

TRANSPORT MECHANISMS OF DECAPOD
LARVAE TO THE NEARSHORE AND
ESTUARINE ENVIRONMENT

by

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A THESIS

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Time series analysis techniques were used to investigate relationships between possible shoreward transport mechanisms and the nearshore abundance of larvae in the mouth of Coos Bay, Oregon, USA. The abundance of *Cancer magister* and *Cancer oregonensis/productus* megalopae was significantly correlated with the tidal cycle; peak abundance just after the spring tide. Hermit crab post-larvae and Porcelain crab zoea were significantly more abundant during onshore winds.

We tested the hypothesis that the depth distribution of *Cancer* spp megalopae changed across the estuary plume at the Coos Estuary. In 1995 more megalopae were caught on the surface waters on the ocean side of the estuary plume front, while more megalopae were caught in the bottom waters on the estuary side of the front. Due to low concentrations of megalopae, the results of the 1997 data were inconclusive .

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CHAPTER I

GENERAL INTRODUCTION

Planktonic larval stages are a fundamental characteristic of the life histories of many near-shore marine invertebrates (Strathmann 1987). The amount of time spent in the plankton can vary from as short as minutes to as long as many months (Strathmann 1987). During the planktonic period, larvae may be dispersed away from a suitable settlement site, thus, creating the need for a return migration. Since larvae are usually unable to swim against horizontal currents, the return migration is probably due to physical processes that induce shoreward movement (Shanks, 1995).

This thesis discusses possible transport mechanisms that function to return decapod larvae back to settling environments. Chapter I investigates mechanisms of shoreward transport of *Cancer magister*, *Cancer oregonensis*, *Cancer productus* megalopae, Porcellanidae megalopae and zoeae and hermit crab megalopae from outer-shelf waters to the nearshore. Daily time series of decapod larval abundance and physical variables were collected to test for relationships between the abundances of larvae and the physical variables. If physical factors influence the transport of larvae, then we predict that the abundance of larvae should vary with the physical variable. For example if

larvae are pushed ashore by currents generated by onshore wind then abundance should be highest during onshore wind events.

Chapter II investigates the distribution of *Cancer magister*, *Cancer oregonensis* and *Cancer productus* megalopae around the estuarine plume front at the mouth of Coos Bay. Coos Bay is probably a two layer estuary with net transport out of the estuary at the surface and landward currents near the bottom of the water column. We tested the hypothesis that *Cancer* megalopae on the estuary side of the plume front inhabit a different portion of the water column than megalopae on the ocean side of the plume front. It has been suggested earlier that blue crab (*Callinectes sapidus*) larvae may migrate into bottom waters to cross the estuarine plume (McConaugha, 1988) and it is possible that *Cancer* spp. may utilize a similar mechanism to enter the Coos Bay estuary. In order to see if there was a difference in abundance, we sampled the surface and bottom waters on the ocean and estuary-side of the plume front.

CHAPTER II

CROSS SHELF TRANSPORT OF DECAPOD LARVAE

Introduction

Many nearshore benthic invertebrates have planktonic larvae (Strathmann, 1987). While some larvae remain nearshore others can be carried over the continental shelf, hundreds of kilometers away from their origin (Lough, 1976). The planktonic larval phase can vary from as short as minutes to multiple months. The amount of time spent in the plankton is usually proportional to the distance these larvae are transported (Shanks, 1995). At the end of this planktonic existence, the larvae are faced with the need to migrate to a suitable environment in which to settle. For organisms which inhabit estuaries, the intertidal zone or the nearshore, larvae may need to migrate shoreward distances greater than a hundred kilometers (Lough, 1976).

Since most larvae are probably unable to swim against prevailing horizontal currents, the migration to the nearshore is probably accomplished by the utilization of shoreward currents. Possible cross shelf transport mechanisms have been reviewed in (Shanks, 1995) and include: 1) wind driven

surface currents; 2) shoreward propagating convergences associated with tidally generated internal waves; 3) shoreward propagation due to tidally generated internal wave bores; 4) relaxation following upwelling events; and 5) currents generated by the density structure over the continental shelf. Larval behavior should have a large effect on which current dominates shoreward transport. For example, shoreward transport by a moving convergence zone requires a larvae to be in the neuston when the larvae contacts the convergence and to remain in the neuston while in the convergence.

The number of larvae transported to the nearshore should fluctuate with the strength of the physical phenomena which causes transport. For example, if wind caused transport you would expect to see a significant correlation between wind duration and the size of larval catch. Time series have been used to infer mechanisms of shoreward transport of blue crab *Callinectes sapidus* megalopae (Rabalais, 1995; Van Montfrans et al., 1995; Morgan et al., 1996; Shanks, in press); *Pachygrapsus crassipes* megalopae (Shanks, 1983); barnacles (Shanks, 1986; Roughgarden et al., 1991; Pineda, 1991); *Cancer* spp. megalopae (Wing et al., 1995a; Wing et al., 1995b) and larval fish (Thorrold et al., 1994).

Cancer magister is an economically important fishery in the northeast Pacific. The *C. magister* fishery is characterized by a high interannual variability in catch (McConnaughey et al., 1992). Many studies have tried to explain variations in interannual catch (Botsford et al., 1989; McConnaughey et

al., 1995; Wing et al., 1995; Johnson et al., 1986). One possibility is that the variability in catch may be related to the number of larvae that migrate from offshore back to suitable coastal settlement sites. A better understanding of the mechanisms of shoreward transport may lead to a better understanding of the variations in interannual catch.

As adults *Cancer magister*, *Cancer oregonensis* and *Cancer productus* inhabit nearshore or estuarine benthic habitats (Jensen, 1996). Planktonic zoeae are released early in the year (January-march) (Strathmann, 1987; Cleaver, 1949). The five zoeae stages develop over the shelf waters. Following stage five zoeae they go through metamorphosis and become megalopae. Once megalopae, the larvae migrate back to nearshore settlement sites (Lough, 1976). This study is the first example of a daily time-series of the abundance of *Cancer* spp. megalopae, the three families of hermit crab post-larvae and Porcelanidae larvae done in the northeast Pacific. By comparing the pattern of daily abundance of larvae to the physical variables which might cause transport, I hoped to determine the mechanisms of shoreward migration of larvae.

Methods

Physical Forcing Mechanisms

Wind speed and direction data were obtained from the NOAA Cape Arago Weather Station (CARO3), which is located 3.6 km south of the sample

site. The wind data were used to calculate cross-shelf and along-shelf wind stress (Pedlosky 1987). In order to obtain true near-shore ocean temperature and not temperature associated with the estuary, temperature was recorded away from the Coos Estuary. Temperature data were obtained from a Hobo temperature logger set approximately 3 m below mean low low water, at Norton Gulch which is 4 km south of the mouth of Coos Bay. Predicted tides were obtained for Charleston, Oregon which is approximately 1 km away from the study site from the Harbor Master tide predictor. The maximum daily tidal range was calculated as the difference between the highest high tide and the lowest low tide between each collection period. All physical data are reported as daily averages.

Time Series of Decapod Laevae Abundance

Organisms that pass through the mouth of the Coos Estuary in southwestern Oregon, USA ($43^{\circ} 20' 10''$ N; $124^{\circ} 20' 0''$ W) (Figure 1) were sampled from 8 April thru 1 July, 1997. Samples were collected with a pair of stationary neuston nets held in a horizontal position by a PVC frame (Figure 2). The net mesh was $500\mu\text{m}$ and each net had a mouth opening of 16 cm X 33 cm. Each net had a reducing cone to increase the ratio of filtering area to mouth area of the net. The net expands from the small mouth out to a 50 cm diameter net and then tailed off in a conical shape. In order to separately sample the flooding and ebbing tides the nets were placed side by side and oriented facing opposite

directions. The PVC frame was held in position with ropes to a buoy in the channel and to the shore. To quantify the amount of water sampled, the nets were equipped with General Oceanics flow meters with high speed rotors. The flow meters were mounted in the mouth of the nets in such a way that they could not rotate when the current switched directions. When current flow was opposed to the net opening, the nets collapsed onto the flow meter preventing rotation of the rotor. To reduce larval loss during periods when each net was not sampling, special cod ends were constructed. The cod ends were bent at a 90° angle so that during non-sampling currents the cod ends pinched the net closed.

Plankton samples were removed from the nets every other low tide. Each day's sample consists of organisms collected over two flooding and two ebbing tides. Net retrieval was conducted at slack tide when there was no active sampling by the nets. Nets were pulled ashore and washed down with fresh water. Samples were preserved with 10% buffered formalin.

Prior to sample inspection, macro-algae were removed from the samples and organisms that stuck to the algae were washed into a sieve. Organisms were identified with standard references (Lough, 1975; Gonor, 1973; Puls in prep) and enumerated under a dissecting microscope. It was impossible to differentiate between *Cancer oregonensis* and *Cancer productus* so they were grouped together (Debrosse et al., 1990). There are three families of hermit crabs (Paguridae, Diogenidae, and Lithodidae) found in the north eastern Pacific

Figure 1: Location of study site in the mouth of Coos Bay, Oregon. Arrow indicates the location of the nets.

Oregon Coast



Coos Bay

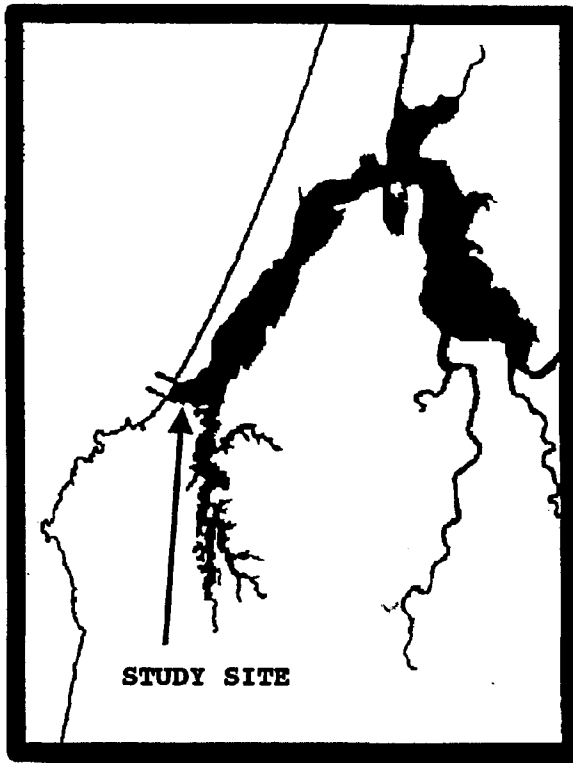
PACIFIC OCEAN

Columbia River

Tillamook Bay

Yaquina Bay

OREGON



STUDY SITE

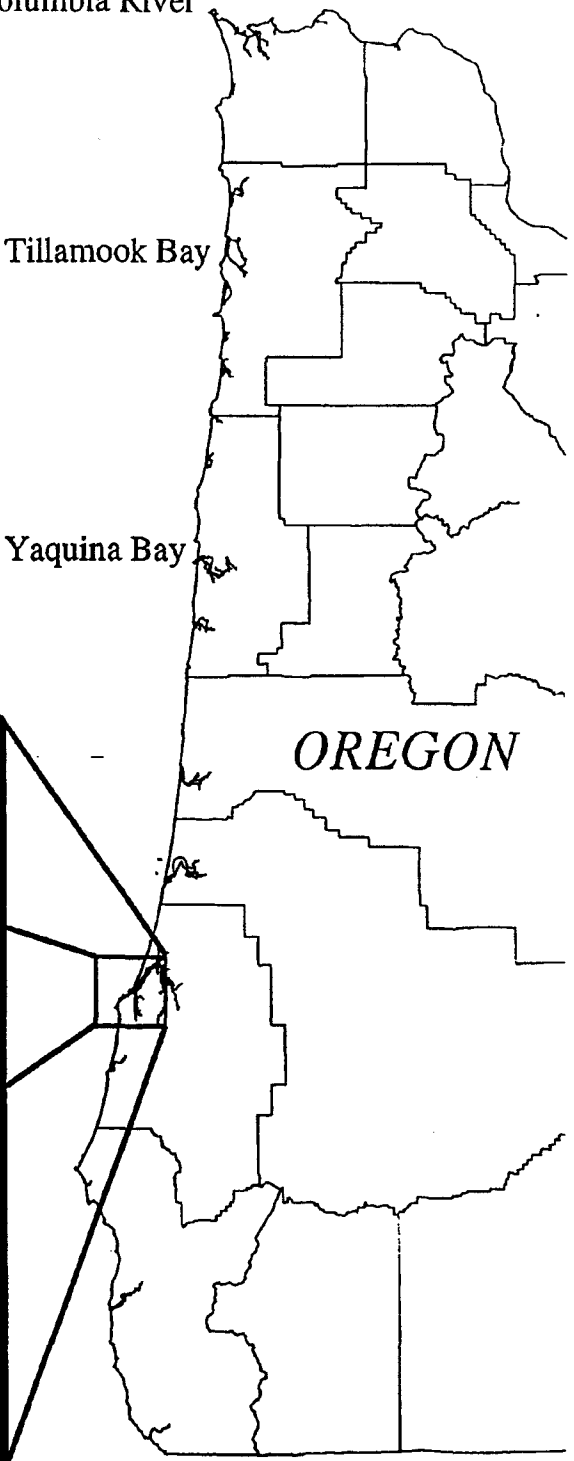
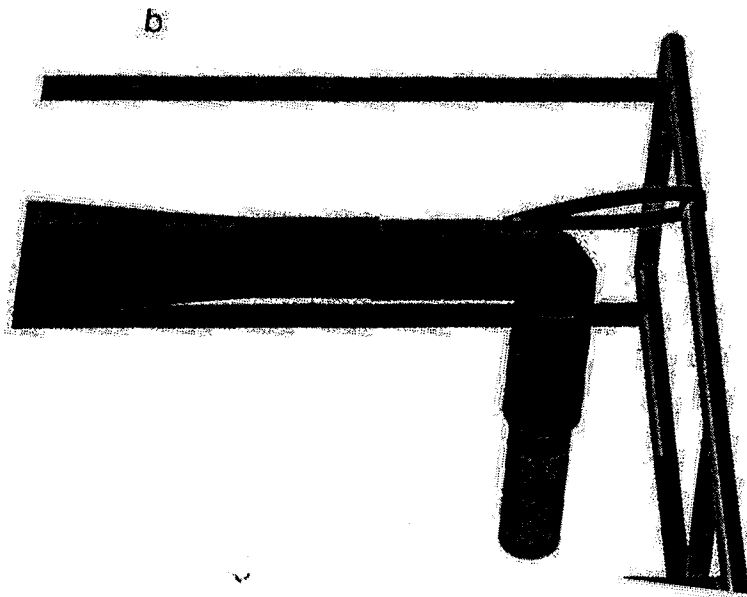
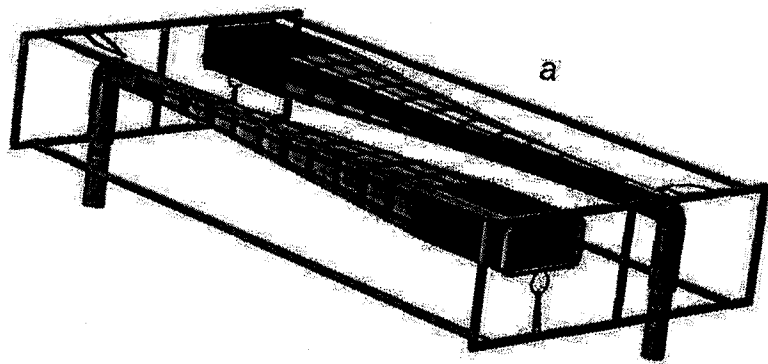


Figure 2: Neuston sampling nets deployed near the mouth of the Coos Estuary. Nets(A) were equipped with flow meters and special cod ends(B) designed to minimize larval loss during non sampling times.



(Strathmann, 1987; Jensen, 1996). No effort was made to differentiate between the families. There are four species of Porcelain crabs (*Pachycheles rudis*, *Pachycheles pubescens*, *Petrolisthes cinctipes*, and *Petrolisthes eriomerus*) along the Oregon coast (Gonor and Gonor, 1973; Jensen, 1996). Both the megalopae and the two zoeae for Porcelain crabs were counted. Species were difficult to differentiate so, Porcelain crab larvae were only identified to family.

In most cases the entire sample was counted but if the number of organisms in a particular group was above two hundred, random squares within the counting tray were counted for that group. Porcelain crab zoeae in most samples were counted using this technique but some of the large samples were split with a plankton splitter, down to smaller samples.

Data Analysis

To minimize the effect of large peaks in the data sets of larval abundance, catches were log transformed ($\log_{10} x+1$) (Thorrold et al., 1994). Daily catches were expressed as either numbers day⁻¹ or concentration day⁻¹ (#'s caught/m³) (Thorrold et al., 1994). The number day⁻¹ was used whenever abundance was not significantly correlated to the amount of water which passed through the net. If the number day⁻¹ was significantly correlated to the amount of water filtered then concentrations day⁻¹ were used in subsequent analysis. Sample dates that were missed (days 15, 16, 56, 80) were estimated by taking the average of the prior and successive data points.

The first step in the analysis was to look for relationships between the biological time-series and the lunar cycle. Fourier analysis was used to look for periodicities in the biological data. Following this, cross-correlations between maximum daily tidal range and catch were run. To account for the effects of significant autocorrelations in the tidal data the corrected standard error of the cross-correlation r was computed (Wing et al., 1995). This corrected standard error was used in cases where it was more conservative than the white noise standard error calculated from the cross-correlation.

To investigate relationships among the physical variables, cross-correlations were run between the tides, wind stress (along and cross shore) and water temperature. Cross-correlations were then run between the physical and the biological time-series. Before these later cross-correlations were run, however, the time series were tested for significant auto-correlations ($\alpha \leq 0.05$) because the autocorrelation may artificially inflate the r values (Thorrold et al., 1994). If significant autocorrelations were found, ARIMA (Autoregressive Integrated Moving Averages) models were fitted to the data using standard techniques (Dunstan, 1993; Jassby, 1990). Cross-correlations were then run between the residuals of the ARIMA's. In this analysis significant cross-correlations with positive lags were disregarded because it was assumed that biological data would not have an effect on the physical data sets. Lags of longer than seven days were also disregarded (Thorrold et al., 1994).

Results

Physical Forcing Mechanisms

During the spring of 1997 the coastal oceanography off of Coos Bay was dominated by a significant El Niño event. Sea surface temperatures (SST) during the spring of 1997 were anomalously high with SST anomalies ranging from 1.11 to 2.77°C (Pacific Fisheries Environmental Laboratory). SST tended to increase with time. At the beginning of the study SST was approximately 11°C and by the end it was around 16°C (FIGURE 3). SST was not significantly correlated with either the along-shore or cross-shore wind stress (Table 1).

The upwelling indices for 45°N, 125°W were an order of magnitude smaller for the spring of 1997 than they were for the two previous springs (Pacific Fisheries Environmental laboratories). The normally strong northwest winds which persist during the spring and summer were not as strong in 1997 as they were in previous years and further, rains persisted well into the normally dry season.

The only significant cross-correlations between the physical variables was a positive correlation between along shore and cross shelf wind stress with a 0 days lag and a significant positive correlation between temperature and the maximum daily tidal range at 3, 2, 1, and 0 days lag (Table 1). There were no

correlations at any days lag between the amount of water sampled by the nets and the maximum daily tidal range.

Time Series of Decapod Larvae Abundance

Cancer magister

Daily catches of *Cancer magister* ranged from 0 to 78 and were highly variable with a few large peaks (Figure 4). Catches of *C. magister* ($\log_{10}(\# \text{ s caught} + 1)$) were significantly correlated with the amount of water filtered through the nets. Because of this correlation the log of the concentration ($\text{Log}_{10}(\# \text{ s caught}/\text{m}^3) + 1$) of *C. magister* was used in further analysis. In the Fourier analysis peridiogram of the daily concentrations of *C. magister* megalopae there is a peak at 12.8 days (Figure 5). The average number of days between spring tides during the sampling was 13.8 days. The similarity between the peaks in the peridiogram and *C. magister* concentrations suggests that *C. magister* concentrations were fluctuating with the fortnightly tidal cycle. There were significant positive correlations at -3, -4 and -5 days lag between the maximum daily tidal range and the concentration of *C. magister* megalopae, which indicates that large catches tended to occur several days after the spring tide. Temperature was significantly negatively cross-correlated at -1 days lag with the concentration of *C. magister* megalopae. There were no

Figure 3: The variation in the physical parameters during the period of the study (April 8 through June 1, 1997). Positive values for cross shelf wind stress are towards the east, while positive values for along shore wind stress are towards the north. Temperature is near surface temperature at Norton Gulch which is approximately 4 km away from the sample site. Maximum daily tidal range is the difference between the highest high tide and the lowest low tide.

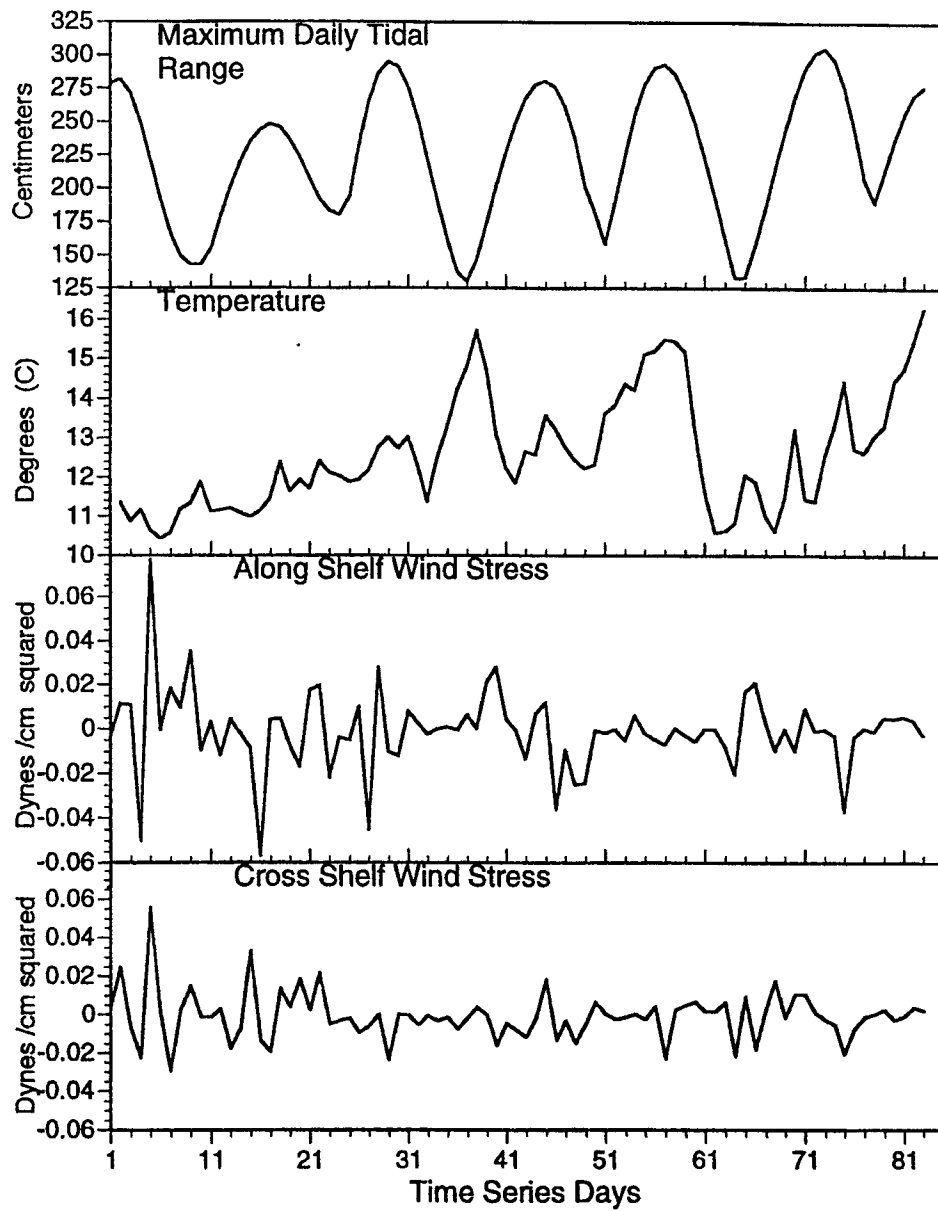
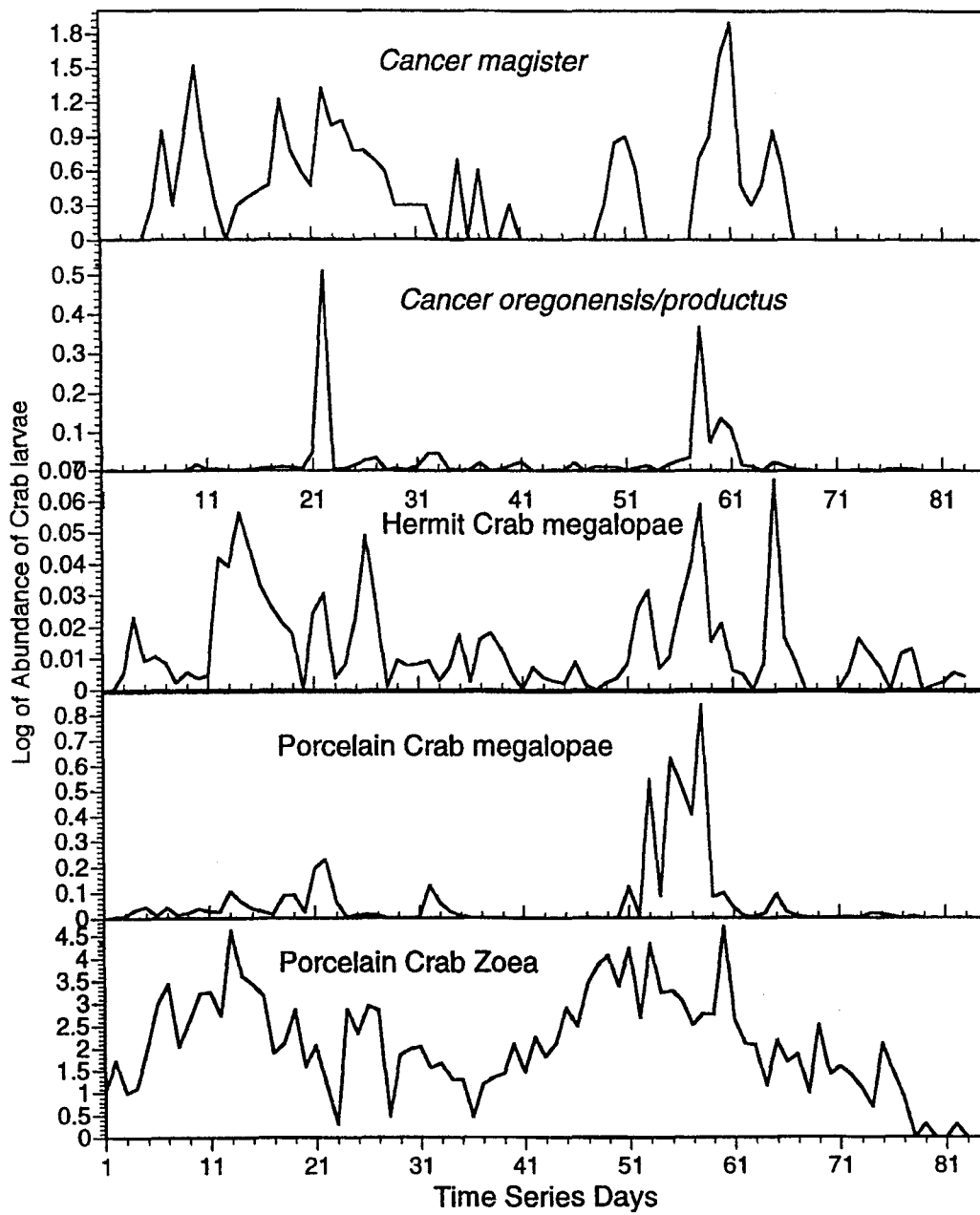


Table 1 : Cross-correlations between nearshore forcing physical variables. Values in parentheses indicate lag(days) while second value is cross-correlation coefficients at which significant($P < 0.05$) cross-correlations were found. NS means that cross-correlation were not significant($P < 0.05$).

	Maximum Daily tidal range	temperature	Cross shore wind stress
Along shore wind stress	NS	NS	(0): 0.4519
Cross shore wind stress	NS	NS	
Temperature	(0): 0.2316 (1): 0.2780 (2): 0.2883 (3): 0.2606		

Figure 4: Time series of the daily abundance (log scale) of organisms caught at the study site from April 8 through June 1, 1997. Organisms sampled include Porcelain megalopae and zoea, *Cancer oregonensis/ productus*, *Cancer magister* and hermit crab post larvae.



significant cross-correlation between either of the along or cross shore wind stress and the concentration of *C. magister* (Table 2).

Cancer oregonensis/productus

Daily catches of *Cancer oregonensis/productus* ranged from 0 to 307 and were highly episodic with two large peaks (Figure 4). Daily catches of *C. oregonensis/productus* were not correlated to the amount of water sampled, so catches were expressed as the $\text{Log}_{10}(\#\text{'s caught}+1)$. The time-series of *C. oregonensis/productus* showed no peaks in the Fourier analysis suggesting that there was no periodicity in the catch. Catch was significantly positively cross-correlated to the maximum daily tidal range at a lag of -3 days suggesting that the largest catches occurred three days after the spring tides. There were no significant cross-correlations between temperature or the along or cross shore wind stress and *C. oregonensis/productus* catch (Table 2).

Hermit crab post-larvae

The daily catch of hermit crab post larvae ranged from 0 to 58 (Figure 4). Because the catch of hermit crab was correlated to the amount of water which passed through the net, concentrations ($\text{Log}_{10}(\#\text{'s caught}/\text{m}^3)+1$) were used in subsequent analysis. The time-series of daily catch showed no large peaks in the Fourier analysis (Figure 5). Catch was not significantly cross-correlated to

Figure 5: Results of time series analysis of the daily abundance of crab larvae catch at the mouth of Coos bay. On the left are the results of Fourier analysis of the daily abundance. On the right are the results of cross-correlations between the maximum daily tidal range and the log transformed daily abundance of organisms. The dashed lines indicate r values needed for significance ($P < 0.05$).

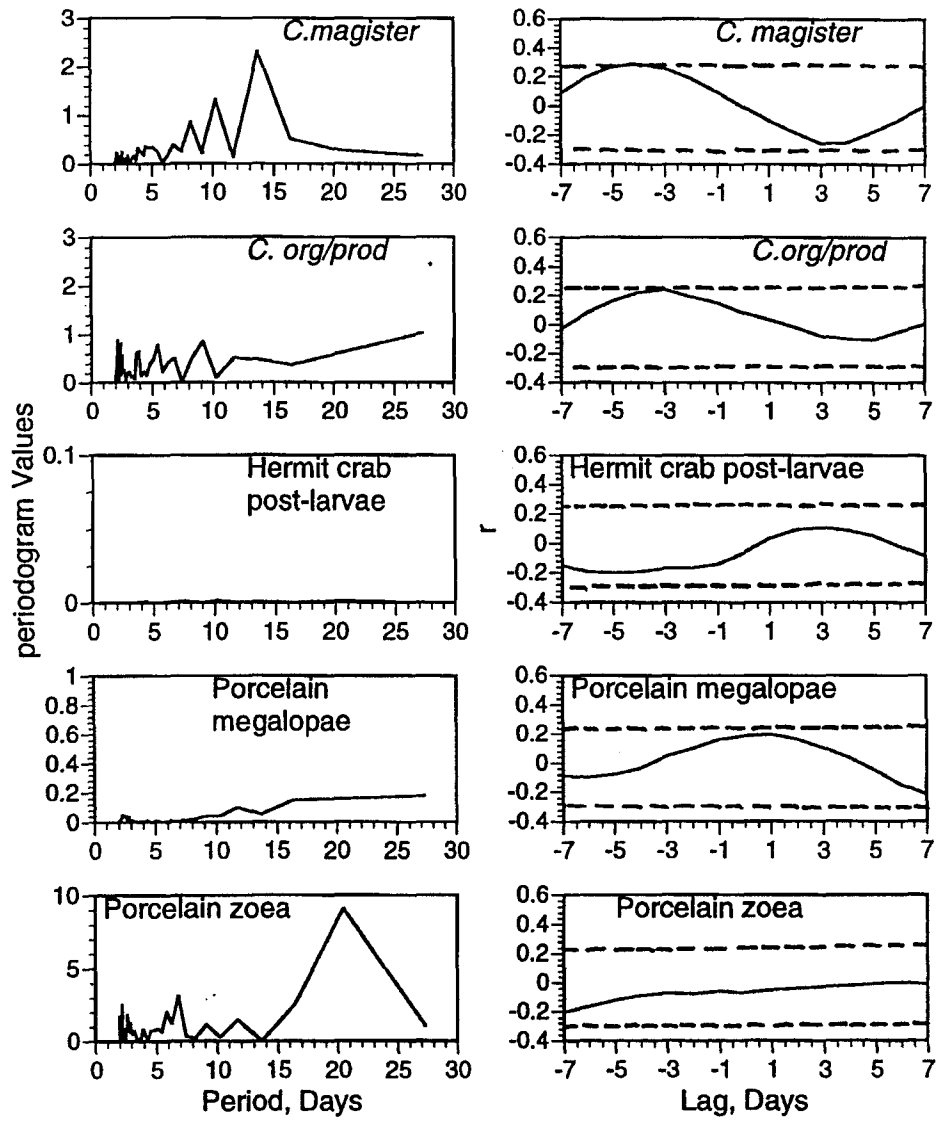


Table 2 : Cross-correlations between log transformed daily abundance of crab larvae and physical variables. Autoregressive integrated moving average models (ARIMA) were fitted to each time series for cross-correlations between the residuals from the models and along and cross-shore wind stress and temperature. Value in parentheses indicate lag(days) and second is cross-correlation coefficients at which significant ($P < 0.05$) cross-correlations were found. NS means that there was no significant cross-correlation.

speciès	Along shore wind stress	Cross shore wind stress	Temperature
Cancer magister	NS	NS	(-1): -0.352
Cancer oregonensis/ productus	NS	NS	NS
Hermit crab post larvae	NS	(-2): 0.2112	NS
Porcelain zoea	(-4): 0.2308	(-4): 0.3101	NS
Porcelain megalopae	NS	NS	NS

maximum daily tidal range (Figure 5). Residuals from the ARIMA of hermit crab concentrations were not significantly cross-correlated to temperature or along-shore wind stress but were significantly positively cross-correlated to cross-shore-wind stress with a lag of -2 days (Table 2). This significant cross-correlation suggests peak catch tended to occur during periods of onshore winds.

Porcelain crab larvae

Catches of Porcelain crab zoeae ranged from 1 to 49,024 (Figure 4). The catches of porcelain crab zoeae were not significantly correlated to the amount of water sampled by the net so $\text{Log}_{10}(\#\text{'s caught}+1)$ was used for analysis. There were no peaks in the Fourier analysis of porcelain zoea in the time-series. Catch was not significantly cross-correlated to maximum daily tidal range (Figure 5) or water temperature (Table 2). There were significant positive cross-correlation with both along and cross-shore wind stress at a lag of -4 days (Table 2).

Catches of Porcelain crab megalopae ranged from 0 to 661 (Figure 4). The catch of porcelain crab megalopae was correlated to the amount of water sampled so concentrations ($\text{Log}_{10}(\#\text{'s caught}/\text{m}^3)+1$) were used in subsequent analysis. There were no peaks in the Fourier analysis of the time-series of porcelain crab megalopae concentrations which suggests a lack of periodicity

(Figure 5). Catch was not significantly cross-correlated with maximum daily tidal range (Figure 5). There were no significant cross-correlation with water temperature or the along shore or cross shore wind stress (Table 2).

Discussion

Physical Forcing Mechanisms

The well documented and publicized El Niño of 1997 caused changes in the oceanography of the southern Oregon shelf. During the spring, the southern Oregon shelf is usually characterized by intermittent upwelling caused by strong northwest winds and short relaxation events associated with southerly winds. In the spring of 1997 the northwest winds were abnormally weak and the sea surface temperature was abnormally high. During the three month sample period of this study, the upwelling indices were much lower than in normal years. Water temperature was not significantly correlated to along shore wind stress, indicating that even when upwelling occurred during the study, the upwelled water was still warm and was probably from above the thermocline. These factors indicate that the spring of 1997 was different from most years and that conclusions drawn in this study may be atypical.

Significant positive correlations between cross-shore and along-shore wind stress indicates that when winds blew toward the north they also blew towards the east. These winds generate downwelling conditions due to Ekman

transport. Neither along-shore or cross-shore wind stress was significantly correlated to an increase in temperature, however, which would be expected in downwelling conditions during non El Niño years.

Temperature was significantly and positively correlated to the maximum daily tidal range. This significant correlation between tides and temperature may be caused by upwelling due to the propagation of internal tidal bores to the coast (Pineda, 1991). A predictable fortnightly pattern of rapid drops in temperature has been described previously in the fortnightly tidal cycle (Pineda, 1991). We also observed a close coupling of temperature to the maximum daily tidal range with predictable drops in temperature. Increases in maximum daily tidal range were correlated to increases in temperature. These relationships were cyclical with decreases in temperature 4 days after the spring tides.

Differences in tidal amplitude did not seem to have an effect on the volume of water sampled, even though one would expect a positive relationship between tidal amplitude and sample volume in an inlet dominated by tidal flow. The lack of correlation between the amount of water sampled and maximum daily tidal range is probably due to the location of the nets. Due to the difficulty of the sampling regime, the nets were placed near the side of the channel. Most of the flow into and out of the Coos Estuary probably occurs in the dredged portion of the navigation channel because it is the deepest region and offers the least resistance to tidal flow. Rapid flow through the middle of the channel and slower flows on the sides (coupled with irregularities in the contour of the sides

of the channel) may form eddies which could have lead to the unexpected lack of correlation between tides and the amount of water sampled. It was possible to observe tidal currents that flowed through the ebb net long after the front signaled the difference between estuary and ocean water had moved upstream past the sample site.

Time Series of Decapod Larvae Abundance

The life cycle of many crustaceans involves a planktonic larval phase during which they can be transported hundreds of kilometers away from a suitable settlement site. Near the end of this planktonic period these larvae must migrate back to an appropriate settlement site. While in the plankton larvae may encounter oceanographic conditions suitable for their transport back to the nearshore. Many of the proposed shoreward transport mechanisms vary in strength within a season and between years. Ideally, a larva would be capable of exploiting more than one mechanism of shoreward transport and avoid currents which might transport them away from possible settlement sites.

The significant correlation of *Cancer magister* and *Cancer oregonensis/productus* catch with the maximum daily tidal range and the roughly fortnightly periodicity of *C. magister* catch, indicates that the catch of these organisms fluctuated on a tidal cycle. On the west coast of the U.S., barnacle settlement (Shanks, 1986; Pineda, 1991) and crab megalopae

abundance (Shanks, 1983) have been significantly correlated to maximum daily tidal range. This correlation has been used to infer transport of larvae shoreward by internal waves or associated phenomenon. On the Atlantic coast of the U.S., blue crab (*Callinectes sapidus*) megalopae have been shown to exhibit peaks in settlement that are coincident or immediately follow the new or full moon (Metcalf, 1995; Olmi, 1995; Montifrans, 1990; Mense et al., 1995; Shanks in press) and after the quarter moons (Boyland and Werner, 1993). Settlement patterns of these larvae could be explained by transport mechanisms that involve internal waves. Shoreward transport of larvae by slicks associated with internal waves has been demonstrated (Shanks, 1983; 1987 and 1988). Further, (Lamb, 1997) modeled internal waves and showed they are able to transport particles residing in the neuston to the nearshore. We propose that a tidally-generated phenomenon, (perhaps internal waves) caused the shoreward transport of *C. magister* and *C. oregonensis/productus*.

Creation of tidally generated internal waves occurs when ebb tidal currents flow across bottom relief on the continental shelf and a lee wave is formed (reviewed in Shanks 1995). When the tide changes back to flood, the lee wave is released and propagates shoreward as a solitary wave (reviewed in Shanks 1995). As this wave moves shoreward it turns into a set of waves (reviewed in Shanks, 1995). The amplitude of tidally generated internal waves is at least in part dependent on the strength of the tidal current, which varies with tidal range. For reasons that are not presently clear, only some internal

waves cause transport (Shanks, 1987, 1988). During a spring-to-spring tidal cycle there may only be a few sets of internal waves which are capable of transporting larvae. The sets capable of transport may only occur at certain stages of the spring-to-spring tidal cycle. If larvae are being transported by only some sets of internal waves during this tidal cycle it may be expected that a correlation exists between catch rates and maximum daily tidal range.

Moving convergences associated with tidally generated internal waves have also been proposed as a mechanism for shoreward transport for larval crustaceans and fish (reviewed in Shanks, 1995). Transport by convergences over internal waves requires that the organisms inhabit the neuston. Buoyant particles, or larvae that maintain themselves in the neuston, can be entrained in the convergence zone between the internal waves. As a result of shoreward movement of the convergence zone, the entrained larvae are also transported shoreward (Shanks, 1995). Megalopae of *Cancer magister* and *Cancer oregonensis/productus* may be transported by internal waves because they inhabit the neuston (Shenker, 1988; Lough, 1976) and are strong swimmers (Lough, 1976). A strong swimming ability is required to maintain position in the neuston in downward flowing convergences.

The significant correlation between daily catch and a decrease in temperature and tidal periodicity could be caused by internal tidal bores that transport the larvae to the nearshore (Cairns, 1967; Pineda, 1991). Internal bores are internal waves which have broken and cause shoreward transport of

masses of water. Oregon has all the physical parameters necessary for internal tidal bore creation (Pineda, 1994) and therefore larvae may be transported by these bores. Although Pineda did not look at temperature anomalies used to infer internal bore creation along the Oregon coast, there is no apparent reason why they could not exist here. The shelf of Oregon has strong density gradients, a large tidal range, and a rough bottom relief, all of which are required for the formation of internal waves and bores. Another possible explanation for the significant correlation between larval catch and tides and temperature is that the larvae are transported by the internal waves associated with internal bores. When sets of internal waves propagate to the nearshore, sometimes one will form a bore (break), but the other waves in the set can continue to propagate shoreward with the bore as internal waves. This means that internal waves and bores can be closely coupled. With daily sampling it is impossible to differentiate between transport of larvae by internal bores and the associated internal waves.

Wing et al. (1995a; 1995b) proposed that upwelling relaxation events caused shoreward transport of *Cancer magister* and *Cancer oregonensis/productus* megalopae. The data presented here indicates that catches varied only with the tides. The difference between the conclusions drawn from these two studies may stem from one or more of the following factors: 1) the differences in temporal resolution of the time-series, 2) the transport mechanisms may differ between regions, 3) transport mechanisms

may vary from year to year. Our samples were collected daily. In contrast Wing et al. 1995a,b sampled on a weekly schedule in northern California. A time series of weekly samples cannot be used to investigate a signal varying on 14 day cycles and, hence, Wing et al. (1995a,b) were unable to discern shorter-term transport mechanisms, (i.e. internal waves, bores). With a weekly time series they were able to document transport back to the nearshore associated with upwelling relaxation events. Wing et al. (1995a,b) also noted that upwelling circulation and coastal topography may cause differences in the temporal pattern of settlement at sample sites further north (Oregon). There is also a possibility that transport mechanisms vary between years. Differences due to daily versus weekly sample collection are probably the primary reason for the differences in conclusions.

Shoreward transport due to relaxation events could be caused by two different mechanisms: 1) the larvae may be transported shoreward in the convergence zone generated by the relaxation front and 2) larvae move shoreward with the water behind the convergence zone. Settlement of barnacles has been correlated with increases in temperature associated with the collision of upwelling fronts with the shore (Roughgarden et al., 1991). Wing et al. (1995a,b) also suggest that some echinoderm and crab larvae are transported to settlement sites by residence within the water behind the relaxation fronts. If relaxation fronts cause transport then a peak in catch or settlement should be associated with a rapid rise in temperature associated

with the fronts arrival at the shore. Because relaxation events are caused by a weakening or reversal of upwelling winds and cause oceanic water to be transported shoreward, larvae may be transported to the nearshore in the water behind a relaxation front consequently catches or settlement should be positively correlated with an increase in temperature and negatively correlated with alongshore wind stress toward the south. Catches of *Cancer magister* and *Cancer oregonensis/productus* megalopae were not significantly correlated to along-shore wind stresses or increases in temperature. This lack of significant correlation suggests that relaxation events were not the dominant transport mechanism during this study.

Because catches of Porcelain crab megalopae were not significantly correlated with any of the physical data, we can draw no conclusions as to the transport mechanism. The catch of Porcelain crab zoeae was positively and significantly correlated with northerly and easterly wind stresses, suggesting that onshore transport occurred during relaxation events or downwelling conditions. If shoreward transport occurred at these times, one would also expect that catch would have been positively correlated with increases in temperature. We did not observe a correlation between catch and temperature increases. If, however, the temperature of the water nearshore is already high, one may not see an increase in temperature when offshore water is pushed ashore. Sea surface temperature was anomalously high during the spring of 1997 and may have masked temperature signatures of relaxation events. It is

our belief that Porcelain crab zoea were not transported by relaxation events, because there was very little upwelling wind in 1997 and therefore relaxation events would have been very weak.

Another possible scenario is that the Porcelain crab zoeae and hermit crab post-larvae reside in the neuston and are transported shoreward by the surface currents generated by shoreward winds. Hermit crab post-larvae and Porcelain crab zoeae were caught in higher abundance when winds were onshore. Transport of larvae by currents generated by easterly winds would require larvae to reside in the neuston. If larvae were at depth, transport would be to the right of the wind direction, due to Ekman transport.

If Porcelain crab zoeae were transported to the near shore via onshore winds they could be farther offshore than hermit crab post-larvae. Porcelain crab zoeae are believed to stay within five km of shore (Lough, 1974) Peaks in catch for Porcelain crab zoeae were not until four days after the onset of wind events, while peaks in hermit crab post-larvae catch occurred only 2 days after shoreward wind events. It is apparent though, that both Porcelain crab zoeae and hermit crab post-larvae abundances are higher when onshore winds are stronger.

There is a second possible explanation for the correlation between onshore winds and the size of the catch of hermit crab post-larvae. On the east coast of the USA, peaks in the catch of blue crab megalopae within estuaries tend to occur during northeast winds (Mense et al., 1995; Jones and Epifanio,

1995;) when coastal water would tend to be pushed into the estuary. If onshore winds were blowing hermit crab post larvae into the estuary, then this significant correlation may disguise a cross-shelf transport mechanism. A time-series of larval abundance on the open coast could be used to resolve this dilemma.

The abundance of both *Cancer magister* and *Cancer oregonensis/productus* megalopae varied with the fortnightly tidal cycle, suggesting that internal waves or bores were responsible for the shoreward transport of the post larvae. Shoreward transport of Hermit crab post-larvae and Porcelain crab zoeae appears to be due to shoreward wind. In conclusion, the correlations between the physical variables and post-larvae abundance varied with species suggesting that the shoreward transport mechanisms may vary by species. Different behaviors and swimming abilities may determine the position of the larvae in the water column which may in turn, be responsible for the differences in transport mechanisms and hence abundance of post-larvae.

Bridge

Chapter I reported on research that investigated mechanisms of cross-shelf transport of *Cancer magister* megalopae, *Cancer oregonensis/productus* megalopae, Porcelain megalopae and zoeae, and hermit crab post-larvae.

Time series analysis was used to evaluate the dominant physical processes affecting shoreward transport. The abundance of *Cancer magister* and *Cancer oregonensis/productus* megalopae appear to be transported shoreward by a physical phenomena which varies with the tides. The abundance of hermit crab post-larvae and Porcelain zoeae were highest during periods of onshore winds. No conclusions can be drawn for Porcelain megalopae because no significant cross-correlations occurred between the physical data sets and the biological time series.

The next chapter investigates the possible mechanisms by which *Cancer magister* and *Cancer oregonensis/productus* megalopae cross the estuarine plume front. We hypothesized that *Cancer* megalopae change their position in the water column following contact with the estuarine plume. On the ocean side of the plume we predict megalopae to be higher in concentration in the upper half of the water column. On the estuary side of the plume we predict megalopae to be higher in abundance in the bottom half of the water column. To test this hypothesis, zooplankton tows were made on the ocean side and estuary side of the estuarine plume front.

CHAPTER II

TRANSPORT OF *CANCER* MEGALOPAE ACROSS AN ESTUARINE PLUME FRONT

Introduction

Many benthic estuarine invertebrates have life cycles that include planktonic larvae (Strathmann, 1987). Larvae spawned in the estuary and that settle in the estuary are either retained within the estuary (Bousfield, 1955) or they go through their development over the continental shelf and then re-enter the estuary for settlement. Larvae that settle in an estuary not only must migrate to shore (reviewed in Shanks, 1995) but they also have to migrate across the estuarine/ocean boundary (reviewed in Boehlert and Mundy, 1988). These two steps to the return migrations may require distinct and separate larval behaviors. Behaviors utilized for shoreward migration may hinder transport into an estuary. For example, residence in the neuston may aid in shoreward transport (see Chapter 1) but may make it impossible to enter an estuary. If entrance into an estuary is required by the larvae they will need to change their behavior in order to maximize their chances of entering the estuary (reviewed in Boehlert and Mundy, 1988).

The benthic brachyuran crabs *Cancer magister*, *Cancer oregonensis* and *Cancer productus* are all near shore or estuarine species whose life cycles include planktonic larvae (Jensen, 1996). Zoea are hatched between January and March (Strathmann, 1987; Cleaver, 1949). The larvae go through five zoeal stages during which time they are dispersed over the continental shelf (Lough, 1976). Toward the end of the planktonic period the zoea metamorphose into megalopae. The megalopae then migrate back to shore where they settle and metamorphose into juvenile crabs (Lough, 1976). The majority of *Cancer* megalopae settle in the nearshore but a significant number enter estuaries (Armstrong and Gunderson, 1985). Those megalopae which enter an estuary must cross the estuarine plume. The estuary has a net outflow of water near the surface and a net inflow of water near the bottom. Residing in bottom waters for crossing the estuarine plume front has been suggested as a plausible mechanism for transport into estuaries (McConaughy, 1988) for blue crabs (*Callinectes sapidus*) and may be possible for *C. magister*, *C. oregonensis* and *C. productus*.

In this thesis I tested the hypothesis that *Cancer* megalopae reside in the bottom waters inside the estuarine plume and that this behavior is different from behaviors expressed by megalopae outside the estuarine plume. This hypothesis was tested with the idea that larvae near the bottom of the water column inside of the front were preferentially selecting the estuary for settlement.

Methods

Samples were collected in front of the mouth of the Coos Estuary, Oregon, USA (43° 20' 10 N; 124° 20' 0 W; Figure 6). The first set of samples were collected on 2 and 3 June 1995. The second set of samples were collected on 30 May, and 10 and 13 June, 1997. In 1995 sampling consisted of three replicate neuston and tucker-trawl tows on the ocean-side and estuary-side of the estuarine front(Figure 7). In 1997 the sampling consisted of one neuston and tucker-trawl tow on either side of the estuarine front on each of the three days. The tucker trawl sampled the bottom and the top half of the water column separately. Prior to the zooplankton tows, a CTD(conductivity, temperature and density) cast was made on both sides of the plume front. Due to computer problems the CTD casts collected on May 30 and June 13, 1997 were lost. The estuarine plume front separating the ocean from the estuary water was located through visual cues. The estuary water was browner in color and more turbid. There was always a line of foam and debris at the convergence zone associated with the front separating the two bodies of water.

The mesh on all nets was 500 μ m. A 1 x 0.2 m mouth opening manta net was used for the neuston tows (Brown and Cheng, 1981) . The mouth of the tucker trawl was 0.5 x 0.5 m. A General Oceanics flow meter was mounted in the mouth of each net to quantify the amount water filtered. Each tucker-trawl tow consisted of an oblique tow of bottom and top waters. Bottom samples were collected from the bottom to the middle of the water column, while top samples

Figure 6: Location of the study site at the mouth of Coos Bay, Oregon. Arrow indicates the approximate location of the zooplankton tows

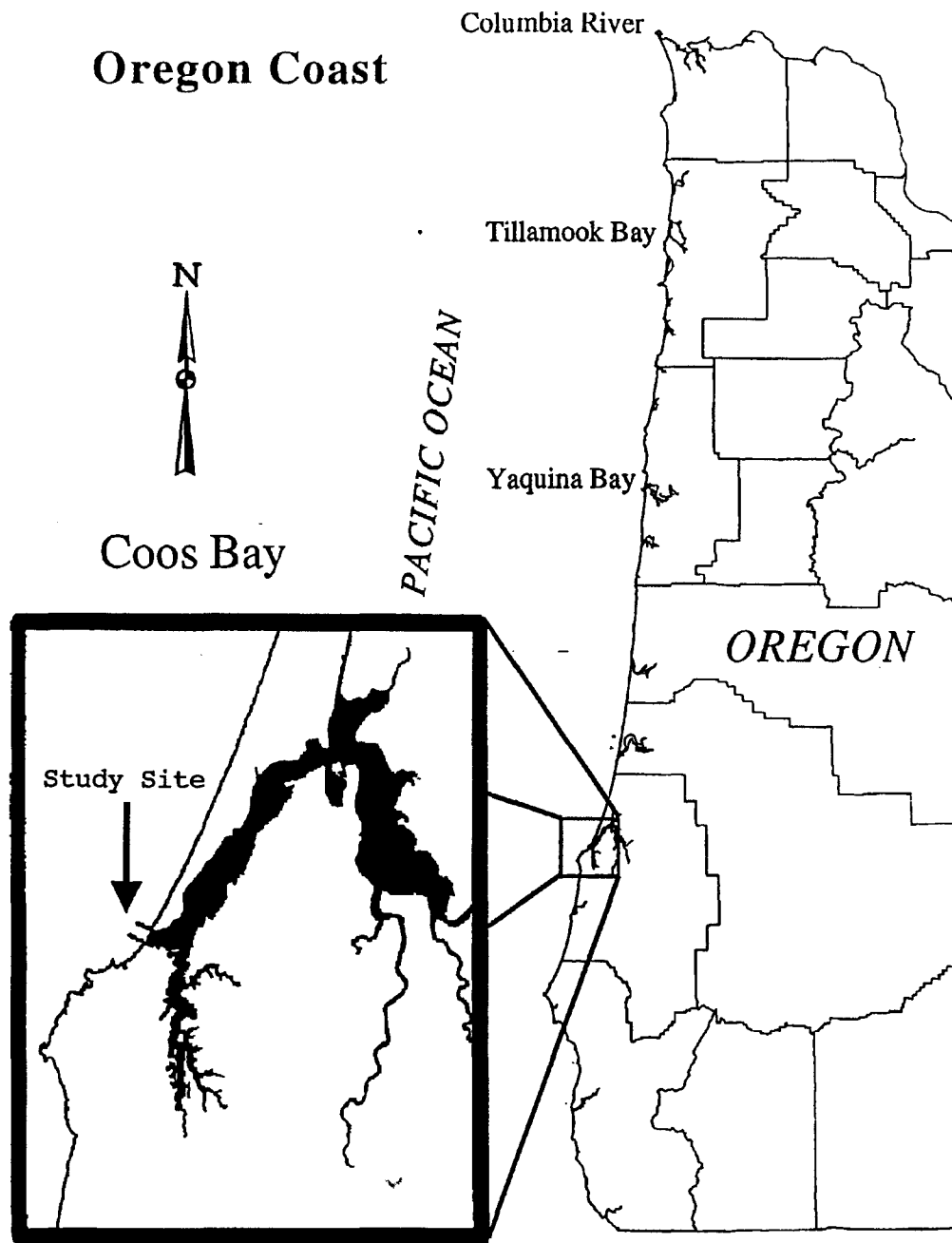
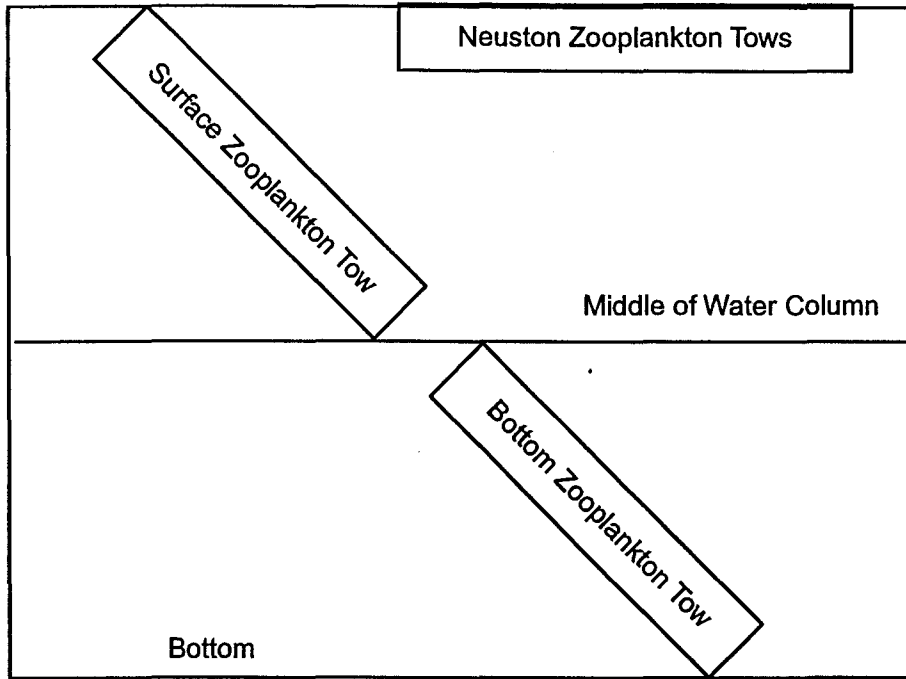
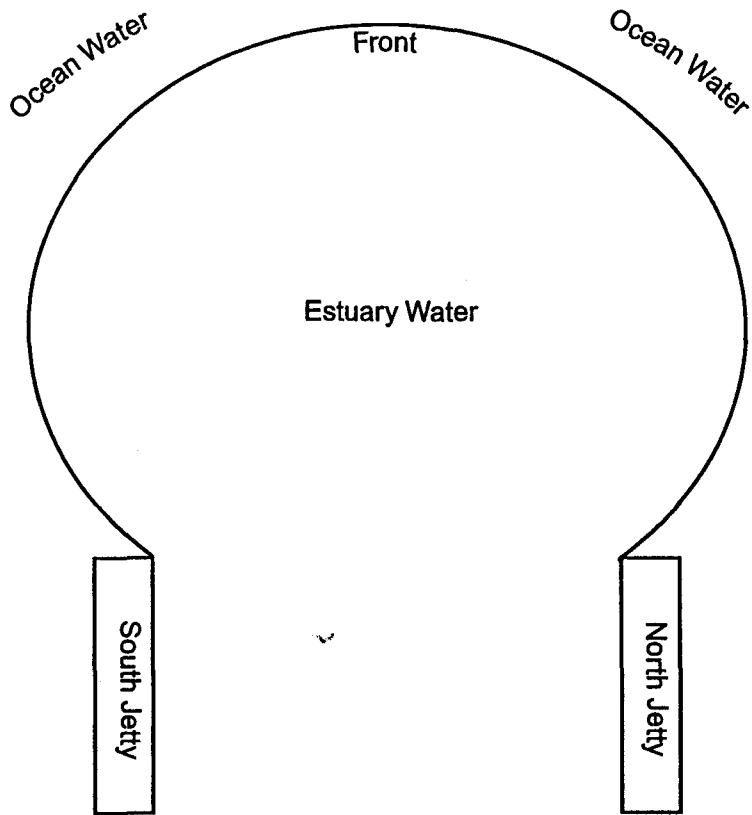


Figure 7: Schematic of depth(a) and location(b) of zooplankton tows. Bottom zooplankton represent tows from the bottom to the middle of the water column while top zooplankton tows represent tows from the middle of the water column to the surface. Neuston tows sample the interface between the sea surface and the air. Tows were made on the ocean and estuary side of the plume.



a



b

were taken from the middle to the top of the water column.

Samples were fixed with 10% buffered formalin. In the lab, megalopae of *Cancer magister* and *Cancer oregonensis/productus* were identified (Lough, 1976; Puls, in prep) and counted under a dissecting microscope. Differentiating between fixed samples of *C. oregonensis* and *C. productus* is not possible (Debrosse et al., 1990), therefore they were combined into one category. Each sample was turned into numbers caught/100m² and arcsine transformed so that the samples were comparable.

Neuston tows and the upper tucker-trawl tows were added together to represent the abundance of megalopae in the surface waters. This combined surface data and the abundance below the middle of the water column was then turned into percent in surface waters. A two factor analysis of variance was run on 1995 data with "date" and "location" being the independent variables and percent in the surface layer being the dependent variable. A one factor analysis of variance was run on the 1997 data with "location" being the independent variable, percent in the surface layer was the dependent variable. The percentages were arcsine transformed prior to running the ANOVAs.

Results

On 2 June, 1995 and 10 June, 1997, CTD casts on the estuary side of the plume front were characterized by a lens of lower salinity, warmer water on the surface. The CTD cast made on 3 June, 1995, indicates that there was a thick

layer of lower salinity water on the surface with a thin layer of colder more saline water near the bottom. The CTD casts on the ocean-side of the plume front found the water column to be vertically mixed with the waters being cooler and more saline (Figure 8, and 9). The CTD cast on the ocean-side of the plume in June 1997 suggests that there was still a shallow lens of less saline, warmer water present (Figure 9). The water column inside the estuary front under the less saline warmer plume water appears to have similar characteristics to the water column outside the front for 1995 data (Figure 8). The front was very obvious during sampling with a distinct line of organic material and debris concentration at the front and a distinct change in water characteristics on the two sides of the front. More megalopae were caught in 1995 than 1997. The largest catches of *Cancer magister* in 1995 and 1997 were 1910/100m² and 55/100m², respectively. Catches of *Cancer oregonensis/productus* were also larger in 1995. In 1995 a higher percentage of megalopae were caught in the upper half of the water column in the waters on the ocean side of the estuarine front (Figure 10). Nearly 100% of the catch in the ocean-side samples were in the surface waters. Inside the estuarine front megalopae were caught in lower abundance in the surface waters. The 2-way ANOVA which investigates the factors which affect the distribution of *Cancer magister* megalopae for 1995 found significant effects of Location (Table 3). The 2-way ANOVA run on *Cancer oregonensis/productus* data found a significant effect of Location (Table 4). So, in summary, the distribution of megalopae changed

Figure 8: CTD data for June 2 and 3, 1995. Data in the figure labeled "Estuary" and "Ocean" are from CTD casts made on the estuary and ocean side of the estuarine plume. Solid lines are temperature($^{\circ}\text{C}$) and dashed lines are Salinity(PSU).

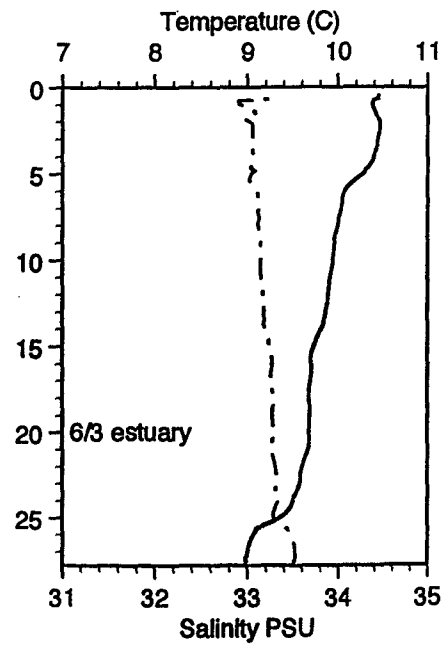
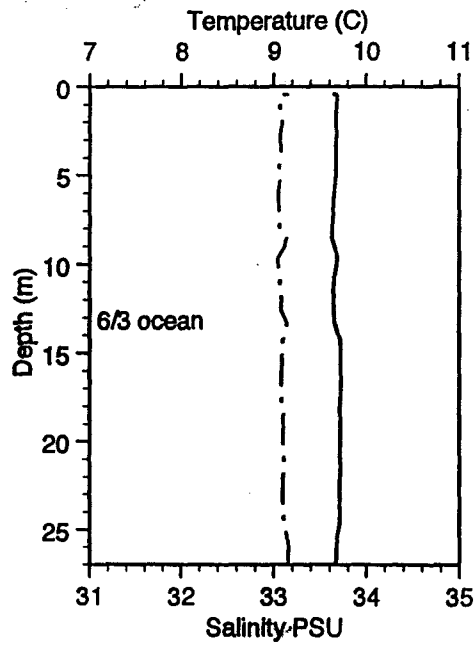
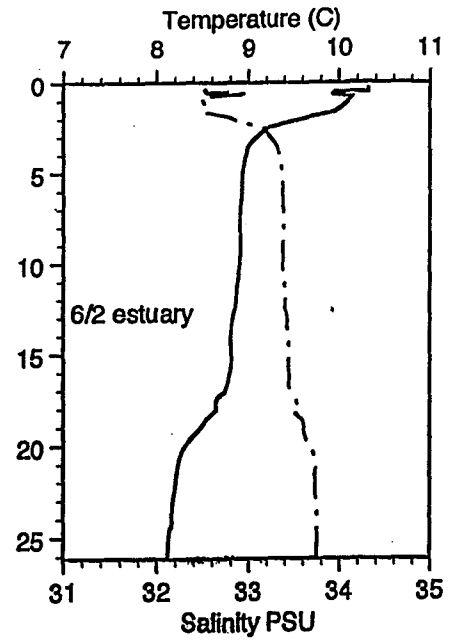
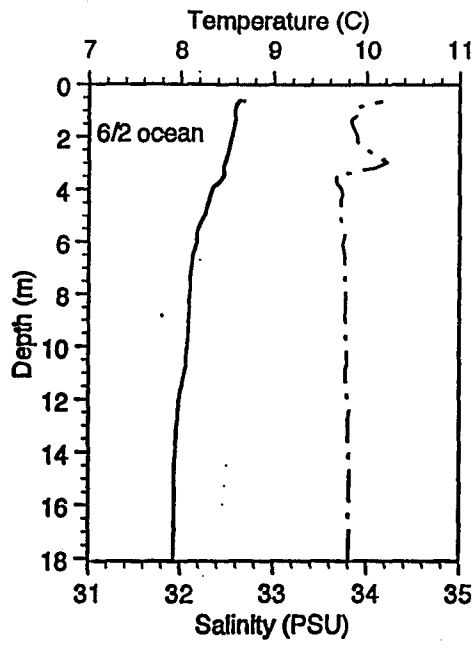
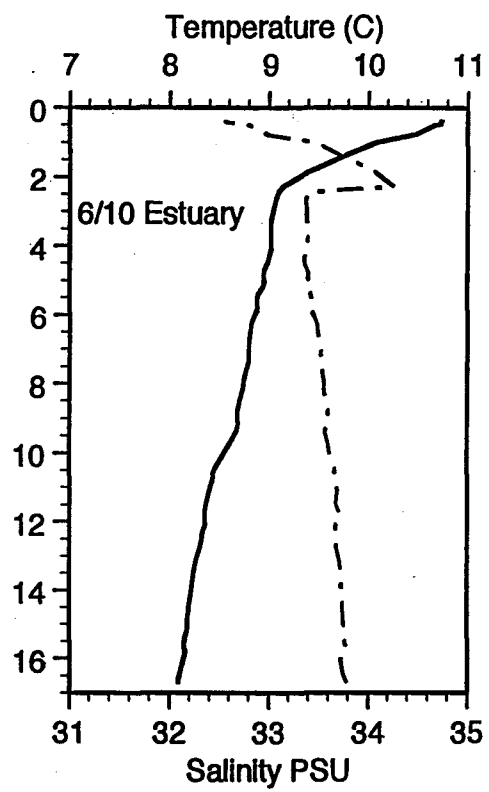
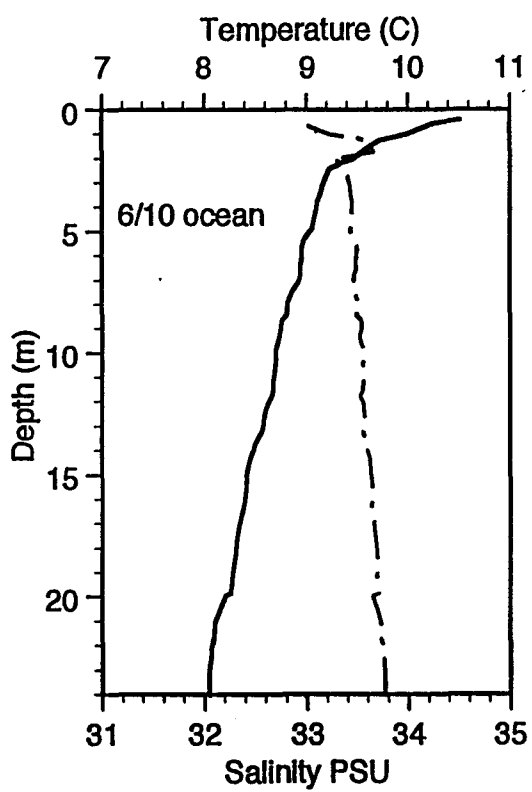


Figure 9: CTD data for June 10, 1997. Data in the figure labeled "Estuary" and "Ocean" were made on the estuary and ocean side of the estuarine plume. Solid lines are temperature($^{\circ}\text{C}$) and dashed lines are Salinity(PSU).



across the estuarine plume front with more megalopae in the surface waters on the ocean-side of the front and more megalopae in the bottom waters estuary-side of the front.

Far fewer megalopae were caught in 1997. A number of the zooplankton tows contained no megalopae (Table 5). The one factor ANOVA run on *Cancer magister* and *Cancer oregonensis/productus* data collected in 1997 found no significant effect of location on the percent of megalopae in the surface (Table 6). This lack of significant effect of location is probably due to the small catches and the high number of zero catches (Table 5).

Discussion

During our sampling there was always a visible estuarine front. The front was marked by a line of buoyant foam and debris, with more turbid water estuary-side of the plume. There was apparent seaward surface flow on the estuarine side of the front. Further evidence of net surface outflow, include a surface layer of less saline (Figure 8 and 9). On the estuary side of the plume front the surface layer of less saline and higher temperature water, coupled with higher salinities and lower temperatures on the bottom, is evidence that the estuarine plume was a two layer system. Like many estuaries with two layered systems, there was probably a net inflow of water near the benthos (Largier, 1992; Pritchard, 1951). Given net outflow at the surface and net inflow near the

Figure 10: Results of 1995, survey. Percent *Cancer oregonensis/productus* (top 2 fig.) and *Cancer magister* (bottom 2 fig.) in the surface waters on the estuary (circles) vs. ocean (squares) side of the estuarine front. Surface waters are defined as the catch in the neuston layer added to the catch of the tucker trawl from the middle of the water column to the surface. Error bars are 95% confidence intervals.

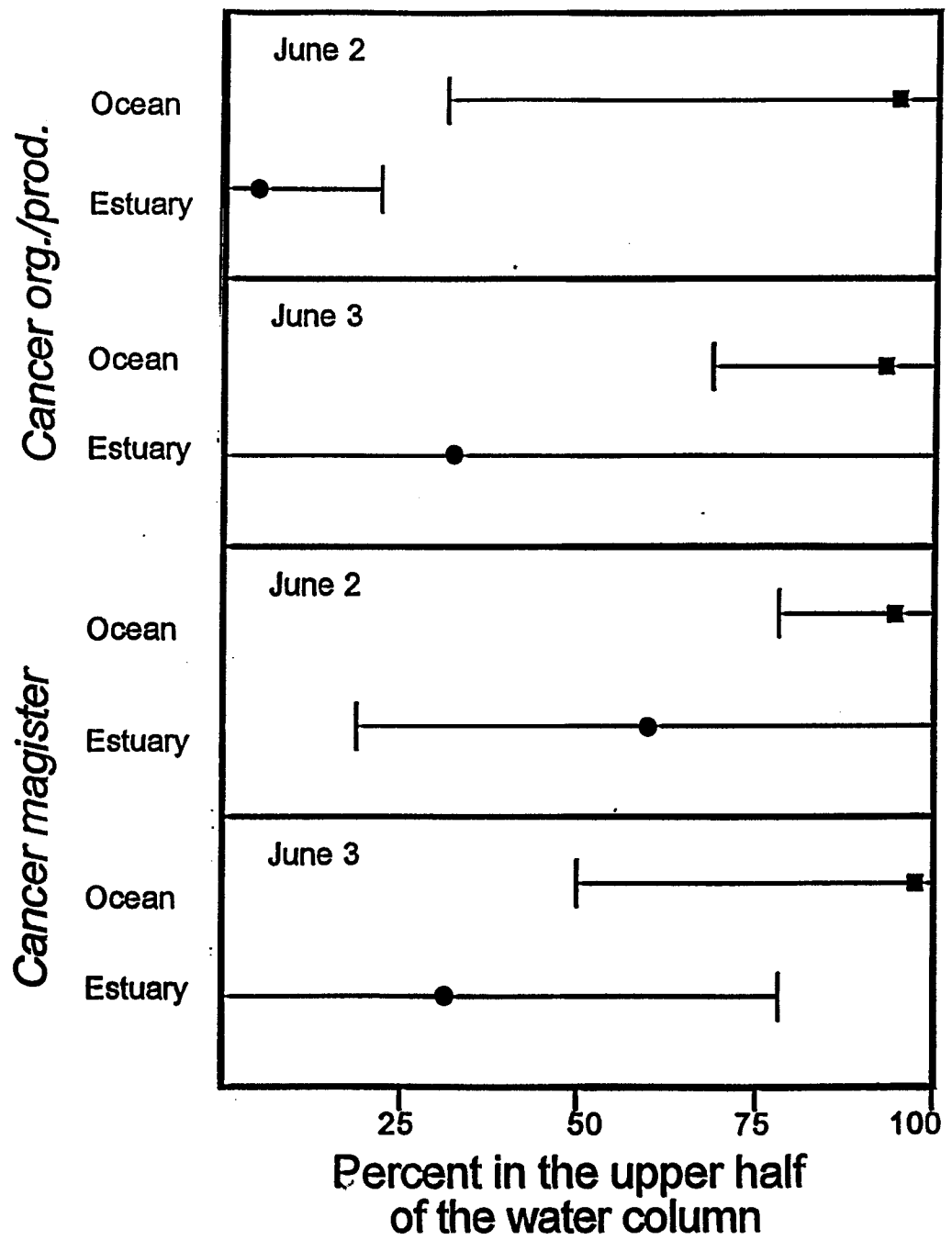


Table 3. Results of 2-way ANOVA comparing the distribution of percent on the surface of *Cancer magister* across the estuarine plume in 1995. The variable Location is whether the sample was collected on the ocean or estuary side of the estuarine plume. The variable Day is whether the samples were collected on 2 or 3 June, 1995.

variables	Sum of Squares	DF	F-Ratio	P
Day	198.209	1	0.330	0.582
<u>Location</u>	5928.714	1	9.863	<u>0.01</u>
Day *Location	1066.910	1	1.775	0.219
Error	4808.671	8		

Table 4. Results of 2-way ANOVA comparing the distribution of the percent on the surface of *Cancer oregonensis/productus* across the estuary front in 1995. The variable Location is whether the sample was on the ocean or estuary side of the estuarine plume, while the variable day is whether the samples were collected on 2 or 3 June 1995.

Variables	Sum of Squares	DF	F-Ratio	P
Day	258.17	1	0.273	0.616
<u>Location</u>	10902.2	1	11.507	<u>0.009</u>
Day*Location	934.21	1	0.986	0.350
Error	1.366	8		

Table 5. Abundances($\#/100\text{m}^3$) and percent caught in surface layer for each station of *Cancer magister* and *Cancer oregonensis/productus* for the three sample dates in 1997. The average amount of water per zooplankton tow was 30.3 m^3 .

<i>Cancer magister</i>	Ocean $\#/100\text{m}^3$		Estuary $\#/100\text{m}^3$		Percent in Surface	
	Surface	Bottom	Surface	Bottom	Ocean	Estuary
5/30/97	0.025	0	0.015	0.062	100	80
6/10/97	0.016	0	0.022	0	100	100
6/13/97	0	0	0.022	0	0	100
<i>Cancer org./prod.</i>	Ocean $\#/100\text{m}^3$		Estuary $\#/100\text{m}^3$		Percent in Surface	
	Surface	Bottom	Surface	Bottom	Ocean	Estuary
5/30/97	0.64	0	0.44	0.124	100	78
6/10/97	0.032	0	0	0.227	100	0
6/13/97	0.048	0.076	0.022	0	38	100

Table 6. Results of 1-way ANOVA comparing the distribution of the percent on the surface of *Cancer magister* and *Cancer oregonensis/productus* across the estuary front in 1997. The variable "Location" is defined as either ocean side or estuary side of the estuarine front.

<i>C. magister</i>				
Source	Sum-of-squares	DF	F-Ratio	P
Location	132.634	1	0.173	0.699
Error	3073.43	4		
<i>C.org./prod</i>				
Source	Sum-of-squares	DF	F-Ratio	P
Location	1616.385	1	1.800	0.251
Error	3591.89	4		

bottom, ingress into the estuary would be optimally accomplished by organisms entering the bottom waters at the mouth of the estuary. We hypothesize that ingress into the estuary by *Cancer magister* and *Cancer oregonensis/productus* is accomplished by the migration of the megalopae into the bottom waters of the estuarine plume. McConnaugha (1988) proposed a similar hypothesis. He suggested that blue crab (*Callinectes sapidus*) megalopae may use the net inflow of water near the bottom in order to enter the estuary

In 1995 the megalopae of the species studied were found in higher abundances on the ocean side of the estuarine plume. On the estuarine side of the plume they were at higher abundances in the bottom waters. In 1997 too few organisms were caught for the statistical analysis. Many samples had zero catch, and the samples that did have catch were usually small. The results from 1995 data suggest that there was a shift in the vertical distribution of the megalopae following contacts with the estuarine plume, while the results from 1997 are inconclusive.

The larvae of *Cancer magister* and *Cancer oregonensis/ productus* reside in the plankton. During their larval development they can be advected further than a hundred kilometers offshore (Lough, 1976). At the end of this planktonic existence the larvae must migrate to shore to settle. *C. magister* megalopae inhabit the neuston (Shenker, 1988; Lough, 1976). They are found at the surface at night, at dusk and dawn and during cloudy days in offshore waters (Shenker, 1988). Recently Roegner et al. (pers. com.) demonstrated that

larvae in the nearshore (less than 15 km offshore) reside in the neuston during the day. We caught megalopae in daytime neuston tows made on the ocean side of the estuarine plume suggesting that they are in fact residing in the neuston in the nearshore. Habitation in the neuston may help with shoreward transport to a settling environment (see Chapter II).

But, due to the flow at the mouth of the estuary, organisms residing at the surface will not be advected into the estuary. We found *Cancer* megalopae in the bottom half of the water column on the estuarine side of the plume, where they should have been advected into the estuary. The shift in the distribution of megalopae across the plume front suggests that the megalopae changed behavior. Possible methods of plume detection were reviewed in Boehlert and Mundy (1988). They suggest that an estuarine plume might be detectable by the salinity gradient, temperature gradient, olfactory cues, changes in turbidity, bottom composition and current speeds. Once the estuary is contacted a behavioral response should then follow. There have been extensive studies showing changes in vertical migration behavior following contact with one or more of these gradients (Tankersley et al., 1994; Tankersley et al., 1995; Forward, 1989; Jacoby, 1982). Hughes (1969) demonstrated that when *Penaeus duorarum* (Pink shrimp) contacted lower salinity water they dropped to the bottom of the test chamber. Changes in the vertical distribution of organism has been studied extensively and may be due to behavioral changes in geotaxis, phototaxis or barokinesis (reviewed by Sulkin, 1984).

The change in the distribution of *Cancer* megalopae across the estuarine plume suggests that entrance into the estuary was due to changes in the behavior of the megalopae. How might ingress into an estuary be advantageous to a *Cancer magister* megalopae? They are known to grow faster in estuaries, possibly due to the generally higher temperature within estuaries (Wainright and Armstrong, 1993). Estuaries may also offer better protection from predators (Fernandez et al., 1994). Lastly, it is possible that there are genotypic differences between megalopae which settle within estuaries and those settling on the open coast (Orensanz et al., 1988). These benefits may also apply to *Cancer oregonensis/productus*. Our data suggests that *C. magister* and *C. oregonensis/productus* may use the net inflow of water near the bottom under an estuarine plume in order to enter the Coos Estuary.

CHAPTER IV

CONCLUSION

The research presented in the preceding pages was an effort to develop a better understanding of the return migration of decapod post-larvae back to coastal settlement sites. Chapter II investigated the relative importance of different mechanisms of shoreward transport. The daily abundance of *Cancer magister* and *Cancer oregonensis/productus* megalopae varied on a tidal cycle with peak abundances tending to occur about three days after the spring tides. These results suggest that transport to the nearshore may be due to physical phenomena associated with the tides. *Cancer* megalopae may be transported shoreward in the convergences over tidally generated internal waves or within internal tidal bores. Internal waves and bores have been previously proposed as mechanisms of shoreward transport for larvae (Shanks, 1983; Pinneda, 1991). Peak abundance of hermit crab post-larvae and Porcelain crab zoea tended to occur during periods of onshore winds, suggesting that they were pushed shoreward by currents generated by onshore winds. No conclusions can be drawn for Porcelain megalopae because no significant correlations were found between their abundance and the physical variables.

Chapter III presents research which investigated the transport of *Cancer magister*, *Cancer oregonensis* and *cancer productus* megalopae across the estuarine plume front at the mouth of Coos bay. Megalopae were found in higher abundance in the surface waters on the ocean-side of the estuarine front and were more abundant in the lower half of the water column on the estuary side of the front. Bottom waters near the mouths of estuaries may be moving up the estuary. If a megalopae were trying to migrate into the estuary, moving into these up estuary bottom currents may enhance transport. These findings suggest that *Cancer* megalopae may change their behavior upon contacting the estuarine plume for preferential ingress into the estuary.

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