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ARTICLE

Life Stage, Gender and Movement of Blue Crabs (*Callinectes sapidus*) in Lake Mattamuskeet and Connecting Canals

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ABSTRACT

In their ranges on east and south coasts of the Americas as well as their established invasions in the Adriatic and Baltic, blue crabs, *Callinectes sapidus*, inhabit estuaries, sounds and coastal oceans and are commercially and ecologically important. How crabs move in response to physical variables is important to management. We monitored life stages at canal control structures, assessed gender ratios with recreational crabbing, learned from crabbers, and studied movements of tagged crabs in a canal connecting Lake Mattamuskeet to the Pamlico sound. Juveniles enter the lake through two of 4 canals connecting to the sounds. Females migrate out through one canal. The lake standing population is about 70% male. Movements of 240 crabs in August 2012 and 102 crabs in October 2014 were quantified using RFID tags with co-located meteorological and oceanographic devices. Non-spawning females and males are nomadic. Crabs released in the canal move in response to changes in water depth and go with the flow, toward the Pamlico Sound (summer 76% and fall 78%). What crabbers describe as a fall migration appears to be concentration of crabs in warmer deeper canals and then southern movement with flow generated by strong north winds. To be effective, management strategies like migratory corridors require understanding of crab movements.

1. Introduction

Blue crabs, *Callinectes sapidus*, range naturally from Argentina to Cape Cod [1] where they occupy aquatic habitats from coastal oceans to fresh to hypersaline sounds and estuaries. Invasive populations are established from Italy to Turkey and in the Baltic [2-5]. The blue crab life cycle is dominated by movements. Understanding movements is a key to effective active

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management.

In lunar tidal systems, early-stage larvae, settlement-stage megalopa, dispersing juveniles, and spawning females migrate using tidal stream transport. Early stage larvae move out of estuaries into the coastal ocean [1-6,7]. Zoea ride falling tides at night out of estuaries [6]. Planktonic, settlement stage larvae change vertical migration patterns in response to estuarine odors [8-11] migrating up-estuary on flood tides [12].

Females migrate to high salinity to spawn in 22 PSU or higher. Migrations are often over 5 km per day [13,14]. The spawning migration is punctuated by foraging [15,16] as migrating females gather energy and mature additional clutches of eggs [17-19]. Spawning female crabs move first to high salinity water and then into the coastal ocean [13,14, 20-22].

Cues that stimulate movements are known for some blue crab life stages. Megalopa respond to salinity, turbulence and light [7,23-25]. Juveniles respond to day vs night and to flow[12]. Spawning females respond to rates of change in salinity and water depth and walk and swim with falling tides [13,22,,26,27]. In strongly tidal systems, spawning females move with the flow on falling tides and walk against the flow with rising tides [13]. In the tidal Chesapeake Bay, movements of spawning females reported by Aguilar et al., [14] were 10 fold higher than movements of spawning females in the tributaries of the non-tidal Neuse River in north Carolina [28]. Spawning females in the South Atlantic Bight are found at least 13 km offshore [29]. In the weakly tidal Gulf of Mexico spawning female crabs are found over 70 km offshore (unpublished GOMEX cruise data). Spawning females have sequential clutches and are likely to complete their life cycle in the coastal ocean.

How non-spawning adult and late stage juvenile blue crabs behave is less well understood. In an embayment in North Carolina [19] and sub-estuary of the Chesapeake, late stage juveniles were found in shallower water than adult males. Both meandered with punctuated times of faster movement. Juveniles meander about 12 m/hour and adults meander about 24 m/hour. Adult males are nomadic. Juveniles and adults overwinter in deeper water [30]. Vertical swimming in juvenile crabs enables rapid planktonic dispersal over tens of kilometers. Thus, the little that is known suggests movements of juveniles and males are a combination of directed and non-directed movements.

Environmental cues that stimulate movement, decision rules, should be universal and work in the vast range of environments crabs occupy. Cues common in all habitats are changes in water height, turbulence, flow and night vs day.

Our goal is understanding the roles of cues in triggering activity, determining movement direction and rates of movement in wind driven systems. This knowledge has potential to inform management decisions for blue crab fisheries and conservation. Whooping cranes mainly eat blue crabs while wintering in Texas. Part of the impetus for doing this study is management maximizing crab populations in and around the Aransas National Wildlife Refuge. For fisheries man is the major crab predator. This information could inform management of large commercial blue crab fisheries in predominantly wind-driven sounds and estuaries such as in the Albermarle-Pamlico Estuarine System, NC and in large tidal fisheries like the Chesapeake.

The massive size of most wind driven estuarine systems and their complexity make experimental approaches intractable. We chose to study movements of crabs in Lake Mattamuskeet National Wildlife Refuge. Lake Mattamuskeet is a large shallow wind driven lake with a robust crab population, an extensive canal system and water control structures. The lake has only a spatially restricted and bag limited recreational fishery. Though still a large and complex body of water the system has features that make experimentation tractable.

Major questions

Five major questions guided this study: (1) do crabs show directioned movements analogous to STST? (2) do male and female crabs behave similarly? (3) does behavior change with season? (4) which environmental variables cue movement behavior? (5) is there a discrete fall migration? We also gathered life stage movement information which could be used in active management of crabs in the refuge.

2. Materials and Methods

2.1 Lake Mattamuskeet

Lake Mattamuskeet is a ~15,400 ha coastal bay lake modified first by settlers of Dutch origin with slave labor and becoming a wildlife refuge during the US great depression [31-33]. Though the mission of the refuge is to manage the lake and wetlands for wild fowl, the lake level is managed to support surrounding agriculture and lake water is used for irrigation. Moorman et al. (2017) [34], provide a succinct history of the lake. In the 19^{th} century, the Lake was connected to the Pamlico sound with a network of canals that enabled draining of swamps for harvest of cypress and conversion to farm land. Today, there are 4 canal systems: 1 to the east, 2 to south and 1 to the west that connect the Lake to the rest

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of the APES (Figure 1A). Each canal is approximately 20 m wide and has a water control structure controlled presently by pressure-activated gates. When the water level in the Lake surpasses that of the estuaries the gates open; conversely, if the estuary water levels exceed that of the Lake, the gates shut [35]. Until 2013, water levels in the canals averaged between 0.61–0.88 m [35]. In 2013 and 2014, the control structures were rebuilt and canals dredged to a depth of 1.2 m. Lake Mattamuskeet averages 46 cm deep. At the beginning of the study, the side of the lake west of highway 94 was phytoplankton dominated and the east side was submerged aquatic vegetation dominated. By the end of the study the lake was virtually entirely phytoplankton dominated [34]. The lake experiences strong wind-driven circulation with very strong wind driven flows though the culverts on Highway 94 as well as into the canals.

Lake Mattamuskeet's status as a National Wildlife Refuge prohibits commercial fisheries. The lake supports a vibrant but spatially restricted recreational crab fishery with catch limits of 12 per person per day. Crabbing is primarily at the control structures on the 4 canals, at five 10 m wide culverts under the Route 94 causeway, which crosses the lake north to south and divides the lake into 1/3 to the west and 2/3 to the east, and at 2 bridges near the refuge headquarters. The lake is famous for crabs of consistently large size. A creel survey funded by the federal government and conducted by NC Fish and Wildlife personnel [36] estimated that 220,000 adult crabs were harvested recreationally that year. We chose a 1-km stretch of the Central Canal for detailed study of tagged crab movements in relation to environmental variables. Tagging studies were conducted in one summer interval and in one fall interval.

2.2 Initial Observational Data

In 2012 from June to August, we spent time learning about the lake. Targets were control structures, north and south culverts on US 94 and two bridges over canals near the refuge office frequented by crabbers. During June and July 2012 crabs were hand captured daily with a net and baited crab lines, photographed and sexed determined at the 7 locations. Flow conditions were noted. This effort was used to determine adult sex ratios and gain experience with where crabs could be most easily and consistently captured for tagging studies. While crabbing we made an effort to meet the resident crabbers and learn from them. Based upon their input, we verified some anecdotal comments with observations.

Figure 1A. Lake Mattamuskeet National Wildlife Refuge [37]

Note: Lake Mattamuskeet is about 0 .5 m deep 10 km wide and 20 km long. Major recreational crabbing is at 5 culverts on NC-94 which crosses the lake, 4 control structures controlling water entry and exit from the lake, and two bridges near the refuge. The area of detailed study by RFID tagging is in the box labled study area.

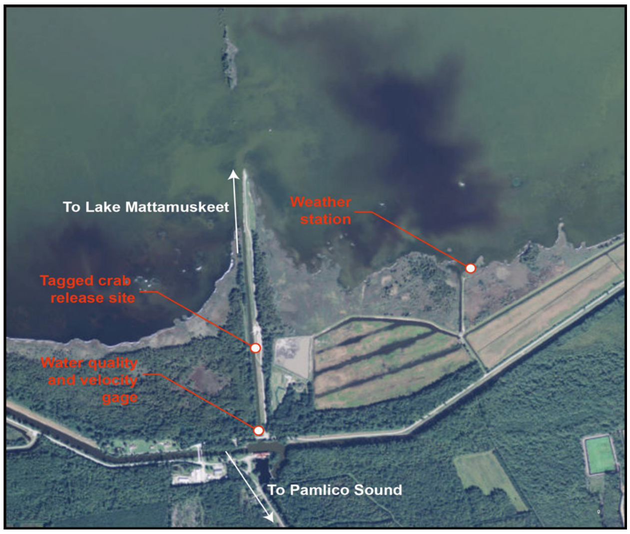

Figure 1B. Satellite view of the study area (Google Maps)

Note: The northern end of the Central Canal is the study area. The canal runs due North to due South. The refuge office is to the south west of the southern end of the location of water instruments under New Bridge. The weather station was located on a treeless area about 1 km east of the canal.

2.3 Study Site and Physical Data Instrumentation

We chose our study site (Figure1B) to maximize security and simplify data collection and interpretation. Major considerations were:

(1) The north/south heading of the canal and consistent canal width and conditions. These features simplified RFID antenna placement in north and south flow patterns.

(2) Approximately 8 miles of lateral canals draining

wetlands immediately south of the study area. These canals and wetlands acted as a buffer enabling wind forced flows in the canal for extended periods even when the control structure was closed.

(3) Security considerations included: proximity to the Refuge Headquarters and staff housing; Restricted access at New Bridge, enabling deployment of expensive and sensitive equipment under New Bridge.

(4) Ease of access by roads on both sides of the canal. A restricted access road west of the canal enabled secure placement of antenna controllers and facilitated battery exchanges.

Physical data were collected with a meteorological station and oceanographic instruments. The meteorological station (Campbell Scientific, WXT-520) was deployed at the end of a restricted access road in a treeless area on a blunt point (Figure 1B) 0.8 km east of the Central Canal. This station measured barometric pressure, air temperature, relative humidity, rainfall, wind speed and wind direction. The sensors were mounted on a tower 5 m above ground and recorded to a self-contained data logger (Campbell Scientific, CR-800) at 10 min intervals.

In concert with the meteorological station, the oceanographic instruments continuously collected data on water velocity, dissolved oxygen, water temperature, water pressure and salinity in the Central Canal. Water velocity was measured with a bottom-mounted 2 MHz acoustic Doppler current profiler (ADP, Nortek AquaDopp), that measured velocity profiles at 1 Hz and recorded at 1 min intervals. In 2012 and 2014 this device was deployed under New Bridge. New Bridge is part of the main access road over the central canal immediately north of the pump house. Water temperature, salinity, and pressure were measured with a bottom-mounted pumped CTD (Seabird SBE-16plus). Dissolved oxygen (DO) was measured with a Seabird SBE-43 cabled into the CTD. All CTD/DO data were recorded at 10 min intervals. In 2014 second instrument was mounted under a no-wake buoy, at the west side of the crab release site. Water velocity, water quality, and meteorological data were post-processed with a 1-hr low pass filter, and then interpolated onto a common time base with 15-min intervals. Weather and oceanographic sensor data products were then used as candidate environmental parameters to test whether they had an effect on crab movement behavior based upon synchronized RFID tag data.

2.4 RFID Antennas

Arrays of radio frequency antennae were deployed across the Outfall Canal. Antennae were constructed of 43 meters of 8 gage insulated copper wire in a loop separated by 1.2 m PVC pipe spacers. The antennae were tuned, activated, and data recorded using multiple antenna readers and control boxes from Oregon RFID, Inc. (Portland, OR). In 2012 two sets of two antennae were deployed (Figure 2). The pair of antennae between the release point and the lake was 112 m from the release point. The pair of antenna south of the release point was 612 meters away from the release point hidden under the New Bridge. Each antenna was comprised of 20 meters of 8 gage coated copper wire in a loop with 1.2m PVC pipe spacers. In 2014 the design was modified to loops with a width of 35 cm to improve excitation and detection and because the larger arrays became rapidly fouled in the fall with detached aquatic vegetation.

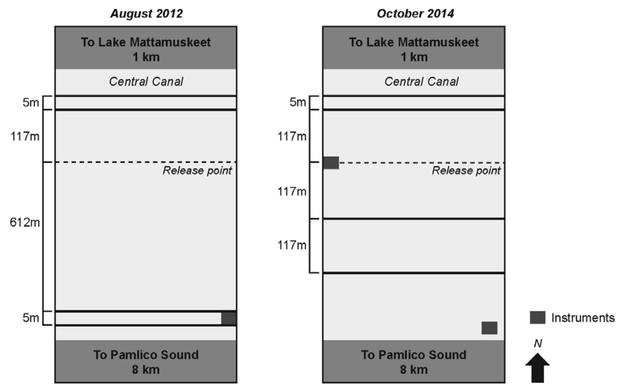

Figure 2. Study area in 2012 and 2014

Note: Sketch of study area, instruments and RFID antenna arrays in August 2012 and October 2014 in the Outfall Canal (not to scale). In 2012 each pair of antenna was approximately 5 meters apart and separated by 624 m. In 2014 the arrays were modified to the pattern depicted due to a combination of our improved understanding and practical equipment limitations. Crabs were released individually in the 2012 experiment and in groups in the 2014 experiment.

In October 2014, based upon what we learned from previous year, we altered the RFID array design (Figure 4). The antennae pair under New Bridge was also separated, with one antenna placed 117 meters south of the release point and one 234 Meters south of the release point. The antenna were 378 and 495 m away from crabbing activity at New Bridge.

2.5 Crab Collection and Tagging

In 2012 we employed a commercial fisher to soak 20 crab pots in the Central Canal from the mouth at the lake to the water control structure. Potting was after sunset when the refuge was closed and small diurnal turtles were inactive. Ten pots were set to the north from about 50 meters above the North antenna array to the lake and south from 50 meters above the release point to the water control structure for the Central Canal. After deployment, pots were

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soaked for 1 hour, emptied and redeployed. Crabs were delivered to the boat ramp where each crab was tagged across the back with a unique 32mm HDX+ PIT tag. The tags were inserted in silicone tag sleeves with a string with a loop at each end. The string was fitted around the large lateral spines across the back and loops were secured on the crab with a cable tie. After tagging a crab was photographed and released immediately. We tagged 202 crabs with the commercial crabber. An additional 38 crabs were captured in the day by net using weighted hand lines baited with chicken. All crabs were photographed with their RFID number displayed on an Agrident AWR 100 tag reader (Figure 3). In October 2014, crabs feeding on chicken were pulled to the surface, netted, and then fitted with across-the-back radio frequency identification (RFID) tags. Tag number and sex were determined from photographs. In 2014, 102 crabs tagged as they were captured were photographed and stored in coolers separated by damp clothes for up to 2 hours until release of a group within 5 minutes.

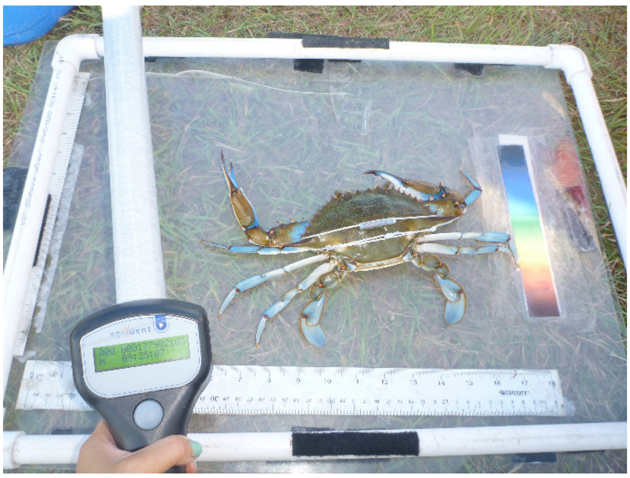

Figure 3. Photograph of a male crab with an RFID tag. All photographs are available on Fickr: Callinectes sapidus

2.6 Analysis

Crab movement and environmental variable data were synthesized using Microsoft Access and Excel. Direction of movement was based on the first detection. Direction of flow was determined for that time. To determine movement velocity we used crabs with a second detection. Time and distance between detections were used to calculate direction as well as movement velocity. We had simultaneous information on flow direction which enabled us to determine crab velocities in relation to water flow speed and direction.

Salinity, water temperature, water velocity, and dissolved oxygen were analyzed for patterns that could explain crab movements between the north (Lake Mattamuskeet) and the south (Pamlico Sound). Frequency analysis, chi square or contingency, was used to accept or reject specific hypotheses described in the text. Two-sided t-tests were performed in order to determine whether there was a significant relationship between direction of movement and each respective environmental variable. Statistical analyses were conducted in R Studio and through web-based statistical packages.

3. Results

3.1 Confirmation of Recreational Crabber Information

Most recreational crabbers were friendly and made every effort to help us. Over the three years that this study was conducted we were able to confirm many of their observations. Although we visited all control structures, most small juvenile crabs were encountered predominantly at Lake Landing and Waupoppin. We hand captured and sampled 100, 4 mm cw crabs with a pool leaf skimmer net in 20 minutes at Lake Landing in late May. As an aside we also found dozens of eel elvers in in the net. Later in the summers, July and August, larger, 30 to 60 mm cc, juvenile crabs were observed on the sound sides of the outfall, Lake Landing, and Waupoppin control structures. Rather than in the hundreds, the number of crabs was 1 to 10 on any particular day. We experienced the "fall migration" at Lake Landing all three years. Finally, we documented the reports of crabbers that most females could be captured at the outfall canal.

3.2 Sex Ratios of Crabs Captured Summer 2012

Seven locations were fished with chicken baited hand lines daily from June until August 2012. If there was flow, crabs were routinely captured at 6 of the 7 locations. No crabs were captured at the Rose Bay control structure. In total, 876 crabs were captured with 70% male and 30% female. Depending on location, crab gender ranged from over 85% male to 60% female (Figure 4). Female crabs were most common at the outfall canal water control structure and next most common at new bridge between the lake and the extensive southern canal system. Male crabs were most common at the North Culvert on highway 94. The largest female crabs, average 170 mm cw, were captured at the north culvert. The largest males crabs, average 178 mm cw. Were captured at the south culvert (data not shown). Episodically, and consistent with local crabber conversations, large numbers (10s to 100s) of small crabs (approximately 4mm to 30 mm cw) were observed

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swimming on the sound side and attached to floating vegetation at the control structures at Waupoppin and Lake Landing when the water control gates were closed.

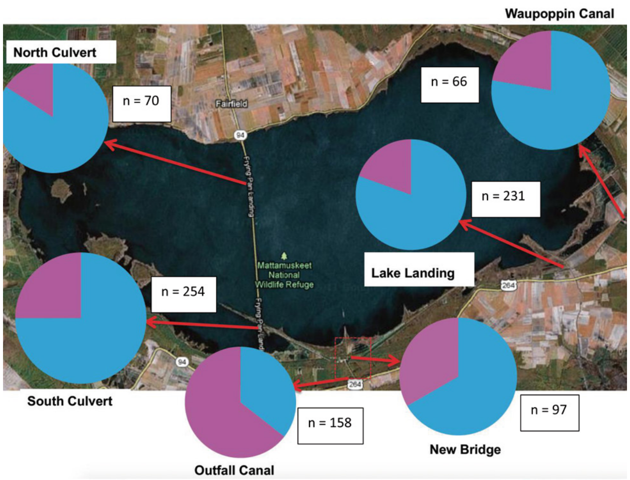

Figure 4. Sex ratios of crabs captured by hand line during the summer of 2012

Note: Seven locations were fished with chicken baited hand lines every week from June until August 2012. Crabs were routinely captured at 6 of the 7 locations. No crabs were captured at the Rose bay control structure. n is the number of crabs caught at the site. Pink is female crabs. Blue is male crabs. Note high proportion of female crabs captured at the Outfall Canal control structure which is beyond the extensive canal system south of the lake. Highest proportions of males were captured at the culverts under the road crossing the lake. Image google earth.

3.3 Environmental Variables

The August 2012 RFID tagging interval was a typical of late summer weather in Coastal NC with prevailing winds from the southwest, gradual changes in air pressure which ranged from 1009 hPa to 1024 hPa, and air temperatures that fluctuated, usually diurnally, between 21°C and 32°C. The canal experienced daily heating and consistently high water temperatures between 26°C and 29°C. In contrast, in the fall (October) variations in pressure ranged between 1001 and 10024 hPa and were related to the passage of fronts. With warm fronts, winds were from the south and west and with cold fronts winds were from the north. Air temperatures were more variable in fall than summer and ranged from to 6°C to 28°C. Cold temperatures were associated with high pressure cold fronts and strong nighttime cooling with clear skies. Water temperatures ranged from about 9°C to 24°C. Fronts with cooling events were exemplified by cold fronts in the 10/07 and 10/ 20 intervals (Figure 5.) The canal experienced daily heating with larger changes than observed in summer. On 10/07 air temperatures dropped from the high 20s to below 10°C , a 19°C change). In the 10/20 interval air temperatures dropped from the Mid 25°C to about 6°C, a 19°C drop. On 10/23 water temperature dropped briefly to a level below 15°C where crabs are reported to be inactive. Maximum wind speeds were about 3 times higher in the fall than in the summer. Thus, August weather and October weather were very different and these differences are summarized in Table 1 and displayed in Figure 5.

Table 1. A summary of environmental conditions in the August and October study intervals

	August 2012		October 2014	
	Minimum	*Maximum*	*Minimum*	*Maximum*
Air Temperature (Celsius)	21°	32°	6°	28°
Barometric Pressure (hPa)	1009	1024	1001	1024
Wind Velocity (min/sec)	-5.0	4.9	-4.0	12.2
Water Temperature (Celsius)	26°	29°	9.0°	24.0°
Salinity (PSU)	–	–	0.74	0.75
Dissolved Oxygen (mg/L)	–	–	6.3	9.3
Water Velocity (min/sec)	-0.228	-.004	-0.330	0.040

Note: Negative numbers indicate winds from the south and water flow in the outfall canal to the south toward the sound. Positive numbers indicate winds from the north and water flows to the north toward the Lake.

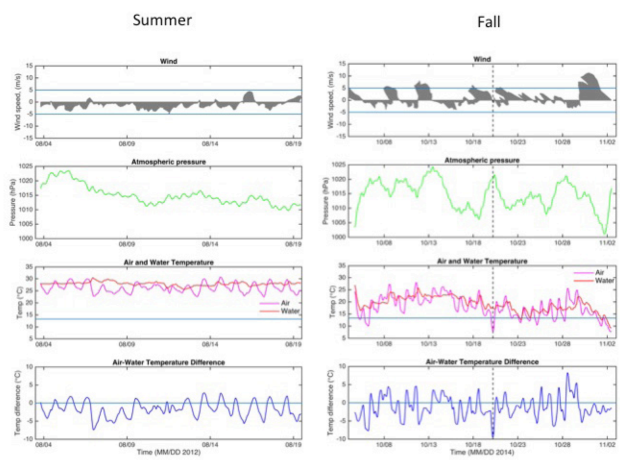

Figure 5. Wind, atmospheric pressure, air and water temperature, and the air-water temperature difference during the two tagging intervals

Note: The line at 13.3°C on the temperature figure is the reported low temperature cutoff for crabs to pot.

3.4 RFID Tagging, Detection, Gender and Direction

Of the 240 crabs caught haphazardly and tagged in 2012, 179 individuals (75%) were detected at least once. Forty-five crabs were female and 134 were male. In 2014, 89 (88%) of the 102 haphazardly caught, tagged and released crabs were detected at least once. For these, of the 60 crabs of known gender 15 were female and 45

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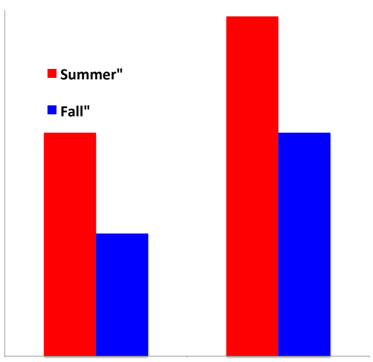
were male. We detected significantly more of the tagged crabs in 2014, rejecting the hypothesis that initial detection was equally likely (chi sq= 6.678, p =0.009 1 d.f.). In both tagging intervals sex ratios of captured and released crabs were similar, approximately 3:1 males to females(2012-2014 comparison chi sq=0.0005 p=0.981 df ns). The null hypothesis that sex ratios were equal was rejected for each year (2012 chi sq = 17.65, p<0.001 1 df; 2014 chi sq = 7.29 p= 0.006, 1 df). Sex ratios were skewed towards males and were similar in both seasons. In general, movements were not randomly oriented, but were primarily toward the sound. The vast majority of adult crabs (76% in summer and 78% in fall) moved toward the sound. In the 2012 and 2014 crab release intervals water flow was predominantly south toward the Pamlico Sound. Most crabs moved with the flow but at a slower pace than flow.

3.5 Rate of Change in Environmental Variables

Previous studies show crabs respond to rates of change in environmental variables [8,25,27].We compared frequencies of summer and fall movement and direction of rate of change in water depth, temperature, salinity, and dissolved oxygen. Using all of the movement data, we tested the hypothesis that overall direction of change made no difference. This hypothesis was accepted for temperature, salinity and dissolved oxygen, fall water depth (chi square = 0.006, 1 d.f., p = ns) but rejected for summer 2012 water depth (chi square = 5.4, 1 d.f., p = 0.02) Figure 6A. Next, we combined directional movements and compared directional responses of crabs in the summer and fall in response to rates of change less than 0 and greater than 0 (Figure 6B). The null hypothesis that there was no difference in total movement responses between summer and fall was accepted for temperature, salinity and dissolved oxygen and rejected for response to water depth (chi sq= 5.41, 1 df, p=0.02; Figure 5). Almost twice as many crabs moved in response to increased water depth than to decreased water depth in the summer (Figure 6B).



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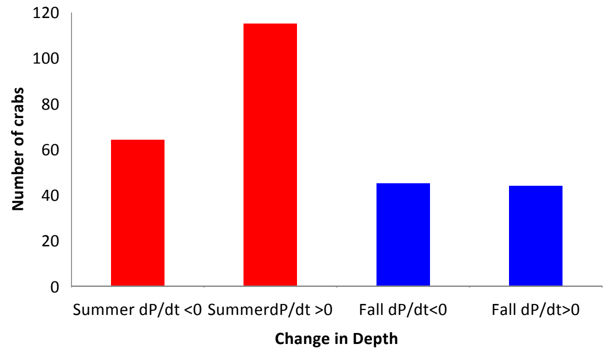

B.

Figure 6. Movement of Crabs and rates of change in water depth in relation to movement in summer (red bars) and fall (blue bars)

Note: In both seasons more crabs moved south than north (6A). Crabs moved more frequently to increases in water depth in summer (6B). In fall the responses were approximately equal (6B).

The clearest example of movement in relation to the direction of flow is from October data before, and then after high pressure cold fronts moved through the region (Figure 7). This set of fronts resulted in flows predominantly to the north as the front approached and then strongly to the south after the front had passed. When flow was to the north, crabs move to the north. When flow was to the south crabs moved to the south. The null hypothesis that there was no effect of flow on movement direction was rejected (chi sq 1 df =19 p<<0.05. Crabs go with the flow.

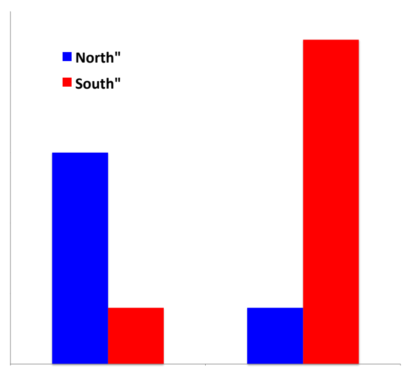

Figure 7. Movements of Crabs with flow predominantly to the north (<October 20) and then with flow predominantly to the south (>October 23)

Note: Blue bars are crabs detected moving north toward lake. Red bars are crabs detected moving south toward sound.

3.6 Crab Movements During the Fall

We were particularly interested in the movements of crabs during what is anecdotally called the fall migration. This is an interval in October where recreational crabbing picks up and a crabber can often catch his limit of 12 crabs in less than an hour. In 2014 the "migration" started when the water temperature dropped below 17°C (Figure 8). Inspection of the figure shows crab movements are usually clustered by direction. Crabs did not move across antennae when the water temperature was below 15. 5°C.

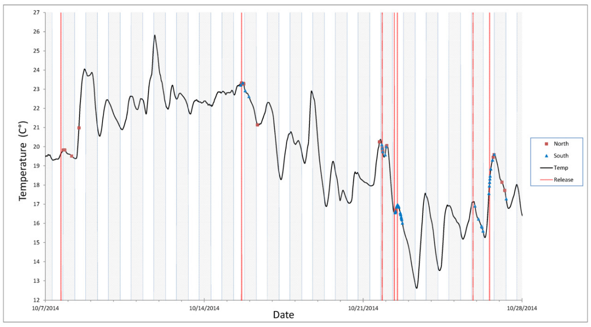

Figure 8. Crab Movement Direction and Temperature

Note: This figure was generated to show that movements are clustered in one direction or the other and that crabs stop moving as the water temperature approaches 15 C and then resume activity when the water warms above 15 C. The lowest temperature a crab was detected was 15.6 C.

3.7 Mean Crab Velocity

Mean crab velocity was computed for 47 crabs detected at more than one antennae for the 2014 data. Velocities were more variable for crabs moving towards the lake than for crabs moving towards the sound (Figure 9.). The October 25th 20:15 release was particularly striking. In that released crabs moving towards the lake moved at a significantly higher velocity than those moving towards the sound.

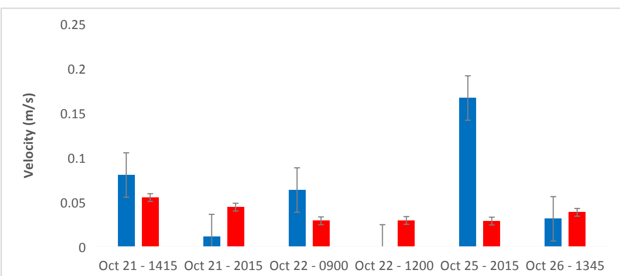

Figure 9. Crab velocities for crabs moving between antennae

Note: Velocities computed for crab detected at two antennae during the 2014 experiment. Velocities were calculated for crabs that were detected at two different antennae after release. Blue is North toward lake, Red is south toward sound. The numbers after the date are the 24 h time of crab releases.

3.8 Individual Crab Velocity

Individual crab velocity computed for the 47 individual crabs used to generate Figure 10. Crab velocity and flow velocity were converted to meters per minute and crab velocity plotted against flow velocity. All but two of the individual crab velocities ranged between a little over 0 m/m to about 4.5 m/min. Crab velocity was low as water flow approached 0 meters per minute and neared 4.5 meters per minute with flows approaching 20 meters per minute. Two individual crabs had movement velocities approximately double the highest velocities observed for the other crabs. These two crab velocities were approximately double the water flow velocity.

3.9 Flow and Crab Movement

Using the absolute value of flow, we binned flow into 15 minute bins and grouped the bins into four categories from slow, less than 0.09 m/s to fast, >0.3 m/s flows. We then grouped crab detections in the same time intervals. We tested the hypothesis that crab detection was equally likely at all flows. We found that significantly fewer crabs were detected at low flows than expected ($G > 7.8$, $p < 0.05$)and significantly more crabs were detected at high flows ($G > 11.34$, $p < 0.01$) than expected (Figure 10).

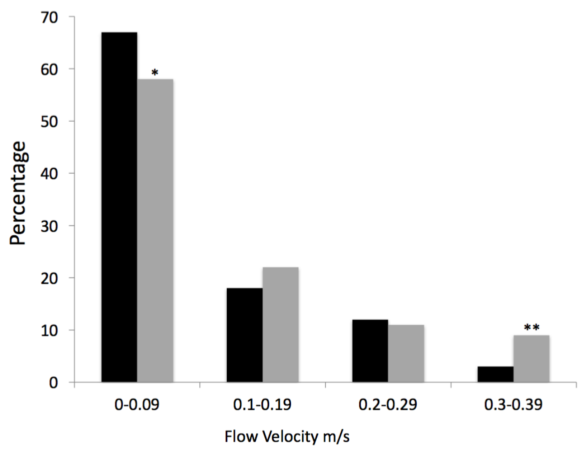

Figure 10. Histogram of percentages of crabs moving at ranges of flow velocities

Note: Statistics were based upon contingency analysis of frequencies. The null hypothesis that crabs were equally likely to move at all flows was rejected. Significantly fewer crabs were detected at low flows than expected and significantly more crabs were detected at high flows than expected. * $p<0.05$; ** $p<0.01$.

4. Discussion

Our primary interest was to determine how adult crabs move in response to environmental variables in the absence signals associated with lunar tides. In the shallow lake system that we chose for our study, flows were due to wind forcing and geometry. We simplified the system by working in a man-made canal oriented in a north-south

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direction with dominant flows to the south about ¾ of the time. Our goal was to compare crab movements in the summer foraging season with movements during the recreational crabber reported “fall migration” in which crabs were reported to move in high numbers from the lake to canals and then to the sounds.

4.1 We Asked 5 Questions:

(1) Do crabs move with the flow analogous to selective tidal stream transport (STST)? We found crabs move with the flow, but movement is not analogous to STST because crabs move with the flow independent of the direction of the flow.

(2) Do male and female crabs behave similarly? Yes, male and female crabs behave similarly. However, based on gender ratios from our early crab capture data, some females, presumably those with mature ovaries appear to actively migrate out of the outfall canal toward the sound. The cues for this movement are unknown.

(3) Does behavior change with season? This is a qualified yes. Basic crab behavior is the same. However, as water cools in the fall crabs concentrate in the deeper warmer canals. Then when the wind blows and water moves concentrated crabs move in the canals and can move though the control structures or back toward the lake.

(4) Which environmental variables cue movement behavior? Change in water depth is the only variable we found that cued movement. We couldn’t test salinity because there is only a weak salinity signal in the lake.

(5) Is there a discrete fall migration? No, there is no evidence of a discrete fall migration. Crab activity increases with increased flows driven by stronger winds associated with the passage of weather fronts. Although the crabs still move with the flow, this is nomadic movement because crabs move with the flow independent of flow direction. Crabbers do not see the crabs moving toward the lake at control structures as we did with Tags in canals with antennae because gates block flow toward the lake.

Crabs move in response to wind forcing when relative water depth changes. Crabs move with the flow. This is consistent with lunar tidal systems in which crabs move in and out of habitats with the tides [19]. In the lake, foraging male and female crabs move similarly. Males and adult females in the first ≈ 2-3 months post molt (the time it takes to mature ovaries and seminal vesicles) would forage and move nomadically, while females physiologically ready to begin spawning would show more directed down-stream movements and reproductive males would periodically spend time on station for breeding.

There are two potential explanations for the observed three to one sex ratio between male and female crabs. One explanation is fewer female crabs migrate to very low salinity water than males. The other explanation is males stay and female crabs begin their spawning migration and actively move down stream after their ovaries mature. In North Carolina, female crabs molt to maturity and mate from March to November.The higher percentage of females at the outfall canal supports he interpretation that small numbers of the females change behavior and actively migrate to high salinity water[39]. This is consistent with our gender data. Our RFID tag data sets are too small to detect the females starting this migration. Pulses of spawning migrations observed in other estuaries[14,22] are probably due to spring and fall synchronization of physiological responses by temperature and other environmental variables.

Based upon the proportions of males and females captured, the Lake Mattamuskeet population is unusual when compared to commercial fishery populations in that mating is not male limited as predicted for US East Coast fisheries populations[17,40-43]. Condition of females in Lake Mattamuskeet would be an interesting comparison with females from male limited populations like the Chesapeake with reduced reproductive output through sperm limitation[17].

Movement velocities of individual crabs provides a sense of how crabs move in flow. Our interpretation is at this life stage, crabs go with the flow and by and large are walking. The slow walking in lower flows suggest crabs are casting laterally as they walk down current. This behavior is consistent with what we observe with crabs foraging in shallow water. We think the slow walking in low flow velocities (near 0 flow) reflects a lack of clear direction and activity and the fast walking in high flow reflects directed movement. The velocities we observed are similar to movement velocities of crabs walking seaward during the spawning migration[13]. They are considerably faster than average 0.3m/min speeds observed in a flume walking up current in response of chemical stimulation [44].

We hypothesize the two very high individual crab movement velocities in Figure 10 are crabs swimming in flow. Although swimming is routine for blue crabs undergoing STST during migrations up or down estuary, it is observed in male and female crabs occasionally in Lake Mattamuskeet. On days when one crab is seen swimming usually others are also seen swimming (Rittschof P.O.). It may be that in the lake and canals nonmigrating crabs swim over a very narrow range of flow velocities (Figure 10). It is likely that swimming can be stimulated by several environmental variables including turbulence[25] and potentially low oxygen at depth.

Clark et al. (1999) [45] followed male crabs by ultrasonic telemetry in a tidal creak in the Chesapeake Bay and provided elegant information on a small number of male crabs spend their days. Hooper (1999) [46] in a sea grant study of recently molted male crabs showed newly molted crabs generally stayed in the area where they were captured until their exoskeletons were calcified. Our data expand these findings to include the observation that males are nomads responding by foraging with the flow at movement rates comparable to those observed for females [19].

Consistent with the extensive literature reporting environmental control of movement behavior, we hypothesized that crabs would move in response to currents in the larger context of physiological state and biological rhythms. Our data support this hypothesis. Rates of change in water depth predict movement of adult male and female crabs in the summer and in the fall. Supporting the hypothesis that crabs at this life stage are nomadic is the result that crabs move with rates of change in water depth independent of direction of the change and crabs go with the flow. Thus crabs are not performing the equivalent of STST by moving in one direction, using STST observed in megalopae and spawning females. However, since the net flow in the lake is out of the lake and into the sound, crabs in canals that move with the flow would eventually end up in the sound.

In the fall, especially after cold shocks, crabs moved in groups. However, our interpretation of the data suggests that rather than a true migration, individual crabs are responding to physical factors that result in their aggregation and then cause them to move in the same direction. During these intervals crab movements are with the direction of the water flow. Thus the reported "fall migration" is a response of individual crabs to environmental conditions that result in the appearance of a coordinated fall migration. These movements are similar to what has been reported for aggregations of mole crabs on ocean beaches [47].

There is a clear seasonality to crab capture in Lake Mattamuskeet [36]. It is easiest to catch crabs in the spring and in the fall when the wind blows the strongest impacting water height and flow. The most difficult times to catch crabs are when the wind blows the least. In our intervals of catching crabs by baited lines, when there was low to no flow one was lucky to catch one crab. In contrast, if there was flow one caught crabs.

In addition to setting the lower limit for crab foraging and movement, temperature may play other important roles in crab activity. In summer, there is less wind forcing, and water temperatures in all portions of the lake support crab activity. Hypothetically crabs are dispersed maximally and less likely to be in canals in the summer. In the spring and the fall, crabs, if they behave as they do in tidal systems tend to move into deeper warmer water as nighttime cooling impacts the shallow water. The deepest water in Lake Mattamuskeet is the canals. Relic canals from when the south side of the lake was a vegetable farm may serve as crab collectors as the lake cools. Thus, when the wind blows and if temperature is high enough to support crab activity, crabs go with the flow and are funneled to specific canals.

There is extensive overlap between the nomadic behavior of crabs and what has been termed Phase I migration[21]. As noted by Aguilar et al. [8], and seen as well in the APES, mature females are routinely the majority of the pot fishery catch during the fall. These mature females are recently molted, nomadic and foraging. In North Carolina these crabs have little value in the basket markets and are sold to the crab meat picking industry.

4.2 Management Implications

In applying our findings to place-based management practices, our most important findings for Lake Mattamuskeet crab management are: (1) juvenile crabs enter the lake through Lake Landing and Waupoppin canal control structures and entry is episodic; (2) female crabs leave the lake though the Outfall Canal; (3) crabs that grow up in the lake are nomadic with movements triggered by changes in relative water depth and movement is in the direction of flow; (4) approximately 70% of the crabs in the lake are male rendering the lake female limited. Active management of the control structures when juvenile crabs are migrating in would maximize the lake population. The lake is a potential source of very large male and female crabs for improving depleted fisheries. However, as managed, the long canals are choke points and filled with commercial crab pots. It is unlikely any crabs survive that gauntlet. Only one canal, the outfall canal appears important to female egress from the lake. Female crabs could be captured by weir at the outfall canal control structure and transported to sanctuaries or there could be a ban on commercial capture of female crabs on some schedule in the outfall canal and sound.

5. Conclusions

The simplicity of the logic of water height change and flow determining movement direction is an attractive decision rule because it applies to lunar tidal as well as wind driven tidal systems. It predicts that if one has a real time model of the physical forcing of flow in an estuary and if one knows where the crabs are that one can predict where and how fast crabs will go. As reported by Carr et al. [13]

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and Darnell et al. [28], and seen here, crab movement rates are a fraction of the actual flow rates. It is likely that expert commercial crabbers know the relation between flow and crab movements and that knowledge explains why some crabbers are consistently more effective at harvesting crabs than others.

That the lake population has a high proportion of males and is not male limited has implications for the reproductive quality of the female crabs. In the lake proper, male and female crabs average approximately 170 mm CW which is routinely larger than all but the very largest crabs in the fishery and in two fecundity studies [18,19] . If Lake Mattamuskeet crabs could travel to high salinity water and spawn, these crabs could help counteract fisheries pressure for smaller more rapidly reproducing males [40] and females [49].

Management of the life stages of crabs such as spawning females using migration corridors requires sophisticated understanding of crab behavior. For example, migrating crabs do not simply move down current and remain in deep channels. Rather crabs migrate using STST and then, if the water is warm, routinely move into shallow water to forage [13,15,48]. Thus establishment of migration corridors as a management tool should also include shallow foraging habitat. Migration corridors would not be an effective management option for the majority of crabs in the fishery as these crabs are nomadic rather than migratory.

The water control structures which function to keep farm fields from flooding are choke points for blue crab movements in and out of the lake. As sea level continues to rise and the land in Eastern NC continues to subside, the water control structures will increasingly impact crab entry and exit as the gates will be closed increasing periods of time. This issue needs to be addressed with an active management plan if the lake is to continue to be a vibrant recreational crab fishery and continue to contribute a large proportion of the anadromous fish spawning habitat in North Carolina and Virginia.

Blue crabs are the most valuable and largest fishery in North Carolina. However this position is threatened by a severely declining stock. Populations have declined steadily since the mid-1990s, with reasons for that decline rooted in anthropogenic [50] and environmental [51] stressors. By more thoroughly understanding the biology of crabs in APES extensive wind-driven estuarine systems, state fishery and wildlife managers can better adaptively manage crab resources—such as crabs in Lake Mattamuskeet National Wildlife Refuge-potentially to enhance the current commercial stock. If science-driven management is an option, then the blue crab fishery in Lake Mattamuskeet could be successfully managed. The success of the blue crab fishery in North Carolina and the sustainability of the state seafood economy are intimately coupled. Potentially, lessons from Lake Mattamuskeet could be applied to the larger fishery.

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