Seasonal variation in age-specific movement patterns of red drum *Sciaenops ocellatus* inferred from conventional tagging and telemetry

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Abstract - We used 25 years of conventional tagging (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 North Carolina. Movement rates of 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, while 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. Telemetered age-2 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 tagging and telemetry programs can provide valuable insights into the complex movement patterns of estuarine fish.

Understanding the movements of individuals within and among populations is critical in order to effectively manage and conserve fish species. Movement information within a population is necessary to identify and prioritize nursery areas (Beck et al., 2001; Gillanders et al., 2003), evaluate marine protected areas (Kramer and Chapman, 1999; Walters et al., 1999; Botsford et al., 2003), and elucidate population dynamics (Turchin, 1998), while movement among populations is crucial to understanding gene flow, metapopulation dynamics, and ultimately, stock structure (Metcalfe, 2006; Shepherd et al., 2006; Cadrin and Secor, in press). Movement is thus a major force structuring fish populations. The quantification of intra- and inter-population movement of fishes, however, lags far behind the well developed methodologies that exist for measuring population density and survival (Turchin, 1998).

Given the commercial and recreational importance of fish that use estuaries at some stage in their life history, a wide variety of methodologies have been employed to try to understand the movement patterns of estuarine fish. Historically, the most common approach has been to reconstruct movement pathways based on fishery catches (e.g., Rulifson and Dadswell, 1995). Mark-recapture techniques have advanced our understanding of fish movement patterns because they explicitly account for individual variation in movement behavior (Able and Hales, 1997; Able et al., 2005; Glover et al., 2008). Otolith microchemistry techniques have recently been employed to understand aspects of the movement ecology of estuarine organisms, such as the importance of substocks or contingents (Secor, 1999) and the natal homing of estuarine fish (Thorrold et al., 2001). The use of biotelemetry represents another major methodological advance because it can provide multiple relocations of individual fish over various spatial and temporal scales (Able and Grothues, 2007; Sackett et al., 2008). Each of these methods has its own strengths and weaknesses, suggesting that a combination of techniques may be optimal to understand the movement of fish in estuaries (e.g., Cunjak et al., 2005).

Red drum *Sciaenops ocellatus* is a long-lived estuarine and coastal fish species found along the Gulf and Atlantic coasts of the United States. Overfishing was responsible for declines of red drum in the 1980s, but strict harvest regulations enacted in the 1990s have promoted the rebuilding of red drum stocks (Bacheler et al., 2008a). Red drum are currently managed such that subadult (i.e., ages 1 – 3) age classes are harvested, while adults are protected in most states. A more thorough description of red drum movement patterns could be used to assess the current spatial scale of management (Metcalfe, 2006), inform the usefulness and design of no-take zones as a management strategy (Collins et al., 2002), and provide information on the ways juveniles move from nurseries to adult habitats (Beck et al., 2001; Gillanders et al., 2003).

The literature on the spatial extent of red drum movement is mixed. Studies conducted over relatively small spatial and temporal scales indicate subadult red drum movement is limited (Osburn et al., 1982; Collins et al., 2002; Jenkins et al., 2004; 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 and Richardson, 1991; Gold et al., 1993; Seyoum et al., 2000). This apparent inconsistency, 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 suggests 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 movement rates by subadults, adult movement rates 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, previous examinations of subadult red drum movement at relatively small temporal and spatial scales may have missed the full extent of subadult movements.

This study describes the movement patterns of subadult and adult red drum in North Carolina, USA, and neighboring states. The objectives of this study were to quantify 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 3 years of ultrasonic telemetry and submersible receiver detections. We use a variety of quantitative approaches to describe subadult and adult movement patterns including passive and active telemetry relocations, geographic mapping, and circular mapping. We explicitly account for differences in movement patterns based on the season and location of tagging. This study improves our understanding of the movement of red drum in 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 tagging data were considered. The first source was the red drum tagging dataset from the North Carolina Division of Marine Fisheries (NCDMF), which has occurred throughout North Carolina (NC) from 1983 – 2007. North Carolina Department of Marine Fisheries captured and tagged red drum opportunistically using pound nets, hook-and-line, runaround gill net, trammel nets, and electrofishing (see Burdick et al., 2007 for a complete description). Volunteer recreational fishers have been involved in tagging since 1984 and primarily target adult red drum. Commercial fishers assisted in tagging until 1990, primarily tagging subadult red drum caught in pound nets and gill nets in conjunction with NCDMF. The second data source was tagging of subadult red drum in 2005 – 2007 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 Floy® internal anchor tags (FM-84, FM-89SL, and FM-95W), while adults were primarily tagged with nylon dart tags (Floy® FT-1 and FT-2), stainless steel dart tags with a monofilament core (Floy® FH-69) or, more recently, a stainless steel core (Hallprint® SSD wire-through). All tags were labeled with a unique tag number, "REWARD" message, and an address to send the tag and phone number to report the tag. A two dollar (US) reward was given for returned NCDMF tags until 1989, and the reward amount increased to five dollars or a hat in 1990. Most NCSU tags were labeled with the "REWARD" message (US$5, hat, or t-shirt reward), but the remaining tags were labeled "$100 REWARD" for a concurrent tag reporting rate study (Bacheler, 2008) and were worth US$100. All tag types were combined and treated equally in this study.

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 NC red drum ageing data from otoliths, and annuli have 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 NC (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. Previous aging work on adult red drum in

NC determined that maximum age was 62 years (Ross et al., 1995), suggesting that age-4+ red drum in our study potentially ranged from age 4 to > 60.

Red drum movement patterns were examined in four regions in NC (Fig. 1). These regions were eastern Pamlico Sound and the adjacent coastal waters (EPS; the Outer Banks from the Virginia state line to Cape Lookout), western Pamlico Sound (WPS; mainland areas of northern NC), Neuse and Pamlico Rivers (NPR), and southern North Carolina (SNC; Cape Lookout southward, including estuaries and coastal waters). These regions were chosen based on preliminary examination of movement patterns of red drum (Burdick et al., 2007) and 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 0º 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) of each individual fish based on tagging and recovery coordinates (Batschelet, 1981).

We were unable to examine the simultaneous influence of age, region, and season of tagging on red drum movement patterns due to 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 ($km \cdot d^{-1}$) among red drum age classes and regions of tagging using ANOVA. Each dependent variable was log-transformed to reduce skewness and 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, while 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 due to the presence of multiple modes (Zar, 1999) and geographic barriers that varied by region.

The second statistical analysis 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 the potential of seasonal movements to be influenced by the age of red drum at tagging. 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; 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 only examined in these plots due to low sample sizes of older age classes. The overall length of each wedge in the plot was the relative frequency of angular observations within 20º 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 a particular direction composed of various distance categories. These unique diagrams allowed for an examination of both direction and distance moved by season for red drum.

Anecdotal reports have suggested that some adult (age-4+) red drum migrate from coastal North Carolina waters northward each spring to Virginia and Maryland, with a 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 survey, (2) Virginia Institute of Marine Sciences (VIMS) shark longline survey, and (3) locations of tagged and recovered adult red drum in coastal waters from North Carolina northward. The NMFS trawl survey was conducted in spring (March) and fall (September – November) in coastal waters from Cape Hatteras northward (Desprespatanjo et al., 1988); we used data from 1963 to 2004. The VIMS shark longline survey has 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 here. Data from these three surveys 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 in a small lateral tributary of the Neuse River, Hancock Creek. Age-2 red drum were implanted with transmitters in Hancock Creek between 2005 and 2007; surgical procedures can be found in Bacheler (2008). Fish were surgically implanted with coded ultrasonic transmitters (VEMCO, Ltd., 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 min). The transmitters operated on a frequency of 69 kHz, and were programmed to be continuously active for a period of 641 d.

Telemetered red drum were manually relocated monthly using a VEMCO VR100 receiver and hydrophone. Upon relocation of a telemetered fish, the latitude and longitude coordinates were recorded, and water depth, temperature, salinity, and dissolved oxygen measurements were taken with a YSI® 85. 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, it was classified as stationary.

Submersible VR2 VEMCO receivers were used at the mouth of each tributary to document emigration events. Preliminary testing suggested that VR2 receivers could detect nearly 100% of 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 a tributary, it was censored from the movement analyses. Approximately 300,000 detections could be stored in a single VR2 receiver, so data were downloaded every 1 – 5 mo to avoid filling the memory.

Preliminary observations of telemetered red drum in Hancock Creek suggested that fish often moved in synchronized ways upstream or downstream among monthly relocation periods. To test for seasonal effects, we related the proportion of fish moving upstream, moving downstream, and remaining stationary in Hancock Creek with the month of relocation using an R x C Test of Independence. Given that the salinity regime in Hancock Creek was near the lower limit for red drum (Crocker et al., 1983; Forsberg et al., 1997), we also tested whether fluctuations in salinity was correlated with upstream and downstream movements, as well as emigrations, of age-2 red drum. We correlated the proportion of telemetered 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 telemetered red drum were excluded from analysis.

Results

Conventional tagging

A total of 48,136 red drum was tagged in this study, of which 6173 were recovered and reported by fishers (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+. A majority of recoveries occurred from fish originally tagged in the Neuse and Pamlico Rivers (59%), but many fish were also recovered from releases in other regions as well (Table 1).

Red drum tagging and recoveries occurred broadly throughout estuaries and the coast of NC (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 NC waters (Fig. 2, A – B). Tagging of age-3 red drum was mainly focused in the Neuse River (NPR) and in Pamlico Sound near Cape Hatteras (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).

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, with age-1 red drum spending 100.8 ± 2.8 d (mean ± SE) at large, while age-4+ fish were at large much longer (693.8 ± 37.9 d; Table 2). Mean distance moved was lowest for age-3 red drum (10.1 ± 1.2 km) and highest 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^{-1}) compared to other age classes, which varied from 0.2 – 0.4 km·d^{-1} (Table 2). In addition, there were significant interactions between region and age for all analyses (all interaction $P < 0.01$).

Prevailing movement directions were region- and age-dependent (Fig. 3). Generally, age-1 and age-2 red drum moved parallel to the coast, except for fish tagged in NPR, which tended to primarily move towards the coast. Rarely did subadult red drum move up rivers and estuaries towards low salinity waters. Age-1 red drum tagged in EPS and WPS primarily moved southwest along the coast, while those tagged in SNC primarily moved 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 were smaller than other age classes. Age-4+ red drum tagged in EPS moved the furthest towards the north and south, but many fish moved shorter distances to the east and west. Movement distances for age-4+ red drum were low in all other regions, with the exception of primarily northeast (downriver) movements in NPR (Fig. 3).

Red drum of all ages had highest movement rates in fall (Fig. 4). 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, while 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 (Fig. 4).

Four observations were apparent for the detailed seasonal examination of directions and distances moved for age-1 and age-2 red drum (Fig. 5). First, higher proportions of long-distance movements occurred in fall months; in fact, a majority of movements in fall months consisted of distances greater than 20.1 km. Second, regional differences were observed in both distances and directions moved, especially in 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, 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 moves of highly variable directionality. Fourth, when comparing age-1 and age-2 red drum movements in fall months, the direction and distances moved 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 compared to 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.

A total of 36 red drum was recovered in states other than NC (0.6% of all recoveries). Most out-of-state recoveries were from fish tagged at age 2 (56%), but some had 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 and tagging showed a seasonal geographic pattern (Fig. 6). In March, adult red drum were observed 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, while 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 2007. Most (77%) ultimately emigrated from the system, but some were harvested by fishers (15%) and others remained alive at the end of the study (7%). One fish (1%) died from the surgical procedure.

Emigration rates from Hancock Creek were bimodal and seasonal ($\chi^2 = 41.6$; $P < 0.001$; Fig. 7A), with most fish emigrating in spring (April – June) or fall months (September – November). No fish emigrated during winter (December – February). Movement rates of telemetered red drum within Hancock Creek (i.e., excluding movements of emigrating fish) were also seasonal (ANOVA: $P = 0.01$), with highest movements in May and lowest in January and February. Last, directionality of movements in Hancock Creek was dependent upon month of relocation (R × C Test of Independence: $\chi^2 = 53.4$, $P < 0.001$), but no obvious seasonal trend was observed (Fig. 7B).

Upstream and downstream movements of telemetered red drum were also significantly correlated with fluctuations in salinity (Fig. 8). 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. 8A), and, similarly, downstream movements were correlated with a negative monthly change in salinity (r = -0.68; F = 16.28; P < 0.001; Fig. 8B). Changes in salinity did not influence emigration rate, however (r = -0.20; F = 0.19; P = 0.67; Fig. 8C).

Discussion

We used a 25-year tagging dataset in combination with 3 years of ultrasonic telemetry and coastal fishery-independent survey data to provide a comprehensive examination of subadult and adult red drum movement. Red drum movement patterns in NC 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.

Movement patterns of red drum were distinctly age-dependent. 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 (Wenner, 1992) and habitat use (Bacheler et al., in press), but it was unknown how these ecological shifts translated to age-dependent and seasonal movement patterns. While 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 has focused on only one age class (Dresser and Kneib, 2007) or has 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.

The use of multiple tag types in our study may have biased our analyses of movement patterns 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). Unequal retention rates of tags 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 likely shown even greater differences in days at large compared to subadult fish if a tag that lasted longer was used for adults.

By tagging and implanting large numbers of fish in this study, we were able to clearly document the strong seasonality of movements of red drum. The limited temporal scope and modest sample size of previous estuarine tagging studies 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 in fall months, especially in northern regions of NC (EPS and WPS); NC 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 furthest southerly migration in 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.

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, while fish tagged in polyhaline waters primarily moved along the coast. This may be due as much to the physiological requirements of red drum as the geography of the NC coast, which constrains the movements of red drum to specific directions (e.g., east – west in NPR, northeast – southwest in SNC).

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 was able to provide a reliable interpretation of North Sea plaice (*Pleuronectes platessa*) movement patterns 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 evaluate conventional tagging with telemetry in our study because the spatial distribution of tagging and telemetry did not overlap. However, we believe conventional tagging movement data were generally robust except for fish tagged in the NPR. A large number of fish were 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 compared to other regions where fish were not tagged out of pound nets. In light of the unusual pound net tagging in the Pamlico River, movement data from NPR should be viewed cautiously.

Our analyses could have been improved if fishing effort data across coastal NC were available. Since heterogeneous fishing effort may influence movement results, recent movement analyses have standardized tag recoveries by regionally-variable fishing effort (e.g., Schmalz et al., 2002; 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 movement probability parameters. Accurate fishing effort data could be useful for future red drum tagging analyses, and may improve both movement and mortality modeling.

The addition of a telemetry component to this study to examine small-scale movement patterns of subadult red drum complemented large-scale analyses that used conventional tagging. Since the salinity in Hancock Creek is near the lower tolerance limit for red drum (Crocker et al., 1983; Forsberg et al., 1997), upstream and downstream movements of telemetered 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), and hatchery-reared juvenile red drum choose salinity regimes that match conditions in which they were reared (Parkyn et al., 2002). Alternatively, telemetered red drum may have been following the movements of prey species (Bacheler et al., in press) that had their own physiological constraints. Regardless, telemetered red drum appeared to remain in salinities around 4 – 5 psu (Bacheler et al., in press), following this gradient up and down the creek with fluctuations in salinity. Our results contrast with 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 the discrepancy.

We developed a conceptual diagram to highlight the ways in which our conventional tagging and telemetry data helped elucidate several critical aspects of red drum life history and ontogeny (Fig. 9). 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. 9). 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 either move westward into NC estuaries or northward to the lower Chesapeake Bay or coastal Virginia/Maryland during spring, and back east or south during fall months. 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 elsewhere (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 takes place.

Small marine reserves have been proposed as a management tool to protect red drum in South Carolina because rebuilding of red drum stocks has been modest and movements of hatchery-raised, stocked red drum has been minimal in the state (Collins et al., 2002; Jenkins et al., 2004). The higher rate of movement we documented for subadult red drum in NC suggests that marine reserves would need to be larger than those proposed in South Carolina to achieve similar gains (Polacheck, 1990). Tremain et al. (2004) examined the movements of tagged red drum inside and outside of the Merritt Island National Wildlife Refuge reserve in Florida and found that more red drum moved into the reserve than out, and that movement rates were higher than previously reported. The authors suggest that the reserve may have been extracting exploitable red drum from adjacent areas, although increased egg production and larval export could have been replenishing nearby areas. The size and location of estuarine reserves in North Carolina could be revisited in the future if the stock declines from current, near-optimal levels (Takade and Paramore, 2007).

Assessment of NC and Virginia red drum together as one stock (Takade and Paramore, 2007) is justified by tagging data. Subadult red drum tagged in NC appear to be much more likely to move northward to Virginia than to any other state, even though interstate movements were generally low. Likewise, subadult red drum tagged in Virginia have consistently been recovered in NC waters (Lucy and Bain, 2007). 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 (Wenner, 1992). The interstate movement patterns of adult red drum appear to mirror those of subadults, showing a northward seasonal migration to Virginia each year, but very limited exchange with states south of NC. Our tagging results suggest that the state line between NC and SC is an important ecological division for red drum and, thus, an appropriate division for management and assessment.

Our results generally contrast with red drum population genetic results that imply significant interstate movement given low observed genetic variability (i.e., low F_{ST}) within Atlantic and Gulf of Mexico basins (Gold and Richardson, 1991; Gold et al., 1993; Seyoum et al., 2000). While low F_{ST} values may suggest a highly mixed population, they can also mean that subpopulations became isolated only very recently, or that just enough gene flow exists to homogenize genetic variability despite extremely limited exchange of individuals on average among sites (Conover et al., 2006). Given the many possible interpretations of low F_{ST} values in genetic studies, we believe tagging and telemetry methods are more appropriate techniques for defining the appropriate management unit for red drum.

Acknowledgements

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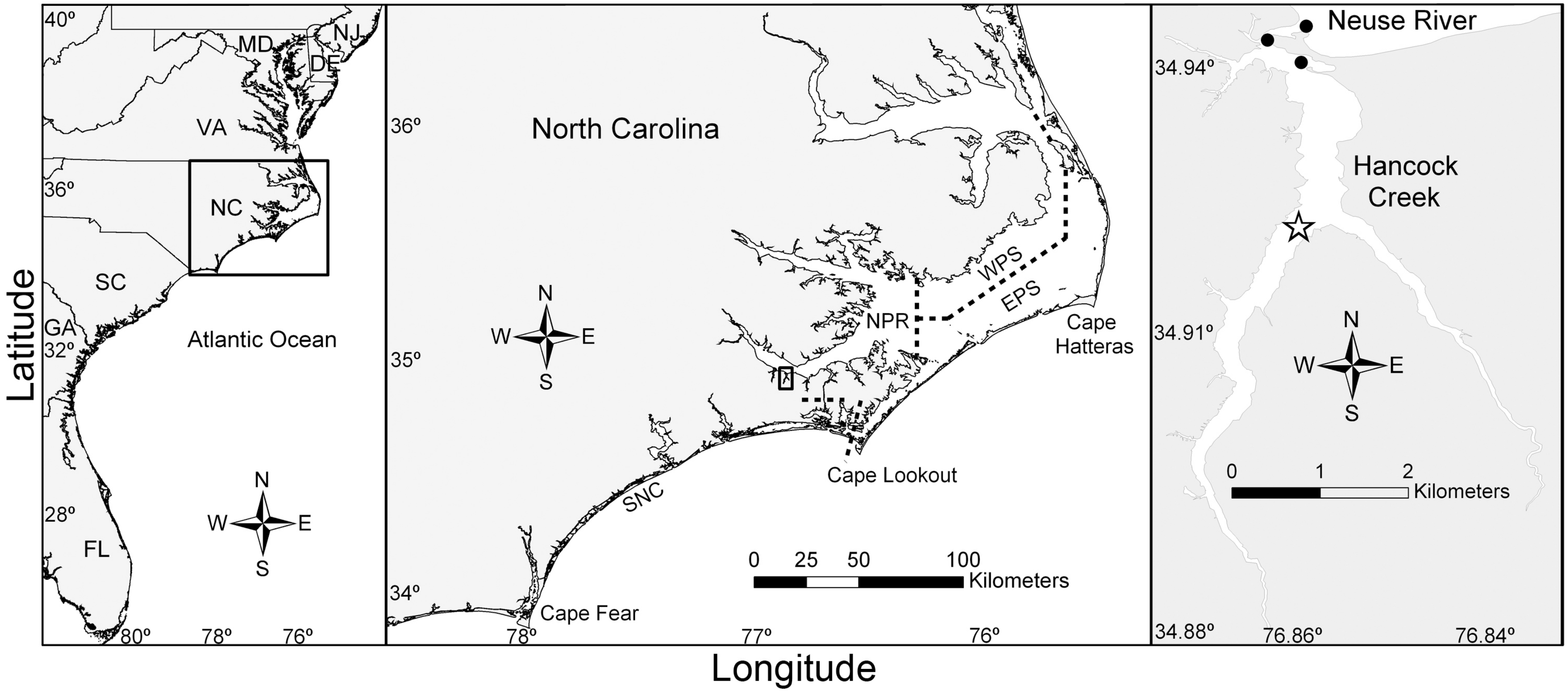
Table 1. Number of recovered North Carolina red drum, classified based on their age, region, and season of tagging, 1983 - 2007. No winter or spring data exist for age-1 red drum because these individuals were too small to be tagged in either tagging program.

	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

Table 2. Summary of movement information for four age groups of red drum in North Carolina, based on their age at tagging. 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 due to low sample sizes in some regions. Shortest distance in water was used for all distance and movement rate calculations.

	Total recoveries	Mean (SE) days at large	Max days at large	Mean (SE) dist moved (km)	Max dist moved (km)	Mean (SE) mov rate (km·d^{-1})	Prop 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



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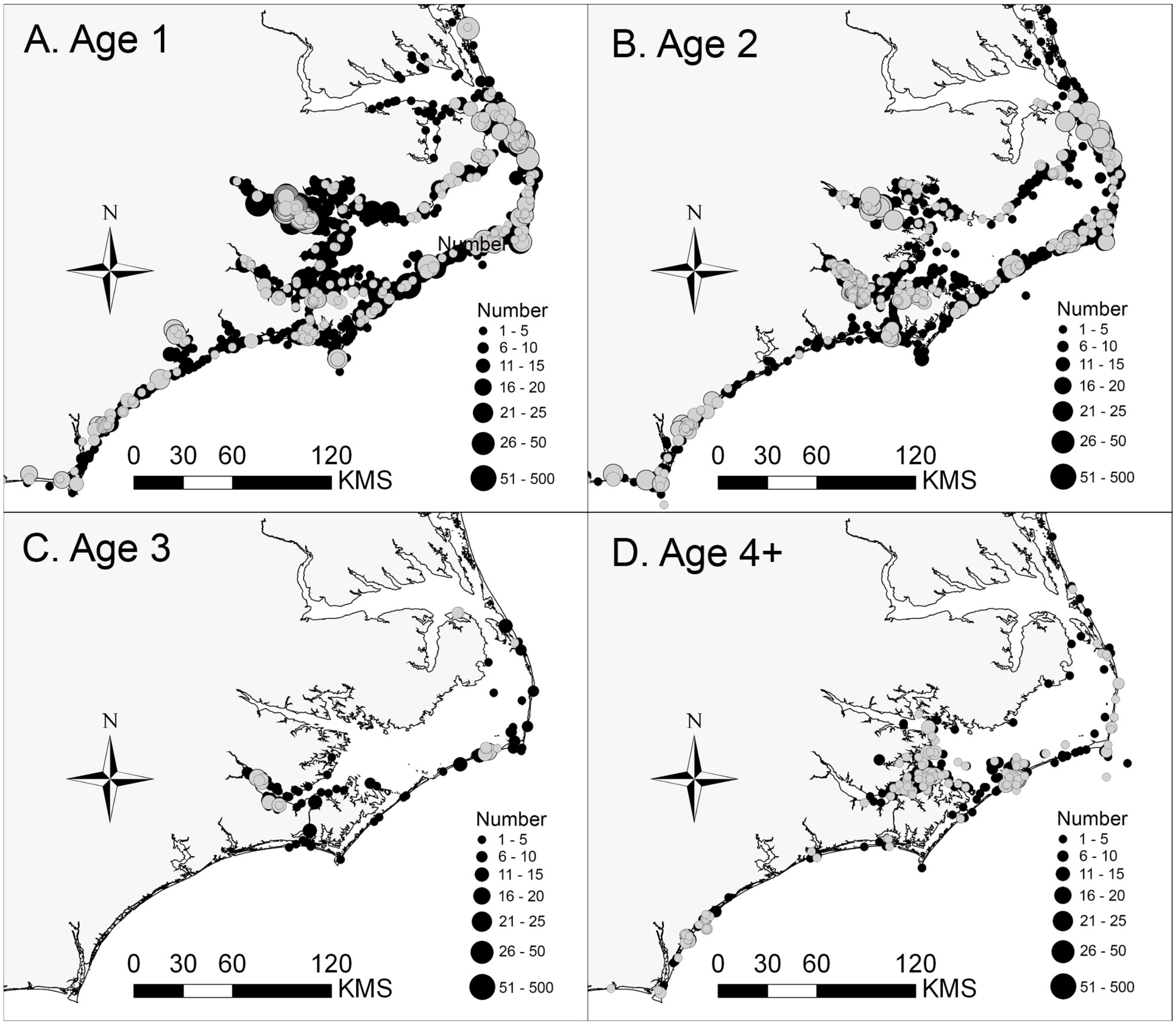

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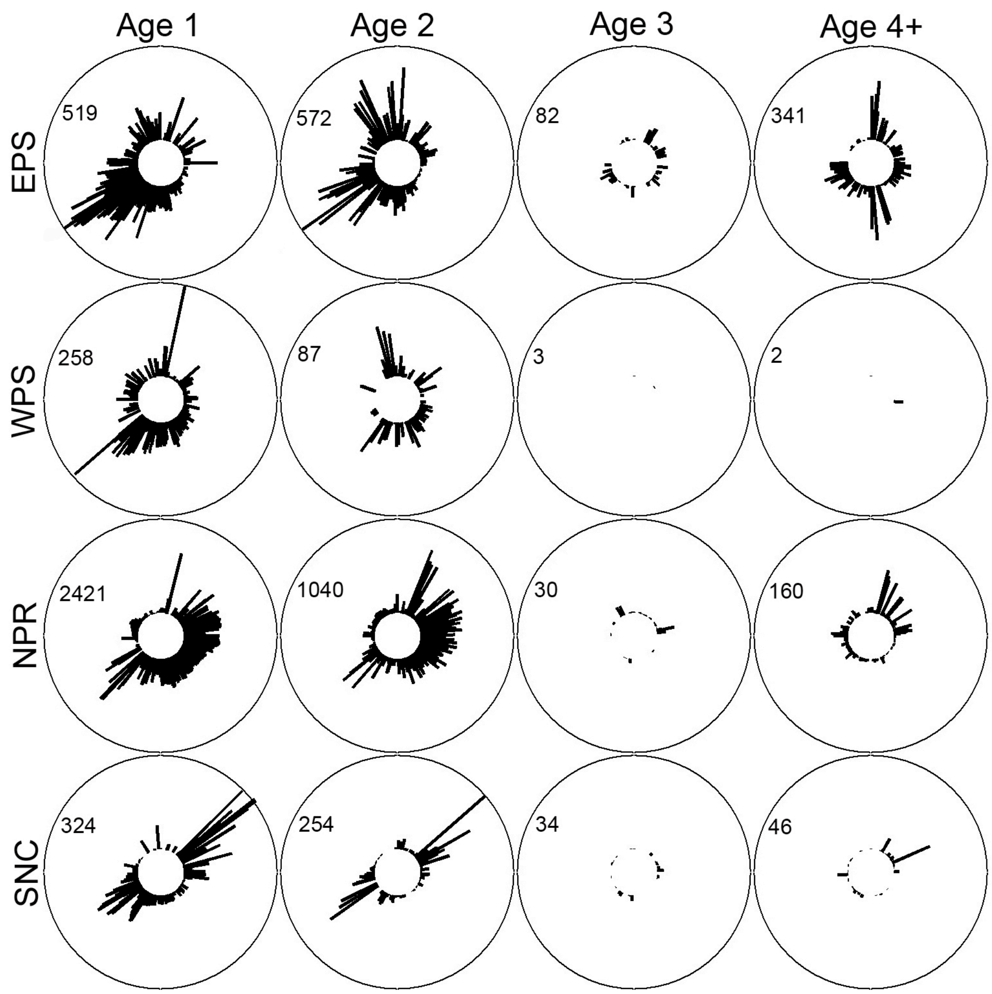

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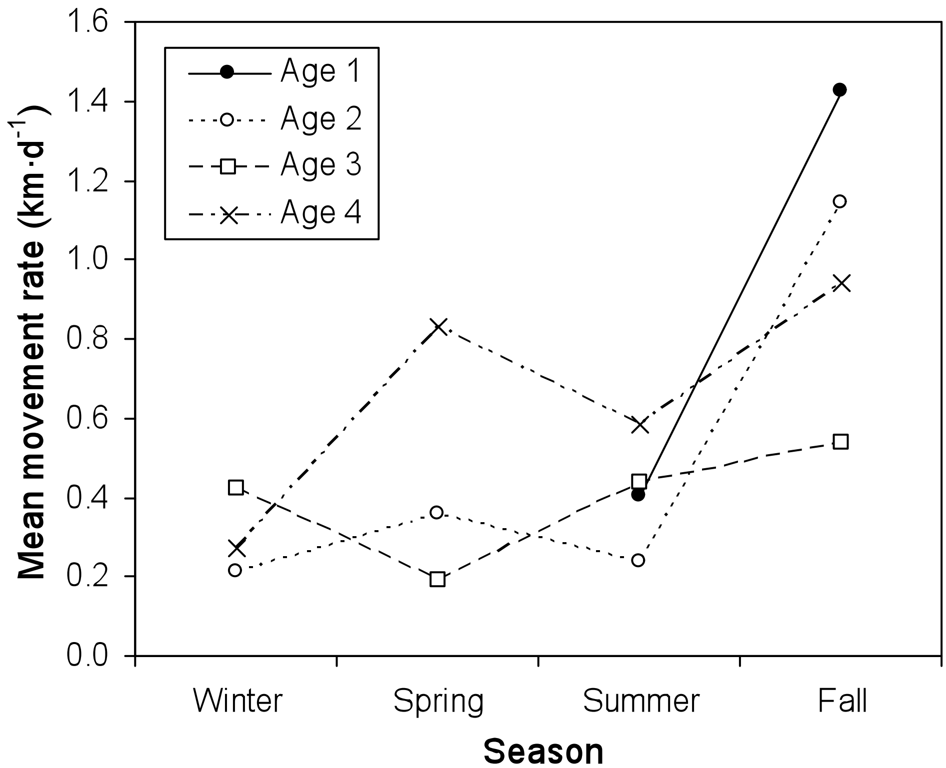

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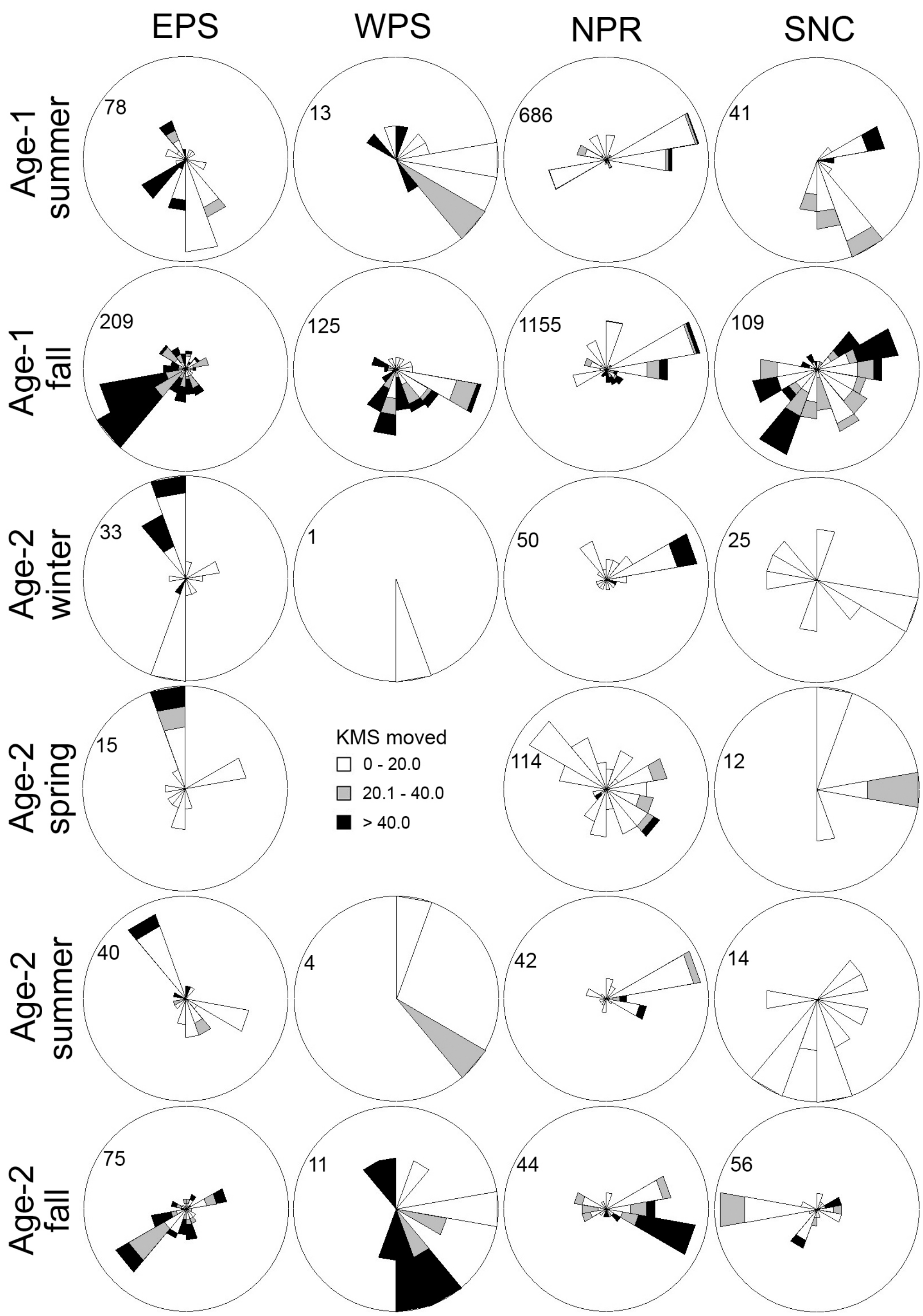

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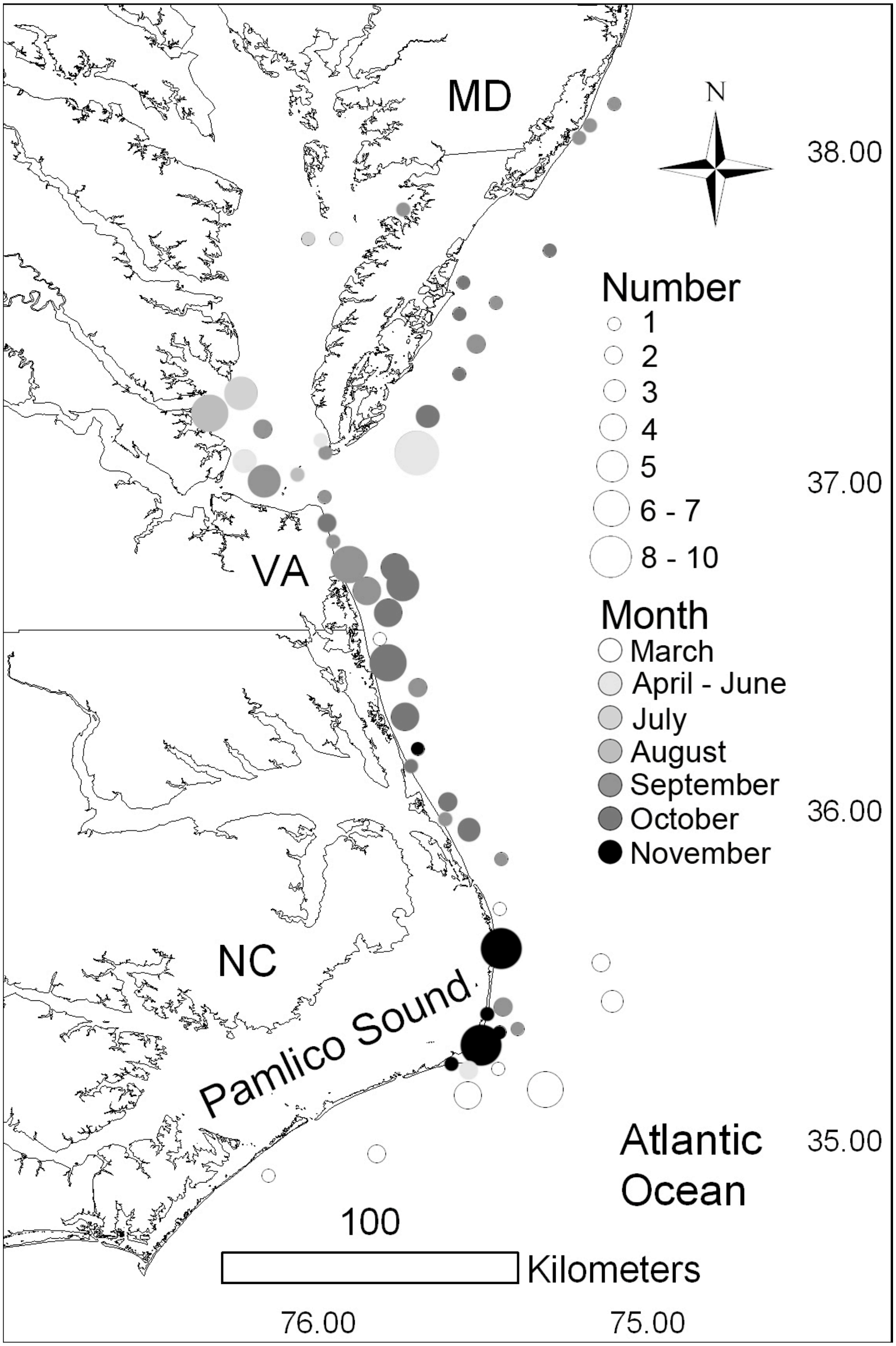

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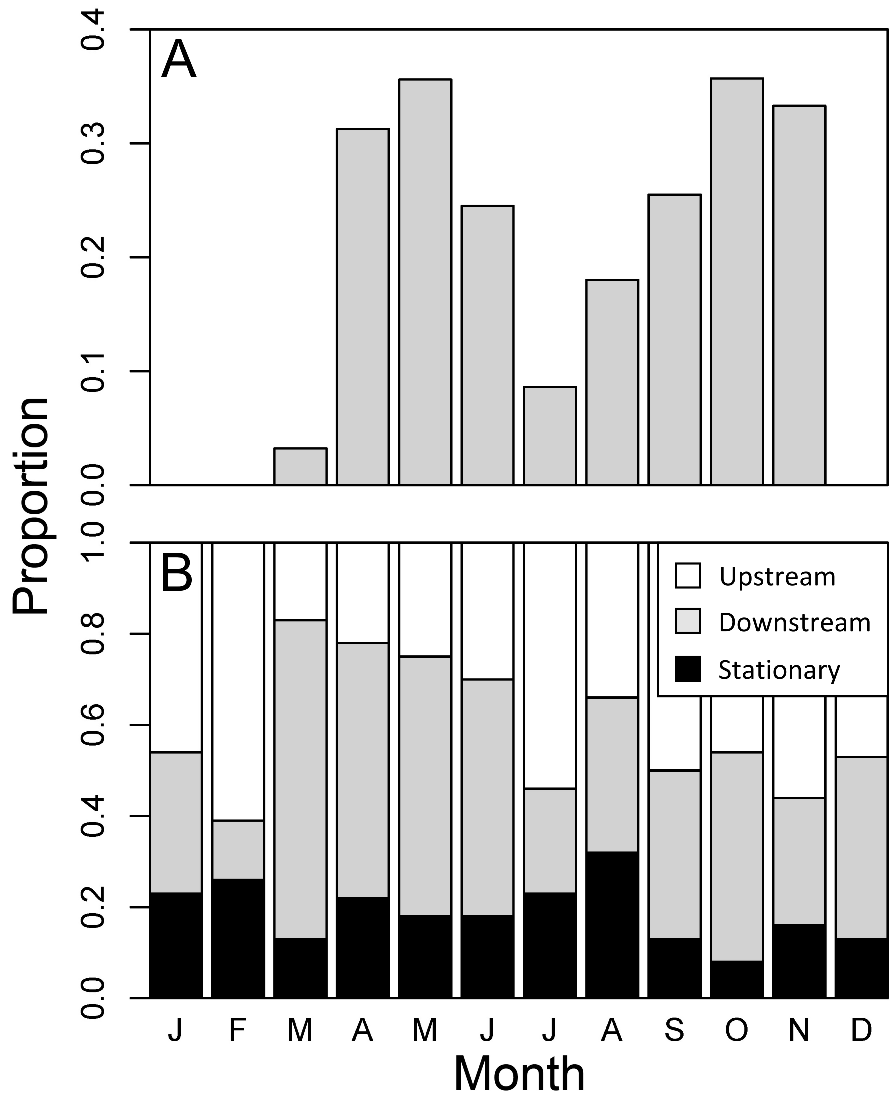

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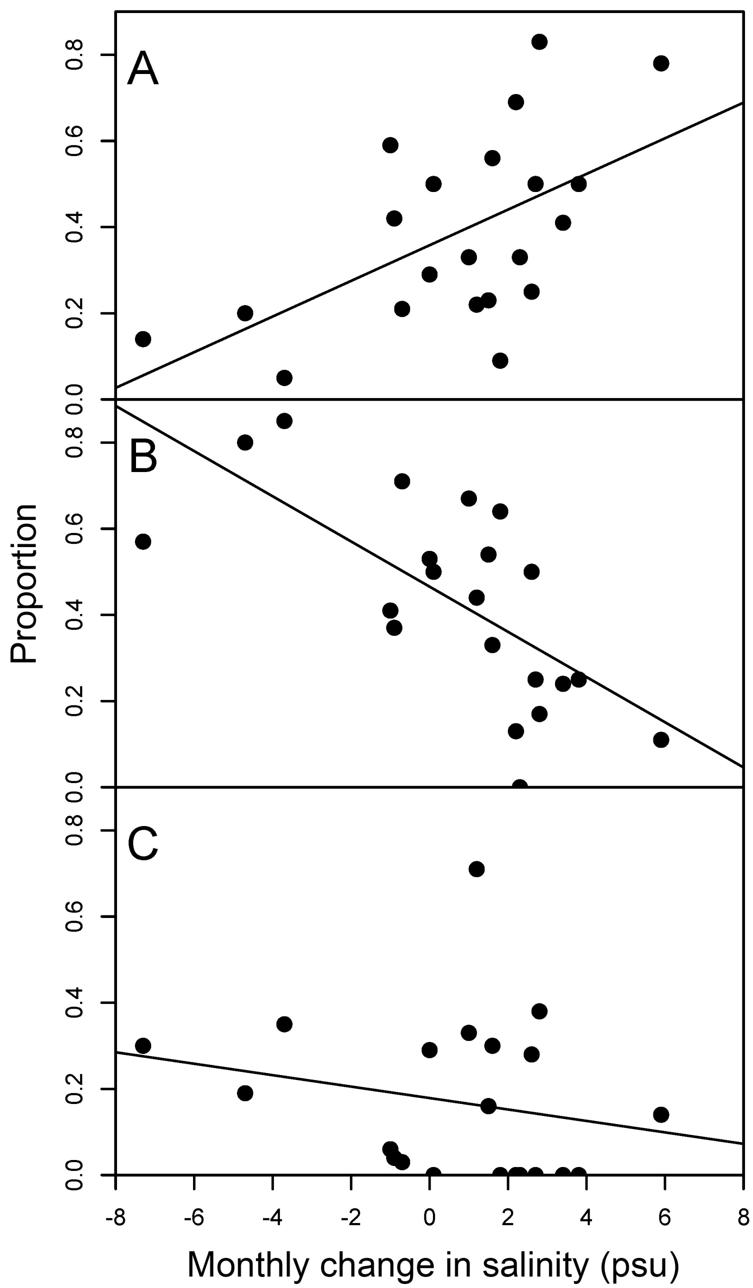

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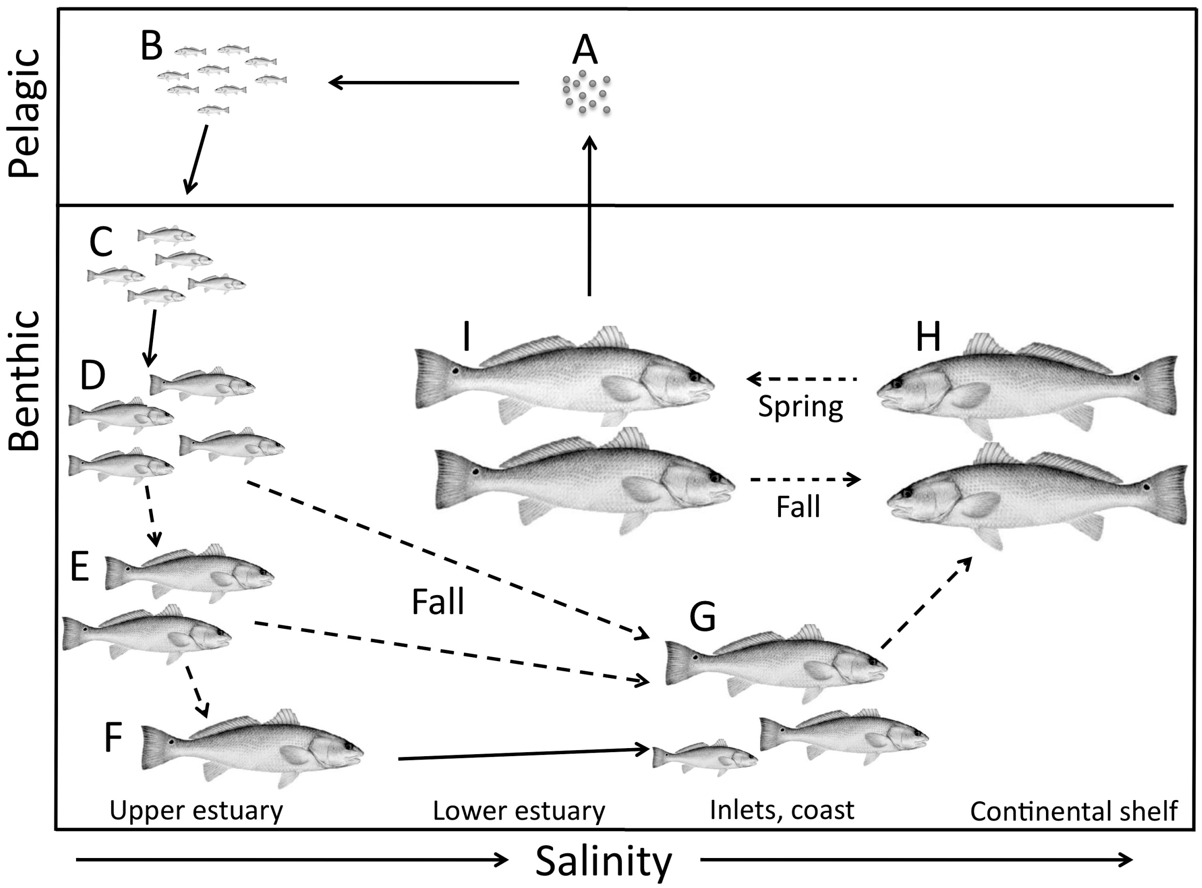

Bacheler. Figure 9.

Figure legends

Figure 1. Map of study areas in North Carolina. Left map shows location of coastal North Carolina (in box) along the Atlantic coast of the U.S.A. Middle map shows view of entire coastline of North Carolina, with the four regions used in the movement analyses demarcated by the dashed lines. The four regions are: eastern Pamlico Sound (EPS), western Pamlico Sound (WPS), Neuse and Pamlico Rivers (NPR), and 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, while the star shows where salinity measurements occurred.

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

Figure 3. Rose diagrams showing the direction and distances moved for tagged red drum in North Carolina, 1983 – 2007. Age classes are shown in columns and region of tagging in rows. Northward movements are straight up, southward movements are straight down, and outer circle is scaled to 300 kms. Sample size is provided on each diagram.

Figure 4. Mean movement rate ($km \cdot d^{-1}$) of four age classes of red drum by season in which tagging occurred. Only movement rates of fish recovered within 60 days of tagging were used.

Figure 5. Frequency distributions of angular directions moved for subadult red drum recovered within 60 days of tagging, with season and age class shown as rows and region tagged as columns. The overall length of each wedge shows the relative frequency of angular observations within 20º 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 6. Seasonality of captures of adult (age-4+) red drum caught in coastal North Carolina, Virginia, and Maryland. Data are from the National Marine Fisheries Service trawl survey, Virginia Institute of Marine Sciences shark longline survey, or tagged or recovered in the North Carolina Division of Marine Fisheries tagging project (1983 – 2007). The National Marine Fisheries Service survey took place in continental shelf waters north of Cape Hatteras in spring (March) and fall (September – November) each year in 1963 – 2004, and the Virginia Institute of Marine Sciences survey was conducted in Chesapeake Bay and coastal Virginia waters in May or June through September or October in 1974 – 2004.

Figure 7. Seasonal ultrasonic telemetry relocation information for age-2 red drum in Hancock Creek, 2005 – 2007. (A) Proportion of telemetered red drum emigrating each month from Hancock Creek, combined across years. (B) Proportion of telemetered red drum moving upstream, downstream, or remaining stationary within Hancock Creek, combined across years.

Figure 8. Proportion of telemetered red drum in Hancock Creek moving upstream (A), moving downstream (B), or emigrating (C) in relation to the salinity change between two consecutive monthly relocation periods. Salinity sampling took place midriver near the boat ramp, and monthly periods are only included if at least four telemetered red drum were relocated in that period.

Figure 9. Conceptual diagram of red drum life history and movement patterns in North Carolina. A, spawned eggs in August/September; B, pelagic larvae 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 inhabiting coastal habitats, eventually joining adults after maturity at approximately age 3 or 4; H, overwintering, nonspawning adult (age-4+) red drum; I, spawning adult red drum during summer months. Dotted lines indicate that a particular pathway is not necessarily followed by all members of a cohort in a particular year.