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The timing and route of movement and migration of post-copulatory female blue crabs, *Callinectes sapidus* Rathbun, from the upper Chesapeake Bay

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Abstract

The movement of mature female blue crabs *Callinectes sapidus* Rathbun from lower salinity areas to spawn near the mouths of estuaries is well documented, but specific details of the post-copulatory phase of their migratory behavior are poorly understood in Chesapeake Bay. To test the hypotheses about the timing and route of this migration, we conducted a mark–recapture study of mature females released in a mesohaline portion of the upper Chesapeake Bay. From June 1999 to October 2002, 1440 mature female blue crabs were obtained from fishers, tagged, and released in the vicinity of the Rhode River, Maryland, approximately 200 km distant from the mouth of the Bay. As of the end of 2002, 167 crabs were recaptured (11.6%), with considerable variation in recapture rates among years. All recaptures except one (in Flagler Beach, Florida) were caught within the Chesapeake Bay proper. Recaptures of female crabs released at monthly intervals from June–November indicated that migration occurred during a short fall period rather than over the prolonged period of summer to fall mating. The distances traveled by crabs before recapture differed significantly among release months. On average, crabs released in September and October traveled greater distances than crabs released in earlier months (June–August). Depths of recapture sites differed significantly among months, with shallow depths in June–August increasing in September to a maximum in November. The locations and bathymetry of recapture sites showed that female crabs used areas near the deep channel, especially the eastern shoulder, of the Bay as a migration corridor to the spawning areas of the lower estuary. The distinct fall season and route of migration should provide valuable management information for protecting the declining spawning stock of Chesapeake blue crabs.

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1. Introduction

Although migratory patterns are best known for anadromous and catadromous fish species, numerous decapod crustaceans also undergo migration across coastal habitats (Herrnkind, 1980; Taylor et al., 1985; Wolcott and Wolcott, 1985; Campbell and Stasko, 1986; Hines et al., 1995; Lovrich et al., 1995; Freire et al., 1999). Females of many of these marine and estuarine species undergo long-distance migrations to release offspring in areas favorable for early development (Allen, 1966). The risks associated with migrating can be costly for the individual female, including acquiring and allocating energy for both migration and oogenesis and increased predatory or mortality risk. However, females are often adapted for differing strategies (e.g., timing, route, mechanisms) that promote successful completion of migration and maximize survival of offspring. Understanding the role of migratory movements in determining life history, distribution, and population dynamics is necessary for effective management of exploited species.

The blue crab *Callinectes sapidus* Rathbun is an ecologically and commercially important brachyuran crab that occurs from Nova Scotia to northern Argentina (Williams, 1984), but along North America it is most common south of Cape Cod. Historically, the Chesapeake Bay has supported an abundant blue crab population with an intense fishery, which currently supplies over one-third of all US commercial blue crab landings (National Marine Fisheries Service, Fisheries Statistics and Economics Division, Silver Spring, MD). However, most likely due to the effects of overfishing and habitat degradation, the Chesapeake Bay blue crab spawning stock abundance and biomass have declined 81% and 84%, respectively, from 1992 to 2000 (Lipcius and Stockhausen, 2002) and remain at record low levels (BBCAC, 2003). Furthermore, larval abundance and post-larval recruitment have declined precipitously in this same time period (Lipcius and Stockhausen, 2002). Regulations have historically protected crabs from harvest from the spawning grounds in the lower Chesapeake Bay during the spawning period (Seitz et al., 2001). However, recent work by Lipcius et al. (2001) proposed protecting females en route to the spawning grounds by establishing an extended sanctuary–corridor complex.

Blue crab mating typically occurs from May to October in mesohaline and oligohaline portions of the Chesapeake Bay (Van Engel, 1958). Males couple with pre-pubescent females prior to the terminal molt to maturity. After ecdysis, mating occurs while the female is soft, and males continue to guard females (Van Engel, 1958) for a period of hours to 3 days (Jivoff, 1997). Following separation, males remain in these lower salinity areas, whereas most females will eventually move to higher salinity areas in the lower estuary to spawn (Van Engel, 1958; Millikin and Williams, 1984). Periods of peak spawning along the Mid-Atlantic Bight have typically been documented to occur from late July through August (McConaughy et al., 1983; Epifanio et al., 1984; Jones et al., 1990; Epifanio, 1995).

The migration of mature female blue crabs has been characterized by two distinct phases (Tankersley et al., 1998). The first phase (Phase I) involves the movement from the location of mating to the lower estuary prior to brood production. The second phase (Phase II) entails the movement of late-stage ovigerous females from the lower estuary to near the estuary mouth or into adjacent coastal waters. During Phase II, females use selective-tidal-stream-transport on nocturnal ebb tides to move seaward to release their larvae at or near nocturnal high tides (Tankersley et al., 1998). After spawning, some females use tidal stream transport on flood tides to return to the lower estuary, where they may produce subsequent broods (Forward et al., 2003), but do not move back into lower salinity zones (Fischler, 1965; Hines et al., 1987, 1990; Medici, 2004). Some mature females may also move into nearshore and offshore coastal waters after spawning (D. Rittschof, Duke Marine Laboratory, personal communication).

Although the movement of post-copulatory blue crabs from lower salinity areas to the mouth of the estuary is well documented, the timing, exact route, and mechanisms of this Phase I portion of the female migration are poorly understood. Turner et al. (2003) studied movement, feeding behavior, and energy allocations of mature females during the period immediately following mating in upper Chesapeake Bay. Their initial results suggested that migration was delayed until fall, when females moved down shallow areas of the mainstem of the Bay.

In Chesapeake Bay, we hypothesize that females could display at least three possible patterns in the seasonal timing of migration. First, migration could be randomly distributed during the year, although this is unlikely as a result of the markedly seasonal fluctuations in water temperature (e.g., 0° to 30° C in the Rhode River) and the biological activity of the crabs. Second, they could begin migrating from the mating area soon after copulation, or after a short post-molt preparatory interval following copulation. Such behavior would most likely produce a fairly steady stream of crabs migrating to the lower bay overlapping with the mating season, possibly following a lag interval. Alternatively, females could display a “pulsed” migration pattern in which peak migration occurred in a season that is distinct from the mating/spawning period. A “pulsed” migration pattern would most likely arise if females require a biotic or abiotic cue, such as declining water temperatures, decreasing photoperiod, or increasing density of individuals (e.g., “cueing behavior” in spiny lobsters; Herrnkind, 1980). This would also allow females to forage extensively to exploit food resources of the upper estuary during warm months, and potentially acquire the energy stores necessary for migration and somatic growth prior to migration and oogenesis (Turner et al., 2003). By exhibiting a migratory response to the seasonal change of conditions in the fall, females could avoid stressful anoxia/hypoxia in the bay mainstem during the summer (Diaz and Rosenberg, 1995) as well as lethal winter conditions of lower salinities in cold climates (Rome et al., *in press*, this volume).

Additionally, we hypothesize that females could use several different routes and habitats during the Phase I migration to the spawning grounds in the lower Chesapeake Bay. First, females could travel randomly, irrespective of bathymetry and habitat. Second, female crabs could utilize shallow nearshore areas of the Bay, where they could take advantage of abundant prey resources (principally infaunal bivalves) that could be reduced in deeper waters by summer time hypoxia/anoxia (Diaz and Rosenberg, 1995). Conversely, post-copulatory females could use the deeper channel portions of the estuary (i.e., the trough and adjoining shoulder areas), where individuals could utilize the salinity wedge as a cue to navigate to the spawning grounds.

The objective of this study was to determine the timing and route of Chesapeake Bay post-copulatory female blue crabs as they move from the upper to the lower estuary to spawn (i.e., Phase I of the spawning migration). Blue crab movements have typically been examined using either biotelemetry or standard mark–recapture techniques (e.g., Fiedler, 1930; Cronin, 1949; Cargo, 1958; Fischler and Walburg, 1962; Tagatz, 1968; Judy and Dudley, 1970; Nye, 1989; Wolcott and Hines, 1989; Steele, 1991; Hines et al., 1995; Schwartz, 1997; Clark et al., 1999; Bell et al., 2003; Turner et al., 2003). However, the long distances traveled by mature females in the Chesapeake Bay have made the tracking of individuals during migration impractical. Previous mark–recapture studies generally have not been designed to address the timing and route of mature females during the first phase of the spawning migration. In this paper, we assess the migration of female blue crabs from the Upper Chesapeake Bay using mark–recapture data spanning four consecutive years. Particular attention is given to the release months, distances traveled, and the depths used by mature females during migration.

2. Methods

2.1. Tagging

The tagging of mature female blue crabs took place approximately monthly from June to October during 4 years, 1999–2002. Crabs were obtained from local fishers operating in the vicinity of the Rhode River (38°51'N, 76°32'W), a small (485 ha) lower mesohaline subestuary of upper-central Chesapeake Bay, and transported to laboratory facilities at the Smithsonian Environmental Research Center (SERC) in Edgewater, Maryland (Fig. 1). Upon arrival, carapace width (CW; to the nearest millimeter) and autotomy (limb loss) were recorded for all crabs that appeared active and in good health, i.e., no more than three missing appendages, limited to only one missing chela or 5th priopod (swimming leg) or no gross indication of injury or disease. Tags were attached to the dorsal surface of the carapace with malleable wire wound around the lateral spines. A crab tag consisted of a double-faced aluminum tag (Forestry Supplies, Inc.)

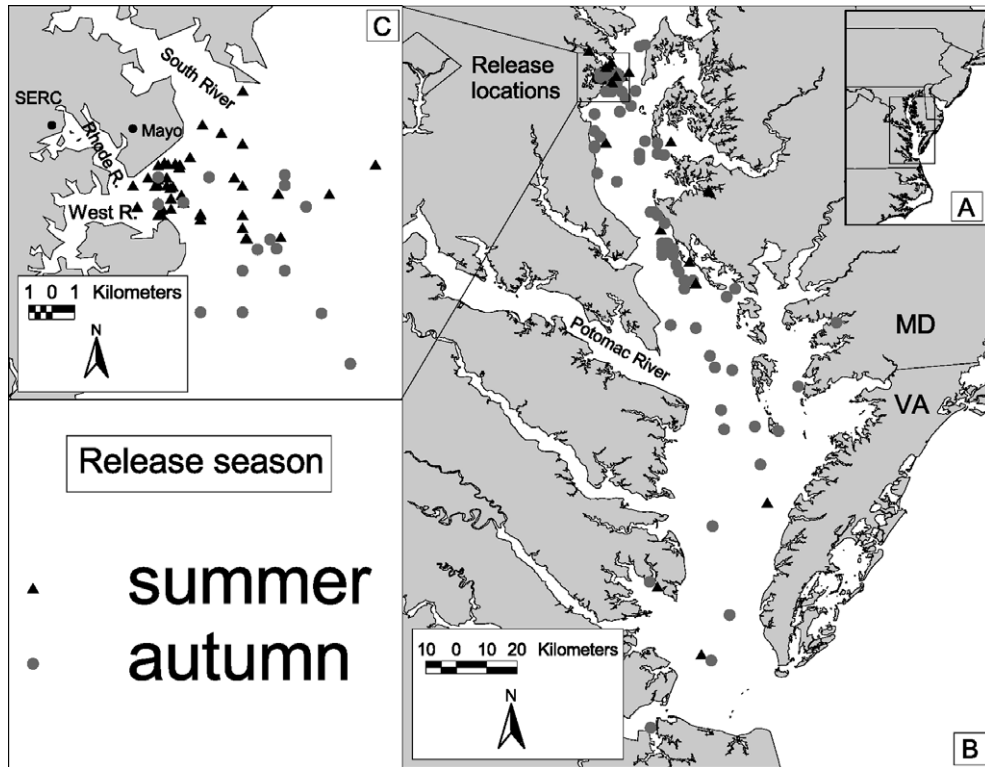


Fig. 1. Map of the recapture locations of mature female blue crabs tagged and released near the mouth of the Rhode River, Chesapeake Bay, 1999–2002. Triangles indicate crabs tagged and released in the summer (June–August) and circles indicate crabs tagged and released in the autumn (September and October). Panel A is the coastal region of the eastern-central United States. Panel B is the Chesapeake Bay. Panel C is the area of release locations of tagged female blue crabs.

with a waterproof label affixed to the outward surface that was coated with epoxy resin. Information printed on labels included “Smithsonian Environmental Research Center,” contact phone number, individual tag number, and “reward.” After tagging, crabs were immediately released at locations near the common mouth of the Rhode and West Rivers. The date and GPS coordinates (longitude and latitude) were recorded for each release event.

Information regarding the present study was disseminated at several public meetings and through publications targeting commercial and recreational fishers. All persons reporting tagged crabs were asked tag number, capture date, capture location, capture depth, and capture gear. Captors received a US\$2 reward for each tag reported and entry into several US\$100 yearly lotteries. Upon recapture, most captors removed the tag and harvested the crab. However, several captors recorded the appropriate information

and released the crab alive with the tag intact, which allowed for potential subsequent recapture of the same crab.

2.2. Analyses

Recapture information was used to compute distance moved, movement direction, rate of movement, time at liberty, and recapture depth for each crab. Straight-line distances between recapture and release locations were calculated using Arcview GIS (ESRI, Environmental Science Research Institute) and the Arcview animal movement extension (Hooge and Eichenlaub, 2000). It is important to note that this method certainly underestimates actual distances traveled, especially for individuals at liberty for extended periods of time, because crabs do not typically move in straight lines (Wolcott and Hines, 1989; Hines et al., 1995).

Data were grouped according to (1) release year (1999–2002), (2) release month (June–October), and (3) recapture month. December through February recaptures were excluded from depth analysis because crabs had most likely ceased migrating due to declining water temperatures and were assumed to be overwintering. April and May recaptures were also removed from depth analysis because most of these crabs had completed the spawning migration (i.e., reached the lower Bay). December through May recaptures were retained in movement analyses because migration is considered one-way; once females reach the lower estuary they do not return to upper portions of the estuary.

An overall recapture rate and individual yearly recapture rates were generated for all years of this study. Individual yearly recapture rates represent the number of crabs caught over the course of this study relative to the number of crabs released within each release year (1999–2002). This method was deemed the most appropriate because after female crabs reach the lower bay they are generally unavailable to the fishery due to seasonal harvest restrictions within the spawning sanctuary and generally do not return to the upper estuary after spawning. Nearly all crabs (93.2%) were caught within the calendar year of release and only one crab was caught after the beginning the next year's releases, i.e., after June of the following year.

Distances moved by recaptured crabs were compared among release years and release months, and recapture depths were compared among release months and release years using a one-way ANOVA followed by Tukey honestly significant difference (HSD) tests (SAS, 1990). Migration rates (km day^{-1}) were calculated for all female crabs that moved >25 km. A one-way ANOVA was used to test for significant differences in migration rates among release years, which was followed by a Tukey HSD test (SAS, 1990). Recaptures depths of crabs were compared among recapture months using a one-way ANOVA followed by a Tukey HSD test (SAS, 1990).

To evaluate the spatio-bathymetric habitat use of migrating female blue crabs the Chesapeake Bay was partitioned into five zones: eastern and western shallow zones, which represent the shallow areas (<6 m) along both shorelines of the Bay; eastern and western shoulder zones, which represent the mid-

depth (6–13 m) areas on both sides of the main channel; and a trough zone, which represents the deepest (>13 m) areas of the Bay. Recapture locations of crabs that traveled >5 km down Bay from their release site were scored by their respective geographic zone and separated by recapture season, i.e., summer (June, July and August) and fall (September, October, and November). All crabs that traveled <5 km and the three crabs that traveled >5 km to the north were omitted to restrict analysis to crabs that were most likely migrating and limit the effect of random movement.

All variables that did not meet the assumptions of univariate normality and homogeneity of variances were log transformed. A significance level of 0.05 was chosen for statistical analyses. All summary statistics were computed using SAS (SAS, 1990).

3. Results

3.1. Recaptures

A total of 1440 adult female blue crabs were tagged and released in 15 events (mean=96 crabs/event) from 18 August 1999 to 24 October 2002. By the end of 2002, 167 (11.6%) individual tags were reported as recaptures; individual yearly recapture rates varied from 4.3% to 17.7% (1999=12.6%; 2000=17.7%; 2001=10.8%; 2002=4.3%). Most recaptured crabs (83%) were reported with complete recapture information (i.e., tag number, recapture date, recapture depth and recapture location). Five crabs were recaptured twice; only the last recapture for each crab was included in data analysis. In these instances, captors released captured crabs alive with the tag intact and crabs were subsequently caught again by other fishers. All recaptures were caught within the Chesapeake Bay proper except one, which occurred in Flagler Beach, Florida, 1040 km from the release site and 234 days after release. This crab was removed from all analyses because it was considered an outlier.

3.2. Distance moved and time at liberty

The distance traveled by crabs from release to recapture sites ranged from 0.1 km to 213.5 km (mean

35.7 ± 4.06 km; Fig. 1.) Most crabs (60%) were recaptured <25 km from release sites. However, the distances traveled by crabs differed significantly among release months (one-way ANOVA, $F_{4,138} = 19.47$, $P < 0.0001$; Fig. 2). In general, crabs released in September and October moved greater average distances (49 km) than crabs released in earlier months of June–August (16 km). Although Tukey's HSD tests indicated that July was not significantly different from September and October, this is most likely due to the low July sample size ($n=5$; Fig. 2).

Time at liberty for crabs varied from 0 to 279 days (mean 32.1 ± 4.59). Most crabs (64.8%) were recaptured within 20 days; recapture rates generally decreased as time at liberty increased. Eleven crabs were recaptured during the following winter or spring (Dec–May). Several of these crabs ($n=6$) were caught in the lower bay; however, five crabs were caught north of the Potomac River, indicating that they most likely overwintered in the upper Chesapeake Bay.

3.3. Depth and recapture location

Crabs were captured at depths ranging from 1.2 m to 21.3 m (mean 6.4 ± 0.37 m). Depth of recapture differed significantly among recapture months (one-

way ANOVA, $F_{5,129} = 13.53$, $P < 0.0001$; Fig. 3). Recapture depths generally increased in September in comparison with June–August, and peaked in November.

In general, crabs in the Chesapeake Bay proper were recaptured in waters >1 km from the shoreline (Fig. 1). During the fall migration months, the locations and bathymetry of recapture sites conformed with the mainstem channel, especially the shoulder that runs primarily along the eastern side the Bay, with recapture sites arrayed mainly along the slope break to the deepest water along the full length of the estuary (Fig. 4). Recaptures during other months generally occurred in nearshore areas.

3.4. Migration rate and year effects

The overall mean (\pm S.E.) migration rate for female blue crabs that moved >25 km was 3.3 ± 0.35 km day⁻¹. The fastest migration rate for a crab that traveled >25 km was 13.0 km day⁻¹ (65.0 km in 5 days). Although the year of tagging did not influence the mean distances traveled by female blue crabs (one-way ANOVA, $F_{3,138} = 0.77$, $P = 0.5119$) or time at liberty (one-way ANOVA, $F_{3,142} = 1.54$, $P = 0.1954$), tagging year appeared to significantly affect migration

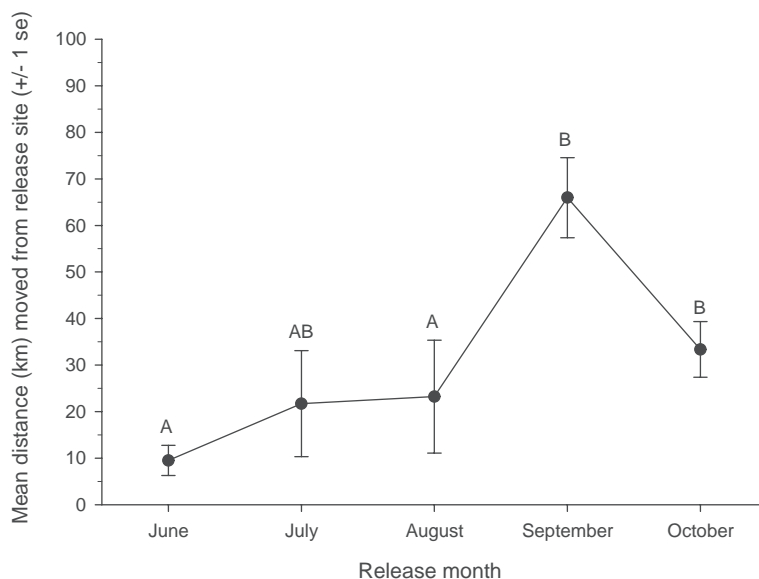


Fig. 2. Monthly mean distances traveled by mature female blue crabs tagged and released near the mouth of the Rhode River, Chesapeake Bay, 1999–2002. Error bars indicate one standard error. Letters represent groups that did not differ significantly ($P > 0.05$) in Tukey HSD tests. Sample sizes by month are: June=32; July=5; August=23; September=42; October=37.

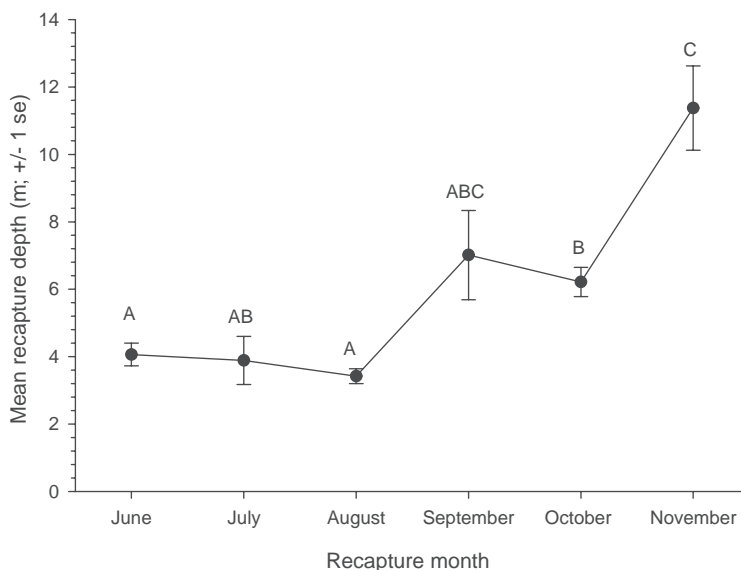


Fig. 3. Monthly mean recapture depths of mature female blue crabs tagged and released near the mouth of the Rhode River, Chesapeake Bay, 1999–2002. Error bars indicate one standard error. Letters represent groups that did not differ significantly ($P>0.05$) in Tukey HSD tests. Sample sizes by month are: June=25; July=8; August=22; September=4; October=44; November=26.

rates (one-way ANOVA, $F_{3,135}=6.31$, $P<0.005$). Crabs released in 2001 ($3.0 \pm 0.58 \text{ km day}^{-1}$) traveled significantly faster than those released in

1999 ($1.0 \pm 0.20 \text{ km day}^{-1}$), 2000 ($1.6 \pm 0.26 \text{ km day}^{-1}$), and 2002 ($1.1 \pm 0.7 \text{ km day}^{-1}$; Tukey HSD Test).

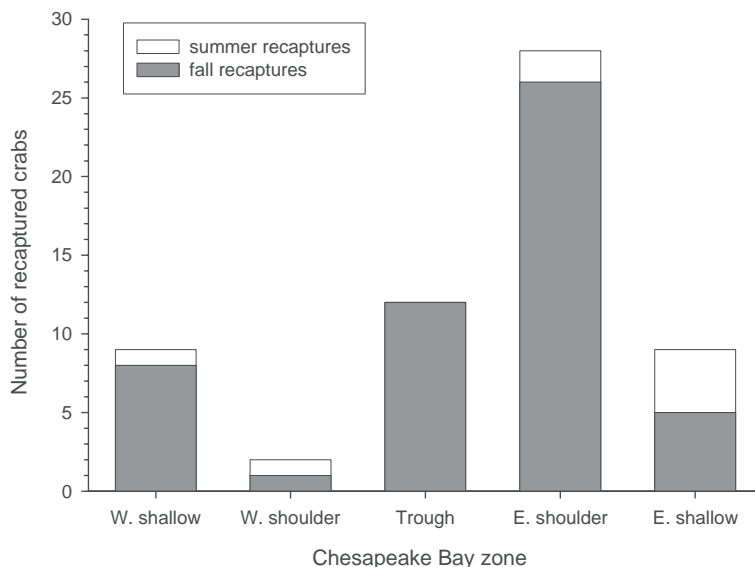


Fig. 4. Number of recaptured female blue crabs that traveled $>5 \text{ km}$ down Bay from their respective release site within each zone of the Chesapeake Bay (W. shallow=western shore, $<6 \text{ m}$; W. shoulder=western shoulder, $6\text{--}13 \text{ m}$; Trough=center trough, $>13 \text{ m}$; E. shoulder=eastern shoulder, $6\text{--}13 \text{ m}$; E. shallow=eastern shallow, $<6 \text{ m}$) by recapture season, summer (June, July, and August) and fall (September, October, and November), 1999–2002.

4. Discussion

Our mark–recapture data clearly indicate that most post-copulatory female blue crabs in the upper Chesapeake Bay remain within the mating areas during the summer, and in the fall most begin their migration to spawning grounds of the polyhaline zone. This pulsed fall migration was consistent in all 4 years of our study, including the initial indications by Turner et al. (2003) for the same release locations. Furthermore, Van Engel (1958) noted most females move to the lower Chesapeake Bay in October and November. However, little is known about environmental or endogenous factors that may trigger migration. Many crustaceans possess endogenous clocks that influence ecdysis, egg hatching, vertical migration, foraging, and other behaviors (e.g., Lipcius and Herrnkind, 1982). In Caribbean spiny lobsters *Panulirus argus*, “cueing behavior” appears to be partially triggered by temperature drops associated with passage of autumnal cold fronts (Kanciruk and Herrnkind, 1978; Herrnkind, 1980). Declining water temperature has been associated with the onset of migration for several marine decapods, including the green crab, *Carcinus maenas* (Edwards, 1958; Crothers, 1968), Dungeness crab *Cancer magister* (MacKay, 1942), snow crab *Chionoecetes opilio* (Lovrich et al., 1995), spider crab *Maja squinado* (Freire et al., 1999), long-clawed hermit crab *Pagurus longicarpus* (Rebach, 1974, 1978), and American lobster *Homarus americanus* (Campbell and Stasko, 1986). Despite numerous examples of seasonal migration, the timing of these behavioral shifts in relation to environmental changes and possible underlying causative mechanisms are poorly understood (Herrnkind, 1980).

Adaptive benefits accrue to female blue crabs that delay migration in Chesapeake Bay. Remaining in meso- and oligohaline areas after mating allows females to forage extensively on benthic prey in these productive zones of the estuary (Hines et al., 1987, 1990). While exploiting these food resources in the Rhode River, post-copulatory female blue crabs first allocated energy to muscle growth in the post-molt recovery process, then to egg development and hepatopancreas reserves (Turner et al., 2003). Even with this delay for feeding, females did not complete ovarian development and the accumulation of hep-

atopancreas reserves while in the subestuary, suggesting that foraging and consequently oogenesis continued en route to the spawning grounds (Turner et al., 2003). Delaying migration until after the fall turn-over of the water column also ensures that migrating crabs do not encounter deleterious low oxygen conditions that are common in the mainstem of the bay during warm summer months (Officer et al., 1984; Pihl et al., 1991).

Waiting until fall to begin the spawning migration could also have adverse consequences for females. Females leaving the upper Chesapeake Bay after September are not able to spawn until the summer following mating, requiring that they over-winter before producing eggs. The increased delay between mating and spawning could reduce viability of stored sperm (Hopkins, 2002). Furthermore, some females may not reach the spawning grounds before the onset of winter and would be forced to overwinter in the upper portions of the bay (as noted by five individuals in the present study), especially in years when onset of cold conditions is rapid. This could increase mortality risk prior to spawning, especially in extreme winters, as lower salinity water decreases tolerance to cold temperatures (Rome et al., in press, this volume). The combination of substantial delay in brood production, potentially reduced sperm viability, and possibly increased mortality, suggest that female crabs from the upper Chesapeake Bay could have a lower reproductive value than crabs from the lower bay. The shorter distance between spawning and mating areas for lower bay crabs may allow them to spawn in the same year that they mated, although this presumption remains untested. Further, by reaching higher salinity areas before the onset of winter, females probably endure reduced overwintering stress. This combination of factors is likely to contribute to the northern geographic limit of blue crab distribution (Rome et al., in press, this volume).

While most female blue crabs migrated in the fall after tagging, a small percentage appeared to move down the Bay earlier in the season. There are at least two possible explanations for this: (1) A small number of female blue crabs begin southerly movement prior to the main fall migration; or (2) Although we have assumed that all crabs in this study mated in the year of their release, the apparent earlier migration results from individuals that mated in the previous year and

overwintered in the upper estuary before they were tagged. Our ongoing tagging studies currently employ larger sample sizes and record shell condition as an index of time since mating to help differentiate between these two possibilities.

The migration rates in this study were consistent with movement rates reported for blue crabs from other tagging studies (Fischler and Walburg, 1962; Judy and Dudley, 1970; Steele, 1991; Schwartz, 1997). These data indicate that crabs migrating from upper portions of the Chesapeake Bay could reach the spawning grounds in approximately a month. This is particularly evidenced by one crab released in October that reached the mouth of the Rappahannock River (approximately 150 km from the release site) in 17 days.

Only a single crab in our study was captured outside of the Chesapeake Bay. This individual was recaptured in the intercoastal waterway near Flagler Beach, Florida, a distance of 1040 km traveled in 234 days. Similar unusual instances of long-distance movement have been noted in other blue crab tagging studies (Fischler and Walburg, 1962; Tagatz, 1968; Judy and Dudley, 1970; Schwartz, 1997), but it is difficult to place much significance in this single unusual record. In a review of blue crab movement and tagging studies, Hines (in press) noted that blue crabs tend to remain within East Coast estuaries, with only occasional individuals moving to neighboring systems (Cargo, 1958; Fischler and Walburg, 1962; Tagatz, 1968; Judy and Dudley, 1970), whereas females along the Gulf Coast of Florida often migrate along shore over long distances of hundreds of km (Oesterling and Evink, 1977; Steele, 1991).

The pattern of recapture sites in our study clearly indicates that most female blue crabs are migrating along the channel of the mainstem of Chesapeake Bay. The array of recapture sites along the eastern side of the bay corresponds well with the channel, and the pattern is contrary to both patterns expected of random migration routes and prediction of migration along the nearshore shallows (Turner et al., 2003). The bathymetry of the recapture sites (ca. 10 m deep) suggests that the crabs may move along the edge of the channel within adjoining shoulder areas, rather than within the trough (>13 m) itself, as surmised by Lipcius et al. (2001). However, many tagged crabs were caught on the eastern side of the main channel.

At the very least, these crabs had to directly cross the center channel of the Chesapeake Bay by walking through the trough, swimming over it, or a combination of both methods. To what degree crabs may have utilized deep trough areas during migration is uncertain. Due to the inherent nature of mark–recapture studies, it is difficult to describe female blue crab use of trough areas in much more detail without more comprehensive, fine-scale behavioral records of migratory movement now under study (Wolcott and Wolcott, 2003). Nevertheless, movement along the channel could reflect use of the salinity wedge as a cue for navigation down estuary. Use of depths along the edge of the channel may allow migrating crabs to forage on benthic prey resources that have been less impacted by deep anoxic waters during the summer months (Officer et al., 1984; Pihl et al., 1991; Diaz and Rosenberg, 1995). Although low oxygen conditions have most likely existed to some extent historically within the mainstem Chesapeake Bay, their severity and duration have increased markedly since European colonization (Officer et al., 1984; Cooper and Brush, 1993).

Although mark–recapture studies examining movement patterns can be biased significantly by the spatial and temporal distribution of recapture effort, especially for studies relying heavily on recaptures from commercial fishers, this did not appear to be a significant source of bias in the present study. The authors acknowledge that the large percentage of crabs recaptured near deep channel areas could be a result of a disproportionate amount of fishing effort within these deeper areas. In the fall, many commercial fishers typically move crab pots from shallow areas to the deeper areas of the mainstem Chesapeake Bay (often as deep as 20 m) which, as expressed by the fishers themselves, is intended to target migrating females. Historically, there has been little quantitative information available regarding the distribution of blue crab fishing effort during the majority of the summer–fall season. However, Maryland has recently begun to assess the spatial and temporal distribution of commercial crabpot and trotline effort within its portion of the Chesapeake Bay and associated tributaries (Christman et al., 2004; Glenn Davis, Maryland Department of Natural Resources, personal communication). In 2002, within the lower section of the Maryland portion of the Bay, the relative

abundance of crab pots in deeper water increased during the fall. During October and November, roughly 50% of commercial crabpot effort occurred in waters 8–10 m, while the remainder of effort occurred in waters <8 m. Furthermore, the majority of recreational effort, which represented approximately 20% of Maryland's commercial harvest (>10 million crabs) in 2001, is typically centered in shallow waters near man-made hard structures, e.g., docks, piers, public boat access points, etc. (Ashford and Jones, 2002). Thus, although it appears that commercial fishing effort was not evenly distributed temporally or spatially, a substantial amount of effort occurred within shallow areas of the Bay during the fall months in 2002, and most likely for all years presented in this study. Moreover, the markedly skewed distribution of recaptures in the eastern shoulder of the Bay indicates that the apparent migration pattern is not an artifact of fishing effort.

The spatio-temporal distribution of fishing effort could also bias the examination of the timing of blue crab migration. For instance, an inaccurate movement pattern could be generated if fishing effort is skewed temporally in the vicinity of the release areas or moves along the vertical axis of the Chesapeake Bay during the migration period. However, our observations indicate that commercial fishing effort in and near the Rhode River appears fairly consistent from the beginning of the fishing season in mid-April until season closure, usually in mid-November.

While the blue crab spawning sanctuary complex in Virginia waters of the Chesapeake mainstem may protect crabs during the spawning period, it leaves a large portion of females (especially those females moving from the upper bay) vulnerable to harvest during their fall migration. Overharvest is considered the major factor responsible for the recent dramatic decline in blue crab spawning stock biomass and larval recruitment (Lipcius and Stockhausen, 2002). Seitz et al. (2001) reported that only 11–22% of the potential blue crab spawning stock reached the historical Lower Bay Spawning Sanctuary (LBSS) and Bayside Eastern Shore Sanctuary (BESS). Our results provide fishery managers with specific information that regulation of fishing pressure along the migration corridor during very limited months (late September to early November, and perhaps shifting down the bay with advancing season) and habitats

(depths >8 m along the mainstem channel) could have great effect in protecting migrating females. Our results also emphasize the importance of further research to determine the cue(s), the mode(s) of movement, and the mechanism(s) of navigation, for this migration.

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