

**A Bayesian multistate approach to evaluate movements of an invasive freshwater
estuarine-opportunist**

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Key Words: Blue Catfish, Tidal River, Salinity, Invasive Species, Acoustic Telemetry,
Colonization, Dispersal, Partial Migration

Abstract

Coastal rivers and estuaries provide habitat and migratory corridors for freshwater estuarine-opportunists. We evaluated movement patterns of 61 blue catfish *Ictalurus furcatus* in the tidal York and Rappahannock rivers in Virginia, USA with acoustic telemetry from July 2015 to June 2016. To evaluate river-specific movements, we utilized a multistate Cormack-Jolly-Seber (CJS) model within a Bayesian framework to estimate probabilities of detection and transition (movement) among established salinity zones (i.e., tidal-fresh [0-0.5 ‰], oligohaline [>0.5-5 ‰], mesohaline [>5-18 ‰]). We considered flow as an environmental covariate. Despite high site fidelity in tidal-fresh zones, some individuals displayed movements into oligohaline and mesohaline habitats indicative of partial migration. Once downstream movement occurred, the probability of staying in the new salinity zone was higher than the probability of movements to other salinity zones. In the Rappahannock River only, movement upstream from mesohaline habitats was associated with below average flow. As flow increased, the probability of remaining in oligohaline and mesohaline zones increased. Our study shows blue catfish can move into downstream areas of tidal rivers with elevated salinities and that increased freshwater flow may allow them to remain in these habitats for extended durations.

Introduction

Movement polymorphism (e.g., resident and migratory contingents; partial migrants) within animal populations is common in nature. An individual's propensity to migrate can be influenced by resource competition and predation risk, and thus density-dependent factors can contribute to movement choice (Chapman et al. 2012b). However, the ability to move is also strongly influenced by physicochemical habitat features along migration routes (Chapman et al. 2012a). In estuaries, freshwater fish species with elevated salinity tolerance may use estuaries as permanent habitat or as temporary migratory corridors during periods of tolerable salinity conditions (Bringolf et al. 2005; Brown et al. 2007; Schofield and Nico 2009; Gutierre et al. 2014).

A strong salinity gradient exists in the Chesapeake Bay, USA varying from fresh (0‰) to euhaline (>30‰; Chesapeake Bay Program 2004). Salinity is determined by precipitation patterns, and distance relative to oceans, which affects fish assemblages, marsh vegetation, and other aquatic fauna (Latham et al. 1994; Wagner and Austin 1999; Martino and Able 2003; Bilkovic et al. 2012). Blue catfish *Ictalurus furcatus*, a nonnative species to Atlantic slope drainages, has shown high phenotypic plasticity in growth and reproduction (Nepal et al. 2020; Hilling et al. 2020), and high movement capabilities (Tuckey et al. 2017), which has led to high abundance (Bunch et al. 2018; Fabrizio et al. 2018) and an expansive colonization pattern across freshwater to mesohaline habitats (Nepal and Fabrizio 2019).

As a freshwater estuarine-opportunist (Potter et al. 2015), blue catfish have a propensity to occupy what are thought to be sub-optimal habitats in mesohaline estuarine reaches. This may be due to density-dependent growth in upstream areas coupled with

abundant high-quality prey resources in downstream areas (Arim et al. 2006; Schloesser et al. 2011; Bachelor et al. 2012) that may partially offset physiological costs imposed by these low-salinity habitats (sensu Glover et al. 2012). Blue catfish occupying estuarine habitats is of particular concern to fisheries managers as predation could negatively impact economically important estuarine species, such as blue crab *Callinectes sapidus*, and allow for population expansion into new locations (Chesapeake Bay Program 2020). In lower tidal river estuaries in elevated salinity conditions, blue crab predation occurs, especially in late summer and fall (Schmitt et al. 2019b).

Although movement studies within the species' native range and invaded lentic and lotic systems have been conducted (Garrett and Rabeni 2011; Tripp et al. 2011; Gerber et al. 2019), with exception of Tuckey et al. (2017), there are no other published studies on blue catfish movement in coastal systems. Furthermore, the effects of flow on blue catfish movement in tidal rivers have not been investigated. River flows can greatly affect spatiotemporal patterns of salinity in coastal systems. Blue catfish which have elevated salinity tolerance compared to most freshwater fish species (Nepal and Fabrizio 2019), may be able to move downstream as freshwater flows increase. Thus, we hypothesized that high flow conditions will increase downstream blue catfish movement, and they will adjust positioning based on salinity conditions. Our primary objectives were to: 1) evaluate blue catfish broad-scale movement patterns in two tidal rivers in Chesapeake Bay among established salinity zones (i.e., tidal-fresh, oligohaline, and mesohaline), and 2) evaluate how flow influenced these movements.

Materials and methods

Study Area

This study focused on two coastal plain tidal river systems in Eastern Virginia, USA, the Rappahannock and York rivers (Figure 1). The Rappahannock River becomes tidally influenced below the fall line and flows as a free-flowing coastal river within our study area. The York River is formed by the confluence of the Pamunkey and Mattaponi rivers, which drain portions of the Virginia Piedmont region (Figure 1). Tidal influence for the Pamunkey and Mattaponi rivers include areas well above the confluence with the York River. The two rivers are vastly different in size and characteristics (Table 1) and experience changes in habitats with downstream distance as they change from relatively narrow meandering channels to indiscernible channels with broad open flats as they approach Chesapeake Bay. These rivers support large populations of blue catfish, which were stocked in the Rappahannock River in 1974, and later in Pamunkey and Mattaponi in 1985 (Schloesser et al. 2011). Population estimates from summer 2015 mark-recapture studies on the Pamunkey was 565 fish per ha; while Rappahannock estimates were nearly double at 1127 fish per ha (Y. Jiao, Virginia Tech).

Standard salinity zone segments have been developed by managers within the Chesapeake Bay (Chesapeake Bay Program 2004). The Chesapeake Bay Program Analytical Segmentation Scheme (CBPASS) uses the Venice system for classifying salinity zones based on historical salinity patterns: tidal-fresh (0-0.5 ‰), oligohaline (>0.5-5 ‰), mesohaline (>5-18 ‰), and polyhaline (18-30 ‰; Chesapeake Bay Program 2004). These established salinity zones were used within our model structure for each river and applied to georeferenced data described below (Figure 1).

Tagging

In mid-July 2015, low-pulse boat electrofishing (15 pps) was used to collect and anesthetize 60 blue catfish for acoustic tagging. Thirty blue catfish were tagged in each river across a broad representation of sizes above 35 cm total length (TL) to mimic river-specific length-frequency patterns. All fish were collected and released in tidal-fresh reaches in both rivers (Figure 1). We used 69 kHz acoustic tags (VEMCO®, V9 or V13) set at 90-180 second intervals with battery life expected to be 347 days (V9) and 657 days (V13). V9 tags were generally placed in smaller individuals. Tags were evenly distributed between rivers (V9, n=15; V13, n=15). Gerber et al. (2019) showed that with proper care and handling, ictalurids can be successfully tagged with very high natural survival. We employed steps similar to those outlined in Gerber et al. (2019). Surgery occurred while fish were under electrosedation (Kim et al. 2017). To reduce the chance of infection, tags and surgical instruments were placed in 100% alcohol solution prior to surgery, and the surgery area was flushed with water between surgeries. Tags were surgically implanted in the abdominal cavity through a small incision ventral to the lateral line and posterior to the pectoral spine with a two-person team. We used dissolvable sutures to close the incision and covered it with a topical antibiotic gel. We placed no more than three freshly tagged fish in a large oxygenated holding tank (approximately 1,000 L) until they displayed normal equilibrium, fin movements, and no ill effects from the surgical procedure. Additionally, we placed an omnidirectional hydrophone from a VR100 manual tracking unit in the holding tank to verify tag functionality prior to release. Each fish received two secondary marks including an anchored T-bar tag with a printed identification number and phone number, and an adipose fin clip. During a tag retention study on blue catfish, Bodine and Fleming (2014) indicated that T-bar tags did not substantially affect survival. If any

functioning acoustic tags were retrieved from known mortalities, they were sanitized and surgically implanted into a new fish. Post-release tracking occurred using a combination of active and passive telemetry techniques.

Telemetry

Passive tracking.—During our study, an extensive network of stationary VR2W acoustic receivers existed within Virginia's tidal rivers and lower Chesapeake Bay. Receiver arrays developed and maintained by the U.S. Navy, Virginia Institute of Marine Science, and Chesapeake Scientific were supplemented to enhance coverage within each river (Figure 1). Some receivers in the upper Pamunkey River were only used seasonally, but high coverage in those areas remained year-round. Receivers were attached to docks, stable fallen trees, or navigation buoys with stainless steel cable adequate to allow the receiver to stay submerged in the center of the water column without contacting the river bottom or risk of air exposure during low tide. Receivers were maintained, and data retrieved on monthly intervals, while cooperators supplied detection data periodically throughout the study. To predict the density of receivers needed to achieve high detection probability p , we employed a non-linear exponential rise-to-maximum model (simple exponent, 2-parameter) based on p and receiver densities within each salinity zone.

Active tracking.—Active tracking occurred weekly during the first six weeks with the manual tracking unit, and monthly thereafter through the study's end (July 2015 through June 2016). A subset of receivers (those owned by Virginia Dept of Wildlife Resources and Virginia Institute of Marine Science) were downloaded and screened for recent detections. For time efficiency purposes, individuals that were not recorded by stationary receivers on the day of each tracking event were targeted during manual tracking. Each river required

two to three days for manual tracking. During monthly manual tracking events, tracking attention was placed in areas where stationary receivers were not located along the mainstem and within small side tributary creeks. Tracking occurred every 300-500 m while drifting with tidal flow for periods of no less than six minutes at each location to detect tags. However, due to small 6.1 m vessel size we were not consistently able to track in large open mesohaline reaches of each river (Figure 1). In cases where multiple tag detections occurred, a directional hydrophone was used to identify each unique individual. Upon detecting a fish, the VR100 logged GPS coordinates, tag number, coordinates, date, and time.

Geospatial data preparation

All detections from both active and passive tracking were georeferenced to GPS coordinates and compiled into a single database for processing. ArcGIS software was used to generate customized centered lines within all river polygon shapefiles. A unit of line segment length (km) was applied to each new line shapefile. Each unique detection was “snapped” to the line segment’s centerline and referenced to a specific km. Further analyses, including multistate encounter histories and distance measures described below, were estimated from the km associated with each unique detection.

Flow data

Flow (m^3/s) data was obtained from the U. S. Geological Survey stream gages on the Rappahannock River (01668000; 38°18'30" N, 77°31'46" W), and the Pamunkey River (01673000; 37°46'03" N, 77°19'57" W). Both gage locations were unaffected by tide schedules as they were upstream of the fall line with no tidal influence. For the model

below, we standardized flow by converting average weekly flow to a z-score ($z = (x - \mu) / \sigma$, where x is average weekly flow, μ is the grand mean, and σ is the standard deviation).

Quantifying individual movement variability

We screened fine-scale daily movement data for lack of movement which may be indicative of tag expulsion, which would affect parameter estimates (Gerber et al. 2017). We examined trends in raw movement data using several approaches. The minimum cumulative distance moved (km) for each individual was estimated as the summation of absolute values from daily movement distances. We categorized the average cumulative number of transitions across all individuals based on the lowest salinity zone each individual occupied. The same categorization strategy was applied to describe size-related movements based on total length (cm) at the time of tagging. We also summarized the number of unique individuals detected weekly by salinity zone and displayed this relative to flow z-scores.

Multistate model

Given the vast differences in river size and characteristics, and no movement between rivers, we modeled each river separately. We fit multistate Cormack-Jolly-Seber (CJS) models to weekly capture histories to estimate transition (movement) probability (ψ), detection probability (p), and apparent survival (ϕ) for tagged blue catfish among three model states that corresponded to established salinity zones. This approach quantifies the probability of movement across all tagged fish and detection probabilities. Apparent survival was modeled as the combined effects of mortality, emigration, or other processes that could cause tags to be lost from the study. As we were unable to separately estimate emigration (or other sources of tag loss) from actual mortality, we did not attempt

to draw biological insights from this survival parameter, which was needed to estimate transition and detection probabilities in our CJS model.

Since continuous salinity data was not available throughout the study areas, we used these established salinity zones to bound our model states. We used these standard salinity zones in a geographical approach similar to Kanno et al. (2020), but instead of defining lower, middle, and upper stream sections, we bounded model states geographically by tidal-fresh, oligohaline, and mesohaline zones which varied in length and size (Table 1; Figure 1). These zones are important for local and regional management of aquatic resources across the Chesapeake Bay region because “differences in water quality and biological communities among similar segments can be identified” (Chesapeake Bay Program 2004). The polyhaline zone was not considered in the model structure because no fish were detected in this zone. We used salinity designations with the understanding that spatiotemporal salinity changes would likely occur and thus we chose to incorporate a freshwater flow covariate into the model structure to determine if movement patterns changed in response to changes in flows (see full description below). In the York system, the Pamunkey and Mattaponi rivers comprised the tidal-fresh and oligohaline zones while the York River (formed at the confluence of the Pamunkey and Mattaponi Rivers) was classified as mesohaline-polyhaline. Model parameters for the tidal-fresh and oligohaline zones of the York system were estimated irrespective of movement into either river (Pamunkey or Mattaponi). For example, a fish moving downstream from the Pamunkey River oligohaline zone to the mesohaline York River could move upstream into the Mattaponi River oligohaline and tidal-fresh zones. This movement pattern was noted, but not modelled explicitly.

All available fish detection data from stationary receivers and manual tracking were condensed to a weekly, state-specific encounter history for each individual fish. Below is an example from fish #34174 from the Pamunkey River across the 51-week study period:

‘AA0AAAAAAAAAABCCCCCCCCBCCCCBBBBBBBBCCCCCCCCCBAAAA’

where “A” was tidal-fresh, “B” was oligohaline, “C” was mesohaline, and “0” represented a week that the fish was not detected. If a fish was detected in multiple states in a single week, the most upstream or downstream state was used in the dataset relative to the previous week’s location. For example, if a fish was detected in A during week t , then detected in both A and B in the following week ($t+1$), we would denote B as the state used in the encounter history for week $t+1$. We constrained transitions from tidal-fresh to mesohaline zones (i.e., ψ_{AC} and ψ_{CA} transitions).

The model used was an adaptation of the Bayesian state-space approach presented by Kéry and Schaub (2012) and was fit to our data using Markov chain Monte Carlo (MCMC) in program JAGS (Plummer 2017) called from Program R (R Core Team 2019) with the ‘jagsUI’ package (Keller 2019). Models were run on the Palmetto Cluster at Clemson University. The hierarchical CJS model was composed of a movement process and an observation process that linked the latent states to observations and accounted for imperfect transmitter detection by the hydrophones. The movement process described state transitions ($\Psi_{i,t}$) between states (i) from week-to-week beginning with the first week (t) in which an individual was captured and tagged. State-transition probabilities were defined by a categorical distribution that included all possible fates at week $t+1$, given their states at week t . The unobserved movement process was governed by a state transition matrix which was populated with conditional probabilities of survival and movement

between salinity zones (Table 2). Given survival, an individual could stay in its current salinity zone or move to another. Survival refers to apparent survival because emigration from the system is unaccounted for. Thus, mortality (due to either fishing or natural causes) and emigration were both included in our apparent survival estimates.

We used an indicator variable selection approach to estimate the importance (w) of a weekly flow (x_t) covariate (β) on ψ between states:

$\text{logit}(\psi_{i,t}) \sim \mu_i + w_i * \beta_i * x_t$ (Equation 1)

where μ_i is the intercept parameter, which is the log odds of staying in zone i under average

flow conditions. For states A and C where only two transitions (i.e., moving or staying) were possible, $\text{logit}(\psi)$ was estimated for the moving transition (e.g., ψ_{AB} for state A), and the staying transition was derived as the complement ($\psi_{AA} = 1 - \psi_{AB}$). For state B, where three transitions were possible (ψ_{BA} , ψ_{BB} , ψ_{BC}), $\psi_{i,t}$ was derived from three hyper-parameters which were constrained to sum to one. Each of the hyper-parameters was estimated with the linear model described above. In each state, β_i represents the difference in the log odds of a transition compared to a baseline transition. Four β parameters were estimated, one for each possible transition (ψ_{AB} , ψ_{BA} , ψ_{BC} , ψ_{CB}). Our indicator variable of importance (w) represents a toggling Bernoulli variable (0,1), whose probability density is equal to the proportion of posterior draws that include the covariate being included in the model. If the probability density of the w variable was greater than 0.5, it indicated that the toggled covariate improved model fit. The product of β_i and w_i gave the model averaged estimate of the covariate. Within the model, we derived the predicted transition probabilities for each state transition over the range of observed flows.

The observation process was represented by another categorical distribution which accounted for imperfect detection probability by the stationary hydrophones in the system. The model assumed no false positive detections, but the probability of false negatives (failure to detect a fish that was truly in a state) was denoted by $1-p$, the probability of detection (Table 3).

Detection probability and φ were estimated for each state on the probability scale with uniform priors (0,1). The slope and intercept parameters of the linear models determining ψ were estimated on the logit scale and given t-distribution priors (Dorazio et al. 2011). The variable importance factors (w), were given Bernoulli prior distributions with probability 0.5 (Table 4). Posterior distributions of model parameters were thinned by taking every 40th sample from 800000 iterations of three chains after a burn-in period of 400000 iterations. Convergence was checked by visually examining plots of the MCMC chains for proper mixing as well as ensuring that the \hat{R} statistic was less than 1.1 for all model parameters (Gelman and Hill 2007). Parameters were considered statistically significant if their 95% credible intervals (CrI) did not include zero. Encounter histories (S1), R code (S2) and covariate (S3) data are available as Supplementary material. A series of diagnostic plots were created to evaluate β_i and w_i using the ‘postpack’ package (Staton 2020).

Results

Detection overview and quantifying individual movement variability

Over the course of the study period, tagged fish generated over 780,228 detections (average per individual = 26,008) in the York River and 523,488 detections (average per

individual = 17,450) in the Rappahannock River. We had broad representation (35-155 cm TL) of blue catfish sizes tagged in each river (Figure 2A). In the Rappahannock, fish that transitioned downstream were generally smaller individuals, but this pattern was not evident in the York (Figure 2B). Individuals from both rivers that moved downstream from tidal-fresh areas showed a higher number of overall transitions among salinity zones (Figure 3B). On average, those that moved to oligohaline and mesohaline zones transitioned among zones more frequently (Figure 3B). Four individuals moved >1000 km with minimum cumulative distances up to 2425 km (Figure 3A). Median cumulative movement for the Pamunkey River was 185 km, and 105 km for the Rappahannock River. Results from the growth-to-maximum model used to predict VR2W receiver densities indicated that the ideal receiver density would be 0.1 - 0.2 receivers per km² area (Figure 4).

Tag loss and mortality

Two weeks following surgical implantation, four fish were collected in subsequent sampling, and although wound site and external marks were present, all fish exhibited absence of sutures and healed surgical wounds. Other than the examples described below, we assumed all tags detected throughout the study were not expelled and fish were alive at the time of detection. We found no evidence from screening individual daily movements to indicate that tag expulsion was pervasive in the dataset. However, we found that a single fish collected 5 weeks post-tagging on the Rappahannock River had not retained its acoustic tag. Additionally, two tagged fish were reported as harvested. A recreational fishing mortality in the York River was reported, and the tag returned. A commercial fishing mortality was also reported from the York River on week 5, but the tag was not

returned. For all three instances above, we only included detection data up until collection/harvest of each fish, and considered weekly detection of 0 for the remainder of the study (S1). The functioning tag from the recreational harvest was sanitized and placed into a new fish in week 8 into the same river which accounts for the overall sample size increase to 61 for the study.

Multistate model

Diagnostics did not detect substantial departures from convergence as all parameters met requirements ($\hat{R} < 1.1$). Visual assessment of MCMC chains indicated proper mixing. If flight response (i.e., tagging effect) from tagging occurred (Cooke et al. 2010), we would expect this to be represented by large ψ_{AB} estimates in the first two weeks, which was not seen (S4). Results revealed similar patterns of high site fidelity to the tidal-fresh zone (Table 5). Models also indicated clear transitions downstream by a small proportion of each tagged population. The overall probability of staying in the tidal-fresh zone (ψ_{AA}) was higher in the York (0.96 [95% CrI = 0.94 – 0.97]) compared to the Rappahannock (0.88 [95% CrI = 0.83 – 0.91]). Conversely, the probability of downstream movement ψ_{AB} was higher in the Rappahannock (0.13 [95% CrI = 0.09 – 0.17]) compared to the York (0.04 [95% CrI = 0.03 – 0.06]). Probabilities of staying in and moving from oligohaline and mesohaline zones were similar in both the York and Rappahannock (Table 5). In both rivers, once downstream movement occurred, the probability of staying in the new salinity zone was higher than movements to upstream or downstream salinity zones (Table 5). For example, the probability of staying in the oligohaline zone in the York was 0.85 (95% CrI = 0.80 – 0.89), with remaining fish either returning upstream to tidal-fresh (0.08 [95% CrI = 0.05 – 0.11]) or making further movements downstream to mesohaline

habitat (0.08 [95% CrI = 0.05 – 0.11]; Table 5). Similar trends were seen in the oligohaline zone of the Rappahannock and the mesohaline zones in both the York and Rappahannock (Table 5). There did not appear to be strong seasonal effects on movement based on an examination of week-to-week movement transitions (S4).

Lower flow conditions occurred in the first half of the time-series (July-December) with higher flows becoming more prevalent during the second half (January-June; Figure 5). According to the variable importance analysis, flow was only a significant predictor for two of the β in the Rappahannock model (ψ_{BB} , ψ_{CB}) and none in the York model. Increased flows corresponded with increased likelihood of staying in the oligohaline zone (ψ_{BB}) compared to moving out of that zone. Increased flows also made it less likely that blue catfish in the mesohaline zone would move back upstream to the oligohaline zone (ψ_{CB}) and resulted in increased probabilities that individuals in the mesohaline zone would remain in the mesohaline zone (ψ_{CC}) for the Rappahannock River (Figure 6). At very low flows in the mesohaline zone, blue catfish in the mesohaline zone were most likely to move upstream to the oligohaline zone rather than remain in the mesohaline zone (Figure 6). This was the only movement transition that was predicted to be more likely than staying in a given zone at any flow level. Our variable importance analysis suggested that transition probabilities from tidal fresh to oligohaline (ψ_{AB}), oligohaline to tidal fresh (ψ_{BA}), and oligohaline to mesohaline (ψ_{BC}) were not strongly influenced by flow (Figure 6).

Temporal patterns of detected individuals showed downstream dispersal across salinity zones, and a higher overall number of detections in the York (Figure 5). Detection probabilities were generally higher in the York (average $p=0.92$) compared to the Rappahannock (average $p=0.60$; Table 5). The oligohaline zone on the Rappahannock had

the lowest detection probability across models and states at $p_B=0.17$. For the York model, the tidal-fresh zone had the lowest detection probability ($p_A=0.83$).

Discussion

Here, a nonnative freshwater estuarine-opportunist exhibited partial migration into heightened salinity conditions. The majority of the tagged population in both York and Rappahannock rivers exhibited high site fidelity in tidal-fresh waters, while a small migratory contingent displayed downstream movement into oligohaline and mesohaline habitats. However, we found no movements into polyhaline zones. Partial migration has been documented in numerous fishes including Arctic charr *Salvelinus alpinus* (Dodson et al. 2013), Atlantic salmon *Salmo salar* (Dodson et al. 2013), threespine stickleback *Gasterosteus aculeatus* (Chapman et al. (2012b), European eel *Anguilla anguilla* (Tsukamoto 1998), and white perch *Morone americana* (Kerr et al. 2009). This phenomenon is common in fishes with an extensive list of partial migrators grouped by family in Chapman et al. (2012b). Partial migration is likely a common response to variable environmental conditions in marine or estuarine systems that allow fishes to take advantage of enhanced environmental conditions for foraging, growth, or reproduction and is likely maintained by genetic inheritance of thresholds (e.g., in growth or condition) that dictate the adoption of one behavior or another based on underlying environmental conditions (Secor 2015).

Chapman et al. (2012b) found that smaller three-spined stickleback *Gasterosteus aculeatus* likely migrate to take advantage of highly productive marine resources which improves growth, and the risk of migrating was offset by future improved fitness. Similarly, Kraus and Secor (2004) showed that slower growing white perch juveniles in

freshwater regions of the Patuxent River estuary (Maryland, USA) became migrants to downstream brackish habitats. Sampling of white perch adults in the same system found that individuals from brackish habitats dominated the adult population and had faster growth than freshwater individuals, suggesting downstream, brackish habitats were more conducive for survival and growth compared to freshwater habitats (Kraus and Secore 2004). Given that smaller blue catfish migrated downstream to oligohaline and mesohaline zones in the Rappahannock, this may suggest similar mechanisms underlie downstream movement for blue catfish. Follow-up studies linking blue catfish growth rates with previous habitat use would be required to test this hypothesis.

Once tagged blue catfish moved downstream, most exhibited high fidelity in downstream oligohaline and mesohaline zones. Gillanders et al. (2015) indicated that migratory contingents typically have advantages of higher growth and fitness due to increased food availability, while they also possess the ability to move from inhospitable conditions. Blue catfish residing in mesohaline habitats are living on the edge of salinity tolerance where trade-offs between higher diet item richness/food availability from marine-derived sources and optimizing bioenergetic processes that influence growth and survival (e.g., osmoregulation) may occur. Bœuf and Payan (2001) indicated that fish growth may improve in intermediate salinities as a result of lowered metabolic rates and increased food intake. However, osmoregulation is also an important physiological cost to consider when attempting to predict species invasions (Behrens et al. 2017).

McCabe (2019) described salinity as the primary abiotic factor influencing blue catfish movements. Nepal and Fabrizio (2019) found high salinity tolerance of blue catfish ($LC_{50}=15.7‰$) relative to most freshwater species and showed that large proportions of

downstream habitats in Chesapeake Bay were likely to become suitable to blue catfish during wet years with above average freshwater flow. Our findings build on this previous work and suggest that blue catfish in the Rappahannock were more likely to remain in the mesohaline zone when flows were elevated and more likely to move back upstream to the oligohaline zone when flows were lower. These movement patterns offer evidence to support the hypothesis that elevated flows can allow blue catfish to reside in downstream mesohaline habitats. In dry years with less freshwater input, increased costs of osmoregulation in the mesohaline zone in the Rappahannock River may outweigh the benefits of marine derived nutrients for blue catfish. This trade-off has been well-documented in largemouth bass *Micropterus salmoides* populations inhabiting freshwater and low-salinity habitats in coastal rivers along the northern Gulf of Mexico (Norris et al. 2010; Glover et al. 2012).

During our study, mean daily flow in the Rappahannock River ($58 \text{ m}^3/\text{s}$) was similar to the long-term mean annual flow ($51 \text{ m}^3/\text{s}$; 1990–2020) and mean daily flow in the Pamunkey River ($19.5 \text{ m}^3/\text{s}$) was slightly below its long-term mean ($24.3 \text{ m}^3/\text{s}$; 2003–2020). As our study was conducted during average to below average years of river discharge and both the Rappahannock (range: 16.6 – $116.1 \text{ m}^3/\text{s}$) and Pamunkey Rivers (range: 4.8 – $47.8 \text{ m}^3/\text{s}$) can experience much wetter years with higher flows, downstream movement may be much greater following periods with elevated flow. Similar flow-related movement patterns have been observed with another freshwater invasive species, the Northern snakehead *Channa argus*, which utilized seasonal high flows to colonize Chesapeake Bay tributaries from their original point of origin in the Potomac River (Love and Newhard 2018; Bunch et al. 2019).

Partial migrants from upper tidal-fresh zones may also interact with sub-populations of blue catfish that occupy lower oligohaline-mesohaline reaches. These sub-populations may exhibit movement characteristics different from those collected in the upstream tidal-fresh reaches (Kwak et al. 2011). Fish collected and tagged in lower river reaches may show differing movement patterns than those tagged in the upper reaches (the tagging location for this study); therefore, further study on blue catfish movement dynamics in mesohaline zones is warranted. For example, blue catfish utilizing mesohaline habitats may occupy side tributaries more frequently to find ample freshwater refugia from salinity; this is known to occur with northern snakehead (Bunch et al. 2019). High densities of blue catfish have been observed in connected freshwater impoundments during periods of low precipitation and increased salinity near tidal river mouths (A. Bunch, personal observation). Given the higher occurrence of tidal-fresh habitats and generally lower salinity in middle to upper reaches of the Chesapeake Bay, our findings support the premise that blue catfish pose risk of inhabiting northerly connected systems in Chesapeake Bay that have not yet been invaded (Tuckey et al. 2017; Nepal et al. 2019).

In flowing habitats in large midwestern US rivers (e.g., Mississippi and Missouri rivers) where blue catfish are native, and in lakes where the species has been introduced, studies have found that some individuals are generally sedentary staying within a close home range near tagging locations, while others dispersed widely (Hunter et al. 2009, Garrett and Rabeni 2011). Similar patterns have been documented for other ictalurid species including flathead catfish *Pylodictis olivaris* and channel catfish *Ictalurus punctatus*. Although, we did not find broad-scale seasonal movements indicated by a lack of clear seasonal patterns in week-to-week transition probabilities, other studies in freshwater

systems have shown that seasonal movements can be triggered by spawning activity, lunar phase, temperature, and increased flows (Wendel et al. 1999, Travnichek 2004, Garrett and Rabeni 2011, Tripp et al. 2011).

This study is the first published acoustic telemetry study on blue catfish in the Chesapeake Bay region. Tuckey et al. (2017) found large and variable movements of blue catfish in the tidal Potomac River (i.e., the next watershed north of the Rappahannock) spanning as much as 113 km into mesohaline waters; however, cumulative distance could not be estimated due to tag type limitations as this study used external T-bar tags. Median cumulative movements were relatively low in the Rappahannock and York, but there were also a few individuals that moved large distances. One individual moved as much as 2425 km in approximately one year, which is, to our knowledge, the highest annual cumulative movement recorded for the species. Other studies for blue catfish have reported annual rates of movements over 640 km (Garrett and Rabeni 2011, Tripp et al. 2011). This is an impressive amount of movement further exemplifying the high mobility documented in this species, as blue catfish are believed to be the most mobile of the ictalurids (Graham 1999). In comparison to a species in the same order (siluriformes), the gilded catfish *Brachyplatystoma rousseauxii* are extreme movers with a maximum known life history migratory cycle of greater than 11000 km in the Amazon River (Barthem et al. 2017). Our study also documented movements among interconnected rivers within the York system with tagged fish from the Pamunkey moving substantially upstream into the Mattaponi River (2 out of 30 transmitted fish).

We focused primarily on broad-scale patterns in blue catfish movement as our objectives were to assess large movement patterns across three large salinity zones with

data condensed to weekly time-steps. With this level of resolution, finer-scale movements within salinity zones were less emphasized. However, studies using passive acoustic receiver arrays in combination with positioning algorithms (such as Vemco Positioning System [VPS; Espinoza et al. 2011] or Yet Another Positioning System [YAPS; Baktoft et al. 2017]) that can track fine-scale movement may be able to provide insight into how daily and hourly movement patterns respond to tidal influences and rapid shifts in salinity.

While we were able to document flow-mediated movements in the Rappahannock River, our detection probabilities were less precise in the Rappahannock compared to the York. These differences in detection probabilities between rivers can likely be attributed to differing hydrophone densities between rivers and river size. Despite our manual tracking efforts aimed at improving overall detection, lower density of receivers in the oligohaline and mesohaline zones of the Rappahannock likely led to lower detection probabilities in these zones. Lower detection probability within the oligohaline and mesohaline zones in the Rappahannock may have contributed to higher variability in transition probability estimates compared to the same zones in the York. Lower detection probabilities in the Rappahannock compared to the York, combined with overall small sample sizes of blue catfish that migrated downstream may have limited our ability to detect river-specific differences in movement between oligohaline and mesohaline zones. Given our findings, future studies in these systems could consider placing 0.1 - 0.2 receivers per km² to maximize efficiency and maintain high detection probabilities.

The use of multistate models for inferring fish movements is becoming more prevalent in fisheries studies (Holbrook et al. 2014; Melnychuk et al. 2017; Dyer and Brewer 2020; Kanno et al. 2020). Our study builds on these approaches by using

established criteria to spatially reference zones of an environmental variable to bound model states. With the flexible modelling structure that the Bayesian CJS approach provides, future research could aim to create model states based on other important environmental conditions.

Understanding blue catfish movement patterns has important implications for fisheries management in the Chesapeake Bay region. The potential for large scale movements of blue catfish creates management challenges as blue catfish may prey on commercially and recreationally important species in downstream habitats. Schmitt et al. (2019a) defined blue catfish in tidal waters as opportunistic generalists that focus consumption on locally abundant food items, particularly aquatic vegetation (e.g., hydrilla *Hydrilla verticillata*), gizzard shad *Dorosoma cepedianum*, and Asiatic clam *Corbicula fluminea*), but still preyed on marine species when encountered (e.g., blue crab). Schmitt et al. (2019b) used a generalized additive model approach to predict the probability of occurrence of blue crab in the diet of blue catfish based on salinity, predator size, and month. They found the highest probabilities of blue crab predation in York tributaries and Rappahannock in mesohaline habitats (6-11‰) in October by 70-80 cm TL blue catfish and suggested some individuals may specialize on blue crabs.

Downstream movement may also complicate other proposed management actions for this invasive species, such as density reductions (Tuckey et al. 2017). Given high densities, long-distance movement capabilities, high phenotypic plasticity, and ability to survive at elevated salinities, managers may need to investigate movement patterns with respect to density to understand if reductions in density are offset by increased movement to areas with lower densities. Previous mark-recapture studies found that blue catfish

densities in the Rappahannock were approximately double those in the York (Y. Jiao, Virginia Tech), suggesting that higher rates of movement out of the tidal-freshwater zone of the Rappahannock could be related to higher densities in this system. We suggest future studies further investigate the potential for density-dependent movement in estuarine blue catfish populations. Given that blue catfish are well-established in the Chesapeake Bay region and provide recreational and commercial fishing opportunities, managers will likely be pressed to maintain blue catfish at levels that minimize ecosystem impacts while maintaining fishery benefits (Chesapeake Bay Program 2020). Our study enhances understanding of blue catfish movement patterns in coastal estuaries and should assist managers in understanding and predicting blue catfish movements in response to changing environmental conditions.

Acknowledgements

The Virginia Department of Wildlife Resources (VDWF) supported this research through U.S. Fish and Wildlife Service Sport Fish Restoration Funds (F-111-R). We sincerely appreciate the efforts of C. Watterson (U.S. Navy), E. Hilton and M. Fisher (Virginia Institute of Marine Science), and C. Hager (Chesapeake Scientific) for collecting, compiling, and dispersing acoustic telemetry data. The project scope and detection capabilities would not have been as extensive without their valuable contributions. J. Kapalczynski provided substantial GIS analysis support. B. Greenlee and M. Bednarski provided valuable feedback and advice throughout the study. We thank all other VDWF staff and volunteers who assisted with field work. B. Staton assisted with Bayesian model development and analysis. Clemson University is acknowledged for the generous allotment

of computer time on the Palmetto cluster. The time and energy of editors and reviewers is highly valued, and much appreciated.

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Table 1. Length and area of salinity zone designations from the Chesapeake Bay Program Analytical Segmentation Scheme (Chesapeake Bay Program 2004).

| River | Zone | Length (km) | Area (km2) |
|------------------|-------------|-------------|------------|
| Rappahannock | Tidal-fresh | 87.1 | 36.5 |
| Rappahannock | Oligohaline | 15.6 | 19.5 |
| Rappahannock | Mesohaline | 78 | 323.8 |
| York (Mattaponi) | Tidal-fresh | 138.3 | 9.3 |
| York (Mattaponi) | Oligohaline | 26.6 | 8 |
| York (Pamunkey) | Tidal-fresh | 110 | 16.2 |
| York (Pamunkey) | Oligohaline | 37.9 | 14.1 |
| York (Mainstem) | Mesohaline | 30.6 | 94.6 |

Table 2. Latent state transition matrix applied to the multistate Cormack-Jolly-Seber (CJS) model.

| True state at week t | True state at week t+1 | | | |
|----------------------|---------------------------|--------------------------------|---------------------------|-----------------|
| | Tidal-fresh | Oligohaline | Mesohaline | Dead |
| Tidal-fresh | $\varphi_A^* \psi_{A,t}$ | $\varphi_A^* (1 - \psi_{A,t})$ | 0 | $1 - \varphi_A$ |
| Oligohaline | $\varphi_B^* \psi_{BA,t}$ | $\varphi_B^* \psi_{BB,t}$ | $\varphi_B^* \psi_{BC,t}$ | $1 - \varphi_B$ |
| Mesohaline | 0 | $\varphi_A^* (1 - \psi_{C,t})$ | $\varphi_A^* \psi_{C,t}$ | $1 - \varphi_C$ |
| Dead | 0 | 0 | 0 | 1 |

Table 3. Observation matrix linking the latent state to the data in the multistate Cormack-Jolly-Seber (CJS) model.

| True state at week t | Observed state at week t | | | |
|------------------------|----------------------------|-------------|------------|---------|
| | Tidal-fresh | Oligohaline | Mesohaline | Dead |
| Tidal-fresh | P_A | 0 | 0 | $1-P_A$ |
| Oligohaline | 0 | P_B | 0 | $1-P_B$ |
| Mesohaline | 0 | 0 | P_C | $1-P_C$ |
| Dead | 0 | 0 | 0 | 1 |

Table 4. Priors used for parameter estimation. η = scale, ν = degrees of freedom

| Parameter | Priors |
|-----------|--|
| w | Bernoulli, $p=0.5$ |
| β | t-distribution, $\eta = 1.566$, $\nu = 7.763$ |
| μ | t-distribution, $\eta = 1.566$, $\nu = 7.763$ |
| p | Uniform 0,1 |
| φ | Uniform 0,1 |

Table 5. Mean parameter estimates and associated 95% credible interval (in parentheses) for probabilities (prob) of detection (p), transition (ψ), and apparent survival (φ) for tagged Blue Catfish among model states. Transition probability estimates were averaged across all weeks for each river.

| Parameters and description | | York | Rappahannock |
|----------------------------|--|---------------------|---------------------|
| p_A | Detection prob in tidal-fresh | 0.827 (0.797-0.854) | 0.953 (0.922-0.978) |
| p_B | Detection prob in oligohaline | 0.969 (0.944-0.991) | 0.168 (0.136-0.204) |
| p_C | Detection prob in mesohaline | 0.976 (0.915-0.999) | 0.656 (0.354-0.884) |
| ψ_{AA} | Prob of staying in tidal-fresh | 0.958 (0.942-0.972) | 0.875 (0.835-0.908) |
| ψ_{AB} | Movement prob from tidal-fresh downstream to oligohaline | 0.042 (0.028-0.058) | 0.125 (0.092-0.165) |
| ψ_{BA} | Movement prob from oligohaline upstream to tidal-fresh | 0.078 (0.049-0.113) | 0.077 (0.048-0.114) |
| ψ_{BB} | Prob of staying in oligohaline | 0.846 (0.799-0.886) | 0.896 (0.846-0.934) |
| ψ_{BC} | Movement prob from oligohaline to mesohaline | 0.076 (0.049-0.108) | 0.027 (0.011-0.055) |
| ψ_{CC} | Prob of staying in mesohaline | 0.703 (0.595-0.802) | 0.596 (0.304-0.858) |
| ψ_{CB} | Movement prob from mesohaline upstream to oligohaline | 0.297 (0.198-0.405) | 0.404 (0.142-0.696) |
| φ_A | Apparent survival prob in tidal-fresh | 0.974 (0.961-0.984) | 0.986 (0.969-0.998) |
| φ_B | Apparent survival prob in oligohaline | 0.992 (0.979-0.999) | 0.980 (0.965-0.991) |
| φ_C | Apparent survival prob in mesohaline | 0.988 (0.956-1.000) | 0.955 (0.848-0.999) |

Figure Captions

Figure 1. A map showing the Eastern coast of Virginia, USA and the lower portion of Chesapeake Bay, with shaded polygons indicative of different salinity zones which were determined by Chesapeake Bay Program (Chesapeake Bay Program 2004), and larger circles with white borders representing the locations of VR2W (VEMCO, Canada) hydrophones. The magnified river sections of the left indicate the regions where tagged fish were released (stars), and show some of the manual tracking locations (small black circles).

Figure 2. A length-frequency plot (A) of all tagged individuals and a dot and whisker plot (B) showing the mean and 95% confidence intervals of total length (cm) based on the lowest salinity zone that an individual occupied at any point during the study period. The Rappahannock River ("Rapp") is represented by pink and the York River ("York") is represented by aqua.

Figure 3. A histogram (A) of the cumulative minimum movement distances (km) of all tagged individuals and a dot and whisker plot (B) showing the mean and 95% confidence intervals of transitions between salinity zones among all individuals based on the lowest salinity zone that an individual occupied at any point during the study period. The Rappahannock River ("Rapp") is represented by pink and the York River ("York") is represented by aqua."

Figure 4. Predicted number of VR2W hydrophones necessary to achieve high detection probabilities which was based on data from both rivers and from all salinity zones.

Figure 5. The total number of unique individuals detected each week among tidal-fresh (TF), oligohaline (OH), and mesohaline (MH) salinity zones for the York (left panels) and Rappahannock (right panels) rivers. Week-1 was the second week of July 2015, while week-51 was in June 2016. The size of each circle is relative to the maximum number of unique individuals detected ($n=30$) within each river. The flow measurement shown is the z-score (i.e., the flow above and below average scaled to zero).

Figure 6. Rappahannock River transition probability predictions associated with standardized flow (z-score).

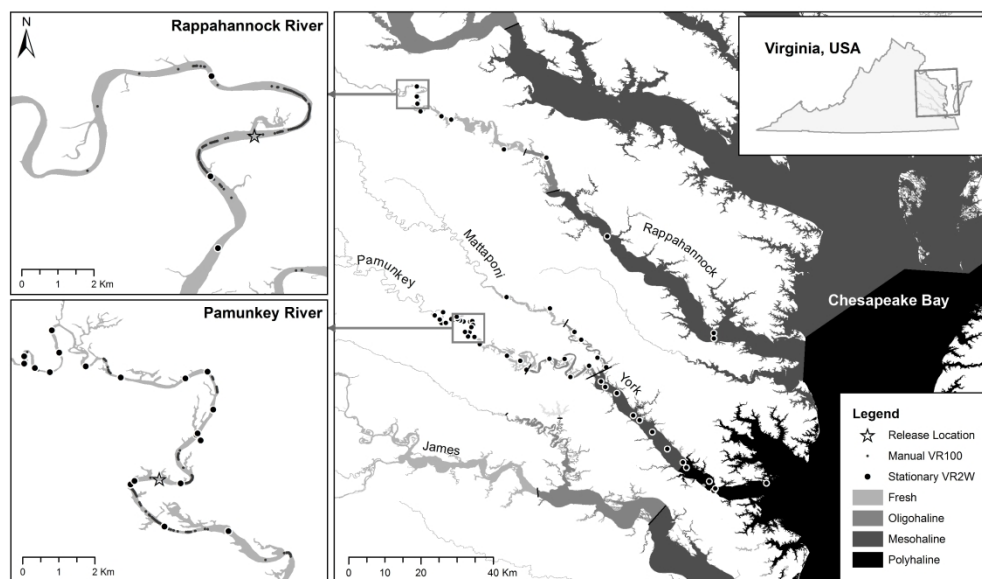


Figure 1

277x168mm (300 x 300 DPI)

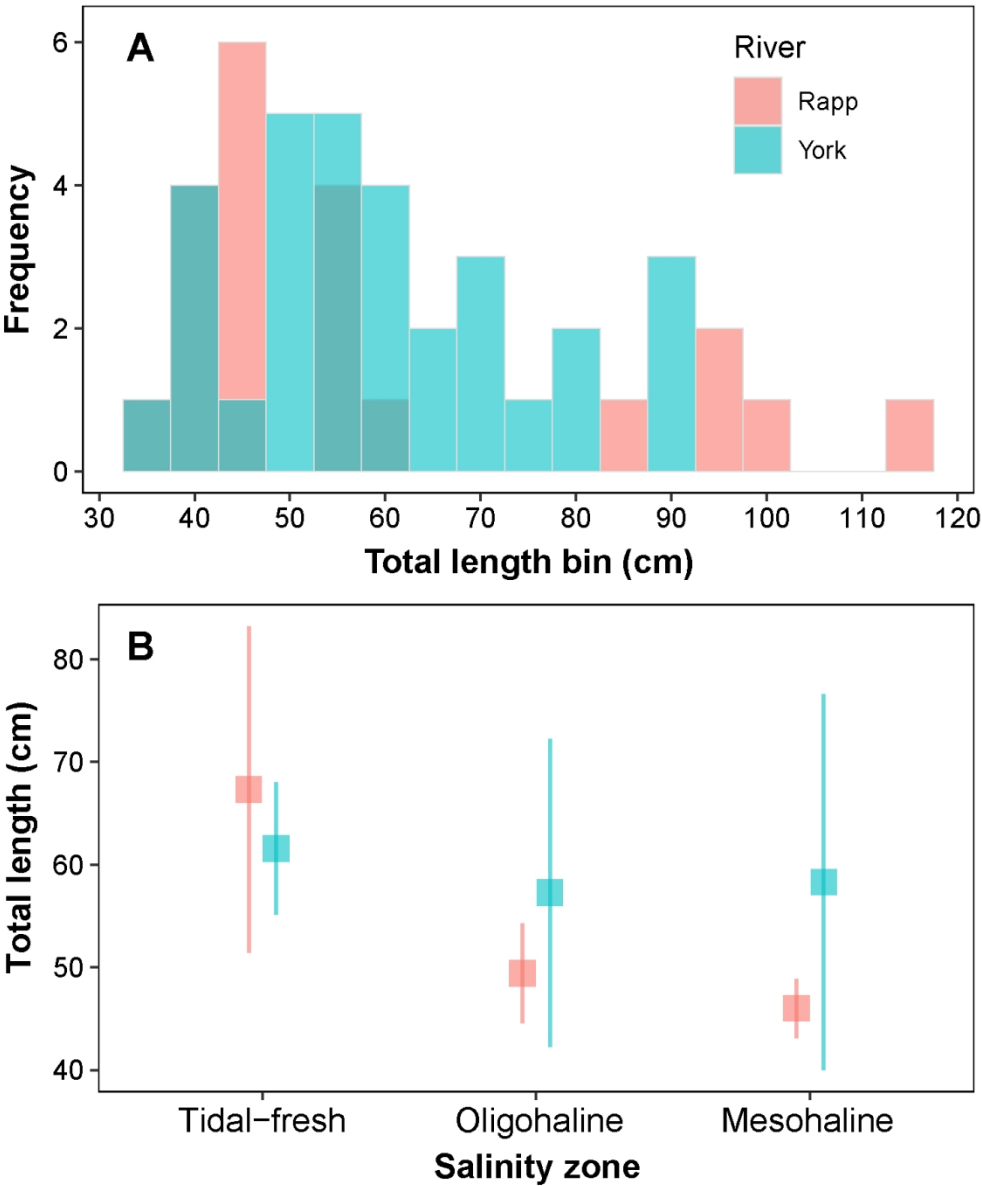


Figure 2

124x149mm (300 x 300 DPI)

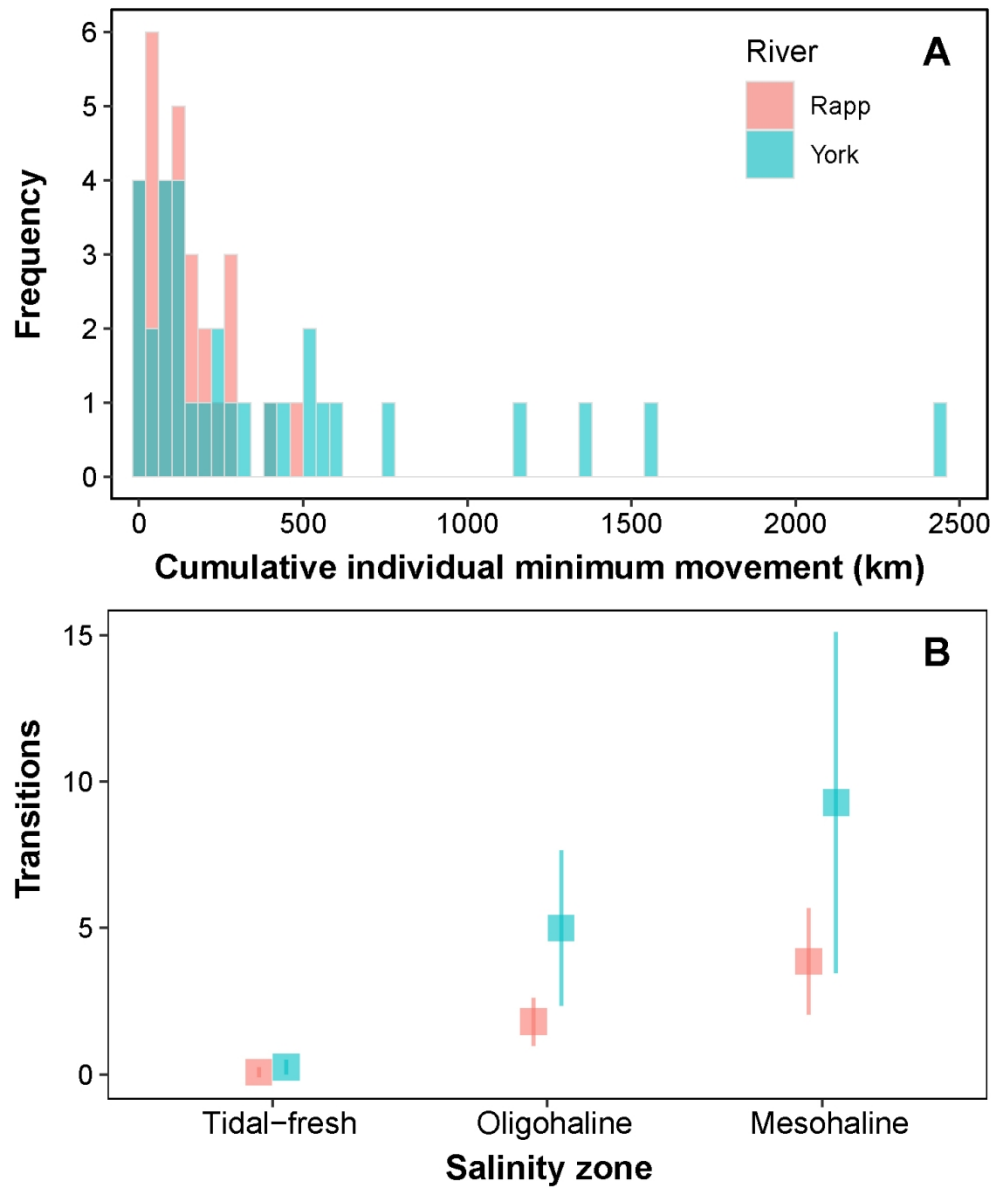


Figure 3

124x149mm (300 x 300 DPI)

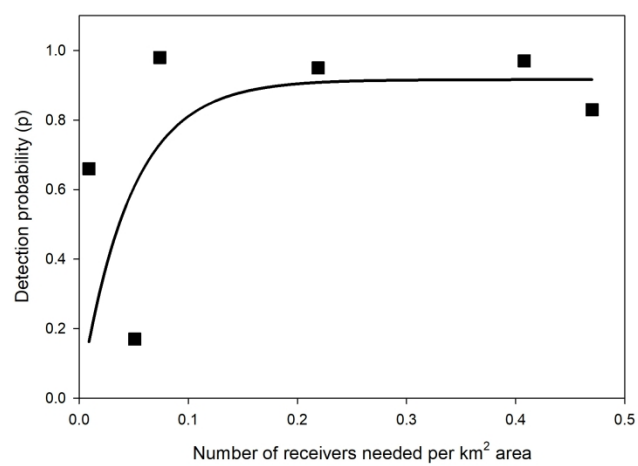


Figure 4

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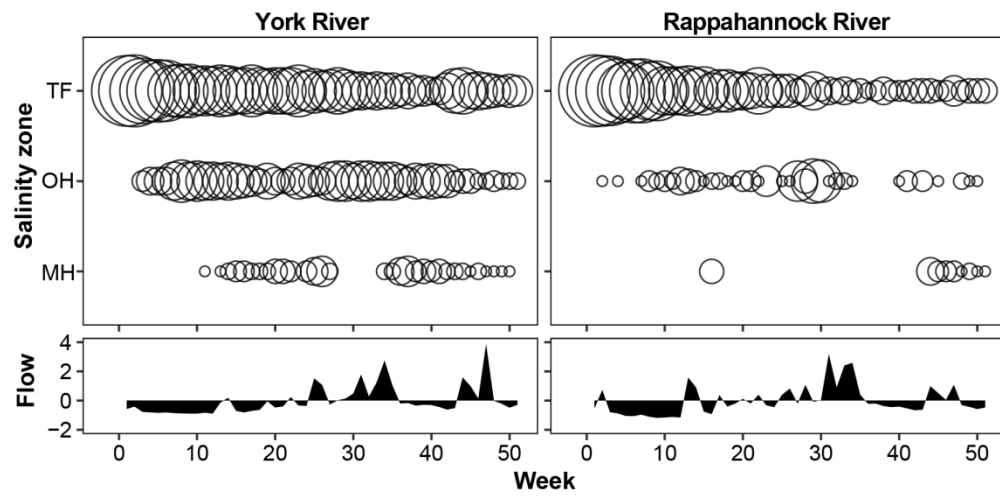
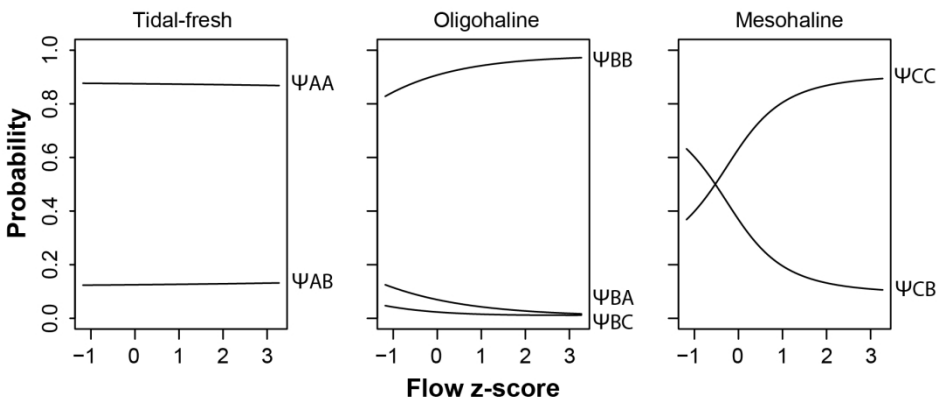


Figure 5

161x78mm (300 x 300 DPI)



166x71mm (300 x 300 DPI)