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Post-mating behavior, intramolt growth, and onset of migration to Chesapeake Bay spawning grounds by adult female blue crabs, *Callinectes sapidus* Rathbun

Heather V. Turner[a,1], Donna L. Wolcott[a,*], Thomas G. Wolcott[a], Anson H. Hines[b]

[a] *Department of Marine, Earth, and Atmospheric Sciences, North Carolina State University, Box 8208, Raleigh, NC 27695-8208, USA*

[b] *Smithsonian Environmental Research Center, P.O. Box 28, Edgewater, MD 21037, USA*

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Abstract

After molting to maturity, female blue crabs must rebuild muscles atrophied to permit molting and grow larger ones commensurate with the larger exoskeleton. They also must acquire energy for oogenesis and for migration to high-salinity spawning habitat, a distance of >150 km for females mating in the Upper Chesapeake Bay. Using telemetry and mark–recapture techniques, post-copulatory females in the upper bay were shown to forage at high rates, alternating between meandering and directed movement in the area of mating for weeks to months, and to begin migrating in October. Consequently, females from the Upper Chesapeake Bay probably do not spawn until the season after mating. Their priority seems to be to acquire energy before migrating. After molting, energy was allocated first into somatic tissue and eventually into hepatopancreas and gonads. Telemetry of feeding and movement showed that habitat utilization, traveling velocities, foraging patterns, and movements were similar to those already determined for males. However, females appeared to invest proportionally more energy (calories per gram dry weight) into their somatic and reproductive tissues than did males. A newly designed transmitter that telemetered depth showed that females moved during both ebbs and floods and remained at or near the bottom of the water column.

Keywords: Female blue crab; *Callinectes sapidus*; Foraging; Growth; Energetics; Migration; Telemetry; Chesapeake Bay; USA

* Corresponding author.
E-mail address: donna_wolcott@ncsu.edu (D.L. Wolcott).
[1] 523 Cliff Court, Winterville, NC, 28590, USA.

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1. Introduction

Migratory activity is costly, since it requires energy (Kilpi and Saurola, 1984; Harrington et al., 1988), can involve moving long distances (Malcolm et al., 1987; Reed et al., 1988), and can require physiological changes (Bone et al., 1995). Other migratory costs can include an increased probability of predation and greater exposure to physical risks (Wolcott and Wolcott, 1985; Reed et al., 1988). However, migration is an essential component of many life history strategies and occurs throughout the animal kingdom (Dingle, 1985). Migrating is advantageous because it allows a variety of organisms to reach locations where they are able to benefit from favorable environmental conditions, e.g., reduced predation rates, greater food availability, seasonally favorable temperatures, higher densities of mates (Kuipers, 1973; Taylor et al., 1985; Wolcott and Wolcott, 1985; Campbell, 1986; Calvert and Brower, 1987; Malcolm et al., 1987; L'Arrivee and Blokpoel, 1988; Harrington et al., 1988; Reed et al., 1988; Omura, 1988; Wibbels et al., 1990; Adamczewska and Morris, 1994; Hines et al., 1995; Gitschlag-Gregg, 1996). Therefore, there is strong selection pressure favoring those animals that can develop mechanisms for dealing with trade-offs—minimizing costs and maximizing benefits.

Female blue crabs offer unique opportunities to examine how animals deal with the costs of migration. Females must migrate from lower salinity waters, where they molt to maturity and mate, to high salinity waters where they produce egg masses and release larvae (Van Engel, 1958; Millikin and Williams, 1984). For females in the Chesapeake, this can involve moving up to 200 km (Churchill, 1919; Fielder, 1930; Van Engel, 1958; Hines et al., 1995; McConaugha, 1995). They also must obtain large amounts of food in a short time. As with any crab following a molt, mature females must rebuild muscles atrophied to make molting possible (Skinner, 1985) and build muscle mass commensurate with their new, larger exoskeleton. They also must build energy stores for migration and oogenesis (Hard, 1942; Lee and Walker, 1995). Females after the terminal molt, therefore, face potentially conflicting needs for energy acquisition (foraging) and allocation (migration, somatic growth, oogenesis)—needs that do not confront females (or males) in other post-molt periods. The trade-offs could be managed in various ways; for instance, post-copulatory female blue crabs might complete somatic (muscle) growth and acquire all the necessary energy reserves prior to migration, maximizing locomotory and defensive abilities and perhaps potential egg production at the expense of delayed reproduction, overwintering mortality, and decreased viability of stored sperm. They might migrate soon after mating and continue to build tissues and energy stores en route, trading a risk of underdeveloped predation defenses and weak locomotion for earlier arrival on the spawning grounds, or they might migrate at their best speed immediately after mating and delay energy acquisition for oogenesis until migration is completed, trading risk of delaying both somatic and gonadal growth (hence, higher predation, possibly lower fecundity) for early arrival. The last alternative is unlikely, since females have been reported to begin ovarian maturation shortly after the molt to maturity (Hard, 1942; Lee and Walker, 1995) and, in some cases, to overwinter with ovaries in advanced stages of development (Churchill, 1919). We examined the post-molt strategies of mature females including foraging patterns, post-molt tissue building, and timing of the onset of migration to gain insight about how they make the energetic trade-offs.

Molting to maturity and mating occur throughout the warm months, and we began with the hypothesis that each individual would begin migration soon after she mated. Reproducing as early as possible after mating would shorten generation time, remove the risk of winter mortality before first reproduction, and ensure that eggs were fertilized with fresh sperm, resulting in an increase in the individual's genetic contribution to the population (Stearns, 1976). Strong selection pressure for this would be expected, and strategies to protect blue crab spawning stocks are based on the assumption that at least some females migrate to spawning grounds promptly after mating. On the other hand, delaying migration until mid- to late fall might offer a selective advantage by allowing females to forage in prey-rich subestuaries and maximize energy acquisition before migrating and overwintering. Peak numbers of females appear to begin their progression downstream when cooler temperatures appear in the fall (Van Engel, 1958; McConaugha, 1995), but those females would not be able to spawn in the same season as mating. They could not reach the spawning grounds before mid-September, when brood production is ending for the year (Churchill, 1919; McConaugha, 1995). Some do not even complete their migration before winter sets in and appear in winter dredge samples from upstream portions of the bay (McConaugha, 1995; Seitz et al., 1998).

Migratory locomotion presumably is a major component of the energy equation. Females might use several locomotory modes to move the long distance from low-salinity mating grounds to high-salinity spawning grounds. Swimming down-estuary would be fast, but probably energetically expensive. It appears unlikely because the crabs have no way to know which direction is seaward. Simple compass orientation (if crabs have the capability) would be of limited use in meandering channels. Although crabs on the bottom might exploit cues in ebb- or flood currents to move in the "right direction" relative to those currents, those swimming in the water column would lose the fixed frame of reference required to extract directional information from currents. Ebb–tide transport ("selective tidal stream transport" or STST), achieved by hovering near the water surface during ebbs and staying on the bottom during floods, would ensure down-estuary transport at a lower energetic cost. Blue crabs possess the necessary behaviors for STST, which is used for transport up-estuary by postlarvae (Little and Epifanio, 1991; DeVries et al., 1994; Olmi, 1994, 1995) and for seaward transport by females about to hatch ripe egg masses (Tankersley et al., 1998). A third option, presumably the least energy intensive, is simply walking on the bottom and relying on tidal currents for directional cues.

We addressed the following questions: What patterns of movement and behavior do females exhibit prior to (when preparing for) migration? Do recently molted adult females build muscle, hepatopancreas (storage), and gonadal tissues simultaneously or sequentially? Are females putting more energy into any of these compartments than are males (which do not need to make eggs or migrations)? Before migrating, how long do post-copulatory females stay in the area where they mated? What transport mechanisms do females use? What is the risk that an adult female from the upper Chesapeake Bay will never reach the spawning grounds, but be caught by the intensive fishery (Miller and Houde, 1998), that may already have caused a decline in the spawning stock biomass (Lipcius and Stockhausen, 2002)?

2. Materials and methods

2.1. Study site

This research was conducted during the summer and fall seasons of 1998 and 1999, in the Rhode River (38°51′ N, 76°32′ W) and in the adjacent Chesapeake Bay (Fig. 1) near the Smithsonian Environmental Research Center (SERC). The Rhode River is a subestuary of northwest Chesapeake Bay located in the lower mesohaline zone. Maximum depth in the river is approximately 4 m, while the depth of the adjacent bay ranges from 0 to 38 m. Because of the northerly location in the bay, there is a single period of reproductive activity beginning in late June and trailing off in September.

2.2. Animal collection

Blue crabs were collected by otter trawl, seine, and trap or purchased by rendezvous with watermen who had just emptied them from crab pots around the mouth of the Rhode River and were promptly placed in aerated water tables supplied with flow-through Rhode River water. Crabs selected for post-molt growth, telemetry, and mark–recapture studies were intact, in molt stage C, had clean carapaces, and were >130 mm in carapace width

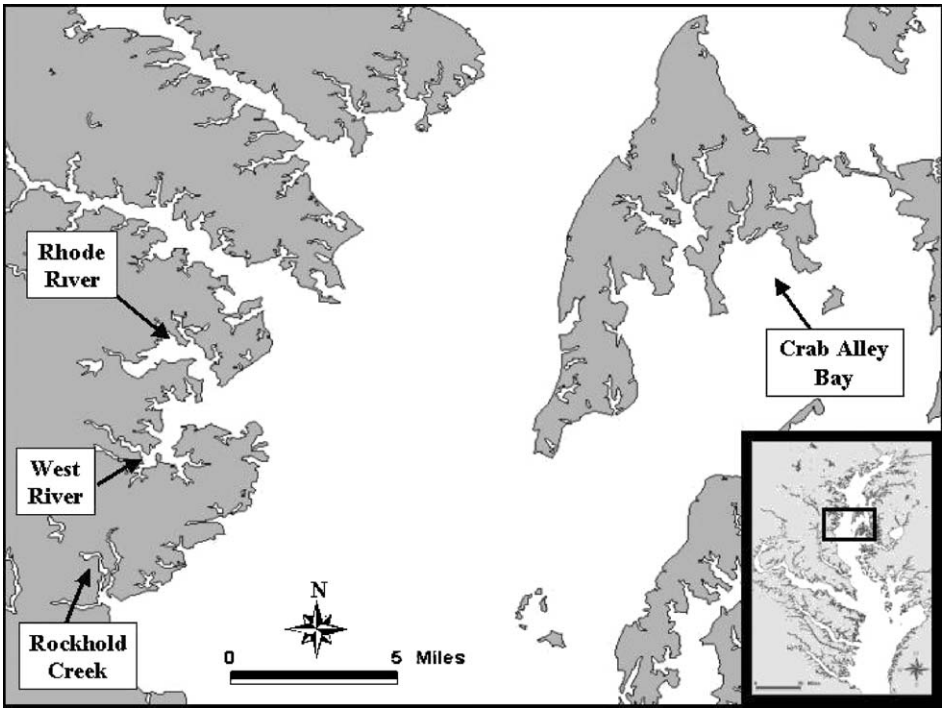


Fig. 1. Map of Chesapeake Bay with inset of Rhode River and adjacent Bay study sites.

(CW). A clean exoskeleton indicated they had molted during that season. We chose to use these field-caught adults, including individuals that had just mated and ones that might be closer to migrating because they had been in the area from days to months since mating. Controlling for time since molt by collecting pubertal ''peelers'', holding them until molt, mating them, and allowing them to harden before release was deemed impractical, a potential source of holding artifacts, and not representative of the actual population. Mature females used in mark–recapture studies were missing no more than two walking legs (loss of one to two walking legs by autotomy is common in the natural population [Smith and Hines,1991] due to molting ''accidents'' and agonistic interactions among crabs and, unlike the loss of chelae, was considered inconsequential). Approximately 10 females and 10 males were selected monthly (July–October 1999) for post-molt growth analyses.

2.3. Movement and behavior

To characterize movement and behavior of females, we tracked them with ultrasonic biotelemetry using location transmitters (''pingers'', $n = 18$) and depth/feeding transmitters ($n = 4$) that we constructed. Pingers were similar in design to those described by Wolcott and Hines (1990), produced regularly recurring pulses at frequencies ranging from 72 kHz to 78 kHz and had an average life of about a year. They were encased in vinyl electrical sleeving (Alpha PVC-80-5/8''), sealed with liquid vinyl cement, and back-filled with mineral oil to eliminate air bubbles. They weighed about 7 g in water, roughly 5% of the crabs' body mass, and in laboratory observations did not interfere with the normal behavior and locomotion of crabs (Hines et al., 1995; Wolcott and Hines, 1989, 1990). Transmitters were affixed to the dorsal carapace of females with copper wire wrapped around their lateral spines.

To determine movement patterns and average residence time of post-molt females in the molting and mating habitat prior to migration, females bearing ultrasonic transmitters were released in the area where they were captured (Rhode River or nearby Chesapeake Bay) within approximately 24 h of capture and typically were located twice per day (except during hazardous boating conditions) using an ultrasonic receiver (Sonotronics USR-5) and a directional hydrophone. Successive locations of the females were recorded along with date and time, and they were followed until they moved beyond tracking range of SERC (approx. 15 km). Eighteen females were released with pingers from 1998 to 1999. Their tracks were plotted as chart overlays with ArcView GIS using the Animal Movement extension (Hooge and Eichenlaub, 1997). To identify directed and undirected movement, weekly meander indices were calculated by dividing net distances traveled by gross distances traveled. Index values of 1 represented no meandering (directed movement), while values of 0 indicated random movement with no net direction (undirected movement). Their velocities and bearings were calculated, and Rayleigh's tests for significant preferred direction were conducted, testing the null hypothesis that their movements were random (Batschelet, 1981).

Four females were fitted with transmitters that telemetered crab depth and feeding activity and tracked (three continuously and one intermittently) to provide insight into behaviors of crabs while resident in the mating habitat. Hundreds of observations on each

of these "focal animals" provided data on the temporal and spatial scales of 10 min and a few meters. The depth/feeding transmitters weighed approximately 10 g in water (approx. 7% of crab's body mass). Laboratory observations of transmitter-equipped females have shown no detectable changes in behavior, motility (Nye, 1989; Clark et al., 1999), or vertical swimming behavior in deep tanks (R. Forward, Duke University, personal communication). Depth was measured by a calibrated pressure transducer, while feeding activity was detected by sensing biopotentials of the crab's mandibular muscle (Wolcott and Hines, 1989; Nye, 1989). Depth/feeding transmitters produced "pings" that allowed us to locate crabs from up to 700 m and transmitted data as 8-bit bytes using audibly different pings for "0" and "1" bits. The telemetered data were the instantaneous depth and the number of bites in the current 20-min period, plus the average depth and total number of bites in each of the three preceding 20-min periods (i.e., archived data for the past hour). Females were fitted with depth/feeding transmitters by first inserting electrodes through their carapace near the mandibular muscle according to the methods of Wolcott and Hines (1989), Nye (1989), and Clark et al. (1999), and then lashing the transmitter to the crab's dorsal surface with copper wire wrapped about the lateral spines (Fig. 2). Correct electrode placement and transmitter output were verified by holding females in laboratory aquaria for approximately 24 h and observing them during a feeding bout.

Females were released at their capture site and tracked continuously by a team of observers using directional and omnidirectional hydrophones and an ultrasonic receiver (Sonotronics USR-5). Crabs were tracked for 96 h (weather permitting) until females were lost or appeared motionless for at least 12 h. Their location (from GPS) was plotted on a chart at 10-min intervals, and the crab's depth compared with bottom depth shown by a depth sounder. Feeding activity over time was also recorded. Depth/feeding tracking was done during the months of July, September, and October. Data were analyzed to identify peaks of feeding activity. The total number of bites taken per hour was calculated for

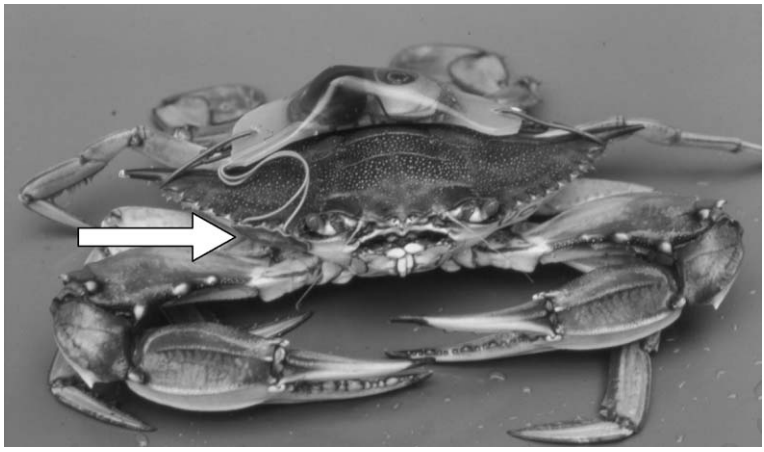


Fig. 2. Photograph of female blue crab fitted with depth/feeding transmitter. Transmitter attached with wire wrapped around lateral spines. Arrow denotes electrodes that are inserted into mandibular muscle.

diurnal, nocturnal, and crepuscular periods. Diurnal hours were 0830–1900 h in July, 0915–1800 h in September, and 0945–1700 h in October; nocturnal hours were 2200–0530 h in July, 2100–0615 h in September, and 2000–0645 h in October; crepuscular hours were 0530–0730 and 1900–2100 h in July, 0615–0815 and 1800–2000 h in September, and 0645–0845 and 1700–1900 h in October. Means of feeding activity for each period were calculated.

2.4. Post-molt tissue growth

To determine patterns of post-molt tissue growth, tissues of premigratory females ($n = 45$) were analyzed using tissues of males ($n = 49$) as controls. Prior to dissection, crabs were stored frozen. At dissection, they were thawed, measured (CW), weighed, and staged by ovarian development (Hard, 1942). Total wet weight was recorded after ancillary water was shaken off. Ovaries (or vasa deferentia plus testes) and hepatopancreas were dissected out separately and weighed wet. Spermathecae were dissected out of females but not included in analysis, since sperm and accessory fluid deposited there by males do not reflect growth or energy investment by females. These tissues and the rest of the body were dried to a constant weight at 60 °C, and dry weights were recorded. To measure total ash-free dry weight (AFDW), each crab was ground in a coffee mill, and approximately 1 g samples were ashed for 2 h at 450 °C in a muffle furnace. Dried reproductive tissues and hepatopancreas were not ashed because initial trials demonstrated their ash content to be insignificant. To measure caloric content (calories per gram), a subset of samples was pressed into pellets (approximately 1 g body, 0.5 g reproductive tissue, and 0.5 g hepatopancreas) and ignited in an Isoperibol Oxygen Bomb Calorimeter (Parr 1261). Calorimetry techniques were conducted according to manufacturer's recommendations.

To ascertain post-molt growth and energetic trends, caloric investment was calculated, and tissue accumulation was determined. Total caloric gain was determined by first estimating the mean calories per gram for each compartment and then calculating total calories (mean calories per gram·dry weight of that compartment). The potential effect of crab size was eliminated as a covariable by dividing total calories by CW^3 (cube of carapace width in millimeters). The cube of a linear dimension is suitable as a surrogate for volume because, within each sex, form is isometric in mature animals (Hines, 1982) and does not change during intermolt.

The relative time course of investment of calories into various tissue compartments was determined based on assumptions about growth in biomass relative to growth in external dimensions for an animal with an exoskeleton. Immediately after molting, a crab's internal volume increases markedly and almost instantaneously while the amount of tissue remains unchanged, so tissue per unit volume is at a minimum, and much of the space is occupied by increased hemolymph volume. As a crab "grows into" its new, larger exoskeleton by increasing muscle mass, etc. (somatic growth), the internal volume of the hard intermolt exoskeleton remains constant. Consequently, tissue per unit volume increases, while hemolymph volume decreases (Millikin and Williams, 1984). To measure post-molt somatic growth while eliminating body size as a covariate, we measured tissue mass as dry weight excluding shell (ash-free dry weight or AFDW). Tissue mass per unit exoskeleton volume (using CW^3 as a surrogate) serves as a relative measure of post-molt

growth, independent of body size. The absolute rate of tissue deposition depends on environmental factors, such as forage quantity and quality (Wolcott and Wolcott, 1984), so AFDW/CW^3 gives an estimate of how far along an individual animal is in the process of tissue deposition post-molt, but not of the time since molt.

To compare caloric content of body compartments between premigratory females and (nonmigratory) males, we used two-way ANOVA to test for effects of gender (male, female) and body size (CW^3) and of gender and total tissue mass (AFDW). When significant interactions between main effects (i.e., gender × CW^3, gender × AFDW) were revealed, graphical analysis of the regressions provided insight about the nature of gender effects on size-specific tissue accumulation since molt (i.e., AFDW/CW^3). When no significant interactions between main effects were revealed, we used ANCOVAs to partition the effect of relative tissue accumulation since molt (AFDW/CW^3) and body size (CW^3) as the covariates and tested for main effect of gender on caloric content of the body compartment. Data were tested for normality and homoscedasticity; no transformations were required.

2.5. Timing of migration

To determine when females begin migrating after mating, we conducted a mark–recapture study using individually numbered across-the-back tags requesting recapture information. Tags were affixed to mature females by wire wrapped around their lateral spines. Four batches of ~ 100 females each (total = 400 crabs) were released in 1999, with the first in mid-August, the second in early September, the third in late September, and the fourth in mid-October. All batches were released in Chesapeake Bay off the mouth of the Rhode River, with the first two at ~ 4 m depth and the last two at ~ 8 m depth. To increase probability of data return, the project and its purpose were publicized and rewards offered: $2/crab, plus entry into a lottery for $100. Watermen who caught tagged crabs reported approximate location, depth, and date of recaptures. Timing of migration was estimated by comparing when/where crabs were released with when/where crabs were recaptured.

We also analyzed movement and behavior data from females ($n = 18$) with ultrasonic pingers. To determine the latency from release to migration, we calculated the number of days between a release in the Rhode River and the crab's loss or capture, or its movement out into the bay (mean, S.E.). Latency from the date of release in the bay (or of movement into the bay from the river) and loss or capture was also determined (mean, S.E.).

2.6. Transport mechanisms

To determine if females use STST, we towed an otter trawl fitted with floats for near-surface sampling and conducted spotlight searches for females swimming near the surface, across the bay axis near the Rhode River during nocturnal ebbs. Cruises ($n = 12$) took place monthly from June to November 1998 and in May and June 1999, primarily during spring tides and extended from 38°52.11N, 76°28.57W to 38°51.88N, 76°27.08W. During the cruises, bottom trawls were also conducted occasionally to determine if mature females were present in deeper water but not migrating near the

surface. Each trawl lasted approximately 15 min. Evidence for STST was also sought in the depth data from females with depth/feeding transmitters. Their vertical movements were compared to tidal phase (ebb or flood) using an ANOVA ($\alpha = 0.05$), and plots of depth vs. time were constructed.

3. Results

3.1. Movement and behavior

Females with location transmitters alternated between quick, directed movements and slow, meandering movements (Fig. 3), at speeds ranging from 0 to 257 m/h. Only 39% of movement patterns were nonrandom (Rayleigh's $z_{0.5}$ for angles ranging from 0.0266 to 17.16), and some of these probably were a consequence of the crabs' movements being constrained by the river banks. Meandering indices were highly variable between and within crab tracks and within months, ranging from 0.041 to 1.000. Due to high variance and low sample size, trends could not be established among months and between years. However, for crabs tracked longer than 1 month, meander indices generally increased just before crabs were lost.

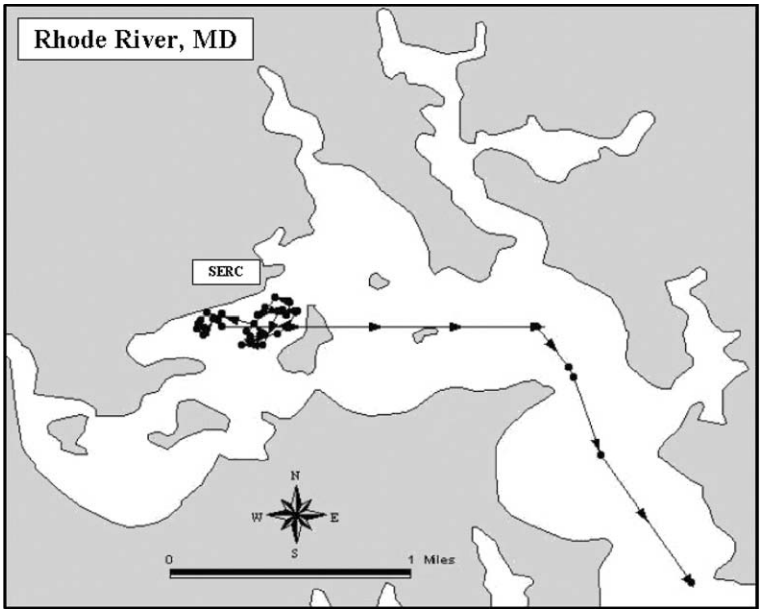


Fig. 3. Movements of a female crab tracked by ultrasonic pinger. The pattern of alternating meandering and directed movements is typical of females tracked in the Rhode River and adjacent bay in this study and of males in previous studies. This individual was released 7 June 1999 near the Smithsonian Environmental Research Center (SERC), tracked for 19 days until it moved out of tracking range and was never recovered. Circles: position fixes (generally twice/day). Arrows: most direct vector of movement.

Table 1
Data from location transmitters

Number	Date of release	Date of recapture	Time tracked (days)	*t* in river (days)	*t* in bay (days)	Mean dly speed (m/h)	Total dist (km)	Mean heading	*Z* values
1 R	July 14, 1998	July 24, 1998	7	4	7	18.21	4.37	127.42	2.98
2 R	August 6, 1998	October 29, 1998	70	25	45	35.72	72.04	134.99	17.16
3 R	August 11, 1998	July 10, 1999	2	×	×	×	×	×	×
4 B	August 24, 1998	September 4, 1998	12	n/a	12	26.24	6.93	16.76	0.41
5 B	August 24, 1998	September 4, 1998	12	n/a	12	24.20	6.39	313.37	0.03
6 R	August 26, 1998	n/a	31	31	n/a	6.03	4.34	136.28	3.32
7 R	September 9, 1998	October 10, 1998	31	31	n/a	7.74	5.76	129.77	0.49
8 R	June 7, 1999	n/a	19	19	n/a	13.80	5.96	99.89	1.60
9 B	June 10, 1999	n/a	3	n/a	3	22.53	1.08	11.35	2.38
10 R	June 23, 1999	July 3, 1999	9	6	3	78.52	18.84	172.02	2.29
11 R	July 12, 1999	July 19, 1999	7	3	5	41.63	6.99	158.92	3.54
12 R	August 16, 1999	August 19, 1999	4	4	n/a	15.37	1.11	151.52	2.15
13 B	August 16, 1999	September 20, 1999	14	n/a	14	26.45	21.59	173.69	7.16
14 R	August 25, 1999	n/a	4	4	n/a	21.49	1.55	11.13	2.59
15 R	September 6, 1999	n/a	42	39	3	4.93	4.85	167.04	8.87
16 R	October 8, 1999	n/a	34	34	n/a	3.35	2.65	336.03	0.17
17 B	October 21, 1999	n/a	28	n/a	28	10.00	6.49	261.44	3.24
18 B	October 21, 1999	n/a	23	n/a	23	12.11	6.41	102.74	0.03
Mean			19.56	18.18	11.91	21.67	10.43	145.30	3.69
Standard deviation			17.56	14.29	11.91	18.16	16.81	90.29	4.19
S.E.			4.14	4.12	3.44	4.28	3.96	21.28	0.07

Average speed, distance, direction, and time spent in the Rhode River or Bay. R = Rhode River, B = Bay, *t* = time, dly = daily, and dist = distance. Number 3R malfunctioned and provided no tracking data. Crabs released in the bay did not move into the Rhode River. All recaptured crabs were returned by the fishery. *Z* = Rayleigh's statistic for significant preferred direction ($z = nr^2$).

Females remained primarily in nearshore regions of the bay < 10 m deep and the deeper regions of subestuaries like the Rhode River where maximum depth = 4 m (Fig. 1). The most common direction of movement (mean bearing with respect to north) was 145.3° (Table 1). Two females moved out from the Rhode River, into the adjacent bay, and up into other tributaries. One moved about 13 km south, then west and into Rockhold Creek (near Deale, MD), while another moved 11 km southeast across the bay, then another 16 km northeast into Eastern Bay, an eastern shore subestuary, and into Crab Alley on its northern margin.

Females with telemetry transmitters fed at irregular intervals around the clock. The mean number of bites per hour during diurnal hours was 34.6, during nocturnal hours, 33.4, and during crepuscular hours, 54.1; the differences were not significant [$F(2,6) = 5.14$, $p = 0.896$].

3.2. Post-molt tissue growth

Females appear to invest proportionally more energy (calories per gram dry weight) into their muscle and reproductive tissues than do males. Mean energy contents of body (muscle) tissue were $2.60 \times 10^3 \pm 138.3$ S.E. cal/g in females ($n = 6$) and $2.26 \times 10^3 \pm 37.5$ S.E. cal/g in males [$n = 27$; $F(1,15) = 6.96$, $p < 0.05$]. Ovaries contained $5.23 \times 10^3 \pm 91.4$ S.E. cal/g ($n = 15$), and vasa deferentia plus testes $4.59 \times 10^3 \pm 27.0$ S.E. cal/g [$n = 22$; $F(1,17) = 30.92$, $p < 0.05$]. Mean investment into hepatopancreas did not differ by gender and was $6.01 \times 10^3 \pm 136.7$ S.E. cal/g for females ($n = 22$), and $5.71 \times 10^3 \pm 120.0$ S.E. cal/g for males [$n = 26$; $F(1,22) = 1.3899$, $p = 0.25$].

Males and females differed significantly in how energy was allocated during tissue growth (Table 2). Both males and females invested energy into muscle (defined as tissue other than gonad or hepatopancreas) from the onset of tissue deposition. Since muscle is

Table 2
Tests for significant differences in caloric content of body compartments between premigratory females and nonmigratory males

Interactions between covariates and factors

	Gender	AFDW/CW^3	Gender × AFDW/CW^3	Gender	Volume	Gender × volume
Gonad	< 0.001	< 0.001	< 0.001	0.4	0.027	0.294
Hepatopancreas	0.165	< 0.001	0.034	0.958	< 0.001	0.938
Muscle	0.351	< 0.001	0.131	0.593	< 0.001	0.509

Analysis of covariance

	Gender	AFDW/CW^3	Volume
Gonad	< 0.001	< 0.001	< 0.001
Hepatopancreas	0.075	< 0.001	< 0.001
Muscle	0.003	< 0.001	< 0.001

Gonad = ovarian AFDW/CW^3, or testes and vas deferens AFDW/CW^3, hepatopancreas = hepatopancreas AFDW/CW^3; muscle = non-gonad, non-hepatopancreas tissue AFDW/CW^3. $N = 45$ females, 49 males.

the bulk of the body's biomass, there is a tight linear relationship between muscle calories/volume and AFDW/volume with an intercept near zero (Fig. 4A). Animals at the lower end of the data range would be the newly molted "empty" or "white-belly"

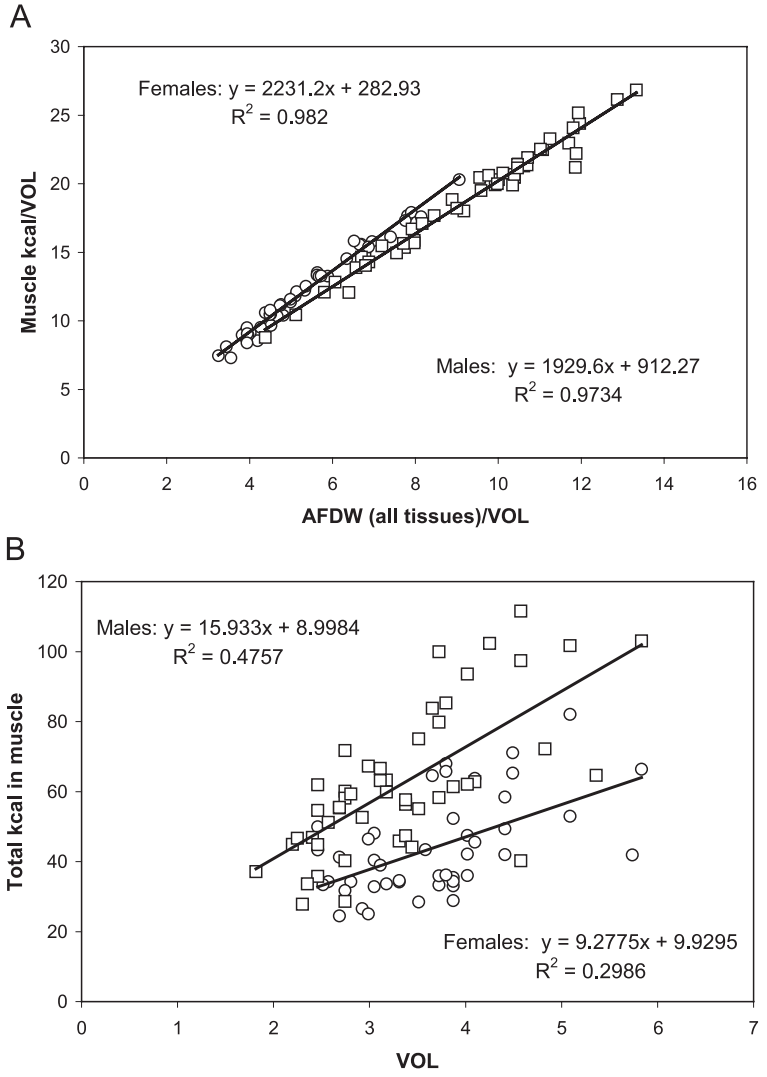


Fig. 4. Caloric investment by female (circles) and male (squares) blue crabs in somatic, reproductive, and hepatopancreatic tissue as a function of total tissue accumulation. Tissue accumulation (grams AFDW/exoskeleton volume) serves as surrogate for time since molt. "VOL", a surrogate for exoskeleton volume, is the cube of carapace width (CW^3)·10^{-6}. (A) Calories in "muscle" (body excepting gonad and hepatopancreas) per unit shell volume vs. tissue accumulation. (B) Total kilocalories in "muscle". (C) Post-molt caloric increase in female reproductive tracts (ovaries) vs. tissue accumulation. (D) Post-molt caloric increase in male reproductive tracts (testes + vasa deferentia) vs. tissue accumulation. (E) Post-molt caloric increase in female hepatopancreas vs. tissue accumulation. (F) Post-molt caloric increase in male hepatopancreas vs. tissue accumulation.

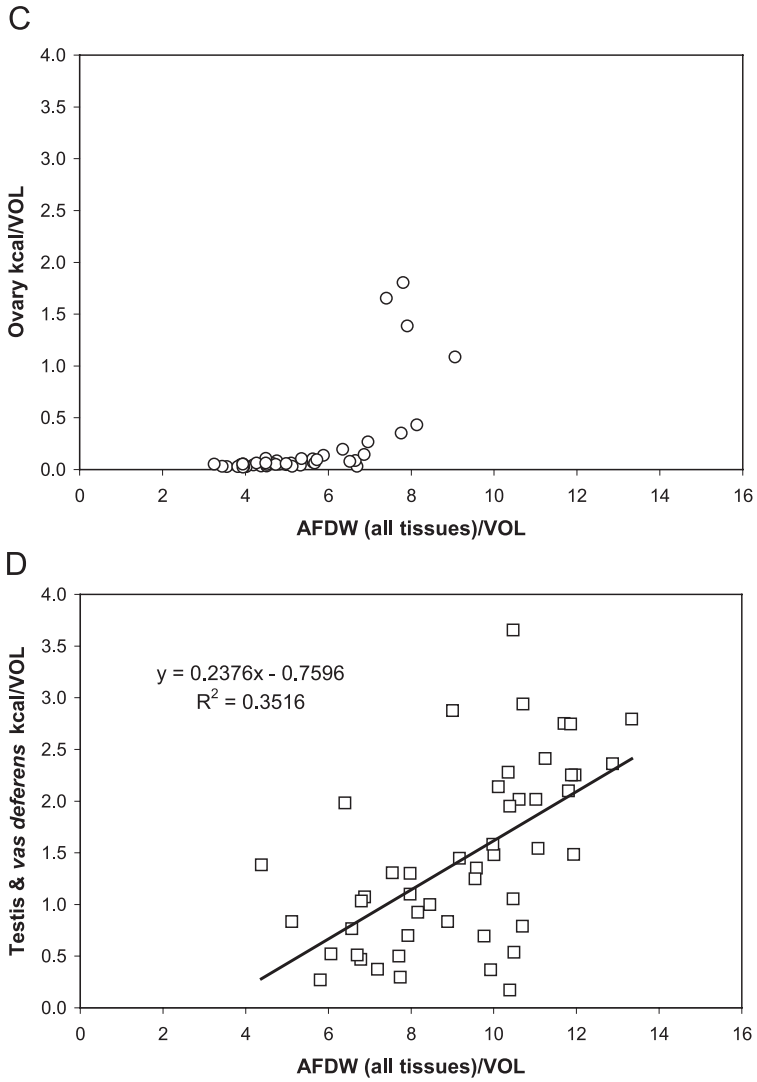


Fig. 4 (*continued*).

crabs; those at the upper end are "filled-out" intermolt animals. Females did not accumulate dramatically larger caloric reserves in muscle than did males. Indeed, their total caloric investment in muscle mass per unit exoskeleton volume appeared significantly smaller than that of males ($p = 0.003$, Fig. 4B). However, because volume was estimated by CW^3, the difference could be accounted for by male–female allometry. Given the small proportion of the variance explained by the regressions, the difference in muscle calories/volume and its apparent increase with increasing volume probably have no biological significance.

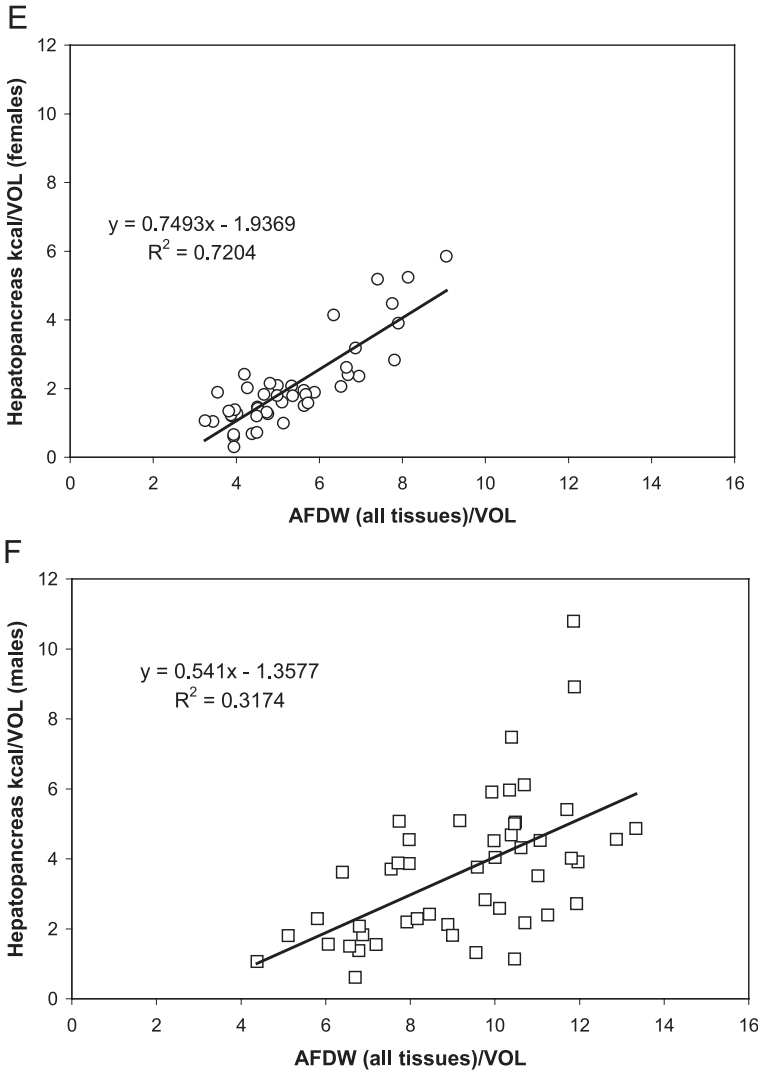


Fig. 4 (*continued*).

Females delay substantial investment in reproduction until total tissue accumulation reaches a threshold value of 7×10^{-6} g/mm^3 (AFDW/CW^3), shown by the dramatically nonlinear relationship in Fig. 4C. Calories in ovarian tissue remained low at $\sim 1.75 \times 10^{-4}$ cal/CW^3 until that ratio of tissue to volume was reached, then began to increase dramatically. Males' caloric investments in vasa deferentia and testes were initially higher than those of females ($p < 0.001$) and variable, ranging threefold from 0.0005 to 0.0015 cal/CW^3 even for a similar stage in tissue deposition (Fig. 4D). The intersect of the regression with the tissue/volume axis suggests that they too invest in

muscle at the outset and begin diverting energy to gonadal development only after reaching a threshold AFDW/CW^3 of about 3×10^{-6}. A very similar pattern is exhibited for investment in hepatopancreas by both sexes (Fig. 4E and F).

3.3. Timing of migration

Females fitted with location transmitters and released in the river ($n = 12$) remained there for an average of 18.2 days (range 3–34 days, S.E. $\pm$ 4.31). Those that were released in the bay ($n = 6$), or entered the bay after release in the Rhode River ($n = 11$) stayed there for an average of 11.9 days (range 3–45 days, S.E. $\pm$ 3.59) (Table 1). No transmitter-bearing females initiated an obvious migration while being tracked. Two were captured and returned after migration had begun. One disappeared in October 1998 after being tracked for over 2 months and was caught 15 days later 59 km downstream off Barren Island, across the bay from the Patuxent River. The other crab was lost in August 1998 due to transmitter malfunction, but was caught in July of 1999 $\sim$ 30 km down-bay on the western shore off Calvert Cliffs, about 18 km north of the Patuxent River. This crab was carrying an egg mass at the time of capture.

The return rate of carapace tags from batch releases was 5–21%. Females often remained near release sites for weeks, but the percentage captured at >50 km from release increased markedly during October. Of recaptures from the mid-August release ($n = 101$, 20.8% returned), 70.8% were caught within 1 week less than 1 km from their release site. After 4 weeks, 4.8% had been caught 1–10 km away, and after 8 weeks, an additional 4.8% were taken within 1–10 km (Figs. 5 and 6). Beyond 8 weeks after release, another 4.8% were recaptured farther than 150 km from the release site. Of crabs recaptured from the early September release ($n = 101$, 5.9% returned), 33.4% of captures were after 4

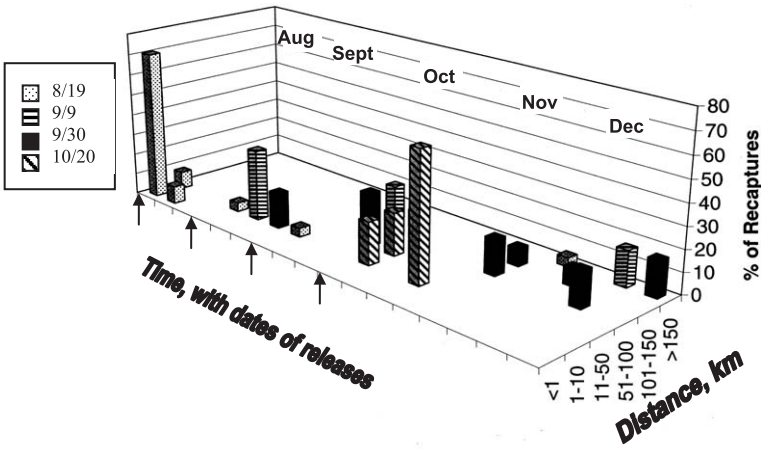
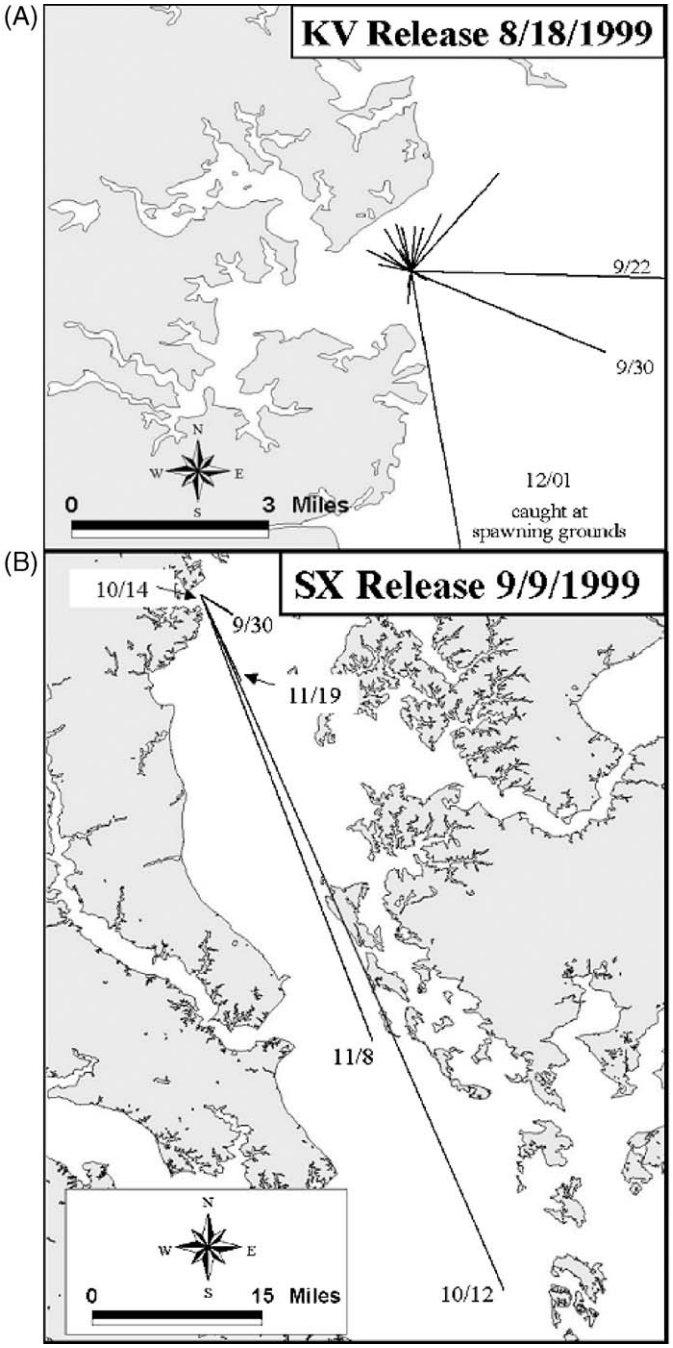


Fig. 5. Migration of mature female blue crabs as a function of season. Bars represent the percentage of recaptured females from each of four release dates caught within a given distance interval (km). Arrows denote release dates (18 August 1999, 9 September 1999, 30 September 1999, and 20 October 1999).


(A)
KV Release 8/18/1999
9/22
9/30
N
W
E
S
0
3 Miles
12/01
caught at
spawning grounds
(B)
SX Release 9/9/1999
10/14
9/30
11/19
11/8
10/12
N
W
E
S
0
15 Miles

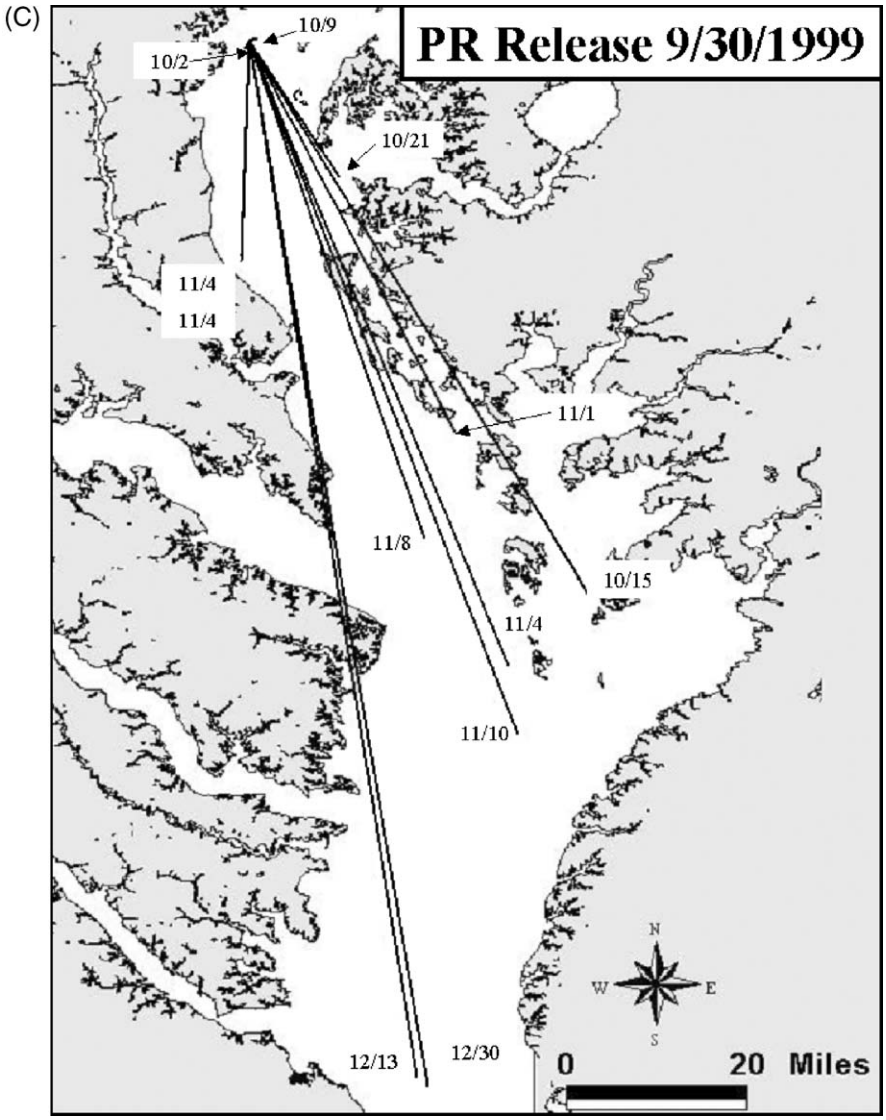


Fig. 6. Mark–recapture maps of individual mature females. Lines indicate most direct vector of movement with recapture location at terminus. Plot lines for animals recaptured less than 2 weeks after release do not include a recapture date. (A) August release, August 19, 1999. (B) Early September release, September 9, 1999. (C) Late September release, September 30, 1999.

weeks and within 1–10 km of their release, and 16.7% were taken after 8 weeks within 10–50 km (Figs. 5 and 6). About 16.7% of recaptures were beyond 8 weeks, from 50 to more than 150 km away from their release site. Of females recaptured from the late September release ($n = 98$, 12.2% returned) 16.7% of recaptures were after 1 week from

within 10 km of the release site, and 25% were after 4 weeks from 10 to 50 km away. A total of 16.7% and 8.3% of returns came after 4 and 8 weeks, respectively, from 100 to 150 km away (Figs. 5 and 6). Beyond 8 weeks after release, another 16.7% of recaptures were reported farther than 150 km downstream. Many of the females released in mid-October ($n = 100$, 6.1% returned) immediately began migrating; 20% of the crabs recaptured had moved between 10 and 50 km from their release site during the first week, although a large proportion was still recaptured within 10 km of the release site after 1 week (20% of recaptures) and even 4 weeks (60% of recaptures; Fig. 5).

Females began to be recaptured halfway down the bay in mid- to late October (Figs. 5 and 6B–D). Four females migrated >190 km, all the way down to the bay mouth, and were captured by winter dredges near the York River starting in December (Fig. 6). The majority of recaptures from this study occurred along the margins of the bay, generally within 1 km of the shoreline in water up to 10 m deep, with only two recaptures at depths greater than 15 m (Figs. 6 and 7).

Releases of females with transmitters and carapace tags were designed to detect the seasonal timing of migration. As noted earlier, we did not control for time since molt because it would have been neither practical nor (even at best) representative of the natural population. The bay contains females that have molted to maturity and mated at various times since waters warmed in spring. So did our sample population, so it is unknown how many days, weeks or even months each individual had remained in the area before we tagged and released it. Our estimates of delay from mating to the onset of migration are therefore very conservative. Based on our recapture data and the seasonal peaks in mating (July and August in the Rhode River) and the onset of peak migration (October) as suggested by previous reports and confirmed by our tag returns,

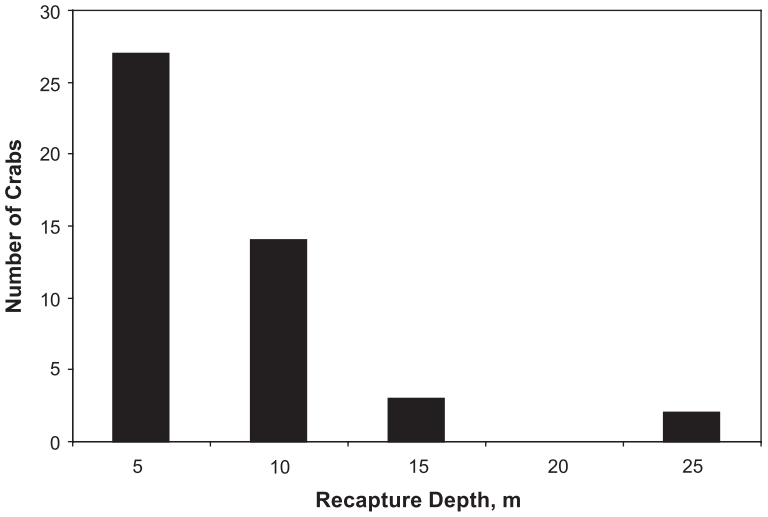


Fig. 7. Depth of capture of mature female blue crabs. Bars represent the number of females caught with across-the-back tags in each 5-m-depth interval, as reported by fishers. Data from August 1999 to January 2000.

we presume that females spend an average of 2 months in or near the molting habitat before migrating down-bay.

3.4. Transport mechanisms

Only one female was caught and another four seen in near-surface waters during multiple nocturnal trawls and observations in late June 1998. A single crab was seen in early September. No adult crabs (either sex) were caught or observed in any of the other cruises. Bottom trawls in the mainstem of the bay yielded no females from depths greater than 5–10 m.

Although the four females tracked with depth/feeding transmitters probably were not actively migrating, two exhibited apparently oriented movement in a generally southward direction. All moved exclusively on (or quite near) the bottom, at up to 240 m/h. Females moved during both ebb and flood tides, and movement was not significantly correlated with tidal phase [$F(1,4) = 7.71$, $p = 0.86$].

4. Discussion

Premigratory females' habitat utilization, traveling velocities, foraging patterns (feeding bouts and number of bites), and movements (slow meandering movements during feeding, rapid directed movements between prey patches) were similar to those of males tracked in previous studies (Nye, 1989; Wolcott and Hines, 1989, 1990; Hines et al., 1995; Clark et al., 1999). Throughout the summer, mature females were not found out toward the center of the main channel of Chesapeake Bay—either on the bottom or swimming in the water column during ebbs. This unexpected finding led to the question, "If they aren't heading seaward in the mainstem, where are they?" Pingers and telemetry transmitters revealed that they stay predominantly in shallow subestuaries and margins of the mainstem of Chesapeake Bay, apparently foraging and building up muscle tissue and energy reserves.

During tissue growth, both females and males invest energy sequentially, first into growth of muscles, then simultaneously into reproductive tissue and hepatopancreas, a strategy also employed by *Carcinus maenas* (Adiyodi, 1978, 1985). Separating periods of somatic and reproductive growth is consistent with the idea that crabs first regain strength for defense, foraging, and locomotion before investing in migration and/or reproductive output. Since females did not have significantly higher caloric content in their hepatopancreas than did males, they do not seem to lay up hepatopancreatic energy stores specifically for migration. Some reserves for migration and/or for oogenesis may be stored in their muscle tissues, which have a higher caloric density than those of males. As in most species, blue crabs' ovaries have higher caloric density than male reproductive tracts, reflecting the high cost of provisioning eggs. Post-molt growth and energy allocation by females appeared less variable than that of males, perhaps because males were analyzed without controlling for stage of spermatogenesis or mating history. After mating, males are depleted in sperm and accessory fluid and require time for recovery (Jivoff, 1997; Kendall and Wolcott,

1999), so vasa deferentia from mature males taken in the field may differ widely in weight and energy content.

Post-molt growth, based on analysis of females' tissues, also provided physiological indications of how they prepare for migration. Post-molt mature females allocate energy first to the synthesis of muscle mass commensurate with the expanded post-molt exoskeleton, then increasingly to ovarian development and energy reserves, and finally to the locomotory costs of migration. Data from tracking and mark–recapture also are consistent with a strategy of acquiring energy prior to migration; females remained where they mated, in prey-rich subestuaries and nearby shoulders of the bay, for weeks to months. Oocytes of females in warmer regions south of the Chesapeake (near Savannah, GA) appear to increase in volume 120-fold within 30 days after the maturation molt (Lee and Walker, 1995), so mature females in the upper Chesapeake Bay probably are also allocating energy to oocyte maturation during the weeks they remain in the molting habitat. Foraging for resources to build oocytes and energy reserves probably continues during migration, since growth of ovaries and hepatopancreas was not completed in the Rhode River. That females are mating throughout the summer but only begin to appear down bay in mid- to late October suggests that migration is triggered not by some corollary of time since molting/mating, but by environmental cues (e.g., changes in water temperature, photoperiod).

Natural selection apparently has favored foraging and tissue growth prior to migration, rather than early arrival at the spawning grounds. The time that females remain near where they mated, building muscles and acquiring some of the energy required for migration and oogenesis, precludes their reaching the bay mouth in time to produce even one brood before winter. Watermen expect a pulse of mature females migrating down-bay in October and move crab pots accordingly, from the shallower waters to those below 10 m. Virginia's migration corridor/spawning sanctuary complex (waters deeper than 10 m) is opened to potting after September 15 and remains open until June 1 (Rugolo et al., 1997; Seitz et al., 1998), leaving a large segment of the spawning stock (at least from the upper bay) vulnerable to intensive fishing pressure. A large proportion of females is presently being caught, reflected by a 70% decline in the biomass of the female spawning stock (Lipcius and Stockhausen, 2002). The high proportion of tags from females in this study that was returned by the fishery despite the small $2 inducement (86% in 1998, 13% in 1999) underscores the potential impact of fishing mortality.

While we observed hardly any females swimming, our limited data do not allow us to reject any of the three hypothetical modes of transport: oriented swimming, STST or walking. The females fitted with telemetry transmitters did not use STST, but we could not be certain that they were actually migrating or track any of them farther than 24 km from the Rhode River. The STST hypothesis is still tenable, because STST requires little energy, provides a mechanism for seaward orientation, and is utilized by other life history stages of the blue crab. Walking on the bottom also remains a plausible transport mechanism. The females we tracked always moved at or near the bottom, at speeds (240 m/h) that could bring them to the spawning grounds in 34 days, a time similar to that extrapolated from progress of a migrating, pinger-carrying female (165 m/h, 37 days). A crab migrating by walking would experience slower current velocities in the boundary

layer (Hill, 1991) and could walk slowly or intermittently as needed. Like the terrestrial Christmas Island red crab, *Gecarcoidea natalis*, they might thereby minimize lactate accumulation associated with more vigorous exercise (Adamczewska and Morris, 1994). Walking females would also have a fixed frame of reference (the bottom), allowing the use of chemical and current cues for orientating down-bay (Barbin, 1998). Unlike crabs swimming in the water column, they also could forage opportunistically at all times of day and night.

Since post-copulatory females do not appear to build up large energy reserves for migration and invest calories in lipid-rich eggs instead, we infer that locomotory costs of migration (and continued ovarian development) are supported by foraging en route to the lower bay spawning grounds. Commercial crabbers confirm that migrating crabs seek food, by catching large numbers of mature females in baited pots in the fall (Rugolo et al., 1997). Crab digestive tracts are "batch processors" (Gibson and Barker, 1979) requiring several hours to process a meal (personal observation), so foraging intermittently during STST (while on the bottom during flood tides) might be nearly as effectively as foraging while continuously walking on the bottom (Penry and Jumars, 1987), depending on the importance of prey search time.

Our recaptures of tagged females indicate that many females are migrating through nearshore regions less than a kilometer from shore and in waters less than 15 m deep and are vulnerable to fishing while in this area. This finding is somewhat biased, since our data are fishery dependent, i.e., we have no data thus far on whether or how females utilize the deeper portions of the bay. Sixteen females clearly swam in, or walked on the bottom of, water as much as 30 m deep. They were recaptured on the bay's eastern margin after crossing the main shipping channel, but only two of them at depths greater than 15 m. If females migrate along the nearshore shallows of the bay, they may encounter more food resources than in the deep mainstem channel and also decrease their exposure to anoxic/hypoxic waters. Given that migration seems to peak in October, this last may be a minor consideration; by the end of October, dissolved oxygen typically is rising above 2 mg/l even in the deepest pools (Wang et al., 2001).

Our evidence indicates that females from upper regions of the Chesapeake Bay probably do not spawn until the season after mating, which raises the risk of mortality from the fishery or from overwintering stress before their first reproduction. In contrast, females in the lower bay have been assumed to migrate and begin brood production in the same summer that they mate. If this is the case, they are afforded protection by Virginia's corridor/sanctuary complex, avoid winter mortality before first reproduction, have a shorter generation time, and may therefore make a disproportionate contribution to reproductive output of the population. It remains to be demonstrated that populations nearer the spawning grounds migrate earlier; fall migration appears to be the pattern in North Carolina's Pamlico Sound, a much smaller estuarine system (T. Wolcott and D. Wolcott, unpublished data). Research now in progress will provide a fuller understanding of any regional or estuarine-scale-dependent differences in behavior and their implications for the ecology of the species and for management of the threatened broodstock to maintain a sustainable blue crab fishery.

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