

ABSTRACT

BACHELER, NATHAN MITCHELL. Factors Influencing the Mortality and Distribution of Subadult Red Drum in North Carolina. (Under the direction of Jeffrey A. Buckel and Joseph E. Hightower.)

Subadult red drum *Sciaenops ocellatus* are ecologically and economically important in North Carolina, but little is known about factors influencing their mortality and distribution in estuaries. I first assessed the effect of fishing on red drum mortality using 24 years of tagging data. The tag-return model incorporated all first returns from fish caught-and-released and accounted for age-dependent selectivities that varied by fate of the fish. Estimated fishing mortality rates (F) were high and variable before regulation changes in 1991, but decreased in magnitude and variability after 1991. A dome-shaped selectivity pattern was estimated to account for migration of older fish into coastal waters. To quantify the natural mortality rate and seasonal F s for red drum, I conducted the first field test of a combined telemetry – tag return approach. Estimated F s were similar in seasonal pattern and magnitude between tagging and telemetry, but joint estimates were influenced primarily by tagging. Natural mortality rate was low and influenced primarily by telemetry. The combined approach provides a new tool to estimate mortality rates for myriad fish species. Next, habitat use of subadult red drum was quantified with a combination of fishery-independent sampling, telemetry, and generalized additive models. At a large scale, red drum were associated with shallow, nearshore waters, sometimes with seagrass. To determine the influence of prey, I examined red drum stomachs and used generalized additive models to relate physicochemical and prey attributes to telemetered red drum at a small scale. Telemetered red drum were negatively related to salinity and

positively related to dissolved oxygen and total prey. Last, I used tagging and telemetry to quantify the large- and small-scale movements of subadult red drum. Movement rates and directions were influenced by age of fish and region and season of tagging, and suggest that the spatial scale of management and regulations currently employed in North Carolina are appropriate. Tagging and fishery-independent surveys have provided valuable information to improve red drum management.

Factors Influencing the Mortality and Distribution of
Subadult Red Drum in North Carolina

by
Nathan Mitchell Bacheler

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APPROVED BY:

Dr. Louis B. Daniel, III

Dr. Kenneth H. Pollock

Dr. James F. Gilliam

Dr. Joseph E. Hightower
Co-chair of Advisory Committee

Dr. Jeffrey A. Buckel
Co-chair of Advisory Committee

BIOGRAPHY

I was born and raised in the small northern Michigan town of Sault Ste. Marie, a place described as having eleven months of winter and one month of poor sledding. I am the oldest son of my parents, Bill and Pam Bacheler, and have one younger brother, Dan. I spent my childhood fishing, hiking, and camping in and around the Great Lakes, often to the detriment of schoolwork. I attended Grand Valley State University in Michigan after graduating from high school, and it was during my undergraduate years when I learned that one could make a career out of studying fish, my childhood passion. Desiring a more temperate climate after graduation, I began a master's project at NC State in 1999 that involved research in Puerto Rico with Dr. Rich Noble. After finishing my master's degree in 2002, my career path became a bit saltier when I began a one-year marine fisheries fellowship with Dr. Jeff Buckel at NC State's Center for Marine Sciences and Technology in Morehead City. I elected to remain at NC State University for a Ph.D., an easy decision given the quality of the mentorship I would be receiving from Jeff Buckel and Joe Hightower, the exciting research project I would be working on, the friendships I had made, and the world-class outdoor opportunities that exist in coastal North Carolina. In 2007, I married Salinda Daley, a former NC State fisheries and wildlife graduate student.

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TABLE OF CONTENTS

List of Tables.....	viii
List of Figures.....	x
Chapter 1. Introduction.....	1
References.....	6
Chapter 2. An age-dependent tag return model for estimating mortality and selectivity of an estuarine-dependent fish with high rates of catch and release	8
Abstract.....	8
Introduction.....	9
Methods.....	12
Results.....	21
Discussion.....	23
Acknowledgements.....	29
References.....	29
Tables.....	33
Figures.....	37
Chapter 3. A combined telemetry – tag return approach to estimate fishing and natural mortality rates of an estuarine fish	40
Abstract.....	40
Introduction.....	41
Methods.....	44
Results.....	61
Discussion.....	66
Acknowledgements.....	73
References.....	74
Tables.....	80
Figures.....	82
Chapter 4. Abiotic and biotic factors influence the habitat use of North Carolina subadult red drum.....	88
Abstract.....	88
Introduction.....	89
Methods.....	92
Results.....	102
Discussion.....	107
Acknowledgements.....	114
References.....	115

Tables.....	121
Figures.....	125
Chapter 5. Movement patterns of subadult red drum in North Carolina, with implications for marine reserves and stock structure.....	130
Abstract.....	130
Introduction.....	131
Methods.....	133
Results.....	138
Discussion.....	142
Acknowledgements.....	147
References.....	147
Tables.....	152
Figures.....	154
Chapter 6. Conclusions.....	160
References.....	165
Appendices.....	167
A. Monthly locations of telemetered red drum in five tributaries of the Neuse River, May 2005 – January 2008.....	168
B. Relocation histories for 148 telemetered age-2 red drum included in the combined mortality model.....	183

LIST OF TABLES

Chapter 2

Table 2.1	Primary size and bag limits for North Carolina recreational and commercial red drum fisheries.....	33
Table 2.2	Number of red drum tagged and recovered in four age classes in North Carolina from 1983 to 2006.....	34
Table 2.3	AIC and QAIC values for the 15 models with varying assumptions about fishing mortality rate (F) and selectivity (Sel) for red drum in North Carolina.....	35
Table 2.4	Estimated reporting rate of tagged red drum at various natural mortality and internal anchor tag retention rates	36

Chapter 3

Table 3.1	Monthly sample sizes of external tagged and telemetered age-2 red drum in North Carolina	80
Table 3.2	Candidate models fitted to tag return data alone, telemetry data alone, or combined tag return and telemetry data	81

Chapter 4

Table 4.1	Age- and region-specific GAMs for red drum abundance in North Carolina	121
Table 4.2	Stomach contents of age-2 red drum from Hancock Creek in the lower Neuse River, North Carolina, 2005 – 2006.....	122
Table 4.3	Information on 36 age-2 red drum with ultrasonic transmitters used to quantify habitat use in Hancock Creek, North Carolina, in 2006.....	123
Table 4.4	Generalized additive models relating the presence of telemetered age-2 red drum to abiotic and biotic explanatory variables	124

Chapter 5

Table 5.1	Summary information for age-1 and age-2 red drum tagged in four regions of North Carolina.....	152
Table 5.2	Results of two-way factorial ANOVAs on the effects of region tagged, age tagged, and their interaction on days at large, distance moved, and movement rate of subadult red drum in North Carolina.....	153

LIST OF FIGURES

Chapter 2

- Figure 2.1 Percentage of yearly tag returns in North Carolina.....37
- Figure 2.2 Adjusted fishing mortality rate (mean \pm SE; solid line) and mortality on tags ($F^?$; dotted line) for fully selected fish (A) and age-specific fishing mortality rates (B) from 1983 to 2006.....38
- Figure 2.3 Selectivity (mean \pm SE) of harvested (A) and caught-and-released (B) red drum in North Carolina as determined by tagging.....39

Chapter 3

- Figure 3.1 Map of study area, showing coastal North Carolina and Pamlico Sound (left panel), and an enlarged view of the Neuse River Estuary (right panel).....82
- Figure 3.2 Tagging (gray circles) and recovery sites (black circles) for red drum.....83
- Figure 3.3 Proportion of telemetered red drum emigrating from Neuse River tributaries in various monthly intervals after initial release84
- Figure 3.4 Monthly fishing mortality rate (\pm SE) for subadult red drum from April 2005 – December 200785
- Figure 3.5 Annual fishing mortality rate of age-2 North Carolina red drum attributed to recreational and commercial fishing sectors.....86
- Figure 3.6 Proportion of emigrating transmitters (black bars) and bottlenose dolphins (white bars) based on estimated swimming speed87

Chapter 4

Figure 4.1	Map of Pamlico Sound and associated rivers showing gill net survey sampling strata (separated from each other by thick black lines) and gill net sites (open circles)	125
Figure 4.2	Cubic spline smoothed generalized additive model plots of the effects of physical habitat features on the abundance of age-1 red drum	126
Figure 4.3	Cubic spline smoothed generalized additive model plots of the effects of salinity on the abundance of age-1 red drum	127
Figure 4.4	Cubic spline smoothed generalized additive model plots of the effects of physical habitat features on the abundance of age-2 red drum	128
Figure 4.5	Cubic spline smoothed generalized additive model plots of the effect of water quality and prey variables on the presence of telemetered age-2 red drum in Hancock Creek	129

Chapter 5

Figure 5.1	Map of study areas in North Carolina	154
Figure 5.2	Tagging (gray circles) and recovery locations (black circles) of age-1 (A-D) and age-2 (E-H) red drum	155
Figure 5.3	Mean movement rate of subadult red drum based on the season and region of the state in which fish were tagged	156
Figure 5.4	Frequency distributions of angular directions moved for subadult red drum recovered within 60 days of tagging	157
Figure 5.5	Seasonal ultrasonic telemetry relocation information for subadult red drum in the tributaries of the Neuse River	158
Figure 5.6	Proportion of telemetered red drum in Hancock Creek moving upstream (A), moving downstream (B), or emigrating (C) in relation to the salinity change	159

CHAPTER 1. INTRODUCTION

Estuarine organisms are rarely distributed uniformly across space and time.

Variation in the density of estuarine and salt marsh organisms is thought to result from a variety of complex abiotic and biotic processes (Bertness 1991; Posey and Hines 1991; Miltner et al. 1995; Lenihan et al. 2001). Our understanding of the mortality and distribution of organisms in estuaries has lagged behind our knowledge of other aquatic environments due to the complexity of estuarine systems in terms of their fresh and salt water mixing patterns, tidal regimes, intricate food webs, and anthropogenic influences (Day et al. 1989; Kennish 1990). Gaining a better understanding of mortality and distribution of estuarine fishes is particularly important for marine fisheries scientists, given that most of the harvested marine fish species use estuaries at some point in their life cycle (Chambers 1992).

The harvest of fish, as measured by the fishing mortality rate, is one of the most direct ways that mortality can be affected. Until recently, however, quantifying the rate of fishing mortality has been difficult because both catch and total stock size were needed (Hilborn and Walters 1992). Recent improvements in tag return methodologies have eliminated the need to estimate total stock size, and instead use tag recoveries from the fishery over time to estimate mortality rates (Brownie et al. 1985). Rates of natural and fishing mortality can be determined using tag return models if the tag reporting rate can be reliably estimated (Pollock et al. 1991, 2001, 2002; Hearn et al. 2003).

Traditional tag return models have been complicated by catch and release fishing and discards from commercial fishing operations. Early tag return models assumed that all reported tags came from harvested (i.e., dead) animals, since these models were originally developed for banded waterfowl (Brownie et al. 1985). However, in situations where catch and release occurs, the assumption that all reported tags are from dead fish would result in overestimated exploitation rates. To avoid this problem, Jiang et al. (2007) developed an age-dependent tag return model that allows for the separation of fish caught and released and harvested by differentiating mortality on harvested fish from “mortality” on tags when the tag is removed and the fish is released alive.

Another factor that can complicate the estimation of fishing mortality rates using tag return models is changes in vulnerability with age. If vulnerability of a fish species declines with age due to emigration, for instance, and the reduced vulnerability is unaccounted for in the model, fishing mortality rates will be overestimated. Latour et al. (2001) removed the upper right hand corner of a matrix of red drum *Sciaenops ocellatus* tag returns in an attempt to exclude older individuals that were most likely to have emigrated from their study system. Jiang et al. (2007) developed an alternative approach that incorporated age-dependent selectivity patterns for striped bass *Morone saxatilis*.

This dissertation describes the factors influencing the mortality and distribution of red drum in North Carolina. Red drum are an estuarine and coastal fish species found along the southeastern Atlantic and Gulf coasts of the USA (Wenner 1992). Red drum support major recreational fisheries as well as a limited bycatch commercial fishery in North Carolina (NCDMF 2001; Takade and Paramore 2007). Released red drum now

outnumber harvested red drum from the North Carolina recreational fishery in most years. They are managed through a variety of regulations in North Carolina including an annual commercial cap, bycatch allowance limits, and minimum and maximum size limits. Most importantly, harvest of red drum now occurs at the subadult stage (i.e., ages 1 – 3), and the long-lived adults are not harvested. Therefore, it is difficult to assess the status of red drum because of the limited information on larger and older fish that comprise the spawning stock. Moreover, mortality rates, habitat use, and movement patterns of subadult red drum are poorly known.

Chapter 2 of this dissertation addresses key extensions to the Jiang et al. (2007) model, using red drum as the model species. I analyzed 24 years of tagging data from the North Carolina Division of Marine Fisheries to assess the efficacy of two regulation changes, occurring in 1991 and 1998, on fishing mortality rate and selectivity patterns of red drum. I used an age-dependent tag return model that accounted for both harvest and catch-and-release fishing. The model advanced the Jiang et al. (2007) approach in three important ways. First, I modeled selectivity of harvested fish separate from that of caught-and-released fish. Second, I developed a method to account for tagging that does not occur at the beginning of each time step, a central assumption of Brownie models. Last, I included external estimates of the tag retention rates of two tag types in our model. I present evidence that historical regulation changes affected the fishing mortality rate and selectivity patterns of red drum in North Carolina. This model can be a useful approach for studying fish populations especially as catch-and-release fishing increases, as long as practical issues such as reporting rate, tag loss, and hooking mortality are addressed.

Chapter 3 builds upon the preceding chapter by addressing uncertainties specifically in the natural mortality rate and the tag reporting rate of subadult red drum. Estimating the rate at which fish die of natural causes is important in a fisheries perspective because the rate can be used to predict the productivity of a population and therefore how much exploitation a stock can sustain. Natural mortality rate is also often included as a fixed parameter in most stock assessments; small changes in the natural mortality rate have been found to translate into very different harvest recommendations (Zheng et al. 1997; Clark 1999; Williams 2002). Unfortunately, the natural mortality is extremely difficult to estimate because natural deaths are rarely observed (Quinn and Deriso 1999).

I provide the first field test of a novel combined ultrasonic telemetry and tag return model to estimate the fishing and natural mortality rates experienced by subadult red drum in North Carolina, based on the earlier simulations of Pollock et al. (2004). By studying telemetered red drum and externally tagged red drum simultaneously, I test whether the combined approach improves estimates of fishing and natural mortality compared to either approach alone. I also use high-reward tagging to estimate the tag reporting rate of red drum directly, the first time this approach has been used in North Carolina. The combined telemetry and tag return approach not only provides precise estimates of fishing and natural mortality rates for subadult red drum, but also provides a new, flexible tool to estimate mortality rates for a wide variety of fish species in closed and open systems.

Chapter 4 addresses the influence of various abiotic and biotic factors on the distribution and habitat use of subadult red drum in North Carolina. Previous work on red

drum has suggested that subadult red drum occupy a wide variety of environmental conditions. While individuals of a species may tolerate a wide range of abiotic and biotic conditions, optimal physiological functioning and highest fitness is often realized over a much narrower range. I used a combination of fishery-independent gill netting, ultrasonic telemetry, and prey and water quality sampling to examine the habitat use of subadult red drum at small (meters to kilometers) and large (10 – 100s of kilometers) scales. These results have implications for the ecology of estuarine organisms generally, as well as in a variety of applied areas such as informing the placement of no-take zones and determining essential fish habitat for red drum. Such a synthetic approach to examine habitat use of red drum had previously been lacking.

Chapter 5 continues to address the distribution patterns of subadult red drum in North Carolina by describing the movement patterns of these important age classes. Movement is one of the least understood aspects of red drum ecology, yet enhanced knowledge of movement in North Carolina could improve management. I used 25 years of conventional tagging data and 3 years of telemetry data to examine movement patterns of red drum at small and large spatial scales. Results of this chapter suggest that the spatial scale of management and regulatory actions currently employed in North Carolina are appropriate.

I summarize the improved understanding of red drum ecology and management created by this research in Chapter 6. I also discuss the usefulness of our various field and modeling approaches for future studies on fish populations.

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CHAPTER 2. AN AGE-DEPENDENT TAG RETURN MODEL FOR ESTIMATING MORTALITY AND SELECTIVITY OF AN ESTUARINE-DEPENDENT FISH WITH HIGH RATES OF CATCH AND RELEASE

Nathan M. Bacheler, Joseph E. Hightower, Lee M. Paramore, Jeffrey A. Buckel, and
Kenneth H. Pollock

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ABSTRACT

Red drum *Sciaenops ocellatus* support commercial and recreational fisheries in North Carolina, but the stock was overfished in the 1980s due to unregulated fishing. Subsequent fishery regulations increased subadult survival into adult age classes but overall stock status is difficult to assess because of migration to ocean waters, prohibited harvest of older fish, and relative importance of catch-and-release. We analyzed 24 years of tagging data from the North Carolina Division of Marine Fisheries to assess the efficacy of two regulation changes, occurring in 1991 and 1998, on fishing mortality rate (F) and selectivity patterns of red drum. We used an age-dependent tag return model that accounted for both harvest and catch-and-release fishing. Using external estimates of natural mortality and annual tag retention rates, we obtained precise estimates of annual F , an overall tag reporting rate, and fate-, age-, and regulation period-specific selectivities. Estimated F s on fully selected red drum were high and variable before 1991 (mean = 2.38) but decreased in magnitude and variability after 1991. A dome-shaped selectivity pattern was observed for harvested fish in all regulation periods, with maximum selectivity

occurring at age 2, when red drum are of harvestable size and found in more accessible estuarine waters. Selectivity for caught-and-released red drum generally decreased for younger ages and increased for older ages in later regulation periods. The tag reporting rate was estimated at 18% and was generally insensitive to changes in the inputs of natural mortality or tag retention rates. Tag return models may be important tools for studying fish populations as catch-and-release fishing increases, as long as practical issues such as reporting rate, tag loss, the timing of tagging, and tagging and hooking mortality are addressed.

INTRODUCTION

The recent surge in popularity of catch-and-release fishing is creating new challenges for management of many fish species (Lucy and Studholme 2002). Many fishery models require knowledge of numbers of fish at age or size that are killed; catch-and-release fishing poses a problem because the sizes of released fish (i.e., selectivity of releases) are often not available. Traditional tag return models are also hindered by catch-and-release fishing because they assume all fish caught are harvested (Brownie et al. 1985; Pollock et al. 1991; Hearn et al. 1998; Hoenig et al. 1998a, 1998b), which would result in overestimated exploitation rates. Smith et al. (2000) developed models to adjust survival given tags clipped due to catch-and-release fishing if natural mortality rate and reporting rate are known and all parameters are age-independent. More recently, Jiang et al. (2007) developed an age-dependent model that allows for the separation of fish caught and released and harvested by differentiating mortality on harvested fish from “mortality” on

tags when the tag is removed and the fish is released alive. However, Jiang et al.'s (2007) model does not allow for the separation of selectivity on harvested and caught-and-released fish. This separation is most critical when suspected differences in selectivity due to size regulations occur.

Red drum *Sciaenops ocellatus* use estuarine and coastal habitats along the southeastern (SE) Atlantic and Gulf coasts of the USA (Wenner 1992), and their management is complicated by catch-and-release fishing. Red drum support major recreational fisheries as well as a limited bycatch commercial fishery in North Carolina (NCDMF 2001) that is focused on subadult age classes (hereafter defined as age-1 to age-3 red drum; Wenner [1992]). Released red drum now outnumber harvested red drum from the North Carolina recreational fishery in most years (NOAA Fisheries, Fisheries Statistics and Economics Division, Silver Spring, Maryland; www.st.nmfs.gov). They are managed through a variety of regulations in North Carolina including an annual commercial cap, bycatch allowance limits, and minimum and maximum size limits. Most importantly, harvest of red drum now occurs at the subadult stage, and the long-lived adults are not harvested. Therefore, it is difficult to assess the status of red drum because of the limited information on larger and older fish that comprise the spawning stock.

Another factor complicating assessment of red drum stocks is their reduced vulnerability to fishing with age because of their migration from estuarine to coastal waters. Harvestable red drum in the SE USA occur in easily accessible inland waters, but age-3 or age-4 red drum move towards coastal beaches and inlets where fishing pressure is likely reduced. Thus, age-independent tag return models, such as the Brownie model or

instantaneous rates versions (Brownie et al. 1985; Pollock et al. 1991; Hearn et al. 1998; Hoenig et al. 1998a, 1998b), are not appropriate. Latour et al. (2001) attempted to ameliorate this problem for subadult red drum in South Carolina by removing the upper right corner of the age-dependent Brownie recovery matrix (i.e., the “chop option”), which corresponded to the oldest fish that are most likely to have emigrated from their study system. Alternatively, Jiang et al. (2007) extended the instantaneous rates tag return model to account for age-dependence in fishing mortality and selectivity; the explicit modeling of selectivity allows for factors such as emigration to be separated from mortality.

Red drum in North Carolina were overfished in the 1980s but size and bag restrictions put in place in the early 1990s increased subadult survival (escapement into adult age classes) significantly (Vaughan and Carmichael 2000). Escapement levels from 1992-1998, however, were still estimated to be below the level believed to be necessary to reach the optimum sustainable yield (Vaughan and Carmichael 2000). The objective of this study was to estimate fishing mortality and selectivity of North Carolina red drum using tag return data from harvest as well as catch-and-release fishing. We extended previous tag return modeling by estimating the tag reporting rate internally by fixing natural mortality rates, accounting for tag loss with two types of tags, incorporating the first capture for all caught and released fish, separating the selectivities of harvested and caught-and-released red drum, and accounting for fish not tagged at the beginning of the year. The study results provide an alternative to traditional stock assessment approaches for red drum management and illustrate how tag returns from catch-and-release fishing can be used to make informed management decisions for other species.

METHODS

Red drum have been tagged since 1983 by North Carolina Division of Marine Fisheries (NCDMF) personnel as well as recreational and commercial fishers. The NCDMF has used various methods to collect red drum opportunistically throughout the study including pound nets, hook-and-line, runaround gill net, trammel nets, and electrofishing (see Burdick et al. 2007 for a full description). Recreational fishers have been involved in tagging since 1984 and primarily target adult red drum. On average, 20 volunteer anglers have tagged red drum each year since recreational tagging began in 1984. Commercial fishers assisted in tagging until 1990, primarily tagging subadult red drum caught in pound nets and gill nets in conjunction with NCDMF. Only healthy fish were tagged and released.

Internal anchor, nylon dart, and steel dart tags were employed throughout the study. Floy® internal anchor tags were used mainly on subadult red drum. Between 1987 and 1998, Floy® FM-84 and FM-89SL were used, while FM-95W was used between 1999 and 2006. Internal anchor tags were inserted into a small incision made by a scalpel approximately 10 mm posterior to the pelvic fin and dorsal to the mid-ventral line. Nylon dart tags (Floy® FT-1 and FT-2) were also used on a limited number of subadult red drum primarily in middle years of the study. These tags were inserted posterior to the trailing edge of the dorsal fin at an acute angle so the dart would lock behind the pterygiophores. From 1984 to 1998, Hallprint® stainless steel dart tags (FH-69) with a monofilament core were used, after which Hallprint® dart tags with a stainless steel wire core were used. Steel dart tags, which were used primarily on adults, were inserted firmly into the muscle

two or three scale rows behind the middle of the first dorsal fin. All tags were labeled with a unique tag number, “REWARD” message, and a mailing address to send the tag. A two dollar reward was given for returned tags until 1989, and the reward amount increased to five dollars in 1990. In addition, three \$100 prizes were given away in annual drawings from each year’s returned tags (Ross and Stevens 1992). Upon receipt of information from a recapture event, NCDMF personnel contacted each fisher about the fate of the fish and tag, gear used, and location of capture. Reporting rate was assumed to be equal for dart and internal anchor tags.

We used a 6-mo age-length key to convert total length of fish at tagging to an estimated age based on a January 1 birthday (Takade and Paramore 2007). The age-length key was based on 17 years of North Carolina red drum ageing data (Ross et al. 1995). A 6-mo age-length key (January - June and July - December) was used because of rapid summer growth rates that subadult red drum experience in North Carolina. The 6-mo age-length key provided very good separation of length groupings of fish until age 4. Therefore, red drum older than age 3 were grouped into a single age bin that we refer to as age-4+ fish, which are all adults and sexually mature (Ross et al. 1995). Thus we used four age groupings for all analyses: age-1, age-2, age-3, and age-4+ red drum. Previous ageing work on adult red drum in North Carolina determined that maximum age was 62 in the 1990s (Ross et al. 1995; NCDMF 2001), suggesting that age-4+ red drum in our study ranged from 4 to a maximum of 62 years old.

We estimated annual fishing mortality rates, an overall tag reporting rate, and fate-, period-, and age-specific selectivities using a modified instantaneous rates formulation of

the Brownie tag return model that extends Jiang et al. (2007). We assumed that the instantaneous fishing mortality rate for fish at age k in year j was $F_{jk} = Sel_k F_j$, where F_j is the instantaneous fishing mortality rate in year j for fully recruited fish ($Sel = 1.0$), and Sel_k is the selectivity coefficient for age- k fish. We extended previous work by modeling selectivity separately for fish that were harvested from those caught-and-released. We allowed selectivity to vary by age but required it to be constant within an age for each of three time periods (1983 - 1991, 1992 - 1998, and 1999 - 2006, hereafter referred to “early,” “middle,” and “late” regulation periods, respectively) that corresponded to major management periods in the red drum fishery in North Carolina (Table 2.1). Based on several trial runs (e.g., switching $Sel = 1.0$ between different age groups), selectivity for harvested fish was set equal to 1 for age-2 fish in all regulation periods. Selectivity for caught-and-released fish was set equal to 1 for age-1 fish in the early and middle regulation periods, and age-2 in the late regulation period.

Jiang et al. (2007) demonstrated how to model tag returns from harvested fish in addition to those caught and released with their tag clipped by separating the “death” of a tag from the death of a fish; fish caught and released with their tag intact were ignored. A large proportion of reported tags in our study, however, came from fish caught and released with their tag intact. If we excluded these reported tags, F would be underestimated because catch and release mortality would not be accounted for. We treated tags reported from fish caught and released with tag intact as though tags were cut off; subsequent captures of those fish were then ignored. By treating released fish the same whether or not their tags was left intact upon release, we were able to account for

catch and release mortality more accurately than if these recoveries were ignored.

Reporting rate was assumed to be equal for harvested and released fish.

The expected number of tags returned, R , from fish tagged at age k and released in year i , and harvested in year j , is:

$$E[R_{ijk}] = N_{ik} P_{ijk}, \quad (2.1)$$

where

$$P_{ijk} = \begin{cases} \left(\prod_{v=i}^{j-1} S_{ivk} \right) (1 - S_{ijk}) \frac{F_j Sel_{k+j-i}}{F'_j Sel'_{k+j-i} + F_j Sel_{k+j-i} + M_k} \lambda \phi^{j-i} & (\text{when } j > i) \\ (1 - S_{ijk}) \frac{T_{Fk} F_j Sel_k}{T_{Fk} F'_j Sel'_k + T_{Fk} F_j Sel_k + T_{Mk} M_k} \lambda & (\text{when } j = i) \end{cases} \quad (2.2)$$

and

$$S_{ijk} = \exp[-(T_{Fk} F_j Sel_{k+j-i} + T_{Fk} F'_j Sel'_{k+j-i}) - T_{Mk} M_k].$$

Here, S is the annual survival rate, N_{ik} is the number of fish that are tagged at age k and released in year i , P is the probability of recovery, F_j is the instantaneous fishing mortality rate experienced by fish, F'_j represents the instantaneous fishing mortality rate for tags of fish caught and released in year j , Sel is the selectivity of harvested fish, Sel' is the selectivity of caught-and-released fish, ϕ is the annual tag retention rate, λ is the tag reporting rate, and T is the proportion of the year remaining after the average tagging date

that is multiplied by fishing and natural mortality rates. A central assumption of Brownie tag return models is that tagging occurs at the beginning of the year, but in our case, most red drum were tagged in the final third of the year. If not accounted for, fishing and natural mortality rates would be biased low in a fish's first year because fish tagged in the fall would have a much shorter time period over which to experience mortality. We accounted for fall tagging by multiplying all fishing and natural mortality rates experienced by fish in their first tagging year (T_F and T_M , respectively) equal to 0.33, based on most tagging occurring in the final third of the year. No adjustment was required for fishing mortality rates ($T_{F1,0} = 1.00$) for age-1 fish, which first recruit to the fishery in the fall, because they only experience F during the last four months of each year.

The expected number of tag returns from fish tagged at age k and released in year i , then caught and released in year j , is:

$$E[R'_{ijk}] = N_{ik} P'_{ijk}, \quad (2.3)$$

where

$$P'_{ijk} = \begin{cases} \left(\prod_{v=i}^{j-1} S_{ivk} \right) (1 - S_{ijk}) \frac{F'_j Sel'_{k+j-i}}{F'_j Sel'_{k+j-i} + F'_j Sel_{k+j-i} + M_k} \lambda \phi^{j-i} & (\text{when } j > i) \\ (1 - S_{ijk}) \frac{T_{Fk} F'_j Sel'_k}{T_{Fk} F'_j Sel'_k + T_{Fk} F'_j Sel_k + T_{Mk} M_k} \lambda & (\text{when } j = i) \end{cases} \quad (2.4)$$

and

$$S_{ijk} = \exp[-(T_{Fk} F'_j Sel_{k+j-i} + T_{Fk} F'_j Sel'_{k+j-i}) - T_{Mk} M_k].$$

Following Jiang et al. (2007), the tag returns due to harvest and catch-and-release (R_{ijk} and R'_{ijk} , respectively) from N_{ik} fish that are tagged at age k and released in year i , follow a multinomial distribution. The likelihood function then is:

$$L = \prod_{k=1}^K \prod_{i=1}^I \left(\begin{matrix} N_{ik} \\ R_{iik}, R_{i+1k}, \dots, R_{ijk}, R'_{iik}, R'_{i+1k}, \dots, R'_{ijk}, N_{ik} - \sum_{j=i}^J (R_{ijk} + R'_{ijk}) \end{matrix} \right) \times \left(\prod_{j=i}^J P_{ijk}^{R_{ijk}} P'_{ijk}^{R'_{ijk}} \right) \left(1 - \sum_{v=i}^J (P_{ivk} + P'_{ivk}) \right)^{N_{ik} - \sum_{v=i}^J (R_{ivk} + R'_{ivk})} \quad (2.5)$$

Maximum likelihood estimates of the model parameters were obtained using SURVIV software (White 1983), which permits coding of the multinomial cell probabilities P_{ijk} .

Our initial estimate of F pertained to harvested fish only and thus did not include any estimate of hooking mortality. To account for effects of hook-and-release mortality on F , we adjusted F upward ($F_{adjusted}$) using a previously estimated catch-and-released mortality (δ) for red drum (10%; Jordan 1990) and F' (representative of fish caught and released) using the following equation:

$$\hat{F}_{j,adjusted} = \hat{F}_j + \delta \hat{F}'_j \quad (2.6)$$

We fixed tag retention rates of dart and internal anchor tags separately based on previous studies. Burdick et al. (2007) analyzed nylon and steel dart double tagging data from 2001 – 2004 for adult red drum and found no difference in tag retention between dart tag types. Overall, they estimated an annual retention of 0.74 for both types of dart tags, which was used in our model. To estimate retention of internal anchor tags, we used the arithmetic mean of four studies on red drum and similar species from double tagging, pond, and tank experiments (Sprankle et al. 1996; Wallin et al. 1997; Henderson-Arzapalo et al. 1999; Latour et al. 2001). Each study examined retention rates using Floy internal anchor tags; only FM-84 estimates were used from Henderson-Arzapalo et al. (1999) because it was the most common internal anchor tag used in our study. Annual retention rates varied between 0.850 and 0.963, and the mean value was 0.91, which was used in our baseline model.

In order to partition fishing and natural mortality rates using tag return data, the tag reporting rate must be known. Unfortunately, the reporting rate is difficult to estimate for fish in general (Pollock et al. 1991; Pollock et al. 2001, 2002; Hearn et al. 2003) and red drum in particular (Denson et al. 2002). We assumed that we had better knowledge of natural mortality than of the reporting rate, so we fixed age-dependent values of M for red drum based on a life history estimator that uses body size as a predictor variable (Boudreau and Dickie 1989). This is the same method used to estimate natural mortality rate in the current North Carolina stock assessment. We converted length for each age at tagging to weight based on the equation provided by Ross et al. (1995). Natural mortality rate was thus set at 0.30 for age-1, 0.22 for age-2, 0.16 for age-3, and 0.10 for age-4+ red drum. By

fixing values of M , we could estimate yearly fishing mortality rates, fate-, regulation period-, and age-specific selectivities, and tag reporting rate. These age-specific values of M were bracketed by lower (chosen by informed judgement) and higher (Lorenzen 1996) values of M over a range of tag retention rates to examine sensitivity of reporting rate estimates to these two parameters.

An assumption of the Brownie et al. (1985) tag return model is that fish mix thoroughly prior to harvest. If newly tagged fish are not able to mix with untagged fish prior to harvest, those individuals may experience a different fishing mortality rate than untagged fish and therefore would not be representative of the larger population. Hoenig et al. (1998b) showed that incomplete mixing could be allowed by estimating mortality in the first time period separately from mortality in the subsequent time periods by using a “nonmixing” model. Because of the nature of our age-dependent model, however, we would lose all information on age-1 fishing mortality and selectivity by using a nonmixing model. Instead, we excluded tag returns within 7 days to allow some time for fish to mix with the larger population, and deleted them from their tagged fish cohorts (e.g., Jiang et al. 2007).

In our full model, fishing mortality rates were allowed to vary by year and selectivities were allowed to vary by fate, age, and regulation period. Reduced models assumed that fishing mortality rates were constant within regulation periods or across all years of the study, or that selectivity was constant across all ages of red drum, constant across all years of the study within a particular age class, or equal for harvested and caught-and-released fish. We compared 14 reduced models to our full model using

Akaike's Information Criterion (AIC), which selects the model with the lowest AIC value based on the best trade-off between the number of parameters and likelihood of the models (Burnham and Anderson 2002). The AIC values were computed as:

$$\text{AIC} = -2 \log \left[l \left(\hat{\theta} \mid y \right) \right] + 2k, \quad (2.7)$$

where $\log \left[l \left(\hat{\theta} \mid y \right) \right]$ is the log likelihood function evaluated at the MLEs $\hat{\theta}$ given the data y and k is the number of parameters.

If tagged fish are not completely independent, overdispersion can result. Burnham and Anderson (2002) recommend a quasiliikelihood AIC approach (QAIC) if overdispersion is the reason for lack of model fit. The QAIC values are computed as:

$$\text{QAIC} = -2 \log \left[l \left(\hat{\theta} \mid y \right) \right] / \hat{c} + 2k, \quad (2.8)$$

where \hat{c} is a variance inflator factor that can be calculated as:

$$\hat{c} = \chi^2 / df, \quad (2.9)$$

where χ^2 and df correspond to the value of the Pearson goodness-of-fit test of the most general model in the model set and its degrees of freedom. We inflated all SEs in this paper by the square root of \hat{c} as suggested by Burnham and Anderson (2002).

RESULTS

Overall, 45,295 red drum were tagged from 1983 to 2006 and used in our analyses. The fewest fish were tagged in 1983 ($n = 92$), while the largest number of fish were tagged in 1994 ($n = 5,054$). Age-1 and age-4+ red drum were tagged much more frequently than age-2 or age-3 fish (Table 2.2). The proportion of fish tagged with internal anchor tags (instead of dart tags) declined with age, from 0.90 at age 1 to 0.74, 0.25, and 0.01 at ages 2, 3, and 4+.

There were a total of 4,722 reported tags (10.4% of total) by commercial and recreational fishers, of which 2,439 were harvested, 1,483 were released with tag intact, and 800 were released after the tag had been cut off. The ultimate fate of the fish and tag depended on year and age at recovery (Figure 2.1). There was generally a decreasing proportion of fish harvested and an increasing trend of fish caught and released over time for all age classes, and this trend was most obvious for age-1 and age-4+ red drum. In most years and age classes, more fish were released with the tag intact than released after the tag had been cut off.

The best model based on AIC and QAIC values was our full model, which allowed F to vary by year and selectivity to vary by fate of the fish, regulation period, and age

(Table 2.3). None of the reduced models were considered viable candidates based on AIC or QAIC values. Our estimate of \hat{c} was 5.68 from the full model, so all SEs were inflated by 2.38 (i.e., the square root of 5.68).

The adjusted fishing mortality rate, which accounted for catch-and-release mortality, was variable over the study period for fully selected fish (Figure 2.2A). During the early regulation period, fishing mortality rate was high and variable (mean = 2.38), with a low of 0.80 in 1991 and a high of 3.90 in 1989. In the middle and late regulation periods, however, the fishing mortality rate was consistently lower, reaching a low of 0.27 in 2004 and never exceeding 2.20 in any year. The mean fishing mortality rate on fully selected fish was similar between the middle (0.59) and late regulation (0.90) periods.

The mortality rate experienced by tags, F^T , generally increased throughout the study (Figure 2.2A). No red drum were caught, released, and reported in 1983 and 1985, so F^T in those years was 0. Excluding those years, F^T has varied between 0.09 and 1.47.

Regulation changes did not affect all age classes of red drum equally (Figure 2.2B). Fishing mortality rate on age-1 red drum dropped from a mean of 1.54 to 0.16 (91% decrease) after the 1991 regulation change and to 0.06 (an additional 74% decrease) after the 1998 regulation change. Fishing mortality rate on age-2 and age-3 red drum, however, only decreased after the 1991 regulation change (80 and 83% decreases, respectively); additional restrictions in 1998 did not result in further decreases in F on age-2 and age-3 red drum. Age-4+ F was low in the early regulation period (0.07), and decreased to 0.03 in the middle and 0 in the late regulation period.

Selectivity of tagged red drum in North Carolina varied by fate, regulation period, and age (Figure 2.3). In all regulation periods, a dome shaped selectivity curve was observed for harvested red drum, with maximum values for age-2 red drum (Figure 2.3A). The selectivity of harvested age-1 red drum decreased with each change in regulation. For red drum that were caught-and-released, selectivity was highest for age-1 fish and decreased for older ages in the early and middle regulation periods (Figure 2.3B); age-2 red drum were fully selected in the late regulation period.

We estimated an overall tag reporting rate in our baseline model of 0.18 (\pm 0.01), with slightly higher estimates when higher rates of natural mortality or lower rates of tag retention were used (Table 2.4).

DISCUSSION

Our tag return modeling technique provided an effective and succinct approach to estimate F and selectivity patterns of an estuarine fish experiencing high rates of catch-and-release fishing. We accounted for catch-and-release mortality associated with the first capture of released fish, separated selectivity parameters for fish of different fates, estimated the reporting rate internally, and incorporated tag loss for two tag types. We also modified the tag-return model to accommodate tagging at times other than the start of the year. By making these modifications with 24 years of tagging and recovery data, we were able to estimate model parameters with high precision and show that F and selectivity patterns of red drum were influenced by regulations in North Carolina. Our methodology

advances the field of fisheries tag return modeling and provides a unique complement to traditional stock assessment techniques (Pine et al. 2003; Walters and Martell 2004).

The fate of the fish and tag in Brownie tag return models is most critical. Developed originally for waterfowl, Brownie models traditionally assumed that all reported tags were from harvested animals. Recent modifications by Jiang et al. (2007) extended the Brownie framework to include fish that were caught and released with their tag cut off. We refined the Jiang et al. (2007) model to include fish caught and released with their tag intact, given the large proportion of fish in this fate category in our study. Failure to include tags reported from fish caught and released with their tag intact would have resulted in an underestimate of catch and release mortality and, ultimately, F . By treating fish released with their tag intact as though tags were cut off, and excluding subsequent recoveries of this group of fish, we could more accurately represent the true impact of catch and release fishing in red drum. A drawback of this approach is the exclusion of 4% of the recoveries that occurred after an initial recovery and report by a fisher. However, this was a much lower loss of information than if all fish caught and released with a tag (35% of recoveries) were excluded. The advantage of including multiple recaptures is slightly better precision but the disadvantage is a much more complex likelihood to compute. The complexity results from recapture events occurring at random times; each fish that is caught and released with an intact tag would have to be modeled separately to account for the unique fraction of the year that each fish was at large after the first catch and release.

By estimating selectivity patterns explicitly in the tag return model, we avoided the situation where data on older fish had to be discarded (e.g., Latour et al. 2001). We refined the Jiang et al. (2007) approach and were able to quantify the complex selectivity patterns of red drum in North Carolina, which we found were influenced by the age, regulation period, and fate of the fish at recovery. It was not surprising that selectivity depended on age of red drum, given the presence of a slot limit centered on one or two age classes of red drum and perceived age-dependent emigration rates (Ross et al. 1995). Our tagging approach also showed that regulations not only influenced the fishing mortality rates experienced by red drum, but clearly affected selectivity patterns as well. For instance, after harvest was prohibited on red drum less than 457 mm TL in 1991, selectivity on harvested age-1 red drum dropped by 91%. Furthermore, the fate of the fish at recovery, whether released or harvested, influenced the selectivity patterns of red drum. For example, selectivity of all age classes of caught-and-released red drum except age-1 fish has increased in recent regulation periods, suggesting recent increases in catch-and-release fishing of red drum in North Carolina.

We estimated a tag reporting rate (18%) that was lower than previous work on red drum. Green et al. (1983) estimated a reporting rate of 36% for red drum that were tagged surreptitiously during creel surveys in Texas. Denson et al. (2002) estimated tag reporting rates of recreational fishers to be 56.7% in South Carolina and 63.4% in Georgia using high-reward tagging methodology. There are three likely reasons that may explain differences in our reporting rate compared to Denson et al.'s (2002) study. First, South Carolina and Georgia lack the significant commercial fisheries that exist in North Carolina

(NOAA Fisheries, Fisheries Statistics and Economics Division, Silver Spring, Maryland; available: www.st.nmfs.gov). This sector is thought to report fewer tags than their recreational counterparts. Future studies should quantify this assumption by examining differences in reporting rate by fishing sector. Second, high-reward tagging was not advertised in the Denson et al. (2002) study in order to avoid influencing the behavior of anglers, but an unintended consequence of no advertising is that fishers may not recognize high reward tags easily and thus not report them (Pollock et al. 2001). Serious positive bias in reporting rate occurs when fishers do not report high reward tags (Conroy and Williams 1981). Lastly, we assumed no tagging mortality and this assumption, if false, could have led to biased low reporting rates (see below).

It is possible that tag reporting rates of NCDMF tags increased beginning in 2005. Since early 2005, high reward tagging of red drum has taken place in North Carolina for a complementary study that is currently in progress. High-reward tagging was advertised widely in the state during these years, which likely resulted in an increase in tag reporting rate of NCDMF tags. If the reporting rate increased, then F in 2005 and 2006 was likely overestimated and should be viewed cautiously. Because the presence of high-reward tagging can influence the reporting rate of low-reward tags, it is recommended that high-reward tagging occurs during the entire tagging study, or not at all (Pollock et al. 2001).

Our analysis would have been improved if external information about tag reporting had been available because we may have been able to estimate the natural mortality rate experienced by red drum. High-reward tagging, surreptitiously planted tags, angler or port surveys, and catch data from multiple fishery components with a 100% reporting rate from

one component have all been used to estimate tag reporting rates (Pollock et al. 2002). Perhaps the best approach is to build into the tagging program an annual experiment to estimate the reporting rate (Pollock et al. 2001). For a situation such as ours where that was not done, a reasonable alternative is to use information about life history to get an assumed rate of natural mortality and to produce a robust estimate of reporting rate conditional on that assumed M . Ultimately, multiple methodologies to estimate reporting rate will allow more accurate quantification of fishing and natural mortality rates.

We had to make assumptions in our tag return model. First, we assumed that by excluding fish recaptured within 7 days, we could limit problems associated with non-mixing. If we had used a non-mixing model (Hoenig et al. 1998b), our estimated fishing mortality rates for age-1 fish would have applied only to fish with tags, and not the population as a whole. Longer exclusionary periods would have led to biased estimates because the numbers of non-reported tags not accounted for when excluding tags would increase. Second, we assumed no deaths of fish occurred from the tagging process. A large proportion of fish tagged early in the study were captured out of pound nets, and recently most younger fish have been collected with electrofishing; these methods of capture likely result in very low post-tagging mortalities. Hook-and-line was used to collect some younger fish and most age-4+ red drum in this study, based on the protocol that only the healthiest fish were tagged and that these were tagged by trained professionals. Latour et al. (2001) employed tank studies in South Carolina to demonstrate that no mortality occurred on red drum that were tagged in water less than 25°C, but some mortalities (19.1%) occurred on large red drum (> 55 cm total length) at water warmer

than 25°C. The majority of fish in this study were tagged during fall months when water temperatures were below 25 °C. If post-tagging mortalities did occur, reporting rate may have been underestimated. Third, we assumed equal reporting rate of tags across all ages as well as from fish that were harvested and fish that were released. We do not know if these assumptions are reasonable; however, there is no evidence in the literature to the contrary. Last, parameter estimates could be biased if tagged fish were assigned an incorrect age because of the use of an age-length key. We view this as an unlikely source of bias because of the rapid growth and clear separation of length modes through age 3.

Tag return studies can also be improved by using telemetry to obtain detailed information about natural mortality (Hightower et al. 2001; Heupel and Simpendorfer 2002). Combining telemetry and tag return methods allows for the reporting rate to be estimated reliably and improves the precision of estimates of natural and fishing mortality rates (Pollock et al. 2004). We also suggest that double tagging experiments be used to estimate tag retention rates (Seber 1982). The timing of tagging should also be done at beginning of year ideally before the fishery begins; if not, the adjustment provided in this paper can be used. Last, high-reward tagging should accompany tag return studies in order to obtain reporting rates (Pollock et al. 2001), and ideally reporting rates should be estimated by fishing sector, fish age, and fate. With the inclusion of auxiliary studies to estimate tag retention, natural mortality, reporting rate, and tagging mortality, tag return models will go even further to provide robust estimates of critical population parameters that could greatly benefit the management of diverse marine and freshwater fisheries.

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Table 2.1. Primary size and bag limits for North Carolina recreational and commercial red drum fisheries within each of the regulation periods examined in this paper. A window limit here means that harvest can only occur on red drum inside the total length window.

Regulation period	Name	Recreational regulations	Commercial regulations
1983-1991	Early	356 mm TL minimum size Only 2 fish over 812 mm TL	356 mm TL minimum size
1992-1998	Middle	Harvest restricted to TL window of 457-686 mm 5 fish bag 1 fish >686 mm TL allowed	250,000 lb commercial cap 457-686 mm TL window
1999-2006	Late	457-686 mm TL window 1 fish bag	457-686 mm TL window 7 fish bag

Table 2.2. Number of red drum tagged and recovered in four age classes in North Carolina from 1983 to 2006. Tagged red drum were aged based on a 6-mo age-length key.

Year	Age at tagging					Age at recovery				
	Age-1	Age-2	Age-3	Age-4+	Total	Age-1	Age-2	Age-3	Age-4+	Total
1983	74	2	0	16	92	16	0	0	0	16
1984	22	52	10	220	304	5	4	0	1	10
1985	42	15	18	224	299	4	3	1	0	8
1986	1,517	44	21	137	1,719	76	4	1	2	83
1987	459	32	9	219	719	95	45	1	5	146
1988	783	36	13	346	1,178	155	21	3	7	186
1989	283	107	51	502	943	76	44	11	12	143
1990	110	149	117	454	830	15	35	10	13	73
1991	2,214	69	31	531	2,845	267	9	1	10	287
1992	1,158	311	41	406	1,916	98	86	2	7	193
1993	1,429	599	152	470	2,650	128	153	29	9	319
1994	3,768	224	205	857	5,054	816	59	32	12	919
1995	428	391	50	616	1,485	26	190	8	24	248
1996	290	132	67	630	1,119	20	20	14	17	71
1997	1,962	124	34	706	2,826	159	30	10	14	213
1998	1,326	1,614	47	708	3,695	50	256	6	25	337
1999	1,011	1,004	186	852	3,053	28	135	38	25	226
2000	602	563	214	1,052	2,431	41	135	44	35	255
2001	171	388	260	921	1,740	8	102	78	35	223
2002	193	112	112	1,003	1,420	7	16	23	45	91
2003	47	338	145	777	1,307	4	21	8	16	49
2004	272	30	141	1,035	1,478	13	2	4	0	19
2005	397	547	129	1,158	2,231	26	75	3	32	136
2006	551	1,802	348	1,250	3,951	42	318	44	67	471
Total	19,119	8,685	2,401	15,090	45,295	2,175	1,763	371	413	4,722

Table 2.3. AIC and QAIC values for the 15 models with varying assumptions about fishing mortality rate (F) and selectivity (Sel) for red drum in North Carolina, 1983 - 2006. “# Parameters” denotes the number of parameters estimated by the model. For F , subscript “ y ” denotes year-specific values. For Sel , subscripts “ a ” and “ f ” denote age- and fate-specific values, respectively. Subscripts that denote regulation-period specific “ p ” or constant “.” values are used for both F and Sel .

Model	# Parameters	log likelihood	AIC	QAIC
$F_y Sel_{fap}$	65	-2,034	4,198.7	1,839.2
$F_y Sel_{fa}$	53	-2,216	4,537.8	1,968.2
$F_p Sel_{fap}$	25	-2,424	4,897.6	2,087.0
$F Sel_{fap}$	21	-2,444	4,930.0	2,095.8
$F_y Sel_{ap}$	56	-2,442	4,995.9	2,164.1
$F_y Sel_a$	50	-2,489	5,077.7	2,191.6
$F_p Sel_{fa}$	13	-2,645	5,316.7	2,248.7
$F Sel_{fa}$	9	-2,667	5,351.8	2,259.2
$F_p Sel_{ap}$	16	-2,807	5,646.4	2,390.8
$F Sel_{ap}$	12	-2,837	5,699.0	2,408.0
$F_p Sel_a$	10	-2,876	5,772.9	2,436.8
$F Sel_a$	6	-2,999	6,010.4	2,532.2
$F_y Sel.$	47	-4,029	8,151.8	3,479.7
$F_p Sel.$	7	-4,471	8,956.5	3,771.1
$F Sel.$	3	-4,556	9,118.8	3,834.6

Table 2.4. Estimated reporting rate of tagged red drum at various natural mortality and internal anchor tag retention rates. The bold value indicates the reporting rate estimated in our baseline model. The different rates of natural mortality rate on age-1, age-2, age-3, and age-4+ red drum are scenario 1 (0.25,0.20,0.15,0.10; low natural mortality rates chosen by informed judgement), scenario 2 (0.30,0.22,0.16,0.10; estimated using Boudreau and Dickie (1989)), and scenario 3 (0.47,0.35,0.26,0.18; estimated using Lorenzen (1996)).

Internal anchor tag retention	Natural mortality rate scenarios		
	Scenario 1	Scenario 2	Scenario 3
0.95	0.16	0.16	0.19
0.91	0.17	0.18	0.20
0.85	0.19	0.19	0.22
0.80	0.20	0.20	0.23

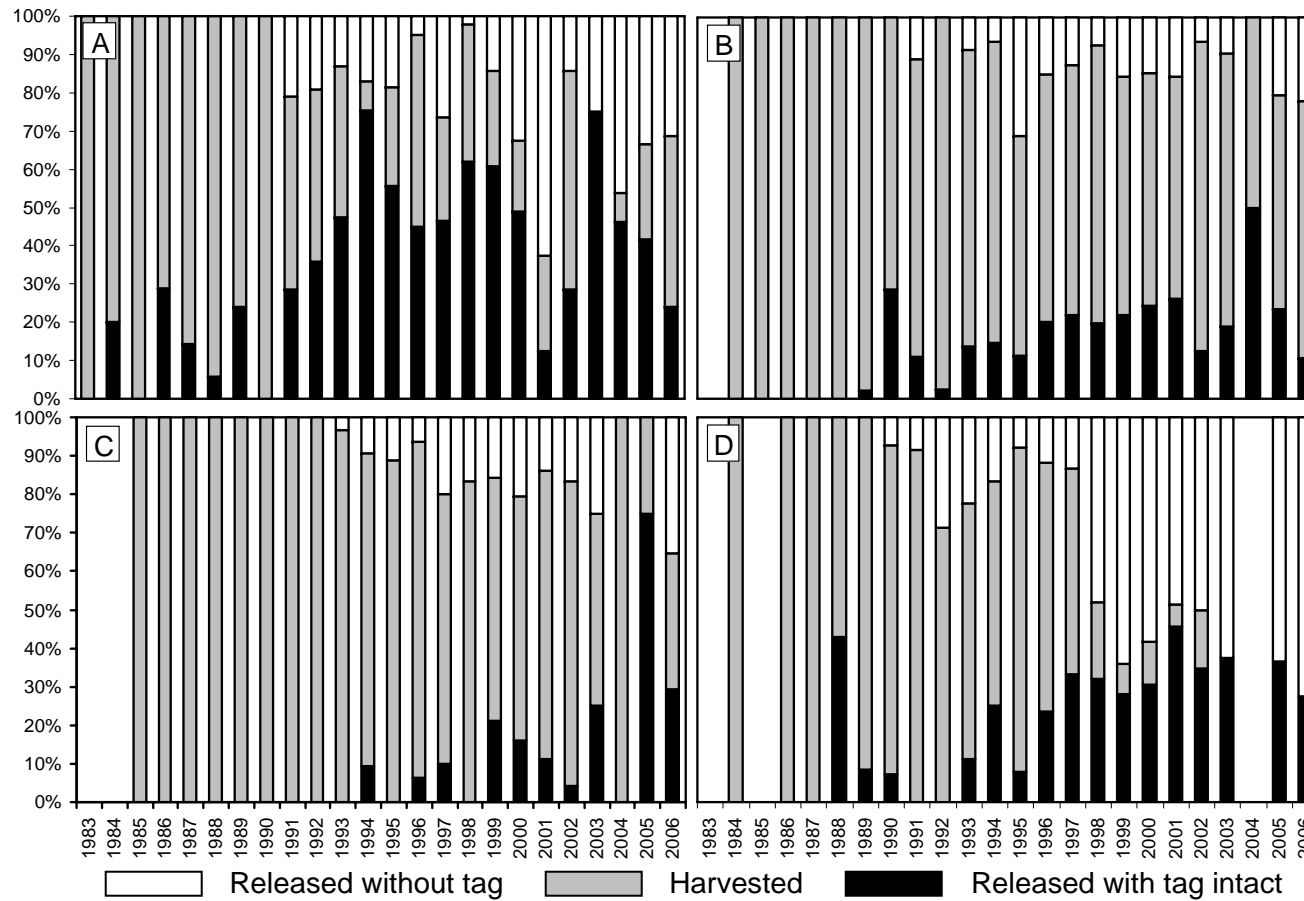


Figure 2.1. Percentage of yearly tag returns in North Carolina that were either caught and released without tag (white bar), harvested (gray bar), or caught and released with tag intact (black bar) for age-1 (A), age-2 (B), age-3 (C), and age-4+ (D) red drum, 1983 – 2006. Fish were classified into age classes based on age at recovery.

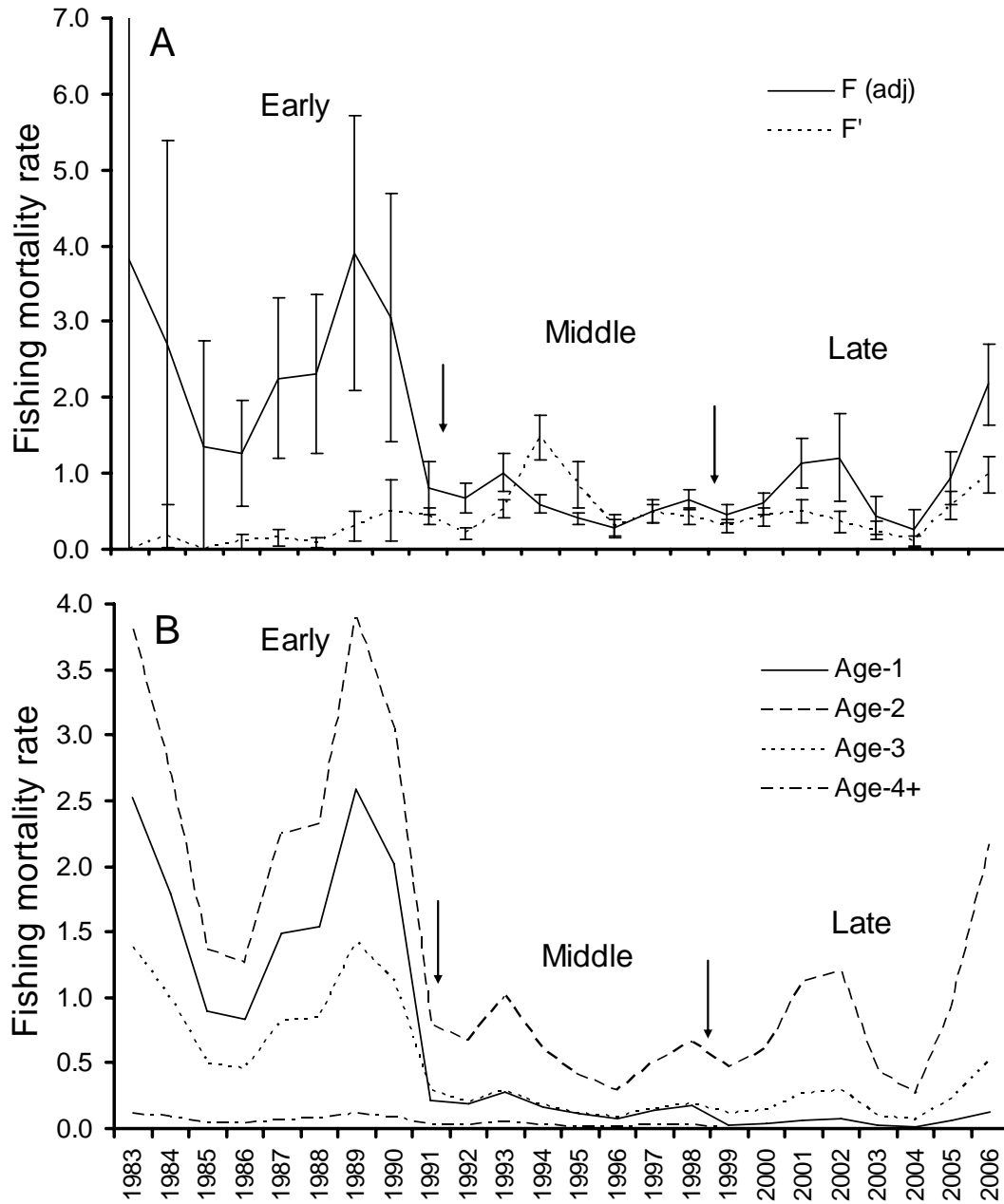


Figure 2.2. Adjusted fishing mortality rate (mean \pm SE; solid line) and mortality on tags (F' ; dotted line) for fully selected fish (A) and age-specific fishing mortality rates (B) from 1983 to 2006. Three regulation periods (i.e., Early, Middle, Late) are denoted by lettering between the arrows, and arrows indicate when regulation changes occurred (see Table 2.1). Note difference in y-axis labels of the two panels.

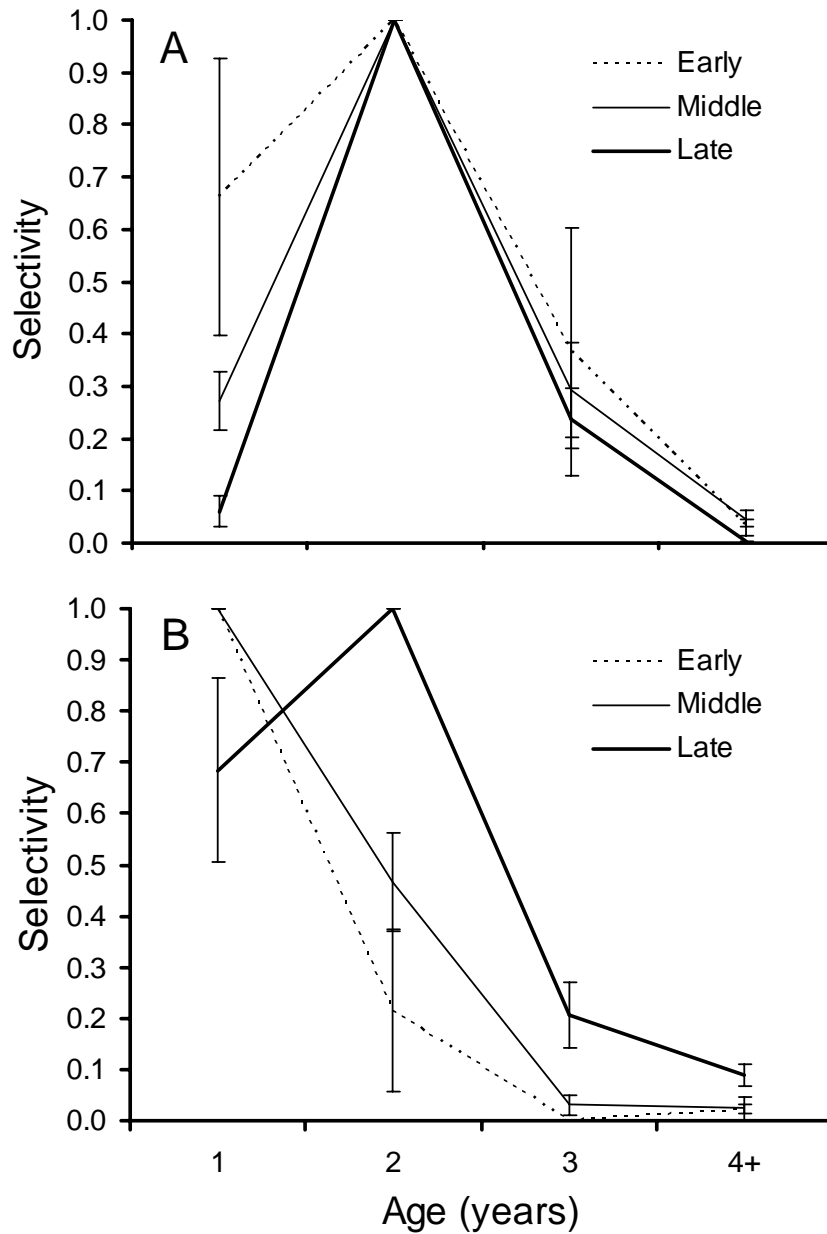


Figure 2.3. Selectivity (mean \pm SE) of harvested (A) and caught-and-released (B) red drum in North Carolina as determined by tagging. Four age classes of red drum are shown across three regulation periods: Early (1983-1991), Middle (1992-1998), and Late (1999-2006). Selectivities set equal to 1 do not have estimates of error.

CHAPTER 3. A COMBINED TELEMETRY – TAG RETURN APPROACH TO ESTIMATE FISHING AND NATURAL MORTALITY RATES OF AN ESTUARINE FISH

Nathan M. Bacheler, Jeffrey A. Buckel, Joseph E. Hightower, Lee M. Paramore, and
Kenneth H. Pollock

ABSTRACT

A joint analysis of tag return and telemetry data should improve estimates of mortality rates for exploited fishes; however, the combined approach has thus far only been empirically tested in terrestrial systems. We tagged subadult red drum *Sciaenops ocellatus* with conventional tags and ultrasonic transmitters over three years in coastal North Carolina, USA, to test the efficacy of the combined telemetry – tag return approach. There was a strong seasonal pattern to monthly fishing mortality rate (F) estimates from both conventional and telemetry tags; highest F s occurred in fall months and lowest levels occurred during winter. Although monthly F s were similar in pattern and magnitude between conventional tagging and telemetry, information on the estimate of F came primarily from conventional tagging. The natural mortality rate (M) in the combined model was low (estimated annual rate \pm SE: 0.04 ± 0.04) and was based primarily upon the telemetry approach. Using high-reward tagging, we estimated significantly different tag reporting rates for state agency and university tagging programs. The combined tag return – telemetry approach can be an effective approach for estimating F and M as long as several key assumptions of the model are met.

INTRODUCTION

Obtaining accurate estimates of the fishing and natural mortality rates experienced by fish stocks is a central goal of fisheries stock assessment and management. Regulation of the fishing mortality rate (F) is commonly used to generate sustainable harvest levels of fish stocks with recreational or commercial importance (Hilborn and Walters 1992). Overestimates of F would result in lost harvest, while underestimates can result in unsustainable exploitation rates.

Natural mortality rate (M) is important because it determines the productivity of a population. Whereas estimates of F are typically produced internally in stock assessment models, M is often estimated externally and included in models as a fixed parameter (Vetter 1988). Changes in M (e.g., 0.05 – 0.20) have been shown to result in very different harvest recommendations (Zheng et al. 1997; Clark 1999; Williams 2002). It is difficult to estimate M because natural deaths are rarely observed (Quinn and Deriso 1999). Moreover, it is hard to separate the effects of M , F , and recruitment on the population dynamics of fish stocks (Hilborn and Walters 1992; Quinn and Deriso 1999). Given the difficulty of estimating M , methods that use life history parameters are often used to develop predictive regression relationships with M (Vetter 1988). These methods usually require minimal data; however, the precision of these estimates is unknown (Vetter 1988; Pascual and Iribarne 1993) and M is often required to be constant among ages, seasons, or years (Hightower et al. 2001).

The unknown accuracy of life history methods and other techniques to estimate M , combined with the need for improved estimates of F , have prompted recent developments

using tag return methods to estimate mortality rates of fish stocks (Brownie et al. 1985; Hoenig et al. 1998a, 1998b; Latour et al. 2001; Polacheck et al. 2006; Jiang et al. 2007). Tag return models can be considered special extensions of capture-recapture models (Seber 1982), except that tagged fish are harvested and tags are returned by the fishery (Brownie et al. 1985; Pine et al. 2003). Rates of F and M can be determined using tag return models if the tag reporting rate (λ) can be reliably estimated with a high-reward tagging study or other methods (Pollock et al. 1991, 2001, 2002).

An alternative approach used to separately estimate F and M for fish populations that has received recent attention is telemetry. Telemetry methods have been used by wildlife researchers to estimate the survival rates of terrestrial animals (White and Garrott 1990; Pollock et al. 1995), but only recently have these methods been applied to aquatic organisms (Hightower et al. 2001; Heupel and Simpfendorfer 2002; Waters et al. 2005; Thompson et al. 2007). Pollock et al. (1995) developed a method to estimate survival of telemetered animals when the probability of relocation is less than one, and Hightower et al. (2001) extended this approach to estimate F and M for fish populations in an aquatic setting. The general methodology is to release a sample of telemetered animals, then locate each individual at fixed time periods until the animal has died, emigrated from the study area, has been harvested, or until the transmitter battery fails. Natural mortalities are inferred from transmitters that stop moving over successive relocation periods, and fishing mortalities are inferred from the disappearance of transmitters from the study system.

A novel approach for estimating F and M is to combine the use of tag return and telemetry data in joint analyses. Combined analyses were first developed for terrestrial

animals to estimate total mortality (Tsai 1996; Barker 1997; Catchpole et al. 1998; Powell et al. 2000; Nasution et al. 2001, 2002), but recent simulations have shown that combining the two techniques may be useful in aquatic systems as well (Pollock et al. 2004). In theory, the combined tag return and telemetry approach improves estimates of F and M compared to either method independently by drawing on the strengths of each (Pollock et al. 2004). Specifically, telemetry methods provide direct information about natural mortalities from transmitters that stop moving, while tag return methods provide direct information about fishery harvests from returned tags (Pollock et al. 2004). Another benefit of combining two independent methods to estimate mortality rates is that if the separate estimates do not agree, the two (independent) methods might help to identify the possible assumption violations that are causing the disparity.

This field test of the combined telemetry and tag return approach used red drum (*Sciaenops ocellatus*) as a model species. Aspects of the biology and management of subadult red drum (i.e., ages 1 to 3) make this species and size class amenable to a combined tag return and telemetry approach. First, subadult red drum are thought to have particularly strong site fidelity (Collins et al. 2002; Dresser and Kneib 2007), allowing for a long-term analysis of telemetered fish in an estuary. Second, subadult red drum in North Carolina are exploited by both commercial and recreational fishers within a slot limit, but estimated F s come from tag return studies (Ross et al. 1995; Chapter 2) and uncertain assessment results (Takade and Paramore 2007). Last, estimates of M for subadult red drum in the most recent stock assessment come from a life history method (Boudreau and Dickie 1989), which has unknown accuracy and precision.

Here, we provide the first field test of a combined tag return – telemetry approach for a fish species. Estimates of F and M from the combined model were compared to the estimates from the tag return and telemetry models separately to assess potential improvements in precision when combining the independent approaches. Results of our study document the ways tag return and telemetry data can be combined to produce robust estimates of F and M for a variety of fish species.

METHODS

Four sources of data were used in this study: (1) low-reward external tags released by North Carolina State University (NCSU), (2) low-reward external tags released by North Carolina Division of Marine Fisheries (NCDMF), (3) high-reward external tags released by NCSU, and (4) ultrasonic telemetry tagging by NCSU. Methods for each data source are described below.

Tag return approach

NCSU low-reward tagging

Tagging was performed by NCSU within the Neuse River Estuary (NRE), the major southern tributary of North Carolina's Pamlico Sound (Figure 3.1). The NRE is a shallow, mesohaline estuary with a watershed of 16,000 km². The NRE is relatively large in size, with a length of over 70 km and an average width of 6.5 km (Buzzelli et al. 2001).

In the winter and spring of 2005 – 2007, approximately 400 red drum (300 – 500 mm total length, TL) were externally tagged each year in the NRE (Table 3.1). Most red

drum were captured using the “strike net” method, whereby a 200-m gill net with 102-mm stretch mesh was set in an arc along the shoreline. A 7.2-m research vessel was then driven between the net and shoreline, scaring fish into the net. The net was then immediately retrieved, and when red drum were captured, the monofilament netting was cut in order to prevent injury to the fish. In the rare case where a red drum was injured, it was released without a tag. Electrofishing was also used periodically to catch red drum for tagging. Healthy fish were placed in 140-L aerated round tanks on board until all fish were ready for tagging. Fish were then removed from tanks and measured (TL; mm).

Fish were tagged with wire core internal anchor tags (Floy® FM-95W). Internal anchor tags were yellow in color and stated “REWARD FOR TAG,” and were additionally labeled with a tag number, a toll-free phone number, and “NCSU.” A t-shirt, hat, or US\$5 check was given to fishers reporting low-reward tags. During the telephone interview, fishers were asked for the tag number, location and date of capture, whether they were a commercial or recreational fisher, fate of the fish and tag (i.e., whether the fish was kept or released and whether the tag was cut off or left on if released), and length of fish.

We used a six month age-length key to convert total length of fish at tagging to an estimated age based on a January 1 birthday. The age-length key was based on 17 years of North Carolina red drum ageing data (Ross et al. 1995). A six month age-length key (January - June and July - December) was used because of rapid summer growth rates that subadult red drum experience in North Carolina (Ross et al. 1995). The six month age-length key reliably separates the age-2 red drum used in this study from older fish.

NCDMF low-reward tagging

The NCDMF tagged between 356 and 1,555 age-2 red drum annually in 2005 – 2007 (Table 3.1). Tagging was done year-round at sites throughout North Carolina but concentrated in the eastern and western Pamlico Sound. Fish were collected primarily using electrofishing and strike netting, and fish were tagged with Floy® FM-95W internal anchor tags. All tags were labeled with “NCDMF,” a unique tag number, “REWARD” message, a mailing address to send the tag, and a toll-free phone number. The NCDMF tags were blue or yellow in color. The NCDMF asked each fisher about the fate of the fish and tag, gear used, total length, and date and location of capture. A hat or US\$5 check was given to fishers returning NCDMF tags.

NCSU high-reward tagging and reporting rate estimation

In order to partition total mortality (Z) into F and M , we estimated λ using high-reward tagging (Hoenig et al. 1998a, 1998b; Pollock et al. 2001). High reward tags were red in color and stated “\$100 REWARD FOR TAG,” in addition to all other information provided on NCSU low-reward tags. Approximately 75 red drum were tagged each March (2005 – 2007) with high-reward tags, and high-reward tagging occurred simultaneously with low-reward tagging by NCSU in the Neuse River (i.e., for every six fish tagged and released with NCSU low reward tags, one was released with an NCSU high-reward tag). In early April of 2006, an additional 150 NCSU high-reward tags were released simultaneously with 850 low-reward NCDMF tags in eastern Pamlico Sound. Laminated advertisements describing the high reward study were placed in local tackle shops, boat

ramps, and fish houses, and advertisements were posted at many popular fishing websites in North Carolina. Tag reporting rates were estimated separately for NCSU and NCDMF low-reward tags.

Mortality rate estimation using tag return data

We estimated monthly F and M , and a constant λ for NCSU and NCDMF tags separately using a modified instantaneous rates formulation of the Brownie tag return model similar to Jiang et al. (2007) and Chapter 2. The NCSU tagging was assumed to occur at the beginning of April each year, while NCDMF tagging was assumed to occur at the beginning of each month throughout the year. Harvest was assumed to occur continuously throughout the year. Since the slot limit is centered directly on age-2 red drum, maximum selectivity occurs on this age class (Chapter 2). Recoveries were only used for age-2 fish; once a fish turned age 3, it was censored due to the low sample size of age-3 fish in our study. Thus, F and M only apply to age-2 red drum in our study.

Jiang et al.'s (2007) tag return model accounts for fish either being harvested or caught and released by separating the “death” of a tag from the death of a fish. We treated tags reported from fish caught and released with tag intact as though tags were cut off; the few subsequent captures of those fish were ignored (see Chapter 2). By treating released fish the same whether or not their tags were left intact upon release, we were able to account for catch and release mortality more accurately than if these recoveries were ignored. Reporting rate was assumed to be equal for harvested and released fish. The

expected number of low-reward tags returned, R , from fish tagged at age 2 and released in month i , and harvested in month j , is:

$$E[R_{ij}] = N_i P_{ij}, \quad (3.1)$$

where

$$P_{ij} = \begin{cases} \left(\prod_{v=i}^{j-1} S_v \right) (1 - S_j) \frac{F_j}{F'_j + F_j + M} \lambda_x & (\text{when } j > i) \\ (1 - S_j) \frac{F_j}{F'_j + F_j + M} \lambda_x & (\text{when } j = i) \end{cases} \quad (3.2)$$

in which $S_{ij} = \exp[-(F_j + F'_j) - M]$. Here, R_{ij} is tag returns due to harvest, N_i is the number of fish tagged in month i , P is the probability of recovery, S is the monthly survival rate, F'_j represents the instantaneous fishing mortality rate for tags of fish caught and released in month j , and λ_x is the tag reporting rate (i.e., lambda), with subscript x referring to the source of tags (i.e., NCSU or NCDMF tags). The expected number of low-reward tag returns from fish tagged and released in month i , then caught and released in month j , is:

$$E[R'_{ij}] = N_i P'_{ij}, \quad (3.3)$$

where

$$P'_{ij} = \begin{cases} \left(\prod_{v=i}^{j-1} S_v \right) (1 - S_j) \frac{F'_j}{F'_j + F_j + M} \lambda_x & (\text{when } j > i) \\ (1 - S_j) \frac{F'_j}{F'_j + F_j + M} \lambda_x & (\text{when } j = i) \end{cases} \quad (3.4)$$

The same equations above were used for the expected number of high-reward tag returns, except that lambda was removed because we assumed 100% reporting of high-reward tags. Following Jiang et al. (2007), the tag returns due to harvest (R_{ij}) and catch-and-release (R'_{ij}) from N_i tagged fish follow a multinomial distribution. The likelihood function then is:

$$L = \prod_{i=1}^I \left(\begin{matrix} N_i \\ R_{ii}, R_{ii+1}, \dots, R_{iJ}, R'_{ii}, R'_{ii+1}, \dots, R'_{iJ}, N_i - \sum_{j=i}^J (R_{ij} + R'_{ij}) \end{matrix} \right) \times \left(\prod_{j=i}^J P_{ij}^{R_{ij}} P_{ij}'^{R'_{ij}} \right) \left(1 - \sum_{v=i}^J (P_{iv} + P'_{iv}) \right)^{N_i - \sum_{v=i}^J (R_{iv} + R'_{iv})} \quad (3.5)$$

Maximum likelihood estimates of the model parameters were obtained using program SURVIV (White 1983), which permits coding of the multinomial cell probabilities P_{ij} .

To account for catch-and-release mortality, we adjusted F upward using a previously estimated catch-and-release mortality (δ) for red drum (10%; Jordan 1990) and F' using the following equation (Jiang et al. 2007):

$$\hat{F}_{j,adjusted} = \hat{F}_j + \delta\hat{F}_j' . \quad (3.6)$$

Our full tag return model was then compared to various reduced models using the Akaike information criteria (see below).

Assumptions of the tag return approach:

- (1) *The tagged sample is representative of the target population or the tagged animals are mixed thoroughly with the untagged ones.*

Based on telemetry and recapture locations, movement rates of red drum appeared to be high enough that tagged fish mixed well with untagged fish. Also, only 57 out of 409 fishers (14%) reported more than one tag, and the majority of these fishers catching multiple tagged fish caught them on separate fishing trips.

- (2) *There is no tag loss, or the rate is reliably known and can be adjusted for.*

Based on a double-tagging study and holding tank experiments with subadult red drum, chronic tag loss of internal anchor tags was minimal (6 of 272 fish [2.2%] lost an internal anchor tag over 14 months; Latour et al. 2001). Therefore, no adjustment was made for tag loss.

- (3) *Survival rates are not affected by tagging.*

Tag-induced mortality was not observed for age-2 red drum based on a holding tank study at various water temperatures (Latour et al. 2001).

- (4) *The fate of each tagged fish is independent of the fate of other tagged fish.*

This assumption may be violated because subadult red drum are thought to aggregate, but the extent of aggregation is not known. Violations of this assumption make the precision appear lower than it really is, but violations do not cause bias (Pollock et al. 2004).

(5) *The month of tag recovery is correctly tabulated.*

We assumed that fishers correctly tabulated the date of tag recovery.

(6) *All tagged fish, within an identifiable class, have the same survival and recovery probabilities.*

As fish were tagged over a narrow size range, we assumed all red drum had the same survival and recovery probabilities.

Ultrasonic telemetry methodology

Study sites for telemetry

Telemetry occurred in five tributaries along the southern shoreline of the NRE: Slocum Creek, Hancock Creek, Clubfoot Creek, Adams Creek, and South River (Figure 3.1). These are long and narrow embayments with average depths of 1 – 3 m. Each tributary has a narrow mouth that can be monitored with an acoustic receiver array to determine timing of emigration by telemetered red drum out of the study site (see below). These tributaries were chosen instead of tributaries on the northern shoreline of the NRE because of accessibility. Since tidal influence in each system is minimal, all habitats were accessible by boat at all times making telemetry feasible. Slocum and Hancock Creeks are designated as nursery areas, and are thus closed to commercial fishing but are open to

recreational harvest (one fish d⁻¹ bag limit). The other three tributaries are open to both commercial (seven fish d⁻¹ bag limit) and recreational fishing.

Transmitter implantation

In total, 180 age-2 red drum were implanted with transmitters in various tributaries of the NRE in 2005 – 2007 (Table 3.1). Surgical procedures can be found in Chapter 4. Fish were surgically implanted with ultrasonic transmitters (VEMCO, Ltd., Nova Scotia, Canada; V16 4H, 10 g in water; 10 mm wide; 65 mm long), and were released once swimming behavior returned to normal (approximately 10 min). The transmitters operated on a frequency of 69 kHz, and were programmed to be active for a period of 641 d. External tags were not placed on telemetered fish so that a fisher's decision to retain or release a captured red drum was not influenced by the external tag (Hightower et al 2001).

Telemetry relocations

Telemetered red drum were manually relocated monthly to determine location using a VEMCO VR100 receiver and hydrophone. The first two weeks of data after surgery were censored for all fish to account for post-surgery deaths that may otherwise appear as natural mortalities.

Submersible VR2 VEMCO receivers were used at the mouths of each tributary to document emigration events, since unaccounted-for emigration from the tributaries would bias estimates of *F*. For example, a fish that swam undetected out of the study estuary would be incorrectly considered a fishery removal. Previous studies have found relatively

high site fidelity for subadult red drum (Collins et al. 2002; Dresser and Kneib 2007), but there has tended to be an increased probability of emigration from estuaries with increasing size (Daniel 1998). In preliminary work, VR2 receivers detected nearly 100% of pulses from V16 tags at 400 m in our study systems. Therefore, submersible receivers were placed a conservative distance of 600 m apart from one another and within 250 m of shoreline. If a fish emigrated from a tributary, it was censored from the mortality analyses. Approximately 300,000 detections can be stored in a single VR2 receiver, so data were downloaded every 1 – 5 mo to avoid filling the memory. Telemetered fish missed by manual relocation during a monthly search were recorded as present in that month if they were detected by a submersible receiver.

Another potential form of bias was if a predator consumed a telemetered red drum and subsequently emigrated from the estuary. Heupel and Simpfendorfer (2002) were able to determine likely predation events upon two telemetered blacktip sharks in Florida by unusual movement patterns of transmitters through an array of stationary receivers. In our study, average swimming speeds were calculated for pods of bottlenose dolphins *Tursiops truncatus* observed opportunistically in our study systems, because subadult red drum composed a small proportion of bottlenose dolphin diets in North Carolina (Gannon 2003). Bottlenose dolphin swimming speeds were compared to the speed at which transmitters exited our study systems (using submersible receiver data). If no overlap was observed, it would suggest that bias from emigrating predators having a telemetered red drum in its stomach was negligible.

Transmitter retention and post-surgical survival experiments

A laboratory study was initiated in 2004 to estimate transmitter retention and post-surgical survival. Six fish (n=6) were captured using hook-and-line (only jaw-hooked fish were retained) and one was captured using a 30 m beach seine. All fish were transported back to the laboratory in plastic tubs filled with 100 L of aerated water. Each fish was released into a separate flow-through holding tank (1.2 m diameter, 1 m deep, filled with 0.7 m deep water) with a continuous air supply. Approximately 38 L of water flowed into (and out of) each tank per hour. Water temperature (°C), salinity (psu), and dissolved oxygen (mg L^{-1}) were recorded each day. Fish were fed daily to satiation with a variety of frozen fish and invertebrates. Seven fish were implanted on November 18, 2004, with “dummy” V16 transmitters of the exact size and shape as used in the field study, using the same surgical procedure as described above. Due to the death of one fish on November 28, 2004, from jumping out of the tank, an additional subadult red drum was caught by hook-and-line on November 30 to replace the dead fish; this fish was surgically implanted on December 14, 2004. Fish were checked daily for loss of transmitter or death, and in the instance where deaths did occur, necropsies were performed by doctors of veterinary medicine to identify the cause of death.

Mortality rate estimation using telemetry

Telemetry data were interpreted according to the criteria described in Hightower et al. (2001). A fish was assumed to be alive if it moved between searches and was dead from natural mortality if a fish was located in the same location after repeated searches.

As red drum were fairly mobile in our study, dead fish were obvious within a few monthly relocation periods and mortality was applied to the period immediately preceding the relocation of the fish when first found at that location. If a fish was not located after repeated searches and was not detected by submersible receivers as having emigrated, it was assumed that the fish was harvested. Our estimates of M may be positively biased if hook-and-release or discard mortality was occurring. Transmitter failure would appear as a fishery removal, positively biasing F , but the likelihood was small given that transmitters from all dead fish in the systems ($n = 4$) and returned transmitters ($n = 7$) remained audible through the end of their suggested battery life. Osprey *Pandion haliaetus* predation could also appear as a fishery harvest, but the sizes of telemetered red drum in this study are beyond the upper limit of previously observed fish prey sizes for osprey (Carss and Godfrey 1996), so avian predation on age-2 red drum is unlikely. Furthermore, most surgeries occurred during winter months when Osprey were not present in the NRE.

Monthly F and M were estimated from telemetry data using the Pollock et al. (1995) general capture-recapture model, with the modification of Hightower et al. (2001). Relocations of dead fish were used as a direct estimate of M , while F was estimated indirectly from the disappearance of telemetered fish over successive months. Relocation probabilities were estimated for each relocation period based on the number of fish missed during one relocation period but found during a later period.

Parameter estimation during each relocation period was based on the expected probabilities of each of the above outcomes for all fish released at time i (Hightower et al. 2001). All fish relocated at time $i - 1$, as well as all newly tagged fish, become part of the

new “virtual” release R_i at time i . Following Hightower et al. (2001), the expected number of fish in release R_i that are first relocated at time $i + 1$ was determined as the product of the number released (R_i), the survival rate from time i to $i + 1$ ($S_i = \exp[-F_i - M_i]$), and the probability of relocating an individual during search $i + 1$ (p_{i+1}):

$$R_i \cdot \exp(-F_i - M_i) \cdot p_{i+1} \quad (3.7)$$

where F_i is the instantaneous rate of fishing mortality and M_i is the instantaneous rate of natural mortality at time i . The expected number of fish first relocated at time $i + 2$ following release R_i would then be

$$R_i \cdot \exp(-F_i - M_i) \cdot (1 - p_{i+1}) \cdot \exp(-F_{i+1} - M_{i+1}) \cdot p_{i+2} \quad (3.8)$$

where $(1 - p_{i+1})$ is the probability of a tagged fish not being relocated at time $i + 1$. The expected number of natural deaths from release R_i first relocated at time $i + 1$ would be

$$R_i \cdot M_i \cdot \frac{1 - \exp(-F_i - M_i)}{(F_i + M_i)} \cdot p_{i+1} \quad (3.9)$$

The expected number of natural deaths from release R_i first relocated at time $i + 2$ would be

$$R_i \cdot \exp(-F_i - M_i) \cdot (1 - p_{i+1}) \cdot M_{i+1} \cdot \frac{1 - \exp(-F_{i+1} - M_{i+1})}{(F_{i+1} + M_{i+1})} \cdot p_{i+2}. \quad (3.10)$$

We used program RELEASE (Burnham et al. 1987) to convert the relocation history into a summary table of relocations for each release. The summary table of relocations (i.e., full-m array) was then used by program SURVIV (White 1983) to estimate model parameters on monthly time intervals. The Akaike information criteria (AIC; Burnham and Anderson 2002) was then used to compare our full model to various reduced models (see below).

Assumptions of telemetry method

- (1) *All marked fish present in the study area at time i (whether alive or dead of non-harvest causes) have the same probability (p_i) of being relocated.*

The tributaries were small enough to be searched thoroughly so that live and dead fish should have been found with equally high probability.

- (2) *All marked fish alive in the study area at time i have the same survival rate to the next time $i+1$.*

Because we tagged fish over a relatively narrow size range, we assumed all telemetered fish had similar survival rates.

- (3) *The probability of transmitter failure or of a transmitter being shed is negligible.*

Hightower et al. (2001) and Heupel and Simpfendorfer (2002) used VEMCO V16 transmitters and neither study found evidence of premature transmitter failure. In our

study, seven transmitters were returned from the fishery and four transmitters from dead fish were relocated monthly, and all functioned for at least the minimum guaranteed battery life. Tag retention was 100% in our holding tank study (see *Results*).

(4) *Marked and unmarked fish have the same survival rates.*

There were no surgery-related deaths in subadult red drum implanted with dummy transmitters in the laboratory holding study (see *Results*).

(5) *All fish behave independently with respect to capture and survival.*

See conventional tag assumption #4.

(6) *Movement patterns can be used to determine whether a tagged fish remains alive or has died due to non-harvest causes (possibly including catch-and-release or discard mortality).*

Movement patterns have commonly been used to identify the fate of individual telemetered fish (Jepsen et al. 1998, 2000; Hightower et al. 2001, Heupel and Simpfendorfer 2002, Waters et al. 2005, Thompson et al. 2007). Red drum movement rates were high enough that natural mortalities were not difficult to detect after a few monthly relocations. We also found no evidence of bottlenose dolphin predation by comparing swimming speeds of emigrating transmitters to emigrating bottlenose dolphins (see *Results*).

(7) *Natural mortality occurs immediately prior to the first relocation.*

By sampling monthly and maintaining high relocation probabilities, the timing of natural mortalities was assumed to occur in the period previous to when it stopped moving.

(8) *Emigrating fish can be detected and censored from the analysis, and censoring is random.*

Emigrating fish were detected with a submersible receiver array and censored from the analysis. Furthermore, no differences were observed in length ($P = 0.64$), weight ($P = 0.84$), or Fulton Condition Factor ($P = 0.84$) between red drum emigrating within 2 months of release ($N = 23$) compared to those emigrating more than 2 months after release ($N = 24$) for fish released in Hancock Creek in March, 2005.

Combined methodology and model selection

The methodology for the combined telemetry-conventional tag return approach was described in Pollock et al. (2004). Monthly estimates were obtained using maximum likelihood methods, where the overall likelihood function (L) was the product of the likelihood functions for the tag return (L_1) and telemetry data sets (L_2) because the two sets of data are independent:

$$L = L_1 \times L_2. \tag{3.11}$$

Tag returns and relocations of live and dead telemetered fish were both assumed to follow multinomial distributions.

We used the Akaike information criterion (AIC), corrected for overdispersion and including a second order bias correction (QAIC_c), to evaluate the likelihood of our full models (separately for tag return alone, telemetry alone, or combined data) compared to various reduced models (Burnham and Anderson 2002). The QAIC_c method provides a benefit for model fit and a penalty for adding parameters, resulting in models that produce the best trade-off between bias and variance (Burnham and Anderson 2002). The QAIC_c is:

$$\text{QAIC}_c = -2 \log \left[l \left(\hat{\theta} \mid y \right) \right] / \hat{c} + 2K + \frac{2K(K+1)}{n-K-1}, \quad (3.12)$$

where $\log \left[l \left(\hat{\theta} \mid y \right) \right]$ is the log likelihood function evaluated at the MLEs $\hat{\theta}$ given the data

y , K is the number of parameters, and \hat{c} is a variance inflation factor. The variance inflation factor can be calculated as:

$$\hat{c} = \chi^2 / df, \quad (3.13)$$

where χ^2 and df correspond to the value of the Pearson goodness-of-fit test of the most general model in the model set and its degrees of freedom (Burnham and Anderson 2002).

The number of parameters of each model was augmented by one to account for the

estimation of \hat{c} , and we inflated all SEs in this paper by the square root of \hat{c} (conventional tagging = 2.04; telemetry = 1.18; combined = 1.89). Both of these modifications are recommended by Burnham and Anderson (2002). We then computed simple differences (Δ_i) between the best model ($QAICc_{min}$) and the i^{th} model ($QAICc_i$) as

$$\Delta_i = QAICc_i - QAICc_{min}. \quad (3.14)$$

For each approach (tag return alone, telemetry alone, and combined), F was allowed to vary in six ways: by month, month and year, quarter, quarter and year, year, or it was held constant. Natural mortality rate and relocation probability were allowed to vary by month, year, or be constant. In addition, parameter estimates were model averaged based on $QAIC_c$ to account for uncertainty in model selection (see Burnham and Anderson 2002 for a full description).

RESULTS

External tags were applied to 4,776 red drum, with a larger percentage (68%) receiving NCDMF tags (Table 3.1). Eight percent of external tags released were high-reward tags.

Overall, there were 116 recoveries of NCSU high-reward tags (33% return rate), 299 recoveries of NCSU low-reward tags (26% return rate), and 512 recoveries of NCDMF low-reward tags (16% return rate) within their first year. Both NCSU and

NCDMF tags were recovered throughout the estuarine and coastal waters of North Carolina, including the Neuse and Pamlico Rivers, Pamlico Sound, Core Sound, all major northern inlets, and coastal beaches from the northern Outer Banks all the way south to Wilmington (Figure 3.2).

Eight red drum were surgically implanted with dummy transmitters and held in the laboratory for 9 months. Fish resumed eating within 0 – 2 d after surgery, and surviving fish healed completely and were healthy at the end of the study. Each red drum in the study retained its transmitter. Three fish died over the course of the holding tank study, but none were judged by veterinarians to have died from the surgery process: one died from jumping out of the tank, one died from a fishing hook found in its stomach during necropsy, and one died from a storm-related poor water quality event affecting the entire laboratory.

Ultrasonic transmitters were surgically implanted in 180 age-2 red drum (mean TL \pm SE = 457.9 \pm 1.9 mm; mean weight = 950.7 \pm 11.2 g). All fish were large enough that the transmitter never weighed more than 1.25% in water of the fish's weight out of water, as recommended by Winter (1996). Telemetered fish were only released into Hancock Creek (n = 105), South River (n = 46), and Slocum Creek (n = 30); thus, detections in Clubfoot and Adams creeks would represent fish migrating from their tagging location. The number of red drum present in all tributaries each month (i.e., new releases plus virtual releases of relocated fish) ranged from 0 to 44 (mean = 13.5; Table 3.1).

Relocations within the first two weeks after tagging were censored to account for surgery-related effects. This resulted in the exclusion of 32 telemetered fish from our

model. During the first two weeks, there were 2 apparent surgery deaths and 4 harvests along with 26 confirmed emigrations. Of the remaining 148 telemetered red drum that were included in the model, 19 were harvested, 1 died of natural mortality, 112 emigrated, and 16 were alive until they reached age 3 and were excluded from the study. Harvest was verified in four of nineteen cases of presumed harvest by returned transmitters from fishers.

Submersible receiver detections were used to document emigration events from the tributaries over the three years of this study. Overall, 30 submersible receivers recorded 1,522,843 detections from telemetered red drum. Most detections came from Hancock Creek ($n = 980,000$), while the least came from Adams Creek ($n = 17, 223$). The residence time of fish ultimately emigrating was 3.8 ± 0.3 months (Figure 3.3).

The spatial coverage of the telemetry and tag return components of this study did not completely overlap, since the telemetry component occurred in Neuse River tributaries while the tag return study occurred throughout North Carolina. If F varied spatially, combining these two components may not be valid. We tested for a spatially-explicit F by constructing an initial model that used QAIC_c to compare a spatially-invariant F (i.e., $F_{tel} = F_{tag}$) to an F that varied by space (i.e., $F_{tel} \neq F_{tag}$). By far the best model was one that assumed a spatially-invariant F , so the subsequent combined model allowed the telemetry and tag return portions of the study to share parameters.

Preliminary modeling using QAIC_c showed that constant M and yearly P parameters outperformed all other forms of these parameters, so these were used in all models. The best model using external tagging data alone according to QAIC_c was one

that had 28 parameters and allowed F to vary by quarter and year, with a constant M (Table 3.2). The best model using telemetry data alone estimated 9 parameters and allowed F to vary by quarter, M to be constant, and relocation probability to vary by year (Table 3.2).

The best model chosen for the combined tag return and telemetry data was the model that estimated 31 parameters and allowed F to vary by quarter and year, M to be constant, and relocation probability to vary by year (Table 3.2).

The tag return model estimated monthly F s that ranged from 0 – 0.08, and monthly relative standard errors (RSE; SE/estimate x 100) of 15 – 101%. Monthly F s were generally low in winter and spring months, increased in summer months, and peaked in the fall (Figure 3.4A). The F s were also variable among years, with highest F in 2006 and lowest in 2007. The mortality rate experienced by tags (F') varied between 0 and 0.04 (RSE = 14 – 101%) and showed a seasonal pattern, being low in winter months and highest in summer months (Figure 3.4A).

The telemetry model estimated monthly F s that were low in winter, spring, and summer months (ranging from 0.01 – 0.03) and highest in fall (0.14). Relative standard errors of monthly estimates ranged from 33 to 107%, similar to RSEs from the tag return model. Monthly F s from the telemetry approach mirrored the seasonal pattern observed in the tag return results, with the exception of higher magnitude in fall months (Figure 3.4B).

Monthly F s in the combined model ranged from 0.01 to 0.07, with RSEs of 11 - 102% (Figure 3.4C). The magnitude and seasonal pattern of monthly F s in the combined model closely mirrored estimates from the tag return data alone, being low in winter and spring, increasing in summer months, and peaking in the fall. Fishing mortality was also

highest in 2006 and lowest in 2007. In addition, F' varied between 0 and 0.04 (RSE = 13 – 101%), and showed a seasonal pattern of being low during the winter months and highest in the summer (Figure 3.4C).

Annual estimates of F from the combined model were partitioned into recreational and commercial components based on the returns of high-reward tags from harvested fish. Commercial F varied from 0.07 in 2007 to 0.13 in 2005 and 2006, while recreational F was generally higher and varied from 0.11 in 2007 to 0.22 in 2006 (Figure 3.5). The recreational sector made up between 50 and 64% of the total F among the three years of the study, with the commercial sector making up the remainder.

Monthly M from the tag return model was estimated to be 0.03 ± 0.02 . Considerably lower estimates were obtained for the telemetry-only model (0.002 ± 0.002) and the combined model (0.003 ± 0.003). Therefore, annual estimates of M were 0.38 (tag return), 0.03 (telemetry) and 0.04 (combined model).

It did not appear that predation upon telemetered red drum by bottlenose dolphins in our systems was frequent, since there was nearly complete separation between the speed of emigrating transmitters and the range of observed speeds of bottlenose dolphins (Figure 3.6). The single red drum that emigrated from South River at an unusually high rate of speed (8.2 km h^{-1}) may have been consumed by a predator such as a bottlenose dolphin. Since possible predation occurred on this fish within the two-week censor period, it was not included in the analysis.

In the tag return model, λ was estimated at 0.82 ± 0.08 for NCSU low-reward tags, but was much lower for NCDMF low-reward tags (0.53 ± 0.05). The estimates changed

slightly in the combined model, resulting in lower λ for both NCSU (0.76 ± 0.07) and NCDMF (0.49 ± 0.04) low reward tags.

Relocation probability for telemetered fish was high for all years of the study, varying from 0.87 ± 0.05 in 2005 to 1.00 ± 0.07 in 2007 in the telemetry model and 0.84 ± 0.05 in 2005 to 1.00 ± 0.08 in 2007 in the combined model.

DISCUSSION

By combining telemetry and tag return data into one joint analysis, we estimated seasonal F s and annual M s for an estuarine fish. Our work provides the first field test of the simulations by Pollock et al. (2004), who suggested that a combined telemetry and tag return approach could provide precise and unbiased estimates of F , M , and λ . The strength of the telemetry method is estimating M , while the tag return method is better at estimating F (Pollock et al. 2004). The combination of these two approaches takes advantage of the relative strengths of each and provided more precise estimates of F and M than either independent approach alone.

Recent work has highlighted the benefits of combining different techniques and data sources to estimate mortality rates of organisms. For instance, improved estimates of mortality have been acquired using multiyear fishery tagging models combined with catch data (Polacheck et al. 2006) or catch-at-age and observer data (Eveson et al. 2007). Coggins et al. (2006) used catches of marked and unmarked fish in a fisheries stock assessment model to estimate capture probabilities, survival, abundance and recruitment. Likewise, previous work from terrestrial systems has shown that combining mark-

recapture techniques with telemetry resulted in improved models that allowed estimation of additional parameters and assessment of assumptions (Tsai 1996; Barker 1997; Catchpole et al. 1998; Powell et al. 2000; Nasution et al. 2001, 2002). For example, Nasution et al. (2001) estimated precise monthly survival rates of snail kites (*Rostrhamus sociabilis*) in Florida when combining a Cormack-Jolly-Seber mark-resight model with Kaplan-Meier radio telemetry analyses. Our combined model provided the same benefits in a fisheries context, but has gone further by being able to partition F and M from total mortality with good precision.

The combined tag return – telemetry model estimated relatively precise monthly F s. We attribute the good precision to four factors: (1) a large number of red drum were tagged and telemetered each month, (2) the annual exploitation rate of red drum while in the slot limit was high (e.g., 0.30 in our study in 2006), (3) λ was high, and (4) relocation probability of telemetered red drum was high (≥ 0.80). Large monthly sample sizes of tagged, recovered, and telemetered fish permitted us to use a monthly model, which clearly demonstrated the strong seasonality in F that peaked in the fall months, but was different among years. Unlike most stock assessments that only produce an annual F , information about the seasonality of F estimated by our combined model could be used by managers to employ seasonal closures that would have maximum impact. For subadult red drum in North Carolina, fishing effort could be reduced or restricted in fall months to reduce F most substantially.

There are additional benefits of using a monthly time step. Although fish are often tagged continuously over time in tagging studies, many applications of tag return models

assume that tagging only occurs at the beginning of each annual time step. Monthly time steps reduce potential problems associated with continuous tagging. It was also encouraging that monthly estimates of F from the tag return and telemetry approaches were similar in seasonal pattern, especially considering their independence. The apparent differences in magnitude of F during the fall months between the tag return and telemetry approaches were not substantial; differences may have been real if F was higher in NRE tributaries compared to the rest of the state. Our results suggest that, although the tag return data drove estimates of F in the combined model, both the tag return and telemetry approaches can be used to estimate monthly F s with reasonable precision given large sample sizes.

Natural mortality is notoriously difficult to estimate because natural deaths are rarely seen and it is often confounded with other parameters in population models (Quinn and Deriso 1999). Our annual estimate of M (0.04) is consistent with recent telemetry research that suggests M may be lower than previously thought for many fish species. For instance, estimates of M ranging from 0.10 to 0.16 have been determined for adult striped bass *Morone saxatilis* in North Carolina reservoirs using telemetry (Hightower et al. 2001; Thompson et al. 2007). Likewise, our estimate of M is substantially lower than previous estimates for subadult red drum. Latour et al. (2001) estimated an annual M of 0.83 – 1.37 for age-2 red drum in South Carolina based on tagging, but the authors noted that these estimates were likely positively biased due to emigration from the study area towards the coast. The rarity of observed natural mortalities in our telemetry study ($n = 1$) made it difficult to compare a constant M model to one that allowed M to vary by shorter time

steps such as months or years. In cases where natural deaths are more common, it will likely be possible to estimate season- or yearly-specific M s using the telemetry approach (e.g., Waters et al. 2005).

It is unlikely that our estimate of M was biased low because of unaccounted-for predation. By using submersible receivers to quantify emigration rates of transmitters and quantifying the average swimming speed of bottlenose dolphin in our systems, we were able to show that in only one instance did a transmitter emigrate at a speed suggestive of a bottlenose dolphin. That particular fish was ultimately censored from our analyses because it emigrated within the two week censor period. Other predators capable of consuming a 2-kg red drum were very rare or absent in these oligohaline tributaries. Future studies using the telemetry approach on small fish in open systems must be able to separate live emigrating fish from those emigrating while in the stomach of a predator. It should be noted that it remains unknown whether M s experienced by subadult red drum in tributaries of the NRE are reflective of rates elsewhere. The value of M estimated using tag return data alone was much higher but it was not a precise estimate, likely because natural deaths are estimated indirectly with this approach.

It is not necessary to assume that all tags are reported to separate F and M in a tag return study, but λ must be known or estimable. There are many methods available to estimate λ , including high-reward tagging (Pollock et al. 2001), planted tags (Hearn et al. 2003), observers in multi-component fisheries (Hearn et al. 1999), and tagging studies with pre- and post-fishing season tagging (Hearn et al. 1998). For recreational species like red drum, high-reward tagging has become the primary method used to estimate λ . There are

some important assumptions of the high-reward method that must be considered before conducting a high-reward tagging study (reviewed in Pollock et al. 2001). Most importantly, high- and low-reward tagging must be spread over a large area to avoid changing the behavior of the fishery and to reduce the chance that individual fishers will catch multiple tags. Furthermore, the high-reward tagging study must be widely advertised and high-reward tags must be obvious in color and message so that fishers recognize high-reward tags when caught. If not, the critical assumption of 100% reporting of high-reward tags will likely not be met, which will cause the λ of low-reward tags to be positively biased (Conroy and Williams 1981). By spreading tagging over a large area, advertising the tagging project widely, and using a unique tag color with an obvious \$100 reward message, we believe our estimates of λ for NCSU and NCDMF tags are accurate.

We estimated λ for NCDMF and NCSU external tags separately. Our estimates of λ (0.49 and 0.76) are consistent with previous work on red drum, which have estimated λ ranging from 0.36 to 0.63 (Green et al. 1983; Denson et al. 2002). We also showed that λ varied substantially between the two sources of released tags. The 0.27 difference in λ could be due to some fishers being less likely to report tags to a management agency compared to an academic institution. For instance, some fishers may be reluctant to return tags to a management organization because of a perceived risk of additional regulations, but they may not have the same fears of returning tags to an academic institution. It is unknown if differences in λ for low-reward tags between a university and a management agency would translate to unequal reporting of high-reward tags from different sources.

Future high-reward tagging studies, especially those conducted by management agencies, must consider this possibility.

Another advantage of using a tagging approach with high-reward tags to estimate mortality rates for fish species is that F can be decomposed into recreational and commercial components. Assuming both sectors reported 100% of all high-reward tags from harvested fish, we found that recreational fishers accounted for 50 – 64% of F in North Carolina from 2005 to 2007. Our results are consistent with estimates of landings in North Carolina that suggest recreational fishers have harvested approximately 56% of the total red drum harvest in the state since 1999 (Takade and Paramore 2007). Furthermore, the observed increase in F from 2005 to 2006 appeared to be due entirely to an increase in recreational F , while the commercial F stayed constant over the same time period. The factors contributing to variability in the magnitude of sector-specific F s for red drum requires more research attention.

We estimated mortality rates of one age class of red drum only because sufficient sample sizes were lacking for other age classes and we were particularly interested in slot-limit (legal) fish in this study. The combined approach can easily be adapted to an age-dependent analysis, however. The model structure for conventional tagging analyses of multiple age classes has been described in Jiang et al. (2007) and Chapter 2; it would be straightforward to combine these analyses with age-dependent telemetry data to produce an age-dependent combined model.

The potential benefit of adding a telemetry component to an on-going tag return study is substantial, as long as it is possible to detect emigration from the study area. For

instance, telemetry can also be used to estimate mixing or emigration rates; this is important because emigration is often confounded with mortality in most tagging models (Pollock et al. 1990). Given variable fishing effort over space, movement and habitat use data can be biased in traditional tagging studies. Telemetry provides much more accurate information about movement and habitat use because it does not rely on the spatial and temporal patterns of the fishery. The telemetry approach also avoids problems associated with estimating λ and tag loss common in traditional tagging studies.

The telemetry mortality approach is most easily used in closed systems such as lakes, reservoirs, or rivers blocked by dams. The telemetry approach can be adapted to open systems, however, by using submersible receivers as gateways through which telemetered fish enter and exit the study system or area. We staggered the release of 180 telemetered red drum over the course of our 34 month study in an attempt to maintain an adequate monthly sample size. Had movement rates of subadult red drum been lower, many fewer transmitters would have been required to maintain adequate monthly sample sizes, but the downside would have been that mixing rates of conventional tagged fish would have been much lower. In our study, it appeared that movement rates of subadult red drum were high enough that substantial mixing of conventionally tagged fish occurred, but it also resulted in a high emigration rate of telemetered fish from Neuse River tributaries.

The combined tag return – telemetry approach may ultimately be a cheaper alternative than traditional stock assessment approaches to control exploitation rates of managed fish populations (Martell and Walters 2002; Walters and Martell 2004).

Traditional stock assessment approaches typically rely on fishery landings and survey data, which are only linearly related to true biomass if catchability (q) remains constant over time (Hilborn and Walters 1992). Variability in q arising from technological advances, range contractions, or any number of other reasons has famously resulted in erroneous stock assessments of many species (see Walters and Martell 2004 for a review). The combined tag return – telemetry approach may be a viable alternative that can be used to directly estimate F and M , as long as several key assumptions (discussed above) are met and benchmarks could be established. Tagging hundreds or thousands of fish annually with high- and low-reward tags as well as releasing a modest number of transmitters may appear to be an expensive way to estimate mortality rates. In many situations, however, this approach may be much less risky and expensive than collecting and analyzing survey and aging data needed for traditional stock assessment approaches (Walters and Martell 2004).

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Table 3.1. Monthly sample sizes of external tagged and telemetered age-2 red drum in North Carolina from April 2005 to December 2007.

Month	External tagging			Telemetry
	NCSU low-reward	NCDMF low-reward	NCSU high-reward	Virtual releases
Apr-05	391	149	74	44
May-05	0	27	0	33
Jun-05	0	86	0	31
Jul-05	0	23	0	25
Aug-05	0	29	0	17
Sep-05	0	11	0	3
Oct-05	0	25	0	4
Nov-05	0	4	0	1
Dec-05	0	2	0	29
Jan-06	0	55	0	32
Feb-06	0	256	0	31
Mar-06	0	502	0	23
Apr-06	391	463	211	24
May-06	0	43	0	19
Jun-06	0	41	0	26
Jul-06	0	19	0	17
Aug-06	0	66	0	12
Sep-06	0	61	0	10
Oct-06	0	40	0	3
Nov-06	0	6	0	0
Dec-06	0	3	0	0
Jan-07	0	0	0	0
Feb-07	0	323	0	0
Mar-07	0	323	0	2
Apr-07	388	114	67	1
May-07	0	326	0	0
Jun-07	0	94	0	0
Jul-07	0	10	0	12
Aug-07	0	8	0	8
Sept-07	0	12	0	8
Oct-07	0	7	0	10
Nov-07	0	45	0	11
Dec-07	0	81	0	10
Total	1170	3254	352	581

Table 3.2. Candidate models fitted to tag return data alone, telemetry data alone, or combined tag return and telemetry data with program SURVIV. Fishing mortality (F) was allowed to vary by month (m), month and year (my), quarter (q), quarter and year (qy), year (y), or be constant (\cdot). Natural mortality rate (M) was held constant and relocation probability (P) was allowed to vary yearly based on preliminary modeling.

Model	Parameters	Log likelihood	AIC	QAIC _c	Δ QAIC _c
Tag return					
$F_{qy}M_{\cdot}$	28	-672.7	1401.4	661.3	0
F_mM_{\cdot}	28	-700.7	1457.4	686.5	25.2
F_qM_{\cdot}	12	-738.6	1501.2	688.3	27.0
$F_{my}M_{\cdot}$	70	-616.0	1372.0	696.1	34.8
F_yM_{\cdot}	10	-887.5	1795.0	818.2	156.7
$F_{\cdot}M_{\cdot}$	6	-918.8	1849.6	838.3	177.0
Telemetry					
F_qMP_y	9	-62.6	143.3	88.8	0
$F_{qy}MP_y$	17	-50.6	135.3	92.1	3.3
FMP_y	6	-72.2	156.5	93.4	4.6
F_yMP_y	8	-71.5	159.1	96.7	7.9
F_mMP_y	17	-55.5	145.0	97.5	8.7
$F_{my}MP_y$	37	-43.0	160.0	127.7	38.9
Combined					
$F_{qy}M_{\cdot}$	31	-745.4	1552.8	831.7	0
$F_{my}M_{\cdot}$	73	-691.7	1529.4	861.9	30.2
F_mM_{\cdot}	31	-774.9	1611.8	862.1	30.4
F_qM_{\cdot}	15	-809.7	1649.4	865.7	34.0
F_yM_{\cdot}	13	-965.6	1957.2	1022.6	190.9
$F_{\cdot}M_{\cdot}$	9	-994.6	2007.2	1044.5	212.8

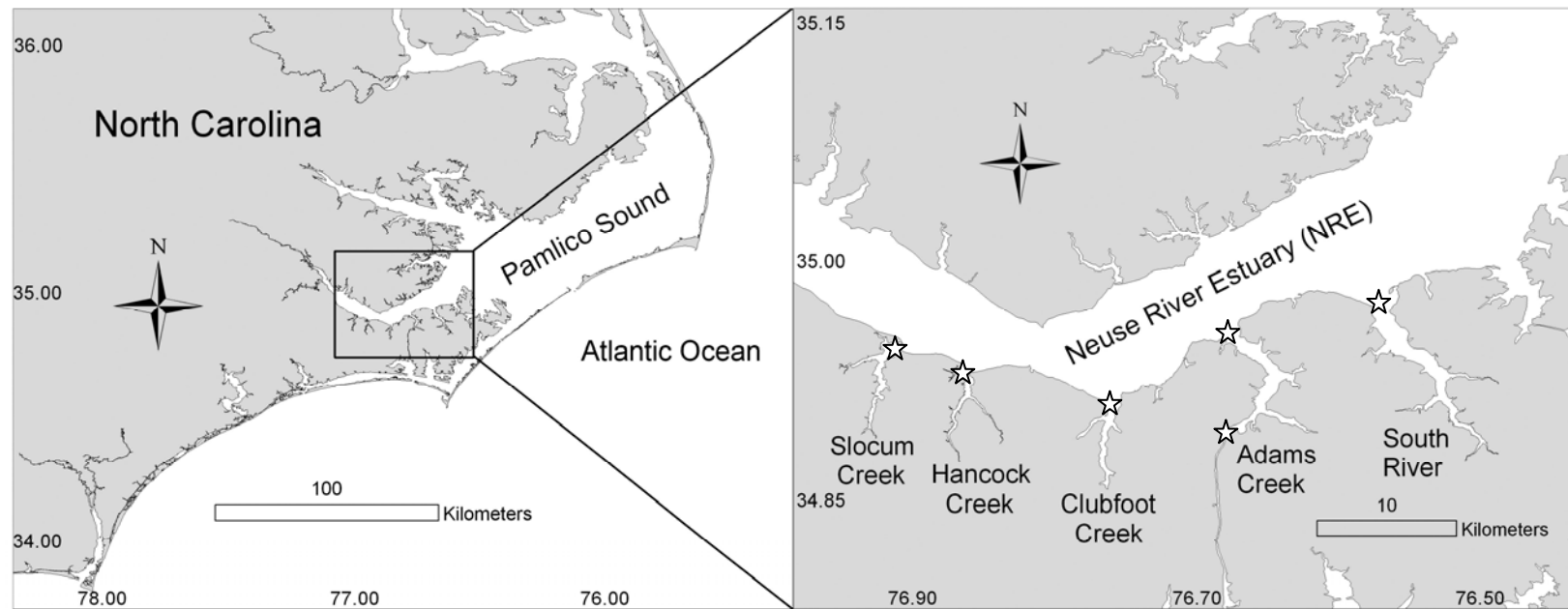


Figure 3.1. Map of study area, showing coastal North Carolina and Pamlico Sound (left panel), and an enlarged view of the Neuse River Estuary (right panel). The conventional tagging took place throughout Pamlico Sound and associated rivers. The telemetry component of the study was conducted exclusively within the five labeled creeks in the Neuse River, and stars indicate location of submersible receiver arrays.

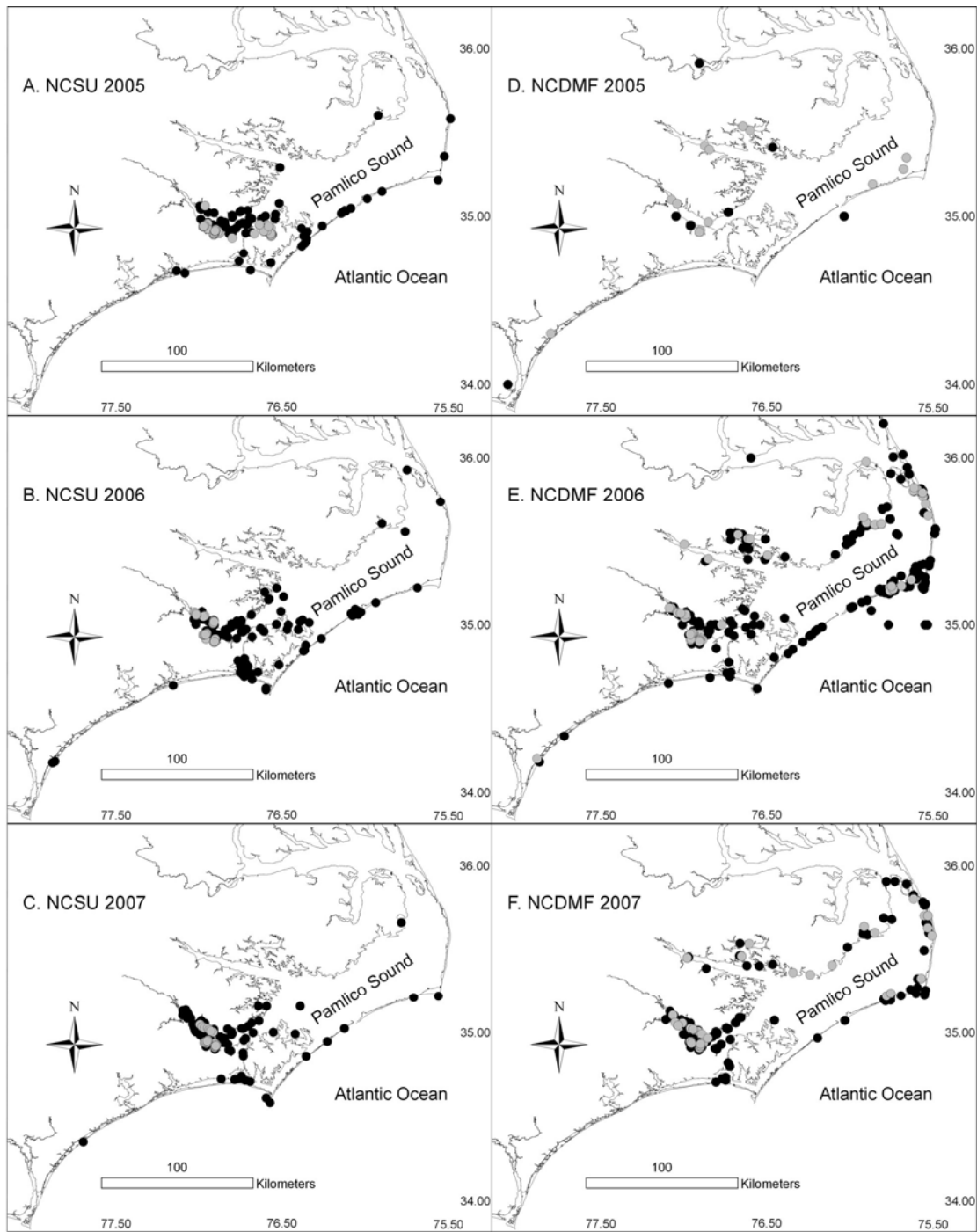


Figure 3.2. Tagging (gray circles) and recovery sites (black circles) for red drum tagged and released by NCSU (A – C) and NCDMF (D – F) in 2005 – 2007.

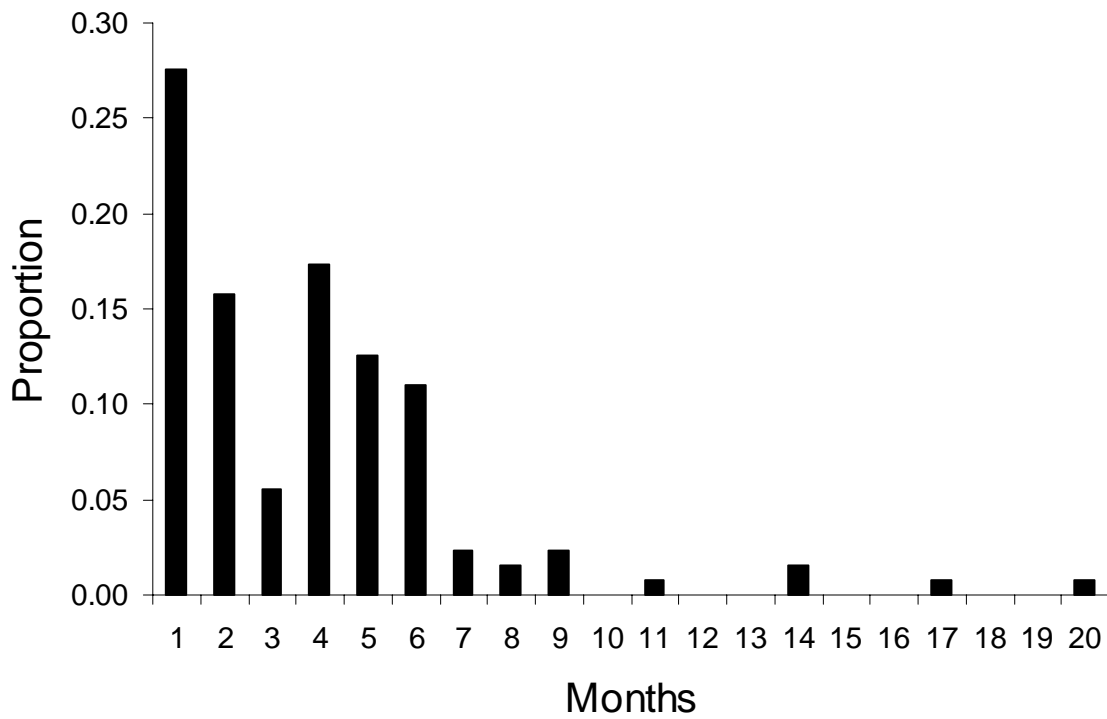


Figure 3.3. Proportion of telemetered red drum emigrating from Neuse River tributaries in various monthly intervals after initial release, 2005 – 2007. Emigration events were documented with submersible receiver arrays at the mouth of each tributary.

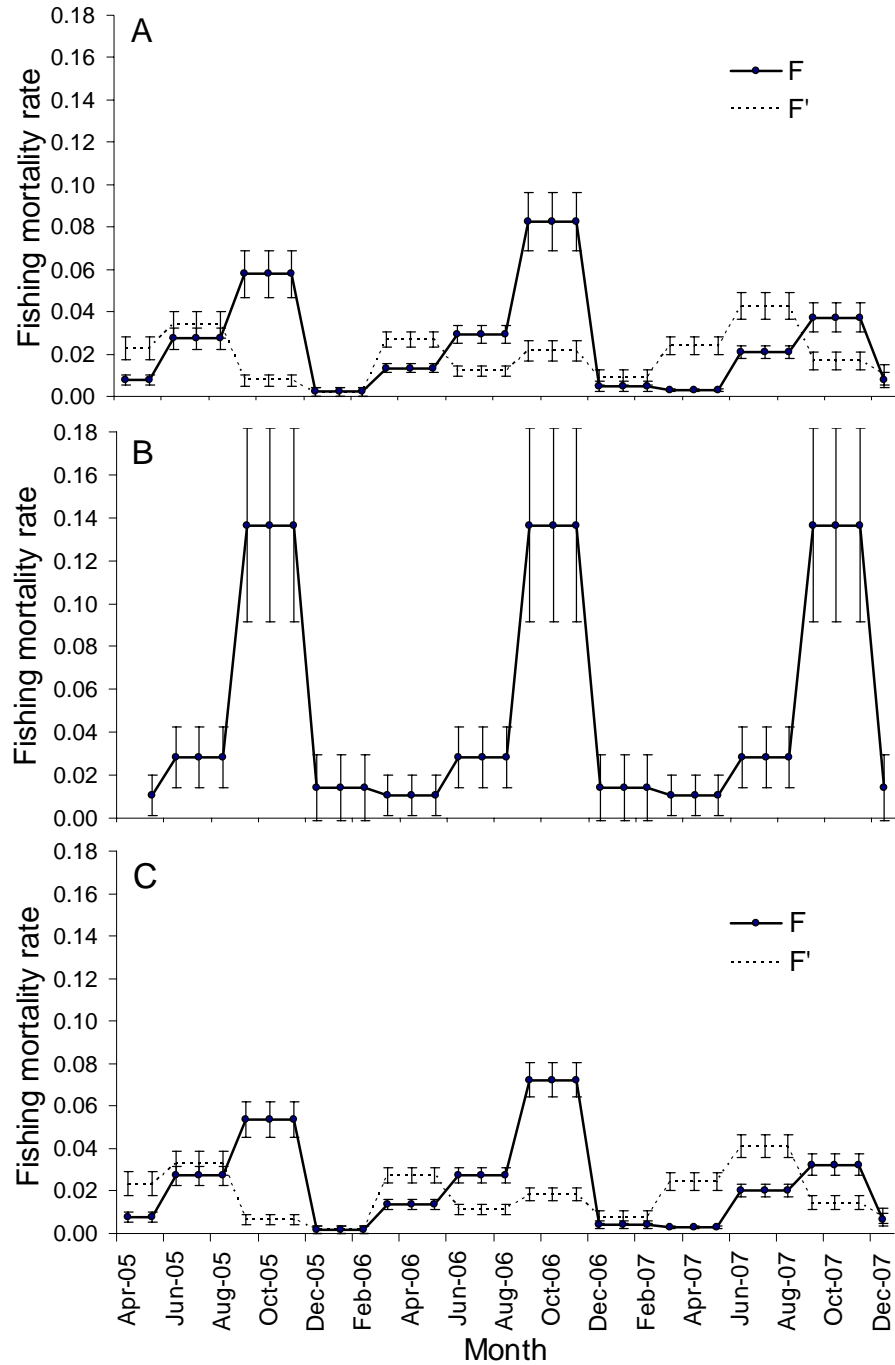


Figure 3.4. Monthly fishing mortality rate (\pm SE) for subadult red drum from April 2005 – December 2007. Fishing mortality rates were estimated by the tag return model alone (A), the telemetry model alone (B), or the combined tag return – telemetry model (C). The mortality rate experienced by tags (F' , for caught-and-released fish only) is shown by the dotted line.

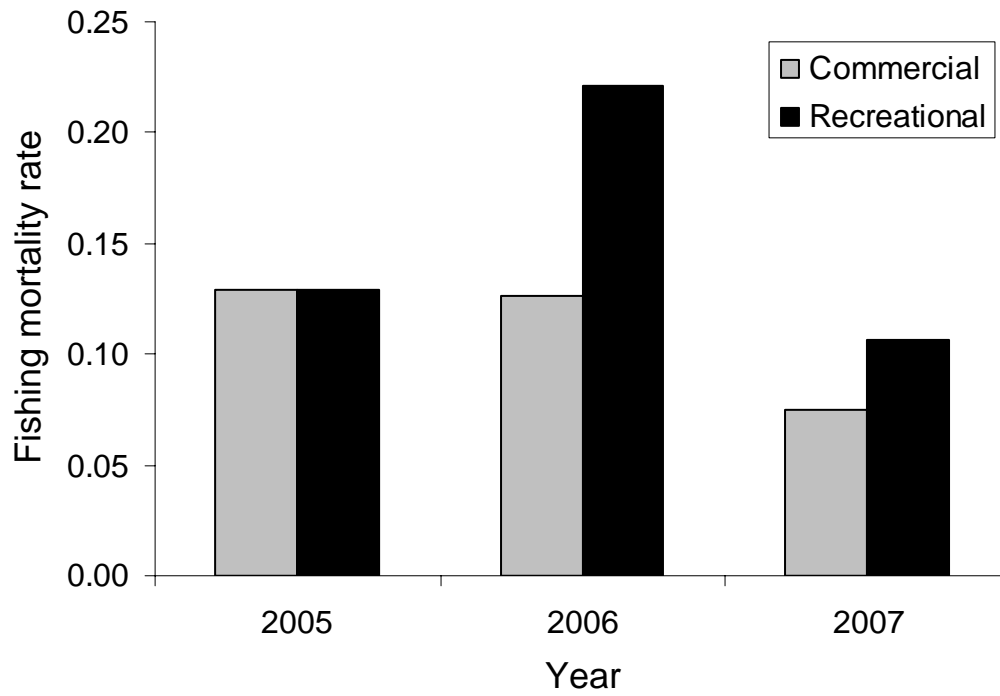


Figure 3.5. Annual fishing mortality rate of age-2 North Carolina red drum attributed to recreational and commercial fishing sectors, estimated by the yearly returns of high-reward tags from harvested fish.

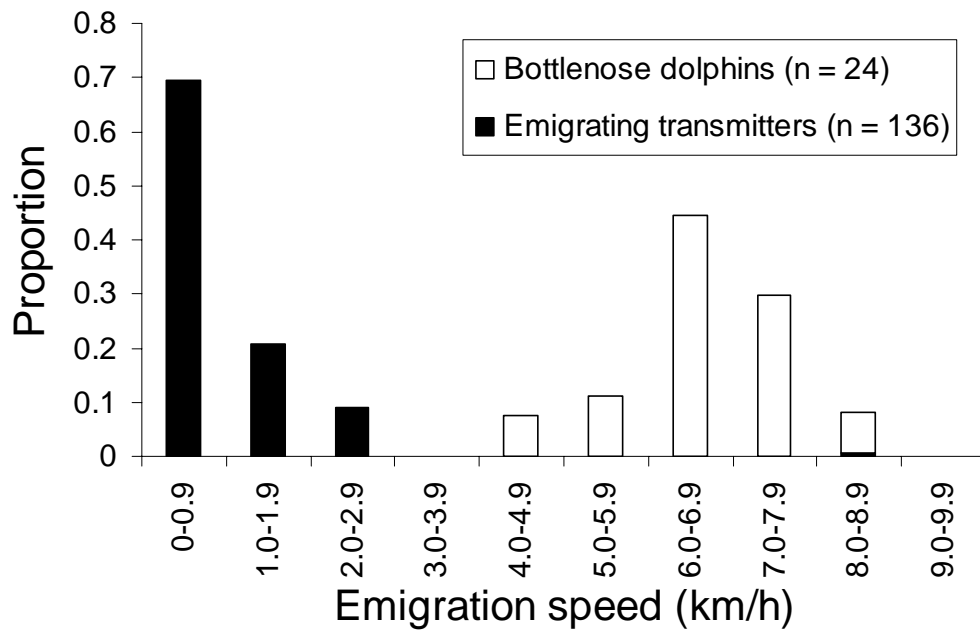


Figure 3.6. Proportion of emigrating transmitters (black bars) and bottlenose dolphins (white bars) based on estimated swimming speed from detections in the receiver arrays.

CHAPTER 4. ABIOTIC AND BIOTIC FACTORS INFLUENCE THE HABITAT USE OF NORTH CAROLINA SUBADULT RED DRUM

Nathan M. Bacheler, Lee M. Paramore, Jeffrey A. Buckel, Joseph E. Hightower

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ABSTRACT

We used generalized additive models (GAMs) to relate water quality, microhabitat, geographic, and temporal factors to catches of two age-classes of subadult red drum *Sciaenops ocellatus* from a 6-year fishery-independent gill net survey in North Carolina. Age-1 and age-2 red drum were most often caught in shallow, nearshore waters; in some regions, both age groups showed a preference for seagrass. Age-1 red drum were primarily captured at two different salinity ranges (0 – 5 and 20 – 30 psu), while age-2 red drum were not related to salinity. To determine the influence of prey on red drum distribution, we examined stomachs of red drum to determine prey eaten and used GAMs to relate water quality and prey attributes to the presence of 36 telemetered age-2 red drum during four seasonal periods in a small tributary of the Neuse River. Telemetered red drum displayed a negative response to salinity, a positive response to dissolved oxygen, a dome-shaped response to prey evenness, and a positive response to total prey in Hancock Creek. Although previous research has determined that subadult red drum can tolerate a wide variety of environmental conditions, our research suggests that they associate with both

abiotic and biotic factors in very specific ways. We determined that habitat use patterns of subadult red drum were age-, scale-, and sometimes region-dependent, highlighting the need for examining habitat use patterns of estuarine organisms at multiple scales for multiple age classes if generalities about how species respond to abiotic and biotic factors are sought.

INTRODUCTION

Recent loss of estuarine habitat due to human development in coastal zones has resulted in increased attention on fish habitats by governments and researchers. Concerns about severe habitat loss and degradation in estuarine environments have prompted government action at state and federal levels to identify, prioritize, and protect essential habitats for estuarine organisms (e.g., Benaka 1999, Street et al. 2005, ASFMC 2007). It has also spurred a suite of reviews on ways to develop robust methods for identifying and prioritizing “nursery” habitats that are used by estuarine organisms (e.g., Beck et al. 2001, Heck et al. 2003, Dahlgren et al. 2006). There are now a variety of approaches to prioritize conservation planning in estuarine and marine environments (e.g., Stewart et al. 2003, Morris & Ball 2006). A basic understanding of the habitat use of the species of interest is required for all of these techniques.

The issue of scale is one of the most fundamental topics in ecology. Relationships of species to their environment can change qualitatively with the scale of observation, so a basic understanding of a species’ ecology requires study of how pattern and variability are influenced by the scale of observation. The importance of spatial scale in terrestrial

ecology is now well established (Levin 1992, Ives et al. 1993, Schneider 2001, Shriner et al. 2006). For example, Shriner et al. (2006) showed that the scale of observation profoundly influenced the spatial distribution of species richness hotspots and thus conservation planning priorities. The topic of scale has also received some attention in freshwater (Essington & Kitchell 1999, Fagan et al. 2005, Kennard et al. 2007, Wilson & Xenopoulos 2008) and marine fish studies (Rose & Leggett 1990, White & Warner 2007). In contrast, estuarine finfish studies rarely deal explicitly with issues of scale.

The red drum (*Sciaenops ocellatus*) is a highly prized recreational estuarine fish species found along the coast of the SE USA and northern Gulf of Mexico. Compared to the well documented habitat use of early juvenile (i.e., age-0) red drum, there is a dearth of habitat information on late state juveniles (i.e., ages 1 – 3, hereafter referred to as “subadults”). Early juveniles of the species occupy seagrass meadows or marsh edge habitats in the Gulf of Mexico (Holt et al. 1983, Rooker & Holt 1997, Rooker et al. 1998, Stunz et al. 2002), but appear to also use small creeks, shorelines, and bays with sand or mud bottom and little cover along the SE USA (Daniel 1988, Wenner 1992, Ross & Stevens 1992). Given that exploitation of red drum generally occurs at the subadult state (Chapter 2), understanding the habitat use patterns of this stage is also important. For instance, habitat use studies are needed to prioritize important habitat types for subadult red drum in North Carolina. Moreover, detailed habitat information could be used to create temporal or seasonal fishing closures to protect high densities of subadult red drum from recreational and commercial exploitation.

Previous research on subadult red drum habitat use has been limited to small systems of 1 to 10s of km, and these results have been mixed. For instance, Adams & Tremain (2000) observed higher catches of subadult red drum in low water temperatures during a year-round gill net survey, but other water quality variables such as salinity and dissolved oxygen were not significantly related to subadult red drum catch. Alternatively, Dresser & Kneib (2007) used ultrasonic telemetry to show that habitat use of subadult red drum was influenced by tidal and diel cycles; fish moved into the flooded marsh at high tide during the day and back into main channel habitats at low tide or during the night. The next logical step for an improved understanding of habitat use in subadult red drum is for study to occur at larger spatial scales to determine the validity and generality of previous work.

In this paper, we quantified habitat use of subadult red drum in Pamlico Sound and associated rivers in North Carolina using a combination of fishery-independent gill netting to address large scale habitat use (1 - 100s of kilometers) and ultrasonic telemetry to quantify small-scale habitat use (meters to kilometers). These two approaches allowed us to quantify small- and large-scale habitat use patterns of subadult red drum and understand the relative influence of abiotic and biotic factors in influencing habitat use. This study improves our understanding of the ways in which organisms use estuaries and how interpretations of habitat use patterns may be dependent upon the scale at which research is conducted.

METHODS

Large-scale habitat use

Pamlico Sound and associated rivers

We quantified the physical habitat that may influence large-scale habitat use patterns of red drum in Pamlico Sound, North Carolina (Figure 4.1). Pamlico Sound is the second largest estuary in North America, and is an important nursery habitat for a wide array of estuarine species (Ross & Epperly 1986). Pamlico Sound is a shallow lagoonal system (mean depth = 5 m) bordered on the east by barrier islands (the Outer Banks), and on the west by mainland eastern North Carolina and multiple rivers. The Neuse, Pamlico, and Pungo Rivers drain eastern North Carolina and empty into Pamlico Sound. Currents and tides are primarily wind-driven; lunar tides only influence the Sound within a few kilometers of the inlets (Pietrafesa & Janowitz 1991). A wide variety of habitats exist in Pamlico Sound and associated rivers, including seagrass and oyster reefs that are thought to be important for subadult red drum.

NCDMF gill net survey

The North Carolina Division of Marine Fisheries (NCDMF) fishery-independent gill net survey began in Pamlico Sound in May, 2001, and in the Pamlico, Neuse, and Pungo Rivers in July, 2003. Five regions are considered in this study: The Outer Banks, Hyde County, Neuse River, Pamlico River, and Pungo River. Sampling in the first year of the study occurred year-round, but was changed thereafter to exclude the month of January due to unsafe working conditions on the water in winter months.

Sampling locations for the gill net survey were selected using a stratified random sampling design based on strata and water depth (Figure 4.1). The Sound was divided into eight strata: Hyde County 1 – 4 and the Outer Banks 1 – 4. The Neuse River was divided into four strata (Upper, Upper-Middle, Middle-Lower, Lower) and the Pamlico River was divided into three strata (Upper, Middle, Lower), while the Pungo River was not divided. A one minute by one minute grid (i.e., one square nautical mile) was overlaid over all strata and each cell was classified as shallow (< 1.83 m) or deep (≥ 1.83 m) or both based on bathymetric maps.

Each stratum was sampled twice a month. One cell was randomly selected within each stratum by using the SAS procedure PLAN for each sampling occasion. If that cell had both deep and shallow habitat then both sets were made in that cell. If the cell lacked either deep or shallow water, then the closest suitable habitat in an adjacent cell was used. Sampling was conducted with a gill net consisting of eight 27.4 m segments of 7.6, 8.9, 10.2, 11.4, 12.7, 14.0, 15.2, and 16.5 cm stretched mesh webbing, totaling 219.5 m of gill net on each sampling date per cell. Shallow cells were sampled with floating gill nets and deep cells were sampled with sinking gill nets; vertical height of nets was between 1.8 and 2.1 m deep. Nets set along the shoreline were most typically set perpendicular to shore, whereas most deep sets (and shallow sets offshore) were typically set parallel to shore along a depth contour. Nets were typically deployed within an hour of sunset and retrieved the next morning, so all soak times were approximately 12 h. This sampling design resulted in a total of approximately 64 gill net samples per month.

Red drum from gill nets were enumerated, measured for fork length (mm), and released. We converted length of red drum from fork to total based on the conversion provided by Ross et al. (1995). We then used a 6-mo age-length key to convert total length of fish at capture to an estimated age based on a September 1 birth and a January 1 birthday for all additional age groups (i.e., age-0 red drum are 0 – 3 months old, age-1 fish are 4 – 16 months old, and so on). The age-length key was based on 17 years of North Carolina red drum ageing data from otoliths (NCDMF, unpublished data); annuli were validated by Ross et al. (1995). A 6-mo age-length key (January - June and July - December) was used because of rapid summer growth rates that subadult red drum experience in North Carolina (Ross et al. 1995). The 6-mo age-length key provided very good separation of length groupings of fish until age 4. However, catches of age-3 and older red drum were rare, so only age-1 and age-2 red drum were considered here. Age-dependent catch-per-unit-effort (CPUE) was calculated as the number of each age group of red drum caught in each gill net set per hour.

Habitat measurements were taken at deployment and retrieval of each gill net set, and average values were used for analyses. Temperature (°C), salinity (psu), and dissolved oxygen (mg/L) were measured with a YSI 85. Sediment size was classified into one of four categories: clay, mud, mud and sand mix, and sand. Above bottom habitat was also visually estimated as being primarily composed of algae, detritus, seagrass, oyster shell, or none. Distance from shore was estimated with a rangefinder and categorized into one of the following bins: 0 – 99 m, 100 – 199 m, 200 – 299 m, 300 – 399 m, 400 – 499 m, 500 – 599m, or greater than 599 m. Depth (m) was determined using an onboard depth finder.

NCDMF gill net survey analyses

We used generalized additive models (GAMs) to examine the relationship between independent variables and the CPUE of red drum caught at a particular location. A GAM is a generalization of generalized linear models and its main advantage over traditional regression techniques is its capability to model nonlinearities, common in ecological studies, using nonparametric smoothed curves (Hastie & Tibshirani 1990). Generalized additive models replace the traditional least squares estimate of multiple linear regression with a local smoother; here, we used the cubic spline smoother *s*. We constructed separate models for age-1 and age-2 red drum. The response variable was CPUE of a particular age-class of red drum; we assumed a Poisson error distribution with a log link function because it is recommended when the response is count data (Swartzman et al. 1992). Explanatory variables included water quality (temperature, salinity, dissolved oxygen), microhabitat (sediment size, above bottom habitat), geographic (distance from shore, depth, region), and temporal (year, month) factors. Given likely differences in habitat availability among regions, we also constructed separate GAMs for age-1 and age-2 red drum within each of the five regions. An added benefit of region-specific GAMs is that they can be used to examine the generality of habitat use patterns of red drum in North Carolina.

A backwards stepwise selection procedure was used to compare different ways of including each variable and to remove those terms that did not improve model fit significantly (Venables & Ripley 1999). There were four possibilities for each variable: a flexible nonlinear smoothed effect with 4 degrees of freedom, a less flexible nonlinear

smoothed effect with 2 degrees of freedom, a linear effect, or exclusion from the model. However, 'Region,' 'Sediment size,' and 'Above bottom habitat' could only enter the model as categorical variables with a linear effect or be excluded. Akaike's Information Criterion (AIC) was used to select the model that provides the best fit with the fewest degrees of freedom used (Burnham & Anderson 2002). Deviance explained by the model was approximated by subtracting residual deviance from null deviance, and then dividing that value by the null deviance (Stoner et al. 2001). All models were constructed and tested using the gam and stepgam procedures in Splus 2000 (Insightful Corporation, Seattle).

Red drum food habits in Hancock Creek

Hancock Creek is a lateral tributary of the lower Neuse River (Figure 4.1). It is shallow (mean depth = 1.5 m) and oligohaline, and is fringed by forest, marsh, and very little shoreline development. Hancock Creek is approximately 7 km long by at most 0.5 km wide. The shallow depth (< 2 m throughout) and narrow width of Hancock Creek reduces the confounding influence of depth and distance offshore as predictor variables, allowing a clearer examination of how prey variables influence the habitat use of red drum.

We used stomach content analysis to identify the major prey of red drum in Hancock Creek that might influence their habitat use. Quarterly diet samples were taken from age-2 red drum during daylight hours ± 12 d around 1 February, 1 May, 1 August, and 1 November 2006. An additional collection of age-2 red drum occurred the previous year, on 8 June 2005, in Hancock Creek, and is included in these analyses to increase sample

size of red drum stomachs examined. Most red drum were captured using the “strike net” method, whereby a 200-m gill net with 102-mm stretch mesh was set in an arc along the shoreline. A 7.2-m research vessel was then driven between the net and shoreline, scaring fish into the net. The net was immediately retrieved, and when red drum were captured, the monofilament netting was cut in order to prevent injury when removing the fish. Electrofishing was used to collect the remaining red drum. Fish were held temporarily in 140-L aerated tanks on board the research vessel for a maximum of 1 h to reduce regurgitation or digestion (Sutton et al. 2004).

Gastric lavage was used to extract stomach contents from individual subadult red drum. Previous studies have shown that gastric lavage is an effective means to remove stomach contents from a variety of fishes (Crossman & Hamilton 1978, Waters et al. 2004). The gastric lavage device was constructed based on the design described by Crossman & Hamilton (1978), and gastric lavage protocol followed Waters et al. (2004). Briefly, a 12-V bilge pump ($1,382 \text{ l h}^{-1}$) was used to flush items out of the stomach into a fine mesh net positioned under the red drum. Once no additional materials were being flushed out (approximately 45 s per fish), the contents from the net were placed into a plastic bag, which was then sealed, labeled, and placed on ice. Fish were then released alive, except for four red drum that were sacrificed to verify the gastric lavage method. All stomach items were taken back to the laboratory and identified, sorted, measured for TL (all items except crabs) or carapace width (crabs), blotted, and weighed wet ($\pm 0.001 \text{ g}$) within 24 h of extraction. Stomach contents of individual red drum within a quarterly sampling period were combined and summarized together in terms of frequency of

occurrence (proportion of stomachs with food containing a prey type) and percent by weight (proportionate contribution of identifiable prey to diet by weight).

Small-scale habitat use

Abiotic and biotic sampling in Hancock Creek

To test the influence of prey abundance and diversity on the distribution of red drum, we examined small-scale habitat use of red drum in Hancock Creek. Quarterly surveys of red drum distribution, potential prey items, and physicochemical characteristics were made in Hancock Creek in 2006. These surveys occurred on 1 – 2 February, 1 – 2 May, 2 – 3 August, and 30 – 31 October. Hancock Creek was divided into 20 strata of similar size, and sampling occurred in all of these 20 strata in each of the four seasonal periods.

Spatial and temporal patterns of habitat use of red drum were quantified using ultrasonic telemetry methods, an approach that can effectively assess the distribution and habitat use of fishes (Cooke et al. 2004). Age-2 red drum were captured using strike netting or electrofishing, and placed in aerated 140-L tanks on board a research vessel. Red drum were anesthetized individually in 20-L aerated water in a covered cooler with 150 mg l⁻¹ tricaine methanesulfonate (Finquel MS-222), measured for total length (mm), weighed (g), and placed dorsal side down on an open-cell foam-cushioned surgical platform fitted onto a 50 L cooler equipped with a re-circulating pump. Water containing anesthetic (75 mg l⁻¹ MS-222) was then pumped over the gills at approximately 680 l h⁻¹.

An incision was made 4 cm caudal to the pelvic girdle and 5 mm to the right of the ventral midline.

Ultrasonic transmitters (VEMCO, Ltd., Nova Scotia, Canada; V16 4H, 10 g in water; 10 mm wide; 65 mm long) were inserted cranially, but pulled back caudally so that the transmitter was positioned directly under the incision. The transmitters operated on a frequency of 69 kHz, and were programmed to be constantly active for a period of 641 d. The incision was closed using a simple interrupted pattern with 3-0 PDS absorbable sutures. Fish were returned to 140-l aerated tanks for recovery, and were released at capture sites once swimming behavior had returned to normal (approximately 10 minutes). Telemetered red drum were located monthly in 2006, but quarterly relocations in early February, May, August, and November are only included in our full Hancock Creek GAM to match up with quarterly prey data. Relocation probabilities of telemetered red drum exceeded 90% on all quarterly search occasions in Hancock Creek (N.M. Bacheler, unpublished data). The response variable used in statistical models was the presence or absence of telemetered red drum in each stratum.

Prey densities were quantified within each stratum and sampling period using an otter trawl. The otter trawl had a 5.0-m headrope length, 25-mm bar mesh wings and body, and a 6.4-mm bar mesh tail bag. Bottom fauna, the main prey of subadult red drum (Scharf & Schlicht 2000), are most reliably and efficiently collected using an otter trawl (Ross & Epperly 1986, Rozas & Minello 1997). Because all sampling took place in shallow water (< 2.0 m), the net opening included the majority of the water column.

To determine the location of trawling within a stratum, each stratum was divided into 10 m x 150 m cells, and one cell per stratum was randomly selected within a quarterly sampling period. The trawl was towed by a 7.2 m research vessel at approximately 77.0 m min⁻¹ for 2 min within the randomly selected cell in each stratum for a total of 20 trawl stations each quarter. All potential prey items (species and sizes) of red drum were enumerated, and a random sub-sample of 30 individuals of each species was measured for total length (fish or shrimp) or carapace width (crabs).

Only species and sizes of prey found in the diet of red drum were included in the model. Three prey metrics were used as independent predictors: prey richness, total prey, and the Shannon Index of prey evenness. For each trawl in a stratum, prey richness was calculated as the total number of prey species while total prey was the total number of individual prey. The Shannon Index (H') combines the number of species and the evenness of the species in a trawl sample (Krebs 1989), and is hereafter referred to as prey evenness. Temporal diet variability was difficult to determine due to low sample sizes of stomach samples from August ($n = 15$) and November 2006 ($n = 7$). Therefore, prey predictor variables used in GAMs (i.e., prey richness, prey evenness, and total prey) were based on red drum diet over the entire study.

Bottom temperature, salinity, dissolved oxygen, and water clarity were sampled at the beginning and end of each trawl within a stratum, and the average of both samples were used in the models. All physicochemical measurements except water clarity were sampled using a YSI-85 environmental monitoring system (Yellow Springs Instruments).

Water clarity was measured with a standard secchi disk at the same locations as water quality samples were taken.

Analyses of small-scale habitat use

We analyzed the relationship between red drum presence-absence and predictor variables using binomial GAMs. Binomial GAMs (with logit link function) were used to analyze relationships in Hancock Creek because they are more appropriate than GAMs using abundance when the relocation probability of telemetered red drum is less than one. We used both abiotic (temperature, salinity, dissolved oxygen, water clarity) and biotic (prey richness, prey evenness, and total prey) factors as predictor variables. Sample size of trawls was too small ($n = 20$) to analyze each seasonal period independently, so we included a categorical “season” variable in the model to account for any potential differences in the numbers of telemetered red drum present during each seasonal period. An added benefit of developing a year-round model is consistency with the gill net survey year-round sampling and analyses described earlier; a drawback is that we could not examine seasonal habitat use patterns.

We were concerned that quarterly sampling in Hancock Creek was not sufficient to provide a useful comparison with the nearly year-round sampling that occurred in the Pamlico Sound gill netting component of our study. To provide more consistency with large-scale GAM, we created an additional GAM model (binomial distribution, logit link function) that related the monthly (January – December, 2006) presence or absence of

telemetered red drum in Hancock Creek to physicochemical parameters only (temperature, salinity, and dissolved oxygen), since prey information on a monthly scale was lacking.

RESULTS

Large-scale habitat use

Overall, 5,961 red drum were caught in the Pamlico Sound gill net survey between 2001 and 2006, ranging in size from 146 to 1341 mm total length (mean = 424.0; SE = 1.6). More age-1 red drum (n = 4,034; CPUE = 1.33) were caught than age-2 fish (n = 1,786; CPUE = 0.59). Age-1 red drum were widely distributed from the upper reaches of the Neuse and Pamlico Rivers all the way to behind the Outer Banks. Age-2 red drum were also widely distributed, but were more frequent in higher salinity (Outer Banks) compared to lower salinity waters (Pamlico and Neuse Rivers).

There were differences in habitat use for age-1 and age-2 red drum (Table 4.1). The overall statewide age-1 GAM regression explained 62% of the variation in CPUE (Table 4.1). Depth, distance offshore, salinity, year, and month had significant nonlinear effects, and above bottom habitat and region had significant linear effects, on the distribution of age-1 red drum (Table 4.1). Age-1 red drum were strongly associated with nearshore shallow water habitats (Figure 4.2). The relationship of age-1 red drum CPUE to salinity was bimodal, with highest CPUE at low (0 – 8 psu) or high salinities (20 – 30 psu), and lowest catches were observed at moderate salinities (10 – 15 psu). Age-1 red drum CPUE was also highest in above bottom habitat of algae, detritus, and shell, while catches were lower in sets with seagrass and no above bottom habitat. Annual variability

in CPUE was apparent; highest CPUE was observed in 2004 and 2005, and lowest was observed in 2001 (Figure 4.2). There was also a strong seasonal pattern with CPUE peaking in late fall.

We also constructed separate GAMs for age-1 red drum in each of the five regions to examine possible regional habitat use differences (Table 4.1). Regional-specific age-1 GAMs explained 63 to 73% of the deviance, and were generally consistent in the variables that were included in the models. For instance, three of five regional models included depth, four of five models included distance offshore, and all six included year and month effects. Regional effects of these four variables were similar to overall statewide trends. In contrast, two variables had regionally-dependent effects: salinity was significant in the Outer Banks and Neuse River only, and above bottom habitat was significant in the Outer Banks and Hyde County only. Higher catches of red drum were associated with seagrass, and to a lesser extent shell bottom, in the Outer Banks, while age-1 red drum in Hyde County were more strongly associated with algae and detritus.

Age-1 red drum were related to salinity in different ways in the Neuse River and the Outer Banks regions (Figure 4.3). In the oligohaline Neuse River, age-1 red drum were associated with the lowest salinities (< 5 psu), and were found less commonly in higher salinity waters. In contrast, age-1 red drum in the Outer Banks were observed in salinities of ~ 20 psu or higher, and CPUE decreased at lower salinities. The regional differences in the response of age-1 red drum to salinity observed in the Neuse River and the Outer Banks appeared to compose the overall statewide bimodal relationship (Figure 4.3).

The statewide age-2 red drum GAM regression explained 44% of the variation in CPUE, and included depth, distance offshore, temperature, above bottom habitat, year, month, and region as predictor variables (Table 4.1; Figure 4.4). Age-2 red drum were found most often in shallow, warm, nearshore waters associated with seagrasses. The CPUE of age-2 red drum was also highest in 2005 and 2006, primarily during the winter, spring, and early summer months.

Regional-specific GAMs for age-2 red drum were somewhat less consistent and explained moderately less deviance than for age-1 red drum (Table 4.1). Age-2 GAMs explained between 36 and 52% of the deviance in red drum CPUE. Depth, distance offshore, temperature, salinity, above bottom habitat, year, and month were included in various regional models. In all cases, the magnitude and slope of regional responses were similar to the overall statewide response. Above bottom habitat was only significant in the Outer Banks, showing a strong positive relationship of age-2 red drum to seagrass; preferences of seagrass by red drum in the Outer Banks was likely driving the overall statewide trend because above bottom habitat was not selected in any other regional model.

Red drum food habits in Hancock Creek

A total of 212 age-2 red drum stomachs was examined from 2005 and 2006 collections in Hancock Creek (Table 4.2). No additional stomach contents were found in the four sacrificed red drum examined after gastric lavage was performed; thus, the likelihood of us missing prey in the released red drum was low. Across all sampling periods, 31% of red drum had empty stomachs. Invertebrate prey dominated the diet of red

drum in all sampling periods except February 2006, when fish prey was slightly more important when percent by weight was used.

The dominant prey of red drum in Hancock Creek was blue crab *Callinectes sapidus*; this prey was found in 25 to 89% of stomachs during all five sampling periods and made up approximately half to nearly all of the diet by weight in three out of five samples (Table 4.2). Other important invertebrate prey included white-fingered mud crabs *Rhithropanopeus harrisi*, amphipods *Gammarus* spp., White River crayfish *Procambarus acutus*, and grass shrimp *Palaemonetes pugio*. Fish prey were also important, occurring in 22 to 100% of stomach samples within a season. Species of prey fish varied substantially among sampling periods with southern flounder *Paralichthys lethostigma*, silver perch *Bairdiella chrysoura*, American eel *Anguilla rostrata*, Atlantic menhaden *Brevoortia tyrannus*, pumpkinseed *Lepomis gibbosus*, and naked goby *Gobiosoma bosc* either contributing substantially to overall diet or occurring in at least three out of five sampling periods (Table 4.2).

Small-scale habitat use

Thirty-six age-2 red drum were surgically implanted with transmitters, released, and relocated at least one time alive during quarterly sampling in Hancock Creek (Table 4.3). More red drum were relocated in February (n = 21) and May (n = 21) than in August (n = 9) or November (n = 7). Individual red drum were relocated between 1 and 4 seasonal periods (Table 4.3); we assumed that the lack of independence did not bias results given

that over half of the fish (19 out of 36) were only relocated in one seasonal period and only four fish were relocated more than two times.

Significant correlations ($P < 0.05$) were present between some pairs of explanatory variables in Hancock Creek. Dissolved oxygen was negatively correlated with temperature ($r = -0.91$) and salinity ($r = -0.69$), and temperature and salinity were positively correlated ($r = 0.76$). Among the prey predictor variables, prey richness was positively correlated with prey evenness ($r = 0.63$) and total prey ($r = 0.48$). All remaining pairs of explanatory variables (16 out of 21) had $r < 0.30$. Colinearities were not deemed numerous enough to drop variables from the Hancock Creek GAM, but care was taken when interpreting results in the case that more than one correlated predictor variable was related to red drum (see *Discussion*).

The full GAM constructed for Hancock Creek explained 32% of the deviance, and included salinity, dissolved oxygen, prey evenness, and total prey in the model (Table 4.4). Telemetered red drum were more often found in lower salinity waters with high dissolved oxygen (Figure 4.5). They also showed a preference for moderate prey evenness, with reduced red drum presence at high and low values of prey evenness. Finally, red drum presence was linearly and positively related to total prey in Hancock Creek. The monthly Hancock Creek GAM (using temperature, salinity, and dissolved oxygen only) supported quarterly results by including only salinity ($P = 0.03$) and dissolved oxygen ($P = 0.04$) as predictor variables, but explaining much less of the deviance (13%) than the quarterly GAM that included prey information in addition to water quality parameters.

DISCUSSION

Habitat use of North Carolina red drum

Most investigations on red drum habitat use have determined that the species is a habitat generalist with broad tolerances for water quality conditions and microhabitat (Buckley 1984, Reagan 1985, Wenner 1992, Ross & Stevens 1992, Procarione & King 1993, Adams & Tremain 2000). While red drum appear to be able to tolerate a wide variety of environmental conditions, we observed specific associations to various water quality, microhabitat, geographic, and prey variables in North Carolina. In some instances, preferences for these factors differed between age-1 and age-2 red drum.

The GAMs were successful at quantifying habitat use patterns for subadult red drum captured by the gill net survey in Pamlico Sound, North Carolina, and for telemetered fish in Hancock Creek, North Carolina. A large amount of the deviance in red drum CPUE was explained by the models (62% for age-1 and 44% for age-2 red drum in gill net survey; 32% for age-2 red drum in Hancock Creek), similar to or higher than most published studies using GAMs to explain the spatial distribution of estuarine organisms. For instance, the annual GAMs developed by Jensen et al. (2005) that describe the winter distribution of mature female blue crabs in Chesapeake Bay in relation to environmental factors explained approximately 10 – 50% of the deviance in catches.

Depth and distance from shore were the most dominant explanatory variables related to age-1 and age-2 red drum spatial distribution from the gill net survey. However, these two predictor variables were correlated (and the only case of colinearities being included in the large-scale model), so it was impossible in our study to distinguish if

subadult red drum were responding to depth or distance from shore, or both. Our results are consistent with the small body of literature that has described habitat use of subadult red drum in other more tidally-dominated estuarine systems. For instance, subadult red drum have been shown to move onto the shallow, intertidal marsh flat at high tides, returning to marsh creeks at low tide (Collins et al. 2002, Dresser & Kneib 2007). Shallow, nearshore areas may provide subadult red drum with increased foraging opportunities (Ross and Epperly 1986, Ruiz et al. 1993, Miltner et al. 1995, Craig & Crowder 2000). It may also minimize predation, because predators of red drum (e.g., bottlenose dolphins *Tursiops truncatus*) primarily occur in deeper waters in North Carolina (Gannon 2003, N.M. Bacheler, unpublished data).

The response of age-1 and age-2 red drum to water quality variables was mixed. The temperature response, whereby age-2 red drum were positively related to temperature, was only observed in the Neuse River and Outer Banks regions. This response to temperature was most likely not a matter of selection of the warmest available water, but instead that more age-2 red drum were caught in spring and summer months when water was warm. We did not observe increased CPUE of red drum to cooler water temperatures as was noted in Indian River, Florida (Adams & Tremain 2000), but the broader examination of habitat use in our study may explain this inconsistency.

In some instances, salinity was significantly related to the distribution of red drum. The Hancock Creek GAM was consistent with the gill net survey GAM, showing higher presence of subadult red drum in the lower salinity waters of Hancock Creek. The selection of the lowest and highest salinities may be due to the physiological requirements

of subadult red drum, but more research is needed to disentangle direct effects of salinity from other covarying factors such as prey or predator distribution. In addition, because salinity and dissolved oxygen were covarying predictor variables, their inclusion in the Hancock Creek GAM should be viewed cautiously.

There were no significant effects of dissolved oxygen concentration on the distribution of any age class of red drum from the gill net survey, but subadult red drum were positively related to dissolved oxygen levels in Hancock Creek. Effects of hypoxia (i.e., areas with dissolved oxygen concentration $< 2 \text{ mg l}^{-1}$) on fishes are well documented, often resulting in behavioral avoidance or reduced growth or survival (Pihl et al. 1991, Eby & Crowder 2002). However, complex interactions between predators and prey may occur during episodic hypoxia, such as increased predator – prey overlap (Breitburg et al. 1999, Eby & Crowder 2002). Hypoxic water was documented at less than 1% of all gill net sets in our study, so the response of red drum to hypoxic waters may not have been well quantified. In contrast, small-scale sampling in Hancock Creek revealed a strong response of subadult red drum to dissolved oxygen, perhaps because telemetry can detect the fine-scale habitat use patterns that may have been changing over the course of minutes or hours (e.g., Bell et al. 2003).

Although all stages of red drum have been documented in seagrass beds, there is a lack of information on the selection or avoidance of seagrasses by subadult red drum. The use of seagrass by red drum in the Outer Banks only may be related to its abundance, since the Outer Banks has by far the highest amount of seagrass of any region in North Carolina (Street et al. 2005). Alternatively, red drum may only associate with certain species of

seagrass that only occur in the polyhaline waters of the Outer Banks, such as eelgrass (*Zostera marina*) or shoalgrass (*Halodule wrightii*). Our results highlight the need, perhaps using telemetry, to specifically examine utilization patterns of seagrass in polyhaline waters by subadult red drum.

There was significant annual variation in the CPUE of age-1 and age-2 red drum over the period from 2001 to 2006 that was observed in all regions. Furthermore, there was reasonably good agreement between the two age groups lagged 1 year (e.g., high value for age-1 red drum in 2004 and age-2 red drum in 2005). Variation in year-class strength, resulting from processes in the early life history of red drum, likely drove these yearly differences in CPUE (Bacheler et al. In Press).

Monthly trends in CPUE for age-1 and age-2 red drum likely represented a combination of changing gear selectivity, migratory behavior, and fishery removals. Age-1 red drum in winter and spring were too small to be sampled by the smallest mesh of the experimental gill nets (7.6 cm), but selectivity slowly increased throughout the year as red drum increased in size until catches became substantial in the fall months. A portion of age-1 red drum migrate from oligohaline creeks on the western Pamlico Sound towards the Outer Banks in the fall months each year (Chapter 5), which could also result in higher fall CPUE when passive gears like gill nets are used to sample red drum. Monthly CPUE of age-2 fish was high in winter, spring, and summer months, but decreased in the fall. Decreased CPUE in fall months for age-2 red drum was likely due to a combination of removals of age-2 fish from intense fishing (Takade & Paramore 2007) and reduced

selectivity of larger fish that begin to associate with inlets or other habitats not sampled in this study (Chapter 2).

By examining habitat use of red drum using telemetry in a non-tidal system such as Hancock Creek, we were able to show a clear response of subadult red drum to total prey. Diet of red drum in our study was diverse as observed in prior studies (e.g., Scharf & Schlicht 2000), so total prey was used instead of focusing on a single prey type. Our results support the accumulating body of literature suggesting that prey distribution is an important determinant of habitat use of estuarine organisms. Estuarine habitat studies have often focused on the role of abiotic factors in determining habitat use of estuarine organisms (e.g., Pietrafesa et al. 1986, Whitfield 1996, Baltz & Jones 2003), while often neglecting the role of prey distribution (see Craig & Crowder 2000 for a review of habitat selection of marsh organisms). However, the distribution of prey has been a major determinant of estuarine fish habitat use in the limited situations where it has been examined (e.g., McIvor & Odum 1988, Miltner et al. 1995, Alofs & Polivka 2004). Previous work found no significant overlap of age-1 red drum with their prey in a tidal salt marsh system in Georgia (Dresser 2003). However, the complicated movement patterns of red drum in Georgia (i.e., movement being influenced by tides and time of day) and limited prey sampling may have obscured the true relationship of red drum to prey organisms (Dresser 2003, Dresser & Kneib 2007).

Importance of scale

Three abiotic explanatory variables (temperature, salinity, and dissolved oxygen) were examined in both our large-scale and small-scale assessments and could be used to understand whether red drum habitat use was scale-dependent. Most notably, the use of salinity by age-1 red drum appeared to be dependent upon the scale at which research was conducted; had we limited our sampling to the Neuse River (or Hancock Creek) only, we would have concluded that subadult red drum were negatively related to salinity. At the larger scale of Pamlico Sound (100s of kms), however, we observed a bimodal relationship of red drum CPUE to salinity. Age-1 red drum showed nearly an identical response to salinity from the Neuse River gill netting and the Hancock Creek telemetry, suggesting that red drum's response was indeed scale-dependent and not a result of the small methodological differences between the two types of analyses.

Our results are consistent with previous work on the scale-dependency of habitat use and suggest that, in order to understand general patterns, habitat use must be analyzed at multiple scales (Thrush et al. 2005). Previous authors have noted that there is no single correct scale at which to quantify the spatial distribution of populations, and have suggested that habitat use must be examined on multiple scales (Weins 1989, Levin 1992). Recently, the importance of scale in the interpretation of spatial distribution of aquatic organisms has been noted (Essington & Kitchell 1999, Maury et al. 2001, Pittman et al. 2004). Essington & Kitchell (1999) showed telemetered largemouth bass distributions in a small Michigan lake were the product of several processes operating at spatial scales of 10, 30, and 180 m. The authors concluded that the small-scale aggregation may have been a

response to patches of aquatic macrophytes, while large-scale variation was a response to selection of the eastern half of the lake, possibly due to warmer water temperatures. In estuaries, the primary work concerning scale has been conducted on the spatial correlations of recruitment variability (Scharf 2000, Manderson 2008, Bacheler et al. In Press).

Assumptions of GAMs

Our modeling approach had some limitations. The flexibility of GAMs allow them to fit observed data very well, but sometimes that flexibility comes at the expense of generality (Jensen et al. 2005). In our study, the age-dependent habitat use patterns of red drum were often consistent across regions and years, suggesting that the patterns we observed were robust and not subject to overfitting. Our correlational approach could also not account for the effects of the spatial arrangement of habitat types, which in some cases has been found to be important (e.g., Essington & Kitchell 1999).

Management implications

Our results have important implications for red drum management in North Carolina and elsewhere. For instance, these results may be used to help reduce commercial or recreational discards of red drum in North Carolina. Subadult red drum are currently managed for commercial fishers as a bycatch fishery; only seven fish day⁻¹ can be retained by commercial fishers and they must make up no more than 50% of the total weight of the catch. The strong influence of depth and distance from shore on the distribution of red drum in nearly all areas of the state suggests that prohibiting gill netting in shallow,

nearshore waters may reduce bycatch and discards substantially. Such actions must be traded-off with the possible reduction of target species caught by commercial fishers. Our results could also be used to create temporal or seasonal fishing closures to protect high densities of subadult red drum from recreational and commercial exploitation.

These results also begin to inform managers on the types of habitats and water quality conditions commonly used by subadult red drum, a central recommendation of the red drum fishery management plan in North Carolina. For instance, seagrasses appear to be important for age-1 and age-2 red drum behind the Outer Banks; loss of seagrass here due to shoreline development or reduced water quality conditions may negatively influence red drum in this region. The positive relationship we observed between telemetered red drum in Hancock Creek and dissolved oxygen concentrations also suggests that increased hypoxia may also be detrimental to red drum. Most importantly, our results highlight the regional dependency of habitat use of red drum in North Carolina, and suggest additional research may be required to determine the generality of our findings to other locations.

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Table 4.1. Age- and region-specific GAMs for red drum abundance in North Carolina. A backwards stepwise selection procedure was used to compare four different forms of each variable: a linear effect (*), a nonlinear effect with 2 degrees of freedom (†), and a nonlinear effect with 4 degrees of freedom (§). Terms with $P > 0.05$ were dropped from the model and denoted as “ns.” Catch-per-unit-effort (CPUE) was determined as the number of red drum per gill net set. The deviance explained (Dev exp) by each model is also given.

Model	# sets	# drum caught	CPUE	Depth	Distance offshore	Temp.	Salinity	Dissolved oxygen	Sed size	Above bottom habitat	Year	Month	Dev exp
Age-1													
Outer Banks	982	979	1.00	<0.001*	<0.001*	ns	0.024†	ns	ns	<0.001*	<0.001§	<0.001§	63
Hyde County	939	1224	1.30	<0.001*	<0.001†	ns	ns	ns	ns	<0.001*	<0.001§	<0.001§	73
Neuse River	551	1087	1.97	<0.001†	ns	ns	<0.001§	ns	ns	ns	<0.001§	<0.001§	68
Pamlico River	424	534	1.26	ns	<0.001*	ns	ns	ns	ns	ns	0.021§	<0.001§	63
Pungo River	139	210	1.51	ns	<0.001*	ns	ns	ns	ns	ns	0.009†	<0.001†	72
All regions	3035	4034	1.33	<0.001†	<0.001†	ns	0.005§	ns	ns	<0.001§	<0.001§	<0.001§	62
Age-2													
Outer Banks	982	759	0.77	<0.001*	ns	<0.001†	ns	ns	ns	<0.001*	<0.001§	<0.001§	46
Hyde County	939	391	0.42	ns	<0.001*	ns	ns	ns	ns	ns	0.025§	<0.001*	36
Neuse River	551	354	0.64	<0.001*	ns	0.002*	<0.001*	ns	ns	ns	<0.001§	<0.001*	52
Pamlico River	424	134	0.32	ns	<0.001*	ns	ns	ns	ns	ns	<0.001†	<0.001†	46
Pungo River	139	148	1.06	<0.001*	ns	ns	ns	ns	ns	ns	<0.001§	ns	52
All regions	3035	1786	0.59	<0.001†	0.016†	<0.001†	ns	ns	ns	<0.001§	<0.001§	<0.001§	44

Table 4.2. Stomach contents of age-2 red drum from Hancock Creek in the lower Neuse River, North Carolina, 2005 - 2006. Red drum were collected by strike netting or electroshocking, and stomach contents were removed by gastric lavage. %F: proportion of stomachs with food containing a particular prey type, %W: proportion of identifiable prey types to overall stomach contents by weight.

Prey type	June 2005		February 2006		May 2006		August 2006		November 2006	
	%F	%W	%F	%W	%F	%W	%F	%W	%F	%W
Invertebrates										
Blue crab	30.4	45.1	24.5	7.9	64.5	58.1	88.9	95.4	33.3	1.1
Mud crab			4.1	2.0	38.7	9.6	11.1	<0.1	33.3	0.8
Amphipoda	4.3	<0.1	71.4	11.9	8.1	<0.1				
White River crayfish	13.0	29.4	2.0	5.2	9.7	3.6				
Grass shrimp			16.3	5.0	21.0	4.0				
Brown shrimp			2.0	4.6			11.1	0.5		
Cyathura			6.1	0.2						
Dragonfly larvae					3.2	2.8				
Isopoda					1.6	<0.1				
Damselfly larvae					1.6	<0.1				
Unid invertebrate	4.3	0.7	2.0	0.7						
Total invertebrates	52.2	75.2	128.5	37.5	148.4	78.1	111.1	95.9	66.7	1.9
Fish										
Southern flounder	8.7	8.5			6.5	2.4			33.3	47.9
Silver perch					1.6	8.3			33.3	42.3
American eel	4.3	0.1			6.5	1.7			33.3	7.9
Atlantic menhaden	13.0	2.3	14.3	16.7						
Lepomis spp.			8.2	16.2	4.8	0.4				
Bay anchovy			4.1	1.9						
Naked goby	8.7	0.7	2.0	0.5	1.6	<0.1				
Inland silverside					1.6	0.2				
Atlantic croaker					1.6	0.1				
Unidentified fish	60.9	9.4	12.2	14.6	12.9	1.4	22.2	<0.1		
Total fish	95.7	21.0	40.8	49.9	37.1	14.6	22.2	<0.1	100.0	98.1
Other^a	30.4	3.8	79.6	12.6	59.4	7.3	66.7	3.8		
Total stomachs	25		74		91		15		7	
Number with prey	23		49		62		9		3	
Mean TL (mm) (SE)	467.3 (5.8)		438.8 (3.9)		441.3 (3.4)		515.6 (8.4)		503.4 (48.1)	
TL range (mm)	425 – 507		360 - 509		385 - 568		450 - 582		318 – 650	
Mean wt (g) (SE)	976.7 (39.6)		843.8 (17.4)		854.8 (15.3)		1190.8 (37.8)		1464.9 (377.4)	
^a Aquatic vegetation and detritus										

Table 4.3. Information on 36 age-2 red drum with ultrasonic transmitters used to quantify habitat use in Hancock Creek, North Carolina, in 2006. Fish listed below were relocated in at least one quarterly relocation period (denoted by an ‘X’): February, May, August, or November.

Fish #	Surgery date	TL (mm)	Weight (g)	Sampling period relocated			
				Feb	May	Aug	Nov
1	21 March 2005	468	890	X	X		
2	21 March 2005	447	875	X	X	X	
3	25 March 2005	445	465	X			
4	25 March 2005	452	929	X	X		
5	28 November 2005	459	1075	X			
6	28 November 2005	444	926	X			
7	28 November 2005	471	1071	X			
8	28 November 2005	456	807	X	X		
9	28 November 2005	431	867	X	X	X	X
10	28 November 2005	456	888	X	X		
11	28 November 2005	452	969	X	X		
12	28 November 2005	453	1011	X			
13	28 November 2005	416	849	X			
14	28 November 2005	449	841	X			
15	28 November 2005	428	872	X			
16	28 November 2005	445	1025	X			
17	24 January 2006	437	863	X			
18	24 January 2006	453	899	X	X		X
19	24 January 2006	452	931	X			
20	24 January 2006	445	821	X	X		
21	24 January 2006	491	1112	X	X		
22	26 April 2006	450	893		X	X	X
23	26 April 2006	443	896		X		
24	26 April 2006	445	858		X		
25	26 April 2006	441	815		X		
26	26 April 2006	442	870		X		
27	27 April 2006	458	935		X		
28	27 April 2006	430	819		X		
29	27 April 2006	481	1058		X		
30	27 April 2006	457	985		X	X	
31	27 April 2006	447	991		X		
32	27 April 2006	468	896		X	X	
33	21 June 2006	446	907			X	X
34	21 June 2006	458	975			X	X
35	21 June 2006	467	1027			X	X
36	21 June 2006	532	1463			X	X

Table 4.4. Generalized additive models relating the presence of telemetered age-2 red drum to abiotic and biotic explanatory variables in Hancock Creek, North Carolina. A backwards stepwise selection procedure was used to compare four different forms of each variable: a linear effect, a nonlinear effect with 2 degrees of freedom, a nonlinear effect with 4 degrees of freedom, or exclusion from the model. Terms with $P > 0.05$ were dropped from the model and not shown.

Parameter	Type of effect	df	F	$\text{Pr}(F)$
<i>Deviance explained = 32%</i>				
Salinity	Nonlinear	2.9	8.33	0.035
Dissolved oxygen	Linear	1.0	10.21	0.002
Prey evenness	Nonlinear	0.9	4.76	0.026
Total prey	Linear	1.0	4.84	<0.001

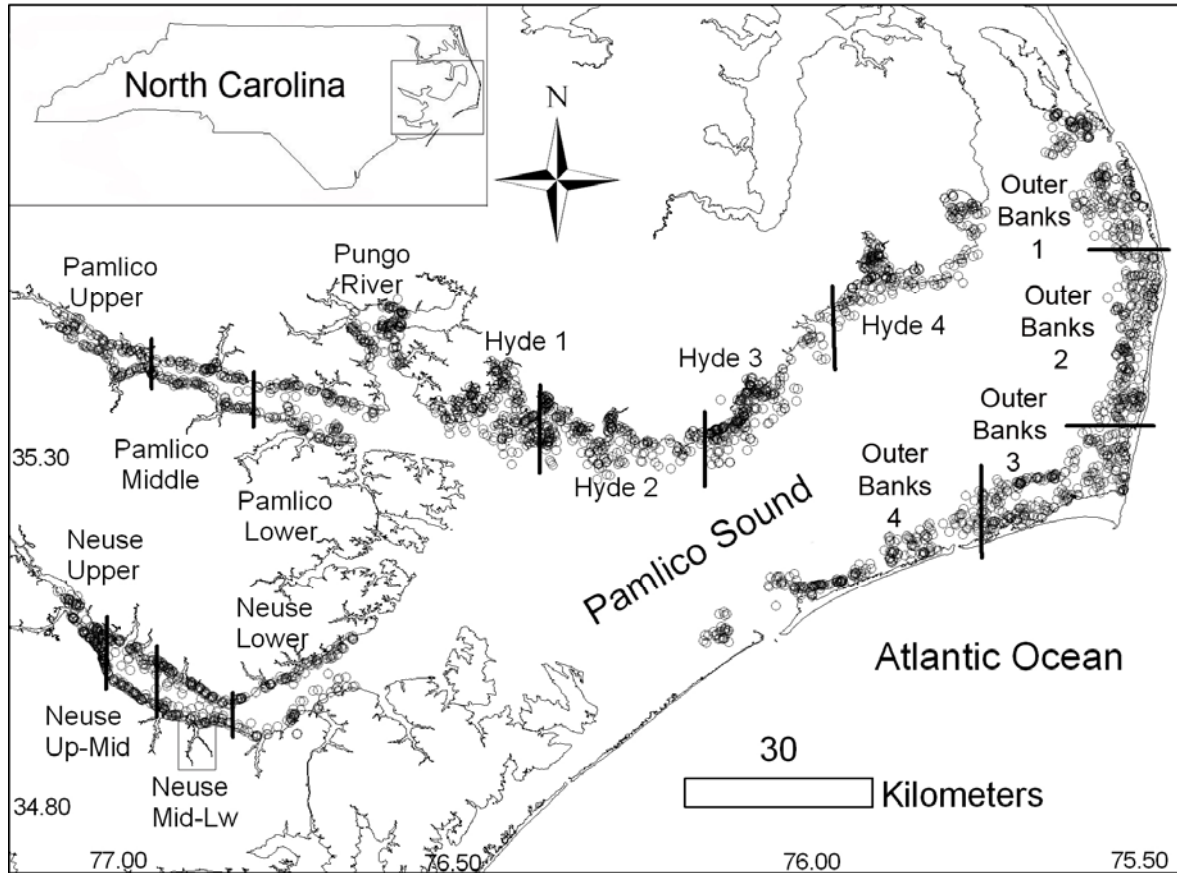


Figure 4.1. Map of Pamlico Sound and associated rivers showing gill net survey sampling strata (separated from each other by thick black lines) and gill net sites (open circles) sampled between 2001 and 2006. Five regions were sampled: the Outer Banks, Hyde County, Neuse River, Pamlico River, and Pungo River. Small scale habitat use of red drum was examined in Hancock Creek, located in the Neuse Mid-Lw stratum, and is surrounded by a box.

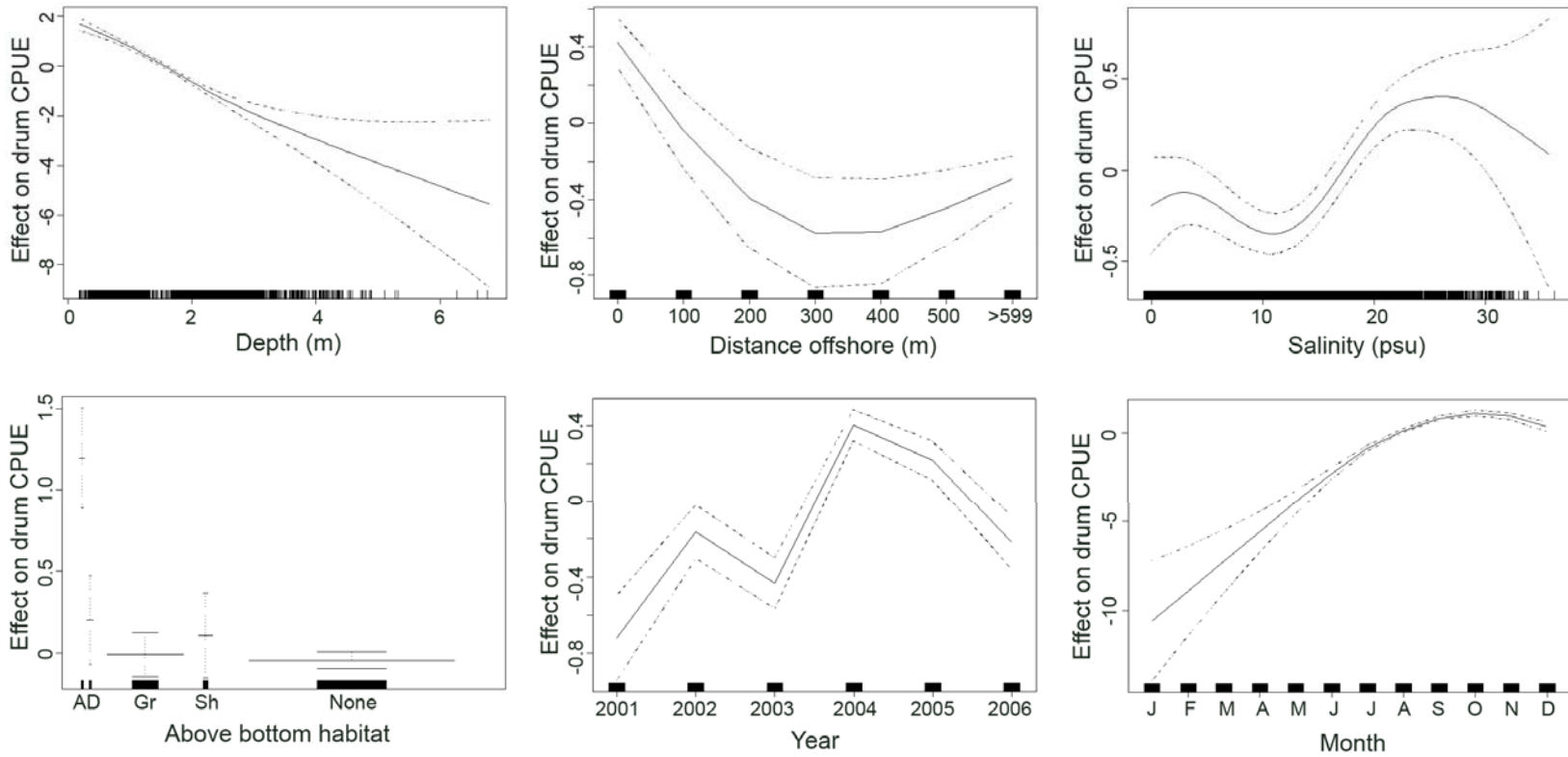


Figure 4.2. Cubic spline smoothed generalized additive model plots of the effects of physical habitat features on the abundance of age-1 red drum captured in the NCDMF gill net survey, 2001 – 2006. Categories of above bottom habitat are algae (“A”), detritus (“D”), seagrass (“Gr”), and oyster shell (“Sh”); width of bars represents sample size. Only significant factors ($P \leq 0.05$) are shown. The y-axis is the effect of the given variable on red drum abundance, and the tick marks on the x-axis indicate sampling intensity. Dashed lines are twice the standard error.

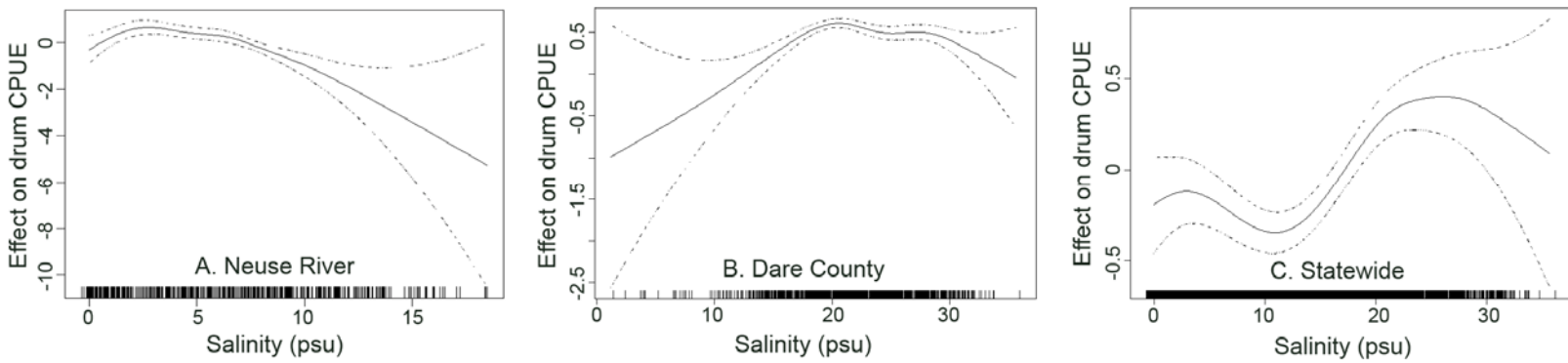


Figure 4.3. Cubic spline smoothed generalized additive model plots of the effects of salinity on the abundance of age-1 red drum captured in the NCDMF gill net survey, 2001 – 2006. The oligohaline Neuse River (A) and the polyhaline Outer Banks (B) regions are shown, in addition to the overall statewide response of age-1 red drum to salinity (C). The y-axis is the effect of the given variable on red drum abundance, and the tick marks on the x-axis indicate sampling intensity. Dashed lines are twice the standard error.

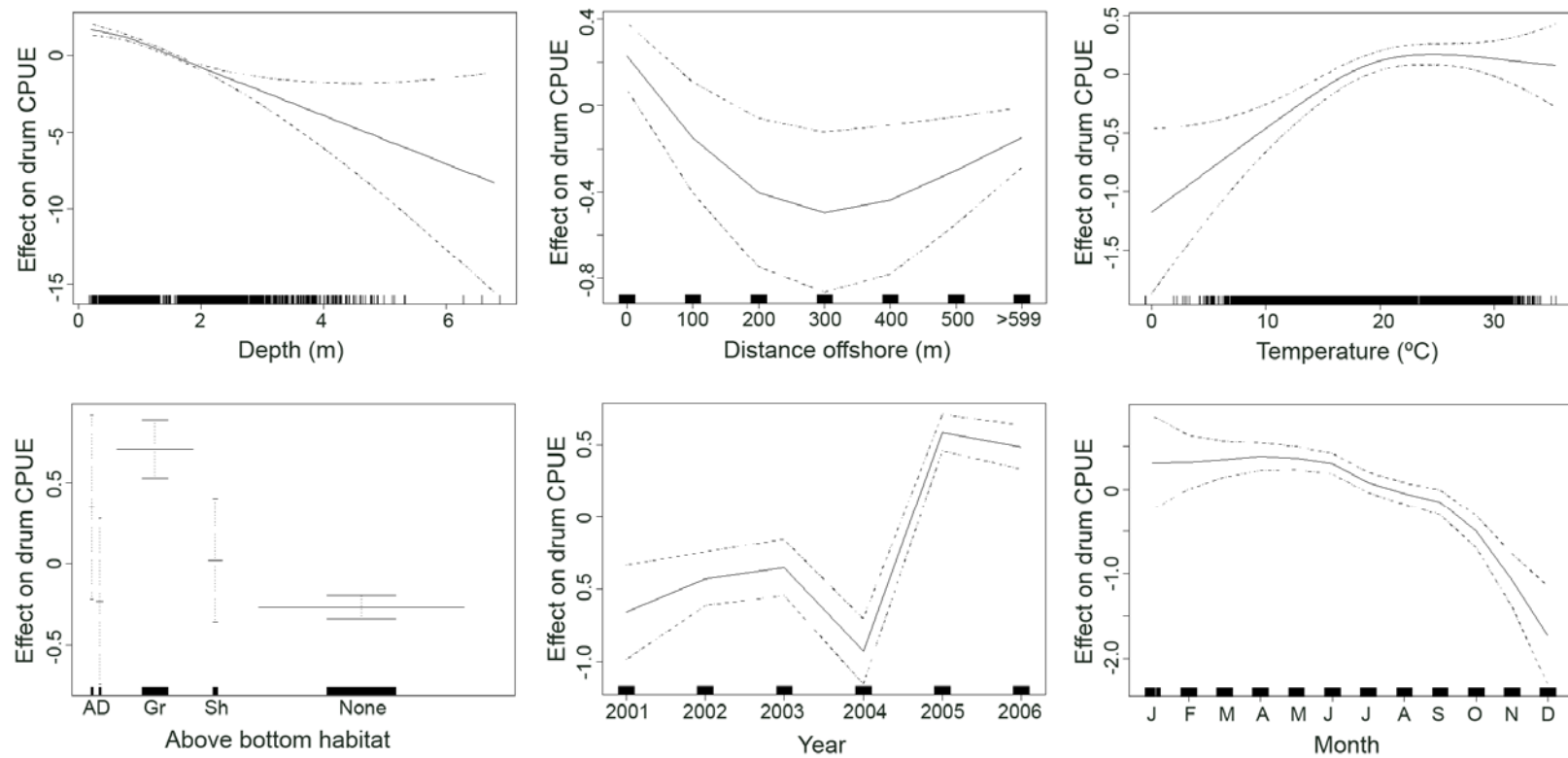


Figure 4.4. Cubic spline smoothed generalized additive model plots of the effects of physical habitat features on the abundance of age-2 red drum captured in the NCDMF gill net survey, 2001 – 2006. Categories of above bottom habitat are algae (“A”), detritus (“D”), seagrass (“Gr”), and oyster shell (“Sh”); width of bars represents sample size. Only significant factors ($P \leq 0.05$) are shown. The y-axis is the effect of the given variable on red drum abundance, and the tick marks on the x-axis indicate sampling intensity. Dashed lines are twice the standard error.

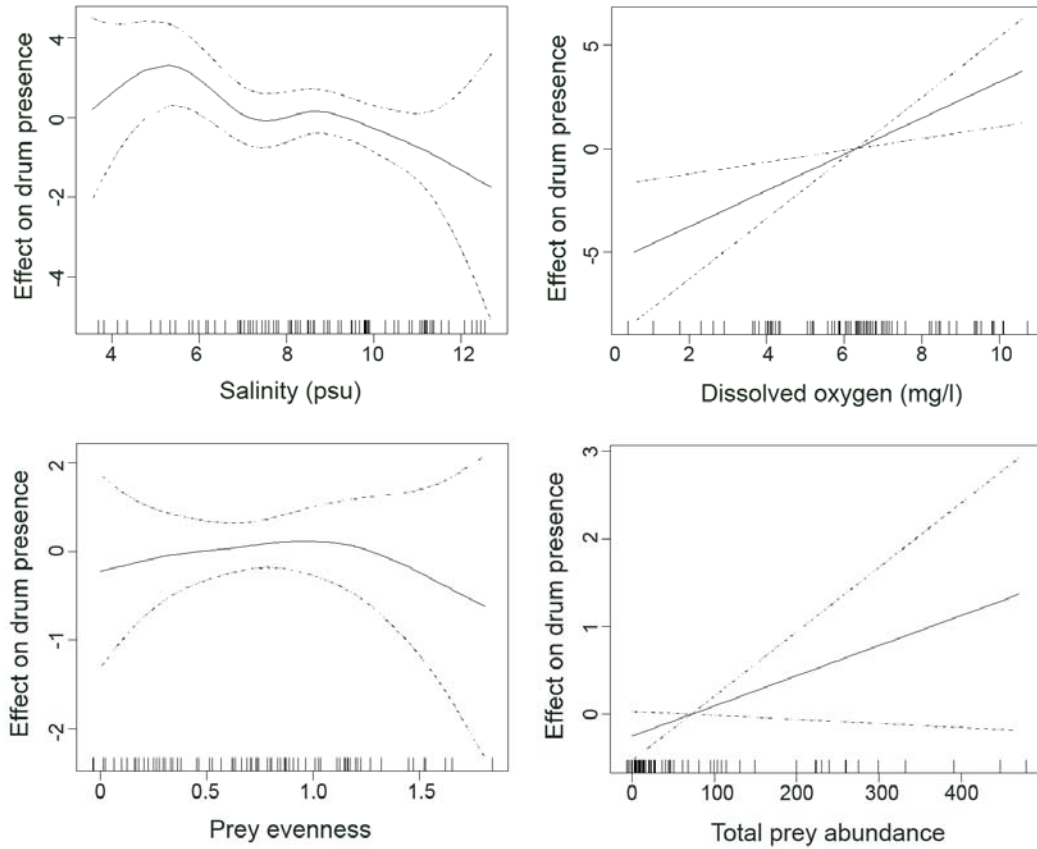


Figure 4.5. Cubic spline smoothed generalized additive model plots of the effect of water quality and prey variables on the presence of telemetered age-2 red drum in Hancock Creek, North Carolina, 2006. Only significant factors ($P \leq 0.05$) are shown. The y-axis is the effect of the given variable on red drum presence, and the tick marks on the x-axis indicate sampling intensity. Dashed lines are twice the standard error.

CHAPTER 5. MOVEMENT PATTERNS OF SUBADULT RED DRUM IN NORTH CAROLINA, WITH IMPLICATIONS FOR MARINE RESERVES AND STOCK STRUCTURE

Nathan M. Bachelier, Lee M. Paramore, Jeffrey A. Buckel, and Joseph E. Hightower

ABSTRACT

We used 25 years of conventional tagging and 3 years of ultrasonic telemetry data to examine movement rates and directional preferences of subadult red drum *Sciaenops ocellatus* in North Carolina. Movement rates of tagged red drum (n = 5,469 recoveries from 29,193 tagged fish) were dependent on the age of the fish at tagging, as well as the region and season of tagging. Fish tagged along the coast generally moved northward in spring and southward in fall, while fish tagged in oligohaline waters far from the coast tended to exhibit coastward movement trajectories primarily in fall months. Few recoveries occurred outside of North Carolina (0.5% of all recoveries), with most of these (77%) occurring in Virginia. Telemetered age-2 red drum (n = 105 fish) in a small tributary displayed seasonal emigration rates (highest in spring and fall), but upstream and downstream movements within the creek were correlated with fluctuating salinity regimes and not season. Our results show that red drum movement behavior is variable and complex. Results also suggest that the spatial scale of management and regulatory actions currently employed in North Carolina are appropriate.

INTRODUCTION

Understanding the movements of individuals within and among populations is critical in order to effectively manage 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 (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). Movement remains one of the least understood aspects of most species' ecology.

The individual movements and population distribution of red drum *Sciaenops ocellatus*, a long-lived Atlantic and Gulf coast estuarine fish species, has lacked the attention that has been given to other aspects of its life history, yet detailed movement information is central to its sustainable management. Red drum are among the most popular recreational species throughout their range (Wenner 1992), and moderate commercial fisheries exist in some states (e.g., North Carolina). After significant declines in the 1980s due to overfishing, strict harvest regulations were enacted in the 1990s to promote the rebuilding of red drum stocks (Vaughan and Carmichael 2000). Now, subadult red drum (i.e., ages 1 – 3) are generally harvested throughout their range, often

with protection for the long-lived adults. Modest rebuilding has occurred since that time (Takade and Paramore 2007; Chapter 2).

The small body of literature that has examined red drum movement has been mixed, and appears to be at least partially dependent on the methodological approach employed. Conventional tagging techniques have generally shown limited movements of subadult red drum, with most fish being recovered within 10 km of their release site (Osburn et al. 1982; Collins et al. 2002; Jenkins et al. 2004). Ultrasonic telemetry has been used to document substantial but consistent daily movements of subadult red drum that were related to diel and tidal cycles (Dresser and Kneib 2007). Otolith microchemistry has been used to show that red drum appear to return to their natal estuary to spawn, which is generally consistent with conventional tagging and telemetry results (Patterson et al. 2004). In contrast, population genetic approaches have shown that genetic variability only exists at the basin-wide scale (i.e., Atlantic and Gulf of Mexico), suggesting that gene flow (i.e., movement) is high enough to overcome any genetic differentiation within each basin (Gold and Richardson 1991; Gold et al. 1993; Seyoum et al. 2000).

A clearer description of the movements of subadult red drum could benefit management in many ways. First, red drum on the Atlantic coast are currently managed as separate northern and southern stocks that are divided at the North Carolina – South Carolina state line (Vaughan and Carmichael 2000), but the validity of this division of stock structure has not been evaluated. Second, movement patterns of subadult red drum can inform the usefulness and design of no-take zones as a management strategy, as has been proposed in South Carolina (Collins et al. 2002). Last, a missing link in our

understanding of the value of estuarine nurseries is the movement of individuals from juvenile to adult habitats (Beck et al. 2001). A regional-based movement analysis would begin to elucidate the spatial connectivity of different life history stages of red drum (Gillanders 2002).

This study describes the movement patterns of two age classes of subadult red drum in North Carolina at two spatial scales. We used 25 years of conventional tagging data to resolve large-scale movements and 3 years of ultrasonic telemetry relocations and submersible receiver detections to quantify movement at a smaller scale. We also explicitly accounted for differences in movement patterns based on the season and location of tagging. This study improves our understanding of the movement of subadult red drum in North Carolina and estuarine fish species more generally, and also provides some analytical techniques that may be more widely applicable.

METHODS

Conventional tagging

Two sources of tagging data were considered here. 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. Fish have been captured and tagged opportunistically by NCDMF 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, but a limited number of subadult fish tagged from

volunteer anglers are included in this study. Commercial fishers assisted in tagging until 1990, primarily tagging subadult red drum caught in pound nets and gill nets in conjunction with NCDMF. Tagging of subadult red drum was also performed in 2005 – 2007 by NCSU personnel within the Neuse River. In all of these studies (1983 – 2007), only healthy fish were tagged and released.

Most subadult fish were tagged with Floy® internal anchor tags (FM-84, FM-89SL, and FM-95W), but a limited number were tagged with nylon dart tags (Floy® FT-1 and FT-2) and stainless steel dart tags (Hallprint® FH-69) with a monofilament core and, more recently, a stainless steel core. 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 “REWARD” message (US\$5, hat, or tshirt), but the remaining tags were worth US\$100 for a concurrent tag reporting rate study (labeled “\$100 REWARD”). 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 January 1 birthday. The age-length key was based on 17 years of North Carolina 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 6-mo age-length key provides complete

separation of age-1 and age-2 red drum used in this study from each other and from older age classes.

Subadult red drum movement patterns were examined in four regions in NC (Figure 5.1). These regions were eastern Pamlico Sound (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). These regions were chosen based on previous examinations 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 0° representing true north). We calculated distance moved both as shortest distance moved in water using ArcGIS 9.1 (ESRI, Redlands, CA) for distance and movement rate calculations, as well as straight-line distance (Batschelet 1981) for circular mapping analyses. We also calculated the whole-circle bearing (in degrees) of each individual fish between tagging and recovery (Batschelet 1981).

To visualize the directionality and distances moved by tagged subadult red drum, we constructed maps showing the tagging and recovery locations of each age class of red drum within each of the four regions of the state using ArcGIS 9.1. We also constructed two-variable vector plots in Oriana 2.0 (Kovach Computing Services, Anglesey, Wales). The length of the bars in these 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 did not

use descriptive statistics on these circular data due to the presence of multiple modes (Zar 1999) and geographic barriers that varied by region.

Movement rates were then calculated separately for each season and age class combination (i.e., age-1 fish in summer through fall for age-2 fish), within each of the four regions of the state. Only fish recovered within 60 days of tagging were included in this analysis so that fish could be classified accurately into a seasonal period. The effects of season and region were tested with a two-way factorial ANOVA, using log-transformed movement rate ($\log(x + 1)$) to homogenize variances, so that main effects as well as the interaction between them could be tested for significance at $P = 0.05$.

We also quantified the ways in which distance moved and directionality was influenced by season using circular plots. Here, we used a stacked and stepped histogram for all subadult red drum recovered within 60 days only, so that the effect of season could be explicitly accounted for. The overall length of each wedge in the plot was the relative frequency of angular observations within 20° bins scaled to the largest number for each plot (because sample size was highly variable). Each wedge was further subdivided into the proportion of movements in a particular direction composed of various distance categories. These unique diagrams allowed for an examination of both direction and distance moved by season for subadult red drum.

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 Chapter 4. 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 to determine location 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 were also measured with a YSI 85 at the estimated location. 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 0.05 km 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. In preliminary work, VR2 receivers detected nearly 100% of pulses from V16 tags at 400 m in our study system. 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, and that such movement appeared unrelated to season. Given that the salinity regime in Hancock Creek is near the lower limit for red drum (Reagan 1985), we hypothesized that fluctuations in salinity would be correlated with upstream and downstream movements, as well as emigrations, of subadult red drum. To test this hypothesis, 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. We also correlated the proportion of red drum emigrating each month with the monthly change in salinity. Months with sample sizes of less than four telemetered red drum were excluded from these analyses.

RESULTS

Conventional tagging

A total of 29,193 age-1 and age-2 red drum was tagged in this study, of which 5,469 fish were recovered and reported by fishers at age 1 or age 2. Overall, 66% of these recoveries were from fish tagged at age 1 and 34% were from fish tagged at age 2. A majority of recoveries occurred from fish originally tagged in the Neuse and Pamlico Rivers (68% of age-1 and 54% of age-2 red drum), but many fish were also recovered from releases in other regions as well (Table 5.1).

Age-1 red drum spent an average of 100.8 ± 2.8 d (mean \pm SE) at large, traveled 24.9 ± 0.6 km between tagging and recovery, and moved 1.1 ± 0.1 km/d (Table 5.1). Age-2 red drum were at large longer (155.6 ± 3.5 d), traveled slightly less far between tagging

and recovery (22.4 ± 0.8 km), and moved at a lower rate (0.4 ± 0.1 km/d). Variability across region of tagging was also apparent (Table 5.1). Log-transformed ($\ln(x + 1)$) mean days at large, mean distance moved, and mean movement rate of subadult red drum were all significantly influenced by both region of tagging and age of the fish (two-way factorial ANOVA; all $P < 0.001$; Table 5.2). In addition, there were significant interactions between region and age for all analyses (all interaction $P < 0.01$; Table 5.2).

Prevailing movement directions also appeared to be region- and age-dependent (Figure 5.2). Generally, subadult red drum moved parallel to the coast, except for fish tagged in the Neuse and Pamlico Rivers, 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 Eastern and Western Pamlico Sound primarily moved southwest along the coast, while those tagged in Southern North Carolina moved primarily northeast and less so to the southwest. Age-2 red drum generally showed more northward movements, especially when tagged in the more northerly regions of Eastern and Western Pamlico Sounds (Figure 5.2).

A total of 30 subadult red drum was recovered in states other than North Carolina (0.5% of all recoveries). Most out-of-state recoveries were in Virginia (77%), but recoveries also occurred in South Carolina (17%), Georgia (3%), and Delaware (3%). Out-of-state recoveries were primarily composed of red drum tagged at age 2 (73%), but some were tagged at age 1 (27%). Most out-of-state recoveries came from fish tagged in Eastern Pamlico Sound (60%), but some also came from Neuse and Pamlico Rivers (13%), Southern North Carolina (13%), and Western Pamlico Sound (13%).

Movement rates of subadult red drum were also influenced by season (Figure 5.3). Movement rates were highest in fall for both age-1 and age-2 red drum recovered within 60 d of tagging, and were lowest in winter and spring for age-2 fish. Both the effects of season ($P < 0.001$) and region ($P < 0.001$), as well as their interaction ($P < 0.001$), were significant. In particular, it appeared that movement rates were higher for fish tagged in Eastern and Western Pamlico Sound, especially in the fall months (Figure 5.3).

We also created a two-variable histogram plot for fish recovered within 60 days of tagging to quantify effects of season and region on distances and directions moved (Figure 5.4). Four observations are apparent. First, higher proportions of long-distance movements occurred in fall months; in fact, most movements in fall months consisted of movements 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.

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 (6%). One fish died from the surgical procedure.

Emigration rates from Hancock Creek were bimodal and seasonal ($\chi^2 = 41.6$; $P < 0.001$; Figure 5.5A), 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: $P = 0.01$; Figure 5.5B), with highest movements in May and lowest in January and February. Last, directionality of movements in Hancock Creek was unrelated to season (R \times C Test of Independence: $\chi^2 = 1.54$, $P = 1.0$; Figure 5.5C).

Upstream and downstream movements of telemetered red drum were, however, significantly correlated with fluctuations in salinity (Figure 5.6). The proportion of red drum moving upstream was correlated with a positive monthly change in salinity ($R^2 = 0.33$; $F = 9.19$; $P = 0.007$; Figure 5.6A), and, similarly, downstream movements were correlated with a negative change in salinity ($R^2 = 0.46$; $F = 16.28$; $P < 0.001$; Figure 5.6B). Changes in salinity did not influence emigration rate, however ($R^2 = 0.04$; $F = 0.19$; $P = 0.67$; Figure 5.6C).

DISCUSSION

We used a 25-year tagging dataset in combination with 3 years of ultrasonic telemetry information to provide the most comprehensive examination of subadult red drum movement to date. Subadult red drum movement patterns in North Carolina were influenced by the age of the fish at tagging, region of tagging, and season of tagging. Longitudinal movements within a small creek in the Neuse River were related to salinity fluctuations, but emigrations from the system were dependent on season and not salinity.

Movements were distinctly different for age-1 and age-2 red drum. Subadult red drum are known to experience major ontogenetic shifts in diet (Wenner 1992) and habitat use (Chapter 4), but it was unknown whether these ecological shifts translated into differences in 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 subadult 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 (Chapter 2) and provides baseline information for the possible use of age-dependent, spatially-explicit models in future red drum stock assessments (e.g., Cadrin and Secor, in press).

By tagging and implanting large numbers of fish in this study, we were able to clearly document the strong effect of season on red drum movements. The limited temporal scope and modest sample size of previous estuarine tagging studies has 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 North Carolina (EPS and WPS); North Carolina happens to be the most significant northern overwintering grounds for subadult red drum on the Atlantic coast (Ross et al. 1995). Atlantic silversides (*Menidia menidia*) are known to migrate offshore in the northern but not the southern part of their range in the Atlantic (Conover and Murawski 1982), presumably to avoid overwintering mortality due to acute cold stress in northerly latitudes (Munch et al. 2003). 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 red drum movement has been observed elsewhere (Osburn et al. 1982) and is likely a result of the ecology of subadult red drum, 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 latitudinally along the coast. This may be due as much to the physiological requirements of red drum as the geography of the North Carolina coast, which constrains the movements of red drum to specific directions (e.g., east – west in NPR, northeast – southwest in SNC).

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) showed, using electronic transmitters, that conventional tagging was found to provide a reliable interpretation of 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 North Carolina 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 would be extremely useful for future red drum tagging analyses, and could be used to improve both movement and mortality modeling.

The addition of a telemetry component to this study improved our understanding of the movement patterns of subadult red drum at a small scale, which complemented large-scale analyses using conventional tagging. Since the salinity in Hancock Creek is near the lower limit for red drum (Reagan 1985), 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). Alternatively, telemetered red drum may have been following the movements of prey species (Chapter 4) that had their own physiological constraints. Regardless, telemetered red drum appeared to remain in salinities around 4 – 5 psu (Chapter 4), 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.

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). We showed that movement rates of wild subadult red drum in North Carolina were variable but highest in fall, which is the time when most red drum harvest occurs in the state (Takade and Paramore 2007; Chapter 3). This was even true for

the smallest (age-1) red drum in our study; surprisingly, these fish had the highest movement rates. The higher rate of movement we documented for North Carolina red drum suggests that marine reserves would need to be larger than those proposed in South Carolina to achieve similar gains (Polacheck 1990). Tremain et al. (2003) 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. Since red drum escapement in North Carolina has improved to near optimal levels (Takade and Paramore 2007), the closing of large areas of estuarine waters to fishing as a tool to increase red drum survival does not appear necessary at this time.

The current practice of assessing North Carolina and Virginia red drum together as one stock (Takade and Paramore 2007) is justified by tagging data. Subadult red drum tagged in North Carolina 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 North Carolina waters (Lucy and Bain 2007). In addition, there is movement of adult red drum from North Carolina to Virginia waters during summer months, with a return in late fall (Burdick et al. 2007). Movements of tagged red drum between North Carolina and South Carolina are low (this study; Wenner 1992).

Tagging 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 panmixia, they can also mean that distinct lineages exist but have diverged too recently to be detected despite no gene flow or that just enough gene flow exists to homogenize neutral markers 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.

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Table 5.1. Summary information for age-1 and age-2 red drum tagged in four regions of North Carolina: eastern Pamlico Sound (EPS), western Pamlico Sound (WPS), Neuse and Pamlico Rivers (NPR), and southern North Carolina (SNC). 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)	Prop moving < 10km
Age-1							
EPS	549	134.2 (7.4)	1079	49.0 (2.3)	353.5	2.0 (0.2)	0.32
WPS	255	186.7 (15.3)	1532	44.7 (2.5)	314.5	2.4 (0.5)	0.25
NPR	2454	77.9 (3.0)	1882	21.0 (0.6)	202.6	1.0 (0.1)	0.66
SNC	355	147.3 (9.3)	1125	27.8 (2.4)	306.7	0.5 (0.1)	0.49
Overall	3613	100.8 (2.8)	1882	24.9 (0.6)	353.5	1.1 (0.1)	0.56
Age-2							
EPS	542	164.8 (7.6)	2056	28.7 (1.9)	622.5	0.7 (0.1)	0.45
WPS	84	179.4 (13.7)	621	43.3 (3.7)	166.7	0.8 (0.1)	0.21
NPR	1007	150.5 (4.0)	816	20.4 (1.0)	220.7	0.2 (0.1)	0.57
SNC	223	151.2 (12.8)	1043	11.9 (2.2)	186.9	0.3 (0.1)	0.74
Overall	1856	155.6 (3.5)	2056	22.4 (0.8)	622.5	0.4 (0.1)	0.54

Table 5.2. Results of two-way factorial ANOVAs on the effects of region tagged, age tagged, and their interaction on days at large, distance moved, and movement rate of subadult red drum in North Carolina. Subadult red drum were tagged between 1984 and 2007, and recoveries by fishers occurred in North Carolina and adjacent states.

	SS	df	MS	<i>F</i>	<i>P</i>
Days at large					
Region	110.2	3	36.7	18.9	<0.001
Age	273.0	1	273.0	140.2	<0.001
Region x Age	306.9	3	102.3	52.5	<0.001
Error	10635.6	5461	1.9		
Distance moved					
Region	559.4	3	186.5	96.5	<0.001
Age	42.3	1	42.3	21.9	<0.001
Region x Age	106.9	3	35.6	18.4	<0.001
Error	10562.6	5467	1.9		
Movement rate					
Region	33.1	3	11.0	40.6	<0.001
Age	40.1	1	40.1	147.6	<0.001
Region x Age	3.6	3	1.2	4.4	0.004
Error	1470.3	5461	0.3		

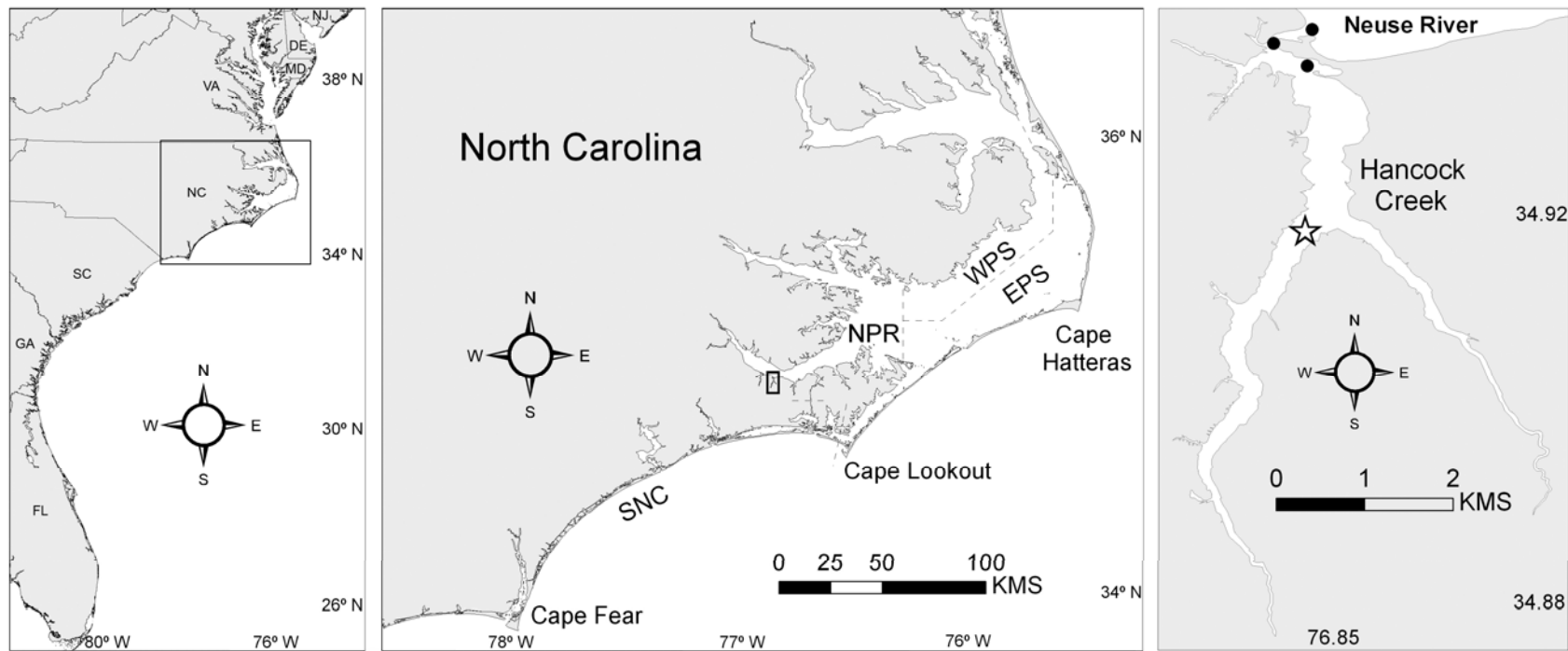


Figure 5.1. Map of study areas in North Carolina. Left map shows location of coastal North Carolina (in box) along the Atlantic coast of the U.S.A. Middle map shows view of entire coastline of North Carolina, with the four regions used in the movement analyses demarcated by the dashed lines. The four 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.

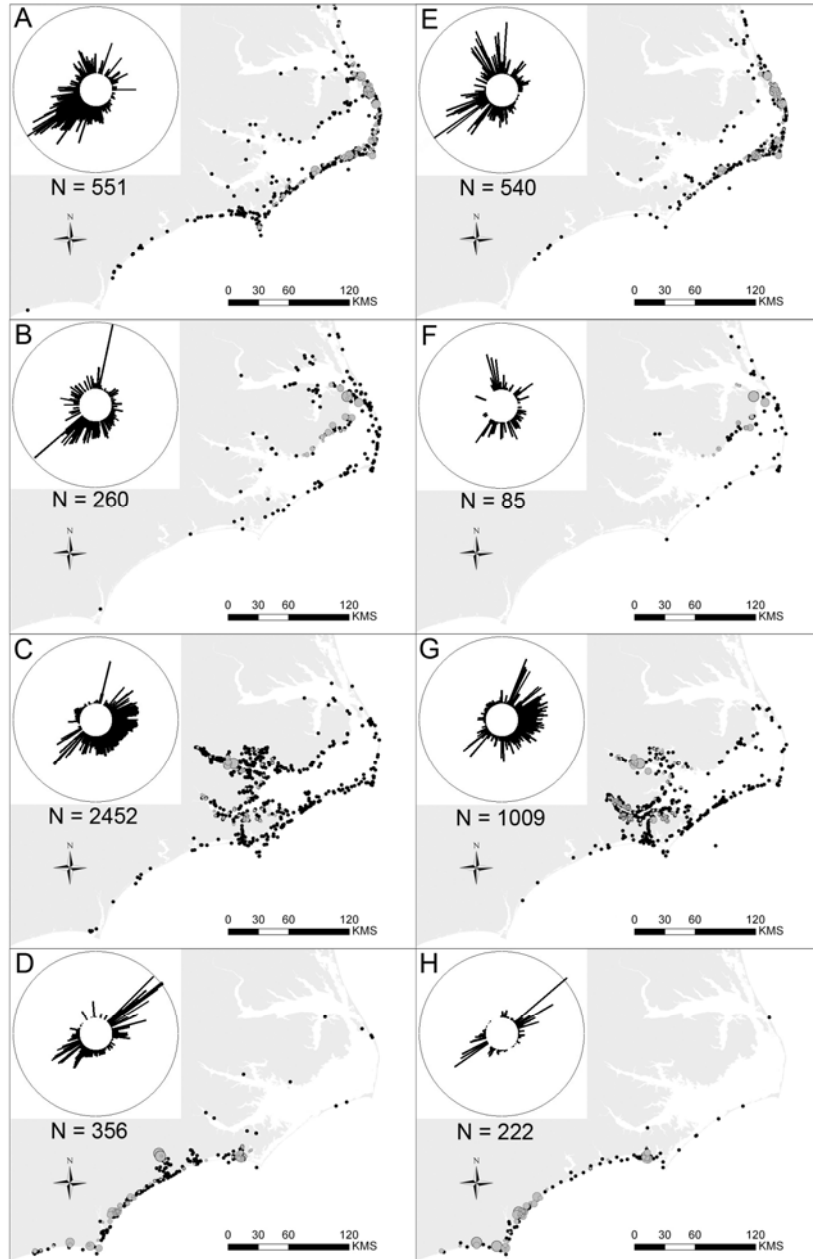


Figure 5.2. Tagging (gray circles) and recovery locations (black circles) of age-1 (A-D) and age-2 (E-H) red drum tagged by NCDMF and NCSU between 1983 and 2007. Panels show different tagging locations: eastern Pamlico Sound (A, E), western Pamlico Sound (B, F), Neuse-Pamlico Rivers (C, G), and southern North Carolina (D, H). Inset rose diagrams show direction and distances moved for all fish in a particular region and age group. Northward movements are straight up, southward are straight down, and outer circle is scaled to 300 kms. Out-of-state recoveries are not shown on map, but are shown on rose diagram.

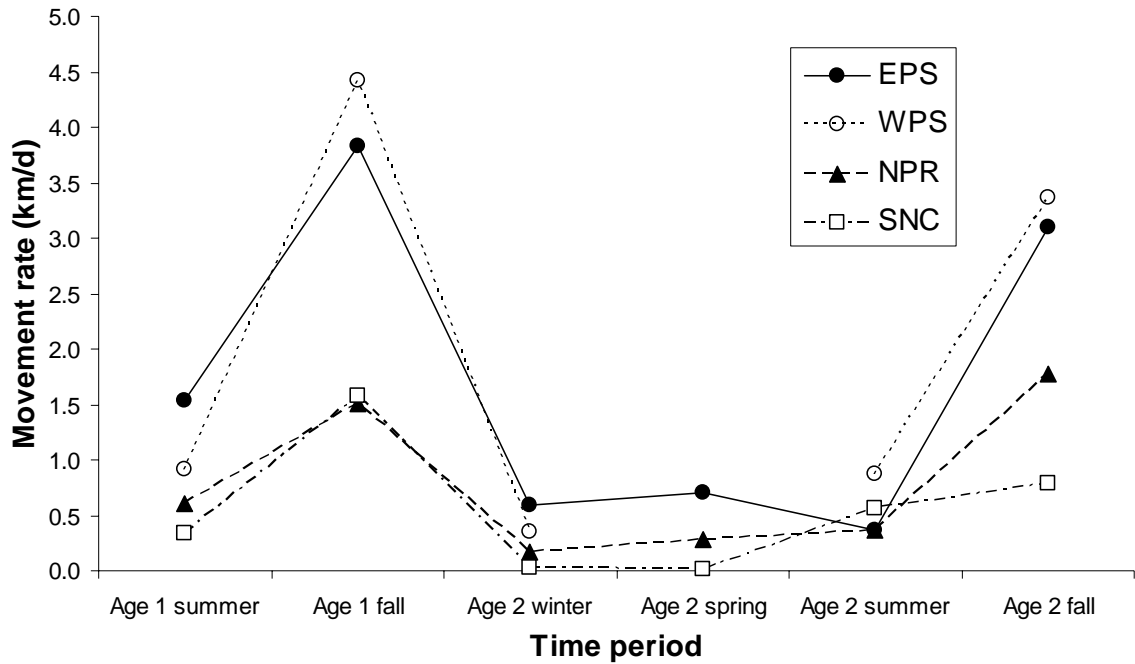


Figure 5.3. Mean movement rate of subadult red drum based on the season and region of the state in which fish were tagged. Only movement rates of fish recovered within 60 days of tagging were used in this analysis. Regions are: Eastern Pamlico Sound (EPS), Neuse – Pamlico Rivers (NPR), Southern North Carolina (SNC), and Western Pamlico Sound (WPS).

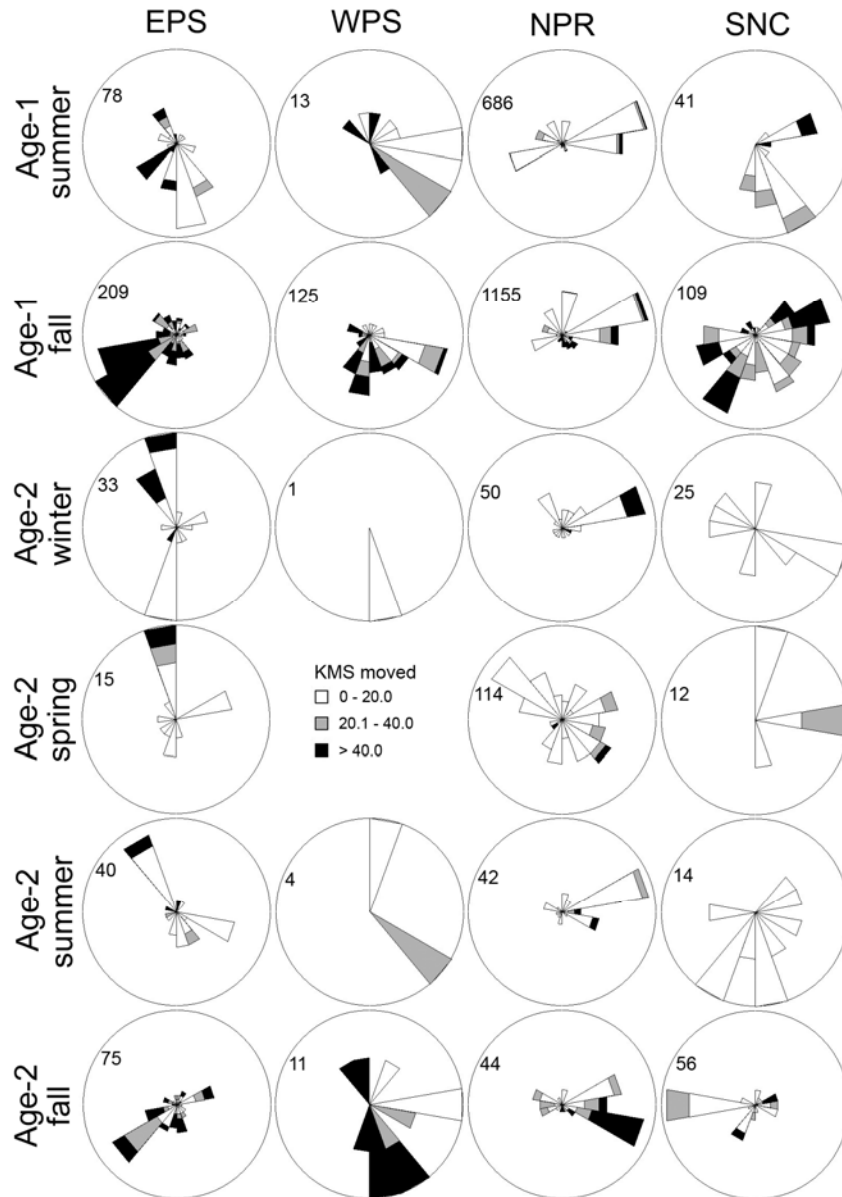


Figure 5.4. Frequency distributions of angular directions moved for subadult red drum recovered within 60 days of tagging, with season and age class shown as rows and region tagged as columns. The overall length of each wedge shows the relative frequency of angular observations within 20° bins scaled to the largest number for each plot. Each wedge is further subdivided into the proportion of movements in a particular direction composed of distances less than or equal to 20 km (white), 20.1 to 40.0 (gray), or greater than 40 km (black). Northward movements are straight up, and southward movements are straight down. Regions are eastern Pamlico Sound (EPS), western Pamlico Sound (WPS), Neuse – Pamlico Rivers (NPR), and southern North Carolina (SNC). Sample size is shown by the number in the upper right corner of each circular plot.

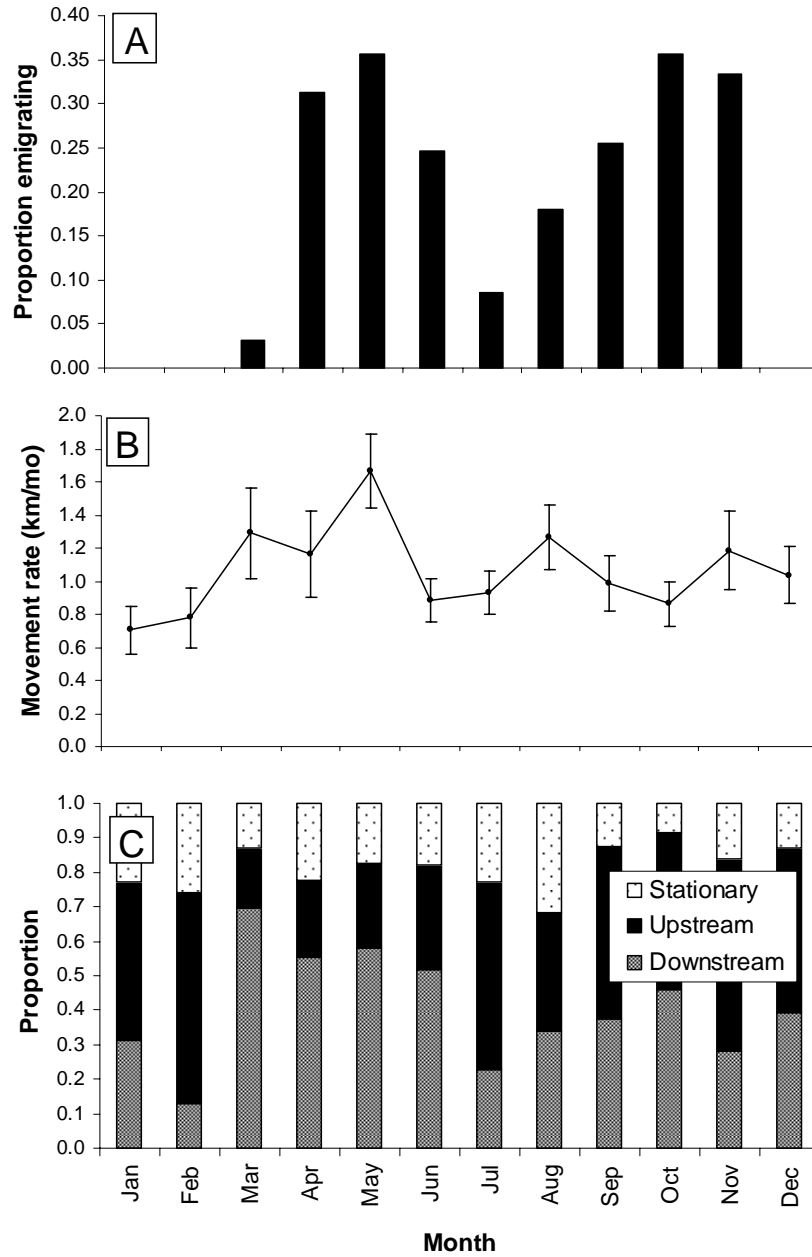


Figure 5.5. Seasonal ultrasonic telemetry relocation information for subadult red drum in Hancock Creek, 2005 – 2007. (A) Proportion of telemetered red drum emigrating each month, combined across years and all Neuse River tributaries. (B) Monthly movement rate of telemetered red drum within each of the Neuse River tributaries (excluding emigrating fish), across all tributaries and years. (C) Proportion of telemetered red drum moving upstream, downstream, or remaining stationary within the Neuse River tributaries, combined across tributaries and creeks

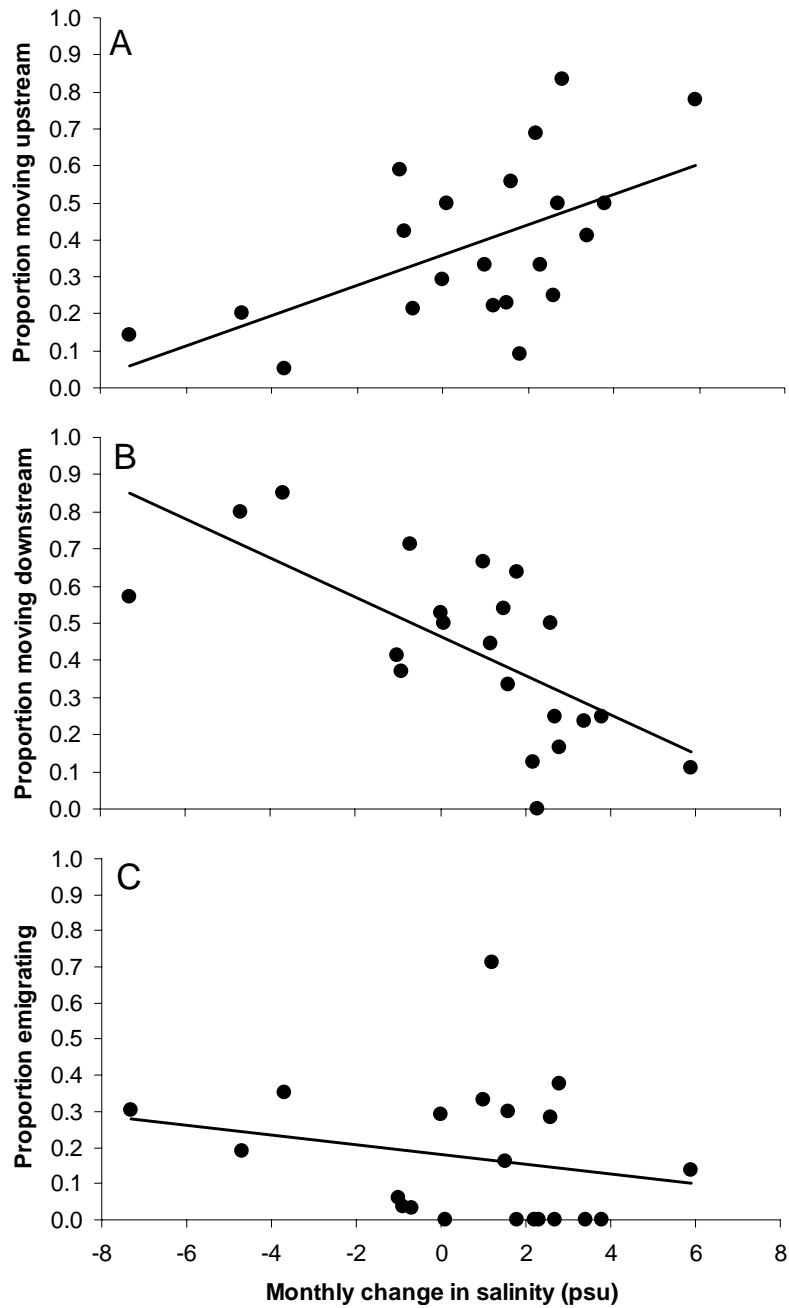


Figure 5.6. Proportion of telemetered red drum in Hancock Creek moving upstream (A), moving downstream (B), or emigrating (C) in relation to the salinity change between two consecutive relocation periods. Salinity sampling took place midriver near the boat ramp, and monthly periods are only included if more than three telemetered red drum were present in a month.

CHAPTER 6. CONCLUSIONS

Red drum ecology and management in North Carolina

This study described the ways that the mortality and distribution of subadult red drum in North Carolina estuaries were influenced by the combined forces of abiotic, biotic, and fishing effects. I showed that most mortalities of subadult red drum could be attributed to fishing, which was not surprising given the substantial harvest of red drum by recreational and commercial fishers. Deaths due to natural causes, however, were extremely rare in tributaries of the Neuse River and it is concluded that predation was infrequent in these systems. These data also indicate that abiotic conditions were generally not lethal and prey was not limiting; or, if they were, red drum emigrated out of the system before death. While abiotic and biotic factors did not often appear to cause direct mortalities, they did combine to strongly shape the distribution of subadult red drum throughout North Carolina. Moreover, the relationship of subadult red drum to abiotic and biotic factors was scale-, region-, and age-dependent, highlighting the complex ways that subadult red drum interact with their environment. Movement of subadult red drum was complex and influenced by age of the fish, region in which tagging occurred, and season of tagging.

These results are already being used in several ways to better manage red drum in North Carolina. First, age-dependent selectivity patterns (Chapter 2) have been incorporated into the most recent stock assessment, which allows separation of red drum disappearing due to fishing mortality from those experiencing reduced selectivity due to

coastward migration (Takade and Paramore 2007); the observed movement patterns (Chapter 5) confirmed the mechanism behind this reduced selectivity. Second, fishing mortality rate estimates produced by this study (Chapters 2 & 3) independently corroborate estimates produced in the most recent stock assessment. Third, given the strong affinity of subadult red drum to nearshore waters (Chapter 4), a buffer zone has been created that prohibits gill netting along the immediate shoreline in North Carolina. Fourth, North Carolina now has small-mesh gill net requirements in areas where sublegal, age-1 red drum have been found in high abundance (Chapter 4 & 5). Last, these results confirm the current practice of assessing North Carolina and Virginia red drum as one unit stock (Chapter 5).

My results also suggest that the natural mortality rate used in the most recent North Carolina stock assessment may be too high. The assessment used external estimates of natural mortality rate (M) based on a life history estimator that predicts M from age-specific body mass (Boudreau and Dickie 1989). An advantage of life history estimators is that they require minimal data, but their accuracy is often questioned and precision is unknown (Vetter 1988; Pascual and Iribarne 1993). Using telemetry in tributaries of the Neuse River, I estimated an M that is substantially lower than the value used in previous red drum stock assessments (Vaughan and Carmichael 2000; Takade and Paramore 2007) and estimates from a previous tagging study in South Carolina (Latour et al. 2001). Our estimates of M should be considered an improvement over estimates from life history and traditional tagging studies because telemetry methods estimate natural deaths directly from transmitters that stop moving (Hightower et al. 2001).

Tagging and fishery-independent sampling programs are extremely important to the success of red drum management in North Carolina. In light of the complex life history and management system for red drum, the North Carolina Division of Marine Fisheries red drum tagging program is vital for providing independent estimates of mortality rates, selectivity patterns, and movement (Chapters 2, 3, and 5). Furthermore, fishery-independent sampling programs, such as the Pamlico Sound fishery-independent gill netting and juvenile red drum seining programs, have been essential to understand habitat use patterns (Chapter 4), spatial and temporal patterns in recruitment (Bacheler et al., in press), and the validity of age-0 red drum catch-per-unit-effort as a tuning index for stock assessment (Bacheler et al., in press).

Methodological advances

The unusual management of red drum, whereby subadult fish are harvested only within a slot limit, has caused substantial difficulties in assessing red drum using traditional stock assessment approaches. To handle problems associated with the slot limit, high rates of catch-and-release, and perceived age-dependent selectivities of subadult red drum, I instead used a tagging approach. I built upon the pioneering tagging work of Brownie et al. (1985), and more recently Jiang et al. (2007), to develop a 24-year age-dependent model that could simultaneously estimate annual fishing mortality rates (F), age-dependent selectivities, and an overall tag-reporting rate (Chapter 2). I extended previous tag return modeling by estimating the tag reporting rate internally by fixing natural mortality rates, accounting for tag loss with two types of tags, incorporating the

first capture for all caught and released fish, separating the selectivities of harvested and caught-and-released red drum, and accounting for fish not tagged at the beginning of the year. With the inclusion of auxiliary studies to estimate tag retention, natural mortality, and reporting rate, tag return models can provide valuable independent estimates of fishing mortality rate and selectivity, as well as critical information often lacking in traditional stock assessment approaches (e.g., lengths or selectivities of released fish).

Although the combined telemetry – tag return approach has been employed in terrestrial environments (Tsai 1996; Barker 1997; Catchpole et al. 1998; Powell et al. 2000; Nasution et al. 2001, 2002), I provided the first field test of the approach for a fish species in an aquatic environment. Based on simulations, Pollock et al. (2004) suggested that a combined telemetry and tag return approach could provide precise and unbiased estimates of F , M , and reporting rate in a fisheries context. My field test confirmed the results of Pollock et al. (2004) by showing that the combined approach could take advantage of the relative strengths of each method and provide more precise estimates of F and M than either independent approach alone. One word of caution is that there may be differences in the spatial coverage of each approach (e.g., telemetry occurs in restricted area and conventional tags released or especially returned over a much larger area). In my work, the seasonal patterns and magnitude of F 's from each approach were similar, but that may not always be the case. Regardless, the combined telemetry – tag return approach should be strongly considered when estimates of both fishing and natural mortality rates for a fish species are required.

Future research

Estimation of natural mortality rate clearly requires additional research attention, both in regards to red drum specifically in North Carolina and for fish species generally. Although I have confidence that M is low in tributaries of the Neuse River using telemetry methods (Chapter 3), it is not known if M varies spatially in North Carolina. For instance, is M similarly low along coastal beaches and estuaries where predators are possibly more abundant? This question will be of particular importance when attempting to choose an appropriate value of M in future red drum stock assessments. The telemetry approach can be used in closed systems such as lakes, or in various open systems by using submersible receivers as gateways through which telemetered fish enter and exit the study system or area (Chapter 3). Future research should continue to estimate M for marine and estuarine species in open systems, either by expanding the telemetry and submersible receiver approach or by developing new approaches.

The future of fisheries stock assessment will likely see increased use of combined analyses of diverse data sources such as catch-at-age, mark – recapture, telemetry, and fishery-independent sampling data. For instance, improved estimates of mortality have been acquired using multiyear fishery tagging models that have been combined with catch data (Polacheck et al. 2006), catch-at-age and tagging combined with observer data (Eveson et al. 2007), and mark – recapture combined with traditional stock assessment approaches (Coggins et al. 2006). Additional research attention on combined fisheries analyses using tagging data will likely be very productive.

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APPENDICES

Appendix A. Monthly locations of telemetered red drum in five tributaries of the Neuse River, May 2005 – January 2008. Maps are shown only if red drum were relocated in that tributary in a particular month. Ordering of creeks listed below is shown from east to west, i.e., Slocum Creek, Hancock Creek, Clubfoot Creek, Adams Creek, and South River.

