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Source: Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science, 7(7) : 450-463

Published By: American Fisheries Society

URL: https://doi.org/10.1080/19425120.2015.1079578

Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science 7:450–463, 2015
Published with license by the American Fisheries Society
ISSN: 1942-5120 online
DOI: 10.1080/19425120.2015.1079578

ARTICLE

Estuarine Residency and Migration of Southern Flounder Inferred from Conventional Tag Returns at Multiple Spatial Scales

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Abstract
An improved understanding of the spatial structure and movements of harvested populations can promote more efficient management of marine resources. Conventional tagging is a valuable approach to study the movements of marine fishes due to its relatively low expense and the typically broad spatial extent over which movements can be characterized. We present the findings of multiple tag return studies initiated in the estuaries of North Carolina during the past two decades to better understand habitat residency and migration patterns of Southern Flounder *Paralichthys lethostigma*, an economically important marine flatfish in the southeastern USA. Tag return data indicated large-scale (>50 km) movements of relatively large fish in the fall, which were presumably associated with offshore winter spawning migrations. Nearly all Southern Flounder that demonstrated large-scale movement were recovered to the south of the system in which they were tagged, suggesting that the spawning activity of fish using North Carolina estuaries may be concentrated mostly off the southeastern U.S. continental shelf. Tag returns from within multiple estuarine systems during the spring and summer were in close proximity to release sites (typically < 1 km), suggesting limited movement during estuarine residency. Recaptures in the spring of fish tagged the previous summer or fall were also in close proximity to release sites, in some cases within the same estuarine creek, indicating limited movement of fish overwintering in the estuary as well. Our findings reveal saltatory movement dynamics of Southern Flounder characterized by limited movement during estuarine residency and large-scale movements in the fall associated with spawning migrations. Our synthesis of several tag return studies across multiple spatial scales should contribute to a better alignment of Southern Flounder management with their spatial dynamics.

Subject editor: Patrick Sullivan, Cornell University, Ithaca, New York

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Received April 13, 2015; accepted July 20, 2015

There is increasing recognition that the stock definition of harvested marine resources is more complex than the traditional view of geographically distinct units with homogenous vital rates that are reproductively isolated from adjacent populations (Stephenson 1999; Quinn 2003; Cadrin and Secor 2009; Hamilton et al. 2011). Many fish populations exhibit complex spatial patterns and movements that generate spatial heterogeneity in demography, population biomass, and realized rates of exploitation (Goethel et al. 2011; Hamilton et al. 2011; Berger et al. 2012). Despite growing recognition that the movements of fish populations can have important implications for understanding harvested ecosystems, spatial dynamics have been largely ignored in the assessment and management of marine resources (Secor 2005).

In many cases, the stock boundaries of harvested populations are based on jurisdictional or management convenience rather than on the life history and ecology of the species under consideration (Cope and Punt 2011; Berger et al. 2012). For example, mismatches between the spatial structure of marine populations and the stock definitions used for management were identified for about one third of harvested stocks in the northeastern Atlantic Ocean (Stephenson 2002). As a result, many stock assessment models violate the basic assumption that emigration and immigration rates are negligible, potentially confounding these demographic rates with other model parameters. Failure to match the spatial scale of fisheries stock assessments to ecologically relevant processes that influence population dynamics can hinder the achievement of fishery harvest and conservation objectives (Fay et al. 2011; Hamilton et al. 2011; Taylor et al. 2011; Ying et al. 2011).

Adequately addressing the spatial aspects of harvested populations is limited more by the lack of reliable field observations on movement dynamics than by the availability of appropriate modeling tools. Conventional tagging studies are a useful approach for understanding movement dynamics because they are relatively inexpensive, can cover a large spatial extent, and generate direct information on individual fish movements (as opposed to indirect information from various molecular and chemical markers). Such studies are particularly useful for defining the appropriate geographic scale at which to monitor, assess, and manage marine resources (e.g., Bacheler et al. 2009; Cadrin and Secor 2009). In addition, recent advances in stock assessment modeling allow tagging data to be incorporated directly into population dynamic models to simultaneously estimate movement, exploitation rate, and the spatial distribution of population biomass (McGarvey et al. 2010; Goethel et al. 2011; Taylor et al. 2011; Hulson et al. 2013).

Southern Flounder *Paralichthys lethostigma* is a harvested marine flatfish that is distributed along the U.S. southern Atlantic and Gulf of Mexico coasts from southern Virginia to the Yucatan peninsula in northern Mexico. Adult Southern Flounder spawn in offshore waters from November to March (Stokes 1977; Miller et al. 1984; Burke et al. 1991), with pelagic larvae recruiting to estuarine habitats at 1–2 months of age. After settlement, Southern Flounder remain in estuaries for the first 2–3 years of life before moving into ocean waters (Powell and Schwartz 1977; Stokes 1977; Wenner et al. 1990). Maturation is typically attained by age 2 (Midway and Scharf 2012), with immature individuals thought to overwinter in the estuary while mature individuals emigrate from estuaries to offshore spawning grounds in the fall. After spawning, mature fish are believed to return to nearshore or estuarine waters in late spring. Southern Flounder support valuable commercial and recreational fisheries, with landings concentrated primarily in estuarine waters. In the southeastern USA, the majority of commercial landings are harvested in North Carolina (>45.4 million kg landed since 1972, ~1.13 million kg annually; http://portal.ncdenr.org/web/mf/statistics/comstat). The fisheries are managed independently by individual states, and North Carolina is presently the only state in the region with a comprehensive management plan for Southern Flounder. A 2009 assessment of the North Carolina Southern Flounder fishery concluded that the stock was overfished (low spawning biomass) and that overfishing (high fishing mortality) was occurring. An important assumption of this stock assessment is that there is no net migration of Southern Flounder outside of North Carolina state waters.

Studies of the movements and habitat use of Southern Flounder have focused mostly on recently settled and young-of-the-year (age-0) fish in estuarine habitats (Powell and Schwartz 1977; Burke et al. 1991; Burke 1995; Glass et al. 2008; Nañez-James et al. 2009; Taylor et al. 2010; Froeschke et al. 2013a, 2013b; Furey and Rooker 2013). Collectively, these studies suggest some level of habitat specificity, with settlement patterns potentially related to the physical transport processes affecting larvae (e.g., Taylor et al. 2010), and habitat selection of age-0 fish driven by several abiotic and biotic factors (e.g., Burke et al. 1991; Walsh et al. 1999; Froeschke et al. 2013a; Furey and Rooker 2013). Estuarine movements of larger age-0 and subadult fish appear to be fairly localized, with fish moving less than 10 km over periods of at least 1 month (Furey et al. 2013). Recent studies using otolith microchemistry suggest more extensive use of low-salinity habitats than previously thought (Lowe et al. 2011; Farmer et al. 2013; Nims and Walther 2014). Despite indications of limited movement, there is little evidence for discrete populations within the Gulf of Mexico or Atlantic basins, though molecular and otolith morphometric studies indicate high levels of genetic divergence between southern Atlantic Ocean and Gulf of Mexico populations (Blandon et al. 2001; Anderson and Karel 2012; Anderson et al. 2012; Midway et al. 2014; Wang et al. 2015). The movements of larger, older (>age-1) Southern Flounder, as well as the migratory patterns associated with maturation, are poorly understood.

There are few published studies of Southern Flounder movement and no quantitative analysis of large-scale movements associated with spawning. Our primary objective was to quantify the spatial scale of Southern Flounder movements in order to better understand the stock structure of this species and its relevance to the management unit assumed for this stock. Our secondary objective was to better understand the localized movements of Southern Flounder during the period of estuarine residency. We investigated the movements of Southern Flounder using three conventional tagging data sets collected from multiple estuarine ecosystems in North Carolina. First, we quantified the directionality of Southern Flounder movements, the total distance moved, and the occurrence of large-scale movements (>50 km) in relation to fish size, season, year, and estuary based on tag return data for fish tagged in the Neuse and New River estuaries during 2005 and 2006. We then integrated these results with similar analyses of prior tagging studies conducted in multiple North Carolina estuarine systems during the 1980s and 1990s and also with data from a small-scale study conducted in a single marsh creek from 2003 to 2005. We interpret our results in terms of their relevance to the spatial dynamics of Southern Flounder and other similar flatfish species, as well as to recent management decisions based on the most current assessment of the stock supporting the fishery in North Carolina waters.

METHODS

Study Systems

Paired tagging studies using identical methodologies were conducted in the Neuse and New River estuaries in 2005 and 2006 (Figure 1). The Neuse River estuary is a large (~75 km in length) riverine estuary located in the central portion of the North Carolina coast that drains into the southwestern corner of Pamlico Sound. The New River estuary is located in a separate drainage basin along the southern portion of the coast and

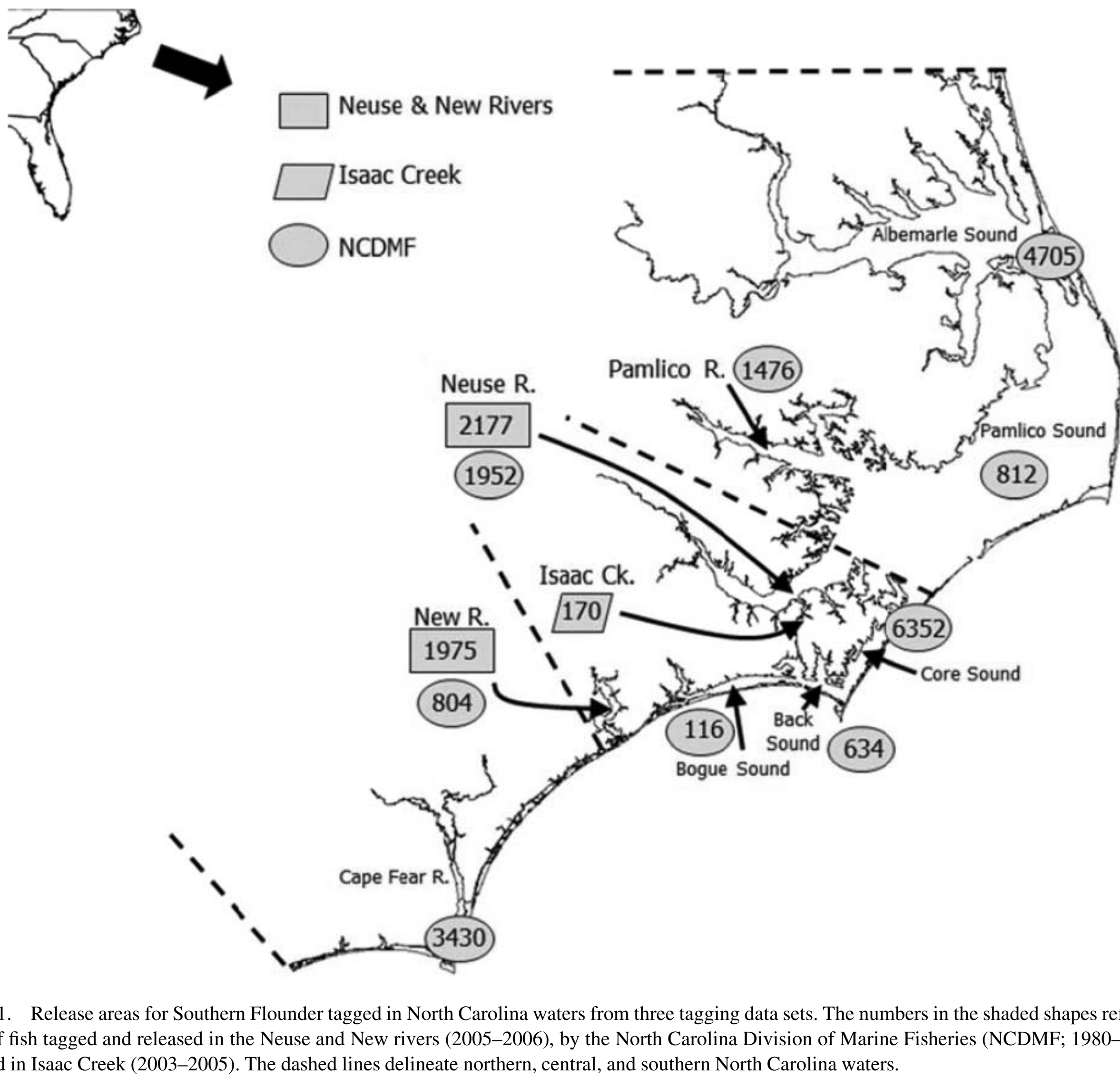

FIGURE 1. Release areas for Southern Flounder tagged in North Carolina waters from three tagging data sets. The numbers in the shaded shapes reflect the total number of fish tagged and released in the Neuse and New rivers (2005–2006), by the North Carolina Division of Marine Fisheries (NCDMF; 1980–1982, 1988–1995), and in Isaac Creek (2003–2005). The dashed lines delineate northern, central, and southern North Carolina waters.

extends over 25 km before emptying into the coastal ocean. Both estuaries range from oligohaline to polyhaline along their length, have slow flushing and high nutrient retention rates, and are considered moderately to severely eutrophic (Mallin et al. 2000). Earlier tagging of Southern Flounder in the 1980s and 1990s was conducted in inshore estuarine waters from Albemarle Sound to the Cape Fear River estuary as part of a long-term tagging program by the North Carolina Division of Marine Fisheries (NCDMF) (Figure 1). These data included riverine estuaries as well as fish tagged in the larger bays and sounds throughout the state. A small-scale tagging study was conducted in Isaac Creek, a small (2.5 km in length) marsh creek adjacent to the Neuse River estuary, from 2003 to 2005.

Tagging Methodology

Neuse and New River study.—Tagging was conducted during the 2005 and 2006 fishing seasons (March to November) in the Neuse River estuary and the New River estuary in collaboration with commercial gill-net fishermen (Figure 1; Table 1). Over the 2-year period, approximately 2,000 Southern Flounder were tagged in each system. Fish were retrieved from overnight sets of 14-cm stretched-mesh gill nets, held in insulated coolers for less than 15 min, tagged with an external orange cinch-up tag (Floy Tag, Seattle), measured for total length (TL), and released within 200 m of the capture location. Tags were inserted into the dorsal region of the caudal peduncle with a stainless steel canula and cinched to allow a remaining space of about 10–15 mm for growth. Each tag was labeled with a cash reward (US$5 or $50), a unique identification number, and contact information. Some undersized fish ($\leq$356 mm) were tagged in the Neuse River, while all tagged fish in the New River were of harvestable size. Over the 2-year period, only 20 Southern Flounder ($<$1%) were recaptured more than once (all in the Neuse River). These fish were measured and re-released. Only the first recapture was retained in the statistical analysis.

Tagging study by NCDMF.—Southern Flounder were tagged as part of a long-term tagging program for paralichthid flounders conducted by the NCDMF from 1980 to 1982 and from 1988 to 1995 (Figure 1; Table 1). Fish were captured primarily in commercial pound nets and trawls from January to December, with 87% of fish captured between April and November. Each fish was held in a holding tank onboard the vessel, tagged with a laminated internal anchor tag inserted into the abdominal cavity, and then returned to the water after a 15–20-min recovery period. Tags were labeled with a $2 reward prior to June 1990 and a $5 reward or cap thereafter. From 1980 to 1982, Southern Flounder greater than 200 mm were tagged, while from 1988 to 1995 all fish greater than 160 mm were tagged. As a result, many more small fish were tagged in the NCDMF study than in the Neuse and New River study (85% $\geq$ 356 mm; Table 1). Over the 11-year period, 20,281 fish were tagged, with most of the tagging conducted in southern Albemarle Sound, the Pamlico River estuary, Core Sound, the Neuse River estuary, and the Cape Fear River estuary (Figure 1).

Isaac Creek study.—From March 2003 to May 2005, 170 Southern Flounder were tagged in Isaac Creek (Figure 1; Table 1). These fish were also captured from overnight sets of gill nets as part of a larger study of the piscivore community in shallow estuarine creeks (Kirby-Smith et al. 2003; J. K. Craig, unpublished data). Gill nets were set weekly to biweekly from March 2003 to April 2004 and monthly thereafter. Captured fish were tagged between the dorsal pterygiophores with 63.5-mm T-bar anchor tags (Floy Tag). Tags were printed with a unique identifying number and contact information. Initially, tags were not labeled with a reward, but a $5 reward was added to the tags midway through the study.

Data Analysis

We conducted separate but parallel analyses of the three data sets (Neuse and New rivers, NCDMF, Isaac Creek) rather than a single integrated analysis due to inherent differences in the data and the types of analyses that could be conducted. In some cases, response variables were defined differently across data sets based on the spatial scale and the resolution of the

TABLE 1. Southern Flounder tagged in North Carolina waters from three tag–recapture studies (Neuse and New rivers, 2005–2006; NCDMF, 1980–1982 and 1988–1995; and Isaac Creek, 2003–2005). Mean total length (TL) is given in millimeters, with the standard deviation given in parentheses. Recap is the percentage of tagged fish that were recaptured, with the number of recaptures given in parentheses. Days at large is given as the median, with the range given in parentheses. Recap location is the percentage of recaptured Southern Flounder that were recaptured within the same system where they were tagged.

Study	Year	Number tagged	Tagging period	Mean TL	Recap	Days at large	Recap location (%)
Neuse River	2005	1,018	Apr–Aug	367 (30.3)	25.0 (255)	7 (1–463)	93.7
	2006	1,159	Apr–Oct	372 (41.6)	24.4 (283)	21 (1–444)	88.0
New River	2005	1,011	Jun–Nov	387 (34.3)	24.3 (246)	19 (1–958)	89.8
	2006	964	May–Oct	390 (29.0)	52.4 (505)	26 (1–432)	96.1
NCDMF	1980–1982, 1988–1995	20,281	Jan–Dec	291 (66.6)	5.7 (1,156)	43 (1–2,429)	78.9
Isaac Creek	2003–2005	170	Jan–Dec	345 (69.8)	8.8 (15)	98.5 (12–206)	80.0

tagging information, and not all predictor variables were available for all data sets. The NCDMF data were unbalanced with respect to season, system, and year and required some degree of pooling across one or more predictors, while the Neuse and New River data were relatively balanced with respect to these factors. Sample sizes from the Isaac Creek study were small (Table 1) and not sufficient to statistically detect the effects of multiple predictor variables; therefore, only a descriptive analysis of these data are presented. Our analytical approach focused on the Neuse and New River study and then used the two other data sets to corroborate our main results and provide additional insights beyond those available in the Neuse and New River data.

Response variables.—Tag returns from the Neuse and New rivers, the NCDMF tagging, and Isaac Creek were divided into two categories and analyzed separately for the three data sets. The first category included fish that were recovered prior to December 1 in the same calendar year they were tagged. These fish represented 86% of all tag returns and are referred to as the "prewinter analysis." The second category included fish that were recovered after having the opportunity to join the winter offshore spawning migration (after December 1 of the calendar year of tagging). Emigration of mature adults from estuaries to the coastal ocean is thought to be completed by December 1 in most years (L. Hollensead and F. S. Scharf, University of North Carolina Wilmington, unpublished data). These fish represented 14% of all tag returns and are referred to as the "overwinter analysis."

Three response variables were developed that reflected different aspects of the movement dynamics of Southern Flounder: (1) the total distance moved, (2) the direction of movement, and (3) a binomial variable indicating whether a fish moved more than 50 km (overwinter analysis only). The total distance moved (km) was calculated in ArcGIS (ESRI 2011) as the shortest distance between tagging and recovery locations that did not cross land. The direction of movement was defined differently depending on the spatial scale and resolution of particular data sets. For the prewinter analysis of Neuse and New River data, the direction of movement was categorized as upstream, downstream, or stationary within the study system (i.e., Neuse or New rivers) because movement out of the river of tagging was generally not observed prior to winter. Stationary was defined as a tag recovery location that was < 1 km from the tagging location. Movement upstream or downstream could not be determined for most fish in the prewinter analysis of the NCDMF data because tagging and recovery locations were defined only broadly and tagging was conducted mainly in the larger bays and sounds rather than in particular river systems. Based on initial tag returns, Monaghan (1992) hypothesized that Southern Flounder begin to move south within the Albemarle–Pamlico estuarine system prior to moving through southern inlets to the coastal ocean. Therefore, the direction of movement was categorized as north, south, or stationary for the prewinter analysis of the NCDMF data. Stationary was defined as a tag recovery occurring within the system of tagging (Figure 1). For the overwinter analysis of both data sets, the direction of movement was categorized as north or south of the study system based on whether the recapture location was north or south of a latitudinal line bisecting the tagging location. Fish that moved >50 km were determined from the total distance moved. All overwinter recoveries of fish that had moved >50 km occurred outside of the estuarine system where they were tagged, and no fish that had left the estuarine system of tagging moved < 50 km. Most of these fish were recovered in other estuarine systems or coastal waters downstream of the tagging location, while a few fish were recovered near inlets in the larger Pamlico Sound and were presumed to be migrating offshore to spawn.

Statistical analysis.—Multiple regression and multinomial logistic regression were used to test the effects of predictor variables on the distance moved, direction of movement, and probability of moving >50 km. For the prewinter analysis of Neuse and New River data, TL at tagging, season of tagging (summer and fall), system (Neuse River or New River), and year (2005 or 2006) were tested for their effects on the total distance moved and the direction of movement. Summer was defined as April−July and fall was defined as August−November. Unbalanced sample sizes with respect to system and season across the 11 years of tagging by the NCDMF precluded the analysis of year and system effects. Therefore, data were pooled across years and systems, and the effects of TL at tagging and season of tagging were tested for their effects on the total distance moved and the direction of movement. Both analyses were conditioned on the days at large of individual fish because we assumed greater movement was possible with increasing days at large. In addition, models of the Neuse and New River data were conditioned on monthly fishing mortality because nearly all returns were from commercial fishermen, and we assumed that the level of fishing mortality would influence the probability of tag return. The monthly fishing mortality rate was estimated separately for the Neuse and New rivers during the 2005 and 2006 fishing seasons using a tag–recapture model applied to these same tag return data (Craig and Rice 2008; Smith et al. 2009). Monthly fishing mortality rates were not available for the NCDMF tagging data set.

For the overwinter analysis of Neuse and New River data, the effects of predicted TL at the beginning of the spawning season (November 1), system, and year were tested for their effects on the probability of moving > 50 km using binomial logistic regression. Due to small sample sizes, only the effect of length on overwinter movement was tested for the NCDMF data set. For both data sets, the length at the beginning of the spawning season was predicted using the length at tagging and the von Bertalanffy growth model parameters estimated in the 2009 North Carolina stock assessment (Takade-Heumacher and Batsavage 2009) and a growth model based on mark–recapture data (Fabens 1965). Southern Flounder growth is sexually dimorphic, with females (maximum observed size = 835 mm TL) reaching a much larger asymptotic length than males (maximum observed size = 495 mm TL) (Takade-Heumacher and Batsavage 2009). Because males and females have different growth schedules and possibly migratory patterns, fish predicted to be less than 356 mm TL on November 1 were removed from the overwinter analysis of both data sets. These smaller fish could have been mature males that might have joined the offshore spawning migration at relatively small sizes or immature females that overwintered in the estuaries. At lengths > 356 mm TL at least 85% of Southern Flounder are estimated to be female (see Figure 4 in Takade-Heumacher and Batsavage 2009); therefore, the overwinter results apply primarily to female fish.

All possible models, including intercept-only models, were compared using the Bayesian information criterion (BIC), and the model with the lowest BIC was selected as the best model. We chose BIC (rather than Akaike information criterion) because it penalizes model complexity more severely and, hence, is more conservative in terms of the predictor variables retained in the best model (Burnham and Anderson 2002). The weight of evidence in support of alternative models was compared using BIC weights. Normal, Poisson, and negative binomial error distributions were tested for models of the distance moved; the negative binomial provided the best fit and was used for all models. Each of the best models' regression coefficients were analyzed for significance using *t*-tests ($\alpha = 0.05$). All statistical analyses were conducted in R 3.1.0 (R Core Development Team 2012).

RESULTS

Recaptures of Southern Flounder ranged from 5.7% to 52.4% depending on the system, year, and data set (Table 1). Most recaptured Southern Flounder were recovered within the same system where they were tagged (79−96%). The mean size of tagged Southern Flounder was similar across systems and years, except for fish tagged by the NCDMF, which were about 20% smaller on average than those tagged in the Neuse and New rivers. Based on the examination of otolith annuli, most recovered Southern Flounder were age 1 and nearly all were less than age 2. The median days at large was similar for fish tagged in the Neuse and New rivers (19−26 d), with the exception of the Neuse River in 2005 (7 d). For fish tagged statewide by the NCDMF, the median days at large was 43 d, with fish recaptured within the year of tagging at large for a median of 20 d, while fish recaptured the following year were at large for a median of 280 d. The median days at large for recaptures of fish tagged in Isaac Creek was 99 d, with those recaptured within the creek at large for up to 206 d.

Prewinter Analysis

Southern Flounder were resident within local riverine and estuarine systems in North Carolina for large portions of the year. Across the 2 years and the two river systems, 69% of Southern Flounder tagged and recovered within the Neuse River or New River did not move considerable distances (i.e., fish were recaptured < 1.0 km from the tagging location). Fish that did move > 1.0 km were recovered at relatively moderate distances from the tagging location, with median distances moved of 3.6 km (range = 1.0–19.5 km) in the Neuse River and 4.2 km (range = 1.0–24.6 km) in the New River. The best model to explain the distance moved prior to winter included only the season of tagging as an explanatory variable (BIC weight = 0.26; Table 2). The null model and models with only a year or system effect were closely ranked (BIC weights = 0.24, 0.18, and 0.15, respectively), however, suggesting the predictor variables were not highly informative about factors affecting the distances Southern Flounder moved within estuaries. Fish moved 0.16 ± 0.01 km/d (mean ± standard error) during the summer season (April to July) and 0.24 ± 0.05 km/d during the fall season (August to November) (Figure 2A).

Similar to the Neuse and New rivers, fish tagged by the NCDMF also showed little movement during the prewinter period. Nearly 80% of the fish were recovered in the same area as the tagging location, and of those that had clearly moved from the tagging location, the median distance moved was only 14 km. Similar to the Neuse and New River study, the best model to predict the distance moved also included only season as an explanatory variable (BIC weight = 0.66; Table 2). On average fish moved 0.33 ± 0.00 km/d during the summer and 0.99 ± 0.11 km/d during the fall (Figure 2B).

The best model of the direction of Southern Flounder movements in the Neuse and New rivers during the prewinter period included the effects of TL, season, and system of tagging (BIC weight = 0.71; Table 3); year was not included. These effects were primarily driven by the downstream movements of relatively large Southern Flounder in the fall (Figure 3). Relative to remaining stationary, Southern Flounder were 2–3 times more likely to move downstream in the fall than in the summer, and relatively large fish (≥450 mm TL) were more than twice as likely to move downstream than were relatively small fish (≤375 mm). Also, downstream movements were slightly more likely to be observed in the

TABLE 2. Results from the best multiple linear regression models of the total distance moved from the prewinter analysis of Southern Flounder, fit separately for the Neuse and New River data set and the NCDMF statewide data set. For both season and TL (mm), model inputs refer to the time of tagging. The *P*-values are defined as follows: three asterisks indicate < 0.001 and two asterisks indicate < 0.01. The "X" indicates terms that were removed during the BIC model selection process.

Data set	*N*	Intercept	TL	Season	System	Year
Neuse and New rivers	789	6.3***	X	1.1**	X	X
NCDMF	728	8.5***	X	0.9***	X	X

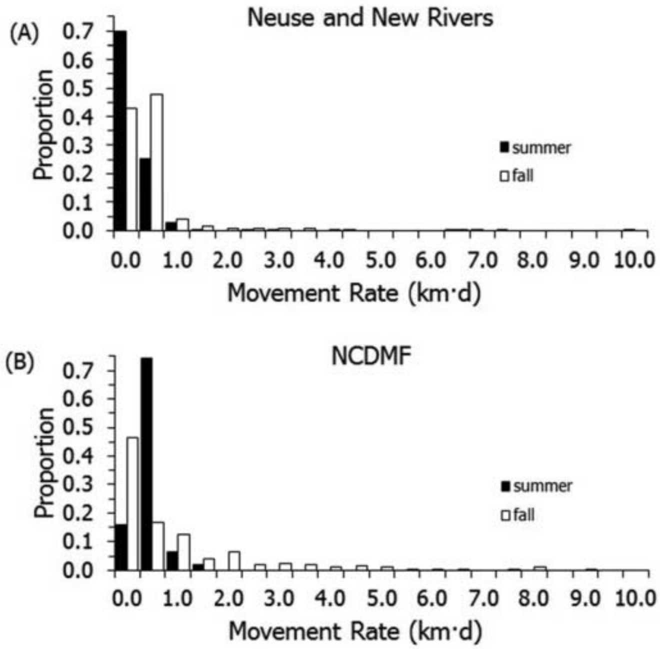

FIGURE 2. Movement rate of prewinter Southern Flounder tagged and recaptured in **(A)** the Neuse and New rivers (2005–2006) and **(B)** by the NCDMF (1980–1982, 1988–1995). Data were pooled across systems and years for each data set.

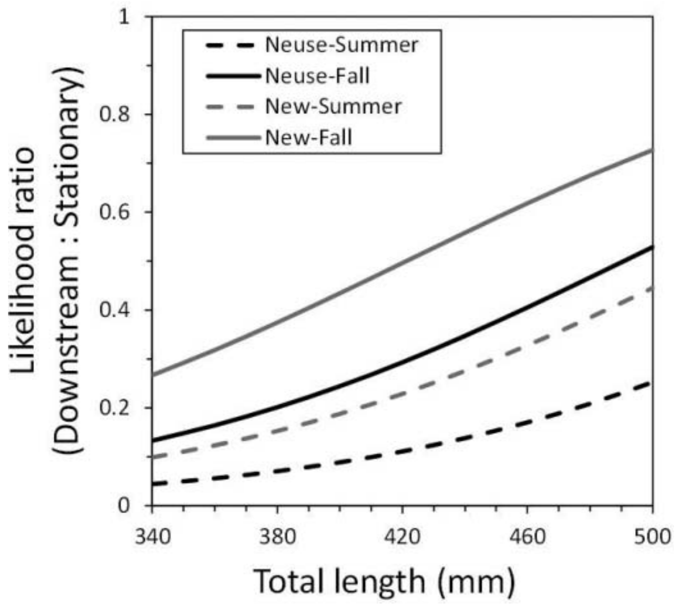

FIGURE 3. Multinomial logistic regression model predictions of the probability ratio of recovering tagged Southern Flounder after downstream movement within the Neuse and New River system (2005–2006). Probability ratios compare the probability of moving downstream to the probability of remaining stationary. Model predictions of upstream movement are not shown because upstream movement parameters were not significant (see Table 3).

New River (66% of moves were downstream) than in the Neuse River (50% of moves were downstream).

In the NCDMF data set, the best model explaining movement direction north or south of the tagging location also included a seasonal effect, but no other effects were significant (BIC weight = 0.69; Table 3). Similar to the Neuse and New River data set, most directional movement was to the south. In contrast to the Neuse and New River data set, however, slightly more southerly movement occurred in the summer (64% of recaptured fish) than in the fall (57% of recaptured fish). The more southerly movement of NCDMF-tagged fish in the summer was probably due to the much greater time at large for NCDMF-tagged fish in the summer (118 ± 94 d [mean ± standard deviation]) than in the fall (22 ± 20 d). As a result, recaptured fish tagged in the fall were less likely to show strong directionality in movement because they had only been at large for a limited time.

In Isaac Creek, 12 of the 170 Southern Flounder tagged were recaptured in the creek prior to winter after 12–154 d at large (Table 1; Figure 4). The average distance moved by fish recaptured within the creek was 0.22 km (range = 0.02–0.40 km). There was no evidence of directional movement at the scale of the creek, with four fish recaptured toward the head of the creek, three recaptured toward the mouth, and the remainder showing no directional movement relative to the tagging location.

Overwinter Analysis

The probability that Southern Flounder tagged in the Neuse and New rivers were recaptured > 50 km from the tagging

TABLE 3. Results from the best multinomial logistic regression models of movement direction during the prewinter period. Movement direction was categorized as upstream, downstream, or stationary (tag recovery < 1 km from tagging location) for the Neuse and New River data set and north, south, or stationary (tag recovery within system of tagging) for the NCDMF data set. For both season and TL, model inputs refer to the time of tagging. Probabilities of upstream or downstream movement are referenced to the probability of remaining stationary as a probability ratio. The *P*-values are defined as follows: three asterisks indicate < 0.001 and ns = not significant. The "X" indicates terms that were removed during the BIC model selection process.

Data set	*N*	Response	Intercept	TL (mm)	Season	System	Year
Neuse and New rivers	789	Upstream	−4.5 (ns)	0.003 (ns)	1.3 (ns)	0.89 (ns)	X
		Downstream	−7.7 (ns)	0.012***	1.2***	0.87***	X
NCDMF	663	North	−1.3***	X	0.3***	X	X
		South	−2.6***	X	1.5***	X	X

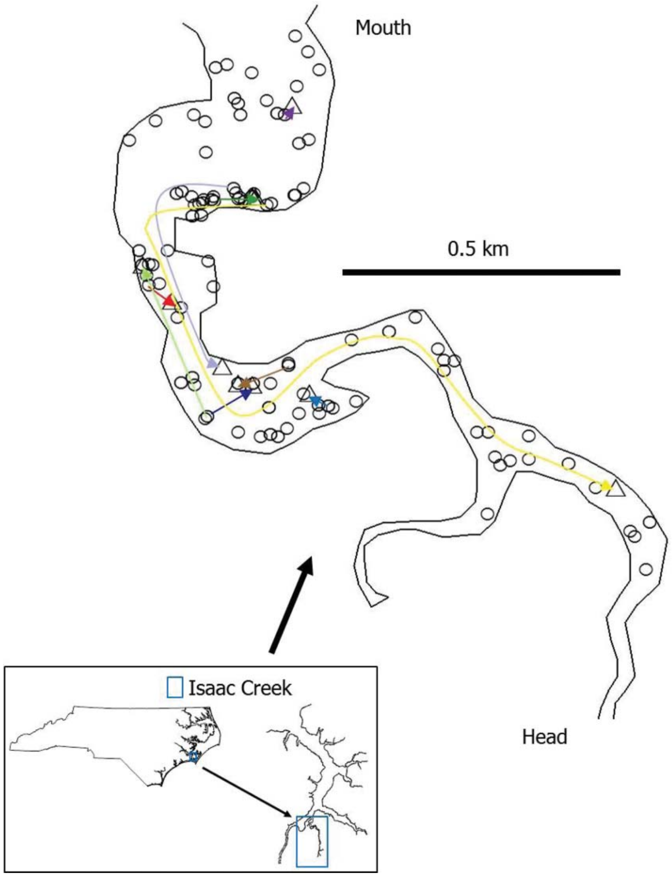

FIGURE 4. Distribution of Southern Flounder tagged and recaptured in Isaac Creek, North Carolina (2003–2005). Each line connects the tagging location (circles) to the recovery location (triangles) for fish recaptured within the creek. Colors indicate individual recaptures that could be uniquely identified.

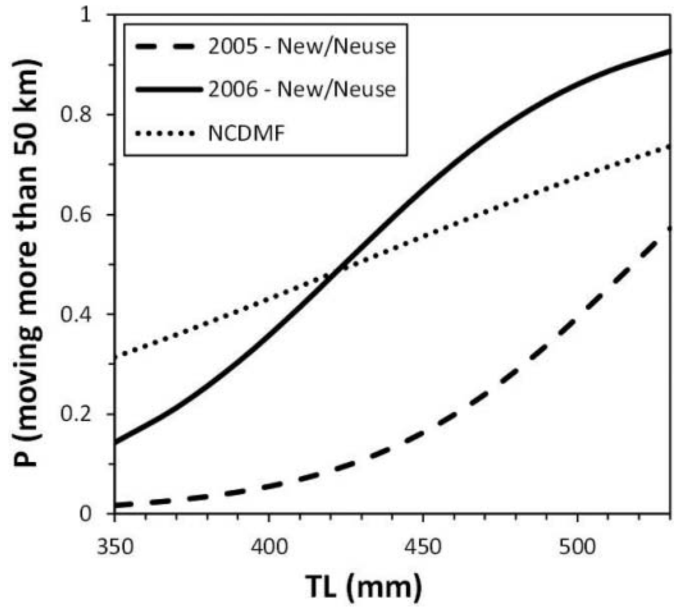

FIGURE 5. Regression model predictions of the probability that Southern Flounder moved more than 50 km from the location of release as a function of total length (TL; mm) for fish tagged in the Neuse and New rivers (2005–2006) and in coastal waters by the NCDMF (1980–1982, 1988–1995).

location was related to TL and year (BIC weight of best model = 0.54; Table 4; Figure 5); system was excluded from the best model. Southern Flounder ≥ 450 mm TL were more than three times as likely to emigrate from the system where they were tagged than were fish ≤ 375 mm TL. Also, fish tagged in 2006 were more likely to be recovered outside of the Neuse and New rivers (34.6%) than were those tagged in 2005

TABLE 4. Results from the best logistic regression models of Southern Flounder emigration from the estuarine system of tagging (tag recovery >50 km from the tagging location) based on the overwinter analysis of fish tagged in the Neuse and New rivers and statewide by the NCDMF. The *P*-values are defined as follows: one asterisk indicates < 0.05 and ns = not significant. The "X" indicates terms that were removed during the BIC model selection process.

Data set	*N*	Intercept	TL (mm)	System	Year
Neuse and New rivers	75	−12.5*	0.024*	X	2.3*
NCDMF	58	−4.4 (ns)	0.010 (ns)	X	X

(20.4%). Due to disparate returns among systems and years, only TL could be tested for its effect on the probability of emigrating for overwintering fish tagged by the NCDMF. The probability of emigrating increased with increasing TL, as for the Neuse and New River data set, but the effect was marginally insignificant ($P = 0.10$; Table 4; Figure 5) and the null model was a better model (BIC weight = 0.65) than the model including TL (BIC weight = 0.35).

All Southern Flounder that left inshore estuarine waters and were recaptured > 50 km from the tagging location were recovered to the south of where they were tagged (Figure 6). Southern Flounder tagged in the New River were recaptured from coastal waters south of the New River to northern Florida, while those tagged in the Neuse River were recaptured in coastal North Carolina waters to the south and in South Carolina. Pooled over the three data sets, 44% of overwintering fish that had moved > 50 km were recaptured across North Carolina state lines in waters to the south. Most of these fish (73.9%) were recaptured in South Carolina, while the remainder were recaptured in Georgia and north Florida.

There was no apparent relationship between tagging location and recapture location. For example, tag returns from state waters to the south (South Carolina, Georgia, and Florida) in the NCDMF data were from fish tagged as far south as the Cape Fear River and as far north as the Pamlico River and the Pamlico Sound in North Carolina. The most rapid movement speeds of emigrating Southern Flounder were > 1 km/d, with the fastest fish moving 5–8 km/d. However, the distance moved was not strongly correlated with the days at

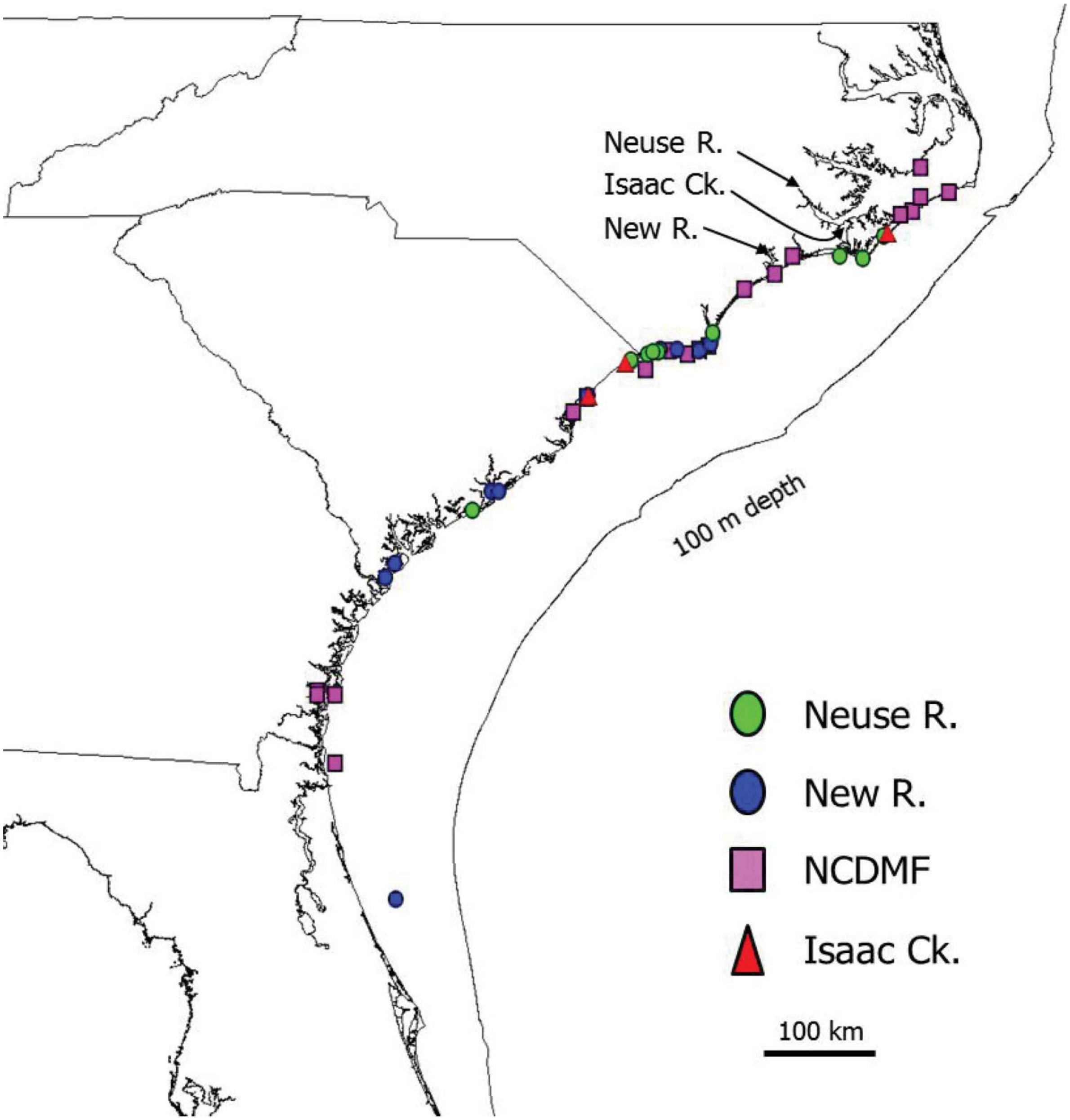

FIGURE 6. Recapture locations for Southern Flounder from three tagging studies: (1) Neuse and New rivers (2005–2006), (2) NCDMF (1980–1982, 1988–1995), and (3) Isaac Creek (2003–2005). Each symbol represents the recapture location of individual fish that had moved greater than 50 km from the tagging location and were recaptured after the overwinter period. The 100-m depth contour approximates the continental shelf–slope break.

large ($r^2 = 0.002$, $P = 0.55$). In fact, the days at large for fish that moved the greatest distances (603–676 km) ranged from 77 to 958 d, and those fish that moved the shortest distances (50–100 km) were at large for 81–647 d. While the data were too limited to evaluate temporal trends, tag returns from the NCDMF data (tagging from 1980 to 1982 and from 1986 to 1995) occurred from 1982 to 1994, with about an equal number of returns in the 1980s (11 recaptures) and the 1990s (15 recaptures).

Recaptures of overwintering fish tagged in Isaac Creek were consistent with the results from the Neuse and New River and NCDMF data sets. Two fish tagged in Isaac Creek in late summer (August) and fall (October) were recaptured in the creek during winter (December; 116 d at large) and during the following summer (June; 206 d at large), suggesting either high site fidelity or overwintering at the scale of the creek. Of the three fish recaptured outside of the creek after being at large for 81–150 d, one was recaptured in Core Sound between two estuarine inlets and two were recaptured in South Carolina waters (Figure 6), consistent with the southerly movement of fish tagged in the Neuse and New rivers and by the NCDMF.

DISCUSSION

Migration Patterns of Southern Flounder

Within the U.S. southern Atlantic Ocean, Southern Flounder appear to make consistent large-scale movements to the south that are most likely associated with migration from inshore estuarine nursery habitats to offshore winter spawning locations. Although findings from conventional tag returns cannot provide definitive insights on individual fish behaviors or migration routes, the collective results from multiple tag return studies indicate that large-scale movement in a southerly direction during fall is a general feature of the life history of Southern Flounder along the U.S. southern Atlantic coast. Many other flatfish species undergo extensive seasonal migrations associated with spawning and feeding, which is common among marine fishes (Secor 2015). Indeed, several aspects of the large-scale migration dynamics of flatfishes, including temporal synchronization, consistent migratory pathways, site fidelity, and complex larval transport processes between offshore spawning areas and inshore nurseries, have been described for selected species (Harding et al. 1978; Bailey and Picquelle 2002; Hunter et al. 2003; Loher and Seitz 2006).

Within North Carolina, the evidence for large-scale southern migration during fall that was observed during the more recent work in the New and Neuse River estuaries aligns well with past observations from the 1980s and 1990s during NCDMF tagging efforts. Furthermore, within the Atlantic range of Southern Flounder, tagging studies conducted in Georgia (Music and Pafford 1984) and South Carolina (Wenner et al. 1990) also demonstrated patterns of large-scale movement to the south, suggesting that offshore spawning activities could be concentrated close to the southern end of the species' Atlantic distribution. The fact that we observed an increased likelihood of downstream movement within the estuary during fall by larger individuals, coupled with an increased probability of large-scale (> 50 km) movement for larger individuals, also suggests that these movements were linked to maturation and spawning behavior. The strong size dependence of Southern Flounder female maturity was recently confirmed (Midway and Scharf 2012), and smaller, immature fish are suspected to primarily overwinter in estuarine systems rather than participate in offshore migrations.

The locations of offshore spawning sites for Southern Flounder are currently unknown, but spawning is suspected to be centered on the outer continental shelf along the southeastern U.S. Atlantic coast. Although sparse, both historic and recent ichthyoplankton data collected off the North Carolina coast support a hypothesized spawning location on the outer continental shelf (Smith et al. 1975; Walsh 2007). In addition, the absence of adult Southern Flounder aggregations in shallow neritic (depth < 40 m) habitats during recent winter scuba surveys also suggests deeper spawning habitats (Watterson and Alexander 2004; Tucker 2011). The combined weight of evidence, thus, points to the outer continental shelf as the most likely spawning site for Southern Flounder. The distribution of conventional tag returns suggests that spawning may be concentrated in more southern outer-shelf habitats, with northward advection of some individuals during the transport of egg and larval stages across the shelf. Depth-specific, cross-shelf circulation patterns may combine with Gulf Stream transport to determine larval pathways for several winter-spawning fishes, including flatfishes, along the southeastern U.S. Atlantic coast (Miller et al. 1984; Kraus and Musick 2001; Hare and Govoni 2005; Walsh 2007).

Estuarine Movements of Southern Flounder

Southern Flounder resided in North Carolina estuaries for extended periods between late spring and early fall, with tagged fish remaining in the New or Neuse rivers for up to 166 d. During this residency period, the vast majority of fish were recaptured less than 10 km from their release site, with many recoveries occurring within 1 km of the release locations. The NCDMF tag returns revealed similar patterns of limited estuarine movement until fall, with nearly 80% of all tag returns occurring within the system of tagging. During spring and summer, most fish were recaptured within the same system in which they were released, with most fish recaptured less than 20 km from their release site. Southern Flounder appear to demonstrate similar localized movement patterns during summer and early fall as was observed for the closely related Summer Flounder *Paralichthys dentatus* occupying U.S. mid-Atlantic estuaries. Both Sackett et al. (2008) and Capossela et al. (2013) detected some Summer Flounder individuals residing in estuarine systems for > 200 d (mean residence times: 86 d in New Jersey, 130 d in Virginia) using acoustic telemetry. In both of these studies, Summer Flounder resided mainly in higher salinity habitats, with Sackett et al. (2008) noting a habitat shift toward the ocean inlet in late summer prior to offshore emigration. Fish demonstrated highly localized movement within the estuary, with large-scale (hundreds of meters) movements uncommon until fish were beginning to emigrate. To our knowledge, no telemetry studies of Southern Flounder habitat use have been conducted at the whole-estuary scale; however, Furey et al. (2013) used a fine-scale positioning system to quantify Southern Flounder habitat use within a confined area of a Texas estuary. They found that individuals also tended to remain within relatively small areas for extended periods but that some individuals did show considerable movement (e.g., > 8 km over ~8 d) within their study area. The strong seasonal and size effects on within-estuary movements that we observed in the present study were most likely associated with the transition to offshore habitats. However, we also noted that Southern Flounder tended to show greater within-estuary movements during fall, including upstream movements not associated with emigration. We suspect that these movements may have been in response to episodic changes in temperature and barometric pressure that occur more frequently during fall or in response to shifts in prey fish distributions.

At a finer spatial scale, the tag return data from Isaac Creek provided additional evidence of limited movement by Southern Flounder when occupying estuarine habitats. Nearly all recaptures occurred in the creek, in some cases after over 100 d at large. For these fish, the average distance between release and relocation sites was 0.22 km, with most recaptures occurring < 0.1 km from the release site. Even after presumably overwintering in the creek, one fish was located only 1.15 km from its release position, providing evidence for habitat fidelity during the overwinter period at the scale of a small marsh creek. Indeed, at the whole-estuary scale, fish suspected of overwintering in the estuary were relocated in the spring in close proximity to their fall release sites (all postwinter relocations in the New and Neuse rivers were < 20 km from the release site). These included mainly smaller individuals that were putatively immature and thus had likely foregone offshore emigration. Our findings support the possibility that individual Southern Flounder often remain confined in relatively small areas throughout estuarine residency but may demonstrate high activity levels within those areas (e.g., Sackett et al. 2008; Furey et al. 2013).

Potential Limitations of Conventional Tagging Results

The use of conventional tag return data means that our conclusions about Southern Flounder movement are inferred only from release and recapture locations and time at large. The data provide no direct evidence that fish participated in spawning or that spawning occurred over the outer continental shelf, nor do they provide direct evidence that fish recaptured close to their estuarine release locations demonstrated limited movement during their time at large. We observed that all fish recovered > 50 km from their tagging location after the overwinter period were recaptured in areas south of the tagging area and inferred southerly movement most likely associated with offshore winter spawning. Alternatively, the potential exists for higher recapture or reporting probabilities to the south of the tagging location. The much higher landings of Southern Flounder in North Carolina waters relative to other states, particularly in the northern area (Figure 7), suggests this possibility is unlikely, and we know of no evidence for regional differences in reporting probabilities. Furthermore, several previous tag return studies for this species obtained similar results pertaining to large-scale movements (Music and Pafford 1984; Wenner et al. 1990). In addition, because most fish that had moved large distances to the south were at large for longer periods, any increase in the probability of tag loss with time at large would create a negative bias for detecting southerly migration. Similarly, our conclusions related to limited within-estuary movement are supported by recent telemetry studies for both Southern Flounder (Furey et al.

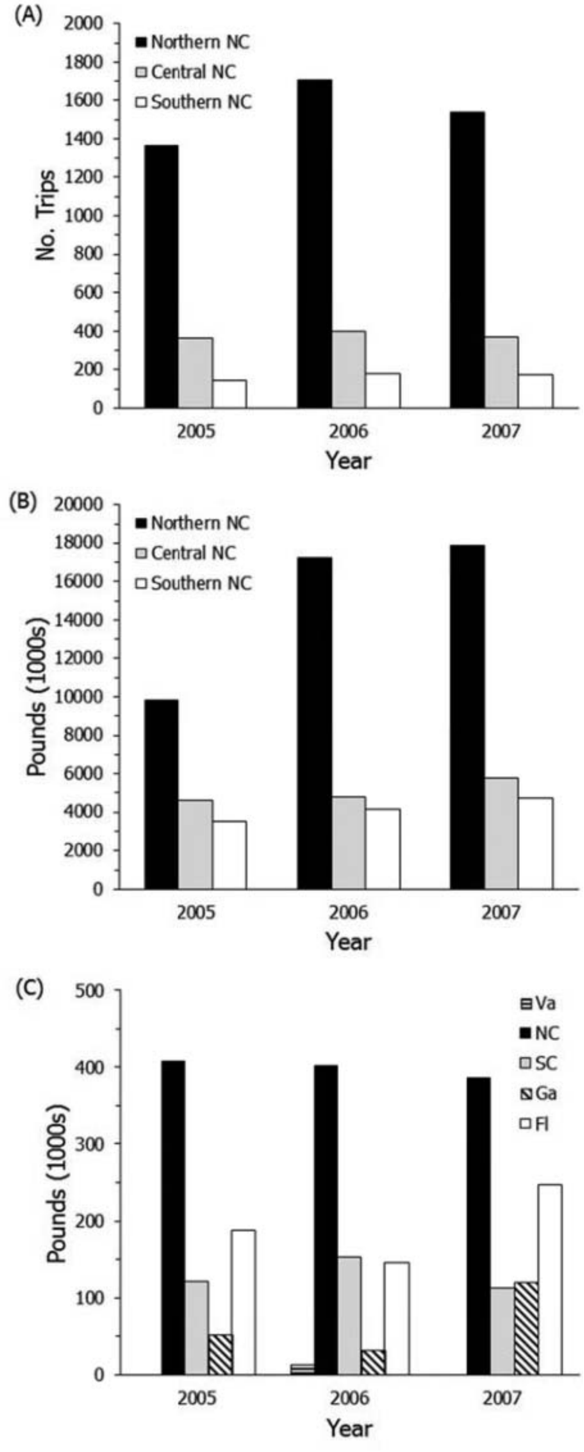

FIGURE 7. Fishing effort and landings for Southern Flounder in North Carolina and U.S. southern Atlantic Ocean waters (2005–2007), showing **(A)** the number of commercial trips and **(B)** commercial landings reported by the NCDMF in different regions of the state and **(C)** the recreational landings by state along the U.S. southern Atlantic coast obtained from the U.S. Marine Recreational Information Program (www.st.nmfs.noaa.gov/recreational-fisheries). State abbreviations are as follows: Va = Virginia, NC = North Carolina, SC = South Carolina, Ga = Georgia, and FL = Florida. Delineations for northern, central, and southern regions of North Carolina are shown in Figure 1.

2013) and the closely related Summer Flounder (Sackett et al. 2008; Capossela et al. 2013). While it is possible that Southern Flounder demonstrate more extensive movement during estuarine residency, which if coupled with strong site fidelity could lead to high rates of recapture near the original release location, a more parsimonious conclusion for our observations is that movement is limited.

Management Considerations

The Southern Flounder stock is currently categorized as "depleted" in North Carolina waters, a status that is believed to be related to a long period of elevated commercial harvest rates beginning in the early 1990s. Outside of North Carolina, only Florida produces any considerable commercial landings (~200,000–300,000 lb annually; Florida Fish and Wildlife Conservation Commission 2015) of Southern Flounder along the southeastern U.S. Atlantic coast. However, recreational landings have increased steadily during the past three decades in all states. Total annual recreational catch of Southern Flounder for southern Atlantic states has averaged more than 0.45 million kg since 2010, more than doubling since the 1980s (National Oceanic and Atmospheric Administration 2015). While South Carolina, Georgia, and Florida each enforce recreational bag and size limits for Southern Flounder in state waters, the regulations are liberal relative to those in North Carolina. Additionally, given that the fishery resource has had only moderate historical importance in those states, none has developed a comprehensive fishery management plan for Southern Flounder. In contrast, North Carolina has recently imposed even stricter management measures in both commercial and recreational fishery sectors intended to lower Southern Flounder harvest rates and reduce interactions with protected species, most notably sea turtles (Cheloniidae; NCDMF 2013). Continued growth of recreational fisheries and any increased participation in estuarine and nearshore commercial fisheries in other states may necessitate the development of more comprehensive management plans in the near future. In that event, there may be an increased need for interstate cooperation through a federal fishery management plan under the auspices of the Atlantic States Marine Fisheries Commission. The cooperative management of the closely related Summer Flounder, a species that demonstrates several life history features similar to Southern Flounder and is harvested by multiple states in the U.S. mid-Atlantic region, could serve as a useful model.

The management of Southern Flounder in North Carolina is based on the assumption that the North Carolina fishery represents a unit stock (Takade-Heumacher and Batsavage 2009; NCDMF 2013). This is primarily due to a lack of available information about migration patterns and stock structure within the U.S. southern Atlantic region. Throughout the range of Southern Flounder, their life history includes offshore spawning during winter, larval transport to estuarine nurseries, and rapid growth during estuarine residency, followed by maturity and spawning-related migration to ocean habitats (Stokes 1977; Wenner et al. 1990; Burke et al. 1991). This basic life history model has also included a return to estuarine habitats by adult Southern Flounder in the spring following spawning, and the unit stock assumption would necessitate that adults emigrating from North Carolina in the fall would return to North Carolina waters in the spring. However, findings from this study, as well as observations from previous conventional tag return studies for Southern Flounder conducted in Georgia (Music and Pafford 1984) and South Carolina (Wenner et al. 1990), demonstrate that most fish that return to inshore waters may do so within the jurisdiction of a neighboring state to the south. Although the available data do not yet allow any definitive conclusions about Southern Flounder migration pathways and behavior, the consistent and considerable movement to waters located south of the tagging location implies that there is high potential for extensive mixing within the southeastern U.S. Atlantic region.

Recently, genetic analysis of Southern Flounder stocks demonstrated clear separation between Gulf of Mexico and southeastern U.S. Atlantic populations (Anderson et al. 2012; Wang et al. 2015). However, stock structure within the southeastern U.S. Atlantic basin remains poorly understood. Analysis of otolith morphometrics was able to detect the Gulf of Mexico–Atlantic separation but only low levels of shape disparities among regions within the Atlantic basin, suggestive of a high level of mixing (Midway et al. 2014). Similarly, using fingerprints from both mitochondrial DNA and amplified fragment length polymorphisms, Wang et al. (2015) detected the presence of only weak genetic structure among possible subpopulations of Southern Flounder along the southeastern U.S. Atlantic coast. If Southern Flounder from North Carolina mix extensively with individuals from other areas within the southeastern U.S. Atlantic region, this has several important implications for effective management of the species. For instance, if fish that emigrate from North Carolina estuaries reenter estuarine waters in another part of the range, they are effectively removed from the harvestable stock in North Carolina. Alternatively, immigrants from other areas may replenish local stocks in North Carolina that are heavily exploited. Importantly, any attempts to estimate spawning stock biomass, a key biological reference point used in management, would be biased if the movements of fish outside of North Carolina state waters were ignored. While our findings suggest that a broad exchange of individuals within the U.S. southern Atlantic region is likely, a more refined understanding of Southern Flounder migration dynamics will be necessary to promote effective fishery management of this important resource species.

ACKNOWLEDGMENTS

We thank the commercial fishermen who participated in this study: H. Bogey, P. Darna, S. Notargiacomo, B. Padgett,

J. Padgett, and B. Sanderford. We thank Z. Tait, J. Williams, and J. Leonard for help with tagging and data processing. Funding for this project was provided by grants to J. A. Rice and J. K. Craig (FEG-05-15), and to F. S. Scharf (FEG-05-16), from the North Carolina Sea Grant Fishery Resource Grant Program. We thank B. Hooper, D. Skinner, C. Batsavage, and K. West of the North Carolina Division of Marine Fisheries and the North Carolina State University Center for Marine Science and Technology for logistical support. We thank N. Bacheler, C. Taylor, and two anonymous reviewers for comments on the manuscript. This work is dedicated to James P. Monaghan (deceased) for his influence on JKC and his contributions to the understanding and management of flatfish populations in North Carolina. The findings and conclusions in this paper are those of the author(s) and do not necessarily represent the views of the National Oceanic and Atmospheric Administration nor any of its subagencies or of the North Carolina Division of Marine Fisheries.

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