

THE INFLUENCE OF VERTICAL MIGRATORY BEHAVIORS ON THE TRANSPORT  
OF MARINE ORGANISMS

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## ABSTRACT

SARAH CARR: The influence of vertical migratory behaviors on the transport of marine organisms

(Under the direction of Dr. Richard A. Luettich, Jr.)

Many marine organisms are dispersed by water currents for all or part of their lives or utilize water currents to migrate between habitats as juveniles or adults. This transport is an important determinant of the distribution of marine populations and can be significantly influenced by organisms' vertical migratory behaviors (VMBs). The importance of VMBs to transport is now widely recognized, but there have been relatively few attempts to give detailed descriptions of them or quantify their influence.

This dissertation describes and quantifies the influence of ebb-tide transport (ETT), a VMB in which crabs ascend into the water column during ebb tides, on the spawning migration of female blue crabs *Callinectes sapidus*, near Beaufort Inlet, North Carolina. Ovigerous female crabs were tracked with ultrasonic telemetry. A detailed behavioral model was developed from this study as well as other field and laboratory studies and was coupled to a hydrodynamic model of the Beaufort Inlet region. The total distances that crabs traveled during ebb tides ranged from 10 – 40 % of the distances that passive particles would have traveled under the same conditions.

This dissertation also describes and quantifies the influence of diel vertical migration (DVM), a common VMB in which organisms reside in near-surface waters at night and at deeper depths during the day, on the transport of zooplankton in a coastal region with strong

seasonal upwelling. Simple behavioral models of zooplankton DVM were coupled to a hydrodynamic model of the Monterey Bay region of California. DVM reduced transport away from the region by as much as  $8 \text{ km d}^{-1}$  relative to passive transport near the surface.

A synthesis of the existing literature supports the assumptions that selective tidal-stream transport behaviors such as ETT enable directed migrations in estuarine and coastal regions while DVM and ontogenetic vertical migrations generally retain organisms near their starting locations. The synthesis also demonstrated that quantification of the influence of VMBs on transport must be carried out for specific behaviors at specific locations because organisms' characteristic VMBs and hydrography vary widely between marine environments.

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## **Chapter 1. Introduction**

### **1.1 Vertical migratory behaviors in the marine environment**

Transport by oceanic currents is an important determinant of the distribution of marine populations because many marine organisms are planktonic throughout their lives (holoplankton) or during a dispersive larval stage (meroplankton; Roughgarden et al., 1988; Cowen et al., 2000). In addition, many nektonic organisms use water currents to migrate between habitats as juveniles or adults (Arnold and Holford, 1995). Understanding transport processes and their variability in the marine environment, particularly the level of self-recruitment in a population and the connectivity between populations, is critical to the effective management of marine fisheries resources. These processes help determine appropriate boundaries for fisheries management units (Strathmann et al., 2002; Warner and Cowen, 2002), potential sites for restoration efforts (Peterson et al., 1996), and the potential utility of and proper design (e.g. size, location) for marine protected areas (Stockhausen et al., 2000; Gaines et al., 2003; Palumbi, 2003).

Vertical migratory behaviors (VMBs) are often cited as important influences on the horizontal transport of marine organisms (Wroblewski and Hofmann, 1989; Werner et al., 1993, 2001; Gaines et al., 2003; Shanks et al. 2003). Vertical current velocities in the marine environment are typically much smaller than horizontal current velocities ( $\ll 1\%$ ), and many organisms that are unable to swim effectively against strong horizontal currents can control their vertical position in the water column. Vertical migratory speeds between 1 - 70

m h<sup>-1</sup> have been observed in most marine invertebrate and vertebrate taxa, including poriferans, cnidarians, ctenophores, chaetognaths, nematodes, annelids, mollusks (including gastropods, bivalves, and cephalopods), arthropods (including euphausiids, copepods, cirripeds, and decapod crustaceans such as shrimp and crabs), bryozoans, and echinoderms (including asteroid and ophiuroids; Mileikovsky, 1973; Chia et al., 1984). Depending on current velocities in a region, organisms that traverse relatively small vertical distances, on the order of 10 - 1000 m, in the water column could theoretically alter their horizontal transport by distances on the order of 10 - 100 km.

VMBs influence an organism's transport when an organism is able to maintain a given position on the bottom or in regions where there is vertical current shear in the water column. Vertical current shear occurs in most marine environments due to the presence of wind-driven surface Ekman layers, benthic boundary layers, and thermal and salinity stratification. Shear is often much stronger (and the potential influence of VMBs on transport much higher) in coastal environments, however, due to coastlines, shallow depths, and freshwater runoff from land. The exact influence of VMBs on transport is a function of how long an organism spends at different depths (i.e. its near-surface depth, depth of migration, and migratory timing and speed) and the relative current velocities at those depths.

There are three main types of VMB: selective tidal-stream transport, diel vertical migration, and ontogenetic vertical migration. Selective tidal-stream transport (STST) is a behavior in which organisms ascend into the water column during one tidal phase and remain at or near the bottom during the opposing tidal phase. STST allows planktonic organisms to make unidirectional migrations in regions with strong oscillatory tidal currents, decreases the energetic costs of migration for nektonic organisms, and gives directional cues to migrating

organisms (Forward and Tankersley, 2001). STST behaviors are generally linked to semi-diurnal tides (generally the  $M_2$  tide), but diel vertical migrations in regions with strong diurnal tides (such as the  $K_1$  tide) may be de facto STST behaviors depending on the phase of the tide relative to the day-night cycle (Hill, 1991; Forward and Tankersley, 2001).

While tides occur in all marine environments to some degree, STST occurs primarily in estuarine and coastal regions (Forward and Tankersley, 2001). Tidal currents in these regions are generally much stronger than in open-ocean environments because the relatively shallow depths and reflection from and funneling by coastlines increases tidal amplitudes. In channelized areas, such as straits, river mouths, or narrow estuaries, tidal currents are rectilinear (i.e. flowing back and forth in a straight line), therefore STST behaviors lead primarily to onshore-offshore (up- and down-estuary) transport. The two variants of STST in these regions are ebb-tide transport (ETT), which results in net seaward transport, and flood-tide transport (FTT), which results in net landward transport. ETT has been observed in numerous crustacean, molluscan, and fish species and is often used for rapid larval dispersal from an estuarine or nearshore region (Forward and Tankersley, 2001). FTT has been observed in numerous crustacean, molluscan, polychaete, and fish species and is often used for larval retention in or entry into an estuarine region (Forward and Tankersley, 2001). In less confined regions, such as continental shelves, tidal currents are rotary (i.e. velocity vectors trace out an ellipse), so STST leads to transport in a particular compass direction. ETT, FTT, and STST in rotary currents are all used by juveniles and adults for directed migrations to nursery, reproductive, and feeding areas (Arnold and Holford, 1995).

While STST behaviors are based on temporal fluctuations in current speed and direction, the presence of vertical current shear or an organism's ability to maintain a given position on

the bottom is critical to achieving net transport. Organisms that are strong swimmers can move to the bottom and maintain themselves there to avoid transport during the unfavorable tidal phase. These organisms can achieve purely unidirectional transport and may be able to further augment their migratory speed by swimming downstream during the favorable tidal phase or swimming or walking upstream during the unfavorable tidal phase. Organisms that remain in the water column during both tidal phases must migrate to depths with slower currents during the unfavorable tidal phase to achieve significant net transport. These organisms generally have much slower net migratory speeds because of the back-and-forth transport.

Diel vertical migration (DVM) is a behavior in which organisms migrate between surface waters and deeper depths with diel periodicity. There are three main variants to this behavior: 1) nocturnal DVM in which organisms ascend into surface waters during the night and descend during the day, 2) reverse DVM in which organisms ascend into surface waters during the day and descend at night, and 3) twilight DVM in which organisms ascend to the surface at dawn and dusk and descend in between these periods (Forward, 1988). Nocturnal DVM is by far the most common variant and has been observed in most marine taxa and almost all marine environments. In terms of biomass, DVM is the largest animal migration on earth (Hays, 2003). It enables zooplankters to feed in relatively productive surface waters during the night and avoid visual predators and intense solar radiation during the day (Haney, 1988; Hays, 2003). While STST behaviors appear to exist solely to influence transport, the influence of DVM behaviors on transport may be largely incidental because DVM imparts other advantages to organisms such as increased foraging opportunities and reduced vulnerability to predation (Hill, 1998).

Ontogenetic vertical migration (OVM) is a behavior in which an organism's mean depth changes as the organism develops. Common OVM behaviors include ascents or descents by eggs because of changes in buoyancy (Werner et al., 1993), ascents or descents to preferred depths by larvae as their swimming capacity increases (Cowen, 2002), and seasonal migrations of long-lived zooplankters such as copepods to cold, deep water to slow metabolism and survive periods of food scarcity (Bartsch and Coombs, 1997; Hannah et al., 1998; Mullon et al., 2003; Stenevik et al., 2003). OVMs are very common in most marine environments, and, as with DVM, the influence of OVM on transport may be largely incidental to the ecological benefits it provides.

Other types of VMBs have also been observed. Hybrids of the above behaviors, such as STST ascents into the water column during nocturnal periods only and increases in DVM amplitudes as organisms develop, are common. VMBs have also been observed in response to short-term, less routine physical phenomena, such as rapid vertical movements of thermoclines or haloclines (Garland et al., 2002). VMBs are also not static over time. Many organisms use different VMB behaviors in different environments (e.g. DVM on the continental shelf and STST near and in estuaries; Forward et al., 2003), and the details of an organism's VMB (e.g. timing, speed, and depth of migration) may vary over time due to intrinsic factors such as age, reproductive condition, and hunger state and environmental factors such as cloud cover, seasonal changes in the photoperiod, and the presence of predators (Haney 1988; Bollens et al., 1994).

## 1.2 Determining the influence of VMBs on transport



Determining the transport of passive and vertically-migrating organisms in the marine environment is extremely difficult. The limited visibility in the marine environment and the small size of many marine organisms means the transport of organisms can only be directly observed for distances on the order of 10s of meters or less (e.g. Olson, 1985; Stoner, 1992). As a result, a variety of other methods, such as mark-recapture, telemetry, autonomous drifters, and hydrodynamic model simulations, are used (Freire and Gonzalez-Gurriaran, 1998).

Marking an organism, releasing it into the marine environment, then recapturing it later (mark-recapture) is used to determine the net transport of organisms between release and recapture. Marks can be artificial tags such as stains, dyes, or physical attachments. Organisms released from identifiable sources such as isolated islands or reefs, newly-established populations of introduced species, or regions with unique geochemical signatures or genetic characteristics can also be considered marked for the purpose of mark-recapture studies. Mark-recapture is one of the oldest methods of determining the transport of organisms and has been widely used to track a variety of invertebrates and vertebrates, including larval stages. Mark-recapture studies can be difficult, however, because many artificial tags have detrimental effects on organisms (e.g. impede their foraging or make them more vulnerable to predators) or are shed when an organism molts, natural tags are rarely unique, and the probability of recovering marked individuals is extremely low (Levin, 1990; Jones et al., 1999; Thorrold et al., 2002; Freire and Gonzalez-Gurriaran, 1998). Mark-recapture studies also do not provide detailed information about organism trajectories or VMBs (e.g. migratory timing, speed, and depth of migration).

Tagged organisms with transmitters that telemeter their position can provide detailed information about trajectories because the organisms can be tracked by boat or have sequential locations recorded by fixed receiving stations. Ultrasonic transmitters are generally used in the marine environment because they have a much greater range in saltwater than radio or satellite transmitters. If organisms remain at or periodically move to the surface of the water column, radio or satellite positioning and telemetry can be used to transmit their position to remote observers for the period of time that they are at the surface. Incorporating pressure transducers into or using them simultaneously with transmitters also makes the telemetry or storage of VMBs possible. Transmitters and pressure transducers are rapidly being miniaturized (Wolcott, 1995), but telemetry is still limited to relatively large, hard-bodied organisms that can carry a transmitter and/or transducer. Moreover, tracking organisms or setting up arrays of receiving stations is often impractical, costly, and/or time-consuming. These difficulties notwithstanding, telemetry is an extremely promising method for determining the transport of passive and vertically-migrating organisms and will yield a tremendous amount of invaluable data in the future. Excellent reviews of the use of telemetry for determining the transport of organisms in the marine environment have been written by Stasko and Pincock (1977), Wolcott (1995), and Freire and Gonzalez-Gurriaran (1998).

Another technology that is also developing rapidly and is extremely promising is the use of autonomous drifters to simulate the trajectories of organisms. The tracking of subsurface drifters is constrained by many of the same factors as tracking live organisms, namely the difficulty of determining and transmitting position underwater. Drifters that mimic the VMB of organisms have been developed (DeRobertis and Ohman, 1999). These drifters can be

programmed to surface periodically and take advantage of radio or satellite positioning and telemetry to determine and transmit their position, but they are still too large to realistically simulate the trajectories of larvae or small organisms. The miniaturization of both passive and vertically-migrating drifters should occur rapidly, however, and make deployment of autonomous drifters extremely useful for determining detailed trajectories of both passive and vertically-migrating organisms. Autonomous drifters have the advantages that they are less vulnerable to injury than live organisms, more readily made identifiable, and more easily recaptured because of the potential for adding transmitters that will telemeter a drifter's position when it grounds or surfaces. They have the disadvantage that they do not fully recreate the VMBs of organisms.

Due to the difficulties of determining the transport of passive and vertically-migrating organisms in the field, many researchers use hydrodynamic models to simulate organism trajectories. Hydrodynamic models solve simplified forms of the Navier-Stokes equations, the equations governing fluid flow, to simulate current velocities and sea surface height (Giske et al., 2001). Models may also include algorithms to simulate other parameters, such as salinity, temperature, light, nutrients, and organism abundance. The trajectories of passive organisms can be simulated by Lagrangian particle-tracking algorithms driven by current velocity output from hydrodynamic models. The trajectories of vertically-migrating organisms can be simulated by incorporating a behavioral algorithm determining the depth of an organism at any given time into Lagrangian particle-tracking algorithms. Behavioral algorithms can range from very simple functions in which simulated organisms swim up and down at fixed times to complex functions in which an organism's depth depends on their developmental stage and other intrinsic parameters, as well as model parameters such as

temperature, salinity, light, nutrients, chlorophyll, turbulence, and prey or predator abundance (Giske et al., 2001; Werner et al., 2001; Gentleman, 2002). Hydrodynamic models have a significant advantage over field methods for determining organism transport because the trajectories of both passive and vertically-migrating organisms can be simulated under a wide variety of hydrographic conditions with relative ease. The ability to do numerous simulations is critical because even minor changes in starting location (horizontal or vertical) or time can lead to significant differences in the net transport of an organism.

While hydrodynamic models provide the most detailed descriptions of current fields available, they may be inaccurate because of the simplification, parameterization, and discretization necessary to solve the governing equations and algorithms as well as inaccuracies in forcing data. In addition, computational time and memory limitations make it impossible for hydrodynamic models to resolve processes at all of the temporal and spatial scales that may be important to an organisms transport (Giske et al., 2001). The development of hydrodynamic models capable of resolving the small temporal and spatial scales critical to the circulation of coastal and estuarine regions is relatively recent; therefore there are relatively few examples of coupling behavioral algorithms with hydrodynamic models to predict the transport of vertically-migrating organisms in these regions (Wroblewski and Hofmann, 1989; Werner et al., 2001; Largier, 2003).

### 1.3 Organization of this dissertation

This dissertation describes and quantifies the influence of two common VMBs, STST and DVM, on transport in the marine environment. Chapter 2 describes the ETT migration of female blue crabs (*Callinectes sapidus* Rathbun) from low salinity estuarine regions to high

salinity regions near the ocean to release larvae. In order to determine the relationship of ebb-tide vertical migrations to local currents and the influence of these vertical migrations on the horizontal transport of blue crabs in the estuary, ovigerous females with mature embryos ( $\sim 1 - 3$  days from hatching) were tracked near Beaufort Inlet, North Carolina (USA), in July and August 2001 and 2002. Crabs were tagged and tracked using ultrasonic telemetry, and currents near the crabs were measured simultaneously with a shipboard acoustic Doppler current profiler. In Chapter 3, a detailed behavioral model of female blue crab ETT is developed from the results of Chapter 2, as well as other previous laboratory and field studies, and is coupled to a hydrodynamic model of the Beaufort Inlet region of North Carolina. This coupled model is then used to simulate the trajectories of migratory female crabs in the region and determine spatial patterns in migratory success, migratory speeds, the residence times of crabs in different regions of the estuary, and potential larval release locations. Chapter 4 describes the influence of DVM on zooplankton transport, the level of recruitment of locally-produced propagules (self-recruitment), and sources of recruits in the upwelling region near Monterey Bay, California, by simulating the trajectories of fixed-depth and vertically-migrating organisms with a drifter-tracking algorithm driven by velocity fields from a three-dimensional hydrodynamic model. Chapter 5 synthesizes the existing literature, including the new work included in this dissertation, to determine the extent to available studies support the commonly-held belief that VMBs have a significant influence on transport in the marine environment.

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## **Chapter 2. Observations of the ovigerous blue crab *Callinectes sapidus* ebb-tide transport spawning migration**

Reprinted from “Carr SD, Tankersley RA, Hench JL, Forward RB, Luettich RA (2004) Movement patterns and trajectories of ovigerous blue crabs *Callinectes sapidus* during the spawning migration. Estuarine, Coastal and Shelf Science 60:567-579” with permission from Elsevier.

### **Abstract**

Female blue crabs (*Callinectes sapidus* Rathbun) migrate from low salinity estuarine regions to high salinity regions near the ocean to release larvae. During this migration, ovigerous females use ebb-tide transport, a vertical migratory behavior in which they ascend into the water column during ebb tides, to move seaward to larval release areas. In order to determine the relationship of ebb-tide vertical migrations to local currents and the influence of these vertical migrations on the horizontal transport of blue crabs in the estuary, ovigerous females with mature embryos (~ 1 - 3 days from hatching) were tracked near Beaufort Inlet, North Carolina (USA), in July and August 2001 and 2002. Crabs were tagged and tracked using ultrasonic telemetry, and currents near the crabs were measured simultaneously with a shipboard acoustic Doppler current profiler.

During the two seasons, eight crabs were successfully tracked for periods ranging from 3.9 – 37.0 h and for distances ranging from 1.9 – 10.6 km. All crabs migrated seaward during the tracking periods. Crabs moved episodically during all tidal phases with periods of movement on the order of minutes to an hour. They moved with local currents in terms of both speed and direction during ebb tides, consistent with ebb-tide transport, and moved

down-estuary (seaward) in opposition to local currents during flood tides. The percentage of time that crabs were active was higher during night ebb tides than during day ebb tides or flood tides and increased with increasing ebb-tide current speed. Mean migratory speeds were 0.11, 0.04, 0.08 and 0.02 m s<sup>-1</sup> during night ebb, night flood, day ebb and day flood tides respectively, and net migratory speeds were on the order of 5 km day<sup>-1</sup>. Due to the episodic nature of the crabs' movements, the total distances that crabs traveled during ebb tides ranged from 10 – 40 % of the distances that passive particles could have traveled under the same conditions.

## 2.1 Introduction

The blue crab *Callinectes sapidus* has a complex life history in which it utilizes both oceanic and estuarine habitats (reviewed in Van Engel, 1958 and Millikin and Williams, 1984). Mating generally occurs in the lower salinity regions of estuaries from spring to fall. After mating, females migrate down-estuary to higher salinity regions, often overwintering en route (Turner et al., 2003). They generally extrude eggs during the summer months and carry them as a mass under their abdomens for a ~ 2 week development period (Sandoz and Rogers, 1944; Millikin and Williams, 1984). Females release larvae near estuary mouths during nighttime and morning ebb tides, and larvae are transported offshore (Provenzano et al., 1983; Epifanio et al., 1984; Natunewicz et al., 2001). Offshore larval development may be important for avoiding low-salinity osmotic stress and estuarine predators (Sandoz and Rogers, 1944; Morgan, 1990). Wind events transport megalopae (post-larvae) back to coastal regions (Epifanio and Garvine, 2001).

During the spawning migration, ovigerous female blue crabs use ebb-tide transport (ETT) to move seaward to coastal larval release areas (Tankersley et al., 1998; Forward et al., 2003a). Organisms using ETT migrate vertically into the water column during ebb tides and are transported seaward as passive or semi-passive particles (reviewed in Forward and Tankersley, 2001). They generally minimize transport during flood tides by remaining at or near the bottom. Adult blue crabs are strong swimmers capable of speeds  $> 1 \text{ m s}^{-1}$  (Spirito, 1972) and long distance migrations of 500 km (Tagatz, 1968), but ETT may enable ovigerous crabs to migrate more rapidly and efficiently in near-coastal areas where currents can exceed  $1 \text{ m s}^{-1}$ . ETT also provides a means of orienting towards suitable larval release areas in the lower estuary and coastal ocean.

Other studies of ETT by ovigerous blue crabs have focused on the timing of vertical migrations into the water column with respect to tidal and diel phases. In a survey of blue crabs migrating at the surface of a North Carolina estuary, Tankersley et al. (1998) observed a relatively large number of ovigerous females with mature embryos ( $< 4$  days prior to larval release) migrating via passive transport during night ebb tides and relatively few ovigerous crabs migrating during night flood tides or the day. In a laboratory experiment in constant low-level light conditions, Forward et al. (2003a) demonstrated that ebb-tide vertical migrations by ovigerous crabs with mature embryos are based on an endogenous circatidal rhythm in vertical swimming and occur at times corresponding to consecutive local ebb tides. Vertical swimming episodes in laboratory tanks were brief ( $< 3$  min), and swimming activity levels varied widely among crabs. In a field study of female blue crabs tethered in a North Carolina estuary, Hench et al. (2004) observed that crabs migrated vertically during all stages of egg development but sojourns into the water column were most frequent in the  $\sim 3$  days

prior to larval release. Most vertical migratory activity occurred when hydrostatic pressure in the estuary was decreasing, suggesting that this environmental cue may be the zeitgeber (“timegiver”) for the endogenous circatidal rhythm. The frequency of vertical ascents was highest during times of maximum ebb currents and when hydrostatic pressure was decreasing most rapidly. Some of the tethered crabs were active during night and day ebb tides, while others were only active during night ebb tides. As with Forward et al. (2003a), vertical migratory episodes were brief ( $< 1$  min), and the frequency of vertical migrations varied widely among crabs.

The goals of the present study were three-fold: 1) to characterize horizontal and vertical movement patterns of ovigerous blue crabs during the spawning migration, 2) to determine the relationship of ETT vertical migrations by free-ranging ovigerous crabs to local currents, and 3) to determine the influence of ETT vertical migrations on the horizontal transport of ovigerous crabs during the spawning migration. Free-ranging ovigerous females were tracked using ultrasonic telemetry, and currents near the crabs were measured with a shipboard current meter. By measuring crab and current velocities simultaneously, the difference between active horizontal movements (walking or swimming) could be distinguished from passive horizontal transport by local currents. Similar tracking methods have been used for striped marlin (*Tetrapturus audax*; Brill et al., 1993) and American eels (*Anguilla rostrata*; Parker and McCleave, 1997), but the simultaneous measurement of both organism and current velocities at high-resolutions is still rare in tracking and migration studies. I am unaware of any comparable prior studies for invertebrate migrations. Previous estimates of travel speeds for ovigerous blue crabs during the spawning migration have been derived from low-resolution mark-recapture studies (reviewed in Millikin and Williams,

1984; Turner et al., 2003). This study provides the most detailed description of the ovigerous blue crab spawning migration to date and allows for estimates of temporal variability in migratory speeds, as well as average migratory speeds.

## 2.2 Materials and methods

Ultrasonic tracking experiments were conducted near Beaufort Inlet, North Carolina, in July and August, 2001 and 2002. Beaufort Inlet is a high-energy tidal inlet that connects the complex, shallow estuarine system of Bogue Sound, the Newport River Estuary, the North River Estuary and Back Sound to Onslow Bay and the South Atlantic Bight (Fig. 2.1). Circulation near the inlet is dominated by semi-diurnal tides, and peak ebb currents speeds are  $> 1 \text{ m s}^{-1}$  near the inlet throat (Logan, 1995; Luettich et al., 1999). Tidal currents are slower inside the estuarine system due to bottom friction and increases in cross-sectional area, and there is a  $\sim 2 \text{ h}$  phase lag between the time of high tide at the inlet and the time of high tide in the upper sub-estuaries (Luettich et al., 1999). Due to low freshwater input, shallow depths and strong tidal currents, the water column near Beaufort Inlet is generally well-mixed with little stratification (Klavans, 1983; Luettich et al., 1999).

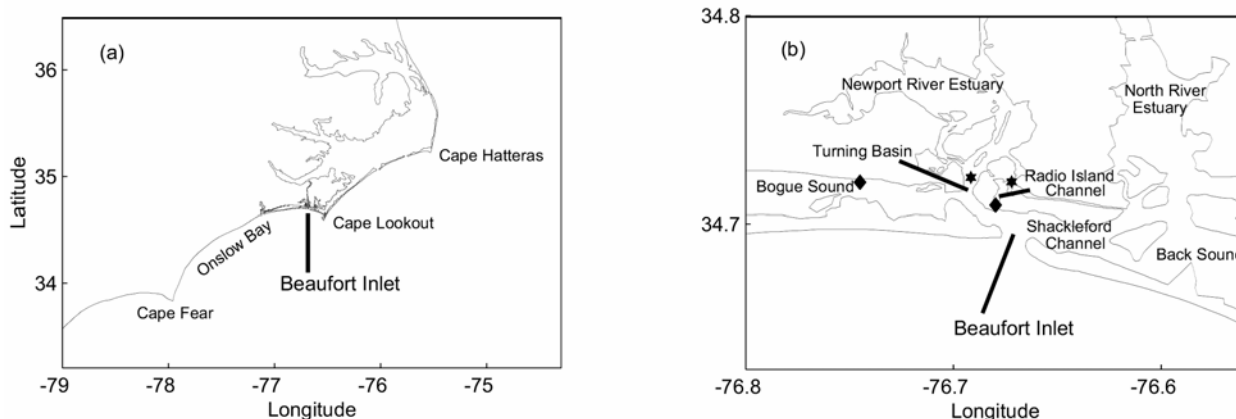


Fig. 2.1. Location of tracking study area: (a) South Atlantic Bight and (b) Beaufort Inlet region. Crab collection sites are marked by hexagons (★), and ADCP mooring sites are marked by diamonds (◆).

Female blue crabs (12 – 17 cm carapace width) with mature embryos (~ 1 - 3 days from hatching) were dipnetted while migrating in surface waters of the lower Newport River Estuary (2001) and the Port of Morehead City turning basin (2002) (Fig. 2.1b). Embryo stage was determined at the time of collection by examining a small sample of eggs with a dissecting microscope. Mature embryos have well-developed eyes and little yolk, giving egg masses with mature embryos a characteristic brown-black color (DeVries et al., 1983).

Ultrasonic transmitting tags (2001: Sonotronics CT-82-3, 10 g in water, 18 mm x 67 mm; 2002: VEMCO V16, 11 g in water, 16 mm x 58 mm) were attached to the crabs' dorsal carapaces by wrapping wire around the crabs' lateral spines. Similar telemetry tags have been used to study a range of crab behaviors, such as movement patterns, foraging and agonistic activity (Hines et al., 1995; Clark et al., 1999; Turner et al., 2003; reviews in Wolcott, 1995 and Freire and González-Gurriarán, 1998). In laboratory tests, these tags do not appear to interfere with normal activities, such as burial, walking and swimming (Hines et al., 1995). Tagging does not have a significant effect on the mean number of vertical migrations, ascent rates or descent rates of ovigerous blue crabs but does decrease the

duration of vertical migratory episodes (Hench et al., 2004). The results in this study should therefore be considered conservative estimates of true migratory speeds.

Tagged crabs were kept in buckets of water from the collection sites and transported by boat to one of three starting sites: the Radio Island Channel (2001), the Shackleford Channel (2001) or Bogue Sound (2002) (Fig. 2.1b). Tracking began 30 - 60 min after crabs were collected and continued for up to 37 h or until the signal from the tagged crab was lost. Crabs were tracked from the 8-m RV *Parker*, which was equipped with a differential Global Positioning System (Northstar 951XD receiver) and a boom-mounted acoustic Doppler current profiler (Hench et al., 2000; RD Instruments Workhorse Monitor ADCP, 1200 kHz, 0.5 m bins, 1.34 s sample interval) that also measured water depth. Ultrasonic signals from the tags were received with a Sonotronics DH-4 directional hydrophone with USR-96 receiver (in 2001) and a VEMCO VH-10 directional hydrophone with VR-60 receiver (in 2002). The hydrophones were mounted on PVC (in 2001) and stainless steel (in 2002) pipes that were held overboard (in 2001) and mounted to the side of the boat (in 2002) so that the hydrophones were below the bottom of the boat hull. During tracking, the hydrophones were rotated by hand to determine the direction of the crab relative to the boat.

Although signal strength varied due to local bathymetry, current strength and direction and water column stratification, strong signals were received at 1 - 20 min intervals and indicated that crabs were < 100 m from the boat. The maximum range for a strong signal was determined by independent tests of the ultrasonic telemetry equipment in the lower Newport River Estuary. The boat position was recorded when strong signals were received, and these positions (fixes) were used for the analysis of crab movement. Crab speeds were calculated by dividing the spatial distances that crabs traveled by the time intervals between

fixes. Current velocities from the ADCP were depth averaged and time averaged for the 40 s bracketing the time of each fix.

Independent current meters were moored in the Radio Island Channel in the summer of 2001 (1200 kHz RD Instruments Workhorse ADCP, 0.5 m bins, 3.33 s sampling interval, 180 samples per average) and in Bogue Sound in the summer of 2002 (1200 kHz RD Instruments Workhorse ADCP, 0.5 m bins, 2.50 s sampling interval, 360 samples per average) (Fig. 2.1b). Current measurements from the moorings were depth averaged and used to determine tidal current phase (i.e. ebb tide or flood tide) when shipboard ADCP measurements were not available. The times of local sunset and sunrise were used as the beginnings and ends of night periods.

Analysis of variance (ANOVA) and Fisher's protected least significant difference (PLSD) post-hoc test at the 5 % significance level were conducted on mean crab speeds during the four tidal-diel phases using StatView (SAS Institute Inc., v. 5.0). Mean angles ( $\pm$  95 % CI) for angular data were calculated using Oriana (Kovach Computing Services, v. 1.01).

## 2.3 Results

### 2.3.1 Crab trajectories

Eight crabs were successfully tracked during the 2001 and 2002 spawning seasons. Tracking durations ranged from 3.9 – 37.0 h with a mean of 21.4 h, and tracking distances ranged from 1.9 – 10.6 km with a mean of 4.8 km (Table 1). All crabs migrated seaward during the tracking periods regardless of their starting location or whether their relocation from capture area to tracking starting location changed the direction (compass bearing) to



Beaufort Inlet (Fig. 2.2a). Crabs 1, 2 and 3 were tracked from the Radio Island Channel, Crab 4 from the Shackleford Channel, and Crabs 5, 6, 7 and 8 in Bogue Sound (Fig. 2.2b). Crabs 1, 2, 3 and 6 were tracked to the inlet strait, while Crab 4 was tracked to ~ 4 km offshore (Fig. 2.2b). Tracking ended for Crabs 1, 2, 3 and 7 because the tag signal was lost and for Crabs 4, 5, 6 and 8 because of adverse weather or time constraints.

Crab No.	Starting Location	Starting Date	Starting Time	Tracking Duration	Tracking Distance
1	Radio Island Channel	7/17/01	21:31	3.9 h	2.2 km
2	Radio Island Channel	7/18/01	22:08	15.9 h	2.4 km
3	Radio Island Channel	7/20/01	00:08	4.9 h	2.1 km
4	Shackleford Channel	8/01/01	22:05	37.0 h	7.4 km
5	Bogue Sound	7/08/02	22:22	14.3 h	1.9 km
6	Bogue Sound	7/17/02	22:05	30.6 h	10.6 km
7	Bogue Sound	8/04/02	21:53	34.9 h	5.5 km
8	Bogue Sound	8/07/02	22:51	29.4 h	5.9 km

Table 1.1. Starting locations, dates and times of tracks and tracking durations and distances.

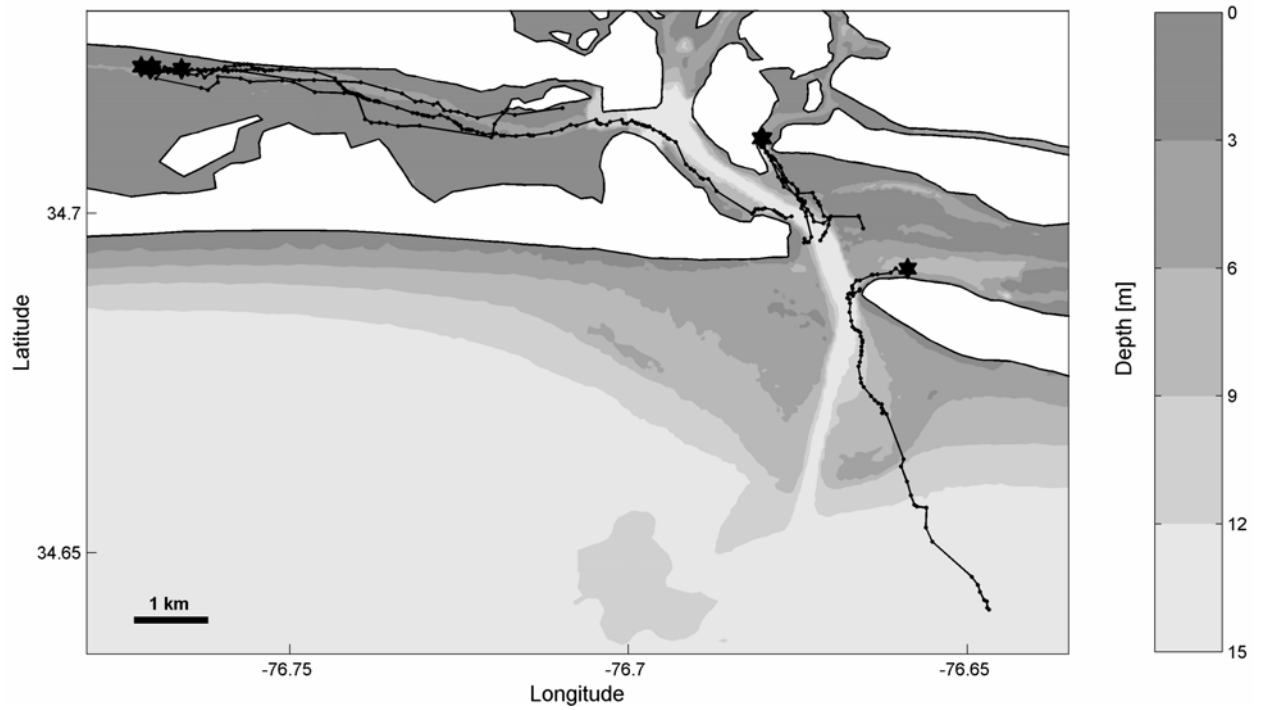


Fig. 2.2a. Eight (8) crab tracks and bathymetry (gray shading) near Beaufort Inlet, North Carolina. Tracks start in the estuary and move towards the inlet. Starting locations are marked by hexagons (★), and subsequent fixes are marked by circles (●).

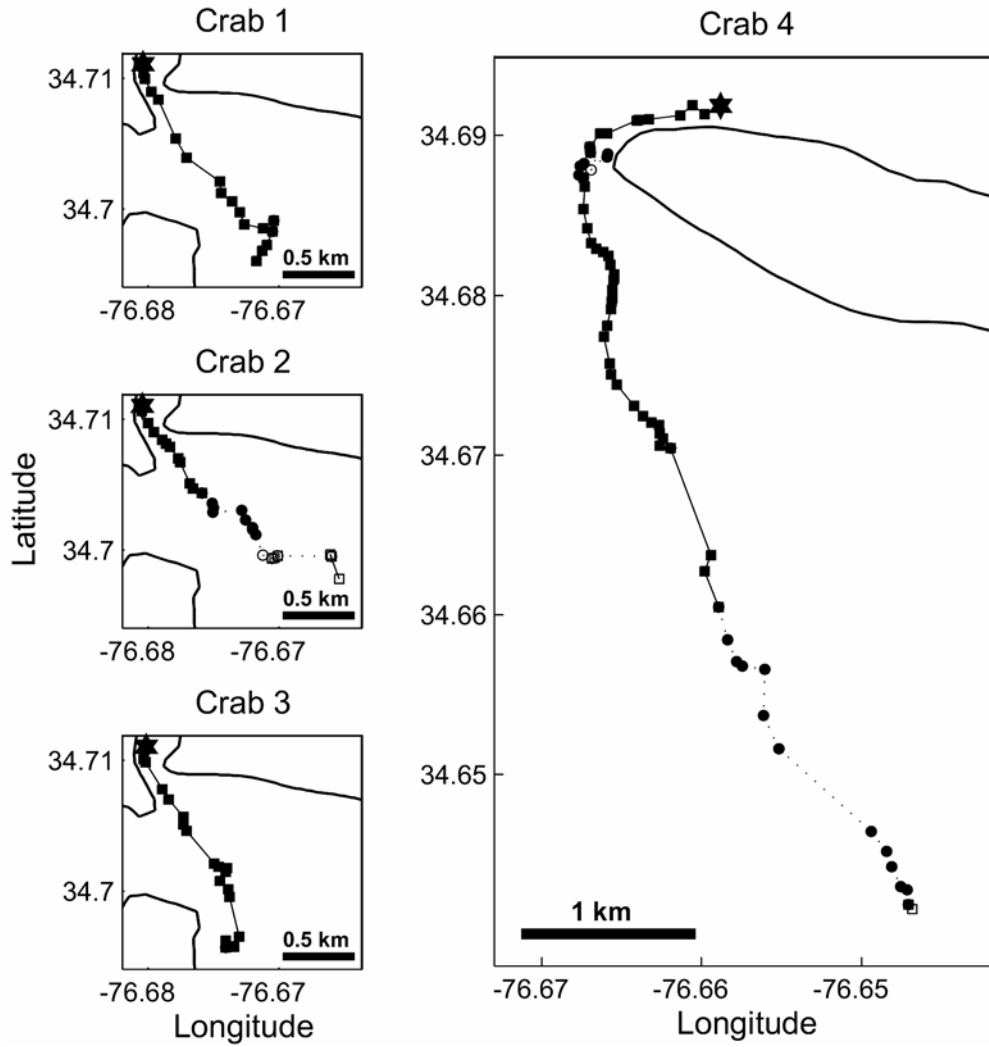


Fig. 2.2b. Crab tracks near Beaufort Inlet, North Carolina. Tracks start in the estuary and move towards the inlet. Starting locations are marked by hexagons (★). Fixes are marked as night ebb (■), night flood (●), day ebb (□) and day flood (○) tides. Solid lines are tracks during ebb tides, and dashed lines are tracks during flood tides.

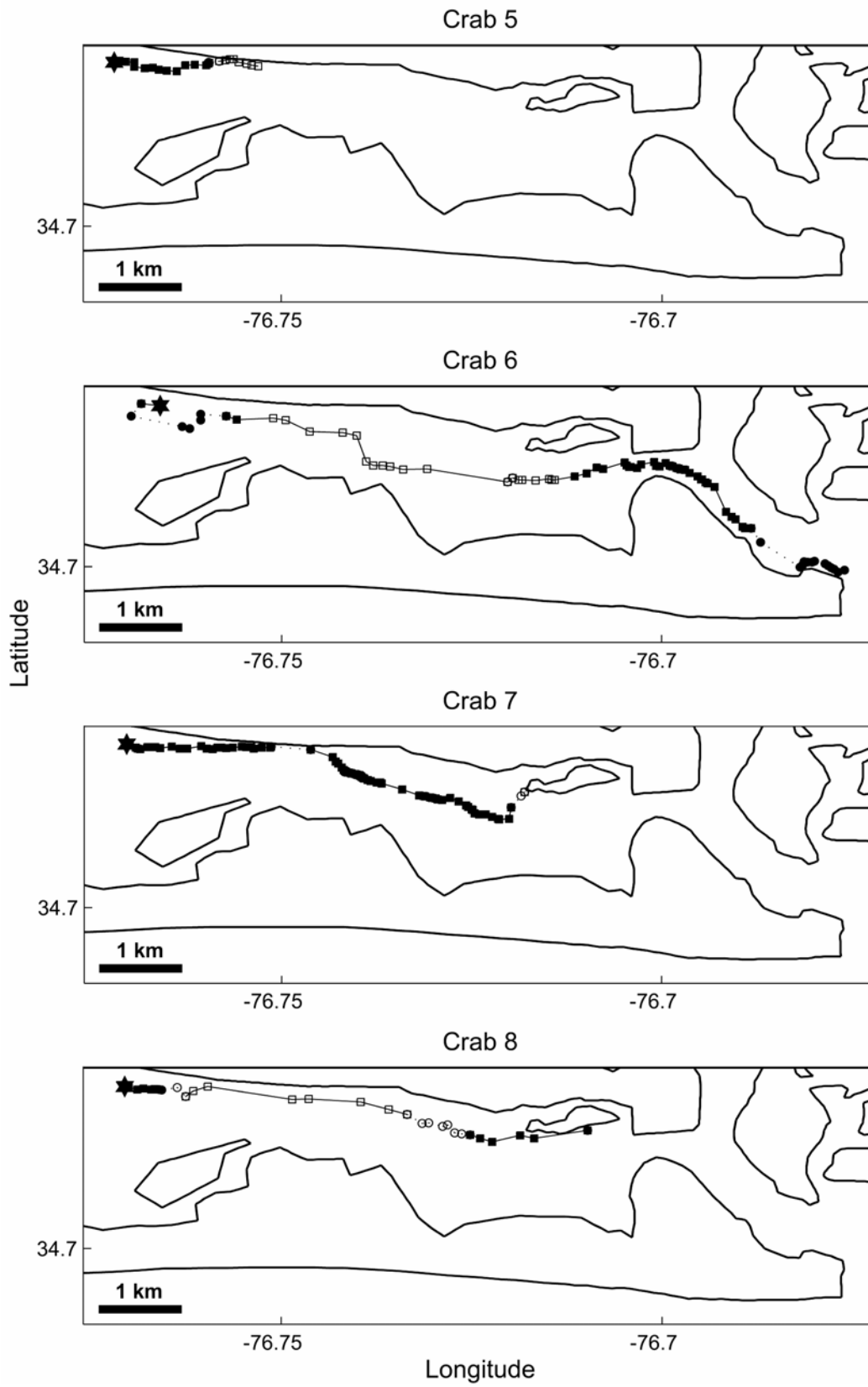


Fig. 2.2b cont.

Crab movements during the tracking periods were highly discontinuous. Crabs tended to move rapidly for periods from several minutes to an hour and remain stationary for periods from several minutes to hours (Fig. 2.3). Some time was required to relocate crabs after periods of movement because the range of the hydrophones was limited. Therefore, some of the crab speeds shown are means of times when crabs were moving and times when they were stationary and underestimate instantaneous crab speeds. Shipboard ADCP measurements were not collected at the ends of the tracks for Crabs 2 and 5 because the crabs moved into shallow areas that were inaccessible to the tracking vessel. Movements during these periods were classified as ebb-tide or flood-tide based on the tidal current phase at the moored current meters, but these periods were not used when direct comparisons between crab and current vectors were made since local current vectors were not available. The local currents at the end of Crab 4's track were very weak ( $< 0.1 \text{ m s}^{-1}$ ) because the crab had migrated offshore, away from the strong tidal influence of the inlet and estuary.

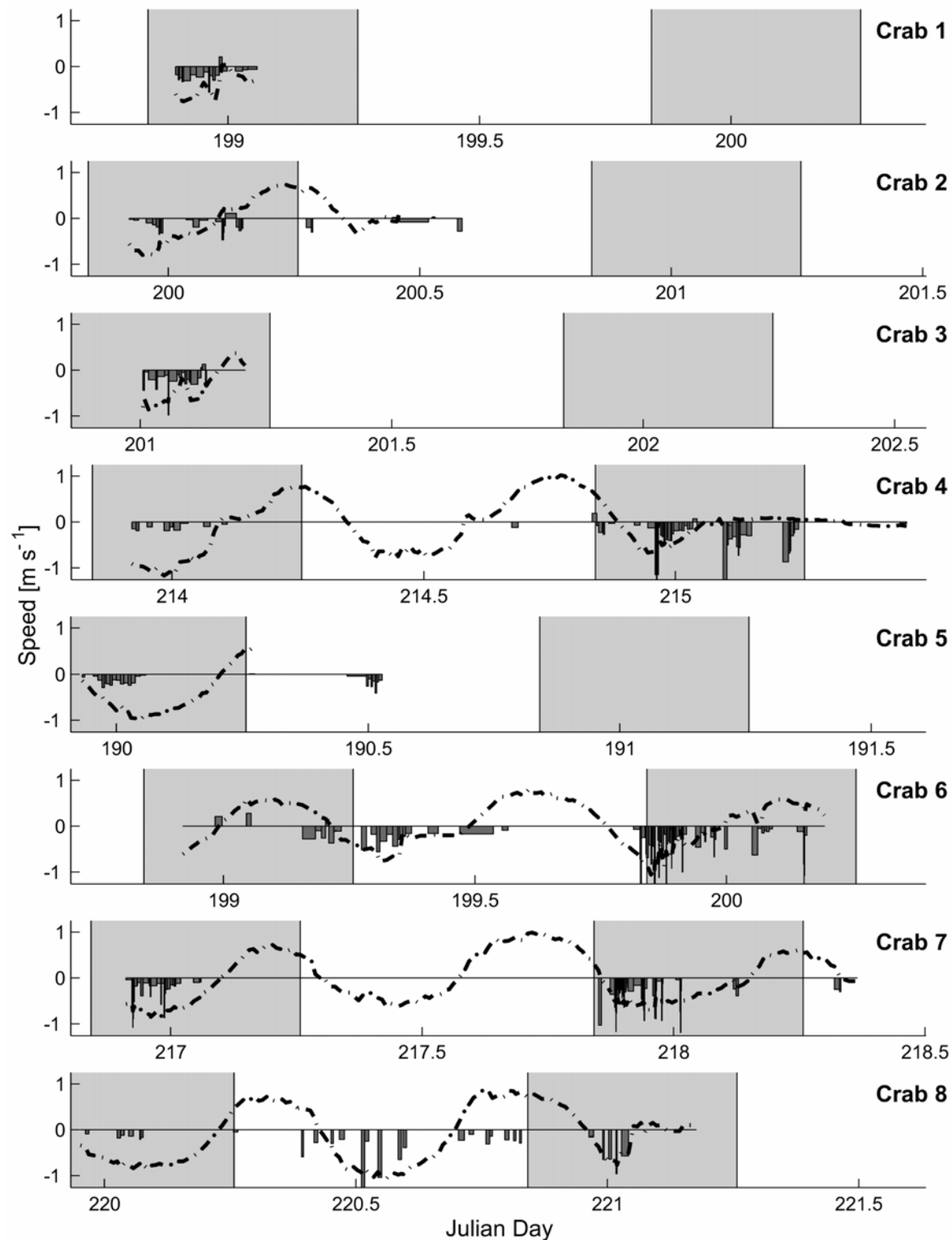


Fig. 2.3. Time series of crab speed (small, dark gray bars) and current speed (-.-). Positive speeds indicate flood tides/up-estuary movement, and negative speeds indicate ebb tides/down-estuary movement. Bar width indicates the time between fixes and period over which mean speed is computed. Night and day periods are indicated by the large light gray and white sections respectively.

### 2.3.2 Relationship of crab movements to local currents

Crabs moved during all tidal and diel phases, but there were distinct differences in movement patterns during different periods. Crab movements were overwhelmingly in the same direction as local currents during ebb tides and against local currents during flood tides (Fig. 2.3), resulting in seaward movement during both ebb and flood tides (Fig. 2.2b). Crab vectors were consistently aligned with current vectors ( $< 30^\circ$  difference) during ebb tides and with the down-estuary flow direction ( $180^\circ$  from the shipboard ADCP current vectors) during flood tides (Fig. 2.4a). When directional data were pooled among the eight crabs and weighted by the time that each fix represented so that every minute of tracking was represented by a single data point, the mean difference ( $\pm 95\%$  CI) between the crab and current vectors during ebb tides was  $1^\circ (\pm 2^\circ)$  (Fig. 2.4b). The mean difference ( $\pm 95\%$  CI) between the crab and current vectors during flood tides was  $187^\circ (\pm 3^\circ)$  (Fig. 2.4b). The close alignment between crab and current vectors during ebb tides is consistent with passive transport, and the close alignment between crab vectors and the down-estuary flow direction during flood tides raises the possibility that crabs may be using flood-tide currents to orient seaward during these periods.

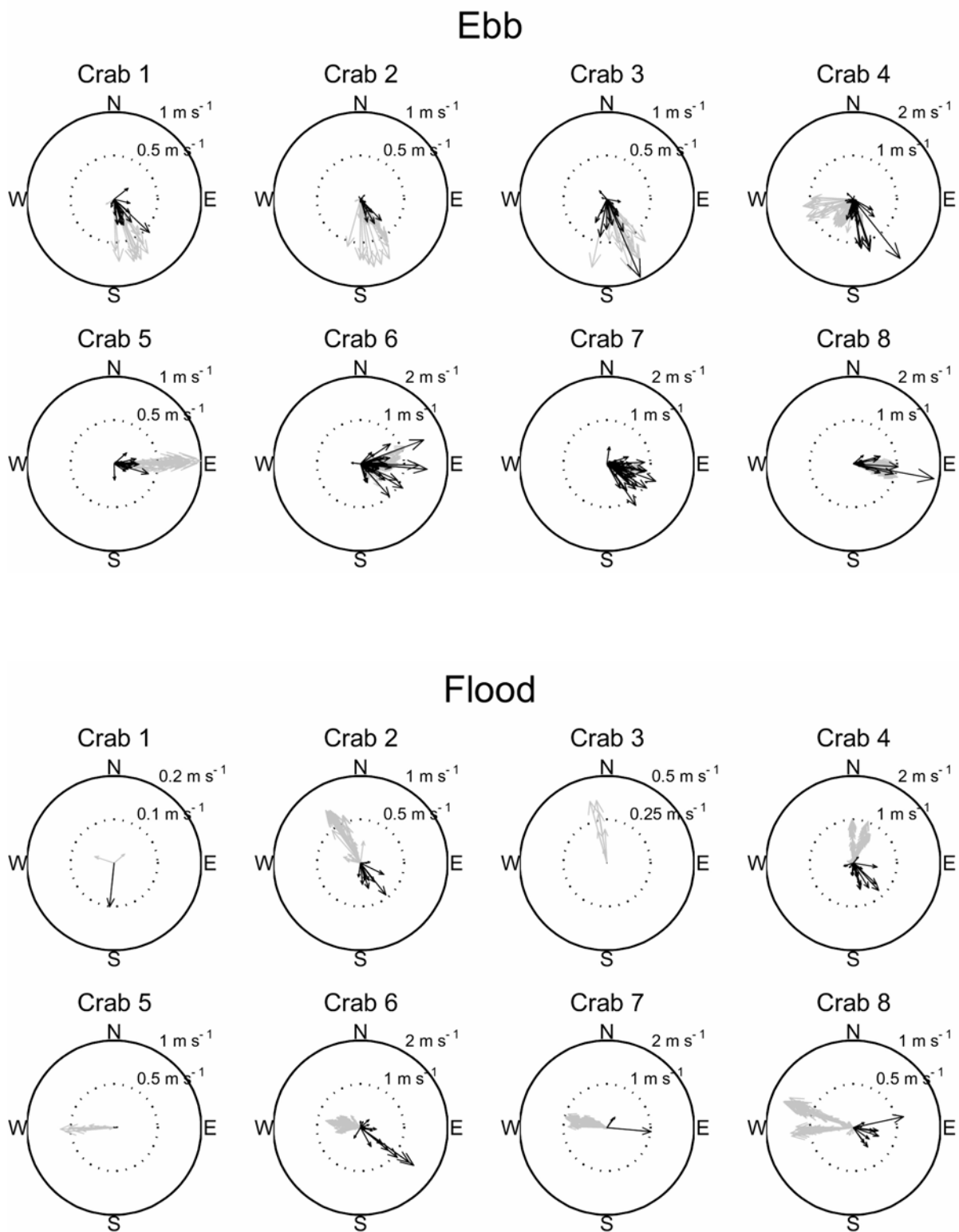


Fig. 2.4a. Crab vectors (black) and current vectors (gray) between fixes during ebb and flood tides.



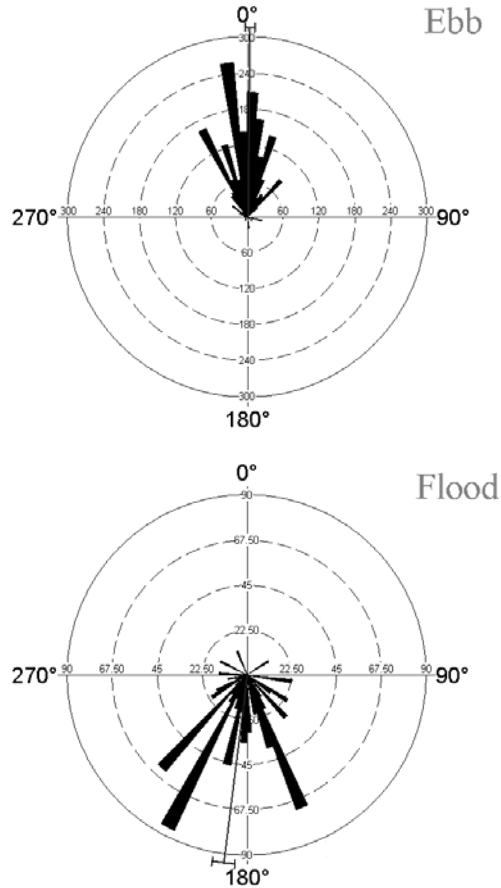


Fig. 2.4b. Histograms of angular difference between crab and current directions during ebb and flood tides. Mean angular differences ( $\pm 95\%$  CI) are indicated.

There were also distinct differences in crab speeds relative to local current speeds during ebb and flood tides. During some ebb tides, the temporal resolution of tracking was sufficient to show crabs moving at approximately the same speeds as local currents, indicating passive transport. Close correspondence between crab and current speeds was seen during the second night ebb of the track of Crab 4 and both night and day ebb tides of the tracks of Crabs 6 and 8 (Fig. 2.3). Movements against local currents during flood tides, on the other hand, were frequently on the order of  $0.25 \text{ m s}^{-1}$  regardless of current speed (Fig. 2.3). These movements suggested down-estuary walking or directed swimming by crabs during flood tides.

Crabs also tended to be more active during ebb tides than during flood tides and during the night than during the day. Figs. 2.5a-b show histograms of crab speed relative to current speed for different tidal-diel phases. To create these histograms, the crab speed at every fix was divided by current speed at the fix. These percentages were weighted by the amounts of time represented by the fixes so that every minute of tracking was represented by a single data point. Percentages were then grouped by value and tidal-diel phase. Since some of the calculated crab speeds are mean speeds between fixes and not necessarily instantaneous speeds, the figures provide lower bounds for the percentage of time that a crab was stationary and for the crab speeds as percentages of current speeds. As a whole, crabs were more active during night ebb tides (~ 50 % of the time) (Fig. 2.5b) than during flood tides or day ebb tides (< 20 % of the time) (Fig. 2.5b), but activity levels among individual crabs varied widely (Fig. 2.5a). Crabs 6 and 8 were equally or more active during day ebb tides than night ebb tides, and Crabs 2, 4, 6 and 8 were frequently active during flood tides.

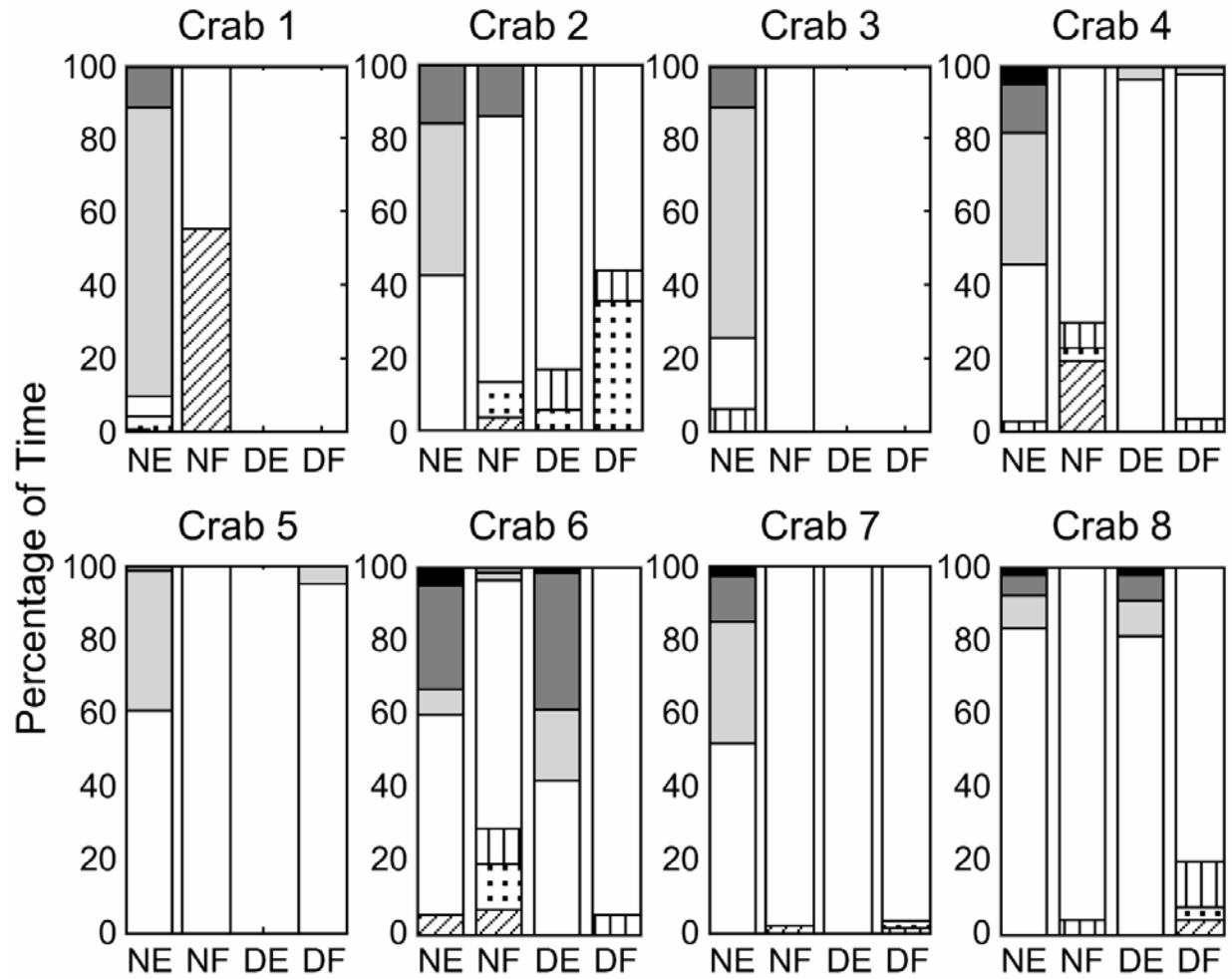


Fig. 2.5a. Relationship between crab speed and local current speed during night ebb (NE), night flood (NF), day ebb (DE) and day flood (DF) periods.

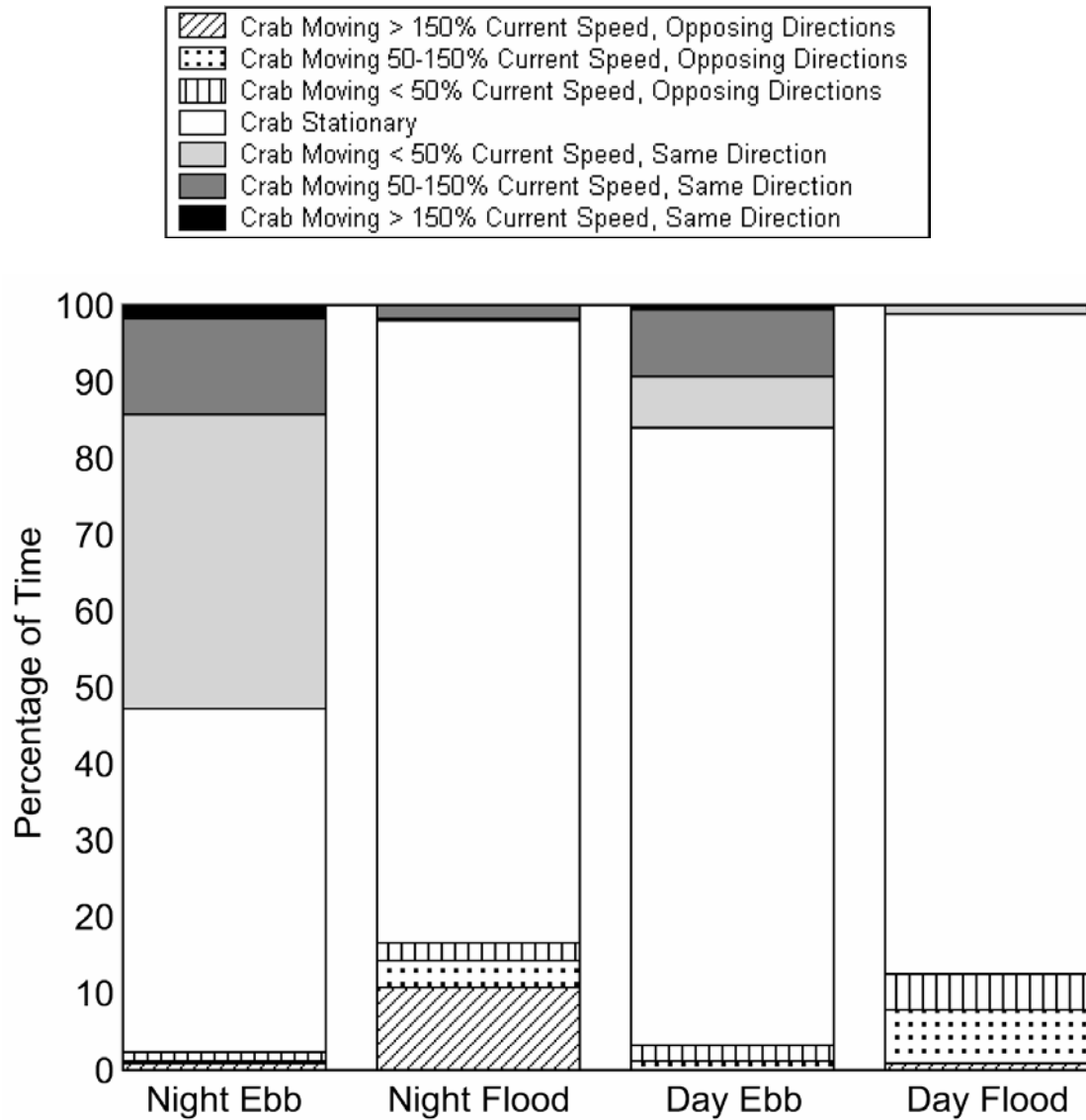


Fig. 2.5b. Relationship between crab speed and local current speed during night ebb, night flood, day ebb and day flood periods (data from all crabs combined).

Crab activity was related to current speed as well as tidal-diel phase. Crabs were more active when ebb-tide current speeds were high than when ebb-tide current speeds were low or during flood tides (Fig. 2.6). Tracking periods were divided into  $0.25 \text{ m s}^{-1}$  velocity bins ( $-1.00 - 1.00 \text{ m s}^{-1}$ ), and the percentages of time that crabs were active when the local current velocity corresponded to each bin were calculated. On average, crabs were active from 45 –

75 % of the time when local currents were ebbing with speeds  $> 0.25 \text{ m s}^{-1}$  and  $< 15 \%$  of the time when currents were flooding  $> 0.25 \text{ m s}^{-1}$ .

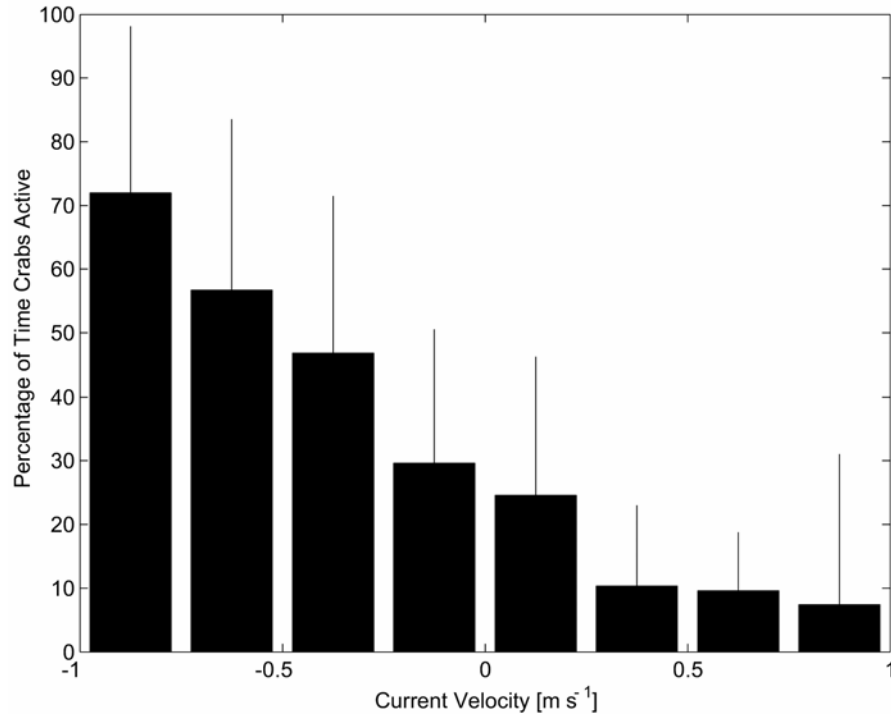


Fig. 2.6. Mean ( $\pm 95 \%$  CI) percentage of time that crabs were active as a function of local current velocity. Positive current velocities are flood tides, and negative current velocities are ebb tides.

### 2.3.3 Horizontal transport

Mean crab speeds were significantly different during the four tidal-diel phases (ANOVA,  $F_{3,24} = 4.49$ ,  $P < 0.05$ ) (Fig. 2.7). The speeds of individual crabs during tidal-diel phases were calculated by dividing the total distance that each crab traveled during a tidal-diel phase by the total time the crab was tracked during that tidal-diel phase. Mean crab speeds ( $\pm 95 \%$  CI) during night ebb, night flood, day ebb and day flood tides were  $0.11 \text{ m s}^{-1} \pm 0.04 \text{ m s}^{-1}$  ( $n = 8$ ),  $0.04 \text{ m s}^{-1} \pm 0.03 \text{ m s}^{-1}$  ( $n = 8$ ),  $0.08 \text{ m s}^{-1} \pm 0.08 \text{ m s}^{-1}$  ( $n = 6$ ) and  $0.02 \text{ m s}^{-1} \pm 0.02 \text{ m s}^{-1}$  ( $n = 6$ ) respectively (Fig. 2.7). Mean crab speed during night ebb tides was significantly

higher than mean crab speeds during night flood tides (Fisher's PLSD,  $P < 0.01$ ) and day flood tides (Fisher's PLSD,  $P < 0.01$ ). There were no significant differences (Fisher's PLSD,  $P > 0.05$ ) between night and day ebb tides or between day ebb tides and night and day flood tides. The high variability in mean speed during day ebb tides was due to relatively high activity levels in some crabs (Crabs 6 and 8) and relatively low activity levels in others (Crabs 4 and 7). When individual crabs were active during the day, their day activity levels were comparable to their night activity levels.

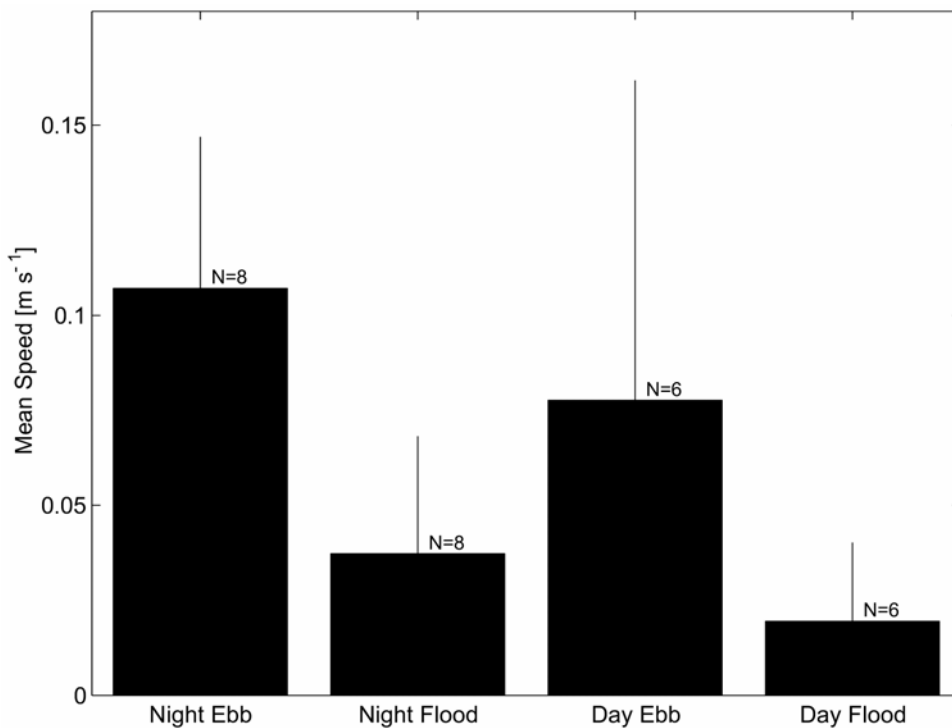


Fig. 2.7. Mean ( $\pm$  95 % CI) crab speed during night ebb, night flood, day ebb and day flood tides.

The crabs' net migratory speeds varied from 3.2 – 13.5 km day<sup>-1</sup> with a mean of 6.5 km day<sup>-1</sup>, but these results were highly dependent on the proportion of tracking time in different tidal-diel phases. For example, Crabs 1 and 3 were tracked primarily during night ebb tides

and had the fastest net migratory speeds (13.5 and 10.3 km day<sup>-1</sup> respectively). The net migratory speeds of crabs tracked for > 24 h ranged from 3.8 – 8.3 km day<sup>-1</sup> with a mean of 5.4 km day<sup>-1</sup>. This corresponds extremely well to a net migratory speed estimate of 5.4 km day<sup>-1</sup> derived from averaging the mean migratory speeds for the four tidal-diel phases (Fig. 2.7).

During ebb tides, crabs traveled 10 - 40 % of the down-estuary distances that passive particles would have traveled (Fig. 2.8). Passive transport distances during ebb tides were calculated by multiplying the local current speeds at each fix by the times that the fixes represented and summing the results. Differences in total transport distances during ebb tides were due primarily to the relatively long periods of time that crabs were stationary during tracking. Migration during flood tides was an important contributor (> 20 %) to the total distance traveled by Crabs 2, 4, 6 and 8 but was not for Crabs 5 and 7. (Crabs 1 and 3 were not tracked long enough during flood tides to be considered.)

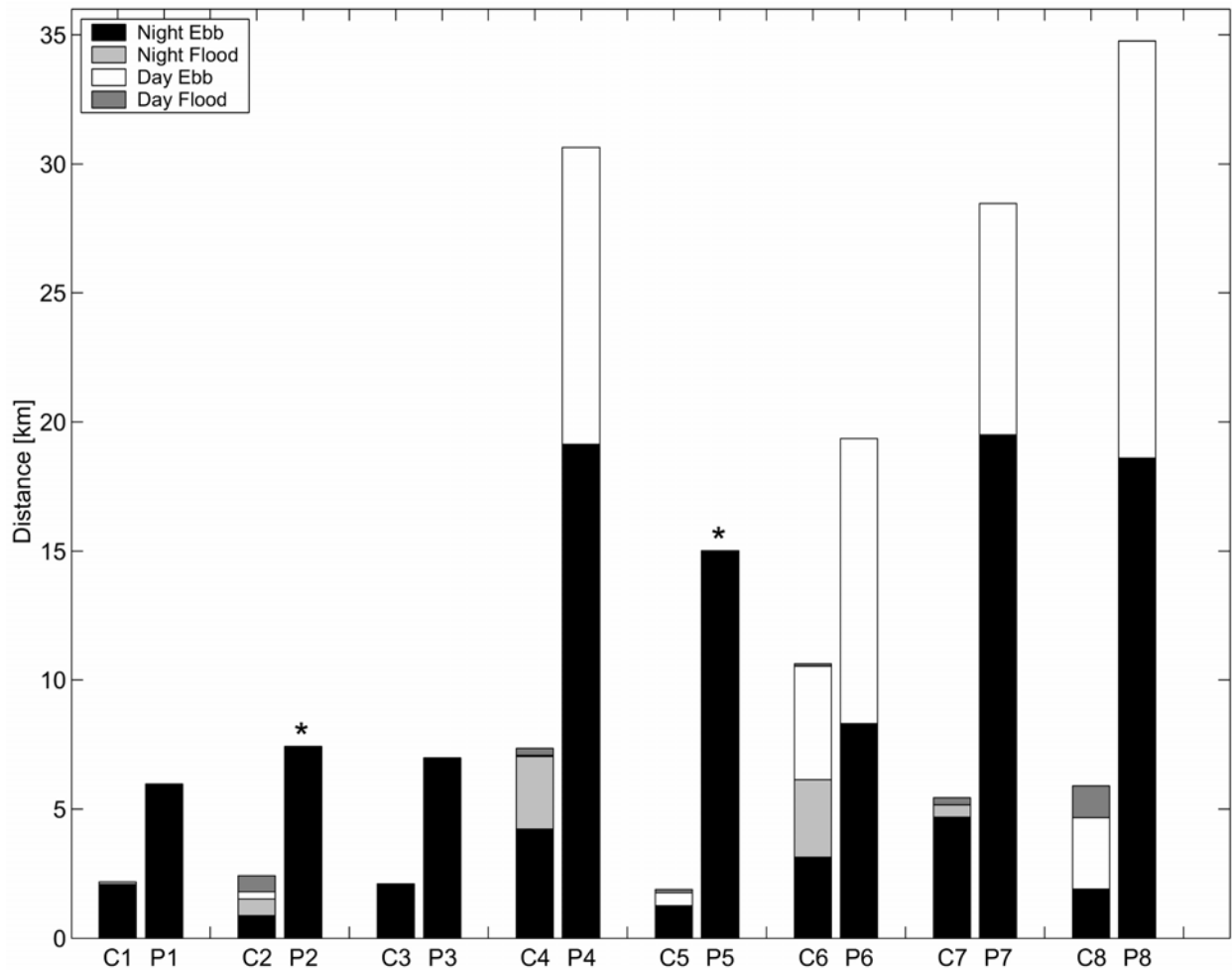


Fig. 2.8. Comparison of distances traveled down-estuary by crabs (C1 - C8) and the down-estuary travel distances predicted for passive particles (P1 - P8). The predicted distances for day ebb tides for Crabs 2 and 5 are not shown because shipboard ADCP data were not available for those periods. Missing ADCP data is denoted by an asterisk (\*).

## 2.4 Discussion

Previous studies have shown that ovigerous blue crabs with mature embryos (< 4 days prior to larval release) use ebb-tide transport (ETT) to migrate seaward to larval release areas (Tankersley et al., 1998; Forward et al., 2003a). This ultrasonic tracking study was the first to examine this behavior in free-ranging crabs and to show the influence of ETT on the horizontal transport of crabs in an estuary. The results are consistent with ETT since crabs moved with the local currents during ebb tides and against them during flood tides and



frequently moved at speeds close to the local current speeds during ebb tides (Fig. 2.3). While some of the periods in which crab speeds were greater than or less than ebb-tide current speeds may represent active horizontal swimming or down-estuary walking respectively, we believe that crabs were passively transported during most of these periods and that there would be closer correspondence between crab and local current speeds during ebb tides if greater temporal resolution of crab location had been possible. It is also possible that passive transport in the lower (upper) water column may have resulted in crab speeds that were less (greater) than depth-averaged local current speeds. Currents in the lower water column are generally slower than depth-averaged currents because of bottom friction. It was not possible to test this hypothesis since the exact vertical position of crabs in the water column could not be determined.

This study provides details about several important aspects of the ovigerous blue crab spawning migration, including the discontinuity of movements by free-ranging migratory crabs in the field. Crab movements were highly episodic with periods of rapid movement, on the order of minutes to an hour, followed by periods when crabs were stationary, on the order of minutes to hours (Fig. 2.3). These movements correspond to the episodic “swimming bouts” observed by Forward et al. (2003a) in laboratory tank experiments and by Hench et al. (2004) in estuarine tethering experiments. They may be more sustained in free-ranging crabs, however, due to the lack of a possible tethering artifact and the presence of strong tidal currents and appropriate environmental cues in the field. High levels of turbulent kinetic energy have been shown to sustain swimming in blue crab megalopae during flood-tide transport (Forward et al., 2003b). The stationary periods between movements may be rest periods for the negatively-buoyant crabs and may provide a means for crabs to sense changes

in environmental conditions (e.g. hydrostatic pressure) that they are not able to sense in a Lagrangian reference frame. The lack of movement by crabs during large portions of the tracking periods resulted in migratory paths that were considerably shorter than ( $< 40\%$ ) the paths predicted for organisms with continuous ETT behaviors.

Although crabs did not move continuously during ebb tides, they moved more frequently when ebb-tide current speeds were high (Fig. 2.6) and transport would be most efficient. Crabs are negatively buoyant and must expend energy to remain in the water column. Therefore, vertical migrations into the water column when currents are strongest will result in faster horizontal transport and will most likely be more energetically efficient than vertical migrations at other times. Hensch et al. (2004) also observed increased ovigerous blue crab vertical migratory activity during times of maximum ebb currents. It is not certain whether the proximal cause of this behavior is environmental cues, such as turbulence or changes in hydrostatic pressure, or whether peaks in the endogenous circatidal activity rhythm (Forward et al., 2003a) correspond to the times of maximum ebb currents in the estuary.

Another important result from the tracking study was the down-estuary migration of crabs during flood tides. Other studies of the ovigerous blue crab spawning migration, involving observation from a fixed platform (Tankersley et al., 1998), activity in laboratory tanks (Forward et al., 2003a) and tethering crabs (Hensch et al., 2004), have been stationary in nature and have not provided data on horizontal migratory behaviors such as walking or swimming against local currents during flood tides. The down-estuary/offshore movements during flood tides in the field cannot be attributed to passive horizontal transport via vertical migration and must involve active horizontal swimming or walking. While all the crabs, except Crab 2, moved farther during ebb tides than during flood tides, down-estuary walking

or swimming during flood tides was an important contributor to the total seaward migration (> 20 %) of half of the crabs during the tracking periods. This behavior may be especially important to migrating crabs when they are in the upper reaches of the estuary where currents are relatively weak. In these areas, vertical migrations into the water column during ebb tides will be relatively inefficient at transporting crabs to suitable larval release areas, but regular seaward movements during flood tides will enable crabs to move to more tidally-energetic regions where rapid ETT is possible.

The close alignment between crab movements during flood tides and the down-estuary/offshore direction (Fig. 2.4b) suggests that ovigerous female blue crabs are able to actively orient down-estuary/offshore. Blue crabs are known to use sun-compass orientation to orient offshore in the intertidal zone (Nishimoto and Hernkind, 1982) and positive rheotaxis for foraging (Weissburg and Zimmer-Faust, 1994), but it is not clear which, if either, of these orientation abilities is involved in down-estuary/offshore movements during flood tides. This observation warrants further investigation.

Another important observation from the tracking study is the high variability in crab behavior during the day. Of the four crabs tracked through a complete 24 hour-period, two were extremely active during the day, while the other two remained relatively stationary during the day. Water depth is a major influence on light penetration in the water column, but there was no apparent relationship between crab activity and water depth during the tracking periods (results not shown). Hench et al. (2004) found that crabs tethered simultaneously in the same environmental conditions often had very different activity levels during day ebb tides. Since all crabs presumably have a circatidal rhythm in vertical migratory activity (Forward et al., 2003a), these results suggest light suppresses vertical

migratory activity under field conditions (Tankersley et al., 1998) but thresholds for suppression vary among individuals.

The speeds that ovigerous crabs travel down-estuary and offshore using ETT will be important determinants of where larval release occurs and whether larvae will be successful at exiting the estuary and reaching suitable offshore development areas. Migratory speeds in the estuary will depend on starting location and the current regime in the estuary, the relationship of the tidal and diel cycles during the migratory period, and other factors, such as the phase of the spring-neap cycle. The mean speeds presented here (Fig. 2.7) are representative of migratory speeds in the lower estuary where currents are relatively strong (maximum speeds of  $\sim 1 \text{ m s}^{-1}$ ) and demonstrate that crabs can migrate rapidly (on the order of  $5 \text{ km day}^{-1}$ ) using ETT. While these transport rates are probably greater than transport rates in the upper estuary where currents are slower, they suggest that the ETT behavior observed in this study will allow crabs from most of the estuarine system north of Beaufort Inlet to reach the lower estuary within  $\sim 4$  days. Currently, very little is known about the exact locations of larval release in the Beaufort Inlet region.

This tracking study provides the first estimates of migratory speeds for ovigerous blue crabs, information that is crucial for the effective management of blue crab spawning stock. The results of this study will also be used to verify a coupled biological-physical model of the migration that can then be used to conduct further investigations of migratory pathways and speeds in the estuary and likely larval release locations. This study poses several questions which require further investigation, including the determination of which, if any, environmental cues help to control the ETT behavior, crab mechanisms for navigating during

the spawning migration, and the variability of crab behavior during the spawning migration among different estuaries with different physical environments.

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### **Chapter 3. Spatial patterns in the ovigerous blue crab *Callinectes sapidus* ebb-tide transport spawning migration**

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#### **Abstract**

Ovigerous blue crabs *Callinectes sapidus* use ebb-tide transport (ETT), a vertical migratory behavior in which crabs ascend into the water column during ebb tides, to migrate from estuarine adult habitats to coastal larval release locations. In this study, we develop a detailed behavioral model of ovigerous blue crab ETT from previous laboratory and field studies and couple this model to a hydrodynamic model of the Beaufort Inlet region of North Carolina. We simulate the trajectories of migratory ovigerous crabs in the region and determine spatial patterns in migratory success, migratory speeds, the residence times of crabs in different regions of the estuary, and potential larval release locations.

Highly active crabs can start their migration from almost anywhere in the estuary and reach suitable larval release locations within a typical 4-day migratory period, whereas crabs with lower activity levels can only reach suitable larval release locations if they start their migration in the lower-mid estuary. Migratory speeds in the estuary range from  $< 1$  to  $> 8$  km day<sup>-1</sup>. Crabs with lower activity levels are resident in the mid-upper estuary for relatively long periods of time, whereas highly active crabs are resident in the lower estuary and coastal ocean for most of the migratory period. Larval release is predicted to occur throughout the

estuary and in the coastal ocean within ~ 5 km of Beaufort Inlet. Fisheries managers can use these spatial patterns to determine management strategies (e.g. spatial closures to fishing) that will protect migratory blue crab spawning stock in tidal regions effectively.

### 3.1 Introduction

Many estuarine and marine species, such as the blue crab *Callinectes sapidus*, make long-distance migrations between habitats and regions. For many of these species, even ones as heavily-exploited and well-studied as the blue crab, spatial and temporal migratory patterns are not well understood (Giske et al., 2001; Pelletier, 2001; Miller, 2003). Historically, the primary sources of information on migratory patterns have been mark-and-recapture studies and observations of spatial and temporal changes in abundance by fishermen and scientists (Millikin and Williams, 1984; Pelletier, 2001). These studies have been unable to address many questions about modes of migration, migratory speeds, residence times in different regions, and the influence of hydrographic processes on migratory success. With the recent development of miniaturized ultrasonic transmitters (Wolcott, 1995; Freire and González-Gurriarán, 1998), gathering high-resolution data on migratory trajectories is possible. It is still prohibitively costly and time-intensive to track large numbers of individuals for long periods of time, however. One way to expand the knowledge gained from limited field sampling is to couple the observed migratory patterns of organisms that utilize water currents to migrate with hydrodynamic models. With these coupled behavioral-physical models, the transport of organisms can be simulated from a wide variety of locations under a variety of hydrographic conditions (e.g. Rothlisberg et al., 1983; Werner et al., 1993; Hare et al., 1999; reviewed in Giske et al., 2001; and Werner et al., 2001). The spatial and temporal migratory

patterns derived from these modeling studies can be used to determine effective means of managing exploited migratory stocks.

In this study, we use a coupled behavioral-physical model to examine spatial patterns in the ovigerous blue crab spawning migration in the shallow, tidally-driven estuarine system behind Beaufort Inlet, North Carolina (Fig. 3.1a). This system is typical of many estuary-inlet systems along the Atlantic and Gulf coasts of the United States and consists of four sub-estuaries, Bogue Sound, the Newport River Estuary, the North River Estuary, and Back Sound, connected to the coastal ocean by Beaufort Inlet (Fig. 3.1b). In these systems, adult blue crabs mate in the upper regions of the estuaries, and inseminated females migrate to the lower regions of the estuaries and coastal ocean to oviposit and release larvae (reviewed in Van Engel, 1958 and Millikin and Williams, 1984). In the final phase of this migration, ovigerous crabs with mature embryos use ebb-tide transport (ETT), a vertical migratory behavior in which organisms ascend into the water column during ebb tides and remain at or near the bottom during flood tides, to migrate seaward (Tankersley et al., 1998; Forward et al., 2003; Carr et al., 2004; Hensch et al., 2004). This behavior may decrease the energetic costs of migration in areas with strong tidal currents (Weihs, 1978; Metcalfe et al., 1990) and provide a means of orienting towards coastal areas suitable for larval release (Forward and Tankersley, 2001). Females release larvae during morning ebb tides, and larvae are transported offshore in near-surface waters (Provenzano, 1983; Epifanio et al., 1984). Offshore larval development is advantageous because it reduces exposure to predators (Morgan, 1990) and harmful low-salinity conditions (Sandoz and Rogers, 1944; Costlow and Bookout, 1959). Female blue crabs are capable of producing multiple egg clutches from stored sperm, and they may continue to use ETT to migrate seaward (Hensch et al., 2004) or

return to estuarine areas after releasing a clutch of larvae (Tagatz, 1968; Tankersley et al., 1998). Our model improves on previous hydrodynamic modeling studies of circatidal vertical migratory behaviors (e.g. Arnold and Cook, 1984; Rothlisberg et al., 1996; Condie et al., 1999; DiBacco et al., 2001) by basing migratory behavior on high-resolution empirical data rather than relatively idealized behaviors.

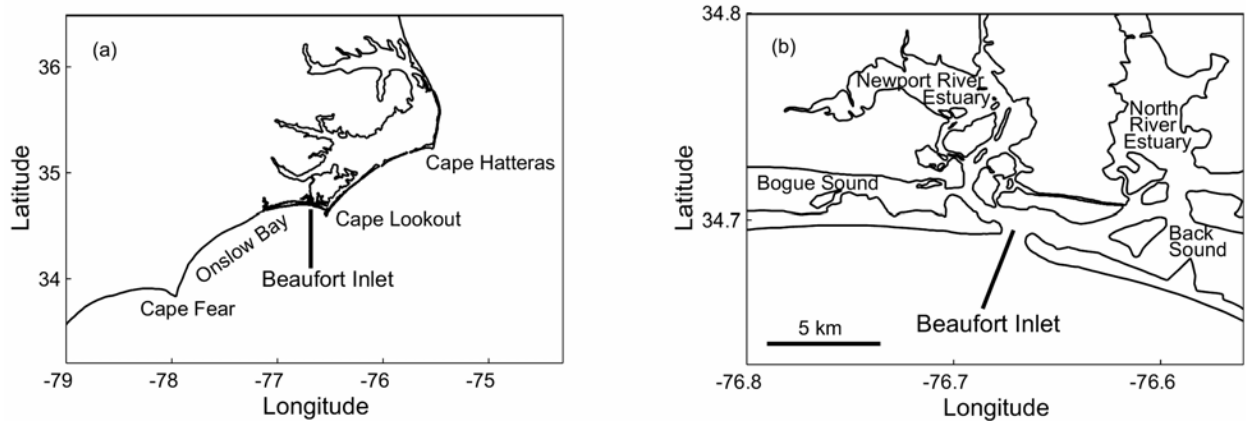


Fig. 3.1. Study location: (a) South Atlantic Bight and (b) Beaufort Inlet region of North Carolina.

## 3.2 Materials and methods

### 3.2.1 Behavioral model

Ovigerous blue crabs migrate seaward by episodically ascending into the water column during ebb tides for passive transport down-estuary (Tankersley et al., 1998; Forward et al., 2003; Carr et al., 2004; Hench et al., 2004) and episodically walking or swimming against local currents (down-estuary) at  $\sim 0.25 \text{ m s}^{-1}$  during flood tides (Carr et al., 2004). Ebb-tide vertical ascents and flood-tide walking/swimming episodes are on the order of minutes (Forward et al., 2003; Carr et al., 2004), and periods in between migratory episodes range from minutes to hours (Forward et al., 2003; Carr et al., 2004; Hench et al., 2004). Since

crab movements are episodic, crabs travel less than half the distances that passive particles would travel during ebb tides (Carr et al., 2004).

Ovigerous blue crab ETT is based on an endogenous circatidal activity rhythm (Forward et al., 2003). Migratory episodes are most frequent during mid-ebb when current speeds are highest (Carr et al., 2004; Hensch et al., 2004) and more frequent during the night than during the day (Tankersley et al., 1998; Carr et al., 2004; Hensch et al., 2004). Migratory behavior and the duration of migratory activity vary widely among individual crabs (Forward et al., 2003; Carr et al., 2004; Hensch et al., 2004) but are highest during the  $\sim 4$  days prior to larval release (Forward et al., 2003; Hensch et al., 2004). Larval release occurs near the beginning of morning ebb tides (Provenzano, 1983; Epifanio et al., 1984; Ziegler, 2002), and there are fortnightly peaks in the number of crabs migrating that correspond to times when slack before ebb (SBE) occurs around sunrise (RA Tankersley, Pers. obs.).

### 3.2.2 Hydrodynamic model

The depth-integrated version of the numerical hydrodynamic model ADCIRC (Luettich et al., 1992) was used to compute tidal velocity fields for the region near Beaufort Inlet, North Carolina. ADCIRC uses a finite element method to solve the fully nonlinear equations of motion on domains discretized into linear triangular elements of varying sizes. This method of discretization permits increased resolution in regions with complex bathymetry, such as Beaufort Inlet. Circulation in the estuarine system is dominated by the M2 semi-diurnal tide (Klavans, 1983) and can be described with a depth-integrated model because strong tidal currents effectively mix the water column and depths within the system are typically less than Ekman depths for the region (Klavans, 1983; Luettich et al., 1999). Wind

forcing is episodically important, and wind-driven currents from routine wind events are on the order of  $0.1 \text{ m s}^{-1}$  in the sub-estuaries (Logan, 1995). These flows are generally of secondary importance to tidal circulation in most of the estuary and were not included in the present model.

A complete description of the model setup is provided in Hench and Luetlich (2003). The model domain encompassed the estuarine system behind Beaufort Inlet, eastern Onslow Bay and the offshore region east of Cape Lookout Bight (Fig. 3.1). Element dimensions ranged from  $< 25 \text{ m}$  in the estuary and coastal ocean near Beaufort Inlet to  $> 2 \text{ km}$  offshore (Fig. 3.2a). Model bathymetry was derived from high-resolution surveys by the National Oceanic and Atmospheric Administration and the University of North Carolina at Chapel Hill (Hench and Luetlich, 2003). The estuary is generally shallow,  $< 3 \text{ m}$ , except for a few narrow navigable channels of  $\sim 5 - 15 \text{ m}$  depth (Fig. 3.2b). For runs with mean tidal conditions, the model was forced at its open boundaries with elevations of the M2, M4, and M6 tidal constituents and a steady residual component derived from the larger domain described in Luetlich et al. (1999). When spring and neap tide conditions were simulated, the S2 tidal constituent, whose velocity amplitude is  $\sim 17 \%$  of the M2 velocity amplitude (Klavans, 1983), was added. Maximum current speeds are  $\sim 1 \text{ m s}^{-1}$  in the lower estuary and decrease with distance up the estuary due to damping by bottom friction and widening of the sub-estuaries (Fig. 3.2c). Both model velocity amplitude and phase corresponded well to previous observational data gathered for the region (Klavans et al., 1983; Luetlich et al., 1999).

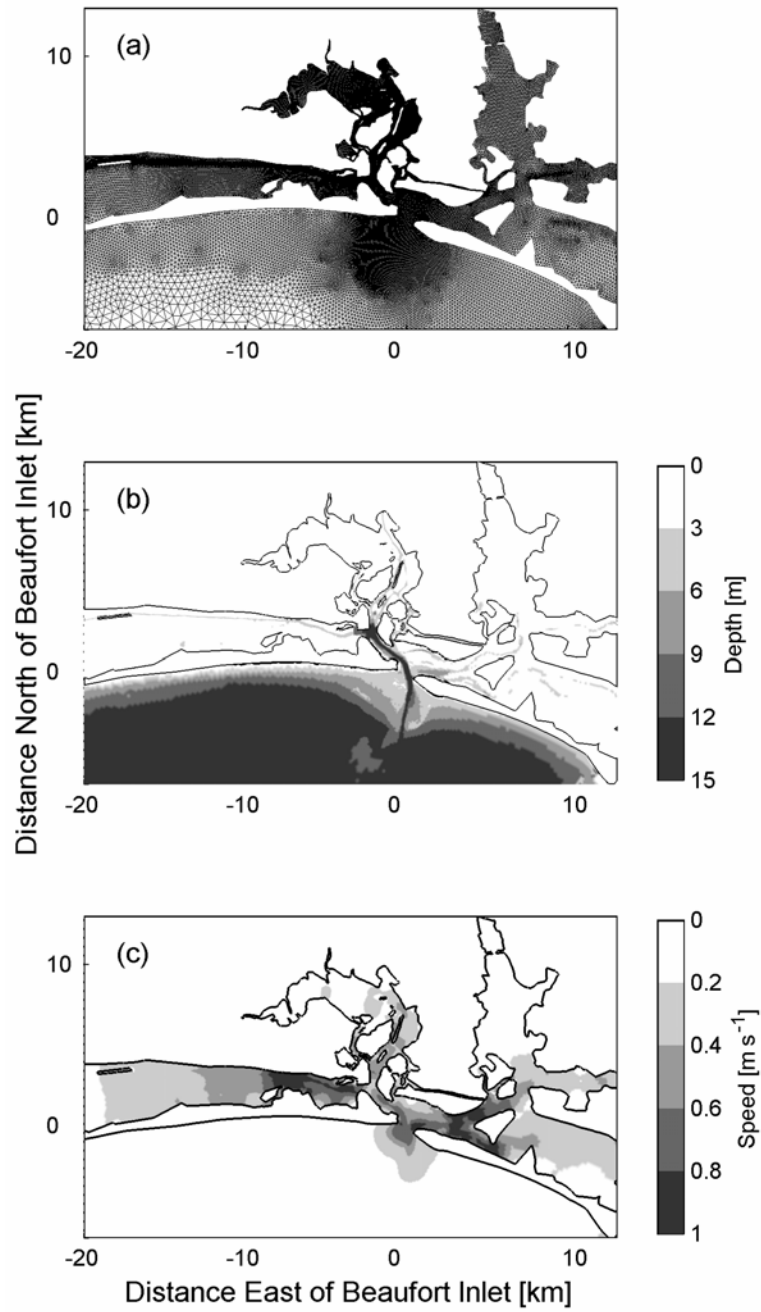


Fig. 3.2. Hydrodynamic model: (a) grid, (b) bathymetry, and (c) maximum ebb current speeds for the Beaufort Inlet region.

### 3.2.3 Coupling of behavioral and hydrodynamic models

The behavioral model was coupled to the hydrodynamic model by incorporating algorithms of the migratory behavior of ovigerous blue crabs into a particle-tracking

algorithm (DROG2D; Baptista et al., 1984; Foreman et al., 1992) driven by velocity fields from the hydrodynamic model. If simulated crabs encountered a land boundary, they were tracked along the boundary using the velocity component parallel to the boundary until ambient velocities transported them away from the boundary. Simulated crabs were tracked using a 2-min time step.

The behavioral algorithms consisted of migratory episodes of fixed duration whose characteristics and frequency were functions of tidal (time relative to SBE) and diel (night:day) phase. When actively migrating during ebb tides, simulated crabs were transported by model currents as passive Lagrangian particles (Tankersley et al., 1998; Carr et al., 2004). When actively migrating during flood tides, simulated crabs were tracked directly against local currents (down-estuary) at a constant speed of  $0.25 \text{ m s}^{-1}$  (Carr et al., 2004). Simulated crabs were stationary when they were not actively migrating (Carr et al., 2004).

Individual migratory episodes lasted 6 min, the median duration of observed migratory episodes (Forward et al., 2003; Carr et al., 2004). To capture the variability in the frequency of migratory episodes over the course of the tidal and diel cycles, the tidal cycle was broken up into half hour bins relative to SBE (e.g. 0.5 – 1.0 h after SBE), and the diel cycle was broken up into night (10 h) and day (14 h) periods. The mean number and standard deviation (SD) of migratory episodes for each half hour bin for night and day periods were derived from a field study of the frequency of vertical ascents by ovigerous blue crabs tethered in Bogue Sound (Hench et al., 2004). To capture some of the variability in crab activity levels during the ovigerous spawning migration, two behavioral algorithms representative of lower and higher activity crabs were created from the mean and the mean + 2 SD of migratory



episodes for each half hour bin (Fig. 3.3). These algorithms were not intended to represent the extremes of crab behavior but rather to show differences in spatial patterns arising from typical variability in crab behavior. Simulated crabs remained stationary for 2 min in between consecutive migratory episodes and after they had completed the designated number of migratory episodes in each half hour bin.

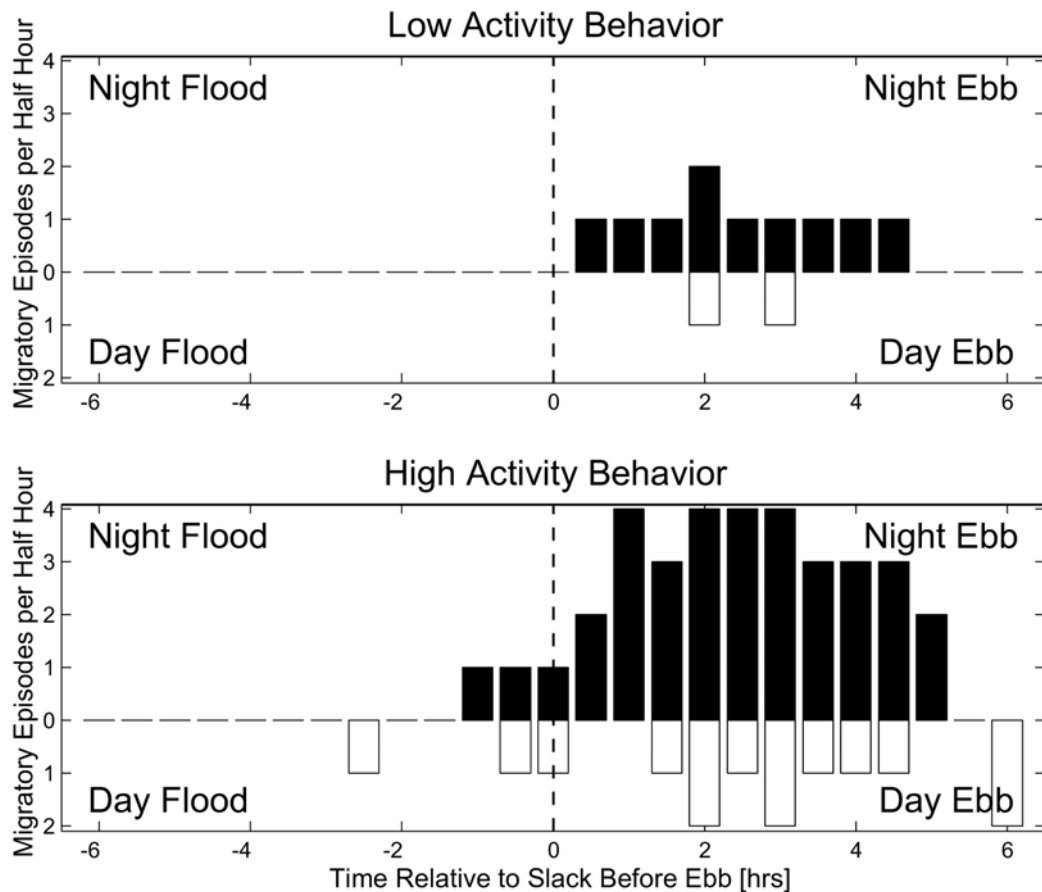


Fig. 3.3. Number of migratory episodes per half hour bin relative to slack before ebb (SBE) for the two behavioral algorithms. Numbers were derived from Hench et al. (2004) and were rounded to the nearest whole number for use in the behavioral algorithms. The mean + 2 SD of migratory episodes from 2 – 3 h after SBE from Hench et al. (2004) was 5, but the use of 6 min migratory episodes with 2 min inactive periods in between limited the maximum number of ascents per half hour in the model to 4.

### 3.2.4 Model simulations

For general model simulations, crabs started from a grid (uniform 500-m spacing) of 579 locations in the estuary (Fig. 3.4) at sunrise and were tracked for 4 days, the approximate duration of ovigerous blue crab ETT (Forward et al., 2003; Hensch et al., 2004). Unless otherwise noted, simulations were run for migratory periods when SBE occurred around sunrise on the last day of migration and with mean tidal conditions (no S2 tidal constituent). Larval release locations were defined as crab locations at the end of the 4-day migratory period.

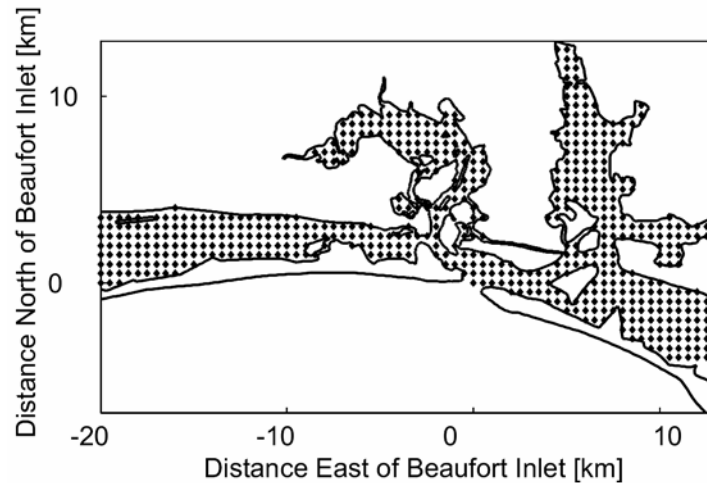


Fig. 3.4. Starting locations of simulated ovigerous blue crabs and blue crab larvae.

*Comparison of observed and simulated crab trajectories-* To evaluate model performance, we compared simulated crab trajectories and mean migratory speeds ( $\pm 95\%$  CI) to the results of a tracking study of ovigerous blue crabs conducted in the Beaufort Inlet region during the 2001 and 2002 spawning seasons (Carr et al., 2004). In that study, eight ovigerous blue crabs were tracked by ultrasonic telemetry for durations and distances ranging from 4 – 37 h and 2 – 11 km. For the comparisons, simulated crabs were tracked from the same eight starting points, started at the same phase in the tidal and diel cycles, and tracked for the same

duration as observed crabs. Paired t-tests ( $\alpha = 0.05$ ) were conducted on overall crab speeds (the total distance each crab traveled divided by the total tracking duration for that crab) and crab speeds during the four tidal-diel phases (the distance each crab traveled during a tidal-diel phase divided by the tracking time in that tidal-diel phase for that crab) using the MATLAB Statistics Toolbox (The MathWorks Inc., v. 3).

*Error estimations-* To get a first order estimate of how much of the difference between the observed and simulated crab trajectories could be attributed to errors in the hydrodynamic model, we compared current velocity measurements made at locations along the observed crab trajectories near Beaufort Inlet (Carr et al., 2004) to hydrodynamic model output at the same times and locations. The eight migratory ovigerous crabs from Carr et al. (2004) were tracked for a total of 171 h, and 948 current velocity measurements were made at 1 – 20 min intervals during this time (Carr et al., 2004). Measurements were made with a boom-mounted acoustic Doppler current profiler (RD Instruments Workhorse Monitor ADCP, 1200 kHz, 0.5 m bins, 1.34 s sample interval; Carr et al., 2004). ADCP current velocities were depth averaged for comparison with the depth-averaged hydrodynamic model output.

*Initial larval transport-* To determine where migratory ovigerous blue crabs need to release larvae to promote rapid offshore transport, we simulated the trajectories of passive Lagrangian particles from starting locations throughout the estuary (Fig. 3.4) at 1 hr after SBE, the approximate time of larval release (Provenzano, 1983; Epifanio et al., 1984; Ziegler, 2002; Hench et al., 2004). If simulated larvae reached the coastal ocean during the

first ebb tide following release, the release location was considered a suitable larval release location.

*Sensitivity of migratory success to the tidal-diel and spring-neap cycles-* A particular tidal phase (e.g. SBE) occurs around sunrise every  $\sim 15$  d (assuming a semi-diurnal tide), and we refer to this cycle as the tidal-diel cycle. To test the sensitivity of migratory success to phase in the tidal-diel cycle, simulations were started at four different times, when SBE, mid-ebb, slack before flood (SBF), and mid-flood at the center of Beaufort Inlet occurred around sunrise on the last day of migration. Phase of the tidal-diel cycle affected the relative proportions of migratory periods that occurred during night ebb, night flood, day ebb, and day flood. When SBE, mid-ebb, SBF, and mid-flood occurred around sunrise on the last day of migration, the percentages of time that were night ebb in the 4-day migratory periods were 16, 18, 26, and 23 %, respectively. To determine the sensitivity of migratory success to the spring-neap cycle, the S2 semi-diurnal tidal constituent was added to the model. Model simulations were conducted for 4-day periods when the M2 and S2 current velocities were approximately in phase (spring tides) and out of phase (neap tides).

### 3.3 Results

#### 3.3.1 Comparison of observed and simulated crab trajectories

The trajectories of the simulated crabs matched the trajectories of the ovigerous crabs observed during the 2001 - 2002 ultrasonic telemetry tracking study closely in terms of migratory routes and total distances traveled (Fig. 3.5). The trajectories of simulated crabs with the low activity behavior matched the observed trajectories of Crabs 2, 5, 7, and 8 best

and were - 50, + 34, - 13, and - 8 % of the distances traveled by the corresponding observed crabs (Fig. 3.5). The trajectories of simulated crabs with the high activity behavior matched the observed trajectories of Crabs 1, 3, 4, and 6 best and were + 11, - 36, - 29, and - 34 % of the distances traveled by the corresponding observed crabs (Fig. 3.5).

The mean overall migratory speed of the simulated crabs with the low activity behavior was significantly lower than the mean overall migratory speed of observed crabs (paired t-test,  $P = 0.04$ ), but there was no significant difference between the mean overall migratory speed of the simulated crabs with the high activity behavior and the mean overall migratory speed of observed crabs (paired t-test,  $P > 0.05$ ; Fig. 3.6). For comparison, the mean overall migratory speed of organisms with a continuous ETT behavior was also determined and was significantly higher than the mean overall migratory speed of observed crabs (paired t-test,  $P < 0.01$ ) and ~ 2 times as high (Fig. 3.6). When observed and simulated crab trajectories were broken down into night ebb, night flood, day ebb, and day flood periods, there were no significant differences between the mean migratory speeds of observed crabs and the mean migratory speeds of simulated crabs with either the low or high activity behaviors during these periods (paired t-tests,  $P > 0.05$ ; Fig. 3.6). The mean migratory speeds of organisms with a continuous ETT behavior were significantly higher than the mean migratory speeds of observed crabs during night and day ebb periods (paired t-tests,  $P < 0.01$ ) and were ~ 3 times as high (Fig. 3.6).

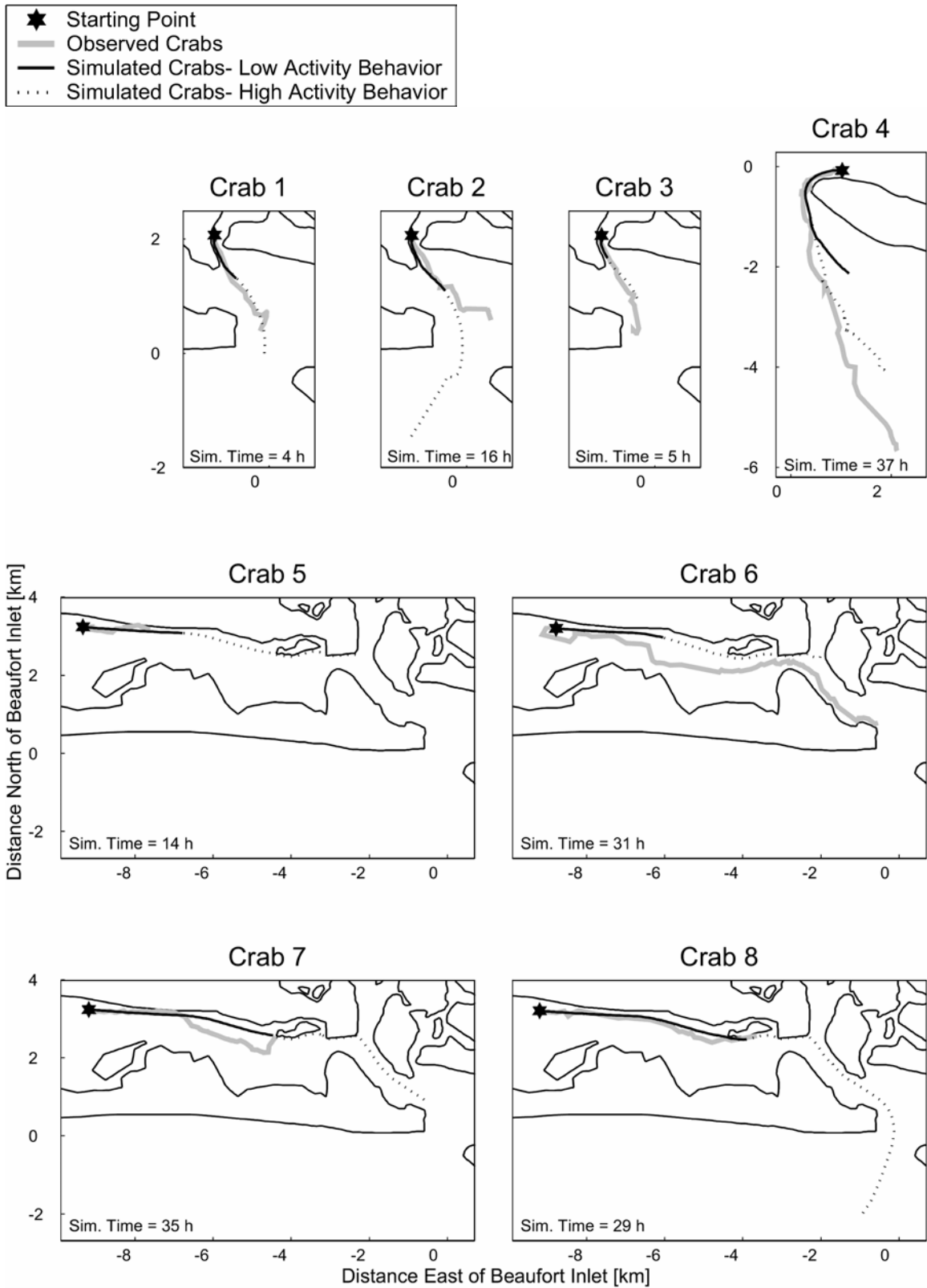


Fig. 3.5. Comparison of trajectories of observed migratory ovigerous blue crabs (from Carr et al., 2004) and simulated crabs with low and high activity behaviors.

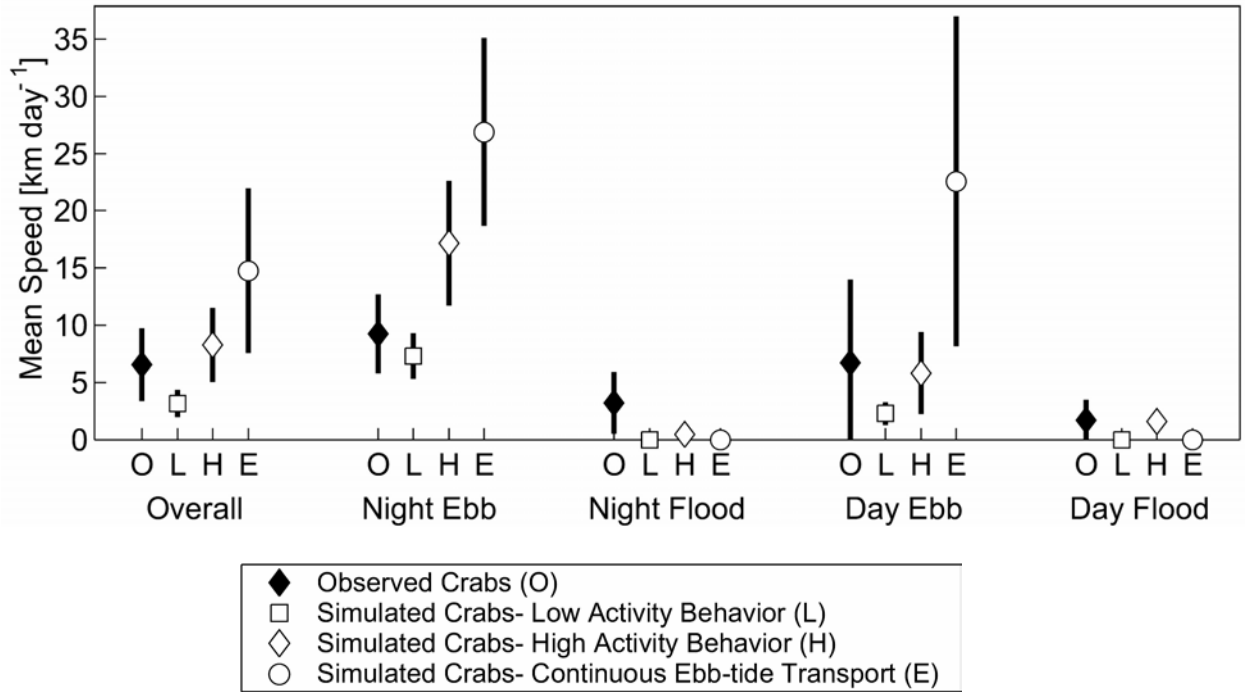


Fig. 3.6. Comparison of mean ( $\pm$  95 % CI) overall and night ebb, night flood, day ebb, and day flood speeds of observed migratory ovigerous blue crabs (from Carr et al., 2004) and simulated crabs with the low activity behavior, the high activity behavior, and a continuous ebb-tide transport behavior.

### 3.3.2 Error estimations

The modeled current speeds were within  $0.1 \text{ m s}^{-1}$  of the observed current speeds  $\sim 41 \%$  of the time and within  $0.2 \text{ m s}^{-1}$  of the observed current speeds  $\sim 69 \%$  of the time (Fig. 3.7). Errors in the hydrodynamic model were relatively evenly divided between overestimations and underestimations of observed currents speeds (Fig. 3.7). There were relatively few instances of the model predicting the wrong tidal phase (i.e. results falling in the upper left and lower right quadrants of Fig. 3.7). The mean difference between the absolute values of the observed and modeled current velocities was  $0.16 \text{ m s}^{-1}$ , and the mean difference between the raw values (allowing positive and negative values for underestimations and

overestimations respectively) of the observed and modeled current velocities was  $+0.01 \text{ m s}^{-1}$

1.

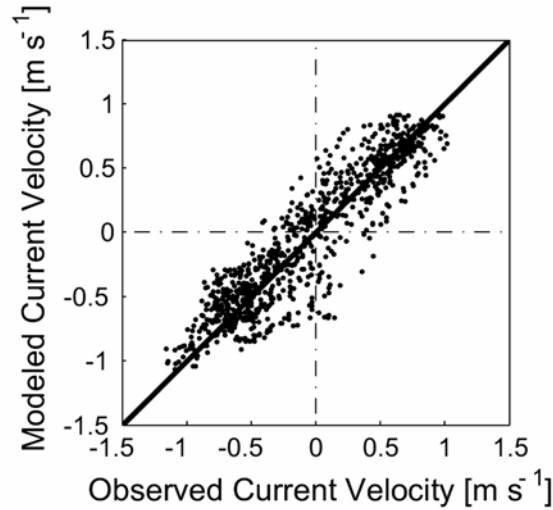


Fig. 3.7. Comparison of observed and modeled current velocities along the observed trajectories of migratory ovigerous blue crabs (from Carr et al., 2004). Ebb and flood current speeds are negative and positive respectively.

The simulated crabs with low and high activity behaviors were passively transported by hydrodynamic model currents for  $\sim 8$  and  $23 \%$  of the total simulation time respectively. Since the hydrodynamic model errors had an approximately zero mean, it is unlikely that they were a source of systematic error in the simulated crab trajectories. Nevertheless, we estimated a reasonable upper limit of possible hydrodynamic model error in the simulated crab trajectories by assuming an error of  $0.05 \text{ m s}^{-1}$  at all times that the crabs were passively transported. With this value, we calculated that hydrodynamic error could account for  $6 - 30 \%$  (mean of  $14 \%$ ) of the distances that the simulated crabs traveled and  $4 - 81 \%$  (mean of  $33 \%$ ) of the differences between the distances that observed and simulated crabs traveled (Fig. 3.5).



### 3.3.3 Suitable larval release locations

Simulated larvae that were released within ~ 8 km of Beaufort Inlet in Bogue and Back Sounds and ~ 5 km of Beaufort Inlet in the Newport River Estuary reached the coastal ocean during the first ebb tide following release (Fig. 3.8).

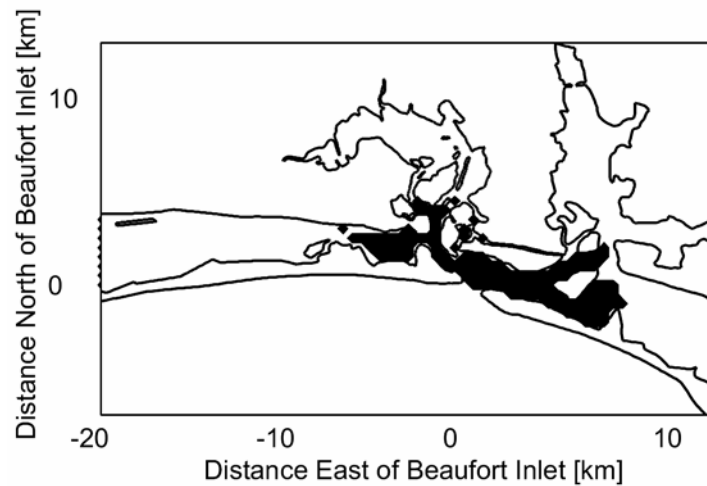


Fig. 3.8. Starting locations of blue crab larvae that reached the coastal ocean during the first ebb tide following release (suitable larval release locations).

### 3.3.4 Migratory success

With the low activity behavior, only simulated crabs within ~ 12 km of Beaufort Inlet reached suitable larval release locations (locations from which larvae will reach the coastal ocean during the first ebb tide following release; Fig. 3.8) during the 4-day migratory period (Fig. 3.9a). With the high activity behavior, crabs from starting locations throughout the estuary, with the exception of the uppermost Newport and North River estuaries, reached suitable larval release locations within the 4-day migratory period (Fig. 3.9b). For both behaviors, crabs that started their migration close to Beaufort Inlet generally reached suitable larval release locations sooner than those that started farther up the estuary (Fig. 3.9).

Approximately twice as many high activity crabs as low activity crabs reached suitable larval release locations within the 4-day migratory period (Fig. 3.9).

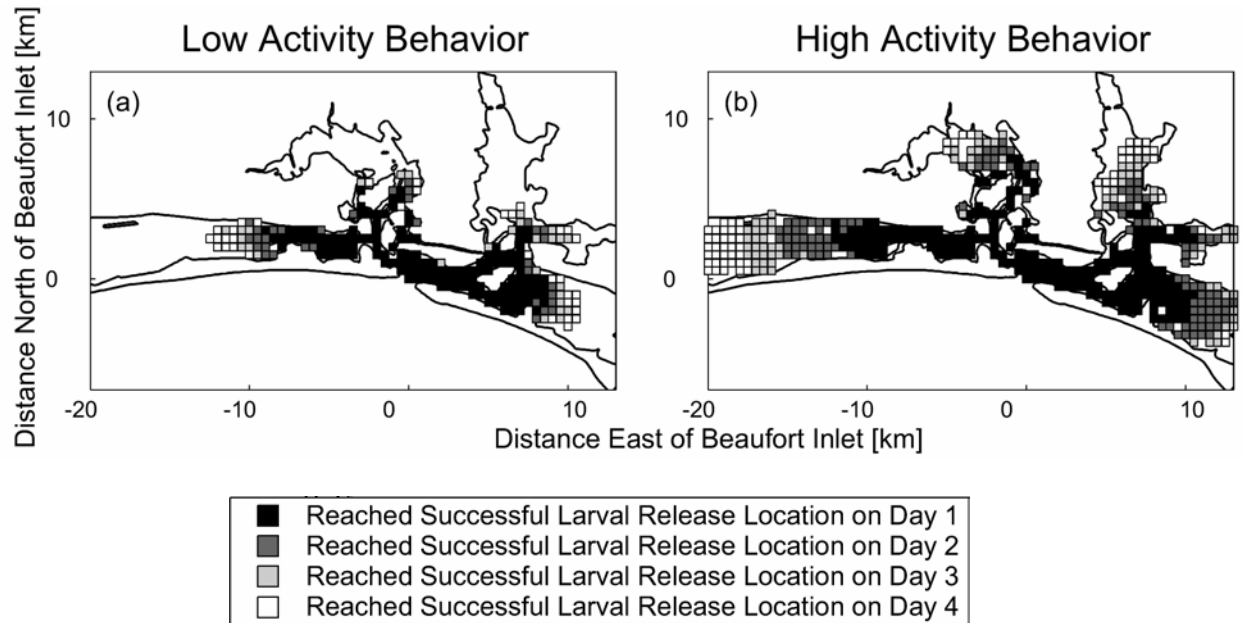


Fig. 3.9. Starting locations of simulated crabs with low and high activity behaviors that reached suitable larval release locations during the 4-day migratory period. Model days are the 24-h periods from sunrise to sunrise.

### 3.3.5 Sensitivity of migratory success to the tidal-diel and spring-neap cycles

There was  $\leq 6\%$  difference in the cumulative percentage of simulated crabs that reached suitable larval release locations during the 4-day migratory period between the four times of migration (i.e. when SBE, mid-ebb, SBF, and mid-flood occurred around sunrise on the last day of migration; Fig. 3.10a). With the low activity behavior, slightly more crabs that migrated when SBF or mid-flood occurred around sunrise on the last day of migration reached suitable larval release locations within the 4-day migratory period (Fig. 3.10a). The daily increase in the percentage of low activity crabs that reached suitable larval release locations was approximately linear during the 4-day migratory period, with increases of 5 – 9

% per day (Fig. 3.10a). The daily increase in the percentage of high activity crabs that reached suitable larval release locations was more asymptotic, with increases of 18 – 24 % from Day 1 to Day 2 and increases of only 4 – 10 % from Day 3 to Day 4 because most crabs (> 70 %) had reached suitable larval release locations by the end of Day 3 (Fig. 3.10a). For both low and high activity behaviors, there was  $\leq 6$  % difference in the cumulative percentage of simulated crabs that reached suitable larval release locations during the 4-day migratory period between spring and neap tides (Fig. 3.10b).

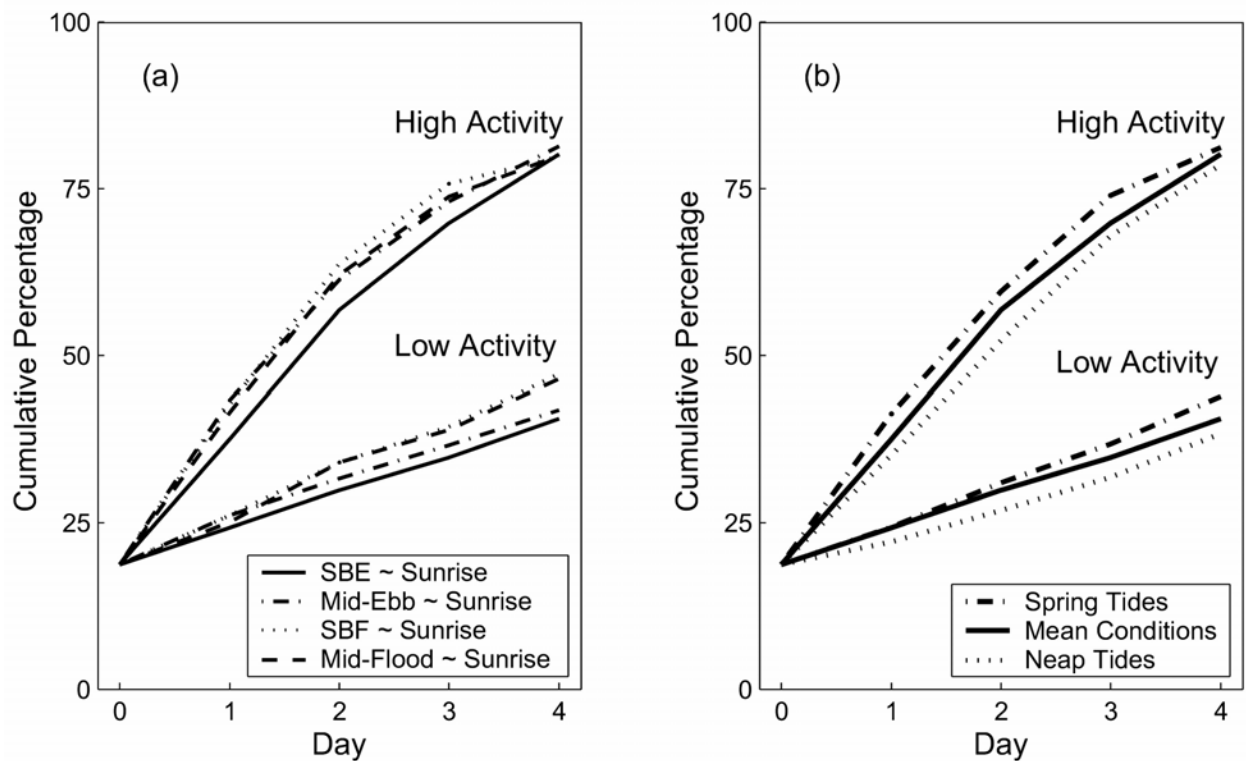


Fig. 3.10. Cumulative percentage of simulated crabs that reached suitable larval release locations during the 4-day migratory period for low and high activity behaviors: (a) when slack before ebb (SBE), mid-ebb (ME), slack before flood (SBF), and mid-flood (MF) occurred around sunrise on the last day of migration under mean tidal conditions and (b) during spring tides, mean tidal conditions, and neap tides when SBE occurred around sunrise on the last day of migration. Nineteen percent (19 %) of the crabs start the migration in suitable larval release locations.

### 3.3.6 Migratory speed

The migratory speed of each simulated crab was calculated by dividing the total distance that the crab traveled in the estuary during the 4-day migratory period by the total time that the crab was in the estuary. The migratory speed in the estuary over the 4-day migratory period for simulated crabs with the low activity behavior was  $< 0.5 \text{ km day}^{-1}$  for crabs starting their migration in the mid-upper Newport and North River estuaries and increased to  $\sim 2 \text{ km day}^{-1}$  for crabs starting their migration in the lower estuary (Fig. 3.11a). The migratory speed in the estuary over the 4-day migratory period for crabs with the high activity behavior was  $< 2 \text{ km day}^{-1}$  for crabs starting their migration in the uppermost Newport and North River estuaries and increased to  $> 8 \text{ km day}^{-1}$  for crabs starting their migration in lower-mid Bogue and Back Sounds (Fig. 3.11b).

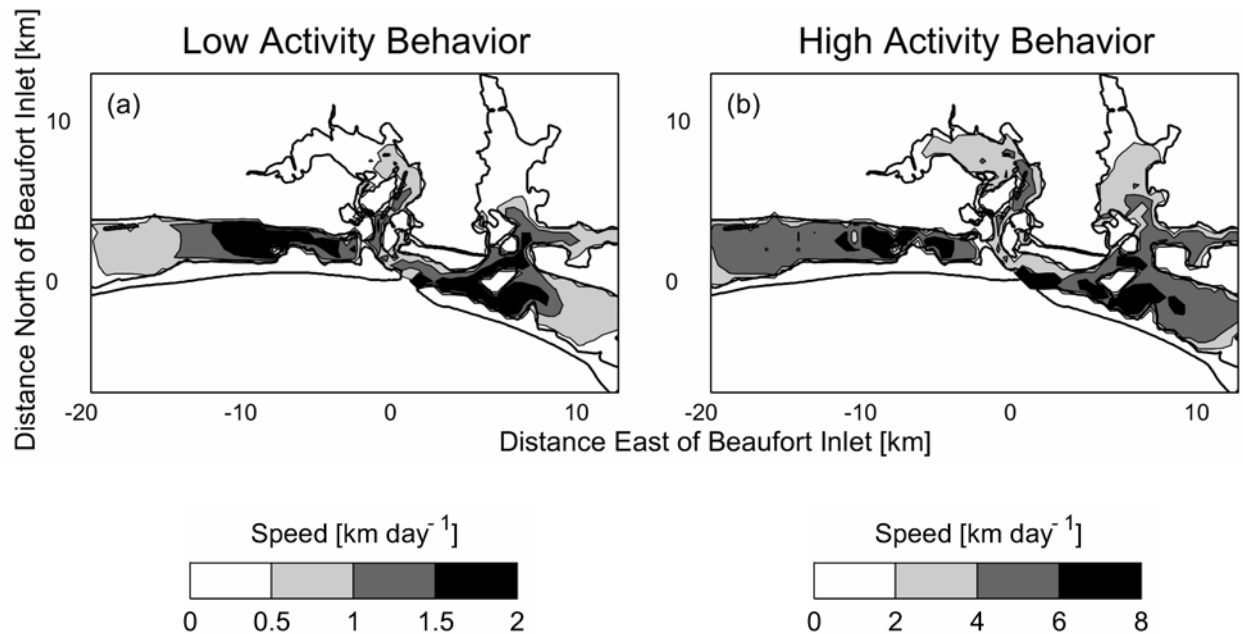


Fig. 3.11. Mean migratory speeds in the estuary for simulated crabs with low and high activity behaviors. The speed at a given location is the speed of a crab starting from that location.

### 3.3.7 Migratory residence times

We defined a migratory residence time as the amount of time a simulated crab spent in a given grid cell (both while moving and while stationary) during the ovigerous spawning migration. Cumulative migratory residence times (the migratory residence times of all the crabs combined) were calculated by matching the location of every simulated crab at every timestep during the 4-day migratory period to the closest node in the grid of starting locations and summing the time that was spent at each grid node (Fig. 3.4). The values for cumulative migratory residence times are dependent on the number of crab trajectories simulated, therefore we emphasize that the spatial patterns in cumulative migratory residence times, rather than the numeric values, are the important result. The cumulative migratory residence time of crabs with the low activity behavior was moderate to high (40 - 120 h) throughout most of the estuary and very high ( $> 120$  h) within  $\sim 4$  km of Beaufort Inlet in the lower estuary and coastal ocean (Fig. 3.12a). The cumulative migratory residence time of crabs with the high activity behavior was moderate (40 – 80 h) in lower-mid Bogue and Back Sounds and throughout the Newport and North River estuaries and very high ( $> 120$  h) in the lower estuary and coastal ocean within  $\sim 5$  km of Beaufort Inlet (Fig. 3.12b).

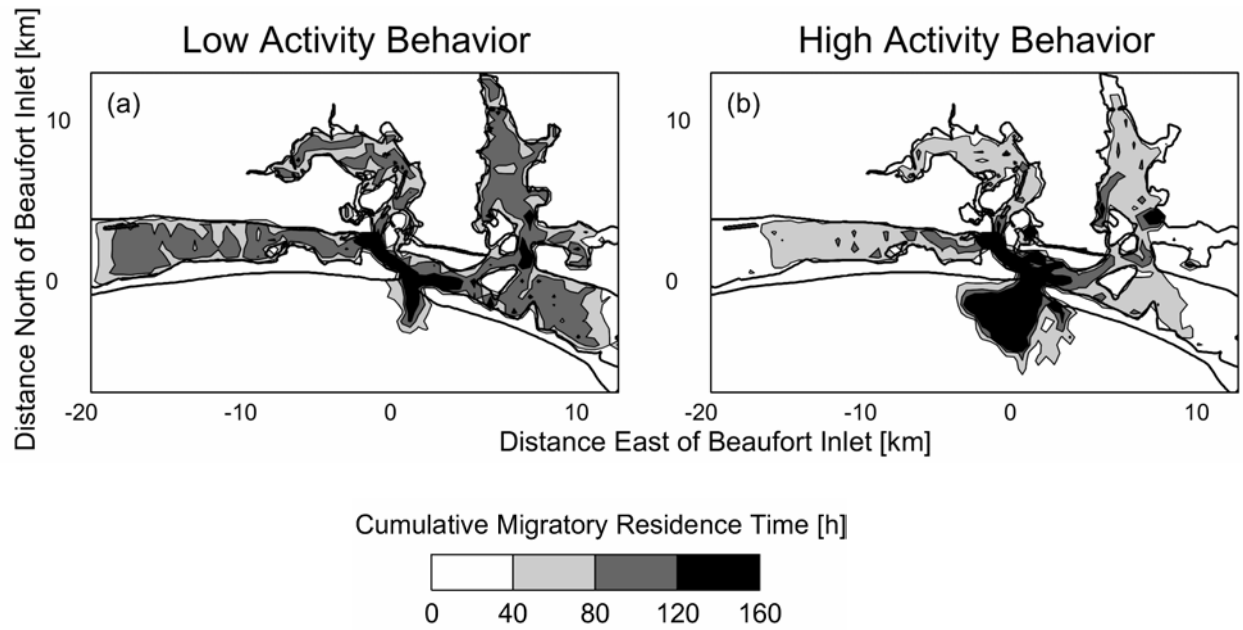


Fig. 3.12. Cumulative migratory residence times during the 4-day migratory period for simulated crabs with low and high activity behaviors.

### 3.3.8 Larval release locations

As with the values for cumulative migratory residence times, the densities of larval release locations are dependent on the number of crab trajectories simulated, and we emphasize that the spatial patterns in larval release locations, rather than the numeric values, are the important result. For simulated crabs with the low activity behavior, there were low to moderate densities ( $0 - 2$  releases per  $0.25 \text{ km}^2$ ) throughout most of the estuary and high to very high densities ( $2 - > 4$  releases per  $0.25 \text{ km}^2$ ) within  $\sim 4 \text{ km}$  of Beaufort Inlet in the lower estuary and coastal ocean (Fig. 3.13a). High activity crabs released larvae predominantly in the lower estuary and coastal ocean within  $\sim 5 \text{ km}$  of Beaufort Inlet (Fig. 3.13b).

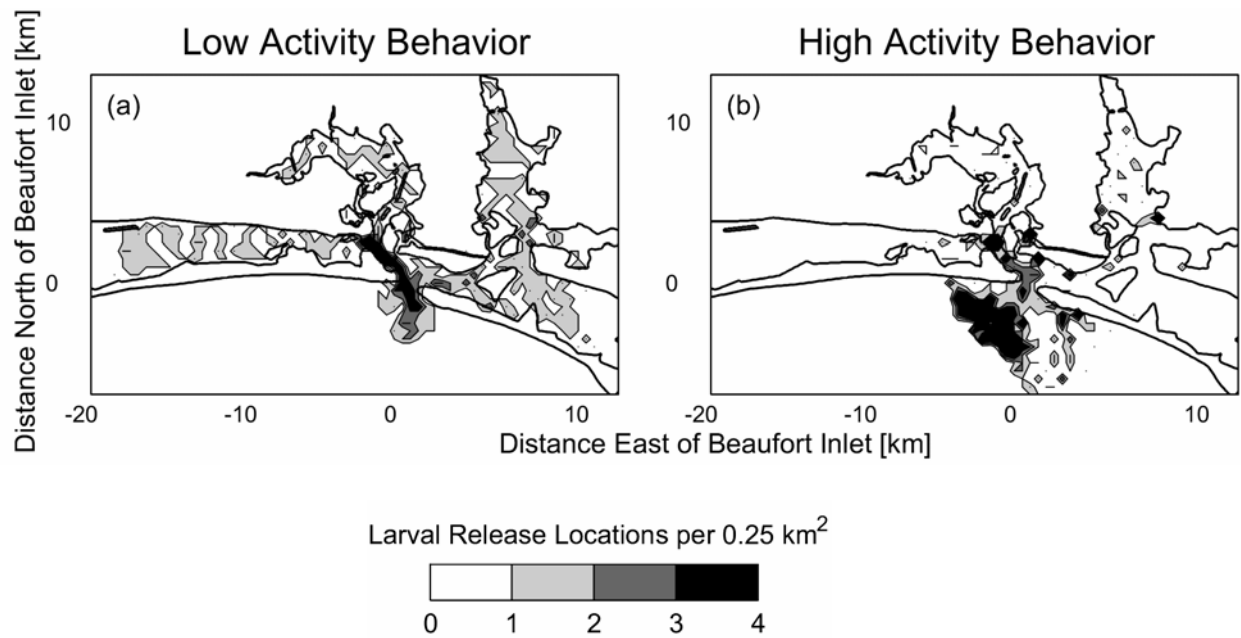


Fig. 3.13. Larval release locations for simulated crabs with low and high activity behaviors.

### 3.4 Discussion

Ovigerous blue crabs use ebb-tide transport (ETT) to migrate from adult estuarine habitats to coastal larval release areas. We developed detailed algorithms of this behavior from empirical data (Tankersley et al., 1998; Forward et al., 2003; Carr et al., 2004; Hench et al., 2004) and coupled these algorithms to a particle-tracking algorithm driven by velocity fields from a hydrodynamic model of the region to simulate the trajectories of migratory crabs and determine spatial migratory patterns. Modeling crab behavior with an idealized behavioral algorithm, such as continuous ETT, would not have been appropriate because it would have overestimated the mean migratory speed of the crabs and portrayed temporal patterns in migratory activity inaccurately (Fig. 3.6). We used two behavioral algorithms, low and high activity, to capture some of the variability in ovigerous blue crab ETT. It is unlikely that activity levels in the crab population are strictly bimodal, however, and these

results should be considered representative low and high values for a continuum of ovigerous blue crab behaviors.

The trajectories and mean speeds of simulated crabs matched the trajectories and mean speeds of observed crabs reasonably well (Figs. 3.5, 3.6). It was not expected that the trajectories of simulated crabs (Fig. 3.5) would match the trajectories of observed crabs exactly since mean values of the behavioral algorithm parameters were used to create the low and high activity behaviors. Nonetheless, improvements could be made to both the physical and behavioral components of the coupled model. We estimated that hydrodynamic model error could account for an average of 33 % of the differences between the distances that observed and simulated crabs traveled and lead to an average of 14 % error in simulated trajectory length. The two most likely sources of the differences between modeled and observed currents are inaccurate bathymetry and a lack of wind forcing in the model. We hope to add wind forcing to subsequent versions of the model to determine possible effects of strong winds and storm events on the ovigerous blue crab spawning migration. The addition of wind forcing will require the use of a three-dimensional hydrodynamic model and the addition of migratory vertical level(s) to the suite of behavioral algorithm parameters. Ovigerous females have been observed migrating at the surface of the water column (Tankersley et al., 1998; Hench et al., 2004), but additional study is required to determine if females are also migrating below the surface.

To improve the design of the behavioral model and the parameterization of the behavioral algorithm, further study of the timing and frequency of migratory episodes, the duration of migratory episodes, and the characteristic range of flood-tide walking/swimming speeds is needed. In the present behavioral algorithms, the low activity behavior, derived from the



mean number of migratory episodes per half hour bin from Hench et al. (2004), appears to underestimate mean crab activity (Figs. 3.5, 3.6). It is likely that tagging and/or tethering effects in the Hench et al. (2004) study resulted in a decrease in the mean number of migratory episodes per half hour relative to natural levels. Despite this uncertainty, these data are the best estimates of the timing of migratory episodes available and allowed us to capture migratory trajectories and temporal patterns in migratory episodes in a realistic manner.

The location of larval release is important because it is one of the primary determinants of whether larvae will be successfully transported to offshore developmental areas. Larvae released in the lower estuary and coastal ocean are the most likely to be transported far enough offshore to escape the tidal influence of the inlet and estuary (Kapolnai et al., 1996). We used larval transport to the coastal ocean during the first ebb tide following release (Fig. 3.8) as a metric for a suitable larval release location because larvae that reach the coastal ocean quickly will spend less time exposed to estuarine predators (Morgan, 1990) and harmful low-salinity conditions (Sandoz and Rogers, 1944). The issue of the larval transport from the estuary merits a more complete description than is given here but is outside the scope of this study. Larval transport outside of the estuary is strongly influenced by wind-driven currents (Luettich et al., 1999), and our depth-averaged hydrodynamic model is inappropriate for further examination of this topic.

Migratory success, the ability of migratory ovigerous crabs to reach suitable larval release locations, is highly sensitive to crab behavior and starting location in the estuary and relatively insensitive to normal variability in estuarine velocities (i.e. the tidal-diel and spring-neap cycles; Figs. 3.9, 3.10). High activity crabs can start their migration from almost

anywhere in the estuary and reach suitable larval release locations within the 4-day migratory period, whereas crabs with lower activity levels can only reach suitable larval release locations if they start their migration in the lower-mid estuary. The insensitivity of migratory success to fortnightly cycles in circulation suggests that the observed fortnightly peaks in migratory activity (RA Tankersley, Pers. obs.) exist because these periods are optimal for larval transport rather than adult migration.

Many simulated crabs starting their migration in the upper Newport and North River estuaries did not reach suitable larval release locations with either activity level (Fig. 3.9) because they were migrating in regions where ebb current speeds are relatively weak ( $< 0.2 \text{ m s}^{-1}$ ; Fig. 3.2c). Many estuaries along the Atlantic and Gulf coasts have similar regions with minimal tidal influence, and much of blue crab mating activity occurs in these areas (Churchill, 1921; Van Engel, 1958). The inability of crabs from these regions to reach suitable larval release locations during the ovigerous spawning migration demonstrates the importance of a down-estuary migratory phase prior to oviposition (Tankersley et al., 1998) and the likelihood that crabs may use other behaviors (e.g. walking along the bottom or directed swimming) to migrate (Turner et al. 2003, Carr et al. 2004). A pre-oviposition, down-estuary migration by mature female blue crabs has been observed in the Chesapeake Bay (Churchill, 1921; Van Engel, 1958; Turner et al., 2003) and the Pamlico Sound (Medici, 2004) but is not well documented for the Beaufort Inlet region (Judy and Dudley, 1970).

The migratory speed of high activity crabs is much higher than that of low activity crabs (Fig. 3.11) because high activity crabs are more active (Fig. 3.3) and migrate more “efficiently” than low activity crabs. High activity crabs are more efficient (i.e. travel farther per time spent actively migrating) because they travel farther down the estuary to areas with

higher current speeds. Down-estuary walking/swimming at  $0.25 \text{ m s}^{-1}$  during flood tides also affects the migratory efficiency of the high activity behavior, although the effect varies with location. Down-estuary walking/swimming at  $0.25 \text{ m s}^{-1}$  increases migratory efficiency in the upper estuary and offshore where maximum ebb current speeds are  $< 0.25 \text{ m s}^{-1}$ , and it enables crabs from the microtidal Newport and North River estuaries to reach areas with stronger currents during the 4-day migratory period. This behavior decreases potential migratory efficiency in regions close to Beaufort Inlet where ebb current speeds are generally  $> 0.25 \text{ m s}^{-1}$  (Fig. 3.2c) because it would be more efficient to increase passive transport during ebb tides in these regions than walk or swim down-estuary during flood tides.

Since crabs with lower activity levels migrate slowly through the estuary, they will reside in the mid-upper sub-estuaries for relatively long periods of time (Fig. 3.12a) and are predicted to release larvae throughout the estuary (Fig. 3.13a). Highly active crabs, on the other hand, migrate to the lower estuary and coastal ocean quickly and therefore reside in these regions for a greater proportion of the migratory period (Fig. 3.12b). They are predicted to release larvae primarily in the coastal ocean within  $\sim 5 \text{ km}$  of Beaufort Inlet (Fig. 3.13b). While these are the best estimates of migratory residence times and larval release locations to date, actual migratory residence times and the distribution of larval release locations will depend on local blue crab population dynamics, including initial starting locations and distribution of behaviors. Very little is known about either of these parameters for the Beaufort Inlet region or for most Atlantic and Gulf coast estuaries, and further study of these factors is necessary to improve model predictions. In addition, this analysis shows spatial patterns for a limited migratory period. Crabs can migrate throughout the summer spawning season and may return to the estuary (Tagatz, 1968; Tankersley et al., 1998) or

migrate farther offshore after larval release (Hench et al., 2004). Therefore spatial patterns in migratory residence times and larval release locations may shift during the spawning season. The concentration of larval release locations in the coastal ocean near Beaufort Inlet is probably realistic, however. Maximum ebb current speeds decrease rapidly to  $< 0.20 \text{ m s}^{-1}$  within  $\sim 3 \text{ km}$  of the inlet in the coastal ocean (Fig. 3.2c), and crabs would need to actively walk or swim offshore or use wind-driven currents to make additional rapid progress away from the estuary.

Recent studies have found a significant positive relationship between spawning stock abundance and recruitment in estuarine blue crab populations and suggest that maintaining a critical level of spawning stock (mature females) may be essential to maintaining viable blue crab populations (Lipcius and Stockhausen, 2002; Eggleston et al., 2004). To protect spawning stock from fishing losses during their migration to and/or residence in spawning areas, spawning sanctuaries, where crabbing is prohibited or restricted, have been created in North Carolina (Henry and McKenna, 1998) and Virginia (Seitz et al., 2001; Lipcius et al., 2001; Lipcius et al., 2003). In North Carolina, five relatively small sanctuaries,  $18 - 35 \text{ km}^2$  each, have been established around inlets in Pamlico and Core Sounds (Henry and McKenna, 1998), while in the Chesapeake Bay, a large migration corridor/spawning sanctuary complex,  $\sim 2400 \text{ km}^2$ , has been created (Virginia Marine Resources Commission Regulation 4 VAC 20-752-10 *et seq.* as adopted July 23, 2003). While the results of this study are specific to the Beaufort Inlet region, they suggest that the five small spawning sanctuaries around other North Carolina inlets ( $\sim 4 - 6 \text{ km}$  in the ebb-tide alongstream direction) may not provide long-term protection for migratory ovigerous crabs because crabs may be able to migrate through the sanctuaries quickly and may spend considerable amounts of time landward and

seaward of the sanctuaries (Figs. 3.11, 3.12; see also Medici, 2004). Consequently, larger sanctuaries and protected migration corridors may be needed to meet management goals. Fisheries managers can use spatially-explicit results such as those determined in this study to estimate what level of protection (percentage of cumulative crab residence time) a sanctuary will provide to migratory ovigerous crabs. Areas that are suitable for larval release and where larval release occurs frequently (Figs. 3.8, 3.13) should also be considered for protection because they may be important source regions for blue crab populations.

The present model provides the first spatially-comprehensive estimates of ovigerous blue crab migratory success, migratory speeds, migratory residence times, and larval release locations in the Beaufort Inlet region. The hydrodynamics of this region are typical of many estuary-inlet systems of the Atlantic and Gulf coasts of the United States, and the migratory patterns determined in this study are likely to be similar for comparable systems. This information is vital to understanding how blue crabs transition from estuarine adult habitats to offshore larval developmental areas and for designing spawning sanctuaries that protect migratory blue crabs effectively.

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## **Chapter 4. The influence of diel vertical migration on zooplankton transport and recruitment in an upwelling region**

### **Abstract**

Diel vertical migration (DVM) is a common zooplankton behavior in which organisms reside in surface or near-surface waters at night and at deeper depths during the day. In many upwelling regions, DVM reduces the transport of organisms away from the region. It is unclear, however, what role DVM plays in recruitment (the arrival of larvae or juveniles to locations where they will become reproducing adults) to upwelling regions. In this study, we determine the influence of DVM on zooplankton transport, the level of recruitment of locally-produced propagules (self-recruitment), and sources of recruits in the upwelling region near Monterey Bay, California, by simulating the trajectories of fixed-depth and vertically-migrating organisms with a drifter-tracking algorithm driven by velocity fields from a three-dimensional hydrodynamic model. We found that DVM into subsurface poleward and onshore currents during the day does not fully compensate for equatorward and offshore transport in the surface Ekman layer at night and does not retain zooplankton in the Monterey Bay region. DVM also tends to decrease the ability of zooplankton to return to the region after being transported away and shift source regions for recruits closer to the Bay. While DVM does not appear to substantially increase the potential for self-recruitment to the region, our results suggest that other mechanisms, such as transport during non-upwelling periods, continuous transport below the surface, increases in mean transport depth over time

(ontogenetic vertical migration), or seasonal changes in hydrography, may still enable relatively high levels of self-recruitment to this highly advective region.

#### 4.1 Introduction

Nocturnal diel vertical migration (DVM) is a common zooplankton behavior in which organisms reside in surface or near-surface waters at night and at deeper depths during the day. This behavior enables zooplankton to feed in relatively productive surface waters at night and avoid visual predators and intense solar radiation during the day (Haney, 1988). In eastern boundary upwelling regions, there are often equatorward and offshore currents at the surface and poleward and onshore currents at deeper depths. Consequently, relatively small vertical migrations (on the order of 10 to 100 m) can reduce the alongshore and cross-shore transport of organisms relative to passive or fixed-depth transport at the surface (Brockmann, 1979; Wroblewski, 1982; Bucklin et al., 1989; Botsford et al., 1994; Batchelder et al., 2002). This reduction in transport away from highly productive upwelling regions may increase food availability for zooplankton (Wroblewski, 1982) and lead to reduced losses to starvation, faster growth rates, increased fecundity, and increased population sizes (Rumsey and Franks, 1999).

It is unclear, however, how much of a role DVM plays in determining recruitment (the arrival of larvae or juveniles to locations where they will become reproducing adults) to holoplanktonic or meroplanktonic populations in eastern boundary upwelling regions. Understanding recruitment patterns, such as the percentage of recruits that are locally-produced (self-recruits), is critical to managing marine populations effectively because they determine stock-recruitment relationships, vulnerability to fishing pressure and habitat

modification, and the efficacy of marine reserves (Strathmann et al., 2002). It is frequently hypothesized that DVM enables self-recruitment to populations in upwelling regions by retaining organisms in a region. In a 1998 review of the subject, Peterson suggested that DVM is not sufficient to retain organisms in narrow upwelling regions over shallow shelves (e.g. the Oregon coast). He instead proposed that ontogenetic vertical migration (OVM), generally an increase in an organism's mean depth as it develops, is the key to retaining organisms in narrow upwelling regions.

In this study, we examine the influence of DVM on zooplankton transport and recruitment in a relatively deep ( $> 100$  m), broad (on the order of 100 km) upwelling region with high mesoscale variability, the Monterey Bay region of central California. We simulate the trajectories of fixed-depth and vertically-migrating organisms in the region with a drifter-tracking algorithm driven by velocity fields from a three-dimensional (3D) hydrodynamic model. With this model, we seek to understand how regional populations are retained in this highly advective upwelling system and address the following questions: 1) What influence does DVM have on the zooplankton transport in the region? 2) What influence does DVM have on zooplankton self-recruitment to the Bay? 3) What influence does DVM have on the source of zooplankton recruits to the Bay? Although we do not model OVM explicitly, our results for fixed-depth organisms transported at deeper depths ( $> 50$  m) indicate what influence OVM may have on zooplankton transport in the region and whether the proposal of Peterson (1998) that OVM rather than DVM is the key to retaining zooplankton populations in upwelling regions is applicable to a broad, deep upwelling system such as the central California coast.

*DVM in the Monterey Bay region-* Almost all of the dominant taxa in the Monterey Bay zooplankton community (e.g. copepods, euphausiids, crab larvae, cladocerans, polychaetes, chaetognaths, siphonophores, ctenophores, larvaceans, and bryozoan larvae) are vertical migrators, although their DVM behaviors are generally not well described. The exceptions are the crustacean macrozooplankton which are typically very strong vertical migrators. Euphausiids in the region migrate from the surface at night to 100 - 600 m depth during the day (Brinton, 1967; Brinton, 1976; Youngbluth, 1976), copepods from the upper 50 m at night to 50 - 350 m depth during the day (Frost, 1988; Dagg et al., 1989; Ohman et al., 1998; Hays et al., 2001), and crab zoeae and megalopae from the surface at night to < 80 m depth during the day (Shanks, 1986; Hobbs and Botsford, 1992).

*Hydrography of the Monterey Bay region-* The influence of DVM on zooplankton transport and recruitment in the Monterey Bay region is likely to vary considerably during the year because of strong hydrographic seasonality. During the spring and summer upwelling season, southeastward winds drive strong southward and offshore (westward) currents at the surface (< 30 m; Rosenfeld et al., 1994; Pennington and Chavez, 2000). The offshore flow of water causes the upwelling of deep, nutrient-rich waters into the photic zone and stimulates high levels of primary and secondary production (Chavez et al., 2002). During the winter, a northward current, the Davidson Current, develops at the surface from shore to ~ 100 km offshore (Collins et al., 2000; Pennington and Chavez, 2000). The fall oceanic season is transitional between the spring-summer upwelling and winter Davidson seasons with reduced upwelling. Throughout the year, the California Undercurrent flows northward from 100 - 250 m deep from shore to ~ 150 km offshore (Collins et al., 2000; Collins et al., 2003). At

intraseasonal time scales (on the order of 10 d), regional circulation is modified by wind fluctuations, such as upwelling relaxation events, and mesoscale features, such as eddies and jets, that result from the instability of the seasonally-varying mean currents (Marchesiello et al., 2003). At interannual time scales, regional circulation is modified by El Niño events which reduce the upwelling of nutrient-rich waters during the spring and summer and prolong and increase northward flow at the surface during the winter (Chavez et al., 2002; Collins et al., 2002).

*Study motivation-* The hydrography and biogeochemistry of the Monterey Bay region of California have been studied extensively (reviewed by Collins et al., 2003), and much attention is now directed at gaining a greater understanding of regional zooplankton population dynamics (e.g. Marinovic et al., 2002). The goal of our study is to determine the influence of DVM on zooplankton transport and recruitment in the Monterey Bay region. There have been very few coupled behavioral-hydrodynamic modeling studies of the influence of DVM on zooplankton transport in eastern boundary upwelling regions (see Brockmann, 1979; Wroblewski, 1982; Batchelder et al., 2002), and the only work we are aware of along the California coast has been extremely preliminary (i.e. simulation of a very limited number of drifters under specific conditions; see Bucklin, 1989; Botsford, 1994). We are expanding upon previous work by using a fully 3D hydrodynamic model which renders realistic seasonally-varying mean velocity fields with realistic mesoscale activity and examining a range of starting times and nighttime near-surface depths. Since we use climatological atmospheric and oceanic fields to force the hydrodynamic model, we are unable to capture some intraseasonal and interannual processes, such as upwelling relaxation

and El Niño events, that may be important to zooplankton advection and dispersion in the region. Nonetheless, given the importance of advection and dispersion processes associated solely with the seasonally-varying mean circulation and accompanying mesoscale activity along the central Californian coast, this study is an important advance in understanding zooplankton transport and recruitment in the region.

## 4.2 Materials and methods

### 4.2.1 Hydrodynamic model and oceanic and atmospheric forcing

We use the three-dimensional (3D) numerical hydrodynamic model ROMS (Regional Oceanic Modeling System; Shchepetkin and McWilliams, 2003; Shchepetkin and McWilliams, 2005) to determine velocity fields for the Monterey Bay region. Our model configuration uses a downscaling grid-nesting capability (Penven et al., 2006) to embed a 2.5 km resolution domain (extending from Pt. Conception in southern California to Heceta Bank in central Oregon) in a 7.5 km resolution domain encompassing the entire California Current System (25°N to 48°N; Fig. 4.1). The large-scale domain has adaptive open boundary conditions (Marchesiello et al., 2003) derived from Levitus climatology. We use 32 vertical (sigma) levels. The sigma levels are concentrated in the upper water column to enable good vertical resolution ( $\geq 3$  m) of near-surface currents. A minimum depth of 10 m depth is imposed in nearshore areas for numerical reasons.

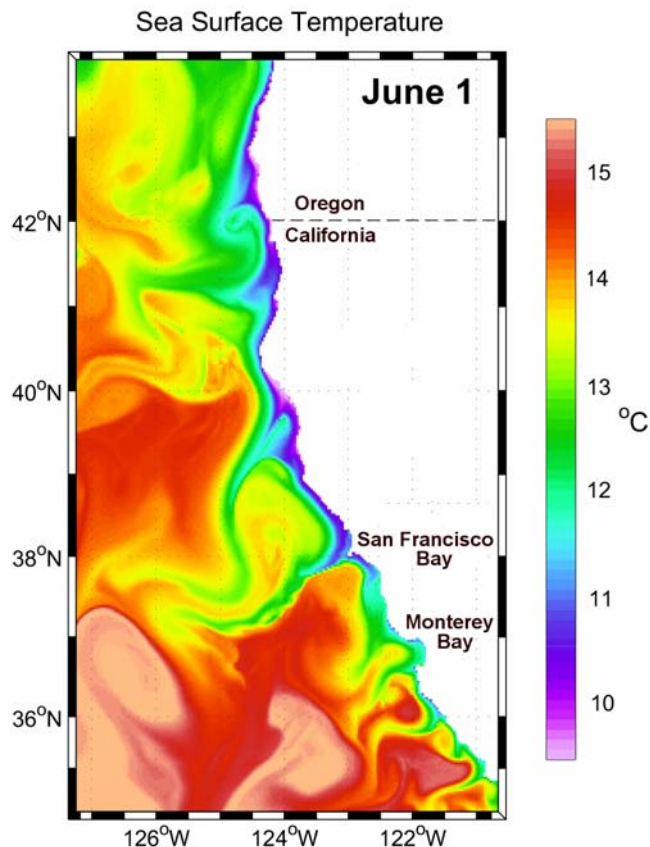


Fig. 4.1. Model domain and simulated sea surface temperature along the U.S. West Coast.

Wind speed decreases rapidly near coastlines, and the form of this decrease has a substantial influence on the strength and nature of upwelling (Capet et al, 2004). There is currently a lack of observational data on atmospheric processes in nearshore regions, and, as a result, different wind products are still being studied to determine how well they reproduce ocean dynamics in upwelling regions (Capet et al., 2004). We use a surface wind field climatology derived from QuikSCAT satellite scatterometer data (Liu et al, 1998; Weissman and Graber, 1999) to force ROMS. QuikSCAT wind fields in the nearshore region (i.e. 25 – 50 km from shore) are contaminated by land and are therefore completed by objective analysis. The resulting wind fields lack observed small-scale coastal features (Winant et al., 1988). To determine if this effect has a significant influence on our results, we performed



additional model simulations forcing ROMS with surface wind fields from the high-resolution atmospheric model COAMPS (Kindle et al., 2002) modified to reduce the likely unrealistic nearshore dropoff in wind velocities (Capet et al., 2004). We found the results presented here to be robust with regard to the wind forcing field.

ROMS is skilled at rendering mesoscale features (e.g. eddies, fronts, and filaments) whose structure and intensity are comparable to observations (Marchesiello et al., 2003), as well as realistic mean velocity fields, for the California Current system. A snapshot of sea surface temperature during the upwelling season demonstrates the ability of our ROMS configuration to reproduce realistic upwelling jets, including the southward jet frequently observed across the mouth of Monterey Bay and the offshore jet frequently observed off of Point Sur (southern tip of Monterey Bay, Fig. 4.1; Rosenfeld et al., 1994; Collins et al., 2003). Mean cross-shore velocities in the Monterey Bay region during the late upwelling season (May 15 – August 15; spatial average between 35.5 - 37.7 °N and temporal average of 3 years) show strong offshore flow in the surface Ekman layer and weak return flow at deeper depths (Fig. 4.2).

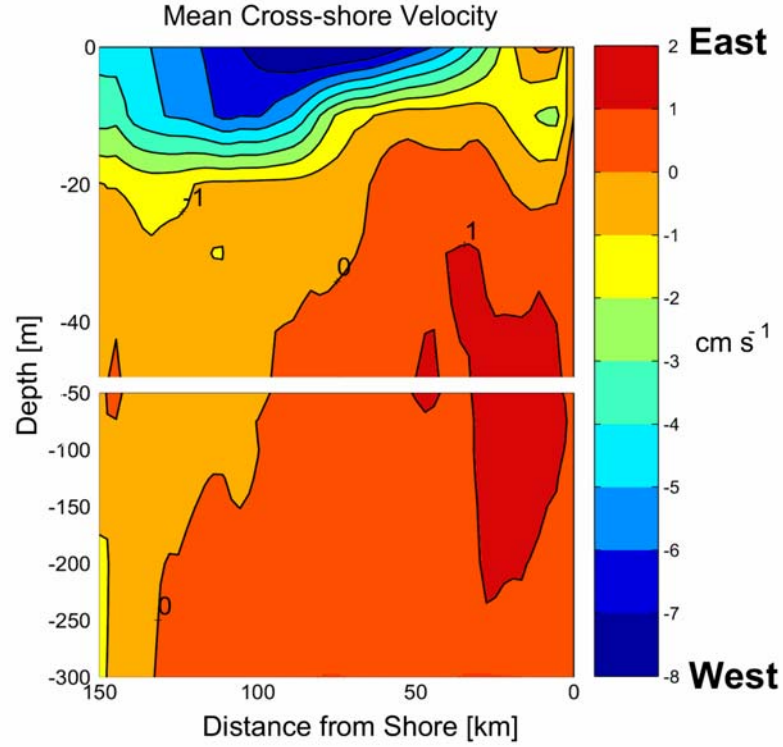


Fig. 4.2. Simulated mean cross-shore velocities in the Monterey Bay region during the late upwelling season (May 15 – August 15; spatial average between 35.5 – 37.7 °N and temporal average of 3 years). Positive and negative values represent eastward and westward transport respectively, and top and bottom panels have different vertical axes. Since velocities are alongshore and temporal means, they do not necessarily represent the instantaneous flows that transport drifters.

#### 4.2.2 Drifter tracking

We use a Lagrangian drifter-tracking code to simulate zooplankton (drifter) trajectories from stored ROMS velocity fields. The code uses a fourth-order accurate Adams-Bashford-Moulton predictor-corrector scheme to integrate  $d\vec{x} / dt = \vec{u}(\vec{x}, t)$  over time given the initial condition  $\vec{x}(t_0) = \vec{x}_0$  and a series  $\vec{u}_{roms}$  of stored 3D ROMS velocity fields. The right-hand side is estimated through a linear interpolation in time and space of the discrete  $\vec{u}_{roms}$  fields.  $\vec{u}_{roms}$  fields are daily averages calculated during ROMS simulations. We verified that using stored ROMS velocity fields yields qualitatively and quantitatively similar results to

analogous “online” experiments in which velocity fields fluctuate with the model time step (400 s) on a subset of simulations. Results are robust with respect to stored or “online” forcing because there is no high frequency variability, e.g. tides and sea breezes, in the ROMS velocity fields.

Using the Lagrangian drifter-tracking code, we simulate the trajectories of drifters from a grid of starting locations in Monterey Bay located just offshore of the 100-m depth contour (Fig. 4.3). All drifters are started at least 5 km from shore because the model does not resolve nearshore processes well. Two types of behaviors are simulated: 1) fixed-depth behaviors in which drifters remain at the same depth night and day and 2) diel vertical migration (DVM) behaviors in which drifters jump from nighttime near-surface depths to deeper daytime depths and vice versa at 0600 and 1800 respectively. Fixed-depth drifters ( $N = 250$ ) are started from 25 horizontal locations at 10 depths (1, 5, 10, 15, 20, 30, 40, 50, 75, and 100 m). DVM drifters ( $N = 200$ ) are started from 25 horizontal locations at 8 depths (1, 5, 10, 15, 20, 30, 40, and 50 m; Fig. 4.3) and have vertical migration amplitudes of 20 and 50 m (Fig. 4.4). Neither fixed-depth nor DVM drifters are advected by ROMS vertical velocity fields. DVM drifters perform partial vertical migrations in regions where the full extent is not possible ( $< 100$  m). The drifter-tracking algorithm is run with a timestep of 5 min, and drifters’ horizontal and vertical positions are recorded once daily unless noted otherwise. We did not account for sub-gridscale dispersion (typically modeled as a random walk) in this study, but it should be of secondary importance because vertical migratory velocities are typically larger than rms vertical velocities associated with upper ocean turbulence and, mesoscale stirring, the primary mesoscale horizontal dispersion process, is adequately resolved (Richardson, 1926).

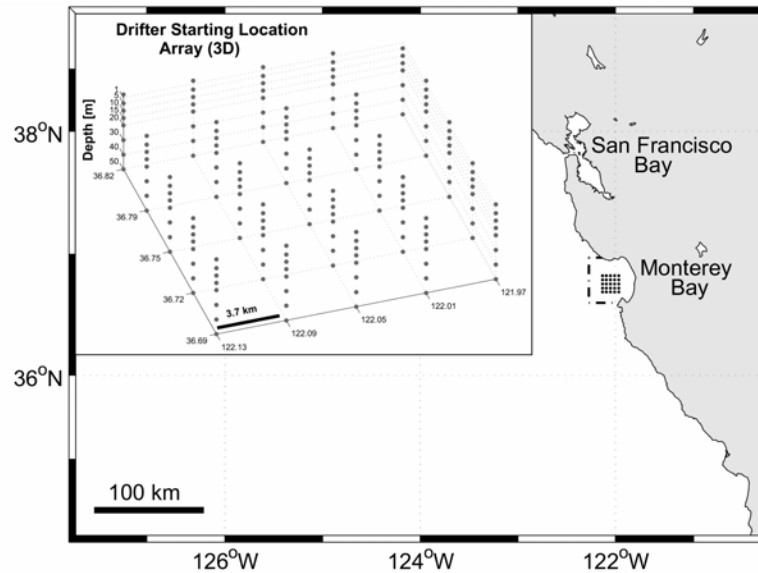


Fig. 4.3. Model domain along the central California coast. Black circles on map are drifter starting locations, and dashed line on map represents Monterey Bay for data analysis purposes. The diagram in the upper left of the map shows the array of drifter starting locations for shallow fixed-depth and all DVM drifters in Monterey Bay.

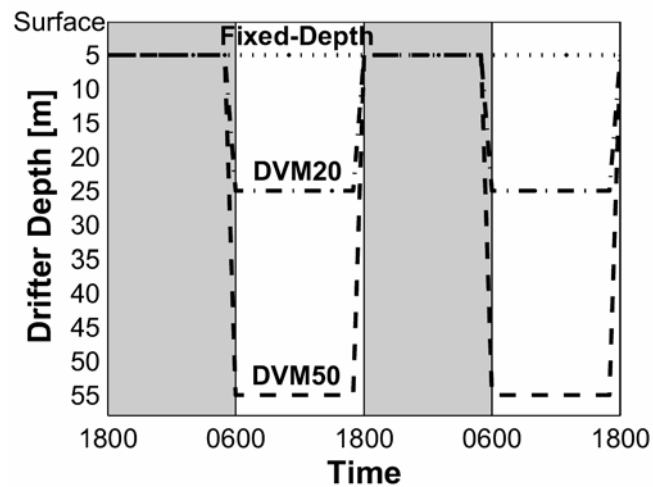


Fig. 4.4. Vertical position of sample fixed-depth, DVM20, and DVM50 drifters with a starting depth of 5 m depth (plotted at 1 h intervals).

#### 4.2.3 Influence of DVM on zooplankton transport

To determine the influence of DVM on the mean alongshore ( $\sim$  north-south) and cross-shore ( $\sim$  east-west) transport of zooplankton in the Monterey Bay region, drifters are started every 5 d for 3 years and tracked for 20 d each. The life spans of holoplanktonic species and larval durations of meroplanktonic species vary considerably ( $< 1$  d to  $> 90$  d; Grantham et al., 2003; Shanks et al., 2003; Siegel et al., 2003). We use 20-d trajectories because they would represent the entire pelagic transport of many species and the initial pelagic transport of longer-lived species (Grantham et al., 2003; Siegel et al., 2003). For each drifter, we use its entire 20-d trajectory or its entire trajectory until it reached an oceanic boundary of the model domain to calculate its mean north-south and east-west transport and determine its final location. Loss of drifters through oceanic boundaries was uncommon ( $\sim 10$  % of fixed-depth drifters at 1 m depth,  $\sim 0.2$  % of all other drifters). Mean cross-shore and alongshore transport are calculated by averaging results from the three simulation years and rotating the north-south and east-west transport vectors  $30^\circ$  counterclockwise.

To determine the spatial distributions of drifters after 20 d of transport, we place a grid with nodes spaced 10 km apart latitudinally and longitudinally over the model domain and match the final location of drifter from the three simulation years to the nearest grid node. Drifter final locations are grouped into the four characteristic hydrographic seasons in the Monterey Bay region: early upwelling (February 15 – May 15), late upwelling (May 15 – August 15), oceanic (August 15 – November 15), and Davidson (November 15 – February 15).

#### 4.2.4 Influence of DVM on self-recruitment

To determine the influence of DVM on self-recruitment to Monterey Bay, drifters are started every 5 d for 2 years and tracked for up to 360 d each. Longer trajectories (i.e. > 20 d) are applicable to organisms with relatively long larval durations, such as many crab and fish species, or long-lived holoplanktonic organisms, such as euphausiids (Brinton, 1976; Grantham et al., 2003; Shanks et al., 2003). A box is defined around Monterey Bay (Fig. 4.3), and drifters are considered recruits to the Bay as long as they remain in the box or when they return to the box after  $\geq 30$  d outside of it. It is assumed that being in the box represents successful recruitment for holoplanktonic organisms and increased potential for transport to shore and recruitment for meroplanktonic organisms. Drifters must exit the box for  $\geq 30$  d to be considered “returns” to Monterey Bay because drifters that are outside of the box for < 30 d generally remain very close to the Bay. Return rates are calculated by dividing the number of drifter that return to the Bay by the number of drifters that actually leave the Bay. Mean time that drifters remain in Monterey Bay and percentage of drifters returning to Monterey Bay are calculated by averaging results of the two simulation years.

#### 4.2.5 Influence of DVM on the source of recruits

To determine the source of recruits to Monterey Bay, we start drifters from the Monterey Bay starting locations (Fig. 4.3) and run the drifter-tracking algorithm backwards in time for 20 d. Otherwise, analyses correspond to those described in Section 4.2 Materials and methods under *Influence of DVM on Zooplankton Transport*.

### 4.3 Results

#### 4.3.1 Influence of DVM on zooplankton transport

*Mean transport of fixed-depth drifters-* There are strong seasonal patterns in the mean transport of fixed-depth drifters started in Monterey Bay (Fig. 4.5) that correspond to the characteristic hydrographic seasons in the region. During the upwelling seasons (mid-February – mid-August), the wind-driven Ekman layer drives near-surface drifters (1 – 15 m depth) rapidly to the south and west of the Bay (Fig. 4.5). Early in the upwelling season (mid-February – mid-June), there is weak southward and westward transport below the Ekman layer, while later in the season (mid-June – mid-August), the California Undercurrent strengthens and drives deeper drifters ( $\geq 50$  m depth) rapidly to the north (Fig. 4.5). During the oceanic and Davidson seasons (mid-August – mid-February), sporadic upwelling interspersed with weak northward flow results in relatively weak southward and westward transport near the surface and northward and westward transport below (Fig. 4.5). There is no strong mean eastward transport at any time or depth because drifters are started close to the California coast.

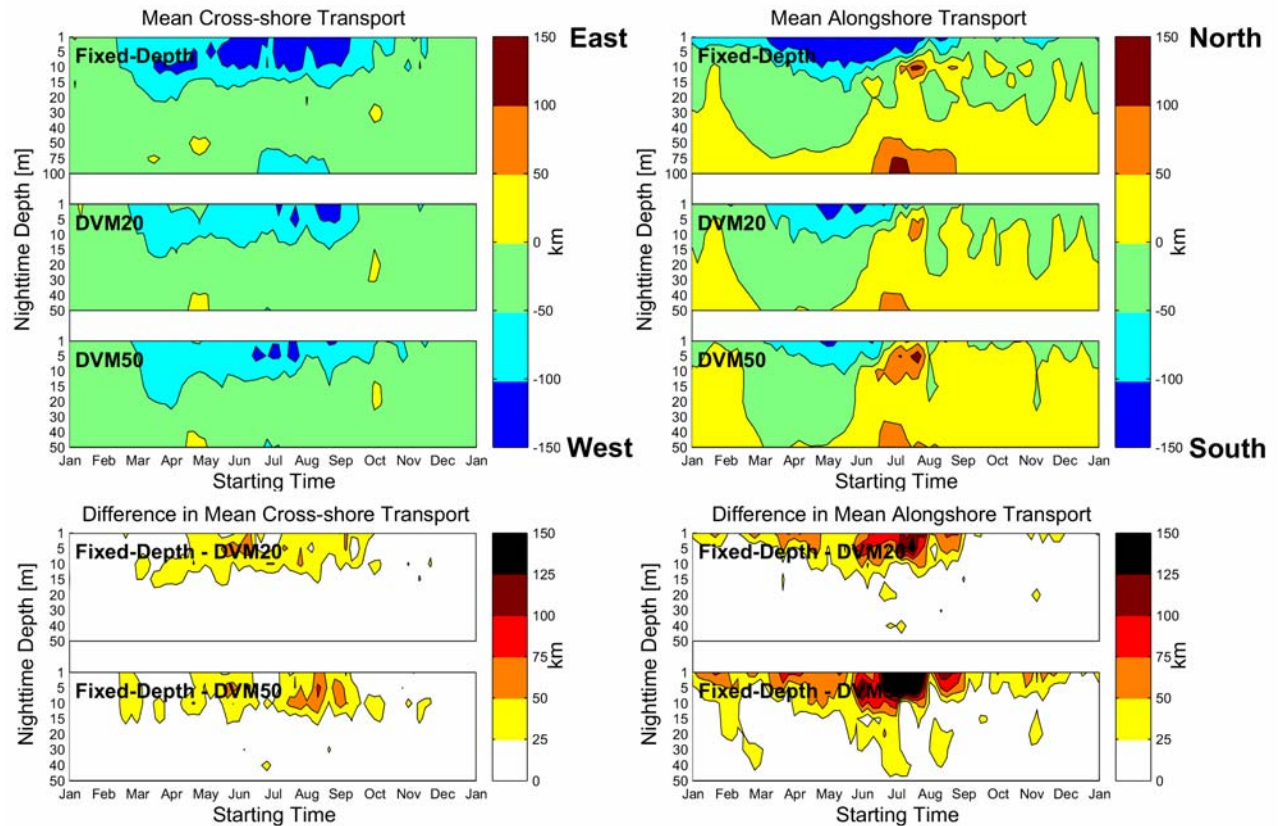


Fig. 4.5. Top: Mean cross-shore and alongshore transport of drifters over 20-d period. Positive values represent eastward and northward transport, and negative values represent westward and southward transport. Bottom: Absolute difference in mean cross-shore and alongshore transport of fixed-depth and DVM drifters over 20-d period.

*Mean transport of DVM drifters-* During periods of active upwelling during the upwelling and oceanic seasons (mid-February – mid-November), DVM drifters migrating from the surface Ekman layer (1 – 15 m depth) at night to weaker or opposing undercurrents during the day have zig-zag trajectories that are shorter than or in a different direction than trajectories for analogous fixed-depth drifters (Fig. 4.6). This means that DVM can substantially reduce the transport away from the Bay of drifters at the surface at night (Figs. 4.5, 4.7). The DVM behaviors simulated generally do not substantially influence the mean transport and final location of drifters with a nighttime depth below the surface Ekman layer



(Figs. 4.5, 4.8), however, because there is less vertical current shear deeper in the water column.

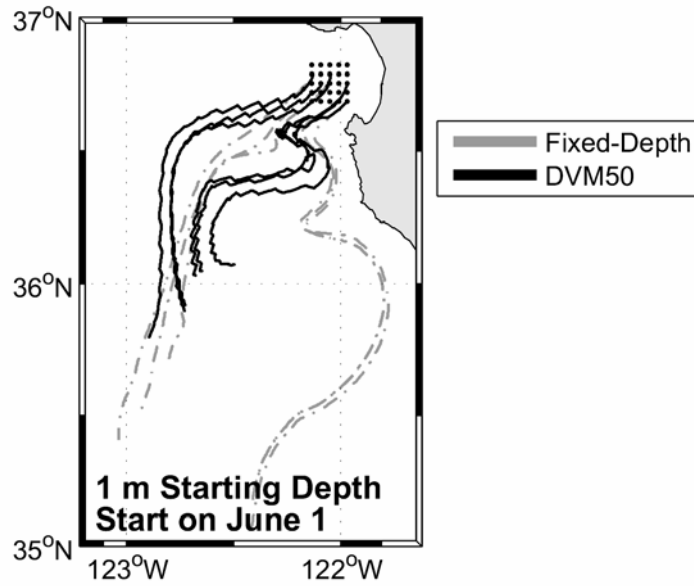


Fig. 4.6. Trajectories of drifters started at the surface (1 m depth) over 20-d period (1 h position intervals).

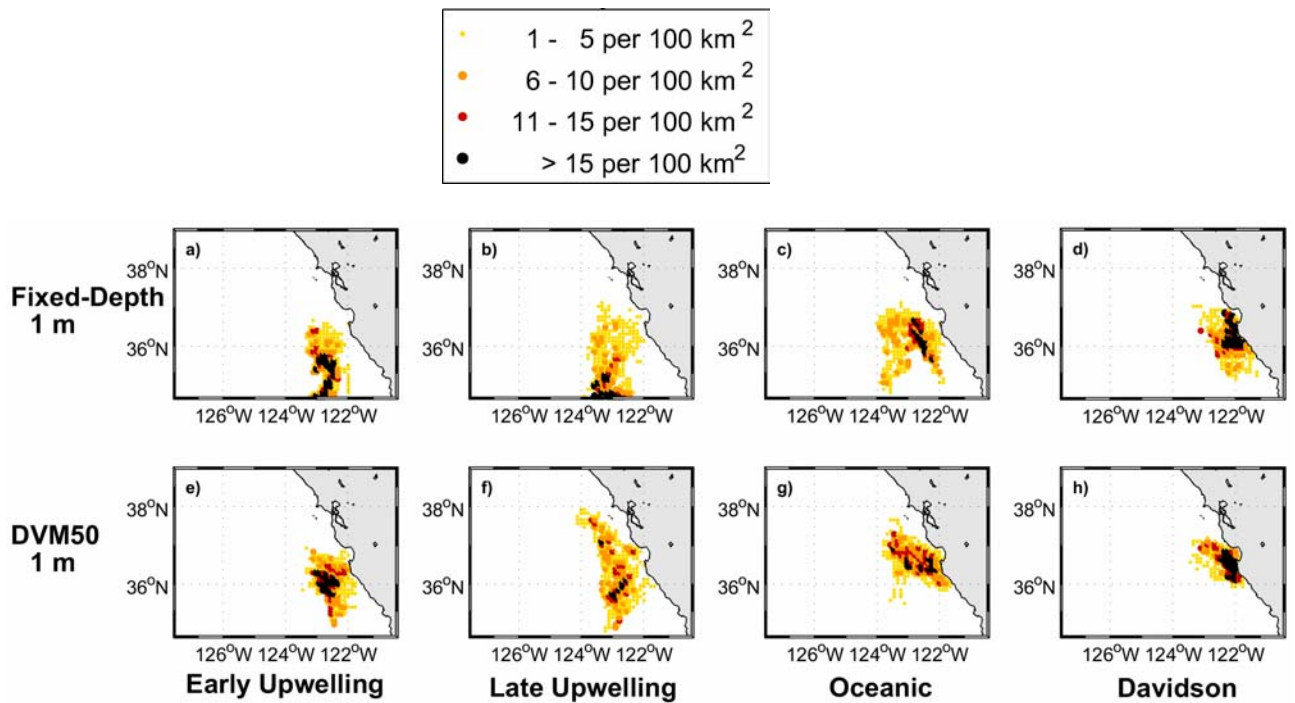


Fig. 4.7. Distribution of drifters started at the surface (1 m depth) after 20 d of transport.

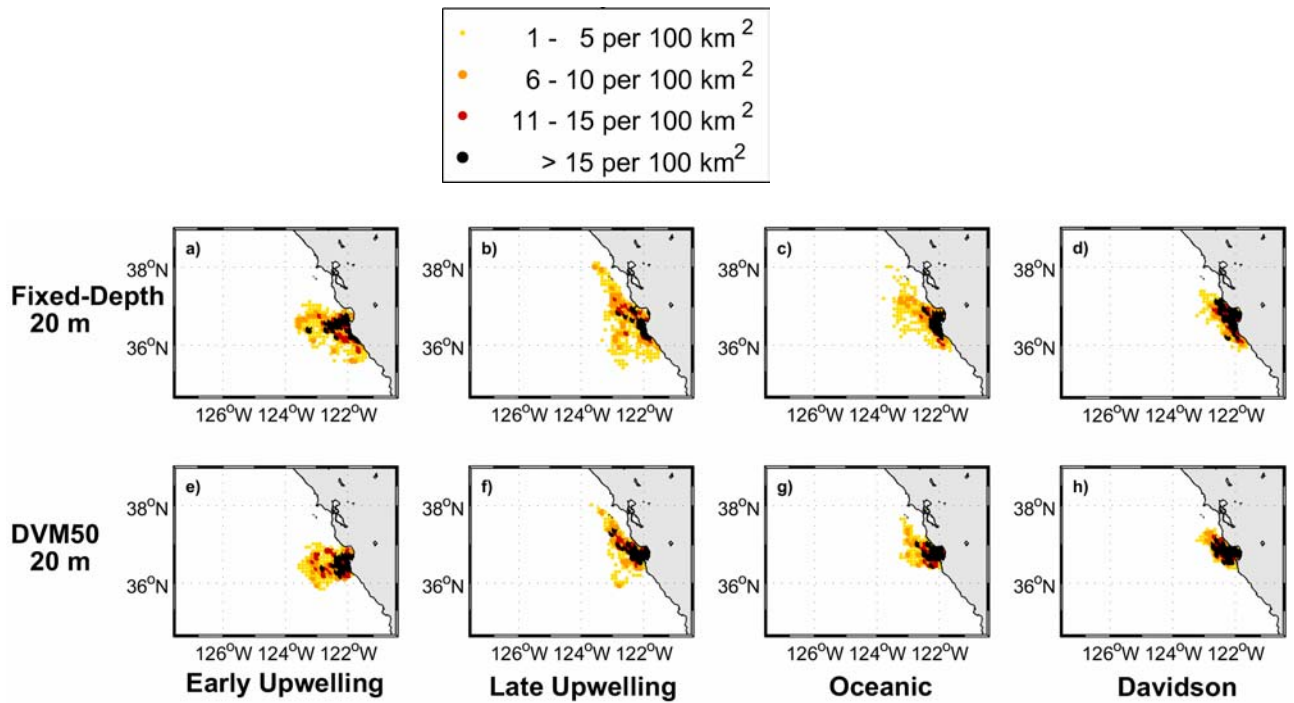


Fig. 4.8. Distribution of drifters started at 20 m depth after 20 d of transport.

#### 4.3.2 Influence of DVM on self-recruitment

*Retention of drifters-* Fixed-depth drifters transported below  $\sim 30$  m depth tend to remain in Monterey Bay much longer than drifters transported at lesser depths (Fig. 4.9) because they are not subject to strong southward and westward Ekman layer currents near the surface. The exception is drifters transported at  $\geq 50$  m depth during the late upwelling season (mid-May – mid-August) and drifters transported at  $\geq 10$  m depth during the Davidson season (mid-November – mid-February; Fig. 4.9). These drifters are transported out of the Bay relatively quickly by northward undercurrents.

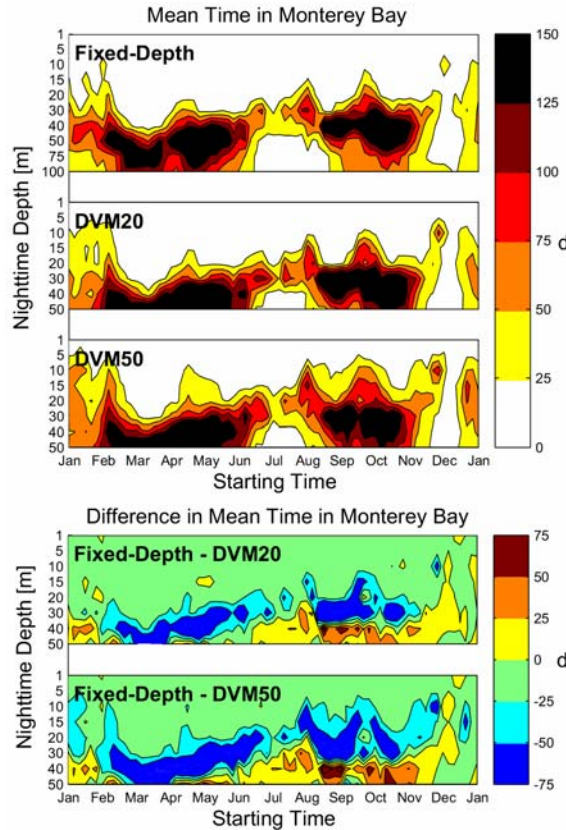


Fig. 4.9. Top: Mean time that drifters remain in Monterey Bay. Bottom: Difference between the mean time that fixed-depth and DVM drifters remain in Monterey Bay.

DVM has relatively little influence on the time that drifters transported above  $\sim 20$  m depth remain in Monterey Bay (Fig. 4.9) because these drifters are still transported rapidly out of the Bay. For drifters transported below 20 m depth during the early upwelling season and the first half of the late upwelling season (mid-February – early June) and drifters transported around 15 - 30 m depth during the oceanic season (mid-August – mid-November), DVM generally increases the time that they remain in Monterey Bay (Fig. 4.9) because they are migrating from southward currents at night to northward currents during the day. During the late upwelling, oceanic, and Davidson seasons (mid-June – early February), DVM tends to decrease the time that the deepest drifters remain in Monterey Bay (Fig. 4.9)

because these drifters are in northward undercurrents throughout the diel cycle with some migrating into stronger northward undercurrents during the day.

*Return of drifters-* During the upwelling and oceanic seasons (mid-February – mid-November), return rates are relatively low ( $< 10\%$ ) for fixed-depth drifters transported near the surface or at deeper depths (Fig. 4.10) because these drifters are transported rapidly away from the Bay in the surface Ekman layer or northward undercurrents. Return rates are high ( $\geq 60\%$ ) for fixed-depth drifters transported from 20 - 40 m depth during the upwelling and oceanic seasons and for fixed-depth drifters transported in the upper 50 m of the water column during the Davidson season (Fig. 4.10) because there is a seasonal reversal of currents at these depths and drifters are generally transported back to the Bay in the season after they exit the Bay (Fig. 4.11). Fixed-depth drifters that return to Monterey Bay during the Davidson and early upwelling seasons are generally transported to the south of Monterey Bay before returning (Fig. 4.12). In contrast, fixed-depth drifters that return to Monterey Bay during the late upwelling and oceanic seasons have widely variable trajectories and may be transported to the north, south, or west of the Bay before returning (Fig. 4.12). Return rates for fixed-depth and DVM20 drifters started during the upwelling seasons, particularly the late upwelling season, may be artificially low because many of these drifters exit the model grid through the southern boundary (Fig. 4.7). It is doubtful, however, that many of these drifters would return to Monterey Bay in subsequent seasons after such substantial southward transport.

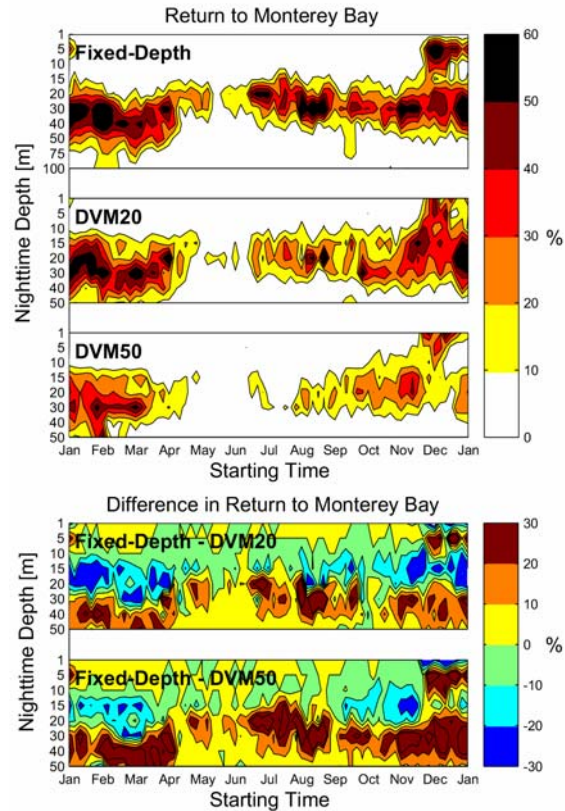


Fig. 4.10. Top: Percentage of drifters exiting Monterey Bay for  $\geq 30$  d that returns to the Bay. Bottom: Difference between the percentages of fixed-depth and DVM drifters exiting Monterey Bay for  $\geq 30$  d that return to the Bay.

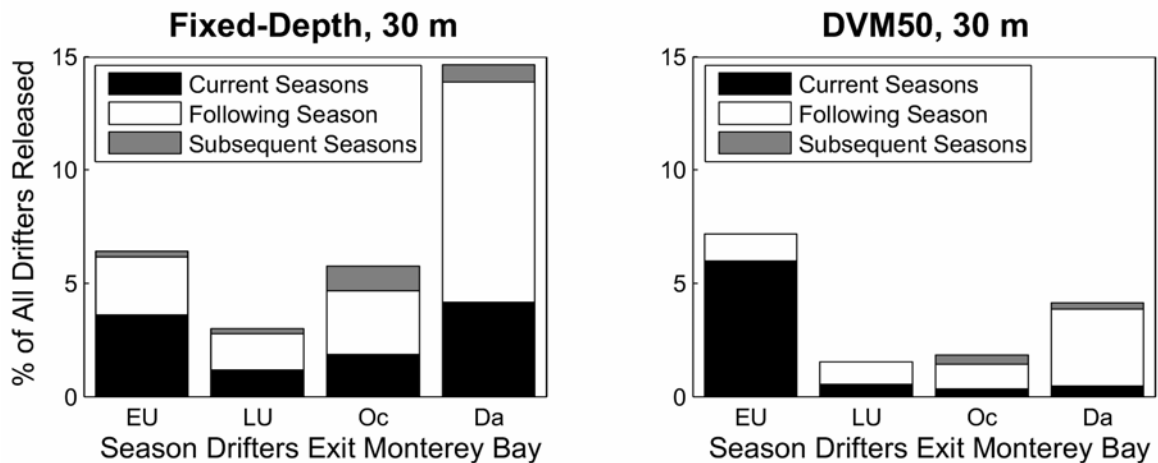


Fig. 4.11. Season of return for fixed-depth and DVM drifters started at 30 m depth (the depth with the highest average return rate) that exit the Bay for  $\geq 30$  d then return.

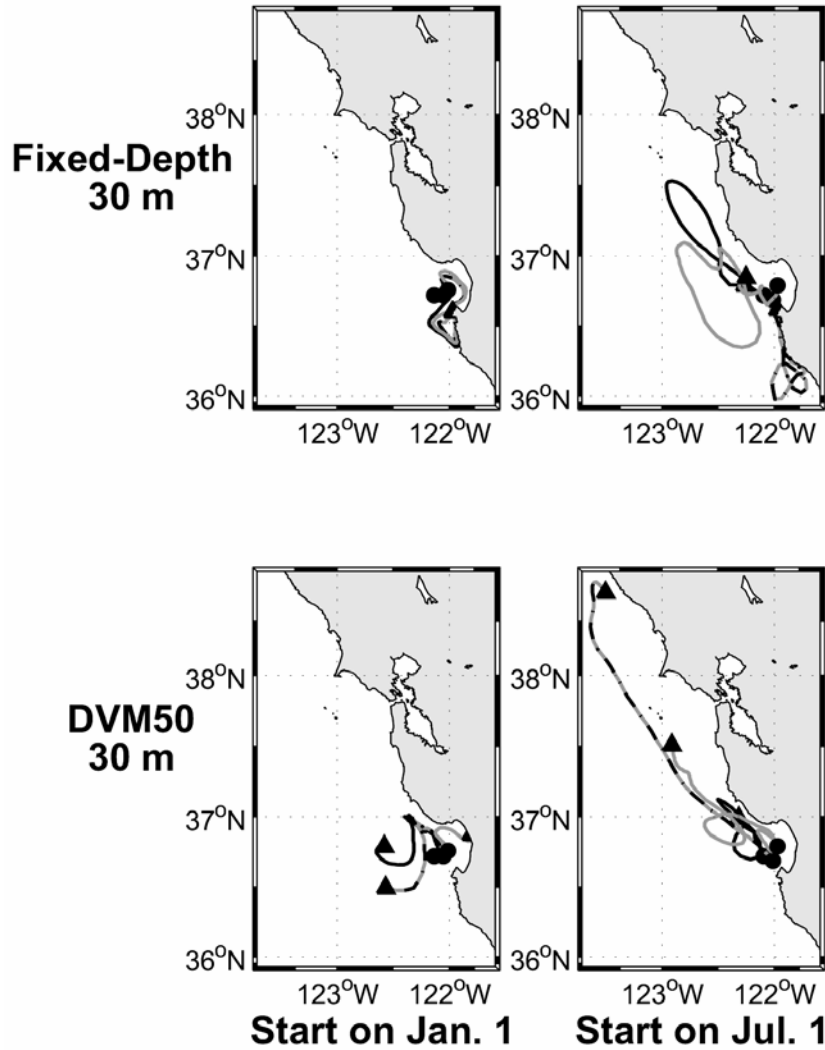


Fig. 4.12. Top: Trajectories of fixed-depth drifters started at 30 m depth that exit Monterey Bay for  $\geq 30$  d then return to the Bay (1 d position intervals). Starting locations are shown by black dots, and reentry locations are shown by black triangles. Bottom: Trajectories of analogous DVM drifters started at the same locations and times. Starting locations are shown by black dots, and ending locations are shown by black triangles. DVM decreases return rates for drifters with a nighttime depth below 20 – 30 m therefore fewer of the analogous DVM drifters return to the Bay.

DVM tends to increase return rates for drifters with a nighttime depth above 20 – 30 m (Fig. 4.10) because their migration to deeper waters during the day reduces transport away from the region and increases their exposure to seasonal reversal in currents. DVM tends to decrease return rates for drifters with a nighttime depth below 20 – 30 m (Fig. 4.10) because

their migration to deeper waters during the day increases their exposure to strong northward undercurrents and decreases their exposure to seasonal reversals in currents (Fig. 4.12).

#### 4.3.3 Influence of DVM on the source of recruits

*Source of fixed-depth recruits-* As with the mean transport of fixed-depth drifters started in Monterey Bay, there are strong seasonal patterns in the source of recruits to Monterey Bay (Fig. 4.13). During the upwelling and oceanic seasons (mid-February – mid-November), the source of fixed-depth recruits in the upper water column (1 - ~ 30 m depth) is to the northwest (Fig. 4.13) because recruits are transported to the Bay by wind-driven southward surface currents. The source of fixed-depth recruits to the Bay is farthest north during the upwelling seasons (mid-February – mid-August), particularly the early upwelling season when the coastal upwelling jet is strongest, and ranges from north of San Francisco Bay to Monterey Bay (Fig. 4.14). During the Davidson season (mid-November – mid-February) and below ~ 30 m depth during the upwelling and oceanic seasons, the source of fixed-depth recruits to the Bay is generally to the southeast (Fig. 4.13) because recruits are transported to the Bay by northward undercurrents. The main source of recruits to the Bay is farthest south during the late upwelling and oceanic seasons and ranges from north of Morro Bay to Monterey Bay (Fig. 4.15). Drifters do not tend to recruit to Monterey Bay from very far offshore because there is little onshore transport in the region at the depths simulated (Figs. 4.13, 4.14, 4.15).



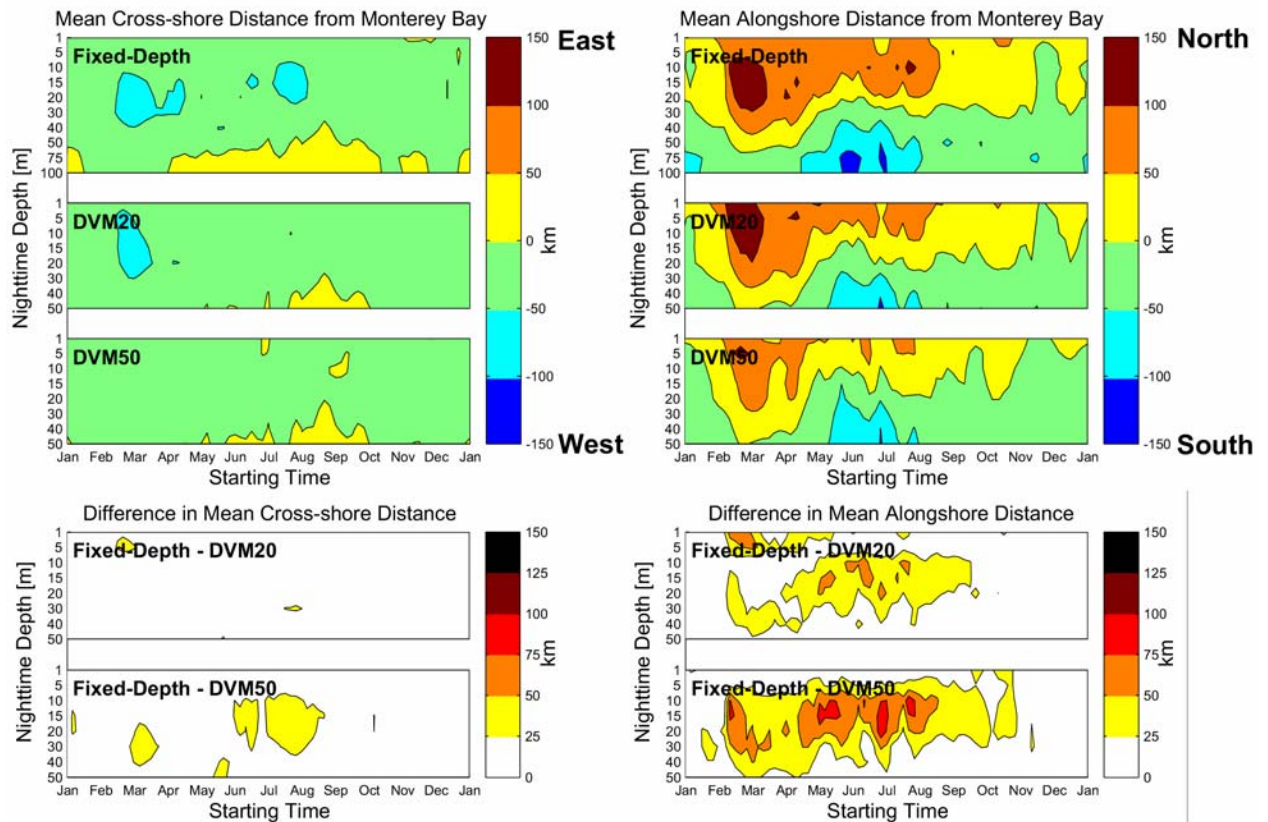


Fig. 4.13. Top: Origin of drifters that recruit to Monterey Bay after 20 d of transport. Positive values represent sources to the east and north, and negative values represent sources to the west and south. Bottom: Absolute difference between origin of fixed-depth and DVM drifters that recruit to Monterey Bay after 20 d of transport. Starting times correspond to when drifters leave their source location.



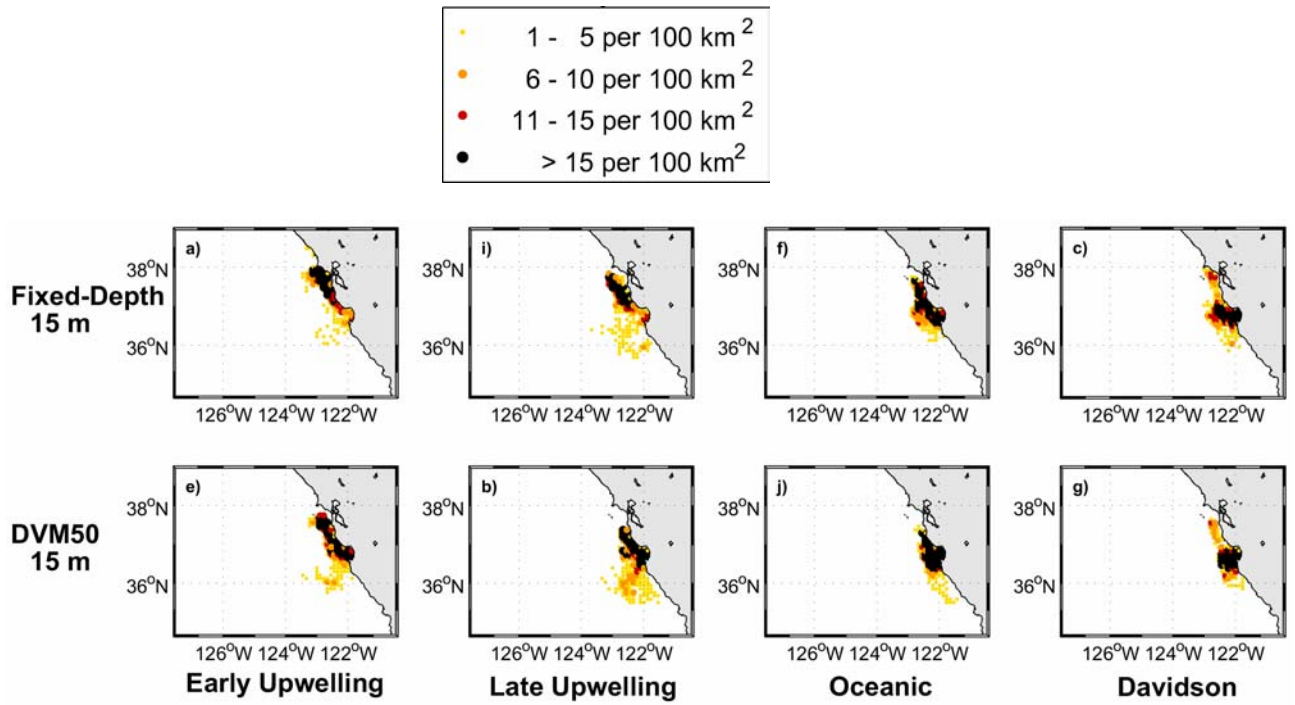


Fig. 4.14. Starting locations of drifters started at 15 m depth that recruit to Monterey Bay after 20 d of transport. Seasons correspond to when drifters leave their source location.

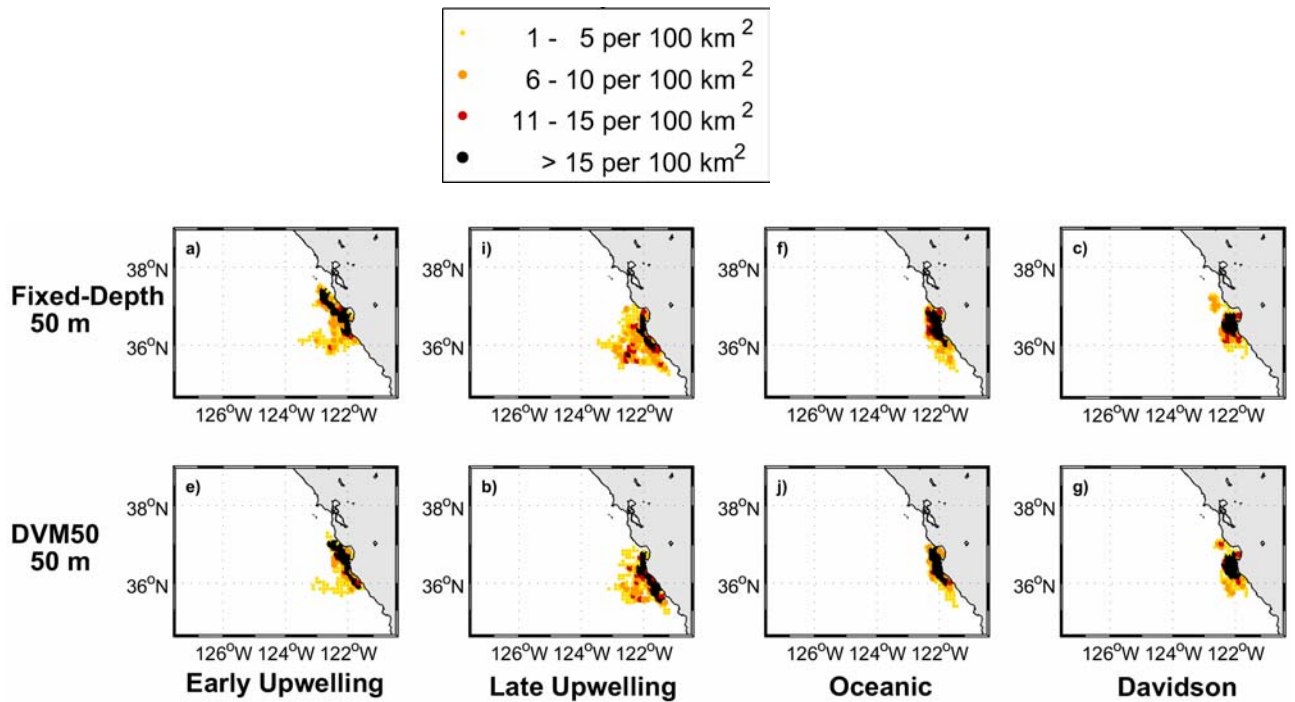


Fig. 4.15. Starting locations of drifters started at 50 m depth that recruit to Monterey Bay after 20 d of transport. Seasons correspond to when drifters leave their source location.

*Source of DVM recruits-* During the upwelling and oceanic seasons (mid-February – mid-November), DVM shifts the main source of recruits in the upper water column ( $\leq 30 - 50$  m depth) farther south and closer to Monterey Bay (Figs. 4.14, 4.15) because migration between the southward, wind-driven Ekman layer and northward undercurrents results in slower net southward transport from source regions. Below 30 – 50 m depth, DVM does not tend to have a strong influence on source regions for recruits to Monterey Bay (Fig. 4.15) because there is generally less vertical current shear at this level in the water column.

#### 4.4 Discussion

A fundamental question in marine ecology is how populations in highly advective regions, such as upwelling regions, are retained. Is it possible for these populations to be self-sustaining or are they necessarily dependent on a constant supply of recruits from upstream regions? It has been hypothesized that zooplankton vertical migration into subsurface poleward and onshore currents during the day compensates for equatorward and offshore transport by surface currents at night and enables retention in upwelling regions (Peterson, 1998). In this study, we test this hypothesis in the Monterey Bay region of central California using a fully three-dimensional (3D) hydrodynamic model coupled to simple diel vertical migration (DVM) behavioral models. We found that under the conditions we simulated (seasonally-varying mean circulation with accompanying mesoscale activity), vertical migration out of the surface Ekman layer during the day decreases transport away from the region but does not fully compensate for nighttime transport and does not lead to nearshore retention (Figs. 4.5, 4.7, 4.9). DVM has little effect on the transport of

zooplankton with deeper nighttime depths or during non-upwelling periods (Figs. 4.5, 4.7, 4.8). It does tend to increase zooplankton retention time in the region (Fig. 4.9).

These results contrast with those of Batchelder et al. (2002) who found that DVM retains copepods nearshore in an Oregon upwelling region. The difference in results arises because Batchelder et al. (2002) used a two-dimensional (2D) hydrodynamic-ecosystem model in which offshore upwelling flow at the surface was balanced by strong onshore return flow in a relatively thin benthic boundary layer. Simulated copepods using DVM were programmed to migrate into this return flow during the day, therefore their daytime onshore transport compensated for nighttime offshore transport and retained them nearshore (Batchelder et al., 2002). In our 3D model, the presence of alongshore pressure gradients means onshore return flow is spread more evenly throughout the interior rather than being restricted to a bottom boundary layer (Marchesiello et al., 2000; Fig. 4.2). Onshore return flow below the surface is weak relative to offshore Ekman transport at the surface even though onshore and offshore transport are roughly balanced (i.e. strong offshore transport in the upper 20 m roughly balances weak return transport in the lower water column; Fig. 4.2). As a result, onshore transport of vertically-migrating zooplankton during the day does not compensate for their offshore transport near the surface at night (Fig. 4.5). Initial results for other regions along the central California coast indicate that full compensation between nighttime and daytime transport of vertically migrating zooplankton near the surface at night does not occur in these regions either but there is generally more compensation than in Monterey Bay (X.J. Capet, UCLA, USA, Pers. Comm.). Greater compensation is also likely on shallow shelves, such as the U.S. East Coast, in which subsurface return flow will be concentrated into a relatively thin vertical layer.

Despite the lack of retention for vertically-migrating zooplankton near the surface at night in our study, retention is likely to be an important self-recruitment mechanism for marine populations in upwelling regions. Our model does not resolve small-scale temporal or spatial recruitment mechanisms, such as upwelling relaxation events (Wing et al., 2003) or upwelling shadows (Graham and Largier, 1997), that may retain organisms in the Monterey Bay region. In addition, transport during the non-upwelling Davidson season decreases zooplankton transport away from the region (Figs. 4.5, 4.7, 4.8), and continuous transport below the surface Ekman layer can lead to relatively long retention times in the region (Fig. 4.9). Both of these transport characteristics have been observed for larval and juvenile fish in upwelling regions (Peterson, 1998; Sponaugle et al., 2002). Fixed-depth transport during the Davidson season or below the surface Ekman layer have the advantage that they eliminate the considerable metabolic costs of vertical migration but the disadvantage that organisms will not be transported during peak annual productivity or in highly productive surface waters.

The use of a fully 3D model also allows us to explore the implications of realistic alongshore transport on zooplankton transport and recruitment in the Monterey Bay region. Upwelling jets in the region are so strong (often  $> 20 \text{ cm s}^{-1}$ ) that even zooplankton that migrate out of the jets during the day have strong net southward transport (Fig. 4.6) and alongshore transport away from the region often exceeds offshore transport (Figs. 4.5, 4.7, 4.8). Despite strong advection away from the region, we found that seasonal changes in hydrography could enable relatively high levels of self-recruitment to the region by allowing zooplankton to return to Monterey Bay after transport away (Fig. 4.10, 12). The influence of

DVM on return to the region is complex but tends to decrease the potential for this means of self-recruitment to Monterey Bay (Fig. 4.10).

The influence of ontogenetic vertical migration (OVM) on self-recruitment to the Monterey Bay region will depend on the amount of time that organisms spend at different depths. If organisms spend relatively little time at the surface, it is likely they can be retained in the Bay (Figs. 4.8, 4.9) or returned to the region via seasonal changes in hydrography (Figs. 4.10, 4.12). These observations support the proposal of Peterson (1998) that OVM rather than DVM could be the key to retaining zooplankton populations in upwelling regions. In contrast, if organisms spend a considerable amount of time near the surface during the upwelling or oceanic seasons, they will be transported away from the region and are unlikely to be able to recruit to the Bay (Figs. 4.5, 4.7, 4.9, 4.10).

Determining self-recruitment levels for marine populations is critical to managing them effectively because self-recruitment levels can determine the vulnerability of local populations to local changes in fishing pressure or habitat modifications. While it is unlikely that zooplankton populations in Monterey Bay are reproductively isolated from alongshore or offshore organisms of the same species, our results suggest the potential for high levels of self-recruitment in the Monterey Bay region for both fixed-depth and vertically-migrating zooplankton with a nighttime depth below 20 – 30 m (Figs. 4.9, 4.10). The potential for high levels of self-recruitment is surprising for such a highly advective upwelling region but adds to a growing body of evidence that self-recruitment in marine populations is more common than previously believed (Warner and Cowen, 2002). Actual self-recruitment levels will vary according to larval duration. Organisms with shorter (longer) larval durations are more (less) likely to be retained in the region (Fig. 4.9). Organisms with relatively long larval durations

(>> 20 d), such as the Dungeness crab *Cancer magister* with a larval duration of ~ 4 months (Botsford et al., 1994), may be able to take advantage of seasonal reversals in currents to return to starting regions (Fig. 4.11).

In addition to determining the influence of DVM on zooplankton transport and self-recruitment in the region, we also determine source regions for recruits to Monterey Bay. Knowing the location of source regions for recruits is important for managing marine resources because habitat alterations and fishing effort in source regions will affect marine stocks in Monterey Bay. Adult migrations to source regions to spawn are another means of enabling self-recruitment to a region and have been observed for fish in upwelling regions (Peterson, 1998; Sponaugle et al., 2002). We found that DVM shifts source regions for recruits closer to the Bay during upwelling periods but has little effect during non-upwelling periods (Fig. 4.13). While these are the first descriptions of source regions for recruits to Monterey Bay to date, actual recruitment levels to Monterey Bay will depend on population distributions and densities in these source regions.

Determining source regions for recruits is also critical for predicting the likelihood of the spread of marine invasive species via alongshore currents. San Francisco Bay is one of the most highly invaded estuaries in the world (Cohen and Carlton, 1998). Our results show that there is seasonal transport of near-surface fixed-depth and vertically-migrating zooplankton from San Francisco Bay to Monterey Bay (Fig. 4.14). This suggests that invasive species in San Francisco Bay could routinely reach Monterey Bay. Transport via alongshore currents has been proposed for the observed spread of the invasive European green crab *Carcinus maenas* along the California coast north of San Francisco (Grosholz and Ruiz, 1995). Green crabs were first observed in San Francisco Bay in 1989 and 1990, spread to Monterey Bay by

1993, and are now found as far south as Morro Bay (Grosholz and Ruiz, 1995; Wasson et al., 2001). DVM should decrease the likelihood, or at least the rate, of spread of invasive species via alongshore currents because vertically-migrating organisms tend to remain closer to their starting points (Figs. 4.14, 4.15). Our results are partially a function of the 20-d larval duration simulated. Source regions are likely to be more (or less) expansive for longer (or shorter) larval durations.

Models inherently involve the simplifications of complex biological systems, and our models of DVM consist of Lagrangian drifters that made vertical jumps in the water column at fixed times of the day (Fig. 4.4). They do not account for many intrinsic (e.g. age, hunger state, reproductive condition, swimming capability) and environmental factors (e.g. cloud cover, seasonal changes in photoperiod and light intensity, presence of predators) that can influence the depth and timing of an organism's migration. For a few organisms (e.g. *Euphausia pacifica*, *Metridia pacifica*), the influence of many of these factors on their vertical migratory behavior is known, and more sophisticated biological models can be created (Eiane and Parisi, 2001; reviewed in Werner et al., 2001). However, the vertical migratory behaviors of most organisms are still poorly described. This study provides a first-order estimate of the influence of DVM on transport and recruitment if basic descriptions of nighttime and daytime vertical distributions are available.

*Conclusions-* While DVM behaviors may not exist solely for their influence on transport, they are potentially important determinants of the spatial dynamics of marine populations. In this study, we use a fully three-dimensional (3D) hydrodynamic model to determine the influence of DVM on zooplankton transport and recruitment in an upwelling region. We

found that zooplankton vertical migration into subsurface poleward and onshore currents during the day does not fully compensate for equatorward and offshore transport in the surface Ekman layer at night and, therefore, does not enable retention in the Monterey Bay region as has been hypothesized for other upwelling regions. DVM also tends to decrease the ability of zooplankton to return to the region after transport away. While DVM does not appear to substantially increase the potential for self-recruitment to the region, our results suggest that other mechanisms, such as transport during non-upwelling periods, continuous transport below the surface, return to the region via seasonal changes in hydrography, and ontogenetic vertical migration, may still enable relatively high levels of self-recruitment to this highly advective region. In addition, we offer the first description to date of potential source regions for recruits to Monterey Bay. Coastal resource managers in the region can use the transport and recruitment patterns determined in this study for assessing the potential for self-recruiting populations, predicting recruitment levels for exploited marine species, designing and assessing marine protected areas, and predicting the natural dispersal of invasive species (Botsford, 2001; Strathmann et al., 2002).



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## **Chapter 5. Do they really matter?: The influence of vertical migratory behaviors on transport in the marine environment**

### **5.1 Introduction**

This chapter synthesizes the existing literature, including the new work included in this dissertation, to determine the extent to which the results of *realistic* and *quantitative* studies support the commonly-held belief that VMBs have a significant influence on transport in the marine environment. Since there are not currently any field studies comparing the transport of fixed-depth and vertically-migrating drifters from the same starting locations at the same time, this review is limited to studies that have used 2D or 3D hydrodynamic models to simulate and compare the trajectories of organisms that are passive or have a fixed depth near the surface with the trajectories of organisms that migrate vertically from near the surface to deeper depths. Only results from 2D and 3D models are included because theoretical or relatively simple models (e.g. 1D progressive vector models) of the influence of VMBs on transport can provide tremendous insight into relevant processes but cannot describe transport in spatially heterogeneous environments (e.g. deGraaf, 2004). Important contributions have been made by a number of studies that incorporated VMB into modeling studies of organismal transport but did not also consider passive or fixed-depth behaviors. These studies have not been explicitly included in this review (e.g. Bartsch et al., 1989; Hermann et al., 1996; Rothlisberg et al., 1996; Condie et al., 1999; Hare et al., 1999).

### **5.2 Synthesis of relevant studies**

### 5.2.1 Selective tidal-stream transport (STST)

Despite the potential importance of VMBs to the transport of marine organisms, there have been relatively few attempts to describe their influence on transport rates and trajectories, particularly for STST behaviors. (See compilation of studies in Table 1.) Although the small number of STST studies limits the scope of conclusions that can be drawn, the studies generally support the assumptions that FTT enables retention in tidal estuaries and embayments (Jacobsen et al., 1990), ETT enables down-estuary transport and export from tidal estuaries and embayments (DiBacco et al., 2001; Carr et al., 2005), and STST enables directed migrations on continental shelves (Arnold and Holford, 1995; deGraaf et al., 2004). Directed transport is likely to be critical to the maintenance of many marine populations because it enables successful migrations to nursery, reproductive, and feeding areas (e.g. deGraaf et al., 2004; Carr et al., 2005).

Study	Organisms	Location	Model	Results	Other
<i>Flood-Tide Transport</i>					
Jacobson et al. (1990)	Oyster larvae	Delaware Bay	3D	FTT retained larvae in bay and enabled return near natal beds.	STST increases potential for self-recruitment in population.
Jenkins et al. (1999)	Fish postlarvae	Port Phillip Bay	3D		Addition of behaviors observed at the mouth of the bay did not improve/decreased predictive capability of the model, possibly because behaviors do not occur throughout the bay.
<i>Ebb-Tide Transport</i>					
DiBacco et al. (2001)	Crab larvae	San Diego Bay	2D <sup>a</sup>	ETT substantially decreased retention in bay.	Larval export is reduced when ETT larvae migrate lower in but do not leave the water column during flood tides.
Carr et al. (2005)	Adult crabs	Beaufort Inlet estuarine system, North Carolina	2D <sup>a</sup>	ETT led to down-estuary transport and export from estuary.	Study used detailed ETT behaviors developed from field and laboratory experiments and validated modeled trajectories with observed trajectories. Transport with observed behaviors is substantially less than transport with idealized behaviors because crabs do not migrate continuously during ebb tides.
<i>Selective Tidal-Stream Transport</i>					
Arnold and Holford (1995) <sup>b</sup>	Adult fish	Southern North Sea and English Channel	2D <sup>a</sup>	STST enabled migration away from spawning grounds.	
deGraaf et al. (2004)	Fish larvae	Southern North Sea	2D <sup>a</sup>	STST directed transport towards coast.	STST increases success at reaching coastal nursery areas. Analogous 1D model fail to predict this effect.

Table 5.1. Influence of STST behaviors in estuarine and continental shelf environments with semi-diurnal currents. <sup>a</sup>Depth-averaged. <sup>b</sup>Update to Arnold and Cook (1984).

### 5.2.2 Diel vertical migration (DVM)

The vast majority of studies of the influence of VMBs on transport have examined DVM. (See compilation of studies in Table 2.) This behavior is widespread in marine environments and has been studied more extensively than STST and OVM. With a few notable exceptions,

DVM tends to increase the retention of organisms near their starting locations relative to continuous transport near the surface. Organisms tend to be retained in regions dominated by  $M_2$  semi-diurnal currents because DVM reduces the time that organisms spend in the water column (e.g. Luettich et al., 1998; Culberson, 2004), regions dominated by estuarine circulation because organisms migrate between seaward currents at the surface and landward currents at deeper depths (e.g. Larson et al., 2003), and regions dominated by wind-driven surface currents (surface Ekman layers) because organisms are migrating between strong wind-driven currents at the surface and weaker and/or opposing currents at deeper depths (e.g. Batchelder et al., 2002; Carr et al., 2005).

While STST behaviors have undoubtedly developed because of their influence on transport, a preponderance of DVM studies demonstrate that these behaviors are also often linked to migratory or recruitment success and are probably critical to the maintenance of many marine populations (e.g. Griffin et al., 2001; Carr et al., In review; Emsley et al., 2005). Retention near parental habitat by DVM may be particularly important to marine populations because parental habitat is likely to be suitable for offspring. Retention (as opposed to random dispersal) may increase developmental and recruitment success (Strathmann et al., 2002). A particularly important example of the benefits of retention is coastal upwelling regions where the retention of organisms in productive nearshore waters likely increases food availability for organisms and leads to reduced losses to starvation, faster growth rates, increased fecundity, and increased population sizes (Wroblewski, 1982; Rumsey and Franks, 1999).

DVM does not necessarily retain organisms near their starting locations, however. In regions with a strong  $S_2$  semi-diurnal tide in which organisms spend periods  $\leq 12$  h at the



surface or in regions with strong diurnal tides, DVM can actually act as a STST behavior and can increase the transport of organisms away from their starting locations (e.g. Rothlisberg et al., 1983; Hill, 1994; Smith et al., 2001; Sentchev and Korotenko, 2004). Since DVM which has a period of 24 h and the  $S_2$  tide which has a period of 12 h are phase-locked, DVM organisms in a given region are transported by currents during roughly the same phase of the  $S_2$  tide every night. The relative phases of DVM and the  $S_2$  tide in that region will determine the magnitude and direction of net transport. DVM can also lead to directed transport over relatively long periods of time in regions with strong diurnal tides. The length of time that the interaction between DVM and a tide will result in net horizontal transport is equal to half the beat period between DVM and the tide in question. The closer the tidal period is to 24 h, the longer the period of time over which net horizontal transport in a given direction is possible, e.g. 85 d in the  $K_1$  tide but only 7 d in the  $M_2$  tide (reviewed in Hill, 1998). As with DVM- $S_2$  tide interactions, the relative phases of DVM and a diurnal tide determine the magnitude and direction of net transport. For a full review of DVM-tidal interactions, see Hill (1991, 1994, 1998). And in cases where organisms do not move to the bottom during one phase of their daily migration or regions which do not have consistent strong vertical current shear, DVM may not have a significant influence on transport (e.g. Gallego et al., 1999) or may not have sufficient influence to enable self-recruitment to the region (e.g. Carr et al., In review).

Study	Organisms	Location	Model	Results	Other
<i>Interaction with semi-diurnal tides</i>					
Hill (1994)	Idealized organisms	Northwest European continental shelf	2D <sup>a</sup>	DVM interacted with the S <sub>2</sub> semi-diurnal tide to produce regions with net horizontal transport.	The relative phases of DVM and the S <sub>2</sub> tide determine whether regions are convergent or divergent.
Arnold and Holford (1995) <sup>b</sup>	Adult fish	Southern North Sea and English Channel	2D <sup>a</sup>	DVM retained fish on spawning grounds.	
Luettich et al. (1998)	Fish larvae	Beaufort Inlet, North Carolina	2D <sup>a</sup>	DVM slowed larval migration through the inlet.	
Culberson et al. (2004)	Fish larvae	San Francisco Bay	3D	DVM slowed larval migration and increased entrainment in the water diversion.	Water diversions in the estuary may entrain larvae and have a negative effect on larval recruitment.
Sentchev and Korotenko (2004)	Fish larvae	Eastern English Channel	3D	DVM interacted with the S <sub>2</sub> semi-diurnal tide to slow the transport of larvae to the north.	DVM decreases larval recruitment to the English coast.
<i>Interaction with diurnal tides</i>					
Rothlisberg et al. (1983)	Shrimp larvae	Gulf of Carpenteria	3D	DVM interacted with diurnal tides to produce net horizontal transport and increase transport towards estuarine nursery areas during the main reproductive season.	Migration to the bottom during day increases horizontal advection. DVM increases range of effective spawning population (i.e. adults whose young will reach nursery grounds) during the main reproductive season.
Smith et al. (2001)	Adult euphausiids and copepods	Juan de Fuca region	3D	DVM interacted with diurnal tides to produce net horizontal transport but the direction of transport varied seasonally.	Addition of behavior helps explain observed zooplankton distributions.
<i>Interaction with estuarine circulation/buoyancy-driven currents</i>					
Hinckley et al. (1996)	Fish eggs and larvae	Shelikof Strait and western Gulf of Alaska	3D	The influence of DVM on transport was not described in detail.	DVM into cold sub-surface waters delays the transition from non-feeding to feeding larval stage and metamorphosis from larvae to juvenile.
Larson et al. (2003)	Idealized organisms	Juan de Fuca region	3D	DVM increased retention in the strait.	The Juan de Fuca Strait has been recommended as a ballast water discharge site

					because of the assumption that seaward transport at the surface would transport potentially invasive species away from coastal habitats where they could reproduce and establish populations. This assumption that is incorrect for DVM organisms.
Emsley et al. (2005)	Adult euphausiids and copepods and fish larvae	Irish Sea	3D	DVM increased retention in the sea through entrainment in a buoyancy-driven gyre.	DVM increases potential for self-recruitment in population.
<i>Interaction with wind-driven surface Ekman layers</i>					
Wroblewski (1982)	Adult copepods	California Current System	2D <sup>c</sup> , 3D <sup>d</sup>	DVM increased nearshore residence time and decreased alongshore transport.	
Bucklin et al. (1989)	Adult copepods	California Current System	3D	DVM decreased offshore transport and increased residence time in an upwelling jet.	
Werner et al. (1993)	Fish larvae	Georges Bank	3D	DVM had little influence on transport relative to passive or fixed-depth transport near the organism's mean depth.	
Botsford et al. (1994)	Crab larvae and megalopae	California Current System	3D <sup>e</sup>	DVM reduced offshore and alongshore transport.	
Hannah et al. (1998)	Adult copepods	Gulf of Maine and Georges Bank	3D	DVM slowed transport to the bank.	
Gallego et al. (1999)	Copepodites	North Sea	3D	DVM did not have a major effect on larval recruitment.	
Jenkins et al. (1999)	Fish postlarvae	Port Phillip Bay	3D	DVM increased westward wind-driven transport relative to the transport of passive organisms dispersed throughout the water column.	Addition of behaviors observed at the mouth of the bay did not improve/decreased predictive capability of the model, possibly because behaviors do not occur throughout the bay.
Jenkins et al. (2000)	Fish postlarvae	Southeast coast of Australia	3D <sup>f</sup>	DVM moved spawning sites offshore.	Field observations suggest that the spawning locations predicted for passive larvae are more likely to be

					accurate, possibly because DVM only develops in the more advanced larval stages.
Griffin et al. (2001)	Lobster larvae	Leeuwin Current System	3D	DVM increased larval retention near Australia west coast.	DVM likely increases recruitment to the fishery.
Batchelder et al. (2002)	Adult copepods	Idealized region similar to California Current System	2D <sup>c</sup>	DVM retained copepods nearshore.	Nearshore retention enables copepods to exploit food resources in productive upwelling regions.
Murphy et al. (2004)	Adult euphausiids	Scotia Sea	3D	DVM decreased northward and increased eastward transport. DVM and mean-field flow trajectories were similar.	
Hinrichsen et al. (2005)	Fish larvae	Baltic Sea	3D	DVM increased retention in deep basins and decreased mixing between basins.	DVM increases potential for self-recruitment in population and may allow genetic heterogeneity between regional populations.
Carr et al. (In review)	Idealized zooplankton	California Current System	3D	DVM reduced offshore and alongshore transport during spring-summer upwelling but did not enable nearshore retention.	3D model results differ from previous 2D results because return currents below the surface are substantially weaker than offshore currents in the surface Ekman layer, therefore onshore transport during the day does not fully compensate for offshore transport at night.

Table 5.2. Influence of DVM behaviors on transport in different environments.

Environments characterized by multiple influences (e.g. semi-diurnal tides and buoyancy-driven currents) categorized by influence with greatest interaction with VMB. All results are relative to the transport of passive or fixed-depth particles near the surface unless specified otherwise. <sup>a</sup>Depth-averaged. <sup>b</sup>Update to Arnold and Cook (1984). <sup>c</sup>Alongshore-averaged. <sup>d</sup>Uniform alongshore topography. <sup>e</sup>Model included southward wind forcing but no surface Ekman layer. <sup>f</sup>Study used reverse simulation, i.e. tracking organisms from their ending to their starting locations by running the model backwards in time.

### 5.2.3 Ontogenetic vertical migration (OVM)

There have been very few studies of the influence of OVM on transport because most OVM studies do not compare the long-term trajectories of vertically-migrating organisms with analogous passive or fixed-depth trajectories (e.g. Slagstad and Tande, 1996; Pederson et al., 2001). (See compilation of studies in Table 3.) Although the small number of OVM studies limits the scope of conclusions that can be drawn, the existing studies lead to conclusions similar to those for DVM, namely that OVM tends to increase the retention of organisms near their starting location relative to continuous transport near the surface. Retention occurs in estuarine circulation because seaward flow near the surface is roughly balanced by landward flow deeper (e.g. Jacobsen et al., 1990) and regions dominated by wind-driven surface currents because organisms are migrating between strong wind-driven currents at the surface and weaker and/or opposing currents at deeper depths (e.g. Stenevik et al., 2003; Paris and Cowen, 2002). Continuous transport below the surface may also increase retention near starting locations and potentially increase self-recruitment levels but has the disadvantage that organisms will not spend as much time in highly productive surface waters (e.g. Werner et al., 1993; Tremblay et al., 1994).

Study	Organisms	Location	Model	Results	Other
<i>Interaction with estuarine circulation/buoyancy-driven currents</i>					
Jacobsen et al. (1990)	Oyster larvae	Delaware Bay	3D	OVM descents increased retention in the bay. Relatively fast descents enabled return near natal beds.	OVM increases potential for self-recruitment in population.
<i>Interaction with wind-driven surface Ekman layers</i>					
Werner et al. (1993)	Fish larvae	Georges Bank	3D	OVM from near-surface to deeper depths decreased retention on bank relative to continual passive or fixed-depth transport below the surface.	
Tremblay et al. (1994)	Scallop larvae	Georges Bank	3D	Deeper OVM ascent termination depths decreased transport from starting locations.	Deeper OVM ascent termination depths increase likelihood of self-recruitment in scallop populations.
Mullon et al. (2003)	Fish eggs and larvae	Southern Benguela Current System	3D	Eggs that were too buoyant were advected offshore. Eggs that were too dense were transported too slowly to reach nursery areas within a suitable developmental window.	OVM occurs because egg buoyancy changes in the first six days of transport. Ascent/descent of eggs to appropriate depths is necessary for successful transport to inshore nursery areas.
Stenevik et al. (2003)	Fish larvae	Northern Benguela Current System	3D	OVM to deeper depths increased retention nearshore.	OVM is assumed to be an adaptation to regional circulation to decrease larval mortality rates.
Paris and Cowen (2004)	Fish larvae	Coral reef off west coast of Barbados	2D <sup>a</sup>	OVM to deeper depths increased retention of larvae near the reef.	OVM increases potential for self-recruitment in population.
<i>Interaction with large-scale circulation patterns</i>					
Bryant et al. (1998)	Adult copepods	Eastern North Atlantic	3D	Seasonal vertical migration from deep water in winter to shallow water in spring enabled return to some regions after a year.	OVM appears to enable some regions to have self-recruiting populations, i.e. copepods return to their origination locations after a year. In simulations without a deep overwintering phase, there was no long-term persistence of copepods originating in the Norwegian Sea.

Table 5.3. Influence of OVM behaviors on transport in different environments. Environments characterized by multiple influences (e.g. semi-diurnal tides and buoyancy-driven currents) categorized by influence with greatest interaction with VMB. All results are

relative to the transport of passive or fixed-depth particles near the surface unless specified otherwise. <sup>a</sup>Depth-averaged.

### 5.3 Management implications

This synthesis has a number of important implications for the management of coastal and marine resources. First and foremost, it demonstrates that VMBs can and do have a significant influence on the transport of organisms in marine environments (results summarized in Table 4) and need to be considered when sponsoring or evaluating research on transport in marine environments. Unfortunately, determining the influence of a VMB on transport in a credible manner is not trivial. The variability in organism behavior (e.g. variability in typical migratory depths and periods; Rothlisberg, 1983; DiBacco et al., 2001; Carr et al., 2005) and spatial and temporal variability of marine currents mean that the influence of VMBs on transport must be quantified for a specific behavior at a specific location. A few behaviors have been studied extensively in a few regions (e.g. DVM and OVM on Georges Bank, STST and DVM in the North Sea, and DVM along the California coast), but some regions (e.g. the South American coast) have received almost no study whatsoever. Modeling studies of idealized behaviors can provide useful first-order estimates of the influence of VMBs on the transport in a region (e.g. Hill 1994; Carr et al., In review) but eventually need to be validated for specific locations because the transport predicted for idealized VMBs or VMBs observed in other locations can differ significantly from actual transport (Jenkins et al., 1999; Carr et al., 2005). Ironically, field observations (e.g. Hench et al., 2004; Carr et al., 2004) have the greatest potential to advance modeling efforts because these observations are desperately needed to parameterize VMBs in models and validate model predictions.

Behavior	Environment	Influence on Transport	References
FTT	Estuary or semi-enclosed bay with semi-diurnal tides	Increased retention near starting locations	Jacobsen et al., 1990
ETT	Estuary or semi-enclosed bay with semi-diurnal tides	Down-estuary transport and export from estuary	DiBacco et al., 2001; Carr et al., 2005
STST	Continental shelf with semi-diurnal tides	Directed transport	Arnold and Holford, 1995; deGraaf et al., 2004
DVM	Continental shelf or other coastal region with $S_2$ semi-diurnal tide	Directed transport or retention depending on relative phases of DVM and tide	Hill, 1994; Sentchev and Korotenko, 2004
	Estuary, continental shelf, or other coastal region with $M_2$ semi-diurnal tide	Increased retention near starting locations	Arnold and Holford, 1995; Luettich et al., 1998; Culberson et al., 2004
	Continental shelf or other coastal region with diurnal tide	Directed transport or retention depending on relative phases of DVM and tide	Rothlisberg et al., 1983; Smith et al., 2001
	Estuary, continental shelf, or other coastal region with estuarine circulation/buoyancy-driven currents	Increased retention near starting locations	Larson et al., 2003; Emsley et al., 2005
	Continental shelf or other coastal region with wind-driven surface Ekman layers	Increased retention near starting locations	Wroblewski, 1982; Bucklin et al., 1989; Botsford et al., 1994; Hannah et al., 1998; Griffin et al., 2001; Batchelder et al., 2002; Murphy et al., 2004; Hinrichsen et al., 2005; Carr et al., 2005
		Little influence on transport	Gallego et al., 1999
OVM	Estuary	Increased retention near starting locations	Jacobsen et al., 1990
	Continental shelf or other coastal region with wind-driven surface Ekman layers	Increased retention near starting locations	Stenevik et al., 2003; Paris and Cowen, 2004

Table 5.4. Summary of influence of VMBs on transport in marine environments. Environments characterized by multiple influences, e.g. semi-diurnal tides and buoyancy-driven currents categorized by influence with greatest interaction with VMB. All results are relative to the transport of passive or fixed-depth particles near the surface.

Secondly, this synthesis demonstrates that coastal and marine resource managers need to account for the interactions between VMBs and currents before undertaking activities which affect current flow (e.g. building jetties, water diversions, or dredging) or zoning marine



areas for living marine resources (e.g. siting ballast water disposal or marine protected areas). For example, Culberson et al. (2004) showed that water diversions in the Suisin Marsh of San Francisco Bay may entrain relatively large numbers of DVM larvae and have a negative effect on larval recruitment, and Larson et al. (2003) showed that potentially invasive species might actually be retained near coastal habitats in a recommended ballast water discharge area because of the interaction of DVM and local circulation. Carr et al. (2005) demonstrated that spawning sanctuaries for migratory female blue crabs in North Carolina inlets are likely to be too small because crabs will migrate quickly through the inlets using ETT. And finally, many of the studies (e.g. Rothlisberg et al., 1983; Hinrichsen et al., 2005; Carr et al., In review) demonstrated that including VMBs in modeling studies will enable fisheries scientists and managers to assess the connectivity patterns and self-recruitment levels for fished stocks more accurately.

Modeling studies which integrate organismal behavior and development may also be able to help coastal and marine resource managers predict the effects of global climate change on living marine resources and the human activities that depend on them. Recent studies have shown that changes in global temperature, and consequently oceanic temperatures and currents, are changing the geographic range, phenology (timing of seasonal activities such as migrations or spawning), and developmental rates of marine organisms, as well as, interactions between marine species (Beaugrand et al., 2002; Walther et al., 2002; Edwards and Richardson, 2004; Sims et al., 2004; Hays et al., 2005). Retention near parental habitat and adaptation to local conditions have previously been assumed to benefit marine populations (Strathmann et al., 2002). If VMBs are closely-timed adaptations to local conditions to promote retention, migratory, and/or recruitment success and organisms using

VMBs are unable to adapt these behaviors to their environments at the same rate that the environments themselves are changing, these behaviors may become a liability for the survival of marine populations (Walther et al., 2002).

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