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Movement patterns and trajectories of ovigerous blue crabs *Callinectes sapidus* during the spawning migration

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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^{-1} during night ebb, night flood, day ebb and day flood tides, respectively, and net migratory speeds were on the order of 5 km day^{-1}. 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.
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Keywords: blue crab; *Callinectes sapidus*; spawning migration; selective tidal-stream transport; ebb-tide transport; ultrasonic telemetry

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; 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

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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 $>1\ m\ s^{-1}$ (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 $1\ m\ s^{-1}$. 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. (submitted for publication) observed that crabs migrated vertically during all stages of egg development but sojourns into the water column were most frequent in the ~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 zeitgeiber (''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. We are 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. 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. 1). Circulation near the inlet is dominated by semi-diurnal tides, and peak ebb currents speeds are $>1\ m\ s^{-1}$ 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 ~2 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).

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. 1b). Embryo stage was determined at the time of collection by examining

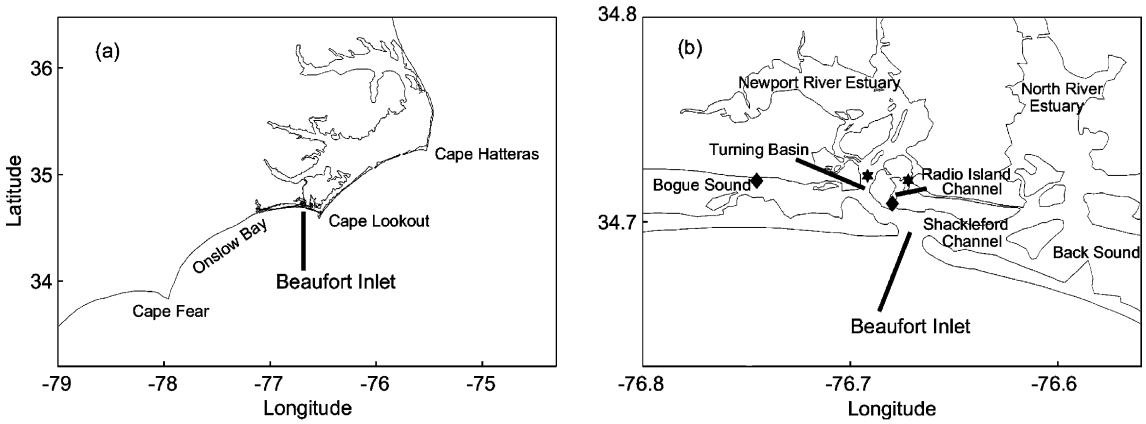

Fig. 1. Location of tracking study area: (a) South Atlantic Bight and (b) Beaufort Inlet region. Crab collection sites are marked by hexagons (✶), and ADCP mooring sites are marked by diamonds (♦).

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 × 67 mm; 2002: VEMCO V16, 11 g in water, 16 mm × 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; 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., submitted for publication). 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. 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. 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 (± 95% CI) for angular data were calculated using Oriana (Kovach Computing Services, v. 1.01).

3. Results

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. 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. 2b). Crabs 1, 2, 3 and 6 were tracked to the inlet strait, while Crab 4 was tracked to ~4 km offshore (Fig. 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 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. 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 ($<0.1\ m\ s^{-1}$) because the crab had migrated offshore, away from the strong tidal influence of the inlet and estuary.

Table 1
Starting locations, dates and times of tracks and tracking durations and distances

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

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. 3), resulting in seaward movement during both ebb and flood tides (Fig. 2b). Crab vectors were consistently aligned with current vectors ($<30°$ difference) during ebb tides and with the down-estuary flow direction (180° from the shipboard ADCP current vectors) during flood tides (Fig. 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 (± 95% CI) between the crab and current vectors during ebb tides was 1° (± 2°) (Fig. 4b). The mean difference (± 95% CI) between the crab and current vectors during flood tides was 187° (± 3°) (Fig. 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.

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. 3). Movements against local currents during flood tides, on the other hand, were frequently on the order of $0.25\ m\ s^{-1}$ regardless of current speed (Fig. 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. Fig. 5a,b shows 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

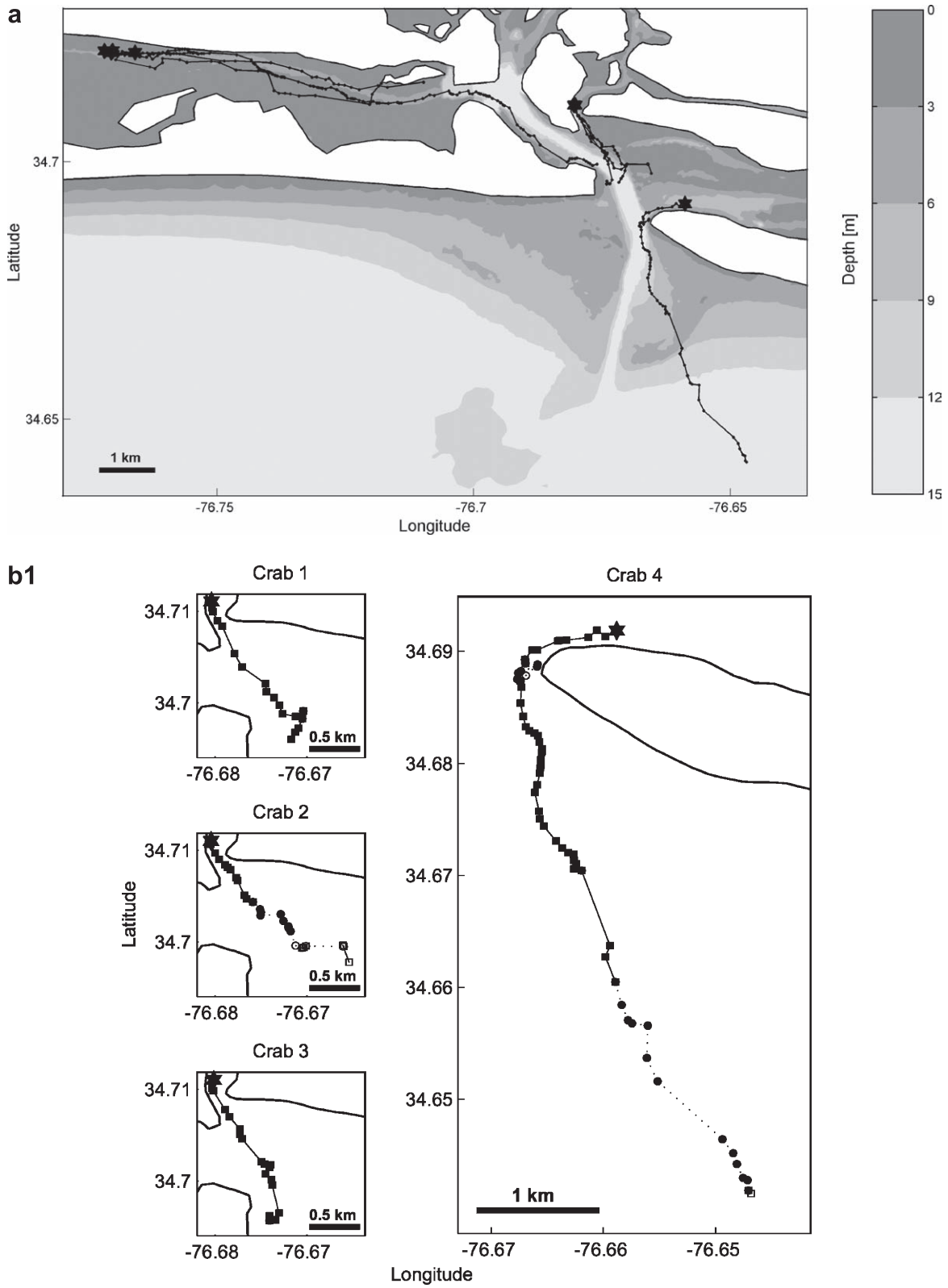

Fig. 2. (a) Eight (8) crab tracks and bathymetry (gray shading) near Beaufort Inlet, North Carolina. Tracks start in the estuary and move towards the inlet. Starting locations are marked by hexagons (✶), and subsequent fixes are marked by circles (●). (b) Crab tracks near Beaufort Inlet, North Carolina. 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.

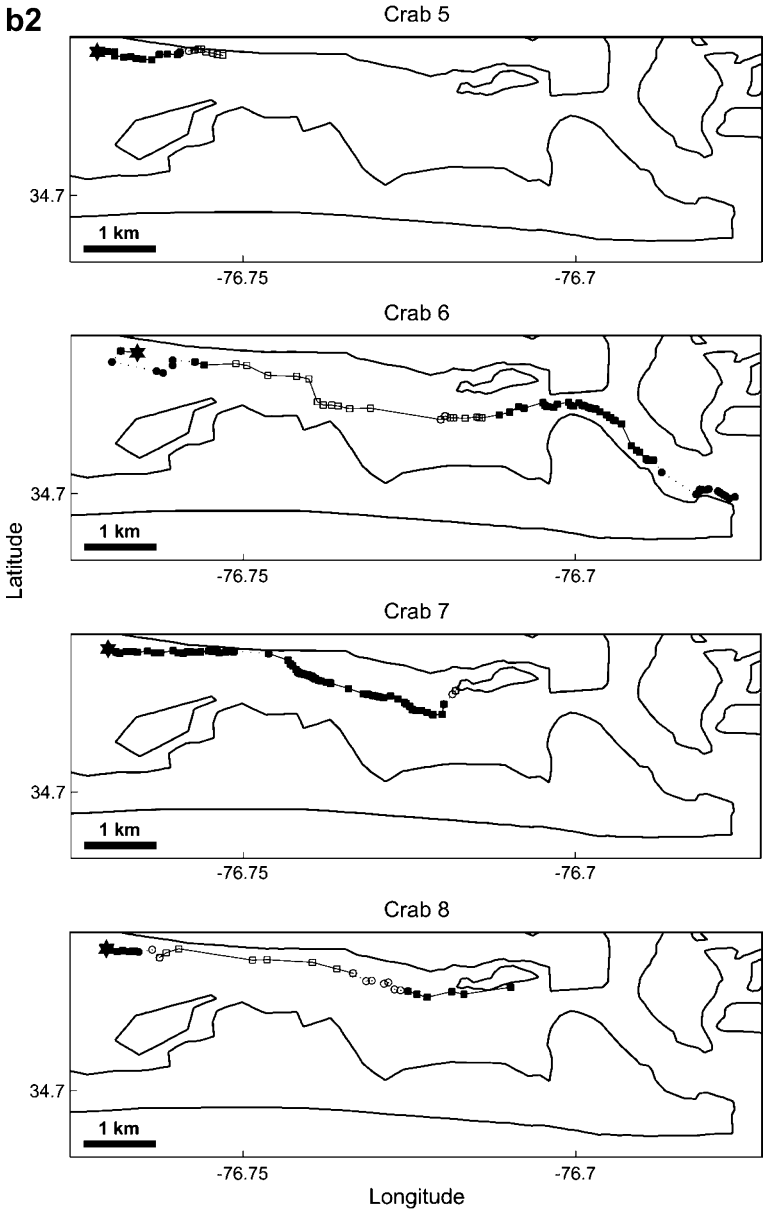

Fig. 2 (*continued*)

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. 5b) than during flood tides or day ebb tides (<20% of the time) (Fig. 5b), but activity levels among individual crabs varied widely (Fig. 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.

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. 6). Tracking periods were divided into 0.25 m s^{-1} velocity bins (−1.00–1.00 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 m s^{-1} and <15% of the time when currents were flooding >0.25 m s^{-1}.

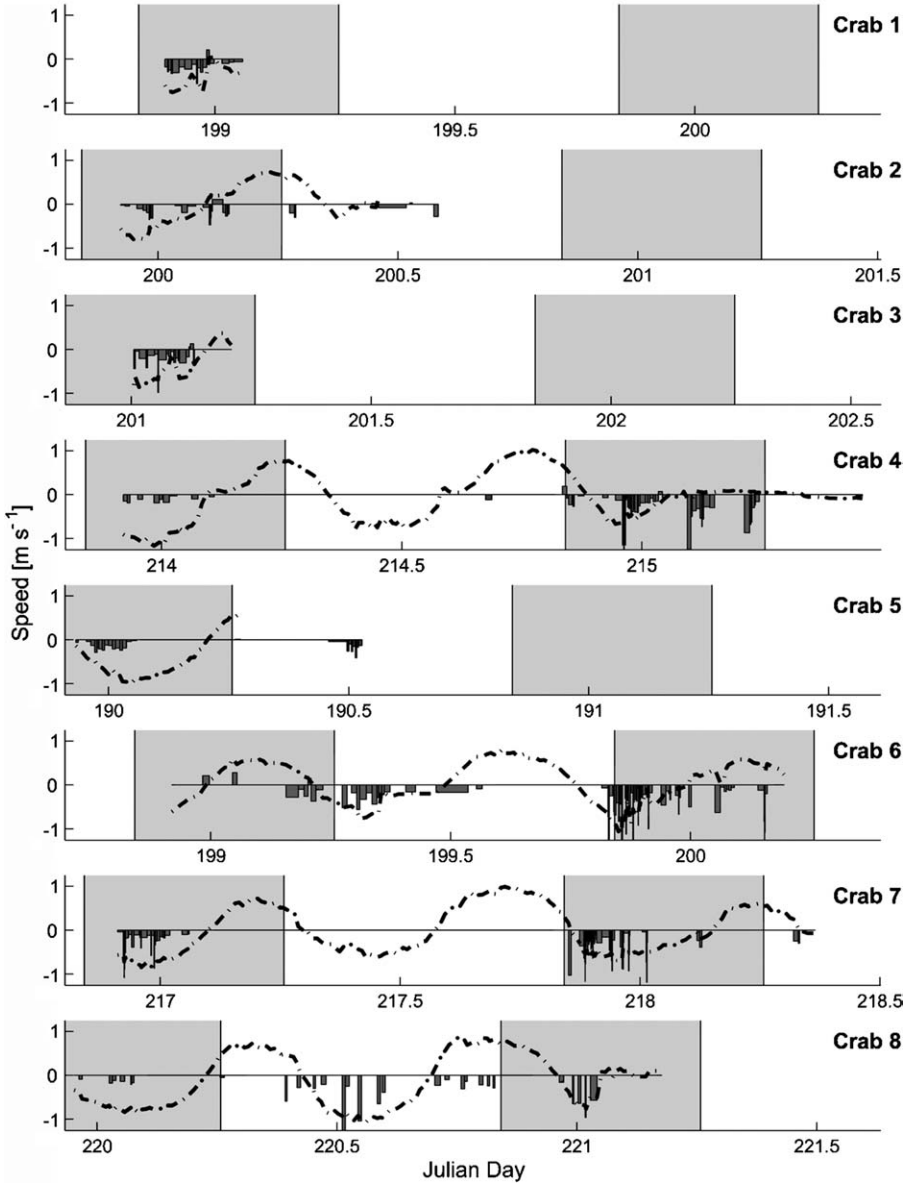

Fig. 3. Time series of crab speed (small, dark gray bars) and current speed (-.-.). Positive speeds indicate flood tides/up-estuary movement, and negative speeds indicate ebb tides/down-estuary movement. Bar width indicates the time between fixes and period over which mean speed is computed. Night and day periods are indicated by the large light gray and white sections, respectively.

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. 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 m s^{-1} $\pm$ 0.04 m s^{-1} ($n = 8$), 0.04 m s^{-1} $\pm$ 0.03 m s^{-1} ($n = 8$), 0.08 m s^{-1} $\pm$ 0.08 m s^{-1} ($n = 6$) and 0.02 m s^{-1} $\pm$ 0.02 m s^{-1} ($n = 6$), respectively (Fig. 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.

The crabs' net migratory speeds varied from 3.2–13.5 km day^{-1} with a mean of 6.5 km day^{-1}, but these results were highly dependent on the proportion of

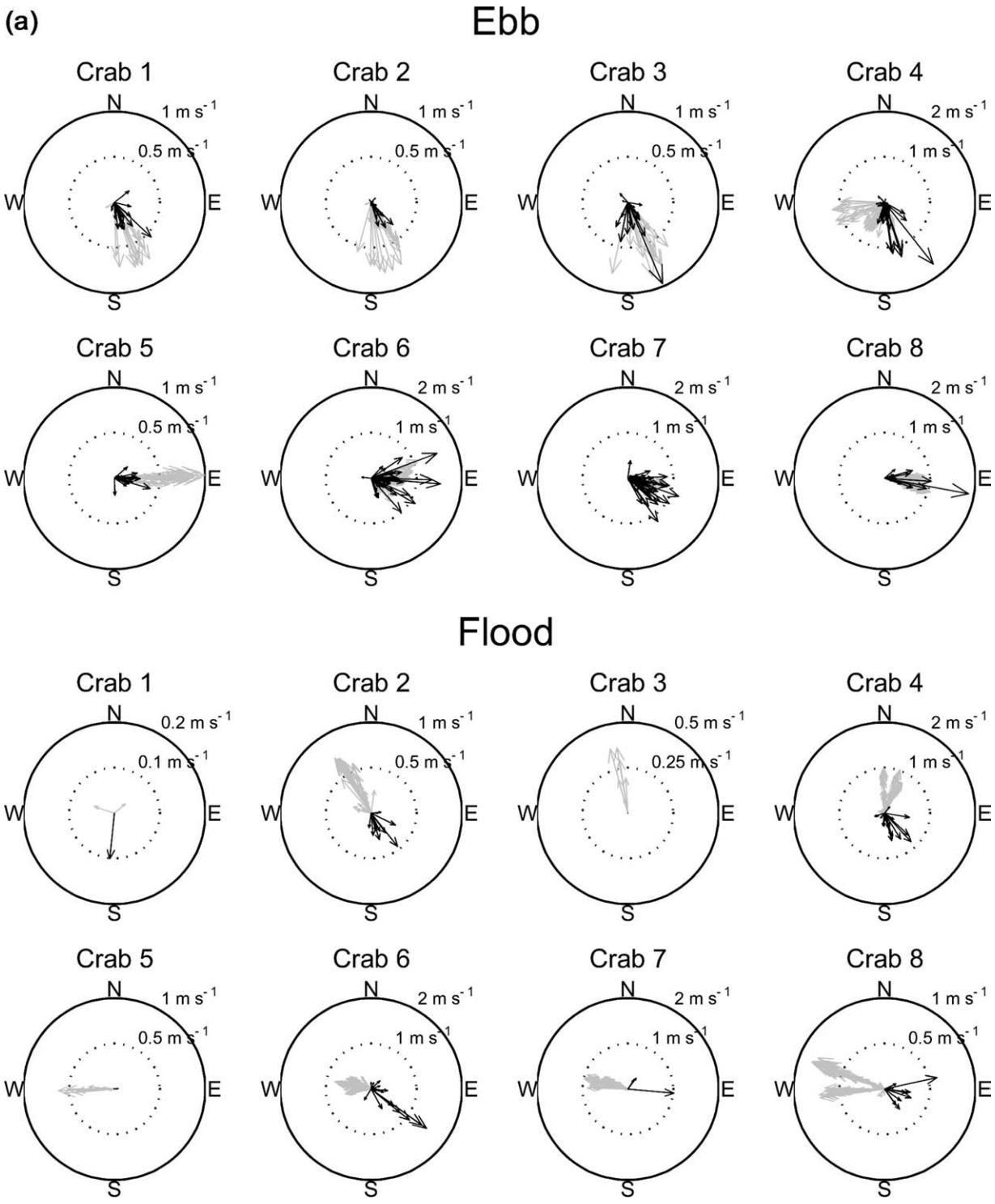

Fig. 4. (a) Crab vectors (black) and current vectors (gray) between fixes during ebb and flood tides. (b) Histograms of angular difference between crab and current directions during ebb and flood tides. Mean angular differences (± 95% CI) are indicated.

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^{-1}, respectively). The net migratory speeds of crabs tracked for >24 h ranged from 3.8–8.3 km day^{-1} with a mean of 5.4 km day^{-1}. This corresponds extremely well to a net migratory speed estimate of 5.4 km day^{-1} derived from averaging the mean migratory speeds for the four tidal–diel phases (Fig. 7).

During ebb tides, crabs traveled 10–40% of the down-estuary distances that passive particles would have traveled (Fig. 8). Passive transport distances during

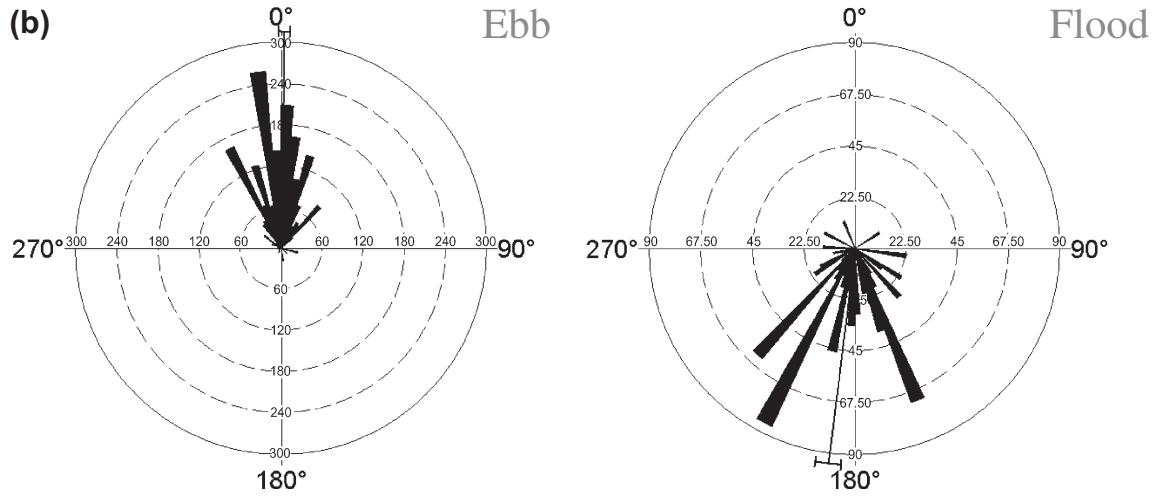

Fig. 4 (*continued*)

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).

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. 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. 3). These movements correspond to the episodic "swimming bouts" observed by Forward et al. (2003a) in laboratory tank experiments and by Hench et al. (submitted for publication) 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. 6) and transport would be most efficient. Crabs are negatively buoyant and must

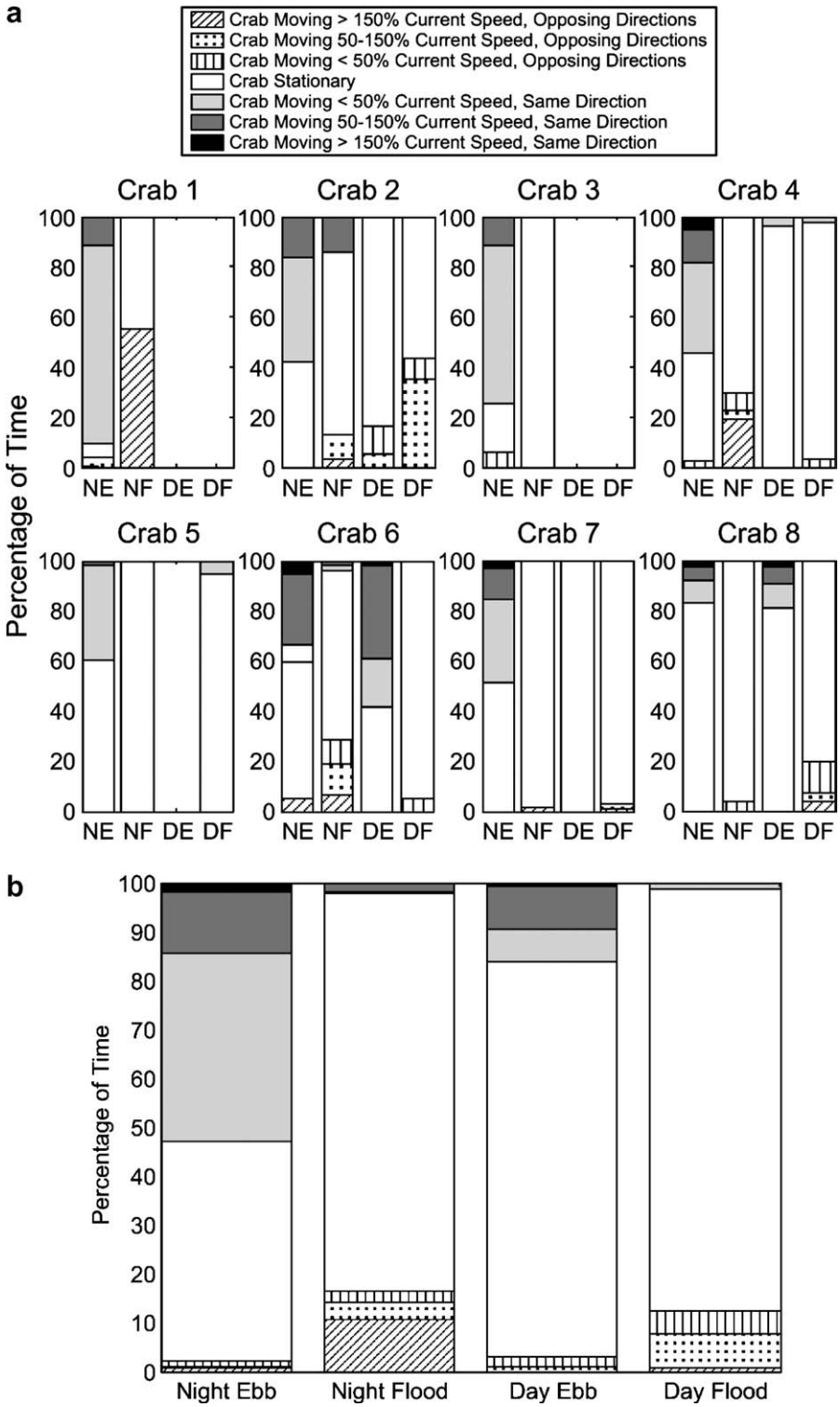

Fig. 5. Relationship between crab speed and local current speed during night ebb (NE), night flood (NF), day ebb (DE) and day flood (DF) periods for (a) individual crabs, and (b) all crabs combined.

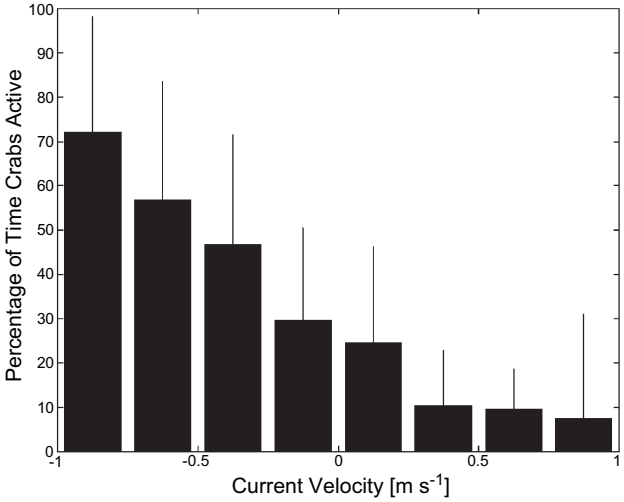

Fig. 6. Mean (± 95% CI) percentage of time that crabs were active as a function of local current velocity. Positive current velocities are flood tides, and negative current velocities are ebb tides.

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. Hench et al. (submitted for publication) 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 (Hench et al., submitted for publication), 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.

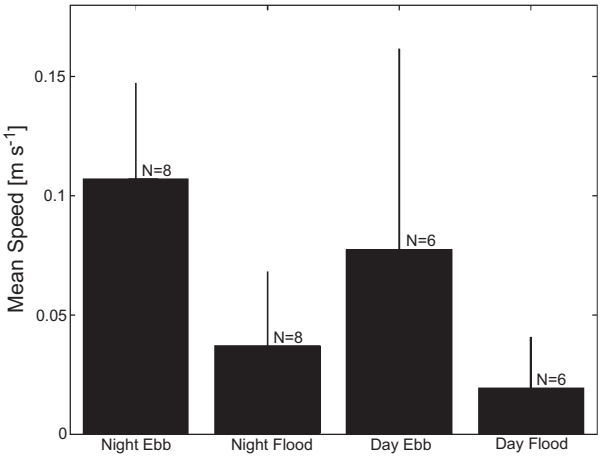

Fig. 7. Mean (± 95% CI) crab speed during night ebb, night flood, day ebb and day flood tides.

The close alignment between crab movements during flood tides and the down-estuary/offshore direction (Fig. 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. (submitted for publication) 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 that 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

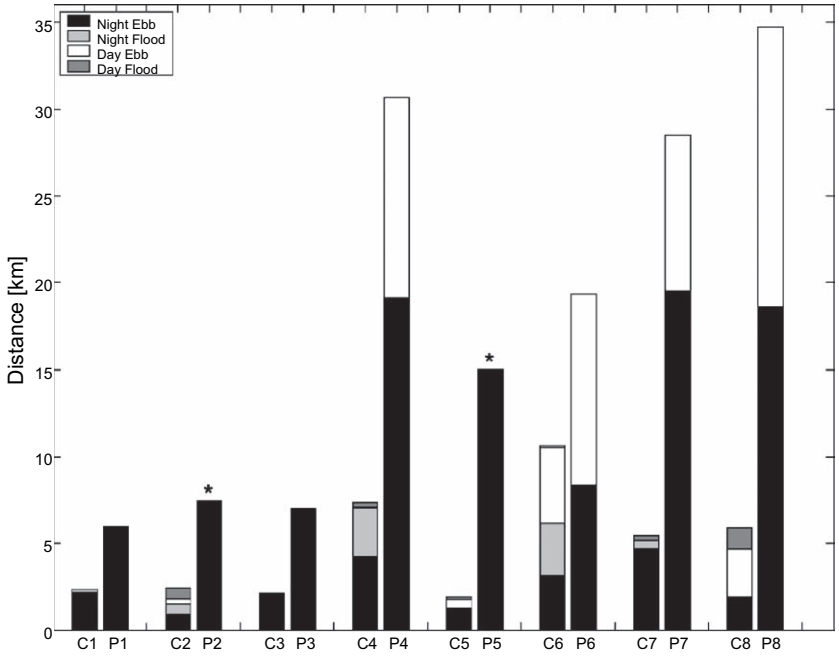

Fig. 8. Comparison of distances traveled down-estuary by crabs (C1–C8) and the down-estuary travel distances predicted for passive particles (P1–P8). The predicted distances for day ebb tides for Crabs 2 and 5 are not shown because shipboard ADCP data were not available for those periods. Missing ADCP data is denoted by an asterisk (*).

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. 7) are representative of migratory speeds in the lower estuary where currents are relatively strong (maximum speeds of $\sim 1\,m\,s^{-1}$) and demonstrate that crabs can migrate rapidly (on the order of $5\,km\,day^{-1}$) 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 ~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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