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Estimating movement and survival rates of a small saltwater fish using autonomous antenna receiver arrays and passive integrated transponder tags

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ABSTRACT: We evaluated the performance of small (12.5 mm long) passive integrated transponder (PIT) tags and custom detection antennas for obtaining fine-scale movement and demographic data of mummichog *Fundulus heteroclitus* in a salt marsh creek. Apparent survival and detection probability were estimated using a Cormack Jolly Seber (CJS) model fitted to detection data collected by an array of 3 vertical antennas from November 2010 to March 2011 and by a single horizontal antenna from April to August 2011. Movement of mummichogs was monitored during the period when the array of vertical antennas was used. Antenna performance was examined *in situ* using tags placed in wooden dowels (drones) and in live mummichogs. Of the 44 tagged fish, 42 were resighted over the 9 mo monitoring period. The *in situ* detection probabilities of the drone and live mummichogs were high (~80–100%) when the ambient water depth was less than ~0.8 m. Upstream and downstream movement of mummichogs was related to hourly water depth and direction of tidal current in a way that maximized time periods over which mummichogs utilized the intertidal vegetated marsh. Apparent survival was lower during periods of colder water temperatures in December 2010 and early January 2011 (median estimate of daily apparent survival = 0.979) than during other periods of the study (median estimate of daily apparent survival = 0.992). During late fall and winter, temperature had a positive effect on the CJS detection probability of a tagged mummichog, likely due to greater fish activity over warmer periods. During the spring and summer, this pattern reversed possibly due to mummichogs having reduced activity during the hottest periods. This study demonstrates the utility of PIT tags and continuously operating autonomous detection systems for tracking fish at fine temporal scales, and improving estimates of demographic parameters in salt marsh creeks that are difficult or impractical to sample with active fishing gear.

KEY WORDS: PIT tags · Mummichogs · Salt marsh · Cormack Jolly Seber

INTRODUCTION

Salt marshes are widely studied ecosystems that serve as important habitats for biological production along the United States East Coast (Seabrook 2012). These habitats provide ecological services (e.g. habitat for secondary and tertiary consumers, carbon storage, and water filtration), which may be hindered by human encroachment (Dame et al. 2000). Salt marshes offer an opportunity to examine specific

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questions such as the behavioral mechanisms of habitat selection over fine time scales due to variation in habitat profitability as a function of tidal cycles (Craig & Crowder 2000). Studies of salt marsh fish production, demographics, habitat use, and movement are often compromised when using traditional gear (e.g. trawls and seines) due to their inefficiency for repeated sampling of soft-bottom creeks (Kneib 1997).

Many species of fish found along the U.S. South Atlantic coast use salt marsh habitats for feeding and for refuge from predation (Kneib & Wagner 1994, Kneib 2003, Bretsch & Allen 2006). However, current knowledge of the use of intertidal marsh habitats by fish is based largely on ebb-tide collections of groups of animals (Kneib 2003, Bretsch & Allen 2006). These batch collections provide little fine-scale (hourly or daily) information about the extent or duration of habitat use by fishes and crustaceans in intertidal marshes (Kneib & Wagner 1994). Additionally, traditional gear does not allow precise estimation of demographic parameters of tagged fish due to the infrequent nature of recaptures (Kneib & Craig 2001, Hewitt et al. 2010, Camp et al. 2011).

Passive integrated transponder (PIT) tags are a tool by which biota in salt marsh systems can be resighted with higher resolution and less effort than traditional techniques (e.g. trapping, seining, and weiring). While used widely in freshwater ecosystems, PIT tags have been used relatively little in saltwater ecosystems. The greater conductivity of salt water compared to fresh water increases the attenuation of electromagnetic wave propagation, and hence reduces the ability of antennas to detect full duplex (FDX) PIT tags carried by animals in these environments (e.g. Bogie 1972, Bass et al. 2012).

The higher resighting rates of PIT tags resulted in greater precision of the estimates of movement and demographic rates than using traditional recapture techniques in freshwater (Prentice et al. 1990, Hewitt et al. 2010) and saltwater environments (Adams et al. 2011). Large (23 mm) half duplex (HDX) PIT tags have been used to determine patterns of saltwater fish spawning (McCormick & Smith 2004), survival (Adams et al. 2006), and movement (Adams et al. 2006, Meynecke et al. 2008, Adams et al. 2011) as the detectability of this type of PIT tag is not hindered by salinity (Castro-Santos et al. 1996). Relatively new, smaller FDX PIT tags (available down to 8 mm) can be used to mark fish that are smaller (see Hering et al. 2010) than what could be tagged with the smallest HDX tag size (23 mm) available when this study commenced.

The mummichog *Fundulus heteroclitus* is the most abundant resident fish species inhabiting salt marsh creeks along the United States East Coast (Kneib 1986, Kneib 1997, Able & Fahay 1998). Given its small home range (Lotrich 1975, Meredith & Lotrich 1979, Teo & Able 2003b) and high site fidelity (Sweeney et al. 1998, Teo & Able 2003b, Skinner et al. 2005), the mummichog is an ideal species for testing the use of FDX PIT tags in a salt marsh system. Mummichogs can be autonomously sampled with PIT tags to potentially improve on published estimates of movement (Kneib & Wagner 1994, Teo & Able 2003b, Bretsch & Allen 2006), survival (Meredith & Lotrich 1979), and production (Teo & Able 2003a) that have resulted from batch collections of multiple species or non-electronic tagging. The marking technique and detection devices used in this study are useful for studying a wide range of salt marsh nekton.

Our objectives were to evaluate the performance of small (12 mm) FDX PIT tags and custom antennas in a salt marsh creek and apply this technology to obtain estimates of movement and survival of a dominant salt marsh fish species via autonomous monitoring. To our knowledge, this is the first study to estimate survival of a saltwater fish species with 12.5 mm PIT tags.

MATERIALS AND METHODS

Study Site

The study site was Porters Creek, North Carolina, USA, a 600-m long, first-order intertidal polyhaline creek in the Newport River Estuary (Fig. 1). The lower 500 m are unrestricted and fringed by vegetated intertidal marsh dominated by saltmarsh cordgrass *Spartina alterniflora* (Loisel), while the upper 100 m are upstream of a culverted road crossing and fringed by forest. Porters Creek has tidal amplitudes of ~1.0 m during spring tides and 0.7 m during neap tides with amplitudes affected primarily by astronomical forcing and secondarily by wind speed, direction, and duration (Kirby-Smith & Costlow 1989). The fringing marsh in Porters Creek is flooded ~3.5 h over each semidiurnal (~12.25 h) tidal cycle. Flooding of the vegetation occurs at a depth (at the PIT tag antenna array) of 0.5 m. Current speeds in the channel of Porters Creek during that portion of the tidal cycle when the marsh platform is not covered by water are ~0.4 m sec^{-1} on ebb tide and 0.2 m sec^{-1} on flood tide where the antennas were

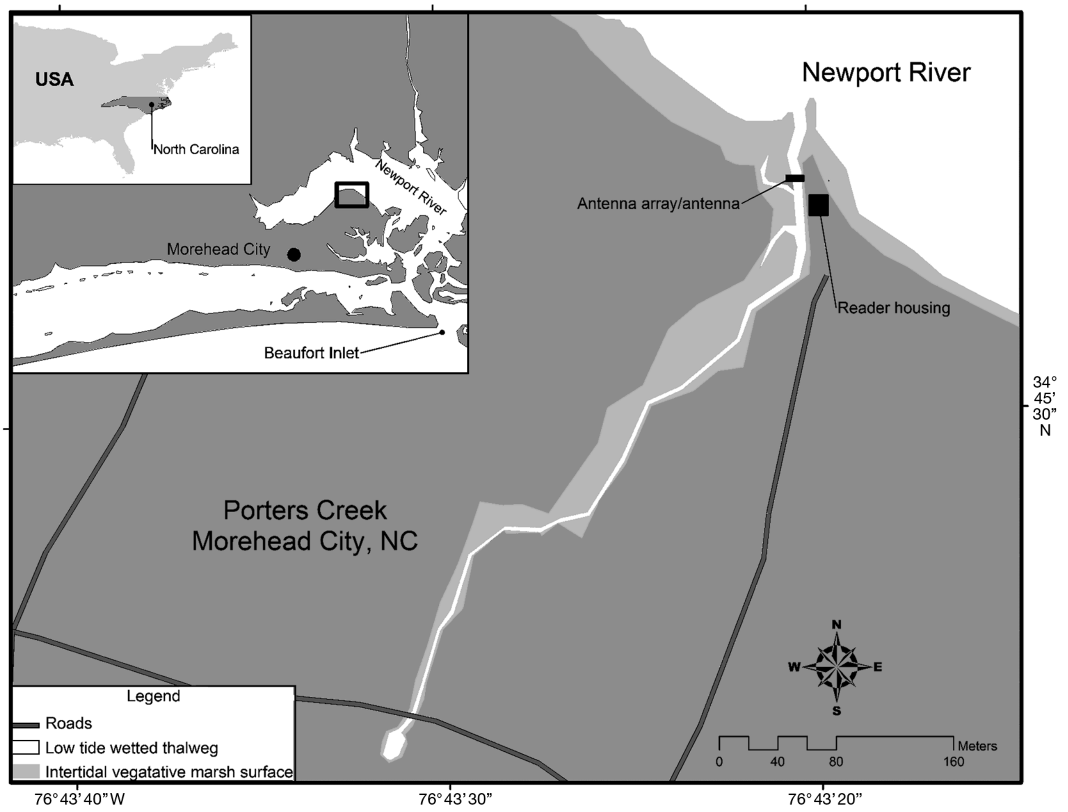

Fig. 1. Porters Creek, North Carolina, USA, showing the location of custom-made autonomous antennas (3 vertical or 1 horizontal) used to detect PIT-tagged mummichogs between 8 November 2010 and 4 October 2011. Large map shows the areas of Porters Creek wetted at both high tide (light gray) and low tide (white). Mummichogs were captured and released in the area of the creek within 50 m of the location of the arrays

located. Salinities taken intermittently in Porters Creek throughout the study ranged from 5 to 39 (mean = 30) throughout the creek.

Fish collection and marking

Mummichogs were collected on 8 November 2010 within 50 m of the detection antennas using minnow traps made of 6 mm square wire mesh. We tagged 44 fish ranging from 50 to 94 mm total length (1.5–13.1 g). We anesthetized fish with tricaine methanesulfate (125 g l^{-1} of seawater) prior to implanting the tag in the peritoneal cavity. We implanted FDX PIT tags (12.5 mm, 0.1 g) (Biomark) with a frequency of 134.2 kHz by making a small (~1 mm) incision on the ventral side of the fish posterior to the pelvic girdle. We used FDX instead of HDX tags because HDX tags were not available in small sizes (≤12.5 mm) when this study commenced. Each tagged fish was then placed in a recovery tank of ambient seawater and later released in the vicinity of the capture location once it was swimming normally.

A laboratory study determined that the overall success rate (probability of retaining the tag and surviving) of PIT tagging in mummichogs (41 to 70 mm) was 87%; all mortality and tag shedding occurred within the first 30 d of a 163 d experiment (authors' unpubl. data).

Tag detection equipment

From 8 November 2010 through 3 March 2011, we used an array of 3 rectangular antennas ('vertical array') to detect PIT-tagged mummichogs moving past a fixed point in the study creek. Each antenna was custom-made from 9 wraps of 10 AWG 1100/40 polyvinyl chloride (PVC) coated Type II Litz wire (New England Wire) encased with controlled spacing in 15-cm diameter schedule-40 PVC pipe. The internal dimensions of each antenna defined the rectangular opening through which fish could pass during movement into or out of the creek. Each antenna had an internal height dimension of 0.7 m (space between the 2 horizontal PVC pipes). The downstream and upstream antennas in the array (numbers 1 and 3, respectively) had internal width dimensions of 1.75 m, while the middle antenna's internal width (number 2) was 2.25 m. Antennas were positioned 4 m apart; at this distance, each antenna had its own detection field. Both the vertical antennas and the horizontal antenna (described below) were secured to- and rested on the substrate with sand screws and ratchet straps.

The 3 antennas were oriented perpendicularly to the channel and placed 50 m upstream from the creek mouth (Figs. 1 & 2A). This location is a transition area at mean low tide between a rivulet of water that persists in the unvegetated channel above the array and standing water that persists over the width of the creek during all tidal cycles below the array. To maximize path efficiency (Zydlewski et al. 2006), plastic weir material (6.4 mm square mesh) was affixed to the top and sides of the upstream and downstream antenna; the side weir material was extended to the high-tide line.

The vertical antenna array and weir material were removed from the creek on 3 March 2011 and replaced with a single antenna on 14 April 2011 that was horizontal (flat) with respect to the creek bottom and placed in the same location as the middle antenna of the vertical array (Fig. 2B). The horizontal antenna was constructed of 9 wraps of 10 AWG 1100/40 PVC coated Litz wire embedded in 20.32 cm diameter schedule 40 PVC. However, no weir material was used with the horizontal antenna. The internal dimensions of the horizontal antenna were identical to vertical antennas 1 and 3 (0.75 × 1.75 m). The switch to a single horizontal antenna was required to permit seasonal use of the study creek by paddle boaters. Each antenna (during both the vertical and horizontal antenna periods) was connected via RG-8 coaxial cable (Belden) to a 24 V FS-1001-M multiplexing receiver (Destron Fearing). The receiver was powered by 2 pairs of 12 V DC batteries connected in series to create two 24 V batteries. A custom-made battery switcher alternately switched charging of each pair of batteries with a charger (Model PS 2408 charger; Interacter) connected to 120 V AC electrical power. The receiver was connected to a cellular modem (Raven XT V2221; Sierra Wireless). The modem provided remote access to the receiver and facilitated automatic daily downloads of text files containing tag codes, dates, and times when tagged mummichogs were detected as well as receiver diagnostics such as electrical current and radio frequency (RF) noise readings (external disturbance to an electrical circuit) of each antenna. The receiver, batteries, battery switcher, recharger, and modem were stored in an electrical box affixed to a sheltered kiosk. There were occasions during the monitoring period (see Appendix 1) when the multiplexing receiver was not operational. During these occasions, a Destron Fearing 24 V FS-1001A receiver was used. Unlike the multiplexer, the FS-1001A does not provide date and time of each detection; detections by the FS-1001A were assigned a date at the midpoint between manual downloads of data (Appendix 1). PIT tag readers are incapable of determining the vertical or horizontal location of a detection within the plane of an antenna.

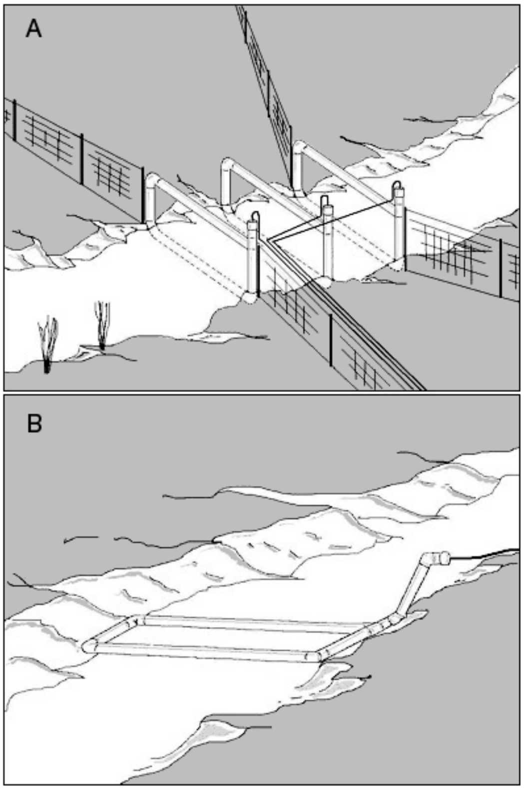

Fig. 2. Antenna arrays placed in the channel of Porters Creek, North Carolina to detect PIT tagged mummichogs by: (A) an array of 3 vertical antennas used between November 2010 and March 2011, and (B) a single horizontal antenna used between March and October 2011

We collected data on water temperature and depth in order to evaluate their relationships with the Cormack Jolly Seber (CJS) model parameter detection probability (see below). We placed a Hobo 20 Titanium logger (Onset) next to Antenna 2; this logger recorded hourly temperature (0.1°C) and water depth (0.1 m) throughout the study. The hourly water depth closest in time to each tag detection was used to evaluate the effects of depth on number of detections for each antenna.

Evaluation of antenna performance and probability of detecting PIT tags

We examined the effect of water depth on electric current (higher current = higher probability of detection) for each vertical antenna from 8 November 2010 through 3 March 2011 by using linear regression models. Fish detections were examined on plots of electric current vs. water depth to determine if reductions in the number of detections with greater water depth resulted from poor antenna performance or real fish behavior. If the number of detections decreased but antenna current remained sufficiently high for detecting fish (>~1 A), it would suggest that fish behavior was responsible for the lack of detections rather than antenna performance. Analysis of covariance (ANCOVA) of electric current (dependent variable) and depth (covariate) was used to determine if the amount of electric current varied by antenna number (factor). Electric current values were ln transformed to linearize the relationship between electrical current and water depth.

The probability of detecting a PIT tag *in situ* was estimated using both a drone tag and live mummichogs. Drone tag testing was conducted to determine how water depth and tag position influenced probability for tag detection using our custom-made antennas. The drone consisted of a 12.5 mm FDX PIT tag embedded in a wooden dowel. We passed the drone tag through a 0.75 × 1.75 m vertical antenna in the field at a water temperature of 26°C and a salinity of 25. This salinity is similar to the average in Porters Creek (~30). Factors examined that are known to influence FDX PIT tag detection included water depth (depth), the height that the tag was passed relative to creek bottom (tag height), and the horizontal location within the antenna perimeter where the drone tag was passed (Horton et al. 2007, Hering et al. 2010, Bass et al. 2012). We selected discrete water depths (0.2, 0.4, 0.6, 0.8, 1.0, and 1.1 m), tag heights (0, 0.2, 0.4, 0.6, 0.8, and 1.0 m), and horizontal locations (0, 0.25, 0.5, and 0.75 m from each vertical side of the antenna) over which to test the drone. Each pass of the drone through the antenna lasted roughly one second. We performed one trial (pass of the drone) for each combination of water depth and tag height because pilot testing of PIT tags in salt water revealed that the outcome of detection trials did not change for any one combination of abiotic conditions and tag position inside the perimeter of the antenna.

Binomial drone tag detection data was fitted to water depth, tag height, horizontal location, and their interactions using generalized linear models (GLM). Model performance was evaluated with quasi-corrected Akaike's information criteria ($QAIC_c$), owing to potential over-dispersion of the data (values of the variation inflation factor frequently >1). We computed a $\Delta QAIC_c$ value for each model, representing the difference between the $QAIC_c$ value and the minimum for the model set ($QAIC_{cmin}$). Models within 2 $\Delta QAIC_c$ units of $QAIC_{cmin}$ were regarded as having substantial support (Burnham & Anderson 2002). Proportional support for each model was estimated using Akaike weights (w_i; Burnham & Anderson 2002).

The *in situ* probability of detecting a tagged mummichog was estimated utilizing fish detection data collected during the period when the vertical array was used. *In situ* detection probability is determined when a live fish or drone is known to be present in the antenna field and, here, represents the performance of a single antenna. In contrast, CJS detection probability includes both *in situ* detection probability of all the antennas in the array (the probability of detecting a fish if it is present) and the probability that the fish is present (available) for resighting. Unlike detection probability estimated in the CJS model (below), *in situ* detection probability does not pool detections across the antennas in a multiple-antenna array.

In situ detection probability was determined for individual mummichogs detected by at least Antennas 1 and 3 within a 10 min period. This provided a group of fish known to have passed through Antenna 2. For those individuals, detection efficiency was then estimated as the number of times a tagged mummichog was detected by Antenna 2 (i.e. all 3 antennas in the 10 min period) divided by the sum of detections on 'all 3 antennas' and 'Antennas 1 and 3 only'. The relationship between *in situ* detection probability and water depth was then modeled with logistic regression.

Using PIT tags to determine movement patterns

Direction of movement of mummichogs was estimated from detection data collected during the vertical array period. We defined a valid movement as detections by at least 2 antennas within a 10 min period with the first and last detections in the direction of movement. This definition avoided the assignment of movement to tagged fish that were occupying the antenna area of the creek for extended periods of time.

We modeled direction of movement through the array with logistic regression by assigning codes of

1 and 0 to upstream and downstream movements, respectively. We developed models that incorporated factors believed to influence direction of movement for mummichogs (Butner & Brattstrom 1960, Lotrich 1975, Teo & Able 2003b). These factors were hourly water depth (to the nearest 0.01 m) and tidal current (flood vs. ebb). Model building with respect to interaction terms, as well as model evaluation, used the same criteria as described for drone tag data.

Using PIT tags to estimate apparent survival using the Cormack Jolly Seber model

Detection probability and apparent survival of tagged mummichogs were estimated using a hierarchical state-space formulation of the CJS model (Cormack 1964, Jolly 1965, Seber 1965, Royle 2008). This version of the CJS model includes in its likelihood a state process (whether a marked individual is alive at sample time *t*) and an observation process conditioned on state (whether individual *i* is observed given that it is alive at time *t* and in the study area). The CJS model assumes that: (1) capture (resighting) periods are instantaneous relative to the time between them; (2) resighted fish are a random sample from the population; (3) behaviors of tagged individuals are independent but all individuals have the same survival and resight probability; (4) tags are not lost or overlooked; (5) individuals are correctly identified; and (6) emigration from the study area is permanent. The study area was both above and below the antenna arrays. We modeled apparent survival (1− [mortality + emigration]) of mummichogs due to the open study area and potential for permanent emigration. Given the small home range size (Lotrich 1975, Meredith & Lotrich 1979) and high site fidelity of this species (Sweeney et al. 1998, Teo & Able 2003b, Skinner et al. 2005), permanent emigration appears unlikely.

Although fish were detected up until 4 October 2011 (see Fig. 7; Appendix 1), we fitted the CJS model to data collected over 167 occasions between 8 November 2010 and 15 August 2011 when detections were continuous (i.e. no long breaks between occasions). The model was implemented using a Bayesian approach within *OpenBUGS* software (version 3.2.1; Spiegelhalter et al. 2010; code available upon request). An occasion is a biologically meaningful unit of time over which independent Bernoulli trials (presence/absence) are conducted on tagged individuals in order to estimate demographic rates (Royle 2008). We elected to define an occasion as one day (24 h) because we felt that this was a sufficiently long enough period to detect a tagged fish moving by the array over a variety of water depths and tidal stages, but a short enough period (high enough temporal resolution) that we could identify any changes in patterns of apparent survival with fluctuations in temperature. Because several occasions were longer than one day, a day vector (number of days per occasion) was used to estimate daily values of apparent survival in the likelihood portion of the model. Some occasions were longer than one day due to equipment issues (Appendix 1).

We developed a form of the CJS model that incorporated covariates believed to influence fish behavior and the likelihood of detection probability (*p*) by each antenna array. Based on plots of numbers of unique individuals detected by occasion, it appeared that occasion-specific variability in *p* was related to water temperature, water depth, and array design (vertical array vs. horizontal antenna). Thus, we elected to fit versions of the CJS model to the individual 'capture' (detection) histories that estimated detection probability by occasion using logistic models (with temperature and depth as continuous covariates) specific to each antenna type; in initial model runs, we eliminated covariates when their slope coefficients had 95% credible intervals (CIs) containing zero. These initial model runs eliminated water depth as a covariate but retained temperature during both the vertical array and horizontal antenna periods. To increase the efficiency of the Markov Chain Monte Carlo sampler within *OpenBUGS*, we centered the variable temperature for each occasion by subtracting its mean value (for all occasions) to reduce autocorrelation between successive samples (McCarthy 2007).

In order to detect potential water temperature effects on apparent survival, we used *OpenBUGS* to estimate a daily value of apparent survival specific to each of 2 periods. These 2 periods were selected based on differences in water temperature patterns. Period 1 included 2 time intervals: from 8 November to 1 December 2010 and 24 January 2011 to 15 August 2011; a preliminary model run found that the CIs regarding estimates of apparent survival overlapped between each of these time intervals. During these time intervals, the water temperature was below 5°C on only one day and often within the range of optimal growth of the species (Garside & Morrison 1977). Period 2 was a late fall-early winter time interval between 2 December 2010 and 23 January 2011, when the water temperature dropped below 5°C on multiple days.

For the Bayesian analysis with *OpenBUGS*, we used uninformative prior distributions. A normal prior distribution with mean of 0 and precision of 1×10^{-6} was given to each coefficient (intercept and slope) of the 2 logistic models of the CJS detection probability. The prior for apparent survival over each of the 2 periods was a uniform distribution with minimum (0) and maximum (1) values of apparent survival. Three Markov chains (independent sample sets) began with a burn-in period of 10 000 iterations (discarded initial values not representative of a stationary distribution). A sufficient burn-in period was determined by examining for convergence of chains of initial values in the trace plots generated in *OpenBUGS*. We then generated 100 000 updates of the model with every 10th iteration saved (thin = 10). This number of updates was selected because changes to the median values and CIs of parameter estimates no longer occurred compared to lesser updates of the same model.

RESULTS

Evaluation of antenna performance and probability of detecting PIT tags

A total of 20 703 individual detections (individual resightings by any antenna at any time) were made by the vertical array from November 2010 to March 2011. The majority of detections by vertical antennas occurred in shallow depths; overall, ~85% of detections occurred at depths less than ~0.5 m. The slopes of linear regressions relating ln-transformed values of electric current to water depth were significantly negative for each antenna ($p < 0.001$) (adjusted r^2 values of 0.867, 0.836, and 0.864 for Antennas 1, 2, and 3, respectively); diagnostic plots did not reveal non-normality or non-constant error variance in the 3 regression models. There was a significant interaction between water depth and antenna in the ANCOVA model ($p < 0.001$); Antenna 2 had lower electrical current at shallow water depths than Antennas 1 or 3 (Fig. 3).

Water depth, tag height, and horizontal location within the antenna, and the interaction between water depth and tag height explained a large amount of variability in the antenna's ability to detect a drone tag *in situ*, and were included in the most parsimonious model (Nagelkerke $R^2 = 0.875$; Table 1). Increasing water depth negatively affected detection probability for the drone while increasing tag height positively affected the detection probability for the drone. Passes of the drone at horizontal distances of 0.25, 0.5, and 0.75 m had a negative effect on detection probability relative to 0 m. At a horizontal distance of 0 m, the probability of detecting the drone remained at 100% for depths ≤~1.0 m (Fig. 4A). At a horizontal distance of 0 m, the probability of detecting the drone remained near 100% for depths <0.8 m (Fig. 4A). For horizontal locations >0 m, the probability of detecting the drone tag generally remained near 100% for depths <0.5 m but dropped to near zero for depths >0.9 m (Fig. 4B). Electric current and percentage of RF ranged from 0.5 A and 84% (at 1.1 m deep) to 3.3 A and 14% (at 0.2 m deep) during drone tag testing.

The *in situ* probability of detecting a tagged fish on Antenna 2 for mummichogs known to have passed through this antenna was 0.933 (642 / 688). Water depth had a significant negative effect on *in situ* detection probability ($Z = -2.897$; $p = 0.004$; Fig. 5). The predicted detection probability of tagged mummichogs declined from near 1.0 at water depths near 0 m to 0.8 at a water depth of 1.0 m (Fig. 5). These data were collected throughout the vertical array period; during these detections, mean water depth was 0.35 ± 0.21 m (SD), electrical current averaged 2.26 ± 1.15 A, and mean RF noise was 21.8 ± 21.8%.

Movement patterns

Based on the criteria used to determine a valid move, the vertical array detected 1112 movements; 624 were ingress and 488 were egress. The vertical antenna array detected subsequent moves in opposite directions in 72.5% of the cases; 27.5% of moves in one direction were not followed by moves in the opposite direction. Mummichogs generally moved upstream through the array with flooding tides and downstream with ebbing tides; 84.5% of the movements occurred in the direction of tidal flow (Fig. 6). Mean water depth when mummichogs moved through the array (±SD) was 0.29 m (±0.21 m) upon ingress and 0.43 m (±0.18 m) upon egress. The probability of movement upstream was negatively related to hourly water depth during ebb tide; at the end of ebb tide (low water depths), some mummichogs would begin their movement upstream (Fig. 6). During flood tides, the probability of ingress remained high across all hourly water depths. Thus, hourly depth, tidal current, and the interaction between the 2 were contained in the most parsimonious model (Nagelkerke $R^2 = 0.702$; Table 2); this model received the vast majority of support.

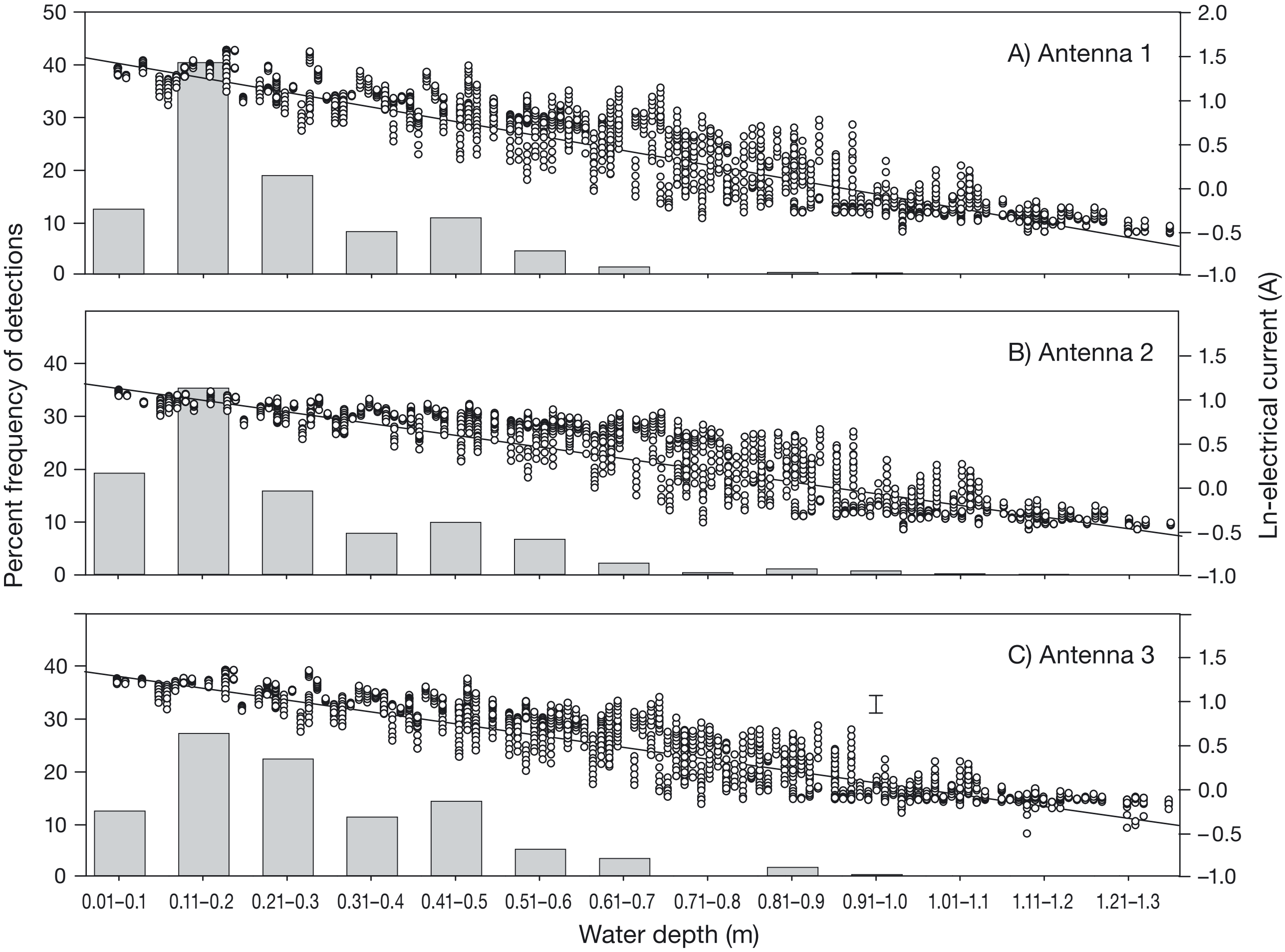

Fig. 3. Percent frequency of detections (left *y*-axis; vertical bars) and the ln values of autonomous electrical current (A) (right *y*-axis; circles) vs. water depth (m) (*x*-axis) for each of 3 vertical antennas used to detect PIT-tagged mummichogs in Porters Creek, North Carolina, USA between 9 November and 3 March 2011. Each pair of values for electrical current vs. water depth is represented by a circle while percent frequency of detections (by water depth bins) is represented by shaded bars. The *x*-axis is scaled for both the binned and the discrete depth data. The straight line in each panel represents a least squares linear regression model (with significant slope) relating the ln values of electrical current to water depth at those time points when electrical current was supplied by the receiver

Cormack Jolly Seber parameter estimates: apparent survival and detection probability

Of the original 44 tagged individuals, 42 were resighted between 9 November 2010 (Occasion 2) and 15 August 2011 (Occasion 167) (Fig. 7). Mean daily water temperature over the study ranged from 0.8°C on 8 December 2010 (Occasion 26) to 34.6°C on 30 May 2011 (Occasion 153; Fig. 7). The greatest CJS detection probability occurred during a 3 wk period after marking (Occasions 2–23) and during February 2011 (~Occasions 80–105); high detection probability during these periods corresponded with warmer water temperatures in autumn and winter. The temperature coefficient was positive (warmer water temperatures led to higher detection probability via greater fish activity) and the 95% CIs did not contain 0 (Table 3) during the vertical antenna period (Occasions 1–111). The temperature effect during the horizontal antenna period (Occasions 112–167) was negative (warmer water resulted in lower detection probability via reduced fish activity). Convergence of chains of initial values to stable posterior distributions occurred within the burn-in period for logistic model parameters used to estimate detection probability by occasion. Median occasion-specific estimates of detection probability fluctuated over the study; the width of the CI for detection probability for each occasion averaged 64% of the median detection probability for each occasion (Fig. 7).

Table 1. Logistic regression models relating drone PIT tag detections by a custom-made vertical antenna to water depth (depth), tag height off the creek bottom, and horizontal location within the perimeter of the antenna (location). The null model includes the intercept term only. $QAIC_c$ = quasi-corrected Akaike's information criteria; a lower $QAIC_c$ score indicates greater model parsimony with the data than a higher score. Models are ranked from lowest to highest $QAIC_c$ scores. k = number of model parameters (including penalty for overdispersion). The Akaike weight (w_i) represents the proportional support for each model

Model	k	$QAIC_c$	$\Delta QAIC_c$	w_i
depth + tag height + location + depth × tag height	8	80.3	0	0.57
depth + tag height + location + depth × tag height + depth × location + tag height × location	14	81.9	1.6	0.26
depth + tag height + location + depth × tag height + depth × location	11	83.7	3.4	0.10
depth + location	6	86.0	5.73	0.03
depth + tag height + depth × tag height	5	87.8	7.46	0.01
depth + tag height + location	7	88.1	7.79	0.01
depth	3	92.1	11.8	0.00
depth + tag height	4	94.1	13.8	0.00
null	2	211.1	130.8	0.00
tag height	3	212.1	131.8	0.00
tag height + location	6	215.4	135.1	0.00

Convergence to a stable posterior distribution of apparent survival occurred rapidly (~1000 iterations). The median estimate of daily apparent survival (2.5 and 97.5% CIs) was greater during period 1 (0.992 [0.988–0.996]; warmer period) than period 2 (0.979 [0.970–0.986]; period with a series of cold snaps); the CIs did not overlap. Mummichogs had higher apparent survival during period 1 than period 2 (Fig. 8). There was low overall apparent survival of tagged mummichogs over the 9 mo monitoring period (~5% remaining after 280 d).

DISCUSSION

This study builds on the growing body of fisheries research using PIT tags to study saltwater fish *in situ* (McCormick & Smith 2004, Adams et al. 2006, Meynecke et al. 2008, Hering et al. 2010, Adams et al. 2011, Barbour et al. 2012). Autonomous detection equipment recorded a large number of resightings on a nearly continual basis throughout the 9 mo monitoring period. The high temporal resolution of resightings allowed for precise estimates of CJS model parameters and temporally fine-scale (hourly) movement patterns of an important salt marsh fish species.

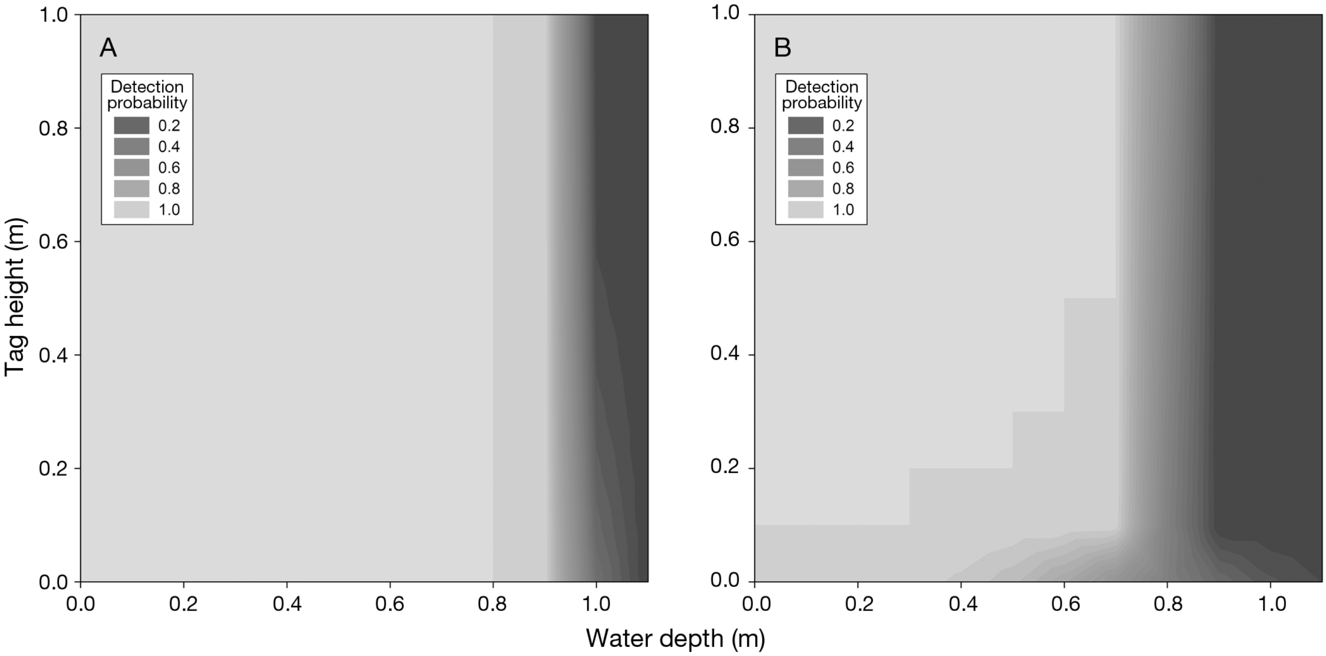

Fig. 4. Predicted probability of detection (gray scale grid; detection probabilities are by increments of 0.2, i.e. 0–0.2 etc.) of a 12.5 mm drone PIT tag passed through a custom-made antenna as a function of water depth (x-axis) and tag height above the bottom of the creek (y-axis). Predicted detection probabilities were separately modeled for (A) a horizontal location (left to right within the perimeter of antenna) of 0 m and (B) at all other horizontal locations (0.25, 0.5, and 0.75 m)

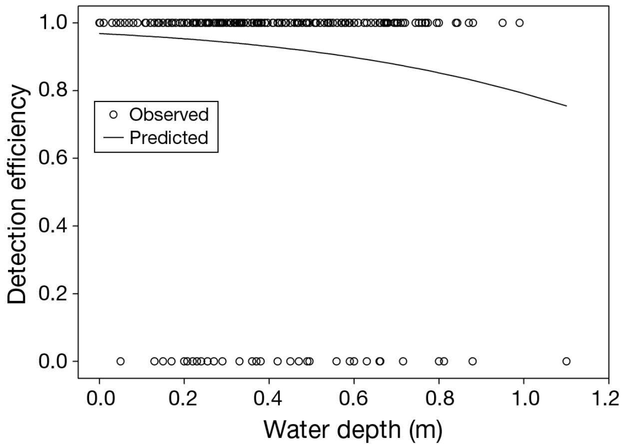

Fig. 5. Predicted *in situ* detection probability (logistic model fit; line) of PIT tagged mummichogs (*y*-axis) moving past an array of 3 vertical antennas in Porters Creek, North Carolina, USA as a function of water depths (*x*-axis). *In situ* detection probability here is the success of the middle antenna of the array to detect a PIT tag. Observed data (open circles) represent moves where a mummichog was detected by all 3 antennas ($y = 1$) or by only the outer 2 antennas and not the middle antenna ($y = 0$)

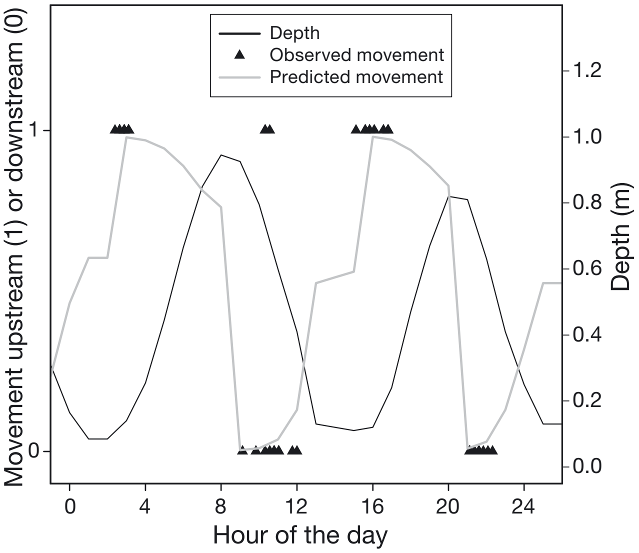

Fig. 6. Observed (black triangles) and predicted (gray line) ingress (1) and egress (0) (left *y*-axis) of PIT tagged mummichogs plotted over a diel cycle with one of the main predictors, hourly water depth (solid black line; right *y*-axis). Data were collected by an array of 3 vertical antennas on 19 November 2010 near the mouth of Porters Creek, North Carolina, USA. See 'Results' section for description of the predictive model

Field estimates of apparent survival and detection probability using CJS model

Our estimate of mummichog apparent survival applies to the entire Porters Creek marsh both upstream and downstream of the antenna array. We were restricted to estimating apparent survival rather than true survival because we worked in an open system where marked fish may have permanently emigrated. However, estimates of apparent survival may be close to true survival for this species, given its small home range size (~100 m^2; Lotrich 1975, Meredith & Lotrich 1979, Teo & Able 2003b) and high site fidelity to home creeks (Sweeney et al. 1998, Teo & Able 2003b, Skinner et al. 2005). Creek fidelity appears to be the case for Porters Creek; out of 300 PIT tagged fish released in Porters Creek in 2013, only 18 were recaptured in 180 traps set (3810 mummichogs captured) outside of Porters Creek (up to 300 m either side of the mouth of the creek; unpubl. data). Of these 18 tagged fish, 15 were subsequently resighted by the antenna array in Porters Creek (83.3% resighting rate). Thus, although some tagged mummichogs were shown to move out of Porters Creek, trapping recaptures suggest that they stay within or in close proximity to the creek mouth and antenna resightings indicate that the vast majority of fish return to the creek after using nearby habitats.

Our results confirm prior work that mummichogs are a short-lived species. Using fish scales, Kneib & Stiven (1978) estimated ages of mummichogs (of similar sizes to this study) that were collected from a nearby North Carolina marsh; those authors reported that in August ~60% of their sample was age-0 fish with few mummichogs making it past their second or third year of life (>age 1 or 2). Similarly, we found low survival of mummichog ≥50 mm total length (TL) (likely older age-0 and younger age-1 fish when tagged). We found that mummichog CJS detection probability and apparent survival varied over a 9 mo period; past research using traditional gear does not have this temporal resolution. However, our overall estimate of apparent survival is similar to that of Meredith & Lotrich (1979). The total annual mortality rate (Z) of 4.49, calculated from our estimate of apparent survival, is close to the Z of 4.74 we estimated from the declines in Meredith & Lotrich's (1979) abundance estimates of mummichogs in a Delaware salt marsh.

During period 2, the temperature dropped to near freezing on multiple occasions. During much of the rest of the occasions during this period, the temperatures were below the thermal optimum for mummichog growth (Garside & Morrison 1977). While low temperatures (<5°C) over multiple days in the colder period may not have directly caused mortality of mummichogs (Fangue et al. 2006 saw high survival

Table 2. Logistic regression models relating movement of PIT-tagged mummichogs (1 = ingress, 0 = egress) through an autonomous array of vertical antennas in Porters Creek, North Carolina, USA. Movement was modeled as a function of hourly depth and tidal current (tide; ebb or flood). The null model includes the intercept term only. $QAIC_c$ = quasi-corrected Akaike's information criteria; a lower $QAIC_c$ score indicates greater model parsimony with the data than a higher score. Models are ranked from lowest to highest $QAIC_c$ scores. Number of model parameters (including penalty for overdispersion) = k. The Akaike weight (w_i) represents the proportional support for each model

Model	k	$QAIC_c$	$\Delta QAIC_c$	w_i
hourly depth + tide + hourly depth × tide	5	679.3	0	0.99
hourly depth + tide	4	689.6	10.3	0.01
tide	3	842.4	163.1	0.00
hourly depth	3	1345.0	665.7	0.00
null	2	1464.7	785.4	0.00

even at freezing temperatures), reduced activity levels may have made them more vulnerable to resident predators such as colonial (Ardeidid) wading birds and double-crested cormorants *Phalacrocorax auritus*.

Some CJS model assumptions may have been violated using PIT tags and autonomous arrays to collect resight data. The readers collected data continuously and this type of sampling violates the assumption of instantaneous resighting. However, Hargrove & Borland (1994) reported that estimates from CJS models are not badly affected by violations of this assumption. Another assumption that was violated is that emigration is permanent. Temporary emigration of tagged mummichogs may have occurred during our study and can negatively bias estimates of CJS detection probability; however, estimates of apparent survival remain unbiased if temporary emigration is random so that all marked individuals have the

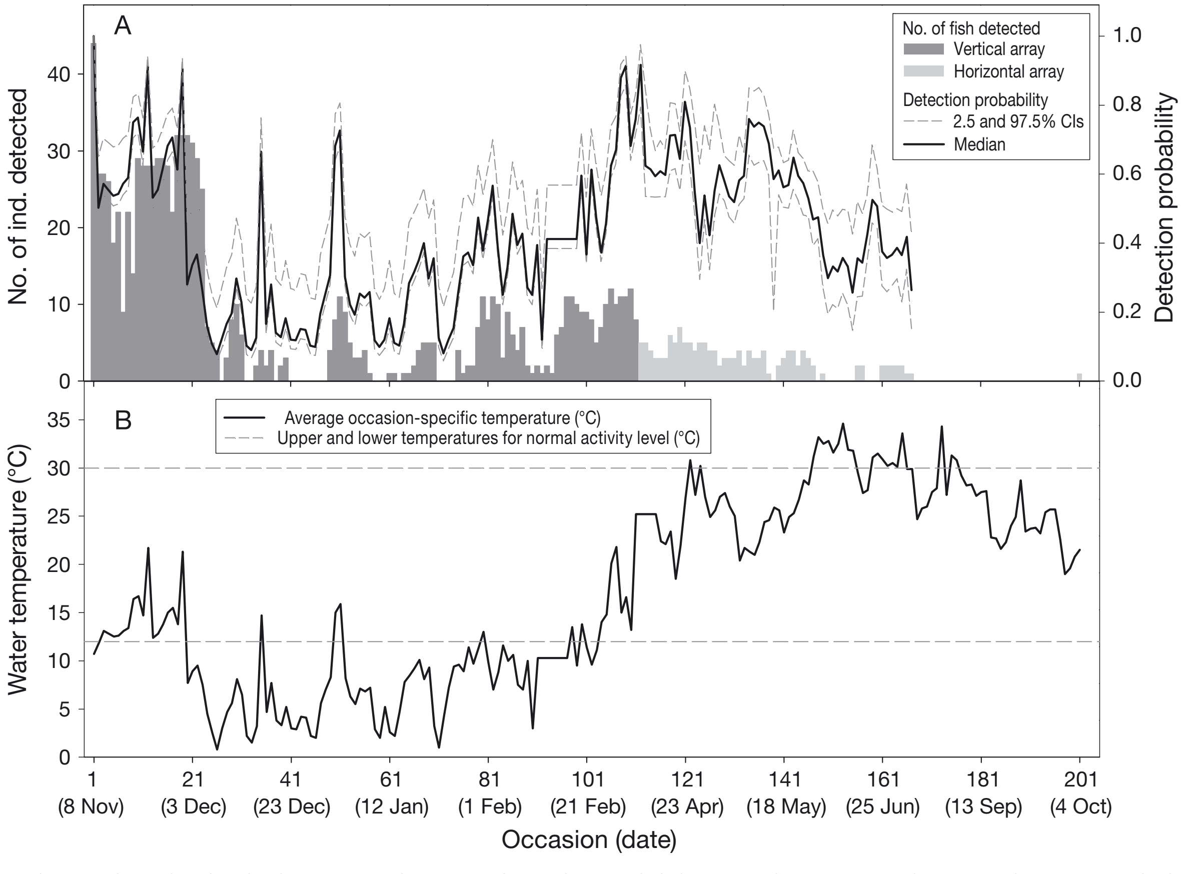

Fig. 7. (A) Number of individual PIT-tagged mummichogs detected (left y-axis) by an array of 3 vertical antennas (dark gray bars) (Occasions 1–111) and by a single horizontal antenna (light gray bars) (Occasions 112–201) in Porters Creek, North Carolina, USA between 8 November 2010 (day of tagging) and 4 October 2011 (last occasion a tagged fish was detected). Detection probability for this figure was estimated by fitting the Cormack Jolly Seber model to antenna detection data for occasions (x-axis) between 9 November 2010 (Occasion 2) and 15 August 2011 (Occasion 167). The occasion corresponding to each date on the x-axis is in parentheses. Median occasion-specific detection probability (right y-axis) is graphed as the solid black line and 2.5 and 97.5 % CIs for detection probability as dashed gray lines. (B) Mean occasion-specific water temperature (°C) (y-axis; solid line) and lower and upper water temperatures for normal activity levels of mummichogs (12 and 30°C, respectively; dashed gray lines) vs. occasion (x-axis). Water temperatures over which normal activity of mummichogs is expected were estimated from Garside & Morrison (1977) and Sidell et al. (1983)

Table 3. Estimating covariates of detection probability when fitting the Cormack Jolly Seber model to detections of PIT tagged mummichogs by 2 antenna arrays in Porters Creek, North Carolina, USA. The table lists median, 2.5% credible intervals (CIs), and 97.5% CIs of regression coefficients when modeling detection probability as a logistic (p-logit) function of water temperature when an array of 3 vertical antennas was used (Occasions 2–111), and when a horizontal antenna was used (Occasions 112–167)

Occasions	Parameter (description)	2.5% CIs	median	97.5% CIs
2–111	β_0 (intercept, logistic model; vertical antennas)	−0.803	−0.709	−0.566
	β_1 (temperature coefficient, vertical antennas)	0.208	0.233	0.255
112–167	β_0 (intercept, logistic model; horizontal antennas)	−0.112	0.056	0.273
	β_1 (temperature coefficient, horizontal antennas)	−0.192	−0.123	−0.066

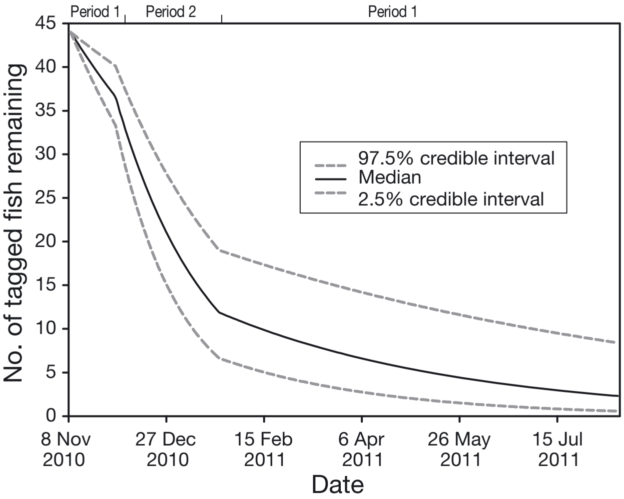

Fig. 8. Estimated number of tagged mummichogs in Porters Creek, North Carolina, USA based on the initial number of tagged fish (n = 44) on 8 November and estimated apparent survival rates from a Cormack Jolly Seber model during period 1 (8 November 2010–1 December 2010 and 24 January–15 August 2011) and period 2 (2 December 2010 and 23 January 2011; see 'Results' section for estimates of apparent survival by period)

same probability of being resighted (Williams et al. 2002). A frequency plot of the total number of occasions an individual was resighted showed no signs of extreme heterogeneity in CJS detection probability (e.g. bimodality) but data were right-skewed suggesting some heterogeneity in detection probability (Abadi et al. 2013). Heterogeneity in CJS detection probabilities among tagged individual has a negligible effect on survival rate estimates (Carothers 1979, Royle 2008, Abadi et al. 2013).

In contrast to these violations, other assumptions of the CJS model were reasonably satisfied. Mummichogs for tagging were randomly selected from traps in order to get a representative subsample from the population inhabiting Porters Creek. The mummichog is not an open-water schooling species, so behavior, movement, or survival of tagged individuals were considered to be independent among tagged fish.

Temperature influenced the CJS detection probability. Mummichogs maintain normal activity at water temperatures between ~12 and 30°C (Garside & Morrison 1977, Sidell et al. 1983). This range of thermal preference is consistent with the positive relationship between CJS detection probability and winter water temperatures which often fell below 12°C. During the horizontal antenna period, detection of mummichogs decreased when the temperature was occasionally above 30°C.

Although water depth influenced the *in situ* probability of detecting a tag, it did not influence CJS detection probability for either array. This result makes sense considering the differences in how the effects of water depth are modeled with these 2 approaches. The *in situ* model estimates the probability of detecting the pass of a drone or fish at a specific water depth. For the CJS model, mean depth over an entire occasion was used to estimate detection probability. Although mean water depth varied among occasions, there was always a period within each occasion when water depths were low and tagged mummichogs could be detected.

Vertical antenna performance and mummichog behavior

The hydroperiod (frequency and duration of flooding) of salt marsh creeks along the U.S. South Atlantic coast affects the patterns of marsh surface use by resident and transient biota (Rozas 1995, Kneib 1997). Tidal frequency and flooding duration control the accessibility to the marsh by fish, while tidal amplitude influences the areal extent of habitat available (Kneib 2003). The vertical antennas did not detect 100% of the tagged fish passing them; 27.5% of movements in one direction were followed by another movement in the same direction rather than being followed by movement in the opposite direction. However, the vertical antennas did document ingress and egress from which we could glean information on mummichog use of the creek.

Attenuation of electric current during deeper water periods reduced the detection of PIT tags. Therefore, any discussion of mummichog behavior has to be interpreted in light of antenna performance (electric current) that declined as water depth increased. Attenuation of electric current led to a 0 *in situ* detection probability of the drone tag at depths >1.0 m when passage was at the vertical parts of the antenna (0 m horizontal locations). For other horizontal locations, the probability of detecting the drone tag dropped at 0.5 or 0.8 m of water depth (depending on the height of the drone tag). This suggests that not all movements of PIT tagged fish were detected by the array during periods of deeper water.

Despite the fact that it generally did not perform as well as other antennas (lower current), the *in situ* detection probability of tagged fish on Antenna 2 was high across a wide range of water depths and remained above 70 % at depths between 0.8 and 1.0 m. Thus, the *in situ* detection probability of tagged mummichogs is mostly consistent with predictions from drone tag data and we infer that mummichogs mostly pass near the vertical parts of the antenna (horizontal location = 0 m) when water depths were less than 0.8 m. Given that water depths were greater than 0.8 m ~26 % of the time over the vertical array period, our antenna configuration did not capture all mummichog movements. This finding is likely the reason for the reduced number of emigrations (occurred during deeper water periods) relative to immigrations. The detection efficiency of the middle antenna in the vertical array (0.933) is comparable to the Hering et al. (2010) study (mean = 0.92) and greater than the Adams et al. (2006) study (0.67); Hering et al. (2010) measured proportional detection of one antenna based on the number of tagged fish detected by both antennas in their array, while Adams et al. (2006) measured the proportion of tagged fish detected that were moved with a net past a single antenna.

Increased detections of FDX PIT tags occur when more of an antenna is out of salt water. For waters of similar salinities, our recommendation for vertical antennas of similar construction and placement (with the long axis of the antenna horizontal) is to work in waters less than ~0.6 m deep if near 100 % detection is required. Even with missed detections, the frequency of resightings is much higher with this gear than with traditional approaches, resulting in robust estimates of CJS model parameters. Not being able to assign a fate to every marked fish (survived, died, or emigrated) does have ramifications for some analytical approaches where all marked animals have to be accounted for, such as survival analyses (Pollock et al. 1990, Williams et al. 2002).

There are several ways to potentially increase *in situ* detection probability to develop increasingly more accurate estimates of movement patterns and demographic parameters of saltwater fishes such as mummichogs. Hering et al. (2010) maintained high detection efficiency of PIT tagged juvenile salmon in relatively deep salt water by having weir material and the long axis of a vertical antenna running vertically (i.e. more of the antenna is in the air across all water depths compared to when the long axis is horizontal). We chose not to use this deployment because we were concerned that it would alter the behavior of mummichogs (and other salt marsh organisms) given the narrow restriction of the Hering et al. (2010) antenna configuration compared to our vertical antenna configuration. Where permitted and feasible based on shoreline stability and impacts to the marsh, orienting antennas with the long axes vertical may help to maximize the perimeter of an antenna that remains exposed to air when used in salt water and help maintain electrical current above a threshold where detections fail, over a wide range of depths. Given imperfect *in situ* detection probability by a single antenna, redundancy in the number of antennas comprising a detection array is one method for increasing the probability of detecting a valid move of a PIT tagged fish. A valid move in our study required detection by at least 2 antennas in appropriate order (i.e. for up- or downstream movement) within a 10 min period. For example, the predicted detection probability of the drone by a single antenna at a depth of 0.6 m, tag height of 0 m, and horizontal location other than 0 m, would be 0.77. This scenario would yield a combined probability of detecting a valid move of 0.59 with a 2-antenna array but 0.86 with a 3-antenna array.

Mummichogs appear to maximize periods over which the vegetated marsh surface can be accessed following low tide (Teo & Able 2003b, Bretsch & Allen 2006) by entering the study creek shortly after it has started flooding. They use the direction of tidal flow to likely reduce energetic expenditures by generally moving in the direction of the tidal current (Sweeney et al. 1998). Our data confirm these observations for mummichogs. Mummichogs ingressed above the array when the water was relatively shallow; this movement occurred during the very late stages of ebb or early flood tides. Previous research (Gibson 1988, Kneib & Wagner 1994) has suggested that the risk of stranding on ebb tide may cause salt marsh fish to egress at depths greater than those upon ingress. Our results confirm this, as mummichogs emigrated from Porters Creek as early as the beginning of ebb tide. The timing of tidal movement likely maximizes growth of the mummichogs, because it maximizes the time that they can feed on the marsh surface (Kneib 1993, Haas et al. 2009). Butner & Brattstrom (1960) observed that mummichogs collected during flood tides in tidal creeks had empty guts while those collected during ebb tides had full guts, suggesting that fish were feeding on the marsh surface.

FDX PIT tags (12.5 mm sizes) have proven effective at studying movements and demographics of small saltwater fishes (Hering et al. 2010, present study) and future comparisons with recently available 12 mm HDX PIT tags are warranted. Further refinements to the construction of PIT tags and custom detection equipment are likely to increase the use of this technique in marine and estuarine habitats. In future studies we plan to estimate survival across multiple systems to gain a better understanding of habitat-specific productivity of mummichogs.

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Appendix 1. Chronology of events related to PIT tagging and detected mummichogs with 2 custom-made autonomous detection arrays near the mouth of Porters Creek, North Carolina, USA between 8 November 2010 and 4 October 2011

Event date(s)	Event(s)	Sampling occasion(s)
8–24 Nov 2010	Tagging (8 Nov 2010) and data collection with 3 vertical antennas	1–17
25–29 Nov 2010	Multiplexer malfunction (no data)	
30 Nov 2010–3 Mar 2011	Data collection	18–111
4 Mar–13 Apr 2011	Antenna maintenance (no data)	
14 Apr–10 May 2011	Commencement of data collection with single horizontal antenna	112–138
11 May 2011	Power failure (no data)	
12 May 2011	Data collection	139
13–16 May 2011	Antenna maintenance (no data)	
17 May–5 Jun 2011	Data collection	140–159
6–23 Jun 2011	Detections not date-stamped	
24 Jun 2011	Download data (Occasion 160 = 6–24 Jun)	160
25–27 Jun 2011	Detections not date-stamped	
28 Jun 2011	Download data (Occasion 161 = 25–28 Jun)	161
29 Jun–1 Jul 2011	Detections not date-stamped	
2 Jul 2011	Download data (Occasion 162 = 29 Jun–2 Jul)	162
3–13 Jul 2011	Detections not date-stamped	
14 Jul 2011	Download data (Occasion 163 = 3–14 Jul)	163
15–20 Jul 2011	Detections not date-stamped	
21 Jul 2011	Download data (Occasion 164 = 15–21 Jul)	164
22–31 Jul 2011	Detections not date-stamped	
1 Aug 2011	Download data (Occasion 165 = 22 Jul–1 Aug)	165
2–7 Aug 2011	Detections not date-stamped	
8 Aug 2011	Download data (Occasion 166 = 2–8 Aug)	166
9–14 Aug 2011	Detections not date-stamped	
15 Aug 2011	Download data (Occasion 167 = 9–15 Aug)	167
16–19 Aug 2011	Detections not date-stamped	
20 Aug 2011	Download data (Occasion 168 = 16–20 Aug)	168
21–31 Aug 2011	Detections not date-stamped	
1 Sep 2011	Download data (Occasion 169 = 21 Aug 21–1 Sep)	169
2–21 Sep 2011	Data collection	170–189
22 Sep 2011	Power failure (no data)	
23 Sep–4 Oct 2011	Data collection through last detection (4 Oct 2011)	190–201

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