

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

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

Résumé : Les gros poissons prédateurs capables de se déplacer sur de grandes distances peuvent améliorer la connectivité du transfert d'énergie entre parcelles d'habitat séparées dans l'espace en étendant les comportements d'approvisionnement sur de grandes superficies. Nous avons vérifié ce concept en suivant les déplacements d'un gros poisson estuarien mobile, le tambour rouge (*Sciaenops ocellatus*). Nous nous sommes plus précisément penchés sur les questions suivantes : (i) quels sont les motifs spatiaux et temporels de déplacement (vitesses de dispersion) et de l'espace d'activité des tambours rouges? (ii) est-ce que les déplacements des tambours rouges améliorent la connectivité entre complexes de marais estuariens? La vitesse de dispersion à partir du lieu de lâcher a atteint un maximum pendant les deux premières semaines de liberté, avant de baisser à moins de 0,5 km-semaine⁻¹ pour le reste de la durée de l'étude. L'espace d'activité a aussi cru rapidement avant d'atteindre une asymptote à 2,5 km² 2 semaines après le lâcher. Les indices de connectivité calculés entre complexes de marais corroborent ces observations, indiquant un fort taux de résidence et des connexions limitées à l'échelle du paysage marin découlant des comportements de déplacement des tambours rouges. Les données font ressortir une possible structure spatiale des poissons mobiles dans les estuaires et pourraient éclairer les efforts visant à suivre les transferts d'énergie dans les réseaux trophiques côtiers, prédire l'empreinte des bénéfices de la restauration d'habitats à l'échelle locale et améliorer la conception de régimes d'évaluation ayant pour but de quantifier la démographie globale des populations. [Traduit par la Rédaction]

Introduction

Marine ecosystems are typically composed of heterogeneous mosaics of distinct habitat patches (i.e., seascapes). Identifying the value and function of habitats within the seascape is a central component of efforts to conserve and protect estuarine habitats (Bostrom et al. 2011). As ecologists and managers incorporate ecosystem-level approaches into research and decision making in marine environments, they have drawn on studies quantifying the degree of connectivity that results from the exchange of nutrients, pollutants, pathogens, sediments, and organisms (i.e., fish, birds, and mobile invertebrates) across habitat boundaries within seascapes (Polis et al. 1997). Fish movement, often considered one of the most influential factors in mediating habitat connectivity (Sheaves 2009), within and among these habitat mosaics can af-

fect species interactions (Baggio et al. 2011), foraging behaviors (Beets et al. 2003), ecosystem resiliency, biodiversity (Olds et al. 2012), reproduction (Bolden 2000), recruitment success (Berkstrom et al. 2012), and nutrient transfer (Meyer et al. 1983). Therefore, enhancing our understanding of fish movement patterns within and between various estuarine habitats is critical to the management and conservation of fish populations and habitats on which they depend (e.g., identifying discrete stock units).

Mobile fish species capable of traveling large distances (i.e., >5 km-day⁻¹) increase the linkages and potential for connectivity among habitats within estuarine seascapes (Rosenblatt and Heithaus 2011; McCauley et al. 2012; McMahan et al. 2012). Fish behavior can be highly variable, with a number of factors affecting a fish's decision to move. For example, movement and habitat choice can

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vary with individual preference and habitat complexity (Popple and Hunte 2005), different degrees of predation pressure (Martin et al. 2010), resource availability (Hammerschlag et al. 2010), seasonally (Barbour et al. 2014; Ketchum et al. 2014), and between contingents of fish (Afonso et al. 2009). Here, we explore the movement behaviors of a relatively large mobile predator among different marsh complexes within a temperate estuary and the potential implications of this behavior on seascape-level connectivity of marsh complexes.

Salt marsh (*Spartina alterniflora*) complexes are composed of a mosaic of salt marsh, seagrass, oyster reef, and interspersed mud-sand flat spatially separated from other structured habitats (most typically other marsh complexes) by deeper channels or expanses of unstructured bottom. Connectivity, resulting from fish movement, has been explored at small (tens of metres) spatial scales in relation to movement of considerably less mobile fish (Able et al. 2012). Estuarine-scale (kilometres) connectivity among marsh complexes, however, is less well characterized. Identifying the level of linkages between individual salt marsh complexes would help frame our understanding of whether whole estuaries function as the fundamental unit of “habitat” for large mobile fishes versus a series of relatively discrete habitat units for subpopulations of a given species.

Red drum (*Sciaenops ocellatus*), common in estuaries from Virginia to Texas, is highly sought after by recreational fishermen. As subadults (up to age 5), red drum inhabit estuarine marsh complexes and nearshore habitats and forage on small fishes and crustaceans (Scharf and Schlight 2000). Individuals are capable of traveling large distances (>10 km-week⁻¹) and are often found occupying a variety of estuarine habitats across a wide range of salinities in temperate estuaries (Bacheler et al. 2009a, 2009b). Because they are considered highly mobile and use a wide range of estuarine habitats, red drum are presumed to increase the connectivity of spatially separated salt marsh complexes within estuaries over tidal, diel, and seasonal scales.

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

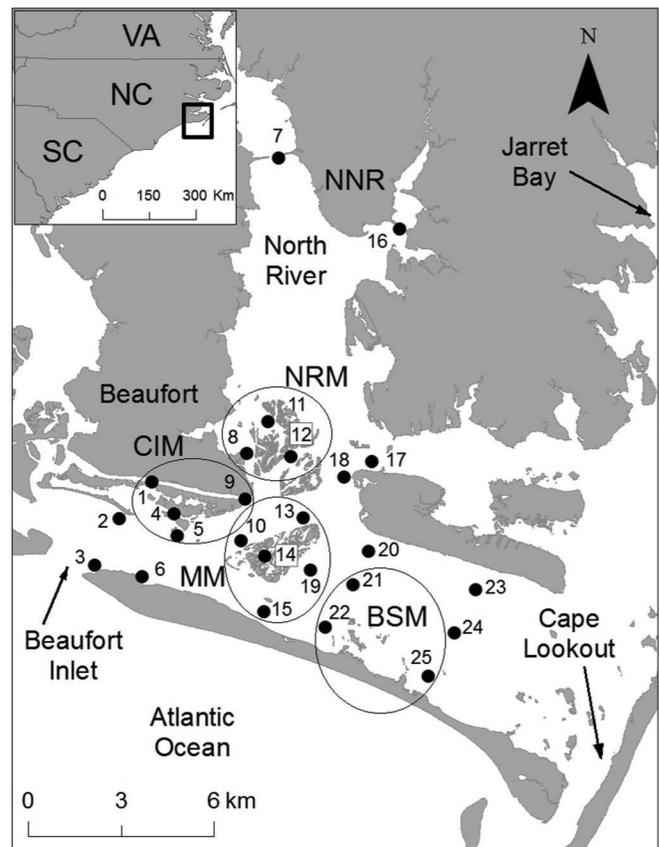
Methods

Study area

We acoustically tracked the movement of 34 subadult red drum over 5 months within a temperate estuary near Cape Lookout, North Carolina (Fig. 1). The shallow estuary of North River and Back Sound covers an area of 68 km² from Beaufort Inlet (western extent of study system) to Bardens Inlet at Cape Lookout (eastern extent). The estuary contains multiple salt marsh complexes, large expanses of shallow unvegetated bottom, and deeper channels. Within the study area, we deployed an array of 25 Vemco VR2W hydrophones to detect red drum movement, specifically among four distinct salt marsh complexes (Fig. 1).

Within each marsh complex, multiple hydrophones were deployed to increase the probability of detection when fish were

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



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

Tagging and tracking

We collected subadult red drum (550 ± 15 mm total length, mean ± 1 standard error (SE)) from different locations within the study area via hook and line (n = 24) or large mesh (12.7 cm mesh) gill nets (n = 10) during July–October 2011 (Table 1). A coded acoustic transmitter (LOTEK Wireless Inc., MM-MR-11-28, also used in a companion fine-scale tracking study; see Fodrie et al. 2015) was implanted into the body cavity of each fish following procedures similar to Dresser and Kneib (2007). These transmitters emitted both LOTEK Wireless and Vemco coded signals and therefore were all detectable with the VR2W (Vemco) receivers. Following tag implantation, fish were held for 24 h for observation before being released into the southwestern-most bay within the MM complex

Table 1. Summary of 34 red drum tagged with acoustic transmitters and tracked within the array of VEMCO hydrophones within the North River and Back Sound Estuary in central North Carolina, 2011.

Fish ID	Capture location	Release date	Total length (mm)	Mass (kg)	Total detections	Stations visited	Marsh complexes visited	Days at liberty (acoustics)	Days at liberty (recapture)	Distance to recapture (km)
RD01	JB	13 July	488	1.1	249	10	3	4	—	—
RD02	JB	14 July	490	1.3	9	1	1	3	—	—
RD03*	JB	14 July	490	1.4	0	0	0	0	420	5.13
RD04	JB	14 July	480	1.1	977	2	1	23	—	—
RD05	JB	15 July	514	1.6	396	4	2	15	—	—
RD06	JB	15 July	515	1.5	15	1	1	3	—	—
RD07	JB	15 July	503	1.3	126	5	1	126	—	—
RD08	NRM	16 Aug.	559	2	550	11	3	76	—	—
RD09	NRM	16 Aug.	520	1.6	499	1	1	37	—	—
RD10	NRM	16 Aug.	365	0.6	101	1	1	35	—	—
RD11	NRM	16 Aug.	505	1	151	4	1	28	—	—
RD12*	NRM	16 Aug.	340	0.6	0	0	0	0	425	14.25
RD13	JB	3 Sept.	565	2	14 140	6	2	62	—	—
RD14	NRM	3 Sept.	341	0.6	138	4	2	30	—	—
RD15	NRM	13 Sept.	775	4	2 159	9	2	46	—	—
RD16	NRM	13 Sept.	755	4.5	38	3	1	1	—	—
RD17*	NRM	13 Sept.	549	1.6	2 610	8	3	34	2	0
RD18*	NRM	30 Sept.	563	1.6	1 199	5	1	32	39	38
RD19	MM	30 Sept.	556	1.5	896	2	1	43	—	—
RD20*	CIM	30 Sept.	568	2	736	7	2	49	54	2.88
RD21	NRM	30 Sept.	600	2.3	2 316	4	1	26	—	—
RD22	MM	4 Oct.	610	2.2	636	5	2	31	—	—
RD23	NRM	4 Oct.	562	1.6	110	6	3	5	—	—
RD24*	NNR	4 Oct.	645	2.6	1 361	7	2	49	50	0
RD25*	NRM	4 Oct.	612	2.3	301	9	2	7	7	5.86
RD26	NRM	4 Oct.	585	1.9	700	6	2	48	—	—
RD27	JB	6 Oct.	600	2	1 128	7	2	21	—	—
RD28	JB	6 Oct.	612	2.3	6 786	10	2	75	—	—
RD29	MM	6 Oct.	556	1.6	193	4	2	52	—	—
RD30*	NNR	6 Oct.	638	2.8	105	3	1	7	10	9.21
RD31	NRM	6 Oct.	555	1.5	1	1	1	1	—	—
RD32	NRM	10 Oct.	550	1.6	12 721	9	3	70	—	—
RD33*	CIM	10 Oct.	602	2.2	314	2	2	25	179	1.83
RD34	MM	10 Oct.	534	1.5	325	7	3	43	—	—

Note: Fish IDs marked with an asterisk (*) are fish that were recaptured by fishermen. Capture location indicates where fish were originally caught for this study: Jarret Bay (JB), North River Marsh (NRM), Middle Marsh (MM), Carrot Island Marsh (CIM), Northern North River (NNR).

(Fig. 1). Fish monitored in this study were the same individuals tracked in a companion project analyzing fine-scale habitat use within MM, therefore requiring all fish to be released in the same location (Fodrie et al. 2015). Individual fish were released intermittently starting 12 July, with the last fish being released on 9 October. At regular 1 min intervals, the transmitter emitted a pulsed chirp unique to each fish, which was used to identify the presence of each individual within range of a hydrophone. For each detection, the hydrophone recorded the transmitter ID, date, and time information, and we downloaded these data monthly. Owing to potential discrepancies in behavior as a result of capture, tagging, and subsequent release back into the environment, we excluded detections during the first 24 h after being released from our movement analyses. Additionally, as a result of using a single-release location, extrapolating patterns and processes to fish being released in other marsh and non-marsh complexes could be limited; however, the faunal communities and the quality and quantity of available habitats in MM are representative of the marsh complexes in this estuary (sensu Baillie et al. 2015). Therefore, we hypothesize that red drum would behave similarly if released in other similar marsh complexes. Prior to conducting analyses, we used the false detections analyzer within VEMCO's data processing software (VUE) to remove any false detections. Additionally, we examined the detection data to ensure that all detections were from live individuals. A deceased individual can be identified when a transmitter is detected continuously at a single

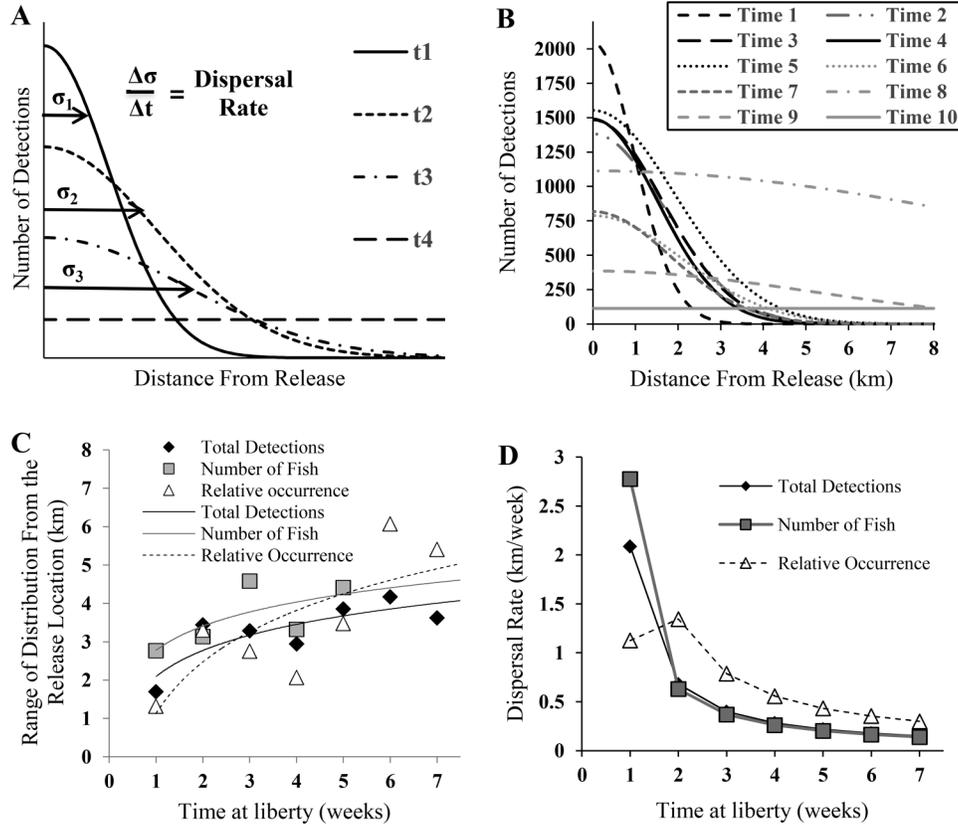
hydrophone, with no detections occurring at any other stations, for extended periods of time.

Dispersal patterns away from Middle Marsh release location

Understanding connectivity in estuarine systems requires knowledge of the rate at which fish move throughout the estuary over hours to months. We calculated the rate of dispersal away from the release location in the southwestern-most embayment within MM. Red drum detections were separated into ten, 6-day time bins, roughly representing weeks since being released into the estuary (weeks at liberty hereinafter). We then established three detection metrics: (1) the raw number of detections (total detections hereinafter), reflecting the number of times all individuals were detected, collectively, at each hydrophone during each week at liberty; (2) the number of individuals that visited each hydrophone during each week at liberty; and (3) a weighted number of detections, defined as "relative occurrence", at each hydrophone during each week at liberty. We chose to look at the number of fish visiting hydrophones to supplement the detection volume data (i.e., total detections). Owing to the fact that the total number of detections for any individual hydrophone or group of hydrophones could result from "residency" of a single fish, we evaluated how many individuals were detected at each hydrophone during each week at liberty (metric 2). The third metric was designed to address a potential bias of individuals with disproportionately higher number of detections "swamping" total

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



detection (metric 1) patterns. To accomplish this, we standardized total detections by dividing a fish's number of detections at each hydrophone by the total number of detections collectively for that individual at all hydrophones. In doing so, "relative occurrence" at individual hydrophones was scaled between 0 and 1 for each week at liberty for each fish. Each fish's relative occurrence value at each hydrophone was then summed to generate final relative occurrence values for analysis.

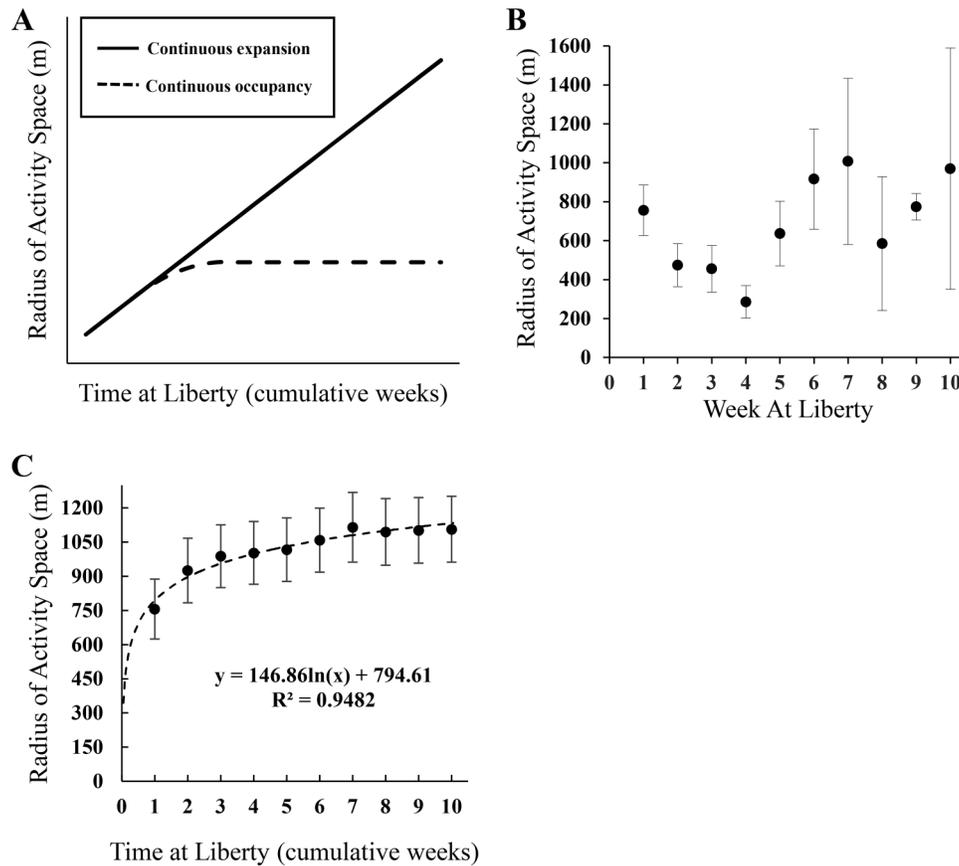
We adopted the general approaches of inspecting animal movement outlined by Ergon and Gardner (2014) by quantifying dispersal patterns as changes in the three detection metrics across our hydrophones, each of known distance from the release point in MM, through time. We first plotted the relationship between our detection metrics at each hydrophone and the straight-line distance from the release location to the respective hydrophone for each weekly time bin. Next, normal distribution curves were fit through the data points to characterize the distribution of the detection metrics for each weekly bin (Fig. 2A). We used the resulting standard deviation (sigma, σ) from the weekly normal distribution curves to represent the relative range of fish distribution (measured in kilometres). For the analysis, we used two standard deviations (2σ) representing 95% of the distribution range. This value therefore represented the distance from the release location in which 95% of fish detections occurred during that week, hereinafter referred to as "relative distribution". As fish dispersed from the release location, the distribution of detections as a function of distance (of hydrophones) from the release location should "flatten", resulting in increasing 2σ values over time (Fig. 2A). By week 7 in our study, the distribution of detections calculated from total detection and relative occurrence metrics had flattened to the point that 2σ values were unreliably large,

and therefore we ceased to evaluate relative distribution beyond this point (Fig. 2B). When analyzing the number of individuals detected at each hydrophone (detection metric 2 listed above), 2σ became unreliably large after week 5. Dispersal rate, the change in 2σ over time ($\Delta 2\sigma/\Delta t$; $t = \text{time}$), was calculated from the logarithmic trend lines fit to weekly relative distribution values. Dispersal rates were calculated through 7 weeks at liberty for each detection metric. Although relative distribution values estimated from analyzing the number of individuals visiting each hydrophone were not obtainable for weeks 6 and 7, we were able to extrapolate dispersal rates for this time frame using the trend line fit to data obtained for weeks 1–5.

Activity space

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

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



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

Residency

To examine patterns of residency and exchange of fish among individual marsh complexes, we calculated the probability of fish moving between each of the marsh complexes in our study area. Each day that an individual red drum was detected, we randomly selected one detection that day and recorded the location of that detection (primary detection). Relative to the time stamp of the primary detection, we identified the location of that same fish 24 h later, or as soon as possible thereafter, based on the marsh complex groupings above (subsequent detection). We chose a 24 h time step to allow for two full tidal cycles and one day-night cycle, both of which can impact fish movement behavior and habitat choice (Pople and Hunte 2005; Dresser and Kneib 2007). This procedure was repeated each calendar day for which each individual was detected throughout the study. We conducted 100 iterations, with replacement, of this sampling procedure to ensure that a representative sample of randomly selected detection data

points were incorporated. Therefore, for each day a fish was detected, we performed this procedure using 100 randomly selected detections. From these observations, we created a connectivity matrix identifying the probabilities that individuals observed in a given marsh complex (primary detection) will be relocated in the same marsh complex, a different marsh complex, or a non-marsh location after 24 h (subsequent detection). Probabilities ranged from 0 (low chance of being detected in subsequent location) to 100 (high chance of being detected in subsequent location). A high probability of being detected within the same marsh complex suggests high residency. Further, we explored the consistency of these behaviors over time by conducting the same analysis with time lags of 48 h and 1 week following the primary detections.

Finally, we assured that the uneven distribution of hydrophones within the marsh complexes (e.g., MM contained five hydrophones while the others had three to four each) did not significantly alter our observations and understanding of movement behavior. We accomplished this by conducting our residency analysis with two hydrophones removed from MM. We selected the three hydrophones with the most detections and ran our analysis again three times with all combinations of two of these three hydrophones being removed from the data set. Therefore, for each subsequent run of the analysis, MM was represented using only three hydrophones. Owing to consistencies in our original test for residency patterns using different time lags as well as the consistency in the reanalysis of the data set with a 24 h lag, we did not perform this test using time lags of 48 h or 1 week. The resulting detection probabilities did not differ notably from the original

analysis; therefore, we proceeded to include all hydrophones from MM in our subsequent analysis of residency patterns.

Fishermen recaptures

Throughout the study, recreational and commercial fishermen reported occurrences of capturing our tagged red drum. Using the date and location of the reported captures, we calculated the number of days at liberty between release and recapture and the straight-line distance from the release location to the recapture location. We examined the correlation between days at liberty and distance from the release location to suggest whether individuals exhibited random (low correlation) or nonrandom (high correlation) movement away from the study area. Correlation analysis was conducted in JMP Pro12.

Results

We recorded 51 987 detections overall, averaging 1625 ± 593 (mean ± 1 standard error) detections per fish from 32 of the 34 tagged individuals (Table 1). The two individuals that were not detected were recaptured outside of the study array by fishermen, indicating that these individuals simply left the array without being detected. Only four of those 32 fish were detected fewer than 100 times. On average, individuals visited 5 ± 1 hydrophone stations and the number of days that individuals were recorded within the hydrophone array ranged between 0 and 126 with a mean of 33 ± 5 days at liberty. Six individuals were detected visiting a combination of three marsh complexes, while another 13 were only detected in two complexes. The remaining 13 fish were detected only in the MM complex. Of the 34 fish released, nine individuals were recaptured by fishermen during or following our 5-month tracking effort. The time at liberty of these nine fish ranged from 2 to 425 days, and the straight-line distance from the release location to the recapture location varied from 0 up to 38 km. There was no distinguishable relationship between days at liberty and distance from release location to recapture location (Pearson's $r = 0.008$).

Dispersal

Over the course of the study, all three dispersal metrics indicated initial dispersal from the release location during the first 2 weeks followed by minimal dispersal within the study area over the remainder of the study (Fig. 2C). Relative distribution calculated from total detections indicated that fish dispersed to a range of 1.69 km during the first week and 3.44 km after 2 weeks. The change in relative distribution each week from week 3 through week 7 was less than 0.50 km. Initial dispersal rate calculated based on total detections was $2.09 \text{ km}\cdot\text{week}^{-1}$ during week 1 before decreasing exponentially to below $0.75 \text{ km}\cdot\text{week}^{-1}$ during the remaining 6 weeks (Fig. 2D). Relative distribution range observed from measurements of relative occurrence was similar to that measured by total detections during the first (1.33 km) and second (3.30 km) weeks at liberty followed by minor fluctuations through week 7 (Fig. 2C). Based on the relative occurrence of fish, the calculated dispersal rate increased slightly from week 1 ($1.13 \text{ km}\cdot\text{week}^{-1}$) to week 2 ($1.34 \text{ km}\cdot\text{week}^{-1}$) followed by an exponential decline through week 7 (Fig. 2D). Finally, relative distribution observed from measurements of the number of fish at each hydrophone displayed the greatest increase during the first week (2.77 km), followed by fluctuating distribution range through week 5 (Fig. 2C). Dispersal rate calculated based on number of fish at each hydrophone was greatest during week 1 ($2.78 \text{ km}\cdot\text{week}^{-1}$), followed by an exponential decline through week 7 ($0.14 \text{ km}\cdot\text{week}^{-1}$; Fig. 2D).

The average of all three detection metrics indicated that after the first 2 weeks at liberty, the range of dispersal was approximately 3.29 km, which was comparable to the distance across the MM complex from the release location (2.73 km). Although dispersal measurements were calculated to represent distribution in all directions, the minimal number of detections at hydrophones one

Table 2. Connectivity matrix indicating the number (N) of randomly selected detections for each marsh complex and non-marsh sites and the location probabilities (%) of subsequent detection after (i) 24 hours, (ii) 48 hours, and (iii) 1 week.

Primary detection location	N	Subsequent detection location				
		BSM	CIM	MM	NRM	Non-marsh
(i) ≥ 24 hours						
BSM	3 108	86.04	0.00	8.72	0.00	5.24
CIM	608	0.00	50.00	26.81	10.69	12.50
MM	53 426	1.12	1.36	93.34	0.21	3.96
NRM	2 291	0.00	0.00	0.09	98.87	1.05
Non-marsh	2 249	11.38	0.00	48.47	0.00	40.15
(ii) ≥ 48 hours						
BSM	2 857	86.66	0.00	9.45	0.00	3.89
CIM	616	0.00	44.97	26.79	28.25	0.00
MM	48 867	1.69	1.20	90.62	0.54	5.96
NRM	2 146	0.00	1.07	0.00	98.93	0.00
Non-marsh	2 124	11.35	0.00	51.84	0.00	36.82
(iii) ≥ 1 week						
BSM	2 457	86.57	0.00	12.70	0.00	0.73
CIM	527	0.00	0.00	29.41	70.40	0.19
MM	43 743	1.89	1.39	88.71	0.94	7.07
NRM	1 805	0.00	0.00	0.00	100.00	0.00
Non-marsh	1 684	14.55	0.00	67.52	0.00	17.93

Note: The connectivity matrix indicates the probabilities of fish remaining in the same location as the primary detection (highlighted values along the diagonal of the matrix) or moving to a new location (nonhighlighted values). Probabilities ranged from 0, low chance of being detected in subsequent location, to 100, high chance of being detected in subsequent location. Marsh complex names: Back Sound Marsh (BSM), Carrot Island Marsh (CIM), Middle Marsh (MM), and North River Marsh (NRM).

through six to the west of MM (0.08% of total) indicated that the dispersal direction was predominantly towards the east and north of the release location, along the main axis of MM.

Activity space

Weekly mean radius of activity space ranged from 286 to 1007 m, with an overall mean (\pm SE) of 686 ± 16.1 m and did not change appreciably over time (Fig. 3B). Calculations of cumulative activity space indicated that the greatest increase in mean radius occurred during week 1 (756 m) and week 2 (925 m; Fig. 3C). The size of the cumulative activity space increased by small increments (<10% per week) over the remaining 8 weeks of observations. Overall, the fish displayed only a 20% increase in the radius of their cumulative activity space between week 2 and week 10. Similar to results from dispersal patterns, the cumulative activity space after 2 weeks at liberty (2.69 km^2) scaled approximately to the area of the MM complex (2.75 km^2).

Residency

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

In general, when fish were not detected in the same marsh complex after 24 h from the primary detection, they were most

likely to be detected in the MM complex during subsequent detections. There was evidence for a lack of direct linkages (i.e., subsequent detection probabilities equal to zero) between several marsh complexes (MM–NRI, BSM–CIM, and NRM–BSM). Finally, none of the fish in this study were detected at either of the two stations located in the northern part of North River (stations 6 and 16), suggesting that tagged fish did not move to marsh complexes in the upper river. Extending the time lag between primary and subsequent detections resulted in very similar patterns of residency within BSM, MM, and NRM. The likelihood of being detected in the same marsh complex 48 h and 1 week later remained >86% in all three marsh complexes. Conversely, fish originally observed in CIM had zero probability of again being detected in that marsh complex after 1 week. When primary detections were observed in CIM, these individuals were now most likely to be detected in NRM after 1 week.

Discussion

Patterns of red drum dispersal, activity space, and residency suggested limited movement between similar salt marsh complexes by a mobile fish during our 5-month study. Dispersal and cumulative activity space metrics indicated that there was minimal sustained occupation of areas outside of the MM complex prior to emigration from the entire study array (further supported by fishermen recapture data). Residency analysis also corroborated dispersal and activity-space data, further suggesting limited movement between the marsh complexes we monitored. Thus, our results imply that red drum induce minimal linkages among these spatially separated habitat complexes on a subannual scale.

Limited seascape connectivity in this study highlights the potential for these salt marsh complexes to represent relatively isolated, discrete food webs within the estuary (Sheaves 2009). This runs counter to suggestions that mobile consumers facilitate nutrient exchange within estuaries through consumption and excretion and may impact primary productivity in adjacent seascapes when consumer movement between habitats is high (Allgeier et al. 2013; Hyndes et al. 2014). Rather, our results suggest that consumer-driven transfer of nutrients may be primarily a local phenomenon, with relatively tighter recycling within each marsh complex. Additionally, red drum could potentially impose greater predation pressure locally on their prey if movement away from their preferred marsh complex is limited. Conversely, seasonally high abundances of food resources throughout the lower estuary could provide fitness incentives to limit movement away from MM or any marsh complex in the lower North River (Dudley and Judy 1973; Williams 1955).

Assigning value to individual habitats and seascapes is an essential component to the management of fish populations and the habitats they use. Preferred habitats, measured by the amount of time fish rely on those habitats and the benefits they provided to the success of the population, weigh heavily when evaluating habitat value (sensu Nagelkerken et al. 2015). Although red drum demonstrated high levels of residency within MM in this study, comparing this marsh complex as a preferred location with the alternative complexes is beyond the scope of this study given a potential bias in releasing all fish within this marsh complex. Nonetheless, we expect that red drum would behave in a similar manner if released in other proximate marsh complexes due to similarities in fauna and habitat (Baillie et al. 2015). The few individuals (three) that moved into one of the alternative marsh complexes for extended periods during the study, with the exception of fish moving to CIM, displayed high residency at their new location. Although two of these fish returned to their initial capture location in NRM, there is little evidence suggesting that red drum movement is influenced by any homing behavior such as that previously documented for some large-bodied fish (Taylor et al. 2017). Fourteen of the 16 individuals initially captured in

NRM remained in the MM system during the study, and only two out of 30 translocated fish were observed returning to their initial capture location.

Ontogenetic migrations of red drum generally shift the distribution of 1- to 3-year-old fish to lower, more saline portions of coastal estuaries (Bacheler et al. 2009b). However, this pattern is not all inclusive, as 2-year-old fish, equivalent to those used in our study, are still known to occupy low salinity (<10 ppt) waters of North Carolina estuaries (Bacheler et al. 2009a), specifically the upper North River estuary (M. Kenworthy, personal observations). Regardless of expectations that red drum in our study system would move to occupy this region of the estuary, none of the tagged red drum were detected at our two upper estuary stations. Furthermore, only a limited number of fish (four) were detected as far up-estuary as NRM (Fig. 1). Our data contribute to the growing consensus in the literature that suggests red drum rarely move upstream as subadults (Dresser and Kneib 2007; Bacheler 2009b). Occupation of the upper estuary by similar age class fish is likely a result of either individuals settling in this region and remaining or individuals arriving during spring months when a large portion of the subadult population re-enter and distribute within the estuaries (Bacheler et al. 2009b). Connectivity among upper estuary and lower estuary seascapes therefore is likely influenced more by seasonal migrations and ontogenetic movement. The mechanism driving this subpopulation structure deserves further research attention.

Overall, red drum displayed high levels of residency within the MM complex with limited seascape linkages. However, some fish were observed making intermittent excursions between MM and both CIM and BSM, potentially establishing linkages with these other complexes. These excursions almost always occurred during nighttime hours and were short in duration. These movement patterns could reflect foraging excursions to the habitats located between the associated marsh complexes. For example, the sandflats between MM and BSM contain isolated patches of seagrass, which red drum could be targeting during preferred crepuscular and nighttime foraging hours (Facendola and Scharf 2012). In comparison, the sandflats between MM and CIM do not contain seagrass patches. This area, located near one of two main channels flowing out of North River, is a potential corridor for crustaceans (crabs and shrimp) emigrating out of the upper North River estuary at night and could be serving as a source of food. Therefore, these excursions could facilitate linkages within the estuarine seascape via nutrient exchange between habitats proximate to MM and the MM complex, similar to that observed in other ecosystems (e.g., coral reefs) (Beets et al. 2003), even if red drum are not consistently connecting distinct marsh complexes within this estuary. Following the flow of energy within coastal ecosystems is important for understanding the values and contributions of individuals towards productivity within an estuary (Heck et al. 2008). Although these assumptions are speculative without direct measurements of nutrient exchange within the system, identifying the movement behaviors of fish with the capacity to facilitate this nutrient exchange is critical to identifying potential energy transport dynamics within this estuary.

The spatial and temporal scale at which ecological processes are observed can influence our understanding of dynamics within an ecosystem (Levin 1992). For instance, over the time frame of this study, the distance between marsh complexes could play a crucial role in assessing linkages among them (i.e., marshes in our study were relatively far apart, and therefore connectivity was low). However, considering previously reported daily movements for red drum (3.4 ± 0.6 km; Dance and Rooker 2015), we do not anticipate that this limited connectivity in our study system. On average, the straight-line distance between marsh complexes in our array was less than 2 km, except for the distances between BSM and both CIM and NRM, which were each ~5 km. We do acknowledge, however, that the location of MM in the middle of the study

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

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

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References

Able, K.W., Vivian, D.N., Petruzzelli, G., and Hagan, S.M. 2012. Connectivity Among Salt Marsh Subhabitats: Residency and Movements of the Mummichog (*Fundulus heteroclitus*). *Estuar. Coasts*, **35**(3): 743–753. doi:10.1007/s12237-011-9471-x.

Afonso, P., Fontes, J., Holland, K.N., and Santos, R.S. 2009. Multi-scale patterns of habitat use in a highly mobile reef fish, the white trevally *Pseudocaranx dentex*, and their implications for marine reserve design. *Mar. Ecol. Prog. Ser.* **381**(2): 273–286. doi:10.3354/meps07946.

Allgeier, J.E., Yeager, L.A., and Layman, C.A. 2013. Consumers regulate nutrient limitation regimes and primary production in seagrass ecosystems. *Ecology*, **94**(2): 521–529. doi:10.1890/12-1122.1. PMID:23691670.

Bachele, N.M., Paramore, L.M., Buckel, J.A., and Hightower, J.E. 2009a. Abiotic and biotic factors influence the habitat use of an estuarine fish. *Mar. Ecol. Prog. Ser.* **377**: 263–277. doi:10.3354/meps07805.

Bachele, N.M., Paramore, L.M., Burdick, S.M., Buckel, J.A., and Hightower, J.E. 2009b. Variation in movement patterns of red drum (*Sciaenops ocellatus*) inferred from conventional tagging and ultrasonic telemetry. *Fish. Bull.* **107**: 405–419.

Baggio, J.A., Salau, K., Janssen, M.A., Schoon, M.L., and Bodin, Ö. 2011. Landscape connectivity and predator-prey population dynamics. *Landsc. Ecol.* **26**: 33–45. doi:10.1007/s10980-010-9493-y.

Baillie, C.J., Fear, J.M., and Fodrie, F.J. 2015. Ecotone effects on seagrass and saltmarsh habitat use by juvenile nekton in a temperate estuary. *Estuar. Coasts*, **38**: 1414–1430. doi:10.1007/s12237-014-9898-y.

Barbour, A.B., Adams, A.J., and Lorenzen, K. 2014. Size-based, seasonal, and multidirectional movements of an estuarine fish species in a habitat mosaic. *Mar. Ecol. Prog. Ser.* **507**: 263–276. doi:10.3354/meps10837.

Beets, J., Muehlstein, L., Haight, K., and Schmitges, H. 2003. Habitat connectivity in coastal environments: patterns and movements of Caribbean coral reef fishes with emphasis on bluestriped grunt. *Gulf Car. Res.* **14**(2): 29–42. doi:10.18785/gcr.1402.03.

Berkström, C., Gullström, M., Lindborg, R., Mwanya, A.W., Yahya, S.A.S., Kautsky, N., and Nyström, M. 2012. Exploring “knowns” and “unknowns” in tropical seascape connectivity with insights from East African coral reefs. *Estuar. Coast. Shelf Sci.* **107**: 1–21. [Elsevier Ltd.] doi:10.1016/j.ecss.2012.03.020.

Bolden, S.K. 2000. Long-distance movement of a Nassau grouper (*Epinephelus striatus*) to a spawning aggregation in the central Bahamas. *Fish. Bull.* **98**(3): 642–645.

Boström, C., Pittman, S.J., Simenstad, C., and Kneib, R.T. 2011. Seascape ecology

of coastal biogenic habitats: advances, gaps, and challenges. *Mar. Ecol. Prog. Ser.* **427**: 191–217. doi:10.3354/meps09051.

Dance, M.A., and Rooker, J.R. 2015. Habitat- and bay-scale connectivity of sympatric fishes in an estuarine nursery. *Estuar. Coast. Shelf Sci.* **167**: 447–457. [Elsevier Ltd.] doi:10.1016/j.ecss.2015.10.025.

Dresser, B.K., and Kneib, R.T. 2007. Site fidelity and movement patterns of wild subadult red drum, *Sciaenops ocellatus* (Linnaeus), within a salt marsh-dominated estuarine landscape. *Fish. Manage. Ecol.* **14**: 183–190. doi:10.1111/j.1365-2400.2007.00526.x.

Drymon, J.M., Ajemian, M.J., and Powers, S.P. 2014. Distribution and dynamic habitat use of young bull sharks *Carcharhinus leucas* in a highly stratified Northern Gulf of Mexico estuary. *PLoS ONE*, **9**(5): e97124. doi:10.1371/journal.pone.0097124. PMID:24841925.

Dudley, D.L., and Judy, M.H. 1973. Seasonal abundance and distribution of juvenile blue crabs in Core Sound, N.C. 1965–68. *Chesapeake Sci.* **14**(1): 51–55. doi:10.2307/1350703.

Ergon, T., and Gardner, B. 2014. Separating mortality and emigration: modelling space use, dispersal and survival with robust-design spatial capture-recapture data. *Methods Ecol. Evol.* **5**(12): 1327–1336. doi:10.1111/2041-210X.12133.

Facendola, J.J., and Scharf, F.S. 2012. Seasonal and ontogenetic variation in the diet and daily ration of estuarine red drum as derived from field-based estimates of gastric evacuation and consumption. *Mar. Coast. Fish.* **4**(1): 546–559. doi:10.1080/19425120.2012.699018.

Fodrie, F.J., Yeager, L.A., Grabowski, J.H., Layman, C.A., Sherwood, G.D., and Kenworthy, M.D. 2015. Measuring individuality in habitat use across complex landscapes: approaches, constraints, and implications for assessing resource specialization. *Oecologia*, **178**(1): 75–87. [Springer Berlin Heidelberg.] doi:10.1007/s00442-014-3212-3. PMID:25669451.

Hammerschlag, N., Heithaus, M.R., and Serafy, J.E. 2010. Influence of predation risk and food supply on nocturnal fish foraging distributions along a mangrove-seagrass ecotone. *Mar. Ecol. Prog. Ser.* **414**: 223–235. doi:10.3354/meps08731.

Heck, K.L., Jr., Carruthers, T.J.B., Duarte, C.M., Randall, A., Kendrick, G., Orth, R.J., and Williams, S.W. 2008. Trophic transfers from seagrass meadows subsidize diverse marine and terrestrial consumers. *Ecosystems*, **11**: 1198–1210. doi:10.1007/s10021-008-9155-y.

Hyndes, G.A., Nagelkerken, I., McLeod, R.J., Connolly, R.M., Lavery, P.S., and Vanderklift, M.A. 2014. Mechanisms and ecological role of carbon transfer within coastal seascapes. *Biol. Rev. Camb. Philos. Soc.* **89**: 232–254. doi:10.1111/brv.12055. PMID:23980752.

Ketchum, J.T., Hearn, A., Klimley, A.P., Peñaherrera, C., Espinoza, E., Bessudo, S., Soler, G., and Arauz, R. 2014. Inter-island movements of scalloped hammerhead sharks (*Sphyrna lewini*) and seasonal connectivity in a marine protected area of the eastern tropical Pacific. *Mar. Biol.* **161**(4): 939–951. doi:10.1007/s00227-014-2393-y.

Levin, S.A. 1992. The problem of pattern and scale in ecology: The Robert H. MacArthur Award Lecture. *Ecology*, **73**(6): 1943–1967. doi:10.2307/1941447.

Martin, C.W., Fodrie, F.J., Heck, K.L., and Mattila, J. 2010. Differential habitat use and antipredator response of juvenile roach (*Rutilus rutilus*) to olfactory and visual cues from multiple predators. *Oecologia*, **162**(4): 893–902. doi:10.1007/s00442-010-1564-x. PMID:20127367.

McCauley, D.J., Young, H.S., Dunbar, R.B., Estes, J.A., Semmens, B.X., and Micheli, F. 2012. Assessing the effects of large mobile predators on ecosystem connectivity. *Ecol. Appl.* **22**(6): 1711–1717. doi:10.1890/11-1653.1. PMID:23092009.

McMahon, K.W., Berumen, M.L., and Thorrold, S.R. 2012. Linking habitat mosaics and connectivity in a coral reef seascape. *Proc. Natl. Acad. Sci.* **109**: 15372–15376. doi:10.1073/pnas.1206378109. PMID:22949665.

Meyer, J.L., Schultz, E.T., and Helfman, G.S. 1983. Fish schools: an asset to corals. *Science*, **220**(4601): 1047–1049. doi:10.1126/science.220.4601.1047. PMID:17754550.

Nagelkerken, I., Sheaves, M., Baker, R., and Connolly, R.M. 2015. The seascape nursery: a novel spatial approach to identify and manage nurseries for coastal marine fauna. *Fish. Fish.* **16**(2): 362–371. doi:10.1111/faf.12057.

Olds, A.D., Pitt, K.A., Maxwell, P.S., and Connolly, R.M. 2012. Synergistic effects of reserves and connectivity on ecological resilience. *J. Appl. Ecol.* **49**(6): 1195–1203. doi:10.1111/jpe.12002.

Polis, G.A., Anderson, W.B., and Holt, R.D. 1997. Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. *Annu. Rev. Ecol. Syst.* **28**: 289–316. doi:10.1146/annurev.ecolsys.28.1.289.

Popple, I.D., and Hunte, W. 2005. Movement patterns of *Cephalopholis cruentata* in a marine reserve in St Lucia, W.I., obtained from ultrasonic telemetry. *J. Fish Biol.* **67**: 981–992. doi:10.1111/j.0022-1112.2005.00797.x.

Reyier, E.A., Lowers, R.H., Scheidt, D.M., and Adams, D.H. 2011. Movement patterns of adult red drum, *Sciaenops ocellatus*, in shallow Florida lagoons as inferred through autonomous acoustic telemetry. *Environ. Biol. Fishes*, **90**: 343–360. doi:10.1007/s10641-010-9745-3.

Rosenblatt, A.E., and Heithaus, M.R. 2011. Does variation in movement tactics and trophic interactions among American alligators create habitat linkages? *J. Anim. Ecol.* **80**: 786–798. doi:10.1111/j.1365-2656.2011.01830.x. PMID:21418209.

Scharf, F.S., and Schlicht, K.K. 2000. Feeding habits of red drum (*Sciaenops ocellatus*) in Galveston Bay, Texas: seasonal diet variation and predator-prey size relationships. *Estuaries*, **23**(1): 128. doi:10.2307/1353230.

Secor, D.H., Rooker, J.R., Zlokovitz, E., and Zdanowicz, V.S. 2001. Identification of

- riverine, estuarine, and coastal contingents of Hudson River striped bass based upon otolith elemental fingerprints. *Mar. Ecol. Prog. Ser.* **211**(1968): 245–253. doi:[10.3354/meps211245](https://doi.org/10.3354/meps211245).
- Sheaves, M. 2009. Consequences of ecological connectivity: the coastal ecosystem mosaic. *Mar. Ecol. Prog. Ser.* **391**: 107–115. doi:[10.3354/meps08121](https://doi.org/10.3354/meps08121).
- Simpfendorfer, C.A., Heupel, M.R., and Hueter, R.E. 2002. Estimation of short-term centers of activity from an array of omnidirectional hydrophones and its use in studying animal movements. *Can. J. Fish. Aquat. Sci.* **59**(1): 23–32. doi:[10.1139/f01-191](https://doi.org/10.1139/f01-191).
- Taylor, M.D., Payne, N.L., Becker, A., and Lowry, M.B. 2017. Feels like home: Homing of mature large-bodied fish following translocation from a power-station canal. *ICES J. Mar. Sci.* **74**: 301–310. doi:[10.1093/icesjms/fsw168](https://doi.org/10.1093/icesjms/fsw168).
- Williams, A.B. 1955. A contribution to the life histories of commercial shrimps (Penaeidae) in North Carolina. *Bull. Mar. Sci.* **5**(2): 116–146.