

A TIME SERIES ANALYSIS OF LARVAL RELEASE AND
LARVAL RECRUITMENT OF THE MOLE CRAB,
EMERITA TALPOIDA

by

MARK ROBERTS AMEND

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“A Time Series Analysis of Larval Release and Larval Recruitment of the Mole Crab, *Emerita talpoida*,” a thesis prepared by Mark Roberts Amend in partial fulfillment of the requirements for the Master of Science degree in the Department of Biology. This thesis has been approved by and accepted by:

Dr. Alan L. Shanks, Chair of the Examining Committee

Date

Committee in charge: Dr. Alan Shanks, Chair
 Dr. Steven Rumrill
 Dr. Richard Emlet

Accepted by:

Vice Provost and Dean of the Graduate School

An Abstract of the Thesis of

Mark Roberts Amend for the degree of Master of Science

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Title: A TIME SERIES ANALYSIS OF LARVAL RELEASE AND LARVAL
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Approved: _____
Dr. Alan L. Shanks

In an attempt to evaluate the effects of nearshore hydrodynamics on larval release and recruitment of *Emerita talpoida*, field observations of late-stage egg condition and field collections of recently recruited individuals were made during the fall of 1994 in Duck, North Carolina. In time series cross-correlations with physical data, the frequency of grey-stage (stage immediately prior to hatching) ovigerous females was positively correlated with temperature and negatively correlated with wave height, suggesting hatching occurred during high wave activity associated with "northeasters."

Daily collections of the smallest crabs were made along 3 randomly selected transects and recent recruits (uncalcified megalopae) were enumerated using image analysis techniques on preserved specimens in the laboratory. A recruitment index was created to account for the gregariousness of crabs on the beach. In cross-correlations with physical data, the recruitment index was positively correlated with onshore winds, warm temperature, and onshore surface currents. Plankton tows taken offshore found late stage zoea in surface and bottom waters while early stage zoea were primarily in bottom waters. Time series correlations and the distribution of late stage zoea suggest that shoreward transport of late stage larvae was due to onshore wind-generated surface currents.

CIRRICULUM VITAE

NAME OF AUTHOR: Mark Roberts Amend

PLACE OF BIRTH: Fort George G. Meade, Maryland

DATE OF BIRTH: October 23, 1970

GRADUATE AND UNDERGRADUATE SCHOOLS ATTENDED:

University of Oregon
University of California at Santa Cruz
University of California at Irvine

DEGREES AWARDED:

Master of Science in Biology, 1997, University of Oregon
Bachelor of Arts in Marine Biology, 1993, University of California at Santa Cruz

AREAS OF SPECIAL INTEREST:

Dispersal of Marine Organisms
Image Analysis Applications in Biological Oceanography
Ecology of Kelp Forest Organisms
Satellite Oceanography Applications in Coastal Environments

PROFESSIONAL EXPERIENCE:

Experimental Biology Aide, Oregon Department of Fish and Wildlife, Newport,
1996
Research Assistant, Oregon Institute of Marine Biology, University of Oregon,
Charleston, 1994-1996

AWARDS AND HONORS:

Student Travel Award, Western Society of Naturalists, 1995
Honors in Thesis, University of California at Santa Cruz, 1993

PUBLICATIONS:

Amend, Mark (1993) Stability in Discrete Overlapping Distributions of Three Species of the Kelp Forest Gastropod, *Tegula*. B. A. Thesis, University of California at Santa Cruz.

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CHAPTER I

GENERAL INTRODUCTION

For an organism with planktonic larvae in its life history, the dispersal process is of extraordinary importance to its reproductive success. Larvae are released from the adult habitat and enter the plankton where, depending upon the species, they undergo several developmental stages over a period of time. Dispersal occurs when these planktonic larvae move some distance during their development. Later larval stages then return to the habitat from which they were released (via some transport mechanism) to settle as new recruits.

In intertidal crabs, larval release occurs when zoea hatch out of the eggs carried on the female. The timing of hatching may be crucial to the survival and dispersal of the early larval stages (Morgan, 1995). If zoea hatch into an unfavorable environment, they may be killed by predators or by physiological extremes of salinity or temperature. If hatching occurs when there is a chance of larval transport to favorable areas (e.g. offshore), this would improve the chances of surviving predation and physical stress and may be physiologically required for the development of certain larval stages (Morgan, 1995).

Does hatching in intertidal crabs occur at a time that ensures transport away from unfavorable conditions? Hatching rhythms are commonly found in intertidal crabs (Forward, 1987; Morgan, 1995). Rhythms are typically endogenous and timed to tidal, lunar, or diel cycles. In almost all cases, offshore transport is attributed to ebbing tidal currents (Forward, 1987; Morgan, 1995). The effects of non-cyclical environmental cues on hatching have not been investigated, however. Hydrographic processes that act in the surf zone may effect the time of hatching of zoea. Chapter II is an investigation of this

possible influence on the hatching of the mole crab, *Emerita talpoida*, using time series analysis.

After the larvae near the end of their planktonic existence, shoreward transport becomes important in the recruitment of individuals to the adult habitat. This element in the life history of intertidal organisms with planktonic larvae is considered crucial to the maintenance of the adult population (Roughgarden et al., 1988). Because currents often flow in different directions at different depths, the depth at which the larvae reside in the water column determines the direction of their horizontal transport (Shanks, 1995b).

Chapter III is a study of the relationship between physical hydrographic variables and the recruitment of recently settled megalopae of the mole crab.. Cross-correlations between daily measurements of recruitment and physical variables are examined using a time series analysis approach. The vertical distribution of late stage zoea is described by replicate plankton tows from offshore waters. The cross-correlations and distribution of late stage zoea are then used to develop hypotheses to explain the shoreward transport.

CHAPTER II

A TIME SERIES ANALYSIS OF LARVAL RELEASE
OF THE MOLE CRAB, *EMERITA TALPOIDA*

Introduction

The timing of reproduction in marine invertebrates can effect the viability of the young (Giese and Pearse, 1974; Giese and Kanatani, 1987). Rhythms in the timing of hatching have been found to be common in intertidal decapods (Forward, 1987). Most of these hatching rhythms are endogenous and approximate environmental cycles such as lunar, tidal, and diel rhythms (DeCoursey 1979; Christy, 1982; Forward, 1987; DeVries and Forward, 1991; Morgan, 1994; Morgan and Christy, 1994; Morgan, 1995a). Hatching rhythms may operate concurrently with environmental conditions to increase the survival of decapod larvae (Morgan and Christy, 1995).

A large portion of the research on decapod larval release has been carried out on intertidal crabs that inhabit estuarine and tropical habitats (Forward, 1987; Morgan, 1995). In a comprehensive review of larval release rhythms, Forward (1987) lists 14 intertidal species that have been shown to exhibit hatching rhythms. Only three of the fourteen species, however, inhabit "exposed" shores (Christy, 1986).

There is a paucity of research done on exposed coastlines, where the intertidal zone is under the influence of surf zone and hence, "inner-shelf," (defined as the area from the surf zone seaward to 30 m depth), processes as well as tides. This lack of research generates the question: are there physical oceanographic influences on hatching in these habitats? Although endogenous rhythms may control the actual time of hatching, could hatching be forced or cued by exogenous oceanographic phenomena? The environmental

processes that define “exposed” or “open coast” (Ricketts et al., 1985) may play a role in determining when hatching occurs and should be evaluated for such an influence.

To determine if inner-shelf physical oceanographic conditions influence hatching, the temporal scale of sampling needs to be addressed. Estuarine and tropical studies that investigate tidal and diel hatching rhythms have generally been time-intensive, and require hourly or more frequent observations (Morgan, 1995; Forward, 1987). To discern reproductive behaviors that could occur at any time of day, fine temporal resolution sampling is needed. On the other hand, the daily nature of most physical oceanographic phenomena on exposed coasts implies that if there was an effect on hatching, it should be detectable on a daily scale.

The eastern coast of North America and, in particular, the Mid-Atlantic Bight (MAB), offers an ideal location for testing hypotheses on oceanographic influences on hatching in intertidal crabs. The physical oceanography over the inner-shelf of the MAB can be characterized by seasonally variable wind-driven circulation (Wright, 1995). Although circulation over the outer-shelf of the MAB has been well described in the literature (Beardsley et al, 1976; Boicourt and Hacker, 1976), inner-shelf circulation is currently under investigation (Butman, 1994; for a detailed description of the dynamically similar inner-shelf of the South Atlantic Bight, see Pomeroy et al., 1994). In general, the intensity and direction of the wind drives inner-shelf circulation. In the winter, strong onshore winds are frequent while weak offshore winds predominate during summer. The fall and spring are times of transition between these characteristic wind regimes. The fall season has been intensely researched by geologists (Birkemeier et al., 1985; Wright, 1995) because the episodic storm events, (known as “northeasters”) provide the opportunity to test sediment transport hypotheses. Northeasters produce strong downwelling events and large waves, phenomena of particular interest to littoral biologists.

In the swash zone of exposed east coast sandy beaches, mole crabs, *Emerita talpoida*, are abundant filter feeders that migrate up and down the beach face with the tides. Reproduction in *E. talpoida* typically occurs from late winter through early fall with a maximum number of ovigerous females in the late summer (Diaz, 1980). Embryos develop while attached to the female's pleopods (Snodgrass, 1952). Following fertilization, the developing eggs are a bright orange color. As development continues, the eyespots of the developing embryos become visible. With further development, the encapsulated larvae with eyespots take on a dirty grey appearance and soon hatch as zoea. There are no determinations of gestation time for *E. talpoida*, but in a related species, *E. analoga*, gestation time in the laboratory (25°C) was 18 days (Fusaro, 1977).

This study, a part of the Coastal Ocean Processes Field Experiment (Butman, 1994), examines the correlations between oceanographic conditions and larval release by *Emerita talpoida*. Physical events were characterized by measurements taken near the site of crab sampling. Hatching was monitored by daily observations of egg condition in mole crabs made along a sandy beach in the MAB.

Methods

The Outer Banks of North Carolina are exposed barrier islands with miles of continuous sandy beaches typical of the east coast of North America. A 500 m stretch of beach south of the research pier at the Army Corps of Engineers Coastal Engineering Research Center Field Research Facility (FRF) located in Duck, North Carolina (36° 10' 54.6", 75° 45' 5.2"), was sampled for *Emerita talpoida* during the fall of 1994 (Figure 1). This beach is described in Birkemeier et al. (1985). Mean annual beach width from foredune edge to mean sea level (MSL) is 40 m, and the mean annual foreshore slope is

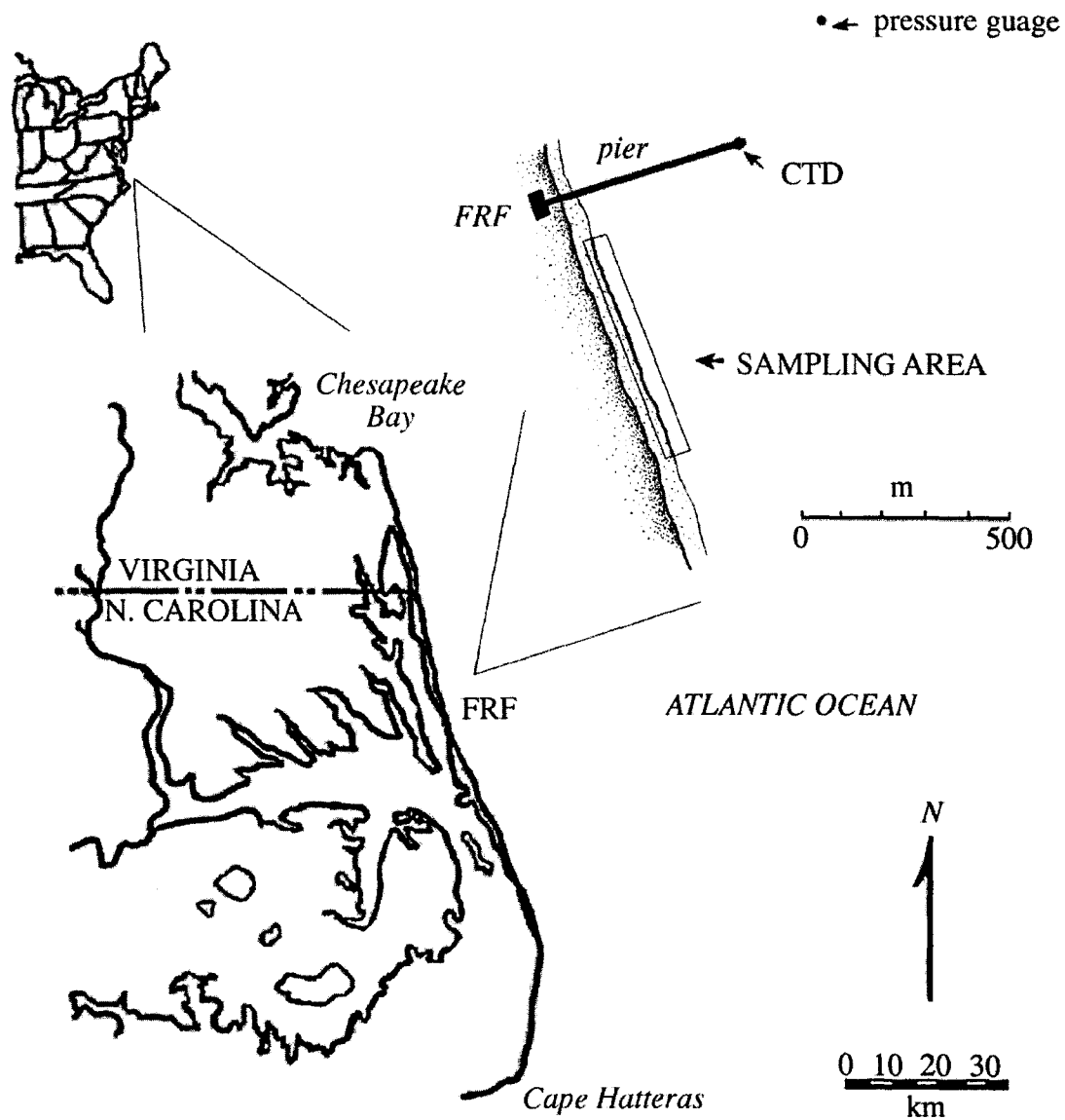


Figure 1. Study site location at Duck, North Carolina. The Army Corps of Engineers Field Research Facility (FRF) was used as the center of operations. A CTD mounted on the end of the pier measured salinity and temperature. A pressure gauge located at 8 m depth measured wave height. A 500 m section of beach on the south side of the FRF pier was sampled for ovigerous *Emerita talpoida*.

0.108. Tides are semidiurnal, with a mean annual range of 1 m. Wave direction is primarily from the south in the summer and from the north in the winter, with a mean annual wave height of 0.9 m (Birkemeier et al., 1985).

The egg condition of *Emerita talpoida* was determined by collection of sexually mature females (carapace length >13.2 mm) and scoring of egg status. Daily sampling extended over 53 consecutive days, from 9 August to 29 September, 1994, at which time the egg-bearing season ceased. Animals were haphazardly collected by taking sand samples of 3 to 5 liters from the lower part of the swash zone at about 1600 Eastern Standard Time each day. Crabs were sorted from the sand and egg condition was examined by lifting the telson and noting the developmental stage. The frequency of ovigerous females with late stage grey eggs was then calculated for each sample day.

The time series of egg condition was compared to alongshore and cross-shore wind stress, wave height, tidal range, salinity, and temperature. Physical variables were acquired from the FRF (Birkemeier et al., 1985) and investigators in the CoOP project (Alessi et al., 1996). Using wind direction and windspeed data provided by the FRF facility, wind stress was calculated with standard techniques (Pedlosky, 1987). Wave height was measured with a pressure gauge located at 8 m depth (referenced to National Geodetic Vertical Datum, NGVD) approximately 400 m east northeast of the pier (36° 11' 14.06", 75° 44' 37.11"). Tidal range was measured with a Baylor tide gauge mounted on the pier. CoOP investigators provided salinity and temperature data measured with a SeaBird SBE-15 SeaCat CTD mounted on the pier at 4 m depth with respect to NGVD (Alessi et al., 1996). All physical variables were converted to 24 hour daily averages to allow temporal comparisons with the time series of egg condition.

Time series correlations were used in testing for relationships between physical variables and between egg condition and physical variables. The steps taken in this

analysis were based on Chatfield (1989) and Dunstan (1993). Intraseres correlations (autocorrelations) may produce spurious interseries correlations (cross-correlations). To remove this bias before performing cross-correlations, each series was reduced to a random noise process with all serial dependencies (i.e. trends) and seasonality (i.e. periodicity) removed. This was achieved by modeling the data and then calculating the residuals between the model and the raw data. The residuals were then tested for cross-correlations.

Prior to the analyses, the frequency of ovigerous females with grey-stage eggs was arcsine-transformed (Sokal and Rohlf, 1995). Following standard procedures (Box and Jenkins, 1976; Chatfield, 1989; Dunstan, 1993), autocorrelations and partial autocorrelations of each variable were used to test for trends and periodicity (e.g. a tidal signal) and to aid in the identification of transformations to be used in modeling.

Significance of all correlations ($p < 0.05$) was determined using white noise standard errors (Box and Jenkins, 1976). Autoregressive integrated moving average (ARIMA) models were fitted for each time series of physical and biological data. Models were chosen based on examination of autocorrelation plots of the model residuals, histograms of the model residuals, normal probability plots of the model residuals, and significance of the model parameter estimates (autoregressive and moving average parameters) (Statistica, Statsoft, Inc.). ARIMA models were selected so that the residuals were normally distributed and there were no autocorrelations left in the residuals. Residuals between the ARIMA models and the raw data were used in cross-correlations. Cross-correlations were run between the residuals to examine significance ($p < 0.05$) at lags of up to five days. This six day (0 through -5 days lag) examination period was based on 10% of the length of the entire time series (Otnes and Enochson, 1975). Negative lags correspond to days prior to the occurrence of the dependent series (e.g. -1 day equals one day before hatching occurred). Positive lags were disregarded due to the unlikely possibility that the dependent series

could occur prior to the independent series (e. g. animals are not likely to “predict” the cross-shore wind stress). A lag of 0 corresponds to both series varying simultaneously.

Results

Physical Data

During the study, winds were strong from the northeast and weaker from the southwest (Figure 2). Maximum alongshore and cross-shore wind stress were -2.717 dynes/ cm^2 and -2.158 dynes/ cm^2 , respectively and occurred during winds from the northeast (so called “northeasters”; Figure 2a). These wind patterns were coincident with changes in other physical variables.

Salinity, temperature, average significant wave height, and tidal range also varied during the study period (Figures 2b, 2c). Salinity varied from 24.9 to 34.7. Temperature ranged from 18° to 23.6° C. Average significant wave height (the average of the largest 1/3 of waves) ranged from 0.28 to 2.57 m. The range of spring and neap tides was from 1.42 to 0.73 m, respectively. All variables except tidal range appear to change with wind direction.

Significant cross-correlations were found between salinity, temperature, and wave height and wind stress (Table 1). Alongshore wind stress was positively correlated with salinity at 0 and -1 days lag. At a -1 days lag, temperature was negatively correlated with alongshore wind stress. Average significant wave height was negatively correlated with alongshore wind stress at 0 days and positively correlated at -1 days lag. Cross-shore wind stress was positively correlated with salinity at 0 days lag. Temperature was negatively correlated with cross-shore wind stress at 0 days lag. Average significant wave height was negatively correlated with cross-shore wind stress at 0 and -1 days lag. In summary, the correlations indicate that onshore winds from the northeast were associated

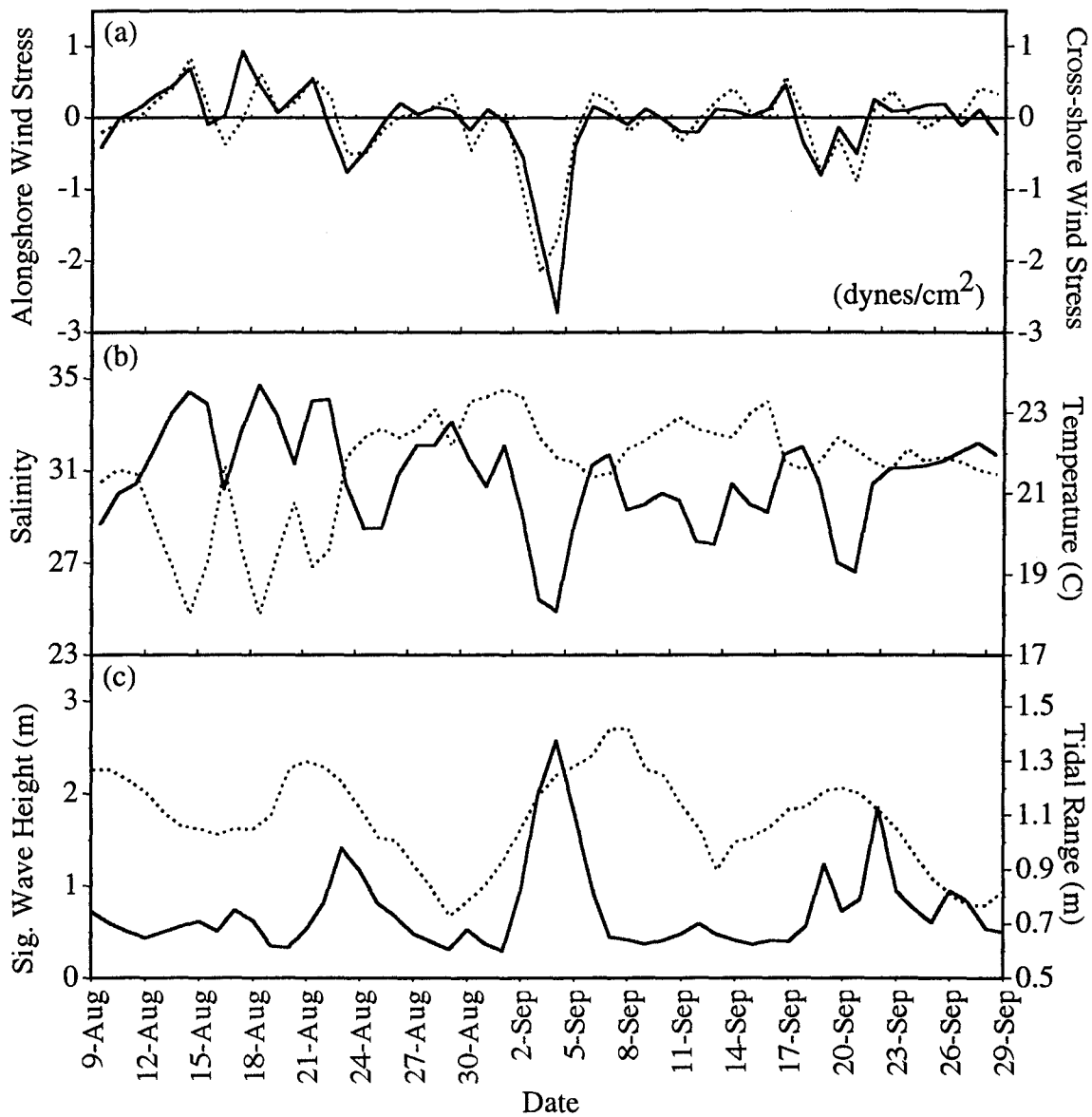


Figure 2. a-c. Physical time series from 9 August to 29 September, 1994. Variables on the left axis represented by solid lines, variables on the right axis are represented by dotted lines. In Fig. 2a, wind stress is positive when winds are from the south and west, negative from the north and east.

Table 1. Results of cross-correlations between ARIMA residuals of wind stress and the physical variables measured. Variables are listed with their corresponding cross-correlation coefficients and lags in days. Only significant lags are shown ($p < 0.05$).

(a) Alongshore Wind Stress			
	<i>r</i>	lag	
Salinity	0.608	0	
	0.316	-1	
Temperature	-0.319	-1	
Significant Wave Height	-0.554	0	
	0.283	-1	
(b) Cross-shore Wind Stress			
	<i>r</i>	lag	
Salinity	0.652	0	
Temperature	-0.325	0	
Significant Wave Height	-0.439	0	
	-0.406	-1	

with warm, lower salinity conditions and an increase in wave height, and offshore winds from the southwest were associated with cold, higher salinity conditions and a decrease in wave height.

Biological Data

The number of crabs sampled (ovigerous and non-ovigerous) per day ranged from 6 to 179 ($x = 94$, S.E. = 5.89; Figure 3). The actual sample sizes are presented to provide a judgment of error in the daily frequency data. Smaller sample sizes early in the study were a result of unforeseen logistical difficulties. During the course of the study, samples were missed on 5 days due to dangerous conditions in the swash zone (2, 3, 18, 21 September) and logistical problems (9 September) (Figure 3). The extremely low numbers of ovigerous crabs late in the study period indicate the end of the reproductive season.

The range in relative frequency of ovigerous crabs with grey-stage eggs was 0.0 to 0.5 (Figure 4). A drop in this frequency was attributed to larval release, the hatching of zoea from grey-stage eggs. The pattern of release was examined during the modeling process.

Autocorrelations of the time series of frequency of grey-staged ovigerous females were performed to examine patterns in the series (trends and/or periodicity) and develop the correct ARIMA model. The upward trend in the frequency data was likely an artifact of the smaller sample sizes of ovigerous females towards the end of the study (Figure 3). The absence of significant correlations around 14 days indicated that there was not an inherent fortnightly hatching rhythm in the time series.

Significant cross-correlations between residuals of the ARIMA models of physical data and the frequency of ovigerous females with grey-stage eggs were found with temperature and average significant wave height (Table 2). The frequency of grey-staged ovigerous females was negatively correlated with average significant wave height at -1 days

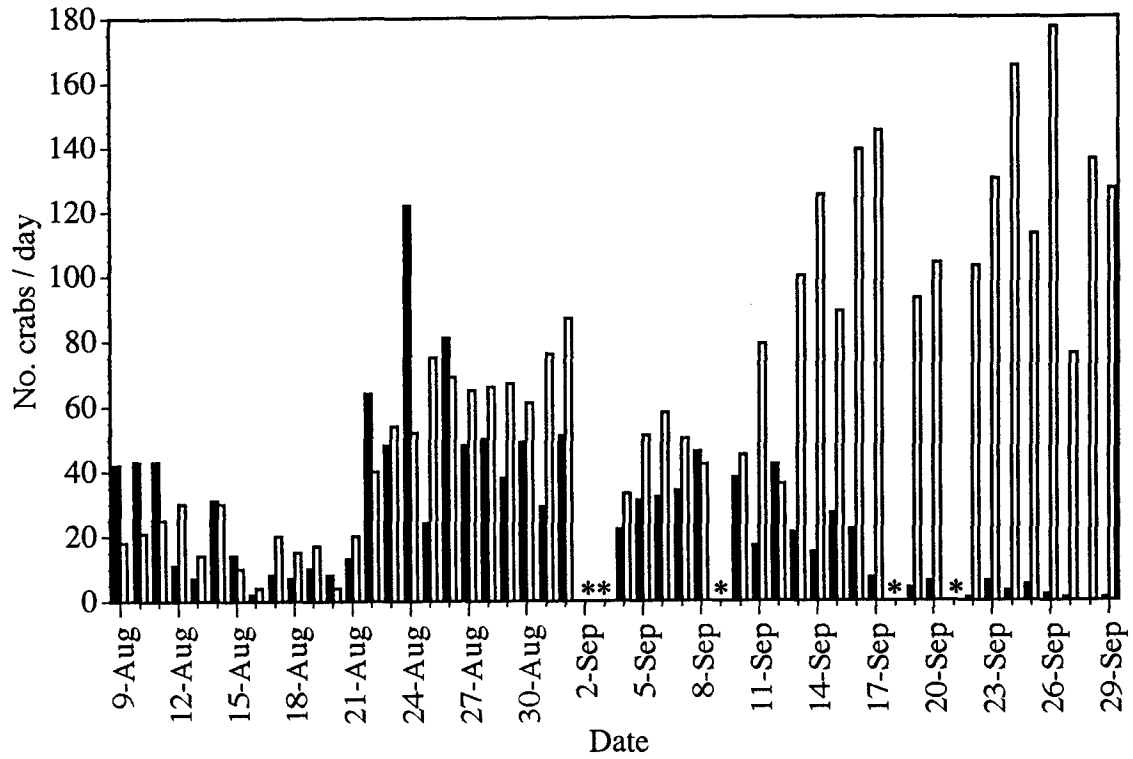


Figure 3. Daily sample sizes of female *Emerita talpoida*. Total females were divided into ovigerous (solid bars) and non-ovigerous (open bars) status. Asterisks indicate missing samples (2, 3, 9, 18, 21 September).

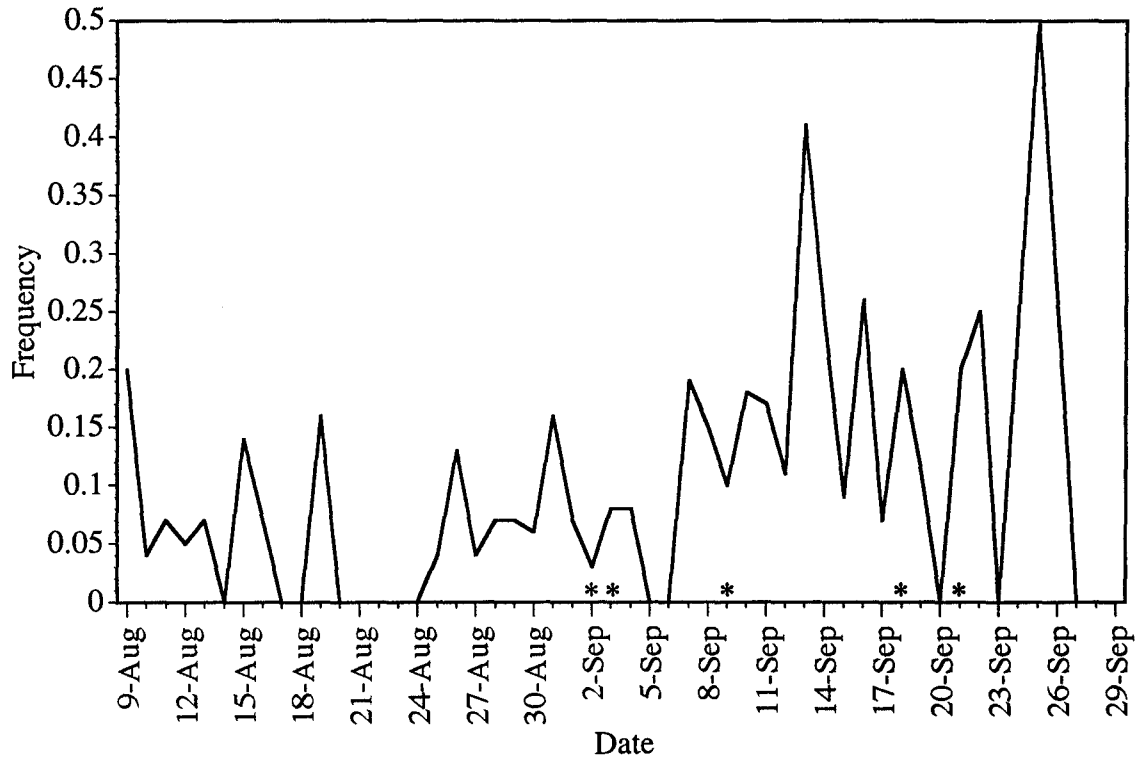


Figure 4. Frequency of grey-stage female *Emerita talpoida* in the ovigerous samples. Missing days (marked by asterisks) were interpolated from adjacent points.

Table 2. Results of cross-correlations between ARIMA residuals of the frequency of grey-stage ovigerous females and physical variables. Physical variables are listed with the corresponding value of the cross-correlation coefficient and the lag in days. Only significant lags are shown ($p < 0.05$)

Grey-Stage Females		
	<i>r</i>	lag
Alongshore Wind Stress	-	
Cross-shore Wind Stress	-	
Salinity	-	
Temperature	0.312	0
Significant Wave Height	-0.394	-1

lag and positively correlated with temperature at 0 days lag. In other words, the frequency of grey-stage ovigerous females was high on days when the temperature was high and low one day after waves were high. Because warm temperature and large waves were both correlated with northeast winds (Table 1), these variables may both influence hatching time in *Emerita talpoida*.

Discussion

Physical data indicate that downwelling and upwelling events occurred over the study period. This is evident in the time series in Figure 2, and is statistically described in Table 1. During northeasters, strong winds from the north and east push warm, low salinity shelf surface waters onshore causing a rise in sea level nearshore and large waves in the surf zone. To compensate for the rise in sea level, there is a downwelling of surface waters and an offshore flow of cold, higher salinity bottom waters. During southwesterers, steady light winds blow offshore from the south and west (southwesterers). This causes a depression of sea level at the coast as the warm, low salinity shelf surface waters are pushed offshore, followed by a compensating upwelling of onshore-flowing cold, higher salinity bottom waters near the coast.

The time series plots and statistical analysis suggest that physical oceanographic events are correlated with the frequency of grey-stage eggs in female mole crabs. Warm temperature, an indication of the onshore flow generated by northeasters, was correlated with an increase in the number of females with grey-stage eggs. High waves, driven by northeasters and lasting several days, were correlated with a decrease in the number of females with grey-stage eggs; suggesting that hatching occurred during periods characterized by large waves. Thus, inner-shelf storm events appear to cause hatching of *Emerita talpoida*.

The effects of temperature on embryonic development rate are well understood (Giese and Pearse, 1974; Giese and Kanatani, 1987). Generally, warm temperatures can cause development time to decrease. A positive correlation between temperature and the frequency of grey-staged females may reflect this relationship. Temperature may accelerate the development of eggs to the grey stage.

While it is generally understood that increased temperature can accelerate embryonic development in marine invertebrates (Giese and Pearse, 1974), not much is known regarding the influence of wave energy on hatching in crustaceans. The hatching patterns in *E. talpoida* raise important questions regarding: (1) the consequences of hatching in large waves, (2) the adaptive significance of release during large waves, and (3) potential cues that might effect the timing of hatching.

What are the consequences of hatching during high wave activity? During periods of high wave action, rip currents rapidly flush the surf zone and the residence time of water within is short (Tam, 1973; Talbot and Bate, 1987). One potential result of hatching into large waves is that larval entrainment may occur in wave-generated rip currents. Larvae that hatch during this time might be rapidly exported from the beach and transported out of the surf zone. Potentially, larvae could be carried several kilometers from shore in wave generated rips (Tam, 1973).

For examples of the fate of a surf zone plankter during high wave activity, one can look at surf zone diatom research. These phytoplankton are characteristic of beaches with intense wave action (Brown and McLachlan, 1990). Surf zone diatoms undergo diel migrations, sinking during the night and rising to the surface during the day where they form patches of foam. These foam patches are concentrated by rip current circulation and often wash up on beaches (Talbot and Bate, 1988). In a study of rip current activity, Talbot and Bate (1987) found that during periods of large waves, surface drogues were retained in the surf zone but dye was flushed from the surf zone. Their research provides

evidence that during high waves positively buoyant particles can be concentrated by wave activity but neutrally buoyant particles can be transported out of the surf zone. If recently hatched *Emerita talpoida* zoea are neutrally buoyant, they should be flushed from the surf zone.

Another consequence of hatching in large waves is that *Emerita talpoida* zoeae might become stranded high on the beach. Examples of stranding on wave-swept sandy beaches are easy to find. The familiar drift lines found above the swash zone on sandy beaches are made of positively buoyant detritus brought ashore by wind and waves. Bowman and Dolan (1984) considered stranding due to intense swash zone runup a potential limiting factor in the upper vertical distribution of postlarval *E. talpoida* in the intertidal. Stranding of larval *Emerita* could also occur as zoea are under the influence of turbulence and probably have little control of their vertical distribution. This seems unlikely, however, since those particles that are so noticeably stranded (i.e. drift) are a result of their positive buoyancy and are likely to be carried in the neuston (Talbot and Bate, 1987). Particles in turbulent currents would likely behave as neutrally buoyant particles (Koehl and Powell, 1994).

Is there an adaptive advantage to hatching during periods of large waves? Predation on larvae is one of the most often cited explanations for selection of hatching rhythms in intertidal decapods (Morgan and Christy, 1995; Morgan and Christy, 1997). The survival of recently hatched larvae is tied to the transport away from the adult habitat, where predation is intense, and into the waters of the inner-continental shelf, where planktonic predators are less abundant (Christy, 1982; Morgan, 1990). By exploiting the rapid transport of water out of the surf zone during large waves (Kam, 1976; Talbot and Bate, 1987), hatching at this time might increase the likelihood of early larval survival and successful planktonic development.

This is the first example of hatching in decapods during high wave activity. Storm-induced spawning, however, has been observed in a number of other taxa. In particular, spawning during large waves has been observed in archaeogastropods (Pilkington, 1971; Grange, 1976; Ohgaki, 1981; Sasaki and Shepherd, 1995). Sasaki and Shepherd (1995) suggested that spawning and dispersal in the subtidal archaeogastropods *Haliotis discus hannai* and *Tegula* spp. occurred during times of maximum wave height. Sampling during and following stormy conditions, they found that typhoons caused large spawning events while less intense storms caused small spawning events. Shanks (in review) monitored the gonadal development of the intertidal limpet, *Lottia digitalis*, on the coast of Oregon and found that spawning tended to occur during periods of both high wave energy and downwelling. Frank and Leggett (1981) found that emergence of larvae of the capelin, (*Mallotus villosus*) was a result of beach disturbance by onshore wind-induced wave action. Grange (1976), studying 3 species of gastropods, induced spawning by vigorous agitation of the water surrounding ripe adults in the laboratory. In the field, larvae were found in the plankton only when the onshore windspeed was greater than 10 knots. These studies provide evidence that there are a number of different marine organisms that spawn during periods of high wave energy.

If spawning in response to large waves is widespread in marine organisms, there might also be selection for hatching in other crabs that are exposed to wave action. Christy (1986), found variations in hatching rhythms between crabs that inhabited the lower intertidal zone of an exposed shore. Variations were attributed to rhythms timed to different environmental cycles (lunar and diel). While these four species showed hatching rhythms in the field, determination of hatching time was made using a protective box around the females from which hatched larvae were extracted. This enclosure method, however, effectively controls for the influence of wave energy on hatching. Hatching in

these species may have occurred during high tides, but the effect of turbulence on hatching was not addressed.

If waves influence the hatching of intertidal crabs, the effect seems likely to act in concert with the widespread patterns of hatching rhythms that are already known. These hatching rhythms, whether lunar or tidal, are thought to act at the embryonic and maternal level (DeVries and Forward, 1991; Morgan, 1995). Embryonic hatching cues are believed to be endogenous and controlled entirely by the embryo, while maternal cues are thought to be exogenously controlled by physiological changes in the female caused by environmental cues. Therefore a wave-driven hatching cue probably acts on the maternal level. Since waves are a composite of mainly physical factors and the water a composition of mostly chemical and biological factors, there are a variety of laboratory experiments that can be done on ovigerous crabs to test for a wave energy influence on hatching.

Wave-driven variation in vibration may act as a hatching cue. Adult *Emerita analoga* are extremely sensitive to vibrations (Enright, pers. comm.). The animals will respond to vibration in the laboratory by showing burrowing behaviors typical of swash migration. Ellers (1995) showed that coquina clams of the genus *Donax* were extremely sensitive to vibrations as well. *Donax* spp. inhabit the swash zone and migrate in a similar fashion to *Emerita*. In Ellers' (1995) study, the clams responded to recorded vibrations from waves that were favorable for swash migration. In *Emerita*, wave-generated vibrations may cause the female to agitate the eggs, maybe mechanically enhancing hatching. It is also possible that turbulence may encourage burrowing and the female may lose the clutch as a consequence. Or, perhaps, vibrations of a certain frequency may signal the female to aerate her clutch, causing the eggs to hatch. Any of these hypotheses could be tested in relatively simple laboratory experiments.

Although this is the first documented case (to my knowledge) of an influence of waves on hatching in an intertidal decapod, the existence of wave-induced spawning in a

variety of organisms provides additional evidence that there is an influence of physical oceanographic variables on larval release. Physical data describing basic oceanographic parameters is often easily available. Typically, ovigerous females are sampled with little difficulty, and hatching in the field can be quickly checked by observing the developmental stage of the eggs. The influence of inner-shelf oceanographic phenomena on hatching in intertidal crabs is an area of research that is ripe for further investigation.

Bridge

Chapter II was the result of research that looked at the release of *Emerita talpoida* larvae by sampling ovigerous females and noting the developmental state of the eggs. Time series correlations were performed to evaluate the effects of physical processes on hatching. Hatching of zoea, as inferred by the frequency of grey-stage ovigerous females, was correlated with temperature and wave height. A positive correlation with temperature and a negative correlation with wave height suggests that hatching was influenced by these variables. The consequences, adaptations, and cues to hatching during storm events were discussed. Warm temperature may cause the development of embryos to proceed to the grey stage. The zoea that then hatch during periods of large waves would likely be transported out of the surf zone in wave-generated rip currents. Hatching in response to wave action has been seen in a number of different organisms. This is the first time, however, that a hatching response has been associated with wave action in a decapod. Further research is necessary to document this response in other crustaceans.

The next chapter is an investigation into the process of shoreward larval transport as inferred by the pattern of recruitment of megalopae to the sandy beach at Duck, North Carolina. Physical variables were measured concurrently with the relative abundance of new recruits and correlations between these data were used to develop a hypothesis to

explain onshore larval transport. The transport of late stage larvae to the adult population completes the planktonic dispersal phase of the mole crab life cycle.

CHAPTER III
A TIME SERIES ANALYSIS OF LARVAL RECRUITMENT
OF THE MOLE CRAB, *EMERITA TALPOIDA*

Introduction

One of the most important steps in the life history of organisms with long planktonic larval stages is the shoreward migration back to the adult habitat or nursery habitat, whereupon larvae settle and begin life as juveniles (Roughgarden et al., 1988). In some cases, this migration is thought to be vertically controlled by larval behavior (Le Fevre and Bourget, 1992; Shanks, 1995a) but horizontally controlled by physical transport mechanisms (Shanks, 1995b) over the inner-continental shelf (defined as the region from the surf zone out to 30 m depth). While larvae may drift passively or swim actively, their horizontal movement is limited by the net horizontal flow of most inner-shelf currents. The shoreward migration is then a largely physical event. The effectiveness of this horizontal shoreward transport has been considered one of the main determinants of recruitment success in certain crustacean fisheries (Botsford and Wickham, 1975; Johnson and Hester, 1989).

While larval transport of some commercially important crab species has been studied extensively, not much is known about larval transport in non-commercial intertidal crustaceans. The few studies that have been done on intertidal species have focused on barnacles. Transport processes are inferred from settlement patterns in the intertidal. Cyprid settlement has been correlated with wind direction (Hawkins and Hartnoll, 1982), the tidal cycle (Shanks, 1986) tidally generated bores (Pineda, 1991), and the collision of fronts with the shore (Farrell et al., 1991; Roughgarden et al., 1991).

Settlement, as defined by Keough and Downes (1982), is the precise moment where an individual takes up permanent residence on the substratum. Because that moment is not usually coincident with sampling, the term recruitment is used. Recruitment is here defined as the measurable input of recently settled individuals to the intertidal.

Recruitment patterns of sessile organisms (i.e. barnacles) are relatively easy to sample in the field (Hawkins and Hartnoll, 1982; Connell, 1985). Recently settled individuals on a natural and artificial substrates are easily examined and enumerated. Yet, in more mobile intertidal crustaceans, there is a lack of information on recruitment patterns due to the difficulty of sampling the habitat for often small and cryptic recently settled individuals.

The mobility of recently settled individuals adds to the difficulty of randomly sampling recruitment to an intertidal population, and inferences regarding larval transport are harder to make. To account for this mobility, Shanks (1983) and others (Epifanio et al., 1988; Jones and Epifanio, 1995; Wing et al., 1995a) sampled the water column and near the substratum for intertidal crab species, using artificial collectors to measure “settlement” of megalopae. These studies, however, did not sample the actual habitat to which the megalopae recruit. They instead sample the last larvae stage before recruitment occurs. A highly mobile species with recently recruited megalopae that are predictably abundant and accessible in the intertidal may allow one to evaluate the effect of physical hydrography on recruitment patterns.

In this study, a sandy beach on the Outer Banks of North Carolina was sampled daily for megalopae of the intertidal mole crab, *Emerita talpoida* (Decapoda: Anomura). In the northern hemisphere, *E. talpoida* is found on beaches from Cape Cod to the Yucatan Peninsula, Mexico. Adult and postlarval *Emerita* generally exist in dense aggregations in the swash zone and feed on particles in retreating waves (Wharton, 1942; Efford, 1965;

Cubit, 1969). Mole crabs are highly mobile and maintain their position in the swash by migrating up and down the beach face with the tides (Wharton, 1942).

On the coasts of North America, the mole crab has been well researched. The east and west coast species, *E. talpoida* and *E. analoga*, respectively, are abundant and easy to sample. Because of these traits, studies have been made on longshore migration (Cubit, 1969; Dillery and Knapp, 1970; Efford, 1970; Perry, 1980), size class zonation on the foreshore (Bowman and Dolan, 1985), biogeography (Wenner et al, 1993; Dugan et al, 1994), seasonality in reproduction (Cox and Dudley, 1968), population biology (Diaz, 1980), growth (Diaz, 1974; Fusaro, 1978), sex differences (Efford, 1967; Wenner et al., 1974; Fusaro, 1977), egg production (Wenner, 1987), adult and larval metabolism (Edwards and Irving, 1943; Schatzlein and Costlow, 1977), larval behavior (Burton, 1979), and larval development (Smith, 1877; Rees, 1959; Harvey, 1993). Despite this wealth of research, there are no studies that have addressed onshore transport mechanisms acting on larval *Emerita*.

Reproduction in *Emerita* typically occurs from late winter through early fall (Cox and Dudley 1969; Efford, 1970). Larval development of *E. talpoida* consists of 5 to 7 zoeal stages (up to 11 molts, however) with an estimated planktonic duration of 30-90 days (Diaz and Costlow, 1987; Harvey, 1993). Late stage *E. talpoida* zoeae can delay metamorphosis and just before settlement, metamorphosis from the last zoeal stage to the megalopa apparently occurs (Harvey, 1993). On the sandy beach, megalopae inhabit the upper portion of the swash and exist in aggregations similar to the adult (Bowman and Dolan, 1985). Megalopae are functionally transitional between the planktonic larval form and the sandy beach adult form in that they can swim in a forward direction (unlike the adults) and also burrow in the sand. Recruitment occurs with the input of megalopae to the swash population.

To develop transport hypotheses, information on the vertical distribution of late stage larvae is needed. Few field observations of the vertical and the cross-shelf distribution of larval *Emerita* have been published, however. Barnes and Wenner (1968) found *E. analoga* zoeae in "surface waters" (depth was not defined) off the Santa Barbara coastline. Unfortunately, they didn't differentiate zoeal stages. Similarly, Johnson (1939) found early stages ("I, II, III") of *E. analoga* at increasing distances offshore, and stage "IV" zoea in "surface waters" 80-90 miles off the Channel Islands, California. He also found, albeit rare, late stage "V" zoea at inshore stations. His observations suggest that larvae are dispersed offshore in early stages and moved onshore at later stages.

No studies to date have closely examined the role of coastal oceanography in the recruitment of *Emerita*. Efford (1970) suggested that low population densities of adult *E. analoga* in Oregon were a result of dispersal and recruitment from a southern (California) population source and described an alongshore countercurrent mechanism that acted over their geographic range to disperse larvae and return them to the adult habitat. He did not address the cross-shelf transport of larvae, however. In another study, Diaz (1974) collected monthly recruitment data for *E. talpoida* over two years on the Bogue Banks of North Carolina. His data were used primarily for calculating demographics; the author didn't examine the role of larval transport in population recruitment.

Studies investigating larval transport have employed physical data, moored experimental instrumentation, satellite imagery, and ship-based sampling, to describe inner-shelf water movement (Ebert and Russell, 1988; Farrell et al., 1991; Roughgarden et al., 1991; Hobbs et al., 1992; Shanks, 1986; Thorrold et al., 1994; Jones and Epifanio, 1995; Nash et al., 1995; Wing et al., 1995a, 1995b; Miller and Emiet, 1997). The more common physical changes over the inner-shelf can be described by any one or combination of these techniques. Using physical data with recruitment data in a time series analysis-approach allows one to test for correlations that may be obscured by the inherent "noise" of the

coastal system (Jassby and Powell, 1990; Thorrold et al., 1991; Wing et al., 1995b; Kope and Botsford, 1988).

The sandy beach of Duck, North Carolina was under investigation from August through October, 1994 as part of the interdisciplinary Coastal Ocean Processes field experiment (CoOP). The CoOP experiment was performed with the broad goal of examining the cross-shelf dispersal of larvae of soft-bottom invertebrates (Butman, 1994). This study was the result of the intertidal portion of the CoOP experiment and examines time series relationships between nearshore physical data and recruitment patterns of *Emerita talpoida* megalopae.

Methods

Study Site

The Army Corps of Engineers' Field Research Facility (FRF) near Duck, North Carolina (36° 10.91' N, 75° 45.09' W), was used as the center of operations for sampling during the fall of 1994. The FRF is located between the mouth of the Chesapeake Bay to the north and Cape Hatteras to the south (Figure 5). This stretch of uninterrupted coastline consists of narrow sandy beaches of relatively uniform characteristics.

A 500 m area on the south side of the FRF pier (561m long), was sampled for recently settled mole crabs (Figure 5). The sandy beach at the FRF is described in Birkemeier et al. (1985). Tides are semidiurnal, with a mean annual range of 1 m. Mean annual beach width is 40m from foredune edge to mean sea level (MSL), and the mean annual foreshore slope is 0.108. The sandy beach classification scheme used by Brown and McLachlan (1990) would classify this beach as intermediate, between seasonal morphs of reflective (summer) and dissipative (winter). Wave direction is primarily from the southwest in the summer and from the northeast in the winter.

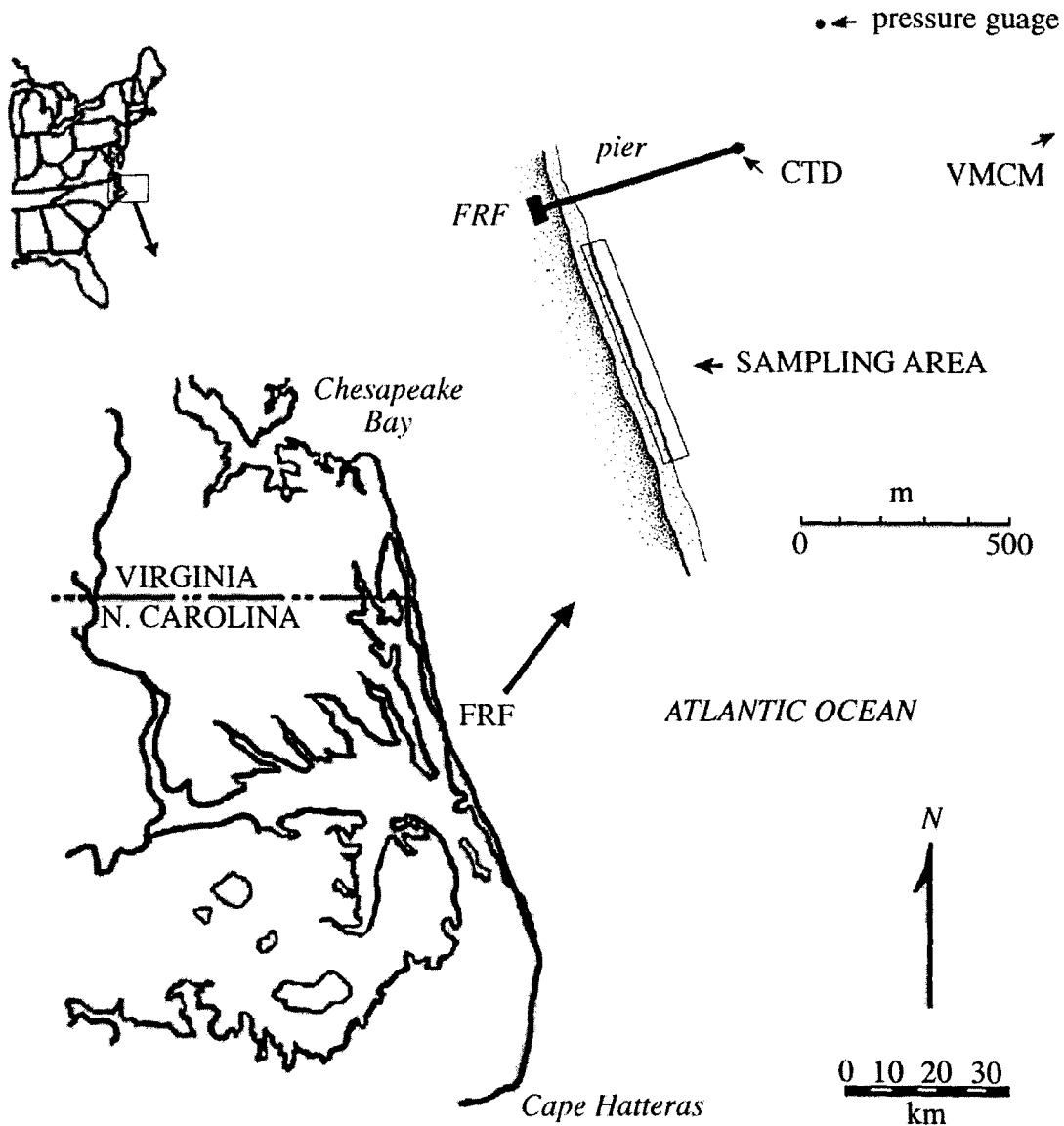


Figure 5. Study site location at Duck, North Carolina. The Army Corps of Engineers Field Research Facility (FRF) was used as the center of operations. Salinity and temperature were measured by a CTD mounted on the pier. Wave height was measured by a pressure gauge located at 8 m depth. Currents were measured by vector-measuring current meters (VMCMs) located east of the pier. A 500 m section of beach south of the pier was sampled for recently recruited *Emerita talpoida*.

Physical Measurements

Physical variables of the nearshore hydrography off of Duck were provided by the FRF and from investigators in the CoOP experiment (Alessi et al., 1996). The FRF measured cross-shelf and alongshore wind speed and direction, significant wave height (defined here as the average of the largest 1/3 of waves), and tidal height. Wind speed and direction were measured with an anemometer mounted on the FRF facility. Alongshore and cross-shore wind stress was calculated using standard techniques (Pedlosky, 1987). Average significant wave height was measured at 34 minute intervals from a pressure gauge located east northeast of the pier in 8 m depth. Tidal height was measured using a Baylor tide gauge mounted on the end of the pier. A SeaCat SBE-15 CTD (SeaBird Electronics, Inc) was mounted on the FRF pier at 4m depth (ref to National Geodetic Vertical Datum, NGVD) by CoOP investigators (Alessi et al, 1996). Measurements were taken every 4 minutes. Alongshore and cross-shore currents were measured by two moored vector- measuring current meters (VMCM) located at 25 m depth east of the pier (Alessi et al., 1996). The surface mooring was located at (36° 14.64' N, 75° 35.00' W), the current meter was at 4 m depth. The subsurface bottom mooring was located at (36° 14.70' N, 75° 35.18' W), the current meter was at 23 m depth. Measurements were made every 4 minutes. Daily averages of all physical data were used in time series analysis.

Biological Sampling

Field

The sandy beach mole crab sampling technique was modeled after that described in Dugan et al. (1993). Three 10 m long vertical transects were randomly placed relative to

the FRF's permanent reference markers (11 poles placed ~45 m apart along the foredune parallel to shore). The transects were placed 2 m to the north or south of the reference markers and were centered in the swash zone, beginning 1 m above the effluent line (Brown and McLachlan, 1990) and extending down to the surf. If undulating beach cusps were present, transects were centered at the apex of the first cusp embayment directly north or south of the chosen marker. Running a transect down the embayment ensured that samples of crabs would be collected because they might be not found on the cusp horns (Cubit, 1969). Along each transect, 20 sediment cores (80 cm² x 15 cm deep) at 0.5 m intervals were drawn using a standard "clam gun" coring device. Cores were drawn quickly so crabs would not burrow away from the corer. The cores were pooled into 1.0 mm mesh bags, and following completion of the transect, the bags were rinsed in the surf. The remaining sand in the bags was divided into several 5 gallon buckets to which seawater was added. The sand and water were swirled by hand to stimulate the movement of the crabs. Once the crabs were swimming in the stirred water, they were poured off into an empty bucket. Stirring and decanting at least 10 times per bucket extracted nearly all crabs from the sediment. The crabs and water were then poured into a stacked series of graded sieves made from 3 gallon buckets with round holes drilled into the bottom of each bucket through which the crabs could burrow (sieve hole sizes changed at approximately 0.7 mm intervals between consecutive sieves; Wenner, 1974). Several buckets of water were poured into the top sieve while the stack was swirled around to help flush the crabs through. The smallest sieve (1.6 mm hole diameter) caught megalopae and juveniles that passed through the next larger sieve (2.3 mm hole diameter). Animals caught in the smallest sieve were preserved with 10% Formalin buffered with calcium carbonate.

Plankton tows were taken at inshore stations to determine the depth distribution of larval *Emerita talpoida*. Approximately 5 km offshore, three replicate samples (15, 17, and 25 September, 1994) from bottom waters, surface waters, and the neuston were taken.

Oblique tows were taken from near the bottom (20 m) to the thermocline (10 m) (bottom tow) and from the thermocline (10 m) to the surface (surface tow). During oblique tows, a 0.25 m diameter plankton net with 330 μm mesh was pulled up at a steady rate for approximately 5 minutes at each depth category (i.e. bottom, surface). Neuston tows were made with a 330 μm mesh net held by a 30 cm x 18 cm PVC frame. Samples from each tow were preserved in 10% buffered Formalin.

Laboratory

Because preserved transect samples of the smallest size class included megalopae and postlarval juveniles, estimation of daily mole crab recruitment required determining an appropriate size range which represented the most recently recruited megalopae. This was achieved using image analysis (IP Lab Spectrum, Signal Analytics, Inc.). Preserved crabs were placed ventral side up in a one crab-thick layer in a water-filled plexiglass dish on a light table. To block out glare from the light table, a polarizing filter was placed on the camera. Using image analysis software, a stationary image was captured and converted to a greyscale intensity-based image. The intensity values were adjusted to maximize the contrast between the white crabs and the black background. The image was then sharpened using a linear filter function. Measurements to the nearest 0.1 mm (\pm 0.01 mm) of the longest body axis (from the rostrum to the joint of the telson) were made for each crab.

Unfortunately, the characteristics that help identify megalopae in live specimens (chromatophores and swimming behavior) were lost during preservation. Therefore to distinguish recently settled megalopae from juveniles in the smallest sieve samples, image analysis was again employed. Using crabs from 4 randomly selected (random number table, Sokal and Rohlf, 1995) transects, a size range for megalopae was established using the refractive optical qualities of the exoskeletons. Megalopae are transparent at

metamorphosis and within a day become opaque as exoskeleton calcification progresses (Harvey, 1993). Preservation, however, impairs this distinction under ambient light. Polarizing filters placed on the camera and on the light table (a cross-polarized setup), helped to restore the calcification distinction. A cross-polarized image was captured with image analysis software (IP Lab Spectrum, Signal Analytics, Inc.) and then enhanced using Photoshop (Adobe Systems, Inc.) to adjust the color levels and color balance. This enhancement helped to emphasize a definitive color difference between the transparent and calcified crabs. The crabs were separated by color and the transparent individuals were measured for body length, as described above. The size range of transparent crabs allowed daily abundance of recently recruited megalopae to be calculated from each transect.

Once recently recruited megalopal abundance was determined, daily recruitment could then be estimated. A “recruitment index” was formulated to address the patchy beach distribution of mole crabs and the tendency for physical changes in the beach shape to alter abundance (Cubit, 1969; Bowman and Dolan, 1985). Due to changes in wave action, the sandy beaches of the Outer Banks undergo rapid changes in morphology (Wright, 1995). When waves are large, cusps form on the beachface. *Emerita* are thought to be physically concentrated within the embayments between the cusps (Cubit, 1969). An index was considered the best estimate of recruitment in these variably abundant crabs. The recruitment index is defined as the number of megalopae per transect, determined by image analysis, divided by the total number of crabs (megalopae and juveniles) per transect. This index is a representative of relative daily recruit (i.e. transparent megalopae) abundance. Therefore, when the mean index increased, it was taken as an indication of an input of recently recruited megalopae to the beach at Duck. When the mean index decreased, it was presumed to be a result of growth out of the smallest size class and mortality of crabs in the smallest size class. The mean recruitment index was used in time series analysis to test correlations with the physical data.

Preserved plankton samples were sorted for larval stages of *Emerita talpoida*. Stages were identified with keys provided by Rees (1959). Zoeal stages were pooled into stages less than stage VI and, because stage VI zoea are competent to molt to megalopae but can delay this metamorphosis by molting several times (Rees, 1959; Harvey, 1993), stages greater than stage VI. Concentrations (no. larvae/ m²) were calculated by multiplying abundance (no. larvae/ m³) by the depths sampled.

Data Analysis

Time series correlations were used in testing for relationships between physical variables and between the recruitment index and physical variables. The steps taken in this analysis were based on Chatfield (1989) and Dunstan (1993) and involved reducing each series to a “pure” random noise process with all serial dependencies (i.e. trends) and seasonality (i.e. periodicity) removed. This was achieved by modeling the data and calculating the residuals between the model and the raw data. Cross-correlations were then run between the residuals of the models at various lags.

Prior to the analyses, the recruitment index, because it is a proportion, was arcsine-transformed (Sokal and Rohlf, 1995). Missing sampling days were filled with values calculated as the median of the two adjacent points. Following standard procedures (Box and Jenkins, 1976; Chatfield, 1989; Dunstan, 1993), autocorrelations and partial autocorrelations of each variable were used to test for trends and seasonality (i. e., a tidal signal) and to aid in the identification of transformations to be used in modeling. Significance of all correlations ($p < 0.05$) was determined with white-noise standard errors (Box and Jenkins, 1976). To remove significant autocorrelations, auto-regressive integrated moving average (ARIMA) models were fitted to each series and the residuals computed by subtracting the model from the raw data (Statistica, Statsoft, Inc.). Models were chosen based on examination of autocorrelation plots of the model residuals,

histograms of the model residuals, normal probability plots of the model residuals, and significance of the model parameter estimates (autoregressive and moving average parameters). ARIMA models were selected so that the residuals were normally distributed and there were no autocorrelations left in the residuals.

Cross-correlations between ARIMA residuals were performed to examine relationships between time series (Box and Jenkins, 1976; Chatfield, 1989). Correlations were run at daily lags in both a negative and positive direction. Negative lags corresponded to days prior to the occurrence of the dependent series. Positive lags were discarded due to the unlikely event that the dependent series could occur prior to the independent series (e. g., megalopae are not likely to recruit days before the winds blow onshore). A significant lag at 0 indicated a concomitant correlation. The examination of lag values of up to eight days was chosen based on the length of the entire time series (Otnes and Enochson, 1978) and the short duration of most nearshore oceanographic phenomena.

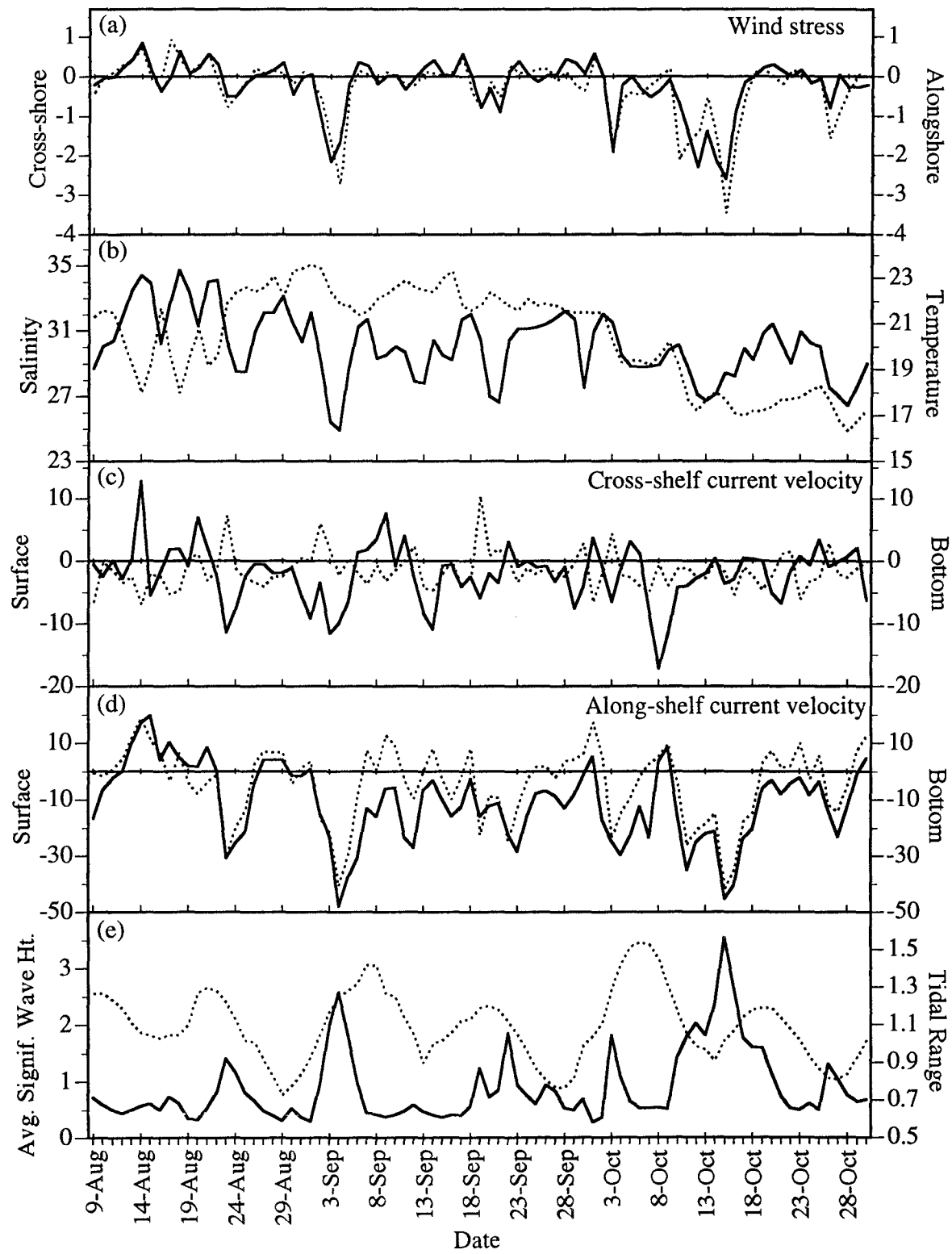
Results

Physical Data

Wind stress during the study tended to be stronger from the north and east than from the south and west (Figure 6a). Maximum cross-shore and alongshore wind stress were -2.59 and -3.44 dynes/ cm^2 , respectively, and occurred during winds from the northeast (so called “northeasters”). Winds from the southwest were less intense, with a maximum cross-shore and alongshore wind stress of 0.84 and 0.93 dynes/ cm^2 , respectively.

Salinity, temperature, wave height, and tidal range varied throughout the study. Mean daily salinity fluctuated between 24.2 and 34.7, and was characterized by a slight decrease in variability over time (Figure 6b). Average daily temperature ranged from 16.3

Figure 6. a-e. Time series of daily-averaged physical variables. Solid and dashed lines correspond to variables on the left and right side of the figure, respectively. The figures are: (a) cross-shore and alongshore wind stress (dynes/ cm²), (b) salinity and temperature (°C), (c) cross-shelf current velocity (cm/ sec), (d) along-shelf current velocity (cm/ sec), and (e) average significant wave height (m) and tidal range (m). Cross-shore parameters are positive to the east. Alongshore parameters are positive to the north.



to 23.6° C (Figure 6b). With the onset of the winter weather regime there was a general cooling trend in the time series. Maximum average significant wave height was 3.54 m; the minimum average significant wave height was 0.28 m. There were several days during the later part of the study when large waves predominated (Figure 6e). Tidal range varied from 0.73 m during neap tides to 1.54 m during extreme spring tides (Figure 6e).

Currents showed striking differences between surface and bottom in the cross-shelf direction but less so in the along-shelf direction (Figures 6c, 6d). Cross-shelf surface currents tended to flow in an opposite direction to the bottom currents (Figure 6c). The highest cross-shelf current velocity was -17.14 cm/ sec, in the onshore direction. Unlike cross-shelf currents, surface and bottom along-shelf current tended to flow in the same direction (Figure 6d). Also, along-shelf currents achieved faster velocities than cross-shelf currents, with a maximum of -47.99 cm/ sec in a southward direction. The differences between maximum cross-shelf and along-shelf currents reflect the dominant pattern of water circulation. Northeast winds drove the onshore and southward flow of surface waters, creating downwelling conditions when bottom waters flowed offshore and southward.

Cross-correlations between residuals from the ARIMA models were used to statistically describe wind forcing. The correlations reflect the dominant effect of downwelling and upwelling in controlling oceanographic conditions during the study (Table 3). Salinity and temperature are significantly correlated with both components of wind stress. Salinity was positively correlated with cross-shore and alongshore wind stress at 0 days and 0 and -1 day lags, respectively. The positive correlation reflects the relationship between wind direction and salinity with respect to upwelling (offshore winds, increase in salinity) and downwelling (onshore winds, decrease in salinity). Temperature was negatively correlated with cross-shore and alongshore wind stress at 0 days lag.

Table 3. Results of cross-correlations between ARIMA residuals of wind stress and measured physical parameters. Significant cross-correlation coefficients ($p < 0.05$) are listed with the corresponding lag in days.

(a) Cross-shore Wind Stress				(b) Alongshore Wind Stress			
		<i>r</i>	lag			<i>r</i>	lag
<i>Salinity</i>		0.626	0	<i>Salinity</i>		0.552	0
						0.423	-1
<i>Temperature</i>		-0.308	0	<i>Temperature</i>		-0.273	0
<i>Cross-shelf currents</i>	Surface	0.325	0	<i>Along-shelf currents</i>	Surface	0.459	0
	Bottom	-0.577	0				0.397
					Bottom	0.442	0
						0.490	-1
<i>Significant Wave Height</i>		-0.502	0	<i>Significant Wave Height</i>		-0.476	0

However, there is a positive correlation with alongshore wind stress at -2 days lag. Temperature decreased during upwelling and increased during downwelling. Average significant wave height was negatively correlated with cross-shore and alongshore wind stress at 0 days lag, indicating northeasters were the major source of waves.

Cross-shelf and along-shelf currents also reflect the patterns of upwelling and downwelling that occurred during the study (Table 3). Cross-shelf surface currents were positively correlated with cross-shore wind stress at 0 days lag. Bottom cross-shelf currents were negatively correlated at 0 days lag and positively correlated at -2 days lag. Along-shelf surface and bottom currents were positively correlated with wind stress at 0 and -1 days lag. Thus, when wind was from the northeast, surface currents were oriented onshore and to the south while bottom currents were oriented offshore and to the south, indicating conditions of downwelling near the coast. When winds were from the southwest, surface currents were oriented offshore and to the north while bottom currents were onshore and towards the north, indicating upwelling conditions near the coast.

Biological Data

Body lengths of transparent uncalcified crabs (N=128) ranged from 2.7 to 4.6 mm (\bar{x} = 3.5 mm, S.D. = 0.36). Recently recruited megalopae were assumed to be the average length of uncalcified crabs + 2 S.D. (maximum of 4.3 mm) and their numbers were used to calculate the daily recruitment index. Crabs larger than this were considered small juveniles.

The patterns of abundance exemplified the need for a recruitment index (Figure 7). Daily abundance of recently recruited megalopae was generally moderate with the exception of a very large peak towards the end of September. The peak in late September was also visible in the pattern of small juvenile abundance. Field notes from this time described cusp formation on the beach following a northeaster that occurred just days before both

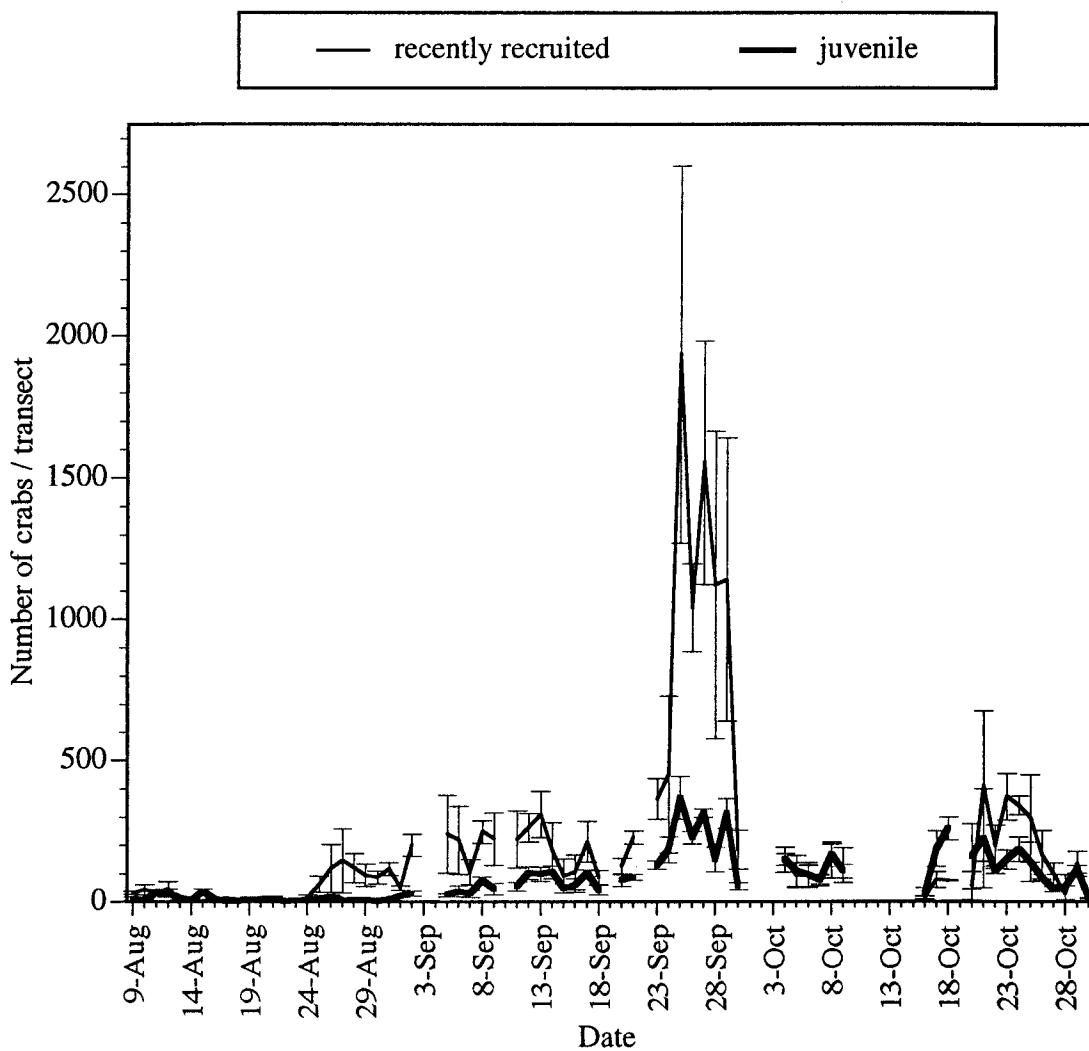


Figure 7. Average daily abundance (± 1 S.E.) of recently recruited (<4.3 mm, thin line) and juvenile (>4.3 mm, thick line) *Emerita talpoida* per transect at the study site. Each transect sample was composed of both megalopae and first crabs. Image analysis was used in distinguishing uncalcified recently recruited crabs from older calcified crabs in the sample. Gaps represent missing sample days.

peaks of abundance. Peaks of both megalopae and juvenile abundance occurring simultaneously indicated that they were both altered by cusp formation. The recruitment index removed this alteration.

The time series of recruitment index was dramatically different than that of abundance (Figure 8). The index was marked by peaks early in the series and then a slight gradual decline thereafter. The largest index values occurred at the beginning of the study period, at one point nearing 100% in late August.

Cross-correlations were made between ARIMA residuals of the arcsine-transformed recruitment index and the physical variables (Table 4). Significant correlations were found between the recruitment index and cross-shore wind stress, temperature, and cross-shelf currents. Cross-shore wind stress was significantly negatively correlated with the recruitment index at 0 and -1 days lag, temperature was significantly positively correlated with the recruitment index at -1 days lag, and cross-shelf currents were significantly negatively correlated with the recruitment index at -2 days lag. These correlations between the recruitment index and winds, temperature, and currents suggest wind-driven onshore transport of larvae may have caused increases in the recruitment index.

Due to the relatively small number of crabs (recruits and juveniles) during the first 15 days of the study (9 to 23 August) (Figure 7), cross-correlations were performed on a shorter time series (24 September to 30 October) to evaluate correlations between the recruitment index and physical variables when crab abundance was high (Table 5). The correlations were slightly different than those found for the entire series, with only cross-shore wind stress significantly negatively correlated with the recruitment index at a 0 day lag. Without the first 15 days of sampling, there is still a correlation between onshore winds and increases in the recruitment index suggesting wind-driven onshore larval transport.

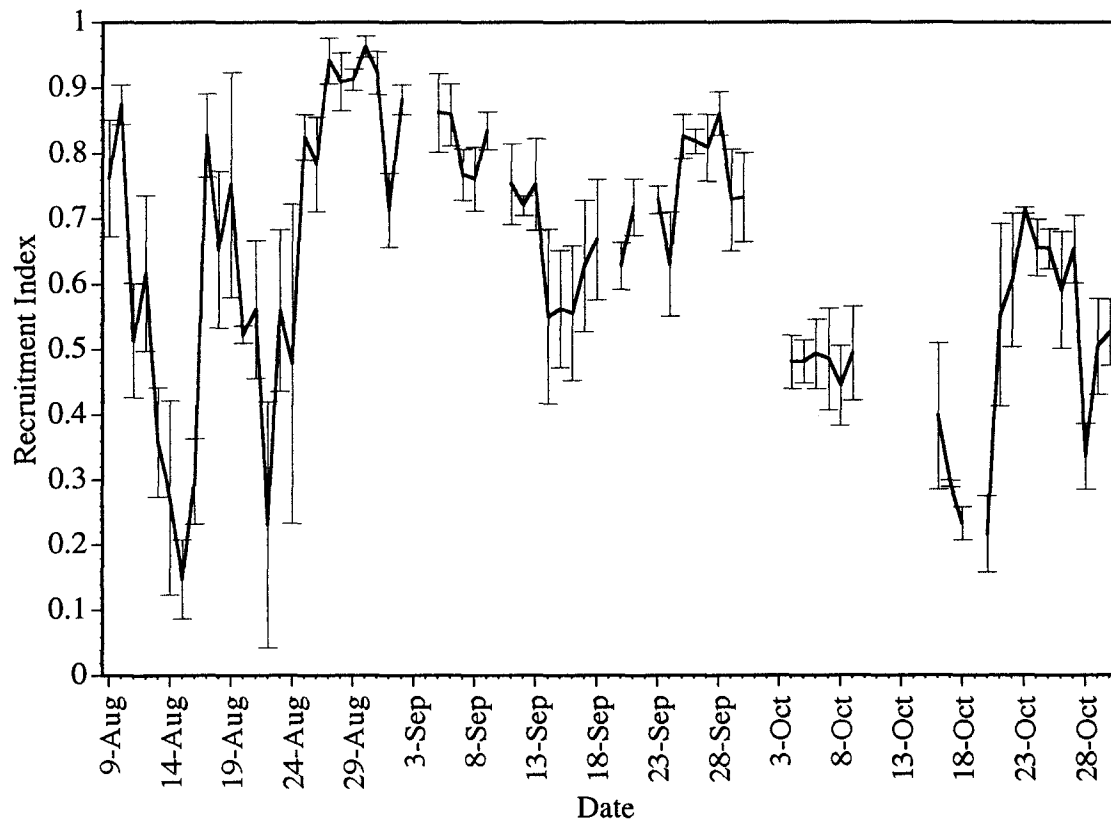


Figure 8. Average daily recruitment index (± 1 S.E.) calculated as the number of recently recruited mole crab megalopae divided by the total number of crabs in each transect. Gaps are missing sample days.

Table 4. Results of cross-correlations between ARIMA residuals of physical variables and the recruitment index, 9 August to 30 October, 1994. Significant cross-correlation coefficients ($p < 0.05$) are listed with the lag in days.

Variable	component	r	lag
<i>Wind Stress</i>	Cross-shore	-0.250	0
		-0.236	-1
	Alongshore	-	
<i>Salinity</i>		-	
<i>Temperature</i>		0.379	-1
<i>Cross-shelf currents</i>	Surface	-0.239	-2
	Bottom	-	
<i>Along-shelf currents</i>	Surface	-	
	Bottom	-	
<i>Average Significant Wave Height</i>		-	

Table 5. Results of cross-correlations between ARIMA residuals of physical variables and the recruitment index, 24 August to 30 October, 1994. Significant cross-correlation coefficients ($p < 0.05$) are listed with the lag in days.

Variable	component	r	lag
<i>Wind Stress</i>	Cross-shore	-0.246	0
	Alongshore	-	
<i>Salinity</i>		-	
<i>Temperature</i>		-	
<i>Cross-shelf currents</i>	Surface	-	
	Bottom	-	
<i>Along-shelf currents</i>	Surface	-	
	Bottom	-	
<i>Average Significant Wave Height</i>		-	

Daytime plankton samples taken from 5 km offshore indicated that *Emerita talpoida* zoea were throughout the water column but were generally in the deeper waters (Table 6). Late stage zoea were found in surface waters on 15 September. On 17 September, late stage zoea were in the neuston and in the deeper waters. On 25 September late stage zoea were found only in the neuston. Zoea at stages prior to stage VI were abundant in bottom samples on 15 and 25 September. On all three sampling dates *E. talpoida* zoea were found in highest abundance in the deeper plankton tows. With respect to zoeal stage, however, *E. talpoida* has a variable vertical distribution.

Discussion

During the study, inner-shelf circulation was characterized by changes from upwelling to downwelling with changes in wind direction. This is evident in the time series (Figure 6) and statistical analysis (Table 3). During northeasters, strong winds from the north pushed warm, low salinity surface waters onshore causing a rise in coastal sea level. To compensate for the rise in sea level, nearshore surface waters downwelled and flowed offshore along the bottom. Large waves were also generated by northeasters. During the southwesterers, steady light winds blew offshore. This caused the warm, low salinity surface waters to move offshore, leaving a depression of sea level near shore. To compensate, cold, higher salinity bottom waters flowed onshore and upwelled near the coast.

Significant correlations between the physical variables and the recruitment index allow one to develop hypotheses explaining larval transport over the inner-shelf. As indicated by the cross-correlations (Table 4, 5), periods of higher recruitment were associated with onshore winds, onshore surface currents, and warm temperature. The mechanism of onshore transport appears to be due to wind-driven onshore flow associated with downwelling events.

Table 6. Concentrations (in number/ m²) of *E. talpoida* zoea integrated over three depth ranges. Samples were taken on 15, 17, and 25 September, at a station located approximately 5 km directly offshore of the FRF pier. Zoel stages I-V were considered early while zoea with stage VI characteristics were considered late.

		September		
depth		15	17	25
Early stages	neuston	0	0	0
	10 m- surface	0.10	0	0
	20 m-10 m	4.8	0.39	3.8
Late stages	neuston	0	0.024	0.049
	10 m- surface	0.28	0	0
	20 m-10 m	0	3.1	0

Plankton samples indicate that late stage zoea are found throughout the water column (Table 6). On all 3 sampling dates, there were low concentrations of late stage zoea at depths <10 m. The greatest concentration occurred at depths >10m on 1 of 3 days sampled. Why there are so few larvae in the neuston if, as the cross-correlations suggest, shoreward transport of *Emerita* occurs in the surface waters is not clear. Note that plankton samples were only collected during the day; *Emerita* might vertically migrate. Early zoeal stages (I-III) of *Emerita talpoida* have been seen to migrate several meters over a 24 hour period (Maris, 1986). If this occurs at later stages, then perhaps the larvae reside in the surface waters primarily at night.

Two characteristics of the larval biology of *Emerita* that may support a wind-driven transport hypothesis: (1) sensitivity to light (Burton, 1979) and (2) delayed metamorphosis at settlement from the zoeal to the megalopal stage (Harvey, 1993). Burton (1979) looked at the responses of laboratory-reared first stage zoea of *E. analoga* and found them to be initially photopositive for the first four hours and then photonegative. The larvae changed behavior when starved. Without food, they remained photopositive. These results suggest that the larvae might be responding to changes in food that are undoubtedly associated with light levels (phytoplankton). If the larvae are optimally exploiting their food resource, starvation (and predation) could be largely avoided by vertical migration to the surface at night. Harvey (1993) found that food and sand effected the duration of the zoeal stages in *E. talpoida*, ultimately affecting the time to molting to megalopae. He found that the zoeal duration was shorter when the larvae were fed and the molt to megalopae was faster in the presence of sand. This study suggested that the molt from zoea may occur only under ideal conditions. Therefore, onshore transport to sandy beaches in surface waters that contain food resources may be beneficial to late zoeal stages by providing favorable conditions for metamorphosis to the megalopal form. These studies on the larval biology of *Emerita* suggest that the larvae have the ability to choose vertical distributions which may be optimal

for development while over the inner-shelf. The demonstrated behavioral and developmental responses to cues that are mostly vertically distributed in nature (food, sand, light) have important implications for the horizontal transport of larvae and ultimately, recruitment patterns.

Studies on blue crab (*Callinectes sapidus*) recruitment to estuaries of the Mid-Atlantic Bight (MAB) exemplify how wind-driven mechanisms can effect recruitment patterns. Blue crabs have planktonic larvae that spend weeks to months developing through zoeal stages over the inner continental shelf (Montfrans et al, 1995). The larvae reside primarily in the neuston and so are carried by surface currents affected by the wind. Although blue crab megalopae have to get into an estuary to settle, they also have to get back to the estuary from shelf waters. Transport back to the estuary has been studied by a number of investigators on the coast of North America (Johnson et al., 1984; Johnson and Hester, 1989; Johnson and Hess, 1990; Blanton et al., 1995; Johnson, 1995; Jones and Epifanio, 1995; Mense et al., 1995; Montfrans et al., 1995; Olmi, 1995; Morgan et al., 1996). The predominant transport mechanism that is believed to bring megalopae to the estuary is shoreward wind-driven transport (Johnson et al., 1984). There is some evidence that there may be tidally-driven transport of *C. sapidus* across the shelf (Shanks, unpublished data). This transport has yet to be as widely documented as wind-driven transport, however. Once the megalopae get near the mouth of the estuary, they are thought to be carried in by tidal currents (Morgan et al., 1996). Two different transport strategies are used by the blue crab, but wind transport across the shelf plays a major role in the success of recruitment (Johnson and Hester, 1989).

Northeasters are onshore winds that result from the passage of low pressure systems over the MAB. Their effect on recruitment has been demonstrated in blue crabs and here, with mole crabs. Onshore winds from the northeast push warm, low salinity surface waters shoreward, resulting in downwelling near the coast. If late stage larvae of

intertidal crustaceans are in these surface waters, there is a good possibility that they will be brought to a suitable settlement site. In *Emerita talpoida*, correlations between recruitment and onshore winds, currents, and salinity, suggest that this larval transport is occurring.

CHAPTER IV

CONCLUSION

The research from the preceding pages was performed as part of the Coastal Ocean Processes (CoOP) experiment. This experiment was designed to address the cross-shelf dispersal of soft-bottom invertebrate larvae over the inner-shelf of the southern portion of the Mid-Atlantic Bight. The intertidal sampling that gave rise to this thesis addressed the beginning and the end of the planktonic dispersal phase of *Emerita talpoida*.

The release of larvae from the intertidal was monitored on a daily basis by examining the developmental state of the eggs held by female crabs. Using physical data provided by the Army Corps of Engineers Field Research Facility (FRF) and other investigators in the CoOP project, a correlative time series analysis was performed with the release data. The results suggest that warm temperature and large waves influence the hatching of zoea from the eggs. The implications of hatching in response to wind-driven downwelling and large waves were discussed. Warm temperatures might accelerate development, while hatching during large waves might export zoea from the surf zone in wave-generated rip currents. This type of hatching response has yet to be seen in other crustacean species, but it seems likely that it could be found with more investigation.

Recruitment of megalopae to the sandy beach from the plankton was monitored daily along with physical variables that affect the nearshore hydrography. After abundance of megalopae was determined using image analysis to isolate the most recently recruited individuals, a recruitment index was calculated. The index removed variations in abundance that may have been attributable to beach morphology rather than recruitment. Cross-correlations between the recruitment index and physical variables resulted in

significant correlations between recruitment and onshore winds, onshore surface currents, and low salinity. Plankton samples taken during the study found late stage larvae in surface waters as well as bottom waters. These results suggest that late stage larvae might be transported shoreward in wind-driven onshore surface currents.

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