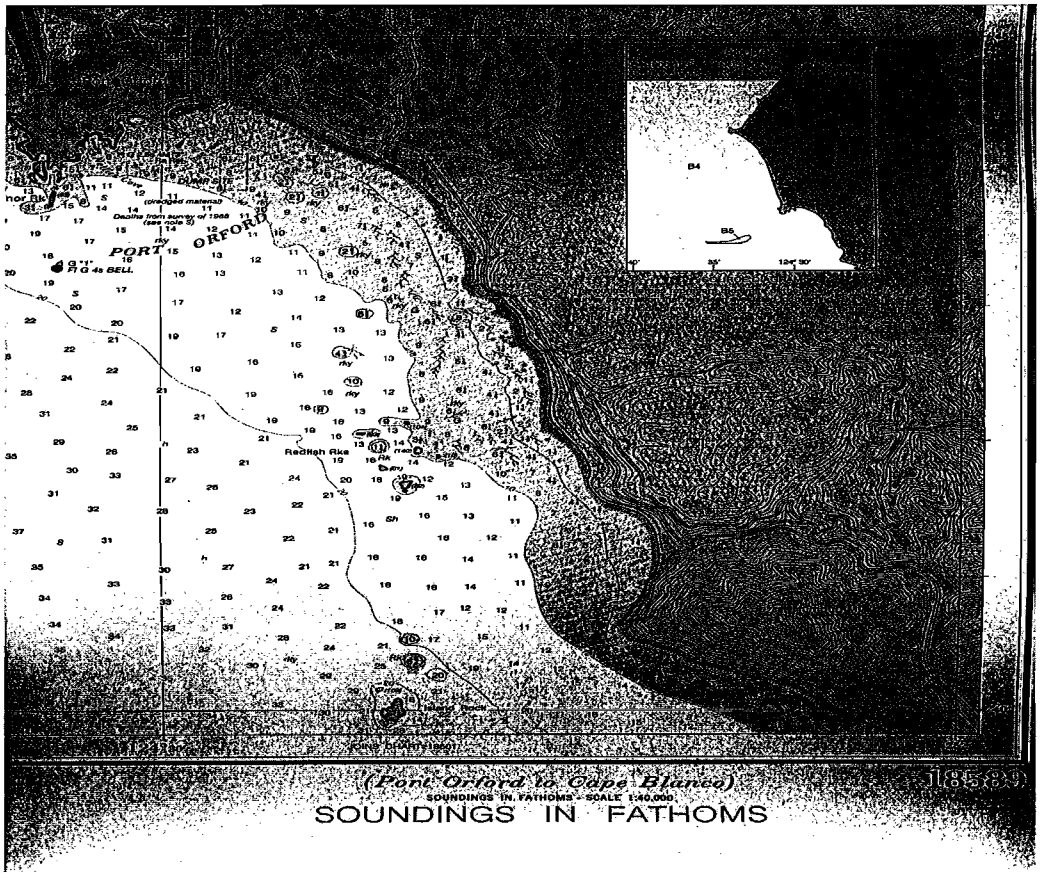
Methods

Study Area

All samples were collected in the waters adjacent to Port Orford, Oregon (42°44.24'N x 124° 29.48'W), which is 12 km south of Cape Blanco, a site characterized by frequent strong upwelling (Figure 1). Port Orford was chosen as a study site because it has a high headland to the north, which provides a lee from strong north winds and shelter from summertime swells. Working downwind from Port Orford Head, I selected

water upon which the wind was blowing, Langmuir cells were present, but, because of the short fetch, large wind waves had not developed. Working in the lee of "The Head" was necessary to avoid surface chop for two reasons: 1) Strong surface chop will obliterate zones of dampened capillary action, making it impossible to see convergence zones. 2) Surface chop and larger waves make sampling from a small boat dangerous and a large boat cannot maneuver properly to sample Langmuir cells. Therefore, Port Orford with its promontory to the north, was an ideal study site to examine Langmuir circulation accurately and safely.

Figure 1: Coast Guard Chart 18589, illustrating the near coastal waters of Port Orford, Oregon.



LC Identification

Sampling was only conducted when NOAA weather station (PORO3) reported north wind within a range of 1.5-8.0 m s^{-1} and a northern swell < 3.5m. (When winds were above 8.0 m S^{-1} I could not see slick lines at the convergence zone). From the bluff in Port Orford, I would determine wind speed and direction with a handheld anemometer and scan the water's surface for indications that Langmuir circulation was occurring.

Accurate identification of LC cells was critical to this study. I used the following two definitions to aid in the identification of the surface manifestation of LC: 1) LC visual surface indication has been defined as a pattern of windrows, made up of surface film, flotsam and debris (Faller & Auer 1988). 2) Stommel (1951) described LC surface manifestation as venous or parallel streaks. LC was positively identified from the presence of multiple slicks aligned parallel to the wind. The convergence zones were indicated by foam, flotsam and slick lines of dampened capillary action on the surface running parallel with the wind. Once it was determined Langmuir circulation was occurring, the sampling process would commence.

Sampling was conducted from a 7m boat, which was launched via crane at the Port of Port Orford. Upon the water, we searched for slicks by motoring perpendicular to the wind until multiple convergence zones oriented parallel to the wind were spotted. Solitary convergences and convergences not running parallel to the wind were not sampled as they were likely due to nearshore fronts or internal waves. In addition, slick lines flowing off a structure; rock, jetty, boat etc. were not sampled. Convergence zones that met the following criteria were sampled: 1) Sufficient wind speed to generate LC.

2) Convergences aligned parallel to the wind. 3) Multiple convergences present. 4) Convergences or slick lines not extending off a topographic structure. 5) Safely within Port Orford Head. All samples were collected downwind of Port Orford Head. Wind speed and direction were determined during sampling with a handheld anemometer and compass.

Neuston Tows

Neuston sampling was conducted on 5 days in July 2006 and on 2 days in August 2007. Once a Langmuir cell was identified, paired neuston tows were conducted. I maneuvered the vessel to the most upwind point of the circulation and towed downwind. The first tow was made in the convergence zone; the net was brought aboard, elevated and thoroughly rinsed three times with buckets of seawater. This rinsing was meticulous to prevent contamination to the next sample. A second tow was then conducted in the same manner midway between two adjacent convergences. Studies have shown that convergence zones, illustrated by a slick line are rather narrow and divergence zones are relatively broad (Weller et al., 1985; Weller & Price, 1988). Since there is no visual surface indication mark of the divergence zone, I was unable to identify the peak of the divergence. However, by sampling the area between the convergences' slick lines I was sampling in the divergence zone.

Plankton samples were collected using a rectangular neuston net, with a mesh of 0.333 mm, attached to a PVC frame; with a mouth opening of 1 x 0.25 m. Floats were fastened to either end of the PVC frame to keep the net at the surface when towed. Tow depth was approximately 0.5 m and tows were 3-4 minutes in duration. After each tow, the net was carefully rinsed and the sample was preserved in ~10% buffered formalin. Two to four Langmuir circulations were sampled each day. Number of samples was determined by wind and sea conditions.

On sample days in July 2006 volume filtered was calculated using the diameter of the net, tow time and boat speed, which was determined with a handheld GPS. On sample days in August 2007 a flow meter was mounted in the mouth of the net and was used to calculate the volume of water filtered.

In the laboratory, the entire plankton sample was inspected and organisms were identified to the lowest possible taxon level. Holoplankters were identified using Smith & Johnson (1996). Meroplankters were identified and staged using keys in Shanks (2001). Organisms occurring in high concentrations were subsampled using the methods in Shanks & Brink (2005). The sample was transferred to a 250mL beaker, and with the aid of an electronic balance the water volume was increased to 200mL. The sample was homogenized with random stirring and a 5mL sub-sample was removed with a stempel pipette (Omori & Ikeda, 1984). Multiple 5mL sub samples were removed until 100 individuals of the common target organisms had been counted. This generated a sample standard deviation of ~10% for abundant organisms and between 10%-20% for less common organisms (Venrick 1978).

All species and associated concentrations are reported in Appendix A. Select organisms were chosen for statistical analysis. Of particular interest were abundant late stage larvae of benthic invertebrates that might be using convergence zones to move shoreward and abundant holoplankters that were expected to be evenly distributed across cells based on ecology. Organisms also needed to be common enough to accurately determine abundance. Statistical comparisons of larval concentration in the convergence and divergence zones on a given day were made using a Wicoxon's two-sample test. This statistical test was used because my samples were paired. The Wilcoxon's statistic first calculates the difference between pairs and then combines replicates to calculate a p-value. P-values were adjusted to fit a 1-tailed test for late stage larvae of benthic invertebrates that were hypothesized to be present in high concentrations in convergence zones a priori. Abundances were considered to be statistically different when $p<0.1$. I adjusted the alpha for this study to 0.1 instead of adhering to the typical alpha of 0.05 to decrease the probability of Type II errors (i.e. missing patterns that are present in the data). Given the nature of this study: few replicates due to logistical restraints and high variance due to the erratic distribution of zooplankton in the surface water, there was a high probability of Type II errors. Seeing as this is the first time this system has been examined in detail, I did not want to miss any potentially important differences in organism concentrations between zones, I accepted the higher probability of alpha errors. For the same reason, I did not choose to make any correction for the multiple statistical tests (i.e. the sequential Bonferroni correction). Such tests tend to be overly conservative when there are many statistical tests, which could lead to disregarding patterns that are

really present in the data (Moran et al., 2003). Therefore, though the multiple tests will increase family wise error, I accepted that in order to achieve the goals of the study.

Vertical Tows

Vertical tows were conducted for two main reasons: 1) To examine the vertical distribution of zooplankton in the top ten meters. 2) To collect zooplankton fecal pellets which will be discussed in Chapter III. Certain elements in the design were done to allow for fecal pellet collection and processing.

Sampling of the top ten meters was conducted on six days in June, 2007. Langmuir circulations were identified as described above. Once a Langmuir circulation was identified and chosen to sample, paired vertical plankton tows were made. The first tow was made in the convergence zone. I maneuvered the boat alongside a fairly wide section of the convergence zone. The net was lowered directly into the convergence zone to ten meters and then pulled slowly through the water column until at the surface. When at the surface, the net was examined for any fouling and then was brought aboard and was gently transferred. The net was then thoroughly rinsed with buckets of seawater to remove any organisms or material and a new cod end (described below) was attached. This rinsing was meticulous to prevent contamination to the next sample. A second tow was then conducted in the same manner in the divergence zone.

Plankton tows were made with circular plankton net with a mesh of 53 *u*m and a mouth opening of 0.26 m. The net was equipped with a modified cod end to enable

gentle sampling. The cod end was made of a one-gallon heavy duty plastic bag, which was hosed clamped onto the base of the net. The metal circular ring and the cod end attachment were weighted. Tows extended from ten meters to the surface. Samples were gently poured into sample containers and preserved in ~10% formalin. Volume filtered was determined from the length of the tow (10m). Three paired convergence and divergence tows were sampled on each day.

In the laboratory, the sample was treated with great care so as to not break fecal pellets, which were collected in these samples and analyzed for another portion of the study. The sample was washed free of formalin by gently pouring it through a 53 *u*m mesh sieve and then the concentrated sample was brought up 1000mL with fresh water. This sample was allowed to settle for 24 hours to determine total settled volume. The sample was homogenized by gently stirring and a 100mL aliquot was transferred with a turkey baster to a tissue culture flask. The flask was capped and transferred to an inverted microscope where it was allowed to settle for one hour. The entire aliquot was inspected for zooplankters, which were identified and enumerated using identification keys in Shanks (2001). Since the organisms were enclosed within the tissue culture flask they could not be manually manipulated, thus species and stages were pooled.

Particular organisms were chosen for statistical analysis because previous knowledge suggested that these organisms might vertically migrate into the surface water to exploit LC as a transport mechanism shoreward for settlement. They were also chosen when organisms were common enough to accurately determine abundance. Statistical comparisons of specific larval concentrations in the convergences and in the divergence

zones on a given day were made using a Wilcoxon's two-sample test. Abundances were considered to be statistically different when $p<0.1$(for reasons explained above).

Results

Nueston Tows:

Wind speeds were measured with a handheld anemometer for each cell sampled and were averaged per day and are presented in Table I. Swell height observed during sampling and measured at NOAA buoy 46015 is reported in Table I. The discrepancy between the two swell sizes is due to location. The NOAA buoy is 16 nautical miles offshore, and the swell is not obstructed. Whereas, Port Orford experiences reduced swell because of the protection of Port Orford Head. I report the observed swell height and add the NOAA recorded buoy swell height as an indication of change across days (Table I).

Table I. Average wind speed, observed swell height and NOAA swell height by date.

Date	Wind Speed (m S^{-1})	Observed Swell Height (m)	NOAA swell height (m)
July 3, 2006	2.5	0.3	1.0
July 7, 2006	3.5	0.3	0.8
July 20, 2006	5.5	0.3	1.0
July 30, 2006	2.4	0.6-1.0	1.3
July 31, 2006	3.0	1	1.1
August 10, 2007	3.3	1	1.3
August 21, 2007	5.1	1	1.8

Meroplankton chosen for statistical analysis and reviewed here are: an unidentified gastropod veliger, Veliger I, *Balanus glandula* cyprids, Pinnotheridae zoea, Spionid nectochaete larvae, *Polydora* sp. and unidentified fish eggs. The holoplankton chosen for statistical analysis and reviewed here are: the cladoceran *Podon* sp., the hydromedusae *Obelia* spp., and the copepod *Acartia hudsonica* .

I was not able to identify Veliger I. Upon preservation with formalin the organism drew its velum inside the shell making identification difficult. For many gastropod taxa, "identification is not possible beyond the level of family or even order"(Goddard, 2001). The veliger larvae collected in this study have a single spiral shell, that coils in one plane, an average size of 600 *u*m and has black and white coloration (Figure 2). Based on the size and development of shell, I believe these organisms to be late stage larvae. Veliger I larvae were collected on the five sample days in July 2006 and were not present in August 2007. Veliger I larvae were found in higher concentrations in the convergence zone than the divergence zone on all five sample days. The Veliger I larvae were 1.6-10.6 more concentrated in convergence zones (Table II). Veliger I were significantly more abundant in the convergence zones than in the water between convergence zones on July 7, July 20 and July 31 (Table II).

Figure 2: Unidentified Veliger, 600um.

Balanus glandula cyprids were collected on the five sample days in July 2006 and were not present in tows collected in August 2007. Cyprids are the final planktonic stage of barnacles before benthic settlement. Cyprids were found in higher concentrations in the convergence zone than the divergence zone on four of the five sample days, concentrating 2-24 times more in the convergence. On July 7 and July 20, *B.glandula* cyprids were significantly more concentrated in convergence than divergence zones (Table III).

Pinnothridae zoeae, were collected on four sample days in July 2006. Zoeae were stages four and five and were pooled for analysis. Although identification to species was difficult I believe the majority were *Fabia subquadrata.* Zoeae were found in higher concentrations in the convergence zones on three days, concentrating 2-80 times more.

Zoeae were significantly more abundant in the convergence zones than divergence zones on July 20 and July 31 (Table IV).

Polydora spp. larvae, which are spionid polychaetes were collected on July 7 and July 20, 2006. Organisms were examined and setigers were counted to determine stage. All organisms were determined to be nectochaetes, the advanced larval stage. Trochophore and metatrochophore stages were not present. Although I am not certain, I believe these larvae to be *P. socialis.* Nectochaetes was found in higher concentrations in the convergence zones on both days, concentrating 1-19 times more in the convergence. *Polydora* spp. were significantly more concentrated on July 7 (Table V).

Unidentified fish eggs were collected on the two sample days in August 2007 and were not present in tows collected in 2006. Fish eggs were yellowish in color. Although preserved in formalin, when the sample was suspended fish eggs appeared to be negatively buoyant. Fish eggs were significantly more abundant in the divergence zones than convergence zones on both days, concentrating 2-8 times more in the divergence than the convergence zone (Table VI).

The holoplankter *Podon* sp. a member of the order Cladocera were collected on three of the seven sample dates in 2006 and 2007. *Podon* has a large eye and an enlarged carapace. Podon were more concentrated in the divergence zones than convergence zones on all three days and were significantly more abundant in the divergence zone on August 21 (Table VII).

The hydromedusa *Obelia* spp. was collected on four sample days in 2006. Specimens varied in size from 1-5mm. Obelia was more concentrated in the convergence

zone than the divergence zones on three dates and significantly more abundant in the convergence on July 20 (Table VIII).

The copepod *Acartia hudsonica* was collected on six sample days. *A. hudsonica* is a pelagic herbivorous calanoid copepod and exhibited a highly variable distribution. *A.hudsonica* was found in higher concentration in the convergence on three days and in higher concentration in the divergence on the other three days. However, *A. hudsonica* was significantly more concentrated in the convergence only on July 31 (Table IX).

Tables II-IX

The abundance of an organism on a given date in convergence zones and divergence zones of Langmuir circulations cells collected in neuston tows. Values are the average no. $100m^3$ with the SE in parentheses. C/D is the ratio of the abundance in the convergence divided by the abundance in the divergence. *p* values are one-tail adjusted results of a Wilcoxon's 2-sample test comparing the convergence and divergence abundances. Statistically significant results at α=0.1 are marked with an *.

Table II. Veliger I distribution within LC

Veliger I	Samples per zone N	Convergence	Divergence	C/D	*p* values
July3, 2006	2	5.5(1.6)	2.8(0.4)	2	_
July 7, 2006	4	297(237)	66(45)	4.5	0.03*
July 20, 2006	4	103(46)	26(13)	4	0.03*
July 30, 2006	3	19(19)	1.8(1.5)	10.6	_
July 31, 2006	3	41(24)	25(23)	1.6	0.05*
August 10, 2007	3	_	_	_	_
August 21, 2007	3	_	_	_	_

Table III. *Balanus glandula* cyprid distribution within LC.

B.glandula Cyprid	Samples per zone N	Convergence	Divergence	C/D	*p* values
July3, 2006	2	3.2(0.8)	0.8(0.8)	4	_
July 7, 2006	4	177(136)	7.4(2.9)	24	0.04*
July 20, 2006	4	125(109)	58(32)	2.2	0.04*
July 30, 2006	3	6.8(5.8)	1.7(0.4)	4	0.5
July 31, 2006	3	6.5(3.4)	7.3(4.9)	0.9	0.5
August 10, 2007	3	_	_	_	_
August 21, 2007	3	_	_	_	_

Table IV. Pinnothridae zoeae distribution within LC.

Pinnothridae Zoeae IV & V	Samples per zone N	Convergence	Divergence	C/D	*p* values
July3, 2006	2	31(22)	16(12)	2	–
July 7, 2006	4	1.3(1.1)	9.2(8.6)	0.1	–
July 20, 2006	4	14(12)	2.1(1.8)	6.7	0.05*
July 30, 2006	3	–	–	–	–
July 31, 2006	3	16(14)	0.2(0.1)	80	0.05*
August 10, 2007	3	–	–	–	–
August 21, 2007	3	–	–	–	–

Table V. *Polydora* sp. distribution within LC.

Polydora sp.	Samples per zone N	Convergence	Divergence	C/D	*p* values
July3, 2006	2	–	–	–	–
July 7, 2006	4	30(19)	1.6(1.1)	19	0.03*
July 20, 2006	4	10(4)	7.9(2.9)	1.3	0.2
July 30, 2006	3	–	–	–	–
July 31, 2006	3	–	–	–	–
August 10, 2007	3	–	–	–	–
August 21, 2007	3	–	–	–	–

Table VI. Unidentified fish eggs distribution within LC.

Fish eggs	Samples per zone N	Convergence	Divergence	D/C	*p* values
July3, 2006	2	–	–	–	–
July 7, 2006	4	–	–	–	–
July 20, 2006	4	–	–	–	–
July 30, 2006	3	–	–	–	–
July 31, 2006	3	–	–	–	–
August 10, 2007	3	3.0(0.9)	5.9(1.3)	2	0.05*
August 21, 2007	3	12(2.3)	92(36)	7.7	0.05*

Table VII. *Podon* spp. distribution within LC.

Podon spp.	Samples per zone N	Convergence	Between Convergence	D/C	*p* values
July3, 2006	2	271(46)	303(264)	1.1	–
July 7, 2006	4	–	–	–	–
July 20, 2006	4	–	–	–	–
July 30, 2006	3	–	–	–	–
July 31, 2006	3	–	–	–	–
August 10, 2007	3	1.4(0.2)	2.5(1.3)	1.8	1.0
August 21, 2007	3	2.4(0.3)	16(6)	6.7	0.1*

Table VIII. *Obelia* spp. distribution within LC.

Obelia spp.	Samples per zone N	Convergence	Divergence	C/D	*p* values
July3, 2006	2	86(16)	13(10)	6.6	
July 7, 2006	4	5.8(3.4)	9.1(6.2)	0.6	0.6
July 20, 2006	4	16(6)	4(2.3)	4	0.06*
July 30, 2006	3				
July 31, 2006	3	5.4(2.7)	0.6(0.3)	9	0.3
August 10, 2007	3	–	–	–	–
August 21, 2007	3	–	–	–	–

Table IX. *Acartia hudsonica* distribution within LC.

Acartia hudsonica	Samples per zone	Convergence	Divergence	C/D	*p* values
July3, 2006	2	562(397)	530(375)	1.0	
July 7, 2006	4	1310(655)	2028(1014)	0.65	0.7
July 20, 2006	4	5390(2695)	1560(780)	3.5	0.5
July 30, 2006	3	266(154)	434(251)	0.62	0.6
July 31, 2006	3	932(538)	650(375)	1.4	0.6
August 10, 2007	3	12(5.3)	9 (3.2)	1.3	0.6
August 21, 2007	3	–	–	–	–

Vertical Tows

Wind speed was determined with a handheld anemometer and mixed layer depth was determined by density readings taken with a CTD, both are reported in Table X. Swell height was determined and recorded as explained above and is reported in Table XI. The meroplankters chosen for statistical analysis were: barnacle nauplii and cyprids; and holoplankters chosen were copepod nauplii and adult copepods. Due to samples being contained within the tissue culture flask, organisms could not be manipulated, making accurate identifcation difficult. Therefore species and stages were often pooled.

Table X. Average wind speed and mixed layer depth by date.

Date	Wind speed (m S^{-1})	Mixed layer (m)
June 5, 2007	3.4	1
June 8, 2007	2.9	10
June 10, 2007	3.5	1
June 22, 2007	3.6	1
June 23, 2007	3.4	2
June 25, 2007	4.3	1

Table XI. Observed swell height and NOAA reported swell height by date.

Date	Observed Swell Height (m)	NOAA swell height (m)
June 5, 2007	0.3-0.6	1.6
June 8, 2007	0.3-0.6	1.5
June 10, 2007	1.6-2	2.4
June 22, 2007	0.6-1	0.8
June 23, 2007	1.3	1.5
June 25, 2007	1	1.4

Barnacle nauplii were collected on all six days of the study. Barnacles have a planktonic nauplius larval stage which undergoes a series of molts, yielding four to six

naupliar stages. Barnacle naupli species and stages were pooled. Although I could not measure or manipulate nauplii, I believe the majority of nauplii were stage 4 and 5 of *B. glandula*. Nauplii were found in higher concentration in the convergence than the divergence zones on all six days collected. Nauplii were significantly more concentrated in the convergence zones than in divergence zones on June 22 (Table XII).

Cyprids were collected on five days and all species were pooled. Cyprids are the second planktonic larval stage of barnacles. Cyprids were highly variable in their distribution and changed from day to day. They were more concentrated in the convergence on three days and more concentrated in the divergence on two days. Cyprids did not differ significantly in their distribution (XIII).

Nauplius larval stages and adult form of copepods were collected on all six sample days. Naupliar stages and species were pooled, although almost all copepods were of the order Calanoida. Copepod naupli can be distinguished from barnacle naupli by the absence of horns. Copepod nauplii were variable in their distribution; they were more concentrated in convergence zones on two days and more concentrated in divergence zones on the other four days. Nauplii did not differ significantly in their abundance between zones on any sample day (Table XIV). Adult copepods were highly variable in their distribution; they were more concentrated in the convergence zone on three days and more concentrated in the divergence on three days. Adult forms were significantly more concentrated in the divergence zone than the convergence zone on June 10 (Table XV).

Tables XII-XV

The abundance of an organism on a given date in convergence zones and divergence zones collected in the upper ten meters of Langmuir circulations cells. Values are the average no. per liter with the SE in parentheses. P values are the results of a Wilcoxan's 2-sample test comparing the convergence and divergence abundances. Statistically significant results at α=0.1 are marked with a *.

Table XII. Barnacle nauplii distribution within LC.

Barnacle nauplii	Samples per zone N	Convergence	Divergence	C/D	*p* values
June 6, 2007	3	129(95)	87(29)	1.5	0.6
June 8, 2007	3	556(260)	306(113)	1.8	0.6
June 10, 2007	3	209(56)	161(137)	1.3	0.3
June 22, 2007	3	161(32)	121(28)	1.3	0.1*
June 23, 2007	3	226(202)	145(48)	0.2	_
June 25, 2007	3	209(116)	105(53)	2.0	1.0

Table XIII. Cyprid distribution wihin LC.

Cyprid	Samples per zone N	Convergence	Divergence	C/D	*p* values
June 6, 2007	3	_	_	_	_
June 8, 2007	3	121(48)	218(114)	0.6	_
June 10, 2007	3	32(21)	16(16)	2	0.3
June 22, 2007	3	8(8)	_	8	_
June 23, 2007	3	_	16(16)	_	_
June 25, 2007	3	24(24)	8(8)	3	_

Table XIV. Copepod nauplii distribution within LC.

Copepod nauplii	Samples per zone N	Convergence	Divergence	C/D	*p* values
June 6, 2007	3	838(233)	975(56)	_	0.6
June 8, 2007	3	3692(1129)	4007(1816)	_	0.6
June 10, 2007	3	1483(293)	806(649)	_	0.3
June 22, 2007	3	1822(644)	2015(854)	_	0.6
June 23, 2007	3	951(481)	846(293)	_	1.0
June 25, 2007	3	1814(608)	2144(1018)	_	1.0

Table XV. Adult Copepod distribution within LC.

Adult Copepod	Samples per zone N	Convergence	Divergence	C/D	*p* values
June 6, 2007	3	258(29)	193(41)	1.3	0
June 8, 2007	3	3539(1464)	3741(2118)	_	1.0
June 10, 2007	3	1217(528)	540(468)	_	0.6
June 22, 2007	3	717(175)	927(187)	_	0.1*
June 23, 2007	3	814(482)	701(384)	_	0.6
June 25, 2007	3	1330(599)	1733(808)	_	0.6

Discussion

This study examines the distribution and compares the concentration of holoplankton and meroplankton in Langmuir circulation convergence zones to concentrations in divergence zones. This study tested the hypothesis that meroplankters would be distributed within LC cells based on taxonomic and ontogentic form, which would define their habitat needs. Holoplankters would be either evenly distributed between zones or retained within a zone due to swimming behavior. These hypothesis were based on two main reasoning's: 1) Stommel's retention zone model, which reasons that organisms that are positively buoyant or swim upward against the downwelling current will be held in convergence zones, whereas animals that are negatively buoyant or swim downward will be retained in the divergence zone. 2) The reasoning that Langmuir circulation sorts organisms based on their taxonomic and ontogentic habitat needs; meaning that certain late stage meroplankton need to be transported shoreward for settlement, while early stage meroplankton are not restricted to the surface water for shoreward movement and holoplankters remain in the water column and do not travel shoreward. If late stage meroplankton utilize Langmuir convergence zones as a mode of transport then concentrations of late stage larvae of benthic invertebrates should be significantly higher in the convergence zone than in divergence zones. Whereas, early stage meroplankters would not be present in the surface water or not concentrated in the convergence zones. In contrast holoplankters which need to remain in the water column

for life would be evenly distributed between zones, cycling with the circulation so they have no net transport shoreward.

Results from the neuston tows provide evidence that late stage meroplankton of benthic invertebrates are frequently concentrated in the convergence zones of LC. Veliger I, *Balanus glandula* cyprids, Pinnothridae zoeae stage IV & V, and *Polydora* sp. nectochaetes were often found more concentrated in the convergence than the divergence zones of LC. These data support Stommel's retention zone hypothesis, that organisms swimming upward will be retained in convergence zones. These four organisms at this developmental stage have the swimming capability to swim upward against the downwelling current at the surface within the convergence zone. The pattern that these organisms are found in higher concentrations in the convergence zones supports the hypothesis that late stage meroplankton are concentrated in convergence zones. This result suggests that they may be using these convergence zones as mechanism to move shoreward.

It should be noted that these late stage meroplankters were not always more concentrated in convergence zones. I attribute this inconsistency to the high variation within the data set. Low number of replicates certainly lends to high variance, however life history of a Langmuir cell and cell size might also explain the high variation in this study. The duration of circulation and wind speed determines the life history of a cell. On each day, the cells sampled may have had different life histories. Cell life history certainly varied across days. Any given wind event will produce varying sized LC cells. Due to the amount of water being circulated, a larger cell would concentrate more

organisms than a smaller cell. On each day several cells were sampled and although size was taken into consideration when choosing cells, size was not measured. I suspect that varying cell life histories and cell sizes contributed to the high variation displayed in the data. Although high variation may have clouded the statistical significance of this study it did not obscure the striking pattern that these four late stage meroplankters were often more concentrated in the convergence zone than the divergence zone.

The ontogentic stages of these four organisms have the appropriate behavior that allows them to be transported shoreward to find suitable habitat for settlement. The adult forms of these organisms are found in the high intertidal to the shallow subtidal. I suspect Veliger I is an intertidal gastropod. Adult forms of *B. glandula* are commonly found in the high to middle intertidal on the outer coast. Pinnotheridae adults are commonly known as "Pea crabs" and are symbiaonts with annelids and mollusks. *Fabia subquadrata* is known to live within *Mytilus californianus,* a common intertidal mussel (Carlton, 2007*)*. *Polydora* sp. is a spionid, that as adults are known for boring into calcareous substrates in the intertidal (Carlton, 2007). *P.socialis* adult forms are known to live in the intertidal to shallow subtidal in fine sands and coarse silts (Carleton, 2007). The intertidal and shallow subtidal of Port Orford, Oregon is composed of rocky outcroppings surrounded by fine sands (personal observation), an ideal settlement site for this spionid.

If these organisms at this late developmental stage do not position themselves so as to move into shallow water for settlement they may perish. The result that these late stage larvae are found concentrating in convergence zones at the surface suggest these

organisms are optimizing downwind drift and exploiting the combination of Langmuir circulation and sea breeze to advect shoreward.

The downwelling current in the convergence and upwelling current in the divergence of LC increases in strength with an increase in depth. Vertical tows made in the top ten meters of the water column passed through varying speeds of flow within the circulation. Nonetheless, late stage barnacle nauplii were more concentrated in the convergence than the divergence zones on all six sample days. Barnacle nauplii have a photo-tactic response, which may stimulate upward swimming against a downwelling current. Nauplii concentrated in the convergence zone provide further support for Stommel's hypothesis, that animals swimming upward are retained in the convergence zone. In contrast, cyprid distribution was highly variable in the vertical tows. This may be due to increased current speed with depth and would explain the discrepancy in the positive concentration in the neuston and sporadic distribution in the top ten meters.

Many larvae can adjust their vertical position in the water column either for feeding or transport purposes. An assortment of larval invertebrates make diurnal vertical migrations into the neuston. In certain decapod species, vertical migration pattern is dictated by ontogentic phase (Temple & Fischer, 1965; Shanks, 1986). Early larval stages typically spend the day at depth and then migrate into the surface waters at night to feed. In contrast, late stage or competent larvae migrate into the surface waters during the day and return to depth in the evening. Being at the surface during the day allows these organisms to make use of the onshore sea breeze. Late stage larvae of other taxonomic groups may migrate into the neuston to employ onshore sea breeze as an

advection tool as well. Larvae that migrate into the neuston during the day, either for behavioral or ontogenic reasons could pair the combination of Langmuir circulation and sea breeze to advect shoreward for settlement.

In contrast to the late stage meroplankton results early stage larvae of benthic invertebrates were not present (or not abundant enough to accurately determine abundance) in the neuston or vertical plankton tows. This result is consistent with the hypothesis that Langmuir circulation is used by meroplankton based on ontogenic habitat needs. Early stage larvae need to disperse and grow through several stages before returning to shore. If an early stage larva was in a convergence zone of LC it may be advected shoreward before it was competent to settle.

Holoplankton as a group collected in neuston and vertical plankton tows either supported Stommel's retention zone hypothesis or the hypothesis that holoplankton would be evenly distributed between zones. When examining individual taxa behavior and swimming speeds, patterns emerged that were consistent with the hypothesis.

Podon was found in higher concentrations in the divergence zones of the neuston on all days it was collected. *Podon* is a member of the Order Cladocera, of which the freshwater *Daphnia* are also a member. George & Edwards (1973) found near surface accumulations of *Daphnia* in between Langmuir circulation convergences. *Podon* possess a large eye that might trigger a negative photo-tactic response resulting in downward swimming, causing *Podon* to be retained in this divergence zone. These data are further evidence for Stommel's model; downward swimming animals will be retained within zones of upwelling.

Obelia spp. was found concentrated in the convergence zone of the neuston, where the LC convergence downwelling current is at its slowest. Although, there are no reported swimming speeds for *Obelia* medusa, I suspect it may be able to control its movement within moderate flow conditions. This medusa is carnivorous and might benefit from being in convergence zones to exploit a potential food source.

Acartia hudsonica is a calanoid copepod collected in neuston tows and was commonly distributed between zones. Adult copepods and copepod nauplii were collected in the vertical plankton tows and both were evenly distributed between zones. These results support the hypothesis that holoplankton would be distributed between zones and provide further evidence that LC zones are utilized by organisms based on habitat need. Copepods are holoplankton which are commonly found in the surface waters and remain in the water column for their whole life. Consequently there does not appear to be a distinct advantage of occurrence within any particular zone of LC.

Unidentified fish eggs are typically considered meroplankton, however when pairing physics with biology they should be regarded as non-regulators or somewhat of a passive particle. Fish eggs cannot change their buoyancy based on a stimulus. Fish eggs were significantly more abundant in divergence zones than in convergence zones, suggesting that they are negatively buoyant Fish eggs may have accumulated in this area by physical forcing, meaning that the diffuse upwelling of the divergence zone would keep eggs from sinking out of the neuston, whereas if eggs were moved into the convergence zone, they would have been pushed below the surface by the downwelling jet.

Due to plankton patchiness, taxonomic life histories and the temporal scale of this study, the organisms collected changed day to day. Organismal data was not pooled but examined by concentration of an organism, zone and collection method used nested within a day. This level of examination enables one to tease out patterns of distribution based on taxonomic and ontogentic form.

In conclusion, these data are consistent with Stommel's retention zone hypothesis that organisms will be retained within zones based on buoyancy or swimming behavior. Late stage meroplankters and medusas, presumed to be relatively strong swimmers, were often concentrated in the convergence zones. *Podon*, which swims down and fish eggs that sank were retained in divergence zones. Copepods that don't exhibit persistent directional swimming were evenly distributed between zones.

The result that late stage meroplankton were concentrated in convergence zones and copepods were evenly distributed support the hypothesis that organisms utilize LC depending on habit need. Given that late stage larvae were concentrated in convergence zones of Langmuir circulation either by behavior or entrained through physical processes, suggests competent larvae are utilizing the pairing of maximum downwind drift in a convergence zone and sea breeze to move shoreward.

The findings in Chapter II support the hypothesis that Langmuir circulation affects zooplankton in the surface waters. Zooplankton have the ability to move and exhibit behaviors which may effect their distribution within LC. Chapter III examines a passively negative particle, zooplankton fecal pellets distribution within zones of Langmuir Circulation.

CHAPTER III

THE EFFECT OF LANGMUIR CIRCULATION ON THE DISTRIBUTION OF FECAL PELLETS IN THE SURFACE WATER

Introduction

The basic mechanics and physics of Langmuir circulation and Stommel's model are described in Chapter I of this Thesis. According to Stommel's model, particles could be retained due to the ratio of settling velocity to circulation velocity. Negatively buoyant particles may be retained in upwelling zones (divergence zones), while positively buoyant particles may be retained in zones of downwelling (convergence zones). Due to turbulent exchange, there may be movement between these two retention zones. Zooplankton fecal pellets are one of many particles in the mixed layer that may be affected by LC.

Zooplankton fecal pellets are negatively buoyant and sink rapidly (Turner, 2002). Fecal pellets are considered a major pathway for surface biogenic material to reach the seafloor (Angel, 1984). Sediment trap studies suggest that the settling of zooplankton fecal pellets, particularly copepod pellets, may contribute and control the

vertical distribution of important elements, such as organic carbon, O2, CO2, N and P (Komar et al., 1981).

The vertical flux of fecal pellets in the water column is determined by a number of factors, including production rate, composition, sinking rate, decay, loss to grazing and localized turbulence. Sinking rate is likely the most important factor in determining successful export to depth (Butler & Dam, 1994). A slowly sinking pellet may decay or be consumed before it exits the euphotic zone. Size, density and shape all contribute to the sinking rate of the pellet (Fowler & Small, 1972; Turner, 1977).

Measured sinking rates of zooplankton fecal pellets in the ocean range from 10 -100 meters a day (Turner & Ferrante, 1979). Fecal pellets produced by macrocrustecans can sink from 18 to 170 meter a day (Alldredge et al., 1987). These high settling velocities strongly suggest that fecal pellets should have a short residence time in the surface water, however, several sediment trap studies have demonstrated that zooplankton fecal pellets, given their production rates in overlaying waters, make up only a fraction of their predicted portion of sedimentary flux (McCave, 1975; Bishop et al., 1977; Poulsen & Kiorboe, 2005). Coprophagy by zooplankton may be an explanation for low export fluxes to depth, however Registad et al. (2005), using *Othiona* spp. as an indicator species, found no evidence for this explanation and suggested that there must be an alternative process retaining pellets in the upper ocean.

The following studies are further evidence that fecal pellets are being retained in the surface waters. Alldredge et al. (1987) found large fecal pellets produced by macro crustaceans in the top 20 m of the water column that were four to ten days old. This is surprising given the sinking rates of these pellets is 18-170 m a day, which is rapid enough to remove them from the surface water in just hours. The accumulation of pellets in the surface waters was partly attributed to turbulent mixing processes. Studies on smaller zooplankton fecal pellets also suggest pellets may be in the surface waters for a long period of time. Krause (1981) over a ten-week study found consistently high concentrations of copepod fecal pellets in the upper 30 m of the North Sea and suggested that pellets were not sinking out of the mixed layer. During a study of the vertical distribution of fecal pellets in the Norwegian Sea, the daily loss of fecal pellets in the upper waters was only 1% of fecal pellet standing stock (Bathmann et al., 1987). These findings demonstrate that pellets are not sinking out of the surface water as fast as expected. This information, combined with the discrepancy of fecal pellets in sediment traps versus standing stock in overlaying waters, suggests that fecal pellets are accumulating and retained in the surface waters due to physical processes.

Langmuir circulation is a physical process that affects surface waters the world over. LC helical vortices create an organized flow in the surface waters and may play a role in the transport potential of fecal pellets. Fecal pellets could be held in Stommel retention zones formed within the divergence zones, where the upwelling current would retard sinking. This would prolong residence time of pellets in the surface water and

combined with turbulent mixing would redistribute them in the mixed layer. No studies to date have investigated the role of Langmuir circulation on fecal pellet suspension.

The purpose of this study is to examine the distribution and concentration of fecal pellets in the divergence and convergence zones of Langmuir circulation cells. Based on Stommel's model, I hypothesized that LC can retain fecal pellets in the surface waters and, as a consequence of retention by LC, fecal pellets would occur in higher concentrations in divergence zones, where the upwelling current would advect pellets upward and retard sinking rates. To test these hypotheses, I made replicate vertical paired plankton tows in divergence and convergence zones of Langmuir circulation cells.

Methods

The study area and methods used to identify Langmuir Circulation are described in Chapter II of this Thesis. Once a Langmuir circulation was identified and chosen for sampling, paired vertical plankton tows were made. The first tow was made in the convergence zone. I maneuvered the boat alongside a fairly wide section of the convergence zone. The net was lowered directly into the convergence zone to a depth of ten meters and then was pulled slowly through the water column until at the surface. When at the surface, the net was examined for any fouling and then was brought aboard and the contents of the cod end were gently transferred. The net was then thoroughly rinsed with buckets of seawater to remove any phytoplankton or pellets and a new cod end (described below) was attached. This rinsing was meticulous to prevent contamination to the next sample. A second tow was then conducted in the same manner

midway between two adjacent convergences. Studies have shown that convergence zones, illustrated by a slick line are rather narrow and divergence zones are relatively broad (Weller et al., 1985; Weller & Price, 1988). Since there is no visual surface indication mark of the divergence zone, I was unable to identify the peak of the divergence. However, by sampling the area between the convergences' slick lines I was sampling in the divergence zone.

Plankton tows were made with circular plankton net with a mesh of 53 *u*m and a mouth opening of 0.26m. The net was equipped with a modified cod end to enable gentle sampling. The cod end was made of a one-gallon heavy-duty plastic bag, which was hosed clamped onto the base of the net. The metal circular ring and the cod end attachment were weighted. Tows extended from ten meters to the surface. Samples were gently poured into sample containers and preserved in ~10% formalin. Volume filtered was determined from the length of the tow (10m). Three paired convergence and divergence tows were sampled on each day. Vertical CTD casts were made each day with a Seabird model 19 CTD to examine the vertical density gradient to determine the depth of the pycnocline and mixed layer.

In the laboratory, the sample was washed free of formalin by gently washing it on a 53 *u*m mesh sieve and then the concentrated sample was brought up 1000 mL with fresh water. This sample was allowed to settle for 24 hours to determine total settled volume. The sample was homogenized by gently stirring and a 100mL aliquot was transferred with a turkey baster to a scored tissue culture flask. The flask was capped and transferred to an inverted microscope where it was allowed to settle for one hour. The

external viewable part of the flask was marked to create a grid of six tracks 8 x 1 cm in surface area. Fecal pellets were enumerated in a randomly chosen track. This methodology for counting fecal pellets was modified from Utermohl (1931).

All pellets counted were intact within a peritrophic membrane and came in two shapes; cylindrical or globular. Only whole pellets were enumerated and pieces and or particles of what might be fecal pellets were not counted. The tissue culture flask enclosed the sample, therefore pellets could not be manipulated, measured or aged. Counts were made for each shape to tease out distributional patterns based on shape. I choose to do separate counts based on the reasoning that shape would likely affect sinking rate, therefore different shaped pellets may have different distributions.

Cylindrical and globular fecal pellet concentrations were log transformed to meet the assumptions of normality and homogeneity of variances. Statistical comparisons of cylindrical and globular fecal pellets in the divergence and convergence zones across days were made using a two-way mixed model ANOVA, with zone as a fixed factor and date as a random factor. A paired t-test examined whether pellet concentrations were different between zones on each date. p values were adjusted to fit a one-tailed test as fecal pellets were hypothesized a priori to be more abundant in divergence zones. Abundances were considered to be statistically different when $p < 0.05$.

Results

Three paired vertical tows were made in the divergence and convergence zones of Langmuir circulations on six sample dates in June 2007. Cylindrical fecal pellets were the shape of a cigar with tapering at both ends. These pellets appear to be similar to those produced by copepods and were present in both zones on all six sampling days. There was no significant difference in cylindrical pellet concentration between zones or days or the interaction of zone and day (Table I; zone, p=0.82; day= 0.17; interaction, p=0.16). Upon examining the data, three samples had abnormally low cylindrical pellet concentrations: FP9 divergence, FP15 convergence and FP16 divergence, marked with an * in Appendix B. I decided to remove these points from the data set and conducted a separate two-way mixed model ANOVA. The results of this ANOVA were no significant difference in concentration between zone but indicated a difference by day (Table II; zone, p= 0.75, day, p=0.03).

Table I. Two-way analysis of variance for cylindrical fecal pellet concentrations with zone and day as main effects (all data points included in analysis).

Effect	df	MS	F	p
Zone	1	0.02	0.06	0.82
Day	5	0.36	1.70	0.17
Zone x Day	5	0.38	0.21	0.16
Residual	24	0.21		

Table II. Two-way analysis of variance for cylindrical fecal pellet concentrations with zone and day as main effects (excluding three data points).

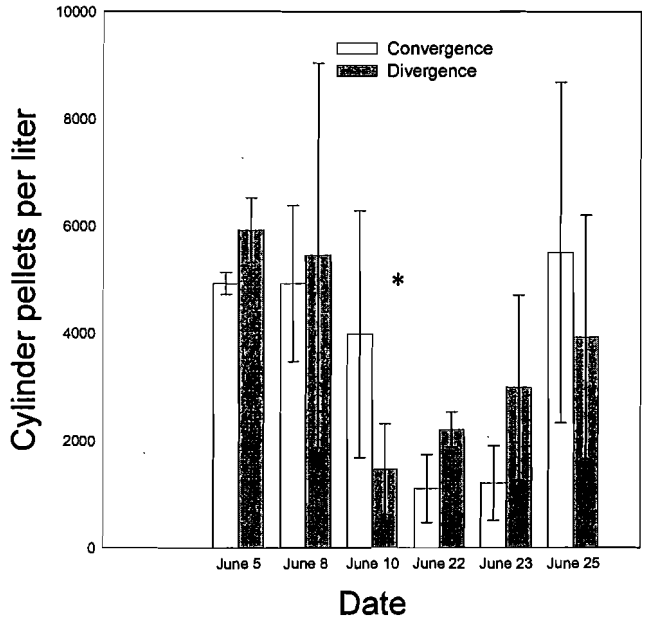
Effect	df	MS	F	p
Zone	1	0.01	0.11	0.75
Day	5	0.33	3.25	0.03*
Zone x Day	5	0.11	1.09	0.39
Residual	21	0.10		

This result prompted me to conduct paired t-test on the cylindrical pellet concentrations in each zone on each date. Cylindrical pellets were significantly more abundant in the convergence zones on June 10, 2007 (Table III). Cylindrical pellets did not differ significantly in their abundance between zones on June 5, 8, 22, 23 or 25 (Table III). Although not significant, on June 25, pellets were more concentrated in the convergence zones and on the other four dates pellets were more concentrated in the divergence zones (Figure 1).

Table III. Paired t-test of cylindrical pellet concentrations in convergence and divergence zones, significant difference marked with an *.

Date	df	T	p	1-tail P
June 5, 2007	2	-1.8	0.21	0.11
June 8, 2007	2	-0.11	0.92	0.46
June 10, 2007	2	8.88	0.01	0.005*
June 22, 2007	2	-1.16	0.36	0.18
June 23, 2007	2	-1.13	0.38	0.19
June 25, 2007	2	0.45	0.69	0.35

Figure 1: Concentration of cylindrical pellets (average/SE; n=3) in convergence and divergence zones of Langmuir circulation cells. Significant difference marked with an *.



Globular pellets were oval and slightly bulbous in shape. These pellets were larger in size and had a slightly less smooth peritrophic membrane than the cylindrical pellets. I am not certain what organism produced these pellets. Globular pellets were observed in both zones on all six sampling days. There was no significant difference in globular pellet concentration between zones but there was a significant difference by day (Table IV; zone, p= 0.52, day, p=0.004).

Table IV. Two-way analysis of variance for globular fecal pellet concentrations with zone and day as main effects.

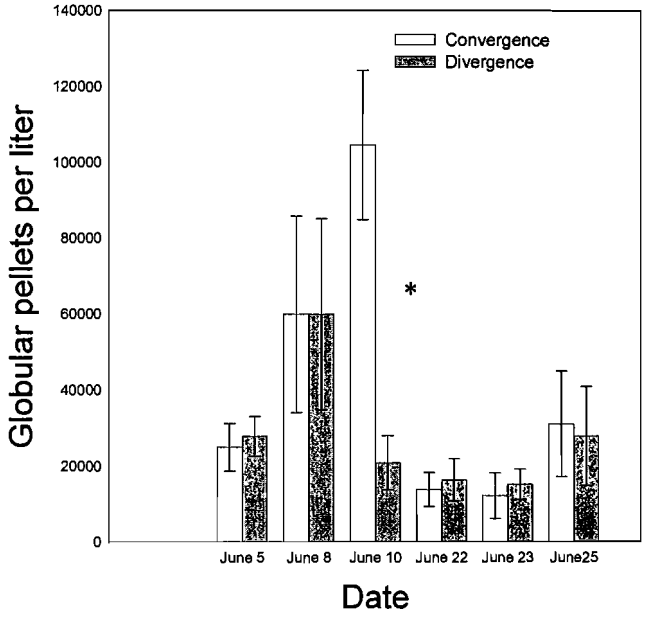
Effect	df	MS	F	p
Zone	1	0.07	0.47	0.52
Day	5	0.40	4.53	0.004*
Zone x Day	5	0.16	1.82	0.15
Residual	24	0.09		

The significant results of day on globular pellet concentration lead me to conduct paired t-test on concentrations in each zone on each day. Globular pellets were significantly more abundant in the convergence zones than in the divergence zones on June 10 (Table V), but were not significantly different in their abundance between zones on June 5, 8, 22, 23, or 25 (Table V). Albeit not significant, on June 25, pellets were more concentrated in the convergence zones and on the other four dates pellets were more concentrated in the divergence zones (Figure 2). On a given day, regardless of pellet shape, pellets were concentrating in one zone. On June 10 and 25 both forms of pellets were more concentrated in the convergence zones. Whereas on June 5, 8, 22 and 23 both types of pellets were more concentrated in the divergence zones.

Table V. Paired t-test of globular pellet concentrations in convergence and divergence zones. Significant difference marked with an *.

Date	df	T	p	1-tail P
June 5, 2007	2	-0.31	0.78	0.39
June 8, 2007	2	-0.001	0.99	0.49
June 10, 2007	2	3.21	0.09	0.04*
June 22, 2007	2	-2.21	0.16	0.08
June 23, 2007	2	-0.37	0.74	0.37
June 25, 2007	2	0.12	0.91	0.46

Figure 2: Concentration of globular pellets (average/SE; n=3) in convergence and divergence zones of Langmuir circulation cells. Significant difference marked with an *.



Wind speed and mixed layer depth on each day is reported in Table VI. Wind speed and mixed layer depth do not appear to be affecting fecal pellet distribution. The winds were strong enough on all days to create Langmuir circulation cells. The mixed layer depth was generally very shallow, one meter or less on all days except June 8, 2007. Swell height observed during sampling and measured at NOAA buoy 46015 is reported in Table VII. The discrepancy between the two swell sizes is due to location. The NOAA buoy is 16 nautical miles offshore, and the swell is not obstructed. Whereas, I was sampling in an area of reduced fetch, in the lee of Port Orford head. Swell height may

have had an impact on circulation. On June 10, when both forms of fecal pellet were found in significantly higher concentrations in the convergence zones swell height was observed to be 1.6 m and the NOAA buoy reported 2.4 m. This was the maximum swell height sampled in the study. On June 25, when both forms were in higher concentration in the convergence zone the swell height observed was 1m, and the buoy reported 1.4 m. Swell height on the four dates when pellets were in higher concentration in the divergence zones was observed to be between 0.3-1.3 m and the outer buoy reported swell heights of 0.82-1.6 m. Thus, pellets of both forms were in higher concentrations in divergence zones on four days when the swell height was relatively small, whereas, pellets of both forms were in higher concentrations in the convergence zones on two days when the swell was large.

Table VI. Average wind speed and mixed layer depth by date.

Date	Wind speed (m S^{-1})	Mixed layer (m)
June 5	3.4	1
June 8	2.9	10
June 10	3.5	1
June 22	3.6	1
June 23	3.4	2
June 25	4.3	1

Table VII. Observed swell height and reported swell height by date.

Date	Observed Swell Height (m)	NOAA swell height (m)
June 5	0.3-0.6	1.6
June 8	0.3-0.6	1.5
June 10	1.6-2	2.4
June 22	0.6-1	0.8
June 23	1.3	1.5
June 25	1	1.4

Discussion

This study compares the concentration of cylindrical and globular fecal pellets in divergence and convergence zones of Langmuir circulation cells and tested the hypothesis that divergence zones would have a higher fecal pellet concentration than convergence zones. This hypothesis was based on Stommel's retention zone model, which reasoned that upwelling currents in divergence zones advects pellets upward counteracting their sinking and thus, retaining pellets in the mixed layer. In contrast, I hypothesized that there would be low fecal pellet concentrations in the convergence zones, as the downwelling jet should advect and accelerate the pellets downward, pushing pellets below the ten meter sample depth.

It is important to note two factors in the design when examining this data. 1) All samples were collected in the morning. 2) All samples were collected in the lee of Port Orford Head. Due to this timing and site of sampling, wind would have had limited time and a potentially weaker effect on the surface water sampled than in the open ocean. Wind was in significant force to achieve Langmuir Circulation, but these factors should be taken into consideration when examining the level of affect.

Both forms of fecal pellets were in higher concentrations in the divergence zone on four of the six sample dates, albeit not significantly so. This pattern suggests that pellets were being retained in the divergence zone and the data supports Stommel's retention zone hypothesis that particles can be retained. Although current velocities and settling rates of pellets were not measured, results from other studies can be used to

evaluate pellet placement within a Langmuir cell. Upwelling current speeds in the divergence zones of Langmuir cells are 0.8-1.5 cm S^{-1}(Weller & Price, 1988) and are known to increase in strength with depth. Reported sinking rates of copepod fecal pellets are 0.006-0.25cm s^{-1}(Smayda, 1971; Turner, 1977; Honjo & Roman, 1978). Therefore a pellet produced at the surface would be able to sink until it enters a depth where the upward current is strong enough to counteract the sinking rate, and then be held in this Stommel retention zone. The plankton tows made in this study were ten meters to the surface, which would pass through the predicted retention zone. These projected numbers of settling velocity and circulation velocity support the theory that a pellet could be retained.

Both forms of pellets were found in higher concentrations in the convergence zone on June 10 (significantly) and June 25. Given the settling rates of fecal pellets and the downwelling speed in the convergence zone, the Stommel retention zone hypothesis suggests that pellets should not be concentrating in the convergence. When examining the environmental variables of wind speed, mixed layer depth and swell height, swell height appears, perhaps, to have affected the distribution of fecal pellets. On June 10, swell height was considerably larger and was running perpendicular to the circulation. Perhaps swell height has a cascade effect on Langmuir circulation.

As swell moves through the surface water as a circular current, it may create turbulence. The larger the swell, the bigger the current and the more turbulence. On June 10, when fecal pellets were concentrated in the convergence zone, the swell's circular current was flowing perpendicular to the helical current of the Langmuir circulation. The

swell's current crossing thorough the LC may have created more turbulence in the helical vortices of LC. This added turbulence may then affect Stommel retention zones, either by shifting them in the vertical or horizontal plane or altogether disintegrating them. I suggest this hypothetical physical cascade would greatly affect particle entrainment and retention.

Based on the results of this study and Stommel's retention zone hypothesis I think the hypothesis that fecal pellets should be in a higher concentration in the divergence zone is still accurate. The result that pellets were more often concentrated in divergence zones supports this hypothesis. However, the result of divergence concentration was not significant. The ability of this study to detect a difference of pellet concentration in zone may have been weakened by high variance or processing problems. Given the logistical restraints of this study, only three tows in each zone were collected on each day, which yielded a very high variance. In regard to processing problems; when examining the cylindrical pellet concentrations three data points were very low, which was unexpected. I recounted these samples and found again a low concentration and ruled out counting error. When looking at the globular pellets and larvae collected in these samples, the numbers seem to be a bit low, which may suggest that the net was not filtering properly. However, the variation in globular pellets and larvae from the normal level was far less than for the cylindrical pellets which makes me think damage occurred to cylindrical pellets in the transfer or processing of samples. These outliers create a high variation in the data set, which lowers the power of the study. On two sample days pellets were in higher concentrations in the convergence zone, which does not support the hypothesis. I

believe this concentration in the convergence to be due to large swell disrupting the stability of Langmuir circulation.

In conclusion, this study was unable to detect a significant difference in fecal pellet concentrations in divergence and convergence zones of Langmuir circulations; nonetheless, interesting patterns emerged that tend to support the hypothesis. Both pellet forms were most often found in higher concentrations in the divergence zones than the convergence zones. This pattern supports Stommel's retention zone hypothesis. The two dates on which pellets were concentrated in convergence zones rather than in the expected divergences I hypothesize to be from turbulence from swell displacing Stommel retention zones.

CHAPTER IV

CONCLUDING SUMMARY

In conclusion, the results of this investigation illustrate and provide evidence that Langmuir circulation has an effect on particles and organisms in the epilimnion. The data are consistent with and support Stommel's retention zone hypothesis that particles and or organisms will be retained within zones of the circulation based on the ratio of settling velocity or swimming velocity versus circulation velocity. Chapter I describes how zooplankton are distributed due to taxonomic, ontogentic and habitat need. The result that late stage meroplankton were concentrated in convergence zones and copepods were evenly distributed support the hypothesis that organisms utilize Langmuir circulation depending on these needs. Given that late stage larvae were concentrated in convergence zones of Langmuir circulation either by behavior or entrained through physical processes or combination, suggests competent larvae are utilizing the pairing of maximum downwind drift in convergence zones and sea breeze to move shoreward. The results in Chapter II that fecal pellets are often concentrated in divergence zones further supports Stommel's model. The result that fecal pellets were significantly more concentrated in the convergence zone on sampling days that experienced a large swell lends to another set of curiosities to be explored.

APPENDIX A

RAW DATA FROM NEUSTON TOWS

Presented below are raw data from 2006 and 2007 Neuston Tows, Table I and Table II respectively (Chapter II).

Table I & Table II:
Cell # include: LC= Langmuir circulation, #, C= Convergence, D=Divergence
Organism: genus and species per 100 m^{3}. Space in the grid indicates a change in date.

Table 1: Raw data from 2006 neuston tows.

Cell #	Unidentified Veliger	*Polydora socialis*	Porcelain zoeae	Porcelain Megalopae
L0C	7.1	0.0	0.0	0.8
L0D	2.4	0.8	0.0	0.0
L0C1	4.0	0.0	4.8	0.0
L0D1	3.2	0.0	0.0	0.0
L1C	40.6	85.2	25.7	0.0
L1D	7.9	5.0	7.9	4.0
L2C	107.7	13.5	38.0	4.0
L2D	33.0	1.5	34.9	2.9
L3C	32.2	3.3	5.9	0.0
L3D	17.2	0.0	5.2	2.6
L4C	1006.6	16.2	113.6	32.5
L4D	200.8	0.0	77.2	15.4
L5C	105.6	21.1	137.2	31.7
L5D	23.0	6.7	21.1	1.0
L6C	28.0	2.1	0.0	21.1
L6D	0.8	3.0	12.8	0.0
L7C	45.8	5.9	16.1	5.9
L7D	15.5	2.7	29.2	8.2
L8C	234.4	11.1	121.1	0.0
L8D	63.6	14.4	16.1	2.5
L9C	56.5	0.0	0.0	0.0
L9D	4.9	0.0	0.0	0.0
L10C	0.0	0.0	1.1	0.5
L10D	0.6	0.0	0.6	0.0
L12C	0.0	0.0	0.0	0.0
L12D	0.0	0.0	0.0	1.0
L13C	17.5	0.0	0.9	8.3
L13D	1.0	0.2	0.0	5.1
L14C	89.5	0.0	0.0	0.8
L14D	71.2	0.0	0.0	6.3
L15C	17.3	0.0	1.0	0.0
L15D	4.3	0.0	0.3	0.6

Cell #	*Obelia* spp.	Amphipods	*B.glandula* cyprid	barnacle molts	Pinnotheridae zoeae
L0C	102.1	3.2	4.0	15.8	53.0
L0D	22.2	0.8	1.6	9.5	28.5
L0C1	69.7	14.3	2.4	100.5	8.7
L0D1	3.2	5.5	0.0	40.4	4.0
L1C	9.9	20.8	56.4	56.4	0.0
L1D	26.7	17.8	5.9	36.6	2.0
L2C	13.5	2.4	55.4	4.0	4.0
L2D	8.7	9.2	1.5	4.4	34.9
L3C	0.0	3.3	12.5	11.2	5.9
L3D	0.9	7.7	6.9	17.2	0.0
L4C	0.0	97.4	584.5	64.9	0.0
L4D	0.0	30.9	15.4	108.1	0.0
L5C	10.6	84.5	453.9	21.1	52.8
L5D	1.9	6.7	139.2	1.9	7.7
L6C	17.9	6.3	14.3	4.2	1.1
L6D	1.5	6.0	9.0	3.0	0.8
L7C	31.4	0.0	25.4	1.7	3.4
L7D	11.0	0.9	5.5	1.8	0.0
L8C	3.2	0.0	4.8	3.2	0.0
L8D	1.7	3.4	76.3	0.0	0.0
L9C	0.0	49.1	0.0	23.8	0.0
L9D	0.0	17.2	1.6	3.3	0.0
L10C	1.6	3.7	2.1	4.2	0.5
L10D	0.6	4.3	2.5	0.0	0.0
L12C	0.0	21.2	18.3	0.0	1.0
L12D	0.0	18.3	1.0	0.0	0.0
L13C	9.2	16.5	11.0	80.9	0.9
L13D	1.0	24.1	2.4	12.2	0.2
L14C	0.0	2.4	0.0	38.0	44.3
L14D	0.8	17.2	17.2	15.7	0.0
L15C	7.0	3.0	8.6	2.7	2.3
L15D	0.0	1.8	2.1	0.9	0.3

Cell #	Siphonophore	*Polyorchis* spp.	Chaetognath	*Podon*	*Sabellaria*	*Acartia hudsonica*
L0C	25.3	2.4	0.8	317.5	0.8	52.3
L0D	86.3	2.4	15.0	567.7	5.5	81.5
L0C1	0.0	0.8	0.0	224.8	0.0	30.9
L0D1	0.0	0.0	0.8	38.8	0.0	26.9
L1C	14.9	5.0	11.9	1.0	20.8	82.2
L1D	36.6	36.6	108.9	1.0	33.7	229.7
L2C	4.0	2.4	0.0	4.8	0.0	199.5
L2D	8.7	2.4	0.0	4.8	0.0	45.1
L3C	5.3	2.6	4.6	2.6	0.7	54.6
L3D	6.0	2.6	7.7	0.0	0.0	43.8
L4C	64.9	0.0	64.9	0.0	16.2	552.0
L4D	15.4	15.4	46.3	0.0	0.0	1297.7
L5C	0.0	21.1	939.5	0.0	31.7	1942.4
L5D	0.0	2.9	239.0	0.0	1.9	215.0
L6C	0.0	1.6	15.8	0.0	0.5	74.9
L6D	0.0	0.8	48.3	0.0	3.8	44.5
L7C	0.0	1.7	33.9	0.0	2.5	119.6
L7D	0.0	9.1	53.9	0.0	1.8	33.8
L8C	4.0	97.4	0.0	0.0	0.0	44.3
L8D	0.0	2.5	125.5	0.0	5.1	165.4
L9C	0.0	0.8	0.0	0.8	0.0	55.7
L9D	3.3	2.5	0.8	0.0	0.0	50.0
L10C	0.5	3.2	7.4	0.0	0.0	11.1
L10D	0.0	1.2	1.2	0.0	0.0	18.5
L12C	0.0	0.0	1.0	0.0	0.0	37.7
L12D	0.0	0.0	0.0	0.0	0.0	71.2
L13C	0.9	1.8	40.4	0.0	0.0	122.3
L13D	0.0	1.0	2.2	0.2	0.0	41.2
L14C	0.8	0.0	0.0	0.0	0.0	78.4
L14D	0.0	0.0	14.1	0.0	0.0	47.0
L15C	0.0	1.0	5.7	0.0	0.0	80.2
L15D	0.0	0.0	1.2	0.0	0.0	25.8

Cell #	*Centropages abdominalis*	*Psuedocalnus mimus*	*Pollicipes*	*pagurus* larvae
L0C	15.0	0.0	0.0	9.5
L0D	32.5	0.0	0.0	26.9
L0C1	3.2	0.0	0.0	0.0
L0D1	6:3	0.0	0.0	1.6
L1C	14.9	0.0	0.0	3.0
L1D	232.7	16.8	0.0	3.0
L2C	148.8	20.6	0.0	0.0
L2D	115.9	12.6	0.0	1.9
L3C	34.8	9.9	0.0	1.3
L3D	9.5	0.0	0.0	0.0
L4C	1152.7	97.4	0.0	0.0
L4D	463.4	77.2	0.0	30.9
L5C	2280.2	52.8	0.0	0.0
L5D	269.7	6.7	0.0	4.8
L6C	1.1	0.0	11.1	0.0
L6D	62.6	14.3	0.0	3.8
L7C	100.9	0.0	29.7	0.0
L7D	60.3	11.0	0.0	0.9
L8C	220.9	0.0	0.0	0.0
L8D	433.5	19.5	0.0	0.0
L9C	100.7	0.0	0.0	0.0
L9D	87.6	0.0	0.0	0.0
L10C	11.1	0.0	0.0	0.0
L10D	15.4	0.0	0.0	0.0
L12C	56.0	0.0	0.0	0.0
L12D	11.6	0.0	0.0	0.0
L13C	250.9	2.8	0.0	0.0
L13D	44.3	0.0	0.0	0.0
L14C	61.0	0.0	0.0	0.8
L14D	118.2	0.0	0.0	1.6
L15C	47.9	1.7	0.0	0.7
L15D	30.4	0.6	0.0	0.6

Table 2: Raw data from 2007 neuston tows

cell #	Insects	Unidentified Veliger	*Polydora socialis*	Porcelain zoeae	Porcelain Meagalopae
LC1C	0.1	0.1	0.0	0.1	0.4
LC1D	0.3	0.0	0.1	0.1	0.1
LC2C	2.2	0.0	0.0	0.2	0.3
LC2D	0.4	0.0	0.1	0.0	0.0
LC3C	0.9	0.0	0.0	0.1	0.0
LC3D	0.4	0.0	0.0	0.0	0.0
LC4C	0.0	0.0	0.0	0.0	0.5
LC4D	0.2	0.0	0.0	0.0	0.7
LC5C	0.0	0.0	0.0	0.0	0.3
LC5D	2.8	0.0	0.0	0.0	13.9
LC6C	0.1	0.0	0.0	0.0	0.0
LC6D	0.5	0.0	0.0	0.0	0.0

cell #	*B.glandula* cyprid	barnacle molts	Pinnotheridae zoeae	Siphonophore	*Polyorchis*	Chaetognath
LC1C	3.4	1.2	0.2	0.1	0.5	1.2
LC1D	0.4	0.0	0.2	0.0	0.3	4.5
LC2C	0.3	0.4	0.1	0.0	0.1	1.5
LC2D	0.1	0.1	0.0	0.0	0.0	0.5
LC3C	0.6	0.0	0.1	0.0	0.1	2.0
LC3D	0.4	0.0	0.0	0.0	0.0	0.7
LC4C	0.0	0.0	0.0	0.0	0.0	2.2
LC4D	0.5	0.0	0.1	0.0	0.0	4.6
LC5C	3.0	0.0	0.1	0.1	0.0	1.9
LC5D	64.1	0.0	0.0	2.8	0.0	25.1
LC6C	1.1	0.0	0.0	0.0	0.0	2.9
LC6D	10.1	0.0	0.0	0.0	0.0	19.2

cell #	*Podon sp.*	*Sabellaria*	*Obelia spp.*	Amphipods	*Acartia hudsonica*	*Centropages abdominalis*
LC1C	0.0	0.1	1.3	4.6	20.5	4.0
LC1D	0.0	0.3	0.1	2.5	3.9	3.8
LC2C	0.0	0.1	0.4	0.9	4.0	1.2
LC2D	0.0	0.1	0.0	5.3	14.4	2.3
LC3C	0.0	0.1	0.2	0.3	5.4	1.0
LC3D	0.0	0.0	1.3	0.7	6.1	1.1
LC4C	0.0	0.0	0.3	0.0	0.0	0.0
LC4D	0.1	0.0	0.6	0.0	0.0	0.0
LC5C	0.2	0.0	0.1	0.5	0.0	0.0
LC5D	0.0	0.0	30.6	19.5	0.0	0.0
LC6C	0.0	0.0	0.0	0.0	0.0	0.0
LC6D	0.0	0.0	0.0	0.5	0.0	0.0

cell #	*Psuedocalnus mimus*	Unidentified fish eggs
LC1C	0.0	2.6
LC1D	0.0	3.6
LC2C	0.0	8.2
LC2D	0.0	3.5
LC3C	0.0	5.8
LC3D	0.0	6.2
LC4C	0.0	10.3
LC4D	0.0	22.1
LC5C	0.0	10.6
LC5D	0.0	111.4
LC6C	0.0	17.3
LC6D	0.0	142.6

APPENDIX B

FECAL PELLET RAW DATA FROM VERTICAL TOWS

Table 1: Fecal pellet raw data from vertical tows: Cell # includes FP= fecal pellet cast #, C=Convergence, D=Divergence. Pellets per liter.

Cell #	Cylindrical Pellet	Globular Pellet
FP1C	4716.98	35849.06
FP1D	4716.98	29716.98
FP2C	4716.98	14308.18
FP2D	6603.77	35691.82
FP3C	5345.91	24528.30
FP3D	6446.54	17924.53
FP4C	4716.98	44811.32
FP4D	471.70	23742.14
FP5C	7547.17	110220.13
FP5D	3459.12	47798.74
FP6C	2515.72	24528.30
FP6D	12421.96	108176.10
FP7C	5503.14	66823.90
FP7D	3459.12	34591.19
FP8C	3301.89	133176.10
FP8D	943.40	16823.90
FP9C	3144.65	113522.01
FP9D	*157.23	11006.29
FP10C	2358.49	13207.55
FP10D	1572.33	15094.34
FP11C	628.93	21698.11
FP11D	2672.96	26415.09
FP12C	314.47	6289.31
FP12D	2358.49	7232.70
FP13C	943.40	7389.94
FP13D	1729.56	8805.03
FP14C	2515.72	24056.60
FP14D	2201.26	13993.71
FP15C	*157.23	4874.21
FP15D	5031.45	22641.51
FP16C	8490.57	58490.57
FP16D	*157.23	5188.68
FP17C	3301.89	21069.18
FP17D	3616.35	27987.42
FP18C	4716.98	13522.01
FP18D	8018.87	50314.47

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