



Movement ecology of a mobile predatory fish reveals limited habitat linkages within a temperate estuarine seascape

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1 **Movement ecology of a mobile predatory fish reveals limited habitat linkages within a**
2 **temperate estuarine seascape**

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24 **ABSTRACT**

25 Large predatory fishes, capable of traveling large distances, can facilitate energy flow
26 linkages among spatially separated habitat patches via extended foraging behaviors over large
27 areas. Here, we tested this concept by tracking the movement of a large mobile estuarine fish, red
28 drum (*Sciaenops ocellatus*). Specifically, we addressed the following questions: 1) What are the
29 spatial and temporal patterns of red drum movement (rates of dispersal) and activity space? and
30 2) Does red drum movement facilitate linkages among estuarine marsh complexes? Dispersal
31 from the release location was greatest during the first two weeks at liberty before declining to
32 less than 0.5 km/week for the remainder of the study. Activity space initially also increased
33 rapidly before reaching an asymptote at 2.5 km² two weeks post-release. Connectivity indices
34 calculated among marsh complexes corroborated these observations, suggesting high residency
35 and limited seascape-scale linkages via red drum movement behaviors. These data highlight
36 potential within-estuary spatial structure for mobile fishes, and could inform subsequent efforts
37 to track energy flows in coastal food webs, predict the footprint of local habitat restoration
38 benefits, and enhance the design of survey regimes to quantify overall population demography.

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40 Key Words: saltmarsh connectivity, spatial ecology, movement behavior, mobile fish, red drum,
41 acoustic telemetry

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47 INTRODUCTION

48 Marine ecosystems are typically comprised of heterogeneous mosaics of distinct habitat
49 patches (i.e., seascapes). Identifying the value and function of habitats within the seascape is a
50 central component of efforts to conserve and protect estuarine habitats (Bostrom et al. 2011). As
51 ecologists and managers incorporate ecosystem-level approaches into research and decision
52 making in marine environments, they have drawn on studies quantifying the degree of
53 connectivity that results from the exchange of nutrients, pollutants, pathogens, sediments, and
54 organisms (i.e., fish, birds, and mobile invertebrates) across habitat boundaries within seascapes
55 (Polis et al. 1997). Fish movement, often considered one of the most influential factors in
56 mediating habitat connectivity (Sheaves 2009), within and among these habitat mosaics can
57 affect species interactions (Baggio et al. 2011), foraging behaviors (Beets et al. 2003), ecosystem
58 resiliency, biodiversity (Olds et al. 2012), reproduction (Bolden 2000), recruitment success
59 (Berkstrom et al. 2012), and nutrient transfer (Meyer et al. 1983). Therefore, enhancing our
60 understanding of fish movement patterns within and between various estuarine habitats is critical
61 to the management and conservation of fish populations and habitats on which they depend (e.g.
62 identifying discrete stock units).

63 Mobile fish species capable of traveling large distances (i.e. >5 km/day) increase the
64 linkages and potential for connectivity among habitats within estuarine seascapes (Rosenblatt
65 and Heithause 2011; McCauley et al. 2012; McMahan et al. 2012). Fish behavior can be highly
66 variable, with a number of factors affecting a fish's decision to move. For example, movement
67 and habitat choice can vary with individual preference and habitat complexity (Poppo and Hunte
68 2005), different degrees of predation pressure (Martin et al. 2010), resource availability
69 (Hammerschlag et al. 2010), seasonally (Barbour et al. 2014; Ketchum et al. 2014), and between

70 contingents of fish (Afonso et al. 2009), Here, we explore the movement behaviors of a relatively
71 large mobile predator between different marsh complexes within a temperate estuary and the
72 potential implications of this behavior on seascape-level connectivity of marsh complexes.

73 Salt marsh (*Spartina alterniflora*) complexes are often the dominant shoreline habitat
74 within temperate estuarine ecosystems, and are typically comprised of a mosaic of salt marsh,
75 seagrass, oyster reef, and mud/sand flat that are separated by deeper channels or extended
76 sand/mud flats from other structured habitats (most typically, other marsh complexes).

77 Connectivity, resulting from fish movement, has been explored at small (10's of m) spatial scales
78 in relation to movement of considerably less mobile fish (Able et al. 2012). Estuarine scale (kms)
79 connectivity among marsh complexes, however, is less well characterized. Identifying the level
80 of linkages between individual saltmarsh complexes would help frame our understanding of
81 whether whole estuaries function as the fundamental unit of "habitat" for large mobile fishes,
82 versus a series of relatively discrete habitat units for subpopulations of a given species.

83 Red drum (*Sciaenops ocellatus*), common in estuaries from Virginia to Texas, is highly
84 sought after by recreational fishermen. As sub-adults (up to age five), red drum inhabit estuarine
85 marsh complexes and near-shore habitats and forage on small fishes and crustaceans (Scharf and
86 Schlicht 2000). Individuals are capable of traveling large distances (> 10 km/week) and are often
87 found occupying a variety of estuarine habitats across a wide range of salinities in temperate
88 estuaries (Bacheler et al. 2009a; Bacheler et al. 2009b). Because they are considered highly
89 mobile and use a wide range of estuarine habitats, red drum are presumed to increase the
90 connectivity of spatially separated saltmarsh complexes within estuaries over tidal, diel, and
91 seasonal scales.

92 Understanding movement behavior of fish is challenging due to limitations in observing
93 individuals directly. Yet, the use of acoustic tracking methods is increasing and overcoming
94 long-standing impediments to monitoring fish movements. In particular, acoustic tracking
95 promotes monitoring of movement and behavior of individual fishes across broader spatial and
96 temporal gradients. The objective of this study was to quantify red drum movement patterns,
97 more specifically temporal variation in dispersal and activity space (home range), with the
98 overarching goal of assessing how fish behavior influences linkages between salt marsh
99 complexes. We asked three primary questions regarding the movement behaviors within this
100 estuarine seascape: 1) At what rate did individuals disperse throughout the estuary and into new
101 areas? (2) What was the activity space of individual red drum, and did it vary throughout the
102 study? And (3) Did individuals express high levels of residency within individual marsh
103 complexes in the study array or frequently move among them?

104 METHODS

105 *Study Area*

106 We acoustically tracked the movement of 34 sub-adult red drum over five months within
107 a temperate estuary near Cape Lookout, NC (Fig. 1). The shallow estuary of North River and
108 Back Sound covers an area of 68 km² from Beaufort Inlet (western extent of study system) to
109 Bardens Inlet at Cape Lookout (eastern extent). The estuary contains multiple saltmarsh
110 complexes, large expanses of shallow un-vegetated bottom, and deeper channels. Within the
111 study area, we deployed an array of 25 Vemco VR2W hydrophones to detect red drum
112 movement, specifically among four distinct salt marsh complexes (Fig. 1).

113 Within each marsh complex, multiple hydrophones were deployed to increase the
114 probability of detection when fish were present. For our analysis, hydrophones were grouped

115 according to their associations with individual marsh complexes or classified as “non-marsh”
116 (Fig. 1). Non-marsh stations were located in deeper channels and mud/sand flats, which were
117 presumed to be travel corridors. The hydrophone stations were grouped as follows: Carrot Island
118 Marsh (CIM) stations: 1, 4, 5, 9; Middle Marsh (MM) stations: 10, 13, 14, 15, 19; North River
119 Marsh (NRM) stations: 8, 11, 12; Back Sound Marsh (BSM) stations: 21, 22, 25; and non-marsh
120 complex stations: 2, 3, 6, 7, 16, 17, 18, 20, 23, 24 (Fig. 1). The VR2W omni-directional
121 hydrophones had a detection range of approximately 350 m in this study system based on range
122 detection tests conducted at the start of the study.

123 *Tagging and Tracking*

124 We collected sub-adult red drum (550 ± 15 mm total length, mean ± 1 standard error
125 [SE]) from different locations within the study area via hook and line ($n = 24$) or large mesh
126 (12.7 cm mesh) gill nets ($n = 10$) during July-October 2011 (Table 1). A coded acoustic
127 transmitter (LOTEK Wireless Inc. MM-MR-11-28, also used in a companion fine-scale tracking
128 study, see Fodrie et al. 2015) was implanted into the body cavity of each fish following
129 procedures similar to Dresser and Kneib (2007). These transmitters emitted both LOTEK
130 Wireless and Vemco coded signals, and therefore were all detectable with the VR2W (Vemco)
131 receivers. Following tag implantation, fish were held for 24 hours for observation before being
132 released into the southwestern-most bay within the MM complex (Fig. 1). Fish monitored in this
133 study were the same individuals tracked in a companion project analyzing fine-scale habitat use
134 within MM, therefore requiring all fish to be released in the same location (Fodrie et al. 2015).
135 Individual fish were released intermittently starting July 12th, with the last fish being released on
136 October 9th. At regular one-minute intervals, the transmitter emitted a pulsed chirp unique to
137 each fish, which was used to identify the presence of each individual within range of a

138 hydrophone. For each detection, the hydrophone recorded the transmitter ID, date, and time
139 information, and we downloaded these data monthly. Due to potential discrepancies in behavior
140 as a result of capture, tagging, and subsequent release back into the environment, we excluded
141 detections during the first 24 hours after being released from our movement analyses.
142 Additionally, as a result of using a single-release location, extrapolating patterns and processes to
143 fish being released in other marsh and non-marsh complexes could be limited; however, the
144 faunal communities and the quality and quantity of available habitats in MM are representative
145 of the marsh complexes in this estuary (sensu Baillie et al. 2015). Therefore, we hypothesize that
146 red drum would behave similarly if released in other, similar marsh complexes. Prior to analysis,
147 we used the false detections analyzer within VEMCO's data processing software (VUE) to
148 remove any false detections. Additionally, we examined the detection data to ensure that all
149 detections were from live individuals. A deceased individual can be identified when a transmitter
150 is detected continuously at a single hydrophone, with no detections occurring at any other
151 stations, for extended periods of time.

152 *Dispersal Patterns Away from Middle Marsh Release Location*

153 Understanding connectivity in estuarine systems requires knowledge of the rate at which
154 fish move throughout the estuary over hours to months. We calculated the rate of dispersal away
155 from the release location in the southwestern-most embayment within MM. Red drum detections
156 were separated into 10, six-day time bins, roughly representing weeks since being released into
157 the estuary (weeks at liberty thereafter). We then established three detection metrics: 1) the raw
158 number of detections (total detections thereafter), reflecting the number of times all individuals
159 were detected, collectively, at each hydrophone during each week at liberty; 2) the number of
160 individuals that visited each hydrophone during each week at liberty; and 3) a weighted number

161 of detections, defined as “relative occurrence”, at each hydrophone during each week at liberty.
162 We chose to look at the number of fish visiting hydrophones to supplement the detection volume
163 data (i.e. total detections). Instead of using just the number of total detections, which for any
164 individual hydrophone or group of hydrophones could result from ‘residency’ of a single fish, we
165 also wanted to evaluate how many individuals were detected at each hydrophone during each
166 week at liberty. The third metric was designed to address a potential bias of individuals with
167 disproportionately higher number of detections “swamping” total detection (metric 1) patterns.
168 To accomplish this, we standardized total detections by dividing a fish’s number of detections at
169 each hydrophone by the total number of detections collectively for that individual at all
170 hydrophones. In doing so, “relative occurrence” at individual hydrophones was scaled between 0
171 and 1 for each week at liberty for each fish. Each fish’s relative occurrence value at each
172 hydrophone was then summed to generate final relative occurrence values for analysis.

173 We adopted the general approaches of inspecting animal movement outlined by Ergon
174 and Gardner (2014) by quantifying dispersal patterns as changes in the three detection metrics
175 across our hydrophones, each of known distance from the release point in MM, through time. We
176 first plotted the relationship between our detection metrics at each hydrophone and the straight-
177 line distance from the release location to the respective hydrophone for each weekly time bin
178 (Fig. 2A). Next, normal distribution curves were fit through the data points to characterize the
179 distribution of the detection metrics for each weekly bin. We used the resulting standard
180 deviation (sigma [σ]) from the weekly normal distribution curves to represent the relative range
181 of fish distribution (measured in kilometers). For the analysis, we used two standard deviations
182 (2σ) representing 95% of the distribution range. This value therefore represented the distance
183 from the release location in which 95% of fish detections occurred during that week, hereafter

184 referred to as “relative distribution”. As fish dispersed from the release location, the distribution
185 of detections as a function of distance (of hydrophones) from the release location should
186 “flatten”, resulting in increasing 2σ values over time (Fig. 2B). By week 7 in our study the
187 distribution of detections calculated from total detection and relative occurrence metrics had
188 flattened to the point that 2σ values were unreliably large, and therefore we ceased to evaluate
189 relative distribution beyond this point. When analyzing the number of individuals detected at
190 each hydrophone (detection metric 2 listed above), 2σ became unreliably large after week 5.
191 Dispersal rate, the change in 2σ over time ($\Delta 2\sigma/\Delta t$) ($t = \text{time}$), were calculated from the
192 logarithmic trend lines fit to weekly relative distribution values. Dispersal rates were calculated
193 through seven weeks at liberty for each detection metric.

194 *Activity Space*

195 In addition to quantifying the mean dispersal rate of tagged red drum over the duration of
196 the study, we quantified weekly activity space size through time to examine if fish revisit the
197 same areas or continuously explore new areas. First, we calculated the center of activity (COA)
198 for each fish using the latitude and longitude coordinates of each hydrophone as suggested in
199 Simpfendorfer et al. (2002). We weighted these values by the number of detections at each
200 hydrophone visited during each week at liberty. Standard deviation (σ) values resulting from
201 calculating the mean latitude and longitude components of the COA were averaged to obtain a
202 single value representing the radius (m) of primary activity space for each week at liberty.
203 Similar to dispersal calculations, we used two standard deviations (2σ) for the radius (m) of
204 weekly activity space, which reflected 95% of all detections (per each individual fish within each
205 week) occurring within these boundaries.

206 Next, we explored temporal variation in the weekly activity space of fish by calculating
207 cumulative activity spaces. Cumulative activity space was calculated in the same manner as for
208 weekly measurements; however, the cumulative measurement included detections from that
209 week and all previous weeks since release. If fish were occupying completely new areas from
210 week to week, we expected to see cumulative activity space continue to grow linearly through
211 time (Fig. 3A). Alternatively, if a fish revisited areas over time, suggestive of higher site fidelity,
212 we expected the cumulative activity would grow initially, then asymptote over time (Fig. 3A).

213 *Residency*

214 To examine patterns of residency and exchange of fish among individual marsh
215 complexes, we calculated the probability of fish moving between each of the marsh complexes in
216 our study area. Each day that an individual red drum was detected, we randomly selected one
217 detection that day and recorded the location of that detection (primary detection). Relative to the
218 time stamp of the primary detection, we identified the location of that same fish twenty-four
219 hours later, or as soon as possible thereafter, based on the marsh complex groupings above
220 (subsequent detection). We chose a twenty-four-hour time step to allow for two full tidal cycles
221 and one day-night cycle, both of which can impact fish movement behavior and habitat choice
222 (Popple and Hunte 2005; Dresser and Kneib 2007). This procedure was repeated each calendar
223 day for which each individual was detected throughout the study. We conducted 100 iterations,
224 with replacement, of this sampling procedure to ensure that a representative selection of
225 randomly selected detection data points were incorporated. Therefore, for each day a fish was
226 detected, we performed this procedure using 100 randomly selected detections. From these
227 observations, we created a connectivity matrix identifying the probabilities that individuals
228 observed in a given marsh complex (primary detection) will be relocated in the same marsh

229 complex, a different marsh complex, or a non-marsh location after 24 hours (subsequent
230 detection). Probabilities ranged from 0, low chance of being detected in subsequent location, to
231 100, high chance of being detected in subsequent location. A high probability of being detected
232 within the same marsh complex suggests high residency. Further, we explored the consistency of
233 these behaviors over time by conducting the same analysis with time lags of 48 hours and one
234 week following the primary detections.

235 Finally, we assured that the uneven distribution of hydrophones within the marsh
236 complexes (e.g. MM contained five hydrophones while the others had 3-4 each) did not
237 significantly alter our observations and understanding of movement behavior. We accomplished
238 this conducting our residency analysis with two hydrophones removed from MM. We selected
239 the three hydrophones with the most detections and ran our analysis again three times with all
240 combinations of two of these three hydrophones being removed from the dataset. Therefore, for
241 each subsequent run of the analysis, MM was represented using only three hydrophones. Due to
242 consistencies in our original test for residency patterns using different time lags as well as the
243 consistency in the re-analysis of the dataset with a 24-hr lag, we did not perform this test using
244 time lags of 48-hr or 1-week. The resulting detection probabilities did not differ notably from the
245 original analysis therefore we proceeded to include all hydrophones from MM in our subsequent
246 analysis of residency patterns.

247 *Fishermen Recaptures*

248 Throughout the study, recreational and commercial fishermen reported occurrences of
249 capturing our tagged red drum. Using the date and location of the reported captures, we
250 calculated the number of days at liberty between release to recapture and the straight-line
251 distance from the release location to the recapture location. We examined the correlation

252 between days at liberty and distance from the release location to suggest whether individuals
253 exhibited random (low correlation) or non-random (high correlation) movement away from the
254 study area. Correlation analysis was conducted in JMP Pro12.

255 RESULTS

256 We recorded 51,987 detections overall, averaging $1,625 \pm 593$ (mean \pm 1 standard error)
257 detections per fish from 32 of the 34 tagged individuals (Table 1). The two individuals that were
258 not detected were recaptured outside of the study array by fishermen indicating that these
259 individuals simply left the array without being detected. Only four of those 32 fish were detected
260 less than 100 times. On average, individuals visited 5 ± 1 hydrophone stations and the number of
261 days that individuals were recorded within the hydrophone array ranged between 0 and 126 with
262 an average of 33 ± 5 days at liberty. Six individuals were detected visiting a combination of three
263 marsh complexes while another 13 were only detected in two complexes. The remaining 13 fish
264 were detected only in the MM complex. Of the 34 fish released, nine individuals were recaptured
265 by fishermen during or following our 5-month tracking effort. The time at liberty of these nine
266 fish ranged from 2 days to 425 days and the straight line distance from the release location to the
267 recapture location varied from 0 km up to 38 km. There was no distinguishable relationship
268 between days at liberty and distance from release location to recapture location (Pearson's $r =$
269 <0.01).

270 *Dispersal*

271 Over the course of the study, all three dispersal metrics indicated initial dispersal from
272 the release location during the first two weeks followed by minimal dispersal within the study
273 area over the remainder of the study (Fig. 2C). Relative distribution calculated from total
274 detections indicated that fish dispersed to a range of 1.69 km during the first week and 3.44 km
275 after two weeks. The change in relative distribution each week from week three through week

276 seven was less than 0.50 km. Initial dispersal rate calculated based on total detections was 2.09
277 km/week during week one before falling below 0.75 km/week during the remaining six weeks
278 (Fig. 2D). Distribution range observed from measurements of relative occurrence was similar to
279 that measured by total detections during the first (1.33 km) and second (3.30 km) weeks at
280 liberty followed by minor fluctuations through week seven (Fig. 2C). Based on the relative
281 occurrence of fish, the calculated dispersal rate increased slightly from week one (1.13 km/week)
282 to week two (1.34 km/week) followed by a continuous decline through week seven (Fig. 2D).
283 Finally, the distribution range observed from measurements of the number of fish at each
284 hydrophone displayed the greatest increase during the first week (2.77 km) followed by
285 fluctuating distribution range through week five (Fig. 2C). Dispersal rate calculated based on
286 number of fish at each hydrophone was high during week one (2.78 km/week), followed by a
287 large reduction in dispersal rate between week two (0.63 km/week) and week five (0.20
288 km/week) (Fig. 2C-D).

289 The average of all three detection metrics indicated that after the first two weeks at
290 liberty, the range of dispersal was approximately 3.29 km, which was comparable to the distance
291 across the MM complex from the release location (2.73 km). Although dispersal measurements
292 were calculated to represent distribution in all directions, the minimal number of detections at
293 hydrophones one through six to the west of MM (0.08% of total) indicated that the dispersal
294 direction was predominantly towards the east and north of the release location, along the main
295 axis of MM.

296 *Activity Space*

297 Weekly mean radius of activity space ranged from 286 m to 1007 m, with an overall
298 average of 686 ± 16.1 m (mean radius \pm SE), and did not change appreciably over time (Fig. 3B).

309 Calculations of cumulative activity space indicated that the greatest increase in mean radius
300 occurred during week one (756 m) and week two (925 m) (Fig. 3C). The size of the cumulative
301 activity space increased by small increments (<10% per week) over the remaining eight weeks of
302 observations. Overall, the fish displayed only a 20% increase in the radius of their cumulative
303 activity space between week two and week ten. Similar to results from dispersal patterns, the
304 cumulative activity space after two weeks at liberty (2.69 km²) scaled approximately to the area
305 of the MM complex (2.75 km²).

306 *Residency*

307 The connectivity matrix indicates the probabilities of fish remaining in the same location
308 as the primary detection (highlighted values along the diagonal of the matrix; Table 2) or moving
309 to a new location (non-highlighted values; Table 2). Movement probabilities indicated that a fish
310 had a >85% probability of being detected in the same marsh complex after 24 hours in three of
311 the four marsh complexes (BSM: 86.04%; MM: 93.34%; NRM: 98.87%). Fish within CIM were
312 the least likely to remain in the same complex (connectivity index = 50%). Fish initially detected
313 at any of the non-marsh locations had a greater likelihood of being detected at MM (48.47%)
314 compared to being detected again at a non-marsh complex location (40.15%).

315 In general, when fish were not detected in the same marsh complex after 24 hours from
316 the primary detection, they were most likely to be detected in the MM complex during
317 subsequent detections. There was evidence for a lack of direct linkages (i.e. subsequent detection
318 probabilities equal to zero) between several marsh complexes (MM-NRM, BSM-CIM, and NRM-
319 BSM). Finally, none of the fish in this study were detected at either of the two stations located in
320 the northern part of North River (stations 6 and 16), suggesting that tagged fish did not move to
321 marsh complexes in the upper River. Extending the time lag between primary and subsequent

322 detections resulted in very similar patterns of residency within BSM, MM, and NRM. The
323 likelihood of being detected in the same marsh complex 48 hours and 1 week later remained
324 >86% in all three marsh complexes. Conversely, fish originally observed in CIM had zero
325 probability of again being detected in that marsh complex after 1 week. When primary detections
326 were observed in CIM, these individuals were now most likely to be detected in NRM after one
327 week.

328 DISCUSSION

329 Patterns of red drum dispersal, activity space, and residency suggested limited movement
330 between similar saltmarsh complexes by a mobile fish during our five-month study. Dispersal
331 and cumulative activity space metrics indicated that there was minimal sustained occupation of
332 areas outside of the MM complex prior to emigration from the entire study array (further
333 supported by fishermen recapture data). Residency analysis also corroborated dispersal and
334 activity-space data; further suggesting limited movement between the marsh complexes we
335 monitored. Thus, our results imply that red drum induce minimal linkages among these spatially
336 separated habitat complexes on a sub-annual scale.

337 Limited seascape connectivity in this study highlights the potential for these saltmarsh
338 complexes to represent relatively isolated, discrete food webs within the estuary (Sheaves 2009).
339 This runs counter to suggestions that mobile consumers facilitate nutrient exchange within
340 estuaries through consumption and excretion, and may impact primary productivity in adjacent
341 habitats when consumer movement between habitats is high (Allgeier et al. 2013; Hyndes et al.
342 2014). Rather our results suggest that consumer-driven transfer of nutrients may be primarily a
343 local phenomenon, with relatively tighter recycling within each marsh complex. Additionally,
344 red drum could potentially impose greater predation pressure locally on their prey if movement

345 away from their preferred marsh complex is limited. Conversely, seasonally high abundances of
346 food resources throughout the lower estuary could provide fitness incentives to limit movement
347 away from MM, or any marsh complex in the lower North River (Dudley and Judy 1973;
348 Williams 1955).

349 Assigning value to individual habitats and seascapes is an essential component to the
350 management of fish populations and the habitats they use. Preferred habitats, measured by the
351 amount of time fish rely on those habitats and the benefits they provided to the success of the
352 population, weigh heavily when evaluating habitat value (sensu Nagelkerken et al. 2015).

353 Although red drum demonstrated high levels of residency within MM in this study, comparing
354 this marsh complex as a preferred location to the alternative complexes is beyond the scope of
355 this study given a potential bias in releasing all fish within this marsh complex. Nonetheless, we
356 expect that red drum would behave in a similar manner if released in other marsh complexes due
357 to similarities in fauna and habitat (Baillie et al. 2015). The few individuals (three) that moved
358 into one of the alternative marsh complexes for extended periods during the study, with the
359 exception of fish moving to CIM, displayed high residency for their new location. Although two
360 of these fish returned to their initial capture location in NRM, there is little evidence suggesting
361 that red drum movement is influenced by any homing behavior such as that previously
362 documented for some large bodied fish (Taylor et al. 2017). Fourteen of the sixteen individuals
363 initially captured in NRM remained in the MM system during the study and only two out of
364 thirty translocated fish were observed returning to their initial capture location. Reflecting the
365 results observed in this study, other fish in the population would be suggested to maintain high
366 levels of residency within the marsh complex they occupy.

367 Ontogenetic migrations of red drum generally shift the distribution of 1-3 year-old fish to
368 lower, more saline portions of coastal estuaries (Bacheler et al. 2009b). However, this pattern is
369 not all inclusive as two-year-old fish, equivalent to those used in our study, are still known to
370 occupy low salinity (< 10 ppt) waters of North Carolina estuaries (Bacheler et al. 2009a)
371 specifically the upper North River estuary (M. Kenworthy, personal observations). Regardless of
372 expectations that red drum in our study system would move to occupy this region of the estuary,
373 none of the tagged red drum were detected at our two upper estuary stations. Furthermore, only a
374 limited number of fish (four) were detected as far up-estuary as NRM (Fig 1). Our data
375 contribute to the growing consensus in the literature that suggests red drum rarely move
376 upstream as sub-adults (Dresser and Kneib 2007; Bacheler 2009b). Occupation of the upper
377 estuary by similar age class fish is likely a result of individuals either settling in this region and
378 remaining or individuals arriving during spring months when a large portion of the sub-adult
379 population re-enter and distribute within the estuaries (Bacheler et al. 2009b). Connectivity
380 among upper estuary and lower estuary seascapes therefore is likely influenced more by
381 ontogenetic migrations or suggested re-entry of the red drum population into the estuary. The
382 mechanism driving this subpopulation structure deserves further research attention.

383 Overall, red drum displayed high levels of residency within the MM complex with
384 limited seascape linkages. However, some fish were observed making intermittent excursions
385 between MM and both CIM and BSM, potentially establishing linkages with these other
386 complexes. These excursions almost always occurred during nighttime hours and were short in
387 duration. These movement patterns could reflect foraging excursions to the habitats located
388 between the associated march complexes. For example, the sandflats between MM and BSM
389 contain isolated patches of seagrass, which red drum could be targeting during preferred

390 crepuscular and nighttime foraging hours (Facendola and Scharf 2012). In comparison, the
391 sandflats between MM and CIM do not contain seagrass patches. This area, located near one of
392 two main channels flowing out of North River, is a potential corridor for crustaceans (crabs and
393 shrimp) emigrating out of the upper North River estuary at night, and could be serving as a
394 source of food. Therefore, these excursions could facilitate linkages within the estuarine seascape
395 via nutrient exchange between unstructured habitats surrounding MM and the MM complex,
396 similar to that observed in other ecosystems (e.g. coral reefs) (Beets et al. 2003), even if red
397 drum are not consistently connecting distinct marsh complexes within this estuary. Following the
398 flow of energy within coastal ecosystems is important for understanding the values and
399 contributions of individual towards productivity within an estuary (Heck et al. 2008). Although
400 these assumptions are speculative without direct measurements of nutrient exchange within the
401 system, identifying the movement behaviors of fish with the capacity to facilitate this nutrient
402 exchange is critical to identifying potential energy transport dynamics within this estuary.

403 The spatial and temporal scale at which ecological processes are observed can influence
404 our understanding of dynamics within an ecosystem (Levine 1992). For instance, over the time
405 frame of this study, the distance between marsh complexes could play a crucial role in assessing
406 linkages among them (i.e., marshes in our study were relatively far apart and therefore
407 connectivity was low). However, considering previously reported daily movements for red drum
408 (3.4 ± 0.6 km; Dance and Rooker 2015), we do not anticipate that this drove our results. On
409 average, the straight-line distance between marsh complexes in our array was less than two
410 kilometers, except for the distances between BSM and both CIM and NRM, which were each ~5
411 km. We do acknowledge, however, that the location of MM in the middle of the study array

412 could have contributed to the higher degree of connectivity of this marsh complex relative to the
413 other complexes we monitored.

414 Identifying variations in spatial and temporal movement patterns of animals can refine
415 our understanding about life history patterns of fish and the value of the habitats they utilize
416 (Secor et al. 2001; Drymon et al 2014; McMahon et al. 2012). Specifically, regional (upper vs
417 lower estuary) and habitat-specific (marsh complexes) isolation of fish groups could have
418 implications for population sampling regimes, identification of essential fish habitats for sub-
419 adult red drum, and management of commercial and recreational fishing efforts. Our results
420 support previous studies suggesting that individual red drum express high residency in specific
421 locations (Dresser and Kneib 2007; Bacheler et al. 2009b; Reyier et al. 2011; Dance and Rooker
422 2015). Even fish that moved out of the study array did not appear to disperse with any apparent
423 regularity. The lack of any defined relationship between time at liberty and distance from where
424 they were released suggests that over the course of that time frame, those individuals likely
425 established temporary residency in other locations along the route to the where they were
426 recaptured. Future research could build off this study to further explore the dynamics of estuarine
427 scale seascape linkages (e.g. between lower and upper estuary) as well as marsh complex
428 specific residency patterns.

429

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450 REFERENCES

- 451 Able, K.W., Vivian, D.N., Petruzzelli, G., and Hagan, S.M. 2012. Connectivity Among Salt
452 Marsh Subhabitats: Residency and Movements of the Mummichog (*Fundulus heteroclitus*).
453 *Estuaries and Coasts* **35**(3): 743–753. doi:10.1007/s12237-011-9471-x.
- 454 Afonso, P., Fontes, J., Holland, K.N., and Santos, R.S. 2009. Multi-scale patterns of habitat use
455 in a highly mobile reef fish, the white trevally *Pseudocaranx dentex*, and their implications
456 for marine reserve design. *Mar. Ecol. Prog. Ser.* **381**(2): 273–286. doi:10.3354/meps07946.
- 457 Allgeier, J.E., Yeager, L.A., and Layman, C.A. 2013. Consumers regulate nutrient limitation
458 regimes and primary production in seagrass ecosystems. *Ecology* **94**(2): 521–529.
459 doi:10.1890/12-1122.1
- 460 Bacheler, N.M., Paramore, L.M., Buckel, J.A., and Hightower, J.E. 2009. Abiotic and biotic
461 factors influence the habitat use of an estuarine fish. *Mar. Ecol. Prog. Ser.* **377**: 263–277.
462 doi:10.3354/meps07805.
- 463 Bacheler, N.M., Paramore, L.M., Burdick, S.M., Buckel, J. a., and Hightower, J.E. 2009.
464 Variation in movement patterns of red drum (*Sciaenops ocellatus*) inferred from
465 conventional tagging and ultrasonic telemetry. *Fish. Bull.* **107**: 405–419.
- 466 Baggio, J. a., Salau, K., Janssen, M. a., Schoon, M.L., and Bodin, Ö. 2011. Landscape
467 connectivity and predator-prey population dynamics. *Landsc. Ecol.* **26**: 33–45.
468 doi:10.1007/s10980-010-9493-y.

- 469 Baillie, C.J., Fear, J.M., and Fodrie, F.J. 2015. Ecotone Effects on Seagrass and Saltmarsh
470 Habitat Use by Juvenile Nekton in a Temperate Estuary. *Estuaries and Coasts* **38**: 1414–
471 1430. doi:10.1007/s12237-014-9898-y.
- 472 Barbour, A.B., Adams, A.J., and Lorenzen, K. 2014. Size-based, seasonal, and multidirectional
473 movements of an estuarine fish species in a habitat mosaic. *Mar. Ecol. Prog. Ser.* **507**: 263–
474 276. doi:10.3354/meps10837.
- 475 Beets, J., Muehlstein, L., Hought, K., and Schmitges, H. 2003. Habitat Connectivity In Coastal
476 Environments: Patterns and Movements of Caribbean Coral Reef Fishes With Emphasis On
477 Bluestriped Grunt. *Gulf and Car. Res.* **14**(2): 29–42. doi:10.18785/gcr.1402.03.
- 478 Berkström, C., Gullström, M., Lindborg, R., Mwandya, A.W., Yahya, S.A.S., Kautsky, N., and
479 Nyström, M. 2012. Exploring “knowns” and “unknowns” in tropical seascape connectivity
480 with insights from East African coral reefs. *Estuar. Coast. Shelf Sci.* **107**: 1–21. Elsevier
481 Ltd. doi:10.1016/j.ecss.2012.03.020.
- 482 Bolden, S.K. 2000. Long-distance movement of a Nassau grouper (*Epinephelus striatus*) to a
483 spawning aggregation in the central Bahamas. *Fish. Bull.* **98**(3): 642–645.
- 484 Boström, C., Pittman, S.J., Simenstad, C., and Kneib, R.T. 2011. Seascape ecology of coastal
485 biogenic habitats: Advances, gaps, and challenges. *Mar. Ecol. Prog. Ser.* **427**: 191–217.
486 doi:10.3354/meps09051.

- 487 Dance, M.A., and Rooker, J.R. 2015. Habitat- and bay-scale connectivity of sympatric fishes in
488 an estuarine nursery. *Estuar. Coast. Shelf Sci.* **167**: 447–457. Elsevier Ltd.
489 doi:10.1016/j.ecss.2015.10.025.
- 490 Dresser, B.K., and Kneib, R.T. 2007. Site fidelity and movement patterns of wild subadult red
491 drum, *Sciaenops ocellatus* (Linnaeus), within a salt marsh-dominated estuarine landscape.
492 *Fish. Manag. Ecol.* **14**: 183–190. doi:10.1111/j.1365-2400.2007.00526.x.
- 493 Drymon, J.M., Ajemian, M.J., and Powers, S.P. 2014. Distribution and dynamic habitat use of
494 young bull sharks *Carcharhinus leucas* in a highly stratified Northern Gulf of Mexico
495 estuary. *PLoS One* **9**(5): 1–12. doi:10.1371/journal.pone.0097124.
- 496 Dudley, D.L., and Judy, M.H. 1973. Seasonal Abundance and Distribution of Juvenile Blue
497 Crabs in Core Sound N.C. 1965-68. *Chesap. Sci.* **14**(1): 51–55. doi:10.2307/1350703
- 498 Ergon, T., and Gardner, B. 2013. Separating mortality and emigration: modelling space use,
499 dispersal and survival with robust-design spatial capture-recapture data. *Methods Ecol.*
500 *Evol.*: 1–10. doi:10.1111/2041-210X.12133.
- 501 Facendola, J.J., and Scharf, F.S. 2012. Seasonal and Ontogenetic Variation in the Diet and Daily
502 Ration of Estuarine Red Drum as Derived from Field-Based Estimates of Gastric
503 Evacuation and Consumption. *Mar. Coast. Fish.* **4**(1): 546–559.
504 doi:10.1080/19425120.2012.699018.
- 505 Fodrie, F.J., Yeager, L.A., Grabowski, J.H., Layman, C.A., Sherwood, G.D., and Kenworthy,
506 M.D. 2015. Measuring individuality in habitat use across complex landscapes: approaches,

- 507 constraints, and implications for assessing resource specialization. *Oecologia* **178**(1): 75–
508 87. Springer Berlin Heidelberg. doi:10.1007/s00442-014-3212-3.
- 509 Hammerschlag, N., Heithaus, M.R., and Serafy, J.E. 2010. Influence of predation risk and food
510 supply on nocturnal fish foraging distributions along a mangrove – seagrass ecotone. *Mar.*
511 *Ecol. Prog. Ser.* **414**: 223–235. doi:10.3354/meps08731.
- 512 Heck Jr, K.L., Carruthers, T.J.B., Duarte, C.M., Randall, A., Kendrick, G., Orth, R.J., and
513 Williams, S.W. 2008. Trophic Transfers from Seagrass Meadows Subsidize Diverse Marine
514 and Terrestrial Consumers. *Ecosystems* **11**: 1198–1210. doi:10.1007/s10021-008-9155-y.
- 515 Hyndes, G.A., Nagelkerken, I., Mcleod, R.J., Connolly, R.M., Lavery, P.S., and Vanderklift,
516 M.A. 2014. Mechanisms and ecological role of carbon transfer within coastal seascapes.
517 *Biol. Rev. Camb. Philos. Soc.* **89**: 232–254. doi:10.1111/brv.12055.
- 518 Ketchum, J.T., Hearn, A., Klimley, A.P., Peñaherrera, C., Espinoza, E., Bessudo, S., Soler, G.,
519 and Arauz, R. 2014. Inter-island movements of scalloped hammerhead sharks (*Sphyrna*
520 *lewini*) and seasonal connectivity in a marine protected area of the eastern tropical Pacific.
521 *Mar. Biol.* **161**(4): 939–951. doi:10.1007/s00227-014-2393-y.
- 522 Levin, S.A. 1992. The Problem of Pattern and Scale in Ecology: The Robert H. MacArthur
523 Award Lecture Author(s): Simon A. Levin Source: *Ecology* **73**(6): 1943–1967.
524 doi:10.2307/1941447.

- 525 McCauley, D.J., Young, H.S., Dunbar, R.B., Estes, J. a., Semmens, B.X., and Micheli, F. 2012.
526 Assessing the effects of large mobile predators on ecosystem connectivity. *Ecol. Appl.*
527 **22**(6): 1711–1717. doi:10.1890/11-1653.1.
- 528 Martin, C.W., Fodrie, F.J., Heck, K.L., and Mattila, J. 2010. Differential habitat use and
529 antipredator response of juvenile roach (*Rutilus rutilus*) to olfactory and visual cues from
530 multiple predators. *Oecologia* **162**(4): 893–902. doi:10.1007/s00442-010-1564-x.
- 531 McMahon, K.W., Berumen, M.L., and Thorrold, S.R. 2012. Linking habitat mosaics and
532 connectivity in a coral reef seascape. *Proc. Natl. Acad. Sci.* **109**: 15372–15376.
533 doi:10.1073/pnas.1206378109.
- 534 Meyer, J.L., Schultz, E.T., and Helfman, G.S. 1983. Fish Schools: An Asset to Corals. *Science.*
535 **220**(4601): 1047–1049. doi:10.1126/science.220.4601.1047
- 536 Nagelkerken, I., Sheaves, M., Baker, R., and Connolly, R.M. 2015. The seascape nursery: A
537 novel spatial approach to identify and manage nurseries for coastal marine fauna. *Fish Fish.*
538 **16**(2): 362–371. doi:10.1111/faf.12057.
- 539 Olds, A.D., Pitt, K.A., Maxwell, P.S., and Connolly, R.M. 2012. Synergistic effects of reserves
540 and connectivity on ecological resilience. *J. Appl. Ecol.* **49**(6): 1195–1203.
541 doi:10.1111/jpe.12002.
- 542 Polis, G.A., Anderson, W.B., and Holt, R.D. 1997. TOWARD AN INTEGRATION OF
543 LANDSCAPE AND FOOD WEB ECOLOGY: The Dynamics of Spatially Subsidized Food
544 Webs. *Annu. Rev. Ecol. Syst.* **28**: 289–316. doi:10.1146/annurev.ecolsys.28.1.289

- 545 Popple, I.D., and Hunte, W. 2005. Movement patterns of *Cephalopholis cruentata* in a marine
546 reserve in St Lucia, W.I., obtained from ultrasonic telemetry. *J. Fish Biol.* **67**: 981–992.
547 doi:10.1111/j.0022-1112.2005.00797.x.
- 548 Reyier, E. a., Lowers, R.H., Scheidt, D.M., and Adams, D.H. 2011. Movement patterns of adult
549 red drum, *Sciaenops ocellatus*, in shallow Florida lagoons as inferred through autonomous
550 acoustic telemetry. *Environ. Biol. Fishes* **90**: 343–360. doi:10.1007/s10641-010-9745-3.
- 551 Rosenblatt, A.E., and Heithaus, M.R. 2011. Does variation in movement tactics and trophic
552 interactions among American alligators create habitat linkages? *J. Anim. Ecol.* **80**: 786–798.
553 doi:10.1111/j.1365-2656.2011.01830.x.
- 554 Scharf, F.S., and Schlight, K.K. 2000. Feeding Habits of Red Drum (*Sciaenops ocellatus*) in
555 Galveston Bay, Texas: Seasonal Diet Variation and Predator-Prey Size Relationships.
556 *Estuaries* **23**(1): 128. doi:10.2307/1353230.
- 557 Secor, D.H., Rooker, J.R., Zlokovitz, E., and Zdanowicz, V.S. 2001. Identification of riverine,
558 estuarine, and coastal contingents of Hudson River striped bass based upon otolith
559 elemental fingerprints. *Mar. Ecol. Prog. Ser.* **211**(1968): 245–253.
560 doi:10.3354/meps211245.
- 561 Sheaves, M. 2009. Consequences of ecological connectivity: the coastal ecosystem mosaic. *Mar.*
562 *Ecol. Prog. Ser.* **391**: 107–115. doi:10.3354/meps08121.

563 Simpfendorfer, C. a, Heupel, M.R., and Hueter, R.E. 2002. Estimation of short-term centers of
564 activity from an array of omnidirectional hydrophones and its use in studying animal
565 movements. *Can. J. Fish. Aquat. Sci.* **59**: 23–32. doi:10.1139/f01-191.

566 Williams, A.B. 1955. A Contribution to the Life Histories of Commercial Shrimps (Penaeidae)
567 in North Carolina. *Bull. Mar. Sci.* **5**(2): 116–146.

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585 TABLES

586 Table 1. Summary of 34 red drum tagged with acoustic transmitters and tracked within the array
 587 of VEMCO hydrophones within the Back Sound Estuary in central North Carolina. Fish ID's
 588 marked with an asterisk are fish that were recaptured by fishermen. Capture location indicates
 589 where fish were originally caught for this study: Jarret Bay (JB), North River Marsh (NRM),
 590 Middle Marsh (MM), Carrot Island Marsh (CIM), Northern North River (NNR).

Fish ID	Capture Location	Release Date	Total Length (mm)	Weight (kg)	Total Detections	Stations Visited	Marsh Complexes Visited	Days at Liberty (acoustics)	Days at Liberty (recapture)	Distance to recapture (km)
RD01	JB	7/13/2011	488	1.1	249	10	3	4	-	-
RD02	JB	7/14/2011	490	1.3	9	1	1	3	-	-
RD03*	JB	7/14/2011	490	1.4	0	0	0	0	420	5.13
RD04	JB	7/14/2011	480	1.1	977	2	1	23	-	-
RD05	JB	7/15/2011	514	1.6	396	4	2	15	-	-
RD06	JB	7/15/2011	515	1.5	15	1	1	3	-	-
RD07	JB	7/15/2011	503	1.3	126	5	1	126	-	-
RD08	NRM	8/16/2011	559	2	550	11	3	76	-	-
RD09	NRM	8/16/2011	520	1.6	499	1	1	37	-	-
RD10	NRM	8/16/2011	365	0.6	101	1	1	35	-	-
RD11	NRM	8/16/2011	505	1	151	4	1	28	-	-
RD12*	NRM	8/16/2011	340	0.6	0	0	0	0	425	14.25
RD13	JB	9/3/2011	565	2	14140	6	2	62	-	-
RD14	NRM	9/3/2011	341	0.6	138	4	2	30	-	-
RD15	NRM	9/13/2011	775	4	2159	9	2	46	-	-
RD16	NRM	9/13/2011	755	4.5	38	3	1	1	-	-
RD17*	NRM	9/13/2011	549	1.6	2610	8	3	34	2	0
RD18*	NRM	9/30/2011	563	1.6	1199	5	1	32	39	38
RD19	MM	9/30/2011	556	1.5	896	2	1	43	-	-
RD20*	CIM	9/30/2011	568	2	736	7	2	49	54	2.88
RD21	NRM	9/30/2011	600	2.3	2316	4	1	26	-	-
RD22	MM	10/4/2011	610	2.2	636	5	2	31	-	-
RD23	NRM	10/4/2011	562	1.6	110	6	3	5	-	-
RD24*	NNR	10/4/2011	645	2.6	1361	7	2	49	50	0
RD25*	NRM	10/4/2011	612	2.3	301	9	2	7	7	5.86
RD26	NRM	10/4/2011	585	1.9	700	6	2	48	-	-
RD27	JB	10/6/2011	600	2	1128	7	2	21	-	-
RD28	JB	10/6/2011	612	2.3	6786	10	2	75	-	-
RD29	MM	10/6/2011	556	1.6	193	4	2	52	-	-
RD30*	NNR	10/6/2011	638	2.8	105	3	1	7	10	9.21
RD31	NRM	10/6/2011	555	1.5	1	1	1	1	-	-
RD32	NRM	10/10/2011	550	1.6	12721	9	3	70	-	-
RD33*	CIM	10/10/2011	602	2.2	314	2	2	25	179	1.83
RD34	MM	10/10/2011	534	1.5	325	7	3	43	-	-

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592 Table 2. Connectivity matrix indicating the number (N) of randomly selected detections for each
 593 marsh complex and non-marsh sites and the location probabilities (%) of subsequent detection
 594 after A) 24 hours, B) 48 hours, and C) 1 week. Marsh complex names are: Back Sound Marsh
 595 (BSM), Carrot Island Marsh (CIM), Middle Marsh (MM), and North River Marsh (NRM).

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A		N	Subsequent Detection Location (=> 24 hours)				
			BSM	CIM	MM	NRM	Non-Marsh
Primary Detection Location	BSM	3108	86.04	0.00	8.72	0.00	5.24
	CIM	608	0.00	50.00	26.81	10.69	12.50
	MM	53426	1.12	1.36	93.34	0.21	3.96
	NRM	2291	0.00	0.00	0.09	98.87	1.05
	Non-Marsh	2249	11.38	0.00	48.47	0.00	40.15

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B		N	Subsequent Detection Location (=> 48 hours)				
			BSM	CIM	MM	NRM	Non-Marsh
Primary Detection Location	BSM	2857	86.66	0.00	9.45	0.00	3.89
	CIM	616	0.00	44.97	26.79	28.25	0.00
	MM	48867	1.69	1.20	90.62	0.54	5.96
	NRM	2146	0.00	1.07	0.00	98.93	0.00
	Non-Marsh	2124	11.35	0.00	51.84	0.00	36.82

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C		N	Subsequent Detection Location (=> 1 week)				
			BSM	CIM	MM	NRM	Non-Marsh
Primary Detection Location	BSM	2457	86.57	0.00	12.70	0.00	0.73
	CIM	527	0.00	0.00	29.41	70.40	0.19
	MM	43743	1.89	1.39	88.71	0.94	7.07
	NRM	1805	0.00	0.00	0.00	100.00	0.00
	Non-Marsh	1684	14.55	0.00	67.52	0.00	17.93

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600 FIGURES

601 Figure 1: Map of the hydrophone observation network labeled with station identification
602 numbers. Hydrophones (marked by black dots) for associated marsh complexes are contained in
603 individual labeled circles. Locations included are Northern North River (NNR), North River
604 Marsh (NRM), Carrot Island Marsh (CIM), Middle Marsh (MM), and Back Sound Marsh
605 (BSM). Map was produced using ArcGis for Desktop (ArcMap 10.5). Shoreline shapefiles
606 obtained from ESRI and the North Carolina Department of Environmental Quality (NCDEQ).

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608 Figure 2: Dispersal patterns for red drum throughout the study based on distributions of the three
609 metrics measured, (total detections, number of fish, and relative occurrence) at hydrophones of
610 known distances from the release location. Panels represent A) theoretical expectations of
611 weekly detection distribution change through time; B) actual total detection distribution curves
612 for each week of the study; C) weekly range of distribution values calculated from distribution
613 curves for each metric used; and D) dispersal rates calculated for the three detection metrics.

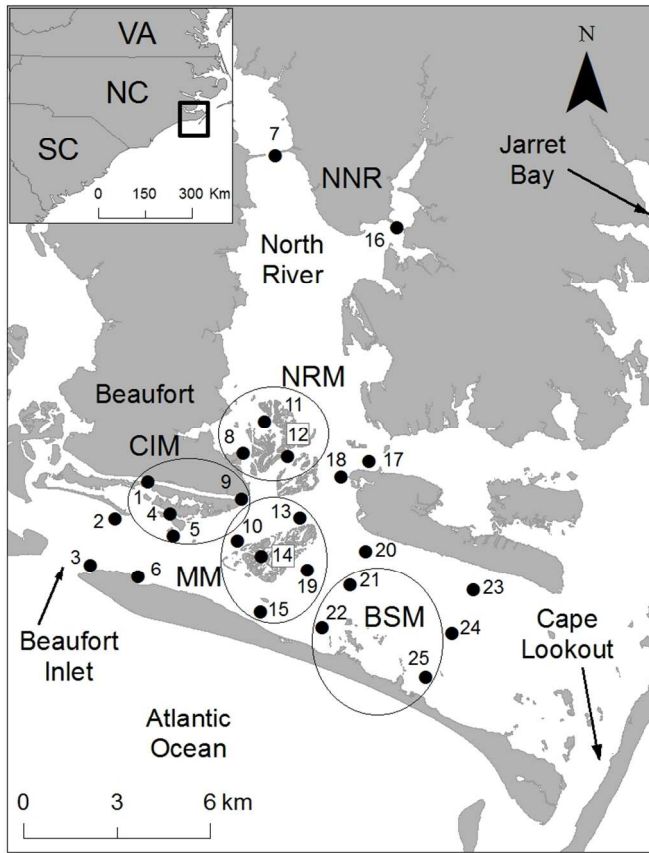
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615 Figure 3: Red drum activity space measured through time. Panels represent A) two theoretical
616 patterns of cumulative activity space growth through time indicating that fish either continue to
617 explore new areas over time (solid line) or continue to occupy the same areas repeatedly (dashed
618 line); B) weekly measurements of the radius of the activity space and C) measured cumulative
619 activity space growth throughout the 10 weeks of the study.

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623 Figure 1.



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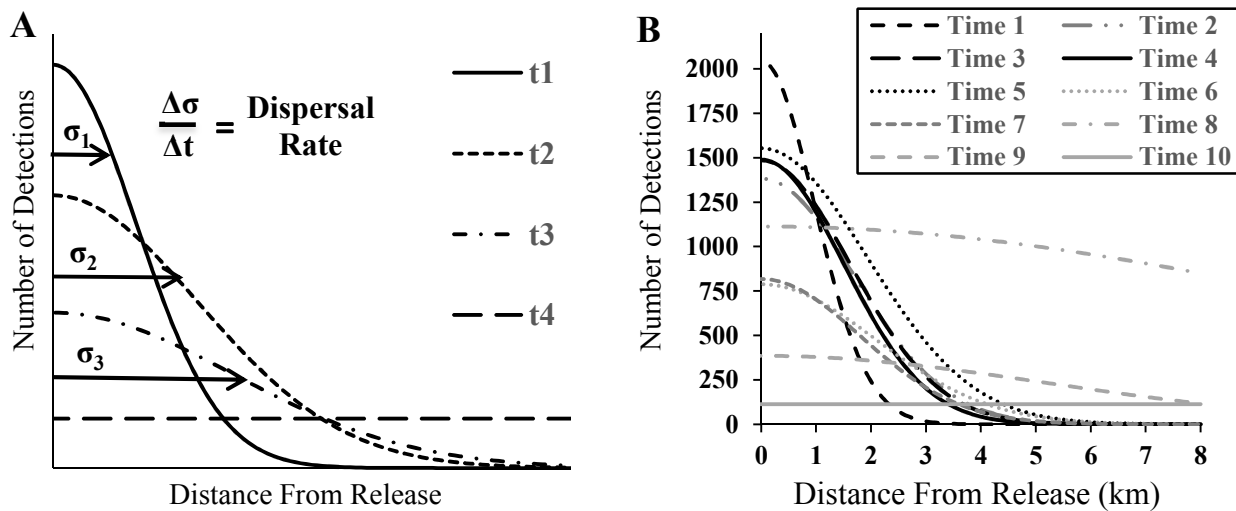
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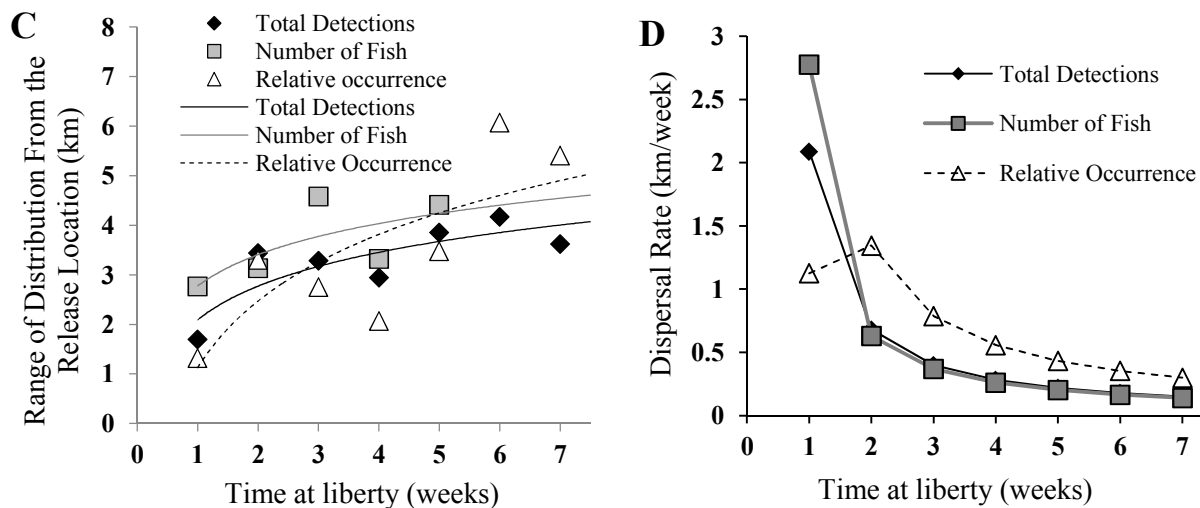
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635 Figure 2.



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