



Seasonal estuarine movements of green crabs revealed by acoustic telemetry

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ABSTRACT: Green crabs *Carcinus maenas* are considered among the most influential invasive species in temperate estuaries worldwide. Yet management can be hindered by the lack of high-resolution data on green crab movement ecology. We addressed this knowledge gap by coupling passive acoustic telemetry and water quality monitoring to examine daily and seasonal movements of individual green crabs in the Webhannet River Estuary (Maine, USA). We tracked 22 adult green crabs (mean [\pm SD] carapace width = 63.8 \pm 6.5 mm) between 2 successive tagging deployments from July 2018–January 2019, with one receiver maintained until mid-April 2019. Overall, our study demonstrated the viability of using acoustic telemetry to assess seasonal movements of green crabs, with an average (\pm SE) individual detection rate of 27.9 \pm 2.8 detections h⁻¹ from July–January. Most crabs remained localized to very specific regions of the estuary, with each region representing a 300–600 m linear distance. Logistic regression models indicated that movements by green crabs to the downstream area were associated with a shift in temperature below 10°C, regardless of sex. From January–April 2019, 9 crabs were found to overwinter in the downstream area, potentially taking refuge in deeper waters. Movement patterns identified in this study further contribute to our understanding of the distances traveled and the areas used by green crabs, as well as further resolve overwintering behavior with consequences for mortality risk due to low temperatures. This additional knowledge of adult green crab movement and dispersal dynamics is valuable to resource managers considering intervention strategies.

KEY WORDS: *Carcinus maenas* · Green shore crab · Seasonal migration · Invasive crustacean · Temperature threshold · Salt marsh · Gulf of Maine

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1. INTRODUCTION

Estuaries are key components of many coastal ecosystems, though they experience constant change and are subjected to a suite of anthropogenic stressors (Wasson et al. 2005, Kennish et al. 2008, Van Coppenolle & Temmerman 2019). Among these stressors, the transport of species through vessel traffic has introduced conspicuous and dominant invasive species into these systems, adversely impacting ecosystem functions and services in novel ways (Ruiz et al. 1997, Weis 2010). The European green crab

Carcinus maenas is one such example, identified as one of the worst global invaders by the IUCN (Lowe et al. 2000). Green crabs have several key traits linked to their success, including a high degree of genetic, behavioral, and physiological plasticity (Roudez et al. 2008, Haarr & Rochette 2012, Tepolt & Somero 2014), a diverse diet (Baeta et al. 2006), and broad environmental tolerances (Young & Elliott 2020). As such, green crabs have expanded extensively in temperate estuaries across 6 continents (Carlton & Cohen 2003, Grosholz et al. 2011) and remain difficult to eradicate (Grosholz et al. 2021).

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In the western Atlantic, green crab presence at their northern range limit was largely suppressed into the 1980s due to cooler sea surface temperatures and associated overwintering mortality (Welch 1968, Berrill 1982, deRivera et al. 2007, MEDMR 2014, MacDonald et al. 2018). However, ocean warming in the region has been correlated with substantial increases in green crab populations (MEDMR 2014, Beal et al. 2016). Once established, high densities of green crabs are known to alter the ecological communities they inhabit. For example, their propensity to burrow not only damages the rhizomes and shoots of eelgrass *Zostera marina*, consequently impacting associated species (Malyshev & Quijón 2011, Matheson et al. 2016), but also compromises marsh vegetation, leading to increased instability and erosion of tidal creek banks and salt marsh platforms (Aman & Wilson Grimes 2016, Raposa et al. 2019, Wasson et al. 2019). In addition, green crabs are frequent predators of bivalves and other shellfish experiencing significant declines in distribution and abundance, such as the commercially valuable softshell clam *Mya arenaria* (Klassen & Locke 2007, MEDMR 2014, Beal et al. 2018).

Although numerous studies in coastal Gulf of Maine waters have explored green crab impacts on estuarine and salt marsh systems (Young et al. 1999, Rosson et al. 2006, Goldstein et al. 2017, Raposa et al. 2019), knowledge of their movements is more limited. Movement patterns of individuals within a population can influence which habitats are impacted as well as population dynamics, such as adult dispersal and mortality rates (Dare & Edwards 1981, League-Pike & Shulman 2009, Gharouni et al. 2015). In particular, ignoring migration can result in poor estimates of population dynamics, hindering fisheries management (Link et al. 2020). Green crab management frequently involves eradication or mitigation by trapping and is dependent on both an understanding of shifting distributions and population densities (Grosholz et al. 2021). Therefore, characterizing movements of individual green crabs within systems vulnerable to invasion, such as estuaries, is needed as a tool for decision-making in considering intervention efforts for this invasive species (Green & Grosholz 2021).

At present, green crab movement behavior has been inferred via shifts in distributions and short-term activity patterns (Lynch & Rochette 2007). Foraging green crabs undertake daily migrations over large areas, congregating in areas with even short-term high prey density (Fairchild et al. 2008, Waser et al. 2018). Yet reports of migration distances are variable and limited (Dare & Edwards 1981, Ameyaw-Akumfi &

Naylor 1987, Waser et al. 2018). Seasonal movements may also be variable, with overwintering green crabs observed both burrowing in vegetated banks of salt marshes (though often found dead; Young & Elliott 2020) and migrating offshore (Crothers 1968, Atkinson & Parsons 1973, Hunter & Naylor 1993). Additionally, sex is widely recognized to influence individual green crab responses to environmental variables and consequently their distributions (Cosham et al. 2016), with early studies following males exclusively to avoid confounding effects (Atkinson & Parsons 1973). Thus, characterizing movements at the individual level, rather than relying on quantifying shifts in population distributions, could help determine the variability of green crab behavior across spatial and temporal scales.

Recently, individual-level tracking of aquatic animal movements has been enhanced by the increasing spatial and temporal resolution of acoustic telemetry and the associated analytical tools that are available (Cooke et al. 2004, Hussey et al. 2015, Crossin et al. 2017). Lynch & Rochette (2007) used radio-acoustic positional telemetry to monitor green crab ($n = 6$) activity patterns over 54 h, and to our knowledge, theirs is the only published biotelemetry research on this species due to concerns regarding the frequency of molting as well as the large distances potentially traveled by green crabs (Young & Elliott 2020). In this study, we used acoustic telemetry in a model estuarine system to track the movements of green crabs over several months to (1) identify behavioral patterns across daily and seasonal scales, (2) relate movements to environmental conditions, and (3) assess the relationship between sex and behavior. We hypothesized that differences exist in the overall movement patterns of females and males based on differential reproductive requirements. As reproductive events wane and abiotic factors indicate seasonal change in the estuary, we also hypothesized that aggregative over-wintering behavior occurs regardless of sex.

2. MATERIALS AND METHODS

2.1. Study area

This study was conducted in the Webhannet River Estuary (WRE; 43° 19' 12.82" N, 70° 33' 48.11" W) in Wells, ME, USA, which connects to the Gulf of Maine via a channel between 2 jetties (Fig. 1). The WRE is a small estuary with notably high abundances of green crabs (Raposa et al. 2019), making it a model system for quantifying green crab movements using

telemetry. Green crab population surveys in the WRE are ongoing (Aman & Wilson-Grimes 2016, Raposa et al. 2019, Crane et al. 2021, K. A. Zarrella-Smith & J. S. Goldstein unpubl. data) and complement our telemetry efforts. The WRE is a barrier beach estuary with an extensive intertidal complex of vegetated marsh, sand and mudflats, and tidal channels (Dionne et al. 2006). A subtidal zone forms the main channel, with predominantly sand and mud substrate (Dionne et al. 2006). The WRE is well-mixed, dominated by semi-diurnal tides (mean tidal prism: $1.96\text{--}2.4 \times 10^6 \text{ m}^3$), and has an average depth of 5–6 m during high tide (Dionne et al. 2006). The downstream region is deepest (Ward 2004), and at low tide, large sections of mixed sand and mud are exposed in all regions.

2.2. Crab collection and tagging

Green crabs were collected in the upstream zone of the WRE using baited Blanchard-style traps (trap dimensions: 93 cm length, 48 cm diameter, 40 cm funnel opening, 1.3 cm mesh; see Young & Elliott 2020 for details) and held for <24 h in floating lobster totes in the estuary prior to all tagging.

Crabs were selected based on the absence of external injuries, sex for equal sample sizes, and carapace width (CW) ≥ 55 mm (age ≥ 1 yr; Behrens Yamada et al. 2017) to minimize the probability of molting and losing the tag.

Green crabs were tagged and released in 2 successive deployments. As acoustic telemetry is not widely used for this species, we initiated our tagging study with a small sample size and equipment available at the time to assess utility before increasing sample sizes. All carapace measurements are reported as mean \pm SD. A total of 4 crabs (1 ovigerous female, 1 non-ovigerous female, and 2 males; CW = 67 ± 9.4 mm) were tagged and released on 10 July 2018. Acoustic telemetry transmitters (Innovasea V9-2x; 69 kHz, 1.8 g in air, 22.5 mm long, 189 d estimated battery life, 40–80 s transmission delay) were affixed externally using an underwater epoxy on the dorsal carapace to maximize detection efficiency (Dance et al. 2016). The epoxy cured for 15–20 min, after which we added lay-

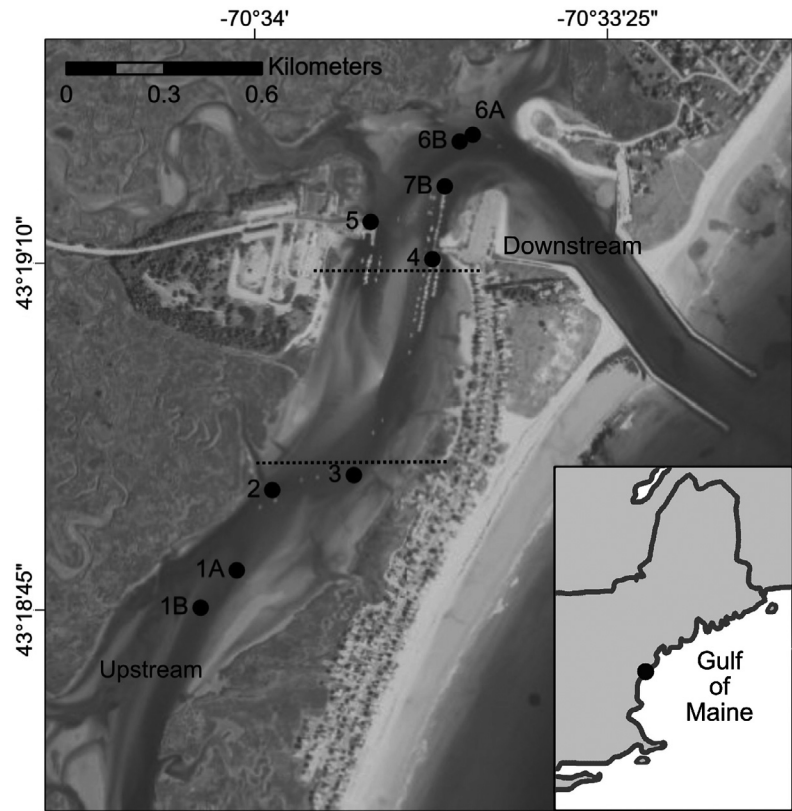


Fig. 1. Main channel of the Webhannet River Estuary, Maine. Dashed lines: boundary between upstream, midstream, and downstream zones used in analyses. Numbers 1–7: acoustic telemetry receivers. Where receivers differed in position between deployments, 'A' represents July deployment and 'B' represents October deployment. The System Wide Monitoring Program station was co-located with receiver 5 and HOBO temperature loggers were co-located with all other numbered receivers. Map services and data available from US Geological Survey, National Geospatial Program and ArcGIS® software (ESRI)

ers of quick-dry and solid epoxy over the tag, reinforced with duct tape. The total weight of the tag and attachment was minimized to limit tag effects on mobility and was low compared to other crustacean studies using telemetry tags (Carr et al. 2004, Guerra-Castro et al. 2007, Lees et al. 2020). Prior to this deployment, we similarly attached Innovasea 'dummy' tags of the same dimensions to a subset of green crabs (tagged: $n = 6$; untagged: $n = 5$; CW = 63 ± 0.6 mm). These crabs were held within individual aquaria and kept at ambient seawater conditions over 2 mo. All crabs retained their tags for the entire period and no crabs were lost or demonstrated impacts to mobility compared to untagged crabs within the tank.

After proof of concept was achieved through the first field deployment, 18 crabs (9 non-ovigerous females and 9 males; CW = 63.1 ± 5.8 mm) were tagged and released in a second deployment on 24 October 2018. We improved the tag type and attachment method to minimize tag burden and handling stress.

Acoustic telemetry transmitters (Innovasea V5-2H; 180 kHz, 0.77 g in air, 12.7 mm long, 140 d estimated battery life, 40–80 s transmission delay) were affixed to animals externally using a harness (Fig. 2). This configuration consisted of the tag shrink-wrapped to a 'spaghetti' poly-tubing wrapped along the carapace and threaded through an oval laminated disc to keep the package flat against the carapace. The disc included a unique identifying number and phone contact if captured. Tag harnesses were additionally secured using a short strip of duct tape reinforced with cyanoacrylate adhesive. To confirm tag retention, we tagged an additional 15 crabs (CW = 66.4 ± 0.23 mm) held in 2 floating totes at ambient conditions in the estuary for 8 wk; no crabs or tag harnesses were lost over this time.

Tagged crabs were placed in a standard lobster trap and transported to the release site (position 1A in Fig. 1). Panels to the release cage were secured using zinc anode pins which readily dissolve in seawater after 2–3 h (temperature-dependent), allowing crabs to exit the cage of their own volition. The release trap was recovered ~12 h after deployment, confirming all tagged crabs had successfully exited.

2.3. Receiver deployments

The 2 successive deployments of fixed underwater acoustic telemetry receivers (Innovasea VR2W; 69 kHz

in the first deployment and 180 kHz in the second to match the tag type used) were set in an array to passively track all tagged crabs (Fig. 1). Receiver site depth varied between 3.6 and 6.1 m. In both deployments, receivers were deployed several ways, including directly attached to opportunistic permanent structures (e.g. pilings and piers), affixed vertically in a PVC tube that was secured within heavily weighted, modified lobster traps and moored using line and buoy (see Goldstein & Watson 2015 for details), or moored to an anchor and affixed to line and buoy using industrial-strength cable ties.

Six 69 kHz receivers were deployed on 10 July 2018 in the main channel of the WRE (1.2 km linear distance maximum between receivers; Fig. 1). Subsequent *in situ* range tests revealed good overlap in detection radii between receivers in the array (200–300 m range; Webber 2009). We also opportunistically supplemented movement data collected via our fixed array with the use of a manually held hydrophone receiver (Innovasea VR100) to track movements outside of the array, as well as to confirm the positions of crabs between receiver data download events. Receivers were routinely checked every 2 wk to document any gear movements or loss. The receivers were recovered 17–24 October 2018; the crabs were at liberty for 100 d for the 6 receiver array.

Six 180 kHz receivers were deployed 17–24 October 2018 in similar locations (within 0–120 m of the locations used in the July deployment). An additional receiver was placed in the WRE ocean channel but was lost in the first week and never recovered, resulting in a 6 receiver array. One receiver within the array was moved further downstream on 17 December 2018 (position 4 to position 7B in Fig. 1) but retained in the same zone of the estuary. Five 180 kHz receivers were recovered in January in anticipation of ice formation in the WRE. Two upstream receivers were recovered on 6 January 2019; subsequently, 3 were recovered between 28–29 January 2019, and the receiver farthest downstream was recovered on 17 April 2019. For the 6 receiver configuration of the October deployment, the crabs were at liberty for 75 d; the total time at liberty until the last receiver was pulled was 176 d.

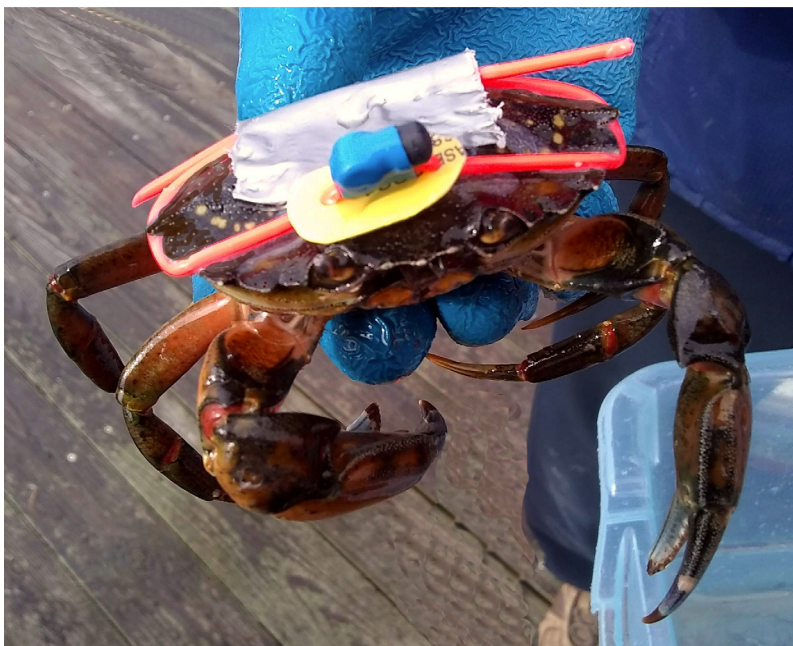


Fig. 2. Acoustic telemetry tag harness attached to a male green crab (carapace width: 66 mm)

2.4. Water quality monitoring

Water quality data in the WRE were collected as part of the NOAA National Estuarine Research Reserve (NERR) System Wide Monitoring Program (SWMP; NOAA NERRS 2020). Parameters collected throughout this study included water temperature ($^{\circ}\text{C}$), dissolved oxygen (mg l^{-1}), salinity (‰), turbidity (NTU), and pH at continuous, 15 min intervals using a YSI EXO2 multiparameter data sonde. SWMP sondes were installed inside a perforated PVC tube mounted ~1 m from the bottom at the Wells Harbor inlet site (Fig. 1). Sondes were calibrated pre- and post-deployment and swapped every 20–30 d to ensure battery life and data accuracy. SWMP data were submitted to the Centralized Data Management Offices (CDMO; <https://cdmo.baruch.sc.edu>) and underwent an automated quality assurance/quality control (QA/QC) process; CDMO-rejected data were not used in these analyses. We also deployed HOBO temperature loggers (UA-002-64; Onset Computer Corporation) fastened to individual receiver buoys (positions 2, 4, 6 in Fig. 1 from 11 July–16 October; position 3 from 17 October–7 February, position 1 from 11 July–7 February).

2.5. Statistical analysis

All analyses were conducted in R version 3.6.3 (R Core Team 2020). Reported results include all telemetry and water quality observations that occurred prior to the removal of any receivers (July deployment: 17 October 2018; October deployment: 6 January 2019), except where otherwise stated. All results are reported as mean \pm SE unless noted otherwise. Turbidity readings from late September–October were rejected through the CDMO QA/QC process due to excessive biofouling of the probe. Salinity values were also impacted 6–23 October 2018 due to instrument biofouling, but these data did not meet rejection criteria through the CDMO QA/QC review and therefore were retained in our analyses. We rejected data from the HOBO temperature logger at position 1 (Fig. 1) and 94 other HOBO readings based on unreliable readings (i.e. below the freezing point of seawater).

A series of rules was applied to the telemetry data to remove potential false detections. First, the Innovasea (formerly Vemco) False Detection Analysis algorithm was used in VUE software to flag suspect interval timing between detections (Pincock 2012) for further manual review. Next, detections with the same timestamp (within <2 min to account for mod-

est clock drift) on multiple receivers were evaluated by the positional relationship between those receivers within the array; for example, detections occurring within 2 min at overlapping receivers (≤ 300 m apart) were classified as valid data as opposed to false detection at one or more of non-overlapping receivers. Lastly, any apparent movements between non-overlapping receivers that resulted in a movement rate exceeding 0.8 m min^{-1} (a conservative estimate of green crab movement rates; Dare & Edwards 1981) were rejected. Rejected detections were $<0.001\%$ of the data (total of 3 detections between release and 6 January 2019 and 215 from 7 January–17 April 2019).

Detection rates were calculated by dividing the total number of detections of an individual by its total time at liberty. Time between detections was calculated as an average of the time between successive detections for an individual. From crab detections, overall residency within the array was calculated. Residency was estimated as the ratio of the number of days individuals were detected and the number of days at liberty, reported as a percentage (Wada et al. 2016). Detection rates and residency values for females and males were compared using the Mann-Whitney U -test with $\alpha = 0.05$.

Detection data were recorded by the receiver position. Due to the overlapping range of receivers within the array, an individual transmission could be recorded by multiple receivers. The location of an individual was therefore estimated using the mean-position algorithm described by Simpfendorfer et al. (2002) to generate centers of activity (COA). Time intervals of 1, 3, 6, 12, 15, 18, 21, and 24 h were used to construct COA using the 'Vtrack' package (Udyawer et al. 2018). COA were visually inspected to identify the temporal resolution that best reflected mean position between receivers (as opposed to position at the receiver) without reducing data resolution; we therefore selected 12 h COA. COA positions were assigned to zones within the WRE. Latitudinal boundaries for the zones were selected based on receiver position. The upstream zone included all southernmost latitudes within the array and encompassed receivers 1–3 plus 20 m on the midstream side (Fig. 1); the downstream zone included all northernmost latitudes and encompassed receivers 4–7 plus 20 m on the midstream side; the midstream zone was the intermediary area. VR100 data were collected ($n = 24$) and all VR100 data positions were consistent with COA zone positions. COA were mapped using the 'ggmap' package (Kahle & Wickham 2013).

To investigate the effects of sex differences and water quality parameters on the movement of green crabs between upstream and downstream zones, generalized linear mixed models (GLMMs) were constructed using the 'lme4' package (Bates et al. 2015). Because <0.01% of the COA data were midstream positions (Fig. 1), we excluded these from the GLMMs in favor of a binary response variable (0 = upstream; 1 = downstream). Candidate explanatory variables included water temperature, dissolved oxygen, salinity, turbidity, and pH, averaged over 12 h periods to match telemetry-based COA. We assessed potential collinearity among water quality parameters (Harrison et al. 2018). We calculated pairwise Spearman's rank correlations between all water quality parameters, with values >0.5 indicating collinearity. Among collinear variables, we retained those we felt would be most important to green crabs (see Section 3.1). In addition, the variance inflation factor (VIF) of remaining variables was assessed in a global model; any variables with VIF > 3 were removed (Zuur et al. 2010). Individual crab ID was included as a random effect in our model to help account for repeated measurements of individuals. We used all-subsets selection to rank models based on their Bayesian information criterion (BIC), with the lowest BIC indicating the most parsimonious model. We also calculated BIC weight (ω_i) for each model, which represents the probability that a given model is the most parsimonious. We reviewed Akaike's information criterion (AIC) results as well and, given our large sample size of positions ($n = 1670$), we choose to report BIC as it penalizes more appropriately for complex models relative to AIC (Link & Barker 2006). Model adequacy was examined by visually inspecting plotted Pearson residuals, a $Q-Q$ plot of the random effect means (Harrison et al. 2018), and residuals from simulations using the fixed effects of the fitted model with the 'DHARMA' package (Hartig 2021). The top-ranked model was then used to generate predictions of zone use across observed values of included explanatory variables. Unconditional 95% CIs were generated using bootstrapping over 500 iterations with the 'ciTools' package (Haman & Avery 2020).

3. RESULTS

3.1. Water quality

There was low variation in the water temperature between the upstream and downstream regions of the subtidal zone throughout the study period (mean difference: $0.56 \pm 0.03^\circ\text{C}$, based on the maximum difference between any downstream HOBO temperature logger in the array and the upstream SWMP station daily from 10 July–6 January; Fig. 3). Notable shifts in water chemistry occurred in October 2018 in the estuary, including a consistent decrease in water temperature and increase in dissolved oxygen along with more variable salinity and turbidity events. The water temperature continued to decrease to -1.8°C in January with a mean temperature of $2.9 \pm 0.02^\circ\text{C}$ between 7 January and 17 April 2019 (i.e. the period between removal of the upstream receivers and the last downstream receiver). Though pH ranged from 7.56–7.96, no apparent trend occurred over the study period.

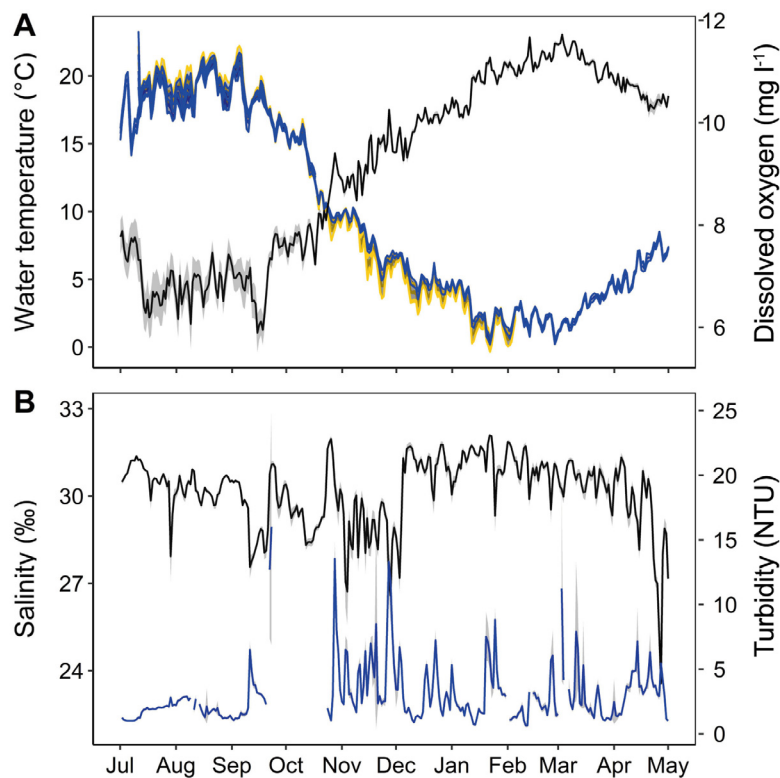


Fig. 3. Water quality trends from 1 July 2018–1 May 2019 in the Webhannet River Estuary, Maine. (A) Blue lines: daily mean water temperature from downstream sites; yellow lines: upstream sites (data is overlapping); black line: dissolved oxygen from a downstream site. (B) Daily mean salinity (black line) and turbidity (blue line) from a downstream site. Breaks in data are due to omitting unreliable observations. Grey bands: 95% CI

Strong correlations were detected among all pairwise combinations of water temperature, dissolved oxygen, and time binned in 12 h periods (Spearman's rank correlation, $p < 0.001$; Table 1). A negative correlation was detected between salinity and turbidity (Spearman's rank correlation, $\rho = -0.61$, $p < 0.001$) and a positive correlation between salinity and pH (Spearman's rank correlation, $\rho = 0.70$, $p < 0.001$). We considered but removed dissolved oxygen and time variables from our GLMM to include water temperature, as it is often linked to seasonal migrations (Crothers 1968, Atkinson & Parsons 1973). We also selected salinity to include as an explanatory variable as opposed to turbidity or pH based on potential movements along salinity gradients by green crabs (Ameyaw-Akumfi & Naylor 1987, McGaw & Naylor 1992). Thus, water temperature and salinity were included in our GLMM prior to all-subsets selection, with a pairwise correlation coefficient < 0.5 ($\rho = -0.30$) and VIFs < 3 (see Section 3.4).

3.2. Green crab residency

All tagged crabs were detected within the array between 10 July 2018 and 6 January 2019, generating 702 323 detections (range of 485 detections over 3 d; 129 105 detections over 100 d crab⁻¹; Fig. 4A). Individual mean detection rate was 27.9 ± 2.8 detections h⁻¹; Table 2). The average time between detections was 280 s, including the 40–80 s tag transmission delay, with individual averages ranging from 1–26 min between detections. More than 99.8% of detections were less than 1 h apart. There was no difference in mean time between detections for females and males when the ovigerous female was included ($U[n_F = 363\ 134, n_M = 339\ 189] = 6.15 \times 10^{10}$, $z = -0.96$, $p = 0.34$). However, when the ovigerous female was excluded, males had significantly less time between detections compared to females ($U[n_F = 234\ 029, n_M = 339\ 189] = 4.48 \times 10^{10}$, $z = 83.83$, $p < 0.001$).

Mean residency within the array among green crabs was $52.1 \pm 7.1\%$. The ovigerous female was detected every day while at liberty, whereas non-ovigerous females had a median residency of 38.6%; the median residency for males was 76.0%. There was no significant difference in residency within the array between females and males, regardless of whether the ovigerous female was included with

all females (female median = 45.3%, $U[n_F = 11, n_M = 11] = 51$, $z = -0.59$, $p = 0.55$) or removed ($U[n_F = 10, n_M = 11] = 40$, $z = -1.02$, $p = 0.31$).

A lack of detections could represent movement outside of the detection range of the array, death of the tagged crab, shedding of the tag, or tag malfunction. The only crab not detected when receivers were removed due to a change in tag type at the end of the July deployment was a male, observed dead in a far upstream reach of the estuary out of range of the receivers, 46 d after the last detection by an upstream receiver. When the upstream receivers were removed due to increasing ice cover, 8 crabs from the October deployment were not being detected. However, we continued to collect detections on the 10 remaining crabs, ultimately using one downstream receiver starting 29 January 2019. Four females and 6 males generated an additional 229 123 detections until 17 April 2019, or 25% of the overall number of detections for the entire study (Fig. 4A).

3.3. COA

Of 1684 calculated 12 h COA, only 14 (0.008%) were in the midstream zone (Fig. 4B). Ten of these midstream positions coincided with transitioning between upstream and downstream zones (or vice versa). An additional 14 zone transitions were made without detection in the midstream zone.

A total of 14 of the 18 crabs (77.8%) from the October deployment were detected moving from the upstream to downstream zone in late October–November 2018. Of the crabs that were not detected making this transition, 3 were lost earlier in tracking and one exhibited a 15 d detection gap during this period, though it did transition to the downstream on 1 December. Three females, including the ovigerous female, moved between zones multiple times whereas no males made multiple zone transitions

Table 1. Spearman's rank correlation coefficients between water quality parameters and time, binned in 12 h periods in the Webhannet River Estuary, Maine. *** $p < 0.001$

	Water temperature	Dissolved oxygen	Salinity	Turbidity	pH
Time	-0.96***	0.95***	0.23***	0.11***	0.39***
Water temperature		-0.94***	-0.30***	-0.04	-0.46***
Dissolved oxygen			0.21***	0.17***	0.41***
Salinity				-0.61***	0.70***
Turbidity					-0.36***

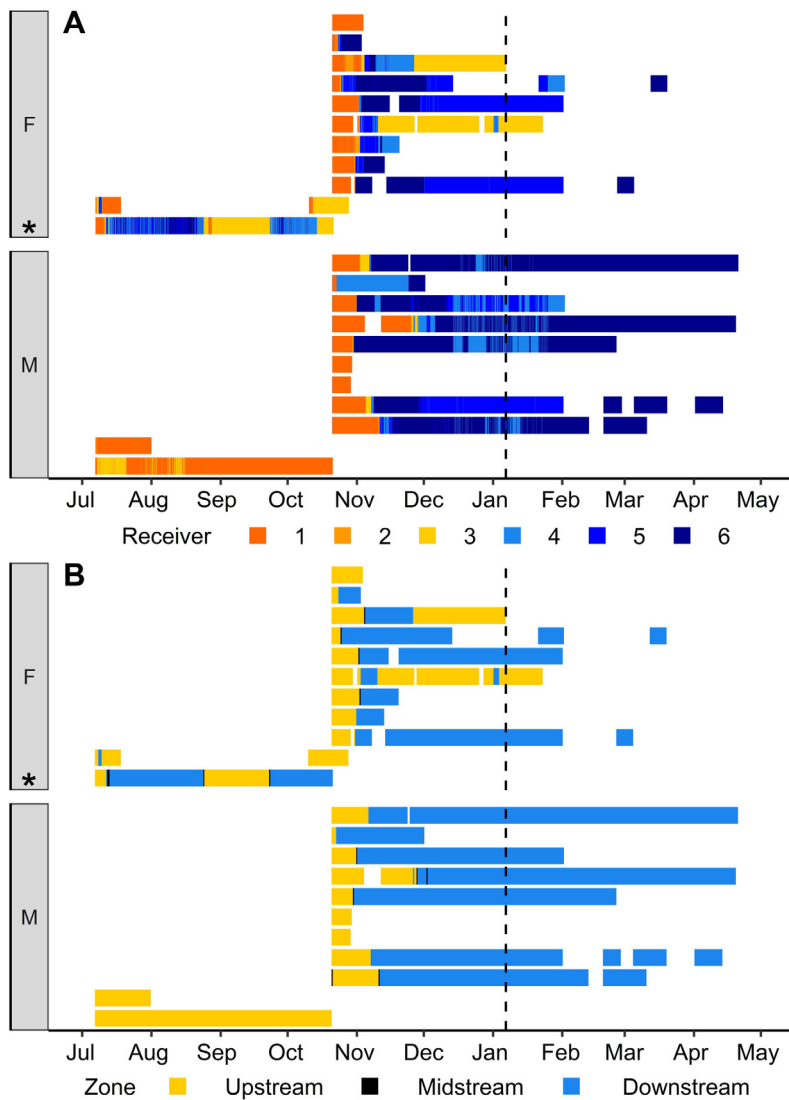


Fig. 4. Movement history of individual green crabs by sex (F: female; M: male). Asterisk: the ovigerous female. Dashed line shows when the first receivers from the second deployment were removed from the array. (A) Raw detection data represents position as equal to the receiver location (receiver numbers as in Fig. 1). The receiver from position 4 was moved to 7 but retained in the general region; therefore, data from position 7 is reported in combination with data from position 4. (B) Position by zone within the estuary (zones as in Fig. 1) using 12 h centers of activity

(Fig. 5). There was no significant difference in the proportion of upstream residency or downstream residency within the array between females and males, regardless of whether the ovigerous female was lumped with all females (upstream: $U[n_F = 11, n_M = 11] = 66, z = -0.33, p = 0.74$; downstream: $U[n_F = 11, n_M = 11] = 54, z = -0.40, p = 0.69$) or removed from the data (upstream: $U[n_F = 10, n_M = 11] = 60, z = -0.32, p = 0.75$; downstream: $U[n_F = 10, n_M = 11] = 49, z = -0.39, p = 0.70$).

3.4. GLMMs

Temperature, salinity, deployment, and sex were included as explanatory variables in the global binomial GLMM. Because there was a strong directional trend in water temperature throughout the study period, we also included a temperature \times deployment interaction. However, there was no directional trend in salinity between deployments to support including a salinity \times deployment interaction. Of the candidate models generated, the top-ranking model included all model terms except sex (Table 3). The marginal R^2 was 0.49, conditional R^2 was 0.76 (Nakagawa & Schielzeth 2013), and ω_1 was 0.97. The top-ranking model was then used to generate predictions of upstream or downstream zone probability by temperature and separately by salinity (Fig. 6). There was a 50% probability of transition between upstream and downstream zones predicted to occur at 8.9°C and 28.6‰.

4. DISCUSSION

Our study investigated the daily and seasonal movements of individual green crabs, demonstrating for the first time, to our knowledge, the value of employing acoustic telemetry on this well-established invasive species over a seasonal timeframe. Over the course of this study, we were able to consistently detect crabs and confirmed that the majority of tracked individuals remained within our fixed subtidal array. The consistency of our detection data (1 detection each ~ 2 min for individuals; the time between detections was < 1 h for 99.8% of all detections) suggests that green crabs remained in the subtidal or submerged intertidal when detected. Half of all observed crabs from a European population moving upshore circatidally did so within a 65 min period (Dare & Edwards 1981). Had individuals been regularly moving to the exposed intertidal, extensive side channels, and fringing salt marsh complex, the movements would have caused longer durations between detections

Table 2. Green crab tagging and detection summary. All reported values are for the 6 receiver array configuration with exception of the day last detected. Tag IDs denote release date (J: 10 July 2018; O: 24 October 2018). The tag type for individuals released in July was 69 kHz and 180 kHz for individuals released in October. The table includes the average detections h^{-1} in proportion to the total time at liberty (July: max. 100 d; October: max. 75 d), residency (%), and the proportion of 12 h centers of activity within upstream, midstream, and downstream zones in the estuary (%)

Tag ID	Sex	CW (mm)	Last detected	Detections h^{-1}	Residency (%)	Upstream (%)	Midstream (%)	Downstream (%)
1-J	F ^a	62	17-Oct-18	53.8	100	34.2	2.0	63.8
2-O	F	59	28-Jan-19	37.2	82.7	20.2	0.8	79.0
3-O	F	57	3-Jan-19	18.2	77.3	67.0	0.9	32.1
4-O	F	69	1-Mar-19	46.6	73.3	3.8	0.0	96.2
5-O	F	58	16-Mar-19	29.8	54.7	10.7	1.3	88.0
6-O	F	59	19-Jan-19	10.8	45.3	67.3	0.0	32.7
7-O	F	59	16-Nov-18	42.1	32.0	54.3	2.2	43.5
8-O	F	59	9-Nov-18	22.4	16.0	45.0	0.0	55.0
9-J	F	57	24-Oct-18	36.6	16.0	90.3	0.0	9.7
10-O	F	55	31-Oct-18	21.7	10.7	100.0	0.0	0.0
11-O	F	56	30-Oct-18	27.7	9.3	50.0	0.0	50.0
13-J	M	78	17-Oct-18	31.2	93.0	100.0	0.0	0.0
12-O	M	67	29-Jan-19	11.8	82.7	6.5	0.9	92.6
14-O	M	57	17-Apr-19	20.5	81.3	12.8	0.0	87.2
15-O	M	68	21-Feb-19	23.4	78.7	10.6	1.0	88.5
16-O	M	67	16-Apr-19	42.6	78.7	37.8	1.8	60.4
17-O	M	73	7-Mar-19	37.9	76.0	12.1	2.0	85.9
18-O	M	70	10-Apr-19	29.9	73.3	11.8	0.0	88.2
19-O	M	66	27-Nov-18	39.6	46.7	4.4	0.0	95.6
20-J	M	71	28-Jul-18	11.6	11.0	100.0	0.0	0.0
21-O	M	68	26-Oct-18	6.7	4.0	100.0	0.0	0.0
22-O	M	68	25-Oct-18	10.8	2.7	100.0	0.0	0.0
Averages (\pm SD)		63.8 \pm 6.5		27.9 \pm 13.2	52.1 \pm 33.3	47.2 \pm 37.4	0.6 \pm 0.8	52.2 \pm 37.1

^aOvigerous female

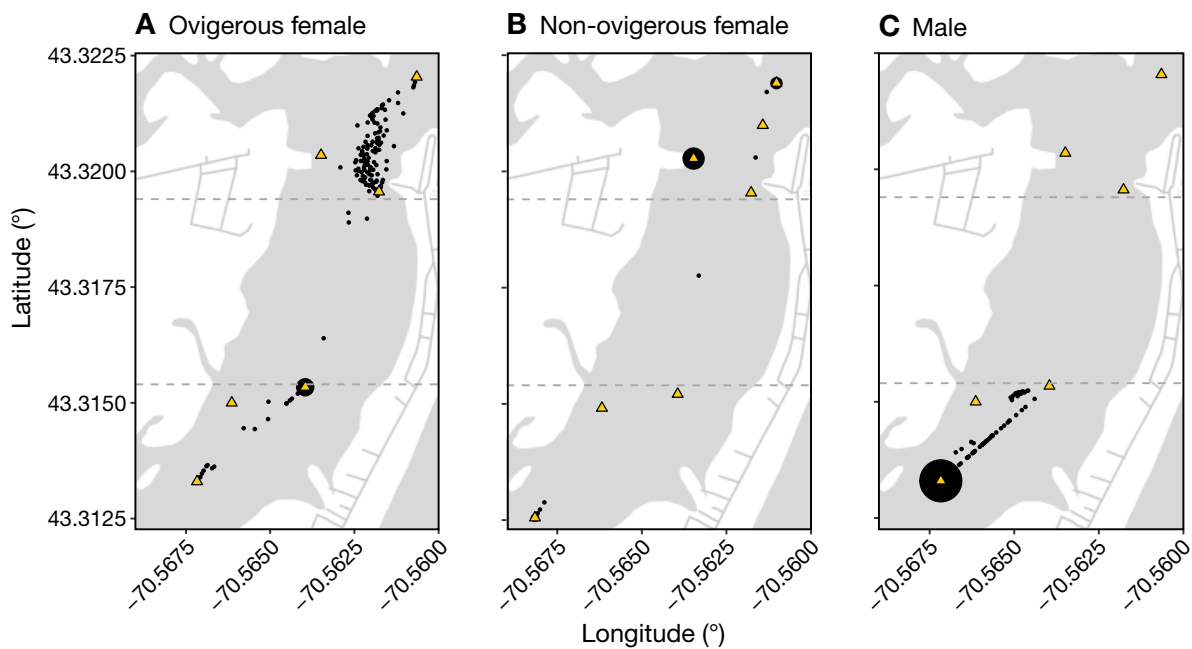


Fig. 5. Example activity patterns of green crabs within the Webhannet River Estuary, Maine, based on 12 h centers of activity (COA) for (A) an ovigerous female (62 mm carapace width [CW], July deployment, detected over 100 d); (B) a non-ovigerous female (59 mm CW, October deployment, detected over 62 d); and (C) a male (78 mm CW, July deployment, detected over 93 d). The zones of the estuary are demarcated by the dashed lines: lower latitudes comprise the upstream zone and higher latitudes comprise the downstream zone. Yellow triangles: receivers; black dots: COA (their size is the relative frequency of the COA with the same position, binned in increments of 5 ranging from 1–105). Map tiles by Stamen Design, under CC BY 3.0; data by OpenStreetMap, under OdbL

Table 3. Top 5 binomial generalized mixed models by Bayesian information criterion (BIC) weight (ω_i). Water temperature (temp), salinity (sal), sex, and deployment (dep) were potential explanatory variables. Two variables within a term indicates an interaction factor

Model	df	Log-likelihood	BIC	Δ BIC	ω_i
~temp + sal + dep + (temp \times dep)	6	-547.78	1140.09	0.00	0.97
~temp + sal + sex + dep + (temp \times dep)	7	-547.68	1147.31	7.22	0.03
~temp + dep + (temp \times dep)	5	-571.41	1179.92	39.83	0.00
~temp + sex + dep + (temp \times dep)	6	-571.30	1187.13	47.04	0.00
~temp + sal	4	-584.17	1198.01	57.93	0.00

due to reduced detection efficiency through signal attenuation (Brownscombe et al. 2019) or a complete loss in signal (e.g. movement out of water or into deep burrows). As our crabs were large, mature individuals, our results support previous studies that report adult green crabs can predominantly inhabit lower intertidal and subtidal zones, especially during colder months of the year (Hunter & Naylor 1993, Warman et al. 1993, Aagaard et al. 1995).

A small subset (0.2%) of the tracking data had longer durations between detections, and 8 crabs were not detected for more than 1 mo by the end of the 6 receiver array tracking period. This lack of detections could indicate that some tagged crabs were regularly active in the exposed intertidal or fringing marsh where detection was not possible or poor, but also could be due to a loss of the tag or death of a tagged crab. In combination with the uncertainty related to absence data from telemetry, our receiver array only provided presence-absence information, and thus we cannot confirm the exact position of crabs ranging between the subtidal and submerged intertidal or whether the cause of loss in detections was the result of movement toward the exposed intertidal or other regions past the boundaries of the array. Further clarification of the proportions of crabs that remain in the subtidal is needed. If contingents of green crabs indeed remain in subtidal habitats, mitigation strategies that employ specific goal-oriented subtidal trapping to limit green crab impacts in the intertidal (e.g. burrowing in salt marsh banks and foraging on commercially harvested soft-shell clams) may overlook potential disconnects between subtidal and intertidal populations and the potential for more limited movements of green crabs. Future studies that utilize positioning telemetry to obtain higher resolution data can further examine connectivity between subtidal and intertidal populations. Given the impact of density dependence on mitigation efforts, the precision of population

or catch per unit effort estimates would need to account for this potential lack of connectivity when designing sampling protocols and predicting outcomes of crab-removal measures (Green & Grosholz 2021, Grosholz et al. 2021).

In addition to an apparent lack of regular migrations to exposed shores, our tagged green crabs remained localized within very specific regions of the estuary. Previous estimates of the distances traveled over a single tide vary from 300 m within the intertidal to 2 km in an estuary (Dare & Edwards 1981, Ameyaw-Akumfi & Naylor 1987). Given the size of the WRE (the dis-

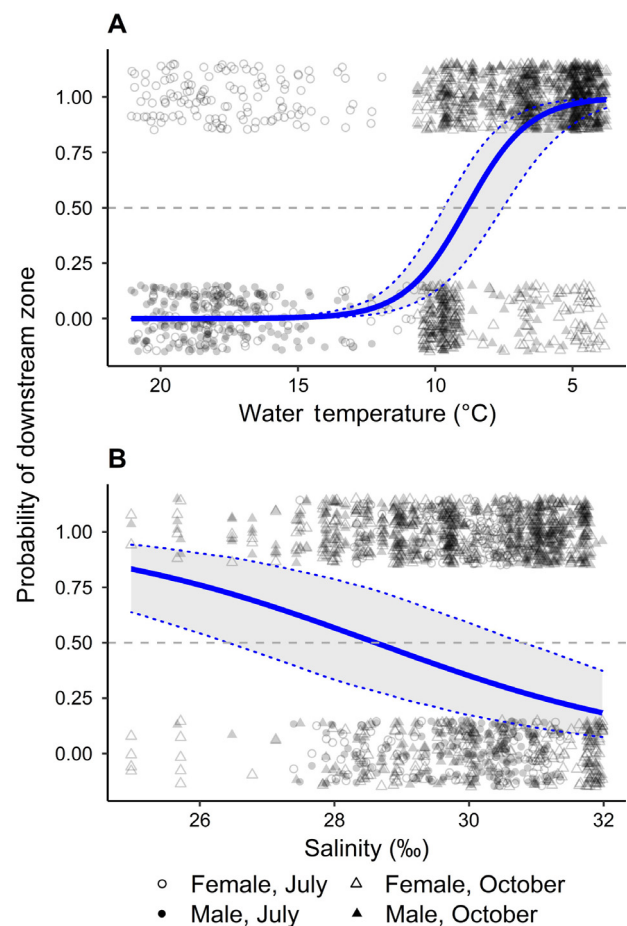


Fig. 6. Logistic regression plots of upstream (0) or downstream (1) zone position of green crabs in the Webhannet River Estuary, Maine, by (A) temperature and (B) salinity. Points are 12 h centers of activity, jittered in the y direction for visibility, and indicate sex and deployment. Horizontal dashed line: inflection point of the regression; dotted lines: bootstrapped unconditional 95% CIs. 50% probability occurs at (A) 8.9°C and (B) 28.6‰

tance between the most upstream and downstream receivers was ~1.2 km), an individual crab could presumably travel the entire length of the main channel multiple times in a single tide. Therefore, we expected frequent transitions of crabs between upstream and downstream zones; however, our data did not provide evidence for these types of movement patterns. Altogether, there was a lack of transition from the upstream and downstream zones (24 transitions in total) over the course of the tracking period among all individuals. Given the high detection rates for individuals that stayed within the array, we were likely able to appropriately detect zone transitions. These data suggest that the distances traveled over a full tidal cycle are more in line with conservative estimates of 300–600 m (Dare & Edwards 1981) and remain limited to particular regions of the estuary in the fall to early winter, and possibly summer.

Although movements between zones were uncommon throughout much of the study, most of the tagged crabs moved downstream in October after water temperatures fell to ~9°C (Fig. 6). And although the timing of the second deployment occurred close to the shift <10°C, causing an interaction effect in our model, these crabs did not remain in the upstream zone where they were released but rather made the transition to the downstream zone and remained there. Notably, reviews by Young & Elliott (2020) and Klassen & Locke (2007) highlight 10°C as an important cold-water threshold for biological and physiological functioning in green crabs. This temperature has also been acknowledged as a significant factor and threshold constraining the range expansion of green crabs (Behrens Yamada et al. 2017).

Though some genetically distinct populations at the northernmost range limit have expanded cold tolerance (Tepolt & Somero 2014), 10°C remains a critical thermal minimum for molting and growth of adults and larvae regardless of population origin (Berrill 1982, Young & Elliott 2020). This 10°C temperature threshold was observed in the estuary during a period of rapid transition from summer to winter conditions and coincided with the move from upstream to downstream habitat use by green crabs. Though tidal-mixing limits the extent of temperature gradients within the WRE, differences in depths may account for the observed transition downstream when colder water temperatures were reached. Shallow regions of the estuary have a higher potential to temporarily expose crabs to suboptimal temperatures that increase the risk of mortality (Ronges et al. 2012). Thus, the fully submerged, deeper regions of the estuary can provide refuge to reduce this mortality risk. As

the Gulf of Maine warms at an accelerated rate (Salisbury & Jönsson 2018), reduced duration of cold water could have significant impacts on the ecology, growth and survival rates, and distribution of green crabs. This may include more crabs residing in shallow regions of estuaries longer, which could have further deleterious impacts on these systems.

Throughout the fall-to-winter transition in the WRE, temperatures met the critical limits of 7 to -1°C for green crab feeding and survival (Ropes 1968, Cohen et al. 1995). Unsurprisingly, migrations from offshore overwintering environments into coastal systems are commonly reported as temperatures increase (>8°C; Aagaard et al. 1995). Although our results suggest that downstream areas close to the estuary mouth are most preferred during the colder months of the year, our ability to detect offshore migration was impaired by the loss of our receiver at the ocean inlet early in the study. It is possible that the 8 crabs from the October deployment that were lost before the end of the study migrated offshore or burrowed into marsh banks where we were not able to detect them, though it is also possible that these crabs shed the tag or died. With only one receiver remaining in the downstream zone from late January to mid-April, 3 females and 6 males continued to be detected (one additional female in the upstream became undetectable after removal of the last upstream receiver). These continued downstream detections demonstrate that the deeper downstream subtidal area of the estuary, with an average temperature of 2.9°C, may be an overwintering ground for a contingent of the green crabs, and thus not all crabs move offshore for the entire winter. Taken together, these data demonstrate the importance of estuarine habitat for green crabs and the potential for continuous ecological consequences to estuaries induced by a year-round green crab contingent, even in suboptimal cold-water conditions. Whereas suboptimal temperatures might be presumed to induce a population-wide risk of mortality, the continued detection of crabs overwintering in the downstream region suggests that these crabs are not representative of those exposed to the higher risk of mortality in shallow regions and observed dead in intertidal burrows, with implications for population dynamics.

In addition to temperature, our top-ranking GLMM included salinity, with increased residence within the upstream zone more probable at higher salinities, particularly >28.6‰. The 12 h mean salinity range within the WRE (25–32‰) is well within the green crab's euryhaline tolerances and is close to the preferred salinity range for adults (27–34‰; Ameyaw-

Akumfi & Naylor 1987). Given that the WRE is heavily influenced by tidal flux, observations of lower salinities or extensive salinity gradients are limited to extreme, episodic events. We expect that such extreme events would prompt the movement of green crabs to the downstream region, especially during periods of cold-water temperatures. The combined effects of temperature and salinity result in higher salinities to be preferable at low temperatures, especially for larvae and consequently ovigerous females (Crothers 1967). Future tracking studies that capture episodic freshwater events or map finer-scale spatial variations in salinity may better inform green crab movement in relation to salinity and its synergy with temperature.

We did not observe significant differences in residency within the array or zone use between female and male green crabs. Additionally, our top candidate GLMM did not retain sex as a predictor of zone use. The strong shift in habitat use from upstream to downstream zones correlated with decreased water temperature suggests that the water parameters during the colder months impose similar cues for both females and males. Yet in the colder months, some females did make multiple transitions between the upstream and downstream zones and had longer times between detections, whereas each male only made one transition from upstream to downstream with shorter times between detections. Additionally, twice as many males were observed to overwinter in the downstream region. During peak mating season from July–October (Berrill 1982), the sample size was too small to compare between the sexes; this is the period during which we would expect males to be localized in the shallower, upstream zone for mating (Hunter & Naylor 1993, Warman et al. 1993), and we would expect females to move between these shallower areas with males and deeper water (Young & Elliott 2020). Once eggs are extruded, trapping studies hypothesize that ovigerous females seek deeper, saline waters, burrow, and are less active (Hunter & Naylor 1993, Warman et al. 1993, Queiroga et al. 1994, Aagaard et al. 1995). However, the highest residency within our array and most frequent transitions between the shallow upstream and deeper downstream zones were made by the ovigerous female when compared to all other individuals. Although we only tagged and documented one ovigerous female, we should note that our finding may be a result of ovigerous females being limited by the combined effects of salinity and temperature on egg viability and maternal care resulting in disparate preferred habitats (Crothers 1967). We suspect that enhanced sample

sizes in future studies may yield further clarification on sex-based differences, especially those for ovigerous females.

This study describes, for the first time, the tracking of adult green crab habitat use within an estuary over a seasonal time frame using acoustic telemetry, with implications for their spatial ecology and management. The localized travel by individual crabs both in up- and down-estuary distance and limited movements to exposed shores points to the potential constraints of cold-water temperatures on populations of green crabs and their survivability during a period with a high risk of mortality (Welch 1968, MEDMR 2014, MacDonald et al. 2018). Intertidal ectotherms exposed to transient near-freezing temperatures are at a higher risk of being killed or incurring major injury, yet some species of crabs can acclimate to freezing temperatures over the length of a tidal cycle and persist at low temperatures (Ronges et al. 2012). Hence, it could be adaptive that green crab movements to areas with highly variable temperatures, such as exposed shores, are restricted and that overwintering occurs in the downstream subtidal zone of the WRE where temperatures reached $<1^{\circ}\text{C}$ on 10 different days but remained consistently below the 10°C threshold. Additionally, the presence of green crabs in the subtidal zone of the estuary during this time of year demonstrates that the offshore environment or marsh complex is not the exclusive overwintering habitat even in cold temperatures; rather, that green crabs are active in the estuary year-round, and consequently, their associated impacts may be seen year-round as well. Knowledge of this basic ecology of green crabs is valuable to resource managers given the ubiquitous nature of green crabs in temperate estuaries and the deleterious impacts that they are capable of inducing. The improved understanding of green crab movement behavior demonstrated in this study can be used in planning for mitigation efforts that require explicit spatial knowledge of populations over time.

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