Variation in movement patterns of red drum (*Sciaenops ocellatus*) inferred from conventional tagging and ultrasonic telemetry

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Abstract—We used 25 years of conventional tagging data (n=6173 recoveries) and 3 years of ultrasonic telemetry data (n=105 transmitters deployed) to examine movement rates and directional preferences of four age classes of red drum (*Sciaenops ocellatus*) in estuarine and coastal waters of North Carolina. Movement rates of conventionally tagged red drum were dependent on the age, region, and season of tagging. Age-1 and age-2 red drum tagged along the coast generally moved along the coast, whereas fish tagged in oligohaline waters far from the coast were primarily recovered in coastal regions in fall months. Adult (age-4+) red drum moved from overwintering grounds on the continental shelf through inlets into Pamlico Sound in spring and summer months and departed in fall. Few tagged red drum were recovered in adjacent states (0.6% of all recoveries); however, some adult red drum migrated seasonally from overwintering grounds in coastal North Carolina northward to Virginia in spring, returning in fall. Age-2 transmitter-tracked red drum displayed seasonal emigration from a small tributary, but upstream and downstream movements within the tributary were correlated with fluctuating salinity regimes and not season. Large-scale conventional tagging and ultrasonic telemetry programs can provide valuable insights into the complex movement patterns of estuarine fish.

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Recent advances in conventional tagging and ultrasonic telemetry methods have substantially increased our understanding of the ecology of myriad estuarine organisms (e.g., Able and Hales, 1997; Able et al. 2005). For red drum (*Sciaenops ocellatus*), a long-lived estuarine and coastal fish species found along the Gulf and Atlantic coasts, conventional tagging and ultrasonic telemetry have been an invaluable tool to understand mortality rates and habitat use. For instance, fishery returns of conventional tags and the tracking of red drum tagged with ultrasonic transmitters have provided important information about the magnitude and seasonal patterns of fishery harvests and natural deaths (Latour et al., 2001; Bacheler et al., 2008a; Bacheler et al., 2009a). Telemetry has also been used to show that habitat-use patterns of subadult (i.e., ages 1–3) red drum are influenced by both abiotic and biotic factors (Dresser and Kneib, 2007; Bacheler et al., 2009b). However, our understanding of the movement patterns of red drum lags far behind our knowledge of mortality rates and habitat use, despite the fundamental implications of movement to the ecology and sustainable management of the species. For example, movement patterns have been used to determine the appropriate spatial scale of management (i.e., stock structure; Metcalfe, 2006) and to provide information on the ways juveniles move from nurseries to adult habitats (Beck et al., 2001; Gillanders et al., 2003).

The available literature on red drum movement is mixed. Studies conducted over relatively small spatial and temporal scales indicate that subadult red drum movement is limited (Collins et al., 2002; Dresser and Kneib, 2007). It also appears that adult red drum return to their natal estuary to spawn (Patterson et al., 2004). However, genetic differences exist only at very coarse scales (i.e.,

Gulf of Mexico and northwest Atlantic Ocean), not at finer spatial scales (Gold et al., 1993; Seyoum et al., 2000). This apparent discrepancy, whereby subadults show limited movements but genetic makeup is relatively homogeneous within each ocean, can potentially be explained in three ways. First, dispersal of larvae may occur over long distances along the coast, although evidence indicates that red drum spawn in inlets and estuaries (Johnson and Funicelli, 1991; Barrios, 2004; Luczkovich et al., 2008) where larvae are likely locally retained (Chen et al., 1997). Second, despite low movements rates (km/day) by subadults, adult movements may be high enough that genetic variability is homogenized at a basin-wide scale; this hypothesis remains untested because adult movement patterns have not been quantified. Third, in previous examinations of subadult red drum movement at relatively small temporal and spatial scales the full extent of subadult movements may have been missed.

We quantified the large-scale movements of subadult and adult red drum (using 25 years of conventional tagging data) and small-scale movement of subadult red drum (using three years of ultrasonic telemetry data. The specific objective of this work was to examine the effects of age, season, and region on movement patterns of North Carolina red drum. Potential differences in red drum movements by age, region, or season have implications for various aspects of the management (e.g., stock structure, spatial or temporal fishery closures, selectivity patterns) and ecology of the species (e.g., timing and spatial scale of gene flow and population connectivity). We used a variety of quantitative approaches to describe subadult and adult movement patterns, including ultrasonic telemetry, geographic mapping, and circular mapping. This study improves our understanding of the movement of red drum in estuarine and coastal waters of North Carolina and estuarine fish species more generally, and also provides some analytical techniques that are more widely applicable.

Materials and methods

Conventional tagging

Two sources of conventional tagging data were used. The first source was from a tagging study conducted by the North Carolina Division of Marine Fisheries (NCDMF) between 1983 and 2007 when red drum were captured opportunistically with pound nets, hook-and-lines, runaround gill nets, trammel nets, and by electrofishing. Volunteer recreational and commercial fishermen also participated in tagging red drum. The second data source was from a tagging study of subadult red drum during 2005–2007 conducted by North Carolina State University (NCSU) personnel within the lower Neuse River estuary (Bacheler, 2008). In both of these studies, only healthy fish were tagged and released.

Most subadult fish were tagged with internal anchor tags (Floy®, Seattle, WA; FM-84, FM-89SL, and FM-95W) and nylon dart tags (Floy® FT-1 and FT-2), whereas adults were primarily tagged with stainless steel dart tags containing a monofilament core (Floy® FH-69) or, more recently, containing a stainless steel core (Hallprint® SSD wire-through, Victor Harbor, Australia). All tags were labeled with a unique tag number and a "reward" message. All tag types were combined and treated equally in this study. The tag recovery location was either provided as latitude and longitude by fishermen or was estimated from the physical description provided by fishermen. For fishery-dependent tag recoveries, it was assumed that fishing effort was homogeneous over space, the implications of which are elaborated upon in the *Discussion* section.

We used a 6-mo age-length key developed by NCDMF to convert total length of fish at tagging to an estimated age based on a 1 January birthday. The age-length key was based on 17 years of North Carolina red drum ages that were estimated from otoliths, the annuli of which had been validated by Ross et al. (1995). A 6-mo age-length key (January–June and July–December) was used because of rapid summer growth rates that subadult red drum experience in North Carolina waters (Ross et al., 1995). The key provided very good separation of length-groups for fish younger than age 4. Sexually mature red drum were grouped into a single age-bin (age 4 and older [4+]; Ross et al., 1995). Thus, we used four age-groups (ages 1, 2, 3, and 4+) for all analyses. Lengths of fish were grouped into the four age bins as follows: for January–June, age 1: 0–253 mm, age 2: 254–558 mm, age 3: 559–761 mm, and age 4+: greater than 761 mm; for July–December, age 1: 0–507 mm, age 2: 508–710 mm, age 3: 711–812 mm, and age 4+: greater than 812 mm. In previous aging studies of adult red drum in North Carolina, maximum age was determined to be 62 years (Ross et al., 1995), indicating that age-4+ red drum in our study potentially ranged from age 4 to greater than 60.

Specific fishery regulations for red drum in North Carolina should not be a major source of bias in age-specific movements. The fishery regulation history for red drum is complex in North Carolina (see Bacheler et al. [2008a] for details), and currently only fish within a window limit (= a size limit with minimum and maximum length requirements, i.e., 457–686 mm TL, corresponding to ages 1–3) can be harvested legally. However, all ages of red drum are encountered in various (popular and targeted) catch-and-release recreational fisheries, and there are no major temporal or spatial restrictions on these fishing efforts.

To understand the generality of movement patterns of red drum in North Carolina waters, we first tested for differences in movement patterns among four regions (Fig. 1). These regions were the following: 1) eastern Pamlico Sound and the adjacent coastal waters (EPS; the outer banks from the Virginia state line to Cape Lookout), 2) western Pamlico Sound (WPS; waters near mainland areas of northern North Carolina), 3) Neuse

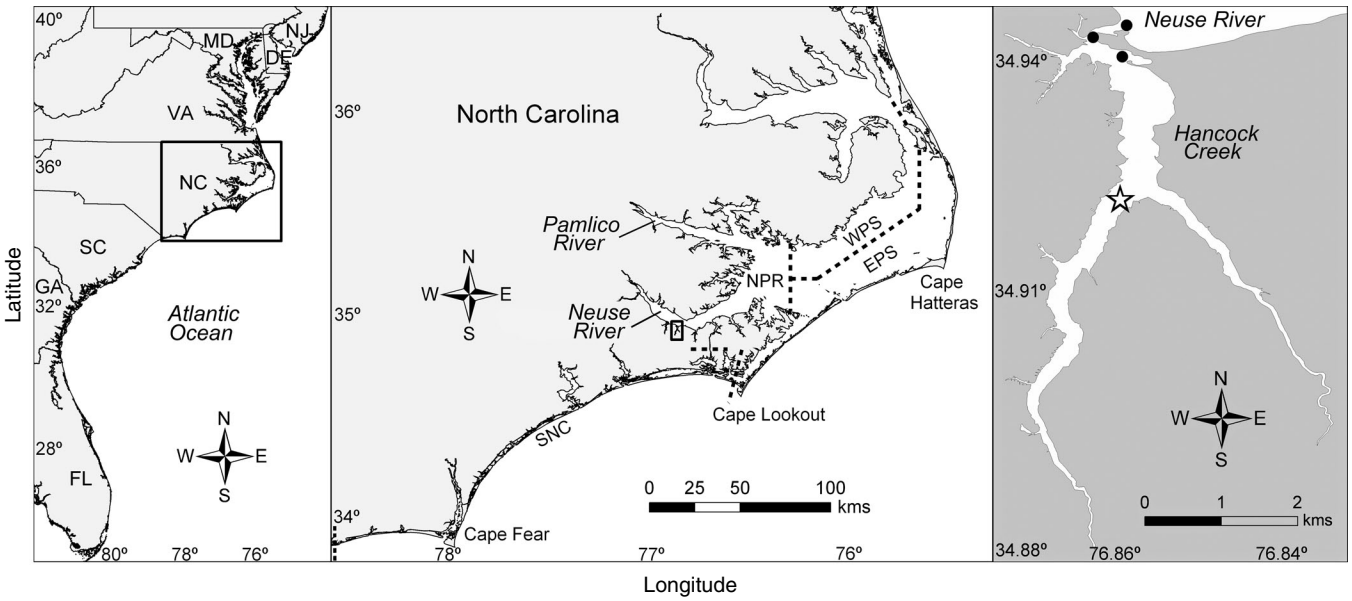

Figure 1

Map of study areas for red drum (*Sciaenops ocellatus*) within coastal and estuarine waters of North Carolina. Left map shows location of coastal North Carolina (in box) along the Atlantic coast of the United States. Middle map shows view of entire coastline of North Carolina, with the four regions used in the movement analyses demarcated by dashed lines. The four regions are the following: eastern Pamlico Sound (EPS), western Pamlico Sound (WPS), Neuse and Pamlico rivers (NPR), and coastal and estuarine waters of southern North Carolina (SNC). The small box in the Neuse River highlights the location of Hancock Creek, which is enlarged in the right panel. Locations of submersible receivers in Hancock Creek are shown by the black dots, and the star shows where salinity measurements were taken.

and Pamlico rivers (NPR), and 4) waters of southern North Carolina (SNC; Cape Lookout southward, including estuaries and coastal waters). These regions were chosen from a preliminary examination of movement patterns of red drum and according to natural geographic divisions.

The latitude and longitude of tagging and recovery locations were used to calculate the distance (km) and angle moved (measured in whole-circle bearing degrees, with 0° representing true north). We calculated distance moved both as shortest distance moved in water, using ArcGIS 9.1 (ESRI, Redlands, CA) for distance and movement rate calculations, as well as straight-line distance (Batschelet, 1981) for circular mapping analyses. We also calculated the angle moved (in degrees) by each individual fish from the tagging and recovery coordinates (Batschelet, 1981).

Next, we tested for the effects of fish age, region, and season of conventional tagging on red drum movement patterns. We were unable to examine the simultaneous influence of these three factors on red drum movement patterns because of low sample sizes of recovered red drum in some age, region, and season combinations. Instead, we conducted two separate statistical analyses. In the first, we tested for differences in days at large, distance moved (km), and movement rate (km/d) among red drum age classes and regions of tagging, using analysis of variance (ANOVA). Each dependent variable was log-transformed to reduce skewness and to homogenize variability. Two-way factorial ANOVAs were used to test the main effects of age and region of tagging and their interaction at $\alpha=0.05$. To visualize these age and region patterns, we first constructed maps of tagging and recovery locations for each age class of red drum, using ArcGIS 9.1. We next constructed two-variable vector plots in Oriana 2.0 (Kovach Computing Services, Anglesey, Wales). The length of the bars in these circular plots represents the straight-line distance moved by individual red drum, and the direction of the bar represents the angular bearing of the fish. Separate graphs were made for each age class and region combination. We were unable to use circular statistics on these data because of the presence of multiple modes (Zar, 1999) and geographic barriers that varied by region.

For the second statistical analysis we tested the influence of tagging season and age class on movement rates of red drum. Age was also included as a variable in this analysis because of its potential influence on seasonal movements. Only red drum recovered within 60 days of tagging were included in this analysis so that fish could be classified accurately into a seasonal period, and the midpoint of time at large for each fish was used to determine its season of recovery. Seasonal periods were classified as spring (March–May), summer (June–August), fall (September–November), and winter (December–February). Differences in log-transformed movement rates by season and age class were tested with a two-way factorial ANOVA.

To visualize this seasonal effect, stacked and stepped histograms of distance moved and directionality were

created within the circular plot. Age-1 and age-2 red drum were examined only in these plots because of low sample sizes of older age classes. The overall length of each wedge in the plot was the relative frequency of angular observations within 20° bins scaled to the largest number for each plot (because sample size was highly variable). Each wedge was further subdivided into the proportion of movements in various distance categories. These unique diagrams allowed for an examination of both direction and distance moved by season for red drum.

Anecdotal reports have indicated that some adult (age-4+) red drum migrate from coastal North Carolina waters northward each spring to Virginia and Maryland, and return southward in the fall. We examined the hypothesis of a seasonal migration of adult red drum with data from three sources: 1) the National Marine Fisheries Service (NMFS) trawl surveys; 2) Virginia Institute of Marine Sciences (VIMS) shark longline surveys; and 3) locations of tagged and recovered adult red drum in coastal waters from North Carolina northward. The NMFS trawl surveys were conducted in spring (March) and fall (September–November) in coastal waters from just south of Cape Hatteras northward (Despres-Patanjo et al., 1988); we used data from 1972 to 2004. The VIMS shark longline surveys have been conducted in the lower Chesapeake Bay and Virginia coastal waters from May or June through September or October (Conrath and Musick, 2007), and data from 1974 to 2004 were used. Data from these three sources were combined to provide a seasonally based map of adult red drum captures along the mid-Atlantic coast.

Ultrasonic telemetry

In order to quantify small-scale movements of subadult red drum, we also used ultrasonic telemetry data in a small lateral tributary of the Neuse River, Hancock Creek. Ultrasonic telemetry data were used in Hancock Creek instead of over a broader area (e.g., Pamlico Sound) because of the accessibility of the creek, ease of tracking, and its narrow mouth that could be monitored with submersible receivers (see below). Age-2 red drum were implanted with transmitters in Hancock Creek between 2005 and 2007; the surgical procedures are described in Bacheler (2008). Fish were surgically implanted with coded ultrasonic transmitters (VEMCO, Ltd., Halifax, Nova Scotia, Canada; V16 4H, 10 g in water; 10 mm wide; 65 mm long) and were released after swimming behavior returned to normal (approximately 10 minutes). Transmitter weight in water was always less than 1.25% of the fish's body weight, as recommended by Winter (1996); there was no evidence that the transmitter affected the behavior of red drum in the laboratory or field (Bacheler et al., 2009a). The transmitters operated on a frequency of 69 kHz and were programmed to be continuously active for a period of 641 days.

Transmitter-tagged red drum were manually tracked (relocated) monthly during daylight hours by using a VEMCO VR100 receiver and hydrophone. Upon relocation of a transmitter-tagged fish, the latitude and longitude coordinates were recorded, and water depth, temperature, salinity, and dissolved oxygen measurements were taken with a YSI® 85 (Yellow Springs Instruments, Inc., Yellow Springs, OH). Monthly movement rates were calculated as the shortest distance in water (km) between two successive relocation events. Upstream or downstream movements were determined for fish moving greater than 50 m in an upstream or downstream direction from its previous monthly location; otherwise, the fish was classified as stationary.

In order to quantify the seasonality and magnitude of emigrations from Hancock Creek, submersible VR2 VEMCO receivers were deployed at its mouth. Preliminary testing indicated that VR2 receivers could detect nearly 100% of the pulses from V16 tags at 400 m in our study system (Bacheler, 2008). Therefore, three submersible receivers were deployed at the mouth of Hancock Creek, each being a conservative distance of 600 m apart from one another. If a fish emigrated from the tributary, it was eliminated from the movement analyses.

We were also interested in potential correlations between movements and emigrations of red drum in Hancock Creek. Preliminary observations of transmitter-tagged red drum in Hancock Creek indicated that fish often moved in synchronized ways upstream or downstream during monthly periods. To test for seasonal effects, we related the frequency of fish moving upstream, moving downstream, and remaining stationary in Hancock Creek with the month of relocation, using an $R \times C$ test of independence. Given that the salinity regime in Hancock Creek was near the lower limit for red drum (i.e., 0–10 psu; Crocker et al., 1983; Forsberg and Neill, 1997), we also tested whether fluctuations in salinity were correlated with upstream and downstream movements, as well as with emigrations, of age-2 red drum. We correlated the proportion of tagged red drum moving upstream or downstream each month with the observed change in salinity near the midpoint (boat ramp) of Hancock Creek (see Fig. 1 for location) using Pearson's product-moment correlation analysis. Months with sample sizes of less than four tagged red drum were excluded from analysis.

Results

Conventional tagging

A total of 48,136 red drum (142–1473 mm total length) were tagged with conventional tags (i.e., internal anchor or dart) in this study, of which 6173 were recovered and reported by fishermen (Table 1). Overall, 58% of these recoveries were from fish tagged at age 1, 30% were from age 2, 2% were from age 3, and 9% were from age 4+ fish. A majority of recoveries occurred from fish originally tagged in the NPR (59%), but many fish were also recovered from releases in other regions as well

(Table 1). Some age and region combinations had small sample sizes, in particular age-3 and age-4+ red drum tagged and recovered in WPS.

Red drum were tagged and recovered broadly in nearshore areas throughout estuaries and the coast of North Carolina (Fig. 2). Age-1 and age-2 red drum were tagged in large numbers in all estuarine and coastal regions of the state, and recoveries occurred throughout North Carolina waters (Fig. 2, A and B). Tagging of age-3 red drum was mainly focused in NPR and EPS, and recoveries generally occurred in nearby areas (Fig. 2C). Tagging of age-4+ red drum was concentrated around Ocracoke Inlet (EPS), the lower Neuse and Pamlico rivers (NPR), and Cape Fear River (SNC); recoveries appeared to be concentrated in these same three areas (Fig. 2D).

Most recoveries occurred within the region in which tagging took place (Table 2). Highest regional fidelity was observed in SNC, where between 94% and 100% of tagged red drum were recovered in SNC. Lowest regional fidelity was observed in WPS, where from 0 to 3% of each age class were recovered in WPS; most fish tagged in WPS were recovered in EPS (50–100% of each age class; Table 2).

There were regional differences in movement metrics among the four age classes of red drum. Log-transformed mean days at large, mean distance moved, and mean movement rate of red drum were all significantly influenced by both region of tagging and age of the fish (two-way factorial ANOVA; all $P<0.001$). Specifically, mean days at large was positively related to age at tagging; age-1 red drum spent 100.8 ±2.8 d (mean ± standard error [SE]) at large, whereas age-4+ fish were at large much longer (693.8 ±37.9 d; Table 3). Mean distance moved was smallest for age-3 red drum (10.1 ±1.2 km) and farthest for age-4+ fish (30.2 ±2.0 km). Movement rates were much higher for age-1 red drum (1.1 ±0.1 km/d) compared to other age classes, which varied from 0.2 to 0.4 km/d (Table 3). In addition, there were significant interactions between region and age for all analyses (all interactions $P<0.01$).

Prevailing directions of movements were region- and age-dependent (Fig. 3). Generally, age-1 and age-2 red drum moved parallel to the coast (in estuarine and coastal waters), except for fish tagged in NPR, which tended to move primarily toward the coast. Rarely did subadult red drum move up rivers and estuaries toward low-salinity waters. Age-1 red drum tagged in EPS and WPS moved mainly southwest along the coast, whereas those tagged in SNC moved mainly northeast and southwest. Age-2 red drum generally showed more northward movements than age-1 red drum, especially in the northern regions of EPS and WPS (Fig. 3). Age-3 red drum displayed limited movements, but sample sizes for this age class were smaller than those for other age classes. Age-4+ red drum tagged in EPS moved farthest toward the north and south, but many fish moved shorter distances to the east and west. Movement distances for age-4+ red drum were minimal in all other regions, with the exception of primarily northeast (downriver) movements in NPR (Fig. 3).

Table 1

Number of conventionally tagged North Carolina red drum (*Sciaenops ocellatus*) that were recovered by fishermen and classified by age, region, and season of tagging, 1983–2007. No winter or spring data exist for age-1 red drum because these individuals were too small to be tagged in the winter and spring tagging program for this age group. Region codes are the following: eastern Pamlico Sound (EPS), western Pamlico Sound (WPS), Neuse and Pamlico rivers (NPR), and southern North Carolina (SNC).

Season of tagging by age	Region				
	EPS	WPS	NPR	SNC	Total
Age 1					
Summer	179	58	871	104	1212
Fall	340	200	1,550	220	2310
Age 2					
Winter	184	48	356	79	667
Spring	171	13	523	47	754
Summer	98	6	102	29	235
Fall	119	20	59	99	297
Age 3					
Winter	12	0	24	2	38
Spring	17	2	4	9	32
Summer	13	0	0	16	29
Fall	40	1	2	7	50
Age 4+					
Winter	1	0	1	4	6
Spring	71	0	0	1	72
Summer	27	0	86	30	143
Fall	242	2	73	11	328
Total	1514	350	3651	658	6173

Red drum of all ages had highest movement rates during fall. Movement rate within 60 days of tagging was influenced by season ($P<0.01$) and age ($P=0.04$); the interaction between season and age was also significant ($P<0.01$). Age-1 red drum showed the highest fall movement rates, and age-4+ displayed the highest movement rate of any age class in spring and summer. Age-3 red drum had the lowest movement rate of any age class in spring and fall.

Four features were apparent for the detailed seasonal examination of directions and distances moved for age-1 and age-2 red drum (Fig. 4). First, higher proportions of long-distance movements occurred during fall months; in fact, a majority of movements during fall months consisted of distances greater than 20.1 km. Second, regional differences were observed in both distances and directions moved, especially during fall months. For instance, most movements of age-1 red drum tagged in eastern Pamlico Sound consisted of long-distance movements (>20.1 km) to the southwest,

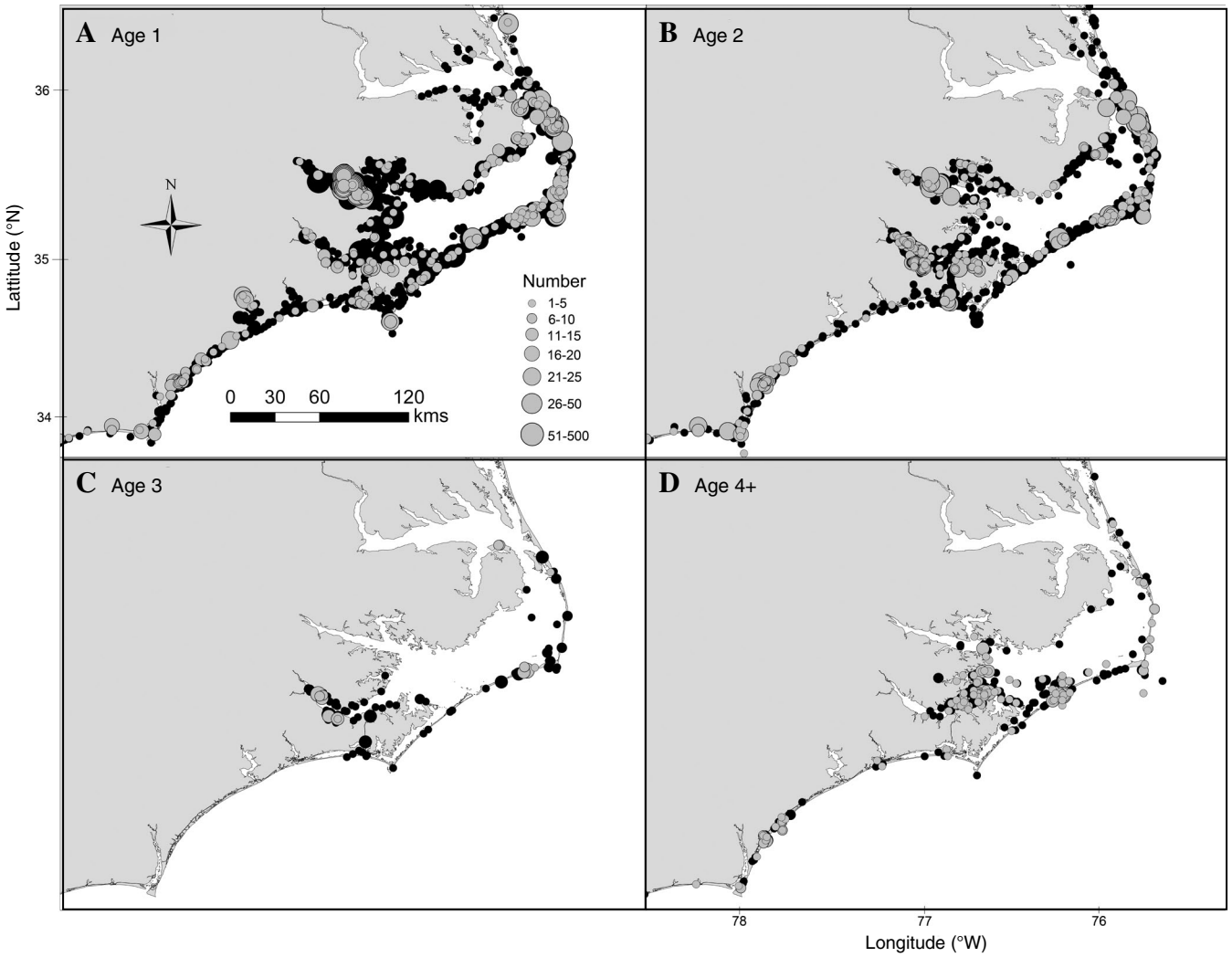

Figure 2

Tagging (gray circles) and recovery locations (black circles) for (**A**) age-1, (**B**) age-2, (**C**) age-3, and (**D**) age-4+ red drum (*Sciaenops ocellatus*) conventionally tagged by North Carolina Division of Marine Fisheries and North Carolina State University, 1983–2007. Only recoveries occurring within North Carolina waters are shown.

whereas age-1 fish in other regions moved primarily south (WPS), east (NPR), or northeast and southwest (SNC). Third, during winter, spring, and summer months, movements of subadult red drum tended to consist of short-distance movements of highly variable directionality. Fourth, when comparing age-1 and age-2 red drum movements in fall months, we found that the direction and distances of movements were mostly similar for EPS and WPS. However, age-specific differences were observed for NPR, which had more long-distance, coastward movements of age-2 than age-1 red drum, and for SNC, which had more westward movement of age-2 fish and highly variable movement of age-1 red drum.

Thirty-six red drum were recovered in states other than North Carolina (0.6% of all recoveries). Most out-of-state recoveries were from fish tagged at age 2 (56%), but some had fish been tagged at age 1 (22%) or age 4+ (22%). Most out-of-state recoveries came from Virginia (78%), but recoveries also occurred in South Carolina (11%), Maryland (5%), Georgia (3%), and Delaware (3%). Most out-of-state recoveries came from fish tagged in EPS (82%), but some also came from NPR (6%), SNC (6%), and WPS (6%).

Catches of adult red drum in coastal waters of North Carolina, Virginia, and Maryland from the NMFS and VIMS fishery-independent surveys showed a seasonal geographic pattern (Fig. 5). In March, adult red drum were located exclusively on the continental shelf of North Carolina. Adult red drum were encountered in lower Chesapeake Bay and coastal Virginia and Maryland in spring and summer months, and catches during late fall were centered back in North Carolina.

Ultrasonic telemetry

In total, 105 age-2 red drum were implanted with transmitters in Hancock Creek from March 2005 to December

Table 2

Region of tagging and number of tagged red drum (*Sciaenops ocellatus*) recovered within North Carolina estuarine and coastal waters, 1983–2007. Region codes are the following: eastern Pamlico Sound (EPS), western Pamlico Sound (WPS), Neuse and Pamlico rivers (NPR), and southern North Carolina (SNC).

Age of fish and region of tagging	Region of tag recovery					
	EPS	WPS	NPR	SNC	Out-of-state	Total
Age 1						
EPS	429	4	7	73	6	519
WPS	236	5	11	5	1	258
NPR	234	1	2119	66	1	2421
SNC	8	1	12	303	0	324
Age 2						
EPS	524	12	10	9	17	572
WPS	80	3	2	1	1	87
NPR	158	4	813	64	1	1040
SNC	6	3	1	243	1	254
Age 3						
EPS	78	0	2	2	0	82
WPS	3	0	0	0	0	3
NPR	1	0	27	2	0	30
SNC	0	0	0	34	0	34
Age 4+						
EPS	225	11	94	4	7	341
WPS	1	0	1	0	0	2
NPR	29	3	127	1	0	160
SNC	1	0	1	43	1	46
Total	2013	47	3227	850	36	6173

Table 3

Summary of movement information for four age groups of red drum (*Sciaenops ocellatus*) in estuarine and coastal waters of North Carolina based on their age at tagging, 1983–2007. Standard errors (SE) are show in parentheses. Age-1 and age-2 red drum were analyzed within each of four tagging regions: eastern Pamlico Sound (EPS), western Pamlico Sound (WPS), Neuse and Pamlico rivers (NPR), and southern North Carolina (SNC). Age-3 and age-4+ red drum movement information was summarized across all regions because of low sample sizes in some regions. Shortest distance in water was used for all distance and movement rate calculations.

Age of fish and region of tagging	Total recoveries	Mean (SE) days at large	Maximum days at large	Mean (SE) distance moved (km)	Maximum distance moved (km)	Mean (SE) movement rate (km/d)	Proportion moving <10km
Age 1							
EPS	519	134.2 (7.4)	1079	49.0 (2.3)	353.5	2.0 (0.2)	0.32
WPS	258	186.7 (15.3)	1532	44.7 (2.5)	314.5	2.4 (0.5)	0.25
NPR	2421	77.9 (3.0)	1882	21.0 (0.6)	202.6	1.0 (0.1)	0.66
SNC	324	147.3 (9.3)	1125	27.8 (2.4)	306.7	0.5 (0.1)	0.49
Overall	3522	100.8 (2.8)	1882	24.9 (0.6)	353.5	1.1 (0.1)	0.56
Age 2							
EPS	572	164.8 (7.6)	2056	28.7 (1.9)	622.5	0.7 (0.1)	0.45
WPS	87	179.4 (13.7)	621	43.3 (3.7)	166.7	0.8 (0.1)	0.21
NPR	1040	150.5 (4.0)	816	20.4 (1.0)	220.7	0.2 (0.1)	0.57
SNC	254	151.2 (12.8)	1043	11.9 (2.2)	186.9	0.3 (0.1)	0.74
Overall	1953	155.6 (3.5)	2056	22.4 (0.8)	622.5	0.4 (0.1)	0.54
Age 3	149	176.7 (35.6)	4752	10.1 (1.2)	80.0	0.2 (0.1)	0.68
Age 4+	549	693.8 (37.9)	5955	30.2 (2.0)	305.8	0.3 (0.1)	0.47

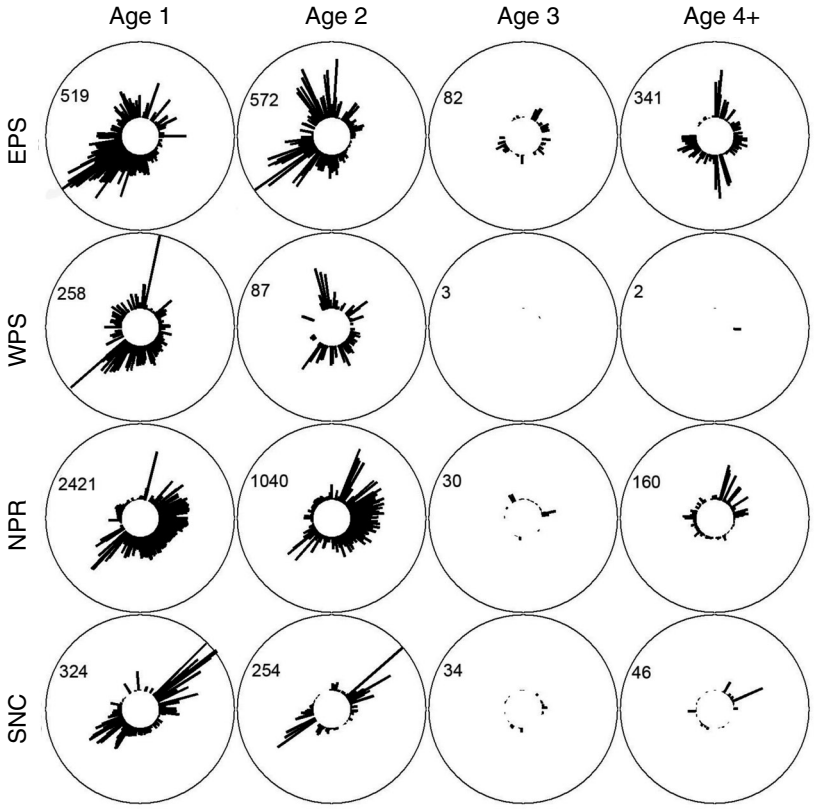

Figure 3

Rose diagrams showing the direction and distances moved for conventionally tagged red drum (*Sciaenops ocellatus*) in the coastal and estuarine waters of North Carolina, 1983–2007. Age classes are shown in columns and region of tagging in rows. The four regions are the following: eastern Pamlico Sound (EPS), western Pamlico Sound (WPS), Neuse and Pamlico rivers (NPR), and southern North Carolina (SNC). Northward movements are straight up, southward movements are straight down, and outer circle is scaled to 300 km. Sample size is provided on each diagram.

2007. Most (77%) ultimately emigrated from the system, but some were harvested by fishermen (15%) and others remained alive at the end of the study (7%). One fish (1%) died from the surgical tagging procedure.

Emigration rates from Hancock Creek were bimodal and seasonal (χ^2=41.6; P<0.001; Fig. 6A), with most fish emigrating in spring (April–June) or fall months (September–November). No fish emigrated during winter (December–February). Movement rates of tagged red drum within Hancock Creek (i.e., excluding movements of emigrating fish) were also seasonal (ANOVA: P=0.01); highest movements occurred in May and lowest in January and February. Lastly, directionality of movements in Hancock Creek was dependent upon month of relocation ($R \times C$ test of independence: χ^2=53.4, P<0.001), but no obvious seasonal trend was observed (Fig. 6B).

Upstream and downstream movements of transmitter-tagged red drum were also significantly correlated with fluctuations in salinity (Fig. 7). The proportion of red drum moving upstream was correlated with a positive monthly change in salinity (r=0.57; F=9.19; P=0.007; Fig. 7A), and, similarly, downstream movements were correlated with a negative monthly change in salinity (r=–0.68; F=16.28; P<0.001; Fig. 7B). Changes in salinity did not influence emigration rate, however (r=–0.20; F=0.19; P=0.67; Fig. 7C).

Discussion

Our analyses on the movement patterns of red drum are innovative and of broad interest for two reasons. First, we provided a thorough treatment of the multiscale movement patterns of subadult and adult red drum by using multiple techniques and sources of data over many years, resulting in a comprehensive examination of movement of an estuarine fish species. Second, we

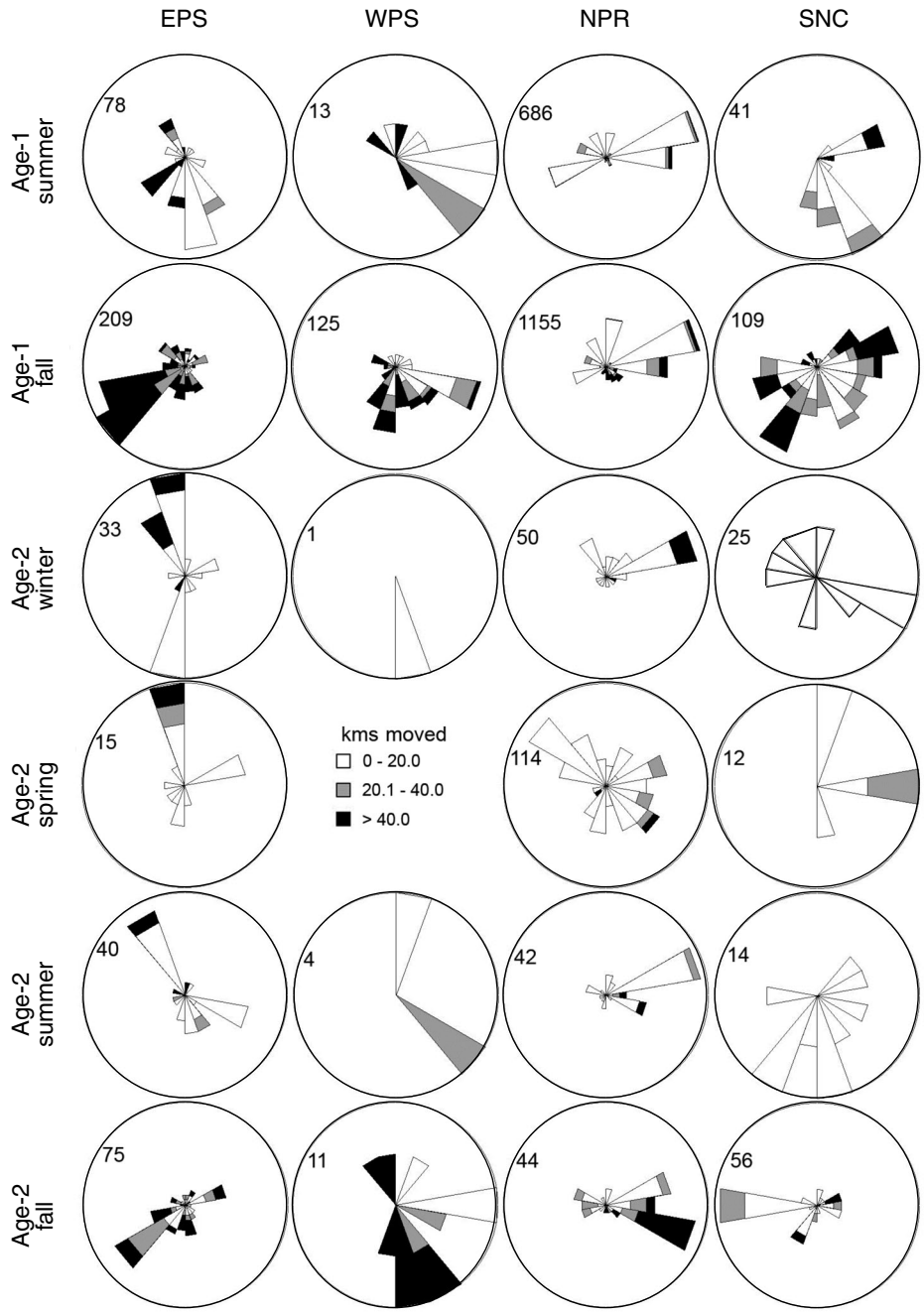

Figure 4

Frequency distributions of angular directions moved for subadult red drum (*Sciaenops ocellatus*) recovered within 60 days of tagging in coastal and estuarine waters of North Carolina, 1983–2007. Season and age class shown as rows and region tagged as columns. The four regions are the following: eastern Pamlico Sound (EPS), western Pamlico Sound (WPS), Neuse and Pamlico rivers (NPR), and southern North Carolina (SNC). The overall length of each wedge shows the relative frequency of angular observations within 20° bins scaled to the largest number for each plot. Each wedge is further subdivided into the proportion of movements in a particular direction composed of distances less than or equal to 20 km (white), 20.1 to 40.0 (gray), or greater than 40 km (black). Northward movements are straight up, and southward movements are straight down. Sample size is given for each diagram.

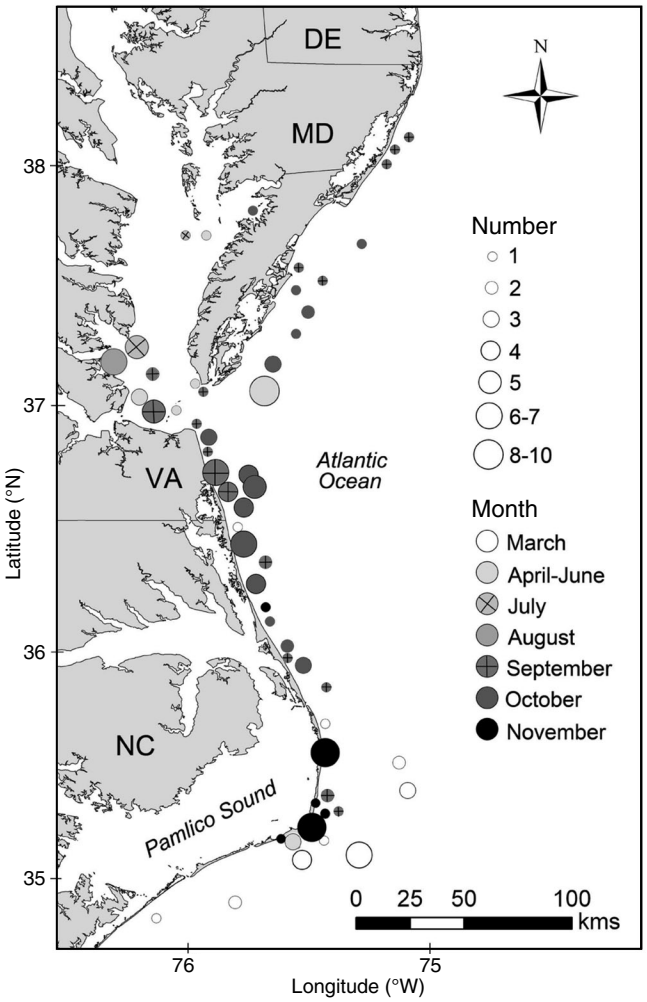

Figure 5

Seasonality and numbers of captures of adult (age-4+) red drum (*Sciaenops ocellatus*) caught in coastal North Carolina, Virginia, and Maryland. Data are from the National Marine Fisheries Service trawl surveys, Virginia Institute of Marine Sciences shark longline surveys, or from fish tagged or recovered in the North Carolina Division of Marine Fisheries tagging project (1983–2007). The National Marine Fisheries Service survey took place in U.S. east coast continental shelf waters from Gulf of Maine to just south of Cape Hatteras in spring (March) and fall (September–November) each year in 1972–2004, and the Virginia Institute of Marine Sciences survey Virginia Institute of Marine Sciences survey was conducted in Chesapeake Bay and coastal Virginia waters in May or June through September or October, 1974–2004.

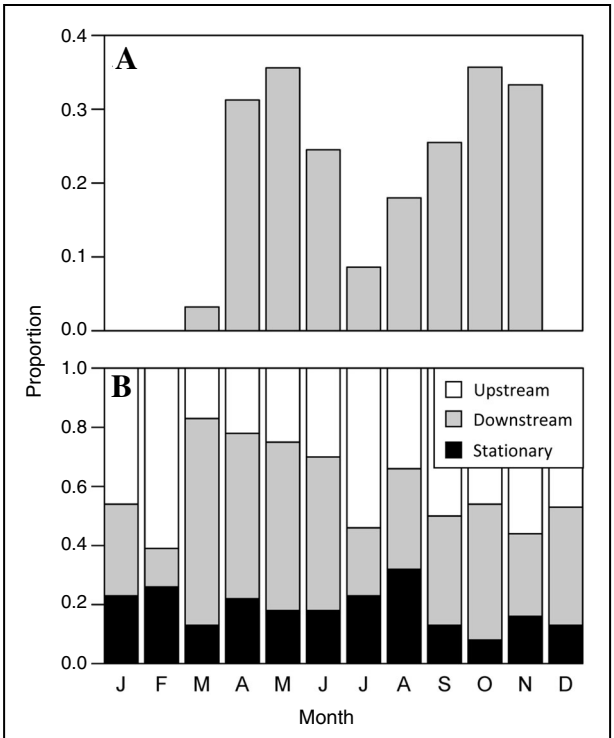

Figure 6

Seasonal ultrasonic telemetry information for age-2 red drum (*Sciaenops ocellatus*) in Hancock Creek, 2005–07. (**A**) Proportion of transmitter-tracked red drum emigrating each month from Hancock Creek, combined across years. (**B**) Proportion of tracked red drum moving upstream, downstream, or remaining stationary within Hancock Creek, combined across years.

developed a series of intuitive figures (e.g., circular mapping) to summarize the ways in which the movement patterns of an estuarine fish species were influenced by a variety of factors. Our results have implications for stock structure, gene flow, and ultimately, the connectivity of estuarine fish populations.

Movement patterns of red drum were distinctly age-dependent. Rates of movement generally declined with age, although the estimates for adult fish may be low if these adult fish were encountered mostly in estuarine waters after returning to spawn. From a physiological perspective, red drum are expected to show preferences for higher salinity with age (Neill et al., 2004), which may at least partially explain the observed age-dependent movement patterns towards the coast. Red drum are also known to experience major ontogenetic shifts in diet and habitat use (Bacheler et al., 2009b), but it is unknown how these ecological shifts translate to age-dependent and seasonal movement patterns. Although movement rates of many fish species have been shown to be age-dependent (e.g., Skalski and Gilliam, 2000), previous work on the movements of red drum focused on only one age class (Dresser and Kneib, 2007) or found no differences among age groups (Osburn et al., 1982). The observation that red drum movement patterns are age-specific is important for explaining age-specific selectivity patterns of the fishery (Bacheler et al., 2008a). In addition, the timing of movement for each age class can also be used to create temporal closures as a fishery management tool to protect red drum during particularly vulnerable periods when movement rates are high (e.g., to protect them from passive gear like gill nets).

The use of multiple tag types and age-dependent selectivity patterns in our study may have biased our analyses of movement patterns of fish by age. Most subadult red drum were tagged with internal anchor tags, which have been shown to have higher retention rates than dart tags that were primarily applied to adult red drum in our study (Bacheler et al., 2008a). Selectivity appears to be dome shaped and centered upon subadult red drum within the window limit for red drum catch (Bacheler et al., 2008a). Unequal retention rates of tags and age-dependent selectivity patterns likely did not bias movement rates or distances moved but may have biased our analysis of days at large. It is likely that adult red drum would have shown even greater differences in days at large compared to subadult fish if a tag with greater retention had been used for adults and there would have been increased selectivity on adult red drum during fewer days at large.

Determining whether estuarine or coastal species exhibit seasonally dependent movements is an important step in developing a broader perspective on the ecology of a particular species. The limited temporal scope and modest sample size of previous estuarine tagging studies have made it difficult to quantify seasonal variability in movement patterns of estuarine fish species like red drum. We documented a high rate of (primarily southward) movement by age-1 red drum during fall months, especially in northern regions of North Carolina (EPS and WPS); North Carolina happens to be the most significant northern overwintering grounds for subadult red drum on the Atlantic coast (Ross et al., 1995). Atlantic silversides (*Menidia menidia*) are known to migrate offshore in the northern but not the southern part of their range in the Atlantic (Conover and Murawski, 1982), presumably to avoid overwintering mortality due to acute cold stress in northerly latitudes (Munch et al., 2003). Adult bluefish (*Pomatomus saltatrix*) on the Atlantic coast appear to consist of three groups that exhibit different migratory behaviors; the group inhabiting the most northerly waters (i.e., New England) in summer months tends to exhibit the farthest southerly migration during fall (Shepherd et al., 2006). Likewise, southerly movements of age-1 red drum during fall months may be an avoidance response to acute cold stress (e.g., Gunter, 1941) that may be particularly hazardous in the northern part of the state.

Despite the low sample size of conventionally tagged and recovered red drum in some age and region combinations, regional variability was apparent. Regional variability in the movement of tagged estuarine fish is likely a result of the physiology of the species, geographic barriers, and the specific fisheries operating in each region. In addition to the seasonal movements described above for age-1 red drum in northerly regions of the state, there appeared to be a coastward (easterly) migration for both age-1 and age-2 fish tagged in oligohaline waters, whereas fish tagged in polyhaline waters primarily moved along the coast. Regionally variable movements may be due as much to the physiological requirements of red drum as to the geography of the North Carolina coast, which constrains the movements of red drum to specific directions (e.g., east–west in NPR, northeast–southwest in SNC).

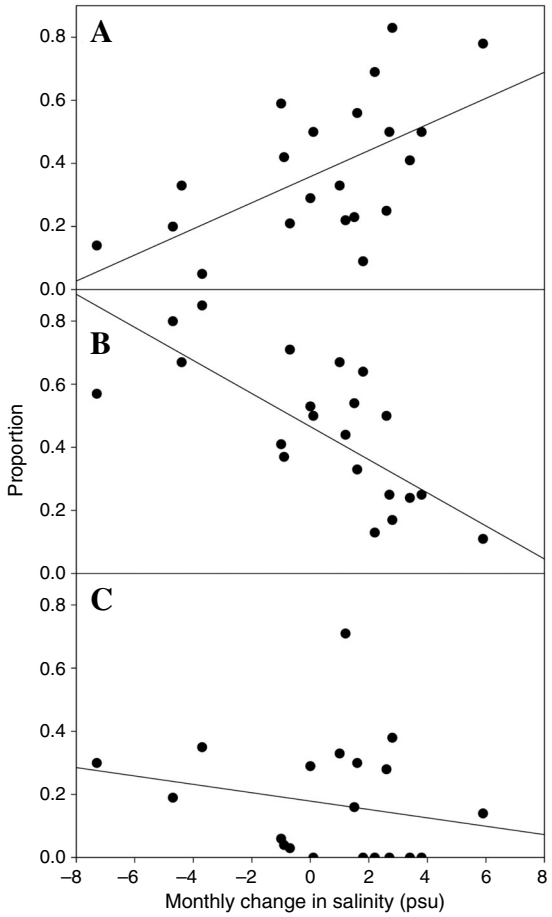

Figure 7

Proportion of transmitter-tracked red drum (*Sciaenops ocellatus*) in Hancock Creek moving upstream (**A**), moving downstream (**B**), or emigrating (**C**) in relation to the change in salinity between two consecutive monthly relocation periods, 2005–2007. Salinity sampling took place midriver near the boat ramp, and monthly periods were included only if at least four tracked red drum were relocated in that period. Trend lines show a linear least-squares fit.

Because tag recoveries come from the fishery, conventional tagging analyses of movement can be biased by spatially heterogeneous fishing effort. The distribution of recoveries may therefore reflect the spatial distribution of fishing more than the true extent of fish movement. Bolle et al. (2005) used electronic transmitters to show that conventional tagging provided a reliable interpretation of the movement patterns of European plaice (*Pleuronectes platessa*) in most areas of the North Sea; the only areas that appeared to be undersampled

by conventional tagging were places where residence time was short, fishing effort was low, and catchability was reduced. We could not compare conventional tagging data with ultrasonic telemetry data in our study because the spatial distribution data from the conventional tags and the ultrasonic telemetry tags did not overlap. However, we believe movement data from conventional tagging were generally robust except for fish tagged in the NPR. A large number of fish were conventionally tagged in conjunction with commercial pound-net operations in the Pamlico River, and many were recovered within a few days in the same or nearby pound nets. Such intense localized fishing pressure adjacent to major tagging operations likely biased NPR movement data, resulting in shorter mean distances moved and days at large than mean distances and days at large from other regions where fish were not tagged from pound nets. In light of the unusual pound-net tagging in the Pamlico River, movement data from NPR should be viewed cautiously. Most recoveries of fish tagged in WPS occurred in EPS, but this result is not surprising given that the primary WPS tagging location was near the dividing line between the two regions. Based on available information, WPS has a similar level of fishing activity as that of other areas of North Carolina.

Our analyses could have been improved if fishing-effort data across coastal North Carolina had been available. Because heterogeneous fishing effort may influence movement results, tag recoveries have been standardized by regionally variable fishing effort in recent movement analyses (e.g., Wang et al., 2007). Building upon the pioneering work of Hilborn (1990), McGarvey and Feenstra (2002) went further and developed a movement model that uses fishing effort or mortality data across space in a maximum likelihood framework to estimate the probability parameters of movement. Accurate fishing-effort data could be useful for future red drum tagging analyses and may improve both movement and mortality modeling.

The addition of an ultrasonic telemetry method in this study to examine small-scale movement patterns of subadult red drum complements large-scale analyses that use conventional tagging. When they could be compared, the two different methods provided similar movement patterns. For instance, the high emigration rate of age-2 transmitter-tracked red drum from Hancock Creek in fall months corresponded with the season when conventionally tagged age-2 fish moved at the highest rate. The direction of movement during fall months was also consistent for the two methods. From data from additional submersible receivers deployed both upstream and downstream of Hancock Creek (see Bacheler et al. [2009a] for description), we determined that most transmitter-tracked red drum (87%) emigrating during fall months moved downstream in the direction of the coast (senior author, unpubl. data). Likewise, conventionally tagged fish in NPR also moved downstream toward the coast during fall months.

Ultrasonic telemetry could also be used to relate smaller-scale movement patterns to environmental variability. Because the salinity in Hancock Creek (0–10 psu) is near the lower tolerance limit for red drum (Crocker et al., 1983; Forsberg et al., 1997), upstream and downstream movements of transmitter-tracked red drum may have been a physiological response to fluctuating salinities. In laboratory experiments, estuarine organisms have been shown to respond to changes in salinity with increased swimming speed and respiration (von Oertzen, 1984). Alternatively, transmitter-tracked red drum may have been following the movements of prey species (Bacheler et al., 2009b) that had their own physiological constraints. Regardless, transmitter-tracked red drum appeared to remain in salinities around 4–5 psu (Bacheler et al., 2009b), following this gradient up and down the creek with fluctuations in salinity. Our results contrast with those of Dresser and Kneib (2007), who showed that subadult red drum movement patterns in a coastal Georgia saltmarsh were primarily influenced by tide and time of day. The lack of lunar tides in Hancock Creek, in addition to much lower salinities, may explain this discrepancy.

We developed a conceptual diagram to highlight the ways in which our conventional tagging and ultrasonic telemetry data helped elucidate several critical aspects of red drum life history and ontogeny (Fig. 8). Spawning occurs in late summer (Barrios, 2004; Luczkovich et al., 2008), and fertilized eggs are advected upstream where they eventually hatch into pelagic larvae and settle to benthic nursery habitats during fall (Bacheler et al., 2008b). Age-0 to age-3 red drum are found in upper estuarine environments, but we have shown that each fall a portion of both age-1 and age-2 cohorts move to high-salinity coastal waters (Fig. 8). It appears that some red drum remain in upper estuary habitats until age 3, the age at which the last remaining red drum move to coastal environments. Subadult red drum in coastal environments join the adult population after maturity at age 3 or 4 (Ross et al., 1995). We have also shown that adults overwinter on the continental shelf and some move westward into North Carolina estuaries, whereas others move northward to the lower Chesapeake Bay or coastal Virginia and Maryland during spring, and back east or south during fall months. The large proportion of conventionally tagged adults recovered near their tagging location in summer months indicates a return to specific spawning areas each year. We could not eliminate the possibility that some adult red drum remain in continental shelf waters year-round and spawn on the shelf or in passes or inlets, as has been observed in another study (Murphy and Taylor, 1990). Therefore, the arrows in our conceptual diagram highlighting the seasonal movements of adult red drum into the estuary were dotted to acknowledge this uncertainty. Taken together, these movement results have direct implications for the use of temporal and spatial management tools and also for the scale at which management and assessment should take place.

Assessment of North Carolina and Virginia red drum together as one stock is justified by tagging data. Subadult red drum tagged with conventional tags in North

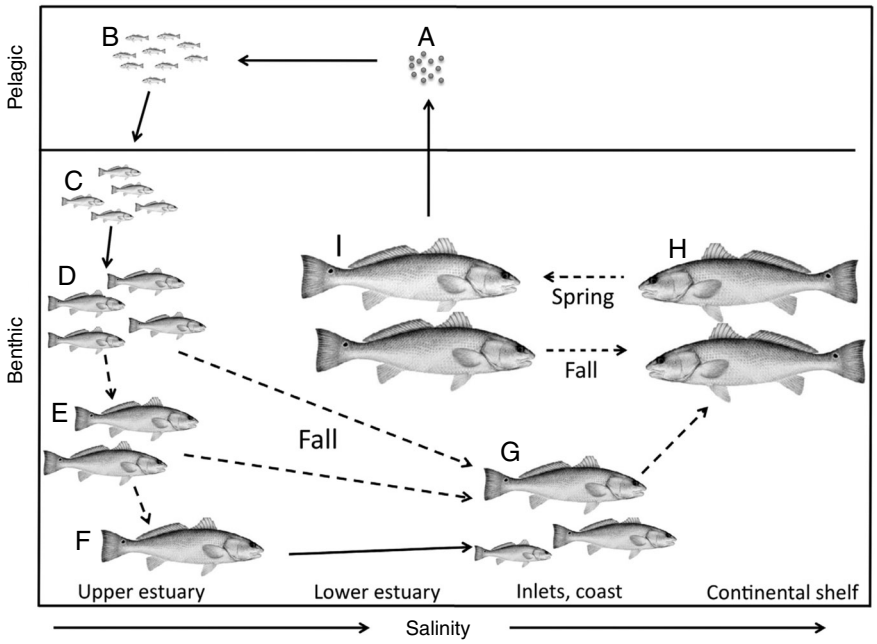

Figure 8

Conceptual diagram of life history and movement patterns of red drum (*Sciaenops ocellatus*) in North Carolina. (**A**) Eggs are spawned in August–September; (**B**) larvae are pelagic in August–November; (**C**) age-0 juvenile red drum settle to benthic habitats in upper estuaries in September–November; (**D** and **E**) age-1 and age-2 red drum either remain in upper estuaries or migrate downstream to coastal habitats in fall; (**F**) age-3 red drum migrate towards the coast throughout the year; (**G**), multiple age classes of subadult red drum inhabit coastal habitats, eventually joining adults after maturity at approximately age 3 or 4 years; (**H**) nonspawning adults on continental shelf (age-4+) overwinter; (**I**) adults spawn during summer months. Dotted lines indicate that a particular pathway is not necessarily followed by all members of a cohort in a particular year.

Carolina appear to be much more likely to move northward to Virginia than to any other state, even though interstate movements were low. Likewise, subadult red drum tagged in Virginia have consistently been recovered in North Carolina waters (J. Lucy, personal commun.[1]). Few subadult red drum were captured in states southward in our study, and, similarly, tagged red drum in South Carolina are rarely recovered in North Carolina (C. Wenner, personal commun.[2]). The interstate movement patterns of adult red drum appear to mirror those of subadults, showing some northward seasonal migration to Virginia each year, but very limited exchange with states south of North Carolina. Our tagging results indicate that the state line between North Carolina and South Carolina corresponds approximately to an ecological division for red drum and, thus, is an appropriate division for management and assessment of the stock.

[1] Lucy, Jon. 2009. Virginia Institute of Marine Science, College of William and Mary, Gloucester Point, VA 23062.

[2] Wenner, Charles. 2009. South Carolina Department of Natural Resources, Charleston, SC 29412.

We used a 25-year tagging data set in combination with three years of ultrasonic telemetry data and coastal fishery-independent survey data to provide a comprehensive examination of subadult and adult red drum movement. Red drum movement patterns in North Carolina were dependent upon the age, region, and season of tagging. Longitudinal movements of age-2 red drum within a tributary to the Neuse River were related to salinity fluctuations, but emigrations from the tributary were dependent on season and not salinity. These results advance our understanding of the seasonality, regional variability, age dependency, and spatial scale of movements of fish in complex estuarine and coastal environments.

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